

## A NEW RECORD OF *MESSAPICETUS* FROM THE PIETRA LECCESE (LATE MIOCENE, SOUTHERN ITALY): ANTITROPICAL DISTRIBUTION IN A FOSSIL BEAKED WHALE (CETACEA, ZIPHIIDAE)

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**Key words:** Odontoceti, Ziphiidae, *Messapicetus longirostris*, *Messapicetus gregarius*, late Miocene, Italy, Peru, palaeoecology, palaeobiogeography, antitropical distribution.

**Abstract.** A new partial fossil skeleton of *Messapicetus longirostris* (Cetacea: Odontoceti: Ziphiidae) collected in Cisterna quarry (Lecce) from Tortonian (upper Miocene) sediments of the “Pietra leccese” is described. It comprises the fragmentary skull (including most of the rostrum), parts of the mandibles, five teeth, the fragmentary right scapula, and one vertebral centrum. This new record, here referred to a juvenile individual, expands our knowledge about the skeletal anatomy of *M. longirostris*; this species was until now only known by the holotype, an almost complete skull from the same Cisterna quarry. Moreover, the new specimen confirms the distinction between *M. longirostris* and *M. gregarius* (late Miocene, Pisco Formation, Peru) based on several osteological characters (e.g. the presence of a distinct maxillary tubercle and prominent notch in the latter species). New dating of layers in Cerro Colorado, the type locality of *M. gregarius*, suggests that *M. longirostris* and *M. gregarius* were contemporaneous sister-species with an antitropical distribution (a biogeographical pattern currently shown by two extant ziphiid genera). Unlike extant ziphiids, feeding predominantly on squid and benthopelagic fish in deep waters, the stem ziphiid *M. gregarius* was recently proposed to have been a raptorial piscivore who may have fed mainly on schools of epipelagic fish. Similarities at the level of the morphology and proportions of the oral apparatus suggest that the two species of *Messapicetus* may have occupied roughly identical ecological and trophic niches, a hypothesis supported by the characterization of the Pietra leccese environment as neritic.

## INTRODUCTION

**The fossil record of marine vertebrates from the Pietra leccese.** Fossil marine vertebrates from the Pietra leccese, a Miocene calcarenite limestone outcropping in Salento (southern Italy), are known since the nineteenth century thanks to the contributions of the famous naturalists Oronzo Gabriele Costa and Giovanni Capellini (Costa 1853, 1856, 1864; Capellini 1878). After these early publications, other important descriptions specifically devoted to cetaceans were produced by Bassani & Misuri (1912), Moncharmont Zei (1950, 1956) and Menesini & Tavani (1968).

Since the end of the 1980's, one of the authors (A.V.), in collaboration with the University of Pisa, started an intensive monitoring of some

quarries and sawmills of Pietra leccese, which led to the discovery and recovery of a large number of fossil marine vertebrates (cetaceans, sirenians, turtles, and fishes). Many of these finds were initially collected by the “Gruppo Naturalisti Salentini” and then became the first nucleus of the fossil vertebrate collection of the Museo dell’Ambiente of the University of Salento. Other specimens are kept in the Museo di Storia Naturale of the University of Pisa. Related to this activity, several publications appeared (Bianucci et al. 1992, 1994a, 1994b, 2003; Bianucci 2001; Bisconti & Varola 2000, 2006; Carnevale et al. 2002; Bianucci & Landini 2006). The most significant result of these studies is the detailed survey of the Cisterna quarry, located ca 2 km southeast of the town of Lecce and north of the village of Cavallino (Fig. 1). From the Tortonian strata outcropping in this quarry, an impressive marine vertebrate fossil assemblage referred to cetaceans

