

A WELL PRESERVED SKELETON OF THE FOSSIL SHARK *COSMOPOLITODUS HASTALIS* FROM THE LATE MIOCENE OF PERU, FEATURING FISH REMAINS AS FOSSILIZED STOMACH CONTENTS

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Abstract. Both the preservation of the poorly mineralized skeleton of sharks and the preservation of stomach contents are rarely observed in the fossil record. Here we report on a partial skeleton of a lamniform shark, including portions of the visceral arches and the anterior segment of the vertebral column, collected from the late Miocene beds of the Pisco Formation exposed at Cerro Yesera (Ica Desert, South Peru). Based on the morphology of the preserved teeth, this specimen was determined as a juvenile of the extinct lamnid species *Cosmopolitodus hastalis*. The shark skeleton includes remains of fish (featuring a pilchard determined as *Sardinops* sp. cf. *S. sagax*) in the abdominal region. These fish remains are interpreted herein as the fossilized stomach contents of the shark. For the first time, piscivory is demonstrated in a juvenile individual of *Cosmopolitodus hastalis*. This result is consistent with the current knowledge about the feeding habits of immature individuals of extant lamniform shark species (including *Carcharodon carcharias* and *Isurus oxyrinchus*). Our report further outlines the fundamental role of schooling pilchards in the late Miocene trophic chains of the highly productive coastal waters off present South Peru. Moreover, the find of this well preserved shark skeleton strengthens the qualification of the Pisco Formation as a Fossil-Lagerstätte, and emphasizes the role of early mineralization processes in cases of exceptional preservation.

INTRODUCTION

Among fossil remains of vertebrates from Miocene marine deposits worldwide, isolated shark teeth are likely the most represented items. In contrast, other typologies of selachian remains (i.e., vertebrae, rostral nodes, etc.) are much less frequent, and articulated shark specimens consisting of both cranial and postcranial skeletal elements represent exceptional finds. This is mainly due to the peculiar anatomical and physiological features of sharks, which bear a poorly mineralized (i.e., largely cartilaginous) axial and cranial skeleton throughout their life cycle, whereas they replace teeth continuously (extant sharks can lose thousands or even tens of

thousands teeth during their lifetime). In spite of being overly rare in the fossil record, articulated fossil shark specimens are highly informative and greatly contribute to shape our comprehension of the anatomy, phylogeny, and ecology of extinct selachian taxa (e.g., Shimada & Cicimurri 2005; Shimada 2007; Ehret et al. 2009a, 2012; Fanti et al. 2016).

Predation and scavenging by sharks on various prey items are testified in the fossil record by various typologies of ichnofossils, including bite marks on bones (e.g., Deméré & Cerutti 1982; Cigala Fulgosi 1990; Aguilera et al. 2008; Cicimurri & Knight 2009; Bianucci et al. 2010; Bianucci & Gingerich 2011; Govender & Chinsamy 2013; Govender 2015; Collareta et al. 2017), shark teeth embedded in (or strictly associated to) remains of the prey (e.g.,

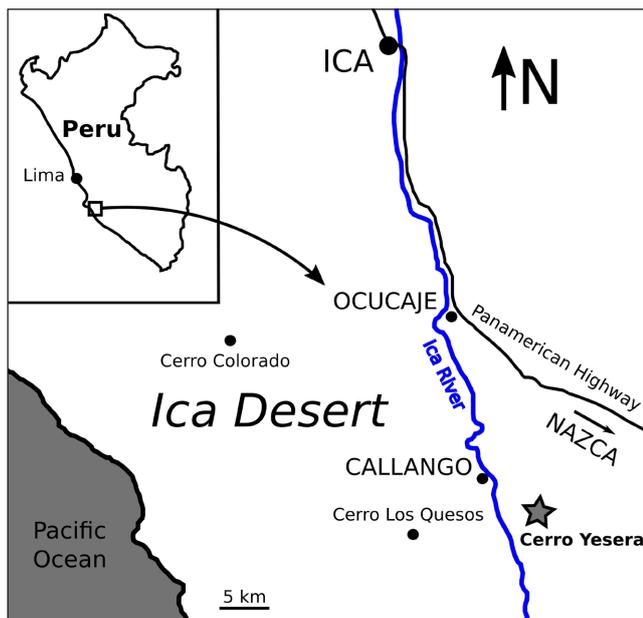


Fig. 1 - Map of the Ica Desert indicating the site of Cerro Yesera c. 8 km south-east to the locality of Callango, southern coast of Peru, where the fossil shark specimen CPI-7899 was discovered. The location of Cerro Colorado and Cerro Los Quesos, two highly fossiliferous sites of the Pisco Formation, is also reported.

Aguilera & Aguilera 2004; Lambert & Gigase 2007; Ehret et al. 2009b; Takakuwa, 2014), coprolites (e.g., Diedrich & Felker 2012; Stringer & King 2012), and stomach contents (e.g., Shimada 1997a; Fanti et al. 2016). Such occurrences, coupled with morphological observations on fossil shark teeth, contribute to depict the ecotrophic habits and preferences of ancient shark taxa. Fossil stomach contents, in particular, often provide the most accurate glimpse into the diet of fossil vertebrates, since both the predator (or scavenger) and prey (or scavenged) taxa can usually be identified (Cicimurri & Everhart 2001).

