



## Research

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# No deep diving: evidence of predation on epipelagic fish for a stem beaked whale from the Late Miocene of Peru

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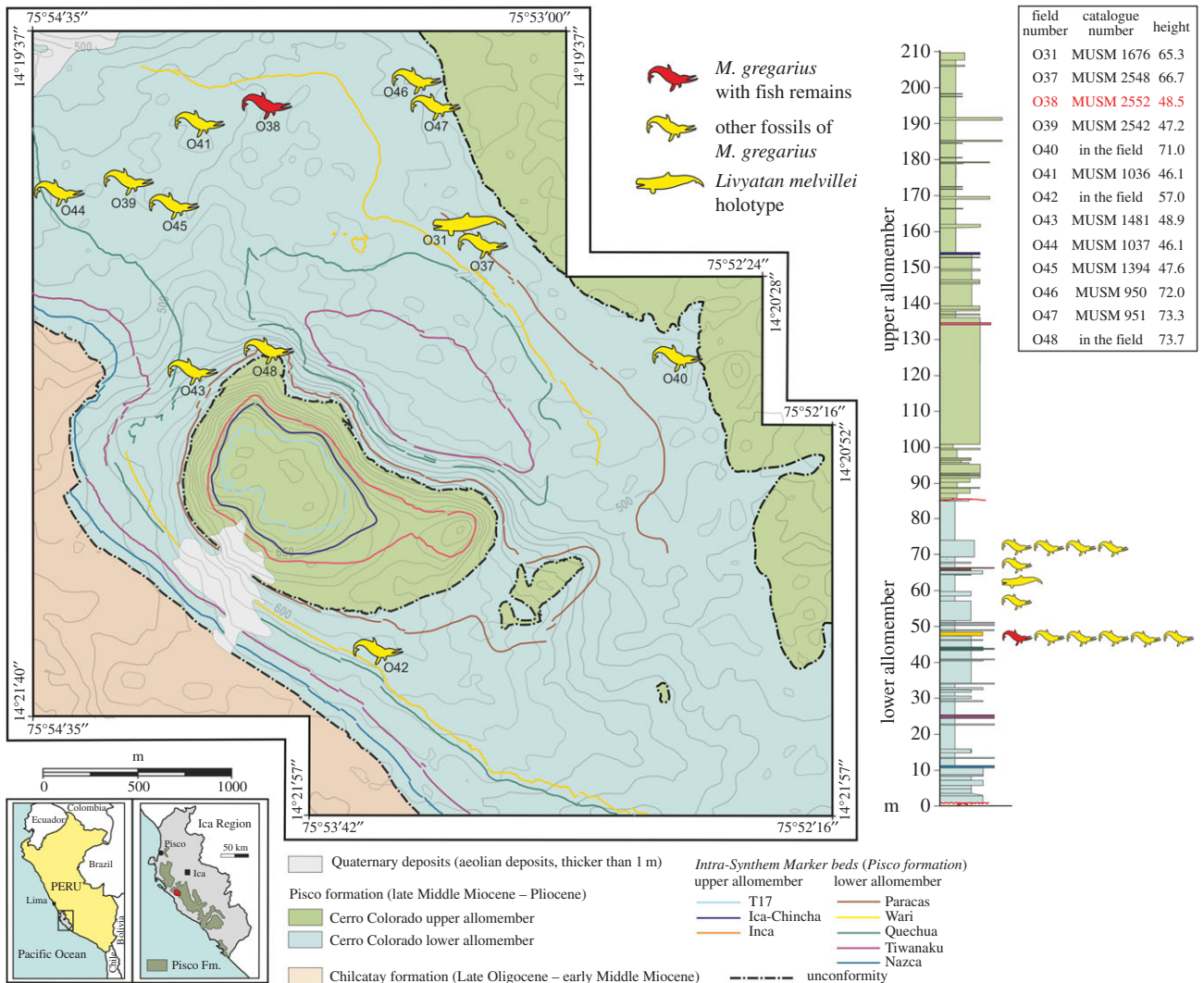
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Although modern beaked whales (Ziphiidae) are known to be highly specialized toothed whales that predominantly feed at great depths upon benthic and benthopelagic prey, only limited palaeontological data document this major ecological shift. We report on a ziphiid–fish assemblage from the Late Miocene of Peru that we interpret as the first direct evidence of a predator–prey relationship between a ziphiid and epipelagic fish. Preserved in a dolomite concretion, a skeleton of the stem ziphiid *Messapicetus gregarius* was discovered together with numerous skeletons of a clupeiform fish closely related to the epipelagic extant Pacific sardine (*Sardinops sagax*). Based on the position of fish individuals along the head and chest regions of the ziphiid, the lack of digestion marks on fish remains and the homogeneous size of individuals, we propose that this assemblage results from the death of the whale (possibly via toxin poisoning) shortly after the capture of prey from a single school. Together with morphological data and the frequent discovery of fossil crown ziphiids in deep-sea deposits, this exceptional record supports the hypothesis that only more derived ziphiids were regular deep divers and that the extinction of epipelagic forms may coincide with the radiation of true dolphins.

