Piscivory in a Miocene Cetotheriidae of Peru: first record of fossilized stomach content for an extinct baleen-bearing whale

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Abstract

Instead of teeth, modern mysticetes bear hair-fringed keratinous baleen plates that permit various bulk-filtering predation techniques (from subsurface skimming to lateral benthic suction and engulfment) devoted to various target prey (from small invertebrates to schooling fish). Current knowledge about the feeding ecology of extant cetaceans is revealed by stomach content analyses and observations of behaviour. Unfortunately, no fossil stomach contents of ancient mysticetes have been described so far; the investigation of the diet of fossil baleen whales, including the Neogene family Cetotheriidae, remains thus largely speculative. We report on an aggregate of fossil fish remains found within a mysticete skeleton belonging to an undescribed late Miocene (Tortonian) cetotheriid from the Pisco Formation (Peru). Micro-computed tomography allowed us to interpret it as the fossilized content of the forestomach of the host whale and to identify the prey as belonging to the extant clupeiform genus *Sardinops*. Our discovery represents the first direct evidence of piscivory in an ancient edentulous mysticete. Since among modern mysticetes only Balaenopteridae are known to ordinarily consume fish, this fossil record may indicate that part of the cetotheriids experimented some degree of balaenopterid-like engulfment feeding. Moreover, this report corresponds to one of the geologically oldest records of *Sardinops* worldwide, occurring near the Tortonian peak of oceanic primary productivity and cooling phase. Therefore, our discovery evokes a link between the rise of Cetotheriidae, the set-up of modern coastal upwelling systems, and the radiation of epipelagic, small-sized, schooling clupeiform fish in such highly productive environments.

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1. Introduction

During their evolutionary history, ancestors of modern baleen whales (Cetacea: Mysticeti) progressively replaced their teeth with keratin structures known as baleen, thus abandoning a primitive raptorial feeding technique in favour of various bulk-filter feeding strategies (Deméré et al. 2008; Clementz et al. 2014; Marx and Fordyce 2015). Among extant mysticetes, Balaenidae (bowhead and right whales) and possibly Neobalaenidae (pygmy right whales) slowly skim for plankton near the sea surface, Eschrichtiidae (gray whales) forage via lateralized benthic suction for invertebrates on shallow seafloors, and Balaenopteridae (humpback whales and rorquals) engulf huge amounts of prey (both fish and krill) and water while swimming fast (a feeding performance widely considered for the blue whale to be the largest biomechanical event that ever existed on Earth) (Pivorunas 1977; 1979; Werth 2000; Croll and Tershy 2002; Berta et al. 2005; Goldbogen et al. 2007; 2011; Johnston and Berta 2011; Pyenson et al. 2012). In turn, although the feeding ecology and diet habits of members of different extinct mysticete families have been discussed based on similarities with other marine tetrapods and/or functional analyses (Fordyce and Barnes 1994; Bisconti and Varola 2000; 2006; Kimura 2002; Bouetel 2005; Bouetel and Muizon 2006; Fitzgerald 2006; 2010; 2012; Deméré and Berta 2008; El Adli et al. 2014; Gol'din et al. 2014; Tsai and Fordyce 2015), no direct evidence about prey has been reported to date.

As redefined by Bouetel and Muizon (2006), Cetotheriidae are a monophyletic group of cosmopolitan, toothless, relatively small-sized baleen-bearing mysticetes. The record of cetotheriids ranges from the middle Miocene to the early or Middle Pleistocene (Boessenecker 2013), although the extant pygmy right whale *Caperea marginata*, traditionally regarded as the only living member of the family Neobalaenidae, has been recently proposed to be a relict cetotheriid (Fordyce and Marx 2013; Marx and Fordyce 2015). From a phylogenetic point of view, cetotheriids generally fall within crown Mysticeti (but see e.g. Bouetel and Muizon (2006) and Deméré et al. (2008) for a more stemward position), either as sister-group to Eschrichtiidae (Steeman 2007; Bisconti 2008),

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sister-group to Eschrichtiidae + Balaenopteridae (Bisconti 2014; El Adli et al. 2014), or as mentioned above in a clade with Neobalaenidae (Fordyce and Marx 2013; Marx and Fordyce 2015). In spite of cetotheriids being an important part of the fossil vertebrate assemblages of many Neogene marine deposits worldwide, their diet(s) and feeding ecology(ies) have never been clearly understood. At the same time, it is widely recognized that such a knowledge would be pivotal in order to fully comprehend the structure and evolution of Neogene marine ecosystems.

Among modern methodologies for studying the diet of cetaceans, stomach content analysis is a powerful tool, which has greatly contributed to our current understanding of the extant marine trophic webs (Pierce and Boyle 1991). Stomach and gut contents are occasionally preserved in the palaeontological record, providing the strongest direct evidence of ancient predator-prey relationships, and greatly helping to reconstruct past trophic chains. With regard to marine tetrapods, fossil stomach contents have been widely reported amongst marine reptiles (e.g., Kear et al. 2003; O'Keefe et al. 2009; Druckenmiller et al. 2014). Unfortunately, preserved stomach contents of ancient marine mammals are overly rare; to date, those have been unambiguously recognized only in a few basilosaurid archaeocetes (Swift and Barnes 1996; Uhen 2004) and in a phocid pinniped (Cozzuol 2001). Bite marks on bones (Harington et al., 2004; Boessenecker and Perry, 2011; Fahlke 2012), fossil remains of ambergris (a byproduct of digestion of sperm whales) (Baldanza et al. 2013; Monaco et al. 2014), and putative gastroliths (Tavani 1973; Pandeli et al. 1998) have also been proposed as direct clues to the feeding activity of ancient marine mammals. Recently, Lambert et al. (2015) interpreted an unusual beaked whale-fish assemblage from the late Miocene of the Pisco Formation (southern Peru) as an evidence of predator-prey interaction. In the same locality of this latter record (Cerro Colorado), we have recently discovered an aggregate of fish remains associated with a baleen whale skeleton. Due to the fragility and peculiar architecture of this aggregate, we investigated it by non-destructive means of high resolution micro-computed tomography (micro-CT) scanning, which allowed us to interpret the fish remains as the fossilized

stomach content of the host mysticete. This finding - the first fossil record of stomach content for a baleen whale worldwide - depicts a predation event involving an undescribed Cetotheriidae and epipelagic fish belonging to the extant clupeiform genus *Sardinops*.

2. Material and Methods

(a) Stratigraphic and palaeoecological framework

The Pisco Formation (East Pisco Basin, southern Peru) is a middle Miocene-late Pliocene sedimentary unit known as one of the most impressive Cenozoic marine Fossil-Lagerstätten worldwide, due both to the diversity of fossil vertebrates and to their extraordinary quality of preservation (Esperante et al. 2015; Bianucci et al. in press). One of the most significant palaeontological sites of the Pisco Formation is Cerro Colorado, the type locality of the giant raptorial sperm whale *Livyatan melvillei* (Lambert et al. 2010). The succession exposed at Cerro Colorado consists of coastal conglomerates, fine-grained sandstones, diatomites and diatomaceous siltstones, a few dolomitic horizons, and volcanic ash layers (Di Celma et al. in press). An erosional discontinuity allows the subdivision of this stratigraphic section into two informal allomembers; most of the fossils of Cerro Colorado, including the ones here examined, are from the lower allomember (Fig. 1). Based on the presence of the diatom species *Lithodesmium reynoldsii*, whose range spans between 9.9 and 8.9 Ma (Barron 2003), the age of the lower allomember was recently constrained to the early late Miocene (Tortonian) (Di Celma et al. in press). The outstanding vertebrate assemblage of Cerro Colorado is dominated by cetacean remains (81% of 318 specimens recorded by Bianucci et al. in press), belonging to both mysticetes (cetotheriids and balaenopteroids) and odontocetes (physeteroids, ziphiids, pontoporiids, and kentriodontid-like delphinidans); phocids, sea turtles, crocodiles, seabirds, sharks, and bony fish are also present (Lambert et al. 2010; Parham and Pyenson 2010; Bianucci et al. 2010; in press).

