



**A rhinopristiform sawfish (genus *Pristis*)
from the middle Eocene (Lutetian) of southern Peru
and its regional implications**

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Abstract: Modern sawfishes (Rhinopristiformes: Pristidae) are circumglobally distributed in warm waters and are common in proximal marine and even freshwater habitats. The fossil record of modern pristid genera (*i.e.*, *Pristis* and *Anoxypristis*) dates back to the early Eocene and is mostly represented by isolated rostral spines and oral teeth, with phosphatised rostra representing exceptional occurrences. Here, we report on a partial pristid rostrum, exhibiting several articulated rostral spines, from middle Eocene strata of the Paracas Formation (Yumaque Member) exposed in the southern Peruvian East Pisco Basin. This finely preserved specimen shows anatomical structures that are unlikely to leave a fossil record, *e.g.*, the paracentral grooves that extend along the ventral surface of the rostrum. Based on the morphology of the rostral spines, this fossil sawfish is here identified as belonging to *Pristis*. To our knowledge, this discovery represents the geologically oldest known occurrence of Pristidae from the Pacific Coast of South America. Although the fossil record of pristids from the East Pisco Basin spans from the middle Eocene to the late Miocene, sawfishes are no longer present in the modern cool, upwelling-influenced coastal waters of southern Peru. Given the ecological preferences of the extant members of *Pristis*, the occurrence of this genus in the Paracas deposits suggests that middle Eocene nearshore waters in southern Peru were warmer than today. The eventual disappearance of pristids from the coastal waters off southern Peru might be interpreted as reflecting the late Cenozoic trend of strengthening of the Humboldt Current.

Key-words:

- East Pisco Basin;
- Elasmobranchii;
- exceptional preservation;
- Humboldt Current System;
- palaeobiogeography;
- palaeoclimatology;
- palaeoenvironments;
- Paracas Formation (Yumaque Member)

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Résumé : Un poisson-scie rhinoprístiforme (genre *Pristis*) de l'Éocène moyen (Lutétien) du Pérou méridional et ses implications régionales.- Les poissons-scies modernes (Rhinoprístiformes : Prístidae) présentent une distribution globale dans les eaux chaudes ; ils sont fréquents dans les habitats marins proximaux et même en eaux douces. Le registre fossile des genres modernes des Prístidés (*i.e.*, *Pristis* et *Anoxyprístis*) remonte à l'Éocène inférieur et est principalement représenté par des épines rostrales isolées et dents orales, ainsi que des rostres phosphatés représentant des événements exceptionnels. Nous rapportons ici un rostre partiel de Prístidae, présentant plusieurs épines rostrales articulées, provenant des couches de l'Éocène moyen de la Formation Paracas (Membre Yumaque) exposées dans la partie orientale du Bassin de Pisco au sud du Pérou. Ce spécimen très bien conservé permet l'observation de structures anatomiques qui sont difficilement fossilisables, par exemple les sillons paracentraux qui s'étirent le long de la face ventrale du rostrum. En se basant sur la morphologie des épines rostrales, ce poisson-scie fossile est identifié ici comme appartenant à *Pristis*. À notre connaissance, cette découverte représente la plus ancienne occurrence géologique connue de Prístidae le long des côtes pacifiques de l'Amérique du Sud. Bien que le registre fossile des Prístidés dans la partie orientale du Bassin de Pisco s'étende de l'Éocène moyen au Miocène supérieur, les poissons-scie ne sont plus actuellement présents dans les eaux côtières du sud du Pérou, eaux fraîches en raison de remontées d'eaux profondes. À la lumière des préférences écologiques des membres actuels du genre *Pristis*, la présence de ce genre dans la Formation Paracas suggère des températures de l'eau de mer plus élevées qu'actuellement dans les environnements littoraux du sud du Pérou au cours de l'Éocène moyen. La disparition finale des Prístidés des eaux côtières du sud du Pérou pourrait être interprétée comme reflétant la tendance au renforcement du courant de Humboldt au Cénozoïque supérieur.

Mots-clefs :

- partie orientale du Bassin Pisco ;
- Elasmobranchii ;
- conservation exceptionnelle ;
- Système du Courant de Humboldt ;
- paléobiogéographie ;
- paléoclimatologie ;
- paléoenvironnements ;
- Formation Paracas (Membre de Yumaque)