## 1. Introduction

One of the most mysterious groups of cetaceans, tusk-bearing beaked whales (Ziphiidae) are a successful family of highly specialized medium to large-size echolocating toothed whales (Odontoceti). Only paralleled by the sperm whale *Physeter*, the feeding ecology of the best-known modern ziphiids generally consists in long dives to great depths (from a few hundred to thousands of metres), where benthic to benthopelagic squid, fish and crustaceans are detected using the sonar and captured via suction [1–4]. Related morphological adaptations shared by most extant ziphiids include changes in the proportions of the vertebral column, decreased size of the flipper, enlarged sinuses on the ventral region of the skull and reduction of the dentition [1,5,6]. Considering that about one-quarter of the extant cetacean species are ziphiids, the prehistoric shift of members of the family to deep-water feeding areas constitutes a major, ecologically important, although poorly studied event in the evolutionary history of cetaceans. Only indirect evidence documents this transition from a hypothetical ancestral, epipelagic–neritic habitat to deeper benthopelagic oceanic regions. First, data on extant ziphiids (stomach contents, satellite recordings of dives, and geographical distribution in relation to sea floor topography; e.g. [2,4,7]) indicate that it is more parsimonious to characterize the last common



**Figure 1.** Map and corresponding composite stratigraphic section of the locality of Cerro Colorado, Pisco Basin, southern coast of Peru, showing the distribution of 12 skeletons of the extinct beaked whale *Messapicetus gregarius* in the outcropping Pisco Formation. Note the concentration of specimens (including specimen O38 associated with fish remains, coloured in red), in a few layers of the lower allomember. Adapted from [17].

ancestor of all modern ziphiids as adapted to deep dives. Second, most stem ziphiids were found in platform deposits, contrasting with the discovery of many fossil crown ziphiid remains in deep-sea deposits [6,8–11]. Finally, a few morphological characters provide clues about the feeding technique and habitat of extinct ziphiids [6].

Complementary to satellite recordings, stomach content analysis is a powerful tool to analyse the dietary preferences and feeding areas of extant marine mammals [2,12,13]. Unfortunately, fossilized gut contents of extinct cetaceans are extremely rarely found (e.g. [14]); apart from a notable record of ambergris tentatively related to a Pleistocene sperm whale [15], there is to our knowledge no other published record for fossil odontocetes. We report here on a ziphiid–fish assemblage from the Late Miocene of the Pisco Basin, Peru, which we interpret as direct evidence of a predator–prey relationship between a stem ziphiid and epipelagic–neritic fish.

