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ON *PLESIOCETUS* VAN BENEDEN, 1859 (MAMMALIA, CETACEA, MYSTICETI)

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Abstract. A new analysis of the "type" *Plesiocetus* collection established by Van Beneden in the 19th century is performed to provide an updated taxonomy of this genus. *Plesiocetus* was established based on isolated finds that were assembled together to reconstruct almost complete skeletons of four species: *P. brialmontii*, *P. dubius*, *P. hupschii*, and *P. burtinii*. *Plesiocetus* has then been used by different authors in taxonomic studies of mysticete faunas and became a taxonomic wastebasked that is now in critical need of revision. Unfortunately, the diagnosis of *Plesiocetus* provided by Van Beneden does not allow to distinguish it from other mysticete taxa. For this reason, the analysis of all the specimens that Van Beneden assigned to *Plesiocetus* was necessary to understand the characters of the genus. The revision was done through a comparative anatomical analysis of all the specimens. The results of this work revealed that, among the specimens used by Van Beneden to set *Plesiocetus*, there is a variety of individuals that must be assigned to different genera in several families. Specimens were assigned to Balaenopteridae, Cetotheriidae, basal thalassotherians, Balaenoidea, Balaenidae, Balaenopteroidea and Balaenopteridae. All the specimens are assigned to gen. et sp. indet. because of their lack of taxonomically-informative characters. The conclusion of this study is that *Plesiocetus* is a *nomen dubium* and must be abandoned by mysticete taxonomists. This result has important taxonomic implications for a number of specimens previously assigned to *Plesiocetus*. We reviewed all these specimens and provided new taxonomic interpretations.

INTRODUCTION

Big numbers of fossil bones were brought to light following the intense excavation activities realized in the Antwerp area during the mid-19th century. Several mysticete remains have been collected in that period that now form a large part of the cetacean collection housed in the Institut royal des Sciences naturelles de Belgique (hereinafter, IRSNB) in Brussels. Most of these fossils were studied and published by Van Beneden and his collaborators in a series of classical monographs and atlases that rapidly became a standard reference for students of the cetacean fossil record.

Van Beneden published his descriptions during the second half of the 19th century and took part in an international debate about the paleontology of cetaceans that he carried out mainly with Brandt and Capellini (Bisconti 2007a, 2009). In that period, these and other authors established many new mysticete taxa following zoological procedures that were somewhat different from those that are being used today, thus, some of the taxa they established are in critical need of revision. As pointed out by Deméré et al. (2005) and others (Bosselaers & Post 2010; Steeman 2010), Van Beneden assigned

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different specimens to different taxa based on a preconceived idea of what might be the general shape of an idealized skeleton of a given mysticete. Individual specimens were assigned to different taxa based on their size and shape but no stable and robust diagnoses were produced by Van Beneden to support his assignments (see Bisconti 2007a for a detailed discussion of a case study). In addition, as previously discussed by other authors (*e.g.*, Whitmore & Barnes 2008; Bosselaers & Post 2010; Steeman 2010), Van Beneden did not designate holotype specimens to which his descriptions had to be referred; rather, he figured all the specimens he assigned to the new taxa he was describing in his later atlases. These specimens form the Van Beneden's "type" collection that is held in IRSNB.

The genus *Plesiocetus* Van Beneden 1859 represents a typical case study as it was established by Van Beneden in 1859, it was re-discussed by Van Beneden (1875), it was figured again by Van Beneden (1880, 1885) and Van Beneden & Gervais (1880), and it was then used as a taxonomical wastebasket by subsequent authors (*e.g.*, Cabrera 1926; Kellogg 1931; Portis 1885; Cuscani-Politi 1961; Caretto 1970; Hampe 1996; Bosselaers et al. 2004).

Deméré et al. (2005) reconstructed the taxonomical history of *Plesiocetus* since its establishment in 1859 by Van Beneden. A list of synonimies and additional interpretations can be found in the Cetacean section of the Paleobiology Database mainly compiled by Uhen (2018, 2010). According to Deméré et al. (2005), Van Beneden (1859) established *Plesiocetus garopii* but subsequently he removed it from *Plesiocetus* (Van Beneden 1872) and assigned it to *Balaenoptera musculoïdes*. Later, Van Beneden (1880) changed opinion again and considered that it was a genus of cetotheriid affinities. Most of this story was reconstructed also by Kellogg (1931).

According to Steeman (2010), Van Beneden (1859) established three *Plesiocetus* species: *P. garopii*, *P. burtinii*, and *P. hupschii* (Fig. 1). He then assigned *P. burtinii* and *P. hupschii* to *Cetotherium* (Van Beneden 1872) and left only *P. garopii* within *Plesiocetus*. Van Beneden (1880) transferred *Plesiocetus garopii* to *Balaenoptera musculoïdes* and returned *Cetotherium burtinii* and *C. hupschii* to *Plesiocetus*; on that occasion, he established also the species *Plesiocetus brialmontii* and referred *Cetotherium dubium* (that he established in 1872) to *Plesiocetus dubius*. Kellogg (1931) stated that *Plesiocetus garopii* is to be considered the type species of the genus *Plesiocetus* based on Van Beneden's (1872) conclusions.

Making things even more complicated, Van Beneden (1875) assigned a nearly complete skeleton from Italy to *Plesiocetus cuvieri*; this skeleton had been previously described by Cortesi (1819) and Cuvier (1823) as the mysticete from Mount Pulgnasco. Bisconti (2007a) reviewed the taxonomical history of this specimen and, after a comparative analysis, concluded that it must be assigned to a different mysticete taxon, namely *Protororqualus cuvieri*.

Bisconti (2007a) reviewed also the taxonomical history of the genus *Plesiocetus* and the history of the different diagnoses provided by Van Beneden during the years. A sort of morphological diagnosis of *Plesiocetus* was provided by Van Beneden & Gervais (1880) as follows: (1) wide head; (2) glenoid fossa of squamosal less vertical than in other mysticetes; (3) tympanic bulla placed more anteriorly than in other mysticetes; (4) wide frontal; (5) supraorbital process of frontal protruding rearward; (6) twelve pairs of ribs; (7) comparatively longer humerus than antebrachium; (8) wide basisphenoid; (9) curvature and general morphology of dentary similar to those of rorquals; (10) well developed coronoid process of dentary; (11) cervical vertebrae free; (12) complete foramen transversarium; (13) scapula long and low; (14) tympanic bulla "pyruliform" (see Bisconti 2010 for a definition of this term) and oval-shaped. As pointed out by Bisconti (2007a), most of these characters are plesiomorphic for mysticetes (*i.e.*, 1, 7, 10, 11, 12) or for particular families (for example, characters 4, 9, and 13 are plesiomorphic for Balaenopteridae), thus this diagnosis is not taxonomically specific and, therefore, cannot be accepted as it shows significant ambiguity.

Van Beneden (1885) provided a different diagnosis of *Plesiocetus* as follows: (1) free and widely separated cervical vertebrae; (2) scapula with rudimentary coracoid and well developed acromion; (3) tympanic bulla "pyruliform"; (4) head robust and wide. This reduced diagnosis is still ambiguously conceived for what concerns characters 1, 3, and 4. Bisconti (2007a, 2010) discussed the shape of the "pyruliform" (pear-shaped) tympanic bulla

Fig. 1 - An example of the illustrations of *Plesiocetus* provided by Van Beneden (1885). In particular, here, Plate 29 is reproduced with illustrations of *Plesiocetus burtinii*. Numbers represent the following specimens: 1, M. 675; 2-6, M. 679; 7-10, M. 678; 11-14, M. 677.

concluding that it is observed in several mysticete taxa including most of the archaic basal thalassotherian species (*sensu* Bisconti et al. 2013).

Plesiocetus has been included in both Balaenopteridae and Cetotheriidae families by different authors. As reconstructed by Bisconti (2007a), *Plesiocetus* was included in the subfamily Cetotheriinae (at the time conceived as part of the family Balaenopteridae) by Brandt (1873). Van Beneden refuted this interpretation and, in a subsequent publication (Van Beneden & Gervais 1880), stated that *Plesiocetus* represented a subgenus of *Balaenoptera* in the family Balaenopteridae. Kellogg (1931, 1965) erected *Plesiocetus* to genus rank again but, later, stated that: "sufficient diagnostic criteria for the recognition of *Plesiocetus* as a valid genus are not presently known" (Kellogg 1965, p. 104). Deméré et al. (2005, p. 125) stated that "because no holotype was designated and the syntypes are almost certainly from different individuals, it is not possible to unambiguously diagnose this taxon". Steeman (2010, p. 69) accepted the opinion presented by Deméré et al. (2005) and acknowledged that "*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 accessibile". She described the ear bones previously assigned to *Plesiocetus garopii*, *P. burtinii*, *P. dubius*, and *P. brialmontii* and assigned the isolated periotic IRSNB M. 676 of *P. burtinii* and the isolated periotic (IRSNB M. 652) of *P. dubius* both to *Aglaocetus burtinii* (respectively as lectotype and as referred specimen) but she did not provide any diagnosis of *Plesiocetus*.

To make order in this complicated situation, Bisconti (2007a) suggested that a revision of *Plesiocetus* should be made based on the "type" materials described by Van Beneden. As it seems that the final opinion of that author on *Plesiocetus* was presented in his paper of 1880, the goal of the present work is to make detailed descriptions and taxonomical decisions on the fossil bones assigned to *Plesiocetus* by Van Beneden (1880). In that paper, Van Beneden distinguished *Plesiocetus brialmontii*, *P. dubius*, *P. hupschii*, and *P. burtinii*; those species are then figured out in Van Beneden (1885) (some specimens are also illustrated in Van Beneden & Gervais, 1880). The present work focuses on the specimens assigned to these species that have been figured out by Van Beneden (1885) and that are now broadly considered "type" materials. Discussions about the status of these specimens are provided below. Most of the specimens consist of postcranial bones including fragmentary vertebrae. As discussed by Steeman (2010), Bosselaers & Post (2010), and Deméré et al. (2005), these specimens are generally not useful to make robust morphological diagnoses; however, no students have provided a clear taxonomic decision on them. The goal of this paper is to provide an up-to-date taxonomic decision on the species that Van Beneden assigned to *Plesiocetus* by means of detailed descriptions and measurements of all the specimens.

CHRONOSTRATIGRAPHIC ASSESSMENT

The specimens come from the vicinity of Antwerp (= Anvers in French; = Antwerpen in Dutch); the different suburbs and small towns where the fossils were found are Borgerhout (= Borgerhaut in French), Borsbeek (= Borsbeck in old French) and the kanaal op Herentals (= canal d'Herentals in French). The latter does not exist anymore. It was an artificial canal to provide drinking water to Antwerp.

All the specimens originally assigned to *Plesiocetus* by Van Beneden are labelled as being from the Diestien that is, according to Laga & Louwye (2006), an antiquate stage of the Belgian Pliocene. The lithological complexes originally included in the Diestien are now placed in the Diest Formation based on the analysis of their content in dinoflagellate cyst by Louwye et al. (2009). These authors suggest a Neogene age for this formation that is chronologically constrained between *c.* 9 and *c.* 7.7 Ma in the late Tortonian (late Miocene). The whole *Plesiocetus* assemblage studied in the present work can be assigned to this age interval.

MATERIALS

The following specimens were studied that represent all the figured materials by Van Beneden (1885) on *Plesiocetus* (all the specimens are housed at IRSNB):

Plesiocetus brialmontii: M. 629a-b, M. 630a-b, M. 631, M. 632, M. 633, M. 634, M. 635, M. 636, M. 637a-b, M. 638a-c, M. 634, M. 640a-d, M. 641, M. 642, M. 643, M. 644.

Plesiocetus dubius: M. 645a-g, M. 646a-b, M. 647a-b, M. 648a-b, M. 649, M. 650, M. 651, M. 652, M. 653, M. 654, M. 655a-c, M. 656, M. 657, M. 658, M. 659, M. 660a-b.

Plesiocetus hupschii: M. 661, M. 662, M. 663, M. 664, M. 665, M. 666, M. 667a-f, M. 668, M. 669a-d (M. 669c is lacking), M. 670, M. 671, M. 672, M. 673, M. 674, M. 675, M. 678.

Plesiocetus burtinii: M. 676, M. 677, M. 679, M. 680a-c, M. 681.

Comparisons were made with the mysticete taxa listed by Bisconti (2009), Bisconti & Bosselaers (2016, 2020) and Bisconti et al. (2020a, b, c).

METHODS

Institutional abbreviations

GLA NW, Geologisches Landesamt Nordrhein-Westfalen, Krefeld, Germany; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MPP, Museo Paleontologico Parmense, Università degli Studi di Parma, Parma, Italia; MSNUT, Museo Regionale di Storia Naturale dell'Università degli Studi di Torino, Torino, Italia; RGM, Naturalis Biodiversity Center, Leiden, Holland.

Anatomical terminology

Anatomical terminology follows Mead & Fordyce (2009) and, when necessary, Nickel et al. (1991), Benke (1994), Schaller (1999) and Ekdale et al. (2011).

The following acronyms are used throughout the paper as anatomical abbreviations: absc, acetabulum of scapula; acsc, acromion process of scapula; aex, articulation surface for exoccipital;

als, anterolateral sulcus; apd, angular process of dentary; apm, ascending process of the premaxilla; app, anterior process of periotic; art, articulation surface of parietal for supraoccipital; brk, broken attachment for posterior process; cpsc, coracoid process of scapula; crt, crista transversa; dpc, deltopectoral crest; dsf, dorsal surface of periotic; eam, external acoustic meatus; elf, endolymphatic duct; eoc, external occipital crest; eof, internal (endocranial) opening of the facial canal; exo, exoccipital; Euo, Eustachian opening; fin, fossa incudis; fms, fossa for stapedial muscle; fpr, falciform process of the squamosal; fr-p, frontal-parietal suture; fsc, fossa for sternocephalic muscle; gfs, glenoid fossa of the squamosal; hiF, hiatus Falloppii; huh, humeral head; hus, humeral shaft; iam, internal acoustic meatus; inv, involucrum; ipr, involucral protrusion; ipp, inner posterior prominence of tympanic bulla; irfr, interorbital region of the frontal; iri, involucral ridge; lbh, lateral border of cranial hiatus; lfu, lateral furrow of tympanic bulla; lof, lateral opening of the facial canal; lat, lateral tuberosity; maf, mallear fossa; mcsc, margo caudalis of scapula; mcrsc, margo cranialis of scapula; mdc, mandibular condyle; mri, main ridge; oc, occipital condyles; olf, facet for articulation with olecranon; ow, oval window; p, parietal; pch, pars cochlearis; pco, posterior concavity in tympanic bulla; pgp, postglenoid process of squamosal; plf, perilymphatic duct; pnc, posterior apex of nuchal crest; prg, promontorial groove; pro, medial protru-

Specimens	Locality	Locality detail	Closest important city	Stratigraphy	Anatomy
M. 631	Borgerhout		Anvers	Diestien, 3rd section	Left tympanic bulla
M. 632	Borgerhout	Turmont	Anvers	Diestien, 3rd section	Right tympanic bulla
M. 629a-b		Fortin N. 1	Anvers	Diestien, 3rd section	Fragments of premaxillae and maxillae
M. 634					Partial right dentary
M. 639					?11th lumbar vertebra
M. 637a		Fortin N. 1, cap. N. 5	Anvers	Diestien, nouvelle, 3rd section	?5th cervical vertebra
M. 637b					?7th cervical vertebra or 1st thoracic vertebra
M. 630a	Borgerhout	Fortin N. 1	Anvers	Diestien, 3rd section	Fragments of squamosal
M. 630b					Right mandibular condyle
M. 633					Right tympanic bulla
M. 644	Borgerhaut	Fortin N. 1, right side	Anvers	Diestien, 3rd section	Right ulna
M. 635	Borgerhaut	Fossée capital	Anvers	Diestien, 3rd section	Atlas
M. 643		Fossée capital	Anvers	Diestien, 3rd section	?left radius
M. 636		Canale d'Hérenthals, Gazometro	Anvers	Diestien, 3rd section	Axis
M. 641	Berchem	Canal d'Hérenthals	Anvers	Diestien, 3rd section	Fragment of left scapula
M. 642					Left humerus
M. 638a	Borsbeck	Fort 3	Anvers	Diestien	?9th thoracic vertebra
M. 638c					?3rd lumbar vertebra
M. 638c					Chevron
M. 640a-d		Fortin N. 1, Caponniére	Anvers	Diestien, 3rd section	?2nd, 8th, 19th, 21th caudal vertebrae

Tab. 1 - Localities of the discovery of the specimens assigned to *Plesiocetus brialmontii* by Van Beneden.

sion; p-sq, parietal-squamosal suture; pty, posterior attachment site for compound posterior process; raf, facet for articulation with radius; rfl, raised anterior portion of tympanic cavity floor; rw, round window; scg, subcondylar groove; sma, suprameatal area; smc, supramastoid crest; sna, attachment site for the nasal bones; soc, supraoccipital; sq, squamosal; sqc, squamosal cleft; stc, subtemporal crest; stf, stylomastoid fossa; tc, temporal crest; ttg, groove for tensor tympani; tty, tegmen tympani; tyc, tympanic cavity; ulf, facet for articulation with ulna; usc, U-shaped sagittal crest of parietal; vgr, vascular groove. The letter i is used to indicate presence of integrated glue to maintain skull integrity.

Taxonomy

A total of 83 skeletal elements were studied in this work that correspond to all the specimens represented by Van Beneden (1885) in the part of his atlas dealing with *Plesiocetus*. These bones were intended by the original author as if they were forming four partial skeletons corresponding to four different species of *Plesiocetus*. As reported in Tabs 1-4, the bones forming each reconstructed partial skeleton have been discovered at different localities. As it is not possible to ascertain the minimum number of individuals in the record examined here, each individual bone is analyzed separately and a taxonomical decision is made for each specimen.

Specimen	Locality	Locality detail	Closest large city	Stratigraphy	Anatomy
M. 645a-g		Fossée de ravelin, left side of the old Fortin N. 1, Caponniére N. 5	Anvers	Diestien, 3rd section	a: atlas; b: axis; c: C3; d: T1; e: T7, f: L3; g: Cd9
M. 646a					Indet.
M. 646b					Indet.
M. 648a-b					a: fragment of exoccipital with condyles and basioccipital; b: partial left squamosal
M. 650					Right tympanic bulla
M. 651					Left tympanic bulla
M. 652					Right periotic
M. 654					Anterior end of left dentary
M. 660a-b		Fossée de ravelin, left side of the old Fortin N. 1	Anvers	Diestien, 3rd section	a: fragment of right scapula; b: left radius
M. 647a-b	Borsbeck	Fort 3	Anvers	Diestien	a: partial skull (supraoccipital and part of the vertex); b: partial skull (squamosal fragment)
M. 657					?C4
M. 649	Borgerhaut		Anvers	Diestien, 3rd section	Right tympanic bulla
M. 653	Borgerhaut			Diestien	Posterior process of periotic
M. 655a-c			Anvers	Diestien, 3rd section	a: fragment of axis; b: cervical vertebra; c: ?cervical vertebra
M. 656	Borgerhaut	Grand fossé in face de l'anc. Fortin n. 1	Anvers	Diestien, 3rd section	?cervical or thoracic vertebra
M. 658	Borgerhaut	Fossé capital	Anvers	Diestien, 3rd section	Fragment of right scapula
M. 659		Nouveau canal d'Hérenthals sur la limite Deurne et de Berchem	Anvers	Diestien, 3rd section	Right humerus
M. 661		Fossé capital et la ch.in de la port d'Hérenthals sous Deurne	Anvers	Diestien, 3rd section	Five skull fragments

Tab. 2 - Localities of the discovery of the specimens assigned to *Plesiocetus dubius* by Van Beneden.

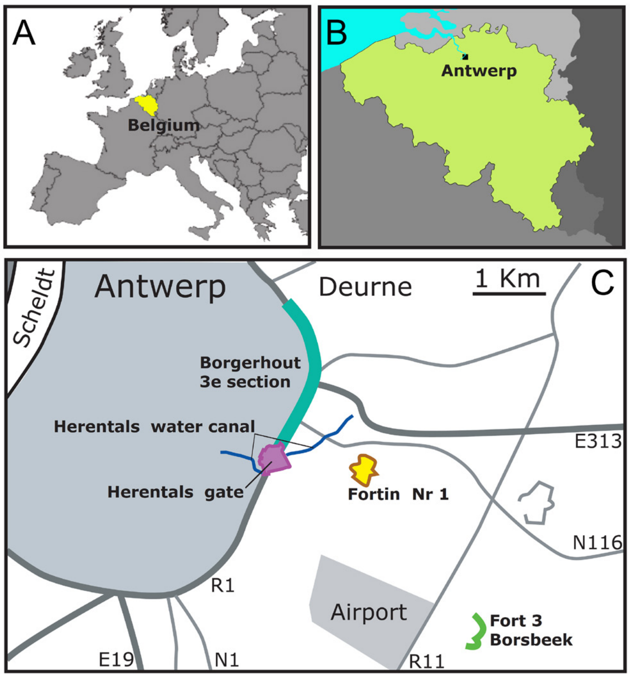


Fig. 2 - Map of the discovery localities of the "type" specimens in the Van Beneden collection of *Plesiocetus*. A) location of Belgium in Europe. B) location of Antwerp in Belgium. C) enlarged view of the localities around Antwerp. "Borgerhout 3rd section" was the section of the fortifications around the city on the territory of Borgerhout. Fortress Nr 3 in Borsbeek is still existent.

RESULTS

General observations on Van Beneden's *Plesiocetus* species

Plesiocetus brialmontii. The bones forming the skeleton assigned to *Plesiocetus brialmontii* by Van Beneden (1880) are from three different Antwerp areas (Tab. 1): Borgerhout, Borsbeek and Deurne and cover a surface of *c.* 6 km^2 (Fig. 2). In addition, 3 specimens are from the the Gate of Herentals (Canal d'Herentals) (at the actual Antwerp ringroad); here, the canal went under the city didge (moat) through a huge steal siphon. Only there the construction pit was deep enough to reach the fossil-bearing horizons (more than 3 m deep). In all the other places the canal did not reach these layers. This location is included in that 6 km^2 area. Therefore, these three specimens are from the location where the siphon of the Herentals canal passes under the city moat (Tab. 5). Based on this observation, common sense suggests that the probability is extremely low that all the specimens Van Beneden assigned to *Plesiocetus brialmontii* represent one individual. If these bones do not belong to the same individual then it is impossible to assign them to the same taxon as they represent different anatomical regions and cannot be compared with each other. Specimens discovered in close connection can be individuated; they are all those bones found in proximity to the Fort Nr. 1 as they are also from the same stratigraphic horizon. These specimens could form one individual. Unfortunately, all the materials discovered in this locality have been sorted out by Van Beneden and assigned to different genera and species based on size and shape but not all these specimens are included here as this paper focuses on *Plesiocetus*. In conclusion, under an optimistic view, the type specimens assigned to *Plesiocetus brialmontii* by Van Beneden represent 6 individuals at least (one from

Specimen	Locality	Locality detail	Closest large city	Stratigraphy	Anatomy
M. 662			Anvers	Diestien, 3rd section	Right supraorbital process of the frontal
M. 678					Right tympanic bulla
M. 663a-b		Fossé du ravelin, left side of the old fortin n. 1	Anvers	Diestien, 3rd section	Fragments of left and right premaxillae
M. 664					Left tympanic bulla
M. 665a-b					Anterior ends of left and right mandibular rami
M. 667a-f					a: atlas; b: axis; c: C3; d: C4; e: C5; f: C6
M. 669a-d					a: C5; b: C7; c: specimen missing; d: T6
M. 671					Left humerus
M. 675					2 unidentified fragments and a partial skull
M. 666	Borgerhaut	Fossé capital	Anvers	Diestien, 3rd section	?right squamosal
M. 670		Fossé capital prés la porte d'Hérenthals sous Deurne	Anvers	Diestien, 3rd section	Right scapula
M. 668	Borgerhaut		Anvers	Diestien, 3rd section	Axis
M. 672					Left ulna
M. 673					Left radius
M. 674			Anvers?	Diestien	Phalanx

Tab. 3 - Localities of the discovery of the specimens assigned to *Plesiocetus hupschii* by Van Beneden.

