



Taxonomy and evolution of the Italian Pliocene Mysticeti (Mammalia, Cetacea): a state of the art

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ABSTRACT - A review of the recent progresses about Italian baleen whale taxonomy and phylogeny is presented together with a summary of the principal studies carried out on this subject in the past 150 years in Italy. A discussion of the chronospecies *Balaenoptera acutorostrata cuvieri* is presented here which dismisses such taxon in the light of a thorough morphological analysis based upon the examination of a number of mysticete skeletons in the collections of many institutions all over the world. An overview of new mysticete taxa established from the Italian fossil record is also presented together with reconstructions of their skulls. The analysis of the Italian record shows that the Mediterranean basin played a role in the preservation of archaic biodiversity especially concerning the *Balaenopteridae*. The presence of *Eschrichtiidae* is also confirmed based on the newly discovered taxon *Eschrichtioides gastaldi*. The study of the Italian record is, thus, of great help in the reconstruction of the past mysticete biodiversity evolution and in the analysis of the phylogeny of this marine mammal group.

RIASSUNTO - [Tassonomia ed evoluzione dei Mysticeti pliocenici italiani: uno stato dell'arte] - Lo stato degli studi sui Mysticeti pliocenici italiani presentato in questo lavoro deriva da una serie di analisi condotte dall'Università di Pisa e dal Museo di Storia Naturale del Mediterraneo di Livorno. Il lavoro, svolto a partire dal 1996, è cominciato attraverso uno studio della letteratura scientifica, in gran parte ottocentesca, e si è poi sviluppato attraverso l'esame di un gran numero di reperti disseminati in istituzioni universitarie e museali in diverse nazioni (Italia, Belgio, Germania, Olanda, Perù, Repubblica Sudafricana, Stati Uniti). Questo studio comparativo ha permesso l'osservazione di una straordinaria diversità nei misticeti a partire dalle forme più arcaiche, oligoceniche, fino alle specie attualmente viventi. Grazie alla disponibilità di questo materiale di confronto è stato possibile intraprendere lo studio delle collezioni fossili italiane con l'obiettivo di decifrare la diversità morfologica esibita dai misticeti fossili della penisola. In questo lavoro l'attenzione si concentra in particolare sullo stato di avanzamento degli studi sui misticeti fossili pliocenici.

Le famiglie *Balaenidae* (balene franche, balena della Groenlandia) e *Balaenopteridae* (balenottere e megattere) sono state intensamente studiate con il risultato che oggi è finalmente disponibile una revisione tassonomica dei balenidi fossili italiani e una serie di diagnosi differenziali che permettono un agile riconoscimento delle specie in presenza di reperti sufficientemente completi. L'analisi filogenetica dei balenidi pubblicata da Bisconti nel 2005 sulla base della revisione tassonomica di cui sopra ha rivelato che la famiglia consta di due grandi radiazioni: una comprendente l'attuale balena franca (genere *Eubalaena*) che risulta strettamente correlata con le specie pigmee incluse nel genere pliocenico *Balaenula*; l'altra formata dai generi *Morenocetus* (il più antico balenide descritto e collocato cronologicamente all'inizio del Miocene, ca 23 Ma), *Balaenella* (un balenide pliocenico nano scoperto recentemente in Belgio) e *Balaena* (l'attuale balena della Groenlandia e le forme fossili ad essa associate).

Lo studio della diversità morfologica esibita dai balenotteridi pliocenici ha rivelato la presenza di diverse linee filogenetiche non riconducibili direttamente alle specie attualmente viventi. In questo senso, l'interpretazione maggiormente accettata in passato della tassonomia dei balenotteridi fossili italiani (proposta da Caretto nel 1970) che collassava questa diversità morfologica all'interno dell'unica specie attuale *Balaenoptera acutorostrata* nella sottospecie *cuvieri* risulta inadeguata a spiegare la notevole diversità osservata. Nei balenotteridi fossili italiani si trovano forme dalla morfologia arcaica scoperte recentemente (*Archaebalaenoptera castriarquati*) o derivanti da revisione tassonomica di reperti già pubblicati (*Protororqualus cuvieri*) e anche taxa appartenenti ad una famiglia diversa, *Eschrichtiidae* (*Eschrichtioides gastaldi*). La ricostruzione del cranio di questi taxa è riportata in questo articolo insieme con una valutazione delle attuali conoscenze sulle loro relazioni filogenetiche.

INTRODUCTION

The evolutionary history of the suborder Mysticeti has been investigated through the study of their fossil record and by means of a wealth of molecular techniques. This effort resulted in the realization of a considerable body of information. Despite such a multidisciplinary effort, however, a consensus view of their phylogeny (and, consequently, of their palaeobiogeography and, in many respects, taxonomy) is still lacking being morphology-based and molecule-based results different in many points (see comparisons in Bisconti, 2003a).

From a paleontological point of view, the study of the fossil record of this suborder has resulted in the development of a noticeable body of knowledge based upon the description of a number of fossil taxa in the last 170 years. The study of Pliocene mysticetes from Italy,

in particular, has started during the second half of the 18th century based upon specimens found in northern Italy and has continued up to now thanks to new discoveries made in several deposits in the northern, central and southern regions of the peninsula (Cuscani-Politi, 1960-1961; Bisconti, 2003b). The new discoveries of the late 20th century allowed more detailed comparative analyses making it possible a revision of the Italian fossil record under the light of modern-day knowledge of cetacean anatomy and techniques of phylogenetic inference.

Anatomical abbreviations

apmx, ascending process of maxilla; eoc, exoccipital; lpmx, irfr, interorbital region of frontal; lateral process of maxilla; mx, maxilla; n, nasal; nf, narial fossa; o, orbit; p, parietal; pmx, premaxilla; pgl,

postglenoid process of squamosal; soc, supraoccipital; sop, supraorbital process of frontal; sq, squamosal; zsq, zygomatic process of squamosal.

