

Evolutionary history of Balaenidae

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Summary

The living species of the family Balaenidae are experiencing a very high extinction risk. Knowledge of their evolutionary history may be helpful in conservation strategies. In this paper a review and osteological diagnoses for the genera and species of the Balaenidae is given. Also palaeoecological features are determined, like the evolution of a large body size, changes in species composition and changes in the choice of reproductive sites over the last five million years. Finally, an overview of the problems encountered in balaenid conservation is made.

The family Balaenidae includes two living genera and three or four species depending on the systematic treatment that is preferred (morphology-based or molecular-based). Here, a review of the fossil record of Balaenidae is given, and the validity of several taxonomic names, based on the revision of type materials held in some European institutions, is assessed. From the comparative analyses of this paper, it is concluded that *Balaenula praediolensis*, *Balaena paronai*, *Balaena primigenius*, and *Balaena etrusca* represent indeterminate Balaenidae genera. Emended osteological diagnoses for the remaining valid taxa are provided: the genus *Eubalaena* (including two or three living species: *E. glacialis*, *E. australis*, and, possibly, *E. japonica*), the genus *Balaena* (including two species: *B. montalionis* and *B. mysticetus*), the genus *Balaenula* (including three species: *B. balaenopsis*, *B. astensis*, and *B. sp. nov.* from Japan), the genus *Balaenotus* (including one species: *B. insignis*). The phylogenetic analyses of Balaenidae, that have been published over the past few years, are revised and a consensus view, based on both molecules and morphology, is proposed. Three themes in the palaeoecology of Balaenidae are assessed: the evolution of large body size, changes in species composition in Pliocene-to-Recent balaenid assemblages, and changes in balaenid preference in choosing reproductive sites over the last five million years. Palaeobiogeographic works on Balaenidae are reviewed based on the distribution of the fossil taxa and recent molecular works. A general overview of the problems encountered in balaenid conservation is made in light of phylogenetic works based on molecular divergences and the fossil record.

Samenvatting

De levende vertegenwoordigers van de familie van de Balaenidae (baleinwalvissen) lopen risico om uit te sterven. De kennis van hun evolutiegeschiedenis zou kunnen helpen om strategieën voor hun behoud te ontwikkelen. In dit artikel wordt een overzicht gegeven van de familie van de baleinwalvissen met osteologische diagnoses (onderscheidingskenmerken aan het skelet) van de verschillende geslachten en soorten. Ook worden er enkele paleoecologische kenmerken behandeld, zoals een toenemende lichaamsomvang, veranderingen in soortensamenstelling en veranderingen in de keus van voortplantingsplaatsen. Tenslotte wordt een overzicht gegeven van de problemen die zich voordoen bij de bescherming van de baleinwalvisachtigen.

Introduction

Balaenids are large, slow-swimming cetaceans. They belong to the family Balaenidae that is included in the suborder Mysticeti, the baleen or whalebone whales. Scientists have known Balaenidae since before the times of Linnaeus (1758) but these whales received their family-level denomination by Gray in 1825, sixty-seven years after Linnaeus' *Systema naturae*. Balaenids differ from other living mysticetes in that they have an arched rostrum, and a body that is deep and stocky (Burns *et al.*, 1993).

Compared to other living mysticetes, balaenids exhibit a low diversity. Only two genera are living today: *Balaena* (the Bowhead whale that includes the only living species *Balaena mysticetus*) and *Eubalaena* (the Right whale which

includes the living species *Eubalaena glacialis* and *Eubalaena australis*; Mead & Brownell, 1993).

Balaenids differ from Balaenopteridae, including rorquals (genus *Balaenoptera*) and humpbacks (genus *Megaptera*), in their arched rostrum, and in that in rorquals and humpbacks the maxilla is transversely expanded while in balaenids it is transversely compressed (Fig. 1b-c); the rorqual's rostrum is flat and wide and that of balaenids is transversely narrow (Fig. 2b-c). Moreover, balaenopterids have ventral throat grooves, which allow them to expand their mouth cavity during feeding in order to accommodate a large quantity of food-containing water; in balaenids the ventral throat grooves are absent, and the mouth cavity cannot be expanded. However, due to the arched rostrum, the mouth cavity of balaenids is very wide and is occupied by the longest baleens

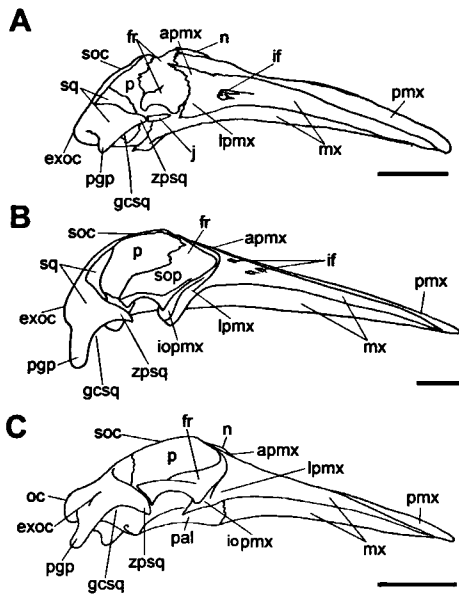


Fig. 1 Right lateral view of selected mysticete skulls. A, *Eschrichtius robustus* (grey whale: family Eschrichtiidae; redrawn from True 1904, pl. 47, fig. 3, with modifications). B, *Megaptera novaeangliae* (humpback whale: family Balaenopteridae, subfamily Megapterinae; re-drawn from True 1904, pl. 31, fig. 1, with modifications). C, *Balaenoptera acutorostrata* (minke whale, a representative of the rorquals: family Balaenopteridae, subfamily Balaenopterinae; re-drawn from True 1904, pl. 26, fig. 1, with modifications). Anterior ends of the skulls on the right side. Scale bars equal 200 mm. See Anatomical abbreviations for explanation

Rechter zijaanzicht van enkele baardwalvis Schedels. A, *Eschrichtius robustus* (grijze walvis: familie Eschrichtiidae; nagetekend van True 1904, pl. 47, fig. 3, met wijzigingen). B, *Megaptera novaeangliae* (bultrug: familie Balaenopteridae, subfamilie Megapterinae; nagetekend van True 1904, pl. 31, fig. 1, met wijzigingen). C, *Balaenoptera acutorostrata* (dwergvinvis, een vertegenwoordiger van de vinvissen: familie Balaenopteridae, subfamilie Balaenopterinae; nagetekend van True 1904, pl. 26, fig. 1, met wijzigingen). De voorkant van de schedels is aan de rechterzijde. Maatstrep is 200 mm. Zie anatomische afkortingen voor uitleg.

among the mysticetes (reaching up to 3.5 meters). Balaenids lack a dorsal fin, which is present in balaenopterids, and have a pectoral fin shorter than that of rorquals and humpbacks. Rorquals and humpbacks are the more streamlined among the living mysticetes. They are high-speed swimmers and represent the only living baleen whales able to perform intermittent so-called ram feeding (Sanderson & Wassersug, 1993). Rorquals and humpbacks display an abruptly

depressed supraorbital process of the frontal, which is wide and does not bear any sharp ascending temporal crest.

There are several other differences between balaenids and other living mysticetes. The balaenids' closest relative is *Caperea marginata* (family Neobalaenidae Gray, 1873) (Fig. 3). Neobalaenidae is a monotypic family characterized by a single genus and species that performs continuous ram feeding on calanoid copepods and other slow-swimming alimentary items in the Southern Oceans. *Caperea* has an arched rostrum, dentary lacking coronoid process, tympanic bullae dorsoventrally compressed, and rostrum transversely narrow. The arrangement of the cranial bones of the neobalaenids is exactly the same as that of balaenids: in fact, in *Caperea* the supraoccipital shield is superimposed on the parietal on the dorsal surface of the skull excluding the parietal itself from the exposition at the cranial vertex.

The Gray whales belong to the family Eschrichtiidae (Fig. 1a, 2a). Today they are restricted to an area localized around the northern border of the Pacific Ocean, from California to the Japan Sea. Eschrichtiidae is a monotypic family including the only living species *Eschrichtius robustus*, the gray whale. *Eschrichtius* has a slightly arched rostrum, dentary lacking coronoid process, and an arrangement of neurocranial bones that is very similar to that of rorquals and some extinct mysticetes known as cetotheres (*Cetotherium*-like *sensu* Kimura & Ozawa, 2002). In fact, in Gray whales the posteromedial corner of the maxilla interdigitates with the frontal generating an ascending process, which reaches a point approximately, placed at the middle of the neurocranium. Moreover, as in rorquals, the supraorbital process of the frontal is abruptly depressed laterally to the short interorbital region.

When compared to the cetotheres, that are considered as a para- or polyphyletic assemblage of early-diverging baleen-bearing whales closely related to Balaenopteridae (Fordyce & Barnes, 1994; Kimura & Ozawa, 2002), balaenids are different in all the morphological features related to hearing and feeding (i.e., the arrangement of rostral bones, the interface between rostrum and neurocranium, the arrangement of the neck musculature forming the head-suspension system). In general, the basicranial architecture of balaenids is different from all the other fossil and living mysticetes because in balaenids the posterior border of the palatines reaches the posterior

limit of the skull, and the palatines cover almost all of the ventral surface of the pterygoids.

Detailed accounts of the morphological features of the various mysticete families can be found in Miller (1923), Kellogg (1928), Barnes (1984), Barnes & McLeod (1984), Fordyce & Barnes (1994), Fordyce & De Muizon (1999). The most recent general analysis of the Balaenidae has been published by McLeod *et al.* (1993) in a special volume on the Bowhead whale *Balaena mysti-*

cetus. In that work, the osteological traits distinguishing the family are analysed and a phylogenetic framework is provided. McLeod *et al.* (1993) re-evaluated the close phylogenetic relationship between Balaenidae and Neobalaenidae, that was proposed earlier by Gray (1825) and re-established the superfamily Balaenoidea. They provided the following morphological diagnoses (McLeod *et al.*, 1993, p. 63):

○ Superfamily Balaenoidea Gray (1825). Glenoid fossa and zygomatic portion of squamosals placed far ventrally on the skull, pterygoids extend far posteriorly beneath basicranium, baleen plates numerous and thin.

○ Family Balaenidae Gray (1825). Rostrum greatly arched and transversely compressed; supraorbital processes greatly elongated, tympanic bulla flattened dorsoventrally, baleen plates greatly elongated.

In this work I will mention other traits supporting the close relationship of Balaenidae and Neobalaenidae. Moreover, I will analyse in detail part of the fossil record of the family Balaenidae to follow the morphological transformations, the ecological adaptations and the paleobiogeographic connections experienced by the balaenids during the last 23 million years. I will conclude with some words about the present health of the living populations of these whales that are under high extinction risk. The family Balaenidae comprises some of the most endangered species in the world; several hundreds million dollars are devoted to their study and conservation each year (Montague, 1993; Fujiwara & Caswell, 2001); the knowledge of their fossil record and the understanding of the forces that have directed their evolution in the past would provide researches with sharper and powerful theoretical and practical instruments for better conservation strategies than those adopted today.

Scopes and format

The principal goal of this work is to provide an overview of balaenid evolution based on the fossil record; recent molecular discoveries are also discussed and compared to the results obtained by paleontologists. A tentative synthesis of the phylogeny of Balaenidae is proposed to stimulate further discussions on this poorly known family. The fossil record is investi-

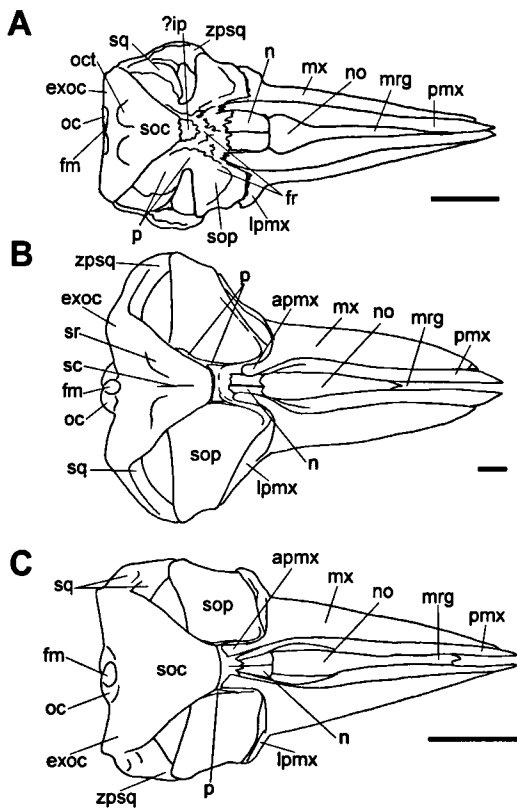


Fig. 2 Dorsal view of selected mysticete skulls. A, *Eschrichtius robustus* (redrawn from True 1904, pl. 47, fig. 1, with modifications). B, *Megaptera novaeangliae* (redrawn from True 1904, pl. 29, fig. 1, with modifications). C, *Balaenoptera acutorostrata* (redrawn from True 1904, pl. 23, fig. 1, with modifications). Anterior ends of the skulls on the right side. Scale bars equal 200 mm. See Anatomical abbreviations for explanation

Bovenaanzicht van enkele baardwalvis Schedels. A, *Eschrichtius robustus* (nagetekend van True 1904, pl. 47, fig. 1, met wijzigingen). B, *Megaptera novaeangliae* (nagetekend van True 1904, pl. 29, fig. 1, met wijzigingen). C, *Balaenoptera acutorostrata* (nagetekend van 1904, pl. 23, fig. 1, met wijzigingen). De voorkant van de schedels is aan de rechterzijde. Maatstrep is 200 mm. Zie anatomische afkortingen voor uitleg

gated also to understand the historical biogeography of Balaenidae and such issues as habitat occupation, reproductive behavior, and community evolution. The present phase of balaenid natural history is one of contraction in diversity and number of individuals; some points on their conservation are discussed in the light of a paleontological approach.

The paper is divided into three parts. In the first part, the living balaenids are presented and compared to the other mysticete families. The second part contains a technical analysis of selected fossil balaenids and a taxonomic revision of some problematic taxa. The third part includes discussions on the paleoecology of Pliocene balaenids and on the phylogeny, paleobiogeography and conservation of this family. The reading of the second part is not a pre-requisite to understand the third part so that also the reader unfamiliar with the skeletal anatomy of mysticetes can reason on the paleoecology, phylogeny, paleobiogeography and conservation of Balaenidae.

Institutional abbreviations

AFS = Museo di Storia Naturale, Sezione Geologica, Accademia dei Fisiocritici, Siena, Italy; IRSN = Institut Royal des Sciences Naturelles du Belgique, Bruxelles, Belgium; LMA = Zoölogisch Museum, Leiden, Holland; MGB = Museo Geopaleontologico "Giovanni Capellini", Bologna, Italy; MSNT = Museo di Storia Naturale e del Territorio, Calci, Italy; NMB = Natuurmuseum Brabant, Tilburg, Holland; USNM = United States National Museum, Smithsonian Institution, Washington D.C., United States of America; ZMA = Zoölogisch Museum, Amsterdam, Holland.

Anatomical abbreviations

alc, anterolateral corner of tympanic bulla; amc, anteromedial corner of tympanic bulla; ap, anterior process of petrosal; apd, angular process of dentary; apmx, ascending process of the maxilla; asph, alisphenoid; atc, ascending temporal crest; bp, broken process; br, broken region; cp, conical process of tympanic bulla; cr, coronoid region of dentary; ct, crista transversa within the internal acoustic meatus; dpb, descending process of basioccipital; dvc, dorsoventral crest-like formation on temporal fossa of *Balaena montalionis*; elf, endolymphatic foramen; eofc, external opening of the facial canal; exoc, exoccipital; fm, foramen magnum; fr, frontal; fs, foramen singulare; fst, fossa for stapedial muscle; gcsq, glenoid cavity of

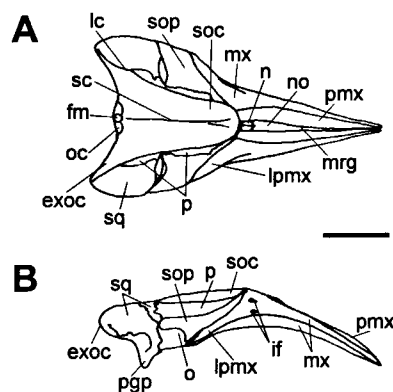


Fig. 3 The skull of *Caperea marginata* (pygmy right whale: superfamily Balaenoidea, family Neobalaenidae; redrawn from Baker (1985) with modifications). A, dorsal view. B, lateral view. Anterior ends of the skull on the right side. Scale bar equals 200 mm. See Anatomical abbreviation for explanation.

De schedel van *Caperea marginata* (dwerfwalvis: superfamilie Balaenoidea, familie Neobalaenidae; nagetekend van Baker (1985) met wijzigingen). A, bovenaanzicht. B, zijaanzicht. De voorkant van de schedel is aan de rechterzijde. Maatstreek is 200 mm. Zie anatomische afkortingen voor uitleg

the squamosal; j, jugal; iam, internal acoustic meatus; if, infraorbital foramina; iofc, internal opening of facial canal; iopmx, infraorbital process of maxilla; ?ip, hypothetical interparietal of *Eschrichtius robustus*; lc, lambdoidal crest; lpap, lateral protrusion of anterior process of petrosal; lpmx, lateral process of maxilla; mc, mandibular condyle; mx, maxilla; mr, mandibular ramus; mf, mandibular foramina; mrg, mesorostral groove; n, nasal; no, narial opening; o, orbit; oc, occipital condyle; oct, occipital tuberosity; ow, oval window; p, parietal; pbsmf, posterior border of stylomastoid fossa; pch, pars cochlearis of petrosal; pgg, postglenoid process of squamosal; plf, perilymphatic foramen; pmx, premaxilla; poc, postorbital corner; pp, compound posterior process of petrosal; ppp, posterior process of tympanic bulla (emergence); prc, preorbital corner; p-sq-s, parietal-squamosal suture; pt, pterygoid; ptf, pterygoid fossa; rw, round window; sc, sagittal crest; sma, suprimeatal area of petrosal; smf, stylomastoid fossa; sms, submeatal sulcus; soc, supraoccipital shield; sop, supraorbital process of frontal; sp, sigmoid process of tympanic bulla; sq, squamosal; sr, supraoccipital roughness; sup, superior process of petrosal; tb, tympanic bulla; tc, tympanic cavity; tma, torsion

on the anteromedial portion of the dentary; tsf, tractus spiralis foraminosus; ttg, tensor tympani groove; vc, ventral concavity of tympanic bulla; vg, vascular groove; zpsq, zygomatic process of squamosal; VII-s, groove for facial nerve.

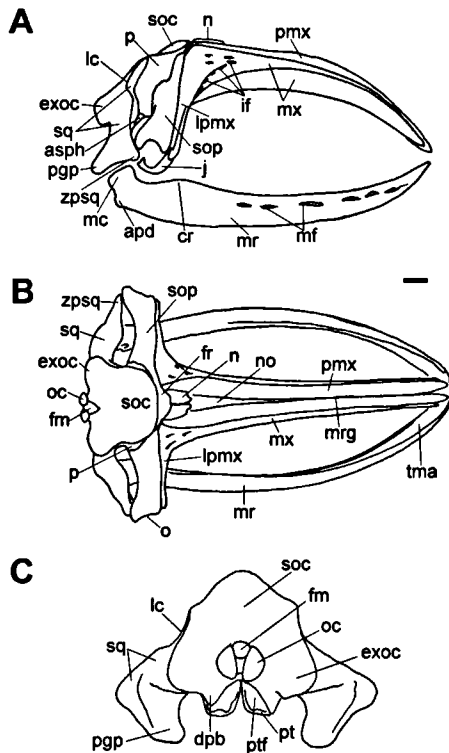


Fig. 4 The skull of *Eubalaena glacialis* (northern or black right whale: superfamily Balaenoidea, family Balaenidae). A, right lateral view (from MSNT 260). B, dorsal view (redrawn from Cuvier 1823, pl. 26, with modifications). C, posterior view (USNM 26712). Anterior ends of the skulls on the right side. Scale bar equals 200 mm. See Anatomical abbreviations for explanation

De schedel van *Eubalaena glacialis* (noordkaper: superfamilie Balaenoidea, familie Balaenidae). A, rechter zijaanzicht (MSNT 260). B, bovenaanzicht (nagetekend van Cuvier 1823, pl. 26, met wijzigingen). C, achteraanzicht (USNM 26712). De voorkant van de schedels is aan de rechterzijde. Maatstreef is 200 mm. Zie anatomische afkortingen voor uitleg

Living balaenids

Living balaenids are represented by two genera characterised by different morphological traits. The Right whales (*Eubalaena glacialis* and *E. australis*) inhabit the North Atlantic, the North Pacific and the waters around Antarctica (Perry et

al., 1999) (Fig. 4). In the Right whales there is a right angle between frontal and maxilla; the anteriormost one-fourth of the premaxilla is directed abruptly downward; the supraorbital process of the frontal is shortened anteroposteriorly and displays a slight ascending temporal crest on its dorsal surface; the supraoccipital shield bears a dome, that is a protruding, nearly globular structure which is placed on the more anterior portion of the bone; the jugal is directed onward so that it is not possible to look at the posterior surface of the temporal fossa from a lateral viewpoint because the fossa is covered by the jugal; the exoccipital is squared in lateral view. Detailed accounts of the morphology of the Right whales are provided, among others, by Cummings (1985), Tomilin (1967), True (1904), Cuvier (1823).

The Bowhead whale *Balaena mysticetus* is endemic of the Arctic Sea (Fig. 5). It is characterised by a continuous arc formed by maxilla and frontal; in fact, in this species the supraorbital process of the frontal is oriented posteriorly so that the small interorbital region is placed more anteriorly than the orbits. In the Bowhead whale the supraorbital process of the frontal is distally flat and does not bear any ascending temporal crest; the supraoccipital shield of *Balaena mysticetus* lacks the dome of the right whales and its anteriormost portion is transversely compressed and narrow; the zygomatic process of the squamosal is directed anterolaterally so that the posterior surface of the temporal fossa can be observed from a lateral viewpoint; the exoccipital is round in lateral view. Detailed accounts of the morphology of the Bowhead whale are provided, among others, by Burns et al. (1993), Reeves & Leatherwood (1985), Tomilin (1967), Cuvier (1823). See also McLeod et al. (1993) for citations of antiquarian literature.

When compared, the living balaenids differ in the arrangements of the rostral-cranial interface, in the robustness and morphology of the exoccipital, and in the shape of the supraoccipital shield. In fact, while in *Eubalaena glacialis* maxilla and frontal form a right angle, in *Balaena mysticetus* they form a continuous arc due to the posterior orientation of the frontal and the posterior placement of the orbit; in the Right whales, the supraoccipital shield is anteriorly wide and round while in the Bowhead whale it is narrow and transversely compressed; in *Eubalaena* the supraoccipital bears an anterior dome while this formation is absent in *Balaena*; in the right whales the jugal bone is directed anteriorly while in the Bowhead whale it is outward directed unco-

ring the posterior surface of the temporal fossa which is formed by the squamosal bone; in *Eubalaena* the supraorbital process of the frontal is shortened anteroposteriorly and bears a slight ascending temporal crest while in *Balaena* it widens distally and does not bear any ascending temporal crest; finally, in the Right whale the exoccipital is squared when observed in lateral view but in the Bowhead whale it is round. Major differences are observed also in the external appearance of these whales; in fact, in the rostrum of *Eubalaena* it is possible to observe callosities which are individual-specific and represent preferential attach sites of cirripeds. These invertebrates do not bear any problem to the life of the Right whales and the pattern of the callosities is considered by biologists as a useful tool in order to get highly precise identifications of single individuals (Gaskin, 1986).