(b) Palaeontological material

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In spring 2014, an almost complete skeleton of a cetotheriid whale was found at Cerro Colorado (coordinates: 14°20'06.8"S-75°53'29.8"W) embedded within a 3 m thick interval of easily friable, white to nearly white, finely laminated diatomite located just above the Wari marker bed of Di Celma et al. (in press) and ca 48.9 m above the basal unconformity with the underlying Chilcatay Formation (Fig. 1; Online Resource file ESM_1.pdf: Fig. S1). This skeleton (labelled M10 in the published map of the fossil vertebrates of Cerro Colorado; Bianucci et al. in press) was partially excavated for taphonomic study. Field excavation revealed the presence of tightly packed fish remains between the left posterior ribs; these bony and dermal elements were labelled T6 by Bianucci et al. (in press). Four small samples of sediment (ranging from 7.5 cm × 5.5 cm × 2.5 cm to 2 cm × 2 cm × 1 cm) containing this intercostal aggregate of fish bones and scales were collected and deposited in the collection of the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM), in Lima (collection number MUSM 2630). Taking account of the poorly preserved head elements of M10, and in order to preserve the extraordinary paleontological heritage of the Cerro Colorado area (Bianucci et al. in press), we did not collect M10 and thus kept the taphonomic aspect of the cetotheriid whale skeleton substantially pristine. In turn, the complete right mandible of a mysticete belonging to the same species as M10 was also collected from Cerro Colorado in order to better identify the new cetotheriid and to undertake a preliminary morphofunctional study. This mandible was prepared at the MUSM (collection number MUSM 2553).

(c) High resolution micro-CT scanning

The four collected samples were analysed with the Xalt micro-CT scanner (Panetta et al. 2012) at Istituto di Fisiologia Clinica (Consiglio Nazionale delle Ricerche, Pisa, Italy), which is a variable-geometry cone-beam CT system with embedded software for geometrical misalignment compensation, equipped with a microfocus X-ray source (20-50 kV) and a digital flat-panel X-ray detector of 2048×1024 pixels with a total active area of 10 cm × 5 cm. All scans were done at the

maximum spatial resolution allowed by the sample size, consisting in 960 projections over 360° and a total scan time of 48 min per bed position, covering a field of view (FoV) of 8 cm × 8 cm × 3 cm. Depending on the sample size, one to three bed positions were necessary to image the entire sample. The X-ray tube settings were 50 kV, 0.7 mA, with an added filtration of 2 mm of aluminium. All images were reconstructed at the isotropic voxel size of 36.9 μm using a modified Feldkamp algorithm (Feldkamp et al. 1984). After reconstruction, all images were visualized and post-processed using ImageJ (Rasband 1997-2014), and volume renderings (VR) were obtained with VolView 3.4, Kitware. Maximum intensity projection (MIP) was used in selected subvolumes to generate a comprehensive view of the bone remains in virtual slabs of arbitrary thickness. Due to the complex spatial arrangement of the bone remains in the scanned samples, the selected thickness of the virtual slabs (at any depth) was always less than 1.5 mm, thus preserving a good compromise between discrimination of the different items and a comprehensive view of the sample.

3. Results

(a) Taphonomy of the whale skeleton M10

The fossil skeleton M10 (Figs. 2a, b) is articulated, lying in dorsal view, and it is represented by the skull, mandibles, most of the vertebrae, and ribs; it lacks the forelimbs. Recent erosion damaged the skull, the mandibles and the distal portion of the ribs and probably destroyed the missing caudal portion of the vertebral column (the posteriormost preserved vertebrae are partially dislocated due to erosion). Cervical, thoracic and lumbar vertebrae are articulated with the skull, but the entire vertebral column is slightly S-shaped. Whereas the bony thorax is flattened dorsoventrally, with the ribs lying sub-horizontally roughly parallel to each other, most ribs (especially the posterior ones) are still articulated with the corresponding thoracic vertebrae. As commonly observed in fossil mysticetes from Cerro Colorado (Gariboldi et al. 2015), M10 exhibits dolomitic concretions filling the endocranial cavity and partially covering several vertebrae and ribs. The fish remains exposed

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between the left posterior ribs were tightly packed and embedded in a yellowish, very fine-grained matrix (Figs. 2c, d). No other fish remains were observed in the sediment surrounding the whale skeleton.

We estimate the total body length of M10 to about 6.0 - 6.5 m (see Online Resource file ESM_1.pdf). A 3D reconstruction of the skeleton M10 can be downloaded as Online Resource (file ESM_2.pdf; methods in file ESM_1.pdf).

(b) Systematic affinities of M10 and other cetotheriid skeletons of Cerro Colorado

As anticipated above, the skull and the mandibles of the skeleton M10 are unfortunately partially eroded, thus being not fully adequate for the purposes of a detailed systematic study. Nevertheless, only three species of Mysticeti - one medium-sized balaenopteroid, one large-sized balaenopteroid, and one small-sized cetotheriid - have been recognized after a detailed census of the fossil vertebrates of Cerro Colorado (Bianucci et al. in press); M10 matches the cetotheriid in terms of general size and proportions, outline of the skull, and length distribution of the vertebral centra. Therefore, anatomical observations were taken in the field for M10, the mandible MUSM 2553 (see description below), and several other mysticete skeletons cropping out at Cerro Colorado and sharing strong similarities with these two specimens (Online Resource file ESM_1: Figs. S2-S11). All these specimens present various characters which, on the whole, are regarded as diagnostic of the family Cetotheriidae: ascending process of the maxilla extended posteriorly as far as the postorbital process of the frontal; premaxilla not as extended posteriorly as the posteriormost extremity of the maxilla; nasals wedge-shaped; posterior edge of the rostral bones V-shaped; facial bones strongly telescoped, causing the vertex to appear X-shaped in apical view; parieto-squamosal suture presenting a ridge-like portion; angular process of the mandible protruding slightly posterior to posterior edge of the mandibular condyle (Bouetel and Muizon 2006; Gol'din et al. 2014; El Adli et al. 2014). They can be assigned to a single new cetotheriid species that shares several similarities with *Piscobalaena nana* (a well-known late Miocene-Pliocene cetotheriid of the Pisco Formation;

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Pilleri and Siber 1989; Bouetel and Muizon 2006): horizontal, sub-rectilinear rostrum in lateral view; posterior limit of narial fossa posterior to the line joining the preorbital processes of the frontals; relatively rounded anterior outline of the supraoccipital shield; prominent nuchal crest; presence of a sagittal crest on the supraoccipital shield; short distance between supraoccipital and maxilla across the vertex; ascending process of the premaxilla ending far from the vertex of the skull; sub-parallel lateral and medial edges of the ascending process of the maxilla. Representing at least 18% of the whole vertebrate assemblage of Cerro Colorado (Bianucci et al. in press), this undescribed cetotheriid species differs from *P. nana* in having a larger size (bizygomatic width of the skull up to 76 cm) and a more reduced contact between the premaxillae and the anteroposteriorly elongated nasals.

(c) Description of the cetotheriid mandible MUSM 2553.

The right mandible MUSM 2553 (Fig. 3; Online Resource file ESM_1: Fig. S12) is almost complete, with the exception of the tip of the coronoid process and part of the dorsomedial edge of the postcoronoid inward elevation (see below). However, a natural cast of the latter can be observed in the dolomitic concretion that embeds the bone. In dorsal view, the horizontal ramus of the mandible is bowed laterally for its whole length. The horizontal ramus shows constant width and height until its anteriormost third, in which it becomes progressively transversely thinner as the mandible rotates moderately clockwise (in posterior view). The lateral face of the mandible is generally strongly convex, while the medial face is almost flat for the whole length of the horizontal ramus and bears a short (about 8 cm long) apical furrow, most likely for the attachment of the ligamentous symphysis. The dorsal edge of the mandible presents a relict alveolar groove that lies medially to a weak dorsal rim and reaches the anterior apex of the bone. The ventral edge of the horizontal ramus forms an angular rim for the attachment of the mylohyoid muscle; this rim is particularly distinct and carina-like in the median portion of the mandible. In this region, the cross-section of the mandible is remarkably D-shaped (Online Resource file ESM_1: Fig. S12). The

coronoid process lacks its tip, which was located at about 18% of the length of the mandible. The coronoid process is robust, roughly triangular, and projects posterolaterally; it is bowed and thus looks hook-shaped. Both the anterior and posterior margins of the anteroposteriorly elongated coronoid process rise gradually. Behind the tip of the coronoid process, the thick posterior margin gradually passes into a massive postcoronoid elevation (preserved in part as bone and in part as a natural cast) that projects inwards. This inward elevation bears a rounded crest (thus being balaenopterid-like, according to Kimura (2002)). Just posterior to the tip of the coronoid process, the mandibular foramen opens posteriorly in the core of the vertical ramus. The anterior end of the mandibular foramen is slit-like, as observed in *Piscobalaena nana* and in some herpetocetine mandibles from upper Miocene deposits of California and Virginia (Baum and Wheeler 1977; Boessenecker 2011: Figs. 3-13). The mandibular foramen passes into a wide, channel-like notch (subcondylar furrow *sensu* Kimura (2002)), which separates the condyle from the angular process on the medial face of the mandible; this channel reaches the posterior end of the mandible. The anteroposteriorly elongated condyle has a planar articular surface (as in *Herpetocetus* spp.) and is inflated both medially and laterally (as in *P. nana*). In lateral view, the articular surface of the condyle stands at high angle (about 60°-70°) with respect to the horizontal plane. The angular process is roughly dorsoventrally flattened and presents a well-defined, inflated lateral edge. It projects posteriorly in a way similar to that of *P. nana* , and as such, represents the posteriormost portion of the mandible. Overall, the mandible MUSM 2553 presents strong similarities with both *P. nana* and the above mentioned late Miocene herpetocetine mandibles, presenting in fact a mix of *Herpetocetus*-like and *Piscobalaena*-like characters; however, the extent of the angular process of MUSM 2553 (which is much posteriorly shorter than in *Herpetocetus* spp.) precludes any tentative attribution to the genus *Herpetocetus*.