## 2. Material and methods

### (a) Geological setting and associated fauna

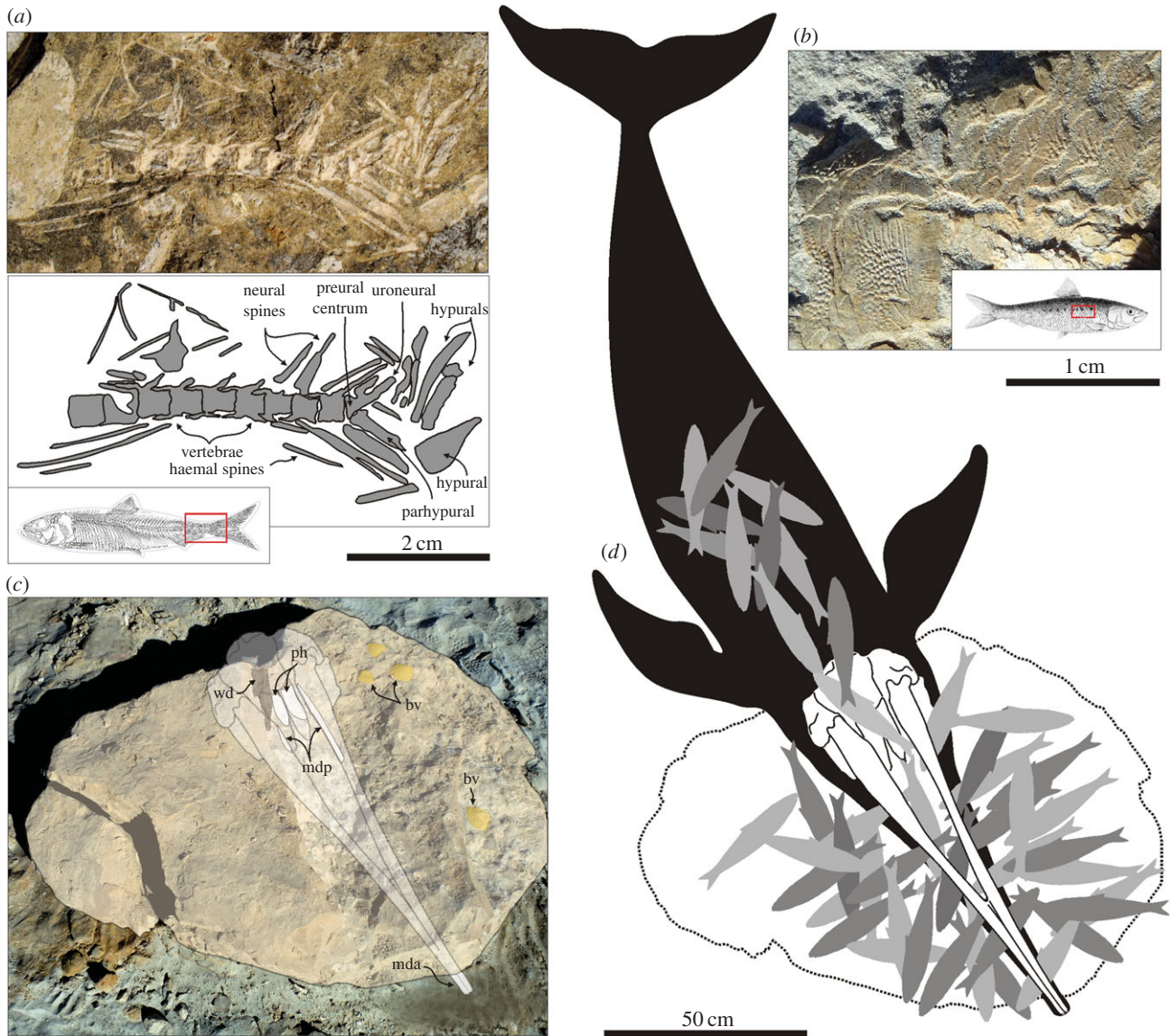
Sediments of the Pisco Formation exposed at Cerro Colorado make up a remarkably thick section spanning about 200 m of

its basal portion. This stratigraphic section, including near-shore conglomerates, fine-grained sandstones, diatomites and diatomaceous mudstones, a few dolomitic horizons, and volcanic ash layers, can be subdivided into two overall fining-upwards packages (allomembers) separated by an intraformational angular unconformity [16] (figure 1). The ziphiid skeleton with associated fish remains examined here originates in the lower allomember, where a large number of other fossil vertebrate remains were found, including sperm whales (e.g. the holotype of *Livyatan melvillei*), beaked whales, several delphinidans (Pontoporiidae and kentriodontid-like delphinidans), cetotheriid and balaenopteroid baleen whales, sea turtles, crocodiles, sea-birds, sharks and bony fish [9,17,18]. These fossiliferous deposits were first tentatively dated from the late Middle to early Late Miocene (Serravallian to early Tortonian, ca 13–11 Ma [9,18]). The recent record of *Lithodesmium reynoldsii*, a diatom species with a range between 9.9 and 8.9 Ma [19], points to a Late Miocene (Tortonian) age [16].

### (b) Palaeontological material

The specimens described here were found northwest to the main Cerro (geographical coordinates: 14°20'59.5" S, 75°53'00.5" W) during a 2014 geological and palaeontological campaign; they are indicated with the field number O38 in the fossil map published by Bianucci *et al.* [17]. The main specimen consists of a partly articulated medium size odontocete skeleton, with the





**Figure 2.** Fossil remains of the extinct beaked whale *Messapicetus gregarius* and associated clupeid fish *Sardinops* sp. cf. *S. sagax* found in Cerro Colorado. (a) Photograph and line drawing of the articulated caudal portion of a skeleton of *Sardinops* sp. in left lateral view (note the typically clupeid urostyle supporting the caudal fin complex), with a complete skeleton of the modern sardine *S. sagax* for comparison (adapted after [21]). (b) Imbricated large cycloid scales of *Sardinops* sp. in right lateral view showing tubercular protuberances in their central region and curved radii-like lines in their lateral fields, with a body of *S. sagax* for comparison reporting the putative collocation of the scale set. (c) Dolomite concretion with the skull and mandibles of *M. gregarius* in ventral view; occipital region, hamular processes of the pterygoids, posteroventral and apical regions of the mandibles emerge from the concretion. bv, articulated bivalve shells; mda, apex of mandibles; mdp, posteroventral part of mandibles; ph, hamular processes; wd, fragment of fossilized wood. (d) Line drawing of the skull of *M. gregarius* inside the concretion with a reconstructed outline of its body. Multiple individuals of *Sardinops* sp. found around the head and in the chest region are schematically represented. Stippled line marks the outline of the concretion.

