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THE OLDEST ESCHRICHTIID MYSTICETE AND A NEW MORPHOLOGICAL DIAGNOSIS OF ESCHRICHTIIDAE (GRAY WHALES)

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Abstract. A close inspection of the dentary of *Eschrichtius robustus* (Cetacea, Mysticeti, Eschrichtiidae) revealed a peculiar organization of the coronoid region. Similar morphologies have been observed in two specimens which are respectively from the Early Pliocene of Piedmont and the Late Miocene of Apulia, Italy. The peculiar organization of the coronoid region consists of the presence of a satellite process parallel or slightly anterior to the coronoid process with a groove interposed between them. The morphology of the dentary is used here to emend the diagnosis of the family Eschrichtiidae and for including the above Italian specimens in this family. Such an emendation is due to the unique mandibular organization shared by *Eschrichtius robustus* and the Italian specimens mentioned above. The new diagnosis allows the establishment of the new genus *Archaeschrichtius* from the Late Miocene of Apulia, which represents the oldest eschrichtiid mysticete to be formally described up to now. Italian specimens extends back to the Late Miocene the fossil record of Eschrichtiidae and document aspects of feeding evolution within Eschrichtiidae for the first time.

Riassunto. Un esame della morfologia della mandibola di *Eschrichtius robustus* (Cetacea, Mysticeti, Eschrichtiidae) ha rivelato una particolare organizzazione della regione coronoidea. Morfologie simili sono state osservate in due reperti fossili provenienti rispettivamente dal Pliocene inferiore del Piemonte e dal Miocene superiore della Puglia. La particolare organizzazione della regione coronoidea consiste nella presenza di un processo satellite parallelo al processo coronoideo e da esso separato da un solco. La morfologia della mandibola è qui utilizzata per emendare la diagnosi di Eschrichtiidae e per includere i reperti italiani di cui sopra all'interno di questa famiglia. Questa nuova diagnosi consente la creazione del nuovo genere *Archaeschrichtius* dal Miocene superiore della Puglia che al momento rappresenta il più antico Eschrichtiidae ad essere formalmente descritto. I reperti italiani estendono la documentazione fossile di Eschrichtiidae indietro fino al Miocene superiore e documentano per la prima volta aspetti dell'evoluzione dei meccanismi alimentari tipici di questa famiglia.

Introduction

The family Eschrichtiidae (Ellerman & Morrison-Scott, 1951) includes only one living species, the gray whale *Eschrichtius robustus* (Lilljeborg, 1861). This species is morphologically well distinct from all the other extant mysticetes in a number of details of the external appearance and of the skeleton. The skeletal morphology of the gray whale has been detailed by True (1904), Wolman (1985), Barnes & McLeod (1984), and Mead & Mitchell (1984); in these papers an emphasis was given to the peculiar skull morphology of the species. The main diagnostic characters of the gray whale skull, as derived from the above works, are summarized as follows: (1) rostrum moderately arched, (2) maxilla and premaxilla not expanded laterally, (3) supraorbital process of the frontal depressed from the interorbital region of the skull, (4) ascending process of the maxilla long and interdigitated with the frontal, (5) nasal rectangular, long and wide, (6) tubercles for the attachment of neck musculature on the dorsolateral surface of the supraoccipital, (7) short zygomatic process of the squamosal, (8) parietal not interdigitated with the posteromedial corner of the rostrum, (9) dentary dorsoventrally arched, (10) coronoid process of dentary highly reduced, (11) in the dentary, articular surface of the condyle faced dorsally, (12) high and strong angular process of the dentary.

Because *Eschrichtius robustus* is the only species assigned to the family Eschrichtiidae, it is difficult to understand if the above characters are diagnostic at family, genus or species level (Ichishima et al. 2006).

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Barnes & McLeod (1984) stated that these characters are not found in any fossil mysticete and that the family has virtually no fossil record. They listed only some subfossil specimens belonging to the now extinct North Atlantic population of *E. robustus* (Barnes & McLeod 1984; Deinse & Junge 1937).

In this paper, we describe new observations on the dentary of the living gray whale that make it possible to emend the morphological diagnosis of Eschrichtiidae. This allows the inclusion of two new fossil taxa within the family. In this way, the fossil record of Eschrichtiidae can be traced back to the Late Miocene of the Mediterranean Basin.

Institutional abbreviations: AMNH, American Museum of Natural History, New York, USA. MAUL, Museo dell'Ambiente, Università di Lecce, Lecce, Italy. USNM, United States National Museum, Smithsonian Institution, Washington DC, USA. ZMA, Instituut voor Systematiek en Populatiebiologie/Zoölogisch Museum, Amsterdam, Holland. ZML, Zoölogisch Museum, Leiden, Holland.

Anatomical abbreviations: ap, angular process; apm, ascending process of maxilla; atc, ascending temporal crest; cd, condyle of dentary; crp, coronoid process; exoc, exoccipital; gsc, groove between coronoid and satellite process; gml, groove for mental ligament; irfr, interorbital region of frontal; mf, mandibular foramen; mhd, mylohyoidal depression; mx, maxilla; n, nasal; p, parietal; pcc, postcoronoid crest; pcf, postcoronoid fossa; soc, supraoccipital; sop, supraorbital process of maxilla; sp, satellite process; sq, squamosal.

