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A new Late Miocene beaked whale (Cetacea, Odontoceti) from the Pisco Formation, and a revised age for the fossil Ziphiidae of Peru

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ABSTRACT - The previously scarce fossil record of Ziphiidae (beaked whales) has greatly increased recently thanks to the serendipitous discovery of high specimen concentrations along deep seafloors as well as to abundant inland finds from the Upper Miocene of the Pisco Formation (East Pisco Basin, Peru). In the latter unit, ziphiid remains are indeed among the most prevalent of the whole cetacean assemblage, being represented by four distinct genera and species plus at least two as-yet unnamed taxa. Here, we describe a fifth ziphiid genus and species from the Pisco strata, Mamaziphius reyesi *n. gen. n. sp., based on a partial cranium from mid-Tortonian (lower Upper Miocene, 9.1-9.0 Ma) strata exposed at the locality of Cerros la Mama y la Hija. Though reminiscent of the extant genus* Berardius*, the holotype skull lacks two diagnostic characters of Berardiinae, namely, an isolated rounded protuberance formed by the interparietal or frontals on the posterior part of the vertex, and a posterior transverse narrowing of the nasals and frontals at the vertex. Our phylogenetic analysis reveals that* Mamaziphius *n. gen. is nested within the crown ziphiids, as sister group of the berardiines. In addition, we introduce two new clade names within Ziphiidae, namely, Messapicetiformes (for the so-called "*Messapicetus *clade") and Vomeroziphii (for Ziphiinae + Hyperoodontinae and closely related forms). Another fragmentary specimen from the Pisco Formation is also briefly described herein. Furthermore, a comprehensive reappraisal of the geological age of the fossil beaked whales of Peru is provided based on new age calibrations, thus restricting the whole rich Peruvian record of this family (including the earliest-branching ziphiid,* Ninoziphius platyrostris*, which comes from Pisco-equivalent strata of the Sacaco area) to a Tortonian-Messinian interval younger than 9.10 Ma. No other inland unit worldwide preserves a record of fossil ziphiids as abundant, diverse and chronostratigraphically well-constrained as the Pisco Formation. In view of this, the absence of Vomeroziphii from the fossil content of the Pisco strata remains quite enigmatic.*

INTRODUCTION

Nowadays, the family Ziphiidae (beaked whales) represents the second most diverse family of cetaceans after Delphinidae (oceanic dolphins), accounting for at least 24 living species (MacLeod, 2018a; Yamada et al., 2019; Carroll et al., 2021). In spite of this, due to their deep-sea habitat, elusive behaviour and apparent low abundance, ziphiids are one of the least known extant groups of mammals, as well as one of the few families of large-bodied animals for which new living species continue to be identified and described to date (Bianucci et al., 2008; Yamada et al., 2019; Carroll et al., 2021). Growing up to about 12 m in total length (the maximum body size of *Berardius bairdii* Stejneger, 1883; MacLeod, 2018b), extant ziphiids are open-sea odontocetes (toothed whales) that feed on squid and other benthic/benthopelagic prey items at great depths (down to more than 3000 m; Schorr et al., 2014). This peculiar lifestyle reflects into a number of distinctive anatomical adaptations for deep-diving, prey detection through echolocation, and prey capture via suction, among which are a strong reduction of the functional dentition as well as wide, anteroposteriorly long pterygoid sinus fossae (Heyning, 1989; Bianucci et al., 2016b). Other typical characters of the ziphiid skeleton include an elevated skull vertex that is anterolaterally bordered by well-distinct premaxillary crests, a more or less elongated rostrum, rostral bones that are often swollen and compact (i.e., pachyosteosclerotic), and relatively small forelimb bones; in addition, sexual dimorphism is

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well-defined in many species, mostly in the form of one or two pairs of (sub)apical tusks that occur on the mandibles of adult male individuals (Heyning, 1989; MacLeod & Herman, 2004; Bianucci et al., 2016b; Marx et al., 2016).

Scanty and fragmentary until the 2000s, the fossil record of the beaked whales has recently been enriched by the serendipitous trawling and long-line fishing of high numbers of specimens (essentially skulls) from various deep seafloor areas worldwide (Bianucci et al., 2007, 2008, 2013, 2023; Gol'din & Vishnyakova, 2013; Post & Jensen, 2013; Ichishima et al., 2017; Miján et al., 2017; Lambert et al., 2018). Overall, such a deep-water record has greatly expanded the past diversity of the family Ziphiidae, shedding new light on the fossil history of the extant subfamilies Berardiinae, Hyperoodontinae and Ziphiinae; however, these finds are often poorly constrained chronostratigraphically, and as such, of somewhat limited potential for comprehensive evolutionary, palaeoecological and palaeobiogeographic reconstructions (Lambert et al., 2023). A similar shortcoming applies to several historical finds from inland sites of Europe and North America that often lack precise geographic and stratigraphic whereabouts (e.g., Leidy, 1877), although micropalaeontological analyses of sediment samples associated with these specimens may result in significantly improving their chronostratigraphic assignment (Lambert et al., 2023).

One of the leading regions for ziphiid palaeontology is the Ica Desert of southern Peru, where a cornucopia of beaked whale fossils belonging to various taxa originates from the Upper Miocene strata of the Pisco Formation. Indeed, in the Pisco strata of the Ica Desert, the family Ziphiidae is represented by as many as four distinct genera and species, as well as by often exquisitely preserved specimens (Bianucci & Collareta, 2022). The geologically oldest ziphiid to have been described from these outcrops is the mid-Tortonian *Messapicetus gregarius* Bianucci et al., 2010: like its Mediterranean congener *Messapicetus longirostris* Bianucci et al., 1992 (Bianucci et al., 2016a, 2019), *M. gregarius* features an extremely elongated rostrum and a complete set of functional teeth. Thanks to a high number of fairly complete specimens, *M. gregarius* represents the best-known fossil beaked whale genus (Bianucci & Collareta, 2022), one for which information is even available with respect to sexual dimorphic variations (skulls with larger mandibular apical tusks were tentatively interpreted as belonging to adult males; Lambert et al., 2010) and trophic palaeoecology (the discovery of a regurgitalite of *M. gregarius* suggests that, unlike its modern relatives, this extinct ziphiid species used to feed on epipelagic prey items, such as schooling fish; Lambert et al., 2015). A roughly coeval form, *Chimuziphius coloradensis* Bianucci et al., 2016b, is known from a single specimen that belongs with the same set of stem-ziphiids as *M. longirostris* and *M. gregarius*, namely, the so-called "*Messapicetus* clade" (a speciose group that went extinct during the Pliocene, when oceanic dolphins radiated explosively to become the dominant odontocete epipelagic predators) (Bianucci et al., 2016b). The other ziphiid species of the Ica Desert, *Nazcacetus urbinai* Lambert et al., 2009 and *Chavinziphius maxillocristatus* Bianucci et al., 2016b, come from geologically younger (uppermost Tortonian and lower Messinian, respectively) deposits of the Pisco Formation. Whereas *N. urbinai* is a small-bodied, archaic crown ziphiid provided with a reduced upper and lower dentition as well as with a small temporal fossa (a combination of characters that suggests some suction feeding capabilities; Lambert et al., 2009), *C. maxillocristatus* has been interpreted as a very early-branching beaked whale, one that features robust rostral maxillary crests and distinct alveoli on the mandible, suggesting the retention of functional lower teeth (Bianucci et al., 2016b). Besides the aforementioned taxa, the occurrence of at least two additional genera of beaked whales in the Pisco strata has been noticed based on the observation of fragmentary, as-yet indeterminate specimens (Bianucci et al., 2016b), whereas another early-branching ziphiid (*Ninoziphius platyrostris* Muizon, 1983) is known from Pisco-equivalent strata of the Sacaco area, South of the Ica Desert (Muizon, 1984; Lambert et al., 2013). Overall, the outstanding Miocene record of beaked whales from Peru stands out as an invaluable source of information on the palaeobiology, palaeoecology, palaeobiogeography and evolutionary history of this family (Lambert et al., 2009, 2010, 2013, 2015; Bianucci et al., 2010, 2016b; Ramassamy et al., 2018).

Our aim here is to further enhance our current understanding of the fossil history of Ziphiidae by describing a new genus and species based on a newly collected skull from a mid-Tortonian outcrop of the Pisco Formation as well as by proposing a new age calibration for the whole Late Miocene beaked whale record from Peru.

MATERIAL AND METHODS

Phylogenetic analysis

The phylogenetic analysis was carried out by modifying the matrix of Bianucci et al. (2023), which in turn was modified from those of Bianucci et al. (2006, 2007, 2016b) and Lambert et al. (2009, 2013). In this new analysis, we considered taxa at the species level instead of the genus level. Consequently, for the outgroups, we replaced the genera with the respective type species or with species for which we were able to score a greater number of characters. For ziphiids, we included all those species known from significant skull material, except for the speciose genus *Mesoplodon*, for which we scored seven species, including the extinct *Mesoplodon posti* Lambert & Louwye, 2016 and *Mesoplodon slangkopi* Bianucci et al., 2007. Furthermore, besides the new species described herein, we added to the matrix *Dagonodum mojnum* Ramassamy, 2016, which belongs to a genus not included in our previous analyses. In total, 55 taxa were considered in this new analysis, 49 of which belong to Ziphiidae.

Eight new characters (chars. 52-59) were added to the analysis:

52. Dorsal margin of each premaxillary crest sloping markedly ventrolaterally and generating an acute dorsal profile of the vertex in anterior view: absent (0); present (1). Cannot be scored for taxa lacking the premaxillary crests.

53. Protuberant rostral maxillary crest medial to the antorbital process: absent (0); present (1); very large rostral crests converging posteromedially (2).

54. Maxillary tubercle and prominential notch anteromedial to the antorbital notch (modified from Ramassamy, 2016): absent (0); present (1).

55. Protuberant vertex pointed in lateral view: absent (0); present (1).

56. Fossa on the anterior surface of the ascending process of the premaxilla, distinct from the premaxillary sac fossa: absent (0); present (1).

57. Mesorostral groove dorsally closed at the level of the antorbital notches by the joined medial margins of the premaxillary sac fossae, forming a prominent ridge posteriorly shifted to the left, and separating the deeply concave anterior portions of the premaxillary sac fossae: absent (0); present (1).

58. Half-circle-shaped anterior margin of the large right premaxillary fossa: absent (0); present (1).

59. Narrow, deep, obliquely oriented jugular notches: absent (0); present (1). We interpret the apparent small jugular notch combined with an unusually distant hypoglossal foramen observed in *Mamaziphius* n. gen. as well as in two crania of *Berardius arnuxii* Duvernoy, 1851 and *Berardius minimus* Yamada et al., 2019 as due to a partial closure of the jugular notch. Consequently, we assign the derived state to these ziphiids as well.

Furthermore, in a few cases, the character states of some taxa were coded differently from previous analyses. For example, in agreement with Lambert et al. (2011) and Acebes et al. (2022), the mesorostral ossification of the vomer was coded as absent (char. 2[0]) in *Indopacetus* and *Hyperoodon*.

The modified matrix includes 59 morphological characters, 35 of which are binary, 17 multistate and ordered, and 7 multistate and unordered (see the Supplementary Online Material file −SOM− for the description of characters and data matrix). The analysis was performed with the software PAUP (v. 4.0a169; Swofford, 2002), using the tree-bisection-reconnection algorithm and the heuristic search option. The characters were analysed under both equal and implied weight. The resulting strict consensus tree was time-calibrated based on the chronostratigraphic ranges reported by Bianucci et al. (2016b, 2023), Ramassamy (2016), Miján et al. (2017), Kawatani & Kohno (2021) and Lambert et al. (2023), and considering also the recalibrated ages of the Peruvian fossil ziphiids as compiled in this work.

Structured-light scanning

A 3D model of the studied specimen was obtained with a SHINING 3D EinScan Pro HD handheld structured-light scanner. It is freely available via Figshare at the following internet address: http://doi.org/10.6084/m9.figshare.25422835

Chronostratigraphy

The $^{40}Ar/^{39}Ar$ ages included in our study are taken from the absolute dating and tephra correlations reported by Gariboldi et al. (2017) and Bosio et al. (2019, 2020a, b). All the biostratigraphic data included herein come from previous works (Gariboldi et al., 2017; Bosio et al., 2020c; Di Celma et al., 2022). However, First Occurrences (hereinafter: FO) and Last Occurrences (hereinafter: LO) were originally calibrated to the Berggren et al. (1995) timescale and are now referred to the Supporting Information of Lazarus et al. (2014), which provides recalibrations to the more recent timescale by Gradstein et al. (2020). Consider, however, that most of the bioevents were originally calibrated for the North and Equatorial Pacific.

Institutional abbreviations

MNHN, Muséum National d'Histoire Naturelle, Paris, France; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru.

GEOLOGICAL SETTING

Stretching along the southern coast of Peru, the East Pisco Basin is an Andean forearc basin whose depositional fill is currently exposed over most of the Ica Desert thanks to the Plio-Pleistocene uplift of the area (Macharé & Ortlieb, 1992) (Fig. 1). The East Pisco Basin is separated from its offshore counterpart, the West Pisco Basin, by the Coastal Cordillera; the latter consists of a NW-trending structural high (the Outer Shelf High) made of Precambrian to Palaeozoic rocks (Thornburg & Kulm, 1981; Di Celma et al., 2022). Between the middle Eocene and the ?Pliocene, the East Pisco Basin saw marine sedimentation as recorded by two megasequences, namely, the Palaeogene Megasequence P and the Neogene Megasequence N (Di Celma et al., 2022) (Fig. 2). Megasequence P includes the Eocene Paracas Formation and the Eo-Oligocene Otuma Formation, whereas Megasequence N consists of the largely Miocene Chilcatay and Pisco formations (Dunbar et al., 1990; DeVries, 1998, 2017; Di Celma et al., 2017, 2022; DeVries & Jud, 2018; Malinverno et al., 2021).

The Pisco Formation is exposed extensively along the lower Ica River valley, whose sides are punctuated by hills (locally known as "cerros") where high concentrations of fossil vertebrates are often observed (Bianucci & Collareta, 2022). It deposited in the semi-protected East Pisco palaeo-area during three major transgressive cycles, hence the genesis of three unconformity-bounded, high-order sequences or allomembers, i.e., the Middle Miocene (Langhian-Serravallian) P0 allomember, the Upper Miocene (Tortonian) P1 allomember and the Upper Miocene (Tortonian-Messinian) to ?Pliocene P2 allomember (Di Celma et al., 2016a, b; Gariboldi et al., 2017; Bosio et al., 2020a, b, c; Collareta et al., 2021a) (Figs 1-2). These sequences are characterised by a deepening-upward trend that indicates transgression; in turn, regressive facies successions are absent (Di Celma et al., 2017). Each allomember starts with a transgressive lag, generally consisting of a *Glossifungites* ichnofacies covered by boulders, passing up-section to a sand-rich shoreface division, which in turn is overlain by siltstones or diatomaceous mudstones that indicate sedimentation in a productive, offshore, shelfal setting (Di Celma et al., 2018). Volcanic ash layers and dolomitised horizons are also present (Bosio et al., 2019; Malinverno et al., 2022).