skull upside down, *in situ* mandibles and several postcranial elements (vertebrae, ribs and ulna) emerging from a large (140 cm wide and more than 25 cm thick) dolomite concretion surrounded by softer diatomaceous sediment, a relatively common condition for the fossil vertebrate remains of Cerro Colorado [20]. The postcranial elements mentioned above were observed in section along the surface of the large block and in smaller detached blocks (<http://doi.org/10.5061/dryad.n27h3>, figure S4). Not protected in the hard concretion, the posterior part of the skeleton was probably lost due to erosion. Removal of fractured peripheral blocks of the concretion provided access to the back of the skull, the palate and the apex of the rostrum (figure 2; <http://doi.org/10.5061/dryad.n27h3>, figures S3 and S5). Numerous partially articulated fish skeletons were found in the exact same layer of the concretion as the odontocete skeleton, around the head and inside the chest region (figure 2a,b,d; <http://doi.org/10.5061/dryad.n27h3>, figures S1–S4). Cranial parts are generally still interconnected, although

the skull architecture appears in each case distorted and the bones are tightly packed. Many fully articulated sections of vertebral column are visible, and a few of them present an almost fully articulated urophore complex displaying a characteristic urostyle. Large, well-preserved cycloid scales are abundant, and many of them are still imbricated. No clear indications of corrosion and no unambiguous bite marks were observed on the exposed scales and other fish remains. A few centimetres above these remains, an accumulation of articulated bivalve shells was noted, following a plane parallel to the odontocete skeleton. Multiple observations, photos and measurements were taken in the field. Several fish specimens were collected, as well as the apex of the mandibles of the odontocete (MUSM 2552; <http://doi.org/10.5061/dryad.n27h3>, figure S5); those are now curated at the MUSM (Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima). Owing to the large size of the concretion block (approx. 1 m<sup>3</sup>), the extremely hard dolomitic matrix surrounding the odontocete skull

and the low degree of mineralization of the bones, part of the specimen could not be prepared for collection with mechanical tools, nor through acid etching. Furthermore, computed tomography (with both hospital CT and microCT) of fragments of the concretion did not yield usable data. Complete skulls of the same species available at the MUSM [9] were used for part of the interpretation and discussion.

### 3. Results

#### (a) Systematic attribution of the odontocete skeleton

Based on (i) the ventrally and anteriorly enlarged hamular processes of the pterygoids and (ii) the presence of apical tusks in the mandibles, this specimen is unambiguously attributed to the family Ziphiidae [6]. Available dimensions for the skull (width across occipital condyles 11.4 cm; maximum width of hamular processes in ventral view 10.5 cm; condylobasal length 107 cm) and for the mandible (maximum width of apex 3.4 cm; diameter of the alveolar tusk  $2.3 \times 1.2$  cm) fitted in the range of the species *Messapicetus gregarius* [9,22]. The general morphology of the outcropping elements perfectly matches the skull morphology in the latter, by far the most commonly found ziphiid in Cerro Colorado (more than 10 specimens, including several skull–mandible sets, among which five specimens originate from a stratigraphic interval 4 m thick, also containing the specimen described here [17]). Therefore, a referral of the studied specimen to a fully grown adult of *M. gregarius* is strongly supported. The maximum width of the apex of the mandible (at the level of the tusks) and the size of the alveolar tusks are lower than in specimens of *M. gregarius* tentatively identified as adult males [22]; this specimen may thus have been a female.

#### (b) Size and weight estimates for *Messapicetus gregarius*

Based on the published postorbital widths for *M. gregarius*, ranging from 31.5 to 35.2 cm [9], and using a regression established in a previous study [23], we estimate the body length of adults of this species between 4.1 and 4.5 m (see the supplementary material). An estimated body weight of 1842 kg is calculated for this specimen when placing the width of the occipital condyles in the regression equation proposed by Pyenson & Lindberg [24], a weight possibly considerably overestimated considering that extant species of *Mesoplodon* with a similar size do not exceed 1540 kg [25].

#### (c) Systematic attribution of the bony fish remains

Based on (i) the overall outline of the cycloid scales (some of them approaching a width of 2 cm) and (ii) the presence of a characteristic urostyle supporting the caudal fin, the fish remains can be attributed to a clupeiform taxon [26]. The morphology of the skull bones (preopercle, opercle, maxilla, dentary and articular) and of the elements of the caudal skeleton (urostyle, hypurapophysis and hypural plates) is fully compatible with the extant monospecific clupeid genus *Sardinops* (Pacific sardine). In particular, we observed a partial opercle with radiating bony striae affecting its ventral part, a diagnostic character of *Sardinops* according to various authors (e.g. [27]). Moreover, most large scales show protuberances in their central portion and curved lines (looking similar to radii) in the lateral fields as typically observed in

*Sardinops sagax* [26]. However, due to (i) the lack of complete and well-preserved elements showing unambiguously apomorphic characters and (ii) the unusually large dimensions of the bony and dermal remains, we prefer to refer the specimens to *Sardinops* sp. cf. *S. sagax*.

