



# HIGH CONCENTRATION OF LONG-SNOUDED BEAKED WHALES (GENUS *MESSAPICETUS*) FROM THE MIOCENE OF PERU

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**Abstract:** Eight skulls of beaked whales (Cetacea, Odontoceti, Ziphiidae), in six cases associated with elements of the mandible, were collected from a limited area (about 1.5 km<sup>2</sup>) and roughly from the same stratigraphic horizon at Cerro Colorado, 35 km south-south-west of the city of Ica (Peru), where the late Middle Miocene basal strata of the Pisco Formation crop out. They represent the highest concentration reported of fossil Ziphiidae. These finely preserved Cerro Colorado fossils are described and assigned to a new species *Messapicetus gregarius*, together with another specimen collected from sediments of the same age at Cerro la Bruja (33 km south-east to Cerro Colorado). *Messapicetus gregarius* shares with *M. longirostris* Bianucci, Landini and Varola, 1992 (Tortonian of Italy), an extremely elongated rostrum, but is clearly different from the Italian species in the more distinct maxillary tubercle and prominent notch, the more robust premaxillary crest, and the abrupt ventrolateral des-

cent of the medial margin of the maxilla from the vertex. A parsimony analysis reveals that *Messapicetus* belongs to a basal clade, which includes other ziphiids with a dorsally closed mesorostral groove and prenarial basin. The high concentration of specimens belonging to the same species (some of them tentatively identified as adult males and females), combined with the presence of a calf, supports the hypothesis of site fidelity; these cetaceans might have lived in a limited region for a long period for both breeding and feeding. Besides the eight specimens of *M. gregarius*, strata at Cerro Colorado include many other cetacean remains (with several specimens of the pontoporiid *Brachydelphis* including a foetus), pinnipeds, turtles, fishes, and birds.

**Key words:** *Messapicetus*, Ziphiidae, Cetacea, phylogeny, Miocene, Peru, palaeobiogeography, taphonomy, palaeoecology.

RECENT studies on fossil beaked whales (Odontoceti, Ziphiidae) trawled from the sea floor revealed an unexpectedly high past diversity of these odontocetes (Bianucci *et al.* 2007, 2008). Although fossils are fairly abundant, they are generally badly preserved and/or lack taphonomic and precise stratigraphical information, which limited the understanding of the morphological intraspecific variation and palaeoecology of these cetaceans. With only some exceptions (see Muizon 1984; Bianucci *et al.* 1994), the same applies to most other fossil ziphiids reported (Bianucci 1997; Bianucci and Post 2005; Lambert 2005a; Lambert and Louwey 2006; Post *et al.* 2008).

Recent field investigations on the Neogene sediments of the Pisco-Ica desert (Peru) have led to the discovery of many exceptionally well-preserved fossil cetaceans, some of them belonging to the family Ziphiidae. One of these finds has been recently described and referred to the new genus and species *Nazzacetus urbinai* Lambert

*et al.*, 2009. This fossil, consisting of a skull, mandible, hyoid bones, and cervical vertebrae, represented at the time of the discovery the most complete fossil of a beaked whale and it provided important information on the phylogeny and the ecology of the ziphiids during the past (Lambert *et al.* 2009). Additional exceptional findings come from a new Miocene fossiliferous locality in the Pisco-Ica desert, where a high concentration of well-preserved ziphiid remains belonging to a new species of *Messapicetus* Bianucci *et al.*, 1992 has been discovered. *Messapicetus* is a Miocene fossil beaked whale previously known from a skull of South Italy (Bianucci *et al.* 1992, 1994) and possibly from fragmentary material from Maryland (Fuller and Godfrey 2007). The new discovery is particularly important because of the high concentration of specimens, all of them collected in a restricted area and approximately in the same fossiliferous layer, and the exceptional preservation of these

fossils. Thanks to these unique conditions, *Messapicetus* is now the best-known fossil beaked whale. The main goals of this work are to provide a detailed morphological description of the new species, highlight some aspect of its intraspecific variation, construct a phylogenetic framework, and give some palaeobiogeographical and palaeoecological hypotheses.

## MATERIAL AND METHODS

**Terminology and measurements.** The terminology for the cranial and ear anatomy mainly follows Kasuya (1973), Heyning (1989), Fordyce (1994), Lambert (2005a), Bianucci *et al.* (2007), and Mead and Fordyce (2009). Measurements were taken following Ross (1984), Bianucci (1997), Lambert (2005a), and Bianucci *et al.* (2007).

**Institutional abbreviations.** IGF, Museo di Geologia e Paleontologia, Università di Firenze, Italy; IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; MAUL, Museo dell'Ambiente, Università di Lecce, Italy; MGPUP, Museo di Geologia e Paleontologia, Università di Padova, Italy; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MSNTUP, Museo di Storia Naturale e del Territorio, Università di Pisa, Italy; MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marco, Lima, Peru; MZUF, Museo di Zoologia, Università di Firenze, Italy; NMR, Natuurhistorisch Museum Rotterdam, The Netherlands; NNML, Nationaal Natuurhistorisch Museum Naturalis, Leiden, The Netherlands; PEM, Port Elizabeth Museum, Port Elizabeth, South Africa; SAM, Iziko South African Museum, Cape Town, South Africa; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; ZMA, Zoologisch Museum Amsterdam, The Netherlands.

**Material.** All the specimens of *Messapicetus gregarius* described here are kept at the MUSM. The comparison with the Italian species *Messapicetus longirostris* is based on our direct examination of the holotype (MAUL no number) and of one undescribed specimen (MSNTUP I15760) collected from the type locality.

The complete list of the specimens described or examined for comparison and phylogeny is the following:

†*Africanacetus ceratopsis*: NMR 9991-00001993 (holotype), SAM PQ 2162, SAM PQ 2235, SAM PQ2708, SAM PQ2709, SAM PQ 2713, SAM PQ 3002, SAM PQ 3062, SAM PQ 69683, SAM PQ69683; †*Aporotus dicyrtus*: IRSNB M.541 (holotype); †*A. recurvirostris*: IRSNB M.1887 (holotype), IRSNB M.1888; †*Archaeoziphius microglenoid eus*: IRSNB M.1853 (holotype), IRSNB M.1854, IRSNB M.1855; †*Beneziphius brevisrostris*: IRSNB M.1885 (holotype), IRSNB M.1886; *Berardius arnuxii*: MNHN no number (holotype), SAM ZM 39296, SAM ZM 37404; †*Caviziphius altirostris*: NNML 447230 (holotype); †*Choneziphius macrops*: IRSNB M.1884; †*C. planirostris*: MNHN no number (lectotype), IRSNB M.1881, IRSNB M.1882, IRSNB M.1883, IRSNB 3767-3773, IRSNB 3776, IRSNB 3779, IRSNB

3780, IRSNB 3790; †*Eurhinodelphis cocheteuxi* du Bus, 1867: IRSNB M.294 (holotype), IRSNB M.1856, IRSNB M.295, IRSNB M.296, IRSNB M.1857, IRSNB M.297, IRSNB M.299, IRSNB 3254; *Hyperoodon ampullatus*: IRSNB 18027, IRSNB 1503, MSNTUP 268; *H. planifrons*: SAM ZM 41123, SAM ZM 41263; †*Ihlangesi saldanhae*: SAM PQ 2792 (holotype), SAM PQ 69673; *Indopacetus pacificus*: MZUF M4854; †*Izikoziphius rossii*: PEM N 3265 (holotype), SAM PQ 2086; †*I. angustus*: SAM PQ 3004 (holotype); †*Khoikhoicetus agulhasis*: SAM PQ 2678 (holotype); *Mesoplodon bidens*: IRSNB 19822, MNHN 1975-111, MNHN 1975-112, MNHN A3541; *M. bowdoini*: MSNTUP 269 *M. densirostris*: SAM ZM 40836, SAM ZM 40858, SAM ZM 4013, SAM ZM 40905, SAM ZM 40663; *M. europaeus*: NMR 9990-00001379, ZMA 25.735, ZMA 25.736, ZMA 25.750; *M. grayi*: MNHN 1877-329, SAM ZM 40622, SAM ZM 40478, SAM ZM 40473, SAM ZM36839, SAM ZM 41391, SAM ZM 36846, SAM ZM 11476, SAM ZM 19470; *M. layardii*: MNHN 1984-038, SAM ZM 38236, SAM ZM 38235, SAM ZM 40051, SAM ZM 35450, SAM ZM 40479, SAM ZM 39566, SAM ZM 39779, SAM ZM 22408, SAM ZM 39786, SAM ZM 35540, SAM ZM 19932; *M. mirus*: SAM ZM 39932, SAM ZM 39840, SAM ZM 38219; *M. peruvianus*: IRSNB 4036; †*Messapicetus gregarius*: MUSM 1037 (holotype), MUSM 950, MUSM 951, MUSM 1036, MUSM 1038, MUSM 1394, MUSM 1481, MUSM 1482, MUSM 1718; †*M. longirostris*: MAUL no number (holotype), MSNTUP I15760; †*Microberardius africanus*: SAM PQ 3003 (holotype); †*Nenga meganasalis*: SAM PQ 69675 (holotype), SAM PQ 2117, SAM PQ 2339, SAM PQ 69676; †*Nazzacetus urbinai*: (holotype) MUSM 949; †*Ninoziphius platyrostris*: MNHN SAS 941 (holotype); †*Pterocetus benguelae*: SAM PQ2803 (holotype), SAM PQ 69684, SAM PQ 2163; *Tasmacetus shepherdi*: SAM ZM 41116, SAM ZM no number, USNM 484878; †*Tusciziphius crispus*: IGF 1594V (holotype), NMR 9991-3020; †*Squalodon bariensis*: MGPUP 26084, MGPUP 20196; †*S. bellunensis*: MGPUP 26131 (holotype); †*S. calvertensis*: USNM 10484 (holotype), USNM 32834; †*Xhosacetus hendeyi*: SAM PQ 2082 (holotype); †*Ziphirostrum marginatum*: IRSNB M.1878 (holotype), IRSNB M.1874, IRSNB M.1875, IRSNB M.536, IRSNB M.537, IRSNB M.1876, IRSNB M.1877, IRSNB M.1879; †*Z. recurvus*: IRSNB M.544 (holotype); †*Z. turniense*: IRSNB M.539 (lectotype), IRSNB M.1880; *Ziphius cavirostris*: MSNTUP M270, MSNTUP M271, MZUF 7466, MZUF 18854, SAM ZM 38237, USNM 550148, USNM 550122, USNM 550111, USNM 550106.

**Cladistic analysis.** The phylogenetic relationships of *Messapicetus* were investigated by means of a matrix of 29 characters partly taken from previous analyses (Lambert 2005a, b; Bianucci *et al.* 2007; Lambert *et al.* 2009). For our analysis, we selected two outgroups (*Squalodon* and *Eurhinodelphis*) and 19 ziphiid genera, including the six Recent genera (Appendix S1). The genus *Mesoplodon*, possibly paraphyletic (Bianucci *et al.* 2007), is represented by the type species *M. bidens*.

The number of characters scored for each taxon is limited by the generally incomplete preservation of the cranial features in the fossil taxa, which are the predominant

component of the matrix. As a consequence, we preferred not to include in our analysis the fossil genera based on too fragmentary material (e.g. *Caviziphius* and *Khoikhoicetus*). In fact, taxa for which too few characters have been scored may be difficult to accurately place on the tree, with a consequent decrease in the phylogenetic accuracy (Wiens 2003).

Character states are designed plesiomorphic (0) or derived (1-n) according to the outgroup comparison method of Maddison *et al.* (1984). The matrix includes 29 morphological characters; 14 binary (5, 6, 12, 16, 17, 19, 20, 21, 23, 24, 25, 26, 27, 29), 11 multistate ordered (1, 3, 7, 9, 8, 11, 13, 14, 15, 18, 22), and four multistate unordered (2, 4, 10, 28). Two characters (23, 24) are parsimony-uninformative in this analysis. Multistate characters were treated as ordered when character states could be arranged so that each state was most similar to the states adjacent to it (e.g., state 1 is most similar to states 0 and 2) (Geisler and Sanders 2003).