A partially complete articulated skeleton of the extinct mackerel shark species *Cosmopolitodus hastalis* (Chondrichthyes: Elasmobranchii: Lamniformes), including part of the cartilaginous visceral arches and the anterior portion of the vertebral column, was recently collected from late Miocene deposits of the Pisco Formation exposed at Cerro Yesera (Ica Desert, South Peru) (Fig. 1). During the preparation of this specimen, skeletal and dermal elements of bony fish appeared in the abdominal region, thus raising the possibility that the last meal of the shark also fossilized (Fig. 2). In this paper, we expand on our first report of these fossil remains (Chacaltana et al. in press) and discuss their paleobiological significance.

STRATIGRAPHICAL FRAMEWORK

The Pisco Formation (East Pisco Basin, South Peru) is a late Neogene marine sedimentary unit known as one of the most significant Cenozoic marine Fossil-Lagerstätten worldwide, due to the abundance, diversity, and excellent state of preservation of fossil vertebrates (e.g., Esperante et al. 2015; Bianucci et al. 2016a, b). In the Ica Desert, the Pisco Formation is late Miocene in age and consists of conglomerates, sandstones, siltstones, tuffaceous beds, dolomitized horizons, and diatomaceous mudstones which depict a shallow-marine environment characterized by high ocean primary productivity (Muizon & DeVries 1985; Brand et al. 2011; Di Celma et al. 2016a, b). The fossil shark skeleton was collected by three of us (C.C., W.V., and M.U.-S.) during the fieldwork related to the realization of the new ‘Carta Geológica Nacional del Perú’ in the site of Cerro Yesera, on the left side of the Ica River (Ocucaje district, Ica department), c. 8 km SW to the locality known as Callango (GPS geographic coordinates: S 14°31’16”, W 75°34’51”), from a silty interval showing flat parallel lamination.

TAXONOMIC REMARKS

Among extinct mackerel sharks, *Oxyrhina hastalis* Agassiz, 1838 represents in various aspects a problematic taxon. The systematic assignment of this species at the genus level is indeed uncertain and debated, with various positions reflecting different phylogenetic hypotheses. Some authors (e.g., Purdy et al. 2001) keep the traditional view to consider *O. hastalis* as a member of the extant genus *Isurus* Rafinesque, 1810. In turn, other sources (e.g., Ward & Bonavia 2001) consider *O. hastalis* as a member of the fossil genus *Cosmopolitodus* Glikman, 1964. Finally, some authors (e.g., Ehret et al. 2012) place *O. hastalis* in the currently monotypic genus *Carcharodon* Smith in Müller and Henle, 1838. Although the ongoing debate about the taxonomy, systematics, and phylogeny of *O. hastalis* will hopefully benefit from the find reported herein, providing an answer to these questions is beyond the purposes of the present paper. Therefore, following what we have already done in three precedent works dealing with the fossil sharks of the Pisco Formation (Bianucci et al. 2010, 2016a, b), we provisionally refer

O. hastalis to the genus *Cosmopolitodus*. The systematic placement of *O. hastalis* and the related phylogenetic issues have been addressed in more detail in a recent work (Landini et al. 2017) based on the fossil record of Lamniformes from Cerro Colorado, a highly fossiliferous site of the Pisco Formation in the Ica Desert (e.g., Bianucci et al. 2010, 2016b; Lambert et al. 2010a, b, 2015; Collareta et al. 2015; Gariboldi et al. 2015; Gioncada et al. 2016).

Some authors considered *C. hastalis* as synonym of the broad-toothed form *Oxyrhina xiphodon* Agassiz, 1838 (e.g., Ehret et al. 2012; Takakuwa 2014). We agree with Purdy et al. (2001) and Cione et al. (2012) in supporting the existence of a separate extinct broad-toothed species that significantly differs from *C. hastalis*. Following Cione et al. (2012), we prefer *Oxyrhina plicatilis* Agassiz, 1843 to *O. xiphodon* as an undoubtedly valid name for this species. Differing from previous name combinations for *O. plicatilis* [reported as *Carcharodon plicatilis* in Cione (2012), Carrillo-Briceño et al. (2015), and Staig et al. (2015)], this species is recombined herein as *Cosmopolitodus plicatilis*. This new combination should be regarded as a mere replacement of the more widespread but allegedly problematic combination *Cosmopolitodus xiphodon*. These critical aspects have also been discussed in a recent work on the chondrichthyan remains of Cerro Colorado (Landini et al. 2017).