(d) Taphonomy and systematics of the fish remains.

The fish remains associated to M10 are preserved just outside dolomitic concretions partially enclosing the whale's skeleton. Fish bones and scales are included in a yellowish, poorly indurated diatomitic matrix containing rare, tiny aggregates of iron oxides and gypsum crystals. This kind of sediment, poorly cemented by ferroan dolomite (which provides the yellowish coloration), is commonly observed nearby dolomitic nodules covering fossil bones in Cerro Colorado (Gariboldi et al. 2015).

The micro-CT investigation of the four samples of the intercostal aggregate succeeded in imaging the complex architecture of the cluster of fossil fish remains (Fig. 4 a-d). All the identifiable fossil elements are fully compatible with the extant monotypic clupeid genus *Sardinops* (only including the Pacific pilchard *S. sagax*). In particular we observed: (1) an abdominal scute including the typical apophysis, that characterizes *S. sagax* among Clupeoidea (Yabumoto 1988); (2) various cycloid scales with characteristic curved fracture lines (looking similar to radii) affecting their lateral fields, as typical of *S. sagax* (see Patterson et al. 2002); (3) a distorted but still well-diagnostic opercle presenting radiating bony striae on its ventral portion (Withehead 1985); (4) a single cranium, squashed and fractured, lacking the distal part of the rostrum (see Online Resource file ESM_3.avi); (5) various other head elements (e.g., maxillary, articular) whose morphologies match those presented by the Pacific pilchard (Fig. 5a, b; Online Resource file ESM_1: Figs. S13-S16). Due to the incompleteness of the studied material, we prefer to refer it to *Sardinops* sp. cf. *S. sagax*. No other vertebrate or invertebrate taxa were recognized; however, the occurrence of a large, indeterminate bone indicates the presence in the aggregate of a bony fish larger than *Sardinops* sp. cf. *S. sagax* (Fig. 5a). For a list of the bony and dermal fish elements recognized in the studied aggregate, see Online Resource file ESM_1.pdf. Two short movies presenting the results of a preliminary, medium-resolution micro-CT 3D reconstruction of MUSM 2630 are in Online resource files (ESM_3.avi and ESM_4.avi for fragment 3 and fragments 1-2-4 respectively).

The observed dermal and bony remains are often fractured and incomplete, especially the long and thin elements (e.g., the vertebral apophyses). Conversely, some complex multi-bone elements are still complete and almost fully articulated (e.g., a few lepidotrichia, Fig. 6). The fish remains are tightly packed and deeply mingled (e.g., head bones lie beside portions of the tail), thus constituting a 3D building of overlapping elements. Interestingly, in spite of being generally fragmentary, all the bony remains and various scales present smooth surfaces, and even the finest details are generally well-defined, lacking evidence of superficial erosion or corrosion; in turn, some scales show a porous, somewhat spongy texture which could be related to those dissolution processes which are believed to affect the fish debris in the upper part of the sediment column (Valdés et al. 2008). The minimum number of *Sardinops* individuals present in the studied aggregate is 1; this result is most likely due to the very limited volume of the fossilized fish remains available for analysis, rather than effectively indicating the ingestion of a single sardine. Based on the width of the scales and the overall size of the bony elements, the *Sardinops* remains can be attributed to one or more young adult specimens whose Standard Length (defined by Phillips (1948) as the length measured from the anterior end of the jaw to the termination of the fleshy part of the caudal peduncle) falls between 15 and 25 cm (i.e., still-growing, but physically and sexually mature individual(s)).

4. Discussion

Various hypotheses could be proposed to account for the cetotheriid-*Sardinops* association found in Cerro Colorado:

1) Fish remains could have been washed by currents between the ribs of the cetacean's skeleton. However, the lack of tractive structures in the embedding sediment, the preservation of delicate and partly articulated fish bones, and the substantial articulation of the bony thorax of the whale discourage from embracing this hypothesis.

2) Fish remains could have been entombed within a small, tube-like burrow dug by a benthic invertebrate (e.g., Boessenecker et al. 2014: Fig. 9). However, the lack of any vertical trace fossil and burrow (e.g., *Ophiomorpha*) as well as any indication of bioturbation affecting the clearly laminated diatomites surrounding the whale skeleton contradicts this hypothesis.

3) Scavenging on the cetotheriid carcass by fish and subsequent death of one or more individuals is also highly unlikely; indeed, extant *Sardinops sagax* is a virtually exclusive planktivore (Whitehead 1985).

4) In turn, several arguments strongly support the hypothesis that the fish remains discovered within the skeleton M10 represent the fossilized prey of the baleen whale, rather than the fortuitous preservation together of ecologically unrelated animals. First of all, fossil fish bones are rare at Cerro Colorado (Bianucci et al. in press). Interestingly, within this scarce record, the only bony remains that have been referred to the genus *Sardinops* are associated to a beaked whale skeleton and are interpreted as representing the undigested or partly digested last meal of the whale (Lambert et al. 2015); in turn, isolated clupeid scales tentatively attributed to *Sardinops* are frequently found within the sediment all over the Cerro Colorado area, and especially near some fossil mysticetes (e.g., the cetotheriid specimen labelled M11; Bianucci et al. in press). Additionally, the fish remains associated with M10 were found between the posterior left ribs (i.e., in the rear left region of the thorax), a location most likely originally occupied by the caudal lobe of the forestomach of the whale (as compared to modern cetaceans; Mead 2002). Furthermore, their state of preservation (high degree of fragmentation, coupled with no evidence of superficial erosion or corrosion) and architecture (tight 3D packing, high degree of mingling) (Figs. 4 and 5) are compatible with the effects of mechanical processing by the forestomach of the host whale. Indeed, in the forestomach of extant piscivorous cetaceans, flesh is stripped from prey and fish bones are ground up and mingled by the powerful contractions of the muscular walls (Berta et al. 2005), whereas chemical attack takes place only farther in the digestive tract (Mead 2002). For all these reasons, we interpret

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the fish remains associated to M10 as part of the fossil stomach (namely: forestomach) content of the cetotheriid whale. The presence of a few still articulated multi-bone elements suggests that, when the whale died, some parts of the fish skeleton(s) (e.g., some fins) were not yet cleaned from their flesh.

Therefore, our discovery represents the first record of a fossil stomach content for a mysticete. Could the fish remains associated with M10 represent an event of accidental ingestion by a non-piscivorous whale? As an example, there are evidences that humpback whales occasionally ingest seabirds while both taxa converge to forage on the same fish school (Dolphin and McSweeney 1983); however, such episodes are rare (Haynes et al. 2013). Therefore, it seems overly unlikely that the only fossilized stomach content of a mysticete recognized to this date features an erroneously ingested object. Moreover, the inferred presence of a fish taxon other than *Sardinops* in MUSM 2630 (testified by a large undetermined bone which does not match the skeletal anatomy of *Sardinops*) strongly suggests that fish were in fact the target prey of M10.

Therefore, the fossil stomach content studied here represents the first direct evidence of piscivory in an ancient edentulous mysticete (Chaeomysticeti). As demonstrated by two fossil stomach contents, at least some of the basilosaurid predecessors of baleen whales fed on fish (Swift and Barnes 1996; Uhen 2004). In basal mysticetes, the progressive substitution of the adult dentition with baleen has been regarded as a transition from a fish-based raptorial behaviour towards a plankton-based trophic ecology; however, the assessment that the adoption of bulk filter feeding necessarily implied giving up of piscivory in favour of microphagy in primitive baleen-bearing whales has recently been questioned (e.g., Deméré and Berta 2008). Therefore, it is a current subject of debate whether piscivory in several Chaeomysticeti (i.e., occasional fish consumption in *Eschrichtius robustus*, regular fish consumption in various extant species within Balaenopteridae, and, by now, piscivory inferred in at least one Cetotheriidae) results from one or more ecological reversions or instead represents the retention of an ancestral feeding habit (see

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discussion in Fitzgerald 2010). A work by Clementz et al. (2014), in which members of the family Eomysticetidae (the earliest edentulous mysticetes) are proposed based on oxygen-stable isotope analyses to have foraged mainly on zooplankton, sustains the hypothesis of an ecological reversion. The results by Clementz et al. (2014) have recently found support in the description of the eomysticetid whale *Waharoa ruwhenua*, for whom a balaenid-like skim feeding method and a diet of zooplankton have been hypothesized by Boessenecker and Fordyce (2015). However, additional stomach contents from other ancient baleen-bearing whales are needed to discuss further these hypotheses.