Based on the available elements, a count of 40–60 individuals is estimated, including about 20 partial vertebral columns. No other bony fish or invertebrate (e.g. Cephalopoda) taxon was detected among the *Sardinops* remains.

#### (d) Size and weight estimates for specimens of *Sardinops* sp. cf. *S. sagax*

We measured the vertebral length for 15 fully articulated and straight segments of vertebral column constituted by eight vertebrae or more; then the average vertebral length was calculated for each vertebral column segment. Using a series of equations relating the average vertebral length to standard length and total body length (see <http://doi.org/10.5061/dryad.n27h3>), we estimated the total body length for each specimen. The average total body length is 38.8 cm, with a standard deviation of 2.3 cm. Finally, the total body length allows the calculation of an estimated body weight (see <http://doi.org/10.5061/dryad.n27h3>). An average body weight of 410 g is obtained, with a standard deviation of 55 g for the analysed sample. Considering a total of 40–60 specimens, the total weight of fish found around the whale is estimated as 16.4–24.6 kg.

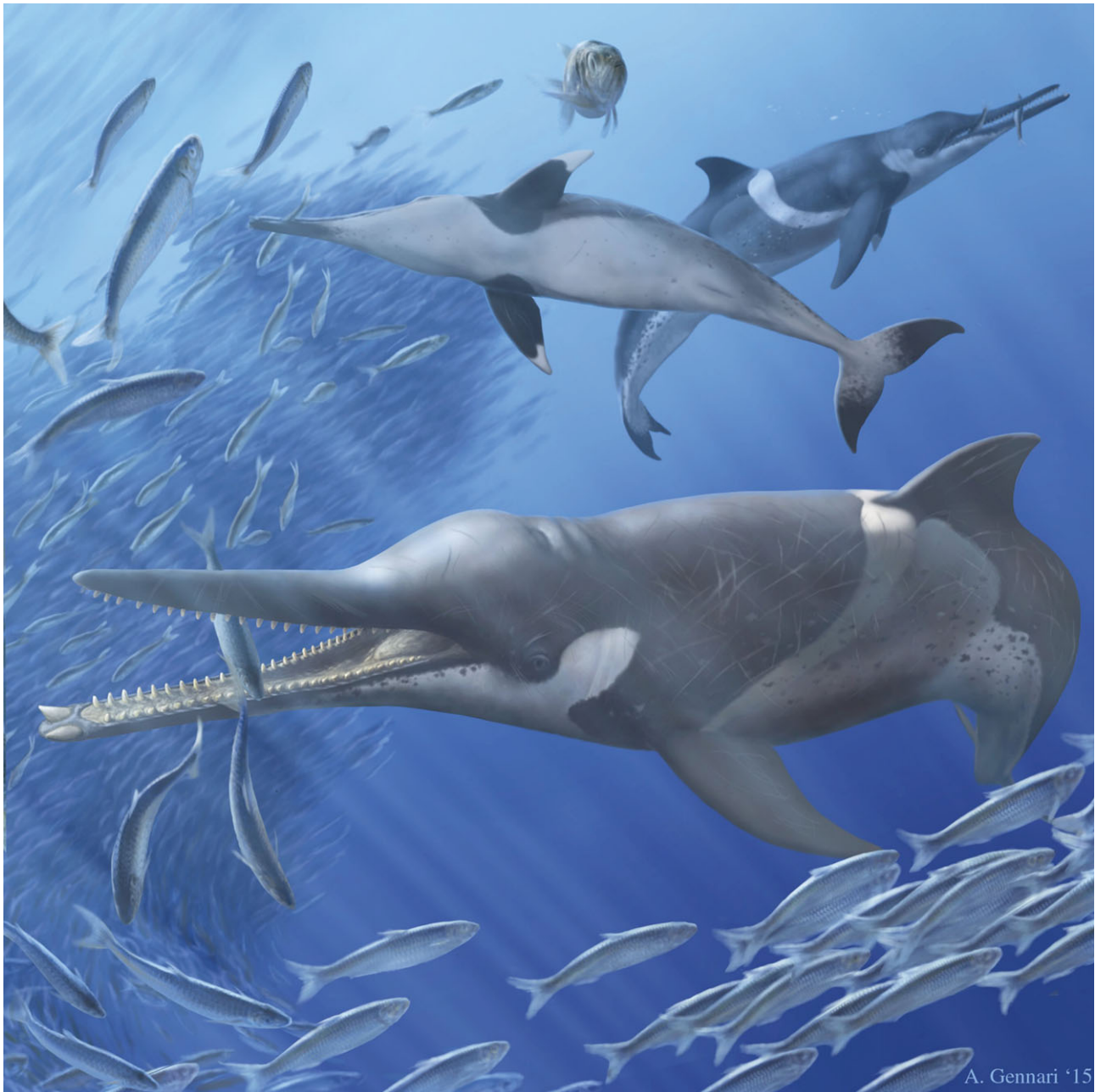
### 4. Discussion

#### (a) Interpretation of the *Messapicetus*–*Sardinops* association

Our favoured interpretation for this unique *Messapicetus*–*Sardinops* association is that it results from the predation of fish by the ziphiid. Several arguments are in support of this hypothesis and/or contradict alternative explanations such as the hypotheses (1) of a fortuitous preservation, in close proximity, of unrelated animals otherwise feeding in different environments and (2) of a high number of fish individuals dying after having scavenged on a whale carcass:

- (1) Fish and ziphiid skeletons are located in the exact same stratigraphic layer, and most specimens are at least partly articulated. This suggests that both the ziphiid and the series of fish died in the same interval of time, and were probably barely disturbed after deposition on the sea floor.
- (2) Fish skeletons are found around the head and in the chest region of the ziphiid. These are the most likely places for prey that would have been swallowed recently and, for some of them, possibly regurgitated (see below).
- (3) No other such concentration of articulated bony fish skeletons is observed elsewhere in the abundantly prospected and fossil-rich Cerro Colorado locality; only isolated scales attributed to *Sardinops* are frequently found [17]. This strengthens the idea that this unique ziphiid–fish association is not fortuitous. Furthermore, careful prospection at some distance around the concretion and in the same horizon did not yield any other bony fish element (which may have suggested the presence of a laterally extensive fossil fish bonebed in which a whale was more likely to be deposited and preserved).