The new ziphiid specimen investigated in the present paper originates from the locality of Cerros la Mama y la Hija, where both P1 and a basal portion of P2 are exposed (Esperante & Poma, 2015; Di Celma

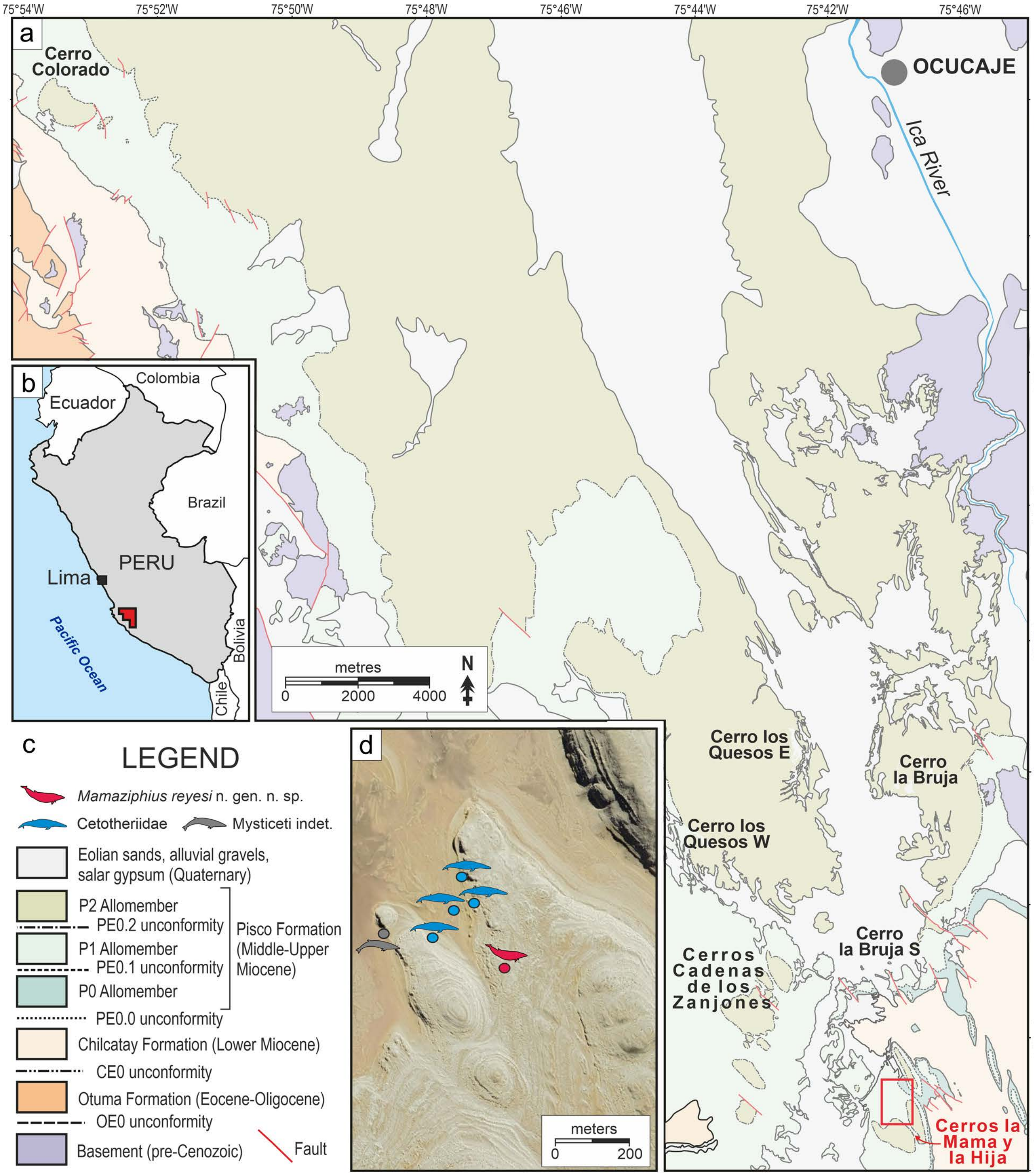

Fig. 1 - (color online) Geographic and geological setting. a) Simplified geological map of the investigated exposures of the Pisco Formation in the Ocucaje area, including the type locality of the holotype of *Mamaziphius reyesi* n. gen. n. sp. (MUSM 4687) and all other localities where remains of Ziphiidae have been recorded (see Figs 2 and 8 for stratigraphic sections showing the position of these fossils). b) Location of the investigated area along the southern coast of Peru. c) Legend of the geological map (a) and satellite image (d). d) Satellite image (obtained under open license from Google Earth) showing the geographic position of the *M. reyesi* n. gen. n. sp. holotype and other nearby cetacean skeletons reported in the stratigraphic log of Fig. 2c.

et al., 2017; Bosio et al., 2020c, 2021; Collareta et al., 2021b; DeVries et al., 2021; Di Celma et al., 2022; Bosio, 2023) (Figs 1-2). Here, a few cetacean fossils occur in P1 strata; most such fossils belong to Mysticeti (baleen-bearing whales), and specifically to the family Cetotheriidae, whereas our specimen represents the only local occurrence of Odontoceti (toothed whales) as well as the sole cetacean find from the diatomaceous part of the local succession (Figs 1d, 2c). Two detailed stratigraphic sections were measured along the eastern and western flanks of the hill, respectively, and an integrated chronostratigraphic framework was established based

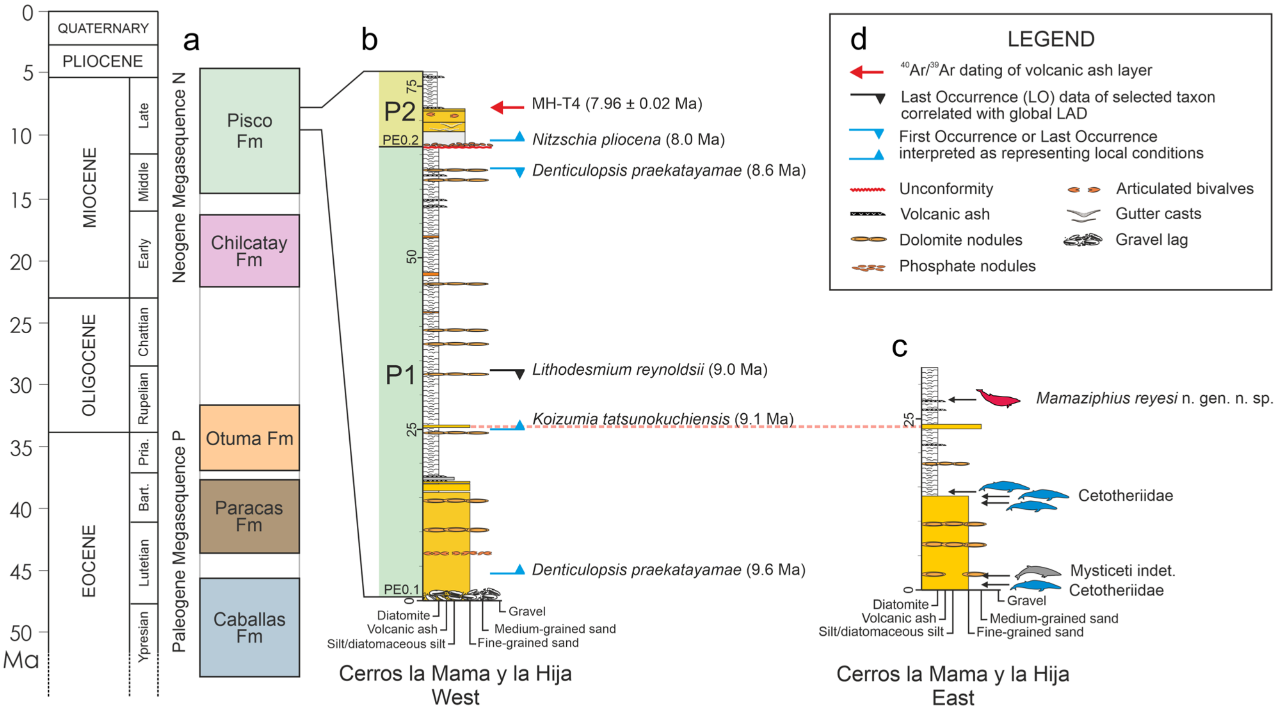

Fig. 2 - (color online) a) Schematic stratigraphic column of the Cenozoic succession exposed in the East Pisco Basin. b) Simplified stratigraphic log of Cerros la Mama y la Hija West reporting the stratigraphic positions of an ash layer (MH-T4) dated by ^{40}Ar/^{39}Ar and of the diatom biostratigraphic events. c) Simplified stratigraphic log of Cerros la Mama y la Hija East showing the exact position of the holotype of *Mamaziphius reyesi* n. gen. n. sp. (MUSM 4687) in the P1 allomember of the Pisco Formation. d) Legend of the stratigraphic sections in panels (b) and (c).

on diatom biostratigraphy, calculated ^{40}Ar/^{39}Ar ages and short-distance lithostratigraphic correlations (Fig. 2). Discovered between a sandy horizon just above the First Occurrence of *Koizumia tatsunokuchiensis* (Koizumi, 1972) Yanagisawa, 1994 and the Last Occurrence of *Lithodesmium reynoldsii* Barron, 1976, both of which are valuable biostratigraphic markers, our new ziphiid fossil dates back to between 9.1 and 9.0 Ma (Lazarus et al., 2014).

SYSTEMATIC PALAEONTOLOGY

Cetacea Brisson, 1762
Odontoceti Flower, 1867
Ziphiidae Gray, 1850

Mamaziphius n. gen.

Type and only known species - *Mamaziphius reyesi* n. gen. n. sp. (by original designation).

Etymology - from the name of the "cerro" (= hill) where the holotype and only known specimen was found. Indeed, the holotype originates from the larger ("Mama", meaning "mother" in Spanish) of a pair of "cerros" known as "la Mama y la Hija" (= "the Mother and the Daughter").

Diagnosis - Same as for the species until other species are described.

Mamaziphius reyesi n. sp.
(Figs 3-6; Tab. 1)

2021	Ziphiidae indet. - Bosio et al., Table S1 (Supporting Information file).
2021b	Ziphiidae indet. - Collareta et al., Table S1 (Supplementary Material file).

Holotype - MUSM 4687, a partial cranium lacking most of the rostrum, the zygomatic processes of the squamosal, the occipital condyles and the ear bones.

Type locality - Cerros la Mama y la Hija, East Pisco Basin, 60 km South of the town of Ica, southern coast of Peru (Fig. 1). Geographic coordinates: 14°35'58.45" S, 75°40'55.15" W; 535 m above sea level.

Type horizon and age - Pisco Formation, P1 allomember, Late Miocene. The age of the type horizon is constrained to the 9.1-9.0 Ma time interval (Tortonian) (see above and Fig. 2 for more details).

Diagnosis - *Mamaziphius* n. gen. belongs to Ziphiidae by having a wide hamular fossa of the pterygoid sinus that extends anteriorly on the palatal surface of the rostrum and a narrow jugular notch combined with an unusually distant hypoglossal foramen that we interpret to be homologous with the deeper, obliquely oriented jugular notch shared by all ziphiids. Furthermore, *Mamaziphius* n. gen. exhibits a large dorsal infraorbital foramen near the base of the rostrum as observed in many (but not all)

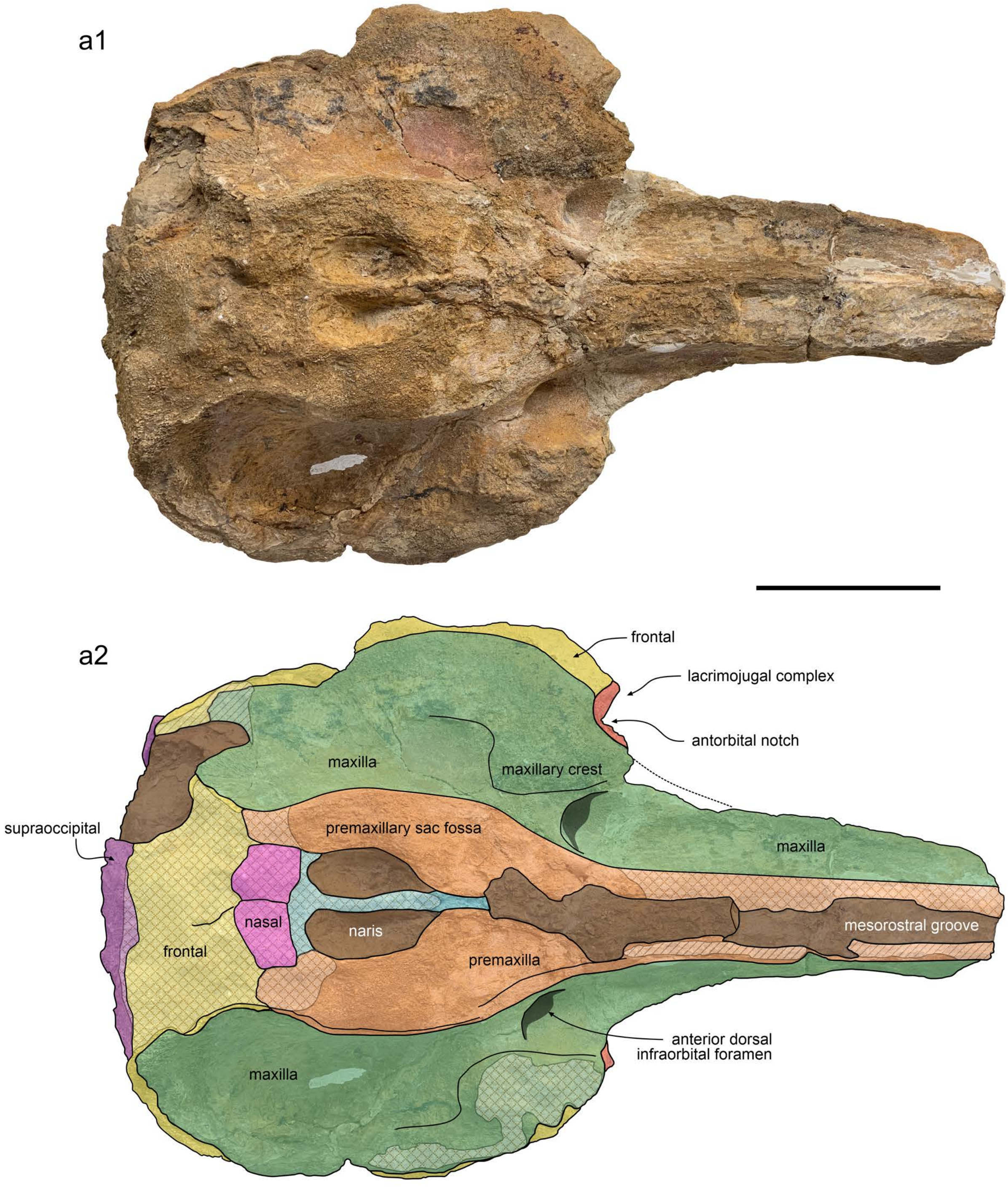

Fig. 3 - (color online) Cranium of *Mamaziphius reyesi* n. gen. n. sp. (MUSM 4687, holotype) in dorsal view; photograph (a1) and corresponding schematic drawing (a2). Linear hatching indicates broken surfaces, crosshatching indicates superficial wear; dark brown indicates areas covered by sediment. Scale bar = 10 cm.

ziphiids. Among Ziphiidae, *Mamaziphius* n. gen. shares with *Archaeoziphius*, *Berardius* (including "*Berardius*" *kobayashii* Kawatani & Kohno, 2021) and *Microberardius* (all of which form the clade Berardiinae) a supraoccipital that does not reach the level of the vertex dorsally; an ascending process of the premaxilla that is slightly concave in lateral view; and a moderate vertex elevation. However, *Mamaziphius* n. gen. differs from the berardiines by lacking two distinctive synapomorphies of this clade: an isolated rounded protuberance, formed by the interparietal or frontals, on the posterior part of the vertex; and a posterior transverse narrowing of the nasals and frontals at the vertex. Moreover, *Mamaziphius* n. gen. further differs from the extant species of *Berardius* by having shorter maxillary crests that do not extend on the rostrum and temporal fossae that are more anteroposteriorly elongated. *Mamaziphius* n. gen. differs from all members of Messapicetiformes (new clade defined below) as the mesorostral groove is

Condylobasal length	+495
Length of rostrum	+240
Length of neurocranium	+275
Width of rostrum base at level antorbital notch	195*
Width of premaxillae at level antorbital notch	68
Preorbital width of skull	159×2 = 318
Postorbital width of skull	160×2 = 320
Length of orbit	77
Length of temporal fossa	126
Height of temporal fossa	63
Total width of premaxillary sac fossae	117
Maximum width of right premaxillary sac fossa	57
Maximum width of left premaxillary sac fossa	47
Width of bony nares	50
Tranverse diameter right dorsal infraorbital foramen	23
Longitudinal diameter right dorsal infraorbital foramen	12
Tranverse diameter left dorsal infraorbital foramen	17
Longitudinal diameter left dorsal infraorbital foramen	19

Tab. 1 - Measurements (in mm) of the cranium of *Mamaziphius reyesi* n. gen. n. sp. (MUSM 4687, holotype) (modified from Bianucci et al., 2007). Abbreviations: e, estimate; +, nearly complete.

not closed by a dorsomedial contact of the premaxillae as well as by the lack of a pachyosteosclerotic development of the premaxillae on the rostrum. *Mamaziphius* n. gen. differs from most members of Vomeroziphii (new clade defined below) as the mesorostral groove is not filled by the mesorostral ossification of the vomer (though this character is absent or less developed in adult females of extant vomeroziphiids).