Based on morphofunctional analyses of well-preserved skeletons, some species of Cetotheriidae (e.g., *Piscobalaena nana*) were proposed to feed via engulfment, like extant balaenopterids (Fordyce and Barnes 1994; Bouetel 2005; Bouetel and Muizon 2006). In turn, a roughly eschrichtiid-like suction feeding method was suggested for two other cetotheriids (*Cetotherium riabinini* and *Herpetocetus morrowi*) (Gol'din et al. 2014; El Adli et al. 2014), whereas stomach content analyses shows the extant putative cetotheriid *Caperea marginata* feeds on copepods and euphausiids, thus suggesting a balaenid-like skimming feeding mode (Kemper 2002). Since among modern baleen whales only Balaenopteridae are known as ordinarily piscivorous, the Peruvian fossil record reported here may support the hypothesis that some extinct members of the family Cetotheriidae already experimented some degree of engulfment feeding. A preliminary morphofunctional analysis of the Cerro Colorado new cetotheriid species reveals that this baleen whale presents some morphological features that have been viewed by various authors as enabling engulfment feeding in mysticetes: a flattened rostrum; a laterally bent dentary with a D-shaped cross section; an angular ventral edge of the median portion of the horizontal ramus; a hook-shaped and posterolaterally projected coronoid process coupled with a significant postcoronoid inward elevation; a well-developed and posteriorly projected angular process; and a V-shaped, interdigitated contact between rostral and cranial bones (Bisconti and Varola 2000; Kimura 2002;

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Bouetel 2005; Bouetel and Muizon 2006; Tsai and Fordyce 2015, and references therein). Other feeding strategies could account for epipelagic fish consumption in cetaceans (e.g., suction feeding, a predation technique most likely used by some early diverging lineages of mysticetes; Fitzgerald 2010; 2012); however, the high predator-prey size ratio estimated for M10 suggests that a feeding mode other than bulk feeding (e.g., a succession of gulping events, each of them involving a single fish) is unlikely for this cetotheriid. A detailed study of the functional anatomy of the Cerro Colorado cetotheriid is in progress; it will hopefully help clarifying its feeding technique.

It is noteworthy that most of the currently known cetotheriids originate from deposits testifying for conditions of high marine primary productivity (Gol'din et al. 2014), as for our record from Cerro Colorado (Dunbar et al. 1990; Brand et al. 2004). Therefore, the finding described here provides further impetus for investigating the relationships between the set-up of modern coastal upwelling systems and the rise of Cetotheriidae. In this respect, the emergence of various genera of small sized, schooling clupeiform fish (e.g., *Sardinops*, *Engraulis*, *Clupea*, etc.) in such highly productive environments may represent a most reliable link. Schools of relatively small epipelagic fish are indeed the preferred target of fish-eating modern mysticetes (e.g., Croll and Tershy 2002), and clupeids are believed to be the main prey of the predominantly piscivorous, small-sized *Balaenoptera acutorostrata* (Lydersen and Weslawski 1991). In this framework, our find that the most ancient evidence of piscivory by a cetotheriid whale from the Southern Hemisphere implies the schooling clupeid *Sardinops* may prove relevant. The origin of the genus *Sardinops* is tentatively set in the Indian Ocean and possibly represented an early Miocene vicariance event within an ancient sardine population following the closure of the Tethys Sea corridor (Parrish et al. 1989; Grant and Leslie 1996; Bowen and Grant, 1997; Grant and Bowen, 1998; Grant et al. 1998). Parrish et al. (1989) proposed that the genus *Sardinops* spread in the Southern Hemisphere "[...] by the late Miocene or early Pliocene, a period when ocean temperatures were decreasing and oceanic productivity was increasing". In turn, the fossil stomach content described in this work, coupled

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with the ziphiid-fish association reported by Lambert et al. (2015) and with the observation of ubiquitous clupeid scales dispersed within the sediment in Cerro Colorado, indicates that *Sardinops* was already abundant along the coast of Peru during early late Miocene times and suggests that *Sardinops* occupied a prominent position in trophic chains of the Cerro Colorado vertebrate fauna. Finally, it is interesting to note that this record matches the Tortonian peak of oceanic primary productivity and cooling phase, a phase that seemingly corresponds to a period of high mysticete diversity (Lambert et al. 2010; Marx and Uhen 2010; Marx and Fordyce 2015), including a radiation within Cetotheriidae (Bisconti 2014).

5. Conclusions

The first fossil record of the stomach content of a mysticete is described from Cerro Colorado, a fossil-rich, early late Miocene locality of the Pisco Formation, Pisco Basin (Peru). The baleen whale is identified as a new species of the chaeomysticete family Cetotheriidae, while its prey is identified as the clupeiform *Sardinops* sp. cf. *S. sagax* (Pacific pilchard). Micro-CT scanning proved to be highly efficient for imaging the complex architecture of the stomach content. Degree of fragmentation and mingling of the observed fish bones and scales are attributed to mechanical processing in the forestomach of the predator whale. Our finding represents the first direct evidence of piscivory in an ancient edentulous mysticete. Based on actualistic considerations and morphofunctional observations, an engulfment-like feeding method is hypothesized to have been experimented by at least part of Cetotheriidae, although other predation techniques (e.g., suction feeding) or combinations of them could be taken in account. We also argue that some of the trophic chains of the vertebrate fauna of Cerro Colorado were based on the presence of schooling pilchards, living within or at the edge of the highly productive Pisco Basin. Together with many recent results in the study of the evolutionary history of baleen whales, this fossil record stimulates further investigation of the relationships between mysticete diversification phases and long-term

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environmental changes in marine environments (e.g., the rise of small-sized, schooling epipelagic fish) with respect to Cenozoic global climatic and oceanographic drivers.

References

Baldanza A, Bizzarri R, Famiani F, Monaco P, Pellegrino R, Sassi P (2013) Enigmatic, biogenically induced structures in Pleistocene marine deposits: a first record of fossil ambergris. Geology 41:1075-1078. doi:10.1130/G34731.1

Barron JA (2003) Planktonic marine diatom record of the past 18 M.Y.: Appearances and extinctions in the Pacific and southern oceans. Diatom Res 18:203-224. doi: 10.1080/0269249X.2003.9705588

Baum GR, Wheeler WH (1977) Cetaceans from the St. Marys and Yorktown Formations, Surry County, Virginia. J Paleontol 51:492-504

Berta A, Sumich JL, Kovacs KM (2005) Diet, Foraging Structures and Strategies. In: Marine Mammals: Evolutionary Biology, 2nd edn. Academic Press, San Diego, pp 312-362

Bianucci G, Celma C, Landini W, Post K, Tinelli C, Muizon C de, Gariboldi K, Malinverno E, Cantalamessa G, Gioncada A, Collareta A, Salas-Gismondi R, Varas Malca R, Urbina M, Lambert O (in press) Mapping and vertical distribution of fossil marine vertebrates in Cerro Colorado, the type locality of the giant raptorial sperm whale *Livyatan melvillei* (Miocene, Pisco Formation, Peru). J Maps. doi:10.1080/17445647.2015.1048315

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. doi:10.1111/j.1475-4983. 2010.00995.x

Bisconti M (2008) Morphology and phylogenetic relationships of a new eschrichtiid genus (Cetacea: Mysticeti) from the Early Pliocene of northern Italy. Zool J Linn Soc-Lond 153:161-186. doi: 10.1111/j.1096-3642.2008.00374.x

19

Bisconti M (2014) Anatomy of a new cetotheriid genus and species from the Miocene of Herentals, Belgium, and the phylogenetic and palaeobiogeographical relationships of Cetotheriidae *s.s.* (Mammalia, Cetacea, Mysticeti). J Syst Palaeontol. doi:10.1080/14772019.2014.890136

Bisconti M, Varola A (2000) Functional hypothesis on an unusual mysticete dentary with double coronoid process from the Miocene of Apulia and its systematic and behavioural implications. Palaeontographia Ital 87:19-35