Tab. 4 - Localities of the discovery of the specimens assigned to *Plesiocetus burtinii* by Van Beneden.

Locality	Locality detail	Closest large city	Stratigraphy	Specimen	Anatomy
	Fossé du ravelin, left side of the old fortin n. 1	Anvers	Diestien, 3rd section	M. 676	Right periotic
				M. 680a-c	a: atlas; b: T1; c: T2
	Left side of the old fortin	Anvers	Diestien, 3rd section	M. 677	Left tympanic bulla
		Anvers	Diestien	M. 679	Left tympanic bulla
		Anvers	Diestien, 3rd section	M. 681	Lumbar vertebra

the vicinity of Fort Nr. 1, one from Fort 3, two from the Canal d'Herenthals, two from the Fossée capital). Unfortunately, the optimistic approach cannot be demonstrated to be valid. Most of the materials assigned to *Plesiocetus brialmontii* consist of fragmentary postcranial bones of scarce diagnostic value.

Plesiocetus dubius. The partial skeleton assigned to *Plesiocetus dubius* by Van Beneden (1880) is formed by bones that have been discovered mostly between Borgerhout and Deurne; these localities are parts of Antwerp that are separated by *c.* 1.5 km (Fig. 2; Tab. 5). Also in this case, the probability that they belong to the same individual approximates zero. Two specimens are from different parts of the Canal d'Herenthals and two are from a different location in Borgerhout (Tab. 2). These represent different individuals. Thirteen specimens are from the vicinity of the Fort Nr. 1 and, given that they are from the same stratigraphic horizon, could represent one individual. Unfortunately, this conclusion is not safe as all the specimens from Fort Nr. 1 should be taken into consideration and re-sorted out but this is currently not possible. In conclusion, based on an optimistic view, the type specimens referred to *P. dubius* represent 6 individuals at least (one from the vicinity of Fort Nr. 1, one from Fort Nr. 3, one from the Herenthals Canal, three from different districts of Borgerhout and Antwerp). However, the optimistic approach cannot be demonstrably valid.

Plesiocetus hupschii. The partial skeleton assigned to *Plesiocetus hupschii* by Van Beneden (1885; Van Beneden and Gervais 1868-1880) is formed by bones discovered in a number of localities between Borgerhout and Deurne (Fig. 2; Tab. 5). It is formed by 6 individuals at least and includes portions of a skull and some postcranial bones of some diagnostic value (Tab. 3).

Plesiocetus burtinii. Van Beneden (1859) established *Plesiocetus burtinii* but this name was then misspelled as *Plesiocetus burtini* by Van Beneden (1880) and Van Beneden (1885), and others. The partial skeleton assigned to *Plesiocetus burtinii* by Van Beneden (1885; Van Beneden & Gervais 1880) consists of bones discovered in the vicinity of the Fort Nr. 1 (Fig. 2; Tab. 5). This is the only species that is based on bones that are not widely scattered (Tab. 5). Van Beneden & Gervais (1880), however, assigned specimens from France and England to this species. Under an optimistic point of view, the Belgian bones could represent one individual. Unfortunately, there is no certainty that the optimistic view corresponds to truth.

SYSTEMATIC PALEONTOLOGY

CETACEA Brisson, 1762
Mysticeti Cope, 1891

Gen. et sp. indet.

Material. IRSBN M. 635, M. 640a-d, M. 644, M. 656, M. 657, M. 658, M. 661, M. 663, M. 667a-f, M. 668, M. 669a-d, M. 672, M. 680.

Descriptions and decisions

Skull. The specimen M. 661 was assigned to *Plesiocetus hupschii* by Van Beneden; this specimen is formed by 5 skull fragments with completely eroded surfaces. Three of these fragments cannot be identified; two fragments include the lateral and posterior portions of the squamosal with an external acoustic meatus and the articular facet for the posterior process of the periotic; one of these fragments includes also the concave lateral surface of the right hiatus cranicus (Fig. 3). The specimen is assigned to Mysticeti gen. et sp. indet. because of the lack of diagnostic characters.

Vertebrae. The specimen M. 635 consists of a single atlas previously assigned to *Plesiocetus brialmontii* (Fig. 4). Measurements are provided in Tab. 6. The

Specimen	Locality	Locality detail	Closest large city	Stratigraphy	Anatomy	Van Beneden's taxonomy
M. 631	Borgerhout		Anvers	Diestien, 3rd section	Left tympanic bulla	*Plesiocetus brialmontii*
M. 649					Right tympanic bulla	*Plesiocetus dubius*
M. 668					Axis	*Plesiocetus hupschii*
M. 672					Left ulna	*Plesiocetus hupschii*
M. 673					Left radius	*Plesiocetus hupschii*
M. 673	Borgerhout	Turmont	Anvers	Diestien, 3rd section	Left radius	*Plesiocetus brialmonti*
M. 643		Fortin N. 1	Anvers	Diestien, 3rd section	Left radius	*Plesiocetus brialmonti*
M. 634					Partial right dentary	*Plesiocetus brialmonti*
M. 639					?11th lumbar vertebra	*Plesiocetus brialmonti*
M. 637a		Fortin N. 1, cap. N. 5	Anvers	Diestien, nouvelle, 3rd section	?5th cervical vertebra	*Plesiocetus brialmonti*
M. 637b					?7th cervical vertebra or 1st thoracic vertebra	*Plesiocetus brialmonti*
M. 630a	Borgerhout	Fortin N. 1	Anvers	Diestien, 3rd section	Fragments of squamosal	*Plesiocetus brialmonti*
M. 630b					Right mandibular condyle	*Plesiocetus brialmonti*
M. 633					Right tympanic bulla	*Plesiocetus brialmonti*
M. 644	Borgerhaut	Fortin N. 1, right side	Anvers	Diestien, 3rd section	Right ulna	*Plesiocetus brialmonti*
M. 635	Borgerhaut	Fossée capital	Anvers	Diestien, 3rd section	Atlas	*Plesiocetus brialmonti*
M. 658					Fragment of right scapula	*Plesiocetus dubius*
M. 666					?right squamosal	*Plesiocetus hupschii*
M. 636		Canale d'Hérenthals, Gazometro	Anvers	Diestien, 3rd section	Axis	*Plesiocetus brialmonti*
M. 641	Berchem	Canal d'Hérenthals	Anvers	Diestien, 3rd section	Fragment of left scapula	*Plesiocetus brialmonti*
M. 642					Left humerus	*Plesiocetus brialmonti*
M. 659		Nouveau canal d'Hérenthals sur la limite Deurne et de Berchem	Anvers	Diestien, 3rd section	Right humerus	*Plesiocetus dubius*
M. 661		Fossé capital et la ch.in de la port d'Hérenthals sous Deurne	Anvers	Diestien, 3rd section	Five skull fragments	*Plesiocetus dubius*
M. 670					Right scapula	*Plesiocetus hupschii*
M. 638a	Borsbeck	Fort 3	Anvers	Diestien	?9th thoracic vertebra	*Plesiocetus brialmonti*
M. 638c					?3rd lumbar vertebra	*Plesiocetus brialmonti*
M. 638c					Chevron	*Plesiocetus brialmonti*
M. 647a-b					a: partial skull (supraoccipital and part of the vertex); b: partial skull (squamosal fragment)	*Plesiocetus dubius*
M. 657					?C4	*Plesiocetus brialmonti*
M. 645a-g		Fossée de ravelin, left side of the old Fortin N. 1, Caponniére N. 5	Anvers	Diestien, 3rd section	a: atlas; b: axis; c: C3; d: T1; e: T7, f: L3; g: Cd9	*Plesiocetus dubius*
M. 646a					Indet.	*Plesiocetus dubius*
M. 646b					Indet.	*Plesiocetus dubius*
M. 648a-b					a: fragment of exoccipital with condyles and basioccipital; b: partial left squamosal	*Plesiocetus dubius*
M. 650					Right tympanic bulla	*Plesiocetus dubius*
M. 651					Left tympanic bulla	*Plesiocetus dubius*
M. 652					Right periotic	*Plesiocetus dubius*
M. 654					Anterior end of left dentary	*Plesiocetus dubius*
M. 660a-b		Fossée de ravelin, left side of the old Fortin N. 1	Anvers	Diestien, 3rd section	a: fragment of right scapula; b: left radius	*Plesiocetus dubius*
M. 676					Right periotic	*Plesiocetus burtini*
M. 680a-c					a: atlas; b: T1; c: T2	*Plesiocetus burtini*
M. 655a-c			Anvers	Diestien, 3rd section	a: fragment of axis; b: cervical vertebra; c: ?cervical vertebra	*Plesiocetus dubius*
M. 662					Right supraorbital process of the frontal	*Plesiocetus hupschii*
M. 678					Right tympanic bulla	*Plesiocetus hupschii*
M. 677		Left side of the old fortin	Anvers	Diestien, 3rd section	Left tympanic bulla	*Plesiocetus burtini*
M. 679					Left tympanic bulla	*Plesiocetus burtini*
M. 681					Lumbar vertebra	*Plesiocetus bustini*
M. 679	Borgerhaut		Anvers	Diestien	Left tympanic bulla	*Plesiocetus dubius*
M. 681			Anvers	Diestien, 3rd section	Lumbar vertebra	*Plesiocetus hupschii*
M. 664					Left tympanic bulla	*Plesiocetus hupschii*
M. 665a-b					Anterior ends of left and right mandibular rami	*Plesiocetus hupschii*
M. 667a-f					a: atlas; b: axis; c: C3; d: C4; e: C5; f: C6	*Plesiocetus hupschii*
M. 669a-d					a: C5; b: C7; c: specimen missing; d: T6	*Plesiocetus hupschii*
M. 671					Left humerus	*Plesiocetus hupschii*
M. 675					2 unidentified fragments and a partial skull	*Plesiocetus hupschii*
M. 674			Anvers?	Diestien	Phalanx	*Plesiocetus hupschii*

Tab. 5 - List of the figured specimens of *Plesiocetus* by Van Beneden (1880) and Van Beneden and Gervais (1868-1880) arranged based on the locality of the discovery.

atlas is damaged in part and lacks half of the neural arch. The surfaces for the articulation with the occipital condyles of the skull are very concave and their ventromedial borders are separated by a notch. The neural canal is dorsoventrally elongated; the lateral borders of the neural canals are straight and converge ventrally. The transverse process is short and shows a small but well developed dorsomedial tubercle. The articular surfaces for the axis are flat. The ventral border of the left articular facet for the axis shows the sign of a possible but unidentified pathology. This atlas presents unique characters in that its foramen magnum is dorsoventrally elongated with straight lateral borders and the transverse

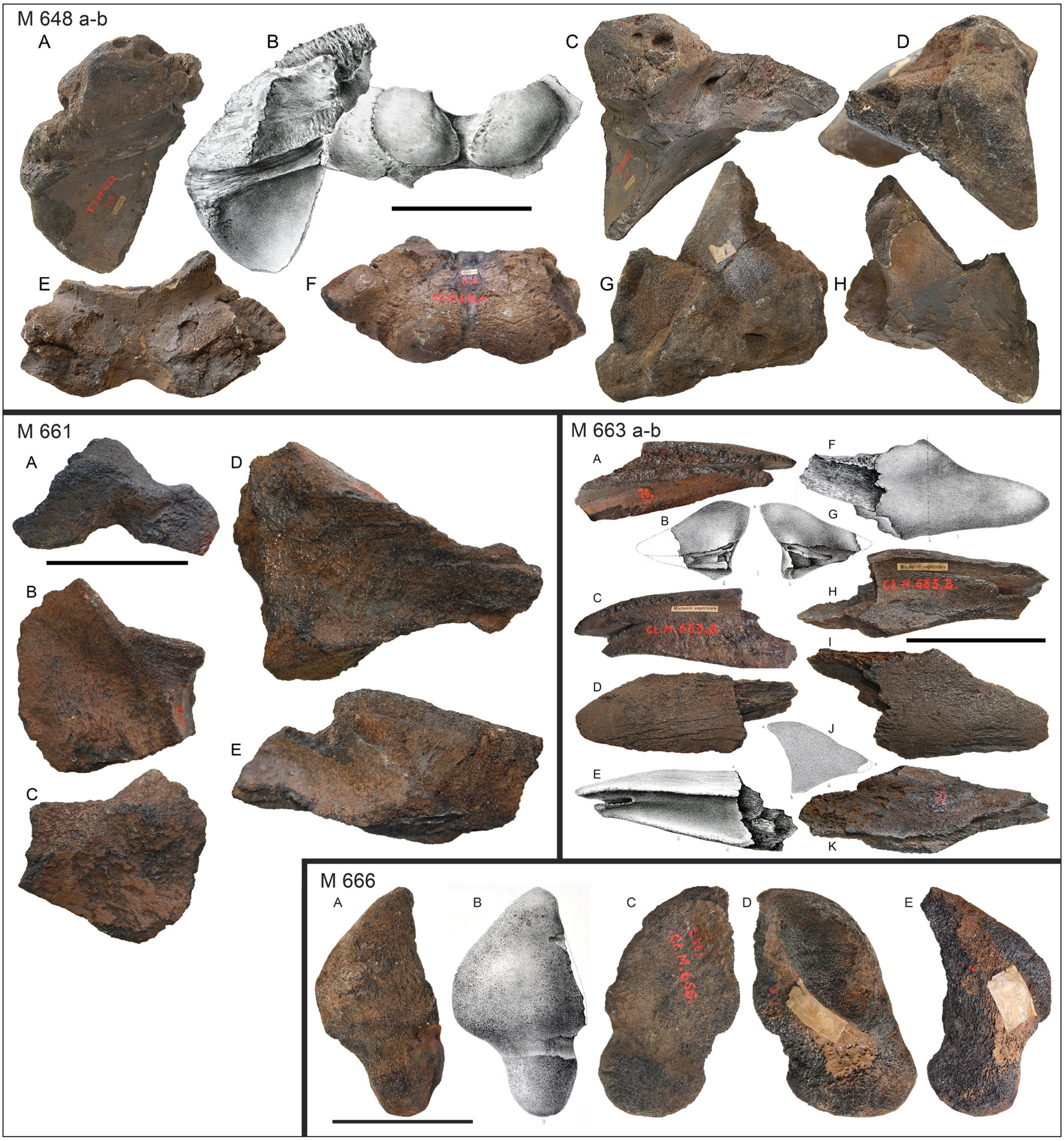


Fig. 3 - Specimen M. 648: A) posterior view of left squamosal (M. 648a) showing the postglenoid process and the external acoustic meatus; B) Van Beneden plate showing the specimens M. 648a and b in articulation; C) left squamosal (M. 648a) in medial view; D) left squamosal in lateral view; E) basioccipital in dorsal view; F) basioccipital in ventral view; G) left squamosal (M. 648b) in dorsal view; H) left squamosal in ventral view. Specimen M. 661: A, B and C) indeterminate fragments; D, E) squamosal. Specimen M. 663: A-to-E) anterior end of left premaxilla; F-K) anterior end of right premaxilla. In particular: B, E, F, G and J are from Van Beneden (1885) with J being the cross section of the right premaxilla at mid-length. Specimen M. 666: A) posterior view of the left mandibular condyle; B) the same from Van Beneden (1885); C) the same in lateral view; D) the same in medial view; E) the same in anteromedial view. Scale bars equal 10 cm.

process shows a dorsomedial tubercle that is well developed. The presence of a dorsomedial tubercle is shared with other mysticete specimens referred by different authors to *Halicetus ignotus*, *Plesiocetus burtinii*, *Burtinopsis similis*, *Burtinopsis minutus*, and *Piscobalaena nana*. However, small differences prevent the safe placement of this atlas in one of these taxa. In *Burtinopsis similis* the transverse process is

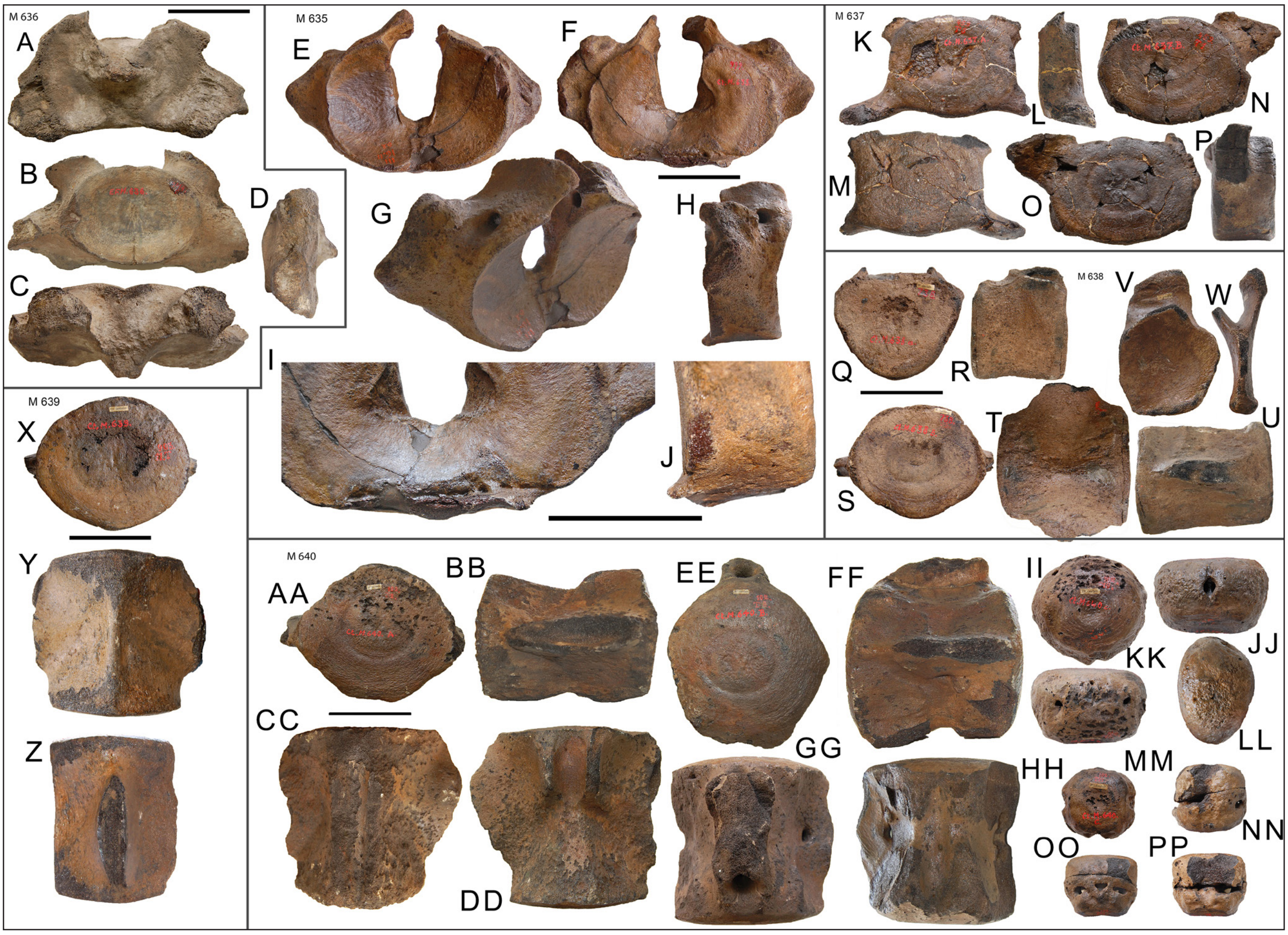


Fig. 4 - Specimen M. 636, axis: A) anterior view; B) posterior view; C) dorsal view; D) right lateral view. Specimen M. 635, atlas: E) anterior view; F) posterior view; G) anterodorsal view from right side; H) left lateral view; I) close-up of ventral border in anterior view; J) close-up of ventral border in left lateral view. Specimen M. 637a-b, cervical vertebrae; M. 637a: K) anterior view; L) right lateral view; M) posterior view; M. 637b: N) anterior view; O) posterior view, P) left lateral view. Specimen M. 638a-c, lumbar vertebrae and chevron; M. 638a, indeterminate lumbar vertebra: Q) anterior view; R) right lateral view. M. 638b: S) anterior view; T) ventral view; U) right lateral view. M. 638c, chevron: V) right lateral view; W) anterior view. Specimen M. 639, indeterminate lumbar vertebra: X) anterior view; Y) ventral view; Z) left lateral view. Specimen M. 640a-d, four caudal vertebrae: AA) anterior-most caudal vertebra of this series (probably Cd2) in anterior view; BB) the same in right lateral view; CC) the same in dorsal view; DD) the same in ventral view; EE) anterior caudal in anterior view; FF) the same in right lateral view; GG) the same in dorsal view; HH) the same in ventral view; II) posterior caudal in anterior view; JJ) the same in ventral view; KK) the same in dorsal view; LL) the same in left lateral view; MM) caudal-most caudal vertebra in anterior view; NN) the same in posterior view; OO) the same in dorsal view; PP) the same in ventral view. Scale bars equal 10 cm.

more delicate and the dorsomedial process is very slightly developed; in *Burtinopsis minutus* the the lateral borders of the foramen magnum are not straight; in *Plesiocetus burtinii* the ventral borders of the articular surfaces for the occipital condyles project medially and the dorsomedial tubercle is much more robust; in *Halicetus ignotus* the transverse processes are much shorter and the ventromedial borders of the articular surfaces for the occipital condyles are in contact along the medial axis of the atlas; in *Piscobalaena nana* the transverse processes are more compressed along the dorsoventral axis and elongated. There are no obvious distinguishing characters for this atlas that is, thus, assigned to Mysticeti gen. et sp. indet.

The specimens M. 640a-d include a partial caudal column (Fig. 4; Tab. 6). All these vertebrae were previosly assigned to *Plesiocetus brialmontii*. The specimen M. 640a is probably a Cd2. It is robust and has short but large transverse processes; the lateral surfaces of the body are concave above and below the transverse process; the attachment sites for the chevrons form two high relieves located anteroventrally. The specimen M. 640b is a caudal vertebra located in the anterior half of the series. It is robust and its neural arch is preserved. The neural channel is tube-like and the neural arch is transversely perforated. The lateral walls of the body are

Tab. 6 - Measurements of the vertebrae described in the text. Data in mm. Abbreviations: Blength, lenght of body along longitudinal axis; Bwidth, widht of body; Bheight, height of body; Maxwidth, maximum width of the vertebra (including transverse processes); Maxheight, maximum height of the vertebra (including neural process); NCheight, height of neural canal; NCwidth, width of neural canal. [a]Reconstructed value. [b]As preserved.