A revision of selected fossil Balaenidae

Introduction

Despite the fact that the diversity of living balaenids is very low, the family has experienced a burst in diversity just a few million years ago. The origin of the modern balaenid species remains obscure but we know that the genera they belong to were present during the Early Pliocene. Van Beneden (1872, 1878, 1880) and Capellini (1873, 1876, 1902, 1904) identified several fossil members of the genus *Balaena*. In particular, Van Beneden (1878, 1880) established the species *Balaena primigenius*, and Capellini (1872, 1904) founded *Balaena etrusca* and *Balaena montalionis*. Del Prato (1900) added *Balaena paronai* to the Pliocene record of this genus. Discoveries from the 20th century were reported by several workers in the northern hemisphere. Abel (1941) and Plisnier-Ladame & Quinet (1969) described *Balaena belgica*, a large balaenid from the Pliocene of Belgium; Whitmore (1994) mentioned a large balaenid from the Pliocene of the eastern United States and stated that it is very close to the living *Balaena mysticetus*; the specimen, however, was not described in detail; Bisconti (2002) described the fragmentary skull of an *Eubalaena* from the early Late Pliocene of Central Italy. These accounts document the presence of balaenids belonging to the living genera as early as Early Pliocene. Unfortunately, the Late Pliocene and Pleistocene history of these forms is not well known. McLeod *et al.* (1993, see also the literature therein) discussed some Pleistocene and Holo-

cene findings in the Arctic, and Nishiwaki & Hasegawa (1967) described a fairly preserved skull of a Pleistocene Right whale of the genus *Eubalaena* from Japan.

The fossil record documents that also other genera belonged to the family Balaenidae. An extensive effort performed during the late 19th and the whole 20th century led to the collection of several fossils representing diverse balaenid taxa. Van Beneden (1872, 1878) described two small-sized balaenids from the Pliocene of Belgium, namely *Balaenula balaenopsis* and *Balaenotus insignis*. Trevisan (1941) described another small balaenid, that he called *Balaenula astensis*, from the Middle Pliocene of northern Italy. Cusani

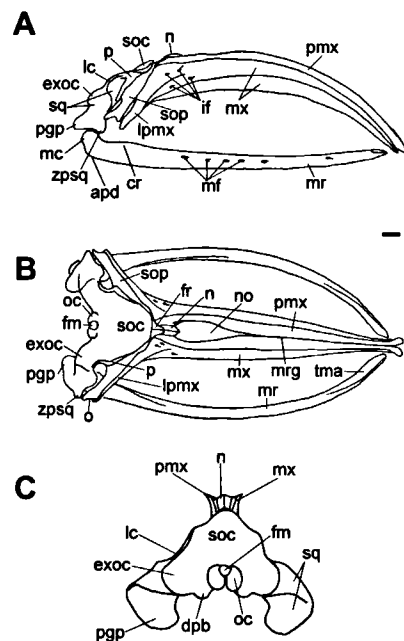


Fig. 5 The skull of *Balaena mysticetus* (Greenland bowhead whale: superfamily Balaenoidea, family Balaenidae). A, right lateral view (redrawn from Cuvier 1823, pl. 26, with modifications). B, dorsal view (re-drawn from Cuvier 1823, pl. 26, with modifications). C, posterior view (USNM 257513). Anterior ends of the skulls on the right side. Scale bar equals 200 mm. See Anatomical abbreviations for explanation

De schedel van *Balaena mysticetus* (Groenlandse walvis: superfamilie Balaenoidea, familie Balaenidae). A, rechter zijaanzicht (nagetekend van Cuvier 1823, pl. 26, met wijzigingen). B, bovenaanzicht (nagetekend van Cuvier 1823, pl. 26, met wijzigingen). C, achteraanzicht (USNM 257513). De voorkant van de schedels is aan de rechterzijde. Maatstreef is 200 mm. Zie anatomische afkortingen voor uitleg

Politi (1961) described *Balaenula praediolensis* from the Early Pliocene of Tuscany. Finally, the Excavation Research Group for the Fukagawa Whale Fossil (1982) reported that another small-sized balaenid belonging to the genus *Balaenula* lived around Japan during the Pliocene. Other balaenid species were established by earlier workers; these were re-evaluated by McLeod *et al.* (1993) that concluded that these forms were too poorly represented by fossil remains and stated that the main part of them were *nomina nuda* or *nomina dubia*. I follow this conclusion and in this work, I re-evaluate other forms whose holotypes I have re-examined in Italian and Belgian collections. In particular, I focus on *Balaena primigenius*, *Balaena etrusca*, *Balaena montalionis*, *Balaena paronai*, *Balaenotus insignis*, and the genera *Eubalaena* and *Balaenula*.

Overview of fossil balaenids

The most ancient balaenid to be formally described is *Morenocetus parvus* from the Early Miocene of Argentina (Cabrera, 1926). This is a small-sized taxon (Fig. 6) characterised by a round and wide anterior process of the supraoccipital shield and supraorbital process of the frontal directed posteriorly and transversely; the supraorbital process of the frontal is mainly flat and does not bear any ascending temporal crest. This taxon is particularly similar to the neobalaenid *Caperea marginata* in the round anterior border of the supraoccipital shield, and in the morphology and the orientation of the supraorbital process of the frontal. Unfortunately, the only description of this intriguing taxon was published early in the 20th century and several data about its basicranium and postcranial are virtually lacking. It is to be hoped that soon a new description of this taxon will appear.

No other Miocene balaenids have been described until now. Barnes (1976) mentioned a *Balaenula* skull from the latest Miocene-to-earliest Pliocene of California but that specimen has not yet been described; Fordyce (1989) stated that some undescribed balaenids were found in Late Miocene-to-Early Pliocene sediments of New Zealand. A fragmentary Tortonian balaenid was discovered in southern Italy that is currently under study; the specimen is represented by a petrosal together with several cranial and postcranial elements. The other fossil balaenids that were formally described and published are from the Pliocene. Fordyce (2002) discussed a primitive and fragmentary Oligocene balaenid from New Zealand and we are waiting for its formal

description and denomination. Contrarily to the rare Miocene record, Pliocene balaenids are abundant and widespread. Several fossil taxa were founded in the last two centuries and in the next section, I will describe some of them in considerable detail.

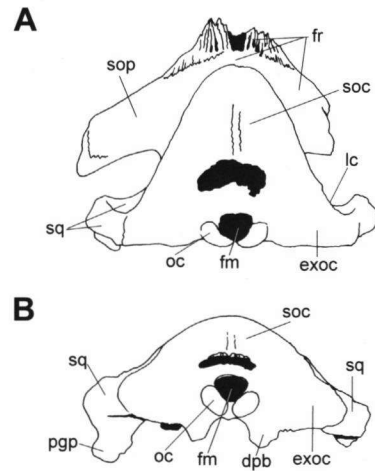


Fig. 6 The skull of the oldest described balaenid: *Morenocetus parvus* (superfamily Balaenoidea, family Balaenidae), Early Miocene (about 23 million year ago), Argentina. A, dorsal view. B, posterior view (images redrawn from Cabrera (1926) with modifications). Scale bar equals 200 mm. See Anatomical abbreviations for explanation

De schedel van de oudst beschreven baleinwalvis: *Morenocetus parvus* (superfamilie Balaenoidea, familie Balaenidae), Vroeg Mioceen (ongeveer 23 miljoen jaar geleden), Argentinië. A, bovenaanzicht. B, achteraanzicht (afbeeldingen nagetekend van Cabrera 1926 met wijzigingen). Maatstreek is 200 mm. Zie anatomische afkortingen voor uitleg

Revision of selected fossil balaenids from Pliocene

Class Mammalia Linnaeus, 1758
 Order Cetacea Brisson, 1762
 Suborder Mysticeti Flower, 1864
 Superfamily Balaenoidea Gray, 1825
 Family Balaenidae Gray, 1825
 Genus *Balaena* Linnaeus, 1758

Type species *Balaena mysticetus* Linnaeus, 1758

Osteological diagnosis of the genus: Anterior process of the supraoccipital shield squared and transversely compressed, rostrum and neurocranium form a continuous arc dorsally, a continuous arc is formed also by the ventrolateral borders of the maxillae and the supraorbital

processes of the frontal, nasals and proximal portions of the rostrum project dorsally and anteriorly, ascending temporal crest absent from the supraorbital process of the frontal distally, anterior process of the parietal not overlapping extensively on the emergence of the supraorbital process of the frontal, squamosal oriented posteriorly, zygomatic process of the squamosal divergent from the longitudinal axis of the skull so that the posterior wall of the temporal fossa can be observed in lateral view, posterior outline of the exoccipital round, pars cochlearis and superior process of the petrosal not protruding cranially, suprameatal area of petrosal very high, dorsal outline of the superior process of petrosal strongly round, scapula lacking both acromial and coracoid processes, very convex and antero-posteriorly expanded radius, olecranon absent or markedly reduced.

Balaena primigenius Van Beneden, 1872

General discussion: I examined only the following type materials of *Balaena primigenius*: CtM 884, CtM 885, CtM 886 (three right tympanic bullae), and CtM 887 (left periotic). The species is poorly known because its remains are very fragmentary. Van Beneden (1878, pls. 18-22) figured some vertebrae, a left partial dentary, humerus, radius, ulna, and some ribs. The humerus has straight anterior and posterior edges and a small articular head; the radius has convex anterior and posterior borders; the ulna bears the olecranon and has a long distal articular facet. The vertebrae are undiagnostic. Measurements of the observed materials are reported in Table 1. The name *Balaena primigenius* was firstly published by Van Beneden (1872) but, subsequently, that name was changed in *Balaena primigenia* (Van Beneden, 1880, 1878; see also Capellini, 1904). However, due to priority reasons, the original name should be maintained, so I call this taxon with its first taxonomic denomination: *Balaena primigenius* Van Beneden (1872), and *Balaena primigenia* should be considered as a junior synonym of the first name.

The left periotic is strong and heavily pachyosteo-sclerotic (Fig. 7c-d). The compound posterior process is not preserved. The anterior process is high and has a round anterior border. The suprameatal area is flat and the superior process is slightly protruding. The internal acoustic meatus is circular and deep, and includes tractus spiralis foraminosus and foramen singulare. The cranial opening for the VII cranial nerve is located anterodorsally to the internal acoustic meatus, it is

tubular, circular and deep. The endolymphatic foramen opens on the floor of a little, elliptical cavity located posterodorsally to the internal acoustic meatus; the perilymphatic foramen is confluent into the round window, a deep groove is observed under the petrosal foramina. The tympanic bulla has a strongly concave ventral surface and an anterolateral corner highly constricted posteriorly. The tympanic cavity is shallow. The anterior border of the bulla is linear-shaped and transversal to the long axis of

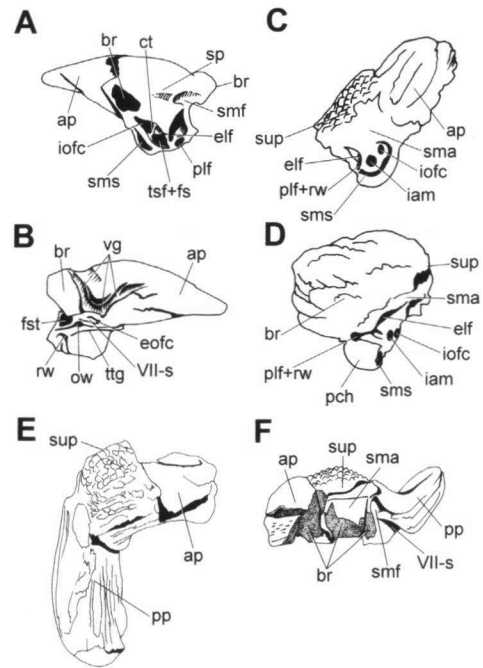


Fig. 7 Schematic representations of petrosals of three fossil balaenids (superfamily Balaenoidea, family Balaenidae). A, *Balaenula balaenopsis* (CtM 858a), right petrosal in cranial view. B, *Balaenula balaenopsis* (CtM 858a), right petrosal in lateral view. C, *Balaena primigenius* (CtM 887), left petrosal in cranial view. D, *Balaena primigenius* (CtM 887), left petrosal in posterior view. E, *Balaenula astensis* (MC CF35), left petrosal in dorsal view. F, *Balaenula astensis* (MC CF35), left petrosal in cranial view. Not to scale. See Anatomical abbreviations for explanation

Schematische weergave van het rotsbeen van drie fossiele baleinwalvissen (superfamilie Balaenoidea, familie Balaenidae). A, *Balaenula balaenopsis* (CtM 858a), rechter rotsbeen, vooraanzicht. B, *Balaenula balaenopsis* (CtM 858a), rechter rotsbeen in zijaanzicht, buitenzijde. C, *Balaena primigenius* (CtM 887), linker rotsbeen, vooraanzicht. D, *Balaena primigenius* (CtM 887), linker rotsbeen, achteraan-zicht. E, *Balaenula astensis* (MC CF35), linker rotsbeen, bovenaanzicht. F, *Balaenula astensis* (MC CF35), linker rotsbeen, vooraanzicht. Niet op schaal. Zie anatomische afkortingen voor uitleg

the bone. The dentary is largely incomplete; it lacks the posterior and the dorsal border that is preserved only along the anteriormost portion of the bone. It bears a long mylohyoidal sulcus on the ventromedial surface and has a poorly developed anterior torsion.

From my analysis and from the images that were published by Van Beneden (1878), there are no characters to link *Balaena primigenius* to the genus *Balaena*. This form clearly belongs to Balaenidae due to the presence of the mylohyoidal sulcus along the ventromedial surface of the dentary, the overall morphology of the tympanic bulla, and the stocky morphology of radius and ulna. However, the phylogenetic relationships of this form are unclear. The periotic documents that *Balaena primigenius* is a different species from the

Table 1 Measurements of the periotic (CtM 887) and tympanic bullae (CtM 884, 885, 886) of "*Balaena*" *primigenius*. Data in mm. ^a: As in Anatomical abbreviations, iam = internal acoustic meatus. ^b: mean thickness resulting from eight measurements at random points on the tympanic wall; methods according to Nummela *et al.* (1999).

Maten van het gehoorgedeelte van de schedel (CtM 887) en de gehoorblaasjes (CtM 884, 885, 886) van "*Balaena*" *primigenius* in mm. ^a: als in anatomische afkortingen, iam = binnenste gehooropening. ^b: gemiddelde dikte samengesteld uit acht maten genomen op willekeurige punten op het gehoorblaasje; methodes volgens Nummela *et al.*, 1999.

	CtM 887	CtM 884	CtM 885	CtM 886
Length of anterior process	65			
Lateromedial diameter of anterior process	79			
Transverse diameter of iam ^a	7,5			
Dorsoventral diameter of iam ^a	8			
Lateromedial diameter of pars cochlearis	26			
Anteroposterior diameter of pars cochlearis	37			
Dorsoventral diameter of oval window	3			
Anteroposterior diameter of oval window	4			
Length of tympanic bulla		130	119	116
Maximum width of tympanic bulla		103	82	82
Minimum width of tympanic bulla (behind anterolateral corner)		67	65	65
Minimum height of tympanic bulla		94	84	82
Maximum height of tympanic bulla		67	65	67
Length of tympanic cavity		87	80	71
Width of tympanic cavity		35	36	28
Height of tympanic cavity		40	45	32
Mean thickness of tympanic wall ^b		6,58	5,69	5,62

other named balaenid species but the diagnostic traits of the known balaenid genera are lacking. The overall size of the vertebrae, humerus, radius and ulna suggest that this form was large-sized and the degree of pachyosteosclerosis observed on the periotic is close to that observed in the living, large-sized balaenids. I conclude that "*Balaena*" *primigenius* is a Balaenidae gen. ind.

Balaena paronai Del Prato, 1900

General discussion: Del Prato (1900) described *Balaena paronai* based on a right dentary and two ribs. The dentary has the typical balaenid features: long mylohyoidal sulcus on the ventromedial surface, coronoid crest reduced to an elongated and low crest, anterior torsion. However, in this dentary, the articular surface of the mandibular condyle is not sharply dorsally exposed; it is, in effect, a little more posterior than usual. I did not re-examine the holotype material but based on the published drawings, I suspect that what is known of this balaenid is too poor to allow for the establishment of a new species. Moreover, there is not enough information to understand which is the genus the specimen belongs to. For this reason I suggest that "*Balaena paronai*" is a Balaenidae gen. et sp. ind.

Balaena etrusca Capellini 1872

Material: the type material is held by MGB and consists of one series of seven cervical vertebrae fused with each other and with the first thoracic vertebra (MGB 9066). Other materials assigned to *Balaena etrusca* consist in the following specimens: the proximal fragment of a right dentary (AFS 4422), eight vertebral elements (AFS 4402, 4403, 4404, 4405, 4418, 4420, 4421), and one indetermined element (AFS 4406); a lumbar vertebra assigned to *Balaena etrusca* is also held by AFS (4419); a proximal fragment of left dentary (MGB 9070), both partial tympanic bullae (9069), a right jugal (9067), the cast of the right humerus (9061), a distal fragment of ulna (9062), four free vertebrae (9063, 9064, 9065, 9068), and another series of fused cervical vertebrae (9066). The measurements and the localities where the specimens were found are reported respectively in Tables 2, 3, 4, and 5. *Balaena etrusca* was presented in the Rendiconto delle Sessioni dell'Accademia delle Scienze dell'Istituto di Bologna (1871), and subsequently discussed by Capellini (1872, 1873, 1876, 1902), Van Beneden (1872), Gervais (1872), and McLeod *et al.* (1993).

Description of the type material: the neck MGB 9066 (Plate 1) comprises seven cervicals plus the

first thoracic vertebra fused to each other. The atlas has articular fossae that are wide and concave; the shape of the fossae resembles the surfaces of the occipital condyles of the *Eubalaena* sp. described by Bisconti (2002) in that both condyles and fossae have very convex outer borders and slightly convex inner borders. The articular fossae are divided along the midline of the atlas. The neural arc is incomplete; its remains are wide and high; it is dorsally covered by a bony plate bearing two slight parasagittal crests formed by the dorsolateral border of the atlas; this bony plate is posteriorly bordered by the neural arc of the axis that develops posteriorly. Dorsally and laterally, the neural arc of the atlas and that of the axis are divided by a round lateral fissure. The atlas bears the alar foramen that perforates the vertebra transversely dorsal to the emergence of the transverse process. The transverse process is squared, anteroposteriorly flat, and projects laterally. The dorsal surface of the cervical vertebrae that is under the neural arc is flat. In mammals the foramen transversarium of the cervical vertebrae is located between the basis of the pedicle of the neural arc (pediculus arcus vertebrae; Schaller, 1999) and the emergence of the transverse process; in balaenids the foramen transversarium is destructed because the pedicle of the neural arc does not generate a transverse expansion dorsal to the emergence of the transverse process. The pedicles of the neural arc of the third and fourth vertebrae are fused with each other and form a strong, long and wide structure that is dorsally broken; the pedicle of the seventh vertebra is stronger than those of the fifth and the sixth ones; its emergence is located on the dorso-lateral border of the centrum of the seventh vertebra; the pedicles of the fourth, fifth and sixth vertebrae are located on the anterodorsal portion of the lateral border of the centra; the emergence of the pedicle of the fourth vertebra is very close to that of the third one. The transverse processes are absent from all the vertebrae. Interarcual foramina were present between the fourth and the fifth pedicles, between the fifth and the sixth vertebrae, and the sixth and the seventh vertebrae. In lateral view, dorsoventral grooves divide the centra of the vertebrae only superficially.

Description of the AFS materials: the materials are figured in Plates 2-4. Only the posteriormost segment of the right dentary is preserved. It is strongly built and it bears a group of cirripeds on its dorsolateral surface, near the condyle. The articular surface of the condyle is dorsal; the posteroventral outline of the angular process is

Table 2. Linear measurements of the dentaries of "*Balaena etrusca*" in mm.

Lineaire maten van de onderkaken van "*Balaena etrusca*", in mm.

	specimens	
	AFS 4422	MGB 9070
Maximum length	790	1750
Anterior height	190	210
Height at condyle	260	430
Height anterior to condyle	210	-
Height at coronoidal region	220	-
Dorsoventral diameter of mandibular foramen	100	128
Lateromedial diameter of mandibular foramen	60	-

rounded; the medial surface of the angular process is strongly concave and is dorsally bounded by a longitudinal crest that is located immediately ventral to the mandibular foramen. The medial surface of the dentary is flat; the dorsal border of the bone is largely eroded so that the coronoid region cannot be described. The mandibular foramen has an elliptic outline and it is bounded dorsally and ventrally by strong protrusions of the medial surface.

The vertebrae do not constitute a series; there are three lumbar and three caudals. The lumbar vertebrae are inventoried as follows: AFS 4403, 4405, 4418, and 4421. The vertebra AFS 4403 is incomplete lacking the anteroventral border and the neurapophysis; its transverse processes are distally eroded and they lack the dorsoventral perforation at their basis; a large *Ostrea* shell is attached on the right ventrolateral surface. The vertebra AFS 4405 is constituted by a portion of the left dorsolateral surface that includes the right anterior zygapophysis and the neural canal; the vertebra is massively built; the right zygapophysis is strong and rectangular; the neural canal is elliptical; a horizontal hole is located on the right posterolateral side of the neural canal; on the left side of the canal, there is a slight concavity in the same position. The vertebra AFS 4418 is the most complete one; the centrum is long and ventrally keeled; the transverse processes emerge from the middle of the lateral surface of the centrum; their distal ends are broken; both the dorsolateral and ventrolateral surfaces of the centrum are strongly concave; the neurapophysis is broken immediately above the anterior zygapophyses; the neural canal is triangular. Only the

ventral half of the vertebra AFS 4421 is preserved; the transverse process exits the centrum from the middle of the lateral surface; there is not a ventral keel but the laterodorsal and lateroventral portions of the sides of the centrum are strongly concave; this morphology suggests that the vertebra was one of the more anterior of the lumbar series.

Another lumbar vertebra assigned to *Balaena etrusca* is held by the Accademia dei Fisiocritici and is inventoried as AFS 4419; it is an anterior lumbar vertebra characterized by the lack of the ventral keel and by concave dorsolateral and ventrolateral surfaces; the transverse processes are broken; the dorsoventral holes on the emergence of the transverse processes are absent; the neurapophysis is absent and the intervertebral discs are fused with the centrum; on the ventral surface there are two longitudinal relieves that border a medial cavity; the longitudinal relieves are the attach sites for the articulation of the chevrons.

Table 3 Vertebral measurements of "*Balaena etrusca*" in mm.

Maten van wervels van "*Balaena etrusca*" in mm.

specimens	centre length	width	height	neural channel height	width
MGB 9063	160	290	290	-	-
MGB 9064	190	280	290	-	-
MGB 9065	200	280	270	-	-
MGB 9068	215	250	230	30	45
AFS 4402	200	170	258 (a)	-	-
AFS 4403	182	200 (a)	220 (a)	-	-
AFS 4404	86	140	145	-	-
AFS 4405	144	172 (a)	190 (a)	19	31
AFS 4408	-	200	180	-	-
AFS 4418	161	165	142	67	50
AFS 4419	260	245	224	-	-
AFS 4420	200	110	160	-	-
AFS 4421	255	240	-	-	-

The caudal vertebrae are inventoried as follows: AFS 4402, 4404, and 4408. The vertebra AFS 4402 is a long caudal vertebra lacking a right dorsolateral portion; it bears attach sites for chevrons characterized by anterior tubercles, transverse perforations and medial cavity; the transverse process is located at the middle of the lateral surface of the centrum and is dorsoventrally bilaterally perforated at the emergence; the transverse process is crest-like; the dorsal surface lacks the neurapophysis and is concave. The vertebra AFS 4404 is largely eroded; the lateral surfaces are missing, the dorsal and ventral surfaces are damaged and eroded; the neurapophysis was probably absent; the posterior surface is flat; the

anterior articular surface is convex; the transverse process is perforated at the emergence bilaterally; ventrally the relieves for the chevrons border a medial cavity; the relieves are transversely perforated. The vertebra AFS 4408 has the anterior articular surface of the centrum flat with a central notch corresponding to the nucleus polposus; the lateral, dorsal, ventral and posterior surfaces are largely missing; a laterodorsal cavity is observed; ventral processes for the attach of the chevrons are present. An unidentified vertebra is marked by the impression of a pine strobyl (AFS 4420).