SYSTEMATIC PALEONTOLOGY

- Class **CHONDRICHTHYES** Huxley, 1880
 Subclass **ELASMOBRANCHII** Bonaparte, 1838
 Order **Lamniformes** Berg, 1958
 Family **Lamnidae** Müller and Henle, 1838
 Genus *Cosmopolitodus* Glikman, 1964

Cosmopolitodus hastalis (Agassiz, 1838)

Figs 2A, 3

Material: CPI-7899, a partially complete articulated skeleton consisting of the Meckel's cartilages, part of the palatoquadrate, part of the hyoid apparatus, possibly fragments of the dorsoventrally compressed chondrocranium, 23 teeth, and the anteriormost 38 vertebrae; dermal and skeletal remains of fish are present in the abdominal region.

Locality: Cerro Yesera (GPS geographic coordinates: S 14°31'16", W 75°34'51"), a site in the Ica Desert (Ocucaje district, Ica department) where the late Miocene fossiliferous beds of the Pisco Formation are exposed.

Repository: CPI-7899 is permanently kept in Lima, in the paleontological collection of the Instituto Geológico Minero y Metalúrgico (INGEMMET).

Description of the shark skeleton CPI-7899. Like many other fossil vertebrates from other sites of the Ica Desert, CPI-7899 (Fig. 2A) is contained within a hardened yellowish matrix interpreted herein as a partially developed concretion. The Meckel's cartilages are well (although partially) preserved (Figs. 3A, B). The two hemimandibles contact each other at the level of the symphysis; they are slightly rotated along their long axis (possibly as a response to lithostatic compaction after burial) so that the lateral aspect of the Meckel's cartilages is exposed ventrally (i.e., upwards). Both hemimandibles are transversely narrow and distinctly convex ventrally in their anterior half, exhibiting mesiodistal curvature; in turn, they widen and flatten posteriorly. Both Meckel's cartilages lack their posterior termination, although the right hemimandible is more complete and exhibits a rather broad posterolateral expansion which is not preserved in its left antimer. On the whole, the Meckel's cartilages of CPI-7899 are very similar to those of various extant species of Lamniformes (including *Carcharodon carcharias* and *Isurus* spp.) illustrated by Mollen et al. (2012). Between the hemimandibles, compressed fragments of the chondrocranium appear to be present below a coating of hardened sediment hosting several disarticulated teeth (see below). Elements of the hyoid apparatus are also preserved. The right hemimandible is bordered medially and posteromedially by the right ceratohyal and, possibly, by the right edge of the basihyal. Likewise, the left hemimandible is medially bordered by the left ceratohyal. Posterior and parallel to the proximal portion of the right ceratohyal, a band of fossilized cartilage (interpreted herein as part of the right palatoquadrate) is exposed; it continues behind (i.e., dorsal to) the anteriormost portion of the vertebral column and disappears below the left ceratohyal. The right hyomandibular can be tentatively recognized, partially hidden by the posterolateral tip of the right palatoquadrate. The putative left hyomandibular contacts the posteromedial corner of the partial left Meckel's cartilage and partially covers a vertebral centrum as a slice of fossilized cartilage.

Twenty-three teeth have been detected in the mandibular region of CPI-7899 (Figs. 3A-D); most of them are disarticulated and displaced from their original position. Twenty-one of them (including functional teeth with intact roots as well as replacement teeth represented only by crowns)