Institutional abbreviations

AMNH, American Museum of Natural History, New York; ChM, The Charleston Museum; IRSN, Institut Royal des Sciences Naturelles du Belgique, Bruxelles; ISAM, IZIKO South African Museum, Cape Town; MCA, Museo Geopaleontologico di Castell'Arquato; MGB, Museo Geopaleontologico, Università di Bologna; MGPT, Museo del Dipartimento di Scienze della Terra, Università di Torino; MPST, Museo Paleontologico di Salsomaggiore Terme; MSNT, Museo di Storia Naturale e del Territorio, Università di Pisa, Calci; NMB, NatuurMuseum Brabant, Tilburg; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington DC; SMNS, Staatliches Museum für Naturkunde, Stuttgart; ZMA, Zoologisch Museum, Amsterdam; ZML, Zoologisch Museum, Leiden.

HISTORY OF 19th CENTURY STUDIES

The history of studies on the fossil record of the Pliocene Italian mysticetes has been partially published by Deméré et al. (2005) and Bisconti (2000, 2003a, 2006, 2007a). In this paper, we provide a historical overview of three phases of this history: (1) the early work of Cortesi (1819) and his influence on the subsequent developments; (2) the works of Capellini with particular emphasis on his 1875 monograph which had a large impact on the scientific thought of subsequent students; (3) and the studies on the fossil record from Piedmont. All these studies are from the 19th century and their present overview is integrative with what has been already published. The analysis of an important work published in 1970 by Caretto is placed in a separate section.

Early works

The first important monograph on Italian fossil mysticetes appeared in 1819 in the form of a series of geological essays written by Giuseppe Cortesi. In his book, Cortesi described several fossil vertebrates including some cetaceans. This work is the first of a series of monographs published over the whole 19th century by many Italian palaeontologists on the mysticete fossil record and its style is a mix of a novel story and a scientific work. That work had surely much more influence than the earlier work of Biancani (1757). Cortesi described three mysticetes that became parts of the collection of the museum (the cabinet) of Parma and Piacenza. One of them is the skeleton from Mount Pulgnasco whose taxonomy and phylogenetic position have been recently re-established (Bisconti, 2007a). The collection of Parma and Piacenza has to be considered the first Italian collection where fossil mysticetes were stored and studied. Cortesi described the morphology of the specimens together with the taphonomic context and the geological situation of the discovery site. He did not provide conclusions concerning the systematic assignments of these specimens but suggested a link

between the skeleton from Mount Pulgnasco (today *Protororqualus cuvieri*) and the minke whale *Balaenoptera acutorostrata*. Cuvier (1823) followed such a suggestion.

Paleontological works carried out during the 19th century resulted in the discovery of several mysticete remains including almost complete skeletons. These records have been intensely studied mainly by Capellini, Strobel, and Portis. Foreign students contributed to the analysis of the Italian Pliocene mysticetes adding detailed observations and descriptions (e.g., Gervais, 1872; Brandt, 1873; Van Beneden, 1875). However, it is a matter of fact that Capellini described the highest number of mysticete taxa from the Italian fossil record. His series titled 'Balene fossili toscane', which was published in several papers (Capellini, 1872, 1873, 1876, 1877, 1902, 1904, 1905) spanning the last quarter of the 19th century and the early 20th century, served as a reference for Pliocene balaenids for most of the following 90 years. In that series, Capellini established such taxa as *Balaena montalionis*, *Balaena etrusca*, and *Idiocetus guicciardinii*. While *Balaena etrusca* is no longer considered a valid taxon (Bisconti, 2003a), the other species are still valid. Del Prato (1900) was the only other worker describing a new fossil balaenid from the Italian Pliocene, *Balaena paronai*. Only Strobel and Portis gave contributions as rich in concepts as those of Capellini. Most of their contributions have been reviewed and discussed by Bisconti (2007a) and will be not detailed here.

The landmark work of Capellini (1875)

Italian Pliocene balaenopterid and balaenopterid-like taxa were the focus of investigations of Italian and foreign palaeontologists since the second decade of the 19th century. Cuvier (1823), Gervais (1872), and Brandt (1873) provided their taxonomic interpretations of the Mount Pulgnasco skeleton (today *Protororqualus cuvieri*) and other rorqual-like taxa. Most of the taxonomic history of balaenopterid-like mysticetes has been recently reviewed by Deméré et al. (2005) and Bisconti (2007a, b, 2008) and is not detailed here.

In his 1875 work, Capellini described a partial skeleton discovered in San Lorenzo in Collina (Bologna). That fossil was found in 1862 and was the subject of a 24 m² excavation ended in 1863.

The study published by Capellini in 1875 represents the first Italian translation of the classification system of mysticetes proposed by Brandt (1873), which has been thoroughly discussed by Bisconti (2007a). A preliminary study of the specimen from San Lorenzo in Collina appeared ten years before (Capellini, 1865) at a time when the specimen was still unprepared. In that paper the author described the geology and the palaeontology of the relevant strata.

Capellini incorporated the Brandt's system as a whole in his paper from 1875. He did not criticize any aspect of such a system (Bisconti, 2007a). More interestingly, in the same paper, Capellini wrote a section on the distribution of remains of archaic rorqual-like mysticetes (Cetotheriidae *s.l.*) from Europe that is, in our knowledge, the first attempt to make a summary of the palaeobiogeography of mysticetes. In that section,

Capellini underlined two points: (1) considering that Russia, Austria, and Italy had Pliocene molluscs and land plants so similar (in his knowledge), it was strange that these countries had different mysticete communities; (2) Italy, Austria, and Russia had, however, more similar mysticete communities than North Sea and for this reason Capellini supposed that there was something similar in the geographic placements of these countries (same latitude). Finally, Capellini suggested that the skeleton from San Lorenzo in Collina represents a taxon that is the ancestor of the modern-day humpback whale, *Megaptera novaeangliae*. The general explanations provided by Capellini appear too simple if compared with the increasing body of evidence provided by mysticete palaeontology during the subsequent century. In particular, Capellini's hypotheses were biased by the lack of a high-resolution stratigraphic framework for the whole Europe. In fact, it seems that what Capellini meant with the term Pliocene is somewhat different from what is meant today. However, the study of 1875 is a landmark because represents a fully modern work in methodological terms: there, descriptions, phylogenetic relationships, and palaeobiogeography of a newly discovered taxon are presented. This study represents the most modern paper dealing with fossil mysticetes published during the whole 19th century by an Italian palaeocetologist.