Bisconti M, Varola A (2006) The oldest eschrichtiid mysticete and a new morphological diagnosis of Eschrichtiidae (gray whales). Riv Ital Paleontol Strat 112:447-457

Boessenecker RW (2011) Herpetocetine (Cetacea: Mysticeti) dentaries from the Upper Miocene Santa Margarita Sandstone of Central California. PaleoBios 30:1-12

Boessenecker RW (2013) Pleistocene survival of an archaic dwarf baleen whale (Mysticeti: Cetotheriidae). Naturwissenschaften 100:365-371. doi:10.1007/s00114-013-1037-2

Boessenecker RW, Fordyce RE (2015) Anatomy, feeding ecology, and ontogeny of a transitional baleen whale: a new genus and species of Eomysticetidae (Mammalia: Cetacea) from the Oligocene of New Zealand. PeerJ 3:e1129. doi: 10.7717/peerj.1129

Boessenecker RW, Perry FA (2011) Mammalian bite marks on juvenile fur seal bones from the late Neogene Purisima Formation of Central California. Palaios 26:115-120. doi: 10.2110/palo.2010.p10-088r

Boessenecker RW, Perry FA, Schmitt JG (2014) Comparative taphonomy, taphofacies, and bonebeds of the Mio-Pliocene Purisima Formation, central California: strong physical control on marine vertebrate preservation in shallow marine Settings. PloS one 9(3), e91419. doi:10.1371/journal.pone.0091419

Bouetel V (2005) Phylogenetic implications of skull structure and feeding behavior in balaenopterids (Cetacea, Mysticeti). J Mammal 86:139-146. doi: http://dx.doi.org/10.1644/1545-1542(2005)086<0139:PIOSSA>2.0.CO;2

Bouetel V, Muizon C de (2006) The anatomy and relationships of *Piscobalaena nana* (Cetacea, Mysticeti), a Cetotheriidae *s.s*. from the early Pliocene of Peru. Geodiversitas 28:319-395

Bowen BW, Grant WS (1997) Phylogeography of the sardines (*Sardinops* spp.): assessing biogeographic models and population histories in temperate upwelling zones. Evolution 51:1601-1610. doi: 10.2307/2411212

Brand LR, Esperante R, Chadwick AV, Poma O, Alomia M (2004) Fossil whale preservation implies high diatom accumulation rate in the Miocene-Pliocene Pisco Formation of Peru. Geology 32:165-168. doi: 10.1130/G20079.1

Clementz MT, Fordyce RE, Peek SL, Fox DL (2014) Ancient marine isoscapes and isotopic evidence of bulk-feeding by Oligocene cetaceans. Palaeogeogr Palaeocl 400:28-40. doi: http://dx.doi.org/10.1016/j.palaeo.2012.09.009

Cozzuol MA (2001) A "northern" seal from the Miocene of Argentina: implications for phocid phylogeny and biogeography. J Vertebr Paleontol 21:415-421

Croll DA, Tershy BR (2002) Filter feeding. In: Perrin W., Wursig B, Thewissen JGM (eds) Encyclopedia of marine mammals. Academic Press, San Diego, pp 428-432

Deméré TA, Berta A (2008) Skull anatomy of the Oligocene toothed mysticete *Aetioceus weltoni* (Mammalia; Cetacea): implications for mysticete evolution and functional anatomy. Zool J Linn Soc-Lond 154:308-352. doi: 10.1111/j.1096-3642.2008.00414.x

Deméré T, McGowen M, Berta A, Gatesy J (2008) Morphological and molecular evidence for a stepwise evolutionary transition from teeth to baleen in mysticete whales. Syst Biol 57:15-37. doi: 10.1080/10635150701884632

Di Celma C, Malinverno E, Gariboldi K, Gioncada A, Rustichelli A, Pierantoni P, Landini W, Bosio G, Tinelli C, Bianucci G (in press) Stratigraphic framework of the late Miocene to Pliocene Pisco Formation at Cerro Colorado (Ica Desert, Peru). J Maps. doi: 10.1080/17445647.2015.1047906

Dolphin WF, McSweeney D (1983) Incidental ingestion of Cassin's Auklets by Humpback Whales. Auk 100: 214

Druckenmiller P, Kelley N, Whalen M, McRoberts C, Carter J (2014) An Upper Triassic (Norian) ichthyosaur (Reptilia, Ichthyopterygia) from northern Alaska and dietary insight based on gut contents. J Vertebr Paleontol 34:1460-1465. doi: 10.1080/02724634.2014.866573

Dunbar RB, Marty RC, Baker PA (1990) Cenozoic marine sedimentation in the Sechura and Pisco basins, Peru. Palaeogeogr Palaeocl 77:235-261. doi: 10.1016/0031- 0182(90)90179-B

El Adli JJ, Deméré TA, Boessenecker RW (2014) *Herpetocetus morrowi* (Cetacea: Mysticeti), a new species of diminutive baleen whale from the Upper Pliocene (Piacenzian) of California, USA, with observations on the evolution and relationships of the Cetotheriidae. Zool J Linn Soc-Lond 170:400-466. doi: 10.1111/zoj.12108

Esperante R, Brand LR, Chadwick AV, Poma O (2015) Taphonomy and paleoenvironmental conditions of deposition of fossil whales in the diatomaceous sediments of the Miocene/Pliocene Pisco Formation, southern Peru - A new fossil-lagerstätte. Palaeogeogr Palaeocl 417:337-370. doi: 10.1016/j.palaeo.2014.09.029

Fahlke JM (2012) Bite marks revisited - evidence for middle-to-late Eocene *Basilosaurus isis* predation on *Dorudon atrox* (both Cetacea, Basilosauridae). Palaeont Electron 15:32A

Feldkamp LA, Davis LC, Kress JW (1984) Practical cone-beam algorithm. J Opt Soc Am A 1:612-619. doi: 10.1364/JOSAA.1.000612

Fitzgerald EM (2006) A bizarre new toothed mysticete (Cetacea) from Australia and the early evolution of baleen whales. P R Soc Lond B Bio 273:2955-2963. doi: 10.1098/rspb.2006.3664

Fitzgerald EM (2010) The morphology and systematics of *Mammalodon colliveri* (Cetacea: Mysticeti), a toothed mysticete from the Oligocene of Australia. Zool J Linn Soc-Lond 158:367-476. doi: 10.1111/j.1096-3642.2009.00572.x

Fitzgerald EM (2012) Archaeocete-like jaws in a baleen whale. Biol Letters 8:94-96. doi:

10.1098/rsbl.2011.0690

Fordyce RE, Barnes LG (1994) The evolutionary history of whales and dolphins. Annu Rev Earth
Pl Sc 22:419-455. doi: 10.1146/annurev.ea.22.050194.002223

Fordyce RE, Marx FG (2013) The pygmy right whale *Caperea marginata*: the last of the cetotheres.
P R Soc Lond B Bio 280:20122645. doi: 10.1098/rspb.2012.2645

Gariboldi K, Gioncada A, Bosio G, Malinverno G, Di Celma C, Tinelli C, Cantalamessa G, Landini
W, Urbina M, Bianucci G (2015) The dolomite nodules enclosing fossil marine vertebrates in
the East Pisco Basin, Peru: field and petrographic insights into the Lagerstätte formation.
Palaeogeogr Palaeocl 438:81-95. doi:10.1016/j.palaeo.2015.07.047

Goldbogen JA, Pyenson ND, Shadwick RE (2007) Big gulps require high drag for fin whale lunge
feeding. Mar Ecol-Progr Ser 349:289-301. doi: 10.3354/meps07066

Goldbogen J, Calambokidis J, Oleson E, Potvin J, Pyenson N, Schorr G, Shadwick R (2011)
Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence
on krill density. J Exp Biol 214:131-146. doi: 10.1242/jeb.048157

Gol'din P, Startsev D, Krakhmalnaya T (2014) The anatomy of the Late Miocene baleen whale
Cetotherium riabinini from Ukraine. Acta Palaeontol Pol 59:795-814. doi:
http://dx.doi.org/10.4202/app.2012.0107

Grant WAS, Bowen BW (1998) Shallow population histories in deep evolutionary lineages of
marine fishes: insights from sardines and anchovies and lessons for conservation. J
Hered 89:415-426. doi: 10.1093/jhered/89.5.415

Grant WS, Clark AM, Bowen BW (1998) Why restriction fragment length polymorphism analysis
of mitochondrial DNA failed to resolve sardine (*Sardinops*) biogeography: insights from
mitochondrial DNA cytochrome b sequences. Can J Fish Acquat Sci 55:2539-2547. doi:
10.1139/f98-127

Grant WS, Leslie RW (1996) Late Pleistocene dispersal of Indian-Pacific sardine populations in an

ancient lineage of the genus *Sardinops*. Mar Biol 126:133-142. doi:10.1007/BF00571385

Harington CR, Ross RL, Mathewes RW, Stewart KM, Beattie O (2004) A late Pleistocene Steller sea lion (*Eumetopias jubatus*) from Courtenay, British Columbia: its death, associated biota, and paleoenvironment. Can J Earth Sci 41:1285-1297. doi: 10.1139/e04-061

Haynes TB, Campbell MA, Neilson JL, López JA (2013) Molecular identification of seabird remains found in humpback whale feces. Mar Ornithol 41:161-166.