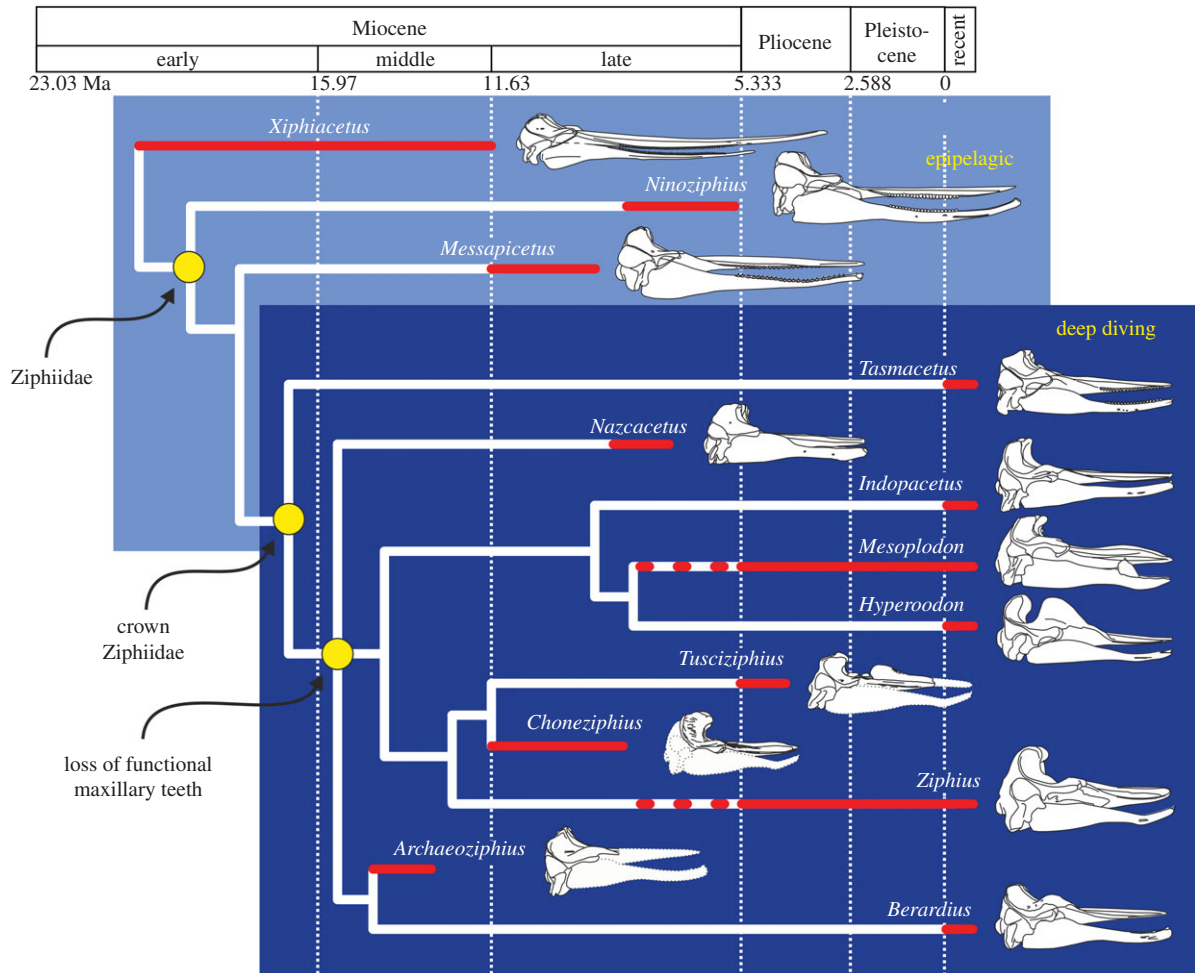




**Figure 3.** Life reconstruction of three individuals of the extinct beaked whale *Messapicetus gregarius* preying upon a school of aged sardines *Sardinops* sp. (average body length 38.8 cm) in the upper part of the water column along the coast of present-day Peru. The front individual is an adult male, whereas the last in the background is a female. Illustration by A. Gennari.

- (4) Extant *Sardinops sagax* predominantly feeds on planktonic crustaceans [27]. Scavenging on the ziphiid carcass and subsequent simultaneous death of a large number of specimens are therefore highly unlikely.
- (5) Extant piscivorous odontocetes with a body length similar to (or even smaller than) *M. gregarius* are capable of consuming fish with a size and weight matching the estimates for the Cerro Colorado *Sardinops* sample (e.g. the ziphiid *Mesoplodon bidens* and the delphinid *Tursiops truncatus* [2,28,29]).
- (6) The number of prey items (40–60) and the corresponding total biomass (no more than 25 kg) do not exceed the quantities obtained from stomach content analyses of similarly sized extant fish-eating odontocetes, and furthermore fall in the range of daily food requirements for medium to large odontocetes (about 2–4% of body mass [13,30–32]).

Interestingly, the body lengths of all the measured fish individuals occupy a narrow range (low standard deviation), close to the maximum body length for extant *Sardinops sagax* [27]. These observations suggest that the individuals found with the ziphiid originate from an age-homogeneous and aged group of prey likely to have been more than 10 years old. Since modern Pacific sardines tend to organize themselves in schools on the basis of their age class from the time they cease to be larvae [33], with aged individuals thought to form assemblages that are distinct from those of younger individuals [34,35], the ziphiid may have preyed upon a single school of relatively old fish (figure 3). The hypothesis of a single predation event is further supported by the observation that fish individuals are undigested or only partly digested, indicating that the whale died no more than a few hours after having caught its prey (see data on digestion rates and stomach clearance in piscivorous marine mammals in previous studies [12,36]).