Discoveries in Piedmont

In the same years as those of Capellini activity, other research efforts were carried out in a different Italian area: the Piedmont. Most of the discoveries from this region have been published by Portis (1885) and his work is still a valid help in the reconstruction of the history of cetacean palaeontology in Piedmont all over the 19th century. All the specimens described there were found in what is now known as the Astian facies of the early Late Pliocene (approximately 3 Ma; Ferrero & Pavia, 1996). In his ponderous volume, Portis (1885) describes *Plesiocetus cortesii* and *Balaenoptera gastaldii* (now assigned to *Eschrichtioides gastaldii* by Bisconti, 2008) and his descriptions are fine and detailed and include also some of the first photographic plates ever published by Italian cetologists. These plates are explicative of morphology and no line drawings are published with interpretative text. Portis (1885) described the complete skeleton of a rorqual-like mysticete he assigned to *Plesiocetus* following the assignment of the specimen from Mount Pulgnasco (now assigned to *Protororqualus cuvieri*; Bisconti, 2007a) made by Van Beneden (1875). However, the specimens from Piedmont are quite different from *Protororqualus cuvieri* but Portis did not study the fossil record within an evolutionary framework thus he was unable to individuate primitive and derivate traits on which to base a classification system.

The work of Portis (1885) is however rich in details and represents the last monograph written on mysticete taxonomy by an Italian specialist of the 19th century. The only other long work on descriptive morphology of the fossil mysticetes from the Italian Neogene is that of Caretto (1970), a monograph that had a profound impact on the Italian understanding of mysticete systematics and evolution.

CARETTO (1970) AND THE PROBLEM OF *BALAENOPTERA ACUTOROSTRATA CUVIERI*

During the 20th century, there have been very few studies on fossil mysticetes from Italy. The works of Trevisan (1941) and Cuscani-Politi (1960-1961) were the only remarkable papers published before 1970. A large-scale work was published in 1970 by Caretto about a Pliocene skeleton of a large rorqual-like mysticete from Valmontasca, northern Italy. Here, such a work is analysed because of the profound influence it had on the subsequent development of Italian mysticete palaeontology.

The paper appeared in a monographic issue of the *Bollettino della Società Paleontologica Italiana* (1970) and its subject was a remarkably complete balaenopterid-like skeleton. The author undertook an extraordinary effort to make a thorough comparative analysis of the skeleton. The specimen was found in 1959 in Valmontasca and its preparation and description required several years; it is now held by the University of Torino. Caretto compared the specimen with the taxa established by Van Beneden, Brandt, Capellini, and Kellogg concluding that it represented a subspecies of the living minke whale, namely *Balaenoptera acutorostrata cuvieri*. Caretto went one step further stating that almost all the previously named taxa belong to the same subspecies. These taxa are the following: *Heterocetus guiscardii*, *Plesiocetus cortesii* (the skeleton from Mount Pulgnasco which is now named *Protororqualus cuvieri*), *Cetotherium* (*Cetotheriophanes*) *capellinii* (the skeleton from San Lorenzo in Collina), '*Balaenoptera*' *gastaldii* (which is now named *Eschrichtioides gastaldii*), *Heterocetus guiscardii*, *Plesiocetus burtini*, *P. garopii*, *P. hupschii*, *Burtinopsis similis*, *Balaenoptera rostratella*, *Heterocetus affinis*, *H. brevifrons*, *H. sprangii*, *M. latifrons*, *Mesocetus laxatus*, *M. longirostris*, *M. pinguis*, *Amphicetus editus*, *A. later*, *A. rotundus*, *A. verus*, *Aglacetus moreni* and *Isocetus depawii*. In this paper, our goal is to demonstrate that the specimen from Valmontasca does not belong to the genus *Balaenoptera* based on morphological evidence. We do not want to discuss the systematics of all the species listed above for which separate papers are necessary. Caretto's extensive revision relies upon the following morphological characters (Caretto, 1970, p. 50):

- (1) mean length of the skeleton of adult individuals not exceeding 10 m;
- (2) relative proportions of the bones relative to the skeleton;
- (3) morphology of the skull especially in the rostral region;
- (4) tympanic size not exceeding 85-90 mm in length;
- (5) whole morphology and mean size of the vertebrae;
- (6) vertebral number not exceeding 50;
- (7) rib number (ranging from 20 in living forms to 24 in fossils);
- (8) whole morphology and relative proportions of the forelimbs.

From his monograph, it seems that the character analysis made by Caretto was based on the direct examination of possibly two individuals of the living

Balaenoptera acutorostrata held by the Museo di Storia Naturale e del Territorio (hereinafter, MSNT) of the University of Pisa (specimens 260 and 261); Caretto wrote that he received data from the Institute Royal des Sciences Naturelles du Belgique (hereinafter, IRSN; two individuals), München and Paris (one individual each). Caretto said that he has analyzed five individuals from MSNT but we were able to find only two adult individuals and one newborn there, which can be assigned to *Balaenoptera acutorostrata*. Moreover, it seems that he did not examine living mysticetes other than *B. acutorostrata*; in fact, he mentioned only rarely the fin whale, *Balaenoptera physalus*.