The Gray Whale dentary

The comparative analysis of the gray whale dentary was carried out through the examination of several specimens which are partially listed in Bisconti (2003, 2005a) and Bisconti & Varola (2000). The dentary of *Eschrichtius robustus* (Figs. 1, 2) shows slight dorsoventral and lateral arcs; the anterior end is acutely rounded; the groove for the mental ligament, which is located anteriorly, is low and short; a mylohyoidal depression is present slightly dorsal to the ventromedial border (in certain specimens this depression is a true groove [i.e., ZML 20350] resembling that of Balaenidae); the coronoid process is strongly reduced and appears as a low and round emergence slightly anterior to the opening of the mandibular foramen; the mandibular foramen is small and round, and its dorsal and ventral borders are prolonged posteriorly as low crests; the condyle of the dentary is higher than the coronoid process, its articular surface faces dorsally and is located over a high neck; the angular process is high and robust, its posteroventral corner is acutely rounded; the presence of grooves separating the condyle from the angular process may vary from individual to individual (grooves were found to be absent in ZML 20350 and present in AMNH 34260).

A close inspection of gray whale dentaries at AMNH (specimens 181374 and 34260) and ZML (specimen 20350) revealed a more complex morphology in the coronoid region (Figs. 1, 2) than previously thought. The height of the coronoid process may vary from individual to individual, being generally quite low. The coronoid process is located slightly anterior to the opening of the mandibular foramen the dorsomedial border of which is marked by strong relief (Figs. 1, 2).

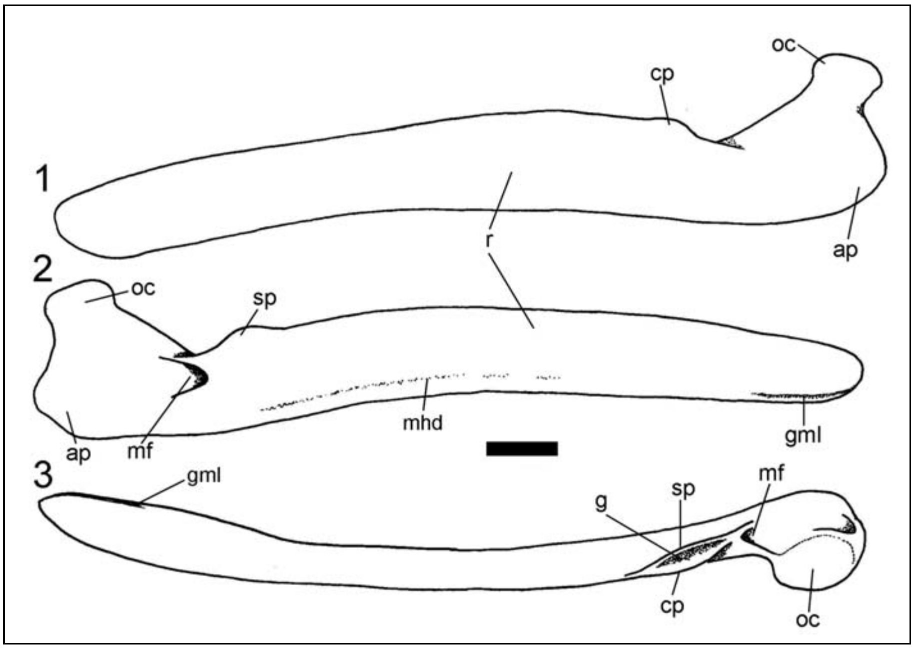


Fig. 1 - *Eschrichtius robustus*, left dentary. 1, lateral view; 2, medial view (borders of mandibular foramen broken); and 3 dorsal view. Scale bar equals 200 mm. Figures 1 and 2: specimen ZML 20350; figure 3: specimen AMNH 34260.

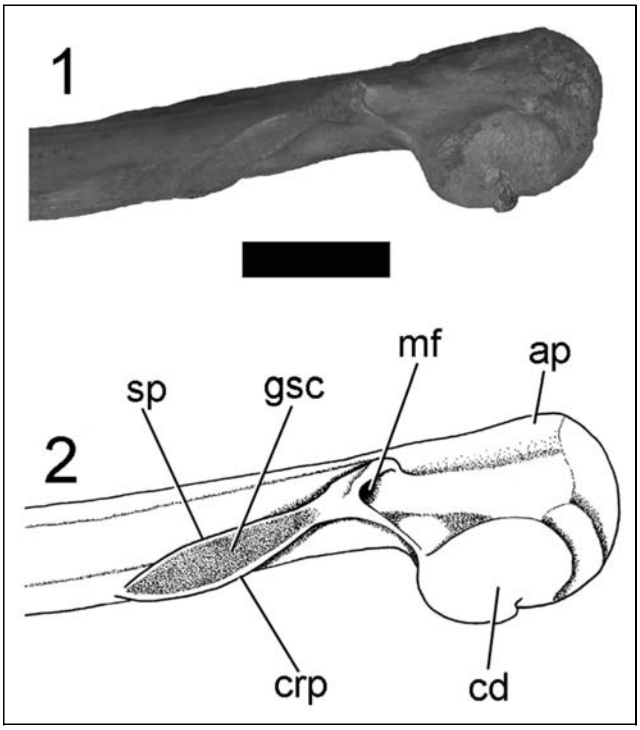


Fig. 2 - *Eschrichtius robustus*, AMNH 34260, left dentary. 1 and 2, close-up view of coronoid region in dorsal view. See Anatomical abbreviations for explanation of acronyms. Scale bar equals 100 mm.