As neither the number of fossil specimens available nor the number of individuals of the living taxa measured were sufficient to lend statistical significance to the standard deviations of the variations within each taxon observed, the continuous multistate characters were transformed into discrete states by placing the divisions between states in correspondence with the largest gaps, following the gapcoding method of Mickevich and Johnson (1976) as modified by Geisler and Sanders (2003) to suit the case of taxa represented by just a few specimens.

The analysis was executed with the software PAUP (version 4.0b10, Swofford 2001), using the Branch-and-bound algorithm with the homoplastic characters down-weighted using the default value of 3 for the constant *k* of the Goloboff method (1993).

At least a part of the characters related to the feeding apparatus are likely to represent homoplasies in odontocetes, specially long-snouted forms like *Messapicetus*. Furthermore, as many fossil beaked whales are fragmentarily known, a significant part of the morphological data is gathered on the rostrum. We therefore preferred to use an objective method for dealing with such potential homoplasies, even if the analysis run with all characters unweighted provided more parsimonious cladograms.

## GEOLOGICAL SETTING

The Pisco Formation consists of coarse- to fine-grained clastic (conglomerates, sandstones and siltstones) and diatomitic outcrops near the southern Peruvian coast and extending, from Pisco to Yauca, for about 300 km (Muizon and DeVries 1985; Dunbar *et al.* 1990; DeVries 1998). These sediments were deposited in the forearc Pisco and Sacaco basins where, over a basement of Palaeozoic and

Mesozoic crystalline rocks, six transgressive sequences have been observed, which range from the middle Eocene to the Late Pliocene (Dunbar *et al.* 1990; DeVries 1998; Uhen *et al.* 2008). The Pisco Formation was deposited in shallow and lagoonal waters from the late Middle Miocene to the Late Pliocene (from about 13–14 Ma to about 2 Ma) and consists of three transgressive sequences separated by two depositional hiatuses. The first hiatus (10–9 Ma) is attributed to an eustatic lowering of the sea level and an Andean compression phase. The second hiatus (5–4 Ma) is attributed to a marked eustatic sea level drop (DeVries 1998). The basal portion of the Pisco Formation lies in angular discontinuity over the older Chilcatay Formation (25–15 Ma) and is covered by disconformable Late Pliocene – early Pleistocene marine terraces (Dunbar *et al.* 1990; DeVries 1998). The stratigraphic thickness of the Pisco Formation, ranging from 200 to 1000 m, and its lithologies vary widely along the sections, as outlined by various authors (e.g., Muizon and DeVries 1985; Dunbar *et al.* 1990; DeVries 1998). In particular, the base of the section (Middle Miocene transgression) consists prevalently of bioclastic conglomerates, sandstones, and tuffaceous siltstones. The middle section (Late Miocene transgression) consists of dolomite-cemented beds and phosphate pebble horizons and coincides with a prolonged subemersion phase. Near the top (Early Pliocene transgression), the Pisco Formation is mostly represented by diatomites and diatomaceous mudstone (about 500 m thick). The marked thickness of the diatomites, locally showing sedimentary structures indicative of the action of currents, has been interpreted as because of a rapid accumulation, at least partly favoured by the transport of diatoms by currents and/or storms from open sea into shallow bays (Brand *et al.* 2004). This rapid burial, combined with a rapid mineralization, is considered responsible for the high concentration of exceptionally well-preserved fossil whales inside these sediments (Brand *et al.* 2004; Esperante *et al.* 2008).

The holotype of *Messapicetus gregarius* and the referred specimens were found in the lowest levels of the Pisco Formation, several metres above the unconformity with the Chilcatay Formation (T. DeVries, pers. comm. 2006). In this area, the first deposits of the Pisco Formation are dated, on the basis of radiolarian, diatom, foraminiferal, and molluscan data, as Middle Miocene (12–13 Ma in Dunbar *et al.* 1990; roughly 14 Ma in DeVries 1998, 2001). This age is corroborated by the discovery in the same strata of a rich mollusc level containing the bivalve *Anadara sechurana* Olsson, 1932, only found in the basal Pisco Formation (DeVries 1998; pers. obs. 2008) and in the Middle Miocene Montera Formation in the northern Peru (Dunbar *et al.* 1990; DeVries 1998). In Cerro Queso Grande, a locality 18 km south-east-east to Cerro Colorado, a section of the Pisco Formation was dated by

radiolarian zones as latest Miocene and K/Ar dating provided an age of  $6.75 \pm 0.18$  Ma (compilation of data in Dunbar *et al.* 1990). With satellite images, it is possible to follow the layers of Cerro Queso Grande towards the north-west; these layers are positioned several tens of metres above the Cerro Colorado layers that yielded the ziphiid remains. The layers at Cerro Colorado are approximately correlated with the cetacean-bearing levels of the locality of Cerro la Bruja, 33 km south-west of Cerro Colorado, where *Brachydelphis mazeasi* and *M. gregarius* have also been recorded (Muizon 1988; pers. obs. 2008).

## SYSTEMATIC PALAEOLOGY

Order CETACEA Brisson, 1762  
Suborder ODONTOCETI Flower, 1867  
Family ZIPHIIDAE Gray, 1850

Genus MESSAPICETUS Bianucci, Landini and Varola, 1992

*Type species.* *Messapicetus longirostris* Bianucci, Landini and Varola, 1992, from South Italy.

*Emended diagnosis.* *Messapicetus* differs from all the other ziphiids in the extreme elongation of the rostrum (roughly 75 per cent of the condylobasal length), the wide nasals (ratio between median length and total width of the nasals lower than 0.35), and the transverse flattening of the post-apical teeth. *Messapicetus* differs from all the other ziphiids except *Aporotus*, *Beneziphius*, *Caviziphius*, *Izikozihius*,

*Tusciziphius*, *Ziphistrostrum*, and *Ziphius* in the anterolaterally directed premaxillary crest, and (with the exception of *Tusciziphius*) in the short posterior contact of the crest with the nasal; except *Beneziphius*, *Caviziphius*, *Tusciziphius*, and *Ziphistrostrum* in the medial fusion of the premaxillae dorsal to the mesorostral groove on the rostrum; and except *Aporotus*, *Beneziphius*, *Ziphistrostrum*, and *Ziphius* in the presence of a developed prenarial basin.

*Messapicetus gregarius* sp. nov.

Text-figures 2–13

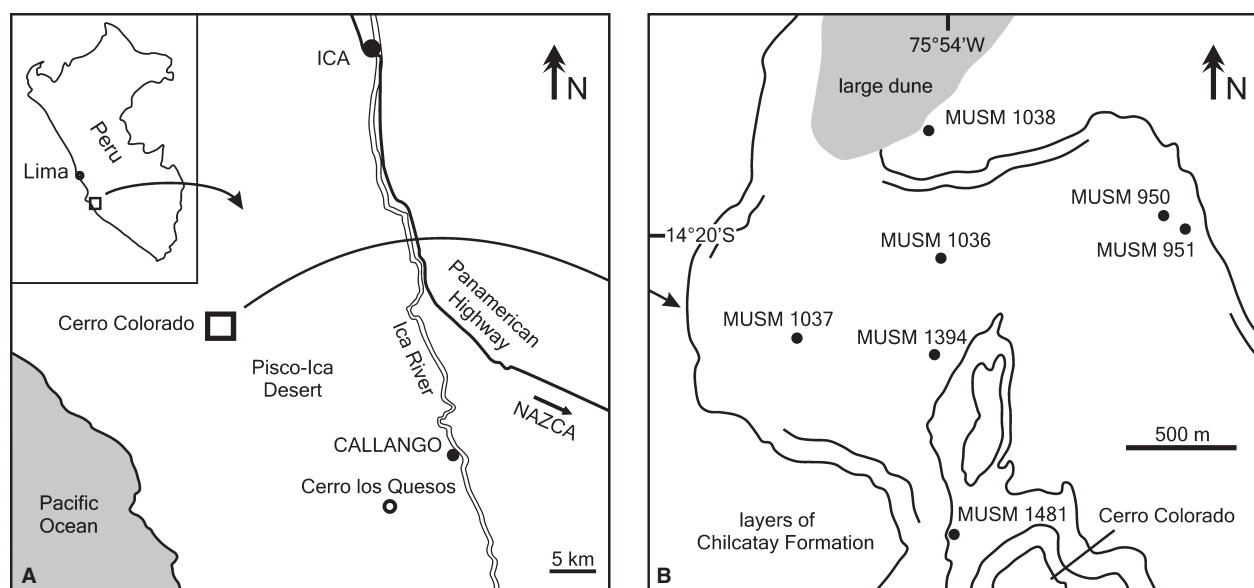
*Derivation of name.* From Latin ‘gregarius’, considering the high number of specimens found in a limited area of outcrops.

*Holotype.* MUSM 1037 (Text-figs 2, 9A, 10), nearly complete skull with damaged basicranium, associated mandible, teeth, right tympanic bulla, and damaged right periotic.

*Type locality.* Cerro Colorado, Pisco-Ica desert, 35 km south-south-west of the city of Ica, southern coast of Peru (Text-fig. 1). Geographical coordinates:  $14^{\circ}20'13.4''S$ ,  $75^{\circ}54'25.2''W$ .

*Type horizon and age.* Lowest levels of the Pisco Formation, several metres above the unconformity with the Chilcatay Formation. The age is Serravallian (Middle Miocene), probably 12–13 Ma (see comments in the Geological Setting section).

*Referred specimens.* Cerro Colorado: MUSM 950, fragments of skull and mandible with associated hyoid bones and left periotic ( $14^{\circ}19'56''S$ ,  $75^{\circ}53'25''W$ ); MUSM 951, fragments of skull,



**TEXT-FIG. 1.** A, maps of the Pisco-Ica desert indicating the locality of Cerro Colorado (square) 35 km south-south-west to the city of Ica, southern coast of Peru, where the holotype of *Messapicetus gregarius* MUSM 1037 and the referred specimens were discovered. B, detail of the investigated area of Cerro Colorado showing the position of each specimen.

including the natural endocranial cast, fragments of ear bones, and mandible (14°19'59"S, 75°53'22"W); MUSM 1036, skull with associated mandible and fragments of ear bones (14°20'02"S, 75°54'01"W); MUSM 1038, skull with facial portion of the cranium damaged, associated mandible, left periotic, left tympanic bulla, and left malleus (14°19'42"S, 75°54'03"W); MUSM 1394, fragmentary skull lacking the basicranium (14°20'17"S, 75°54'04"W); MUSM 1481, skull with associated right periotic and right tympanic bulla (14°20'43"S, 75°54'02"W); MUSM 1482, anterior fragments of the rostrum and mandible. Cerro la Bruja: MUSM 1718, right periotic, fragmentary right tympanic bulla, and left malleus (14°33'29"S, 75°40'17"W); the associated very fragmentary skull and mandible of this last specimen were not collected.

*Diagnosis.* *Messapicetus gregarius* differs from *M. longirostris* in the more distinct maxillary tubercle and prominent notch; the robust premaxillary crest; and the abrupt ventrolateral descent of the medial margin of the maxilla from the vertex.

*Remarks.* Among ziphiids, some of the most striking skeletal characters used to diagnose extant species belonging to a same genus are related to the size, shape, and position of the mandibular tusks (for *Mesoplodon*, see Mead 1989b; Dalebout *et al.* 2008); preserved in *Messapicetus gregarius*, these elements are unknown in *M. longirostris*. Nevertheless, our detailed examination of large samples of specimens for several extant ziphiid species (see Material and Methods section) indicate that the characters considered here distinctive for *M. gregarius* display a clear interspecific variability and a low intraspecific variability.

### Description

*Remarks.* The description is based on the specimens considered to be adults or subadults. MUSM 1394 (presumed to be from a calf) is commented in the text separately.