Caretto assessed also the individual variation of morphological traits in *B. acutorostrata* concluding that the following characters should be diagnostic for the Pliocene subspecies:

- (1) mean length of rostrum;
- (2) length and width of neurocranium;
- (3) development of supraorbital process of the frontal;

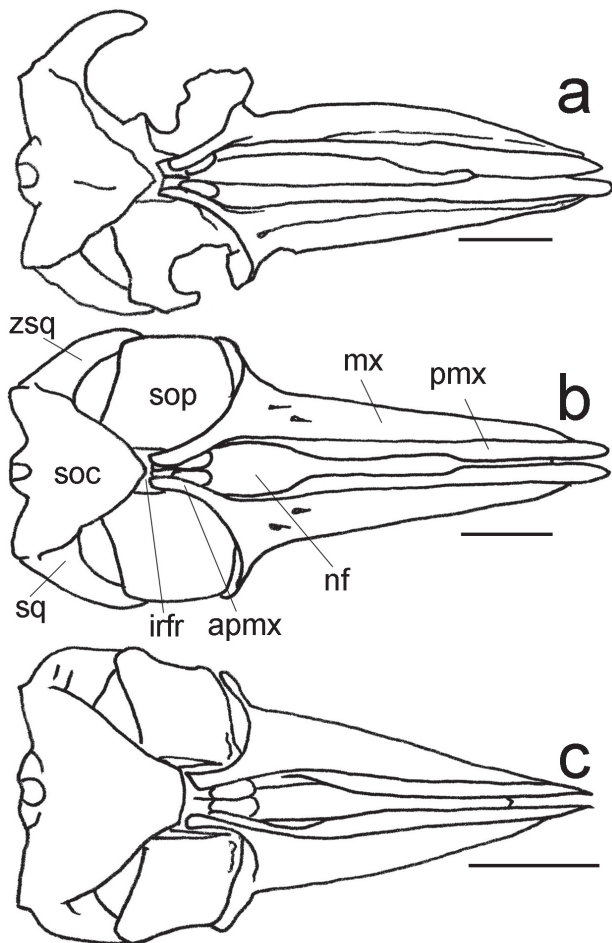


Fig. 1 - The skull of the Valmontasca rorqual-like mysticete described by Caretto (1970) and a modern-day minke whale (*Balaenoptera acutorostrata*) in dorsal view. A) The skull of the Valmontasca whale (redrawn from Caretto, 1970 with modifications). B) Reconstruction of the skull of the Valmontasca whale. C) The skull of a minke whale (*Balaenoptera acutorostrata*) in dorsal view (from True, 1904). See Anatomical abbreviations for explanation of acronyms. Scale bars = 20 cm.

- (4) whole morphology of the dentary and its mean length relative to the skull length;
- (5) morphology of cervical vertebrae with emphasis on atlas and axis;
- (6) position and inclination of neurapophyses;
- (7) position of transverse processes in thoracic and lumbar vertebrae;
- (8) morphology of the olecranon of the ulna (which is markedly similar to an axe).

Following Caretto (1970), the Pliocene subspecies *Balaenoptera acutorostrata cuvieri* is defined by the following features:

- (1) size of rostrum similar to the living minke whale;
- (2) supraorbital process of the frontal not markedly rearward oriented;
- (3) anterior process of the parietal elongated;
- (4) twelve thoracic vertebrae and twelve pairs of ribs.

The revision made by Caretto provided a new rationale to ground systematic identifications of mysticete remains stored within museums and universities. Consequently, almost all of the fossil Italian non-balaenid mysticetes have been assigned to *Balaenoptera acutorostrata cuvieri* independent from their ages, morphology and provenance. This situation is firstly due to the lack of other detailed works on Italian fossil mysticetes in the last 50 years of the 20th century reflecting a major gap in the studies of this group.

Status of the chronospecies Balaenoptera acutorostrata cuvieri

Certainly, the ponderous work of Caretto (1970) represented a landmark study in the field of fossil mysticetes forming a sort of synthesis of the taxonomic and evolutionary knowledge about the group in the late 20th century of Italy. Such a synthesis was considered valid until the late 90s when a new revision of the Italian material started at the University of Pisa resulting in two theses and one doctoral dissertation (Bisconti, 1998, 2003b; Marsili, 2003). A preliminary discussion of the

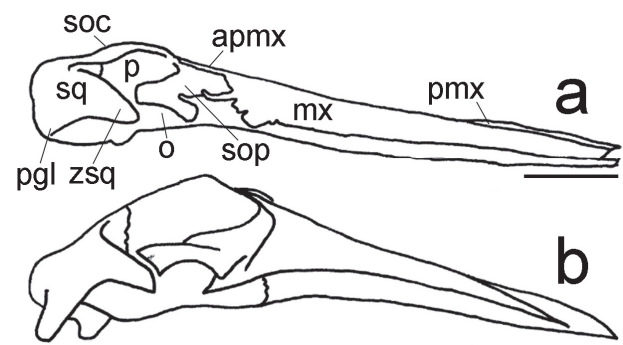


Fig. 2 - The skull of the Valmontasca rorqual-like mysticete described by Caretto (1970) and a modern-day minke whale (*Balaenoptera acutorostrata*) in lateral view. A, the skull of the Valmontasca whale in lateral view (redrawn from Caretto, 1970 with modifications). B, the skull of a minke whale (*Balaenoptera acutorostrata*) in lateral view (from True, 1904). Scale bars = 20 cm. Acronyms as in Anatomical abbreviations.

conclusions of Caretto was made by Deméré (1986) in his description of *Balaenoptera davidsonii*. The preliminary discussions of Caretto's interpretation were substantially focused on the appreciation of the morphological diversity exhibited by Pliocene non-balaenid mysticetes, a point which was totally denied by Caretto. After a careful examination of the morphological evidence, it does not appear justifiable to collapse the whole non-balaenid fossil record of the Italian mysticetes from the Pliocene into a single taxonomic entity, an entity that has been considered,

moreover, con-specific of the modern minke whale, *Balaenoptera acutorostrata* Lacépède.