Specimen	Blength	Bwidth	Bheight	Maxwidth	Maxheight	NCheight	NCwidth
M. 635	69.86	290.4	149	320[a]		102.8	54.7
M. 636	103.8			295[b]	139.78[b]		
M. 637a	52	152	122	229[b]	132[b]		
M. 637b	70	172	118	219[b]	116[b]		
M. 638a	117	141.5	118.5	156[b]	134[b]		61
M. 638b	164.4	165	138	219[b]	137[b]		
M. 639	205	186	161	242[b]			
M. 640a	218	205	174	254[b]	177[b]		31
M. 640b	194	182	185	190[b]	220[b]		23.06
M. 640c	86.04	109.37	116.31	139.15[b]	130.95[b]		
M. 640d	74.06	82.19	79.08		86.09[b]		
M. 645a	68	203	130	281[b]			62
M. 645b	70.91	145.63	86.56	219[b]	189[b]		
M. 645c	43	120	121	150[b]			
M. 645d	56	141	110	200[b]	147[b]		85
M. 645e	121	128	117	178[b]	143[b]		58
M. 645f	152	139	125	156[b]			51
M. 645g	139	123	144				49
M. 655a		150	100	255[b]	155[b]		80
M. 655b	37	140	102	152[b]	135[b]		70
M. 655c	46	140	117	171[b]	132[b]		90
M. 656	43	142	121				90[b]
M. 657	194	156	144				24
M. 667a		68	106	252[b]	155[b]	85	52
M. 667b		145	83	244[b]	110[b]		73
M. 667c	35	139	96				87
M. 667d	32	131	105	140[b]	110[b]		93
M. 667e	30	125	109	141[b]	124[b]		95
M. 667f	42	124	99	139[b]	105[b]		93
M. 668		164	102	232[b]	118[b]		72
M. 669a	30	134	112	150[b]	102[b]		83
M. 669b	44	143	102	167[b]	133[b]		85
M. 669d	109	107	99		114[b]		48
M. 680a	65	182	125	237[b]	129[b]	86[b]	43
M. 680b	38	118	97	161[b]	98[b]		80[b]
M. 680c	43	131	97	161[b]	132[b]		80
M. 681	144	132	120	142[b]			31

concave above and below the transverse processes that are longitudinally elongated and show a dorsoventral foramen located at their emergences. The attachment sites for the chevrons are anteriorly and posteriorly relieved; they form a ventromedial fossa including a large nutrititious foramen. The specimen M. 640c is a caudal vertebra that should be part of the posterior half of the caudal series. It lacks neural arch and transverse processes. The ventral surface of its body shows two foramens located on both sides of a sagittal crest. These foramina are prolonged into canals that cross the body of the vertebra and open on the dorsolateral surfaces. The specimen M. 640d is one of the posterior-most caudal vertebrae (Fig. 4; Tab. 6). It shows dorsolateral foramina but its ventral surface is badly preserved. None of these specimens (M. 640a-d) can be safely assigned to any known mysticete taxon; they are, therefore, assigned to Mysticeti gen. et sp. indet.

The specimen M. 656 represents a cervical vertebra with elliptical outline of the body in anterior view. Ventrolateral tuberosities are present as well as flat anterior and posterior surfaces of the vertebral epiphyses (Fig. 5; Tab. 6). The specimen M. 657 is a caudal vertebra with convex anterior face and circular outline (Fig. 5; Tab. 6). The neural canal is transversely narrow; the transverse processes are broken; their medial parts are dorsoventrally perforated. The attachment sites for the chevrons are relieved anteriorly and posteriorly and a deep elliptical fossa is developed amid them. Both M. 656 and M. 657 were previously assigned to *Plesiocetus dubius* but are now assigned to Mysticeti gen. et sp. indet. because of their lack of diagnostic characters.

The specimens M. 667a-f represent a partial cervical section of a vertebral column (Fig. 6; Tab. 6); these vertebrae were previously assigned to *Plesiocetus hupschii*. The atlas (M. 667a) shows an oval

Fig. 5 - Specimen M. 645a-g. M. 645a, atlas: A) posterior view; B) anterior view; C) right laterodorsal view; D) right lateral view. M. 645b, axis: E) posterior view; F) anterior view; G) right lateral view. M. 645c, ?C3: H) right lateral view; I) anterior view. M. 645d, ?T1: J) posterolateral view; K) posterior view; O) left lateral view; P) anterior view. M. 645e, indeterminate thoracic vertebra: L) posterior view; M) right lateral view; N) ventral view. M. 645f, indeterminate lumbar vertebra: Q) anterior view; R) ventral view; S) left lateral view. M. 645g, indeterminate caudal vertebra: T) anterior view; U) right lateral view; V) ventral view. Specimen M. 656, indeterminate cervical vertebra: W) anterior view; X) right lateral view; Y) dorsal view. Specimen M. 655a-c. M. 655a, axis: Z) posterior view; AA) anterior view; BB) right lateral view. M. 655b, indeterminate cervical vertebra: CC) posterior view; DD) anterior view; EE) right lateral view. M. 655c, indeterminate cervical vertebra: FF) posterior view; GG) right lateral view. Specimen M. 657, indeterminate caudal vertebra. HH) dorsal view; II) right lateral view; JJ) ventral view; KK) posterior view. Scale bar equals 10 cm.

neural canal; the transverse processes are broken but their emergences are located at the middle of the height of the lateral surface of the vertebra; the inferior face of the body is transversely straight and shows squared ventrolateral corners. The axis (M. 667b) is badly damaged and shows a ventrolaterally protruded ventral transverse process and transversely wide, oval-shaped neural canal. The specimens M. 667c-d represent the other cervical vertebrae that have pentagonoid-shaped epiphyses in anterior view; ventrolateral tubercles and transversely wide neural canals. The specimen M. 667e shows an hexagon-like outline in anterior view while M. 667f shows an oval shape. The neural canal is transversely wide in all of them.

The specimen M. 668 was previously assigned to *Plesiocetus hupschii* (Fig. 6; Tab. 6) and is represented by a partial axis with ventrolaterally protruded transverse processes; the neural canal is oval-shaped and the dens is low.

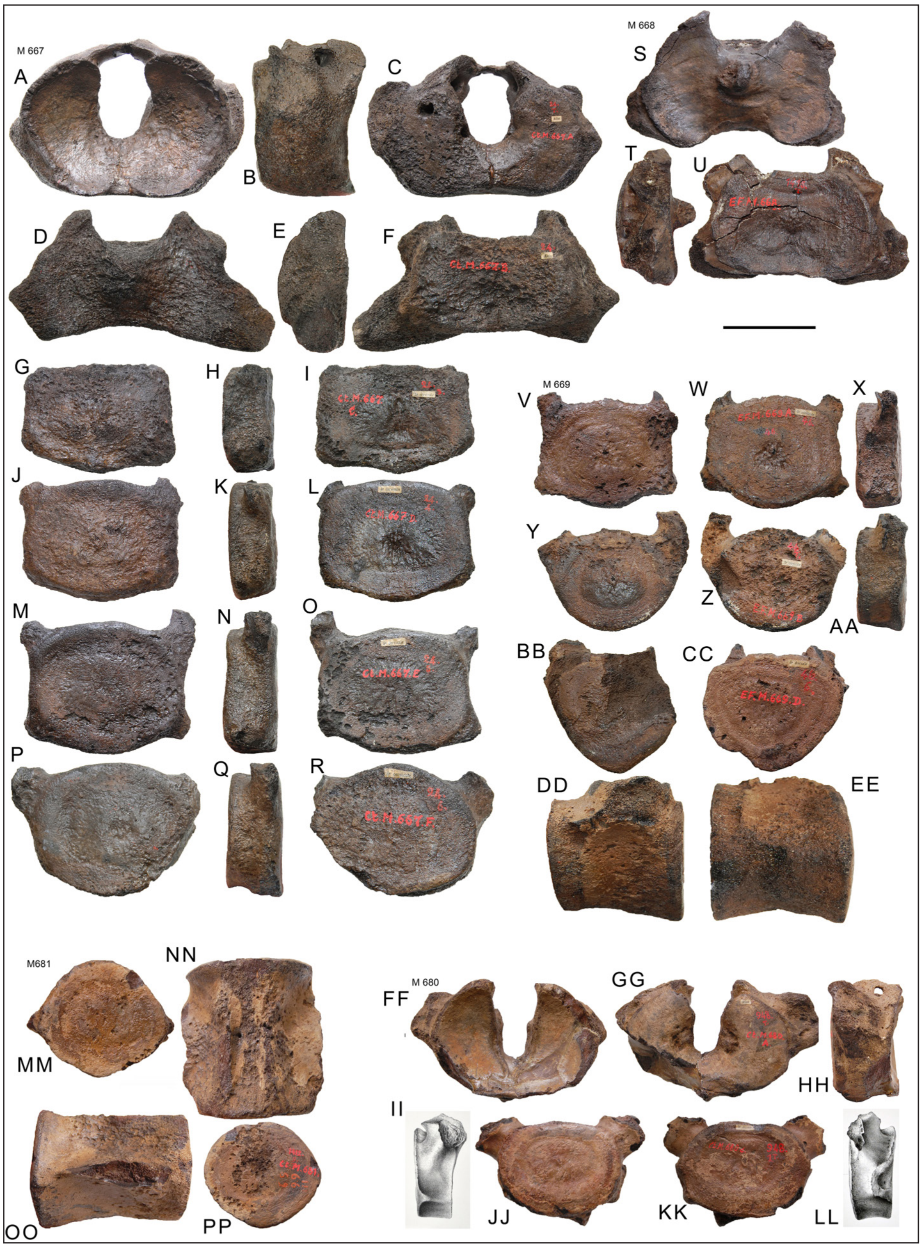


Fig. 6 - Specimen M. 667a-f. M. 667a, atlas: A) anterior view; B) right lateral view; C) posterior view. M. 667b: axis: D) anterior view; E) left lateral view; F) posterior view. M. 667c, possible C3: G) anterior view; H) right lateral view; I) posterior view. M. 667d, possible C4: J) anterior view; K) right lateral view; L) posterior view. M. 667e, possible C5: M) anterior view; N) right lateral view; O) posterior view. M. 667f, possible C6: P) anterior view; Q) right lateral view; R) posterior view. Specimen M. 668, axis: S) anterior view; T) right lateral view; U) posterior view. Specimen M. 669a, b, d. M. 669a, indeterminate cervical vertebra: V) anterior view; W) posterior view; X) right lateral view. M. 669b, indeterminate cervical vertebra: Y) anterior view; Z) posterior view; AA) right lateral view. Specimen M. 669d, indeterminate thoracic vertebra: BB) anterior view; CC) posterior view; DD) right lateral view; EE) ventral view. M. 680a, atlas: FF) anterior view; GG) posterior view; HH) left lateral view. M. 680b, possible T1: II) right lateral view; JJ) anterior view. M. 680c, possible T2: KK) anterior view; LL) left lateral view. Scale bar equals 10 cm.

The specimens M. 669a, b and d are two cervical vertebrae and M. 669d is a thoracic vertebra (Fig. 6; Tab. 6). All of them are assigned to Mysticeti gen. et sp. indet. Because of their lack of diagnostic characters.

The specimen M. 680a-c are three badly preserved vertebrae (Fig. 6; Tab. 6) that were previously assigned to *Plesiocetus burtinii*. M. 680a is an atlas with triangular neural canal and short and stocky and squared transverse process. This atlas resembles that of the living *Megaptera novaeangliae* in the shape of the transverse process. The specimen M. 680b is a possible first thoracic vertebra with transversely wide neural canal. The specimen M. 680c is a possible T2 with a pathology on the ventral surface. Finally, M. 681 (Fig. 6; Tab. 6) is a lumbar vertebra with ventral keel and transvers processes emerging from the middle of the height of the lateral wall of the body. The neural canal is transversely narrow and is perforated by several nutritional foramina. These specimens are too incomplete to warrant a correct taxonomic placement and for this reason they are assigned to Mysticeti gen. et sp. indet.

Forelimb. The specimen M. 644 was previously assigned to *Plesiocetus brialmontii* and is represented by a right ulna (Fig. 7). Both proximal and distal epiphyses are damaged and the olecranon is destroyed. The medial side of this ulna is flat-to-slightly convex; the lateral side is strongly convex. The proximal articular facet is convex. The posterior border of the ulna is concave. The proximodistal diameter is 445 mm; the anteroposterior diameter at mid-length is 67.97 mm, at the proximal end it is 106.74 mm and at the distal end it is 80 mm. The anteroposterior diameter of the proximal articular facet is 75.11 mm. This specimen lacks taxonomically-informative characters and is assigned to Mysticeti gen. et sp. indet.

The specimen M. 658 was previously assigned to *Plesiocetus dubius*. It includes a fragment of a right scapula with acetabulum and partial coracoid and acromion processes (Fig. 17C-E). The acetabulum is oval-shaped with dorsally concave medial border and straight lateral border. The external border of the scapula projects posteriorly and slightly dorsally forming a slight ventral concavity. The coracoid process is stocky at its base; it projects anteriorly and medially. The emergence of the acromion is robust and projects anteriorly and dorsally. The Medial face of the scapula is concave dorsally to the acetabulum. The anteroposterior diameter of the acetabulum is 128 mm and its transverse diameter is 94 mm. The maximum length of the scapula is 322 mm from the anterior end of the coracoid process to the posterior-most point as preserved on the bone. The maximum height is 140 mm. It is not possible to assess extension and morphology of the other characters of the scapula as they are not preserved on this poorly-preserved bone. The lack of informative characters implies the assignment of this specimen to Mysticeti gen. et sp. indet.

The specimen M. 672 was previously assigned to *Plesiocetus hupschii* and is represented by a partial left ulna (Fig. 7). This ulna has an anteriorly convex anterior border while the posterior border is eroded in part. The olecranon is missing because of post-depositional processes. The proximodistal length of the ulna is 408 mm and its anteroposterior diameter at mid-length is 53 mm. The proximal articular facet is highly inclined; its anteroposterior diameter is 75 mm and its transverse diameter is 62 mm. The lateral side of the ulna is convex but the medial side is rather flat. The specimen lacks taxonomically-informative characters and is assigned to Mysticeti gen. et sp. indet.

Chaeomysticeti Mitchell, 1989
Gen. et sp. indet.

Material. IRSNB M. 636.

Description and decision

The specimen M. 636 was assigned to *Plesiocetus brialmontii* and consists of an axis (Fig. 4; Tab. 6) with elongated dens and robust ventral transverse processes. The posterior facet for articulation with the third cervical vertebra is very concave. The specimen is so poorly preserved that it is not possible to safely assign it to a known mysticete genus or species. The strongly-protruding odontoid process observed in this axis can be observed also in Thalassotherii and in Eomysticetidae (i.e., genus *Tokarahia*; see Boessenecker & Fordyce 2015) but not in Balaenoidea. It is therefore assigned to Chaeomysticeti gen. et sp. indet.

Balaenomorpha Geisler & Sanders, 2003
Gen. et sp. indet.

Materials. IRSBN M. 663 (skull), M. 666 (dentary). M. 641, M. 643, M. 671, M. 673, M. 674 (forelimbs). Vertebrae: M. 637a-b, M. 638a-c, M. 639, M. 645a-g, M. 655a-c, M. 681 (vertebrae).

Descriptions and decisions

Skull. The specimen M. 663 consists of two fragments of right and left premaxillae (Fig. 3). The surface of these premaxillae are anteroposteriorly and transversely convex; the left one shows the real border that is straight. The total length of the right one is 173 mm and of the left one is 166 mm. The maximum width of the right one is 62 mm and of the left one is 75 mm. The specimen, previously assigned to *Plesiocetus hupschii*, is shown in Fig. 3. It is not possible to assign this specimen to any of the known mysticete genera. However, it lacks alveoli and this prevents its inclusion within Eomysticetidae. For this reason, it is assigned to Balaenomorpha gen. et sp. indet.

The specimen M. 666 includes a mandibular fragment with eroded surfaces (Fig. 3) and was assigned to *Plesiocetus hupschii* by Van Beneden. It It is *c.* 160 mm in length and 80.89 mm in transverse width. The specimen includes a mandibular condyle faced posterodorsally and a small-sized angular process. The groove between the mandibular condyle and the angular process is low and wide. The poor

Fig. 7 - Specimen M. 641a: A) lateral view of right scapula; B) the same in medial view; C) the same in ventral view. Specimen M. 674: D) from left to right, anterior, medial, lateral, posterior, distal (upper image) and proximal (lower image) views of an unidentified phalanx. Specimen M. 672: left ulna (E) distal view; F) lateral view; G) proximal view; H) medial view; I) anterior view; J) the same specimen from Van Beneden (1885) in medial view; K) cross section of diaphysis at mid-length from Van Beneden (1885); L) distal section). Specimen M. 671, right humerus: M) medial view; N) lateral view; O) superior view of the humeral head; P) inferior view of distal epiphysis showing articulation facets for radius (on the left) and ulna (on the right); Q) posterior view showing the articulation facet for olecranon. Specimen M. 643, left radius: R) lateral view; S) anteroinferior view showing the distal cross section; T) medial view from Van Beneden (1885); U) cross section of diaphysis at mid-length from Van Beneden (1885). Specimen M. 673, right radius: V) lateral view; W) medial view; X) proximal epiphysis; Y) distal epiphysis. Scale bar equals 5 cm in D and 10 cm in all the other images.

preservation prevents a detailed taxonomic decision. Here it is assigned to Balaenomorpha gen. et sp. indet because it differs from the eomysticetid mandible in having the condyle located not dorsally. It It is *c.* 160 mm in length and 80.89 mm in transverse width. Morphology is almost unreadable. The poor preservation prevents a detailed taxonomic decision. Here it is assigned to Balaenomorpha gen. et sp. indet.

Forelimbs. The specimen M. 641 (Fig. 7) was previously assigned to *Plesiocetus brialmontii*. It includes a fragment of a left scapula with acetabulum and emergences of acromion and coracoid process. The supraspinous fossa is very reduced. The acetabulum is elliptical with convex lateral and dorsomedial borders. The main body of the scapula shows a strong medial concavity. The anterior border of the scapula projects dorsally and anteriorly; the posterior border projects posteriorly and dorsally resembling the scapulae of balaenopterids and cetotheriids. The anterior border is convex and the posterior border is concave. The acetabulum shows the fused epyphysis supporting the hypothesis that the animal was a subadult or an adult individual. The anteroposterior diameter of the acetabulum is 127.81 mm and its transverse diameter is 85.09. The length of the coracoid process is 32.33 mm and its height at base is 50.77 mm. The total length of the scapular fragment is 379 mm and its total height (as preserved) is 168 mm. The specimen does not belong to Balaenidae, Eomysticetoidea, Eschrichtiidae because it shows a conspicuous anteroposterior expansion. Such a reduction is observed, i.e., in *Caperea marginata* but the transverse expansion of the scapula of M. 641 is developed in a degree unobserved in Neobalaenidae. Reduction in the development of the supraspinous fossa is observed in basal thalassotherians (Kellogg

1965, 1968) and balaenopterids (e.g., *Plesiobalaenoptera hubachi*; see Bisconti 2011) suggesting that the specimen M. 641 could belong into basal thalassotherians or Balaenopteridae. Lacking additional information useful for a taxonomic decision, M. 641 is assigned to Balaenomorpha gen. et sp. indet.

M. 643 is represented by a left radius and was previously assigned to *Plesiocetus brialmontii* (Fig. 5). The anterior and posterior borders are badly preserved; the bone is anteriorly convex. The proximal epiphysis is wider than the distal epiphysis. The proximal epiphysis was not fused with the diaphysis. The length of the bone is 506 mm, its width at mid-length is 79 mm, its transverse diameter is 47.27 mm. The anteroposterior diameter of the proximal articular facet is 110 mm and of the distal articular facet is 66 mm. Archaic mysticete characters (i.e., the sharp curve observed in the radius of *Yamatocetus*, *Waharowa*, and *Horopeta*) are not observed in this radius thus preventing its inclusion within Eomysticetidae (Okazaki 2012; Boessenecker & Fordyce 2015b; Tsai & Fordyce 2015). There are no additional taxonomically-useful characters on this radius that is here assigned to Balaenomorpha gen. et sp. indet.

The specimen M. 671 is represented by a left humerus previously assigned to *Plesiocetus hupschii* (Fig. 7). The posterior border of this humerus is straight distally to the head; the anterior border is concave. The proximodistal length is 305 mm; the maximum anteroposterior diameter at mid-length is 98 mm. The head is 128 mm in anteroposterior length and has a rounded shape; its articular surface is especially developed dorsally and posteriorly. The distal epiphysis is anteroposteriorly elongated and shows an anterior facet for articulation with radius (71 mm in anteroposterior length) separated from the posterior facet for articulation with ulna (60 mm in anteroposterior length) by a protruding and triangular crest. Posterior to the articular facet for articulation with the ulna is the facet for the articulation with the olecranon process that is located on the distal portion of the posterior border of the humerus. The facet for the olecranon is small; the facet for the radius is longer than that of the ulna. The deltopectoral crest is squared and is developed up to the middle of the humerus; its proximal-most portion is badly eroded. This humerus shows some resemblance to the humerus of *Piscobalaena nana* in the shape of the anterior border and the straight posterior border. Differences from *P. nana* are observed in the direction of the development of the articular surface of the head in that in M. 671 the head is developed more proximodistally. An additional difference from *P. nana* is found in the articular facet for the radius that is longer than that of the ulna. *Thinocetus arthritus* and *Pelocetus calvertensis* have humeri that are comparatively more elongated. Living mysticetes have more proximodistally compressed humeri. Eomysticetid humeri have different shapes, flatter heads and longer deltopectoral crests; this excludes that this humerus belongs to Eomysticetidae. The specimen M. 671 is, therefore, assigned to Balaenomorpha gen. et sp. indet.

The specimen M. 673 was previously assigned to *Plesiocetus hupschii* and consists of a large sized left radius (Fig. 7). The proximodistal length of the bone is 420 mm and its anteroposterior diameter at mid-length is 82 mm. The proximal articular facet is inclined and its anteroposterior diameter is 72 mm and its transverse diameter is 54 mm. This bone has both anterior and posterior borders anteriorly convex and does not display any taxonomically-informative characters. It lacks the strong anterior curvature observed in Eomysticetidae and this prevents its inclusion within this group. It is, thus, assigned to Balaenomorpha gen. et sp. indet.