1. Introduction

Among extant cartilaginous fishes, members of the family Prístidae are large-sized, shark-shaped rays characterised by an elongated, dorsoventrally flattened rostrum whose lateral margins bear lancet-like, continuously growing, highly modified placoid scales (*e.g.*, CAPPETTA, 2012; WELTEN *et al.*, 2015). These dermal elements were described under several different terms, including "rostral teeth" and "rostral spines". Following CARRILLO-BRICEÑO *et al.* (2015) and COLLARETA *et al.* (2017a), the latter term is here preferred. Prístids are active predators that use their saw-like rostrum to uncover infaunal food items, immobilise potential prey, and stun or slash small fish and invertebrates (WUERINGER *et al.*, 2009, and references therein); as such, they are popularly known as "sawfishes". Extant prístids are classified into two genera: *Pristis* LINCK, 1790, which includes four living species, and *Anoxyprístis* WHITE & MOY-THOMAS, 1941, for which a single living species is known (LAST *et al.*, 2016; WEIGMANN, 2016). These aquatic representatives of the charismatic megafauna (here intended as large-sized animal species whose widespread appeal or symbolic value is seen as pivotal for attracting popular attention on conservation goals and policies; see *e.g.* DUCARME *et al.*, 2013) are circumglobally distributed in warm waters and are common in proximal marine and even brackish and freshwater habitats (*e.g.*, WUERINGER *et al.*, 2009; DULVY *et al.*, 2014). The fossil record of modern prístid genera dates back to the early Eocene and is mostly represented by isolated rostral spines and subordinate oral teeth (CAPPETTA, 2006, 2012; but see also CASE, 1994, for a re-

cord of *Pristis* from possibly upper Palaeocene strata of the Tusahoma Formation of Mississippi, USA); in addition, exceptional occurrences of phosphatised rostra have also been reported from a few localities worldwide (*e.g.*, VIGLIAROLO, 1891; LERICHE, 1905; ZBYSZEWSKI, 1947; CASIER, 1949; FARRÉS, 2003; CICIMURRI, 2007; CARRILLO-BRICEÑO *et al.*, 2015).

Decades of research on the celebrated fossil content of the East Pisco Basin of southern Peru has produced numerous noteworthy palaeontological papers dealing with various groups of aquatic vertebrates, including marine mammals (*e.g.*, MUIZON, 1988; BRAND *et al.*, 2004; ESPERANTE *et al.*, 2008; LAMBERT *et al.*, 2010, 2017, 2019; BIANUCCI *et al.*, 2010, 2016a, 2016b) and seabirds (*e.g.*, CLARKE *et al.*, 2007, 2010). In turn, the current knowledge of the fossil history of cartilaginous and bony fishes from this region is still scanty. In particular, for a long time, contributions dealing with the record of the cartilaginous fishes have been mostly limited to plain faunal lists (*e.g.*, MUIZON & DEVRIES, 1985; BIANUCCI *et al.*, 2010). However, recent investigations have focused on exceptionally preserved specimens (COLLARETA *et al.*, 2017c), rare and elusive taxa (SHIMADA *et al.*, 2017), and outstandingly productive tooth-bearing horizons from a handful of Miocene localities (*e.g.*, BIANUCCI *et al.*, 2018; LANDINI *et al.*, 2017a, 2017b, 2019). These studies provide a more comprehensive picture of the Neogene shark and ray assemblages from the basin infill.

In the present paper, we report on a partial prístid rostrum that exhibits several articulated rostral spines, from middle Eocene strata of the Paracas Formation exposed in the vicinity of the Zamaca locality, in the eastern sector of the East



Pisco Basin. This finely preserved specimen is here figured, described, and referred to the extant genus *Pristis*. The palaeobiogeographic, palaeo-environmental, and palaeoclimatic implications of this remarkable fossil are then briefly discussed.

2. Geological framework

The East Pisco Basin is a northwest-southeast elongated Andean forearc basin that extends along a desertic coastal plain between the towns of Pisco and Nazca (Ica Region, southern Peru). It is located just landward of where the aseismic Nazca Ridge impinges on the Peru–Chile trench (PILGER, 1981; HSU, 1992; MACHARÉ & ORTLIEB, 1992; HAMPEL, 2004) (Fig. 1.A). This basin is filled with a Cenozoic sedimentary succession that comprises, in ascending stratigraphic order, the Eocene Caballas and Paracas formations, the Oligo–Miocene Chilcatay Formation, and the Mio–Pliocene Pisco Formation (DUNBAR *et al.*, 1990; DEVRIES, 1998, 2017; DI CELMA *et al.*, 2016) (Fig. 1.B). These sedimentary units are lithologically complex and are bounded by regionally extensive unconformities marked by pavements of pebble- to boulder-sized igneous clasts. The unconformities reflect periods of subaerial exposure and document major breaks of the sedimentary history of the East Pisco basin; moreover, intraformational unconformities are also present (DEVRIES, 1998; DI CELMA *et al.*, 2017, 2018a). Therefore, following to the nomenclatural approach proposed by the NACSN (2005), the aforementioned unconformity-bounded formations might rather be regarded as alloformations (DI CELMA *et al.*, 2017).