The modern minke whale can be clearly identified based on a series of morphological characters including the following ones which are not subject to individual variation based upon the examination of a number of specimens (see Tab. 1 for a list of examined specimens): (1) the rostrum is approximately the same length as the neurocranium; (2) the supraoccipital is clearly inclined being its anterior portion higher (Figs. 1-2); (3) in the tympanic bulla, the Eustachian opening

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- Protocetus atavus*: SMNS 11084 (holotype); Middle Eocene.
Georgiacetus vogtlensis: Hulbert et al. (1996), Hulbert (1998); Middle Eocene.
Zygorhiza kochii: USNM 4748, 16638, 449538; Late Eocene.
Chonecetus goedertorum: Barnes et al. (1994); Late Oligocene.
Aetiocetus polydentatus: Barnes et al. (1994); Late Oligocene.
Eomysticetus whitmorei: ChM PV4253 (holotype); Late Oligocene.
Caperea marginata: AMNH AMO 36692, IRSN 1536, ISAM ZM 41126, 19944, 40626, 14407; Recent.
Balaena mysticetus: USNM 257513; ZML 1680, 3997, 2563, 2001, 'Balaena japonica' (1-2); Recent.
Balaena montalionis: MSNT MC CF 31 (holotype); Bisconti (2000, 2003a); Early Pliocene. *Balaenula astensis*: MSNT MC CF 35 (holotype); Early Pliocene.
Eubalaena glacialis: AMNH 42752, 256803, 90241; MSNT 264; USNM 267612, 3339990, 23077, 301637; Recent.
Eubalaena australis: ISAM ZM 2284, 40710, 48950, 13370; Recent.
Pelocetus calvertensis: USNM 11976 (holotype); Early Miocene.
Isanacetus laticephalus: Kimura and Ozawa (2002); Early Miocene.
Parietobalaena palmeri: AMNH 128885; USNM 10677, 16570, 24883, 10909; Early Miocene.
Diorocetus hiatus: USNM 16783 (holotype), 205990; Early Miocene.
Cetotherium rathkei: Pilleri (1986); Middle Miocene.
Mixocetus elysius: Kellogg (1934); Middle Miocene.
Metopocetus durinasus: USNM 60460 (holotype); Middle Miocene.
Eschrichtius robustus: AMNH 181374, 34260, 1750 ('*Eschrichtius cephalum*'), A; NMB 42001; USNM 364969, 364580, 571931, 364969, 364977, 364970, 364973, 504305; ZML St20350, St13130, 630 ('*Eschrichtius gibbosus*'); Recent.
Eschrichtioides gastaldii: MGPT 13802 (holotype); Early Pliocene.
Titanocetus sammarinensis: MGB 9073 1CMC172 (1-6) (holotype); Middle Miocene.
Archaeobalaenoptera castriarquati: MCA 240536 (inventory of the Soprintendenza per i Beni Archeologici dell'Emilia Romagna; holotype); Bisconti (2003b, 2007b); Middle Pliocene.
Protororqualus cuvieri: Cortesi (1819), Cuvier (1823), van Beneden (1875), Strobel (1881), Bisconti (2007a); Middle Pliocene.
 MPST 240505 (inventory of the Soprintendenza per i Beni Archeologici dell'Emilia Romagna); Bisconti (2003b); Late Miocene.
Balaenoptera borealina: IRSN CtM775a-b, 774 (holotype), 777, 778; Early Pliocene.
Parabalaenoptera baulinensis: Zeigler et al. (1997); Late Miocene.
Megaptera hubachi: Dathe (1983); Middle Pliocene.
Megaptera miocaena: Kellogg (1922); Late Miocene.
Megaptera novaengliae: AMNH 24679; MSNT 263; USNM 269982, 486175 (1-2), 13656 / 16252, 21492; ZMA 14964-14967, 14953 (1-2), 14952 (1-2); ISAM ZM 39781, 2288; Recent.
Balaenoptera acutorostrata: AMNH 181411, 35680; IRSN 1537; MSNT 260, 261; ZMA 12873; ISAM ZM 40626, 36715, 39672; Recent.
Balaenoptera physalus: AMNH 35026, 256796; MSNT 251-253, 255, 257, 258; ZMA 14950 (1-2), 14927 (1-2), 14935 (1-2), 23353, 14947; Recent.
Balaenoptera musculus: AMNH 234949, 256797, 256798; MSNT 250; ZMA 23354-23356, 14946, 14942, 14961; Recent.
Balaenoptera edeni: USNM 504692, 236680 (1-3); ISAM ZM 12962, ZM 40449; Recent.
Balaenoptera omurai: Wada et al. (2003); Recent.
Balaenoptera borealis: USNM 504698, 504699, 504701, 504244, 486174; Recent.
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Tab. 1 - List of specimens examined for comparative analysis.

is lower than that observed in the other living members of the genus *Balaenoptera*. However, a full comparison will be published elsewhere. When these characters are not found in a fossil specimen, it is not justifiable to assign such a specimen to the species *Balaenoptera acutorostrata*. The establishment of a chronospecies to explain the differences observed in the fossil forms when compared to the modern minke whale appears even more arbitrary in the absence of a clear and well-supported morphological ground. If such a ground is lacking then the hypothesis of a close phylogenetic affinities of the fossil taxa with the modern minke whale cannot be supported.

A comparison between the skull of a modern-day minke whale and the rorqual-like mysticete from Valmontasca is presented in Figs. 1 and 2 and shows that there are clear morphological differences that cannot be explained following Caretto (1970). In the Valmontasca skull the rostrum is much longer than the neurocranium (Figs. 1-2) while in the minke whale rostrum and neurocranium are approximately the same size. The supraoccipital of the Valmontasca specimen is not as inclined as that of the minke whale but its anterior portion is almost horizontal. These features show that the skull geometry of the Valmontasca whale is different from that of the minke whale. Additional evidence is found in the cranio-mandibular joint. The postglenoid process of the Valmontasca whale (Fig. 2) does not project ventrally as that of the minke whale and the other balaenopterids and the glenoid fossa of the squamosal is not crescent-shaped as it is typical of the genus *Balaenoptera*.

The morphological pattern of the minke whale periotic has never been found in the extensive collections of mysticete earbones of the Italian collections and, more importantly, in these collections there are no earbones that can be unambiguously assigned to modern balaenopterid species. This point raises the problem of the first arrival of the modern balaenopterid species in the Mediterranean basin, a problem that cannot be solved with the evidence at hand. The periotic of the Valmontasca balaenopterid does not show the lateral crest-like border of the pars cochlearis typical of *Balaenoptera acutorostrata*, and has a large and massive anterior process (the anterior process of the minke whale is delicate). Finally, for these reasons, the Valmontasca skull cannot be assigned to *Balaenoptera acutorostrata* and needs to be newly studied to understand its taxonomy and phylogenetic relationships.