Johnston C, Berta A (2011) Comparative anatomy and evolutionary history of suction feeding in cetaceans. Mar Mammal Science 27:493-513. doi: 10.1111/j.1748-7692.2010.00420.x

Kear BP, Boles WE, Smith ET (2003) Unusual gut content in a Cretaceous ichthyosaur. P R Soc Lond B Bio 270:S206-S208. doi: 10.1098/rsbl.2003.0050

Kemper CM (2002) Distribution of the pygmy right whale, *Caperea marginata*, in the Australasian region. Mar Mammal Science, 18:99-111. doi: 10.1111/j.1748-7692.2002.tb01021.x

Kimura T (2002) Feeding strategy of an Early Miocene cetothere from the Toyama and Akeyo Formations, central Japan. Paleontol Res 6:179-189. doi: http://doi.org/10.2517/prpsj.6.179

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. P R Soc Lond B Bio 282: 20151530. doi: 10.1098/rspb.2015.1530

Lambert O, Bianucci G, Post K, Muizon C de, Salas-Gismondi R, Urbina M, Reumer J (2010) The giant bite of a new raptorial sperm whale from the Miocene epoch of Peru. Nature 466:105-108. doi: 10.1038/nature09067

Lydersen C, Weslawski JM (1991) Stomach content analysis of minke whales *Balaenoptera acutorostrata* from the Lofoten and Vesterålen areas, Norway. Holarct Ecol 14:219-222. doi: 10.1111/j.1600-0587.1991.tb00655.x

Marx FG, Fordyce RE (2015) Baleen boom and bust: a synthesis of mysticete phylogeny, diversity and disparity. R Soc Open Sci 2:140434. doi: http://dx.doi.org/10.1098/rsos.140434

Marx F, Uhen MD (2010) Climate, critters, and cetaceans: Cenozoic drivers of the evolution of modern whales. Science 327:993-996. doi: 10.1126/science.1185581

Mead JG (2002) Gastrointestinal Tract. In: Perrin WF, Wursig B, Thewissen JGM (eds.) Encyclopedia of marine mammals. Academic Press, San Diego, pp 488-495

Monaco P, Baldanza A, Bizzarri R, Famiani F, Lezzerini M, Sciuto F (2014) Ambergris cololites of Pleistocene sperm whales from central Italy and description of the new ichnogenus and ichnospecies *Ambergrisichnus alleronae*. Palaeontol Electron 17:20.

O'Keefe FR, Street HP, Cavigelli JP, Socha JJ, O'Keefe RD (2009) A plesiosaur containing an ichthyosaur embryo as stomach contents from the Sundance Formation of the Bighorn Basin, Wyoming. J Vertebr Paleontol 29:1306-1310. doi: 10.1671/039.029.0403

Pandeli E, Vannucchi P, Monechi S (1998) Possible crystalline gastroliths of large marine Vertebrata from Oligocene pelitic sediments of the Northern Apennines, Italy. Geology 26:775-778. doi: 10.1130/0091-7613(1998) 026<0775:PCGOLM> 2.3.CO;2

Panetta D, Belcari N, Del Guerra A, Bartolomei A, Salvadori PA (2012) Analysis of image sharpness reproducibility on a novel engineered micro-CT scanner with variable geometry and embedded recalibration software. Phys Medica 28:166-173. doi: http://dx.doi.org/10.1016/j.ejmp.2011.03.006

Parham JF, Pyenson ND (2010) New sea turtle from the Miocene of Peru and the iterative evolution of feeding ecomorphologies since the Cretaceous. J Paleontol 84:231-247. doi: 10.1666/09-077R.1

Parrish RH, Serra R, Grant WS (1989) The monotypic sardines, *Sardina* and *Sardinops*: their taxonomy, distribution, stock structure, and zoogeography. Can J Fish Aquat Sci 46:2019-2036

Patterson RT, Wright C, Chang AS, Taylor LA, Lyons PD, Dallimore A, Kumar A (2002) Atlas of common squamatological (fish scale) material in coastal British Columbia and an assessment of the utility of various scale types in paleofisheries reconstruction. Palaeontol Electron 4:88

Pierce G, Boyle P (1991) A review of methods for diet analysis in piscivorous marine mammals. Oceanogr Mar Biol 29:409-486

Phillips JB (1948) Growth of the sardine, *Sardinops caerulea*, 1941-42 through 1946-47. Calif Fish Game 71:33p.

Pilleri G, Siber, HJ (1989) Neuer spättertiärer cetotherid (Cetacea, Mysticeti) aus der Pisco-Formation Perus. In: Pilleri G (ed) Beiträge zur Paläontologie der Cetacean Perus. Hirnanatomisches Institut, Ostermundingen, pp 108-115

Pivorunas A (1977) The fibrocartilage skeleton and related structure of the ventral pouch of balaenopterid whales. J Morphol 151:299-314. doi: 10.1002/jmor.1051510207

Pivorunas A (1979) The feeding mechanisms of baleen whales. Am Sci 67:432-440

Pyenson ND, Goldbogen JA, Vogl AW, Szathmary G, Drake RL, Shadwick RE (2012) Discovery of a sensory organ that coordinates lunge feeding in rorqual whales. Nature 485:498-501. doi: 10.1038/nature11135

Rasband WS (1997-2014) ImageJ. U. S. National Institutes of Health, Bethesda, Maryland, USA. http://imagej.nih.gov/ij/

Steeman ME (2007) Cladistic analysis and a revised classification of fossil and recent mysticetes. Zool J Linn Soc-Lond 150:875-894. doi: 10.1111/j.1096-3642.2007.00313.x

Swift CC, Barnes LG (1996) Stomach contents of *Basilosaurus cetoides*: implications for the evolution of cetacean feeding behavior, and evidence for vertebrate fauna of epicontinental Eocene seas (abstract). Paleontol Soc Sp Pub 8:380

Tavani G (1973) Ipotesi sulla presenza di grossi frammenti di gneiss e di calcare nella "Pietra leccese" della Puglia. Atti Soc Tosc Sci Nat Mem Ser A 80:121-125

Tsai CH, Fordyce RE (2015) The earliest gulp-feeding mysticete (Cetacea: Mysticeti) from the Oligocene of New Zealand. J Mamm Evo. doi: 10.1007/s10914-015-9290-0

Uhen MD (2004) Form, function, and anatomy of *Dorudon atrox* (Mammalia, Cetacea): an

archaeocete from the middle to late Eocene of Egypt. Univ Mich Pap Paleontol 34:1-222

Valdés J, Ortlieb L, Gutierrez D, Marinovic L, Vargas G, Sifeddine A (2008) 250 years of sardine and anchovy scale deposition record in Mejillones Bay, northern Chile. Progr Oceanogr 79:198-207. doi: 10.1016/j.pocean.2008.10.002

Werth AJ (2000) Feeding in marine mammals. In: Schwenk K (ed) Feeding: form, function, and evolution in tetrapod vertebrates. Academic Press, San Diego, pp 487-526

Whitehead PJP (1985) Clupeoid fishes of the world (Suborder Clupeoidei): an annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies, and wolf-herrings. Part 1 - Chirocentridae, Clupeidae and Pristigasteridae. FAO Fisheries Synopsis, Rome

Yabumoto Y (1988) Pleistocene clupeid and engraulidid fishes from the Kokubu group in Kagoshima Prefecture, Japan. Bull Kitakyushu Mus Nat Hist 8:55-74

Figure captions

Fig. 1 Map and corresponding composite stratigraphic section of the locality of Cerro Colorado (Pisco Basin, southern Peru) showing the location of M10 and 56 other mysticete skeletons attributed to the same undescribed new cetotheriid species. All these fossils are from the late Miocene (Tortonian) lower allomember of the outcropping Pisco Formation. Note that the holotype of the macroraptorial sperm whale *Livyatan melvillei* was found a few hundred meters from M10. Modified after Bianucci et al. (in press).

Fig. 2 The cetotheriid skeleton M10 with associated fish remains from Cerro Colorado. **a, b** the fossil after partial excavation (dotted lines mark the outline of hidden ribs). **c, d** Close up of **a**, showing the aggregate of tightly packed, deeply mingled fish scales and bones exposed between the left posterior ribs of M10.