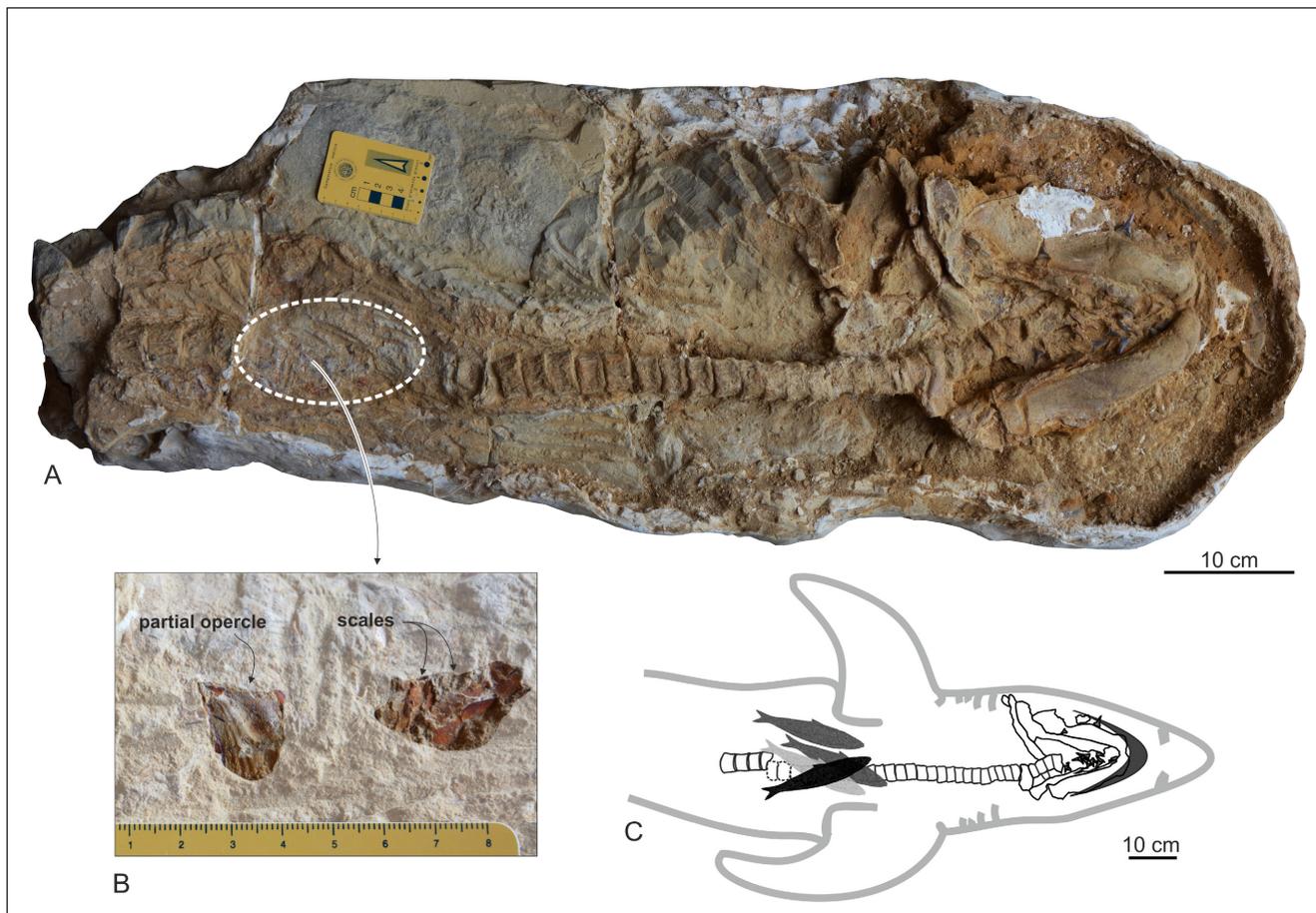


Fig. 2 - Fossil remains of the extinct mackerel shark *Cosmopolitodus hastalis* (specimen CPI-7899) and associated fish elements found in Cerro Yesera. A) Overview of CPI-7899, with the area where the fossilized stomach contents were found encircled. B) Fish remains (a partial opercle and a cluster of scales) attributed to the clupeid fish *Sardinops* sp. cf. *S. sagax*. C) Line drawing of the shark specimen CPI-7899 with a reconstructed outline of its carcass lying ventral-side up on the seafloor. Some individuals of *Sardinops* sp. cf. *S. sagax* are schematically represented in the abdominal region of CPI-7899.

are preserved between the two hemimandibles (e.g., Fig. 3C). A single lower lateral tooth takes place on the ventrolateral face of the right Meckel's cartilage (Fig. 3D). A single tooth is still articulated along the posterior portion of the dentigerous margin of the right Meckel's cartilage. Even though all the teeth but one are not in anatomical connection, their disposition between the hemimandibles recalls a somewhat anatomical order: the few preserved anterior teeth are indeed located anterior to the numerically predominant lateral teeth. All the detected teeth present crowns with smooth cutting edges, not displaying either lateral cusplets or basal serrations. Of the twenty-three teeth identified, about half of them can be referred as belonging to the upper dental series. The upper anterior teeth are labiolingually compressed, and their tips show an evident labial curvature, a character shared by *Isurus oxyrinchus* and *Cosmopolitodus hastalis* according

to Purdy et al. (2001). The height of the crown of the observed upper teeth does not exceed 25 mm. The lower teeth are less robust and less laterally hooked than those of *I. oxyrinchus*; their root lobes are more transversely elongated and less massive than those of *Cosmopolitodus plicatilis*. As characteristically observed in *C. hastalis* and *Isurus paucus*, and differing from *I. oxyrinchus*, the cutting edges of the lower anterior teeth are sharply defined from the tip to the base of the crown. On the whole, the observed teeth differ both from the more mediolaterally broad, strongly triangular teeth of juveniles and adults of *C. plicatilis*, and from the mediolaterally narrower, labiolingually thicker, nearly semicylindrical, and somewhat flexuous teeth of juveniles and adults of *I. oxyrinchus*. Based on these observations, we refer CPI-7899 to *C. hastalis*.