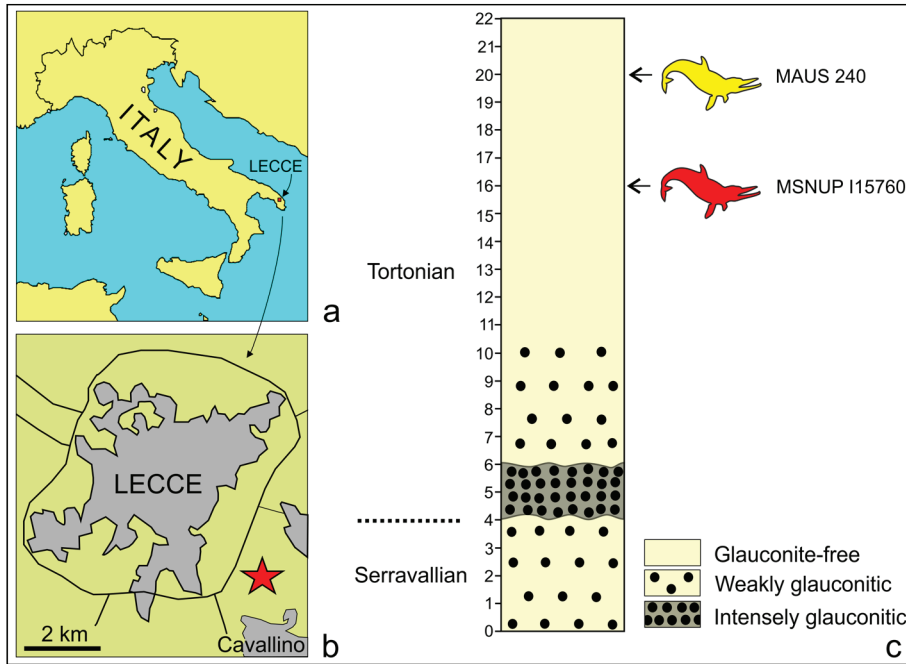


Fig. 1 - Location and stratigraphic section of Cisterna quarry near Lecce, southern Italy, where the holotype (MAUS 240) of *Messapicetus longirostris* and the referred specimen (MSNUP I15760) here described were found. a) Map of Italy with Lecce town. b) Map of Lecce and surrounding area with Cisterna quarry (star). c) Section of Cisterna quarry (from Mazzei et al. 2009) with the stratigraphical position of the two *M. longirostris* specimens.

(mysticetes and odontocetes), sirenians, fishes (teleosts and elasmobranchs), and turtles was collected. Part of this material has been already the object of publications, and three significant specimens were described as holotypes of three new genera and three new species: *Archaeoschrichtius ruggieroi* Bisconti & Varola, 2006, the currently oldest known grey whale (Eschrichtiidae), *Zygophyseter varolai* Bianucci & Landini, 2006, a stem raptorial sperm whale (stem Physeteroidea), and *Messapicetus longirostris* Bianucci et al., 1992, an archaic long-snouted beaked whale (stem Ziphiidae). Although other remains from Cisterna quarry are still under preparation, another interesting ziphiid specimen was recently freed from the hard limestone matrix and fully prepared. It is here described in detail, compared to other fossil ziphiids, and referred to the species *Messapicetus longirostris*.

#### Beaked whales and their fossil record.

Among extant cetaceans, beaked whales are one of the most mysterious families, due to their deep-sea habitat, elusive habits, and apparent low abundance. Despite their relatively large size (4-12 m in length) and high diversity (at least 22 extant species), these toothed whales are one of the least known groups of mammals. Their skull and teeth exhibit specialized morphological features linked to suction feeding (e.g. reduction of the functional dentition) and to sexual dimorphism (e.g. mandibular tusks, rostral pachyosteosclerosis in the genus *Mesoplodon*,

and great development of rostral maxillary crest in *Hyperoodon*) (Mead 2008).

Scarce until recently, their fossil record is now one of the best documented among cetaceans. Recent research on specimens from phosphorite layers outcropping on the bottom of deep oceanic areas and from inland deposits resulted in the description of 17 new genera and 22 new species.

Several new genera and species recovered by trawling and long-line fishing from phosphorite deposits along the Indian and Atlantic oceanic floor off the coasts of South Africa, Portugal, and Spain were described (Bianucci et al. 2007, 2008, 2013). Two main features distinguish the fossil ziphiid assemblages recovered from the ocean floor: an unexpectedly high diversity (10 new genera and 14 new species), and the occasional presence of unusual, aberrant traits (for example the enormous spherical rostral premaxillary protuberance of *Globicetus hibernus* Bianucci et al., 2013).

Inland deposits yielded the oldest ziphiid records, from early and middle Miocene of Ecuador (Bianucci et al. 2004) and Belgium (Lambert & Louwye 2006), as well as many other specimens from the Neogene of Belgium (Bianucci and Post 2004; Lambert 2005), Italy (Bianucci 1997), the eastern coast of U.S.A. (Post et al. 2008; Lambert et al. 2010), Argentina (Buono & Cozzuol 2013), and Peru (Muizon 1984; Lambert et al. 2009, 2010; Bianucci et al. 2010). Another putative fossil beaked whale, *Squaloziphius emlongi* Muizon, 1991 from

the early Miocene of Washington state, was recently considered either in a more basal position within Odontoceti (e.g. Geisler et al. 2011; Lambert et al. 2013) or as sister group of all ziphiids (Lambert et al. 2015b).

All the Peruvian ziphiids come from late Miocene levels of the Pisco Formation, where the best preserved ziphiid remains, referred to the species *Messapicetus gregarius* Bianucci et al., 2010, *Nazcacetus urbinai* Lambert et al., 2009, and *Ninoziphius platyrostris* Muizon, 1983 (Muizon 1984; Lambert et al. 2013) were found. The record of *M. gregarius* is especially interesting, as eight cranial specimens from a few layers of a single locality were described, providing a unique opportunity to describe intraspecific variation (Bianucci et al. 2010). More recently, new investigations in Cerro Colorado, the type locality of *M. gregarius*, evidenced an even higher concentration of fossils attributed to this species: on the whole, 12 specimens, some including postcranial remains, were reported in a geological map and positioned along a stratigraphical section, together with all other vertebrates outcropping in this highly fossiliferous area (Bianucci et al. in press). Interestingly, one of these fossils was found associated with numerous skeletons of a clupeiform fish (*Sardinops* sp. cf. *S. sagax*); this association is tentatively interpreted as representing the last meal of the beaked whale (Lambert et al. 2015a). Thanks to these recent discoveries from Peru, *Messapicetus* represents the best-known fossil beaked whale to date.