Vertebrae. The specimens M. 637a and b are poorly preserved cervical vertebrae (Fig. 4; Tab. 6). The specimen M. 637a is a C5 and it shows a long ventral transverse process and a slightly concave anterior surface of the body; the posterior surface is convex. The specimen M. 637b is a possible C7 (or T1); it has an anteroposteriorly compressed body and the articular surface has an oval outline. The ventral transverse process is reduced to a tubercle.The specimens M. 638a and b (Fig. 4; Tab. 6) are respectively a posterior thoracic vertebra and a lumbar vertebra. The anterior face of the body of the thoracic vertebra has a triangular outline; the lumbar vertebra shows a ventral keel, concave lateral surfaces of the body, and transverse process emerging from the middle of the lateral surfaces; the transverse process projects transversely and not lateroventrally thus preventing its inclusion in Eomysticetidae. The specimen M. 638c is a chevron (Fig. 4) whose height is 178 mm and maximum length is 118.5. The specimen M. 639 is a lumbar vertebra (Fig. 4; Tab. 6) with a sharp ventral keel and concave dorsolateral and ventrolateral surfaces of the body; the outline of the articular facets for the other vertebrae are dorsoventrally compressed oval-shaped; even in this case the inclusion in Eomysticetidae is excluded based on the transverse protrusion of the transverse process of the lumbar vertebra. All these specimens (M. 637, M. 638a-c, M. 639), previously assigned to *Plesiocetus brialmontii*, cannot be assigned to any known mysticete taxon because of their poor preservation and because of their lack of diagnostic characters. However, given that they cannot be assigned to Eomysticetidae, they can be included within Balaenomorpha gen. et sp. indet.

The specimens M. 645a-g represent a partial vertebral column that was previously assigned to *Plesiocetus dubius*. The atlas (M. 645a) shows concave anterior articular facets that are ventrally separated by an interposing notch (Fig. 5); transverse processes are stocky and show a robust dorsomedial tubercle. The neural channel is triangular with borders that converge ventrally. Measurements are provided in Tab. 6 The axis (M. 645b) shows a protruding, large dens (Fig. 5; Tab. 6). The posterior articular surface is elliptical in shape and very concave. The dorsal transverse process is delicate and tiny; the ventral transvers process is large and protrudes laterally and ventrally. Both these processes are broken distally. A possible C3 (M. 645c; Fig. 5; Tab. 6) is represented by a badly damaged vertebra with broken dorsal transverse process and short ventral transverse process. The ventral process is complete and demonstrates that the foramen transversarium was not fully surrounded by bone in this whale. The specimen M. 645d (Fig. 5; Tab. 6) is a possible first thoracic vertebra. The outline of the body is elliptical being it dorsoventrally compressed. The surface of the anterior epiphysis is flat wherever the epiphysis is preserved. The ventrolateral corners of the body show low tuberosities; the dorsolateral corners are occupied by the emergences of the transvsers processes that are distally broken. The specimen M. 645e is a thoracic vertebra that can be located at the mid-length of the thoracic series (Fig. 5; Tab. 6). It shows a ventral keel and the epiphyses have a triangular outline. The lateral surfaces of the body are concave. The specimen M. 645f is one of the first lumbar vertebrae. It shows a ventral keel, wide neural channel perforated by nutritional foramens, and transverse processes emerging from the middle of the height of the lateral sides of the body. The specimen M. 645g is a caudal vertebra with transversely compressed body; transversely narrow neural canal and relieved attachment sites for the chevron. A deep fossa is developed between the attachment sites for the chevron. The tubercles located dorsomedially of the transverse process of the atlas suggest that this partial vertebral column could belong to a cetotheriid mysticete. However, it is not possible to ascertain which species is represented by these specimens and our knowledge of the morphology of the vertebral column in these mysticetes is too limited to support a detailed taxonomic decision. Therefore, it is assigned to Balaenomorpha gen. et sp. indet.

The specimens M. 655a-c represent a partial axis and two additional cervical vertebrae (Fig. 5; Tab. 6) previously assigned to *Plesiocetus dubius*. The axis shows a squared neural canal and a protruding odontoid process. The other cervical vertebrae show very short ventrolateral apophyses demonstrating that the foramen transversarium was incompletely surrounded by bone; moreover, these vertebrae show a sagittal tuberosity along the ventral surface. Eomysticetiid axes are different in that the transverse processes are much shorter and the neural spine is longer. After excluding the specimen from belonging to Eomysticetidae, there is no possibility to assign these vertebrae to any other known mysticete genus and species, therefore they are assigned to Balaenomorpha gen. et sp. indet.

Superfamily Balaenoidea Flower, 1864
Gen. et sp. indet.

Material: IRSNB M. 676 (right periotic).

Description

The specimen M. 676 consists of a right periotic without posterior process that was previously assigned to *Plesiocetus burtinii* by Van Beneden (1885) (Fig. 8). The anterior process is triangular with convex medial border and concave lateral border. Its length is 37.11 mm and its width at base is 49.72 mm. The central portion of the anterior process is thick; its dorsal surface is dorsally concave as the anterior process descends from a raised suprameatal part. A narrow but well evident groove runs laterally to the emergence of the anterior process being posteriorly delimited by a strong tubercle. The pars cochlearis does not protrude medially. Its transverse diameter is 28.05 mm, its height is 27.81 mm and its anteroposterior diameter is 34.03 mm. The internal acoustic meatus includes foramen singulare, trac-

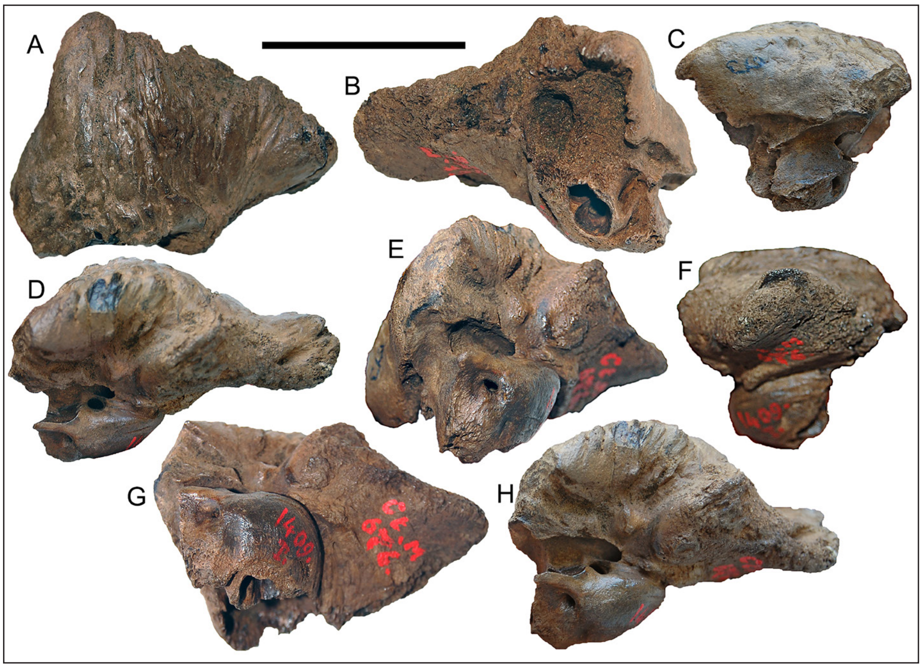


Fig. 8 - Specimen M. 676, right periotic. A) dorsal view; B) medial view; C) posterior view; D) lateral view; E) ventrolateral view; F) anterior view; G) ventral view; H) lateral view. Scale bar equals 5 cm.

tus spiralis foraminosus and endocranial opening of the facial canal (maximum diameter, 6.65 mm; minimum diameter, 4.8 mm); the latter is separated from the cavity including tractus spiralis foraminosus and foramen singulare by a subtle crista transversa (Fig. 9). The suprameatal area is concave with a wide anterior fossa. It is likely that the fossa and the shape of the surface of the suprameatal area are the result of erosive, *post mortem* processes. The oval window is very small being 4.48 mm its maximum diameter and 5.21 its minimum diameter. The round window is oval-shaped and is 4.62 in maximum diameter and 3.36 in minimum diameter. The perilymphatic foramen opens posteriorly to the pyramidal process and is rather wide in size (maximum diameter, 8.89 mm and minimum diameter, 4.17 mm). The endolymphatic foramen is located below the perilymphatic foramen and is 6.63 mm in maximum diameter and 2.20 mm in minimum diameter. The anterior surface of the pars cochlearis is separated from the ventral side of the anterior process by a sharp groove for the tensor tympani muscle. The stapedial muscle fossa is concave and is separated from the round window by a rounded crest. The fossa for the head of the malleus is relieved and has a pyramidal shape. The stylomastoid fossa is very concave and is developed on the posterior surface of the pars cochlearis.

Comparisons and discussion

This periotic closely resembles that of Balaenidae because of its robust dorsal portion, internal acoustic meatus and endocranial opening of the facial canal included in a single cavity, the stocky and grossly rectangular anterior process and the shallow stylomastoid fossa. Among basal thalassotherian taxa, only *Pelocetus*, *Atlanticetus patulus* and *Uranocetus* show a robust dorsal surface of the periotic and the internal acoustic meatus and the endocranial opening of the facial canal included in a single cavity. All the other thalassotherians (with the exclusion of crown Balaenopteridae) show a separation between the endocranial opening of the facial canal and the internal acoustic meatus. This separation is also observed in foetal balaenopterid periotics but disappears in older individuals (Bisconti 2001).

Unfortunately, this specimen is the only remnant of a possible balaenoid individual from the late Miocene of the North Sea basin and represents the first clue to the presence of early-diverging balaenoids in the area before the appearance of the typical genera observed later (i.e., *Balaena*, *Balaenula*, *Antwerpibalaena*, *Eubalaena*, and *Balaenotus*; see Bisconti 2003 for a review). Only a handful balaenoid taxa are known from the Miocene and these include the well preserved *Morenocetus parvus* from the Burdigalian of Argentina (Cabrera 1926; Buono et al. 2018). The periotic of *M. parvus* shows the typical balaenoid characters including a stocky anterior process, a well-developed promontorial groove and a single cavity including the internal acoustic meatus and endocranial opening of the facial canal. Interestingly, this periotic differs from the periotics of *Balaena*, *Ba-*

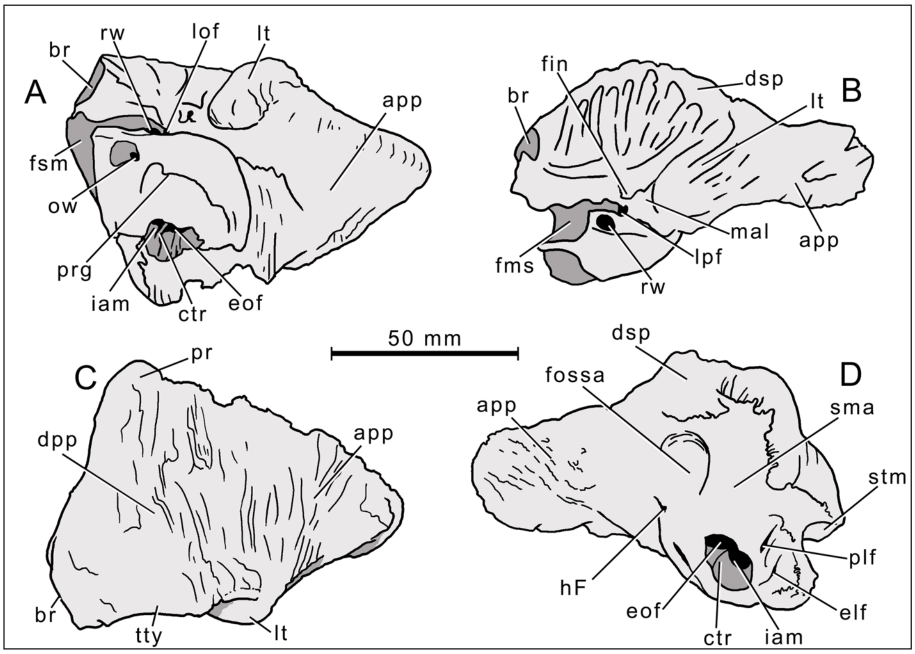


Fig. 9 - Specimen M. 676, right periotic, anatomical interpretations. A) ventral view; B) lateral view; C) dorsal view; D) medial view. Scale bar equals 5 cm. See Anatomical abbreviations for explanation of acronyms.

laenula (as from *Balaenula astensis*), *Antwerpibalaena* and *Balaenotus* in lacking a well-developed and triangular lateral process of the anterior process. The same is observed in M. 676 and in the neobalaenid *Caperea marginata* and *Miocaperea pulchra* (Bisconti 2012; Ekdale et al. 2011). The distribution of this character suggests that the typical lateral process of the anterior process developes from the lateral margin of the anterior process as a strong, triangular protrusion in the later balaenid species forming a unique synapomorphy of Balaenidae and further supporting the exclusion of *Morenocetus parvus* from Balaenidae as from the results of Bisconti et al. (2019, 2020). This specimen shares with Balaenidae the morphology of the stylomastoid fossa, the strong and robust construction of the periotic and the overall morphology of the pars cochlearis. However, the lack of the lateral process of the anterior process and the presence, instead, of a squared and robust lateral tuberosity excludes that it is part of Balaenidae. This specimen differs from Neobalaenidae in being much more robust and in having a dorsal surface of the periotic highly relieved and pachyosteoschlerotic.

Based on the characters of this periotic, we assign the specimen M. 676 to Balaenoidea gen. et sp. indet. suggesting that it may represent a stem-balaenoid species. However, we do not go further and we do not establish a new taxonomic denomination because we think that more osteological evidence is necessary to better understand the taxonomy and phylogenetic relationships of the taxon this periotics belongs to.

Family Balaenidae Gray, 1825
Gen. and sp. indet.

Materials: IRSBN M. 660a (scapula); M. 660b (radius).

Descriptions and decisions

The specimens M. 660a and b include a fragment of right scapula and a left radius and were previously assigned to *Plesiocetus dubius* (Fig. 10). Both M. 658 and M. 660a scapulae have been assigned to *Plesiocetus dubius* but they do not share species-specific morphological traits. On the contrary, the M. 660a scapula shows balaenid affinities. In fact, its external border projects dorsally and slightly posteriorly thus preventing the scapula from being anteroposteriorly expanded as in M. 658. The acetabulum is broadly circular in outline (anteroposterior diameter, 95 mm as preserved; transverse diameter, 84 mm). The articular surface exposed at the acetabulum is perforated by nutritional foramina thus suggesting that the specimen belonged to an immature individual. Most of the anterior part of the scapula is missing. The dorsoventral length of the scapula (as preserved) is 300 mm; the length of the external border is 344 mm; the distance from the inferior angle and a point located on a line crossing the center of the acetabulum is 249 mm. Balaenopterid, neobalaenid, eschrichtiid and cetotheriid (both *s.s.* and *s.l.*) scapulae have a concave external border and anteroposterior expansion. In Balaenidae the scapula

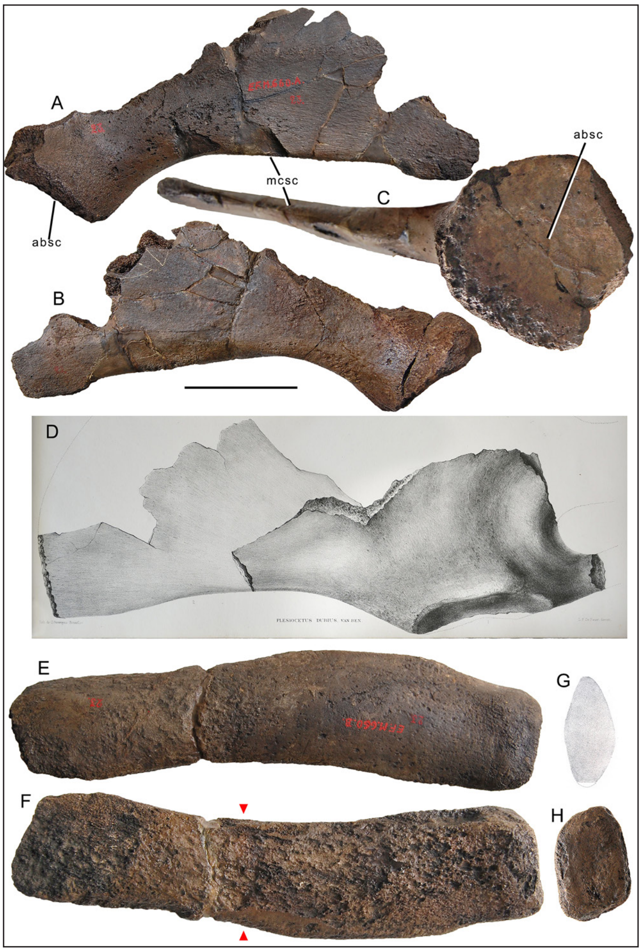


Fig. 10 - Specimen M. 660. A) specimen M. 660a, right scapula in lateral view; B) the same in medial view; C) the same in ventral view; D) the same in lateral view from Van Beneden (1885). E) specimen M. 660b, left radius in lateral view; F) the same in medial view; G) section at the level of the red triangles in F from Van Beneden (1885); H) inferior view of proximal epiphysis. Scale bar equals 10 cm. See Anatomical abbreviations for explanation of acronyms.

shows a straight external border and lacks an anteroposterior expansion. For this reason, this specimen is assigned to Balaenidae gen. et sp. indet.

The specimen M. 660b is a poorly preserved left radius (Fig. 10). Anterior and posterior borders are anteriorly convex; a slight relief is located distally to the proximal articular facet (anteroposterior diameter of the facet, 71 mm). The whole distal portion of the bone is missing. The anteroposterior diameter of the radius at mid-length is 101 mm, its proximodistal length is 469 mm. The morphology of this specimen is not incompatible with the assignment of M. 660a to Balaenidae. As specimens M. 660a and b have been found in close proximity, both of them can be assigned to Balaenidae gen. et sp. indet.

Thalassotherii Bisconti, Lambert & Bosselaers, 2013

Gen. and sp. indet.

Materials: IRSBN M. 648a-b, M. 662 (skull); M. 652 (periotic); M. 631, M. 632, M. 633, M. 649, M. 650, M. 651, M. 664, M. 677, M. 678, M. 679 (tympanic bullae); M. 654, M. 665a-b (mandibular rami); M. 642, M. 659, M. 670 (forelimb elements).

Descriptions and decisions

Skull. Specimens M. 648a and b have been assigned to *Plesiocetus dubius* by Van Beneden but their poor conditions prevent a safe assignment to any mysticete genus or species. M. 648a represents a fragment of an exoccipital with occipital condyles and a partial basioccipital (Fig. 3). The internal face of the basioccipital is transversely flat-to-slightly concave and shows nutritional foramina. It digrades laterally. The occipital condyles are damaged; they are vaguely kidney-shaped. Ventrally, the basioccipital descending process is damaged and displays a ventral pointed apex. The foramen magnum is wide (69 mm in transverse diameter; distance between the external borders of the occipital condyles through the foramen magnum: 201 mm). The maximum transverse diameter of the basioccipital is 264 mm and the maximum length of the fragment is 101 mm.

M. 648b (Fig. 3) includes a partial squamosal with glenoid fossa and postglenoid process. The glenoid fossa is concave; the zygomatic process of the squamosal has broken off and is missing from the specimen. The ventral border of the squamosal and the posterior face of the temporal fossa form an acute angle in lateral view. Ventrally and medially, a fissure is observed running laterally and dorsally from the pterygoid fossa through the squamosal but it is not clear whether this can be the squamosal cleft or not. The pterygoid fossa is concave. The foramen pseudo-ovale is located between the squamosal and the pterygoid. Posteriorly, the external acoustic meatus is developed along the posterior face of the squamosal. Its transverse diameter is 115 mm and its anteroposterior width is 39 mm. The total length of the fragment is 225 mm and its total transverse width is 260 mm. None of the pieces described above show characters of Eomysticetidae, Aetiocetidae and Mammalodontidae. The specimen M. 648b, in particular, shows a triangular zygomatic process of the squamosal that precludes its inclusion in Balaenoidea. Due to their poor pres-

Fig. 11 - Specimen M. 662, right supraorbital process of frontal. A) (inferior part) lateral view; A (top portion), section at red triangles in D from Van Beneden (1885); B) dorsal view; C) close-up of ventral view; D) ventral view. Scale bar equals 10 cm.

ervation, M. 648a and b are here assigned to Thalassotherii gen. et sp. indet.

Another skull fragment is represented by the specimen M. 662 that consists of the right supraorbital process of the frontal of an indetermined basal thalassotherian genus and species (Fig. 11). The supraorbital process is 265 mm in length, its medial length is 40 mm and its distal end (from postorbital corner to antorbital corner) is 120 mm. The process is thus long and narrow. Its dorsal surface is flat being the temporal ascending crest lacking. The postorbital corner is more robust than the antorbital corner and has a rounded shape. The antorbital corner is significantly smaller in size. The Orbit is dorsoventrally concave. The optic canal is developed on the whole ventral surface of the process; it is anteriorly bordered by a ventrally-protruding crest that is crossed by a foramen located approximately 180 mm from the orbit. This specimen was assigned to *Plesiocetus hupschii* but judging from its morphology it could be assigned to different basal thalassotherians. It is thus assigned to Thalassotherii gen. et sp. indet.

Periotic. The specimen M. 652 was previously assigned to *Plesiocetus dubius* by Van Beneden (1885) and consists of a single right periotic lacking the posterior process (Fig. 12). Steeman (2010) referred it to *P. burtinii*. The anterior process is approximately squared in dorsal view. It is 36.15 mm in length and 55.76 mm in width at its base. There is a strong projection laterally to the emergence of the anterior process; this projection is separated from the anterior process by a concavity that runs laterally, posteriorly and ventrally. The central portion of the periotic has a raised dorsal surface whose maximum dorsal protrusion is located anteriorly to the internal acoustic meatus. The pars cochlearis includes an internal acoustic meatus separated from the endocranial opening of the facial canal by a subtle crista transversa (Fig. 13). The opening of the Facial canal is located at the medial end of a groove; its maximum diameter is 4.63 mm (as preserved). The perilymphatic foramen is elongated and narrow (dorsoventral diameter, 3.53 mm; anteroposterior diameter, 2.23 mm); the endolymphatic foramen is wider (dorsoventral diameter, 5.47 mm; anteroposterior diameter, 2.83 mm). The stylomastoid fossa is triangular and is prolonged on the posterior surface of the pars cochlearis and is dorsally edged by a subtle relief. The round window is relatively enormous (anteroposterior diameter, 8.05 mm; dorsoventral diameter, 5.82 mm). The groove for the tensor tympani muscle is present; the groove under the internal acoustic meatus is present. The oval window is surmounted by the external opening of the facial canal. The oval window is smaller than the round window (dorsoventral diameter, 3.90 mm; anteroposterior diameter, 5.82 mm). The fossa for the stapedial muscle is well developed and concave and is separated from the round window by a rounded crest.