*General features of the skull.* The cranium has a size in the range of the Recent ziphiids *Mesoplodon bowdoini* and *M. densirostris* (Table 1). As in *Messapicetus longirostris* the rostrum is considerably elongated, around 75 per cent of the condylobasal length, more than in all other ziphiids (Bianucci *et al.* 1994) and only slightly shorter than in e.g. the eurhinodelphinid *Eurhinodelphis cocheteuxi*. The rostrum is dorsoventrally flattened, wider than high on its whole length. The temporal fossa is longer than the orbit, and moderately dorsoventrally flattened. The cranium is proportionally wider than in the holotype of *Messapicetus longirostris*, but the Italian specimen shows evidence of diagenetic compression so good comparison of this feature is difficult.

*Premaxilla.* The premaxillary anterior portion of the rostrum is 170 mm long, roughly similar to *Messapicetus longirostris* (Text-fig. 2). This portion does not bear alveoli, in contrast to *Tas-*

*macetus*, reminiscent of the long edentulous premaxillary end of the rostrum of eurhinodelphinids. A sulcus marks the lateral surface of the premaxilla from the apex for 300 mm backwards. A similar condition is seen in *M. longirostris*, *Ziphirostrum turniense*, and *Z. recurvus* and is possibly related to the extended dorsomedial closure of the mesorostral groove. The elevated thick premaxillae contact each other dorsomedially, with a sutural contact on more than one half of the rostrum length, not as elevated as in *Aporotus*, and anteriorly diverging contrary to *Choneziphius*. This sutural medial contact between the premaxillae on the rostrum has been proposed to decrease the risk of fractures, possibly during intraspecific fights (Lambert *et al.* in press). The section of the premaxillae on the rostrum is half-circled anteriorly, becoming more triangular in the posterior portion. As in *Ziphirostrum marginatum* and the holotype of *M. longirostris*, the prenarial basin (excavation on the premaxillae and vomer immediately anterior to the external bony nares, possibly homologous to the prenarial basin observed in *Ziphius cavirostris*, see Mead and Fordyce 2009) is deep (maximum depth ranging from 18 to 20 mm), including the premaxillary foramen in its anterolateral corner and located considerably anterior to the antorbital notch. The prenarial basin is shallower in *Beneziphius* and virtually absent in *Choneziphius* (see Lambert 2005a for a discussion of this character in the fossil ziphiids). The slightly concave premaxillary sac fossae are moderately asymmetric (ratio between widths of left and right fossae ranging from 0.75 to 0.95), and they do not overhang the maxilla laterally. The ascending process is transversely constricted before the moderately thickened anterolaterally directed premaxillary crest. The premaxillary crest is thicker than in the holotype of *M. longirostris*. The anterior surface of the crest is roughly vertical.

*Maxilla.* The maxillary alveoli are individually indistinct, shallower than the mandibular alveoli, but the alveolar groove is still deeper than in *Beneziphius*, *Choneziphius*, and *Ziphirostrum* (Text-figs 2, 3). The first posterior alveolus is 255 mm anterior to the antorbital notch in MUSM 1036, 150 mm in MUSM 1481. A total of 18 alveoli occupy 463 mm in the incomplete alveolar groove of MUSM 1481. Lateral to the prenarial basin of the holotype, the left maxilla is somewhat dorsally thickened (rostral maxillary crest, *sensu* Mead and Fordyce 2009), as in *Ziphirostrum marginatum*, whereas the right maxilla remains flat. A low maxillary tubercle separates the V-shaped antorbital notch from the shallow prominent notch (better seen in MUSM 1036). The maxillary tubercle and the prominent notch are clearly more distinct than in the *Messapicetus longirostris* holotype and in another undescribed *M. longirostris* specimen (MSNTUP I15760) from the type locality, both having an almost rectilinear lateral margin of the rostrum base. One or two dorsal infraorbital foramina pierce each maxilla medial to the antorbital notch. From the vertex, the medial margin of the maxilla descends more abruptly lateroventrally than in *M. longirostris*; in lateral view, the dorsal outline of the cranium is therefore truncated compared to the latter.

*Nasal.* The nasal is wider than long, with a narrow lateral process between the premaxillary crest and the frontal (Text-fig. 2A,

**TABLE 1.** Measurements of the skull, ear bones, and mandible of the holotype (MUSM 1037) of *Messapicetus gregarius* and of referred specimens.

	MUSM 1037	MUSM 950	MUSM 951	MUSM 1036	MUSM 1038	MUSM 1394	MUSM 1481
Condylbasal length	+1120	–	–	+1030	e1060	–	+969
Length of rostrum	844	–	–	+771	e795	+540	+710
Length of premaxillary portion of rostrum	170	–	–	+119	–	–	–
Longitudinal distance antorbital notch – anterior end of maxilla	674	–	–	e652	–	–	–
Longitudinal distance bony nares – apex of rostrum	920	–	–	840	e860	+600	+774
Width of rostrum at mid-length	69	–	–	–	64	–	e70
Width of premaxillae at mid-length of rostrum	41	–	–	–	41	–	–
Height of rostrum at mid-length	–	–	–	–	–	–	e39
Width of premaxillae at rostrum base (antorbital notches)	92	–	–	–	105	e109	80
Minimal distance between maxillae in rostrum base area	e48	–	–	–	47	e50	42
Width of rostrum base at level prominent notch	127	–	–	–	123	e110	125
Width of rostrum base at level antorbital notch	217	–	–	–	208	e208	203
Height of rostrum base at level antorbital notch	–	–	–	–	–	–	136
Maximum width of prenasal basin	20	–	–	–	42	e38	36
Length of cranium	+276	–	–	+259	–	–	259
Preorbital width of skull	313	–	–	–	e290	+234	296
Postorbital width of skull	e352	–	–	–	e315	–	323
Bizygomatic width of skull	–	–	–	–	310	–	313
Height of cranium	–	–	–	243	–	–	247
Length of antorbital process of lacrimal	25	–	–	22	–	–	–
Length of orbit	86	e87	–	88	+72	–	80
Length of temporal fossa	–	136	–	136	138	–	e140
Height of temporal fossa	–	89	–	92	–	–	77
Total width of premaxillary sac fossae	140	–	–	–	136	e130	142
Maximum width of right premaxillary sac fossa	59	–	59	–	67	–	61
Maximum width of left premaxillary sac fossa	47	–	–	55	50	–	58
Longitudinal distance right pmx foramen – anterior bony naris	–	–	–	–	157	–	128
Width of bony nares	e85	–	–	70	–	e90	73
Minimum width of ascending process of right premaxilla	e30	–	29	23 left	–	–	30
Transverse width across premaxillary crests	e172	–	–	–	–	–	161
Width right premaxillary crest	52	–	45	–	–	–	53
Width left premaxillary crest	e48	–	–	41	–	–	48
Minimum distance between premaxillary crests	e90	–	–	72	–	–	77
Maximum width of nasals	e102	–	–	–	–	e84	e86
Width of right nasal	58	–	54	–	–	e42	–
Length of medial suture between nasals	34	–	34	41	–	26	–
Minimum posterior distance between maxillae on the vertex	99	–	–	–	–	e88	72
Length of medial suture between frontals on the vertex	29	–	22	–	–	e27	–
Minimum distance between temporal fossae in posterior view	–	–	–	–	175	–	181
Width of occipital condyles	–	–	–	–	120	–	110
Width of foramen magnum	–	–	–	–	36	–	47
Maximum width of right occipital condyle	–	–	–	–	47	–	–
Maximum height of right occipital condyle	–	–	–	–	65	–	67
Distance between ventromedial margins of exoccipitals	–	–	–	–	165	–	–
Length of left pterygoid hamulus	–	–	–	–	195	–	195
Maximum width of left pterygoid hamulus	–	–	–	–	52	–	e55
Maximum length of periotic	–	41.5	–	–	+36.0	–	+36.6
Maximum lateromedial width of periotic	–	25.1	–	–	25.0	–	22.7

TABLE 1. (Continued).

	MUSM 1037	MUSM 950	MUSM 951	MUSM 1036	MUSM 1038	MUSM 1394	MUSM 1481
Maximum length of tympanic bulla (excl. posterior process)	45.0	–	–	–	+43.5	–	42.0
Maximum lateromedial width of tympanic bulla	25.1	–	–	–	24.3	–	23.5
Length of mandible parallel to longitudinal axis	e1023	–	–	–	930	–	–
Length of symphyseal portion of mandible	385	–	–	–	390	–	–

Measurements in mm; e, estimate; +, nearly complete; –, no data.

C). The ratio between medial length and total width of the nasals is lower than in other ziphiids, below 0.35. The dorsal surface of the nasals is roughly flat and horizontal, only moderately medially depressed in MUSM 1481 and possibly MUSM 951, a character not as pronounced as in *Messapicetus longirostris*. The anterior point of the nasals is slightly posterior to the anterior level of the premaxillary crest, differing from the possibly closely related *Ziphirostrum*.

*Frontal*. On the vertex, the frontal has roughly the same length as the nasal and it is only slightly transversely compressed. The frontal-supraoccipital suture is posteriorly convex. In lateral view, the preorbital process is barely thickened (Text-fig. 4A, B). The postorbital process is long and slender, contacting the zygomatic process of the squamosal. Considering the preservation state of the skulls, this condition is much likely not due to diagenetic compression.

*Jugal/lacrimal*. The slender zygomatic arch of the jugal, preserved on the left side in MUSM 1481, displays a wide contact with the zygomatic process of the squamosal. Lateral to the base of the arch is a prominent ventrolateral projection of the bone (Text-fig. 4E, F), more conspicuous than in other similar-sized ziphiids, reminiscent of the condition in *Eurhinodelphis* (see Lambert 2005b, fig. 3). The jugal-lacrimal suture is distinctly visible.

*Supraoccipital*. The dorsomedial area of the supraoccipital is concave, erected along the frontals. At mid-height, the supraoccipital of MUSM 1037 bears a pair of lateral robust protuberances, for the insertion of neck muscles, probably the semispinalis capitis (Text-fig. 2A–C). In the smaller MUSM 1481, the surface of the bone is more regularly convex. In posterior view, the dorsolateral outline of the supraoccipital shield is less rounded than in *Messapicetus longirostris*.

*Exoccipital*. The occipital condyles are robust, with a circular outline (Text-fig. 3B). They are dorsolaterally margined by a deep depression (=dorsal condyloid fossa). The foramen magnum is relatively small and circular.