## INSTITUTIONAL ABBREVIATIONS

MAUS, Museo dell'Ambiente, Università del Salento, Lecce, Italy; MSNUP, Museo di Storia Naturale, Università di Pisa, Italy; MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marco, Lima, Peru; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

## SYSTEMATIC PALEONTOLOGY

Order **Cetacea** Brisson, 1762  
 Suborder **Odontoceti** Flower, 1867  
 Family Ziphiidae Gray, 1850  
 Genus *Messapicetus*  
 Bianucci, Landini & Varola, 1992

**Type species:** *Messapicetus longirostris* Bianucci, Landini & Varola, 1992, from the Tortonian beds of Pietra leccese (southern Italy).

**Referred species:** *Messapicetus gregarius* Bianucci, Lambert & Post, 2010, from the Tortonian beds of the Pisco Formation (Peru).

### *Messapicetus longirostris*

Bianucci, Landini & Varola, 1992

Figs 2-5, Tab. 1

1992 *Messapicetus longirostris* Bianucci, Landini & Varola, p. 261, fig 1-2.

1994 *Messapicetus longirostris* - Bianucci, Landini & Varola, p. 232, fig 1-7.

**Holotype:** MAUS 240, nearly complete skull lacking small portions (antorbital process, premaxillary crest and part of nasal) of the left side of cranium, collected in 1987 by one of the authors (A.V.) from the Tortonian beds of Cisterna quarry, near Lecce (southern Italy).

**Emended diagnosis:** *Messapicetus longirostris* differs from *M. gregarius* in the lesser posterior extension of the dorsomedial closure of the mesorostral groove by the premaxillae; lacking a distinct maxillary tubercle and prominent notch; the more slender premaxillary crest; the more gradual posteroventral descent of the medial margin of the maxilla from the vertex; and the presence of two or three dorsal infraorbital foramina on the right maxilla (contra only one foramen in *M. gregarius*).

#### The new record from Cisterna quarry

**Referred specimen:** MSNUP I15760, fragmented skull consisting of most of the rostrum, fragmentary portions of basioccipital and of exoccipitals (including incomplete occipital condyles), a portion of the postalveolar part of the left mandible, a fragment of the symphyseal portion of the mandibles, five teeth, one deformed centrum of a ?caudal vertebra, and a fragment of scapula, all from the same individual.

**Horizon and locality:** The specimen was found in 1987 by one of the authors (A.V.) during stone mining activities in the Cisterna quarry, ca 2 km southeast to the town of Lecce and north to the village of Cavallino (Salento, southern Italy, Fig. 1a, b), in the informally named "Pietra leccese" formation. This unit consists of generally massive, uniformly fine-grained planktonic foraminiferal biomicrites (Mazzei et al. 2009). At the Cisterna quarry, a stratigraphical section ca 22 m thick was measured and dated to the Langhian (lower portion) and Tortonian (middle and upper portions) ("Section 20" in Mazzei et al. 2009). MSNUP I15760 was collected ca 6 m below the top of the section. The holotype of *Messapicetus longirostris* (MAUS 240) was found in the same quarry at a horizontal distance of about 50 meters from MSNUP I15760 and 4 m higher in the section (Fig 1c). The 12 m upper portion of this section, including MSNUP I15760 and MAUS 240, consists of a yellowish glauconite-free biomicrite showing a planktonic foraminiferal association referable to the *Neoglobobadrina acostaensis* zone of Iaccarino & Salvatorini (1982), sensu Foresi et al. (2002), ranging between about 10.5 and 8.14 Ma (middle Tortonian).

#### Description and comparison

**Skull:** Typical for *Messapicetus* spp., the rostrum appears extremely elongated; in dorsal view, it tapers progressively from the proximal to the distal portion (Fig. 2).