**Figure 4.** Phylogenetic tree illustrating the relationships between extant and part of the extinct ziphiids, modified from [6]. The outgroup is the eurhinodelphinid *Xiphiacetus*. Grey (red in online version) lines indicate stratigraphic ranges. Dotted lines indicate uncertainty for the age of some members of a genus. Separation between epipelagic and deep-diving taxa is based on morphology, platform versus deep-sea deposits for fossil taxa, stomach content analysis for *Messapicetus*, and optimization of the deep-diving ecology of most extant genera on the phylogenetic tree. (Online version in colour.)

Because sick marine mammals are often found with an empty stomach [37], and considering that the whale was capable of capturing several tens of fish, it was probably a relatively healthy animal. How can we explain the death of an animal only a short time after a copious meal? No signs of predation or scavenging were noted on the few visible bones. Furthermore, a predator would have been expected to eat the fish remains surrounding the ziphiid's carcass. Although the unlikely hypothesis of an attack by a large predator (for example, the giant raptorial sperm whale *Livyatan melvillei* or the large sharks *Carcharocles megalodon* and *Cosmopolitodus hastalis*) cannot be completely excluded, it is tempting to propose that the death of the ziphiid resulted from the consumption of fish. Trophic transfer of algal toxins along the food web, from dinoflagellates to planktonic crustaceans, fish and ultimately marine mammals, is known to be occasionally responsible for the death of cetaceans [38,39]. Harmful algal blooms were even convincingly proposed as the cause of large accumulations of marine mammal and seabird carcasses in several Neogene marine deposits [40,41]. The stratigraphic column of the Pisco Formation in Cerro Colorado indeed includes several diatomite layers resulting from extensive algal bloom. Although we could not identify remains of toxic algae around the ziphiid remains and in the surrounding deposits, some neurotoxins are produced by dinoflagellates that do not build a mineralized skeleton (e.g. *Karenia concordia* [42]) and thus fossilize rarely. The proposed rapid death of

the ziphiid and the possible regurgitation of part of the prey items support the scenario of a toxin poisoning, a hypothesis that should be tested on a larger scale with the high number of fully articulated whale carcasses found in successive levels of the Pisco Formation in Cerro Colorado [17].