From a comparative point of view, the specimen M. 652 shows a number of basal thalassotherian characters including the separation between the internal acoustic meatus and the endocranial open-

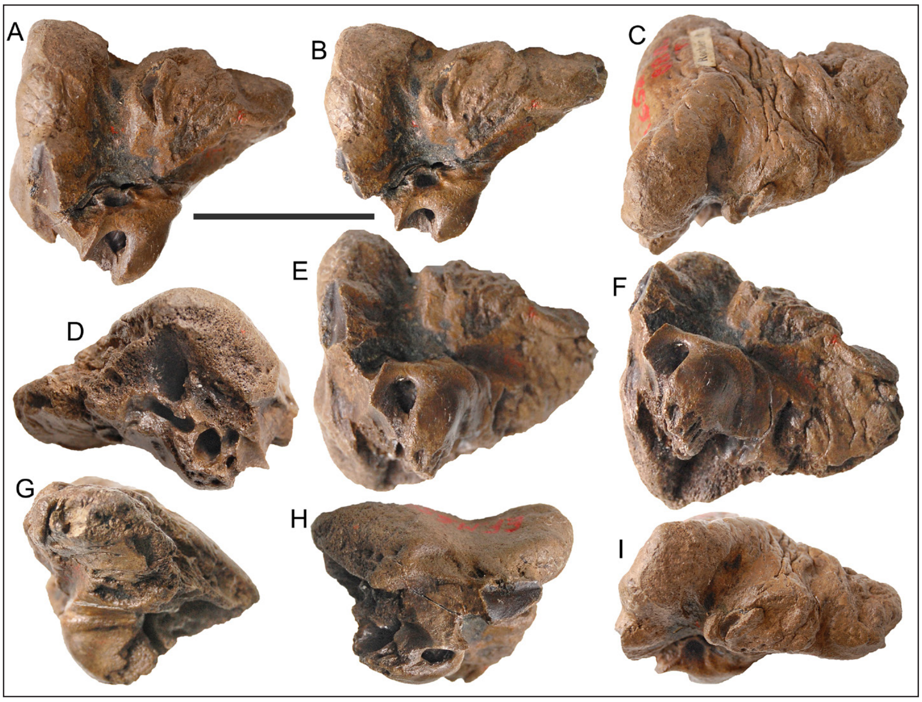


Fig. 12 - Specimen M. 652, right periotic. A) ventrolateral view; B) lateral view; C) dorsal view; D) medial view; E) ventral view; F) ventromedial view; G) anterior view; H) posterior view; I) dorsolateral view. Scale bar equals 5 cm.

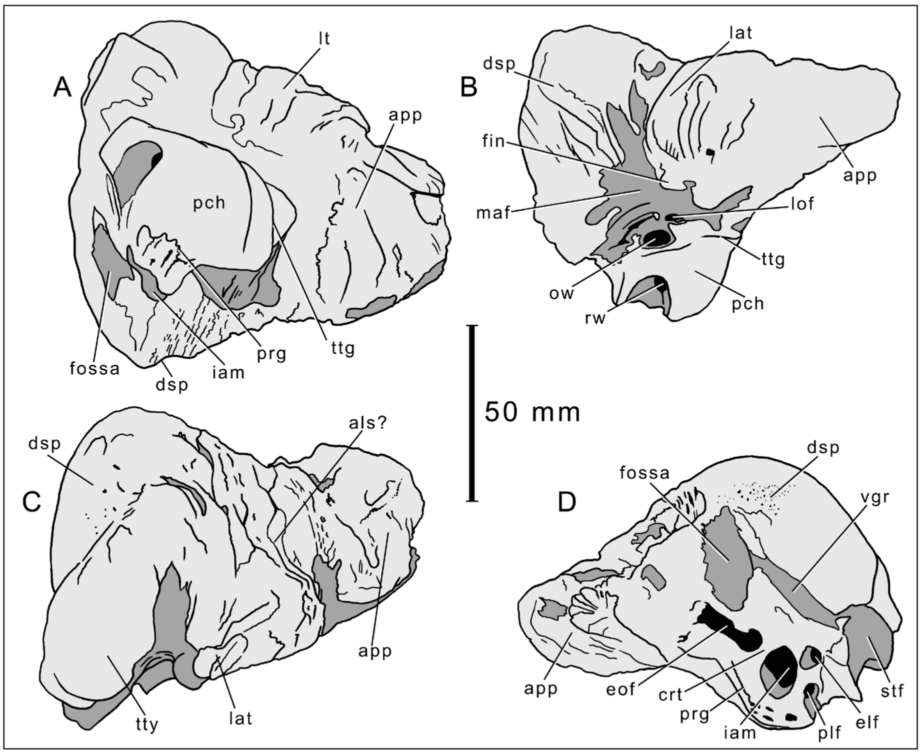


Fig. 13 - Specimen M. 652, right periotic, anatomical interpretation. A) ventral view; B) lateral view; C) dorsal view; D) medial view. Scale bar equals 5 cm. See Anatomical abbreviations for explanation of acronyms.

ing of the facial canal, the presence of a groove starting from the endocranial opening of the facial canal and a deep stylomastoid fossa that was probably continued on the medial side of the posterior process. The above characters dealing with the distribution of the endocranial foramina are typical of basal thalassotherian taxa with the exception of the wide-rostrum forms including *Pelocetus*, *Uranocetus*, *Atlanticetus patulus,* and *Isanacetus laticephalus* in which the endocranial opening of the facial canal and the internal acoustic meatus are included in a single cavity. Unfortunately, there are no additional clues about the skull characters and this prevented us to establish a new taxonomic denomination for this specimen that is, thus, assigned to Thalassotherii gen. et sp. indet. Pending the discovery of more

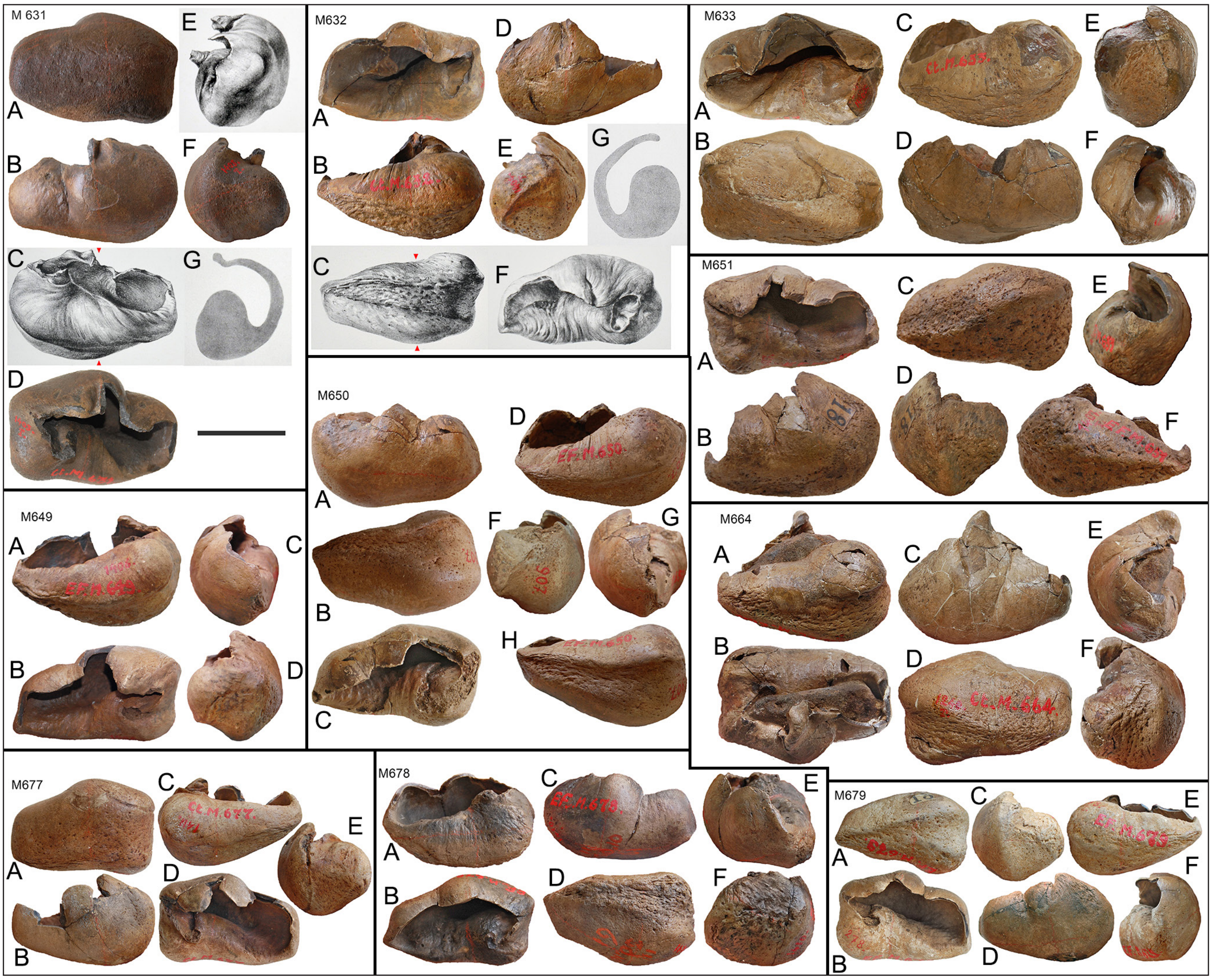


Fig. 14 - Tympanic bullae previously assigned to different *Plesiocetus* species and now assigned to Thalassotherii gen. et sp. indet. M. 631 in A) ventral; B) lateral; C) medial; D) dorsal; E) anterior; F) posterior views; G) cross-section at mid-length; C, E, G from Van Beneden (1885). M. 632 in A) dorsal; B) medial; C) ventral; D) lateral; E) posterior; F) dorsal views; G) cross-section at mid-length; C, F, G from Van Beneden (1885). M. 633 in A) dorsal; B) ventral; C) medial; D) lateral; E) posterior; F) anterior views. M. 649 in A) medial; B) dorsal; C) anterior; D) posterior views. M. 650 in A) lateral; B) ventral; C) dorsal; D) medial; F) posterior; G) anterior; H) ventromedial views; H is in tangent light to show the ridges and the ventral concavity M. 651 in A) dorsal; B) lateral; C) ventral; D) posterior; E) anterior; F) medial views. M. 664 in A) medial; B) dorsal; C) lateral; D) ventral; E) anterior; F) posterior views. M. 677 in A) ventral; B) lateral; C) medial; D) dorsal; E) posterior views. M. 678 in A) medial; B) dorsal; C) lateral; D) ventral; E) anterior; F) posterior views. M. 679 in A) ventral; B) dorsal; C) posterior; D) lateral; E) medial; F) anterior views. Scale bar equals 5 cm.

complete materials and the establishment of a new name for the basal thalassotherian taxa, which is outside the scope of the present paper.

Tympanic bullae. Tympanic bullae are usually considered important by both early and modern students for taxonomic purposes in regard to mysticetes. In some literature, a single tympanic bulla is used to establish the presence of a taxon in a given area in a given time interval (*e.g.*, Tsai & Chan 2019, 2017; Tsai & Boessenecker 2017). However, in most cases tympanic bullae are only useful to individuate the presence of family-level taxa. Bisconti (2010) presented three types of tympanic bullae observed in living and fossil mysticetes with the exclusion of Balaenoidea (Balaenidae and Neobalaenidae). That analysis was unexhaustive but can be used here to understand if these different types are present in the Van Beneden *Plesiocetus* "type" collection and sort out different family-level taxa (Fig. 14). Bisconti (2010) distinguished a first type characterized by pyruliform bulla with flat posterior border and without anterolateral expansion; a second type characterized by bilobated posterior border and with anterolateral expansion; a third (balaenopterid) type characterized by pointed posterior border and with anterolateral expansion. Two of these types are

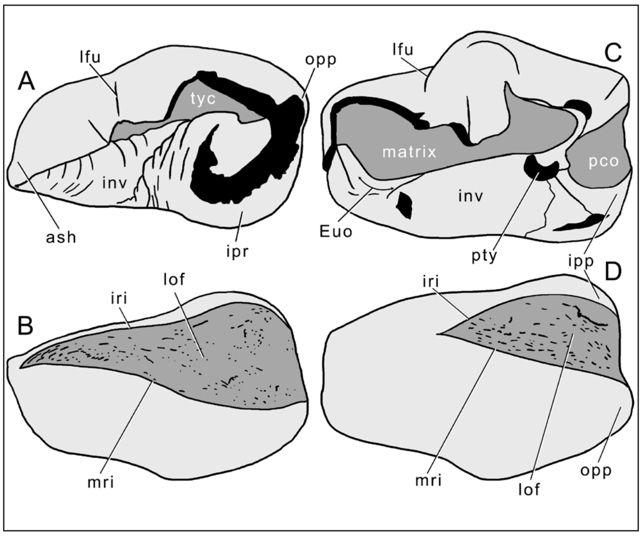


Fig. 15 - Schematic representation of tympanic bullae. First type represented by M. 650 in A) dorsal and B) ventral views. Intermediate type represented by M. 664 in C) dorsal and D) ventral views. See Anatomical abbreviations for explanation of acronyms. Not to scale.

found amongst the bullae described below, together with an additional one that seems to be intermediate between the first and the second type. Measurements of the bullae are presented in Tab. 7.

First type – Specimens M. 631, M. 633 (that were both previously assigned to *Plesiocetus brialmontii*), M. 650, M. 651 (both previously assigned to *Plesiocetus dubius*), and M. 677 (previously assigned to *Plesiocetus burtinii*) show the typical character of the first type described by Bisconti (2010) (Fig. 15). All of these bullae are pyruliform in shape if observed in dorsal view, lack the lateral lobe and show a flat posterior border. All these bullae present a concave area included between the ventral border of the involucrum and the ventral part of the typanic plate. The involucrum is concave in dorsal view in M. 631, M. 633, M. 650, and M. 677 but it is convex in M. 651. The apex is pointed in M. 633 and M. 650 but it is flat in all the other bullae.

Intermediate type – In specimens M. 649 (previously assigned to *Plesiocetus dubius*), M. 664, M. 678 (both were previously assigned to *Plesiocetus hupschii*), and M. 679 (previously assigned to *Plesiocetus burtinii*) the pyruliform shape of the anterior portion of the bulla coexist with a bilobate posterior end (Figs 14, 15). Specimens M. 649, M. 678, and M. 679 shows clearly protruding outer and inner posterior prominences as they are separated by a shallow interprominential notch. In specimen M. 664 the outer posterior prominence is posteriorly pointed in dorsal view and the anterior end is flat and transversely elongated.

Possible second type – The only specimen with characters compatible with the second type described by Bisconti (2010) is M. 632 (previously assigned to *Plesiocetus brialmontii*; Figs 14, 15). However the anterolateral expansion of this bulla is not as clearly developed as in those of *Pelocetus* and *Atlanticetus* and the assignment to the second type is only tentative.

Mandibular rami. The specimen M. 654 was previously assigned to *Plesiocetus dubius* by Van Beneden (1880). It is represented by a fragment of the anterior-most portion of the left mandibular ramus that is 405 mm in length (Fig. 16). In medial view, the specimen shows the presence of a long and dorsally concave groove for the mental ligament that is 240 mm in length and that is mainly located close to the ventral border of the fragment. The medial surface of the fragment is flat and the lateral surface is slightly convex. The alveolar

Specimen	Length	Antwidth	Postwidth	Spwidth	pwidth	Cpheight	Tcdepth	Thickness
M. 631	95.99	30.73	43.57	68.88	62.14		32.87	3.264
M. 632	92.67	27.04	42.5	55.4	52.02		31.94	2.256
M. 633	105.71	28.34	46.96	59.01[a]	58.11[a]		37.17	3.614
M. 649	91.65	37.32	43.65	53.58	51.29	60.41	32.97	3.372
M. 650	85.39	33.96	39.95	51.84	53.98		30	2.958
M. 651	91.33	25.60	48.04	55.28	51.94	64.26	30.6	3.44
M. 664	92.02	29.96	50.47	59.48	56.79	65.26		2.84[b]
M. 677	82.74	33.63	41.71	63.08	48.77	54.35	27.45	2.858
M. 678	80.9	29.25	31.35	53.37	50.18		31.98	2.482
M. 679	74.75	30.53	36.91	51.45	47.81	47.76	32.24	2.09

Tab. 7 - Measurements of tympanic bullae previously assigned to *Plesiocetus*. Data in mm. Abbreviations: Antwidth, anterior width; Postwidth, posterior width; Spwidth, width of bulla at sigmoid process; Cpwidth, width of bulla at conical process; Cpheight, height of bulla at conical process; Tcdepth, depth of tympanic cavity; Thickness, mean thickness of lateral wall obtained by 5 different measurements in different parts of the wall. aAs preserved. bMean value based on 3 measurements.

Fig. 16 - Thalassotherii genera et sp. indet. Specimen M. 654, anterior end of left dentary: A) lateral view; B) medial view; C) posterodorsal view showing the damaged surface. Specimen M. 665a, anterior end of right dentary: D) lateral view; E) medial view; F) dorsal view; G) natural cross-section of posterior end. Specimen M. 665b, anterior end of left dentary: H) lateral view; I) medial view; J) dorsal view; K) natural cross-section of posterior view. Scale bar in G and K equals to 5 cm; all the other scale bars equal 10 cm.

groove is visible anterodorsally together with some gingival foramina and sulci. The anterior end is 115 mm in height and shows a rounded border; the posterior end is 120 mm in height and is truncated. The ventral border is eroded; the medial face is flat; the lateral face is slightly convex. The anterior termination of the dental sulcus is evident anteriorly together with some gingival grooves. The specimen is assigned to Thalassotherii gen. et sp. indet.

The specimen M. 665a-b, that was previously assigned to *Plesiocetus hupschii*, includes the anterior ends of the right (M. 665a) and left (M. 665b) mandibular rami (Fig. 16). The right ramus is 323 mm in length and its anterior height is 85 mm. It shows 7 gingival foramina, an evident dental sulcus, a long groove for the mental ligament and a rounded ventral border. One mental foramen is inferred by the presence of the corresponding groove. The lateral and medial faces are convex but the medial one is less convex than the lateral one. M. 665b is very similar in morphology but its length is 310 mm, its anterior height is 96 mm and its posterior height is 88 mm. It shows 5 gingival foramens and an eroded ventral border. The mandibular canal is elliptical with the longer axis developed dorsoventrally. The specimen is assigned to Thalassotherii gen. et sp. indet. because the lack of mylohyoidal groove excludes it belongs to Balaenidae. The degree of the convexity of the medial side suggests it belongs to Thalassotherii but it is impossible to assign it to a definite genus and species.

Forelimbs. The specimen M. 642 previously assigned to *Plesiocetus brialmontii* consists of a left humerus (Fig. 17). The surface of the bone is poorly preserved. Anterior and posterior borders are straight; the deltopectoral crest is largely destroyed. The head of the humerus is fused with the diaphysis of the bone suggesting that it belonged to a fully adult individual. The diaphysys is comparatively long (maximum length, 354 mm; maximum width at head of humerus along anteroposterior axis, 168 mm). The humerus is 150 mm in width at mid-length. The transverse width is 94 at mid-length. The articular facet for the ulna is flat and longer than that for the radius. Articular facets for the radius and for the olecranon process of the ulna are badly damaged. The head is spherical and protrudes laterally and posteriorly. The length/width ratio of this specimen suggest that it belonged to some primitive but unidentified baleen whale. In the modern forms, in fact, the humerus is longitudinally compressed and the anterior and posterior borders are usually concave. Small differences are observed between this humerus and the humerus of *Piscobalaena nana* (Bouetel & de Muizon 2006); in *P. nana*, anterior and posterior borders are both concave but in this specimen they are straight. Among the basal thalassotherians described by Kellogg (1965, 1968, 1969) it shows some similarities with both *Pelocetus calvertensis* and *Thinocetus arthritus* but the poor preservation prevents its placement within one of these genera. It is here assigned to Thalassotherii gen. et sp. indet.

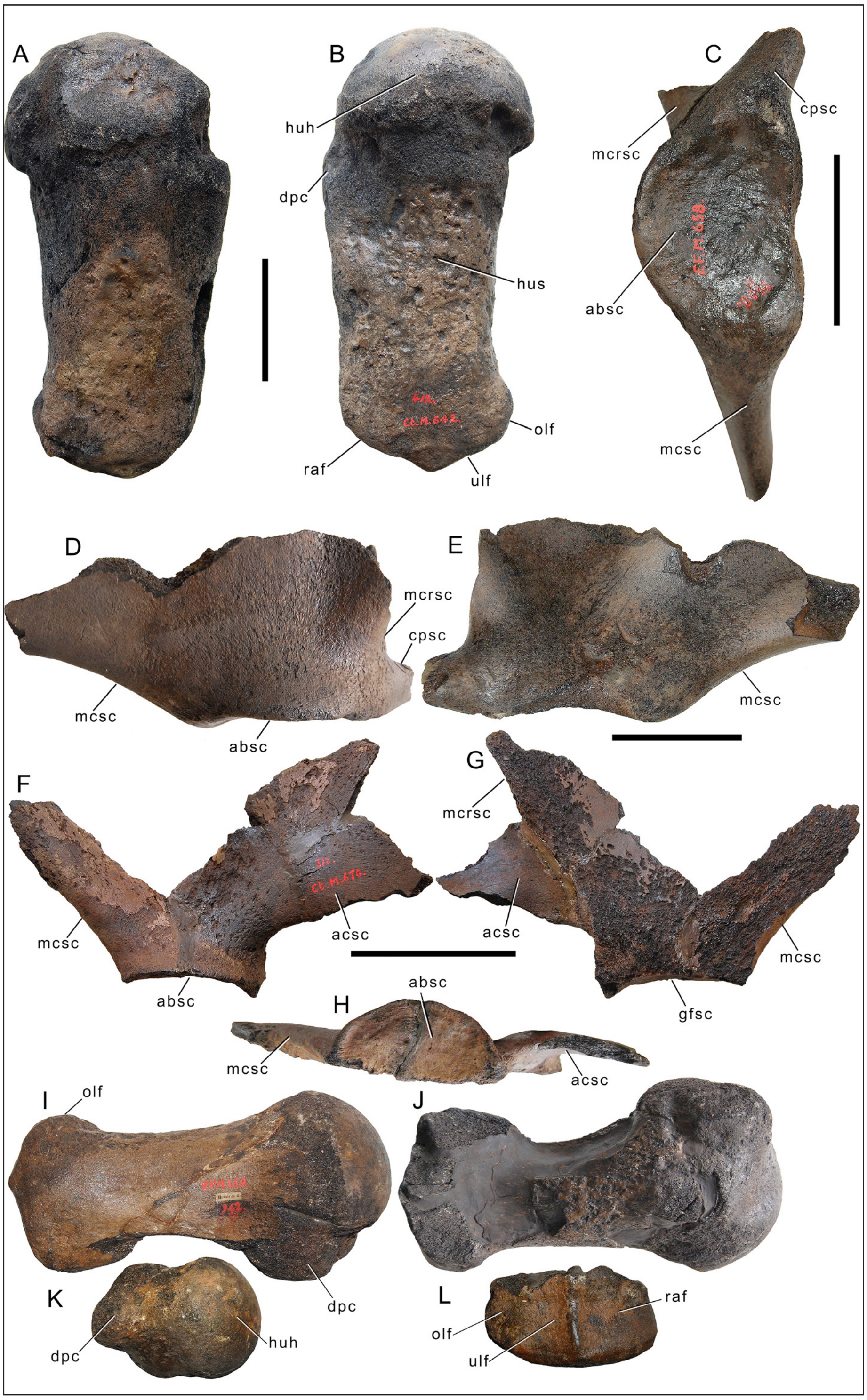
The specimen M. 659 consists of a right humerus and was previously assigned to *Plesiocetus dubius* (Fig. 17I-L). The specimen is poorly preserved and has been partially reconstructed. The anterior border is destroyed; the posterior border is highly concave. The humerus is proportionally very long (maximum proximodistal length, 325 mm; maximum anteroposterior length from posterior border of the head to the anteriorborder of the deltopectoral crest, 140 mm). The deltopectoral crest is robust and is separated from the head of the humerus by a wide and concave groove. The articular facet for the ulna is short but the articular facet for the radius is longer. The articular facet for the olecranon process is long and is developed on an anteroposterior expansion of the distal portion of the bone. The head of the humerus is developed on the proximal face of the bone and is not developed along the lateral and posterior faces. This humerus resembles that of *Pelocetus calvertensis* and *Thinocetus arthritus* but it is not possible to assign it to one of these taxa because of its poor preservation. This humerus shows unique characters in the placement of the head and in the robust development of the deltopectoral crest but these characters are insufficient to warrant a sound taxonomic assignment, therefore, the specimen is assigned to Thalassotherii gen. et sp. indet. Based on the general resemblance of this specimen and *Pelocetus calvertensis* and *Thinocetus arthritus*. Hampe (1996) described a partial skeleton from the Miocene of north-west Germany that he referred to *Plesiocetus* sp. The humerus belonging to this skeleton shares with M. 659 the proximal placement of the humeral head and a proximally-protruded deltopectoral crest. The German specimen shows an anteroposteriorly elongated scapula that suggests it could belong to basal Thalassotherii, Cetotheriidae, or Balaenopteridae. Its posterior process of the periotic bears a deep facial groove that strongly suggests that it belongs to Cetotheriidae. Unfortunately, the specimen M. 659 is badly preserved and there is no possibility to ascertain whether it belongs to the same species as the German specimen.