Similar to the holotype of *M. longirostris*, the

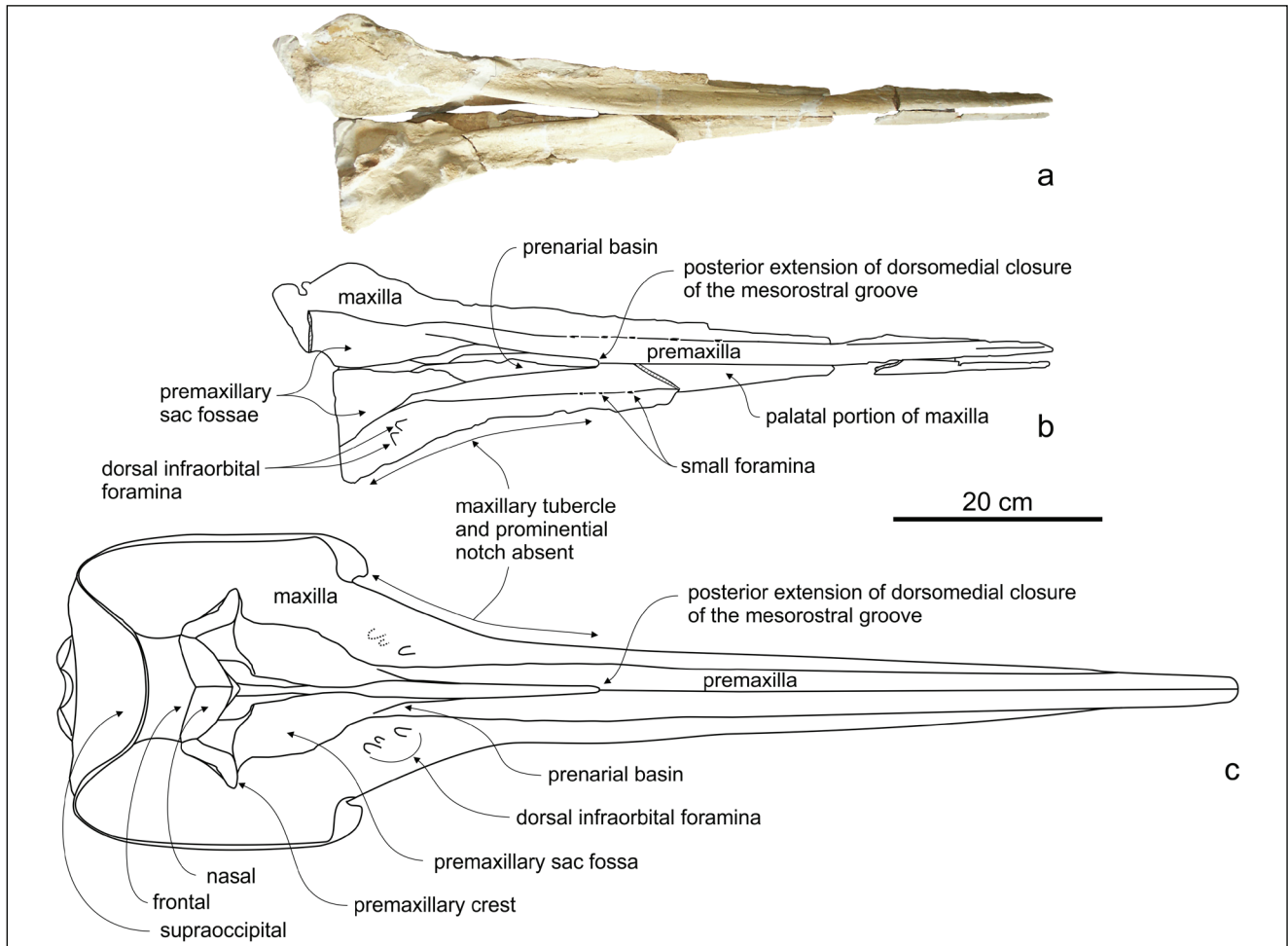


Fig. 2 - *Messapicetus longirostris* from Cisterna quarry (Lecce, southern Italy). a) Incomplete rostrum of the referred specimen MSNUP I15760 in dorsal view. b) Corresponding line drawing. c) Reconstruction of the skull in dorsal view, based on the holotype MAUS 240.

posterior portion of the lateral margin of the rostrum is rectilinear, without the distinct maxillary tubercle and prominent notch observed in the holotype and all the referred specimens of *M. gregarius* (Bianucci et al. 2010). This is the most distinctive feature separating *M. longirostris* from the Peruvian species. The preserved dorsal anterior portion of the rostrum is formed only by the premaxillae. The surface is marked by a longitudinal sulcus also observed in the holotype of *M. longirostris* and in *M. gregarius*. The premaxilla-maxilla suture is marked by a shallow sulcus along the distal half of the rostrum; the sulcus becomes almost invisible in the proximal half of the rostrum, where the suture is marked by several small foramina followed anteromedially by short sulci (a feature not observed in other specimens of *Messapicetus* spp.). The cross section of the premaxilla on the rostrum seems less dorsally convex than in the holotype and in *M. gregarius*, al-

though this character is difficult to assess due to the incompleteness and breakage of the specimen. In the closely related *Ziphirostrum marginatum* du Bus, 1868, intraspecific variation at the level of the elevation of the premaxillae on the rostrum was similarly noted (Lambert 2005). The medial margins of the premaxillae contact each other with a suture extending from 505 mm to 230 mm from the rostrum base. Consequently the medial closure of the mesorostral groove extends for 41% of the rostrum length, less than in *M. gregarius* ( $> 50\%$ ). Due to the diagenetic lateral compression of the skull of the holotype of *M. longirostris*, artificially closing the mesorostral groove both anteriorly and posteriorly to the portion with a medial sutural contact, it was originally not easy to estimate the actual extension of this sutural contact in the latter; nevertheless, thanks to further preparation of the fossil, the posterior end of the sutural contact is now clearly visible at ca 206





Fig. 3 - *Messapicetus longirostris* from Cisterna quarry (Lecce, southern Italy), incomplete mandibles of the referred specimen MSNUP I15760. a) Fragment of ankylosed symphyseal portion of mandibles in dorsal view. b) the same in ventral view. c) Posterior portion of left mandible in lateral view.