### (b) Broader palaeoecological outcome

The large number of specimens of *Messapicetus gregarius* found in Cerro Colorado strongly supports the hypothesis that this species was a regular occupant of this area, which shows a high diversity of marine vertebrates corresponding to upwelling-related high primary productivity and long trophic chains starting with phytoplankton (predominantly diatoms) [17,43]. Therefore, we propose that *M. gregarius* fed either in this shallow, coastal region or in a more open area a short distance away. If our hypothesis of a predator–prey relationship between *M. gregarius* and *Sardinops* sp. cf. *S. sagax* is correct, considering the neritic, epipelagic habitat of modern *Sardinops sagax* [27], our interpretation contrasts markedly with the consumption of benthic to benthopelagic prey by extant beaked whales. This single record of stomach contents nevertheless does not completely exclude the less likely possibility that such prey was not a predominant part of the diet for *M. gregarius*, and that members of this species did occasionally forage in deeper water.

*Messapicetus* being considered in recent phylogenies as a stem ziphiid [6,10], the epipelagic to neritic habitat of this Miocene taxon possibly represents the ancestral condition for ziphiids,

preceding the shift to a deep-water habitat (figure 4). Interestingly, the contrasted fossil records of stem ziphiids (predominantly in platform deposits) and crown ziphiids (many of them in deep-sea deposits) [6,8–11] indirectly support this hypothesis.

In addition to palaeoecological signals coming from stomach contents and phylogenetic analyses, morphology is revealing too. Together with the other best-known stem ziphiid *Ninoziphius*, *Messapicetus* is characterized by a set of morphological features pointing to an ecology less specialized in suction feeding and deep diving than in extant ziphiids: (i) a rostrum proportionally longer than in the vast majority of crown ziphiids; (ii) upper and lower jaws retaining a full set of functional teeth regularly displaying extensive subhorizontal apical wear, contrasting with nearly all extant ziphiids; (iii) a lower number (or the lack) of fused cervical vertebrae on a proportionally longer neck; and (iv) a proportionally longer humerus [6,44,45] (see <http://doi.org/10.5061/dryad.n27h3> for a comparison of proportions and degree of ankylosis of cervical vertebrae and proportions of the humerus between *Messapicetus* and other ziphiids). Most of these traits are shared with members of several Miocene odontocete clades recorded in platform to coastal deposits (e.g. Allodelphinidae, Eurhinodelphinidae and Pomatodelphininae).

The oldest record for a crown ziphiid is a small berardiine from the Middle Miocene (late Langhian to early Serravallian, 15–13.2 Ma) of the North Sea [6,46] (figure 4); although from platform deposits, this record provides a minimum date for the emergence of deep diving in ziphiids, still younger than some (but not all) molecular divergence date estimates provided from Crown Ziphiidae [47–49]. On the other hand, the locality of the youngest stem ziphiid (*Ninoziphius platyrostris*, Sud-Sacaco, Sacaco Basin, Peru; Muizon, 1984 [44]) was recently re-dated to the Late Miocene (possibly early Messinian [50]). The extinction of stem ziphiids may thus be roughly synchronous with the Late Miocene appearance and early diversification of modern delphinoid families, including delphinids for which divergence date

estimates fall within the Tortonian or—a less likely result considering the fossil record—the latest Messinian [47–49,51–53]. If, as proposed above, stem ziphiids were predominantly feeding on epipelagic prey, then they may have entered into competition with delphinids for the resources available there, unlike deep-sea crown ziphiids. Nowadays, a trophic position similar to the one proposed for *M. gregarius* in coastal waters off Peru is occupied by delphinids (*Lagenorhynchus obscurus*, *Tursiops truncatus*), feeding on *Sardinops sagax* and other neritic fish [29,54].

**Data accessibility.** Data available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.n27h3>.

**Authors' contributions.** All authors took part in the fieldwork and collected field data. O.L., G.B., K.P. and B.R. identified and interpreted the ziphiid remains. O.L. and G.B. made calculations for ziphiid size and weight estimates. B.R., G.B., O.L. and K.P. collected data on the postcranial skeleton of ziphiids. A.C. and W.L. identified fish remains, made calculations for fish size and weight estimates, and wrote the electronic supplementary material on fish. C.D. made the geological and stratigraphical prospection and located the fossil ziphiid along the section. O.L. wrote the paper. G.B. prepared the illustrations. All authors discussed the results and commented on the manuscript at all stages.

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