Fig. 3 Right mandible (MUSM 2553) of the undescribed new cetotheriid species from Cerro Colorado. **a** Medial view. **b, c** Dorsomedial view.

Fig. 4 Four micro-CT images showing the main fragment (fragment 4) of the fossilized stomach content MUSM 2630 in four different views. Note the complex architecture of the fish remains (tight 3D packing and deep degree of mingling and fragmentation) and the absence of evidence for chemical corrosion, which are fully compatible with the content of the forestomach of extant piscivorous cetaceans.
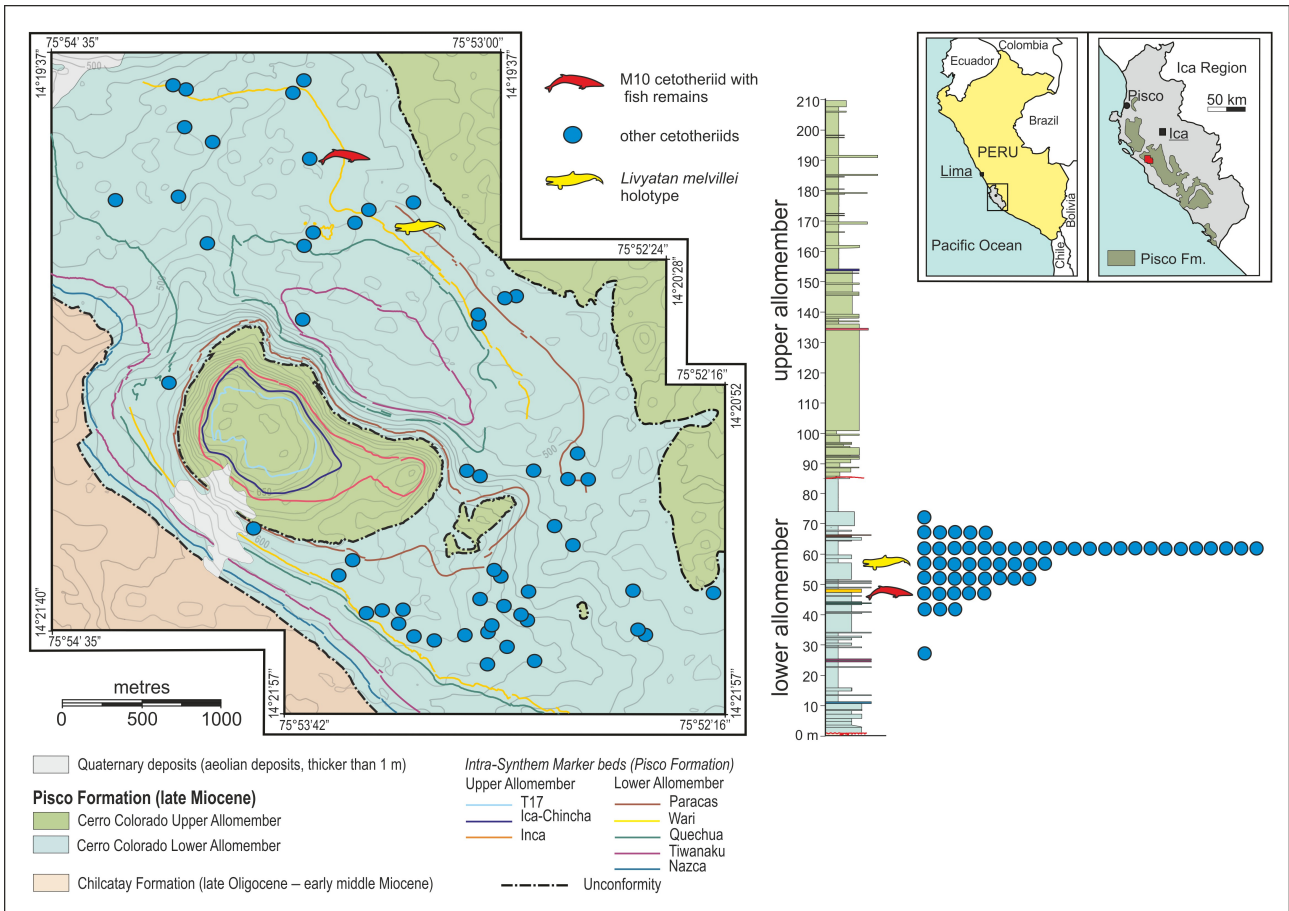
Fig. 5 Examples of fish bones and scales based on micro-CT 3D reconstructions of the fossilized stomach content MUSM 2630. **a** Various bony and dermal elements detected in fragment 4 (note the

characteristically striated opercle). **b** Various bony and dermal elements detected in fragments 1 and 2 (note the typical cycloid scales, the partial maxillary, and the abdominal scute). All identified elements, except for a large undetermined bone, are attributed to the clupeid fish *Sardinops* sp. cf. *S. sagax*. Line drawing of extant *S. sagax* (Pacific pilchard) skeleton modified after Yabumoto (1988).
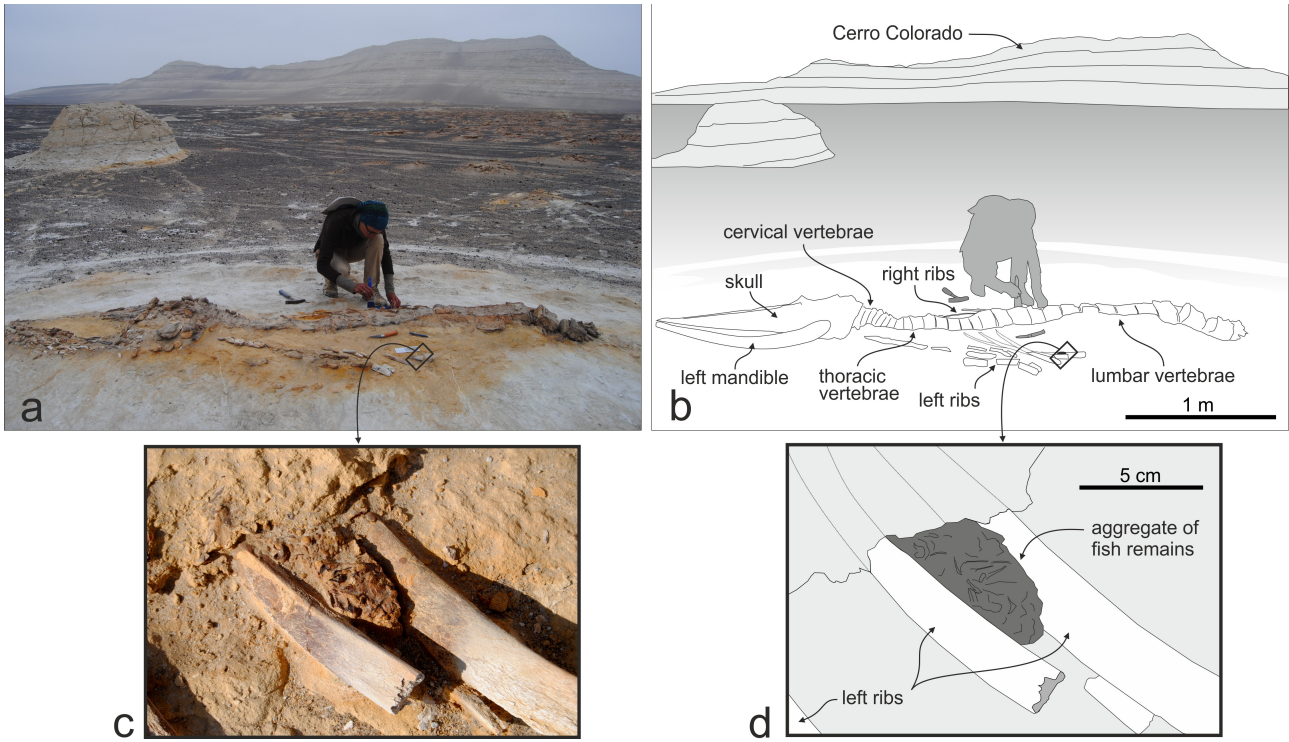