Descriptions of the MGB materials: the materials are figured in Plates 5-7. The dentary MGB 9070 is represented by the posterior third of a bone that was possibly about 5 m in length. The specimen is very strongly built. The mandibular condyle has an articular surface exposed dorsally; the angular process is rounded and it bears a slight ventral protrusion; the mandibular foramen is wide and is located near the dorsal border of the dentary, slightly anterior to the condyle. The medial surface of the bone is highly concave anterior to the mandibular foramen while the lateral surface is strongly convex. More anteriorly, the medial surface of the bone is flat. The coronoid region lacks a true coronoid process; the site for the attachment of the muscle temporalis is a long and low crest developed along the dorsal border of the bone. The ventral border of the dentary is crest-like. A gingival groove begins anteriorly to the convex coronoid crest and bears a gingival foramen. A mylohyoidal sulcus is present along the ventromedial surface.

The jugal MGB 9067 is small; in medial view, it is anteromedially concave and posteriorly flat. It is dorsally concave, and ventrally straight.

The right tympanic bulla is divided into two halves (one corresponding to the ventrolateral wall and the other to the medial wall) that are inventoried as MGB 9069. The two halves cannot be articulated with each other. The cast of the lateral side shows a highly protruded anterolateral corner that is strongly constricted posteriorly, slight anterior to the emergence of the sigmoid process. The conical process is very low and nearly flat. The strong lateral protrusion of the anterolateral corner of the bulla is very marked and it should be regarded as a putative diagnostic trait of a new species.

The right humerus MGB 9061 is represented by a gypsum cast, the original being in Florence (not examined here). The head of the humerus is

globular; it protrudes posteriorly and dorsally. Below the head of the humerus there is a strong and squared deltopectoral prominence that is located on the medial side of the anteroproximal end of the diaphysis. It is evident that both the proximal and the distal epiphyses are not completely fused to the humeral shaft; this suggests that the humerus belonged to an animal that was not completely mature. The diaphysis of the humerus is transversely compressed; its anterior and posterior borders are straight. The distal epiphysis bears a flat articular facet for the radius, and a posterior facet for the ulna; these facets are divided by the interposition of a lateromedial crest; the facet for the ulna continues onto the posterior side of the diaphysis by producing an additional facet for the olecranon process of the ulna.

The distal fragment of the ulna MGB 9062 has a slightly convex lateral surface and a flat medial surface; the bone is transversely compressed; the distal epiphysis is convex and has a rounded outline.

The vertebral remains comprise a complex formed by the neck region and five vertebral elements. The vertebra MGB 9065 belongs to the thoracic region; it is divided into two halves and has transverse processes emerging from the dorsal half of the centrum; the lateral surface of the centrum is flat. The caudal vertebra MGB 9064 bears attachment areas for the chevrons that, at the anteroventral border, look like tubercles, while they are reduced to slight relieves near the posteroventral border; these sites border a deep ventral concavity; the lateral surfaces of the centrum are concave. The caudal vertebra MGB 9068 has concave lateral sides, broken transverse processes emerging from the middle of its height, medial cavity bordered by attach sites for chevrons, and small neurapophysis. The last caudal vertebra is inventoried as MGB 9063; it belongs to the posterior portion of the caudal series; it is circular in outline, lacks transverse processes, and convex articular facets.

From the above descriptions it is immediately evident that the fossil record of *Balaena etrusca* is constituted by a few fragments discovered in different localities (Table 5) and belonging to several individuals. It is yet unclear if all these specimens are of the same age. The main part of the specimens cannot be identified as Balaenidae (e.g., the fragmentary thoracic, lumbar and caudal vertebrae); the two mandibular rami (AFS 4422 and MGB 9070) exhibit different characteris-

Table 4 Measurements of tympanic bullae (MGB 9069) and humerus (MGB 9061) of "*Balaena etrusca*", and cervical vertebrae (MGB 9066) of "*Balaena etrusca*" in mm. ^a: values to the left refer to the left object, those on the right to the right object.

Maten van de gehoorblaasjes (MGB 9069) en opperarm (MGB 9061) van "*Balaena etrusca*", en nekwerfels (MGB 9066) van "*Balaena etrusca*" in mm. ^a: waarden aan de linkerkant betreffen het linker object, die aan de rechterkant het rechter object.

	MGB 9069	MGB 9061	MGB 9066
Length of tympanic bulla	110 - 106 ^a		
Maximum width of tympanic bulla	42 - 75 ^a		
Maximum height of tympanic bulla	67 - 60 ^a		
Height of humerus (from the articular head to the crest dividing ulnar and radial facets)		500	
Maximum anteroposterior diameter of proximal epiphysis		330	
Maximum anteroposterior diameter of distal epiphysis		267	
Anteroposterior diameter of radial facet		190	
Anteroposterior diameter of ulnar facet		110	
Height of deltopectoral tuberosity		105	
Length of cervical block (hereinafter = cb)			300
Posterior transverse diameter of cb			310
Anterior transverse diameter of cb			690
Transverse distance between the outer edges of articular surfaces of atlas			340
Height of articular surfaces of atlas			230 - 221 ^a
Maximum width of articular surfaces of atlas			160 - 140 ^a
Height of neural channel			160
Width of neural channel			170

tics in the morphology of the angular process that is laterally concave in AFS 442 while it is not in MGB 9070 and could belong to different species. It seems that there is no reason to believe that all the specimens listed by Capellini (1873, 1876, 1902) under the taxonomic denomination *Balaena etrusca* belong to the same species.

Moreover, Capellini (1872, 1873, 1876, 1902) listed only one morphological character to distinguish *Balaena etrusca* from other balaenids: the co-ossification of the first thoracic vertebra together with the seventh cervical; this phenomenon makes the

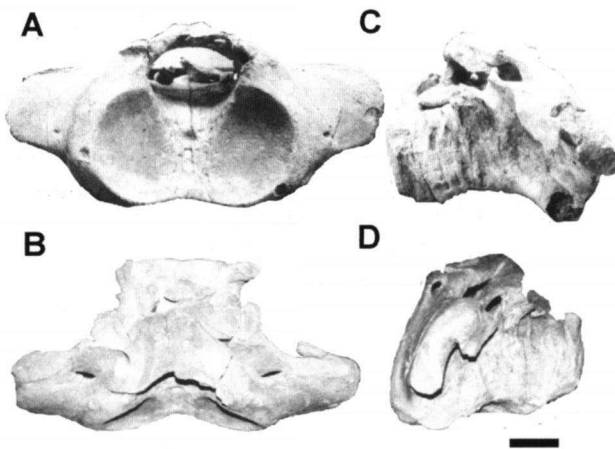


Plate 1 *Balaena etrusca*, MGB holotype (MGB 9066). Cervical vertebrae. A, anterior view. B, dorsal view. C, right lateral view. D, left lateral view. Scale bar equals 100 mm.

Balaena etrusca, MGB holotype (MGB 9066). Nekwervels. A, vooraanzicht. B, bovenaanzicht. C, rechter zijaanzicht. D, linker zijaanzicht. Maatstreef is 100 mm

neck complex incorporate seven cervical and one thoracic vertebrae. This character is somewhat ambiguous; in fact, the co-ossification of vertebral centra occurs frequently in old-aged individuals belonging to living whales and several accounts of co-ossification are reported in the literature (e.g., Kompanje, 1999). However, in the case of the neck MGB 9066 it seems that the vertebrae were not pathologically changed. For this reason I conclude that the neck MGB 9066 belongs to a balaenid species that is different from those living today and from *Balaenula balaenopsis* and *Balaena belgica*. However, I am unable to discriminate between this species and *Balaena montalionis* because the neck of the latter is yet unknown. So, I conclude that the neck MGB 9066 is too scanty to diagnose a new balaenid species and I do not name it.

After this discussion it is evident that there is not any reason to believe that the material previously assigned to "*Balaena*" *etrusca* actually belong to a single species. Moreover, there are no diagnostic traits to distinguish this putative species from other ones with the exception of the neck MGB 9066. This situation makes "*Balaena*" *etrusca* a *Balaenidae* gen. et sp. ind.

Balaena montalionis Capellini, 1904

Material. The holotype and only specimen referred to this species consists in a partial neurocranium with the proximal portion of the left maxilla; The specimen is held by MSNT; Bianucci (1996) reported that it is inventoried as MC CF31 but the specimen is marked as 12357.

Diagnosis. Middle-sized balaenid species whose inferred body length ranges from 11 and 14 m; it is distinguished from *Balaena mysticetus* by shorter nasals (ratio length - width of both nasals), and by the presence of a relief developed dorsoventrally and anteroposteriorly from the lambdoidal suture along the parietal squama.

Description. The specimen has been recently redescribed by Pilleri (1987) and Bisconti (2000) and is only briefly outlined below (Fig. 8); the measurements are reported by Bisconti (2000). The skull lacks the rostrum with the exception of the proximal portion of the left maxilla; a large part of the basicranium is missing together with the more distal portions of the glenoid fossa of the squamosal and the earbones. The supraoccipital, parietals, frontals, exoccipital, and squamosals are preserved together with some portions of the vomer and the pterygoids.

The supraoccipital shield is approximately triangular with a squared anterior border; the lateral edges of the anterior supraoccipital process are transversely constricted so that they appear concave; the remaining posteriormost borders of the supraoccipital are convex. The lateral borders of the supraoccipital shield together with the dorsal borders of the parietals overhang the temporal fossa in dorsal view by forming laterally protruded lambdoidal crests. The supraoccipital is long and wide; its maximum transversal diameter is reached slightly anterior to the foramen magnum. The dorsal surface of the supraoccipital bears a longitudinal relief, which is bordered by pronounced depressions. The exoccipitals are squared in dorsal and posterior view; they are round in lateral view. Compared to the total width of the supraoccipital shield, the foramen magnum is small. The occipital condyles are not really protruding and their articular surfaces are flat.

The supraoccipital shield is superimposed onto the parietals and reaches the posterior surface of the interorbital region of the frontal; for this reason the parietals are excluded from being exposed in the intertemporal region, at the vertex of the skull, anterior to the anterior supraoccipital

process. The parietals are anteriorly elongated and interdigitated with the supraorbital process of the frontal but not with the posteromedial elements of the rostrum. The parietal squama, which forms the medial side of the temporal fossa, is concave and bears a relief that is developed from a point located anterodorsally to a point located posteroventrally; this relief probably marks the suture of parietal and squamosal and reaches the lateral border of the supraoccipital at a point where a small protrusion is developed. The parietals are slightly superimposed onto the emergence of the supraorbital processes of the frontal; they did not spread onto the emergence of these processes as in members of the genera *Eubalaena* and *Balaenula*.

The squamosal is a massive and stocky bone. The posterior wall of the temporal fossa (that pertains to the squamosal) is strongly concave and is laterally defined by an anteriorly protruded, acute lateral squamosal crest. The lateral surface of this crest is flat. The squamosal is oriented posteriorly. The remains of the zygomatic process of the squamosal are projected laterally and transversely relative to the longitudinal axis of the skull so that the posteroventral surface of the posterior wall of the temporal fossa can be observed in lateral view, a typical character of *Balaena*.

The supraorbital process of the frontal projects laterally and posteriorly; it can be inferred that the rostrum formed a continuous arc under the supraorbital process of the frontal. The ascending temporal crest is absent and the supraorbital process is flat. Unfortunately, the more distal portions of the process are missing so that it is impossible to describe the orbit of the specimen. The interorbital region of the frontal is exposed in dorsal view for a small length; in fact, the anterior process of the supraoccipital shield reaches a point very close to the posteromedial elements of the rostrum and the nasals.

The nasal bones are elongated, rectangular and bear a notch on their anterior surface. The longitudinal length of the medial wall of the nasals is smaller than the lateral diameter of both bones taken together (*sensu* Tomilin, 1967) and this is a character distinguishing *Balaena montalionis* from *Balaena mysticetus*. The left nasal is flanked by the proximal portion of the left maxilla that projects anteriorly and dorsally paralleling the nasal bones.

The pterygoids form a deep and dorsoventral pterygoid fossa; the foramen pseudo-ovale is

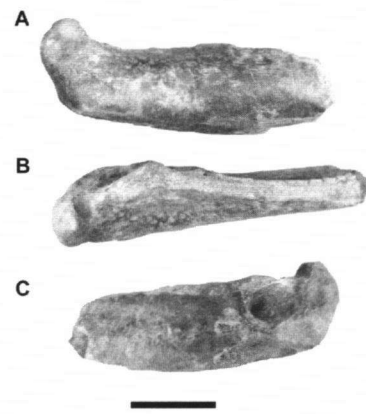


Plate 2 "*Balaena etrusca*", AFS, incomplete right dentary. A, lateral view (anterior end on the right side). B, dorsal view. C, medial view (anterior end on the left side). Scale bar equals 200 mm.

"*Balaena etrusca*", AFS, incomplete rechter onderkaak. A, zijaanzicht, buitenkant (de voorkant is aan de rechterzijde). B, bovenaanzicht. C, zijaanzicht, binnenkant (de voorkant is aan de linkerzijde). Maatstreek is 200 mm.

missing. Other observations on the fragmentary basicranial bones are reported in Bisconti (2000).

Discussion. The holotype of *Balaena montalionis* was originally described by Capellini (1904) and subsequently re-studied by Pilleri (1987), McLeod *et al.* (1993), and Bisconti (2000). Capellini (1904) suggested that this neurocranium represented a new species of the genus *Balaena* but Pilleri (1987) rejected that opinion and stated that the specimen belonged to the same species as *Balaenula astensis*. Pilleri (1987) coined the new combination *Balaenula montalionis* to incorporate both forms. McLeod *et al.* (1993) did not discuss the analysis of Pilleri (1987) and considered the identification of Capellini (1904) to be right. Bisconti (2000) re-analysed the holotype skull and concluded that the name *Balaena montalionis* should be maintained and provided two characters to distinguish that species: first, the dorsoventral and anteroposterior relief located on the parietal squama, and, second, the length/width ratio of the nasal bones. In *Balaena mysticetus* and *Eubalaena glacialis* the suture of the parietal and the squamosal is marked by a tubercle protruding from the dorsal edge of these bones; in *Balaena montalionis* a relief is developed from that tubercle which continues posteriorly and ventrally. In *Balaena mysticetus* the length/width ratio of the nasal bones is higher than one while in *Balaena montalionis* the same ratio is less than 1. *Balaena montalionis* belongs to

the genus *Balaena* because it has squared and transversely compressed anterior process of the supraoccipital shield, and the proximal rostrum and the nasal bones projecting upward and onward. This systematic assignment is confirmed also by a cladistic analysis (Bisconti, 2000).

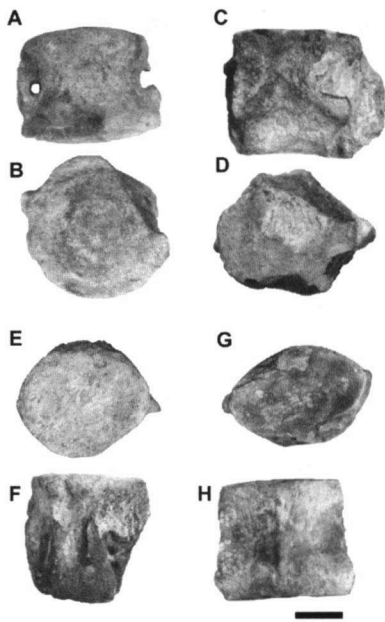


Plate 3 "*Balaena etrusca*", AFS, vertebrae. A, 4402, dorsal view. B, 4402, anterior view. C, 4403, dorsal view. D, 4403, anterior view. E, 4419, anterior view. F, 4419, dorsal view. G, 4421, anterior view. H, 4421, ventral view. Scale bar equals 50 mm.

"*Balaena etrusca*", AFS, wervels. A, 4402, bovenaanzicht. B, 4402, vooraanzicht. C, 4403, bovenaanzicht. D, 4403, vooraanzicht. E, 4419, vooraanzicht. F, 4419, bovenaanzicht. G, 4421, vooraanzicht. H, 4421, onderaanzicht. Maatstreek is 50 mm.

Genus *Balaenotus* Van Beneden, 1872

Type species. *Balaenotus insignis* Van Beneden, 1872

Osteological diagnosis of the genus. The genus is monotypic, its diagnosis is the same as the type species (see below).

Balaenotus insignis Van Beneden, 1872

Materials. The IRSN collection comprises the type materials originally described by Van Beneden (1878, 1880); these materials include the following: CtM832, CtM833a-b (right and left petrosals), CtM837 (left squamosal), CtM836a-c (fragments of the supraorbital process of the frontal, premaxilla, and left maxilla), CtM 838

(right supraorbital process of the frontal), CtM834, CtM835 (left and right tympanic bullae), CtM838, CtM840, CtM841a-b, CtM842a-b, CtM843, CtM844a-b (several blocks including fused cervical vertebrae belonging to different individuals), CtM850 (a partial left scapula), CtM856 (proximal portion of left dentary).

Diagnosis. *Balaenotus insignis* is a balaenid because of its petrosal morphology, tympanic bulla and the presence of a mylohyoidal sulcus on the ventromedial surface of the dentary; its distinctive characters are the lack of anterior torsion of the dentary, ventral opening of the mandibular canal, and the lack of fusion of the atlas to the other cervical vertebrae.

Description of the type material. In this work I re-examine in detail some selected materials that were referred to *Balaenotus insignis* by Van Beneden (1878, 1880). In particular, I re-analyze the petrotympanic complexes, the tympanic bullae, a few skull remains, and the cervical vertebrae. The materials are figured in Fig. 9.

The skull is poorly known. Only the right supraorbital process of the frontal, two fragments of premaxilla and maxilla, the left squamosal with the left exoccipital yet articulated, and a fragmentary left dentary are preserved. The supraorbital process of the frontal is anteroposteriorly narrow and lacks the ascending temporal crest; it is substantially flat; ventrally, there is a wide and shallow optic channel that is continuous with the orbit; the postorbital process is longer than the antorbital process; the orbit has a longitudinal diameter of 105 mm; the optic channel has a proximal longitudinal diameter of 40 mm. The right supraorbital process of the frontal has the same morphology (orbital longitudinal diameter = 115 mm; anteroposterior diameter of the optic channel at base = 40 mm). The fragmentary maxilla bears two maxillary foramina and it is transversely compressed. The premaxilla is very similar to that of *Balaenula astensis* in its overall shape. The partial left squamosal is very strongly built, and is oriented dorsoventrally; the anterior face of the squamosal (corresponding to the posterior wall of the temporal fossa) is concave; the lateral squamosal crest is high and convex. In posterior view, the exoccipital has a round outline and a ventral, pointed apex.

Two left periotics are preserved; their measurements are reported in Table 6. The periotic CtM 832 (Fig.9a-c) has a stocky and tongue-like posterior process that is at right angle with an approximately squared anterior process; the lateral

projection of the anterior process is broken; in dorsal view, the anterior process is divided from the central portion of the periotics by an irregular groove starting from the cranial wall; the posterior limit of the stylomastoid fossa is marked by a small projection on the medial side of the posterior process. The stylomastoid fossa is well defined and long; it continues on the posterior face of the pars cochlearis where it becomes more convex. The superior process is round and it is ventrally bounded by a horizontal, shallow groove. The suprimeatal surface is flat. The petrosal foramina are located in the ventral half of the pars cochlearis. The internal acoustic meatus includes the tractus spiralis foraminosus and the foramen for the VIII cranial nerve (foramen singulare); it is divided from the foramen for the VII cranial nerve (the facial nerve) by the interposition of a transverse crest; the cavities of the internal acoustic meatus and the foramen for the VII cranial nerve are deep and tubular. The latter is higher than the former. A small accessory foramen for the VII cranial nerve is placed more anteriorly and dorsally to the other petrosal foramina; it is usually observed in mysticete earbones. The perilymphatic and endolymphatic foramina are small; they are placed posterior to the internal acoustic meatus and anterior to the fenestra vestibuli (round window) that is wide and almond-shaped. The groove for the tensor tympani muscle is present. The oval window is very wide (lateromedial diameter = 4 mm; dorsoventral diameter = 3 mm) and is separated from the ventral groove for the VII by a crest; the groove projects on the ventral surface of the compound posterior process under the stylomastoid fossa. The stapedial muscle fossa is evident, elliptical, and deep. There is not any neck between the compound posterior process and the remaining part of the petrosal; the stylomastoid notch is slightly developed. The pars cochlearis does not protrude and has a round ventral outline.

The petrosal CtM 833 is more gracile (Fig. 9d-f), has an elongated and narrower compound posterior process, and preserves a long and triangular lateral projection of the anterior process. It represents a juvenile individual because the suture between the round window and the endolymphatic foramen is not completely fused; moreover, the internal acoustic meatus is shallow and very wide and the foramen for the VII cranial nerve is yet included into a larger cavity comprising also the internal acoustic meatus. The posterior limit of the stylomastoid fossa is placed more

cranially than CtM832. The suprimeatal groove placed under the superior process is anteriorly enlarged and it relies above an irregular suprimeatal area. The petrosal CtM832 and CtM833 are so different that they should be regarded as belonging to different species. In fact, while the condition observed in the internal acoustic meatus, and the suture between the round window and the endolymphatic foramen suggest that CtM833 is younger than CtM832, CtM833 has a longer compound posterior process and an irregular suprimeatal surface, both characters being expected to be found in older individuals.

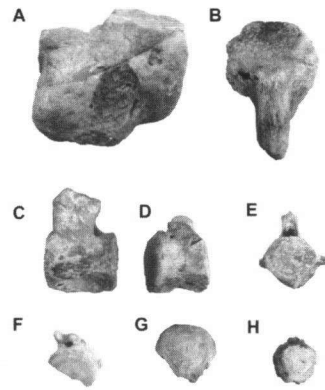


Plate 4 "*Balaena etrusca*", AFS, vertebrae. A, 4420, lateral view (note the pinewood mark). B, 4406, indeterminate piece. C, 4418, left lateral view. D, 4405, left lateral view. E, 4418, anterior view. F, 4405, anterior view. G, 4408, anterior view, H, 4404, anterior view. Not to scale

"*Balaena etrusca*", AFS, wervels. A, 4420, zijaanzicht (let op de beschadiging door dennenhout). B, 4406, ongedetermineerd stuk. C, 4418, linker zijaanzicht. D, 4405, linker zijaanzicht. E, 4418, vooraanzicht. F, 4405, vooraanzicht. G, 4408, vooraanzicht. H, 4404, vooraanzicht. Niet op schaal

The tympanic bullae are typically balaenid-shaped (Fig. 10). The ventral surface is flat-to-slightly concave; the tympanic cavity is shallow; the anterior expansion of the anterolateral corner is strong. Other details are not preserved.