Etymology - The species name honors Julio Cesar Reyes Robles, the eminent Peruvian cetologist who described the extant ziphiid species *Mesoplodon peruvianus* Reyes et al., 1991 (see also Reyes & Van Waerebeek, 2018).

Total body length estimate - By inserting the postorbital width of the *Mamaziphius reyesi* n. gen. n. sp. holotype skull (about 320 mm) in the equation proposed by Bianucci et al. (2008) for ziphiids we obtained a body length estimate of 4.165 m, a size value that is slightly smaller than that of the extant Blainville's beaked whale, *Mesoplodon densirostris* de Blainville, 1817 (Ross, 1984).

Description -

General cranial morphology - The preserved portion of the rostrum is relatively narrow, exhibiting an oval cross section at the preserved anterior end (the transverse width to height ratio approximates 0.70). The well-preserved right margin of the posterior part of the rostrum indicates the absence of a maxillary tubercle and associated prominential notch. The dorsal surface of the neurocranium lacks any clear asymmetry, as the right and left premaxillary sac fossae have nearly the same transverse width (see below), and both the external nares and the right and left nasals are roughly symmetrical with respect to the sagittal plane. Despite some degree of abrasion on the vertex, the missing portion is estimated to be less than 1 cm thick, thus confirming the moderate elevation of the cranium compared to most other beaked whales. Specifically, the ratio between the vertical distance from the dorsal margin of the rostrum to the top of the vertex and the width of the premaxillary sac fossae falls between 0.80-0.90, a moderately high value, yet still lower than typically observed in the extant beaked whales. The degree of elongation of the temporal fossa (the ratio between the horizontal length of the fossa and the total length of the neurocranium is about 0.42) aligns closely with *Chavinziphius* (0.41); it is lower than observed in the functional tooth-bearing *Messapicetus* (0.52-0.54) and *Tasmacetus* (0.48), and much higher than observed in the almost edentulous *Berardius*, *Hyperoodon*, *Mesoplodon*, and *Ziphius* (ratio close to 0.30). In light of these comparisons, and given the apparent absence of an alveolar groove in the preserved rostrum portion, one can hypothesise that *Mamaziphius* n. gen., akin to *Chavinziphius*, may have retained an intermediate, reduced dentition, thus resembling some physeteroids with small yet functional upper teeth along a shortened upper tooth row.

Maxilla - The dorsal maxillary surface of the preserved posterior portion of the rostrum features a longitudinal depression that deepens posteriorly, reaching a single dorsal infraorbital foramen bordered laterally by a prominent maxillary crest (Fig. 3). This foramen is notably large and displays a circular outline (diameter 2 cm) when viewed anteriorly (Fig. 5a). A similar configuration is also observed in *Berardius* (including "*Berardius*" *kobayashii*) and *Tasmacetus.* The presence of a prominent maxillary crest medial to the antorbital notch is a derived character shared by *Mamaziphius* n. gen. with many but not all ziphiids (for example it is absent in most members of Messapicetiformes, *Nazcacetus*, and many species of *Mesoplodon*). However, the maxillary crest of *Mamaziphus* does not extend anteriorly on the rostrum (a clear difference with *Chavinziphius* and the extant species of *Berardius*, which display an elevated rostral maxillary crest). As already mentioned, there are no traces of distinct alveoli or an alveolar groove on the palatal surface of the preserved proximal portion of the rostrum (Fig. 5b).

Premaxilla - In dorsal view, the premaxillae are transversely narrow on the rostrum, their lateral margins being parallel to each other as well as to the main axis of the skull for most of the length of the preserved portion of the rostrum (Fig. 3). These margins weakly diverge posteriorly, yet their transverse distance at the rostrum base accounts for just 28% of the overall rostrum width. Among other ziphiids, such a limited transverse distance between the lateral margins of the premaxillae at the rostrum base (≤30% of the rostrum width) is observed in most hyperoodontines as well as in *Choneziphius*, *Imucetus*, and

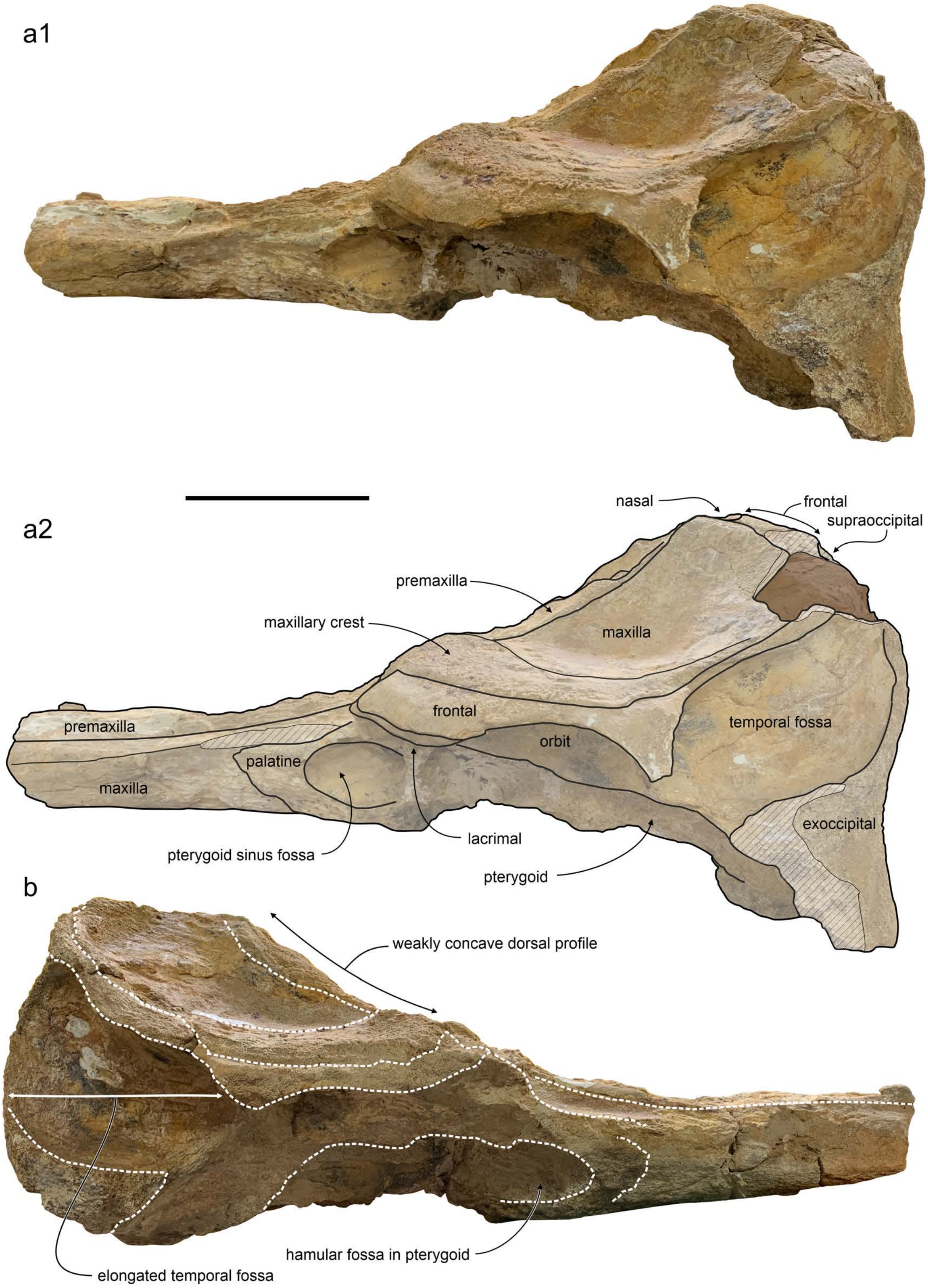

Fig. 4 - (color online) Cranium of *Mamaziphius reyesi* n. gen. n. sp. (MUSM 4687, holotype) in left (a1, a2) and right (b) lateral views; photographs (a1, b) and corresponding schematic drawing (a2). Linear hatching indicates broken surfaces. Scale bar = 10 cm.

Tusciziphius. The dorsal surface of the premaxillae on the rostrum displays evidence of heavy erosion and is partially obscured by sediment. Consequently, it is not possible to assess whether the premaxillae contacted each other dorsomedially to roof the mesorostral groove. However, judging by the U-shaped cross section of the mesorostral groove seen at the broken anterior end of the rostrum, the mesorostral groove was likely open dorsally. Additionally, despite the presence of sediment, the premaxillae do not appear to be excavated near the rostrum base (i.e., a prenarial basin is not present), thus differing from most members of Messapicetiformes. The premaxillary sac

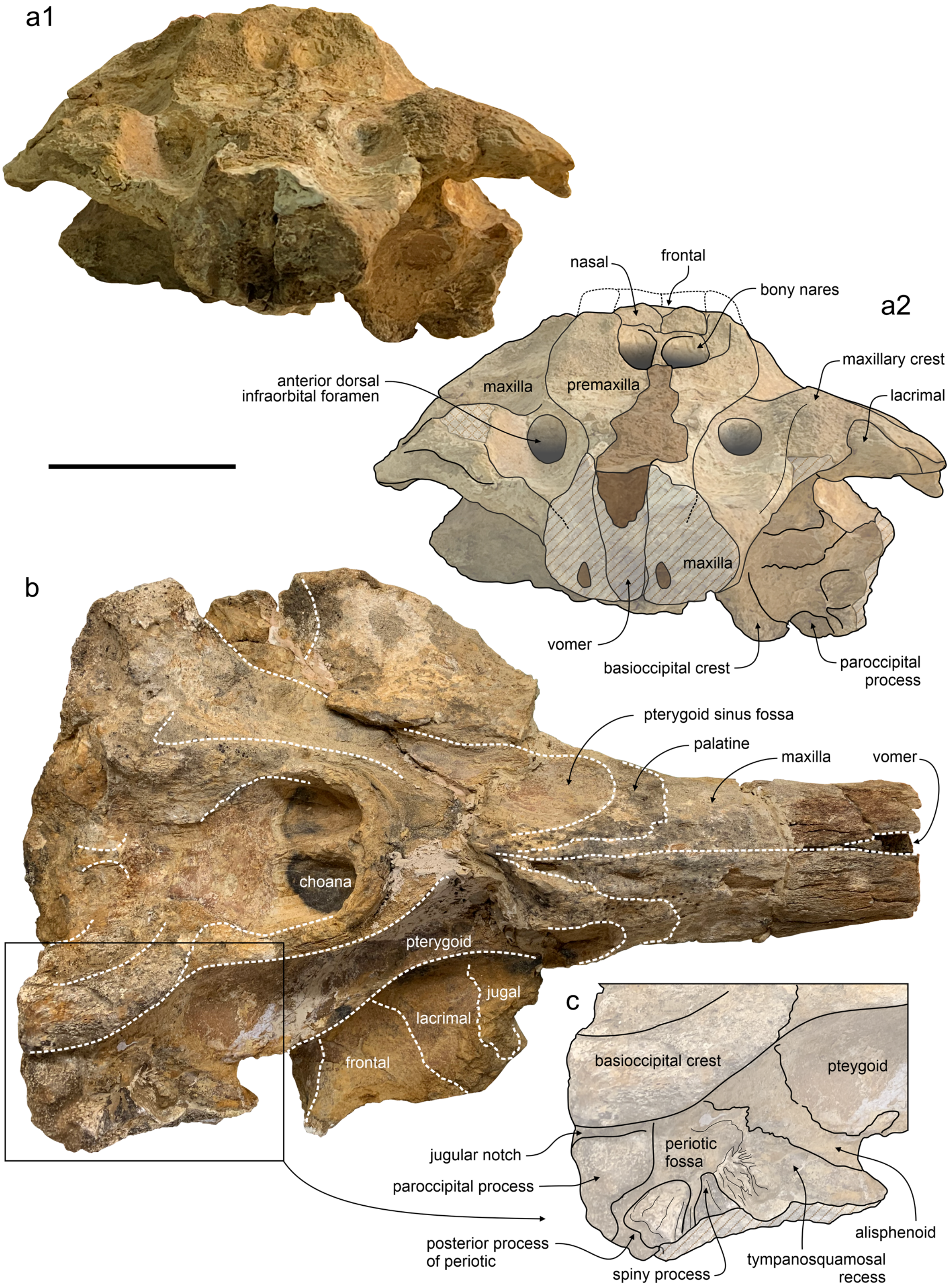

Fig. 5 - (color online) Cranium of *Mamaziphius reyesi* n. gen. n. sp. (MUSM 4687, holotype) in anterior (a1, a2) and ventral (b, c) views; photographs (a1, b) and corresponding schematic drawings (a2, c). Linear hatching indicates broken surfaces, crosshatching indicates superficial wear. Scale bar = 10 cm.

fosse are slightly concave and weakly asymmetrical (ratio between the width of the left and right premaxillary fossae = 0.82). The lateral margin of each premaxillary sac fossa does not overhang the corresponding maxilla. Partially due to the anteroposterior narrowness of the nasals, each premaxilla contacts the lateral margin of the corresponding nasal along the entire anteroposterior extension of the latter. The shape and size of the premaxillary crests are unknown due to erosion of the vertex. In lateral view, the ascending process of the premaxilla gradually rises towards the vertex, thus generating a slightly concave dorsal profile (Fig. 4) as observed in the berardiines and

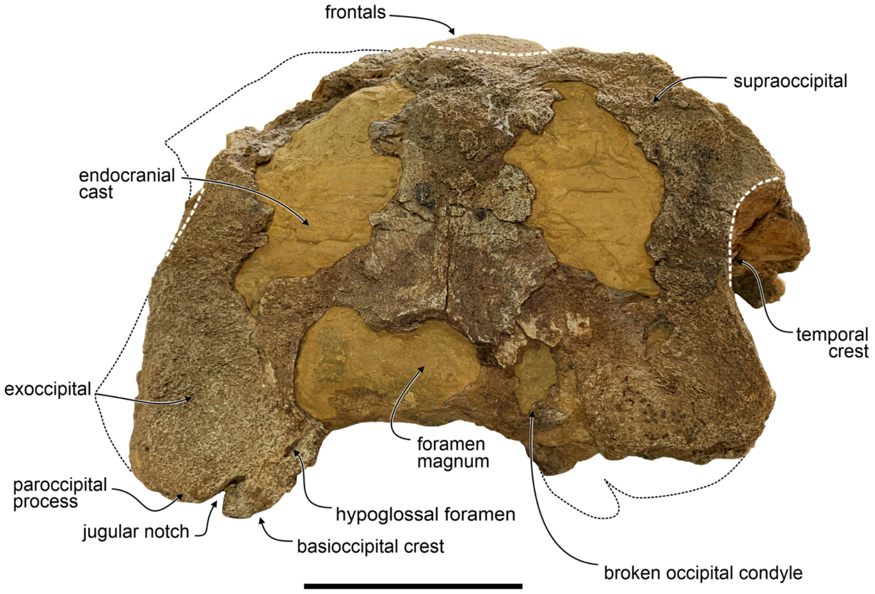

Fig. 6 - (color online) Cranium of *Mamaziphius reyesi* n. gen. n. sp. (MUSM 4687, holotype) in posterior view. Scale bar = 10 cm.

some members of Messapicetiformes. In anterior view, the ascending process of each premaxilla does not exhibit any significant constriction at approximately half its height, although this character may be underestimated due to the erosion of the premaxillary crests (Fig. 5a).

Nasal - Although superficially eroded, the nasals retain their original outline in dorsal view (Fig. 3). Their anterior margin is slightly concave, whereas the posterior margin is slightly convex, except near the median suture where the frontals wedge between the nasals to form a short anterior point. The ratio between the length of the medial suture of the nasals and their maximum width (ratio = 0.37) indicates that the nasals are not anteroposteriorly elongated. This contrasts with all other beaked whales, where the ratio is typically greater than 0.40, with the notable exception of *Messapicetus*.