The specimen M. 670 was previously assigned to *Plesiocetus hupschii* and is represented by a fragmentary right scapula (Fig. 17). It is characterized by a highly inclined external border that projects dorsally and posteriorly and a strongly concave infraspinous fossa immediately dorsal to the acetabulum (anteroposterior diameter of acetabulum, 97 mm; estimated transverse diameter, 80 mm); a long and robust acromion (height of acromion base, 100 mm; length or preserved part of acromion, 98 mm). The acetabulum is anteroposteriorly scarcely concave and transversely flat. The coracoid process is largely missing but its base projects ventrally. There is no trace of a supraspinous fossa. The superior border projects dorsally and anteriorly but it is less inclined than the external border. In comparison with modern mysticete taxa, the absence of the infraspinous fossa prevents its inclusion in Balaenopteridae; the moderate anteroposterior elongation prevents its inclusion in Eschrichtiidae, Balaenidae and Neobalaenidae. In comparison with cetotheres described by Kellogg (1965, 1968, 1969), this scapula shows a general shape consistent with *Thinocetus arthritus* in the orientations of the external and internal borders and in the robustness of the acromion process. The coracoid process of *Thinocetus arthritus* is, however, rectangular and short and projects anteriorly while the coracoid process of M. 670 projects ventrally. The specimen M. 670 is thus assigned to Thalassotherii gen. and sp. indet. based on its general resemblance to *Thinocetus arthritus*.

Discussion and decisions

The periotic M. 652 attracted the attention of Steeman (2010) who provided a first taxonomic revision. A deep groove is located posterolaterally to the emergence of the anterior process in this periotic and this groove is posteriorly delimited by a strong

Fig. 17 - Specimen M. 642, right humerus: A) lateral view; B) medial view. Specimen M. 658, right scapula: C) ventral view showing the acetabular fossa; D) lateral view; E) medial view. Specimen M. 670, right scapula: F) lateral view; G) medial view; H) ventral view. Scale bars equal 10 cm. Specimen M. 659, humerus: I) lateral view; J) medial view; K) superior view; L) inferior view. See Anatomical abbreviations for explanation of acronyms.



relief emerging from the lateral border of the central portion of the periotic. Such a character is found in *Atlanticetus patulus* and in *'Aulocetus' calaritanus* and, based on this character, Steeman (2010) assigned M. 652 to *Aglaocetus* revising *Plesiocetus burtinii* in *Aglaocetus burtinii*. However, M. 652 was originally assigned to *P. dubius* and its designation as a type specimen of *Aglaocetus burtinii* is questionable. In fact, she based her arguments on the consideration of *'Aglaocetus' patulus* being a well established species of the genus *Aglaocetus* (Steeman 2010, p. 65). However, from the phylogenetic analyses presented by Bisconti (2011), Bisconti et al. (2019, 2020a), Bisconti & Bosselaers (2020), Marx (2011), Peredo & Uhen (2016), and Boessenecker & Fordyce (2015a, b) the genus *Aglaocetus* is polyphyletic as *'Aglaocetus' patulus* is now reassigned to *Atlanticetus patulus* by Bisconti et al. (2020b). However, M. 652 shows a mix of basal thalassotherian characters: the dorsal bulge of the periotic and the groove for the facial nerve in the medial surface of the pars cochlearis suggest that it could represent a taxon similar to *Parietobalaena* but the large anterior process suggests that it could represent a taxon more similar to *Atlanticetus*. Presently, in the absence of additional diagnostic characters, we assign it to Thalassotherii gen. et sp. indet.

Bouetel & de Muizon (2006) described in detail the tympanic bulla of *Piscobalaena nana* showing that it is pyruliform and with bilobate posterior border. This bulla shows a pointed anterior end and has a well developed and elongated inner posterior prominence that allows its safe identification. In general, however, it is not easy to distinguish the tympanic bullae of different mysticete species. While it is rather easy to distinguish bullae of Balaenoidea from bullae of all the other mysticete clades, it is not that easy to distinguish bullae within thalassotherian taxa and Balaenopteroidea. At least three types of bullae are found among thalassotherians (excluding Balaenopteroidea): first and second type of Bisconti (2010) and the intermediate type described above. The bulla of *Piscobalaena nana* belongs to the intermediate type and is different from bullae assigned to other Cetotheriidae (*e.g.*, *Herpetocetus transatlanticus* and *H. bramblei*; see Whitmore & Barnes 2008) that are pyruliform in shape without bilobated posterior border. Pyruliform bullae with bilobated posterior ends appear early in the evolution of mysticetes as they are described in the Oligocene *Eomysticetus whitmorei* and *Micromysticetus rothauseni* by Sanders and Barnes (2002a, b). In these taxa, however, the interprominential notch is perforated by the elliptical foramen that disappears in later forms.

It is noteworthy that none of the bullae that Van Beneden (1859) and Van Beneden (1885) assigned to *Plesiocetus* show typical balaenopteroid characters (third type of Bisconti 2010). In addition, it is also impossible to assign either of them to Cetotheriidae and therefore they are all assigned to Thalassotherii genus and species indeterminate.

Family Cetotheriidae Cabrera, 1926
Genera and species indeterminates

Materials: IRSBN M. 647a-b (partial skull) and M. 630b (mandibular ramus).

Descriptions, comparisons and taxonomic decisions

Skull. The specimen M. 647a-b was assigned to *Plesiocetus dubius* and is figured in Figs 18, 19. It includes two portions of a skull with the ventral side still immersed within the matrix. Specimen M. 647a includes portions of the supraoccipital, parietals and frontal; specimen M. 647b includes part of the right squamosal. The whole skull is 278 mm in length.

Only the posterior portion of the interorbital region of the frontal is preserved (Fig. 18). The dorsal surface of the ascending process of the maxilla is absent but its inferior portion (including the articulating crests with the interorbital region of the frontal) is present. The crests of the ascending process of the maxilla are deeply inserted within the articular grooves of the frontal. These structures are the only remnant of the posteromedial elements of the rostrum. The coronal (frontal-parietal) suture is very concave suggesting that the posterior ends of the ascending processes of the maxillae meet posteriorly to the nasals at a small distance from the anterior border of the supraoccipital. The length of the frontal (as preserved and along the sagittal axis) is *c.* 120 mm.

Only the anterior part of the parietal squama is preserved on both sides of the skull. This squama is anteroposteriorly and dorsoventrally concave. The dorsal border of the parietal protrudes laterally to contribute to form the temporal crest. Anteriorly, the parietal is interdigitated with the posteromedial elements of the rostrum as demostrated by the presence of articular grooves in the interorbital region of the frontal. The anterior-most point reached by the parietal is located more anteriorly than the posterior end of the posteromedial elements of the rostrum. The dorsal exposure of the parietal at vertex is very small (8 mm in length); the sagittal suture is partially eroded.

The supraoccipital is anteriorly narrow and rounded; its lateral borders are concave; an external occipital crest is evident on the dorsal surface that anteriorly broadens to become a tubercle located at the anterior border of the supraoccipital. On both sides of the external occipital crest, the surface of the supraoccipital is transversely concave and longitudinally flat. The external occipital crest ends 130 mm posteriorly to the anterior end

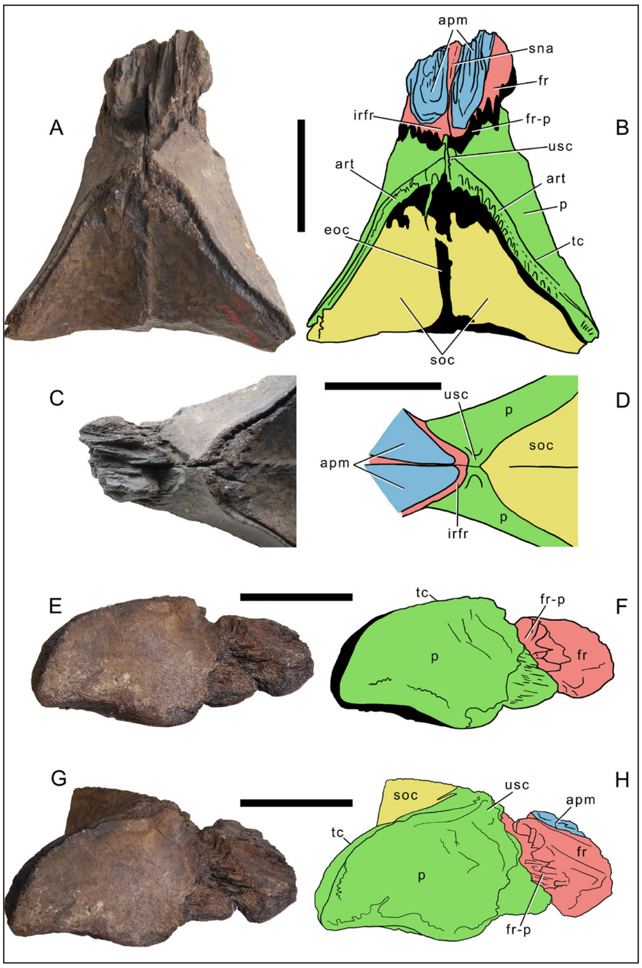


Fig. 18 - Cetotheriidae gen. et sp. indet. Specimen M. 647a, partial skull: A) dorsal view; B) anatomical interpretation of the same; C) vertex; D) anatomical interpretation of the same; E) right lateral view; F) anatomical interpretation of the same; G) dorsolateral view of right side; H) anatomical interpretation of the same. Scale bars equal 10 cm. See Anatomical abbreviations for explanation of acronyms. Black areas represent damaged borders.

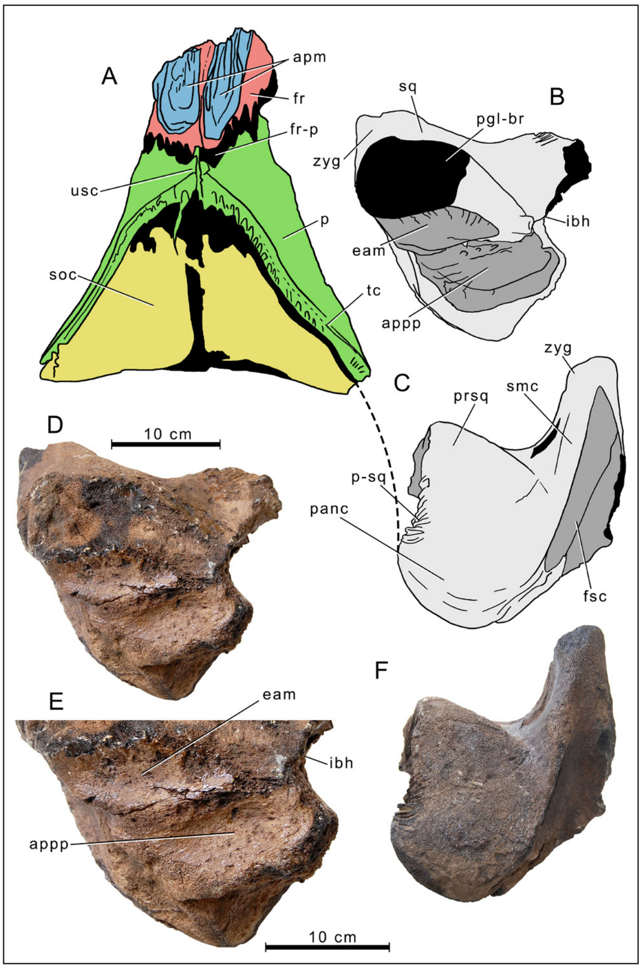


Fig. 19 - Cetotheriidae gen. et sp. indet. Specimen M. 647a, b partial skull. A) dorsal view of neurocranium and inferred articulation (broken line) with right squamosal. B) anatomical interpretation of right squamosal in ventral view. C) anatomical interpretation of right squamosal in dorsal view and with inferred articulation with M. 647a. D) right squamosal in ventral view. E) close-up view of otic region of right squamosal in ventral view. F) right squamosal in dorsal view. Scale bars equal 10 cm. See Anatomical abbreviations for explanation of acronyms. Black areas represent damaged portions.

of the supraoccipital; at that point, the posterior inclination of the supraoccipital changes and the supraoccipital is more vertical. The lateral borders of the supraoccipital do not overhang the lateral surfaces of the parietals in dorsal view. The supraoccipital is 155 mm in length, 145 mm in width at mid-length and 224 mm in width at its posterior termination (as preserved).

The squamosal (M. 647b) is largely eroded (Fig. 19). The zygomatic process is apparently parallel to the longitudinal axis of the skull in dorsal view; it is stocky; its apex is missing. The glenoid cavity is lateromedially convex and anteroposteriorly flat. The ventral projection of the postglenoid process is limited but its lateral projection is significant. The supramastoid crest is evident but its border is rounded; it projects posteriorly to form a posteriorly rounded nuchal crest. The surface located anteriorly to the posterior apex of the nuchal crest is flat. On the external side of the supramastoid crest, a concavity is located that is broadly triangular and shows an anteriorly rounded anterior border.

Medially to the zygomatic process, the squamosal is highly concave but, reaching the posterior wall of the temporal fossa, it becomes highly convex and protrudes within the temporal fossa. A long squamosal cleft is present; it is straight and starts from the parietal-squamosal suture; it develops laterally and dorsally and approximates the medial side of the lateral squamosal crest. More dorsally, the posterior wall of the temporal fossa becomes flat as it approaches the posterior apex of the nuchal crest.

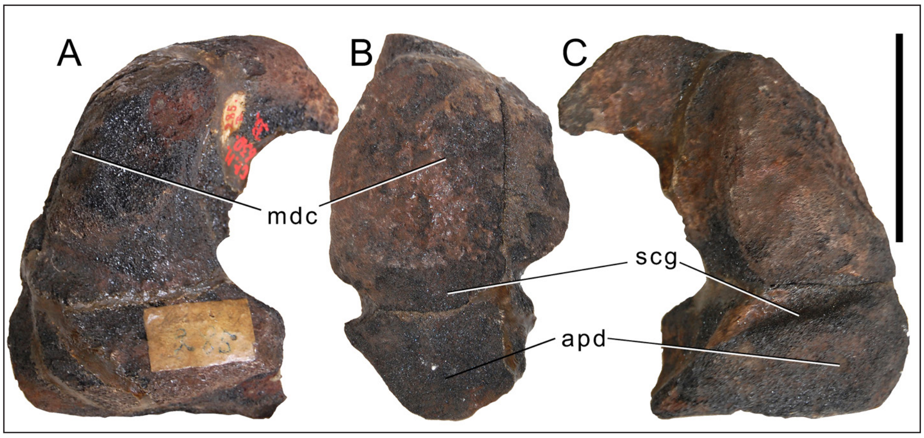
In ventral view, the external acoustic meatus is evident and is scarcely concave; the lateral border of the cranial hiatus shows a laterally convex lateral border. The surface for the attachment of the posterior process of the periotic is wide and developed from the posterolateral corner of the hiatus cranicus to the posterolateral corner of this squamosal. It shows an elliptical outline. The foramen pseudo-ovale is missing.

From a comparative viewpoint, this specimen shows typical characters of Cetotheriidae in the posterior elements of the rostrum and in the squamosal. In dorsal view, the interorbital region of the frontal is crossed by the grooves for the articulation of the posterior elements of the rostrum for all its length; this suggests that the whole interorbital region was covered by the posteromedial elements of the rostrum when these bones were in place. Moreover, judging from the observed pattern, the ascending proceses of the maxilla met along the midline of the skull posteriorly to the nasofrontal suture over a short length. The above characters are observed in Cetotheriidae. In Cetotheriidae and M. 647a, the dorsal exposure of the parietal at vertex is very reduced while in basal thalassotherian taxa the dorsal exposure of the parietal at vertex is much longer. Moreover, the sagittal crest is a true crest in basal thalassotherian taxa but it is reduced to a relieved area characterized by externally concave sides in Cetotheriidae, Balaenopteroidea and M. 647a. Finally, in Cetotheriidae, the squamosal bulges into the temporal fossa forming a strongly convex posterior wall of the temporal fossa and this character is observed also in M. 647b. All these observations provide morphological support to the inclusion of M. 647 to Cetotheriidae.

As far as the relationships with other Cetotheriidae are concerned, the presence of a squamosal cleft is shared by M. 647 and the cetotheriid *Metopocetus durinasus*, *M. hunteri*, and *Herentalia nigra*. The lack of postparietal foramen in M. 647 and the short contact between the ascending processes of the maxilla along the midline prevent its inclusion within Herpetocetinae as defined by Whitmore & Barnes (2008). The ascending processes of the maxilla meeting for a short distance along the midline and the triangular nasals (as inferred from the morphology of the medial borders of the ascending processes of the maxillae) suggest a possible relationship to *Metopocetus durinasus*. The pointed supraoccipital, the presence of a small exposure of the interorbital region of the frontal interposed between the ascending processes of the maxillae and the parietal, the short interdigitation between parietal and posteromedial elements of the rostrum, the wide nuchal crest suggest affinity with *Brandtocetus chongkulek* (Gol'din & Startsev 2014). Unfortunately, the lack of the posterior portion of the neurocranium prevents our attempts to compare the peculiar arrangement shown by the temporal crest of *Brandtocetus chongkulek* and M. 647 in a way that we cannot state with certainty that the structure of the posterior half of the skull shows the same characters in both the specimens. For this reason, a prudent approach should be followed here because the morphological evidence for a taxonomic assignment of M. 647a, b is scanty. Therefore, we prefer to avoid including the specimen in a known cetotheriid genus and assign it to Cetotheriidae gen. et sp. indet.

Mandibular ramus. The specimen M. 630b was assigned to *Plesiocetus brialmontii* by Van Beneden (1880). It includes the posterior-most portion of a right dentary with mandibular condyle and angular process (Fig. 20). The mandibular condyle is inclined dorsally and anteriorly; the angular process projects posteriorly but not ventrally and is separated from the condyle only medially by a deep pterygoid fovea. The maximum height of the specimen is 115.8 mm (from the dorsal surface of the condyle to the ventral border) and the maximum transverse width (across the condyle) is 103 mm. The morphology of the projecting angular process suggests that the specimen could be assigned to basal thalassotherians as this feature is observed in *Parietobalaena palmeri* and *Diorocetus hiatus*. However, in these basal thalassotherians, the angular process projects also ventrally but this ventral projection is absent in the present specimen. A posterior projection is present in Cetotheriidae; here, the specimen is assigned to Cetotheriidae for this reason.

Fig. 20 - Cetotheriidae gen. et sp. indet. Specimen M. 630, posterior end of mandibular ramus. A) lateral view; B) posterior view; C) medial view. See Anatomical abbreviations for explanation of acronyms. Scale bar equals 5 cm.



Epifamily Balaenopteroidea Flower, 1864 (Epifamily *sensu* Bisconti et al. 2013; Balaenopteroidea *sensu* Deméré et al. 2005)

Family Balaenopteridae Gray, 1864

Genera and species indeterminates.

Materials: RBINS M. 675 (partial skull); M. 634 (mandibular rami); M. 674 (forelimb).

Description of M. 675

The following description is focused on a partial skull that Van Beneden (1859) assigned to *Plesiocetus burtinii*. The specimen shows characters of both Balaenopteridae and Eschrichtiidae and it can be correctly placed within Balaenopteroidea *sensu* Deméré et al. (2005). As it presents a singular character combination, it is tempting to use this skull to make a morphological diagnosis of *P. burtinii* and make this specimen the lectotype of the species. However, the specimen is poorly preserved and some characters cannot be definitively understood. For this reason, the specimen is assigned to Balaenopteroidea gen. and sp. indet.

The specimen M. 675 consists in a partial neurocranium lacking the anterior-most elements (Fig. 21). The whole skull is *c.* 320 mm in length and 191 mm in maximum height. The anterior portion of the parietal is dorsoventrally and anteroposteriorly concave; the posterior-most portion of the parietal is anteroposteriorly convex. The anterior part is overwhanged by the temporal crest. The parietal-squamosal suture is very concave. Anteriorly to the supraoccipital, the dorsal-most portion of the parietal is absent. However, laterally, the preserved portion of the parietal shows that the parietal forms a bilateral relief developed paraxially with respect to the longitudinal axis of the skull. This morphology is typically observed in Cetotheriidae and Balaenopteroidea. The coronal (frontal-parietal) suture is highly concave; the anterior end of the parietal squama reached a point located more anteriorly than the posteromedial portion of the interorbital region of the frontal.

The parietal-squamosal suture is highly concave. The ventrolateral portion of this suture broadens in correspondence of a possible exposure of the alisphenoid. From this part of the suture, a squamosal cleft develops laterally and posteriorly paralleling the ventral border of the posterior wall of the temporal fossa formed by the squamosal. The squamosal cleft is straight and is developed in the ventral-most part of the squamosal. The posterolateral termination of the squamosal cleft is located 78 mm far from its starting point.

The nuchal crest is posteriorly protruded but it does not protrude more posteriorly than the occipital condyle. Its outline is transversely narrow and its apex is rounded in dorsal view. The squamosal protrudes into the temporal fossa as its anterior face is convex approaching the parietal-squamosal suture; more laterally, it becomes more concave medially to the emergence of the zygomatic process. Anteriorly to the nuchal crest, it is transversely concave and anteroposteriorly flat.