The cervical vertebrae are preserved in several specimens that are not directly referable to the type material, with the only exception of CtM840. They were longitudinally sectioned to study the pattern of co-ossification of the vertebral centra. All of them lack the atlas and are anteroposteriorly compressed. The apophyses of the axis and the third cervical vertebra are preserved only in CtM844 where they project anterodorsally and form long and triangular structures. It seems that

the atlas did not co-ossify with the axis in these specimens; it is unclear if this pattern is due to the young ontogenetic age of the individuals or if it represents a character of taxonomical value. The cervical vertebrae CtM850 are the only that could belong to the same individual represented by the squamosal plus exoccipital, dentary and frontal because it is the only one that comes from the same stratigraphic interval (third section). The neck CtM850 lacks the atlas and comprises axis, and third-to-seventh cervicals. The axis has a strong and bulbous dens, and concave articular face. The other cervical vertebrae are largely co-ossified even though their anterior and posterior borders can be appreciated in the sagittal section. The last cervical vertebra is slightly longer than the others are.

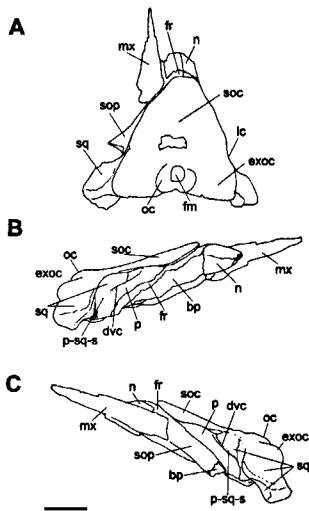


Fig. 8 The skull of *Balaena montalionis*, MSNT holotype (MC CF31) (superfamily Balaenoidea, family Balaenidae). A, dorsal view. B, left lateral view. C, right lateral view. Scale bar equals 200 mm. See Anatomical abbreviations for explanation

De schedel van *Balaena montalionis*, MSNT holotype (MC CF31) (superfamilie Balaenoidea, familie Balaenidae). A, bovenaanzicht. B, linker zijaanzicht. C, rechter zijaanzicht. Maatstreef is 200 mm. Zie anatomische afkortingen voor uitleg

The proximal fragment of the left dentary bears an articular condyle with dorsally exposed articular surface; the angular process is round; a longitudinal crest divides a concave ventral area belonging to the angular process from a dorsal, concave area slightly ventral to the articular surface of the condyle. The distal fragment is long and pertains to the anterior end of the dentary where the groove for the mental ligament and the anterior torsion are absent. Van Beneden (1878,

pl. 24) figured the remaining part of the left dentary; three features are worth noting: first, the mylohyoid sulcus is present along the ventromedial surface of the bone only in the posterior half of the dentary; second, the anterior torsion is almost absent; and third, the mandibular canal opens anteriorly at a ventral position and the sulcus for the mental ligament is ventrally-displaced.

The scapula is incomplete; it is high but short; both the coracoid and the acromial processes are present, but their extremities are broken. A suprascapular fossa is evident. The acromion is directed medially. Van Beneden (1878) figured humerus, radius and ulna; the ulna is olecranon-bearing, the radius has a straight-to-slightly convex anterior border, the humerus has a ball-like articular head, straight anterior and posterior borders, fossa for the olecranon process, and a small and squared deltopectoral tuberosity.

Discussion. The type material referred to *Balaenotus insignis* is very poor. The periotics are the best-preserved portions of that genus but they belong to different individuals and display enough differences to belong to different taxa. The petrotympanic complexes of *Balaenotus insignis* are represented by rather generalized balaenid earbones that lack the distinctive characters of *Eubalaena glacialis* (protruding pars cochlearis and superior process; see Fig. 11) and those of *Balaena mysticetus* (higher suprimeatal area with round dorsal border of the periotics in cranial view). However, the periotic CtM833 and the supraorbital process of the frontal CtM836a are closer to the corresponding bones of the Bowhead whale than the Right whales. In this sense, these specimens are similar to the new genus and species represented by NMB 42001; the type material of *Balaenotus insignis* differs from NMB 42001 in the morphology and the size of the squamosal that is more strongly built and more laterally oriented, and in the morphology of the exoccipital that has a ventral, pointed apex.

The most distinctive features of *Balaenotus insignis* are found in the dentary. The lack of the anterior torsion and the ventral anterior opening of the mandibular canal are not found in other balaenid taxa but for this reason these traits are not useful in establishing the relationships of this form. The proximal region of the dentary of *Balaenotus insignis* has a very concave ventrolateral surface in the proximity of the angular region; this trait is observed also in a dentary of "*Balaena etrusca*" (AFS 4422; Capellini, 1902); however,

these two dentaries differ in the morphology of the articular condyle that is more raised and has a sharper anterior border in *Balaenotus insignis*. I observed these features in a dentary held in NMB, Tilburg (NMB 42002; old inventory number: 752). The Tilburg dentary is represented by a left proximal portion 280 mm in length in which the angular process, the condyle and the mandibular foramen are preserved. The condyle has a sharply angulated anterior border and it is strongly raised; the angular process is laterally round and convex but medially flat; the condyle is posteriorly divided by the angular process by a transverse pterygoid groove; the mandibular foramen is wide and has an external outline that is triangle-shaped. A groove starts from the posteroventral border of the mandibular foramen; this groove is continuous with the posteriormost portion of the mylohyoidal sulcus, which is sharp and is located in the ventromedial surface of the dentary. Unfortunately, despite the good preservation of the Tilburg dentary, the lack of the anteriormost extremity and the convex lateral surface of the angular process prevent us to unambiguously place this specimen in the genus *Balaenotus*. The same is true for the dentary AFS 4422. Moreo-

ver, the Italian specimen has a size that is approximately twice than the type of *Balaenotus insignis* while the Tilburg specimen is of the same size. However, the ontogenetic age of *Balaenotus insignis* type is younger than that of the "*Balaena etrusca*" dentary and this could explain the difference in size.

In conclusion, *Balaenotus insignis* is primitive in the lack of the anterior torsion of the dentary, the morphology of the earbones, the olecranon-bearing ulna, and the straight-edged humerus; it has a *Balaena*-like supraorbital process of the frontal (that is distally flat and lacks the ascending temporal crest); it shares with the Tilburg dentary the sharply angulated anterior border of the mandibular condyle but differs from it in the morphology of the angular process; it shares with the dentary of "*Balaena etrusca*" the concave area lateral to the angular process but differs from it in the overall size and the morphology of the condyle; it is small-sized like the genus *Balaenula* and the new genus from North Sea. In conclusion, *Balaenotus insignis* is represented by a mixture of elements suggesting different relationships and is presently difficult to understand which of these elements are due to convergence and which derive from phylogenetic inheritance. However, *Balaenotus insignis* can be easily diagnosed when the anteriormost portion of the dentary is taken into account; in fact, the lack of the anterior torsion and the ventral opening of the mandibular canal are diagnostic traits of this form. I conclude that the name *Balaenotus insignis* is a valid one and represents a primitive *Balaena*-like form with particular feeding adaptations as observed in the morphology of the dentary.

A new genus and species from North Sea

The skull of a small-sized balaenid is held by the NatuurMuseum Brabant, Tilburg, Holland. The specimen is inventoried as NMB 42001 and it was discovered at Kallo, North-West Antwerp, Belgium, in 1974. The skull was discovered by vicar E.T.H. Van Tuyll and comes from the Kattendijk Sands that are Early Pliocene in age.

The skull represents a new genus and species of a small-sized balaenid from the North Sea and was approximately contemporaneous to *Balaenula balaenopsis* (Fig. 12). It does not belong to the genus *Balaenula* because it shows differences in the position of the glenoid fossa of the squamosal, the orientation of the zygomatic process of the squamosal, in the morphology of the supraoccipital shield and the supraorbital process of the frontal. Moreover, it lacks the derivate traits exhi-

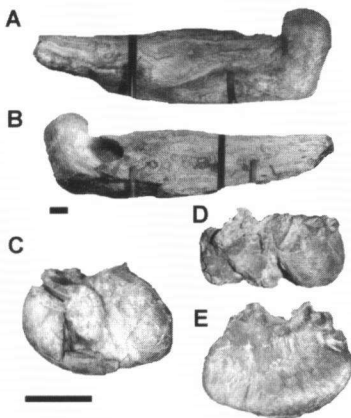


Plate 5 "*Balaena etrusca*", MGB. A, 9070, left dentary in lateral view (anterior end on the left side). B, 9070, left dentary in medial view. Scale bar equals 100 mm. C, 9069, right tympanic bulla in lateral view. D, 9069, right tympanic bulla in dorsal view. E, 9069, right tympanic bulla in medial view. Scale bar equals 50 mm.

"*Balaena etrusca*", MGB. A, 9070, zijaanzicht van de buitenkant van de linker onderkaak (de voorkant is aan de linkerzijde). B, 9070, zijaanzicht van de binnenkant van de linker onderkaak. Maatstreep is 100 mm. C, 9069, rechter gehoorblaasje in zijaanzicht (buitenkant schedel). D, 9069, rechter gehoorblaasje in bovenaanzicht. E, 9069, rechter gehoorblaasje in zijaanzicht (binnenkant schedel). Maatstreep is 50 mm.

bited by *Balaenula balaenopsis* in the periotic bone and by *Balaenula astensis* in the size of the brain. The specimen NMB 42001 seems close to the genus *Balaena* with which it shares the morphology of supraorbital process of the frontal and aspects of the supraoccipital morphology. However, it displays also derivate and distinct features in the nasal bones and the articulation of the rostrum to the frontal. The specimen is presently under study, and a more detailed description with a comparative analysis and taxonomy will be provided elsewhere.

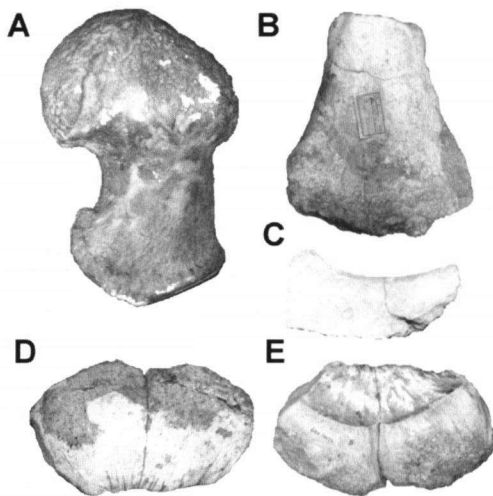


Plate 6 "*Balaena etrusca*", MGB. A, 9061, cast of the humerus. B, 9062, distal end of radius. C, 9067, jugal. D, 9069, tympanic bulla in lateral view. E, 9069, tympanic bulla in medial view. Not to scale

"*Balaena etrusca*", MGB. A, 9061, model van het opperarmbeen. B, 9062, onderzijde van het spaakbeen. C, 9067, jugale. D, 9069, Gehoorblaasje in zijaanzicht; buitenkant schedel. E, 9069, gehoorblaasje in zijaanzicht; binnenkant schedel. Niet op schaal

Genus *Balaenula* Van Beneden, 1872

In 1872, Van Beneden founded the genus *Balaenula* to give a taxonomical designation to the fossil remains of some small-sized balaenids. He considered that the members of *Balaenula* were distinct from *Balaenotus* in the morphology of the earbone and the dentary. Over the years, the genus *Balaenula* has been used as a taxonomical basket, where all the small-sized balaenids were put. During the 20th century, in fact, three new species of *Balaenula* were described: one from Japan and two from Italy. Moreover, both Barnes (1976), and Whitmore (1994) mentioned the presence of *Balaenula* respectively in California and in the eastern United States. Finally, Oishi &

Hasegawa (1994) assigned to *Balaenula* some tympanic bullae, and Pilleri (1987) employed that name to designate the new combination "*Balaenula montalionis*" (see above). None of the previous authors provided a sound morphological diagnosis of this genus, so that it should be regarded as one of the most problematic taxa among the Mysticeti.

Here, I review this genus based on my own observations of Van Beneden's type materials and the Italian taxa. I provide an emended diagnosis of the genus and of two of its species, and discuss its general affinities.

Type species. *Balaenula balaenopsis* Van Beneden, 1872

Osteological diagnosis of the genus. Small-sized balaenid whose estimated body length approaches 5 m, anterior process of the supraoccipital shield wide and round, temporal and lambdoidal crests do not protruding laterally, lateral squamosal crest low and round, ascending temporal crest well developed and high, anteriormost one-fourth of the rostrum abruptly depressed, the ventrolateral border of the maxilla and the supraorbital process of the frontal form a right angle, nasal and proximal rostrum horizontal, olecranon-bearing ulna, squamosal directed ventrally and anteriorly, ventral surface of the exoccipital at the level of the orbit, posterior surface of the exoccipital round in lateral view, glenoid fossa of the squamosal under the orbit.

Balaenula balaenopsis Van Beneden, 1872

Material. I examined only some of the type materials described by Van Beneden (1878, 1880) and held by IRSN; these consist in the following specimens: CtM858a-b (right petrosal and stapes), CtM859, CtM853d, CtM860, CtM861, CtM863, CtM862 (tympanic bullae), CtM865a-b, CtM869a-b, CtM868, CtM867a-c (cervical vertebrae). I have also examined several materials referred to this taxon by Capellini and others and held by MGB but in this work, I focus on the Van Beneden's (1878, 1880) type materials and especially on the petrosal.

Diagnosis. Well defined stylomastoid fossa, the cranial foramen for the VII cranial nerve is triangular, very wide perilymphatic foramen, long and dorsoventrally narrowed anterior process of the periotic.

Description. The type petrosal is figured in Fig. 7a-b. The type materials of Van Beneden comprise a partial skeleton with a fragmentary

skull. The skull as figured by Van Beneden (1878, pl. 1) shows all the traits present in the other forms belonging to the genus *Balaenula* as emended in this work (see above): i.e., the anteroventral development of the squamosal, the low ventral border of the exoccipital (that is at the same height of the orbit), the high ascending temporal crest on the supraorbital process of the frontal, and the glenoid fossa of the squamosal under the orbit. The Belgian form, however, differs from *Balaenula astensis* (another species of the genus *Balaenula*, see below) in its retaining a small endocranial volume and in a peculiar petrosal bone. Some linear measurements are provided in Table 7.

The petrosal (or periotic) lacks the compound posterior process (Fig. 7a-b). It is extremely peculiar and resembles that of the cetothere *Amphicetus*. However, it differs from it in the higher suprimeatal area and the morphology and location of the cranial foramina. In *Balaenula balaenopsis* the anterior process of the petrosal is long and dorsoventrally narrow; it is triangular in cranial view and is divided from the central portion of the bone by a subtle groove; the anterior process has a pointed anterolateral corner. The high suprimeatal area is continuous with a round and not-protruding superior process. The posterior limit of the suprimeatal area is in continuity with a well-defined stylomastoid fossa whose anteriormost area is dorsal to the endolymphatic foramen. Posterior to the subtle groove dividing the anterior process from the central portion of the petrosal, a large cavity should be interpreted as an accessory route for the exit of the VII nerve. The endolymphatic foramen opens on the floor of a wide and triangular cavity; it is placed above the perilymphatic foramen. The internal acoustic meatus is small and deep; it includes the tractus spiralis foraminosus and the foramen singulare for the VIII cranial nerve. The cranial foramen for the VII cranial nerve is slightly anterodorsal to the internal acoustic meatus; the dorsal and ventral borders of this foramen converge anteriorly so that the foramen has a triangular shape. In lateral view, the main feature of the petrosal is the presence of an U-shaped groove that is located above the large lateral opening of the VII (Fig. 7b: vg). This groove corresponds to the vascular groove of Geisler & Luo (1998, p. 179; see their fig. 5) and serves to the transit of the middle meningeal artery. The middle meningeal artery is a ramus of the promontorial branch of the internal carotid artery whose path is marked by a groove

on the ventrolateral wall of the pars cochlearis. This groove is present in the petrosal CtM858. The fossa for the stapedia muscle is wide and well defined by a posterior crest; the oval window is very wide (anteroposterior diameter = 5.4 mm; dorsoventral diameter = 3.65 mm); the groove for the tensor tympanic muscle is present. The stapes is 5.5 mm in height and is perforated by a small and triangular stapedia foramen.

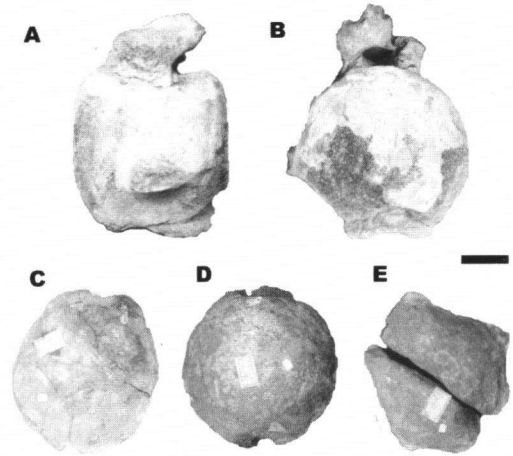


Plate 7 "*Balaena etrusca*", MGB. A, 9068, dorsal view. B, 9068, anterior view. C, 9064, anterior view. D, 9063, anterior view. E, 9065, anterior view. A to D are caudal vertebrae, E is a thoracic vertebra. Scale bar equals 50 mm.

"*Balaena etrusca*", MGB. A, 9068, bovenaanzicht. B, 9068, vooraanzicht. C, 9064, vooraanzicht. D, 9063, vooraanzicht. E, 9065, vooraanzicht. A tot en met D zijn staartwervels, E is een borstwervel. Maatstreek is 50 mm.

Discussion. It is not clear if the petrosal bone of *Balaenula balaenopsis* was found in close connection with the type skull. In fact, in the list of the materials referred to this taxon, Van Beneden (1880: 52) cited several bones representing several individuals. However, he figured only one right petrosal that is the same that I have re-analysed (Van Beneden, 1878: pl. 3). Van Beneden (1880) did not designate a holotype of *Balaenula balaenopsis* and for this reason I focused my analysis on the petrosal that he figured and indicated as characteristic for the species. The materials referred to *Balaenula balaenopsis* come from three different localities that are approximately of the same age (Van Beneden, 1880). A thorough study of the provenances and the morphological compatibilities of the specimens should be undertaken to better characterise this species.

The morphology of the figured petrosal is very different from all the other balaenid taxa. The arrangement and shape of the cranial foramina, the sharply defined stylomastoid fossa, the virtual absence of the usual strong pachyosteo-sclerosis, and the vascular groove for the middle meningeal artery are features unobserved in all the other balaenid periotics that I have examined until now. However, despite this periotic resembles very closely that of *Amphicetus*, it differs from it in a number of details. These details are explained in the above description.

Balaenula balaenopsis differs from *Balaenula astensis* in the brain size and the morphology of the periotic; *Balaenula balaenopsis* differs from the Japanese *Balaenula* sp. in the morphology of the periotic. All these forms share the same antero-

Table 5 Specimens previously assigned to "*Balaena*" *etrusca*: repository, anatomical element, locality and year of discover, and references to first description. References cited in table: 1 = Capellini (1873), 2 = Capellini (1876), 3 = Capellini (1902).

Vondsten die oorspronkelijk toegeschreven waren aan "*Balaena*" *etrusca*: huidige bewaarplaats, anatomisch onderdeel, plaats en jaar van ontdekking, en de eerste beschrijving. Geciteerde referenties: 1 = Capellini (1873), 2 = Capellini (1876), 3 = Capellini (1902).

Repository	Anatomical region	Locality, year of discovery (and references to first description)
AFS 4422	right dentary	Vicolo di Tone, Siena, Tuscany, 1859 (1)
MGB 9070	right dentary	Poggio di Stabicone, Trequanda, Siena, Tuscany, 1879 (3)
MGB 9069	right tympanic (natural cast)	Orçiano, Pisa, Tuscany (3)
MGB 9067	jugal	Ricavo, Chiusi, Siena, Tuscany
not observed	earbones	Pieve di Santa Luce, Pisa, Tuscany, 1875 (3)
not observed	two fragmentary premaxillae	unknown locality, Tuscany (3)
MGB 9062	ulna	Poggio di Stabicone, Trequanda, Siena, Tuscany, before 1888 (3)
MGB 9061	right humerus	Grillo, Val di Chiana, Tuscany, 1857 (2)
MGB 9066	cervical vertebrae	Poggio di Pasqualone, Chiusi-Cetona area, Val di Chiana, Tuscany, 1871 (1)
AFS 4419	lumbar vertebra	unknown locality, Tuscany (1)
MGB 9064	caudal vertebra	Guistrigona, Siena, Tuscany, before 1875 (1)
not observed	caudal vertebra	Guistrigona, Siena, Tuscany, before 1875 (1)
MGB 9065	caudal vertebra	unknown locality, Tuscany (1)
MGB 9063	caudal vertebra	Poggio di Stabicone, Trequanda, Siena, Tuscany, before 1888 (3)
MGB 9062	caudal vertebra	Poggio di Stabicone, Trequanda, Siena, Tuscany, before 1888 (3)
Siena	caudal vertebra	Sarteano, Siena, Tuscany (3)
Siena	2 vertebrae	Monte Follonico? Siena, Tuscany
MGB 9068	caudal vertebra	Valle della Fine? Siena, Tuscany

ventral development of the squamosal, the position of the glenoid fossa under the orbit, high ascending temporal crest on the supraorbital process of the frontal, and the morphology of the exoccipital. All these traits support the monophyly of the genus *Balaenula*. However, the described members of this genus are different in the details explained above and represent three different species. The Japanese form (not examined in this work) is the more primitive species of the genus because it lacks the derived characters expressed by the other ones; *Balaenula balaenopsis* and *Balaenula astensis* exhibit different derived characters suggesting that these forms evolved independently.

Balaenula astensis Trevisan, 1941

Material. A nearly complete neurocranium with earbones and fragments of both dentaries (MSNT MC CF35). The specimen was described by Trevisan (1941) who recognized it as a new species of *Balaenula*; Pilleri (1987) rejected the systematic assignment by Trevisan (1941) and put the specimen into his new combination *Balaenula montalionis* together with the holotype skull of *Balaena montalionis* Capellini, 1904. Bisconti (2000) reviewed the systematics of the specimen based on cladistic analysis and concluded that the original assignment of Trevisan was correct.

Diagnosis. Endocranial volume approaching 4200 cc, temporal fossa small, hypoglossal foramen present, concave paroccipital process, anterior process of petrosal long, narrow and high, compound posterior process short and tongue-like.

Description. The skull is fairly preserved (Fig. 13). The maxillae are largely missing with the exception of their posteriormost elements. The rostrum is represented by the left premaxilla that is strongly arched. The posterior two-thirds of the premaxilla is nearly horizontal but the anterior third abruptly projects downward and onward. The lateral process of the maxilla does not project under the supraorbital process of the frontal; in fact, the rostrum is completely anterior to the frontal and the maxilla, and the frontal forms a right angle. The premaxilla is transversely compressed for its whole length; the nasal fossa is anteroventrally bordered by an ascending crest placed on the medial wall of the premaxilla. The posterior elements of the maxilla are preserved as flat and wide pieces of bone; these elements document that the maxilla did not interdigitate with the frontal in the same manner as that of *Balae-*

nopteridae. Measurements are provided by Bisconti (2000).

The nasal bones are rectangular and long; they bear a notch on their anterior face; their length/width ratio is 1.5, and this represents the higher value between the known fossil and living mysticetes. The supraorbital process of the frontal is prismatic; i.e., it is gently descending from the small interorbital region of the frontal, and bears a strong ascending temporal crest onto its dorsal surface; the ascending temporal crest is developed from the postorbital corner of the orbit to the posterolateral corner of the nasal. The ventral angle between the supraorbital processes of the frontal approximates 90°; this is a typical character of this species because in living mysticetes and *Balaena montalionis* this angle is slightly less than 180°.

The parietals do not appear dorsally at the cranial vertex anterior to the anterior process of the supraoccipital shield. The parietal squama forms the medial side of the temporal fossa and is flat; the temporal fossa is not overhanged by the temporal crests generated by the dorsal borders of parietal and supraoccipital. Anteriorly, the parietal spreads onto the emergence of the supraorbital process of the frontal as in *Eubalaena glacialis* and other members of the genus *Balaenula*.