Frontal - In dorsal view, the supraorbital and preorbital processes of the frontal are not completely covered by the maxilla (Fig. 3). Furthermore, the frontals are extensively exposed at the vertex, between the nasals and the supraoccipital, thus forming a flat trapezoidal surface that gently slopes posteroventrally. In spite of displaying some degree of abrasion, the wide extension of the frontals at the vertex, which is somewhat atypical for a beaked whale, appears to be genuine. When viewed laterally, the preorbital process of the frontal is unusually elongated anteroposteriorly (Fig. 4) compared to most other beaked whales. The supraorbital process displays a moderate thickening, with a height at mid-orbit that is intermediate between the notably elevated process of *Berardius* and the significantly low process observed in some species of *Mesoplodon* (e.g., *M. peruvianus*). The anteroposterior length of the orbit comprises approximately 40% of the postorbital width of the cranium, a value slightly higher than observed in most other beaked whales (ca. 30%) and significantly higher than in the largest ziphiid species, namely, *Berardius bairdii*, *B. arnuxii* and *Hyperoodon* spp. (ca. 20%). Conversely, this ratio is smaller than observed in the holotype of *Nazcacetus urbinai* (ca. 50%). The postorbital process is triangular and distally wide.

Lacrimal and Jugal - The preserved right antorbital notch is margined by the anterior portion of the jugal (maxillary process of the jugal sensu Mead & Fordyce, 2009), which is also visible in dorsal view (Fig. 3). In lateral view, the lacrimal exhibits a dorsoventrally narrow exposure along the anterior and posterior borders of the preorbital processes of the frontal (Fig. 4). In ventral view, the preorbital process of the frontal appears to be nearly completely covered by the lacrimal and jugal (Fig. 5b).

Palatine and Pterygoid - The W-shaped maxilla-palatine sutures are distinctly visible on the ventral surface of the rostrum (Fig. 5b). As in all other ziphiids, the wide pterygoid sinus fossae extend anteriorly from the base of the rostrum. The lateral lamina of the pterygoid is transversely broad and extends posteriorly to reach and suture with the alisphenoid.

Vomer - The broken surface at the anterior end of the rostrum reveals that the transverse section of the vomer is V-shaped (as typical for most odontocetes) and does not display any significant pachyostosis (Fig. 5a), thus differing from most of members of Vomeroziphii. Consequently, the mesorostral groove is deep, yet filled with sediment (Fig. 3).

Squamosal - Only the right squamosal is partially preserved; it lacks the zygomatic process. In ventral view, distinct sutures are seen between the squamosal and the alisphenoid anteriorly, and between the squamosal and the exoccipital posteriorly (Fig. 5b). The periotic fossa, the spiny process and the tympanosquamosal process are also discernible. The broken, enlarged posterior process of the periotic is preserved in situ, being sutured with the squamosal (Fig. 5c).

Supraoccipital and Exoccipital - The supraoccipital and exoccipital bones are significantly abraded and incomplete, yet some important characters are still observable. If our interpretation of the frontal-exoccipital suture is correct, the anteroposterior exposure of the supraoccipital is very limited in dorsal view (Fig. 3). The supraoccipital does not reach the dorsal level of the vertex, a feature that is clearly observed in posterior and lateral views. Among the other ziphiids, this character is only shared with *Archaeoziphius*, *Berardius* (including "*Berardius*" *kobayashii*), and *Microberardius*. In posterior view, two large "windows" resulting from the breakage of the thin supraoccipital and exoccipitals expose the endocranial cavity, which in turn is filled with sediment (Fig. 6). The occipital condyles are almost completely missing, whereas the outline of the foramen magnum is only partially preserved. The jugular notch is preserved between the left paroccipital process and the corresponding basioccipital crest as a narrow, short fissure. Approximately 2 cm posteromedial to the jugular notch, a small opening is identified herein as the hypoglossal foramen. The unusually wide distance between the hypoglossal foramen and the jugular notch may be due to a partial closure of the latter. Indeed, we observed that in most beaked whales for which this part of the cranium is known the jugular notch is narrow, deep, and obliquely oriented. Further supporting this hypothesis, we found a similar pattern (a hypoglossal foramen far removed from a small jugular notch) in two crania of *Berardius arnuxii* and *B. minimus*. Among other toothed whales, we only found such a distance between the hypoglossal foramen and the jugular notch in the extant delphinid *Globicephala macrorhynchus* Gray, 1846.

Basioccipital - The basioccipital basin is wide and the preserved left basioccipital crest is massive (Fig. 5b). We estimate that the left and right crests drew an angle just over 50 degrees in ventral view, which is higher than observed in most other odontocetes, but smaller than in other ziphiids, except for *Messapicetus* and a referred specimen (MNHN SAS 1628) of *Ninoziphius.*

PHYLOGENY

As for the phylogeny in Bianucci et al. (2016b, 2023), the best resolved results were achieved by means of an implied weight analysis with constant K = 3 (Goloboff, 1993). This analysis generated 270 equally parsimonious trees, with a tree length = 232, Goloboff fit = -43.04, consistency index (CI) = 0.40 and retention index (RI) = 0.80 (Fig. 7). The addition of new taxa (partially due to considering species rather than genera as operational units) and new characters did not substantially alter the tree topology compared to the trees published by Bianucci et al. (2016b, 2023).

Indeed, consistent with earlier analyses, the stem Ziphiidae are almost entirely represented by the monophyletic group previously known as the "*Messapicetus* clade" (Bianucci et al., 2016b), which is formally designated herein under the New Clade Name (NCN) Messapicetiformes. On the other hand, the crown Ziphiidae are split into two clades: one including the extant genera *Berardius* (the type genus of Berardiinae), *Tasmacetus* and their fossil relatives; and another that comprises the newly named Vomeroziphii (NCN). The latter encompasses the extant genera *Ziphius* (the type genus of Ziphiinae), *Hyperoodon*, *Indopacetus* and *Mesoplodon* (all of which fall within the subfamily Hyperoodontinae) along with their fossil relatives. Further supporting the clade Vomeroziphii is that *Ziphius*, *Hyperoodon* and *Mesoplodon* form a clade in recent molecular phylogenies (e.g., McGowen et al., 2020). Conversely, we avoided giving a name to the large sister clade of Vomeroziphii both because it is not defined by any synapomorphy and because it is not supported by recent molecular phylogenies, all of which feature *Berardius* as the earliest branching crown ziphiid (e.g., McGowen et al., 2020). The new clades Messapicetiformes and Vomeroziphii are defined below following the rules reported in the International Code of Phylogenetic Nomenclature (Cantino & de Queiroz, 2020).

Messapicetiformes (NCN)

DEFINITION - The branch-based clade Messapicetiformes consists of the extinct *Messapicetus longirostris* and all species that share a more recent common ancestor with *M. longirostris* than with *Notoziphius bruneti* Buono & Cozzuol, 2013.

ETYMOLOGY - From *Messapicetus*, the best-known genus of the clade, due to the abundance and completeness of referred fossil skeletons.

DIAGNOSIS - The members of Messapicetiformes are stem Ziphiidae that share the following synapomorphies: 1) mesorostral groove roofed by the dorsomedial contact or fusion of the premaxillae; and 2) pachyosteosclerotic development of the premaxillae along the rostrum.

Vomeroziphii (NCN)

DEFINITION - The branch-based clade Vomeroziphii consists of the extant *Ziphius cavirostris* Cuvier, 1823 and all species that share a more recent common ancestor with *Z. cavirostris* than with *Berardius arnuxii*.

ETYMOLOGY - From the Latin "vomer", for the pachyosteosclerotic vomer that characterises most of the members of this clade; and from *Ziphius*, the type genus of the family Ziphiidae and one of the extant representatives of this clade.

DIAGNOSIS - The members of Vomeroziphii are crown Ziphiidae that share (with only a few exceptions) the following synapomorphy: mesorostral groove filled by a mesorostral ossification of the osteosclerotic vomer.

Small differences between our new phylogeny and that published by Bianucci et al. (2023) include the following:

1. *Chavinziphius maxillocristatus*, previously interpreted as the earliest branching ziphiid, has been moved to a more derived position, as the earliest branching representative of the large, as-yet unnamed crown ziphiid clade that includes the extant *Beradius* and *Tasmacetus* besides various extinct genera such as *Nazcacetus*.
2. Among the stem Ziphiidae, *Notoziphius bruneti* now occupies a more basal position outside Messapicetiformes, which is also more consistent with the fact that this extinct ziphiid displays neither of the two synapomorphies of the clade.

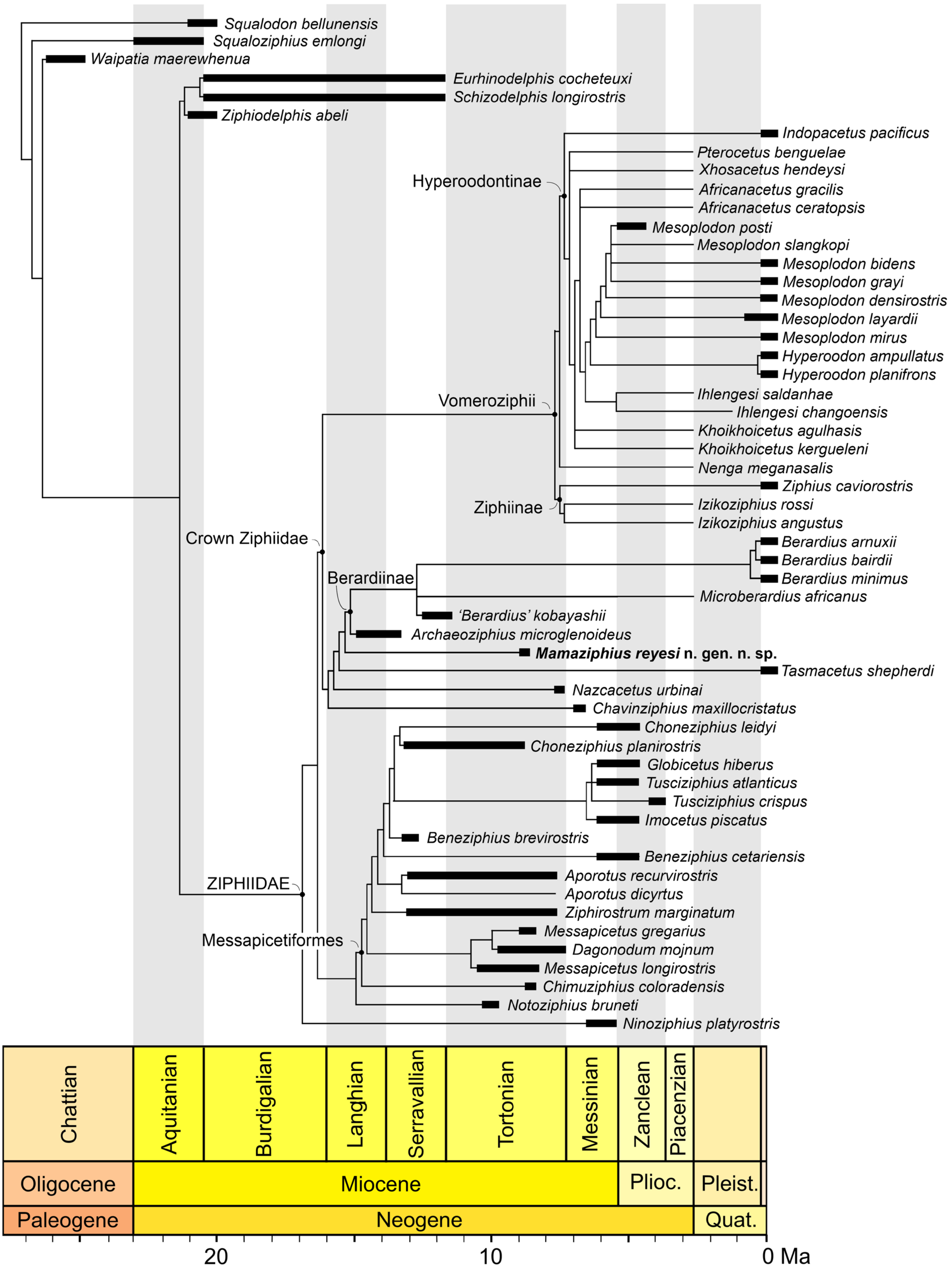

Fig. 7 - (color online) Time-calibrated strict consensus tree of 270 most parsimonious trees describing the phylogenetic relationships of *Mamazihius reyesi* n. gen. n. sp. among Ziphiidae. Homoplastic characters were down-weighted using the method of Goloboff (1993). Tree length = 232, Goloboff fit = -43.04, ensemble consistency index (CI) = 0.40, and ensemble retention index (RI) = 0.80. See the main text for information on the chronostratigraphic ranges, and the Supplementary Online Material for the description of characters and data matrix. The chronostratigraphic scale follows Gradstein et al. (2020).

3. *Dagonodum mojnum*, which was not included in our previous analyses, is recovered herein as the sister group of *Messapicetus gregarius* (contra the results of Ramassamy, 2016), with *Messapicetus longirostris* being placed in a more basal position. This suggests either that the genus *Messapicetus* is paraphyletic or that *D. mojnum* –whose holotype and only known specimen consists of a rather fragmentary skeleton– is a congener of *M. gregarius* + *M. longirostris.*

4. Among the crown Ziphiidae, the positions of *Tamacetus* and *Nazcacetus* have been reversed, with *Nazcacetus* being now regarded as branching before *Tasmacetus*.

5. *Archaeoziphius,* the geologically oldest ziphiid among those included in our analysis, is recovered as the earliest branching taxon within the subfamily Berardiinae, a position that was previously occupied by *Microberardius*.

6. "*Berardius*" *kobayashii* appears to be outside the well-defined clade formed by the three extant species of *Berardius*, including the recently described *B. minimus*. Therefore, our analysis further questions the assignment of "*B.*" *kobayashii* to the genus *Berardius*, as already evidenced by the phylogeny accompanying the original description of this species (Kawatani & Kohno, 2021).

7. Within the clade Vomeroziphii, *Indopacetus* has become the earliest-branching member of Hyperoodontinae, whereas *Mesoplodon* has moved to a more derived position, as sister taxon of *Hyperoodon.*

With respect to *Mamaziphius reyesi* n. gen. n. sp., two synapomorphies support its assignment to the family Ziphiidae: 1) the wide hamular fossa of the pterygoid sinus, extending anteriorly on the palatal surface of the rostrum (char. 35[1]); and 2) the deeper, obliquely oriented jugular notch (char. 59[1]). Specifically, our new phylogeny indicates that *M. reyesi* n. gen. n. sp. belongs with the crown Ziphiidae, as the sister group of Berardiinae. Indeed, *M. reyesi* n. gen. n. sp. shares three synapomorphies with the berardiine clade: 1) an ascending process of the premaxilla that is slightly concave in lateral view (char. 7[1]); 2) a moderate elevation of the vertex (char. 9[1]); and 3) an anteromedial margin of the supraoccipital that is distinctly lower than the dorsal margin of the vertex (char. 18[1]). That said, *M. reyesi* n. gen. n. sp. is excluded from the berardiines owing to the lack of two synapomorphies of this subfamily, namely: 1) an isolated rounded protuberance formed by the interparietal or frontals on the posterior part of the vertex (char. 17[1]); and 2) a posterior transverse narrowing of the nasals and frontals at the vertex, narrower than the nasals (char. 50[1]).

STRATIGRAPHIC DISTRIBUTION AND AGE OF THE FOSSIL ZIPHIIDS FROM PERU

In the Ica desert, fossil remains of Ziphiidae are known from Upper Miocene strata of the Pisco Formation cropping out at the sites of Cerros la Mama y la Hija (*Mamaziphius reyesi* n. gen. n. sp.), Cerro la Bruja South (*Messapicetus gregarius*), Cerros Cadenas de los Zanjones (Ziphiidae indet.), Cerro los Quesos West (Ziphiidae genus and sp. indet. 1), Cerro los Quesos East (*Chavinziphius maxillocristatus*, *Nazcacetus urbinai* and Ziphiidae genus and sp. indet. 2) and Cerro Colorado (*Messapicetus gregarius* and *Chimuziphius coloradensis*) (Fig. 1). Here, we provide an updated assessment of the stratigraphic distribution and geological age of these fossils based on the integration of diatom biostratigraphy and $^{40}Ar/^{39}Ar$ dates on volcanic ash layers through six high-resolution stratigraphic logs (Figs 8-9). In addition, the stratigraphy and age of the holotype and referred specimens of *Ninoziphius platyrostris* –another fossil ziphiid from the Upper Miocene of the Sacaco area of southern Peru– is also reassessed.