The lateral squamosal crest projects laterally and anteriorly; a low but long triangular fossa is developed on the lateral side of the lateral squamosal crest; this fossa is located above the postglenoid process. The apex of the zygomatic process of the squamosal is broken and is missing; what remains of the zygomatic process suggests that this process was developed paralleling the longitudinal axis of the skull.

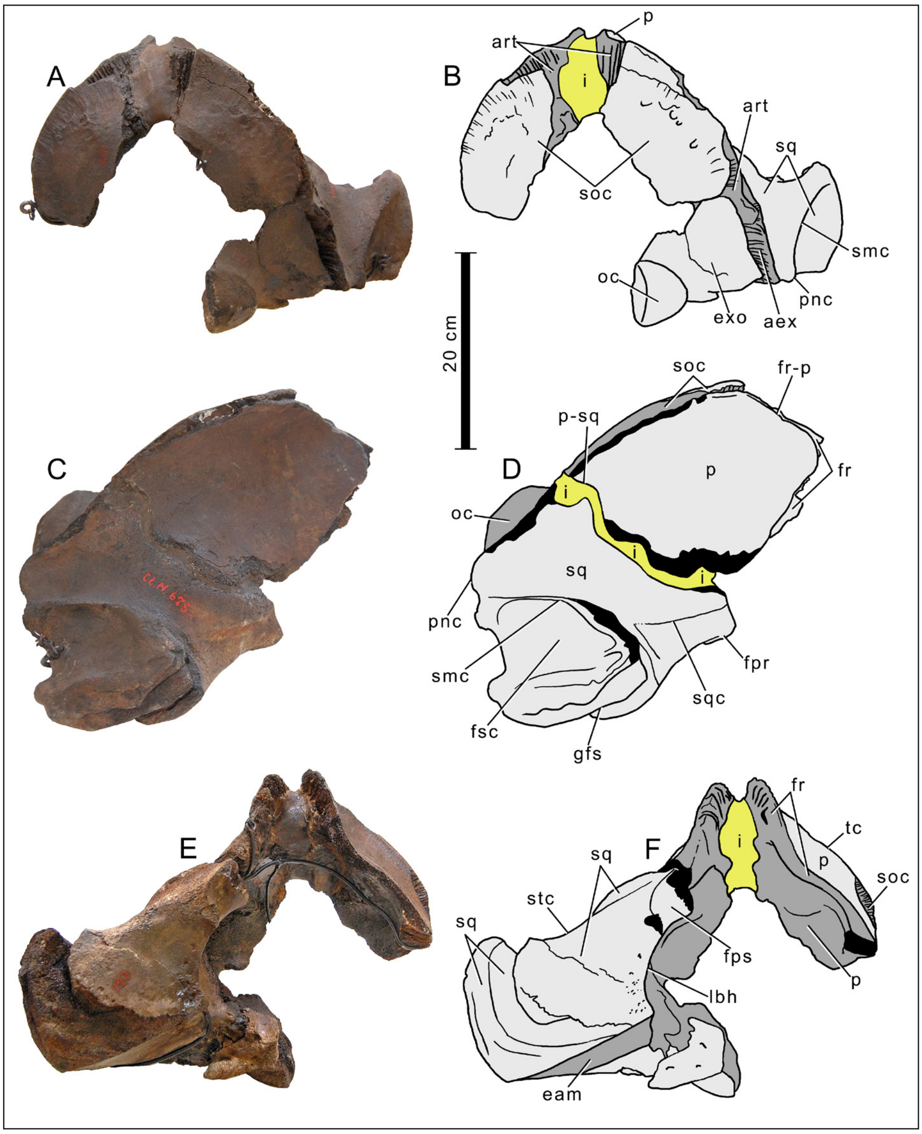


Fig. 21 - Balaenopteroidea gen. et sp. indet. Specimen M. 675, partial neurocranium: A) posterodorsal view; B) anatomical interpretation of the same; C) right lateral view; D) anatomical interpretation of the same; E) ventral view; F) anatomical interpretation of the same. See Anatomical abbreviations for explanation of acronyms. Scale bar equals 20 cm.

In ventral view, the glenoid cavity of the squamosal is flat. Part of the external acoustic meatus is evident; this structure is only slightly concave and has an anteroposterior diameter of 20 mm and a lateromedial length of 107 mm. Posteriorly to the external acoustic meatus, a wide portion is present that lodged the (missing) posterior process of the periotic.

The lateral border of the foramen lacerus posterius is highly concave and projects directly into the cranial cavity. This border is 70 mm in length. The dorsal border of the foramen "pseudo"-ovale is present; the estimated diameter of the foramen is 18 mm and its location is supposed to be between squamosal and pterygoid.

The supraoccipital is wide and its lateral borders are uniformly convex. Even though the lateral border of the supraoccipital is not preserved, the sutural surfaces of the parietal are preserved showing that the temporal crest (and thus the anterolateral portion of the supraoccipital) overhangs the parietal but its posterior part does not. That portion of the supraoccipital surface that is preserved is convex. The anterior end is missing but it is supposed to have been round based on the shape and distribution of the articular groove present on the underlying parietal. The supraoccipital length is estimated to be around 230 mm and its maximum width (between the posterior apices of the nuchal crests) is estimated to be around 275 mm.

The right exoccipital is preserved and shows part of the right condyle that is dorsoventrally convex but transversely flat; the articular surface is located in the ventral half of the condyle. Laterally to the articular surface is a short neck. The condyle is 90 mm in height and 45 mm in transverse width.

As most of the supraoccipital is missing, it is possible to directly look at the internal sides of the cranial cavity. A small anteromedial fossa is present in the parietal that is developed paraxially with respect to the longitudinal axis of the skull; a larger lateral fossa is bilaterally present that approaches the suture parietal-squamosal. Both fossae are superimposed by the supraoccipital. The maximum diameter of the small anteromedial fossa is 95 mm and the minimum diameter is 35 mm; the maximum diameter of the lateral fossa is 110 mm and the minimum diameter is 50 mm.

Comparisons, discussion and taxonomic decision about M. 675

Even if M. 675 resembles the Balaenopteridae, it shows several archaic characters. In particular, the bulging of the squamosal in the temporal fossa is a character observed in Cetotheriidae, Eschrichtiidae and in the basal balaenopterid *Fragilicetus velponi*. The presence of this character in M. 675 is not incompatible with its placement among the earliest-diverging balaenopterid sub-clades. A straight squamosal cleft is also typical of some cetotheriids such as *Metopocetus hunteri* and *Herentalia nigra* and this provides further support to the placement of the specimen in early-branching balaenopterid ramus.

Uniformly convex borders of the supraoccipital are rarely observed in mysticete taxa. They are present in *Titanocetus sammarinensis* (Bisconti 2006), *Eschrichtioides gastaldii* (Bisconti 2008) and *'Balaenoptera' siberi* (Pilleri 1989). However, in *T. sammarinensis*, the supraoccipital surface is uniformly and deeply concave; in *E. gastaldii* the attachment sites for the neck muscles form strong and relieved tubercles; in *'B.' siberi*, the supraoccipital is superimposed on the interorbital region of the frontal in dorsal view. None of these characters is observed in the specimen M. 675.

One of the characters that lend support to the inclusion of M. 675 in Balaenopteridae, is the shape of the parietal exposure anteriorly to the anterior border of the supraoccipital. As in Balaenopteridae, the parietal forms an anteroposterioly shortened stripe of bone that parallels the anterior border of the supraoccipital and forms an anteriorly concave coronal suture. In Cetotheriidae, the parietal exposure at the cranial vertex is transversely narrower and more relieved than in M. 675 where it is more transversely expanded as in Balaenopteroidea.

All the above comparisons suggest the placement of M. 675 within Balaenopteridae. In fact, it is possible to distinguish this specimen from basal thalassotherians because it shows (1) parietal forming two opposite concavities anteriorly to the supraoccipital, (2) presence of squamosal cleft, (3) anteriorly protruded parietal. However, we do not establish a new taxonomic name for this specimen because it lacks critical diagnostic characters able to unambiguously distinguish it from other balaenopterid taxa.

Descriptions and decisions about M. 634 and M. 674

The specimen M. 634 was assigned to *Plesiocetus brialmontii* by Van Beneden (1880). It is represented by the anterior portion of the right manidbular ramus. Mandibular condyle, coronoid process and mandibular foramen are missing because of post-depositional damage. The dentary is subdivided into 4 pieces (Fig. 22). The anterior-most piece

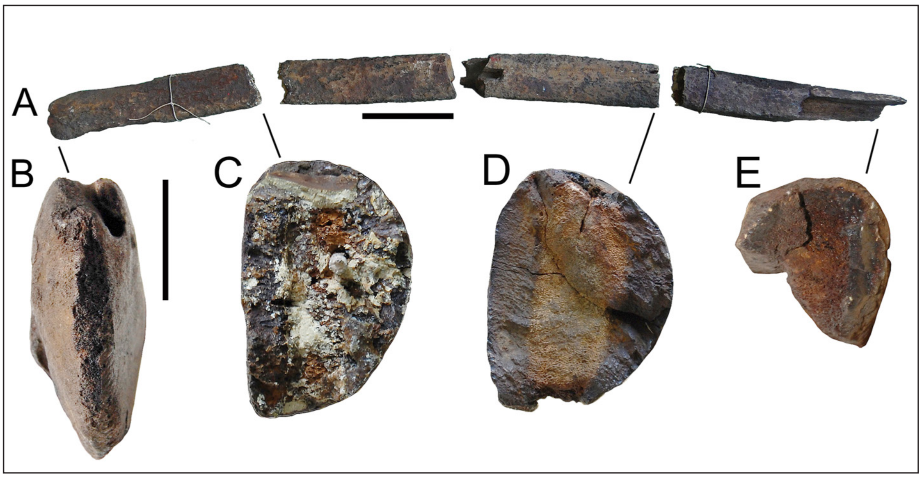


Fig. 22 - Balaenopteridae gen. et sp. indet. Specimen M. 634, right mandibular ramus: A) the four segments forming the ramus in medial view; B) natural cross-section of anterior end of anterior-most segment; C) natural cross-section of posterior end of anterior-most segment; D) natural cross-section of posterior end of penultimate segment; E) natural cross-section of posterior end of posterior-most segment. In A, scale bar equals 10 cm and 5 cm in B.

is 495 mm in length and includes the anterior end of the dentary with a 24.5 mm long groove for the mental ligament. The anterior border is 102.5 mm in height and projects ventrally. Posteriorly, a 370 mm long piece is 105 mm in height at the anterior end. It is rectangle shaped and has a flat medial surface. Posteriorly, a 429 mm long piece is 96 mm in anterior height; this piece is anteriorly broken and has a flat medial surface. The posterior-most piece is 500 mm in length and 97 mm in anterior height. These pieces form a continuous sequence demonstrating that this dentary did not posses a dorsoventral arch and did not have a mylohyoidal groove. Moreover it does not show a lateral curve in dorsal view. Four mental foramens are present on the dorsolateral surface of the ramus. The cross-sections of this dentary are presented in Fig. 22 showing that the lateral surface of the dentary is consistently outward bowed and the medial surface is flat; the ventral border is sharply-edged. The crest-like ventral border and the lack of a consistently convex medial border allow assignment of this dentary to Balaenopteridae gen. et sp. indet.

The specimen M. 674 was previously assigned to *Plesiocetus hupschii* and is represented by an individual metacarpal bone of the last digit (Fig. 5). It is short and shows an undulated posterior border. The length of the metacarpal is 69.54 mm, its anteroposterior diameter at mid-length is 38.52 mm, the anteroposterior diameter of the proximal facet is 57.16 and its transverse diameter is 35.37 mm, the anteroposterior diameter of the distal facet is 43.74 mm and its transverse diameter is 31.09 mm. The proximal border is highly inclined with respect to the distal border resembling the last metacarpal of the extant fin whale, *Balaenoptera physalus*, and of the humpback whale, *Megaptera novaeangliae* (Struthers 1884; Cooper et al. 2007). In comparison, the last metacarpal of balaenid whales appears more slender and lacks the oblique proximal border. Kellogg (1968) reported the metacarpals of *Pelocetus calvertensis*, a basal thalassotherian from North America, but none of the described bones presents the oblique proximal border. Bouetel & De Muizon (2006) showed that one of the metacarpals of *Piscobalaena nana* showed this character but at much lesser extent than that in the balaenopterid species mentioned above. For these reasons, we assign the specimen M. 674 to Balaenopteridae gen. et sp. indet.

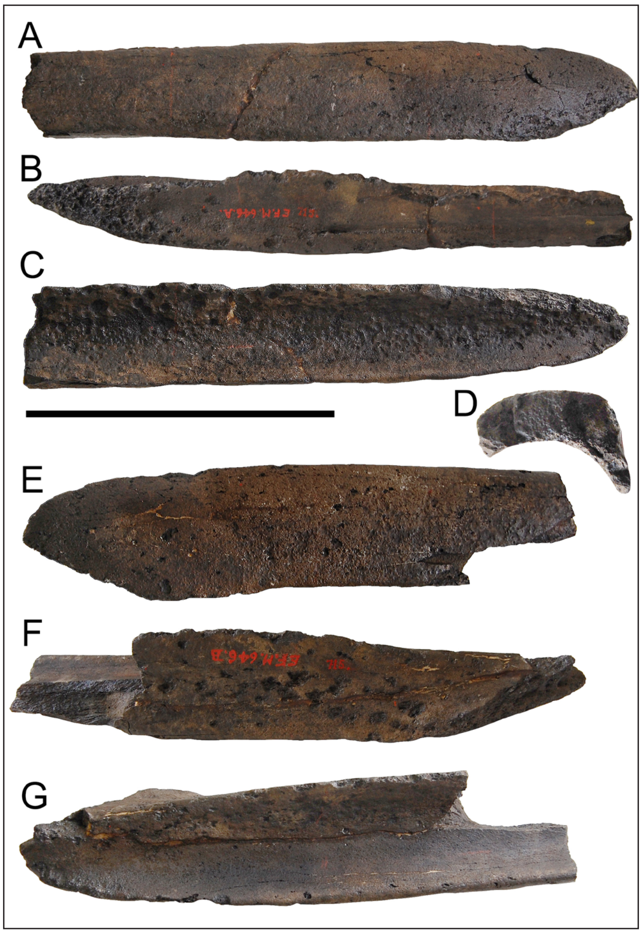


Fig. 23 - Mysticeti gen. et sp. indet. Specimen M. 646a, anterior end of right maxilla or premaxilla: A) dorsal; B) lateral; C) ventral views; D) natural cross-section at posterior end. Specimen M. 646b, anterior end of left maxilla or premaxilla: E) dorsal; F) Lateral; G) ventral views. Scale bar equals 10 cm.

Indeterminate Bones

Materials: IRSBN M. 646a-b.

Description and decision

These specimens were interpreted as the anterior-most portion of the mandibular ramus but their morphology is not compatible with that anatomical region. Both of the specimens were assigned to *Plesiocetus dubius*. The specimen M. 646a is an elongated and flat bone with a V-shaped section (Fig. 23). In one of the walls of the V-shaped section there is a groove whose morphology is compatible with the foramen for the vasculature of the baleen-bearing epithelium. The specimen M. 646b shows the same morphology but represents the contralateral bone and lacks the foramen. There is no possibility to safely assign these bones to a mysticete anatomical district and it is not possible to assign them to any known mysticete genus and species.

GENERAL DISCUSSION

Van Beneden (1880, 1885) gave his last conclusions on *Plesiocetus* and assigned four species to this genus, namely *P. brialmontii, P. dubius, P. burtinii,* and *P. hupschii*. Previously, Van Beneden (1875) had established *Plesiocetus cuvieri* on a specimen from Italy. The latter has been transferred to *Protororqualus cuvieri* by Bisconti (2007a) leaving only the four species presented above in need of revision.

In the Van Beneden "type" *Plesiocetus* collection, two partial skulls deserve particular attention. One of them (M. 647a-b) is here assigned to Cetotheriidae gen. and sp. indet. and the other (M. 675) to Balaenopteridae gen. and sp. indet. It will still be possible to attempt to make more detailed taxonomic assessments after a new comprehensive re-examination of the morphological diversity of Cetotheriidae. While it is tempting to assign the specimen M. 647a-b to *Metopocetus hunteri* based on their respective resemblances, clear morphological differences in the supraoccipital prevent us from taking such a step. Our reluctance is further reinforced by the observation of different details in the sagittal crest in these whales. However, we think that it is important to have found evidence of the cetotheriid affinities of M. 647 because this observation provides further evidence to prove the presence of Cetotheriidae taxa in the southern North Sea basin in the late Tortonian.

The periotics included in the *Plesiocetus* "type" collection revealed interesting relationships. Their disparate morphologies showed affinities with basal thalassotherian taxa (M. 652) and Balaenoidea (M. 676) increasing our knowledge of the taxonomic composition of the mysticete fauna of the late Miocene of Belgium.

The skull M. 675 is here interpreted as a member of Balaenopteroidea. Other specimens found in the "type" Van Beneden collection show morphological characters of Balaenopteroidea even if they were assigned to non-balaenopteroid genera by Van Beneden. Revisions of these materials are currently in progress by the present authors and new conclusions are anticipated. We are still far from knowing the whole diversity of basal balaenopterid mysticetes.

In the end, as shown in Tab. 8, our revision shows that the specimens assigned by Van Beneden to different *Plesiocetus* species cannot be included in a single genus or even in a single family. The "type" *Plesiocetus* collection includes specimens that may be assigned to indeterminate genera and species of Mysticeti, Balaenomorpha, Balaenoidea, Thalassotherii, basal thalassotherians, Balaenopteroidea, and Balaenopteridae. For this reason, we conclude that, as no specimen is sufficiently complete to unambiguously represent a genus or species, *Plesiocetus* is a *nomen dubium* and must be abandoned.

BROADER TAXONOMIC IMPLICATIONS

It is undeniable that the revision of *Plesiocetus* expanded the morphological sample of the balaenomorph mysticetes. Interesting additions include the stem-balaenoid taxon represented by M. 676, the stem-basal thalassotherian taxon represented by M. 652 and two possible new species represented by M. 647 and M. 675. We expect that other revisions, that we are carrying out based on the Belgian historical collections, will reveal new taxa and help to better clarify the phylogenetic relationships of the baleen-bearing whales from the southern North Sea.

However, our conclusion that *Plesiocetus* is a *nomen dubium* has necessary consequences on the taxonomy of non-Belgian mysticetes previously assigned to this genus. Many mysticete fossils were assigned to *Plesiocetus* by several authors as, in a sense, *Plesiocetus* became a sort of taxonomic wastebasked including balaenopterid-like and cetotheriid-like mysticetes. A search in the Paleobiology Database (performed on 22 October 2020) revealed that at least 32 occurrences were listed in 23 collections in Europe, North and South America. Most of the occurrences are referred to as *Plesiocetus* sp. and are represented by largely incomplete fossil records that we will discuss at the end of this section. However, four reasonably complete *Plesiocetus* specimens from Europe and South America, identified at species level, are now in need of taxonomic revisions. These specimens include the following: (1) *Plesiocetus dyticus* Cabrera, 1926 from Cerro del Castillo, Trelew, which is in an Aquitanian/Burdigalian shallow subtidal sandstone in the Gaiman Formation of Argentina; (2) *Plesiocetus notopelagicus* Cabrera, 1926 from Carmen de Patagones, which is in a Pliocene marine horizon in Argentina; (3) *Ple-*

Tab. 8 - Results of the taxonomic revision of *Plesiocetus brialmontii, P. dubius, P. burtinii,* and *P. hupschii* based on the present work.

Specimen No.	**Anatomy**	**Previous taxonomy**	**Revision (present work)**
M. 630a-b	skull and dentary	*Plesiocetus brialmontii*	Cetotheriidae gen. et sp. indet.
M. 631	tympanic bulla	*Plesiocetus brialmontii*	Basal Thalassotherii gen. et sp. indet.
M. 632	tympanic bulla	*Plesiocetus brialmontii*	Basal Thalassotherii gen. et sp. indet.
M. 633	tympanic bulla	*Plesiocetus brialmontii*	Basal Thalassotherii gen. et sp. indet.
M. 634	dentary	*Plesiocetus brialmontii*	Balaenopteridae gen. et sp. indet.
M. 635	atlas	*Plesiocetus brialmontii*	Mysticeti gen. et sp. indet.
M. 636	axis	*Plesiocetus brialmontii*	Chaeomysticeti gen. et sp. indet.
M. 637a-b	vertebrae	*Plesiocetus brialmontii*	Balaenomorpha gen. et sp. indet.
M. 368a-c	vertebrae	*Plesiocetus brialmontii*	Balaenomorpha gen. et sp. indet.
M. 639	vertebra	*Plesiocetus brialmontii*	Balaenomorpha gen. et sp. indet.
M. 640	vertebrae	*Plesiocetus brialmontii*	Mysticeti gen. et sp. indet.
M. 641	scapula	*Plesiocetue brialmontii*	Balaenomorpha gen. et sp. indet.
M. 642	humerus	*Plesiocetus brialmontii*	Basal Thalassotherii gen. et sp. indet.
M. 643	radius	*Plesiocetus brialmontii*	Balaenomorpha gen. et sp. indet.
M. 644	ulna	*Plesiocetus brialmontii*	Mysticeti gen. et sp. indet.
M. 645a-g	vertebrae	*Plesiocetus dubius*	Balaenomorpha gen. et sp. indet.
M. 646a-b	indet.	*Plesiocetus dubius*	Indet.
M. 647a-b	skull	*Plesiocetus dubius*	Cetotheriidae gen. et sp. indet.
M. 648a-b	skull	*Plesiocetus dubius*	Thalassotherii gen. et sp. indet.
M. 649	tympanic bulla	*Plesiocetus dubius*	Basal Thalassotherii gen. et sp. indet.
M. 650	tympanic bulla	*Plesiocetus dubius*	Basal Thalassotherii gen. et sp. indet.
M. 651	tympanic bulla	*Plesiocetus dubius*	Basal Thalassotherii gen. et sp. indet.
M. 652	periotic	*Plesiocetus dubius*	Basal Thalassotherii gen. et sp. indet.
M. 654	dentary	*Plesiocetus dubius*	Basal Thalassotherii gen. et sp. indet.
M. 658	scapula	*Plesiocetus dubius*	Balaenomorpha gen. et sp. indet.
M. 659	humerus	*Plesiocetus dubius*	Basal Thalassotherii gen. et sp. indet.
M. 660a	scapula	*Plesiocetus dubius*	Balaenidae gen. et sp. indet.
M. 660b	radius	*Plesiocetus dubius*	Balaenidae gen. et sp. indet.
M. 661	skull	*Plesiocetus hupschii*	Balaenomorpha gen. et sp. indet.
M. 662	skull	*Plesiocetus hupschii*	Basal Thalassotherii gen. et sp. indet.
M. 663	skull	*Plesiocetus hupschii*	Mysticeti gen. et sp. indet.
M. 664	tympanic bulla	*Plesiocetus hupschii*	Basal Thalassotherii gen. et sp. indet.
M. 665a-b	skull	*Plesiocetus hupschii*	Basal Thalassotherii gen. et sp. indet.
M. 666	skull	*Plesiocetus hupschii*	Balaenomorpha gen. et sp. indet.
M. 667a-e	vertebrae	*Plesiocetus hupschii*	Balaenomorpha gen. et sp. indet.
M. 668	vertebrae	*Plesiocetus hupschii*	Balaenomorpha gen. et sp. indet.
M. 669a-b	vertebrae	*Plesiocetus hupschii*	Balaenomorpha gen. et sp. indet.
M. 670	scapula	*Plesiocetus hupschii*	Basal Thalassotherii gen. et sp. indet.
M. 671	humerus	*Plesiocetus hupschii*	Balaenomorpha gen. et sp. indet.
M. 672	ulna	*Plesiocetus hupschii*	Mysticeti gen. et sp. indet.
M. 673	radius	*Plesiocetus hupschii*	Balaenomorpha gen. et sp. indet.
M. 674	metacarpal	*Plesiocetus hupschii*	Balaenopteridae gen. et sp. indet.
M. 675	skull	*Plesiocetus burtinii*	Balaenopteridae gen. et sp. indet.
M. 676	periotic	*Plesiocetus burtinii*	Balaenoidea gen. et sp. indet.
M. 677	tympanic bulla	*Plesiocetus burtinii*	Basal Thalassotherii gen. et sp. indet.
M. 678	tympanic bulla	*Plesiocetus hupschii*	Basal Thalassotherii gen. et sp. indet.
M. 679	tympanic bulla	*Plesiocetus burtinii*	Basal Thalassotherii gen. et sp. indet.
M. 680a-c	vertebrae	*Plesiocetus burtinii*	Balaenomorpha gen. et sp. indet.
M. 681	vertebra	*Plesiocetus burtinii*	Balaenomorpha gen. et sp. indet.

siocetus occidentalis Kellogg, 1931 which is probably from the Tortonian Monterey Formation of California, and (4) a *Plesiocetus* sp. described by Hampe (1996) from the Upper Miocene of the Lower Rhine Embayment in Germany. These specimens are discussed below.