Thirty-eight clearly lamniform precaudal vertebrae are preserved in CPI-7899 (Fig. 2A). Almost

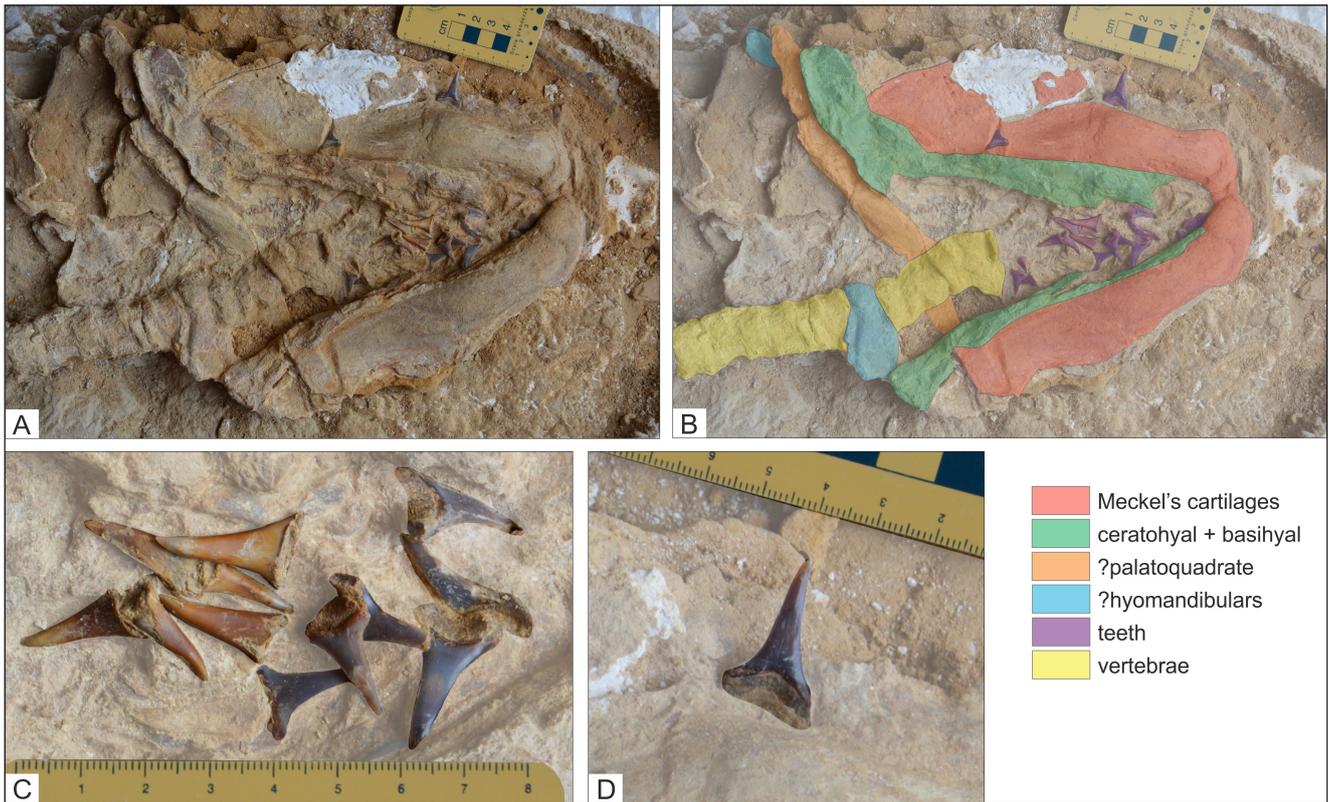


Fig. 3 - Anatomical features of the extinct mackerel shark *Cosmopolitodus hastalis* (specimen CPI-7899). A) Head region of CPI-7899. B) Line drawing of the head region of CPI-7899, with some preserved elements of the oral apparatus highlighted. C) Close-up on a group of disarticulated teeth preserved between the Meckel's cartilages of CPI-7899. D) Close-up on a lower posterior tooth still placed on the tooth-bearing margin of the right Meckel's cartilage of CPI-7899.

all them are preserved in anatomical position, forming a slightly S-shaped segment of vertebral column; only the 25th vertebra is disarticulated from the adjacent centra. The vertebrae between the 26th and the 32nd centra are partially covered by sediment, and only their outline is discernible. The preservation quality of the vertebrae is excellent, and fine anatomical details, such as the plates of mineralization radiating from the double cone-shaped centrum and the concentric accretion lamellae, are readily observable.

Description of the fish remains associated to CPI-7899. In the abdominal region of CPI-7899, between the 25th and the 33rd vertebra, an assemblage of dermal and skeletal remains referable to a small-sized bony fish is present (Fig. 2B); unfortunately, large part of this material was lost during the first phases of preparation of CPI-7899. Fish scales dominate this assemblage; fragmentary and disarticulated fish bones are also present. Scales are typically cycloid and about 1 cm-sized; they are often found imbricated and arranged in clusters

(Fig. 2B). Some well-preserved large scales display grainy protuberances in their central portion and curved fracture lines (looking similar to radii) in the lateral fields. An almost complete opercle is in large part preserved as an impression (and, partially, as a thin film of bone); the opercle shows dorsoventrally orientated bony striae which gradually expand towards the ventral portion of the bone (Fig. 2B). The estimated dorsoventral length of the opercle is 27 mm. A very fragmentary articular has also been observed.