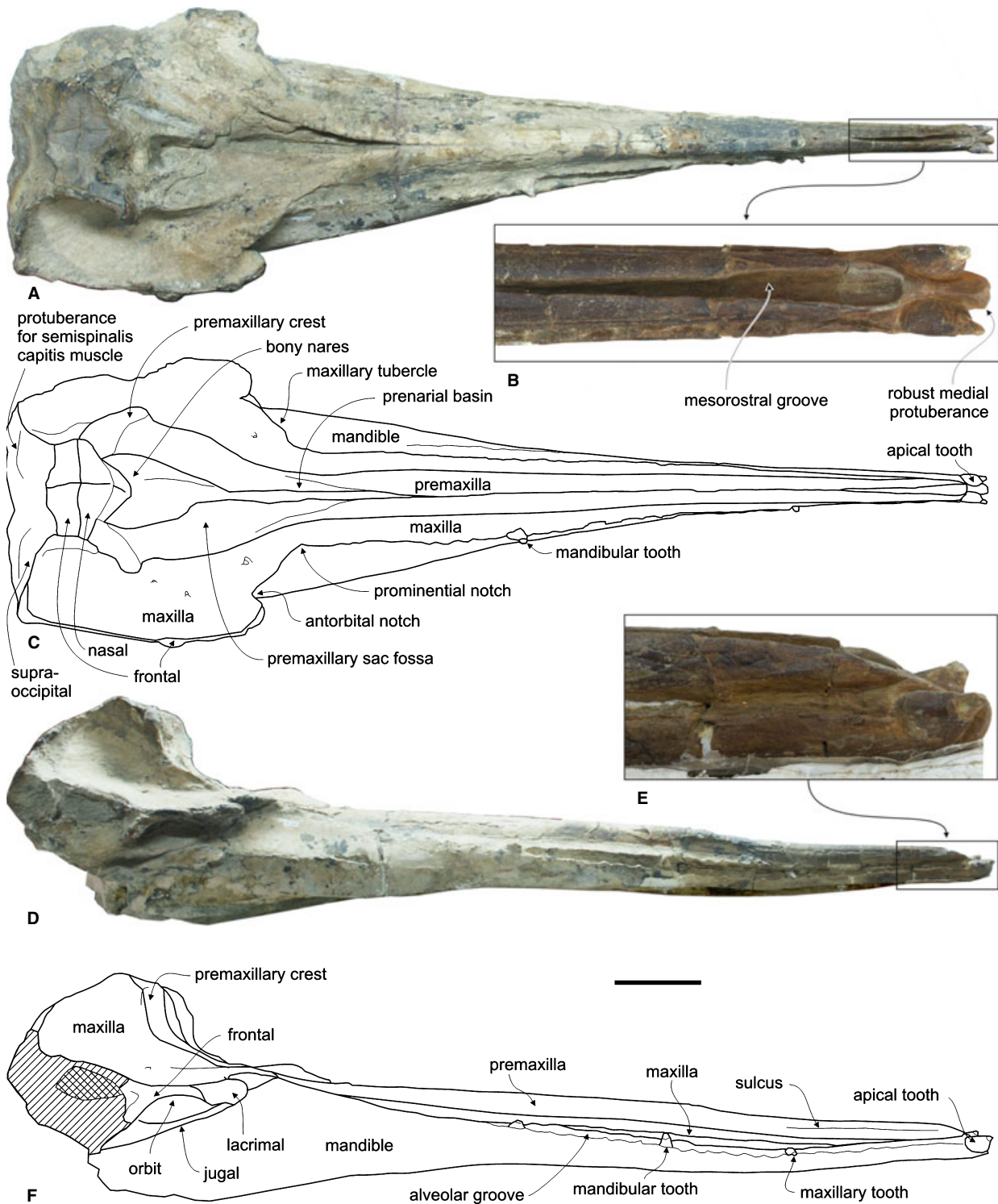
*Basioccipital*. The basioccipital crests are moderately divergent, forming an angle (about 40 degree in MUSM 1481, Text-fig. 4E, F) smaller than in all the extant ziphiids and all fossil ziphiids where this feature could be quantified. The large angle formed by the basioccipital crests is a derived condition (character 19 in the

Appendix S1) considered as a synapomorphy of the clade Ziphiidae + Physeteridae by Muizon (1991) and Geisler and Sanders (2003). Considering the plesiomorphic state of this character in the basal ziphiid *Messapicetus*, we propose that this condition was acquired independently in both the sperm whale and beaked whale lineages, supporting recent phylogenies based on morphological (Lambert 2005b) and molecular (e.g. Cassens *et al.* 2000; Agnarsson and May-Collado 2008) data that exclude a sister-group relationship between these two odontocete lineages.

*Squamosal*. The zygomatic process of the squamosal is elevated, dorsally and transversely swollen (Text-figs 3C–E, 4A, B). In ventral view, the deep tympanosquamosal recess extends on the whole medial margin of the process (Text-fig. 4E, F); in the posteromedial part of the recess, the surface is excavated with irregular pits, a condition commonly observed in ziphiids. The glenoid surface is vast. The falciform process is a thin, narrow, and relatively elongated lamina, different from the spike present in many extant ziphiids and *Physeter*. The robust postglenoid process is rounded apically, shorter ventrally than the exoccipital.

*Periotic*. The three complete periotics (MUSM 950, MUSM 1038 and MUSM 1481) vary in the length (from the apex of the anterior process to the posterior end of the posterior process) between 36.0 and 41.5 mm, whereas the mediolateral width ranges between 22.7 and 25.1 mm (Text-fig. 5). The mediolateral thickening of the anterior process and the slight anterior shift of the pars cochlearis (better seen in dorsal view) are two features observed in these periotics allowing the distinction between a ziphiid periotic and a eurhinodelphinid periotic. The thickening of the anterior process is moderate, less pronounced than in *Nazcacetus* and even less than in the Recent ziphiids, closer to the condition in *Ninoziphius*. The anterior process of MUSM 1038 is shorter and more dorsoventrally compressed than in MUSM 950. The anterior bullar facet is elliptical and anteroposteriorly elongated; the lateral tuberosity is less laterally expanded than in the extant ziphiids; the fossa for the malleus is wide and opens posteromedially. Only a fragment of the accessory ossicle is preserved in MUSM 950, but a complete ossicle is attached in MUSM 1038 and MUSM 1481.

The pars cochlearis is proportionally higher than in other ziphiids, except *Ninoziphius*. It is wider in MUSM 1038 and MUSM 1481 than in MUSM 950. The pars cochlearis lacks the high cochlear spine of *Ninoziphius*, even if in all the periotics with the exception of MUSM 950 a small crest is present because of the thin protuberant posteromedial margin of the internal auditory

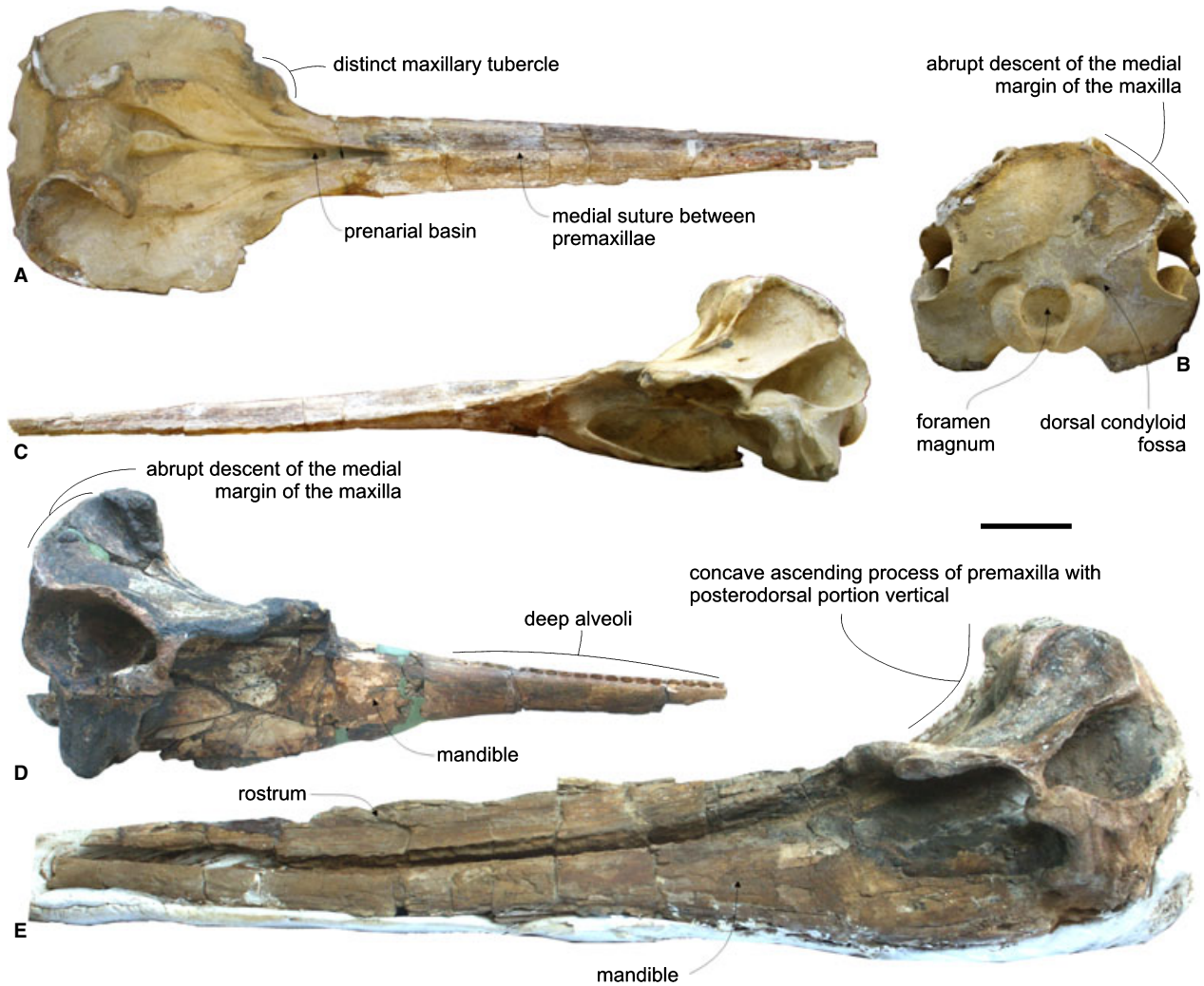


**TEXT-FIG. 2.** Skull and mandible of *Messapicetus gregarius*, sp. nov. MUSM 1037 (holotype). A, dorsal view. B, detail of the apical portion of the rostrum in dorsal view showing the large anterior teeth. C, line drawing of A. D, lateral view. E, detail of the apical portion of the rostrum in lateral view showing the large anterior teeth. F, line drawing of D. Scale bar represents 100 mm.

meatus. The internal auditory meatus is almost circular. The distance between the aperture for the endolymphatic duct and the small aperture for the cochlear duct varies between the periotics

of *M. gregarius*: it is small, as in *Nazcacetus*, *Ninoziphius*, and Recent ziphiids, in MUSM 1481 and MUSM 1718, whereas it is relatively large in MUSM 950 and MUSM 1438.





**TEXT-FIG. 3.** Specimens referred to *Messapicetus gregarius*, sp. nov. A–C, MUSM 1481, skull in dorsal (A), posterior (B), and lateral (C) views. D, MUSM 950, incomplete skull and right dentary in lateral view. E, MUSM 1036, skull and mandible in lateral view. Scale bar represents 100 mm.

The posterior bullar facet is narrower, less fan-shaped than in *Nazcacetus* and Recent ziphiids and more similar to *Ninoziphius* and eurhinodelphinids. The posterior process of MUSM 951 is somewhat shorter than in the other periotics. This process lacks an acute dorsal keel, a feature often present in eurhinodelphinids and retained in *Nazcacetus* and some Recent ziphiids (e.g. *Mesoplodon bidens* IRSNB 14.194).