Mamaziphius reyesi *n. gen. n. sp., 9.1-9.0 Ma (Tortonian)*

The holotype and only known specimen of *M. reyesi* n. gen. n. sp. was collected from P1 strata exposed on the eastern side of Cerros la Mama y la Hija. The fossil laid in diatomites that are found 28.4 m above the base of the local measured section (hereinafter, abs). Thanks to high-resolution correlations with a longer section measured on the western side of the same hill, the fossil ziphiid can be positioned between the FO of *Koizumia tatsunokuchiensis* (which is observed at 25 m abs) and the LO of *Lithodesmium reynoldsii* (33.5 m abs). These bioevents have been calibrated at 9.1 and 9.0 Ma, respectively (Lazarus et al., 2014).

Messapicetus gregarius*, 9.1-8.6 Ma (Tortonian)*

The holotype of *M. gregarius* (MUSM 1037) was collected from P1 strata exposed at Cerro Colorado (Bianucci et al., 2010). The fossil occurred 46.1 m abs, and its age is well constrained between the FO of *Koizumia tatsunokuchiensis* (28 m abs) and the LO of *Lithodesmium reynoldsii* (54 m abs), which date back to 9.1 and 9.0 Ma, respectively (Lazarus et al., 2014). Moreover, the absolute dating of a volcanic ash layer (CC-T1b) at 31 m abs provided a $^{40}Ar/^{39}Ar$ age of 9.10 ± 0.03 Ma (Gariboldi et al., 2017). Thirteen additional specimens of *M. gregarius* were recorded at Cerro Colorado, nine of which (MUSM 950, 951, 1036, 1038, 1394, 1481, 2542, 2548 and 2552) were collected (Lambert et al., 2015; Ramassamy et al., 2018; Bosio et al., 2021). Apart from MUSM 1038, whose precise locality data are unknown (the coordinates reported by Bianucci et al., 2010 were later found to be incorrect), all these fossils come from a stratigraphic interval spanning from 46.1 m to 73.7 m abs. The top of this interval is placed just a few metres below the P1-P2 unconformity, for which an age of 8.60 ± 0.11 Ma has been proposed on the basis of the $^{40}Ar/^{39}Ar$ dating of a volcanic ash layer (ZANJ-T3) occurring at the top of P1 at Cerros Cadenas de los Zanjones (Bosio et al., 2020c). The fragmentary specimen from Cerro la Bruja South (MUSM 1718) was collected in sands of the P1 allomember, 28 m above the P0-P1 unconformity and 29 m below the P1-P2 unconformity. At present, there are no age data available for the P1 strata at Cerro La Bruja, such that the age of the only record of *M. gregarius* from this locality is only loosely bracketed between 9.6 and 8.6 Ma based on its assignment to the aforementioned P1 allomember. In conclusion, the stratigraphically informative record of *M. gregarius* can be constrained between 9.1 and 8.6 Ma.

Chimuziphius coloradensis*, 9.0-8.6 Ma (Tortonian)*

The holotype and only known specimen of *Chimuziphius coloradensis* (MUSM 2548) was collected from P1 strata

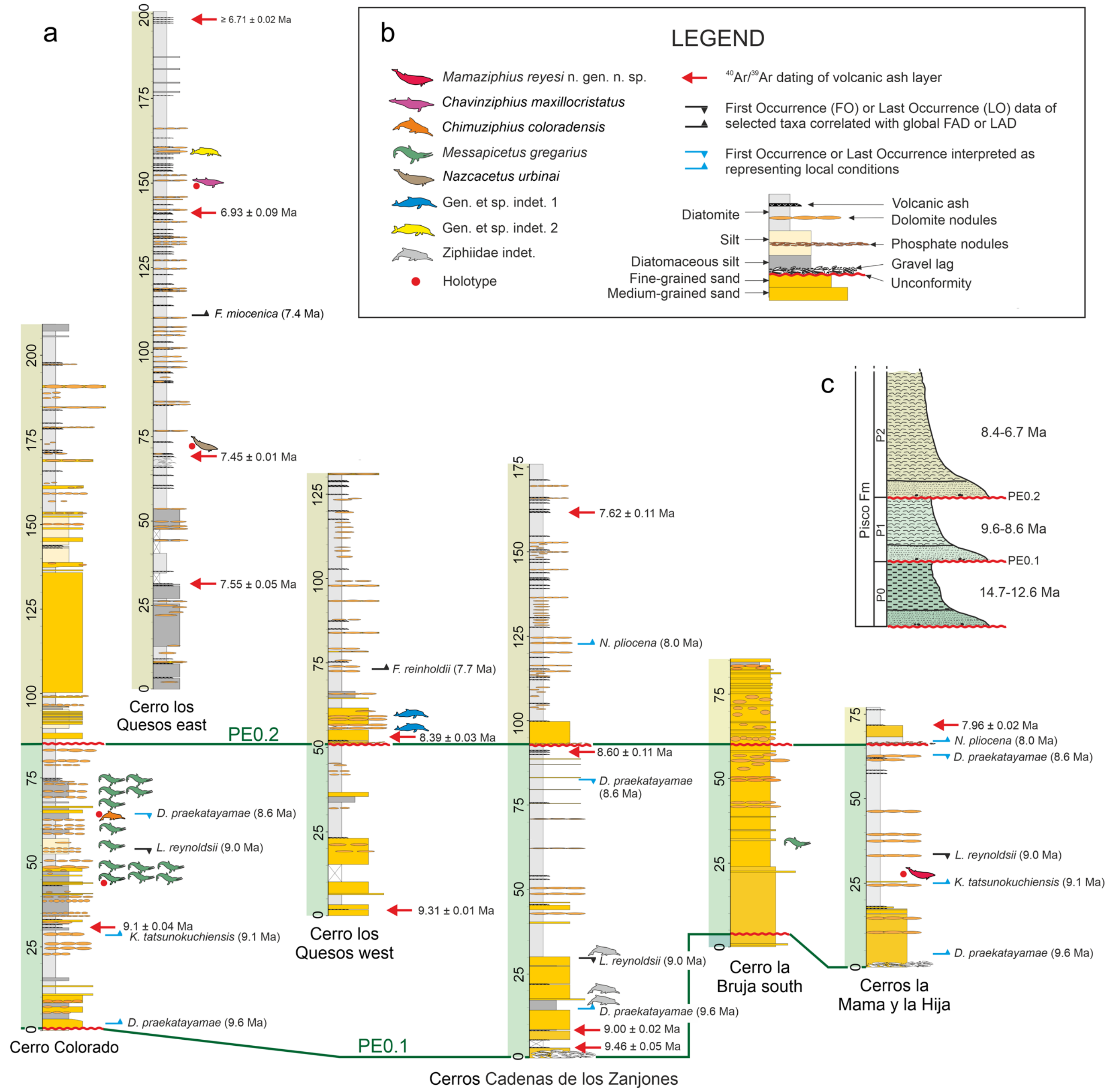

Fig. 8 - (color online) a) Simplified stratigraphic logs (in meters) of six localities of the East Pisco Basin, showing the distribution of fossil Ziphiidae (silhouettes) in the Upper Miocene portion of the Pisco Formation; the position of the holotype of *Mamaziphius reyesi* n. gen. n. sp. (MUSM 4687) is also shown. b) Legend of the stratigraphic logs. c) Schematic stratigraphic column of the Pisco Formation and its internal subdivision into allomembers (P0, P1, P2) (modified after Di Celma et al., 2018). PE0.1 and PE0.2 indicate the unconformities that mark the base of allomembers P1 and P2, respectively (see also Fig. 1). Absolute (^{40}Ar/^{39}Ar ages of volcanic ash layers) and biostratigraphic (diatom) age constraints for the fossil ziphiids are partially modified from Gariboldi et al. (2017) and Bosio et al. (2019, 2020c, 2021) (see the main text for details).

exposed at Cerro Colorado (Bianucci et al., 2016b). The stratigraphic horizon of the fossil is found 61.5 m abs and corresponds to the LO of *Denticulopsis praekatayamae* Yanagisawa & Akiba, 1990, which has been dated at 8.6 Ma (Lazarus et al., 2014). However, this bioevent is here registered 20 m below the P1-P2 unconformity for which an age of 8.6 Ma was reconstructed at Cerros Cadenas de los Zanjones based on the aforementioned dating of the ZANJ-T3 volcanic ash layer. This apparent discrepancy can be explained by considering the slightly angular nature of the P1-P2 unconformity (Di Celma et al., 2022) as well as the fact that the LO of *D. praekatayamae* at Cerro Colorado is interpreted as reflecting local conditions (Fig. 8). Therefore, although the age of *C. coloradensis* can only be bracketed between 9.0 and 8.6 Ma (corresponding to the LO of *L. reynoldsii* and the estimated age of the top of P1 allomember, respectively), an age as recent as 8.6 Ma (corresponding to the disappearance of *D. praekatayamae* as calibrated by Lazarus et al., 2014) is somewhat unlikely for MUSM 2548.

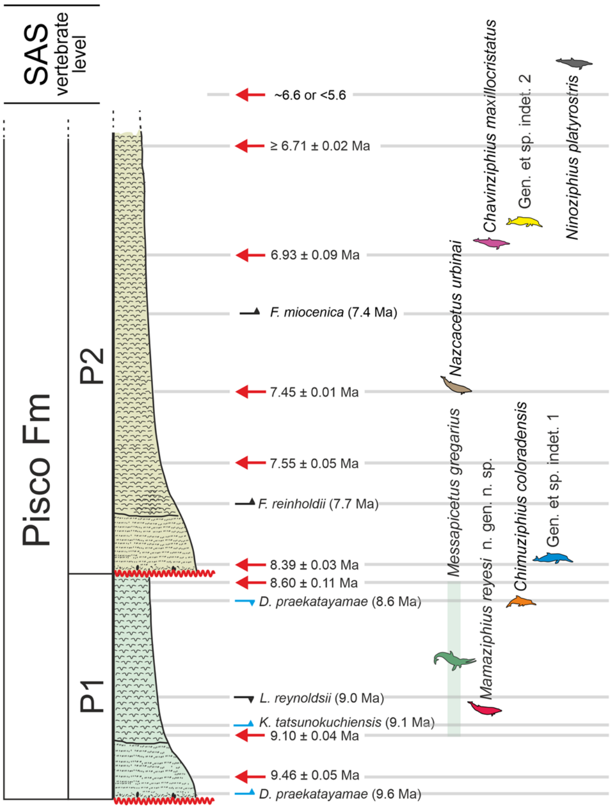

Fig. 9 - (color online) Schematic representation of the stratigraphic distribution and geological age of the fossil ziphiids from the Peruvian deserts of Ica (Pisco Formation) and Sacaco (SAS vertebrate level).

Genus and sp. indet. 1, 8.39 Ma (late Tortonian)

This as-yet unnamed ziphiid taxon is based on a fragmentary skull (MUSM 3237) that was reported by Bianucci et al. (2016) from Cerro los Quesos West (Fig. 10c, d). It was found 38.6 m abs, in strata belonging to the P2 allomember. MUSM 4966, another fragmentary skull consisting of rostral and mandibular fragments as well as three teeth (including the left apical tusk; Fig. 10a, b), may belong to the same ziphiid taxon as MUSM 3237. This second specimen was collected 44.9 m abs, some 2 km south of MUSM 3237. A few metres above the two fossils, at 52 m abs, a volcanic ash layer (ANF-T4) yielded a ^{40}Ar/^{39}Ar age of 8.39 ± 0.03 Ma (Bosio et al., 2020c).

The similarities between MUSM 3237 and MUSM 4966 mainly concern the mandibles. Indeed, the symphyseal portions of the left mandible of these specimens strongly resemble each other in terms of shape, size, diameter of the dental alveoli, and presence of the same pattern of lateral sulci associated with the mental foramina (Bianucci et al., 2016) (Fig. 10d). The only significant difference concerns the shape of the alveoli, which are weakly transversely compressed in MUSM 4966 and roughly circular in MUSM 3237. The anteriormost part of the symphyseal fragment of MUSM 4966 and the associated apical tooth provide new data on this unnamed ziphiid. In particular, the apical portion of the mandible is not particularly robust, as it lacks an anterior protuberance, and the apical tooth is not significantly enlarged, which may indicate that these remains belong to a female (MacLeod & Herman, 2004; Dalebout et al., 2008; Lambert et al., 2010). The apical mandibular tooth is transversely flattened (ratio between the transverse and mesiodistal diameters of the root = ca. 0.45), thus recalling the condition observed in *Messapicetus gregarius*; by contrast, judging from the shape of the corresponding alveolus, the apical mandibular tooth of *Ninoziphius* was likely circular (Lambert et al., 2013). Interestingly, the apical tusk of MUSM 4966 is followed posteriorly by an alveolar groove without distinct alveoli, a condition reminiscent of the diastema observed in the same symphyseal area of *Messapicetus gregarius*, *Ninoziphius* and the extant *Tasmacetus* (Muizon, 1984; Bianucci et al., 2010). However, the diastema of MUSM 4966 is significantly shorter than that of *M. gregarius* (approximately 8-10 cm versus 14-18 cm); furthermore, it lacks the secondary bone exostoses that fill the alveoli of *M. gregarius* as well as of *Ninoziphius* and *Tasmacetus*. All these characters further support the hypothesis that an unnamed beaked whale taxon is present in the lower strata of the P2 allomember. The hopeful discovery of a more complete specimen may allow for a more detailed systematic description of this elusive ziphiid species.

Nazcacetus urbinai*, 7.45 Ma (late Tortonian)*

The holotype and only known specimen of *Nazcacetus urbinai* was collected at Cerro los Quesos East, in strata referred to the P2 allomember (Lambert et al., 2009). Its type horizon occurs 72.4 m abs, that is, 3 m above the volcanic ash layer LB-T11 that was dated at 7.45 ± 0.01 Ma by means of ^{40}Ar/^{39}Ar geochronology (Bosio et al., 2019, 2020c). This age is further supported by diatom biostratigraphy: indeed, the FO of *Fragilariopsis miocenica* (Burckle, 1972) Censarek & Gersonde, 2002, which is dated at 7.4 Ma (Lazarus et al., 2014), occurs 38.6 m above the type horizon of *N. urbinai*.

Chavinziphius maxillocristatus*, 6.93-6.71 Ma (early Messinian)*

The holotype and only known specimen of *Chavinziphius maxillocristatus* was collected from P2 strata exposed at Cerro los Quesos East (Bianucci et al., 2016b). The stratigraphic horizon of the fossil is found 150 m abs, some 9 m above the volcanic ash layers CLQ-T1a, which in turn gave a ^{40}Ar/^{39}Ar age of 6.93 ± 0.09 Ma. Another volcanic ash layers (CLQ-T9b) located 48 m above the *C. maxillocristatus* horizon was ^{40}Ar/^{39}Ar dated at ≥6.71 ± 0.02 Ma (Gariboldi et al., 2017; Bosio et al., 2020c). Therefore, the age of *C. maxillocristatus* can be constrained between 6.93 and 6.71 Ma.

Genus and sp. indet. 2, 6.93-6.71 Ma (early Messinian)

This as-yet unnamed ziphiid taxon is based on a fragmentary skull (MUSM 1609) that was reported by Bianucci et al. (2016) from Cerro los Quesos East. It was collected 159.5 m abs, in strata belonging to the P2 allomember. This fossil laid ca. 10 m above the *Chavinziphius maxillocristatus* holotype and its age is constrained by the same two ^{40}Ar/^{39}Ar dates as the latter, namely: 6.93 ± 0.09 Ma for the volcanic ash layer CLQ-T1a (141 m abs); and ≥6.71 ± 0.02 Ma for the volcanic ash layer CLQ-T9b (198 m abs).