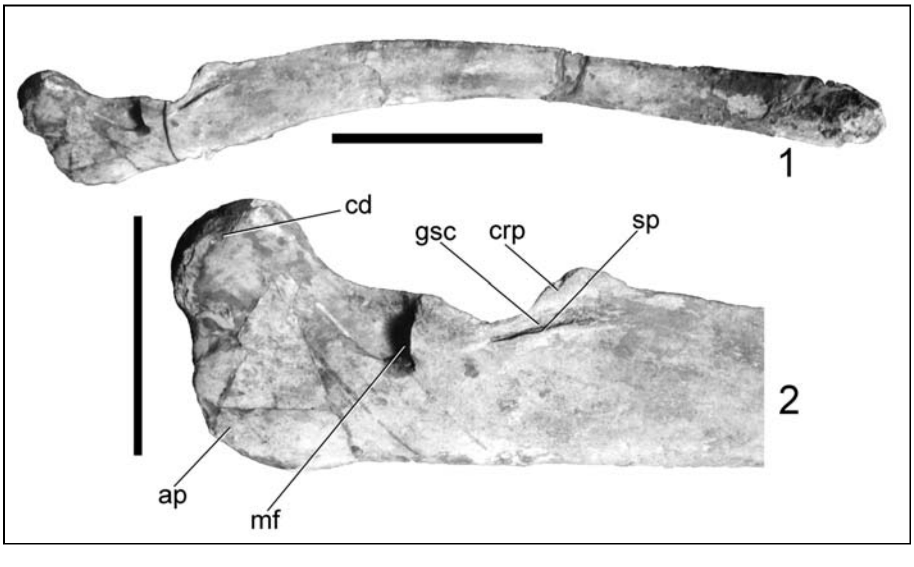
The medial surface of the coronoid process is concave and is continuous with a groove-like surface located on the dorsomedial edge of the dentary. Medial to this surface there is a low, rounded, and elevated feature that parallels in part the coronoid process. Here, we call this feature *satellite process*, new term (Fig. 2). Apart from *Eschrichtius robustus*, we found only two mysticete taxa in which the satellite process was present in the dentary: *'Balaenoptera' gastaldii* (Portis, 1885) from the upper Early Pliocene of Piedmont, North-West Italy (Fig. 3), and an unnamed mysticete from the Late Miocene of Apulia, South-East Italy, preliminarily described by Bisconti & Varola (2000) (Figs. 4-6). There are several morphological traits in the dentary and the skull of *'Balaenoptera' gastaldii* suggesting a close affinity to *Eschrichtius robustus* (compare Figs. 1, 2, and 3). A preliminary study of *'Balaenoptera' gastaldii* has been provided by Bisconti (2003) and a fuller description together with an analysis of phylogenetic relationships is currently under preparation; for this reason, the taxonomy of this specimen is not further investigated here. Here, the specimen previously described by Bisconti & Varola (2000) is used to establish a new eschrichtiid genus and species based on a new morphological diagnosis for Eschrichtiidae derived from the above observations of the gray whale dentary. This new genus represents the oldest eschrichtiid taxon yet described.

Systematic Paleontology

Class **Mammalia** Linnaeus, 1758
Order **Cetacea** Brisson, 1762
Suborder **Mysticeti** Flower, 1864
Family Eschrichtiidae Ellerman & Morrison-Scott, 1951

Emended diagnosis of family. Dentary with presence of a crest-like emergence (satellite process) parallel to the coronoid process but separated from it by a wide sulcus (this emergence may be high and pointed or low and blade-like); dentary ramus continuously arched dorsoventrally; mylohyoidal concavity present in the medial surface of the dentary; well developed angular process of the dentary; ascending temporal crest on the supraorbital process of the frontal which distinctly projects posterior in the proximity of the orbit; robust bilateral prominence in the anterolateral surface of the supraoccipital forming a strong attachment point for neck musculature.

Fig. 3 - *'Balaenoptera' gastaldii* (Portis, 1885) Early Pliocene of Piedmont (northern Italy), left dentary. 1, medial view (scale bar equals 200 mm); 2, close-up view of coronoid region in medial view (scale bar equals 100 mm). See Anatomical abbreviations for explanation of acronyms.



Included taxa. The gray whale *Eschrichtius robustus* (Lilljeborg, 1861), Pleistocene to Recent. *'Balaenoptera' gastaldii* (Portis, 1885), Pliocene, Italy; this taxon represents a new eschrichtiid genus that is under description (Bisconti in prep.). *Archaeschrichtius ruggieroi*, n. gen. et sp. (this paper), Late Miocene, Italy.

Discussion. Characters listed in the above diagnosis are observed in *Eschrichtius robustus*, *'Balaenoptera' gastaldii* and, when preserved, in *Archaeschrichtius ruggieroi* n. gen. et sp. The above diagnosis differs from the previous characterisation of Eschrichtiidae in the following points (numbers in brackets refer to the morphological traits discussed in the Introduction):

(1-2) Characters of the rostrum are not considered here because the rostra of *E. robustus* and *'B.' gastaldii* are different, thus the narrow and arched rostrum of the living gray whale is though to represent a species-level apomorphy.

(3) The depression of the supraorbital process of the frontal from the interorbital region is excluded from the diagnosis because this character is observed also in Balaenopteridae.