mm from the rostrum base (contra 120 mm as erroneously reported by Bianucci et al. 1994b). Consequently, the dorsally open posterior portion of the mesorostral groove represents ca 30% of the rostral length in the holotype, a value similar to that of the referred specimen MSNUP I15760 (32%) and proportionally longer than in the holotype of *M. gregarius* (25%) and the referred specimen MUSM 1481 (ca 23%). Therefore, the lesser extension of the dorsomedial closure of the mesorostral groove may be an additional character distinguishing *M. longirostris* from *M. gregarius*, although this character was observed as variable in *Ziphirostrum marginatum*. This open posterior portion of the mesorostral groove is anteriorly delimited by a clear U-shaped medial notch in the referred specimen MSNUP I15760, with the posteriorly diverging medial margins of the premaxillae forming an angle of ca 14 degrees. The medial margins of the premaxillae are not optimally preserved on the posteriormost portion of the rostrum. Nevertheless, in this area the premaxillae are clearly excavated, forming the typical prenarial basin of *Messapicetus* and other related genera (e.g. *Beneziphius*, *Ziphirostrum*). The incomplete premaxillary sac fossae are slightly transversely concave. Two dorsal infraorbital foramina pierce the right maxilla near the rostrum base: in the same position, the holotype of *M. longirostris* exhibits three foramina, contrasting with the single foramen present in the holotype and referred specimen of *M. gregarius*. This is apparently another minor difference between *M. longirostris* and *M. gregarius*. Only the posterior portion of the maxillary alveolar groove is preserved: it is transversely narrow, without distinct alveoli.

**Mandibles:** The two mandibles are ankylosed (Fig. 3a, b) and the posterior part of the symphyseal portion is half-circled in cross section. The total width at the posterior end of the symphyseal portion is 60 mm, narrower than in the holotype of *M.*

*gregarius* (69 mm) and the referred specimen MUSM 1038 (72 mm). The alveoli on this symphyseal portion are large and conspicuous; seven alveoli are counted on the right side, with an anteroposterior diameter of 21-25 mm and a transverse diameter of 12-13 mm. Three mental foramina are visible on the left ventrolateral surface. The posterior portion of the left mandible (Fig. 3c) is too fragmentary for significant observations (mandibular condyle and most of the coronoid process are missing). Judging by these fragments, the mandibles do not exhibit significant differences with those, well known, of *M. gregarius*.

**Teeth:** The largest tooth (Fig. 4a) is similar to several detached teeth associated to the holotype of *M. gregarius* (Bianucci et al. 2010: fig. 10f-k), with the transversely flattened root and the maximum anteroposterior width located at its proximal end. The crown is conical, slightly transversely flattened with a ratio between minimum and maximum diameters at the crown base equal to 0.9 (0.6 to 0.8 in *M. gregarius*), and medially curved. The enamel is smooth, without longitudinal striations and keels. Apart from the larger size, this tooth does not differ significantly from part of the teeth of *Ziphirostrum marginatum* (Lambert 2005: fig. 9). Unlike the holotype of *M. gregarius*, no apical wear and no indication of occlusal wear on the mesial and distal surfaces could be detected. The four other detached teeth (Figs 4b-e) are significantly smaller and have a proximal widening of the root lower than in the largest tooth. Moreover their root exhibits a swelling at about two thirds of their length from the proximal end. Their crowns are pointed and similarly lack apical and occlusal wear. These smaller teeth share similarities with teeth of members of several non-ziphiid odontocete families, for example eurhino-delphinids. Considering the narrow alveolar row on the proximal portion of the rostrum and the large

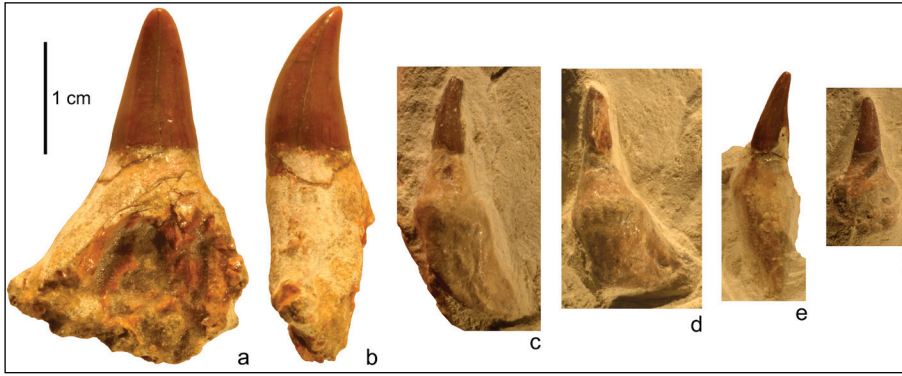


Fig. 4 - *Messapicetus longirostris* from Cisterna quarry (Lecce, southern Italy), five detached teeth of the referred specimen MSNUP I15760. a) Largest tooth in medial view. b) The same in distal view. c-f) Small teeth still partially enclosed in sediment.