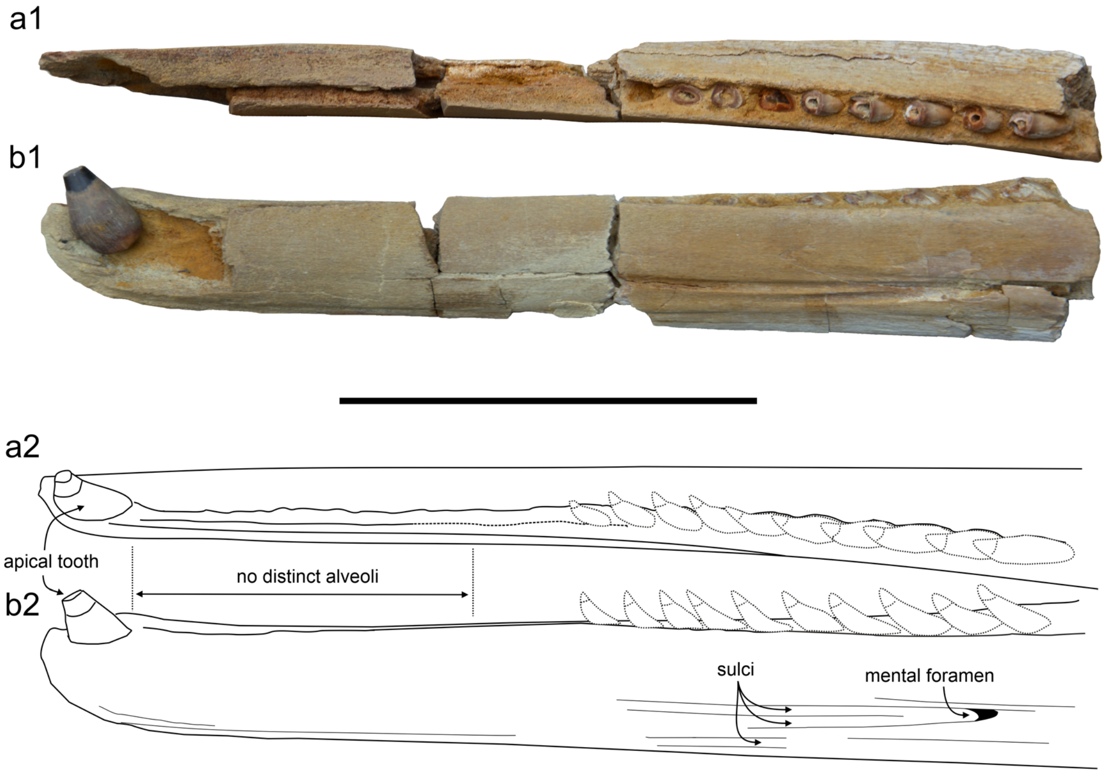

Fig. 10 - (color online) a-b) Symphyseal fragment of left mandible and associated apical tooth of Ziphiidae genus and sp. indet. 1 (MUSM 4966) from the upper Tortonian of Cerro los Quesos West, in dorsal (a1) and left lateral (b) views, and corresponding schematic drawings (a2, b2). c-d) Incomplete symphyseal portion of the fused mandibles of Ziphiidae genus and sp. indet. 1 (MUSM 3237) from the upper Tortonian of Cerro los Quesos, in dorsal (c) and left lateral (d) views. Note that the apical tooth is not shown in panel (a1). Scale bar = 10 cm.

Ninoziphius platyrostris*, ~6.6-5.9 Ma or <5.6 Ma (late Messinian)*

The holotype and referred specimens of *N. platyrostris* come from the Sacaco Desert, which stretches along the southern Peruvian coastline from El Jahuay (some 60 km South of Nazca) to Yauca (Muizon, 1983, 1984; Lambert et al., 2013). In spite of being sometimes referred to as the "southern Pisco Basin" (e.g., Ehret et al., 2012), the Sacaco area is separated from the present-day Ica Desert by the basement structural high of Cerro Huaricangana. Thus, for most of their Cenozoic history, the East Pisco and Sacaco areas may have been separated from each other, which accounts for different palaeoecological and depositional settings (Collareta et al., 2021b; but see also Marocco & Muizon, 1988: fig. 9). As a consequence, although the upper Neogene marine sediments of the Sacaco area have long been regarded as belonging to the Pisco Formation (e.g., Muizon, 1984, 1988; Muizon & DeVries, 1985; Ehret et al., 2009, 2012; Lambert et al., 2013; Ochoa et al., 2021, 2022), they may rather be referred to as "Pisco-equivalent" deposits (Bianucci & Collareta, 2022).

The first attempts to develop a stratigraphic assessment of the Pisco-equivalent strata of the Sacaco area were based on the identification of several vertebrate-bearing stratal packages based on their specific faunal assemblages (Muizon, 1984; Muizon & DeVries, 1985). One such levels is the "Sud-Sacaco vertebrate level", or SAS, which was named after the eponymous locality in the southern part of the Sacaco Desert and is home to the holotype and referred specimens of *N. platyrostris*. As for many other outcrops of the Sacaco Desert (Muizon & DeVries, 1985; Ochoa et al., 2022), the sedimentary successions exposed at Sud-Sacaco are dominated by sandy sediments that evoke a more proximal marine palaeoenvironment than those reflected by most upper Neogene exposures of the Ica Desert. In particular, the SAS vertebrate level is represented by a ca. 20-m-thick, fossil-rich interval featuring abundant barnacle debris, mollusc shell accumulations and vertebrate remains, all of which are capped by vertebrate-bearing tuffs and fining-upward cycles of sandstone (Muizon & DeVries, 1985; Ehret et al., 2012).

The chronostratigraphic and geochronological framework of the Pisco-equivalent strata of the Sacaco area, including the SAS vertebrate level, is constrained at present by diatom and molluscan biostratigraphy, strontium isotope stratigraphy, and radiometric (K-Ar, Ar-Ar and U-Pb) dates (Muizon & DeVries, 1985; Muizon & Bellon, 1986; Ehret et al., 2012; DeVries, 2020; Ochoa et al., 2022). Recent investigations at various localities of the Sacaco area (Ehret et al., 2012; Ochoa et al., 2021, 2022) have shown that most of the Pisco-equivalent deposits belong to the Upper Miocene rather than to the Pliocene as previously thought (e.g., Muizon, 1984, 1988; Muizon & DeVries, 1985; Muizon & Bellon, 1986; Lambert & Muizon, 2013).

The type horizon of *N. platyrostris* corresponds to the SAS vertebrate level, which has long been referred to the Zanclean based on its molluscan content as well as on the observation of serrated *Carcharodon* teeth of purported Pliocene age (Muizon, 1984; Muizon & DeVries, 1985). Ehret et al. (2012) re-assigned this interval to the Late Miocene (Messinian) based on the strontium isotope analysis of mollusc shells (yielding preferred ages of 6.59 and 5.93 Ma) and U-Pb dating on zircon grains from the vertebrate-bearing tuff (resulting in an age range of 7.1 ± 1 Ma), hence Ochoa et al.'s (2021) referral of the SAS vertebrate level to ~6.6-5.9 Ma. That the fossil content of the SAS is Messinian was further supported by Ochoa et al. (2022) based on new strontium-ratio and radiometric data on zircons that basically confirmed Ehret et al.'s (2012) results. At the same time, however, Ochoa et al. (2022) recorded the presence of the diatom biostratigraphic marker *Thalassiosira oestrupii* (Ostenfeld, 1900) Hasle, 1972, whose appearance in the Pacific Ocean has been calibrated to 5.6 Ma (Barron, 2003), at the base of the Sud-Sacaco (West) succession. Notwithstanding this discrepancy between the available age data, Ochoa et al. (2022) regarded the SAS vertebrate level as reflecting deposition during the latest Messinian, later than 5.6 Ma. On the other hand, Ochoa et al. (2022) supported a slightly older age of 5.9 to ~5.7 Ma for the Sacaco (SAO) vertebrate level, which has long been regarded as geologically younger than the SAS vertebrate level (e.g., Muizon, 1984, 1988; Muizon & DeVries, 1985; Ehret et al., 2012; Lambert & Muizon, 2013; Ochoa et al., 2021).

All things considered, we concur with Ochoa et al. (2022) that the SAS level can be confidently assigned to the Messinian; however, we contend that its maximum age is only weakly constrained, as different methods yield results as disparate as ~6.6-5.9 Ma and less than 5.6 Ma.

DISCUSSION

No other formation or lithological unit worldwide preserves a record of fossil beaked whales as abundant, diverse, and stratigraphically well-constrained as the Pisco Formation of Peru. This outstanding palaeontological heritage includes stem ziphiids (*Chimuziphius coloradensis* and *Messapicetus gregarius*, both of which belong with Messapicetiformes), as well as early-branching representatives of the ziphiid crown group (*Chavinziphius maxillocristatus*, the newly described *Mamaziphius reyesi* n. gen. n. sp. and *Nazcacetus urbinai*); in addition, a very early-branching stem ziphiid (*Ninoziphius platyrostris*) is known from the Pisco-equivalent strata of the Sacaco area. Crucially, no remains of Vomeroziphii have ever been found in the Pisco strata, nor in other Neogene deposits of Peru. Overall, these fossils provide unvaluable information on the evolutionary history of Ziphiidae, and especially on the basal ziphiid and messapicetiform radiations as well as on the origin of Berardiinae, whereas several aspects of the evolution of the vomeroziphiids remain quite enigmatic. Some of these aspects are further developed in the following paragraphs.

Ninoziphius platyrostris*: a testament to the early ziphiid radiation*

As highlighted by our review, *Ninoziphius platyrostris* represents a latest Miocene (late Messinian) species, not older than ~6.6 Ma; as such, it postdates all the ziphiid records from the Ica Desert. Interestingly, despite its recent geological age, *N. platyrostris* is recovered in all recent phylogenetic analyses (Kawatani & Kohno, 2021; Bianucci et al., 2023; this work) as a very early-branching ziphiid basal to the origin of Messapicetiformes – one that diverged from the rest of the family before the geologically older (Tortonian; Buono & Cozzuol, 2013) *Notoziphius bruneti*, which in turn appears to be basal to the origin of Messapicetiformes (this work). Thus, the geological age of *N. platyrostris* evokes the as-yet elusive existence of a long-lived lineage of archaic beaked whales coexisting with more derived forms (including both the messapicetiforms and the crown ziphiids) as recently as in late Messinian times.

This "ghost lineage" (sensu Sidor & Hopson, 1998) should have existed since at least the Langhian or early Serravallian (15-13.2 Ma), that is, the age range of *Archaeoziphius microglenoideus* Lambert & Louwye, 2006, the geologically oldest named ziphiid species (Lambert et al., 2023) and a bona fide member of Berardiinae. If the as-yet unnamed, purported vomeroziphiid from Turkana is also taken into account, then the very origin of the family Ziphiidae would be even older, and in fact at least as old as the Burdigalian, ca. 17 Ma or more (Wichura et al., 2015a; see further comments below). All things considered, the first few million years of the evolutionary history of the basal ziphiids are seemingly still off the radar of palaeontologists, which makes the hypodigm of *N. platyrostris* a precious testament to the early beaked whale radiation.

The Peruvian record of Messapicetiformes in a global context

It is generally recognized that the Pisco Formation is home to the best-known fossil species of Ziphiidae, namely, *Messapicetus gregarius* (Bianucci & Collareta, 2022). Actually, it is no overstatement to say that this extinct species is better known at present that the most elusive among its extant confamilials. Within Messapicetiformes, *M. gregarius* forms a clade with *Dagonodum mojnum* and *Messapicetus longirostris*, which are known from roughly coeval deposits of the North Sea and the Mediterranean, respectively; in addition, a fragmentary skull of cf. *Messapicetus* sp. has been reported from the Northwestern Atlantic (Fuller & Godfrey, 2007; Godfrey & Lambert, 2023). This distributional pattern suggests that the then-open Central American Seaway acted as a major route of dispersal for the early Late Miocene messapicetiforms (Bianucci et al., 2016a, 2019). Thus, albeit the geologically oldest member of Messapicetiformes (i.e., *Beneziphius brevirostris* Lambert, 2005) originates from the lower to mid-Serravallian (13.2-12.8 Ma; Lambert et al., 2023) of the North Sea Basin, that the earliest-branching members of Messapicetiformes (i.e., *M. gregarius*, and the slightly more basal *Chimuziphius coloradensis*) come from the Tortonian strata of the Pisco Formation may indicate that the nutrient-rich coastal waters of Pacific South America comprised an important area for the early messapicetiform radiation (see also Bianucci & Collareta, 2022).

As highlighted elsewhere (Lambert et al., 2015), *M. gregarius* was likely a raptorial piscivore that used to feed on epipelagic, schooling fish, and the same seems to apply to a large stock of stem ziphiids, including other early-branching members of Messapicetiformes (Bianucci et al., 2016a, b) as well as the even more basal *Ninoziphius platyrostris* (Lambert et al., 2013). More derived members of Messapicetiformes, however, resemble the vomeroziphiids by evolving characters that have been proposed to be related to suction feeding and deep diving, including: 1) a progressive reduction of dentition; 2) an increase in the compactness and thickness of the rostral bones; 3) similar changes in facial morphology (e.g., through the development of an elevated vertex); and 4) increasing body size values (Bianucci et al., 2016b). Thus, the fossil messapicetiforms of the Pisco Formation witness to the epipelagic, macroraptorial habits and adaptations of the early-branching members of Messapicetiformes as well as to the dramatic adaptive changes underwent by their more derived confamilials, both along the ziphiid stem and in the crown ziphiid clade.

Mamaziphius reyesi *n. gen. n. sp. and the berardiine origins*

The crown ziphiid clade is well represented in the Peruvian fossil record, where it accounts for three out of six formally named genera and species, namely, *Chavinziphius maxillocristatus*, *Mamaziphius reyesi* n. gen. n. sp. and *Nazcacetus urbinai*. In our phylogenetic analysis, all these species cluster with the unnamed clade that includes the extant genera *Tasmacetus* and *Berardius*. In particular, in spite of its relatively old geological age, *M. reyesi* n. gen. n. sp. is here recognized as the most crownward of the Pisco ziphiids, and specifically as the sister group of the berardiines. Though branching earlier than *M. reyesi* n. gen. n. sp., and actually even earlier than the extant *Tasmacetus shepherdi* Oliver, 1937, *Nazcacetus* may be the most modern-looking of the Pisco beaked whales as far as the feeding adaptations are taken into account (Lambert et al., 2009).

Once again, it is worth stressing here that our phylogenetic analysis strengthens the uncertainties existing about the genus-level assignment of "*Berardius*" *kobayashii*. In fact, in our cladogram, "*B.*" *kobayashii* is included in a polytomy with *Microberardius africanus* Bianucci et al., 2007 and a monophyletic group formed by the three living species of *Berardius*. As a consequence of this, although the berardiine affinities of "*B.*" *kobayashii* are well established, this recently described extinct species should not be regarded as a bona fide member of the genus *Berardius*, which at present has no unambiguous fossil record.

On the surprising absence of Vomeroziphii from the Peruvian Miocene

As already mentioned, no vomeroziphiid remains have ever been found in the Pisco strata, nor in other Neogene deposits of Peru. This seemingly curious absence may be due to chronostratigraphic reasons. At present, most fossil representatives of Vomeroziphii come from various deep-marine areas, with consequent uncertainty on their geological age. This is especially true for the most diverse accumulation of ziphiid fossils worldwide, which consists of cranial materials recovered by trawling from the seafloor off South Africa (Bianucci et al., 2007, 2008). Representing as many as ten genera and eleven vomeroziphiid species, this assemblage has been tentatively assigned to the Middle or Late Miocene, but a younger (i.e., Pliocene) age is also possible, at least for some finds (Bianucci et al., 2007), and the same can be said for another rich deep-seafloor assemblage from off the Crozet and Kerguelen islands (Lambert et al., 2018). Excluding a handful of Quaternary records (e.g., Lambert et al., 2018), only a few time-constrained fossil occurrences of Vomeroziphii exist worldwide. The earliest such record was first published by Mead (1975) and then reappraised by Wichura et al. (2015a). It consists of a poorly preserved cranium, including the rostrum and the facial region, from the Lower Miocene (Burdigalian; 17.1±1.0 Ma) of West Turkana, Kenya. What is unique to this specimen is its occurrence in continental alluvial deposits, some 600 km from the nearest palaeocoastline. Based on a phylogenetic analysis, Wichura et al. (2015a) interpreted the Turkana specimen as representing a hyperoodontine, as seemingly demonstrated by the observation of a mesorostral ossification of the vomer. However, judging by the CT scans of the rostrum (Wichura et al., 2015b) the presumed filling of the mesorostral groove does not appear to be made of compact (osteosclerotic) bone, a condition that differs from the microstructure of the thickened vomer as observed in many members of Vomeroziphii (Lambert et al., 2011). Therefore, the referral of the Turkana fossil to this clade of crown group ziphiids should be regarded as tentative at best (see also the observations contained in Mead, 1975: 746). The occurrence of ?*Mesoplodon longirostris* (Cuvier, 1823) in the Tortonian of the Mediterranean Basin was mentioned by Bianucci & Landini (2002) based on skull materials from Calabria, southern Italy (note that *M. longirostris* is now regarded as a "wastebasket taxon" for a variety of ziphiid taxa displaying a osteosclerotic vomer; Bianucci et al., 2007; Lambert et al., 2016). Regrettably, these materials have since been held in private collections (G. Carone, pers. comm. to GB), and as such, cannot be further analysed at present. Another time-constrained occurrence of Vomeroziphii, consisting of the holotype and referred specimens of the extinct hyperoodontine species *Mesoplodon posti* Lambert & Louwye, 2016, comes from the Lower Pliocene (Zanclean; 4.86-3.9 Ma) of Antwerp, Belgium. As confirmed by our phylogenetic reconstruction, the hypodigm of *M. posti* reveals that the origin of the most speciose extant genus of Cetacea (Dalebout et al., 2008) is at least as old as the Early Pliocene. Other more fragmentary cranial remains (mostly isolated rostra with a conspicuous mesorostral ossification of the vomer) come from various Pliocene localities worldwide, most notably from northern and central Italy (Bianucci, 1997). Although the assignment of these specimens to Vomeroziphii is well supported by the observation of a pachyostotic vomer, they are too incomplete to be determined at the genus level (Bianucci et al., 2007).