The squamosal is more slender than that of the genera *Balaena* and *Eubalaena*. The anterior face of the squamosal (which is the posterior wall of the temporal fossa) is flat; the lateral squamosal crest is reduced to a slight relief located at the middle of the height of the squamosal bone; the lambdoidal crest is low and rounded; none of the sites for the attachment of the cranial musculature appears well-developed with the exception of the ascending temporal crest located onto the dorsal surface of the supraorbital process of the frontal. As usual in the genus *Balaenula*, the squamosal is developed ventrally and anteriorly so that the glenoid fossa for the articulation with the dentary is placed approximately at the middle of the length of the neurocranium. The glenoid fossa represents the cranio-mandibular joint (CMJ) and is oblique-to-vertical in the genus *Balaenula*. The CMJ is located immediately below the orbit.

The supraoccipital shield is characterized by a rounded and wide anterior process that is superimposed onto the parietals and it excludes them from being exposed at the cranial vertex. The lateral borders of the supraoccipital are convex. The dorsal relief of the supraoccipital is slight and is bordered by a pair of anterior nuchal fossae and

a pair of posterior nuchal fossae for the attachment of neck musculature. The exoccipitals are round in lateral and dorsal view. They show a tuberosity above the paroccipital process that is flat and well developed. The foramen magnum is very wide; it is bordered by flat and low occipital condyles.

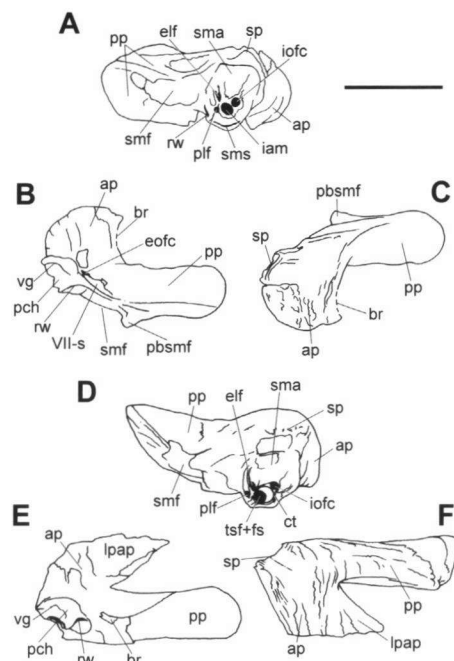


Fig. 9 Type periotics of *Balaenotus insignis* (IRSN). A, CtM 832, cranial view. B, CtM 832, ventral view. C, CtM 832, dorsal view. D, CtM 833, cranial view. B, CtM 833, ventral view. C, CtM 833, dorsal view. Scale bar equals 50 mm. See Anatomical abbreviations for explanation

Type periotics (gehoorgebied) of *Balaenotus insignis* (IRSN). A, CtM 832, vooraanzicht. B, CtM 832, onderaanzicht. C, CtM 832, bovenaanzicht. D, CtM 833, vooraanzicht. B, CtM 833, onderaanzicht. C, CtM 833, bovenaanzicht. Maatstreef is 50 mm. Zie anatomische afkortingen voor uitleg

The basicranium is fragmentary; the basioccipital is ventrally flat; the vomer was removed from the skull during postmortem processes; the palatines that were described by Trevisan (1941) are detached from the skull; they are flat and wide and reach a point posterior on the basicranium. The pterygoids are preserved in part; there is the anterior portion of the right pterygoid that shows a deep and wide pterygoid fossa. The falciform process of the squamosal is robust and long. The basisphenoid and the presphenoid are observed on the ventral wall of the skull; the alisphenoid is preserved and its surface is rough. The basicap-

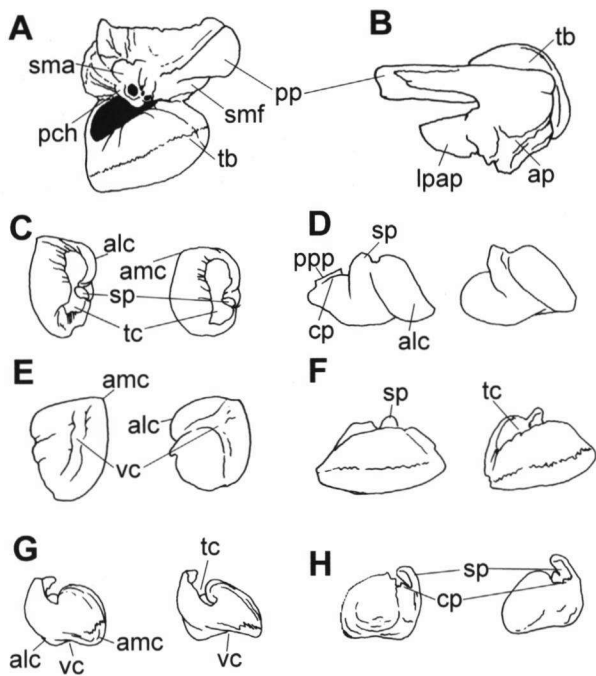


Fig. 10 Petrosal (periotic) and tympanic bullae of bowhead whale *Balaena mysticetus* and southern right whale *Eubalaena australis*. A, right petrotympanic complex in cranial view (bowhead whale, ZML 1680). B, right petrotympanic complex in dorsal view (southern right whale, ZML, periotics associated to a skeleton; compare this petrotympanic with that shown in Fig. 11 to assess morphological variation among northern and southern right whales). C, two tympanic bullae of *Balaena mysticetus* in dorsal view (in all figures, ZML 2563 on the right, ZML without number on the left). D, bullae in lateral view. E, bullae in ventral view. F, bullae in medial view. G, bullae in anterior view. H, bullae in posterior view. Not to scale. See Anatomical abbreviations for explanation

Rotsbeen (periotic) en gehoorblaasjes van de Groenlandse walvis *Balaena mysticetus* en de zuidkaper *Eubalaena australis*. A, rechter gehoorcomplex in vooraanzicht (Groenlandse walvis, ZML 1680). B, rechter gehoorcomplex in bovenaanzicht (zuidkaper, ZML, periotica verbonden met een skelet; vergelijk dit gehoorcomplex met dat in fig. 11 om de variatie in vorm tussen de noordkaper en de zuidkaper vast te stellen). C, twee gehoorblaasjes van *Balaena mysticetus* in bovenaanzicht (in alle figuren, ZML 2563 aan de rechterkant, ZML zonder nummer aan de linkerkant). D, blaasjes in zijaanzicht, buitenkant schedel. E, blaasjes gezien vanaf de onderkant. F, blaasjes in zijaanzicht, binnenkant schedel. G, blaasjes in vooraanzicht. H, blaasjes in achteraanzicht. Niet op schaal. Zie anatomische afkortingen voor uitleg

jugular notch is well developed ventrolateral to the occipital condyles. The descending processes of the basioccipital are triangular in posterior view.

The mesethmoid is worth noting because of its exceptional preservation. It is characterized by a perpendicular lamina that is bordered by two concave surfaces that are round in outline; there is a pair of olfactory foramina on these surfaces, together with a series of crest-like formations that are homologized to ethmoturbinates. Maxilloturbinates are not observed on the specimen probably due to the lack of the relevant portions of the maxillae.

The holotype skull has an endocranial volume that Trevisan (1941) estimated to be around 4200 cc. This volume is the largest among the Balaenidae and suggests that *Balaenula astensis* was a highly encephalized animal. Due to the enormous expansion of the brain, the braincase expanded and the temporal fossa became smaller. The increase in brain size was probably the reason for the round morphology of the sites for the attach of the muscle temporalis (temporal crest, lambdoidal crest, and lateral squamosal crest).

The petrosal and the tympanic bullae were not described in detail by the previous authors. Their detailed description is provided here (Fig. 7e-f). Both petrosals are incomplete and lack the ventralmost portion of the pars cochlearis. The compound posterior process is short and stocky; in dorsal view, it is wide and tongue-like; its dorsal surface is deeply grooved while its ventral surface is flat and projects dorsally. The stylomastoid fossa is long and has a concave roof formed by the petrosal component of the compound posterior process. Posterior and anterior processes are at a right angle to each other. The anterior process is unusually high and long for a balaenid. It is as long as the anteroposterior diameter of the pars cochlearis as measured at its emergence from the central part of the periotic; the cranial face of the anterior process forms a vertical wall slightly concave and oblique. The lateral projection of the anterior process is broken. The dorsal surface of the periotic is strongly pachyosteosclerotic; the superior process is cranially rounded and is ventrally bounded by a horizontal, shallow groove. The suprimeatal area is high and flat. In ventral view, the fossa for the stapedial muscle and the fossa incudis are completely destroyed. The facial groove is widened anteriorly and posteriorly; it

sular fissure is small and elliptical in outline. The

continues posteriorly on the ventral surface of the compound posterior process. Only the dorsal border of the oval window is preserved; the tracks of two semicircular canals are visible. Compared to other balaenids, the ventral surface of these periotics is wider and longer.

The left tympanic bulla is very incompletely preserved while the right one lacks only some fragments of the lateral wall and the pedicles for the articulation to the periotics. Only the posterior wall together with a small portion of the ventral wall of the left bulla are preserved. The bulla is dorsoventrally compressed and has a longitudinally concave ventral surface; the tympanic cavity is shallow and transversely wide; the anteromedial corner is round but forms a right angle with the medial edge of the bone; an anterolateral transversal expansion is posteriorly bounded by a dorsoventral constriction slightly anterior to the sigmoid process; the posterolateral wall of the bulla (below the inferred position of the sigmoid process) is slightly convex. The conical process is very low and straight. There is a shallow notch between the conical process and the transversal, posterior wall of the bulla. This notch is marked in the left bulla.

The dentary is long and straight. It shows the anterior torsion and the mylohyoid sulcus in the ventromedial surface. The condyle has a dorsally exposed articular surface and the angular process is round and low. The coronoid process is absent; in its place, there is a long and low coronoid crest. Several mental and gingival foramina are present along the dorsolateral and dorsomedial borders of the bone. More details are provided by Bisconti (2000).

Discussion. *Balaenula astensis* represents an advanced small-sized balaenid characterised by high endocranial volume and low and round attach sites for the cranial musculature. The endocranial cast reveals that the brain has very large Gasserian ganglia and large olfactory pedicles. However, the cast is under study and its anatomical characteristics will be made clear elsewhere. The expansion of the brain is correlated to a reduction of the temporal fossa caused by the lateral movement of the lateral sides of the skull. The reduction of the volume of the temporal fossa seems paralleled by a reduction of the posteromedial attach sites of the muscle temporalis; on the contrary, the ascending temporal crest located on the supraorbital process of the frontal is very high and marked suggesting a strong anterior attachment of the muscle. The skull of *Balaenula astensis*

is more slender and streamlined than that of *Eubalaena* and *Balaena*. Unfortunately, the lack of the postcranial skeleton prevents us to analyse its swimming abilities. The periotic is primitive in its retaining of a short posterior process. In fact, in other small-sized balaenids such as *Balaenotus insignis* and NMB 42001 the posterior process is long despite the small size of the skull. The shape of the suprareteal area and the superior process resemble the Japanese *Balaenula* sp. but differ from *Balaenula balaenopsis*. Bisconti (2000) found a close relationship between *Balaenula astensis* and *Balaenula balaenopsis* and found that these forms are closer to the living *Eubalaena glacialis*.

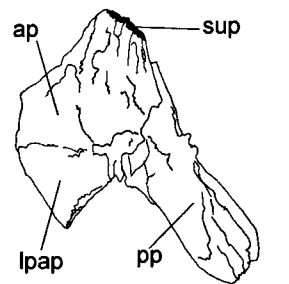


Fig. 11 Petrosal bone of the right whale *Eubalaena glacialis* (MSNT 260). Scale bar equals 50 mm. See Anatomical abbreviations for explanation

Rotsbeen van de noordkaper *Eubalaena glacialis* (MSNT 260). Maatstreek is 50 mm. Zie anatomische afkortingen voor uitleg

Balaenula praediolensis Cuscani Politi, 1961

Pietro Cuscani Politi was a teacher in a high school in Siena during the 50s, 60s, and 70s and did a lot of paleontological work as an amateur who was informed into scientific principles. In a paper that appeared in 1961, he made a general overview of the fossil mysticetes held by the Italian institutions, and described a new species of *Balaenula* under the name *Balaenula praediolensis*.

Materials. The specimen was discovered in November 1958 near San Casciano dei Bagni about 90 km South of Siena, Central Italy. It comes from Middle Pliocene sands that were deposited approximately 3 Ma ago. The remains of the balaenid consist in the partial left mandibular ramus (AFS 7149), the left tympanic bulla (AFS 7132), a fragment of petrosal (AFS 7133), three fragments of premaxilla (AFS 7143), and a fragment of rib (AFS 7144). The holotype and only specimen referred to *Balaenula praediolensis* is held by the Geological Section of the Natural

History Museum of the Accademia dei Fisiocritici.

Diagnosis. The holotype of *Balaenula praediolensis* shows one diagnostic feature at the level of species: very thick lateral wall of the tympanic bulla. This feature distinguishes this form at the level of species but there are no diagnostic traits at the level of genus; for this reason we cannot include "*Balaenula*" *praediolensis* into any of the presently known genera of balaenids. We can only refer this specimen to a species of Balaenidae gen. ind., and wait for further discoveries of more complete and morphologically comparable specimens.

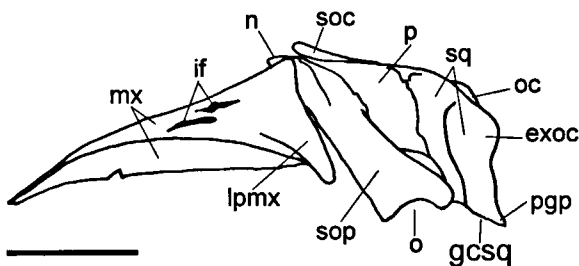


Fig. 12 The skull of a new genus and species of small-sized balaenid in right lateral view (anterior end of the skull on the left side) (NMB 42001, holotype). Scale bar equals 200 mm. See Anatomical abbreviations for explanation

Rechter zijaanzicht van de schedel van een nieuw geslacht en een nieuwe soort van een kleine baleinwalvis (voorkant van de schedel is aan de linkerkant) (NMB 42001, holotype). Maatstrep is 200 mm. Zie anatomische afkortingen voor uitleg

Description. The left dentary is represented by a partial ramus formed by two segments (Plate 8). It is approximately 980 mm in length and 112 mm in height (see Table 8 for measurements). The condyle and the anteriormost portion of the mandible are missing. The dentary bears 5 or 6 mental foramina; the mandibular canal is partially exposed because the dorsal border of the bone is eroded. As it is customary in Balaenidae, the coronoid process is absent. The mylohyoid sulcus is well developed along the ventromedial surface of the bone; it disappears 197 mm posterior to the anterior end of the dentary as preserved in the specimen. Approximately 197 mm posterior to the anterior end, the dentary raises and curves medially toward the mental region. In dorsal view, the dentary is straight for almost its entire length; the only region where it is

bowed is when its anterior end approaches the mental region. The lateral surface of the dentary is highly convex for almost all of its length; this surface begins to be flat only from 197 mm from the anterior end. The medial surface is flat-to-slightly convex.

The left tympanic bulla is incompletely preserved (measurements in Table 8). It lacks the anterior apex, the whole lateral surface, and the pedicles for the attachment to the petrosal. The ventral surface is concave and wide; there is a sharp ventromedial keel; the involucrum (*sensu* Oishi & Hasegawa, 1994) is continuous for the whole length of the bulla; the tympanic cavity is shallow; the involucrum protrudes into the tympanic cavity and the cavity is not observed posterior to the broken posterior pedicle for the attachment of the bulla to the petrosal. The dorsal surface of the medial portion of the involucrum is wide and highly convex; the posterior wall of the bulla is concave and vertical immediately posterior to the posterior pedicle for the attachment to the petrosal. The ventral surface of the bulla is perforated by numerous, small vascular foramina. The fragment of the left petrosal consists in a distal portion of the posterior process. It has a triangular shape and is very robust and pachyosteosclerotic.

The largest fragment of premaxilla represents a portion of the lateral surface of the bone; it has a vertical lateral side; the dorsolateral border is acute and eroded; the dorsal surface descends medially and is concave; the dorsomedial border is lower than the dorsolateral and descends anteriorly. The smallest piece of premaxilla has a ventromedial surface eroded; the dorsal surface is flat and the lateral surface is vertical. The third premaxillary fragment has a dorsal surface flat-to-slightly convex that descends laterally; the lateral surface is concave and has a crest-like ventral border; the ventromedial surface is flat.

The only remains referable to the postcranial are a fragment of a left rib that represents a segment close to the proximal end of the bone. It is medially flat and laterally convex; it is slightly bowed near the proximal end but is straight for the main part of its development.

Discussion. Despite its poor preservation, the holotype of *Balaenula praediolensis* preserves enough information to discriminate it as a separate balaenid species. Unfortunately, based on the fragmentary referred material, it is presently impossible to understand what is the genus it belongs to. "*Balaenula*" *praediolensis* is a species of

an indeterminate genus of balaenids. Its distinctive trait is observed in the tympanic bulla. The thickness of the lateral wall of the tympanic bulla is a crucial factor in the functioning of the cetacean earbones (Nummela *et al.*, 1999). The thicker the bulla, the higher the ability to perceive low-to-very low frequency sounds (Nummela, 1997, 1995). In fact, the mass of the tympanic depends partially on the thickness of the lateral wall of the bulla and the mass is the factor that influences the capacity of a bulla to be resonant with low-to-very low sounds (Hemilä *et al.*, 2001). In "*Balaenula*" *praediolensis* this thickness is maximum among balaenids suggesting that this animal sensed probably very low sounds. It is likely that the increase in the thickness of the lateral wall of the tympanic bulla was a way for "*Balaenula*" *praediolensis* to preserve the high mass of the tympanic that is necessary to perceive very low sounds despite its extreme reduction in size.

Genus *Eubalaena* Gray, 1864

Type species. *Eubalaena australis* Desmoulins, 1822

Osteological diagnosis of the genus. Gigantic body size (maximum body length approaching 22 m), rostrum and supraorbital process of frontal form a right angle, nasal and proximal rostrum horizontal, ascending temporal crest well developed on the dorsal surface of the supraorbital process of the frontal, vertically-developed squamosal, zygomatic process of the squamosal directed anteriorly so that the posterior wall of the temporal fossa cannot be observed in lateral view, protruding lambdoidal and temporal crests, convex and protruding lateral squamosal crest, exoccipital squared in lateral view, dome-bearing supraoccipital shield with sagittal crests, wide anterior process of supraoccipital, pars cochlearis cranially-protruded, superior process of petrosal cranially-protruded.

General discussion of the fossil record. There are two fossil specimens closely related to the living right whales. These are reviewed in the following text. Abel (1941) and Plisnier-Ladame & Quinet (1969) described the skull of *Balaena belgica*; I examined the skull and some other portions of this form held by IRSN (CtM 879a-f); the skull (Fig. 14) is strongly built and larger than *Balaenula*. The supraoccipital shield is large and has a widely round anterior process; the supraorbital process of the frontal is anteroposteriorly narrowed and bears a low ascending temporal crest; the reconstruction of the original position of the supraorbital process of the frontal as made by

Plisnier-Ladame & Quinet (1969) suggests that there was a right angle between the frontal and the maxilla. The squamosal is robust and has an anteriorly convex lateral squamosal crest; the posterior wall of the temporal fossa is very concave. The zygomatic process of the squamosal is anteriorly oriented so that the posterior wall of the temporal fossa cannot be seen in lateral view. All these characters suggest a close relationship of "*Balaena*" *belgica* and the genus *Eubalaena*. Other comments on this specimen can be found in Bisconti (2000, 2002).

Bisconti (2002) described the partial neurocranium of a Pliocene right whale of the genus *Eubalaena* from the early Late Pliocene of Central Italy. This is the most ancient fossil of this genus to be formally described. In fact, the report of Nishiwaki & Hasegawa (1967) of a large partial neurocranium of a right whale from the Kisagata shell bed, was relative to a subfossil individual that probably died in the 18th century.

Balaenidae diversity at the species level: a reassessment

The taxonomy of Balaenidae as derived from this work and that of McLeod *et al.* (1993) is presented in Table 9. The names "*Balaena paronai*" and "*Balaena*" *etrusca* should be considered as unvalid. "*Balaena*" *belgica*, "*Balaenula*" *praediolensis* and "*Balaena*" *primigenius* have wrong generic names; in fact, "*Balaena*" *belgica* is now

Table 6 *Balaenotus insignis*, type material, measurements of periotics CtM 832 and 833, in mm.

Balaenotus insignis, type materiaal, maten van het gehoorsgedeelte (perioticum) van CtM 832 en 833, in mm.

	CtM 832	CtM 833
Anteroposterior diameter of anterior process	39	44
Lateromedial diameter of anterior process	37	36
Lateromedial diameter of pars cochlearis	21	18.5
Dorsoventral diameter of iam	11+	12+
Dorsoventral diameter of round window	4	4
Transverse diameter of round window	3	3
Dorsoventral diameter of oval window	9.5	7.3
Transverse diameter of oval window	4.3	5
Length of posterior process	110	105
Width of posterior process	39	29.6
Length of lateral process of anterior process	-	68

put in the genus *Eubalaena*, "*Balaenula*" *praediolensis* and "*Balaena*" *primigenius* represent species of indeterminate balaenid genera. The diagnosis of the genus *Balaenula* is now emended and the genus is not monotypic including at least three different species: *Balaenula balaenopsis*, *Balaenula astensis* and a Japanese *Balaenula* sp.

The systematics of Balaenidae comprises the following valid taxonomical names: *Morenocetus parvus*, *Eubalaena glacialis*, *Eubalaena australis*, *Eubalaena belgica*, *Balaena mysticetus*, *Balaena montalionis*, *Balaenotus insignis*, *Balaenula balaenopsis*, and *Balaenula astensis*. These taxa should be considered in future phylogenetic works on Balaenidae. New balaenid taxa are the following: the skull NMB 42001 (new genus and species), the Japanese *Balaenula* sp. (new species), "*Balaena*" *primigenius* (indetermined genus but

valid species), and "*Balaenula*" *praediolensis* (indeterminate genus but valid species).

Paleoecology of Pliocene balaenids

Very few data are available about the evolution of balaenids during the Miocene time, but the Pliocene fossil record is enough abundant to allow the generation of paleoecological and behavioural inferences. Living balaenids have different reproductive and feeding behaviours. The Greenland Bowhead whale (*Balaena mysticetus*) spends its whole lifetime in the Arctic seas and makes only limited migrations along the parallels (Moore & Reeves, 1993); it feeds and breeds in the Arctic waters. The Right whales *Eubalaena glacialis* and *E. australis* feed in cold waters (respectively North Atlantic and North Pacific, and Antarctic seas) and migrate to reach more temperate areas for breeding and calving. Judging from the distribution of fossil balaenids we should speculate that the Pliocene taxa behaved differently. In fact, several Early Pliocene forms were discovered in Mediterranean sediments associated with rather warm faunas. The presence of balaenids in the warm, sub-tropical Mediterranean Pliocene conflicts with the distribution of the living species and suggests that the ancient taxa had different physiologies. In the following sections I focus on three aspects of the paleoecology of Balaenidae: body size evolution, change in species composition, and reproductive biology.