	a-b	c	d	e	f
Total length	31.9	21.8	20.3	18.3	+12.2
Root length	18.8	15.3	12.9	12.6	
Crown length	14.7	6.5	7.4	5.7	5.3
Maximum mesiodistal diameter of root	21.6	5.7	5.3	9.5	-
Mesiodistal diameter at crown base	8.5	3.7	3.7	3.5	2.9
Transverse diameter at crown base	7.4	-	-	-	-

Tab. 1 - Measurements (in mm) of the detached teeth of the referred *Messapicetus longirostris* specimen (MSNUP I15760) from Cisterna quarry (Lecce, southern Italy). Letters a-f refer to the elements of Fig. 4. +, incomplete; -, no data.

and distinct alveoli in the symphyseal portion of the mandible, it is possible that this marked difference in size for the preserved teeth (also observed in the detached teeth of the holotype of *M. gregarius*) is linked to their origin in different regions of the tooth row. In *Tasmacetus shepherdi*, the only extant ziphiid with a complete series of functional post-apical upper and lower teeth, the size of the crown and the extent of the root vary markedly along the tooth row, with the smaller teeth positioned anteriorly (Oliver 1937: pl. 4; Mead & Payne 1975: fig.

1c; USNM 484878).

*Scapula*: While the lateral surface of the fragmentary right scapula has been prepared, the medial surface of the delicate blade remains embedded in the hardened micritic matrix. The general outline of the flat and thin blade cannot be reconstructed due to the erosion of its anterior, posterior, and suprascapular (dorsal) borders; however, the ventral-most portion of the posterior border is preserved and draws a rectilinear line posterodorsally (Fig. 5a). Only the proximal portions of the acromion and coracoid process are preserved. With respect to the acromion, which projects anteriorly and upwards, the coracoid process is more downward-oriented, starting from the anterior end of the glenoid fossa. The glenoid fossa is well preserved and roughly oval-shaped; its medial border is less convex than the lateral border. As observed in many odontocetes (e.g. Ichishima & Kimura 2000; Sanchez & Bertta 2010), the wide fossa for the attachment of the infraspinatus muscle is posteriorly bordered by a ridge-like, poorly salient crest whose height decreases towards the dorsal edge of the scapula. The teres major muscle presumably originated posterior to this crest. Due to the fragmentary state of this bone, it was not possible to make detailed comparisons with the scapula of other ziphiids.

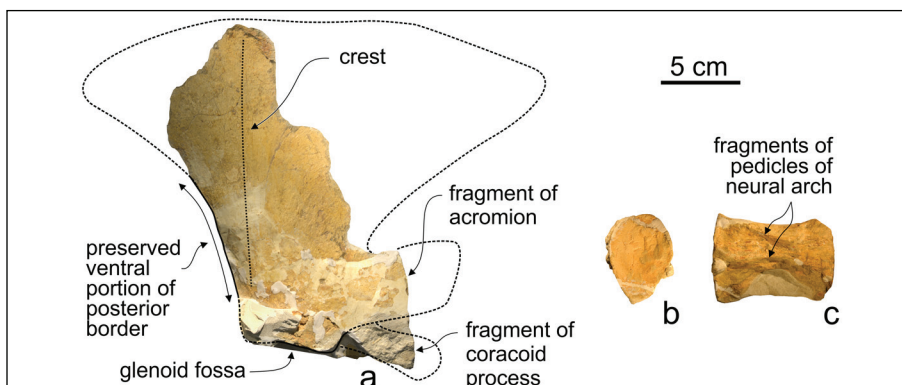


Fig. 5 - *Messapicetus longirostris* from Cisterna quarry (Lecce, southern Italy), fragmentary remains of the poscranial skeleton of the referred specimen MSNUP I15760. a) Right incomplete scapula in lateral view (dotted lines indicate a speculative reconstruction of the outline of the scapula). b) Deformed centrum of ?caudal vertebra in anterior view. c) The same in dorsal view.