A distinctly striated opercle is a character shared by three extant clupeid genera: *Alosa*, *Sardinia*, and *Sardinops* (e.g., Whitehead 1985; McPhail 2007). In turn, the co-presence in some large scales of central protuberances and symmetrical radiating fracture lines is considered well characteristic of the extant Pacific pilchard *Sardinops* and permits to discriminate this currently monotypic genus from other clupeid genera (including *Alosa* in which the scales are differently arranged (Patterson et al. 2002; pers. obs.)). Therefore, large part of the preserved fish remains found in association with CPI-7899

could be attributed to a single clupeid species fully compatible with *Sardinops sagax*. According to molecular investigations, an early Miocene vicariance event due the closure of the Tethys Sea corridor splitted an ancient sardine population in an Atlantic clade (represented by the genus *Sardina*, whose fossil record is to our knowledge limited to the Atlantic Ocean and the surrounding Mediterranean and Paratethyan basins) and an Indo-Pacific clade (represented by the genus *Sardinops*, known as a fossil along the margins of the Pacific Ocean from a few published records) (see Collareta et al. 2015, and references therein). Following what we have already done when dealing with similarly incomplete and not fully diagnostic material (Collareta et al. 2015; Lambert et al. 2015), and considering that no fossil species of *Sardinops* has been described to date, here we refer all the anatomically identified fish remains to *Sardinops* sp. cf. *S. sagax*.

DISCUSSION

More than ten species of lamnid sharks are currently known from the Neogene sedimentary units infilling the East Pisco basin (Altamirano-Sierra 2012). In these deposits, *Cosmopolitodus hastalis* is represented by isolated teeth that are commonly found in the early Miocene beds of the Chilcatay Formation (Alvan De la Cruz 2008; Altamirano-Sierra 2012; pers. obs.) and in the late Miocene beds of the Pisco Formation (e.g., Muizon & DeVries 1985; Kindlimann 1990; Alvan De la Cruz 2008; Ehret et al. 2009a, 2012; Altamirano-Sierra 2012; Bianucci et al. 2010, 2016a, b; Landini et al. 2017). To our knowledge, CPI-7899 represents one of the few associated and articulated fossil specimens of Neogene Lamniformes worldwide, as well as one of the most complete and better preserved specimens of *C. hastalis* known to date. As far as regards this extinct species and its closest relatives, three fossil occurrences are especially noteworthy for their state of preservation. From the Pisco Formation, Ehret et al. (2009a) described an exceptionally well-preserved fossil shark specimen from the latest Miocene (or basal Pliocene) deposits exposed at Sud Sacaco (Bella Union district, Arequipa department), which they referred to an undescribed species in some way intermediate between *Carcharodon carcharias* and “*Isurus*” spp. [in particular “*Isurus*” *bas-*

talis, mentioned by the authors as *Carcharodon hastalis* and considered as including also the broad-toothed form “*Isurus*” *xiphodon* (= *Cosmopolitodus plicatilis*)]. The specimen described by Ehret et al. (2009a) preserves more than two hundred teeth, forty-five vertebrae, and most of its jaws; it was later designated by Ehret et al. (2012) as the holotype of the new species *Carcharodon hubbelli*. Another substantially complete lamniform shark skeleton from the Pisco Formation, collected from Correviento (another Late Miocene site in the Ica Desert), is currently exhibited in Lima at the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM) with catalogue number MUSM 638; although this specimen is labelled as belonging to “*Isurus*” *hastalis*, its dentition was largely reconstructed on the basis of isolated teeth of *C. plicatilis*. Therefore, it is not possible to provide an unambiguous determination for MUSM 638. Outside the Pisco Formation, Uyeno et al. (2007) described a nearly complete tooth set and several vertebrae of “*Isurus*” *hastalis* from the Pliocene of Chiba (Japan); this specimen features no remains of the mandibular arch, hyoid apparatus, or chondrocranium. Based on the morphology of the preserved teeth (Uyeno et al. 1990: Fig. 6), the specimen from the Pliocene of Chiba could perhaps be better attributed to *Cosmopolitodus plicatilis*. To our knowledge, no other associated skeleton attributed to *C. hastalis* has been reported from outside the Pisco Formation; therefore, CPI-7899 stands out as one of the most complete and well-preserved specimens of *C. hastalis* known worldwide to date.

As reported above, the height of the crown of the preserved upper teeth does not exceed 25 mm, thus suggesting that CPI-7899 is a juvenile individual. Moreover, these teeth are distinctly more slender than adult teeth of *C. hastalis*, in agreement with the pronounced ontogenetic heterodonty recognized in this fossil taxon (Marsili 2007). Observations on the postcranial skeleton of CPI-7899 also support an immature condition. Data regarding total vertebral counts of several modern mackerel sharks (including *Alopias* spp., *Carcharodon carcharias*, *Cetorhinus maximus*, *Isurus* spp., *Lamna* spp., and *Pseudocarcharias kamoharui*) show that counts range between 152 and 362, with a maximum value of 419 vertebrae in the common thresher shark (*Alopias vulpinus*) (Springer & Garrick 1964; Bass et al. 1975); similar vertebral counts (150-230) were estimated

in various fossil lamniform species (including *Carcharocles megalodon*, *Cretoxyrhina mantelli*, and *Scapanorhynchus lewisii*) (Cappetta 1980; Gottfried et al. 1996; Shimada 1997b). In turn, only thirty-eight centra are preserved in CPI-7899 (Fig. 2A); they could approximately correspond to about 40% of the total length of the vertebral column of the shark. Therefore, the total body length of CPI-7899 can be estimated at about 230–240 cm; a similar value is also obtained by applying the equations proposed by Gottfried et al. (1996) and Shimada (2008) for some lamniform taxa. This result confirms that CPI-7899 represents a physically immature specimen of *C. hastalis*.