Until recently, it was believed that general rules would influence the size of animals, especially mammals (i.e., Allen's and Bergmann's rules). In particular, the Allen's rule says that animals living in cold environments are larger than their closest relatives living in warm environments; the Bergmann's rule says that the appendages of animals living in cold environments are smaller than those of their close relatives living in warm environments. These rules seem to follow a logical development: in fact, larger animals have a low-to-very low surface/volume ratio that prevents them to exchange high amount of heat with the environment. Smaller animals have a high-to-very high surface/volume ratio so that they loose high amount of heat into the environment. The same is true for the size and shape of appendages. Following these rules it would be expected to find small-sized animals in warm environments and larger forms in cold environments. This is generally true but I must remark

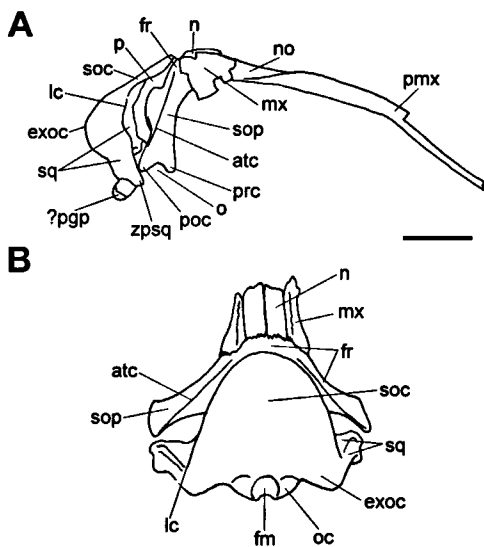


Fig. 13 The skull of *Balaenula astensis* (superfamily Balaenoidea, family Balaenidae). A, left lateral view (anterior end of the skull on the right side), MSNT holotype (MC CF35). B, dorsal view without the premaxilla (anterior end of the skull corresponds to the apex of the nasals and on the upper side). Scale bar equals 200 mm. See Anatomical abbreviations for explanation

De schedel van *Balaenula astensis* (superfamilie Balaenoidea, familie Balaenidae). A, linker zijaanzicht (voorkant van de schedel is aan de rechterzijde), MSNT holotype (MC CF35). B, bovenaanzicht zonder de premaxilla (de voorkant van de schedel komt overeen met de top van het neusbeen en met de bovenzijde). Maatstreep is 200 mm. Zie anatomische afkortingen voor uitleg

that presently the larger terrestrial animals are found in the sub-tropical savannahs (i.e., the elephants) and not in the Arctic; moreover, the most abundant proboscidean of the last ice age (the mammoth) was smaller than its ancestor living in warmer periods (Maschenko, 2002). Therefore, something seems wrong with both Allen's and Bergmann's rules. In recent times, several studies have addressed the relationship between climate and animals focusing on mammals (Prothero, 1999; Dayan *et al.*, 1991; Maas *et al.*, 1988). All these studies concluded that this relationship is very weak or definitively absent.

When one has to assess the physiology of an animal that is known only as a fossil, data from living forms close to the fossil one are crucial (Witmer, 1995). Living balaenids are quite known in terms of their physiology and thermal needs (Lowry, 1993 and references therein) but it seems that there is no rule governing their distributions. In fact, while the Right whales of the genus *Eubalaena* need to breed and calve in temperate waters, the females of the genus *Balaena* need not to migrate so extensively in order to find waters of the right temperature for their parturitions. However, while the living *Balaena mysticetus* spends its whole life cycle in the Arctic, its closest relatives from the Pliocene time are known from the sub-tropical Mediterranean and the North Sea. This point marks a substantial difference between the living species and its fossil relatives. There are no particular differences in size between the living Greenland Bowhead whale and its Pliocene fossil record; in fact, Capellini (1902) estimated that the dentary MGB 9070 ("*Balaena*" *etrusca*) belonged to an approximately 18-m-long individual, a length that approaches very closely the upper limit of variation of the living *Balaena mysticetus*. Other Pliocene balaenids were very large animals: "*Balaena*" *primigenius* has long and strong vertebrae suggesting that it was more than 10-m in length; *Balaena montalioni* was approximately 12-m-long and approached a size similar to that of *Eubalaena belgica* (Bisconti, 2000). Further, Bisconti (2002) estimated that the body length of the early Late Pliocene *Eubalaena* from Tuscany ranged from 11 and 13 m and suggested that the individual was not fully-grown. This is another demonstration that the Allen's rule does not substantially reflect the true distribution of body sizes in relation to the climate.

However, the Early Pliocene was also a time when several small-sized balaenids were living.

In particular, the genus *Balaenula* had a flourishing diversity in the North Atlantic, Mediterranean, and North Pacific. All members of the genus *Balaenula* were small-sized, reaching approximately 5 meters in total body length. These forms lived together with gigantic balaenids such as "*Balaena*" *primigenius*, "*Balaena*" *etrusca* and "*Balaena*" *paronai*". The coexistence of small-sized and gigantic balaenids during the Pliocene represents an ecological situation that has not any present counterpart and raises some problems. Firstly, were balaenids primitively small-sized or large-sized? Secondly, how did the Pliocene small-sized and large-sized balaenids interact with each other? Thirdly, why did small-sized balaenids become extinct?

Table 7 *Balaenula balaenopsis*, type material, measurements of petrosal CtM 858a in mm.

Balaenula balaenopsis, type materiaal en maten van het rotsbeen CtM 858a in mm.

Anteroposterior diameter of anterior process	32
Lateromedial diameter of anterior process	43.5
Anteroposterior diameter of pars cochlearis	54
Lateromedial diameter of pars cochlearis	30
Dorsoventral diameter of iam	4.3
Anteroposterior diameter of iam	6.75
Dorsoventral diameter of round window	3.35
Transverse diameter of round window	4.3
Dorsoventral diameter of oval window	3.65
Transverse diameter of oval window	5.4

The fossil record allows us to answer the first question. Judging from the size of the most ancient balaenid that was formally described (i.e., *Morenocetus parvus* Cabrera, 1926), the size of balaenids was primitively small; large sizes were attained subsequently by at least two different genera, namely *Balaena* and *Eubalaena*. Therefore, it is more parsimonious to consider the small size of the genus *Balaenula* and the new genus from the North Sea as the preservation of a primitive condition.

The nature of the interactions between small-sized and large-sized balaenids has not yet been investigated in scientific publications. Surely, this interaction represents an ecological situation that has not any analogous situation in the living cetacean communities around the world. Other similar situations in which the fossils document ancient coexistences among terrestrial mammals that live now in separate areals have been

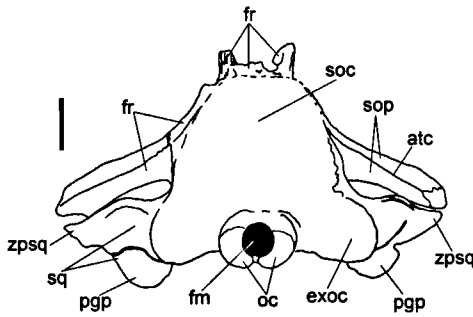


Fig. 14 The skull of *Eubalaena belgica* (superfamily Balaenoidea, family Balaenidae) in dorsal view (anterior end of the skull on the upper side), IRSN holotype. Scale bar equals 200 mm. See Anatomical abbreviations for explanation

Bovenaanzicht van de schedel van *Eubalaena belgica* (superfamilie Balaenoidea, familie Balaenidae) (voorkant van de schedel aan de bovenzijde), IRSN holotype. Maatstreep is 200 mm. Zie anatomische afkortingen voor uitleg

recently documented (Stafford *et al.*, 1999). The high abundance of balaenid species during the Pliocene raises the question of the amount of resources that were available to these animals in that time. In fact, the living balaenids have largely allopatric geographic ranges and rely on rather different food reservoirs, but the Pliocene forms had sympatric distributions and it would be expected that they exploited the same food reservoirs. What was the amount of difference between the Pliocene marine ecosystems and the present ones?

The climate can be invoked to explain the abundance of small-sized balaenids during the Pliocene. In fact, based on traditional rules, it is expected to find small-sized forms during periods characterised by warm climates; however, as argued above, this expectation seems not to be corroborated by fossil and current evidence. The coexistence of small-sized and large-sized balaenids could depend on three main factors:

1. Weak competition. The Pliocene ecosystems were so rich in nutrients and plankton that both large-sized and small-sized forms could survive without interfering with each other. Alternatively, it would be hypothesized that small-sized and large-sized balaenids were differently adapted to prey on different food items. In effect, the genus *Balaenula* has a rather streamlined skull when compared to the large *Balaena* and *Eubalaena*. This would lead to suppose that *Balaenula*

was more agile than the large forms that are presently living. A study of the vertebral column of this genus would be useful to assess its swimming performances as compared to those of the larger taxa. To quantify the amount of resources that were available to the Pliocene cetaceans is yet a complicated issue. Reconstructions of paleoproductivity evolution in the Cenozoic support the availability of highly abundant nutrients in the Pliocene waters all around the world (Compton *et al.*, 2000; Rothmann, 2001; Zachos *et al.*, 2001). This increase in nutrients is generally associated to a raise in planktonic biomass and this represents the basis for the oceanic food webs in which mysticetes are involved. A working hypothesis to explain the co-existence of so diverse balaenid taxa in the Early and Middle Pliocene consists in supposing that major food sources existed that could support several balaenid species and genera. It is yet unclear if the balaenids partitioned the ecosystems by means of diverse trophic specializations or if they were able to exploit the same food reservoirs experiencing low competition.

2. Small-sized species are relict. The presence of small-sized forms in the Pliocene may represent a pale image of the abundance of primitive balaenids that were all small-sized. This scenario derives from the first; in fact, archaic, less advanced forms can survive only if the competition with the more derivate ones is low. Judging from the morphology of periotics, it seems that the genus *Balaenula* was more primitive than *Balaena* and *Eubalaena*, and one would be tempted to consider this genus as a relict. However, at least one member of *Balaenula* displays a highly advanced trait, i.e. a high encephalization. *Balaenula* should be considered as a more conservative form but not primitive. Moreover, the new genus from the North Sea (NMB 42001) is represented by a skull with the most advanced process of nasal reduction ever seen in a mysticete; this form cannot be considered as a relict or a primitive taxon. So, it seems that the small-sized species preserved the primitive condition of a little body but they evolved their own specializations as expressed by derivate character states (e.g., small nasals and large brain).

3. High diversity in balaenid body sizes is promoted by specialized predation. This point was firstly analysed by Bisconti (1998). In ecosystems characterised by a small area (i.e., a lake), the diversity of the zooplankton is promoted by the action of a specialized predator (Beisner *et al.*, 1997); the removal of the predator causes the

collapse of prey's diversity; the lack of a specialized predator allows a prey species to dominate above the others (Kerfoot, 1987; Mills *et al.*, 1987; Kitchell & Carpenter, 1987; Vanni, 1987). The dominant prey undergoes an increase in body size and excludes the main part of the other prey species from the access to the resources (Mittelbach & Chesson, 1987; Power, 1987); the final consequence is that the other prey species become demographically marginal. Bisconti (1998) applied this idea to the problem of the coexistence of small-sized and large-sized balaenids during the Pliocene of Mediterranean. He simulated by a computer program the conditions under which two species of Balaenidae with different metabolic requirements can coexist under the pressure of a predator and in the presence of competitive exclusion. The competitive exclusion is an ecological rule that applies when a dominant species interacts with weak competitors; in general, the dominant species is a better competitor and excludes the other species from the resources leading them to the edge of the extinction. It is reasonable to assume that large individuals are better competitors than smaller ones. The results obtained by Bisconti (1998) suggested that the coexistence is possible when a large part (~40%) of the population of the dominant species is removed by specialized predators like great sharks (i.e., *Carcharocles megalodon*, *Carcharodon carcharias*). It seems counterintuitive to suppose that giant balaenids may be highly preyed by sharks but there is enough evidence supporting this point. Bianucci *et al.* (2002), Purdy (1996), and Deméré & Cerutti (1982) provided many data suggesting strong trophic interactions between white sharks and baleen whales. In particular, Bianucci *et al.* (2002) documented shark interactions with large balaenids during the Pliocene of central Mediterranean. Therefore, it is not so strange to suppose that the sharks had some influence on the distribution of body sizes in fossil balaenid communities. The pattern of community evolution that is obtained by the simulation model is as follows: 1) large- and small-sized balaenids coexist under the pressure of a specialized predator (such as a large shark species), 2) the predator is removed from the ecosystem (i.e., it becomes extinct or it changes its range due to global changes), 3) the large balaenid species becomes dominant and excludes the smaller forms from the access to the resources, 4) the small-sized balaenids become extinct. This model is largely speculative and is based on plankton community evolution and for this reason it should be considered as a starting point.

Table 8 "*Balaenula praediolensis*", type material, measurements in mm. a = as preserved. b = mean thickness was assessed from five measurements of the tympanic wall taken at random positions; method for the larger part in accordance with Nummela *et al.* (1999).

"*Balaenula praediolensis*", type materiaal en maten in mm. a = zoals bewaard. b = gemiddelde dikte samengesteld uit vijf afzonderlijke maten genomen op het gehoorblaasje op willekeurige plaatsen, grotendeels volgens de methode van Nummela *et al.* (1999).

Length of dentary (2 pieces)	983
Posterior height of dentary	125
Anterior height of dentary	108
Height at middle of dentary	112
Length of tympanic bulla ^a	84
Anterior width of tympanic bulla ^a	37
Posterior width of tympanic bulla ^a	69
Posterior height of tympanic bulla ^a	44
Maximum depth of tympanic cavity ^a	32
Mean thickness of tympanic wall ^b	9.8
Length of rib fragment	190
Anteroposterior diameter of rib fragment at proximal end	41
Anteroposterior diameter of rib fragment at distal end	41
Maximum thickness of rib fragment	19

New studies should be carried out for a better understanding of the evolution of balaenid communities over time.

One of the points yet unclear is represented by the evolution of balaenid reproductive behaviour since the Pliocene. Living balaenids perform different reproductive behaviours in that the Greenland bowhead whale completes its whole life cycle in the Arctic waters, while the Right whales need temperate, sub-tropical waters to breed and calve. It is not clear if Pliocene balaenids performed migratory behaviours similar to those of the living Right whales or not. It is also unclear if the breeding and calving areas employed by Pliocene balaenids had peculiar characters such as those used today by members of the genus *Eubalaena*.

The Italian collections of fossil balaenids are really full of remains of juvenile individuals. However, in general, these fossils represent subadult and weaned individuals and do not document that a given area was a reproductive site for Pliocene balaenids. The only exception is repre-

sented by the remains of a newborn of an unidentified species of a balaenid from Orciatico (Tuscany, Central Italy) held by MGB and inventoried as CMC 8911. The specimen consists of an incomplete vertebral column that can be assigned to the family Balaenidae due to the cervical vertebrae that are fused with each other. In the specimen, five cervicals are preserved (atlas and sixth vertebra are lacking) from which the axis is the largest. This neck is illustrated in Fig. 15

where it is compared to the cervical complexes of other small-sized balaenids. I consider the specimen as a newborn individual due to its overall size: the whole complex is 41 mm in length, 60 mm in width, and 58 mm in height. Unfortunately, the information concerning this specimen is scanty so that we do not know the precise locality where it was found. For this reason we have no information on the exact chronostratigraphic age of the specimen. Therefore, we have to assign the specimen to Pliocene *sensu lato*. The neck CMC 8911 is important because it documents that the Central Mediterranean sea, and especially the shallow seas around the islands that were present in the place of the present Central Italy, was a reproductive area used by balaenids sometime during the Pliocene.

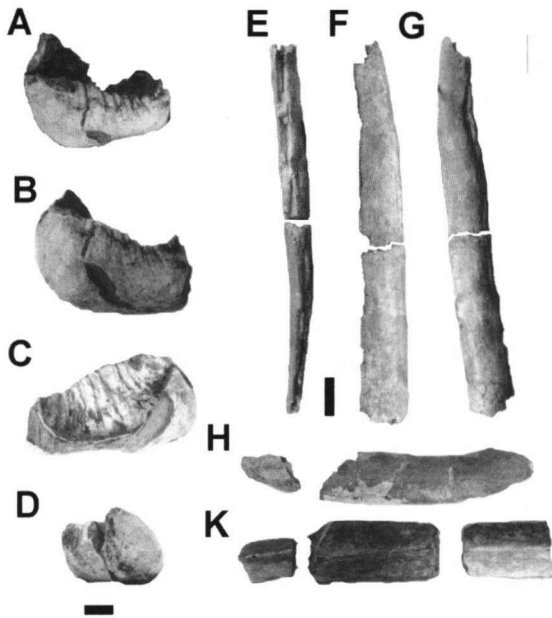


Plate 8 "*Balaenula*" *praediolensis*, AFS holotype. A, 7132, tympanic bulla in lateral view. B, 7132, tympanic bulla in dorsal view. C, 7132, tympanic bulla in medial view. D, 7132, tympanic bulla in posterior view. Scale bar equals 20 mm. E, 7149, dentary in dorsal view. F, 7149, dentary in lateral view. G, 7149, dentary in medial view. Scale bar equals 100 mm. H, 7133 on the left (petrosal fragment), 7144 on the right (rib fragment). K, 7143, premaxillary fragments. H and K not to scale

"*Balaenula*" *praediolensis*, AFS holotype. A, 7132, gehoorblaasje in zijaanzicht, buitenkant schedel. B, 7132, gehoorblaasje in bovenaanzicht. C, 7132, gehoorblaasje in zijaanzicht, binnenkant schedel. D, 7132, gehoorblaasje in achteraanzicht. Maatstreek is 20 mm. E, 7149, onderkaak in bovenaanzicht. F, 7149, onderkaak in zijaanzicht, buitenkant. G, 7149, onderkaak in zijaanzicht, binnenkant. Maatstreek is 100 mm. H, 7133 aan de linkerkant (fragment van een rotsbeen), 7144 aan de rechterkant (ribfragment). K, 7143, fragmenten van de premaxilla. H en K niet op schaal

Phylogeny of Balaenidae

As usual in the study of mysticete evolution, the phylogeny of Balaenidae and their position among Cetacea is not yet completely understood. This is because the phylogeny of the whole Mysticeti is under debate, being a case where morphology and molecules conflict. However, a detailed phylogenetical analysis of Balaenidae would be very useful in shaping conservation strategies to save the living species from extinction. In this sense, the study of balaenid phylogeny and evolution can provide invaluable data to a field in expansion, that of conservation biology. In the next section, I make an overview of previous phylogenetic studies and propose some suggestions to future works on the evolution of Balaenidae.

The morphological evidence

Balaenids are morphologically very different from the other mysticetes. Their transversely compressed rostrum, their vertically developed squamosal, and their squared, low and wide tympanic bulla make them very characteristic. Unfortunately, these peculiar morphologies seem so specialized that it is difficult to link balaenids to other mysticetes in a phylogenetic study of mysticete evolution.

Morphological evidence suggests that Balaenidae and Neobalaenidae are closely related (for accounts of morphology of neobalaenids see Baker, 1985; Beddard, 1901; Oliver, 1922). Gray (1868) suggested putting both families into a superfamily, namely Balaenoidea, a concept subsequently resurrected by McLeod *et al.* (1993).

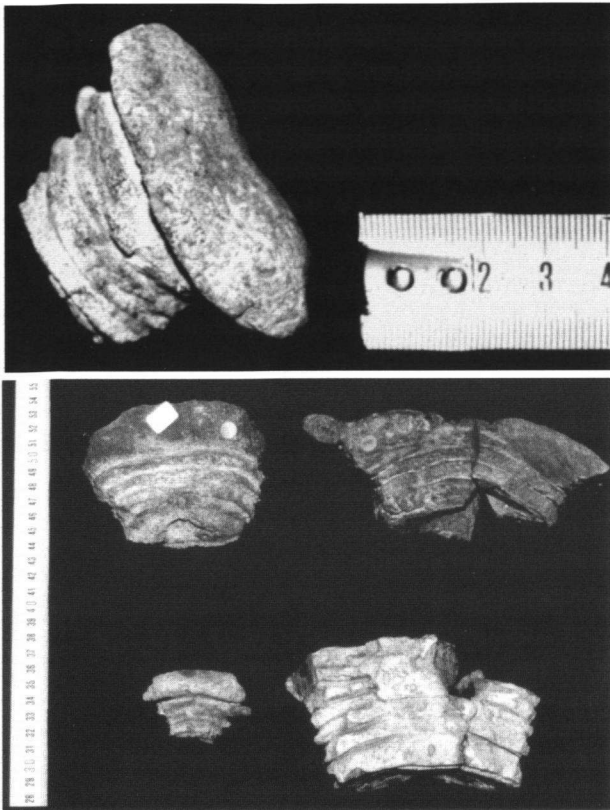


Fig. 15 The cervical vertebrae of a newborn balaenid from the Italian Pliocene (MGB CMC 8911). A, the neck in lateral view (scale bar in cm). B, the neck (on the lower left corner) is compared to other cervical blocks of Pliocene small-sized balaenids held in MGB; length of CMC 8911 = 41 mm, height of the anteriormost centrum = 58 mm, width of the anteriormost centrum = 60 mm.

Nekwervels van een pasgeboren baleinwalvis uit het Pliocene van Italië (MGB CMC 8911). A, de nek in zijzicht (maatstreep in cm). B, de nek (in de linker benedenhoek) vergeleken met andere nekgebieden van kleine Pliocene baleinwalvissen aanwezig in MGB; lengte van CMC 8911 = 41 mm, hoogte van het voorste centrum = 58 mm, breedte van het voorste centrum = 60 mm.

McLeod *et al.* (1993) supported the close connection of balaenids and neobalaenids observing that they share the ventral displacement of the glenoid fossa and zygomatic portion of the squamosal, the posterior extension of the pterygoids beneath the basicranium, and the presence of numerous and thin baleen plates (Fig. 16a). In a previous attempt to explain the phylogeny of mysticetes with emphasis on the relationships of gray whales, Barnes & McLeod (1984) added to this evidence also the sharing of fused cervical vertebrae. The close relationship of Balaenidae and Neobalaenidae was subsequently confirmed by Bisconti (2000) on a cladistic ground.

McLeod *et al.* (1993) and Bisconti (2000) considered Balaenidae as a rather derivate family. This opinion disagrees with those expressed by Winge (1921), Kellogg (1928), and Fraser & Purves (1960) who considered that balaenids and neobalaenids are quite basal among the mysticetes. A primitive status for Balaenidae was also suggested by Barnes (1984) who, in his fig. 1, hypothesized that the ancestors of Balaenidae should be searched among the direct derivatives of archaic toothed mysticetes (Aetiocetidae). Barnes (1984) suggested also that the Neobalaenidae are close relatives of Balaenidae. That analysis was not supported by a list with shared derivate characters by Neobalaenidae and Balaenidae to the exclusion of other mysticete families. Barnes (1984) spent some words about the Early Miocene *Morenocetus parvus* and stated that it does not provide an obvious link to other mysticete families, an observation subsequently remarked also by Fordyce & Barnes (1994).

However, when one looks at the skull of *Morenocetus parvus* (Fig. 6), it is evident that this form displays a combination of characters that is shared with both balaenids and neobalaenids: in particular, the flat and posteriorly-oriented supraorbital process of the frontal, and the round anterior process of the supraoccipital shield. Apart from these two connecting features, the other aspects of the skull morphology of this form are more balaenid-like.

Only two studies addressed the problem of the intra-family relationships of Balaenidae. McLeod *et al.* (1993) did an extensive effort and reviewed the whole fossil record of Balaenidae but their phylogenetic analysis focused on the living species only (Fig. 16a). They were able to confirm the monophyly of Balaenidae but did not analyse the relationships of the fossil taxa to the living ones. Bisconti (2000) provided a cladistic treatment of the balaenid fossil record recognizing two main groups: one formed by *Balaena mysticetus* and *Balaena montalionis*, and another formed by the genus *Balaenula*, *Morenocetus parvus*, *Eubalaena glacialis* and "*Balaena*" *belgica* (Fig. 16b-c). However, the position of "*Balaena*" *belgica* was not completely solved and the close relationship between *Morenocetus parvus* and the genus *Balaenula* is not convincing. I am currently studying the phylogeny of Balaenidae including the fossil record and new results are anticipated that should shed light on the intra-family relationships of these sophisticated organisms.