Therefore, the interpretation of Caretto (1970) cannot be accepted in the light of a detailed morphological analysis of the Pliocene mysticetes from Italy. The establishment of a chronospecies to explain slight differences observed among fossil and living taxa makes sense if the diagnostic features of the living species can be observed also in the fossil forms. If such characters are lacking then we cannot think of the fossil forms that they are closely related to the modern ones and assign them to the same species as the modern ones. In such cases, the establishment of chronospecies is not useful to clear the taxonomy and the evolutionary relationships of the fossil forms. The dismissal of *Balaenoptera acutorostrata cuvieri* implies

that most of the assignments of the Italian fossil non-balaenid mysticetes have to be reviewed.

RECENT DEVELOPMENTS

A large-scale project on the study of the Italian Pliocene mysticetes started at the University of Pisa in 1996 and resulted in two graduation theses (Bisconti, 1998; Marsili, 2003), one doctoral dissertation (Bisconti, 2003b) and a series of scientific papers (Bisconti, 2000, 2001, 2002, 2003b, 2005a, b, 2006, 2007a, b, 2008; Bisconti & Varola, 2000, 2006; Bianucci et al., 2002; Landini et al., 2005a, b). The main results of these works were: (1) a substantial revision of the family Balaenidae, (2) a partial revision of the family Balaenopteridae together with the description of new taxa, *Archaeobalaenoptera castriarquati*, *Protororqualus cuvieri*, and (3) the discovery of the family Eschrichtiidae in the Mediterranean Pliocene.

Balaenidae

The revision of the family Balaenidae (Bisconti, 2003a, 2005) supplemented an earlier work (McLeod et al., 1993) and provided, for the first time, a diagnosis for the problematic genus *Balaenula* (Fig. 3). This genus is now defined based upon its cranial morphology in the following terms:

- (1) the skull has right whale characters in the orientation of the supraorbital process of the frontal and the discontinuously curved rostrum;
- (2) the squamosal is oriented anteriorly and ventrally;
- (3) the cranio-mandibular joint is located ventrally and slightly posteriorly to the orbit;
- (4) the maximum posterior protrusion of the exoccipital is located at a level below the orbit.

These characters are unique of a group of specimens including the Italian *Balaenula astensis* from Villafranca d'Asti (late Early Pliocene; Trevisan, 1941; Bisconti, 2000, 2003a), *Balaenula balaenopsis* from Antwerp (Early Pliocene; Van Beneden, 1878, 1880), and a Japanese *Balaenula* sp. (Early Pliocene; Excavation Research Group for the Fukagawa Whale Fossil, 1982). The revision of the balaenid fauna from the Italian Pliocene led to the resurrection of *Balaena montalionis* Capellini (1904) after its dismissal by Pilleri (1987), which incorporated it in the combination '*Balaenula*' *montalionis*. This combination is now rejected based on comparative and phylogenetic

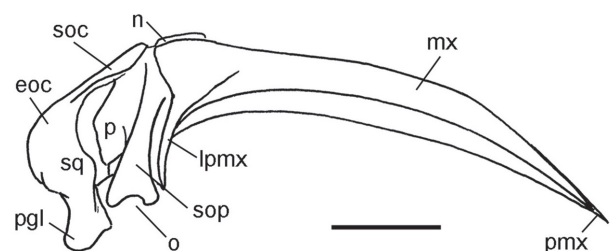


Fig. 3 - Reconstruction of the skull of *Balaenula astensis* in lateral view. Scale bar = 20 cm. Acronyms as in Anatomical abbreviations.

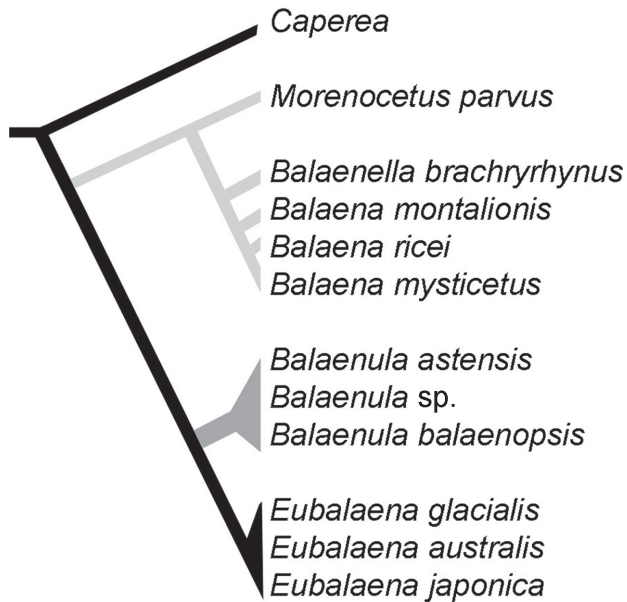


Fig. 4 - A hypothesis for the phylogeny of Balaenidae (from Bisconti, 2005 with modifications).

analyses. The revision of the historical balaenid records included also the assignment of a previously supposed physeterid skull (Pilleri, 1987) to *Eubalaena* sp. (Bisconti, 2002); such a specimen represents the oldest record of right whales in the Mediterranean basin up to now.

The phylogenetic analysis of Balaenidae (Bisconti, 2005a; Fig. 4) revealed that the family includes two large radiations: a clade formed by the genera *Balaenula*

and *Eubalaena*, and a clade formed by *Morenocetus*, *Balaenella*, and *Balaena*. Being *Balaena*, the genus which incorporates the modern-day Greenland bowhead whale (*Balaena mysticetus*), and *Eubalaena*, the genus incorporating the modern-day right whales (*Eubalaena glacialis*, *E. australis*, and *E. japonica*), the close link observed between *Balaena* and the Early Miocene *Morenocetus* means that the living species shared a common ancestor which was living around the beginning of the Miocene or the end of the Oligocene (Bisconti, 2005a; Fitzgerald, 2006). This discovery has profound importance in the assessment of the genetic health of the modern species and should be taken into account by international institutions that are planning conservation strategies (Bisconti, 2005a; Santangelo et al., 2005).