(4) A sharp ascending process of the maxilla is observed in Balaenopteridae and in several 'cetotheriids' such as *Cetotherium rathkei* (Brandt, 1873) and *Mixocetus elysius* (Kellogg, 1934).

(5) Size and shape of the nasals are not included into the diagnosis because these bones are large in *E. robustus* and small in *'B.' gastaldii*, thus large nasals are an apomorphy of *E. robustus*.

(6) The sharp tubercles in the supraoccipital are retained as diagnostic of Eschrichtiidae because present in *E. robustus* and *'B.' gastaldii.*

(7) A short zygomatic process of the squamosal is not included because it is observed in *Cetotherium*-like 'cetotheriids' (e.g., *Cetotherium rathkei* and *Mixocetus elysius*).

(8) The lack of interdigitation of parietal and posteromedial elements of the rostrum is observed in Balaenidae, Neobalaenidae, and some Miocene 'cetotheriids' such as *Parietobalaena palmeri* (Kellogg, 1923) and *Pelocetus calvertensis* (Kellogg, 1965).

(9) The continuous dorsoventral arc of the dentary is considered diagnostic of Eschrichtiidae because it is present in all three taxa included in this family (the dentary of Balaenidae and Neobalaenidae has a dorsoventral arc located in the anterior portion of the bone; thus, in these taxa the arc is not continuous).

(10) The reduction of the coronoid process is not included within the diagnosis because it is not observed in *Archaeschrichtius ruggieroi*.

(11) The dorsal position of the condyle of the dentary is not considered diagnostic of Eschrichtiidae because it is observed also in Balaenidae and Neobalaenidae.

(12) The strong angular process of the dentary is retained in the diagnosis because it is observed in *E. robustus* and *'B.' gastaldii* (in *A. ruggieroi* the angular process is not preserved) and because it is not observed in all the other balaenomorph mysticetes (sensu Geisler & Sanders 2003).

In the present diagnosis higher emphasis is given to the morphology of the coronoid region of the dentary and to the ascending temporal crest. The latter corresponds to the anterior site for the attachment of the temporalis muscle and represents the anterior continuation of the temporal crests formed by the dorsal border of the parietal and the lateral border of the supraoccipital (Fig. 4). In *E. robustus* and *'B.' gastaldii* the ascending temporal crest projects distinctly posteriorly in the proximity of the orbit, near to the lateral border of the supraorbital process of the frontal (Fig. 4).

Occurrence. *Eschrichtius robustus* occurs in present-day northern Pacific Ocean with distinct Korean, Japanese, and Californian populations; a North Atlantic population was living until 17th century when it was exterminated by European whalers (Bryant 1995; Fraser 1970). *'Balaenoptera' gastaldii* occurred in the late Early Pliocene of Piedmont, northern Italy, northern portion of central Mediterranean basin (Portis 1885; Bisconti 2003). *Archaeschrichtius ruggieroi* n. gen. and sp. occurred in the Late Miocene of Apulia, southern Italy, central Mediterranean basin (Bisconti & Varola 2000; this paper).

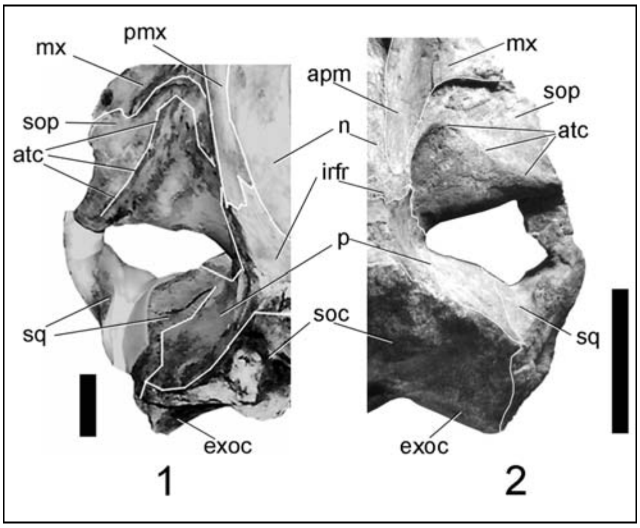


Fig. 4 - Dorsal views of (1) *Eschrichtius robustus* and (2) *'Balaenoptera' gastaldii* skulls showing the distinctive morphology of the ascending temporal crest. The left half skull of *E. robustus* and the right half skull of *'B.' gastaldii* are shown. See Anatomical abbreviations for lettering. Scale bars correspond to 100 mm.

Archaeschrichtius gen. n.

Etymology. *Archaios* (Greek): old, archaic; *Eschrichtius*: gray whale.

Diagnosis. *Archaeschrichtius ruggieroi* differs from *Eschrichtius robustus* and *'Balaenoptera' gastaldii* in having much more developed coronoid and satellite processes, in the presence of a more developed postcoronoid crest and postcoronoid fossa (sensu Bisconti & Varola 2000), and in a more dorsal location of the groove for the mental ligament.

Type species. *Archaeschrichtius ruggieroi* n. gen. et sp.

Range. Late Miocene (Tortonian, see below) of the Pietra Leccese Formation, Apulia, South-East Italy (Fig. 4), central Mediterranean basin.