In conclusion, while the whole morphological evidence points to a close link of balaenids and neobalaenids, there is no complete agreement concerning the phylogenetic position of Balaenidae among the Mysticeti. In fact, early studies considered balaenids as an early-diverging group, and more recent works considered them as derivate forms.

The molecular evidence

In the past ten years, several gene sequences have been investigated to get a complete reappraisal of mysticete phylogeny. Mitochondrial DNA (mtDNA), ribosomal DNA (12S and 16S rDNA), cytochrome *b*, γ -fibrinogen, κ -casein exon 4, β -casein exon 7, β -casein intron 7, and protamine P1, were all used in phylogenetic analyses of

baleen whales including Balaenidae. However, results were discordant.

The position of Balaenidae among the mysticetes was assessed by cytochrome *b* and chromosomal quantitative traits by Árnason & Gullberg (1994), Árnason & Ledje (1992), and Gatesy (1998) who found similar results in that Balaenidae were basal to the other living mysticete families (Fig. 16d-e). Árnason & Gullberg (1994) found that Balaenidae were not closely linked to Neobalaenidae and their results received supports from other previously published sources of molecular and chromosomal evidences (Árnason & Ledje, 1992; Árnason *et al.*, 1993). In these works, Neobalaenidae are more closely related to Balaenopteridae than Balaenidae. These results strongly

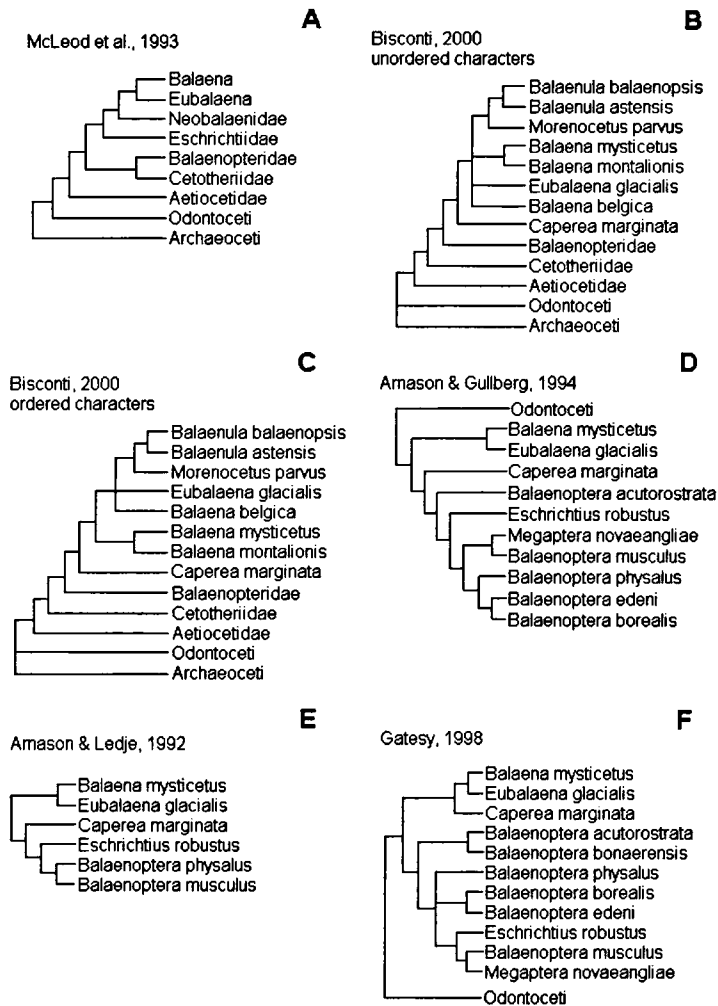


Fig. 16 Hypotheses on phylogenetic relationships of Balaenidae. A, McLeod *et al.* (1993). B and C, Bisconti (2000). D, Árnason & Gullberg (1994). E, Árnason & Ledje (1992). F, Gatesy (1998)

Enkele veronderstelde fylogenetische verwantschappen van de familie van de baleinwalvissen. Voor de bronnen, zie Engelstalig onderschrift

contrast with those provided by Gatesy (1998) who, in his extensive treatment of mammalian genome, found that Balaenidae and Neobalaenidae form a monophyletic group (Fig. 16f), a result according with the morphology-based outputs of McLeod *et al.* (1993) and Bisconti (2000).

Árnason & Gullberg (1994) found also that the molecular variation of cytochrome *b* is so reduced in balaenids that there should not be any reason to distinguish the living forms into two different genera; Árnason & Gullberg (1994) suggested using only one taxonomical name for the living balaenids, i.e., *Balaena*.

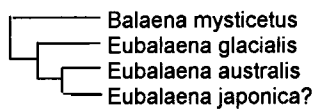


Fig. 17 Rosenbaum *et al.*'s (2000) hypothesis of phylogenetic relationships within Balaenidae

Rosenbaum *et al.*'s (2000) hypothese van de fylogenetische verwantschappen binnen de familie van de Balaenidae (baleinwalvissen)

In recent years, the phylogeny of Balaenidae has been assessed by molecular analyses of mtDNA extracted from baleen of museal specimens and from living individuals (Rosenbaum *et al.*, 2000; Malik *et al.*, 2000; Perrin & Brownell, 2001). The analyses did not focus on the position of balaenids among the mysticetes, but they were centered on the reciprocal relationships of the three main balaenid populations belonging to the genus *Eubalaena*. Despite the small variation observed by Árnason & Gullberg (1994), Rosenbaum *et al.* (2000) found enough differences to distinguish three different groups within the genus *Eubalaena* that correspond to differently-distributed populations: a population inhabiting the North Atlantic ocean, another inhabiting the North Pacific ocean, and a third one inhabiting the Antarctic waters (Fig. 17). These three populations received different taxonomical names under a phylogenetic concept of species: the North Atlantic right whales correspond to *Eubalaena glacialis*, those from the Antarctic waters correspond to *Eubalaena australis*, but it was necessary to propose another name for the right whales inhabiting the North Pacific. This population was given the name *Eubalaena japonica*.

The molecular study of Rosenbaum *et al.* (2000) provided the first attempt to characterise the molecular diversity of the genus *Eubalaena*, and it strongly suggests that three different species belonging to this genus are currently living. Bisconti (2002) critically discussed the study of Rosenbaum *et al.* (2000) remarking the absence of morphological characters distinguishing *Eubalaena glacialis* and *E. australis* from *E. japonica*. This is a major limit of the molecular results of Rosenbaum *et al.* (2000) when applied to the fossil record.

A synthesis?

After this survey, it appears that the evolutionary history of Balaenidae is a field open to new investigations. The lack of agreement of molecular and morphological data points to more detailed treatments of both phenotypic and genotypic sources of evidence until a consensus of view will emerge. It is obvious that molecular works cannot include fossil forms into their analyses and this is a major limit of gene-based phylogenetic studies (Smith, 1998). However, morphological analyses cannot use as many characters as those using molecules (see Peterson & Eernisse, 2001 for analyses using high amount of DNA information). Each approach has its proper advantages and shortcomings.

What emerges from the above outline of phylogenetic studies on Balaenidae is that there is some consensus about the close relationship of Balaenidae and Neobalaenidae, a consensus deriving from both morphology (McLeod *et al.*, 1993; Bisconti, 2000) and molecules (Gatesy, 1998). Another consensus of view emerging from both fields concerns the relationships of the living balaenids; in fact, McLeod *et al.* (1993), Bisconti (2000) and Rosenbaum *et al.* (2000) found that the living forms are different enough to belong to different genera. I think that before accepting the further subdivision of the genus *Eubalaena* as proposed by Rosenbaum *et al.* (2000), a thorough morphological test should be carried out on significant samples of the three different populations of Right whales. This test could be performed by a geometrical-morphometrical approach or traditional qualitative morphological analyses; if morphological differences will be found, it is likely that they are very small. However, small differences are sufficient to subdivide the genus *Eubalaena* in three different species under a phylogenetic species concept.

A thorough phylogenetic analysis of Balaenidae should include the fossil record. This is because

the fossil taxa provide the chronology of the branching events along the rami of the phylogenetic tree of the family. The chronology is necessary to get complete information about the timing of divergence of the living forms from their last common ancestor. This information is crucial in studies assessing the genetic health of the Bowhead and Right whales (Eldredge & Novacek, 1985; Smith, 1998; Gingerich & Uhen, 1998; Bajpai & Gingerich, 1998; O'Leary & Uhen, 1999; Wilf *et al.*, 2000). Unfortunately the relationships of living and fossil balaenids were insufficiently treated in previous studies mainly because it was difficult to have a realistic picture of how many of the established fossil taxa were valid and how many of them were *nomina dubia* or *nomina nuda*. McLeod *et al.* (1993) provided a first detailed revision of the fossil record and the present study represents a further development of that work. After these two studies, the taxonomical situation of Balaenidae would be clear enough to allow a detailed phylogenetic analysis including the fossil record.

The first expected result of such a study would be the close relationship between *Eubalaena* and *Balaenula* as defined in this work. In fact, these genera share the right angle between frontal and rostrum, the irregular arc formed by the dorsal outline of the skull, and the irregular arc formed by the rostrum. A close connection between *Eubalaena* and "*Balaena*" *belgica* is also expected given their sharing of the supraoccipital and frontal morphology; this result would put "*Balaena*" *belgica* into the genus *Eubalaena*. The genus *Balaena* is expected to comprise *Balaena mysticetus* and *Balaena montalionis*; the new genus and species from North Sea (NMB42001) is expected to be the closest relative to the genus *Balaena*. The relationships of *Morenocetus parvus* and *Balaena primigenius* remain unclear.

The position of Balaenidae among the Mysticeti needs to be assessed, also including those characters that seem to link balaenids to eschrichtiids and those making neobalaenids more similar to balaenopterids. A close relationship of balaenids and eschrichtiids would be supported by the sharing of an arched rostrum (however, the rostrum of eschrichtiids is not so arched). The connection of neobalaenids to balaenopterids seems more robust because it is supported by the sharing of a manus with four digits, antibrachium (radius and ulna) longer than humerus, triangular occipital condyles located mainly under the foramen magnum, straight radius, and absence of the tensor tympanic groove from the periotic.

However, there are at least ten derivate characters that link neobalaenids to balaenids (angular process of dentary round and small, supraoccipital superimposes onto the parietal and excludes it from the exposition at cranial vertex, coronal suture always posterior to the anterior process of supraoccipital shield, anterior attach for muscle temporalis developed from the postorbital corner of the supraorbital process of frontal to the posterolateral corner of nasal bone, dorsoventrally compressed tympanic bulla, conical process of tympanic bulla low, tympanic bulla transversely enlarged, internal opening of the facial canal small (relative to the internal acoustic meatus), deep and cylindrical, zygomatic process of squamosal shortened, cervical vertebrae fused) and these should be enough to further affirm the monophyly of the superfamily Balaenoidea.

A biogeographic perspective

Despite the lack of consensus about the intra-family relationships of Balaenidae, it is unanimously recognized that the ranges of the living species are quite well distinct (Perry *et al.*, 1999). It is especially worth noting that the right whales inhabit both northern and southern oceans and the northern populations are divided from the southern ones by the tropics (Fordyce, 1984; Davies, 1963). This is what is said to be an antitropical distribution (see Briggs, 1987 for further explanations of the terms).

There are clues suggesting that Balaenidae originated in the southern hemisphere. In fact, the most ancient and primitive balaenid occurs in Early Miocene sediments of South America, and the most likely close relative of Balaenidae, (i.e., the neobalaenid *Caperea marginata*) is distributed in the southern oceans. The fossil record is not of help in determining when the balaenids invaded the northern hemisphere. It is a matter of fact that early in the Pliocene, balaenids were highly diversified in both the North Atlantic and the North Pacific and this points to an earlier invasion of those areas.

Rosenbaum *et al.* (2000) proposed that the genus *Eubalaena* originated in the northern hemisphere and subsequently invaded the southern oceans during a period characterised by cold climate. In fact, *Eubalaena* filter feeds in cold waters and it is likely that during one of the glaciations occurring during the Pliocene or Quaternary it expanded its range including also what are now the tropics. The re-establishment of temperate conditions

would have caused the subdivision of the genus' range by the interposition of the present tropical zone. Fordyce (1989) mentioned the presence of balaenids from the Late Miocene and Early Pliocene of New Zealand that are however not yet formally described. These fossils could help to chronologically place the entrance of modern Right whales into the southern waters.

The Pliocene distribution of the genus *Balaenula* is an interesting case study in balaenid paleobiogeography. This genus is known from the Early Pliocene of the North Sea, the Mediterranean, the North West and North East Pacific. This distribution suggests that an earlier dispersion led to the invasion of all these ocean basins. This dispersion would be basal Pliocene or latest Miocene in age. Barnes (1976) reported of a Late Miocene-to-Early Pliocene *Balaenula* from California, which suggests that the genus was living before the beginning of the Pliocene. The genus *Balaenula* became globally extinct during the Pliocene, or more precisely, after three million years ago, the date which corresponds to the age of the Italian *Balaenula astensis*. The extinction occurred after the evolution of advanced traits in two different species (i.e., a high encephalization in *Balaenula astensis*, and a differently-shaped periotic in *Balaenula balaenopsis*). These differences suggest that each of the three described species evolved separately from the others. It is yet unclear if the Californian form was co-specific of the Japanese one or if it represents another species of the genus.

Another case study in balaenid paleobiogeography is represented by the absence of the genus *Eubalaena* from the Mediterranean. *Eubalaena glacialis* is only occasionally sighted in this sea (Capellini, 1877; Gasco, 1878; Maio *et al.*, 2001) but its presence has been recently documented in the early Late Pliocene (Bisconti, 2002). Cetacean communities of the Mediterranean waters are presently dominated by the fin whale *Balaenoptera physalus* while other mysticetes are demographically marginal (Notarbartolo di Sciara *et al.*, 1993). This situation seems a case of competitive exclusion but it is yet unclear why and when the Right whales were excluded from the basin. A working hypothesis could be that the exclusion occurred when the orogeny of the Appennines (that form the North-West to South-East axis of the Italian peninsula) erased the breeding areas in the waters of Central Italy, as documented by the presence of newborn remains during the Pliocene time. However, this hypothesis needs further studies to be tested positively or negatively.

Conservation issues

Balaenids are among the most endangered mammal species in the world. The status of the living Right whales (*Eubalaena glacialis* and *australis*) has been recently assessed as critical in the North Pacific, the North Atlantic, and the Antarctic seas (Perry *et al.*, 1999). The status of the Bowhead whale *Balaena mysticetus* is even more critical due to the massive contraction experienced by its populations during about two centuries of intense hunting (Gaskin, 1986). Each year, several million dollars are provided by different national and international organizations to study and manage balaenid populations (Montague, 1993; Fujiwara & Caswell, 1999) but there is not yet any accord about the amount of their recovery or if a recovery really exists (Christensen *et al.*, 1992; Best *et al.*, 1993; Caswell *et al.*, 1999; Fujiwara & Caswell, 2001; but see also NOAA, 2001; Pittman, 2001; Stevens, 2002).

It seems that there is not any industrial whaling currently in progress on balaenid populations but only some forms of aboriginal hunt are performed by different human cultures especially in the Russian and Canadian Arctic (Reeves, 2002; Clapham, 1999). In Canada, this kind of hunt has been responsible of the removal of about 280 Bowheads in the last five years but Canadian authorities say that this aboriginal whaling is sustainable (Reeves, 2002). The aboriginal whaling is a kind of human behavior that some people want to preserve because it represents a source of human diversity in culture and economy, and because it has relevance in our understanding of the cultures of people inhabiting North America and northern Russia before their coming into contact with the European civilization (Reeves, 2002). However, there are evidences that the way in which some of these aboriginal whalers perform their hunts are profoundly influenced by modern technology; in fact, aboriginal whalers from Alaska are known to be occasionally assisted by aircraft and oil industry support vessels to move the bodies of the killed whales; moreover, the weapons used to kill the whales by Alaskan and other aboriginal whalers are modern darting or shoulder guns (Stoker & Krupnik, 1993).

Clapham (1999) listed several factors affecting the extinction risk of baleen whales: among them, there are the aboriginal hunt, collisions with vessels, entanglement in net traps, and destruction of habitats. It is likely that these factors interact in complex ways and their net effect on

Table 9 Revised taxonomy of fossil Balaenidae. References indicated in the table: 1, Van Beneden (1872, 1878, 1880); 2, Trevisan (1941); 3, Pilleri (1987); 4, Bisconti (2000); 5, Cuscani-Politi (1961); 6, Excavation Research Group for the Fukagawa Whale Fossil (1982); 7, Del Prato (1900); 8, Capellini (1873); 9, Capellini (1876); 10, Capellini (1902); 11, Abel (1941); 12, Plisnier-Ladame & Quinet (1969); 13, McLeod *et al.* (1993); 14, Capellini (1904); 15, De Meuter & Laga (1976); 16, Ferrero & Pavia (1996); 17, Gandin & Sandrelli (1992); 18, Signorini (1967); 19, Monegatti & Raineri (1987); 20, Dominici *et al.* (1995); 21, Janssen (1974); 22, Nuyts (1990); 23, Hoedemakers & Marquet (1992).

Herziene taxonomie van fossiele walvisachtigen (Balaenidae). Voor referenties in de tabel, zie het Engelstalige bovenschrijft.

Old designation	New designation	References	Age (and stratigraphic references)
<i>Balaena primigenius</i>	Balaenidae gen. ind.	1	Pliocene s.l. (Scaldisian) (15)
<i>Balaenotus insignis</i>	<i>Balaenotus insignis</i>	1	Pliocene s.l. (Scaldisian) (15)
<i>Balaenula balaenopsis</i>	<i>Balaenula balaenopsis</i>	1	Pliocene s.l. (Scaldisian) (15)
<i>Balaenula astensis</i>	<i>Balaenula astensis</i>	2, 3, 4	Early Piacenzian (16)
<i>Balaenula praediolensis</i>	Balaenidae gen. ind.	5	Early Zanclean (17, 18)
<i>Balaenula</i> sp. (Japan)	<i>Balaenula</i> sp. nov.	6, 13	Early Zanclean (6, 13)
<i>Balaena paronai</i>	Balaenidae gen. et sp. ind.	7	Early Piacenzian (19)
<i>Balaena etrusca</i>	Balaenidae gen. et sp. ind.	8, 9, 10	Early Zanclean (17, 18)
<i>Balaena belgica</i>	<i>Eubalaena belgica</i>	11, 12, 13	Early Pleistocene (Merxemien) (15)
<i>Balaena montalionis</i>	<i>Balaena montalionis</i>	14, 3, 4	Early Zanclean (20)
NMB 42001	Balaenidae gen. et sp. nov.	in progress	Late Zanclean (21, 22, 23)

balaenid populations is difficult to predict. Current efforts are devoted to the study of the genetic health of Balaenidae (in terms of DNA variability) and toward saving single individuals from entangling traps (Center for Coastal Studies, 2001).

A study of the genetic health of living balaenids has been recently performed by Rooney *et al.* (2001) who analyzed the genetic variation of *Balaena mysticetus*. They considered that the Bowhead diverged from the living Right whales during the Pliocene (about 4 million years ago) and based their analyses of mutation rate on this date. Bearing these assumptions in mind, they found that the genetic variation of the living Bowheads is good and there is enough variability to support the recovery of the species. However, the divergence between Bowhead and Right whales may be much older than estimated by Rooney *et al.* (2001) based on McLeod *et al.* (1993) data. In fact, a comprehensive phylogeny of Balaenidae is necessary to estimate the divergence of these whales from their last common ancestor. The estimate made by McLeod *et al.* (1993) was based on a balaenid phylogeny including only the living species. A more comprehensive analysis of balaenid phylogeny is required to confirm or reject that estimate; this new study should comprise all living and fossil balaenids. If analyses of the genetic health of mysticetes will be taken into ac-

count, which contribute to conservation plans, then paleontological data will be of extreme importance to provide phylogenies from which dates of divergence can be extrapolated by statistical or stratigraphic inferences. In this sense, paleontology can help balaenids and other baleen whales escape from extinction.

Summary and prospectus

The evolutionary history of Balaenidae is not yet completely understood. Several taxa are known from the fossil record but their relationships to the living forms are far from being completely solved. The phylogenetic position of *Balaenotus* and *Balaenula* should be cleared far better in the future and the times of divergence of the principal balaenid radiations should be obtained from a well-solved phylogeny of the family. These goals are of interest not only for paleontologists and evolutionary biologists, but also for conservation biologists and national and international organizations that plan conservation strategies for these whales. A better understanding of balaenid spatio-temporal use of past environments (e.g., the Central Mediterranean sea during the Pliocene) should help in planning what habitats to preserve today in order to assist Right and Bowhead whales in their recovery from the

human-induced population contraction of the last century.

Balaenids represent a unique combination of adaptive characters that allow them to exploit enormous reserves of slowly moving zooplankton. These characters were in place about 23 million years ago and maybe before. The subsequent evolution of these animals included a wide radiation of large-sized and small-sized taxa that co-existed in several ocean basins. The nature of this co-existence is still poorly understood.

The maximum abundance of fossil balaenids is observed in Early-to-Middle Pliocene sediments of the Mediterranean, the North Sea, the North-West Atlantic, and the North-West Pacific. The reason of this Pliocene rise of balaenids is unclear but it can probably be connected to the massive turnover experienced by mysticete communities all around the world during the transition from Miocene to Pliocene. In fact, in this period, the previously dominant cetotheres became largely extinct and a modern fauna comprising medium-to-large sized balaenopterids and balaenids became dominant (Whitmore, 1994).

Future studies on balaenid evolution should focus on the description of new fossil records and the interpretation of their phylogenetic history. In fact, a well-solved and unambiguous phylogeny can be highly helpful in obtaining paleobiogeographic, paleoecological, and temporal information to use in planning conservation strategies to preserve these fascinating but vulnerable marine mammals.

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Post scriptum

After the submission of the present paper, a new Pliocene species of Balaenidae has been described by Westgate & Whitmore (2002) from the Yorktown Formation of the eastern United States. It has been named *Balaena ricei* and very closely resembles the living *Balaena mysticetus*. This new species seems more closely related to the living bowhead whale than the fossil *Balaena montalionis*. The phylogenetic position of *Balaena ricei* has not yet been investigated but it deserves attention, because its close resemblance to *B. mysticetus* suggests that *B. montalionis* is a representative of a rather different Balaenidae lineage, a lineage maybe more closely related to the new genus from North Sea outlined in this paper.