In view of this, the fact that no member of Vomeroziphii has ever been found in the Pisco Formation may reflect the chronostratigraphic extent of this lithostratigraphic unit, whose upper strata may be roughly coeval to the origin of Vomeroziphii. It should be noted, however, that the sister group of Vomeroziphii (i.e., Berardiinae and kin, including *M. reyesi* n. gen. n. sp.) is known from fossils as old as the Middle Miocene (e.g., the berardiine *Archaeoziphius microglenoideus*). This suggests that, if the earlier discussed vomeroziphiid assemblage from the seafloor off South Africa is not Middle-Late Miocene (as first proposed by Bianucci et al., 2007; Lambert & Louwye, 2016), then there exists a ghost lineage of crown ziphiids leading to the origin of Vomeroziphii that spans the second half of the Miocene.

Palaeobiogeographic patterns may also have had a role. Assuming for a moment that the origin of Vomeroziphii dates back to the Middle or early Late Miocene, it is interesting to note that the earliest branching members of Ziphiinae (i.e., *Izikoziphius*) and Hyperoodontinae (i.e., *Pterocetus* and *Xhosacetus*) come from the Southern Ocean, and the same holds true for *Nenga* (an archaic relative of the hyperoodontines). Thus, the possibility that the vomeroziphiids originated in the Southern Ocean and only colonised the lower latitudes after the decline of the mostly tropical and warm-temperate Messapicetiformes across the Miocene-Pliocene transition should also be taken into account. Competitive exclusion between two morphologically convergent ziphiid clades (Bianucci et al., 2016b, 2023) may be the key mechanism at play here (see also Collareta et al., 2021c for a similar hypothesis to explain the paucity of cetotheriid fossils from the Mediterranean region).

A third possible explanation for the absence of Vomeroziphii from the Late Miocene Peruvian assemblages may deal with the palaeoenvironmental preferences of the members of this clade. As observed elsewhere (Lambert et al., 2015, 2023; Bianucci et al., 2016a, b), the earliest diverging stem ziphiids (including the early-branching members of Messapicetiformes) may have been epipelagic raptorial feeders that dwelt in shallow, shelfal waters, whereas more derived members of the ziphiid stem group, displaying morphological clues for suction feeding adaptations (e.g., an extreme reduction of the functional dentition), were possibly open-ocean deep-divers; in addition, the fossil record of the ziphiid crown group (including Vomeroziphii) is mostly housed in deep-water sediments, thus paralleling the habitat preferences of the extant ziphiines and hyperoodontines (MacLeod et al., 2003, 2006; Tyack et al., 2006; Schorr et al., 2016). During the Late Miocene, the present-day East Pisco Basin was shaped as a semi-enclosed, shallow embayment, and this palaeoenvironmental setting is thought to be reflected in the autoecological traits of most of the vertebrate taxa (Collareta et al., 2021b). If the Late Miocene representatives of Vomeroziphii shared the palaeoenvironmental preferences of their modern counterparts, they would have likely avoided the shelfal, relatively nearshore waters of the East Pisco embayment.

CONCLUSIONS

We described *Mamaziphius reyesi* n. gen. n. sp., a new genus and species of Ziphiidae from the highly fossiliferous Pisco Formation of Peru, based on cranial remains from a mid-Tortonian (9.1-9.0 Ma) horizon exposed at the Cerros la Mama y la Hija locality of the Ica Desert. While somewhat similar to the extant genus *Berardius*, *Mamaziphius* n. gen. lacks the signature skeletal traits of Berardiinae, being recovered in our phylogenetic reconstruction as sister group of the berardiines. Furthermore, we introduced the new clade names Messapicetiformes (for the so-called "*Messapicetus* clade", aka the messapicetiforms) and Vomeroziphii (for Ziphiinae + Hyperoodontinae and closely related forms, aka the vomeroziphiids). We also described the second known specimen of an as-yet unnamed ziphiid genus and species from the Pisco strata while providing a comprehensive reappraisal of the stratigraphy and age of the eight Peruvian fossil taxa of Ziphiidae, six of which have been formally named to date. Our revision restricts this outstanding record –which includes the earliest branching ziphiid, namely, *Ninoziphius platyrostris* from the Sacaco Desert– to a Tortonian-Messinian interval younger than 9.10 Ma. No other inland deposit worldwide preserves a fossil record of beaked whales as abundant, taxonomically rich and chronostratigraphically refined as the Pisco Formation, but the reasons behind the curious absence of vomeroziphiids from the Miocene outcrops that stretch along the southern Peruvian coast remain difficult to decipher.

SUPPLEMENTARY ONLINE MATERIAL

Supplementary data of this work are available on the BSPI website at: https://www.paleoitalia.it/bollettino-spi/bspi-vol-631/

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REFERENCES

Acebes J.M.V., Yamada T.K., Poniente J.A., Matsuda A.T., Dolar M.L.L., Espiritu M.M., Tan J.M.L. & Santos M.D.

(2022). Stranding of Longman's beaked whale (*Indopacetus pacificus*) in the Philippines. *Journal of Cetacean Research and Management*, 23: 81-105.

Barron J.A. (1976). Revised Miocene and Pliocene diatom biostratigraphy of upper Newport Bay, Newport Beach, California. *Marine Micropaleontology*, 1: 27-63.

Barron J.A. (2003). Planktonic marine diatom record of the past 18 my: appearances and extinctions in the Pacific and Southern Oceans. *Diatom Research*, 18: 203-224.

Berggren W.A., Kent D.V., Swisher III C.C. & Aubry M.-P. (1995). A revised Cenozoic geochronology and chronostratigraphy. *In* Berggren W.A., Kent D.V., Swisher III C.C., Aubry M.-P. & Hardenbol J. (eds), Geochronology, Time Scales and Global Stratigraphic Correlation. *SEPM Special Publication*, 54: 129-212.

Bianucci G. (1997). The Odontoceti (Mammalia Cetacea) from Italian Pliocene. The Ziphiidae. *Palaeontographia Italica*, 84: 163-192.

Bianucci G. & Collareta A. (2022). An overview of the fossil record of cetaceans from the East Pisco Basin (Peru). *Bollettino della Società Paleontologica Italiana*, 61: 19-60.

Bianucci G. & Landini W. (2002). Change in diversity, ecological significance and biogeographical relationships of the Mediterranean Miocene toothed whale fauna. *Geobios*, 35: 19-28.

Bianucci G., Lambert O. & Post K. (2007). A high diversity in fossil beaked whales (Odontoceti, Ziphiidae) recovered by trawling from the sea floor off South Africa. *Geodiversitas*, 29: 5-62.

Bianucci G., Post K. & Lambert O. (2008). Beaked whale mysteries revealed by sea floor fossils trawled off South Africa. *South African Journal of Science*, 104: 140-142.

Bianucci G., Lambert O. & Post K. (2010). High concentration of long-snouted beaked whales (genus *Messapicetus*) from the Miocene of Peru. *Palaeontology*, 53: 1077-1098.

Bianucci G., Miján I., Lambert O., Post K. & Mateus O. (2013). Bizarre fossil beaked whales (Odontoceti, Ziphiidae) fished from the Atlantic Ocean floor off the Iberian Peninsula. *Geodiversitas*, 35: 105-153.

Bianucci G., Collareta A., Post K., Varola A. & Lambert O. (2016a). A new record of *Messapicetus* from the Pietra leccese (Late Miocene, Southern Italy): antitropical distribution in a fossil beaked whale (Cetacea, Ziphiidae). *Rivista Italiana di Paleontologia e Stratigrafia*, 122: 163-174.

Bianucci G., Di Celma C., Urbina M. & Lambert O. (2016b). New beaked whales from the late Miocene of Peru and evidence for convergent evolution in stem and crown Ziphiidae (Cetacea, Odontoceti). *PeerJ*, 4: e2479.

Bianucci G., Llàcer S., Cardona J.Q., Collareta A. & Florit A.R. (2019). A new beaked whale record from the Upper Miocene of Menorca, Balearic Islands, based on CT-scan analysis of limestone slabs. *Acta Palaeontologica Polonica*, 64: 291-302.

Bianucci G., Sielfeld W., Olguin N.A. & Guzmán G. (2023). A new diminutive fossil ziphiid from the deep-sea floor off northern Chile and some remarks on the body size evolution and palaeobiogeography of the beaked whales. *Acta Palaeontologica Polonica*, 68: 477-491.

Blainville H. de (1817). *In* Desmarest A.G. (ed.), Nouveau dictionnaire d'histoire naturelle. Tome 9. 151 pp. Deterville, Paris.

Bosio G. (2023). A Pompeii-like preservation for *Dosinia ponderosa* (Gray, 1838): two volcanic ash casts from the East Pisco Basin (Miocene, Peru). *Bollettino della Società Paleontologica Italiana*, 62: 219-229.

Bosio G., Gioncada A., Malinverno E., Di Celma C., Villa I.M., Cataldi G., Gariboldi K., Collareta A., Urbina M. & Bianucci G. (2019). Chemical and petrographic fingerprinting of volcanic ashes as a tool for high-resolution stratigraphy of the upper Miocene Pisco Formation (Peru). *Journal of the Geological Society*, 176: 13-28.

Bosio G., Gioncada A., Di Celma C., Villa I.M., Pichavant M., Urbina M. & Bianucci G. (2020a). Two-mica rhyolitic tephra in the East Pisco Basin (Peru): new age and dispersion constraints for the eruptions of the Eastern Cordillera of Central Andes. *Bulletin of Volcanology*, 82, 1-22.

Bosio G., Malinverno E., Collareta A., Di Celma C., Gioncada A., Parente M., Berra F., Marx F.G., Vertino A., Urbina M. & Bianucci G. (2020b). Strontium Isotope Stratigraphy and the thermophilic fossil fauna from the middle Miocene of the East Pisco Basin (Peru). *Journal of South American Earth Sciences*, 97: 102399.

Bosio G., Malinverno E., Villa I.M., Di Celma C., Gariboldi K., Gioncada A., Barberini B., Urbina M. & Bianucci G. (2020c). Tephrochronology and chronostratigraphy of the Miocene Chilcatay and Pisco formations (East Pisco Basin, Peru). *Newsletters on Stratigraphy*, 53: 213-247.

Bosio G., Collareta A., Di Celma C., Lambert O., Marx F.G., Muizon C. de, Gioncada A., Gariboldi K., Malinverno E., Varas-Malca R., Urbina M. & Bianucci G. (2021). Taphonomy of marine vertebrates of the Pisco Formation (Miocene, Peru): Insights into the origin of an outstanding Fossil-Lagerstätte. *PLoS ONE*, 16: e0254395.

Brisson A.D. (1762). Regnum Animale in Classes IX. Distributum, sive synopsis methodica. Edito altera auctior. 296 pp. Theodorum Haak, Leiden.

Buono M.R. & Cozzuol M.A. (2013). A new beaked whale (Cetacea, Odontoceti) from the Late Miocene of Patagonia, Argentina. *Journal of Vertebrate Paleontology*, 33: 986-997.

Burckle L.H. (1972). Late Cenozoic planktonic diatom zones from the eastern Equatorial Pacific. *In* Simonsen R. (ed.), First Symposium on Recent and Fossil Marine Diatoms. *Beihefte zur Nova Hedwigia*, 39: 217-246.

Cantino P.D. & de Queiroz K. (2020). International Code of Phylogenetic Nomenclature (PhyloCode). Version 6. International Society for Phylogenetic Nomenclature. Available online: http://phylonames.org (accessed 20.03.2024).

Carroll E.L., McGowen M.R., McCarthy M.L., Marx F.G., Aguilar N., Dalebout M.L., Dreyer A., Gaggiotti O.E., Hansen S.S., van Helden A., Onoufriou A.B., Baird R.W., Baker C.S., Berrow S., Cholewiak D., Claridge D., Constantine R., Davison N.J., Eira C., Fordyce R.E., Gatesy J., Hofmeyr G.J.G., Martín V., Mead J.G., Mignucci-Giannoni A.A., Morin P.A., Reyes C., Rogan E., Rosso M., Silva M.A., Springer M.S., Steel D. & Olsen M.T. (2021). Speciation in the deep: genomics and morphology reveal a new species of beaked whale *Mesoplodon eueu*. *Proceedings of the Royal Society B: Biological Sciences*, 288: 20211213.

Censarek B. & Gersonde R. (2002). Miocene diatom biostratigraphy at ODP Sites 689, 690, 1088, 1092 (Atlantic sector of Southern Ocean). *Marine Micropaleontology*, 45: 309-356.

Collareta A., Di Celma C., Bosio G., Pierantoni P.P., Malinverno E., Lambert O., Marx F.G., Landini W., Urbina M. & Bianucci G. (2021a). Distribution and paleoenvironmental framework of middle Miocene marine vertebrates along the western side of the lower Ica Valley (East Pisco Basin, Peru). *Journal of Maps*, 17: 7-17.

Collareta A., Lambert O., Marx F.G., Muizon C. de, Varas-Malca R., Landini W., Bosio G., Malinverno E., Gariboldi K., Gioncada A., Urbina M. & Bianucci G. (2021b). Vertebrate Palaeoecology of the Pisco Formation (Miocene, Peru): Glimpses into the Ancient Humboldt Current Ecosystem. *Journal of Marine Science and Engineering*, 9: 1188.

Collareta A., Marx F.G., Casati S., Di Cencio A., Merella M. & Bianucci G. (2021c). A cetotheriid whale from the upper Miocene of the Mediterranean. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 301: 9-16.

Cuvier G.L.C.F.D. (1823). Recherches sur les ossements fossiles. Tome 5 (1$^{\text{ère}}$ partie). 405 pp. G. Dufour & E. d'Ocagne Libraires, Paris.

Dalebout M.L., Steel D. & Baker C.S. (2008). Phylogeny of the beaked whale genus *Mesoplodon* (Ziphiidae: Cetacea) revealed by nuclear introns: implications for the evolution of male tusks. *Systematic Biology,* 57: 857-875.

DeVries T.J. (1998). Oligocene deposition and Cenozoic sequence boundaries in the Pisco Basin (Peru). *Journal of South American Earth Sciences*, 11: 217-231.

DeVries T.J. (2017). Eocene stratigraphy and depositional history near Puerto Caballas (East Pisco Basin, Peru). *Boletín de la Sociedad Geológica del Perú*, 112: 39-52.

DeVries T.J. (2020). Lithostratigraphy and biostratigraphy of Pliocene and Pleistocene marine deposits and age of the highest marine terrace from the Sacaco basin and its environs (southern Peru). *Boletín de la Sociedad Geológica del Perú*, 114: 20-48.

DeVries T.J. & Jud N. (2018). Lithofacies patterns and paleogeography of the Miocene Chilcatay and lower Pisco depositional sequences (East Pisco basin, Peru). *Boletín de la Sociedad Geológica del Perú*, Volumen Jubilar 8: 124-167.

DeVries T.J., Barron J.A., Urbina M., Ochoa D., Esperante R. & Snee L.W. (2021). The Miocene stratigraphy of the Laberinto area (Río Ica Valley) and its bearing on the geological history of the East Pisco Basin (south-central Peru). *Journal of South American Earth Sciences*, 111: 103458.

Di Celma C., Malinverno E., Cantalamessa G., Gioncada A., Bosio G., Villa I.M., Gariboldi K., Rustichelli A., Pierantoni P.P., Landini W., Tinelli C., Collareta A. & Bianucci G. (2016a). Stratigraphic framework of the late Miocene Pisco Formation at Cerro Los Quesos (Ica Desert, Peru). *Journal of Maps*, 12: 1020-1028.