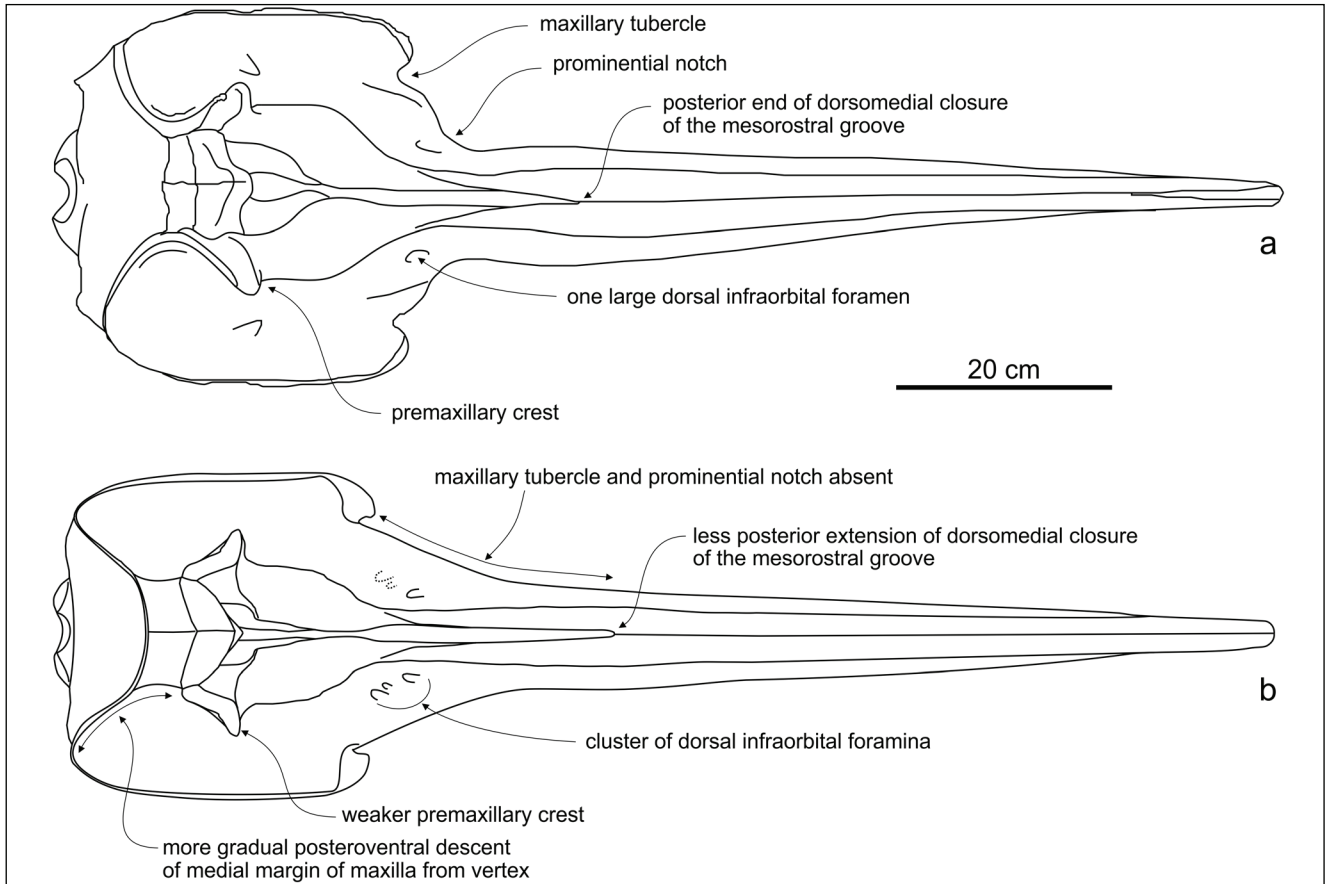


Fig. 6 - Comparison between the reconstructions of the skulls in dorsal view of: a) *Messapicetus gregarius* from Cerro Colorado (southern Peru); b) *Messapicetus longirostris* from Cisterna quarry (Lecce, southern Italy). Characters distinguishing the two species are indicated.

**Vertebra.** Only a partial vertebra, consisting of a 78 mm long centrum, is preserved (Fig. 5b-c). This vertebral centrum appears to have been heavily deformed by diagenetic compression and consequently its transverse section is ellipsoidal. In the dorsal surface a short proximal portion of the two pedicles are still preserved evidencing that originally the neural arch was transversely narrow. The small size, the anteroposterior elongation of the centrum, and the narrow neural arch suggest that this centrum belongs to a caudal vertebra.

## DISCUSSION

**Morphological characters separating *M. longirostris* and *M. gregarius*.** Three characters observed in this specimen further support the specific separation between *M. longirostris* (known until now from a single specimen) and *M. gregarius* (with a larger sample of eight specimens described): 1) the absence of a distinct maxillary tubercle and of a prominential notch, as already pointed out by Bia-

nucci et al. (2010); 2) the lesser extension of the dorsomedial closure of the mesorostral groove, clearly visible in MSNUP I15760 and partly obscured due to lateral diagenetic compression in the holotype of *M. longirostris*; 3) the presence of a cluster of two-three dorsal infraorbital foramina on the right maxilla, contra only one foramen in *M. gregarius*. Two other differences between *M. longirostris* and *M. gregarius* underlined by Bianucci et al. (2010) concern portions of the skull unfortunately lacking in MSNUP I15760: the more slender premaxillary crest and the more gradual descent of the medial margin of the maxilla from the vertex (Fig. 6).

**Age of the animal.** Several observations support the attribution of the remains MSNUP I15760 to an immature individual:

The size is smaller than in the holotypes of *M. longirostris* and *M. gregarius*, both considered as adult animals. In fact the nearly complete rostrum of MSNUP I15760 is 660 mm in length vs. 775 and 844 mm respectively in the holotypes of *M. longiro-*



*stris* and *M. gregarius*. An even shorter rostrum (ca 540 mm) was observed in the skull of *M. gregarius* MUSM 1394, interpreted as a calf (Bianucci et al. 2010). Differences in the length of the rostrum much likely relate to an allometric rostral elongation during ontogeny, as observed in extant ziphiid species (references in Bianucci et al. 2010): in fact, the ratio between the width of the rostrum at base and the length of the rostrum is 0.26 in the holotype of *M. gregarius*, ca 0.30 in MSNUP I15760, and ca 0.39 in the calf MUSM 1394. Moreover, judging by the width at the posterior end of the symphyseal portion (see above), the mandibles appear narrower in MSNUP I15760 than in the holotype of *M. gregarius* and in the referred adult specimen MUSM 1038 (mandibles unknown in the holotype of *M. longirostris*).