Discussion. The new genus and species is based on a single dentary with condyle and angular process missing. The establishment of new cetacean taxa based on incomplete skeletal materials is usually not encouraged, and for that reason Bisconti & Varola (2000) decided to regard this dentary as genus and species indeterminate in a family *incertae sedis*. However, the new observations of the eschrichtiid dentary allow the unambiguous placement of the dentary within Eschrichtiidae. Bisconti & Varola (2000) excluded the possibility that the peculiar morphology of the coronoid region of this dentary was due to pathology. Thus, the particular morphology shown by the type specimen, together with the new diagnosis of Eschrichtiidae, allow to unambiguously characterise this dentary as the new genus and species *Archaeschrichtius ruggieroi*.

Archaeschrichtius ruggieroi n. sp.

Figs. 5-7

2000 - Gen. et sp. indet. Bisconti & Varola, p. 20, pl. 1, fig. 1-3

Etymology. The patronymic *ruggieroi* is given to this species to acknowledge the scientific importance of the work of Professor Livio Ruggiero, University of Lecce, to whom the species is dedicated.

Holotype. MAUL 230/1, a left dentary lacking condyle and angular process (Figs. 5, 6).

Diagnosis. As for genus.

Description. Left dentary lacking condyle and angular process. Dentary slightly arched dorsoventrally and lateromedially. Mylohyoidal depression present in the medial side of the dentary (Figs. 5 and 7). Mental foramina along the dorsolateral border seemingly absent; 7 gingival foramina along the dorsomedial border, which, anterior to the coronoid and satellite processes, bears a sharp groove; such a groove has been observed in the living *E. robustus* and in an early Miocene 'cetotheriid' (AMNH 128885; MB, personal observation, 2005) tentatively referred to *Parietobalaena palmeri*. Groove for mental ligament ending at anterodorsal corner of dentary and projecting ventrally and posteriorly. Coronoid process high with round posterolateral profile; posterior border of the coronoid process prolonged posteriorly as a postcoronoid crest (Fig. 6). Postcoronoid crest long with concave lateral surface (postcoronoid fossa; Fig. 6). Satellite process pointed and high, located anteromedial to the coronoid process and separated from it by a deep and wide groove-like depression. In Fig. 7, cross-sections of the dentary are presented showing the wide mylohyoidal depression, the coronoid crest, and the fossa between coronoid and satellite processes. In cross section, the dentary of *A. ruggieroi* differs from that of mysticetes other than Eschrichtiidae in having a medial side largely concave (in 'cetotheriids' the medial side is usually convex; in Balaenopteridae it is flat; in Balaenidae and Neobalaenidae it is flat-to-slightly convex with a ventromedial mylohyoidal groove). In Table 1 linear measurements of the dentary of *A. ruggieroi* are reported in mm. The height of the ramus increases slightly from the anterior end toward the posterior portion of the bone. The height of the ramus increases abruptly in correspondence of

Fig. 5 - *Archaeschrichtius ruggieroi* n. gen. et sp., MAUL 230/1 (holotype), Late Miocene of Apulia (southern Italy), left dentary. 1, lateral view; 2, medial view; 3, dorsal view. Scale bar equals 200 mm.

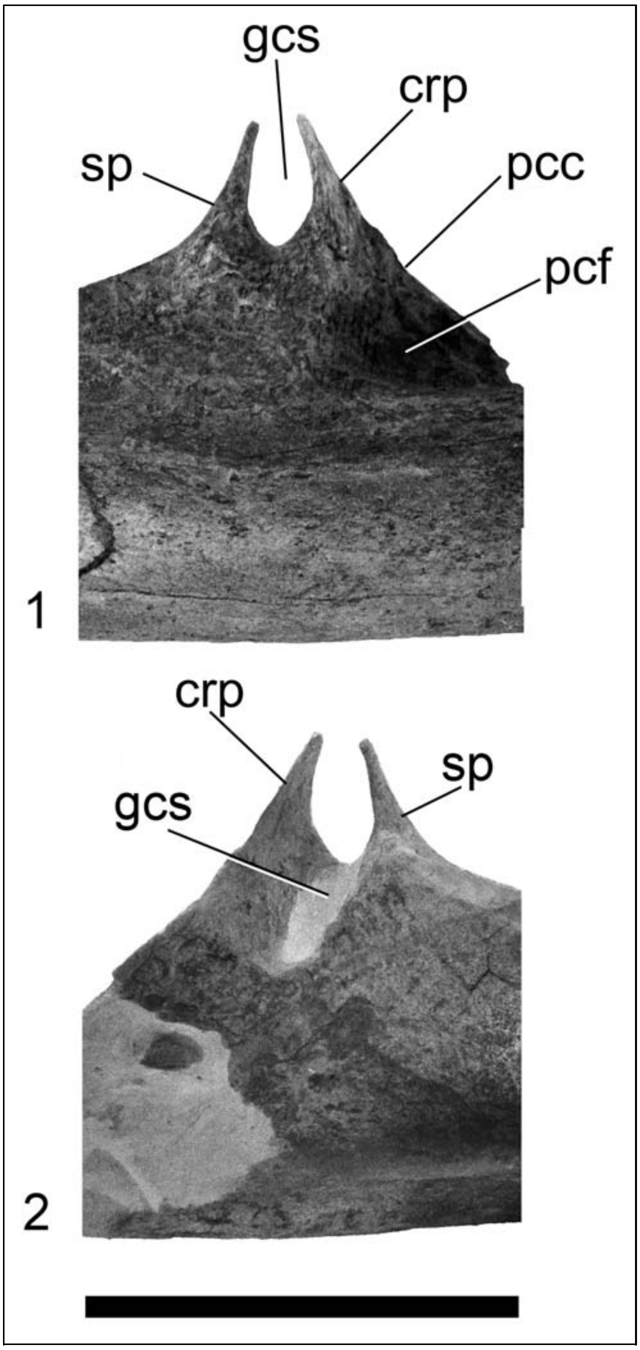


Fig. 6 - *Archaeschrichtius ruggieroi* n. gen. et sp., MAUL 230/1 (holotype). Close-up view of coronoid region: 1 lateral view; 2, medial view. See Anatomical abbreviations for explanation of acronyms. Scale bar equals 100 mm.

the satellite and the coronoid process and decreases abruptly immediately posterior.