Fig. 6 Micro-CT image of an incomplete but still articulated lepidotrichium referred to *Sardinops* sp. cf. *S. sagax* found in the fossilized stomach content MUSM 2630 (fragment 4).
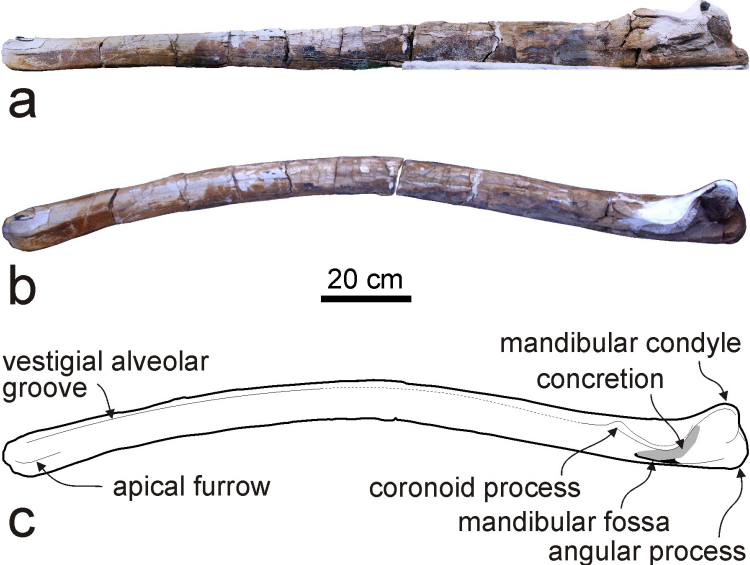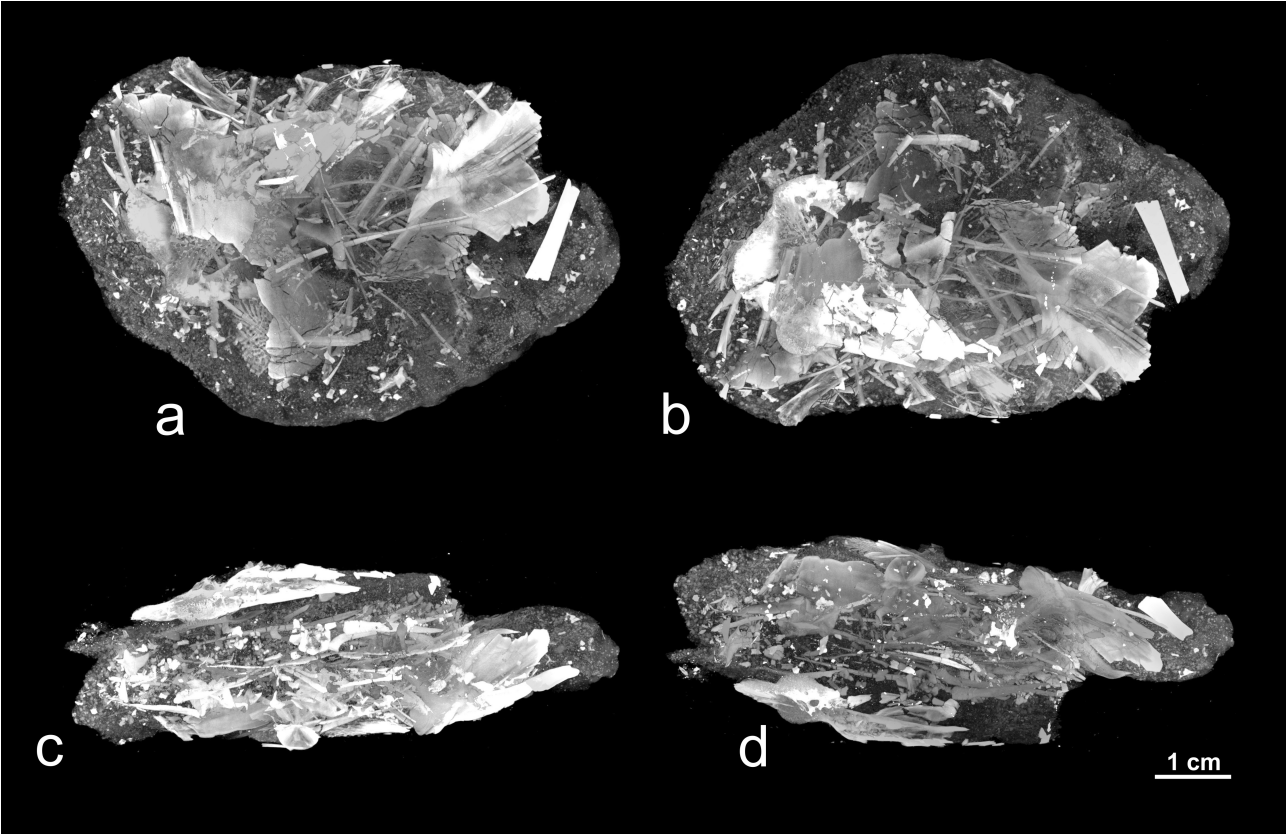
Figures

Fig. 1

Fig. 2

Fig. 3

a

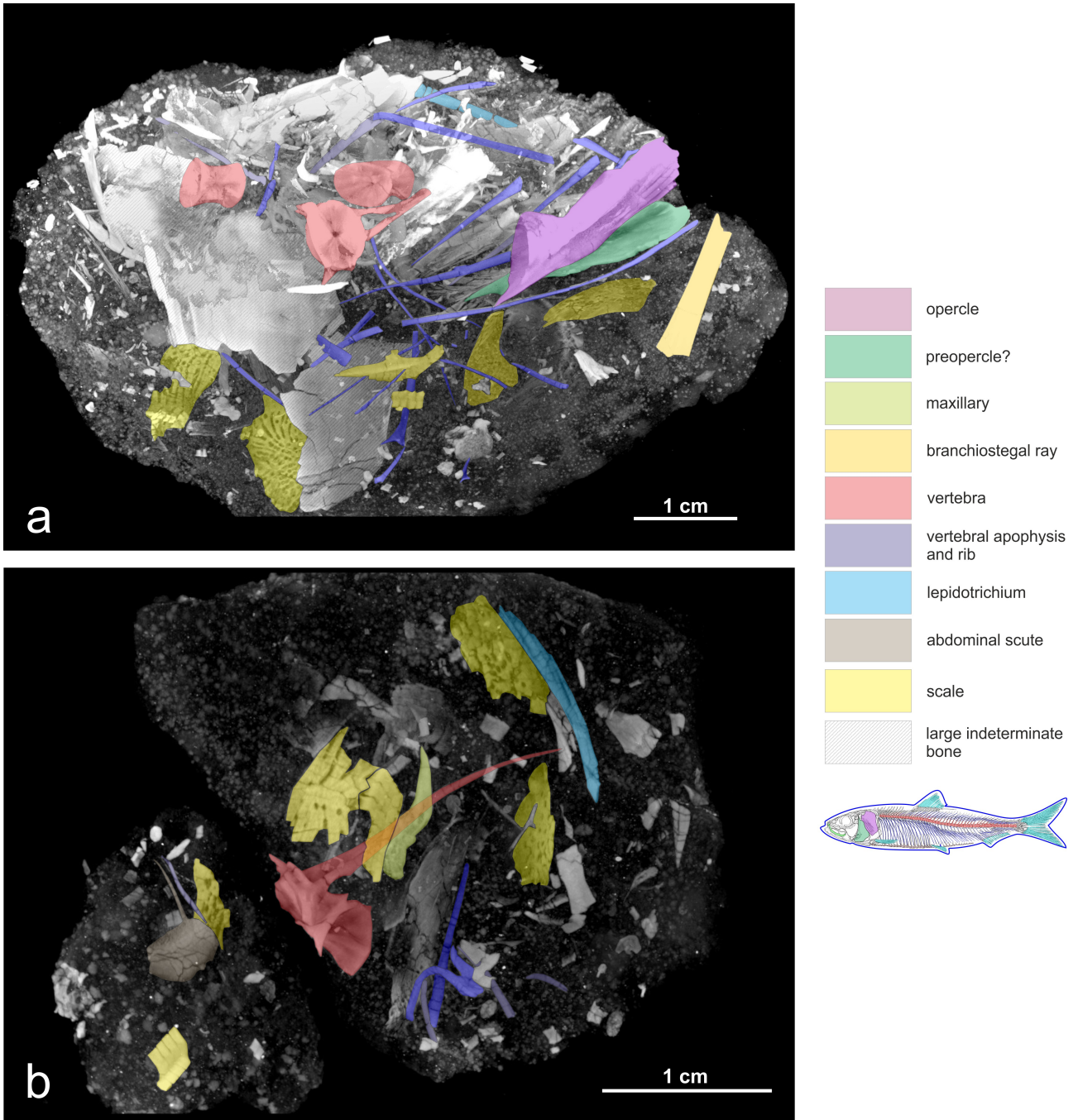**b**

20 cm

vestigial alveolar
groove

mandibular condyle

concretion

apical furrow

coronoid process

mandibular fossa

angular process

c

Fig. 4

Fig. 5

Fig. 6