Compared with the holotype of *M. longirostris*, the bones of the rostrum of MSNUP I15760 appear thinner, a feature also observed in the calf of *M. gregarius* MUSM 1394.

The preserved proximal portion of the maxillary alveolar row is narrower than in the holotype of *M. longirostris*.

The five teeth preserved do not display any apical or occlusal wear, whereas both wear types are observed in the teeth of the holotype of *M. gregarius* (teeth unknown in the holotype of *M. longirostris*).

#### **Palaeobiogeography and palaeoecology.**

As previously outlined (Bianucci et al. 2010), the fossil record suggests a wide geographic distribution for *Messapicetus*, with fossils from Italy (*M. longirostris*), Peru (*M. gregarius*), and possibly Maryland (cf. *Messapicetus* sp., Fuller & Godfrey 2007). Open during the late Miocene (Jacobs et al. 2004), the Central American Seaway allowed a direct communication between the Pacific and Atlantic oceans. Among other fossil ziphiids the genus *Ninoziphius* was also reported from both the southern coast of Peru (in younger deposits of the Pisco Formation) and the east coast of USA, similarly supporting a faunal link between south-eastern Pacific and North Atlantic (Muizon 1984). The assignment to *Ninoziphius* of the presumably early Pliocene North American fragmentary specimens was nevertheless recently questioned (Lambert et al. 2013).

Similar skull size and similar morphology of the oral apparatus suggest that the two species of *Messapicetus* may have occupied roughly identical

ecological niches. Based on this hypothesis, allopatric speciation may better explain the separation of the two species than sympatric speciation. Even if in different oceans, *M. gregarius* and *M. longirostris* might be considered as sister-species with an antitropical distribution, as for species of the extant ziphiids *Berardius* and *Hyperoodon* (see Davies 1963; Hare et al. 2002). Interestingly, the fossiliferous beds from Peru containing the holotype and most of the referred specimens of *M. gregarius* were recently reassigned, based on diatom biostratigraphy, to an age ranging between 9.9 and 8.9 Ma (Tortonian) (Di Celma et al. in press; Lambert et al. 2015a), younger than in previous works (13-11 Ma; Bianucci et al. 2010; Lambert et al. 2010). As a consequence, this new dating suggests that *M. longirostris* (10.5-8.14 Ma) and *M. gregarius* (9.9-8.9 Ma) were contemporaneous species with distinct geographical distributions.

Based on a high number of bony fish skeletons found associated with a partial skeleton of *M. gregarius* in the type Peruvian locality, Lambert et al. (2015a) suggested that unlike the extant ziphiids this stem beaked whale fed on clupeid fish in neritic and/or epipelagic environments. A similar feeding behaviour could be proposed for *M. longirostris*, a hypothesis that is supported by 1) the external neritic depositional environment of the Pietra leccese (Bossio et al. 2006); 2) the discovery in the same quarry and approximately the same stratigraphic horizon as the two known specimens of *M. longirostris* of four well preserved skull remains of Atlantic blue marlin *Makaira* sp. cf. *M. nigricans* (see Carnevale et al. 2002), a large fish whose extant relatives capture epipelagic prey in a similar way to that hypothesized for *M. gregarius*.

#### **CONCLUSIONS**

The fragmentary fossil described here provides new data about the stem beaked whale species *Messapicetus longirostris*, previously only known on the basis of the holotype, a nearly complete skull. In particular the mandibles and the teeth are described for the first time in this species; these parts do not differ significantly from the corresponding bones in the sister species *M. gregarius*. The fragment of scapula and the vertebral centrum represent the only described postcranial elements of *Messapicetus* and contribute to the very scarce record



of fossil postcranial remains of ziphiids worldwide. The relatively well-preserved rostrum of MSNUP I15760 confirms that the most significant character allowing the distinction between *M. longirostris* and *M. gregarius* is the absence of a distinct maxillary tubercle and of a prominent notch in the former. Moreover, two other potentially distinctive features are observed in *M. longirostris*: 1) the lesser extension of the dorsomedial closure of the mesorostral groove and 2) the presence of a cluster of two-three dorsal infraorbital foramina (contra only one foramen in *M. gregarius*). The small size, the relatively short rostrum, thin skull bones, small posterior maxillary alveoli, and the absence of apical or occlusal wear on teeth all together support the identification of MSNUP I15760 as an immature individual. Finally, this record confirms that *M. longirostris* and *M. gregarius* were probably contemporaneous species, living in distinct geographical area, but occupying a similar ecological niche.

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