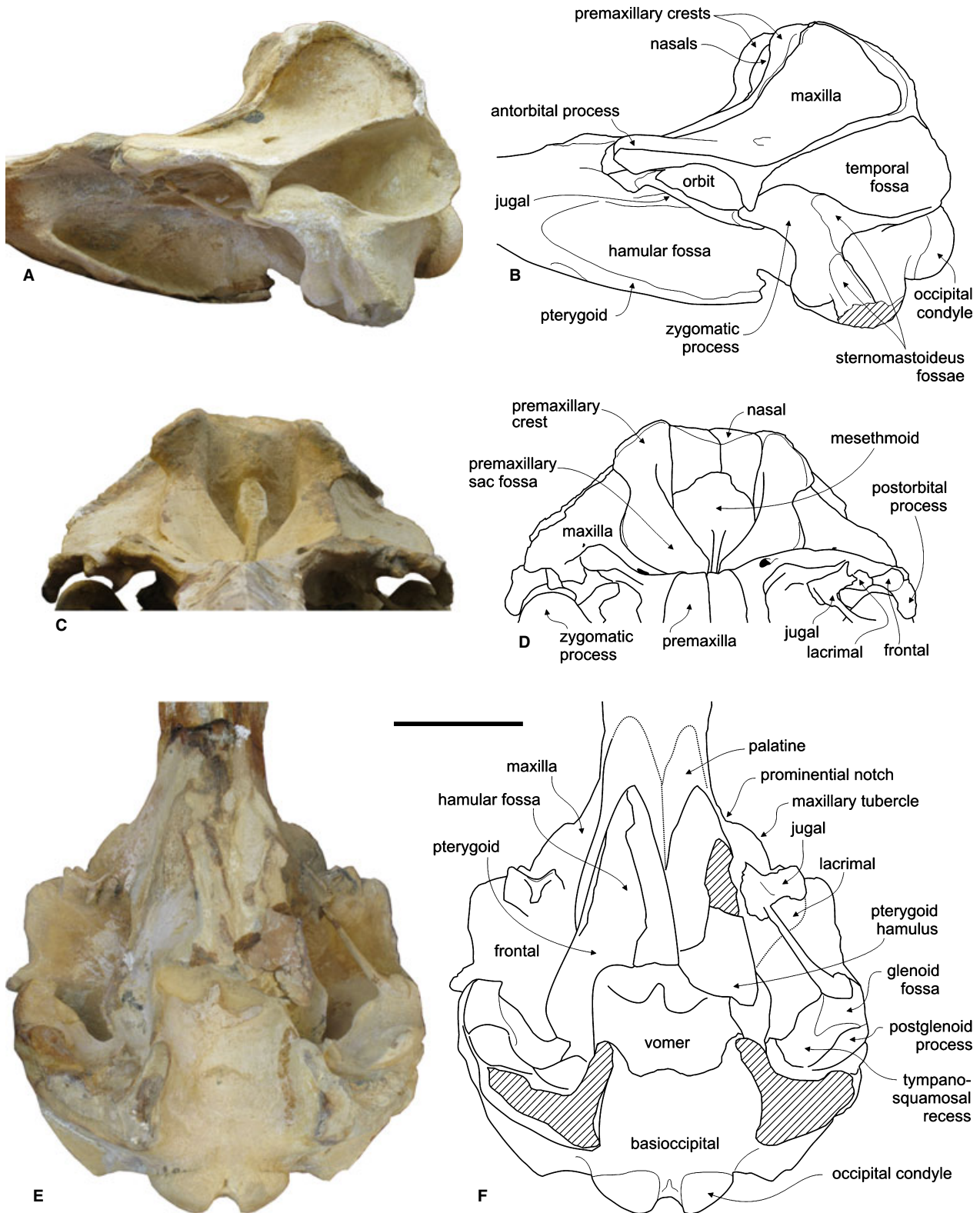
**Tympanic bulla.** The incomplete tympanic bulla of the holotype (posterior process lost) and the complete ones of MUSM 1038 and MUSM 1481 are very similar in size and shape (Text-fig. 6). The total length, excluding the posterior process, ranges between 42 and 45 mm and the mediolateral width between 23.5 and 25.1 mm. The general shape is close to *Ninoziphius*: in ventral view, the outer posterior prominence is much wider than the inner posterior prominence and both prominences are separated by a deep medial groove extending in the posterior half portion of the tympanic bulla. The outer posterior prominence extends a

little bit more posteriorly than the inner posterior prominence and its lateral margin abruptly bends medially, anteriorly to the lateral furrow. The inner prominence exhibits an acute keel, which bends medially in its anterior portion. The anterior margin is well preserved in the holotype only and shows a rather developed anterior spine.

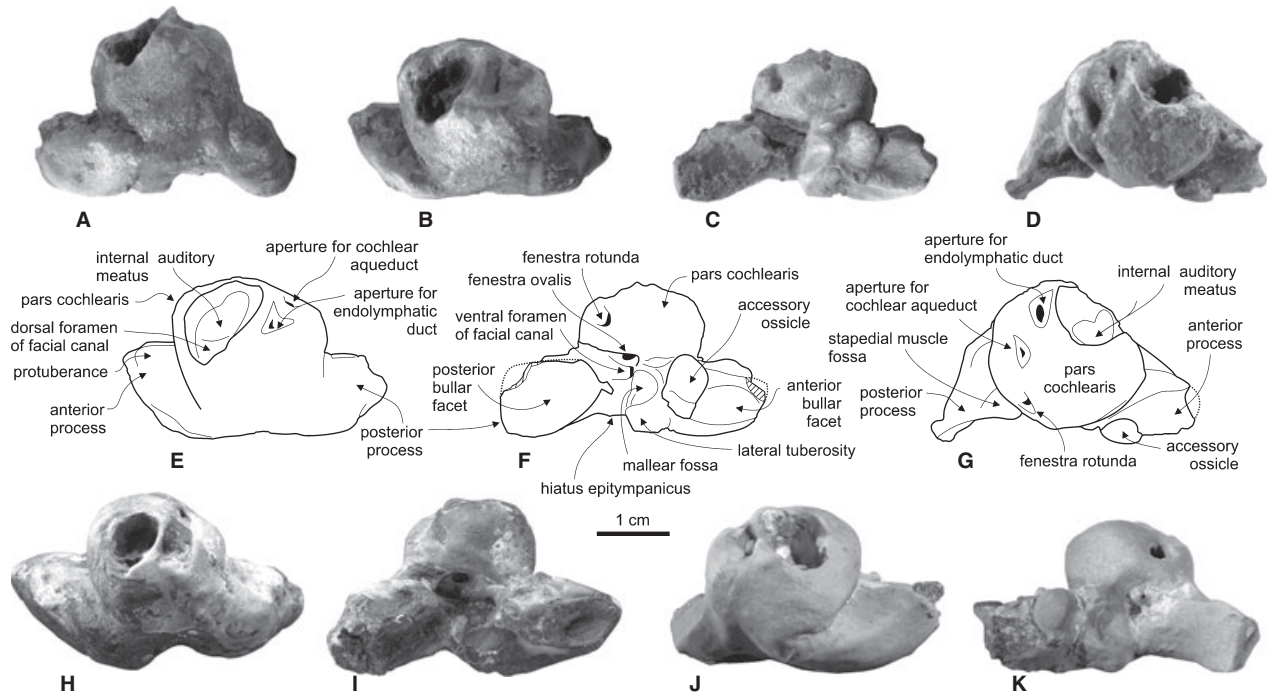
In lateral view, the lateral furrow is shallower than in extant ziphiids, as in *Ninoziphius*. The sigmoid process is rectangular, slightly anteriorly bent and posteriorly projected, forming a distinct posteroventral angle as in *Nazcacetus*, *Ninoziphius*, and the extant ziphiids. The dorsoventral length of the sigmoid process ranges between 12.5 and 12.6 mm.

The involucrum displays an indentation of its dorsal margin less marked than in *Ninoziphius* and, generally, than in the extant ziphiids.

The posterior process is ventrolaterally bent and the articular facet for the posterior process of the periotic is rectangular (15.5 × 10.3 mm and 14.7 × 12.3 mm respectively in MUSM



**TEXT-FIG. 4.** Detail of the cranium of *Messapicetus gregarius*, sp. nov. MUSM 1481. A, lateral view. B, corresponding line drawing. C, anterior view. D, corresponding line drawing. E ventral view. F, corresponding line drawing. Scale bar represents 100 mm.



**TEXT-FIG. 5.** Periotics of *Messapicetus gregarius*, sp. nov. A–D, left periotic (MUSM 1438) in dorsal (A), dorsomedial (B), ventral (C), and medial (D) views. E–G, corresponding line drawing of the dorsomedial (E), ventral (F), and medial (G) views. H–I, left periotic (MUSM 950) in dorsomedial (H) and ventral (I) views. J–K, left periotic (MUSM 1481) in dorsomedial (J) and ventral (K) views. Scale bar represents 10 mm.

1038 and MUSM 1481). As in *Ninoziphius*, the posterior process of *Messapicetus* lacks the hypertrophied distal portion observed by Geisler and Sanders (2003) in the extant Ziphiidae and in the Physeteroidea.

**Malleus.** Two left mallei are preserved: one (MUSM 1718) is in a good state of preservation (Text-fig. 7), the other (MUSM 1038) is rather worn. In posteromedial view, the malleus MUSM 1718 has an elliptical outline with the main vertical axis (va) 6.8 mm long and the minor horizontal axis (ha) 4.2 mm long. A similar elliptical shape is observed in *Eurhinodelphis* ( $ha/va = 0.66$  vs  $0.62$  in *Messapicetus*) and in many other odontocetes (e.g. *Delphinus*: 0.67, *Squalodon*: 0.64), whereas an approximately circular shape is observed in the extant ziphiids ( $ha/va = 0.93$ – $1.10$ ) and in the physeteroids ( $ha/va = 1.00$ – $1.16$ ).

The tuberculum is very short (22 per cent of va), as in the extant ziphiids (19–32 per cent), and in *Eurhinodelphis* (33 per cent) (Text-fig. 8). The tuberculum, instead, is relatively elongated (>50 per cent) in mysticetes and in other odontocetes, except in extant physeteroids that display an even stronger reduction of the tuberculum (*Physeter*, 4 per cent; *Kogia*, 17 per cent). Moreover, in *Physeter* and *Kogia*, as already observed by Lambert (2005b), the reduction of tuberculum is associated with a concomitant lateral shift, absent in the extant ziphiids, *Eurhinodelphis*, and *Messapicetus*.

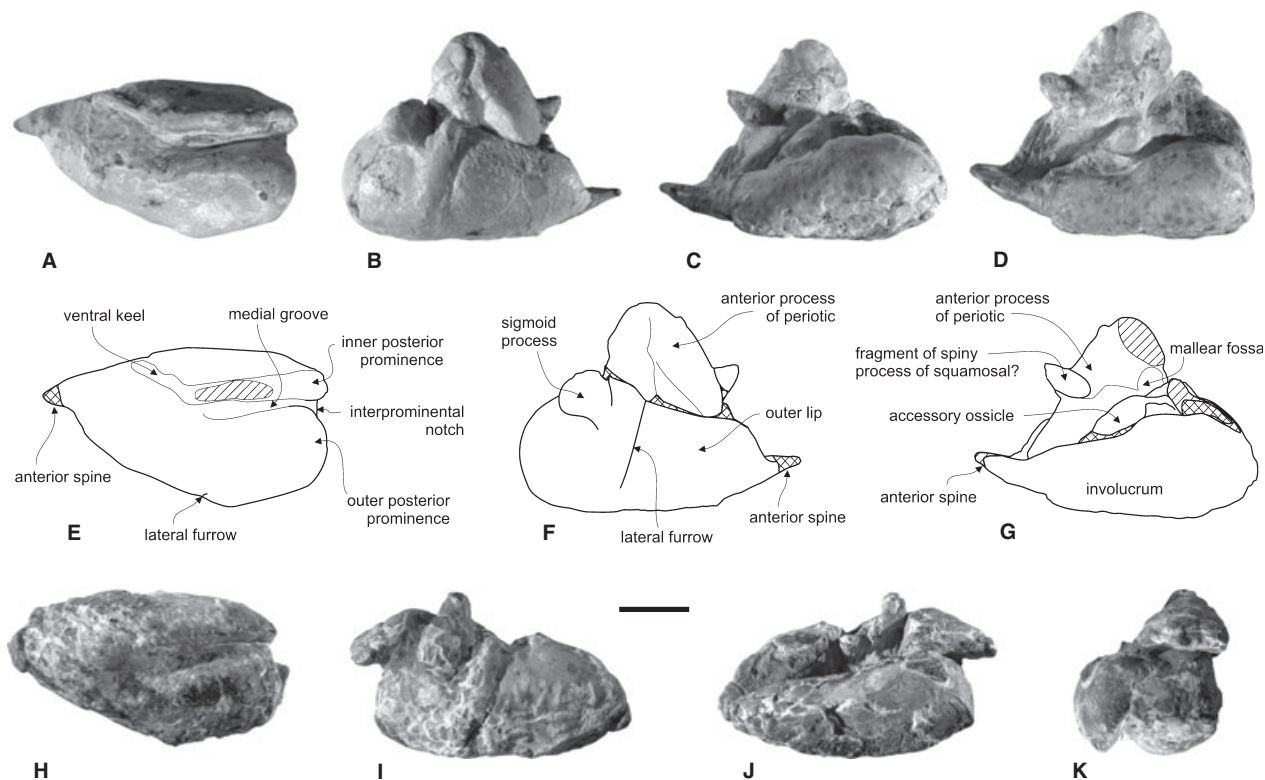
The malleus of an undescribed stem physeteroid from the Miocene of South Italy exhibits the same lateral shift of the tuberculum but the shortening of the tuberculum (22 per cent) is less than in the extant sperm whales (pers. obs., 2009), evidencing

that the extreme reduction of the tuberculum could have occurred in parallel in the extant physeteroids and in some extant ziphiids (e.g. *Ziphius* 19 per cent).