Comparisons. The dentary of *Archaeschrichtius ruggieroi* differs from Balaenidae in having a continuous dorsoventral arc rather than an arc located in the anterior half of the bone, and in having well developed coronoid and satellite processes. The mylohyoidal depression of *Archaeschrichtius ruggieroi* differs from that of Balaenidae because in Balaenidae such a depression has the shape of a true groove. *Archaeschrichtius ruggieroi* differs from Balaenopteridae in having a dorsoventral arc in the dentary and in having well developed satellite process and mylohyoidal depression (both features are absent in balaenopterid dentaries). *Archaeschrichtius ruggieroi* differs from nominal 'cetotheerid' grade mysticetes in having a satellite process, a mylohyoidal depression in the medial side of the dentary, and a dorsoventral arc in the dentary (all of these features are absent in 'cetotheriid' dentaries). For further comparisons and related literature, see Bisconti & Varola (2000).

Horizon and locality. The holotype was found in the Cisterna quarry near the village of Cavallino (geographic coordinates of Cavallino are the following: 40° 19' 0" N in Latitude, 18° 12' 0" E in Longitude), 5.5 kilometres from Lecce (Apulia, South-East Italy) in the Pietra Leccese Formation (Fig. 8). The Pietra Leccese is a biomicrite commonly used for building purposes since the 14th century. Analyses of the geological and paleontological characters of the Pietra Leccese Formation have been provided, among others, by Bossio et al. (1994, 1998), Margiotta (1996), Margiotta & Varola (2004), and Landini et al. (2005). The thickness of the Pietra Leccese outcrop at the Cisterna quarry is about 20 m. The lower portion (0-3 m from the bottom of the quarry) is grey-green in colour, due to a high content in glauconite. The sediments of this portion are rich in *Orbulina suturalis* supporting a Langhian age. In the overlying 2 meters (3-5 m from the bottom of the quarry), the biomicrite is poor in glauconite. A second cycle follows, rich in glauconitic biomicrite (5-6 m from the bottom of the quarry), with abundant *Globorotalia siakensis*, suggesting a Serravallian age (Middle Miocene). Again, from m 6 to 8 from the bottom of the quarry, the biomicrite is poor in glauconite. A third sedimentary cycle, rich in glauconite (approximately 8-20 m from the bottom of the quarry) is placed within the *Globorotalia acostaensis* Zone of Iaccarino & Salvatorini (1982) corresponding to a Tortonian age. Micropaleontological analyses were carried out and discussed by Margiotta (1996). The holotype MAUL 230/1 was discovered in the third cycle and the matrix is rich in *Globorotalia acostaensis* and *Globigerinoides extremus*, confirming the Tortonian age (11-7.5 Ma).

Mode of life

In previous interpretation, the peculiar morphology of the dentary was thought to be consistent with a feeding behavior known as intermittent ram feeding (sensu Sanderson & Wassersug 1993) or engulfing (sensu Pivorunas 1979). That behavior is typically performed by living balaenopterid mysticetes (Bisconti &

Tab. 1 - Linear measurements of MAUL 230/1. Data in mm.

Total length of the dentary (linear)	940
Total length of the dentary along the external curvature	1020
Length from the anterior end to the apex of satellite process (linear)	900
Height of the dentary 100 mm from the anterior end	70
Height of the dentary 200 mm from the anterior end	75
Height of the dentary 300 mm from the anterior end	79
Height of the dentary 400 mm from the anterior end	82
Height of the dentary 500 mm from the anterior end	90
Height of the dentary 600 mm from the anterior end	90
Height of the dentary 700 mm from the anterior end	100
Height of the dentary 800 mm from the anterior end	115
Height of the dentary 900 mm from the anterior end (apex of satellite process)	175
Height of the dentary 940 mm from the anterior end (apex of coronoid process)	190
Height of the dentary 1020 mm from the anterior end	120

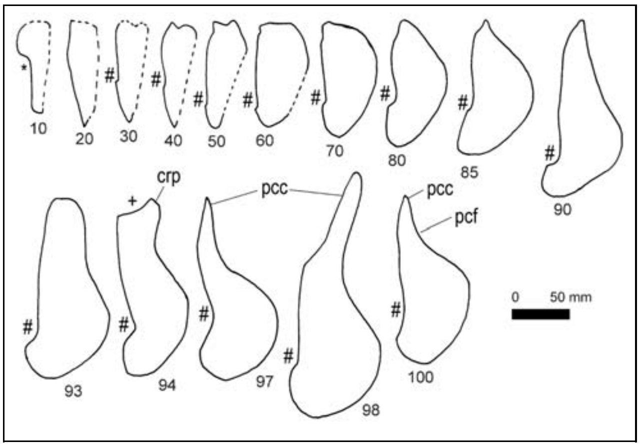


Fig. 7 - *Archaeschrichtius ruggieroi* n. gen. et sp., MAUL 230/1 (holotype), Late Miocene of Apulia (southern Italy), cross-sections of left dentary. Numbers above the sections represent the distance (in mm) from the apex of the dentary. Broken lines represent damaged borders. Scale bar equals 50 mm. Symbols: *, groove for mental ligament; #, mylohyoidal depression; +, sulcus between satellite and coronoid processes. See Anatomical abbreviations for explanation of acronyms.