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Literature

- Abel, O., 1941. Vorläufige Mitteilungen über die Revision der fossilen Mysticoceten aus dem Tertiär Belgiens. *Bulletin du Museum Royal d'Histoire Naturelles du Belgique* 17, 32: 1-29.
- Árnason, U., & A. Gullberg, 1994. Relationship of baleen whales established by cytochrome *b* gene sequence comparison. *Nature* 367: 726-728.
- Árnason, U., & C. Ledje, 1992. The use of highly repetitive DNA for resolving Cetacean and Pinniped phylogenies. In: Szalay, F.S., Novacek, M.J., & M.C. McKenna (eds). *Mammal Phylogeny* 2: 74-80. New York: Springer Verlag.
- Árnason, Ú., Gullberg, A., & B. Widegren, 1993. Cetacean mitochondrial DNA control region: sequences of all extant baleen whales and two sperm whale species. *Molecular Biology and Evol.* 10, 5: 960-970.
- Bajpai, S., & P.D. Gingerich, 1998. A new Eocene archaeocete (Mammalia, Cetacea) from India and the time of origin of whale. *Proceedings of the National Academy of Sciences USA* 95: 15464-15468.
- Baker, A.N., 1985. Pygmy right whale *Caperea marginata* (Gray, 1846). In: Ridgway, S.H., & R. Harrison (eds). *Handbook of marine mammals* 3: 345-354. New York: Academic Press.
- Barnes, L.G., 1976. Outline of eastern North Pacific fossil cetacean assemblage. *Syst. Zoology* 25: 321-343.
- Barnes, L.G., 1984. Whales, dolphins and porpoises: origin and evolution of the Cetacea. In: Gingerich, P.D., & C.E. Badgley (eds). *Mammals. Notes for a short course. Studies in Geology* 8: 139-154.
- Barnes, L.G. & S.A., McLeod, 1984. The fossil record and phyletic relationships of Gray Whales. In: Jones, M.L., Leatherwood, S., & S. Swartz (eds). *The Gray Whale*: 3-32. Orlando: Academic Press.
- Beddard, F.E., 1902. Contribution towards a knowledge of the osteology of the Pygmy whale (*Neobalaena marginata*). *Transactions of the Zoological Society* 16: 87-115.
- Beisner, B.E., McCauley, E., & F.J. Wrona, 1997. The influence of temperature and food chain length on plankton predator-prey dynamics. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 586-595.
- Best, P.B., 1993. Increase rates in severely depleted stocks of baleen whales. *ICES Journal of Marine Sciences* 50: 169-186.
- Bianucci G., 1996. I cetacei fossili del museo di Storia Naturale dell'Università di Pisa. *Atti della Società Toscana di Scienze Naturali* 103: 63-68.
- Bianucci, G., Bisconti, M., Landini, W., Storai, T., Zuffa, M., Giuliani, S., & A. Mojetta, 2002. Mediterranean white shark-cetaceans interactions through time: a comparison between Pliocene and Recent data. In: Vacchi, M., La Mesa, G., Serena, F., & B. Séret (eds). *Proceedings of the 4th European Elasmobranch Association Meeting, Livorno (Italy), ICRAM, ARPAT & SFI, 2000*: 33-48.
- Bisconti, M., 1998. Revisione dei crani fossili di Mysticeti del Museo di Storia Naturale dell'Università di Pisa. *Considerazioni anatomo-comparative e filogenetiche*. University of Pisa, 188 pp; unpubl.
- Bisconti, M., 2000. New description, character analysis and preliminary phyletic assessment of two Balaenidae skulls from the Italian Pliocene. *Palaeontographia Italica* 87: 37-66.
- Bisconti, M., 2002. An early Late Pliocene right whale (genus *Eubalaena*) from Tuscany (Central Italy). *Boll. della Società Paleontologica Italiana* 41, 1: 83-91.
- Briggs, J.C., 1987. Antitropical distribution and evolution in the Indo-West Pacific ocean. *Systematic Zoology* 36, 3: 237-247.
- Burns, J.J., Montague, J.J., & C.J. Cleveland, 1993. The Bowhead Whale. *The Society for Marine Mammalogy Special Publication* 2: 1-787.
- Cabrera, A., 1926. Cetáceos fósiles del Museo de La Plata. *Revista del Museo de La Plata* 29: 363-411.
- Capellini, G., 1872. Resoconto della Riunione Straordinaria della Società Italiana di Scienze Naturali a Siena nel Settembre 1872. *Atti della Società Italiana di Scienze Naturali* 15: 219.
- Capellini, G., 1873. Sulla *Balena etrusca*. *Memorie dell'Accademia delle Scienze dell'Istituto di Bologna* 3: 3-23.
- Capellini, G., 1876. Sulle balene fossili toscane. *Atti della Reale Accademia dei Lincei* 3: 3-8.
- Capellini, G., 1877. Della balena di Taranto confrontata con quelle della Nuova Zelanda e con talune fossili del Belgio e della Toscana. *Atti dell'Accademia delle Scienze dell'Istituto di Bologna* 7: 1-34.
- Capellini, G., 1902. Balene fossili toscane. I. *Balaena etrusca*. *Memorie della Regia Accademia delle Scienze dell'Istituto di Bologna* 5, 9: 759-783.
- Capellini, G., 1904. Balene fossili toscane. II. *Balaena montalioniis*. *Memorie della Regia Accademia delle Scienze dell'Istituto di Bologna* 6, 1: 45-57.
- Caswell, H., Fujiwara, M., & S. Brault, 1999. Declining survival probability threatens the North Atlantic right whale. *Proceedings of the National Academy of Sciences USA* 96: 3308-3313.
- Center for Coastal Studies, 2001. Review of the 2001 Atlantic large whale disentanglement season. At <http://www.coastalstudies.org/rescue/01summary.htm>
- Christensen, I., Haug, T., & N. Øien, 1992. Seasonal distribution, exploitation and present abundance of stocks of large baleen whales (Mysticeti) and sperm whale (*Physeter macrocephalus*) in Norwegian and adjacent waters. *ICES J. of Marine Science* 49: 341-355.

- Compton, J., Mallinson, D., Glenn, C.R., Filippelli, G., Föllmi, K., Shields, G., & Y. Zanin, 2000. Variations in the global Phosphorus cycle. Society for Sedimentary Geology Special Publication 66: 21-33.
- Cummings, W.C., 1985. Right Whales *Eubalaena glacialis* (Müller, 1776) and *Eubalaena australis* (Desmoulin, 1822). In: Ridgway, S.H., & R. Harrison (eds). Handbook of marine mammals 3: 275-304. New York: Academic Press.
- Cusciani Politi, P., 1960-61. Ancora una nuova specie di *Balaenula* pliocenica con considerazioni introduttive su alcuni mysticeti dei nostri musei. Atti dell'Accademia dei Fisiocritici in Siena 2, 8: 3-31.
- Cuvier, G., 1823. Recherches sur les ossemens fossiles, où l'on rétablit les caractères de plusieurs animaux dont les révolutions du globe ont détruit les espèces. Paris: Dufour et d'Ocagne, pp. 308-396.
- Dayan, T., Simberloff, D., Tchernov, E., & Y. Yom-Tov, 1991. Calibrating the paleothermometer: climate, communities, and the evolution of size. Paleobiology 17, 2: 189-199.
- Del Prato, A., 1900. Balena fossile del piacentino. Rivista italiana di Paleontologia 6, 3: 136-142.
- Deméré, T.A., & R. Cerutti, 1982. A Pliocene shark attack on a cethotheriid whale. Journal of Paleontology 56, 6:1480-1482.
- De Meuter, F.J., & P.G. Laga, 1976. Lithostratigraphy and biostratigraphy based on benthonic Foraminifera of the Neogene deposits of northern Belgium. Bull. de la Société Belge de Géologie 85, 4: 133-152.
- Dominici, S., Mazzanti, R., & C. Nencini, 1995. Geologia dei dintorni di San Miniato tra l'Arno, l'Elsa e l'Era. Quaderni del Museo di Storia Naturale di Livorno, Suppl. 1: 1-35.
- Eldredge, N., & M.J. Novacek, 1985. Systematics and paleobiology. Paleobiology 11, 1: 65-74.
- Excavation Research Group for the Fukagawa whale fossil, 1982. Research report on the Pliocene *Balaenula* (Suborder Mysticoceti) collected from Fukagawa City, Hokkaido. Fukagawa City, 131 pp.
- Ferrero, E., & G. Pavia, 1996. La successione marina pre-villanoviana. In Carraro, F. (ed.). Revisione del Villafranchiano nell'area-tipo di Villafranca d'Asti. Il Quaternario 9, 1: 36-38.
- Fordyce, R.E., 2002. Oligocene origins of skim-feeding right whales: a small archaic balaenid from New Zealand. At <http://www.vertpaleo.org/meetings/Abstracts02.pdf>.
- Fordyce, R.E. & L.G. Barnes, 1994. The evolutionary history of whales and dolphins. Annual Review of Earth and Planetary Sciences 22: 419-455.
- Fraser, F.C., & P.E. Purves, 1960. Hearing in cetaceans. Bulletin of the British Museum (Natural History), Zoology 7, 1: 1-140.
- Fujiwara, M. & H. Caswell, 2001. Demography of the endangered North Atlantic right whale. Nature 414: 537-541.
- Gandin, A., & F. Sandrelli, 1992. Caratteristiche sedimentologiche dei corpi sabbiosi intercalati nelle argille plioceniche del Bacino di Siena. Giornale di Geologia 54, 1: 55-65.
- Gasco, F., 1878. Intorno alla balena presa in Taranto nel febbrajo 1877. Rendiconti dell'Accademia di Scienze Fisiche e Matematiche 1877, 12: 1-47.
- Gaskin, D.E., 1986. The ecology of whales and dolphins. London: Heineman, 459 pp.
- Gatesy, J., 1998. Molecular evidence for the phylogenetic affinities of Cetacea. In: Thewissen, J.G.M. (ed.). The emergence of whales. Evolutionary patterns in the origin of Cetacea: 63-112. New York and London: Plenum Press.
- Geisler, J.H., & Z. Luo, 1996. The petrosal and inner ear of *Herpetocetus* sp. (Mammalia: Cetacea) and their implications for the phylogeny and hearing of archaic mysticetes. J. of Paleontology 70, 6: 1045-1066.
- Gervais, P., 1872. Coup d'oeil sur les Mammifères fossiles de l'Italie. Bulletin de la Société Géologique de France 29: 92-103.
- Gingerich, P.D., & M.D. Uhen, 1998. Likelihood estimation of the time of origin of Cetacea and the time of divergence of Cetacea and Artiodactyla. Palaeontologia Electronica 1, 2: 1-28.
- Gray, J.E., 1825. Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently appertaining to each tribe. Philosophical Annals 26: 337-344.
- Hemilä, S., Nummela, S., & T. Reuter, 2001. Modeling whale audiograms: effects of bone mass on high-frequency hearing. Hearing Research 151: 221-226.
- Hoedemakers, K., & R. Marquet, 1992. Lithostratigraphy of Pliocene deposits in the Liefkenshoek-tunnel construction works near Kallo (NW Belgium). Contributions to Tertiary and Quaternary Geology 29, 1-2: 21-25.
- Janssen, A.W., 1974. Met profiel van de bouwput onder het Eerste Kanaaldok nabij Kallo, Provincie Oost Vlaanderen, België. Med. van de Werkgroep voor Tertiaire en Kwartaire Geologie 11, 4: 173-185.
- Kellogg, R., 1928. The history of whales - Their adaptation to life in the water. The Quarterly Review of Biology 3, 1: 29-76, and 3, 2: 174-208.
- Kerfoot, W.C., 1987. Cascading effects and indirect pathways. In: Kerfoot, W.C. & A. Sih (eds). Predation: 57-70, Hanover: University Press of New England.
- Kimura, T., & T. Ozawa, 2002. A new cetothere (Cetacea: Mysticeti) from the early Miocene of Japan. Journal of Vertebrate Paleontology 22, 3: 684-702.
- Kitchell, J.F., & S.R. Carpenter, 1987. Piscivores, planktivores, fossils, and phorbins. In: Kerfoot, W.C. & A. Sih (eds). Predation: 132-146. Hanover: University Press of New England.

- Kompanje, E.J.O., 1999. Considerations on the comparative pathology of the vertebrae in Mysticeti and Odontoceti; evidence for the occurrence of discarthrosis, zygarthrosis, infectious spondylitis and spondyloarthritis. *Zoölogische Mededelingen* 73, 5: 99-130. Leiden.
- Linnaeus, C., 1758. *Systema naturae, per regna tria naturae*. Lugduni: J.B. Delamolliere (1789), 1: 1-506; Lipsia: Jeorg Emanuel Beer (1791), 2: 1-884.
- Lowry, L.F., 1993. Foods and feeding ecology. In: Burns, J.J., Montague, J.J., & C.J. Cleveland (eds). *The Bowhead Whale*. The Society for Marine Mammalogy Special Publication 2: 201-238.
- Maas, M.C., D.W. Krause, & G. Strait, 1988. The decline and extinction of Plesiadapiformes (Mammalia: ?Primates) in North America: displacement or replacement? *Paleobiology* 14, 4: 410-431.
- Maio, N., Picariello, O., & L. Cagnolaro, 2001. I cetacei del Museo Zoologico dell'Università di Napoli Federico II (Mammalia, Cetacea). *Catalogo della collezione con note osteometriche*. *Natura, Società Italiana di Scienze Naturali del Museo Civico di Storia Naturale, Milano* 90, 2: 71-83.
- Malik, S., Brown, M.W., Kraus, S.D. & B.N. White, 2000. Analysis of mitochondrial DNA diversity within and between North and South Atlantic right whales. *Marine Mammal Science* 16, 3: 545-559.
- Maschenko, E.N., 2002. Individual development, biology and evolution of the woolly mammoth. *Cranium* 19, 1: 4-120.
- McLeod, S.A., Whitmore, Jr., F.C., & L.G. Barnes, 1993. Evolutionary relationships and classification. In: Burns, J.J., Montague, J.J. & C.J. Cowles (eds). *The Bowhead whale*, The Society for Marine Mammalogy, Special Publication 2, 45-70.
- Mead, J.G., & R.L. Brownell Jr., 1993. Order Cetacea. In: Wilson, D.E., & D.M. Reeder (eds). *Mammal species of the world*: 349-364. Washington: Smithsonian Institution Press.
- Miller, Jr., G.S., 1923. The telescoping of the cetacean skull. *Smithsonian Miscellaneous Coll.* 76, 5: 1-55.
- Mills, E.L., Forney, J.L. & K.J. Wagner, 1987. Fish predation and its cascading effect on the Oneida Lake food chain. In: Kerfoot, W.C., & A. Sih (eds). *Predation*: 118-131. Hanover: University Press of New England.
- Monegatti, P., & G. Raineri, 1987. Osservazioni paleoecologiche sulla sezione pliocenica di Rio Stramonte (Piacenza). *Bollettino dell'Accademia Gioenia di Scienze Naturali* 20: 287-308.
- Montague, J.J., 1993. Introduction. In: Burns, J.J., Montague, J.J., & C.J. Cleveland (eds). *The Bowhead Whale*. The Society for Marine Mammalogy, Special Publication 2: 1-21.
- Moore, S.E., & R.R. Reeves, 1993. Distribution and movement. In: Burns, J.J., Montague, J.J., & C.J. Cleveland (eds). *The Bowhead Whale*. The Society for Marine Mammalogy, Special Publ. 2: 313-386.
- Nishiwaki, M., & Y. Hasegawa, 1969. The discovery of the right whale skull in the Kisagata Shell Bed. *Scientific Reports of the Whales Research Institute* 21: 79-84.
- NOAA, 2001. Fourteen Right Whale Calves Sighted in Southern US Waters - January 26, 2001. At <http://whale.wheelock.edu/rightwhale/RightWhaleCalves/>
- Notarbartolo di Sciara, G., Venturino, M.C., Zanardelli, M., Bearzi, G., Borsani, F.J., & B. Cavalloni, 1993. Cetaceans in the central Mediterranean Sea: distribution and sighting frequencies. *Bollettino di Zoologia* 60: 131-138.
- Nummela, S., 1997. Scaling and modeling the mammalian middle ear. *Comments Theoretical Biology* 4, 5: 387-412.
- Nummela, S., 1995. Scaling of the mammalian middle ear. *Hearing Research* 85: 18-30.
- Nummela, S., Wägar, T., Hemilä, S., & T. Reuter, 1999. Scaling of the cetacean middle ear. *Hearing Research* 133: 71-81.
- Nuyts, H., 1990. Note on the biostratigraphy (benthic Foraminifera) and lithostratigraphy of Pliocene deposits at Kallo (Oost-Vlaanderen; Belgium). *Contr. to Tertiary and Quaternary Geology* 27, 1: 17-25.
- Oishi, M., & Y. Hasegawa, 1994. Diversity of Pliocene mysticetes from eastern Japan. *The Island Arc* 3: 436-452.
- O'Leary, M.A., & M.D. Uhen, 1999. The time of origin of whales and the role of behavioral changes in the terrestrial-aquatic transition. *Paleobiology* 25, 4: 534-556.
- Oliver, W.R.B., 1922. A review of the Cetacea of the New Zealand Seas. *Proceedings of the Zoological Society of London* 40: 557-585.
- Perrin, W.F., & R.L. Brownell, 2001. Update of the list of recognised species of cetaceans. *Journal of Cetacean Research and Management* 3, Supplement: 364-367.
- Perry, S.L., DeMaster, D.P., & G.K. Silber, 1999. The right whales. In: Perry, S.L., DeMaster, D.P., & G.K. Silber (eds). *The great whales: history and status of six species listed as endangered under the U.S. Endangered Species Act of 1973*. *Marine Fishery Review* 61, 1: 7-23.
- Peterson, K.J., & D.J. Eernisse, 2001. Animal phylogeny and the ancestry of bilaterians: inferences from morphology and 18S rDNA gene sequences. *Evolution & Development* 3, 3: 170-205.
- Pilleri, G., 1987. *The Cetacea of the Italian Pliocene*. Berne: Brain Anatomy Institute, 155 pp.
- Pittman, C., 2001. Baby boom at sea. At http://www.sptimes.com/News/032001/State/Baby_boom_at_sea.html
- Plisnier-Ladame, F., & G.E. Quinet, 1969. *Balaena belgica* Abel 1938 Cetace du merxemien d'Anvers. *Bulletin de l'Institut Royal des Sciences Naturelles du Belgique* 45, 3: 1-6.

- Prothero, D.R., 1999. Does climatic change drive mammalian evolution? *Geological Society of America Today* 9, 9: 1-7.
- Purdy, R.W., 1996. Paleocology of fossile white sharks. In: Klimney, A.P., & D.G. Ainley (eds). *Great White Sharks: 67-78*. London: Academic Press.
- Reeves, R.R., 2002. The origins and character of 'ab-original subsistence' whaling: a global review. *Mammal Review* 32, 2: 71-106.
- Reeves, R.R., & S. Leatherwood, 1985. Bowhead whale *Balaena mysticetus* Linnaeus, 1758. In: Ridgway, S.H., & R. Harrison R (eds). *Handbook of marine mammals* 3: 305-344. New York: Academic Press.
- Rendiconto delle Sessioni dell'Accademia delle Scienze dell'Istituto di Bologna, 1871. Sessione ordinaria 25 Maggio 1871, 2 pp.
- Rooney, A.P., Honeycutt, R.L., & J.N. Derr, 2001. Population size change of Bowhead whales inferred from DNA sequence polymorphism data. *Evolution* 55, 8: 1678-1685.
- Rosenbaum, H.C., Brownell, Jr., R.L., Brown, M.W., Schaeff, C., Portway, V., White, B.N., Malik, S., Pastene, L.A., Patenaude, N.J., Baker, C.S., Goto, M., Best, P.B., Clapham, P.J., Hamilton, P., Moore, M., Payne, R., Rowntree, V., Tynan, C.T., Bannister, J.L., & R. DeSalle, 2000. World-wide genetic differentiation of *Eubalaena*: questioning the number of right whale species. *Molecular Ecology* 9, 11: 1793-1802.
- Rothman, D.H., 2001. Global biodiversity and the ancient carbon cycle. *Proceedings of the National Academy of Sciences USA* 98, 8: 4305-4310.
- Sanderson, L.R., & R. Wassersug, 1993. Convergent and alternative designs for vertebrate suspension feeding. In Hanken, J., & B.K. Hall (eds). *The Skull* 3: 37-112. Chicago: University Press of Chicago.
- Schaller, O., 1999. *Nomenclatura anatomica veterinaria illustrata*. Roma: Antonio Delfino Editore, 637 pp.
- Signorini, R., 1967. Foglio 120-Siena. Note illustrative della Carta Geologica d'Italia: 1-41. Roma: Servizio Geologico d'Italia.
- Smith, A.B., 1998. What does Palaeontology contribute to Systematics in a molecular world? In: Adoutte, A., Tillier, S., & R. DeSalle (eds). *Molecules and Morphology in Systematics. Molecular Phylogenetics and Evolution, Special Issue* 9, 3: 437-447.
- Stafford, Jr., T.W., Semken, Jr., H.A., Graham, R.W., Klippel, W., Markova, A., Smirnov, N.G., & J. Southon, 1999. First accelerator mass spectrometry ¹⁴C dates documenting contemporaneity of nonanalogue species in late Pleistocene mammal communities. *Geology* 27, 10: 903-906.
- Stevens, L., 2001. Baby boom buoys northern right whale population. At <http://www.fishresearch.org/Articles/2001/03/RightWhale.asp>
- Stoker, S.W., & Krupnik, I.I., 1993. Subsistence whaling. In: Burns, J.J., Montague, J.J. & C.J. Cowles (eds). *The Bowhead Whale*. Society for Marine Mammalogy Special Publication 2: 579-629.
- Tomilin, A.G., 1967. Cetacea. In: Heptner, V.G. (ed.). *Mammals of the USSR and adjacent countries* 9: 1-717. Jerusalem: Israel Program for Scientific Transl.
- Trevisan, L., 1941. Una nuova specie di *Balaenula pliocenica*. *Palaeontographia Italica* 40: 1-13.
- True, F.W., 1904. The whalebone whales of the western North Atlantic compared with those occurring in European waters with some observations on the species of the North Pacific. *Smithsonian Contributions to Knowledge* 33: 1-332.
- Van Beneden, P.-J., 1880. Description des ossements fossiles des environs d'Anvers. Cétacés Genres *Balaenula*, *Balaena* et *Balaenotus*. *Annales du Musée Royal d'Histoire Naturelle de Belgique (Text)* 4, 2:1-83.
- Van Beneden, P.-J., 1878. Description des ossements fossiles des environs d'Anvers. Balénides. *Annales du Musée Royal d'Histoire Naturelle du Belgique (Atlas)* 4, 2: 1-38 plates.
- Van Beneden, P.J., 1872. Les baleines fossiles d'Anvers. *Bulletin de l'Academie Royal de Belgique* 34: 6-20.
- Vanni, M.J., 1987. Indirect effect of predators on age-structured prey populations: planktivorous fish and zooplankton. In: Kerfoot, W.C., & A. Sih (eds). *Predation: 149-160*. Hanover: University Press of New England.
- Westgate, J.W., & F.C. Whitmore, Jr., 2002. *Balaena ricei*, a new species of bowhead whale from the Yorktown Formation (Pliocene) of Hampton, Virginia. In: Emry R.J. (ed.). *Cenozoic mammals of land and sea: Tribute to the career of Clayton E. Ray*. *Smithsonian Contributions to Paleobiology* 93: 295-312.
- Whitmore, Jr, F.C., 1994. Neogene climatic change and the emergence of the modern whale fauna of the North Atlantic ocean. In: Berta, A., & T.A. Deméré (eds). *Contributions in marine mammal paleontology honoring Frank C. Whitmore, Jr*. *Proceedings of the San Diego Society of Natural History* 29: 223-227.
- Wilf, P., Labandeira, C.C., Kress, W.J., Staines, C.L., Windsor, D.M., Allen, A.L. & K.R. Johnson, 2000. Timing the radiations of leaf beetles: hispines on gingers from latest Cretaceous to Recent. *Science* 289: 291-294.
- Winge, H., 1921. A review of the interrelationships of the Cetacea. *Smithsonian Miscellaneous Collection* 72: 1-97.
- Witmer, L.M., 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In: Thomason, J.J. (ed.). *Functional morphology in vertebrate paleontology: 19-33*. Cambridge: Cambridge University Press.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E. & K. Billups, 2001. Trends, rhythms, and aberrations in global climate 65 Ma to Present. *Science* 292: 686-693.