Di Celma C., Malinverno E., Gariboldi K., Gioncada A., Rustichelli A., Pierantoni P.P., Landini W., Bosio G., Tinelli C. & Bianucci G. (2016b). Stratigraphic framework of the late Miocene to Pliocene Pisco Formation at Cerro Colorado (Ica Desert, Peru). *Journal of Maps*, 12: 515-557.

Di Celma C., Malinverno E., Bosio G., Collareta A., Gariboldi K., Gioncada A., Molli G., Basso D., Varas-Malca R., Pierantoni P.P., Villa I., Lambert O., Landini W., Sarti G., Cantalamessa G., Urbina M. & Bianucci G. (2017). Sequence stratigraphy and paleontology of the upper Miocene Pisco Formation along the western side of the lower Ica valley (Ica Desert, Peru). *Rivista Italiana di Paleontologia e Stratigrafia*, 123: 255-274.

Di Celma C., Malinverno E., Bosio G., Gariboldi K., Collareta A., Gioncada A., Landini W., Pierantoni P.P. & Bianucci G. (2018). Intraformational unconformities as a record of late Miocene eustatic falls of sea level in the Pisco Formation (southern Peru). *Journal of Maps*, 14: 607-619.

Di Celma C., Pierantoni P.P., Volatili T., Molli G., Mazzoli S., Sarti G., Ciattoni S., Bosio G., Malinverno E., Collareta A., Gariboldi K., Gioncada A., Jablonska D., Landini W., Urbina M. & Bianucci G. (2022). Towards deciphering the Cenozoic evolution of the East Pisco Basin (southern Peru). *Journal of Maps*, 18: 1-16.

Dunbar R.B., Marty R.C. & Baker P.A. (1990). Cenozoic marine sedimentation in the Sechura and Pisco basins, Peru. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 77: 235-261.

Duvernoy G. (1851). Mémoire sur les caractères ostéologiques des genres nouveaux ou des espèces nouvelles de cétacés vivants ou fossiles. *Annales des Sciences Naturelles, Paris, Série 3, Zoologie*, 15: 52-68.

Ehret D.J., Hubbell G. & MacFadden B.J. (2009). Exceptional preservation of the white shark *Carcharodon* (Lamniformes, Lamnidae) from the early Pliocene of Peru. *Journal of Vertebrate Paleontology*, 29: 1-13.

Ehret D.J., MacFadden B.J., Jones D.S., DeVries T.J.., Foster D.A. & Salas-Gismondi R. (2012). Origin of the white shark *Carcharodon* (Lamniformes: Lamnidae) based on recalibration of the upper Neogene Pisco Formation of Peru. *Palaeontology*, 55: 1139-1153.

Esperante R. & Poma O. (2015). Taphonomy and palaeopathology of two mysticete whales, upper Miocene Pisco Formation, Peru. *Spanish Journal of Palaeontology*, 30: 1-14.

Flower W.H. (1867). Description of the skeleton of *Inia geoffrensis* and of the skull of *Pontoporia blainvillii*, with remarks on the systematic position of these animals in the order Cetacea. *Transactions of the Zoological Society of London*, 6: 87-116.

Fuller A.J. & Godfrey S.J. (2007). A late Miocene ziphiid (*Messapicetus* sp.: Odontoceti: Cetacea) from the St. Marys Formation of Calvert Cliffs, Maryland. *Journal of Vertebrate Paleontology*, 27: 535-540.

Gariboldi K., Bosio G., Malinverno E., Gioncada A., Di Celma C., Villa I.M., Urbina M. & Bianucci G. (2017). Biostratigraphy, geochronology and sedimentation rates of the upper Miocene Pisco Formation at two important marine vertebrate fossil-bearing sites of southern Peru. *Newsletters on Stratigraphy*, 50: 417-444.

Godfrey S. & Lambert O. (2023). Miocene toothed whales (Odontoceti) from Calvert Cliffs, Atlantic Coastal Plain, USA. *In* Godfrey S.J. (ed.), The Geology and Vertebrate Paleontology of Calvert Cliffs, Maryland, USA – Volume 2. Turtles and Toothed Whales. *Smithsonian Contributions to Paleobiology*, 107: 49-186.

Gol'din P.E. & Vishnyakova K.A. (2013). *Africanacetus* from the sub-Antarctic region: the southernmost record of fossil beaked whales. *Acta Palaeontologica Polonica*, 58: 445-452.

Goloboff P.A. (1993). Estimating character weights during tree search. *Cladistics*, 9: 83-91.

Gradstein F.M., Ogg J.G., Schmitz M.D. & Ogg G.M. (eds) (2020). Geologic time scale 2020. 1357 pp. Elsevier, Amsterdam.

Gray J.E. (1846). On the British Cetacea. *Annals and Magazine of Natural History, Series 1*, 17: 82-85.

Gray J.E. (1850). Catalogue of the specimens of Mammalia in the collections of the British Museum. Part I. Cetacea. 153 pp. Richard & John E. Taylor, London.

Heyning J.E. (1989). Comparative facial anatomy of beaked whales (Ziphiidae) and a systematic revision among the families of extant Odontoceti. *Contributions in Science, Natural History Museum of Los Angeles County*, 405: 1-64.

Ichishima H., Augustin A.H., Toyofuku T. & Kitazato H. (2017). A new species of *Africanacetus* (Odontoceti: Ziphiidae) found on the deep ocean floor off the coast of Brazil. *Deep Sea Research Part II: Topical Studies in Oceanography*, 146: 68-81.

Kawatani A. & Kohno N. (2021). The oldest fossil record of the extant genus *Berardius* (Odontoceti, Ziphiidae) from the Middle to Late Miocene boundary of the western North Pacific. *Royal Society Open Science*, 8: 201152.

Koizumi I. (1972). Marine diatom flora of the Pliocene Tatsunokuchi Formation in Fukushima Prefecture. *Transaction and Proceedings of the Paleontological Society of Japan, New Series*, 86: 340-359.

Lambert O. (2005). Systematics and phylogeny of the fossil beaked whales *Ziphirostrum* du Bus, 1868 and *Choneziphius* Duvernoy, 1851 (Cetacea, Odontoceti), from the Neogene of Antwerp (North of Belgium). *Geodiversitas*, 27: 443-497.

Lambert O. & Louwye S. (2006). *Archaeoziphius microglenoideus*, a new primitive beaked whale (Mammalia, Cetacea, Odontoceti) from the Middle Miocene of Belgium. *Journal of Vertebrate Paleontology*, 26: 182-191.

Lambert O. & Louwye S. (2016). A new early Pliocene species of *Mesoplodon*: a calibration mark for the radiation of this species-rich beaked whale genus. *Journal of Vertebrate Paleontology*, 36: e1055754.

Lambert O. & Muizon C. de (2013). A new long-snouted species of the Miocene pontoporiid dolphin *Brachydelphis* and a review of the Mio-Pliocene marine mammal levels in the Sacaco Basin, Peru. *Journal of Vertebrate Paleontology*, 33: 709-721.

Lambert O., Bianucci G. & Post K. (2009). A new beaked whale (Odontoceti, Ziphiidae) from the middle Miocene of Peru. *Journal of Vertebrate Paleontology*, 29: 911-922.

Lambert O., Bianucci G. & Post K. (2010). Tusk-bearing beaked whales from the Miocene of Peru: sexual dimorphism in fossil ziphiids? *Journal of Mammalogy*, 91: 19-26.

Lambert O., Buffrénil V. de & Muizon C. de (2011). Rostral densification in beaked whales: diverse processes for a similar pattern. *Comptes Rendus Palevol*, 10: 453-468.

Lambert O., Muizon C. de & Bianucci G. (2013). The most basal beaked whale *Ninoziphius platyrostris* Muizon, 1983: Clues on the evolutionary history of the family Ziphiidae (Cetacea: Odontoceti). *Zoological Journal of the Linnean Society*, 167: 569-598.

Lambert O., Collareta A., Landini W., Post K., Ramassamy B., Di Celma C., Urbina M. & Bianucci G. (2015). No deep diving: Evidence of predation on epipelagic fish for a stem beaked whale from the late Miocene of Peru. *Proceedings of the Royal Society B: Biological Sciences*, 282: 20151530.

Lambert O., Muizon C. de, Duhamel G. & van der Plicht J. (2018). Neogene and Quaternary fossil remains of beaked whales (Cetacea, Odontoceti, Ziphiidae) from deep-sea deposits off Crozet and Kerguelen islands, Southern Ocean. *Geodiversitas*, 40: 135-160.

Lambert O., Bosselaers M. & Louwye S. (2023). Past beaked whale diversity in the North Sea: reappraisal through a new Miocene record and biostratigraphic analyses. *Geologica Belgica*, 26: 117-126.

Lazarus D., Barron J., Renaudie J., Diver P. & Türke A. (2014). Cenozoic planktonic marine diatom diversity and correlation to climate change. *PLoS ONE*, 9: e84857.

Leidy J. (1877). Description of vertebrate remains, chiefly from the Phosphate Beds of South Carolina. *Journal of the Academy of Natural Sciences of Philadelphia*, 8: 209-261.

Macharé J. & Ortlieb L. (1992). Plio-Quaternary vertical motions and the subduction of the Nazca Ridge, central coast of Peru. *Tectonophysics*, 205: 97-108.

MacLeod C.D. (2018a). Beaked whales, overview. *In* Würsig B.G., Thewissen J.G.M. & Kovacs K.M. (eds), Encyclopedia of Marine Mammals, 3rd Edition. Academic Press: 80-83.

MacLeod C.D. (2018b). *Berardius* beaked whales: *Berardius bairdii* and *B. arnuxii*. *In* Würsig B.G., Thewissen J.G.M. & Kovacs K.M. (eds), Encyclopedia of marine mammals, 3rd Edition. Academic Press: 97-99.

MacLeod C.D. & Herman J.S. (2004). Development of tusks and associated structures in *Mesoplodon bidens* (Cetacea, Mammalia). *Mammalia*, 68: 175-184.

MacLeod C.D., Santos M.B. & Pierce G.J. (2003). A review of data on diets of beaked whales: Evidence of niche separation and geographic segregation between three genera. *Journal of the Marine Biological Association of the United Kingdom*, 83: 651-655.

MacLeod C.D., Perrin W.F., Pitman R., Barlow J., Ballance L., D'Amico A., Gerrodette T., Joyce G., Mullin K.D., Palka D.L. & Waring G.T. (2006). Known and inferred distributions of beaked whale species (Cetacea: Ziphiidae). *Journal of Cetacean Research and Management*, 7: 271-286.

Malinverno E., Bosio G., Di Celma C., Gariboldi K., Gioncada A., Pierantoni P.P., Collareta A., Molli G., Bagnoli G., Sarti G., Urbina M. & Bianucci G. (2021). (Bio)stratigraphic overview and paleoclimatic-paleoceanographic implications of the middle-upper Eocene deposits from the Ica River Valley (East Pisco Basin, Peru). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 578: 110567.

Malinverno E., Bosio G., Gioncada A., Cimò R., Andò S., Mariani L., Coletti G., Boschi C., Gariboldi K., Galimberti L., Bianucci G., Urbina M. & Di Celma C. (2022). Laterally-continuous dolomite layers of the Miocene Pisco Formation (East Pisco Basin, Peru): a window into past cyclical changes of the diagenetic environment. *Marine and Petroleum Geology*, 147: 105977.

Marocco R. & Muizon C. de (1988). Le Bassin Pisco, bassin cénozoïque d'avant arc de la côte du Pérou central: Analyse géodynamique de son remplissage. *Géodynamique*, 3: 3-19.

Marx F.G., Lambert O. & Uhen M.D. (2016). Cetacean Paleobiology. 319 pp. John Wiley & Sons, Chichester.

McGowen M.R., Tsagkogeorga G., Álvarez-Carretero S., dos Reis M., Struebig M., Deaville R., Jepson P.D., Jarman S., Polanowski A. & Morin P.A. (2020). Phylogenomic resolution of the cetacean tree of life using target sequence capture. *Systematic Biology*, 69: 479-501.

Mead, J.G. (1975). A fossil beaked whale (Cetacea: Ziphiidae) from the Miocene of Kenya. *Journal of Paleontology*, 745-751.

Mead J.G. & Fordyce R.E. (2009). The therian skull: a lexicon with emphasis on the odontocetes. *Smithsonian Contributions to Zoology*, 627: 1-261.

Miján I., Louwye S. & Lambert O. (2017). A new *Beneziphius* beaked whale from the ocean floor off Galicia, Spain and biostratigraphic reassessment of the type species. *Acta Palaeontologica Polonica*, 62: 211-220.

Muizon C. de (1983). Un Ziphiidae (Cetacea) nouveau du Pliocène inférieur du Pérou. *Comptes rendus de l'Académie des Sciences de Paris,* 297: 85-88.

Muizon C. de (1984). Les vertébrés de la Formation Pisco (Pérou). Deuxième partie: Les Odontocètes (Cetacea, Mammalia) du Pliocène inférieur du Sud-Sacaco. *Travaux de l'Institut Français d'Etudes Andine*s, 27: 1-188.

Muizon C. de (1988). Les vertébrés de la Formation Pisco (Pérou). Troisième partie: Les Odontocètes (Cetacea, Mammalia) du Miocène. *Travaux de l'Institut Français d'Etudes Andines*, 42: 1-244.

Muizon C. de & Bellon H. (1986). Nouvelles données sur l'âge de la Formation Pisco (Pérou). *Comptes rendus de l'Académie des sciences, Séries 2*, 303: 1401-1404.

Muizon C. de & DeVries T.J. (1985). Geology and paleontology of late Cenozoic marine deposits in the Sacaco area (Peru). *Geologische Rundschau*, 74: 547-563.

Ochoa D., Salas-Gismondi R., DeVries T.J., Baby P., Muizon C. de, Altamirano A., Barbosa-Espitia A., Foster D.A., Quispe K., Cardich J., Gutiérrez D., Perez A., Valqui J., Urbina M. & Carré M. (2021). Late Neogene evolution of the Peruvian margin and its ecosystems: A synthesis from the Sacaco record. *International Journal of Earth Sciences*, 110: 995-1025.

Ochoa D., DeVries T.J., Quispe K., Barbosa-Espitia A., Salas-Gismondi R., Foster D.A., Gonzales R., Revillon S., Berrospi R., Pairazamán L., Cardich J., Perez A., Romero P-, Urbina M. & Carré M. (2022). Age and provenance of the Mio-Pleistocene sediments from the Sacaco area, Peruvian continental margin. *Journal of South American Earth Sciences*, 116: 103799.

Oliver W.R.B. (1937). *Tasmacetus shepherdi*: a new genus and species of beaked whale from New Zealand. *Proceedings of the Zoological Society of London, Series B*, 3: 371-381.

Ostenfeld C.H. (1900). Plankton. *In* Knudsen M. & Ostenfeld C. (eds), Iagttagelser over Overfladevandets Temperature, Saltholdighed og Plankton paa islandke og gronlandske Skibsrouter i 1899. Kjobenhavn: 45-93.

Post K. & Jensen J.K. (2013). On diamonds, a mammal fossil from the Faroe Islands, and the northernmost occurrence of fossil beaked whales. *Cranium*, 30: 19-21.

Ramassamy B. (2016). Description of a new long-snouted beaked whale from the Late Miocene of Denmark: evolution of suction feeding and sexual dimorphism in the Ziphiidae (Cetacea: Odontoceti). *Zoological Journal of the Linnean Society*, 178: 381-409.

Ramassamy B., Lambert O., Collareta A., Urbina M. & Bianucci G. (2018). Description of the skeleton of the fossil beaked whale *Messapicetus gregarius*: searching potential proxies for deepdiving abilities. *Fossil Record*, 21: 11-32.

Reyes J.C. & Van Waerebeek K. (2018). The lesser beaked whale *Mesoplodon peruvianus* Reyes, Mead and Van Waerebeek, 1991 revisited, with biological observations on new specimens from Peru. *Journal of Marine Biology and Oceanography*, 7: 1-10.

Reyes J.C., Mead J.G., & Van Waerebeek K. (1991). A new species of beaked whale *Mesoplodon peruvianus* sp. n. (Cetacea Ziphiidae) from Peru. *Marine Mammal Science*, 7: 1-24.

Ross G.J.B. (1984). The smaller cetaceans of the south east coast of southern Africa. *Annals of the Cape Provincial Museums: Natural History*, 15: 173-410.