Cabrera (1926) published brief descriptions of *Plesiocetus dyticus* and *P. notopelagicus* showing only the dorsal and posterior views of the skull of the former and the posterior view of the latter. Judging from Cabrera's descriptions and illustrations, the lack of the anterior border of the supraorbital process of the frontal prevents the assessment of the length of the posteromedial elements of the rostrum. Apparently, the grooves for the articulation with the ascending process of the maxilla, located in the interorbital region of the frontal, are short but this observation could be biased by the lack of the anterior portion of the frontal itself. Cabrera (1926) observes that the temporal crest largely overhangs the medial wall of the temporal fossa as in Balaenopteridae. The balaenopterid affinity of

Plesiocetus dyticus is reinforced by the outline of the supraoccipital that closely resembles that of the genus *Protororqualus* as described by Bisconti (2007a) and Bisconti & Bosselaers (2020). *Protororqualus*, in fact, is characterized by a sinuous lateral border of the supraoccipital with triangular and pointed anterior apex. This pattern is observed in both the species assigned to *Protororqualus* (*i.e.*, *P. cuvieri* and *P. wilfriedneesi*). We thus suggest that *Plesiocetus dyticus* is to be reassigned to Balaenopteridae cf. *Protororqualus* sp. pending a new description of the specimen. If our new taxonomic interpretation will be confirmed, then this would be the only Miocene *Protororqualus* specimen known up to now (Bisconti 2007; Bisconti & Bosselaers 2020).

Cabrera (1926) provided only a short description of *Plesiocetus notopelagicus* which suggests close resemblance to *Mesocetus latifrons*. As the latter is in need of revision, we do not express our opinion on the Argentinan specimen pending a more detailed morphological description and full illustration. As *Plesiocetus* is a *nomen dubium*, *P. notopelagicus* becomes now *'Plesiocetus' notopelagicus* pending a new generic denomination.

Kellogg (1925) provided a detailed description of *Plesiocetus occidentalis* based on two skulls illustrated in dorsal and lateral views. The characters shown by these skulls include an elongated basis of the supraorbital process of the frontal and a frontonasal suture well inserted within the interorbital region of the frontal. Both these characters suggest some affinity of the specimens described by Kellog to the Balaenopteridae. The supraoccipital is compressed at about mid-length and the parietal is exposed at the cranial vertex. These characters suggest that the specimens that Kellogg referred to *Plesiocetus occidentalis* are closely related to *'Balaenoptera' cortesii* var. *portisi* (Portis 1885) that is based on Italian specimens currently under revision by one of us. We then suggest that *Plesiocetus occidentalis* is to be included within the same genus as *'Balaenoptera' cortesii* var. *portisi*. Deméré et al. (2005) suggested that *'Balaenoptera' cortesii* var. *portisi* may be congeneric with *Cetotheriophanes capellinii*. Here, we follow this opinion and assign *Plesiocetus occidentalis* to cf. *Cetotheriophanes capellinii* pending a redescription of the specimen.

The almost complete skeleton assigned to *Plesiocetus* sp. by Hampe (1996) is heavily fractured and damaged by taphonomic processes mainly identified as a transportation process during the Saalian glacial period (Hampe 1996). Only a few bones show diagnostic potential and these include the right posterior process of the periotic. This structure shows a deep and long facial sulcus along its ventral surface; the facial sulcus is bounded by strong and squared relieves laterally and medially as observed in some Cetotheriidae taxa such as *Herpetocetus transatlanticus* (Marx & Fordyce 2016). A cetotheriid affinity for this specimen is reinforced by the outline of the lateral border of the tympanic bulla in dorsal view that shows the absence of the lateral lobe resembling the pyruliform bulla (*sensu* Bisconti 2010; first type of the present paper) of cetotheriid mysticetes. We thus suggest that the *Plesiocetus* sp. described by Hampe (1996) may belong to Cetotheriidae gen. et sp. indet. pending further morphological analysis of the specimen to support a genus-level assignment.

Plesiocetus is mentioned in a number of references retrieved from the Paleobiology Database. We examined all the references to assess the taxonomic status of the specimens. Van Beneden & Gervais (1868-1880) described a partial skull from the Pliocene of Suffolk and assigned it to *Plesiocetus hupschii*. This specimen is figured out by Steeman (2010) too and is represented by an incomplete basicranium with the right periotic in articulation. Steeman (2010) followed Kellogg's (1931) opinion and placed it within *Plesiocetopsis*. As this specimen is not in the "type" collection and its current repository is unknown, we do not investigate further on this specimen and leave it in *Plesiocetopsis*.

Van Beneden & Gervais (1880, pl. 17, Nos 1-3) figured out a partial neurocranium from the surroundings of Bayeux that, in their opinion, shows the same morphological characters as the Belgian *Plesiocetus hupschii*. Based on the published illustrations, this skull shows strong and ovoid tubercles for the attachment of neck muscles in the supraoccipital and a less posteriorly-protruded nuchal crest than the neurocrania referred to *Plesiocetus* by Van Beneden & Gervais (1880). Interestingly, the nuchal crest is similar to that of living Balaenopteridae but the frontal-parietal suture, observed in lateral view, does not project anteriorly to interdigitate with the posteromedial elements of the rostrum. Even though this is an interesting skull, it does not belong into the "type" *Plesiocetus* collection but represents, rather, a specimen referred to *Plesiocetus*. Compared to the two neurocrania in the "type"

Plesiocetus collection (M. 647 and M. 675), this skull shows different morphology in the supraoccipital, in the nuchal crest and in the frontal-parietal suture and cannot be assigned to the same species represented by them. Moreover, its current repository is unknown. For these reasons, we do not investigate this specimen further and assign it to Thalassotherii gen. et sp. indet.

A major taxonomic problem is related to the name *Plesiocetus cortesii*. As detailed by Bisconti (2007a, 2009), this name was created by Brandt (1873) to accommodate a specimen discovered in 1816 by Giuseppe Cortesi in the Argille azzurre Formation outcropping along a river between Montezago and the Rio Chiavenna, *c.* 30 km south of Piacenza, northern Italy (Cortesi 1819). Brandt included in this taxon also a specimen discovered by Alessandro Portis in 1862 in Cortandone, *c.* 50 km south-east of Torino. Strobel (1881) stated that the specimen from Cortandone represented a different taxon and called it *Cetotherium gastaldii*. Portis (1885) pulled out this specimen from *Cetotherium* and assigned it to *Balaenoptera* by defining the species *Balaenoptera gastaldii*. Bisconti (2008) observed that the specimen is a Pliocene record of the family Eschrichtiidae, assigned it to the new genus *Eschrichtioides* and defined the new species *Eschrichtioides gastaldii*.

Portis (1885) described and figured out several specimens from the Pliocene of Piedmont that he assigned to *Plesiocetus cortesii* by assuming that the specimens from Piedmont and the specimen discovered in 1816 represented the same species. Sacco (1890) pulled out the specimens from Piedmont (excluding the skeleton from Cortandone) from *Plesiocetus* and assigned it to *Balaenoptera* by defining the new taxon *'Balaenoptera' cortesii* var. *portisi*. Apparently, only the specimen from 1816 can be still included within *Plesiocetus cortesii*. This specimen is still partially covered by the original matrix and most of it is not accessible to visual inspection. However, wide and flat supraorbital processes of the frontal are free from the matrix and can be observed suggesting inclusion of the specimen within Balaenopteridae. As from our revision, none of the specimens included in the "type" *Plesiocetus* collection of Van Beneden can be used as a syntype, therefore the name *Plesiocetus* is a *nomen dubium* and for this reason, the specimen from 1816 must now be labeled as Balaenopteridae gen. et sp. indet. pending a new study of the skeleton that is now the item MPP-107 in the Museo di Paleontologia of the Università degli Studi di Parma (Freschi 2014; Francou 1994; Cigala Fulgosi 1980). Based on the available illustrations, it is still unclear whether MPP-107 and the specimens from Piedmont represent the same species. In particular, the skeleton from Montafia discovered in 1862 that was described by Portis (1884), and the partial skeleton from Bagnasco described by Borson (1830) appear to be morphologically close and are currently included within *'Balaenoptera' cortesii* var. *portisi*. Whether or not these specimens are conspecific to MPP-107 will be the subject of another work. From this analysis, it is clear that a new study of these records is critically needed to understand the taxonomy and phylogenetic relationships of this important Italian paleontological heritage.

Flot (1895) reported the presence of *Plesiocetus dubium* from the Burdigalian of Mont-de-Marsan, France. This species was reviewed by Steeman (2010) who considered it is a *nomen dubium*; we confirm this decision thus the taxonomy of these French specimens is to be re-assessed based on a new examination of the available materials.

Van Deinse (1931) assigned three incomplete tympanic bullae (RGM 86355, 86359, 86369) to *Plesiocetus/Megaptera affinis* even though the Van Beneden original designation of the species was *Heterocetus affinis*, hence we suppose that this cannot be a valid name. The tympanic bulla RGM 86355 (Fig. 24) is from Pas Van Neuzen Terneuzen and was collected by Van Deinse himself. It was assigned to *Plesiocetus* sp. by Van Deinse (1931). This specimen represents a left tympanic bulla lacking most of the outer lip. Judging from the preserved portion, this bulla lacks the lateral lobe showing a pyruliform outline in dorsal view. The thick involucrum protrudes medially at the posteromedial corner forming a rounded boss in dorsal view. The Eustachian opening is positioned close to the anteroventral border of the bulla. The main ridge is weakly developed and is medially bordered by a ventral concavity. The ventromedial portion of the involucrum is developed in the shape of a secondary ridge running parallel to the anteroposterior axis of the bulla. The tympanic cavity is deep in the posterior portion and shallow in the anterior portion. In fact, the floor of the tympanic cavity raises anteriorly from the posterior-most deepest part. The maximum anteroposterior length of

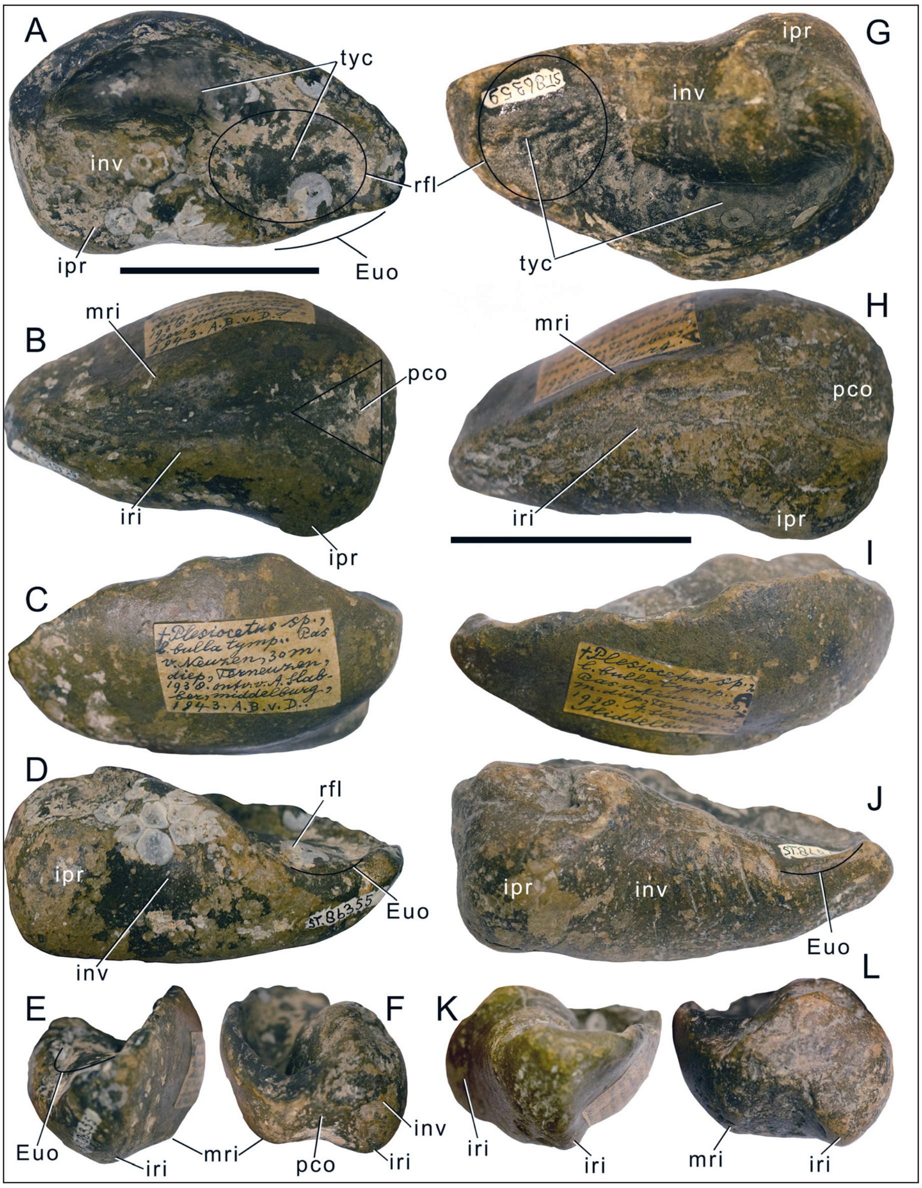


Fig. 24 - Tympanic bullae previously assigned to *Plesiocetus* by Van Deinse (1931). RGM 86355 in: A) dorsal view; B) ventral view; C) lateral view; D) medial view; E) anterior view; F) posterior view. RGM 86359 in: G) dorsal view; H) ventral view; I) lateral view; J) medial view; K) anterior view; L) posterior view. See Anatomical abbreviations for explanation of acronyms. Scale bars equal 5 cm.

this bulla is 93.07 mm; its maximum width at mid-length is 54.53 mm and its maximum height at the inferred level of the conical process is *c.* 26 mm. This bulla does not show the typical characters of the balaenopterid bulla (Ekdale et al. 2011; Bisconti 2010) in that it lacks the lateral lobe and a keen main ridge along its median axis. It may not be assigned to Balaenoidea because the tympanic cavity is deep and the ventral surface of the bulla is not flat-to-concave as seen in Balaenoidea. The pyruliform shape and the raising floor of the tympanic cavity suggest affinity with basal thalassotherian taxa such as *Atlanticetus* (Bisconti et al. 2020b). The lack of diagnostic characters, however, prevents us to assign this specimen to any known mysticete taxon; therefore, we assign the specimen RGM 86355 to Thalassotherii gen. et sp. indet.

The left tympanic bulla RGM86359 was collected by Van Deinse at Pas Van Neuzen Terneuzen and was assigned to *Plesiocetus* sp. indet. This specimen represents a large bulla which is 98.33 mm in maximum length, 22 mm in maximum width at anterior border, 51.77 mm in maximum width at the inferred position of the sigmoid process, and 56.97 mm in maximum width at the inferred position of the conical process. The height at the inferred position of the conical process is 19.64 mm and the maximum height is 43.96 mm. The bulla is largely incomplete lacking most of the lateral wall. Judging from what is preserved, the anterolateral lobe is missing and the bulla shows a pyruliform outline in dorsal view. The involucrum is concave in dorsal view and

Specimen	Original taxonomy	Authority	New taxonomy (this work)
MDLP 5-13	*Plesiocetus dyticus*	Cabrera (1926)	*Protororqualus* sp. nov.
MDLP 5-45	*Plesiocetus notopelagicus*	Cabrera (1926)	*'Plesiocetus' notopelagicus*
UCMP 1351	*Plesiocetus occidentalis*	Kellogg (1931)	*'Balaenoptera' cortesii* var. *portisi*
GLA NW Ter 460	*Plesiocetus* sp.	Hampe (1996)	Cetotheriidae gen. et sp. indet.
Suffolk specimen	*Plesiocetus hupschii*	Van Beneden	*Plesiocetopsis* sp. following Kellogg (1931) and Steeman (2010)
MSNUT PU13802 (Cortandone specimen)	*Plesiocetus cortesii*	Brandt (1873)	*Eschrichtioides gastaldii* following Bisconti (2008)
MPP-107	*Plesiocetus cortesii*	Brandt (1873)	Balaenopteridae gen. et sp. indet.
MSNUT PU13808 (Montafia specimen)	*Plesiocetus cortesii*	Portis (1884)	*'Balaenoptera' cortesii* var. *portisi*
MSNUT PU13809 (Bagnasco specimen)	*Plesiocetus cortesii*	Portis (1884)	*'Balaenoptera' cortesii* var. *portisi*
Mont-de-Marsan	*Plesiocetus dubium*	Flot (1895)	Mysticeti gen. et sp. indet.
RGM 86355, 86359, 86369	*Plesiocetus* sp.	Van Deinse (1920)	Thalassotherii gen. et sp. indet.

Tab. 9 - Taxonomic revision of *Plesiocetus* occurrences in European and American institutions.

protrudes medially from the posteromedial corner forming a boss. The main ridge is well developed and terminates posteriorly at the posteromedial corner of the bulla. The ventral surface of the bulla is concave posteriorly; the ventral concavity is bordered by the main ridge, laterally, and a well developed involucral ridge, medially. The Eustachian opening is very close to the anteroventral border of the bulla and the floor of the tympanic cavity raises anteriorly from a deep posterior-most portion. Anteriorly, the floor of the tympanic cavity forms a sort of platform (Fig. 24). In dorsal view, the bulla is slender showing considerable differences with the bullae of Balaenoidea. The lack of the anterolateral lobe and the presence of a well developed involucral ridge exclude that this bulla may belong to Balaenopteroidea. The anteriorly raised floor of the tympanic cavity and the general pyruliform shape in dorsal view suggest some affinity with basal thalassotherians or Cetotheriidae. We, therefore, assign the specimen RGM 86359 to Thalassotherii gen. et sp. indet.

The right tympanic bulla RGM 86369 was collected by Van Deinse at Groeve Wiegerink Bij Groenlo and the associated label states that it is from the late Miocene. It was No. 57 of the original Van Deinse collection and is identified as *Plesiocetus affinis?* Its maximum length is 59.61 mm, its maximum width at mid-length is 33.54 mm and its maximum height at the inferred level of the conical process is 18.56. This bulla is largely incomplete. It is small-sized and lacks most of the lateral border. The involucral border is broken and there is not any evidence of involucral ridge. The main ridge is well developed. The general outline in dorsal view is pyruliform due to the lack of the anterolateral lobe. The Eustachian opening is located only slightly dorsal to the anteroventral border of the bulla. The lack of a well developed main ridge and of the anterolateral lobe prevents the inclusion of this specimen within Balaenopteroidea. The round ventral border and the deep tympanic cavity exclude that this bulla may be included in Balaenoidea. The pyruliform shape in dorsal view suggests affinity with basal thalassotherian taxa or Cetotheriidae. Based on these observations, we assign the specimen RGM 86369 to Thalassotherii gen. et sp. indet. Our review, therefore, assigns all the specimens that Van Deinse (1931) had previously assigned to *Plesiocetus* to Thalassotherii gen. et sp. indet.

The results from the Paleobiology Database included a mention of *Plesiocetus* sp. from the Navidad Formation of Argentina in Nielsen et al. (2004). After careful reading, we were unable to find any mention of *Plesiocetus* in that paper, therefore we dismiss this reference and conclude that no *Plesiocetus* occurrence is reported in literature from the Navidad Formation of Argentina. Our taxonomic revisions of non-"type" *Plesiocetus* specimens are presented in Tab. 9.

CONCLUSIONS

We re-examined the *Plesiocetus* "type" collection described and figured in Van Beneden (1885) in order to obtain morphologically well-established taxonomic identifications of the different specimens originally assigned to this genus. Our taxonomic decisions are summarized in Tab. 8. Our analyses revealed what follows:

(1) each type *Plesiocetus* species is based on several individuals coming from different localities and represented by not comparable parts;

(2) as a whole, the materials forming these four type species represent individuals that can be assigned to different mysticete clades including Balaenomorpha, Balaenoidea, Balaenidae, Thalassotherii, basal thalassotherian taxa, Cetotheriidae, Balaenopteroidea and Balaenopteridae;

(3) one periotic (M. 676) is a representative of an early-diverging balaenoid taxon that is still undescribed but the lack of additional osteological data prevents the establishment of a new taxonomic denomination;

(4) another periotic (M. 652) belongs to an undescribed basal thalassotherian species but the lack of additional skeletal materials prevents the formulation of an unambiguous diagnosis;

(5) the partial skull M. 647 represents a member of Cetotheriidae with elective affinity to *Metopocetus hunteri* but the lack of additional evidence prevents the establishment of a new taxon and morphological differences prevent the inclusion of this specimen within *M. hunteri*;

(6) the partial skull M. 675 shows several primitive character states that support its inclusion in an early-diverging branch of Balaenopteridae;

(7) in the light of the above revision, we reviewed the European and North American records of *Plesiocetus* and provided new taxonomic assessments.

Our conclusions support the hypothesis that *Plesiocetus* is a *nomen dubium*, therefore, we suggest that this name is to be abandoned by cetacean taxonomists. The broad consequences of this decision are analyzed and resulted in the re-assignment to different superfamily-, family- and genus-rank taxa of the specimens previously included in *Plesiocetus* (Tab. 9). In the end, the revision of the whole materials belonging to the Van Beneden "type" collection promises to reveal new taxa that can help in retrieving a more realistic view of the past diversity within the baleen-bearing whales.

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