The manubrium is extremely reduced; its dorsal extremity is near the dorsal margin of the posterior articular surface of the incus and lower than that of the anterior articular surface. Among other cetaceans, a similar reduction of the manubrium is only observed in *Kogia* and *Physeter*. However, in these physeteroids the reduction also involves the processus muscularis, whereas in *Messapicetus* this process is relatively developed. The processus muscularis higher than the manubrium was actually also observed by Muizon (1985) in Inoidea and Delphinoidea, even if in these odontocetes the reduction of the manubrium is not as marked as in *Messapicetus*.

The articular surfaces for the incus have a circular outline in posteromedial view formed mostly by the margin of the anterior facet and, for a small portion, by the posterior margin of the much reduced posterior facet. The two facets lay perpendicular one to the other and are ventrally delimited by a wide and protuberant margin, also observed in *Tasmacetus*. An opposite condition is observed in *Ziphius*, *Physeter*, and *Kogia*, where the very wide facets occupy almost all the posteromedial surface of the malleus and where the space between the ventral margin of the facets and the ventral margin of the malleus is extremely reduced (*Ziphius* and *Kogia*) or absent (*Physeter*).

**Pterygoid.** In ventral view, the large and robust hamular processes have a posterior outline delimiting a widely open concavity, with less pointed apices than in *Ninoziphius* and most



**TEXT-FIG. 6.** Tympanic bullae of *Messapicetus gregarius*, sp. nov. A–D, right tympanic bulla with associated fragment of right periotic (MUSM 1037, holotype) in ventral (A), lateral (B), medial (C), and dorsomedial (D) views. E–G, corresponding line drawing of the ventral (E), lateral (F), and medial (G) views. H–K, right tympanic bulla (MUSM 1481) in ventral (A), lateral (B), medial (C), and posterior (D) views. Scale bar represents 10 mm.

Recent ziphiids (Text-fig. 4E, F). The vast pterygoid sinus fossa is laterally limited by a thin flange of bone that reaches a maximum height of 25 mm in MUSM 1481.

*Endocranial cast.* The volume of the endocranial cast of MUSM 951 has been estimated, by immersion in water, to be 2159 cm<sup>3</sup>. This volume is an overestimate of the actual brain size. Indeed, it includes the volume of the cranial rete mirabile, which was estimated for the archaeocete *Dorudon atrox* at 19.5 per cent of the total endocranial volume (Marino *et al.* 2000). To apply a similar percentage, the brain size volume of the MUSM 951 animal might be estimated at 1738 cm<sup>3</sup>. This value can be used (considering the brain density to be about 1) to calculate the encephalization quotients (EQ) of *M. gregarius*, using the following equations of Marino *et al.* (2004):

$$EQ_{0.53} = \text{Brain weight (g)} / 1.6 (\text{body weight (g)})^{0.53}$$

$$EQ_{0.67} = \text{Brain weight} / 0.12 (\text{body weight (g)})^{0.67}$$

$$EQ_{0.75} = \text{Brain weight} / 0.055 (\text{body weight (g)})^{0.75}$$

The body weight is estimated using the regression equation of Pyenson and Lindberg (2003):

$$\text{Body weight} = 0.4628 \times (\text{OCB})^{3.2087}$$

OCB is the width across the occipital condyles. This portion of the basicranium is not preserved in MUSM 951, but in the similar size MUSM 1038, OCB equals 120 mm. With this value the body weight of adult *M. gregarius* is estimated to be 1343 kg. Based on the estimated values of the brain and body weight, the following EQ values have been calculated for *M. gregarius*:

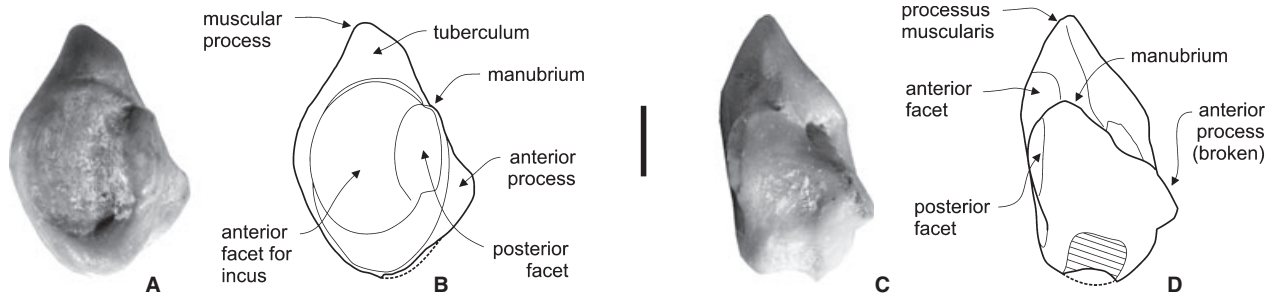
$$EQ_{0.53} = 0.61$$

$$EQ_{0.67} = 1.14$$

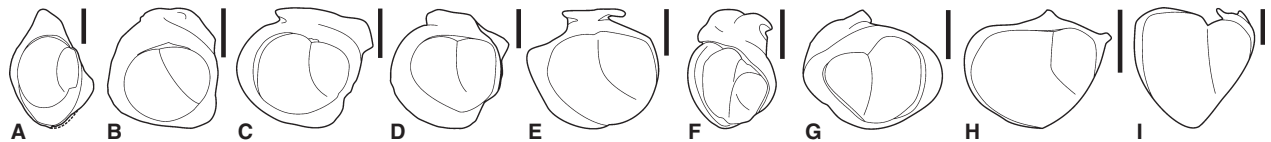
$$EQ_{0.75} = 0.80$$

These EQ values are similar to those of other ziphiids, themselves somewhat lower compared to most other odontocetes (Marino *et al.* 2004).

*Mandible.* The mandible is long and slender; its height increases posteriorly very progressively, in a way similar to *Ninoziphius* (Text-fig. 9). The low and moderately dorsally bent anterior portion corresponds to the long symphysis (38 per cent of the total length of the mandible in MUSM 1037 and 42 per cent in the smaller MUSM 1038); this is longer than in *Nazcacetus* and most Recent ziphiids, and close to *Ninoziphius*. The section of the symphyseal portion is half-circled. The mandible of the holotype is 30 mm longer anteriorly than the rostrum, the robust apical portion corresponding to the presence of a pair of large teeth. A



**TEXT-FIG. 7.** Left malleus of *Messapicetus gregarius*, sp. nov. MUSM 1718. A, posteromedial view. B, corresponding line drawing. C, posteroventrolateral view. D, corresponding line drawing. Scale bar represents 2 mm.



**TEXT-FIG. 8.** Comparison of mallei of *Messapicetus gregarius*, sp. nov. with other odontocetes species. A, *Messapicetus gregarius* (MUSM 1718). B, *Mesoplodon bidens* (MHNP 1963-259). C, *Mesoplodon europaeus* (USNM 504473). D, *Tasmacetus shepherdi* (SAM ZM41116). E, *Ziphius cavirostris* (USNM 504347). F, *Eurhinodelphis cocheuteuxi* (IRSNB M1856). G, *Physeteroidea* indet. (MAUL not catalogued). H, *Kogia breviceps* (USNM 22016). I, *Physeter macrocephalus* (USNM 49488). All in posteromedial view and reduced to the same length. All scale bars represent 2 mm.

similar feature is observed in the Recent ziphiids displaying enlarged apical teeth, and particularly conspicuous in *Berardius* or *Ziphius*. The large anterior alveolus is transversely compressed and oblique, opening anterodorsally (see description of the tooth

below). The maximum and minimum diameters of the apical alveolus are smaller in MUSM 1038 (23 and 12 mm), intermediate in MUSM 1037 (28 and 15 mm), and larger and strangely asymmetric in MUSM 1482 (33 and 18 mm on the right side;



**TEXT-FIG. 9.** Mandibles of *Messapicetus gregarius*, sp. nov. A, MUSM 1037 (holotype) in ventral view. B–C, MUSM 1038 in lateral (B) and ventral (C) views. Scale bar represents 100 mm.

35 and 24 mm on the left side). These differences in size have been proposed to be related to sexual dimorphism (Lambert *et al.* 2010).

The apex of the rostrum perfectly fits in the concave medial surface just posterior to the apical alveoli. This depression is followed anteriorly by a thick sagittal crest, projecting forwards beyond the teeth as a robust protuberance. This layout might correspond to a protection for the anterodorsally directed tusks; any contact is only possible from an anterodorsal direction (Lambert *et al.* 2010). It is noteworthy that the protuberance is stronger in the less complete MUSM 1482 and nearly absent in MUSM 1038. Between the apical alveolus and the next distinct alveolus is a diastema 140–180 mm long, an area where the alveolar groove is partly filled with secondary bone outgrowth. The extent of the diastema roughly corresponds to the anterior edentulous premaxillary part of the rostrum. A similar diastema is observed in *Tasmacetus*, and to a lesser extent in *Ninoziphius* (see discussion in Muizon 1984). Behind this diastema, about 25 alveoli are counted in the right dentary of MUSM 1037 (10 of them in the symphyseal portion) and 25–26 in MUSM 1038, a number close to *Tasmacetus* (Mead 1989a) and lower than in *Ninoziphius* (Muizon 1984). The size of these transversely flattened alveoli (differing from the more circular alveoli of *Ninoziphius* and *Tasmacetus*) varies in a same portion of the mandible; the maximum anteroposterior diameter of an alveolus is 25 mm. The septa between the alveoli are weakly developed. The alveoli are shallower in MUSM 1036 and considerably deeper in MUSM 950, a variation possibly related to age differences between individuals. The last posterior alveolus is 300 mm anterior to the mandibular condyle in MUSM 1038.

**Teeth.** The *in situ* apical mandibular tooth of the holotype has a maximum and minimum diameter at the crown base of 10 and 6 mm, respectively (Text-fig. 2B, E). The apical tooth is similarly transversely flattened in the Recent *Mesoplodon hectori* and *M. perrini* (see Dalebout *et al.* 2002), and in a lesser extent *M. mirus*. In other Recent genera with one pair of apical teeth, namely *Hyperoodon*, *Indopacetus*, *Tasmacetus*, and *Ziphius*, it tends to be more conical (Moore 1968; Dalebout *et al.* 2003) whereas in other *Mesoplodon* species the transversely flattened tooth is located more posteriorly on the mandible (Mead 1989b). In *Ninoziphius* the alveolus for the lost apical tooth is roughly circular (Muizon 1984) and in *Nazcacetus* the area is too abraded to estimate the outline of the apical alveolus (Lambert *et al.* 2009). From the contact with the alveolus the tooth

has a height of 27 mm, anterodorsally and slightly laterally directed. The apex of the short crown is damaged; nevertheless, no apical wear could be detected.

Thirteen detached postapical teeth of the holotype could originate either from the mandible or from the maxilla (Text-fig. 10). In the largest teeth (total length ranging from 20.6 to 28.6 mm), the root is strongly transversely flattened, with a ratio between minimum and maximum diameters ranging from 0.3 to 0.5, differing from the nearly square section of the postapical teeth in *Ninoziphius* and the more circular section in *Tasmacetus*. The proximal margin of the root is irregular. The crown of these large teeth is low (crown height ranging from 5.6 to 8.5 mm), moderately transversely flattened (ratio between minimum and maximum diameters at the crown base ranging between 0.6 and 0.8), and medially curved. The apex of the crown is regularly worn, as in the holotype of *Ninoziphius platyrostris*. A second wear surface on the anterior/posterior surface of the crown corresponds to the contact with the opposite tooth (Text-fig. 10J, K). Two smaller teeth with an anteroposteriorly shorter root do not display any apical wear.