Apart from these results, it is expected that in the next years new data will emerge about the taxonomy and phylogeny of the Italian Pliocene balaenids. In fact, new skeletons are now available for study that should help in resolving the status of the genus *Balaenotus* Van Beneden (1878, 1880) and the diversity of the Pliocene *Eubalaena*.

Balaenopteridae and Eschrichtiidae

The partial revision of the Pliocene record of Italian Balaenopteridae led to the conclusion that the chronospecies *Balaenoptera acutorostrata cuvieri* has to be dismissed based upon the comparative analysis presented in this paper. Moreover, the anatomical study of skull morphology allowed to assign '*Balaenoptera*' *gastaldii* to the family Eschrichtiidae (which includes the modern-day gray whales) based upon the morphology of the frontal, the dentary and the supraoccipital (Bisconti, 2003b; Bisconti & Varola, 2006; Deméré et

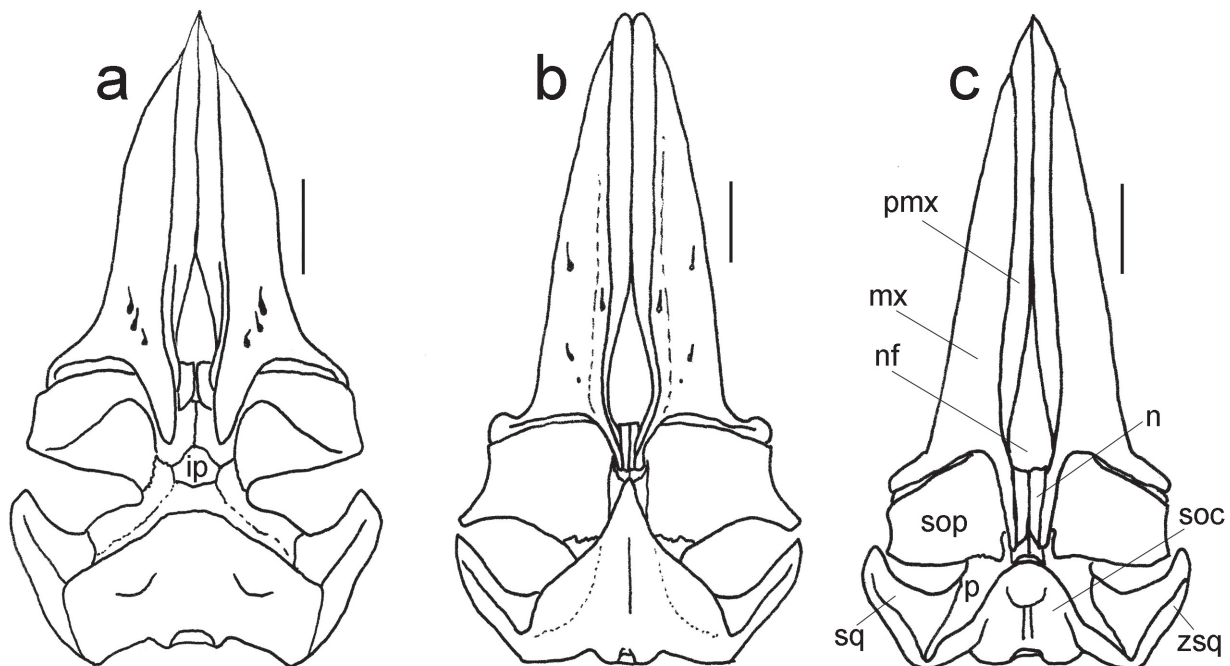


Fig. 5 - Reconstructions of the skulls of representatives of Eschrichtiidae and Balaenopteridae from the Italian Pliocene in dorsal view. A, *Eschrichtioides gastaldii*. B, *Prototorqualus cuvieri*. C, *Archaeobalaenoptera castriarquatii*. Scale bars = 20 cm. See Anatomical abbreviations for explanation of acronyms.

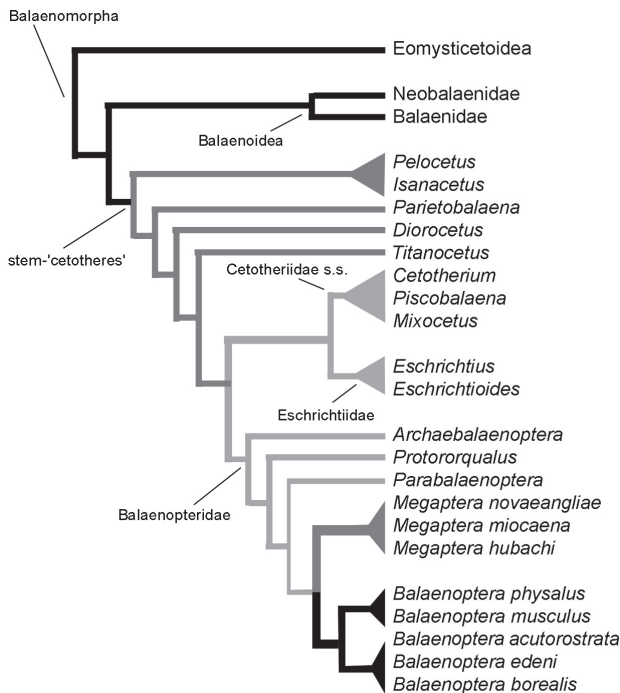


Fig. 6 - Simplified representation of the phylogenetic relationships of Balaenopteridae, Eschrichtiidae, and Cetotheriidae (see Bisconti, 2008 for a fuller description of this cladogram and phylogenetic methods).

al., 2005). Such a specimen is assigned to the new genus *Eschrichtioides gastaldii* (Bisconti, 2008) and demonstrates the presence of Eschrichtiidae in the Mediterranean Pliocene (Fig. 5A).