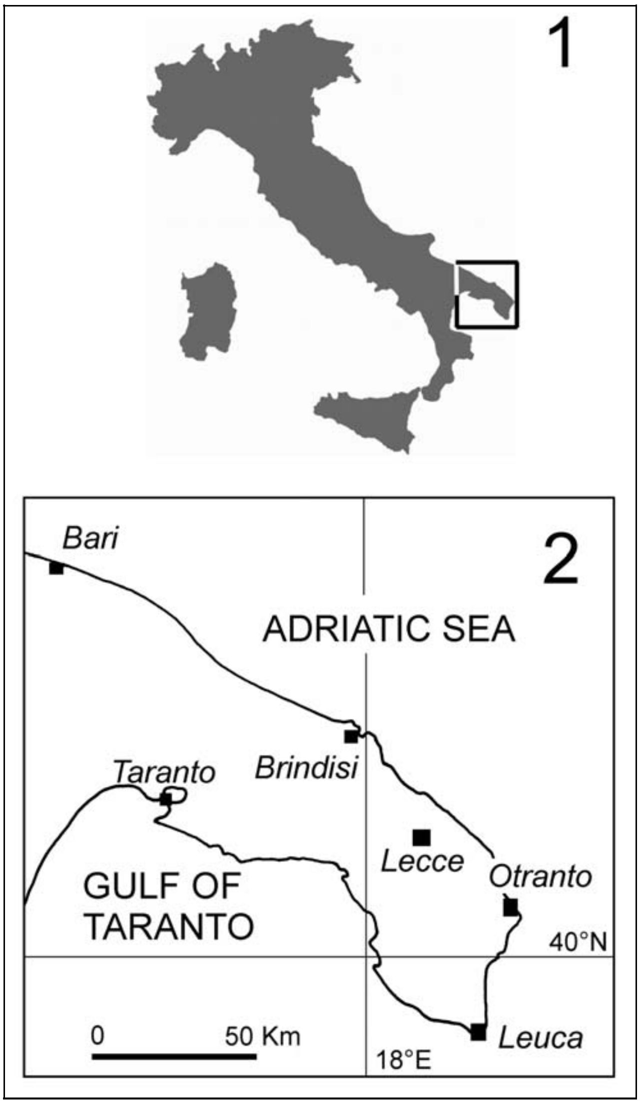


Fig. 8 - Geographic map showing the geographic location of discovery site of *Archaeschrichtius ruggieroi* n. gen. et sp. 1, Italy, the rectangle shows Apulia region. 2, Close-up view of Apulia region, the specimen has been discovered very near to Lecce.

Varola 2000; Bisconti & Marsili 2003). The presence of a postcoronoid fossa for the attachment of part of the temporalis muscle and the deep fossa between the coronoid process and the satellite process were supposed to form wide surfaces for attachment of muscles necessary for the adduction of the dentary during the closure of the mouth (Bisconti & Varola 2000). A postcoronoid fossa is also found in some 'cetotheriids' (e.g., *Parietobalaena palmeri* Kellogg, 1924 and *Diorocetus hiatus* Kellogg, 1968) in which the shape of the skull is highly consistent with the morphological patterns observed in living intermittent ram feeders (e.g., balaenopterids; Sanderson & Wassersug 1993; Werth 2000). The presence of a mylohyoidal depression in the medial side of the dentary supports a strong muscular organization of the tongue; this hypothesis is further supported by the observation that living gray whale calves feed by intermittent suction which needs strong tongue work (Sanderson & Wassersug 1993 and ref. therein). Within the mouth of the gray whale, a muscular-driven depression of the tongue mediated by the mylohyoidal muscle generates negative pressure that allows the mouth to fill rapidly with water. In *Archaeschrichtius ruggieroi*, despite the fact that the muscular attachments in the coronoid region of the dentary were more developed than in *'B.' gastaldii* and *E. robustus* (thus suggesting a more massive participation of muscles in the closure of the mouth than in Balaenopteridae and later Eschrichtiidae), the presence of the mylohyoidal depression in the medial side of the dentary supports the hypothesis that in this species the capture of prey was assisted by a suction mechanism as in the living gray whale. It is impossible to know if *A. ruggieroi* was feeding on bottom invertebrates as *E. robustus* or if it was a pelagic filter feeder. We speculate that the powerful muscular system attached to its dentary (Bisconti & Varola 2000) enabled *A. ruggieroi* to close the mouth faster than the living gray whale, making it possible for it to filter feed on pelagic prey such as euphausiids and schooling fishes, which are able to perform complex escape manoeuvres. At present, the function of both the satellite process and the fossa between the coronoid and satellite processes is unclear, but it is quite reasonable to conclude that they are related to intermittent suction feeding because they are found only in eschrichtiid mysticetes.