**Hyoid bones.** The roughly complete right stylohyal MUSM 950 is 148 mm long; its maximum width and thickness are 32 and 23 mm, respectively (Text-fig. 11). The proportions are close to similarly sized *Mesoplodon* species and *Nazcacetus* (Lambert *et al.* 2009). The anterior part of the stylohyal of the Pliocene Mediterranean ziphiid *Tusciziphius crispus* Bianucci, 1997 is similar, but its posterior portion displays a stronger constriction, closer to the condition in *Ziphius*. A 93-mm-long distal fragment of the left thyrohyal was found associated; it is distinctly narrower than in *Ziphius*.

#### MUSM 1394, calf

Found in the same level of Cerro Colorado and bearing typical features of *Messapicetus* (dorsomedially elevated premaxillae on the rostrum, deep prenasal basin, nasals wider than long), this specimen (Text-fig. 12) displays some differences with other specimens of *M. gregarius*.

(1) Although more or less complete, its rostrum is considerably shorter (ratio between preorbital width and rostrum length is estimated to 0.45, vs respectively 0.37 and 0.36 in MUSM 1037 and MUSM 1038). (2) The dorsal infraorbital foramina are larger. (3) The premaxillary crests are lost on both sides, whereas



**TEXT-FIG. 10.** Four detached teeth of *Messapicetus gregarius*, sp. nov. MUSM 1037 (holotype). A, C, F, H, in medial view. B, D, G, I, in anterior view. J, detail of tooth H–I showing wear facet from opposite tooth. K, corresponding line drawing. Scale bars represent 10 mm.

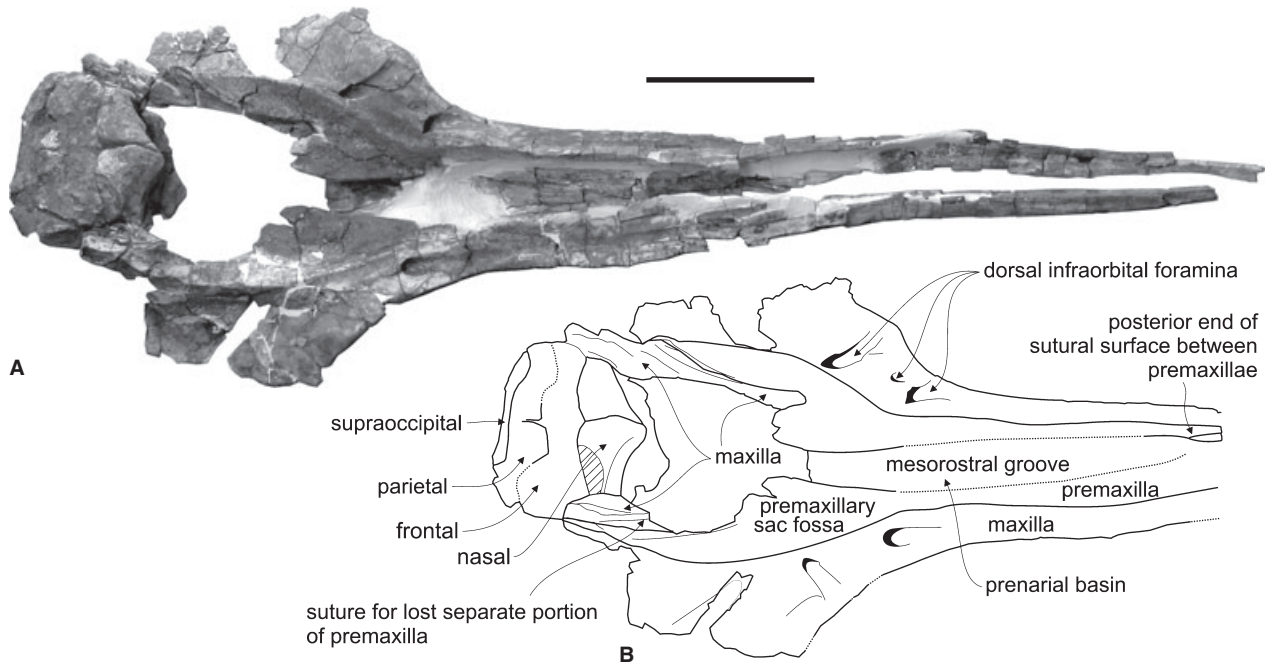


**TEXT-FIG. 11.** Hyoid bones of *Messapicetus gregarius*, sp. nov. (MUSM 950). A–B, right stylohyal in dorsal (A) and lateral (B) views. C–D, ?left thyrohyal in lateral (C) and ventral (D) views. Scale bar represents 50 mm.

they are present in all the other specimens with the vertex preserved. (4) A pair of bones interpreted as the parietals occupy a portion of the vertex, anteriorly margined by the porous frontals. (5) All bones are less thick (for example each premaxilla is 6 mm thick just posterior to the median contact dorsally closing the mesorostral groove in MUSM 1394, vs 11 mm in MUSM 951).

An allometric elongation of the rostrum is observed in growth series of Recent odontocetes, including the ziphiids (e.g. measurements in Dalebout *et al.* 2003; Omura 1972; Reyes *et al.* 1991; Ross 1984). Occurrence of relatively larger dorsal infraorbital foramina in younger individuals is not a general rule among Recent ziphiids, but it has been occasionally noted, for example in *Berardius arnuxii* (pers. obs.) and *Ziphius cavirostris* (Kernan 1918, pl. 21; Fraser 1942, pl. 1). Parietals or interparietal retained on the vertex of the skull is a feature commonly observed in young specimens from various odontocete groups (e.g. Perrin 1975; Arnold and Heinsohn 1996; Lambert 2008). An oblique suture between, on the one side, the premaxillary sac fossa and the lateral portion of the ascending process and, on the other side, the medial portion of the ascending process and the premaxillary crest is observed on the skull of an immature individual of *Mesoplodon peruvianus* (IRSNB 4036; Text-fig. 13B). This feature, associated with the observation of the loss of both premaxillary crests in a young individual of *Berardius arnuxii* (SAM 37404; Text-fig. 13A), supports the hypothesis that the premaxillary crest and the medial part of the ascending process constitute a separated ossification centre in ziphiids, fusing with the remainder of the premaxilla early in the life of the individuals. This suture could be homologous to the premaxillary cleft observed in the platanistoid *Waipatia* and more distinctly in the archaic odontocete *Simocetus* (Fordyce 1994, 2002).

Taking all these elements into account, the interpretation of this specimen as a calf of *M. gregarius* is reinforced. In his large sample of specimens from the Recent ziphiid species *Mesoplodon mirus*, Ross (1984) provided the skull measurements for two stranded lactating mother/calf couples. For the first couple (calf with only one thin postnatal growth layer on teeth), the ratio between the rostrum length of the calf and of the mother is



**TEXT-FIG. 12.** Fragmentary skull (MUSM 1394) of a calf tentatively referred to *Messapicetus gregarius*, sp. nov. A, dorsal view. B, line drawing of the face. Scale bar represents 100 mm.



**TEXT-FIG. 13.** Immature skulls of extant ziphiids. A, *Berardius arnuxii* (SAM 37404), dorsal view of the face. Both premaxillary crests are lost. B, *Mesoplodon peruvianus* (IRSNB 4036), anterodorsal view of the face. Broken lines indicate the medial and lateral sutures of the portion of premaxilla formed by the premaxillary sac fossa and a part of the ascending process, excluding the premaxillary crest. Scale bars represent 100 mm.

0.47, whereas for the second couple (calf with first and part of the second postnatal growth layers), this ratio reaches 0.77. Calculating the same ratio between MUSM 1394 and other specimens of *M. gregarius* from Cerro Colorado, values between 0.66 and 0.72 are obtained, closer to the values for the second *M. mirus* couple, suggesting that MUSM 1394 was a not yet weaned calf.

It is interesting to note that the prenarial basin of this presumed calf is as deep and wide as in the adults of *M. gregarius*, whereas in *Ziphius* only the adult males bear a vast basin (Heyning 1989). This difference might suggest a different function for the basin in the two taxa.

## PHYLOGENY

The cladistic analysis produced 155 equally parsimonious trees, with tree length 87, Goloboff fit – 21.63, Consistency Index (CI) 0.56 and Retention Index (RI) 0.70. The consensus tree of these cladograms is presented in the Text-figure 14 and discussed below.

*Messapicetus* is placed inside a basal clade (below named ‘*Messapicetus* clade’) together with *Beneziphius* and *Ziphirostrum*. These three genera share a dorsally closed mesorostral groove (character 3 in the Appendix S1) and a prenarial basin laterally margined by the premaxilla (state 1 of character 4 in the Appendix S1). Although the relationships within this clade are unresolved, *Messapicetus* is more similar to *Ziphirostrum*, from which it substantially differs in the longer rostrum and the wider nasals.

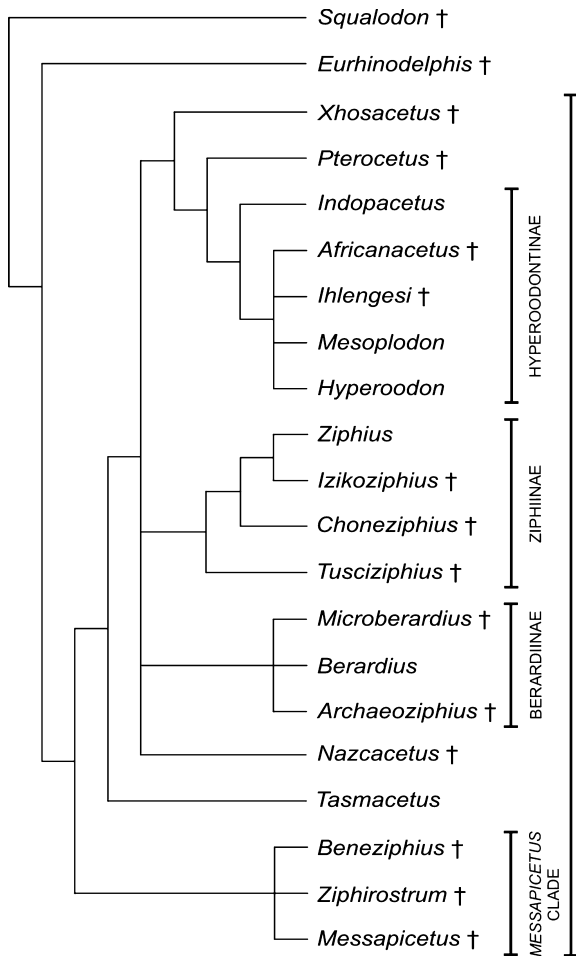
Unlike in previous analyses (Lambert 2005a, b; Lambert *et al.* 2009), *Beneziphius* and *Ziphirostrum* are not closely

related to *Choneziphius*, *Izikoziphius*, *Tusciziphius*, and *Ziphius* (=Ziphiinae), suggesting that the closure of the mesorostral groove observed in the three genera of the *Messapicetus* clade and in *Choneziphius* and *Tusciziphius* among the Ziphiinae might be the result of convergent evolution. The same can be inferred for the prenarial basin of *Ziphius*; laterally margined by the elevated premaxilla, it could actually be considered as analogue to the basin margined by the maxilla of the members of the *Messapicetus* clade.