A recent revision of the Mount Pulgnasco specimen today assigned to the new genus *Protolorqualus cuvieri* (Bisconti, 2007a), showed that it represented an early-diverging balaenopterid whale characterized by primitive conditions in the supraoccipital and dentary (Fig. 5B). In particular, in this specimen, the anterior border of the supraoccipital is triangular and pointed as in Early-to-Middle Miocene Cetotheriidae (Kellogg, 1965, 1968), and the dentary is mainly straight rather than strongly bowed. The balaenopterid dentary is shaped in a way that is closely linked to the peculiar feeding behaviour of this family, which is called intermittent ram feeding or engulfing (Pivorunas, 1979; Sanderson & Wassersug, 1993; Lambertsen et al., 1995). The way the dentary is depressed by the whale changes in relation to its degree of lateral bowing (Lambertsen et al., 1995; Arnold et al., 2005); a straight dentary cannot be depressed in the same way as a laterally bowed dentary does. In this sense, the Mount Pulgnasco whale, fed differently from modern-day balaenopterids.

The presence of early-diverging lineages of balaenopterids in the Mediterranean during the Pliocene is also documented by a newly discovered genus, *Archaeobalaenoptera castriarquati* Bisconti, 2007b from the Castell'Arquato Formation of Rio Carbonari, northern Italy. Such a taxon (Fig. 5C) is characterized by diverging zygomatic processes of the squamosal,

transversely compressed supraoccipital, very long nasal bones, and straight dentary.

From a phylogenetic view, *Archaeobalaenoptera castriarquati* is the basal-most balaenopterid mysticete described up to now (Bisconti, 2007b) (Fig. 6). The main results of the phylogenetic analysis of Balaenopteridae published by the present author (Bisconti, 2007a, b, 2008) accord with the taxonomy of the family proposed by Zeigler et al. (1997) resulting in the subdivision of the family into three subfamilies: Parabalaenopterinae, Megapterinae, and Balaenopterinae. Original result of the more recent studies is the discovery of two stem-balaenopterids, *Archaeobalaenoptera castriarquati* and *Protolorqualus cuvieri*. However, the phylogenetic conclusions are temporary because new taxa are currently under description whose combinations of characters are thought to influence the shape of the mysticete cladogram.

Evolutionary considerations

The revision of the Italian mysticete fauna from the Pliocene was possible thanks to an extensive comparative work carried out in a series of international institutions (see Tab. 1). This effort allowed to describe one new Pliocene balaenid from Belgium and, more importantly, enabled one of the authors (MB) to analyze the morphological diversity of Pliocene, Miocene and Oligocene mysticetes from several sites in the northern and southern hemispheres. The main phylogenetic results of such a study have been presented in the cladograms of Figs. 4 and 6, which show the following points:

1. The family Balaenidae is among the more basal mysticete groups. It is likely that its divergence is from the Oligocene time. This result is in accord with previous interpretations by Kimura & Ozawa (2002) and Fordyce & Muizon (1999). New records from the Late Miocene balaenid diversity from Italy and Holland are under description that should help in deciphering the still poorly-known Miocene history of the family. Balaenidae includes two large radiations: one formed by the genera *Balaenula* and *Eubalaena*, the other including the genera *Morenocetus*, *Balaenella*, and *Balaena*.

2. The family Eschrichtiidae is represented in the Italian Pliocene by the genus *Eschrichtioides*. The particular morphology of this taxon suggests a close link between Eschrichtiidae and the Miocene-to-Early Pliocene Cetotheriidae *sensu* Bouetel & Muizon (2006). An additional Late Miocene eschrichtiid whale was described by Bisconti & Varola (2006), the species *Archaeoschichtius ruggieroi*, which supports the presence of Eschrichtiidae in the Mediterranean since about 10 Ma.

3. The family Balaenopteridae is closely related to Eschrichtiidae and Cetotheriidae and shows high diversity. While the early evolution of the family is now under study through the description of several new stem-balaenopterids, the origin of the modern-day balaenopterid species is still not understood. There is not a clear link between the living rorquals and the fossil taxa described up to now. A deeper investigation on this point should help in the reconstruction of the origin of the most speciose mysticete family of the world.

CONCLUSIONS AND FUTURE DIRECTIONS

The study of the Pliocene mysticete fauna from Italy revealed a number of unrecognized lineages that have been assigned to new taxa. Far from being complete, the taxonomic revision of the specimens already in the collections of Italian institutions will be further complicated by the discoveries of new and well preserved materials from Tuscany, Umbria, and Piedmont. The new specimens that have been excavated in the last ten years are now in the preparation labs of different institutions and some of them are ready to be studied in detail. Preliminary observations on these new records revealed that we are far from having completed the descriptions of the whole mysticete diversity from the Pliocene of Italy.

The rebuttal of Caretto's interpretation of the morphological diversity of Pliocene balaenopterids opens a new and wide horizon concerning the taxonomic revision of previously reported records of Balaenopteridae. The current evidence supports the existence, in the Pliocene, of many lineages of balaenopterids and it is very likely that many of them represents taxa that are new to science.

A clear taxonomic understanding and a well resolved hypothesis of phylogeny are required before focusing the attention to broader palaeobiological problems such as the palaeobiogeographic relationships of the Italian Pliocene mysticetes and the calibration of their extinctions preceding the arrival of the modern fin whale. The latter is a major problem that has been only preliminarily addressed (Bisconti, 1998, 2003a) but it represents a problem with global consequences (Bisconti, 2005b; Santangelo et al., 2005). The general idea, which is emerging from the work already done, is that the Mediterranean trophic web was profoundly different from that of the modern-day Mediterranean Sea. In fact, the presence of balaenids, eschrichtiids and many balaenopterid species strikingly contrasts with the current situation in which only one large-sized balaenopterid species is common, the fin whale (*Balaenoptera physalus*). The assessment of extinction and origination patterns in the Mediterranean Pliocene and the search for global triggers of faunal changes are only in their preliminary phase but they represent the most important future directions in the study of mysticete evolution.

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