Do the dermal and skeletal fish remains found along the vertebral column of CPI-7899 represent the stomach contents of the fossil shark? Alternatively, do they represent a fortuitous postmortem association? The lack of tractive structure in the sediment in which CPI-7899 is contained, coupled with the substantial articulation of some cluster of scales, indicates that the possibility that fish remains were washed by currents into the abdominal region of the shark is highly unlikely. In the same way, scavenging on the shark carcass by fish and consequent death of one or more individuals is also unrealistic, as the extant Pacific pilchard is known as an epipelagic schooling fish which almost exclusively forages on plankton, and only occasionally feeds on the eggs of other fish (Espinoza et al. 2009). Moreover, the absence of vertical trace fossils and burrows in the matrix surrounding CPI-7899 strongly suggests that the concentration of fish remains within the skeleton due to the action of benthic invertebrates is unlikely. In turn, hypothesizing that the fish remains associated to CPI-7899 are the fossilized stomach contents of the shark does not pose critical taphonomic issues. The placement of the fish bones and scales along the vertebral column of CPI-7899 (i.e., scattered between the 25th and the 33rd vertebra) is consistent with the location of the anterior portion of the stomach of extant mackerel sharks. As reported above, during the first phases of preparation of CPI-7899 a significant part of the fish remains went lost, and therefore their architecture and 3-D packaging cannot be ascertained. Nevertheless, the observation of clusters of still imbricated scales suggests that the fish hosted in the stomach of CPI-7899 were at least partially undigested when the shark died. It is well-known that the stomach of sharks can retain food in an undigested state for

long periods of time, up to several weeks (Wetherbee et al. 1990, and references therein). Based on these considerations, we suggest that the pilchard remains represent the last meal of the shark fossilized within the carcass of the predator (Fig. 2C).

The discovery of fossilized stomach contents associated to CPI-7899 represents a snapshot on the trophic habits of *Cosmopolitodus hastalis*. The feeding ecology of this extinct mackerel shark species has been addressed in previous works (e.g., Bianucci et al. 2010; Ehret et al. 2012; Takakuwa 2014). Unfortunately, in most of these works, the broad-toothed form *Cosmopolitodus plicatilis* is considered a synonym of *C. hastalis*; therefore, they could lead to oversimplified paleodietary reconstructions. In their monographic study of the fossil fish from Lee Creek Mine North Carolina, USA, Purdy et al. (2001) noted that teeth of *C. plicatilis* are absent in the early to middle Miocene Pungo Formation, which lacks fossil pinnipeds, whereas both teeth of *C. plicatilis* and pinniped remains are abundant in the late Miocene to Pliocene Calvert Formation; in turn, teeth of *C. hastalis* are well distributed and abundant in both formations. As far as regards the Mediterranean basin, Marsili (2007) proposed that, during the Miocene, *C. plicatilis* and *C. hastalis* were sympatric and occupied similar trophic niches in the same ecosystems; in turn, *Cosmopolitodus* is represented by the sole *C. plicatilis* in Mediterranean Pliocene deposits, which feature also a very rich and diversified marine mammal fauna (including pinnipeds and small-sized cetaceans; e.g., Bianucci et al. 2009). Commenting these data, Marsili (2007) proposed that adults of *C. plicatilis* were characterized by a diet primarily focused on small-sized marine mammals, with a trophic spectrum somewhat similar to that of the extant great white shark *Carcharodon carcharias*, whereas adults of *C. hastalis* were in large part piscivorous. We agree with this interpretation, and outline that the broad teeth of adult *C. plicatilis* could have been more adapted for consuming large prey (i.e., marine mammals) than those of adult *C. hastalis*, which in turn could have been more suitable for foraging on smaller vertebrates (i.e., various taxa of fish). To date, indirect evidences of feeding on marine mammals have been provided by Noriega et al. (2007) for *C. plicatilis*. However, size-based ontogenetic shifts in diet (e.g., changes in trophic level from mesopredator to apex predator) are well known in most extant selachian taxa (Lowe et al. 1996; New-