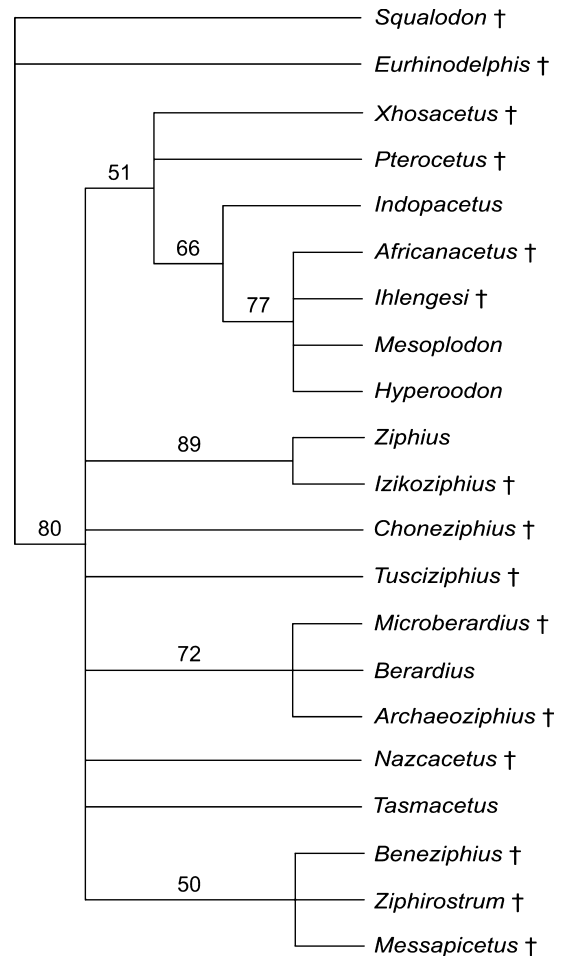
Relationships between the ziphiids outside the *Messapicetus* clade are similar to those proposed in previous analyses (Bianucci *et al.* 2007; Lambert *et al.* 2009), except for the more derived position of the Berardiinae (*Archaeoziphius* + *Berardius* + *Microberardius*). In fact, this subfamily is included in a large clade, sister group of *Tasmacetus*, also including *Nazcacetus*, the Ziphiinae, and the Hyperoodontinae + stem relatives (*Pterocetus* + *Xhosacetus*). In accordance with Bianucci *et al.* (2007), *Pterocetus* and *Xhosacetus* are not included in the Hyperoodontinae because they lack the key character of this subfamily: the deep anteromedian excavation of the dorsal surface of the nasal.

The fifty per cent majority rule strict consensus bootstrap tree (Text-fig. 15) supports the monophyly of the *Messapicetus* clade, the Berardiinae, and the Hyperoodontinae, whereas the unresolved position of *Choneziphius* and *Tusciziphius* indicates that the above proposed content of the subfamily Ziphiinae needs further study. Moreover, the bootstrap analysis does not confirm the hypothesized basal position of the *Messapicetus* clade.





**TEXT-FIG. 14.** Consensus tree of 155 equally parsimonious cladograms showing the relationships of *Messapicetus* with all fossil and extant ziphiid genera. Tree length 87, Goloboff fit – 21.63, CI 0.56 and RI 0.70. See text for discussion and Appendix S1 for description of characters and data matrix. †, strictly fossil taxa.



**TEXT-FIG. 15.** Bootstrap 50 per cent majority rule consensus tree with 300 full heuristic bootstrap replicates from the data matrix in the Appendix S1. See text for discussion and Appendix for description of characters and data matrix. Numbers associated with the branches are bootstrap support values.

The addition in future phylogenetic analyses of more fossil taxa based on complete skulls with associated ear bones and mandible will be necessary to better elucidate the phylogeny of the Ziphiidae.

### PALAEOBIOGEOGRAPHY

The presence of related species in Peru (*Messapicetus gregarius*), Italy (*M. longirostris*), and possibly Maryland (cf. *Messapicetus* sp., Fuller and Godfrey 2007) corroborates the extensive communication between the Pacific and Atlantic oceans during the Middle–Late Miocene (Central American Seaway open, Jacobs *et al.* 2004). It suggests that these fossil ziphiids had a pelagic habitat and a wide geographical distribution. Similarly, four of

the six extant ziphiid genera are found worldwide, two with a cosmopolitan distribution (*Mesoplodon* and *Ziphius*) and two in cold to temperate waters of both northern and southern hemispheres (*Berardius* and *Hyperoodon*). Moreover, two extant beaked whale species (*Mesoplodon densirostris* and *Ziphius cavirostris*) have a wide distribution including the coasts of Peru, Maryland, and Italy (Reeves *et al.* 2002).

In the ziphiid fossil record, the Late Miocene genus *Choneziphius* has been reported from both sides of the North Atlantic (Leidy 1877; Lambert 2005a), the Late Miocene – Early Pliocene genus *Tusciziphius* from the east coast of USA and the Mediterranean Sea (Bianucci 1997; Post *et al.* 2008), and the Early Pliocene genus *Ninoziphius* from the coast of Peru and the east coast of USA (Muizon and DeVries 1985; Morgan 1994).

## TAPHONOMY AND PALAEOECOLOGY

Besides the eight specimens of *M. gregarius*, our field investigations in a restricted area of about 1.5 km<sup>2</sup> around Cerro Colorado lead to the discovery of many cetacean remains belonging to at least five families of both odontocetes (four) and mysticetes (one). Additionally, there is abundant non-cetacean material, including turtles, fish (frequent teeth of *Cosmopolitodus hastalis* and *Carcharocles megalodon*), birds and a fragmentary pinniped (see Table 2, faunal list).

The huge majority of the cetacean remains found in Cerro Colorado correspond to articulated skeletons; several tens of mysticetes and odontocetes display a skull-vertebral column association. Contrasting with this condition, all the *Messapicetus* specimens are represented by isolated skulls, in six cases (plus the Cerro la Bruja specimen) associated with elements of the mandible. A possible cause of this peculiar taphonomic condition could be the separation of the long-snouted and relatively heavy head from the rest of the body during the drifting of the carcass at the surface of the sea. This hypothesis is supported by Schäfer's observations on floating extant dolphin carcasses. According to Schäfer (1972), the head detaches from the drifting body in the early stages of decomposition, as the mandible does from the skull. The very elongated rostrum of *Messapicetus* could have favoured the incipient break of the neck and the head detachment. Additionally, the tight fit of the anterior portion of the rostrum on the dorsal surface of the mandible, as observed in MUSM 1036, MUSM 1037, MUSM 1038, and MUSM 1482, kept the mouth closed and likely hampered separation of the mandible from the skull. In only two cases the mandible separated before the head loss, so that jaws were not found associated with the skull. Post-cranial skeleton of *Messapicetus* presumably drifted away; they have not yet been found at Cerro Colorado.

The high fossil concentration in Cerro Colorado allowed us to identify specimens belonging to different ontogenetic stages: a skull attributed to a calf of *M. gregarius* (see above) and some bones belonging to a foetus, possibly of *Brachydelphis mazeasi*. Similar to *M. gregarius*, this fossil pontoporiid genus characterized by a very short rostrum and a small size (Muizon 1988) is well represented in Cerro Colorado, with several skulls (see Simon Gutstein *et al.* 2009) and other skeleton remains. Among the fragmentary bony remains of the foetus are elements of the skull (part of the zygomatic process of a squamosal, the supraoccipital and a maxilla), a humerus twice shorter than in adults, and several rib fragments (MUSM 1042). Furthermore, adult males and females have been tentatively identified for *M. gregarius* (Lambert *et al.* 2010).

**TABLE 2.** Preliminary faunal list of the marine vertebrates from the lowest levels of the Pisco Formation found in Cerro Colorado.

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<i>Pisces</i>
Chondrichthyes
Elasmobranchii
Carcharhinidae
<i>Carcharhinus brachyurus</i>
<i>C. aff. macloti</i>
<i>Carcharhinus</i> sp.
<i>Galeocerdo aduncus</i>
Sphyrnidae
<i>Sphyrna cf. media</i>
Lamnidae
<i>Cosmopolitodus hastalis</i>
Myliobatidae
Myliobatidae indet.
Otodontidae
<i>Carcharocles megalodon</i>
<i>Reptilia</i>
Chelonia
Chelonia indet.
<i>Aves</i>
Ciconiiformes
Sulidae
<i>Sula</i> sp.
Pelecaniformes
Phalacrocoracidae
<i>Phalacrocorax</i> sp.
Procellariiformes
Procellariidae
Procellariidae indet.
<i>Mammalia</i>
Cetacea
Odontoceti
Ziphiioidea
Ziphiidae
<i>Messapicetus gregarius</i>
Physeteroidea
Physeteroidea gen. et sp. nov.
Physeteroidea indet.
Delphinoidea
Kentriodontidae
Kentriodontidae gen. et sp. nov.
Iniodea
Pontoporiidae
<i>Brachydelphis mazeasi</i>
Pontoporiidae gen. et sp. nov.
Mysticeti
Cetotheriidae s.s.
Cetotheriidae gen. et sp. nov.
Cetotheriidae indet.
Pinnipedia
Phocidae
Phocidae indet.

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The absence of abrasion and the scarcity of breakage and encrustation on the bones of the Cerro Colorado deposits exclude their interpretation as a condensed deposit because of the limited sedimentation and bottom current transport, an hypothesis recently proposed for a Middle Miocene marine bonebed deposit from California (Pyenson *et al.* 2009). The abundance of fossils at Cerro Colorado seems to rather reflect an original abundance of life. High food availability attributed to the intensification of the coastal upwelling system (Dunbar *et al.* 1990) and/or to the arrival of volcanic ash and runoff from the continent (Brand *et al.* 2004) might have been the cause of such a high concentration and diversity of marine vertebrates. Moreover, the high concentration of specimens from the same species (including a calf and specimens tentatively identified as adult males and females) supports the hypothesis of a site fidelity: these cetaceans might have stayed for an extended period in a defined neighbouring area both for breeding and feeding, as noted for some extant ziphiids (Gowans *et al.* 2000; Hooker *et al.* 2002; Wimmer and Whitehead 2004; McSweeney *et al.* 2007). The continuous presence of cetaceans and other marine vertebrates made the area attractive for predators as is shown by the large and middle-sized sharks abundantly recorded in Cerro Colorado.

## CONCLUSIONS

1. The eight specimens of *Messapicetus gregarius* sp. nov. collected at Cerro Colorado, 35 km south-south-west to the city of Ica (Peru) from a limited area (about 1.5 km<sup>2</sup>) and roughly from the same stratigraphical horizon, represent the highest known concentration of a fossil Ziphiidae.
2. At Cerro Colorado and Cerro la Bruja, 33 km south-west to Cerro Colorado, where another *M. gregarius* specimen was collected, the Serravallian oldest strata of the Pisco Formation crop out, indicating for this new Peruvian species an age only slightly older than for the Tortonian Italian species *M. longirostris*.
3. *M. gregarius* shares with *M. longirostris* the extremely elongated rostrum. It differs from the Italian species in the more distinct maxillary tubercle and prominent notch, the more robust premaxillary crest, and the abrupt ventrolateral descent of the medial margin of the maxilla from the vertex.
4. *M. gregarius* exhibits several plesiomorphic characters; a part of them (e.g. moderately divergent basioccipital crests, elongated facets for the incus on the malleus) support the hypothesis that some derived characters shared by modern ziphiids and physeteroids are attributed to convergent evolution.
5. A parsimony analysis suggests that *Messapicetus* belongs to a basal ziphiid clade, also including *Beneziphius* and *Ziphirostrum* and defined by a dorsally closed mesorostral groove and the development of a prenarial basin. Unlike in previous analyses *Beneziphius* and *Ziphirostrum* are excluded from the Ziphiinae, suggesting that some apparently similar features of the skull might be attributed to convergent evolution.
6. The observed wide geographical distribution of *Messapicetus* (Peru, Italy and possibly Maryland) further stressed the extensive communication between the Pacific and Atlantic oceans during the Middle–Late Miocene.
7. The high concentration of specimens of a given species (some of them tentatively identified as adult males and females), combined with the record of a calf, supports the hypothesis of a site fidelity. These cetaceans might have stayed for a long period in a defined neighbouring area for both breeding and feeding.
8. Most of the nine specimens of *M. gregarius* are nearly complete skulls (ear bones included) with associated mandibles, but unlike other cetacean remains collected in the same areas, lacking the postcranial skeleton. Separation of the long-snouted and relatively heavy head from the rest of the body during the drifting of the carcass at the sea surface might have led to this peculiar taphonomic condition.
9. Together with the *M. gregarius* specimens, our field investigations at Cerro Colorado led to the discovery of many other vertebrate remains represented by odontocetes (including a foetus tentatively attributed to the pontoporiid *Brachydelphis mazeasi*), mysticetes, pinnipeds, turtles, fishes, and seabirds. Such abundance of fossils likely reflects an original abundance of life that might be attributed to the local high food availability.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** List of characters used in the cladistic analysis and data matrix.

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