Implications for eschrichtiid fossil record and paleobiogeography

The recognition of two fossil eschrichtiid genera extends the fossil record of Eschrichtiidae back to the Late Miocene. This past unsuspected diversity of eschrichtiids shows that the intermittent suction feeding originated well after the divergence of Balaenomorpha, possibly among 'cetotheriid'-grade intermittent ram feeders which possessed a well developed postcoronoid crest. Two fossil eschrichtiids are now known from the Mediterranean Basin, but today there are no gray whale populations inhabiting this basin. Given that only two fossil records are found in the Mediterranean over a period of around 11 million years, it is impossible to know if there has been a continuous presence of eschrichtiids in the Mediterranean or if extinction and subsequent re-colonization events affected eschrichtiid populations in this basin over time.

The presence of a highly developed postcoronoid fossa in the Late Miocene *A. ruggieroi* suggests that the ancestry of Eschrichtiidae must be sought among intermittent ram feeders in which this structure was present possibly in the early and middle Miocene cetotheriids. From a chronostratigraphic view, this suggestion does not conflict with recent molecular-based phylogenetic hypotheses that consider *E. robustus* as a true balaenopterid or as the sister taxon of Balaenopteridae (e.g., Rychel et al. 2004; Sasaki et al. 2005). In fact, the origin of Balaenopteridae is estimated to have occurred between 6 and 12 Ma (Upper and Middle Miocene; Whitmore 1994; Zeigler et al. 1997; Sasaki et al. 2005), and the estimated age of *Archaeschrichtius ruggieroi* is between 11 and 7.5 Ma. Thus, the discovery of *Archaeschrichtius ruggieroi* makes it reasonable to infer an age of divergence for Eschrichtiidae of about 10 Ma, and supports a view of the Mediterranean Basin as the centre of origin of the family (Bisconti 2005b). Eschrichtiids were present in the Mediterranean at least until the Early Pliocene, which is the age of *'B.' gastaldii*. Pleistocene and Holocene records show the presence of Eschrichtiidae in the northern Atlantic until three centuries ago, and in the northern Pacific until the present time (see Ichishima et al. 2006 for a recent discovery of a Neogene eschrichtiid from Japan).

Discussion

Compared to *E. robustus* and *'B.' gastaldii*, *A. ruggieroi* has a more anterior placement of the satellite process and a long postcoronoid crest that projects posteriorly and medially. The postcoronoid crest is lacking in *E. robustus* and is only vestigial in *'B.' gastaldii* (Bisconti 2003, in prep.; Bisconti & Varola 2000). However, the dorsoventral arc and the mylohyoidal depression make the dentary of *A. ruggieroi* more closely similar to that of later eschrichtiids than to other mysticetes. *A. ruggieroi* being much older than *E. robustus* and *'B.' gastaldii*, the more anterior placement of the satellite process can be interpreted as the primitive condition for Eschrichtiidae, the more medial position of that process being the advanced state. Other primitive traits of *A. ruggieroi* are the dorsal position of the anterior end of the groove for the mental ligament and the more developed coronoid and satellite processes. In fact, a dorsal localisation of the groove for the mental ligament is present in dentaries of 'cetotheriids' such as *Parietobalaena palmeri*, *Diorocetus hiatus*, *Pelocetus calvertensis* (Kellogg, 1965), *Aulocetus sammarinensis* (Capellini, 1901), and living balaenopterids. A high coronoid process is typical of early Miocene 'cetotheriids' and Balaenopteridae. Late Miocene and Pliocene 'cetotheriids' may have a reduced coronoid process and a long angular process (e.g., *Herpetocetus* Van Beneden, 1872). Here, it is hypothesised that the shift toward a ventral position of the groove for the mental ligament and the marked reduction of the coronoid and the satellite process are related to the fuller development of the intermittent suction feeding behavior typical of the living *E. robustus* and possibly already fully developed in the Pliocene *'B.' gastaldii.*

Conclusions

An emended diagnosis of Eschrichtiidae allows the recognition of two new eschrichtiid taxa from the Mediterranean Basin. One of them is from the Pliocene of northern Italy and will be more fully described elsewhere (Bisconti in prep.; see Bisconti 2003 for a preliminary analysis). The other, here named *Archaeschrichtius ruggieroi* is from the Late Miocene of southern Italy and represents the oldest known eschrichtiid mysticete. The recognition of a complex morphological architecture in the coronoid region of the dentary of the living *Eschrichtius robustus* was crucial in discriminating between species-level and family-level diagnostic traits among the Eschrichtiidae.

The discovery of *Archaeschrichtius ruggieroi* in the Pietra Leccese Formation of Apulia suggests that the Late Miocene divergence of Eschrichtiidae took place in a basin subsequently incorporated within the present-day Mediterranean. The presence of a strong postcoronoid crest and fossa in *Archaeschrichtius ruggieroi* suggests that the origin of the intermittent suction feeding (sensu Sanderson & Wassersug 1993) typical of the living gray whale should be sought in some functional change in the mandibular architecture of early and middle Miocene 'cetotheriids'.

The presence of *Archaeschrichtius ruggieroi* in the Late Miocene of the Mediterranean Basin supports the hypothesis that this basin was the centre of origin of the Eschrichtiidae. The family was present in the Mediterranean during the Late Miocene and late Early Pliocene, but it is currently impossible to know if this presence was continuous or if it was punctuated by extinctions and subsequent re-colonization events. Although eschrichtiids were present in the North Atlantic until the 17th century AD, they are now restricted to the northern Pacific Ocean.

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