man 2003; Heupel et al. 2014); larger prey are consumed with increasing predator size, whereas small prey items are generally retained in the diet. Extant mackerel sharks are not an exception to this rule (e.g., Hussey et al. 2012); therefore, small- to medium-sized fish and invertebrates are important in the diet of juvenile individuals of large-sized, mammal-eating species of Lamniformes. In particular, in areas of high primary ocean productivity related to conditions of coastal upwelling, schooling clupeid fish like *Sardinops* are currently found as stomach contents of both juveniles of the shortfin mako *Isurus oxyrinchus* (e.g., one shark individual, measuring 115 cm in fork length, reported by Sepulveda et al. 2014) and juveniles of the great white shark *Carcharodon carcharias* (e.g., three shark individuals, ranging between 227 cm and 240 cm in total length, reported by Hussey et al. 2012). Furthermore, along the coasts of KwaZulu-Natal (South Africa), sardines form an important component of the diet of juveniles of *C. carcharias* during the so-called sardine run (Dudley & Cliff 2010). Therefore, our find of fish remains in the region of a juvenile of *Cosmopolitodus hastalis*, likely measuring about 230–240 cm in total length, is consistent with what we know about the trophic habits of young extant lamnid sharks like *Isurus oxyrinchus* and, especially, *Carcharodon carcharias*. Interestingly, in the fossil-rich site of Cerro Colorado, young teeth of *Cosmopolitodus hastalis* and *C. pliocatilis* are frequently found in the same stratigraphic horizons, thus suggesting that the juvenile stages of these two extinct species were fully sympatric and displayed largely superimposed (i.e., strongly similar) trophic spectra (Landini et al. 2017).

Our find indicates that, during the late Miocene, fish (especially pilchards) were part of the diet of young individuals of *C. hastalis* living off the coasts of South Peru. Two similar snapshots on the trophic relationships between the marine vertebrates of the Pisco Formation were recently reported from Cerro Colorado. Collareta et al. (2015) described the fossilized stomach content of a cetotheriid whale, whereas Lambert et al. (2015) interpreted an unusual beaked whale–fish assemblage as an evidence of predator–prey interaction. It is somewhat surprising that in both instances, as well as in the case study reported in this work, the stomach contents (or prey items) consists (or feature remains) of the Pacific pilchard *Sardinops* sp. cf. *S. sagax*. This observation emphasizes the fundamental

role of schooling pilchards in the late Miocene food chains of the highly productive coastal waters off present South Peru. Nowadays, the Humboldt Current System off Peru is known as one of the most productive coastal upwelling systems in the world, sustaining huge populations of both pilchards and anchovies (*Engraulis ringens*) which currently experience out-of-phase fluctuations over periods of about 50 years (Chavez et al. 2003; Gutierrez et al. 2003). As remains of *Engraulis* have not been documented from this sedimentary unit, shifts between a ‘sardine regime’ and an ‘anchovy regime’ are not documented in the late Neogene fossil record of the Pisco basin; nevertheless, our finds evoke a long history of coastal upwelling, high primary productivity, and long food chains in which small-sized, epipelagic, clupeiform schooling fish represented a fundamental trophic link hunted by a wide variety of marine vertebrates.

Both the fossilization of the poorly mineralized skeleton of a juvenile shark and the preservation of stomach contents are considered as very rarely occurring events; nevertheless, they surprisingly co-occurred in CPI-7899. Our find, together with other recently reported examples of extraordinary fossil preservation (Brand et al. 2004; Ehret et al. 2009a, 2012; Esperante et al. 2008; Bisconti 2012; Collareta et al. 2015; Lambert et al. 2015; Gioncada et al. 2016), contributes to qualify the Pisco Formation as a true Konservat-Lagerstätte. Furthermore, the presence of a partially developed concretion enclosing CPI-7899 further supports the hypothesis that the early formation of diagenetic minerals around vertebrate carcasses, coupled with the mineralization of poorly calcified tissues, is one of the most relevant processes responsible for exceptional fossil preservations observed in the Pisco Formation assemblage – a view already proposed by Gariboldi et al. (2015) and Gioncada et al. (2016).

CONCLUSIONS

- 1) CPI-7899 is a well-preserved fossil lamnid shark specimen collected from the late Miocene beds of the Pisco Formation (South Peru). It preserves part of the cartilaginous oral apparatus and the anterior portion of the vertebral column; fish remains are also present in the abdominal region of the fossil shark.

2) Based on tooth morphology, CPI-7899 was described and identified as a juvenile of the extinct species *Cosmopolitodus hastalis*. CPI-7899 represents one of the most complete and better preserved specimens of *C. hastalis* known to date.

3) The fish remains associated to CPI-7899 were also described; among them, an opercle and various scales of a pilchard (*Sardinops* sp. cf. *S. sagax*) were recognized. These fish remains were interpreted as the fossilized stomach contents of CPI-7899. For the first time, piscivory is demonstrated in *Cosmopolitodus hastalis*. This result is consistent with the trophic habits of young lamniform sharks like *Isurus oxyrinchus* or *Carcharodon carcharias*, considered by several authors as close relatives of *C. hastalis*.

4) This find, coupled with the recently published record of stomach contents from the Pisco Formation, confirms that - during the late Miocene - schooling pilchards played a key role in the trophic chains of the highly productive coastal waters off present South Peru.

5) Our report outlines the role of early mineralization processes as promoters of exceptional preservation in the Pisco Formation Fossil-Lagerstätte.

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