The sawfish fossil reported here was found in deposits belonging to the middle to upper Eocene Paracas Formation (following the nomenclatural revision of DEVRIES, 2017) (Fig. 1.B). Similar to the transgressive sequences that comprise the geologically younger Chilcatay and Pisco formations (*e.g.*, DI CELMA *et al.*, 2017, 2018a; COLETTI *et al.*, 2018; DEVRIES & JUD, 2018), the Paracas Formation is comprised of a coarse-grained lower portion (*i.e.*, the Los Choros Member, consisting of conglomerates and mixed siliciclastic-bioclastic sandstones characterised by abundant tests of large benthic foraminifera) that is overlain by a package of finer sediments (*i.e.*, the Yumaque Member, consisting of silty sandstones and siltstones that feature a rich planktic assemblage) (RIVERA, 1957; TSUCHI *et al.*, 1988; DUNBAR *et al.*, 1990; DEVRIES, 1998, 2017; DEVRIES *et al.*, 2006; LEÓN *et al.*, 2008; UHEN *et al.*, 2011; COLETTI *et al.*, 2019) (Fig. 1.B). Note that a different stratigraphic scheme considers the Paracas Group as comprised of the Los Choros and Yumaque formations (*e.g.*, DÁVILA, 1989; DUNBAR *et al.*, 1990; DEVRIES, 1998; LEÓN *et al.*, 2008), which is the official position of the Peruvian Geological Survey (Instituto Geológico Minero y Metalúrgico, hereinafter referred to as the INGEMMET). The chondrichthyan specimen described herein comes from the basal strata of the Yumaque Member exposed in the vicinity of the Zamaca locality, along the eastern side of the lower Ica valley

(geographic coordinates of the collection site: 14° 38'27.1" S, 75°35'46.4" W) (Fig. 1.C). In the same area, *ca.* 6 km WSW of the collection site, the depositional age of the lower Yumaque beds has been recently reconstructed as close to 42.37 Ma (*i.e.*, Lutetian Stage) by means of calcareous nannoplankton biostratigraphy (COLETTI *et al.*, 2019; Fig. 1.C). This age estimate is here projected to the fossiliferous horizon where our sawfish specimen was found. Previous investigations on the sedimentological characteristics of nearby outcrops concur in indicating an inshore, inner shelf depositional palaeoenvironment situated below wave base (*e.g.*, DUNBAR *et al.*, 1990; UHEN *et al.*, 2011).

Marine vertebrates from the Paracas Formation include the holotype of the early branching penguin *Perudyptes devriesi* CLARKE *et al.*, 2007, and the holotypes of four archaic cetaceans, *i.e.*, the basilosaurids *Supayacetus muizoni* UHEN *et al.*, 2011, and *Ocucajea picklingi* UHEN *et al.*, 2011, the early diverging mysticete *Mystacodon selenensis* LAMBERT *et al.*, 2017, and the recently described protocetid *Peregocetus pacificus* LAMBERT *et al.*, 2019.

3. Systematic paleontology

Class CHONDRICHTHYES HUXLEY, 1880

Subclass ELASMOBRANCHII BONAPARTE, 1838

Infraclass NEOSELACHII COMPAGNO, 1977

Superorder BATOMORPHII CAPPETTA, 1980

Order RHINOPRISTIFORMES NAYLOR *et al.*, 2012

Family PRISTIDAE BONAPARTE, 1838

Genus *Pristis* LINCK, 1790

Pristis sp.

Figs. 2.A-B, 3.A-B, 4.A-E

Material and repository. CPI-7937, an incomplete rostrum, partially entombed in the surrounding siltstone and featuring at least 50 associated rostral spines (no oral teeth appear to co-occur with the specimen). 'CPI' is the acronym for 'Colección Paleontológica del INGEMMET' (=INGEMMET palaeontological collection), housed in Lima, Peru, where CPI-7937 is permanently kept.

Occurrence. Middle Eocene siltstones exposed in the Zamaca area, Ica Province, southern coast of Peru; GPS geographic coordinates: 14°38'27.1" S, 75°35'46.4" W (Fig. 1C). The sediment embedding the sawfish specimen belongs to the basal strata of the Yumaque Member of the Paracas Formation, whose deposition in the vicinity of the study site has been referred to the late Lutetian (see the geological framework for more details).

Rostral cartilage. CPI-7937 is preserved in two distinct blocks of siltstones. The main block (Fig. 2) enables the observation of the 425-mm-



long anterior-most portion of the rostrum, exposed in ventral view, based on the bending direction of the rostral spines (see description below) and still partly embedded in a silty matrix. The main block also preserves 34 rostral spines, 31 of which are still articulated with the rostral cartilage. The second block consists of tens of morphologically uninformative fragments of rostral cartilage with associated shreds of entombing sediment that are distributed on a 485-mm-long, 175-mm-wide area; moreover, at least 16 disarticulated, partly fragmentary rostral spines are also present. By comparing the reconstructed length of the rostrum (totalling *ca.* 90 mm) with the corresponding dimension in extant pristids (e.g., SEITZ & HOOVER, 2017, tab. 1), an adult or late juvenile ontogenetic stage is suggested for CPI-7937.

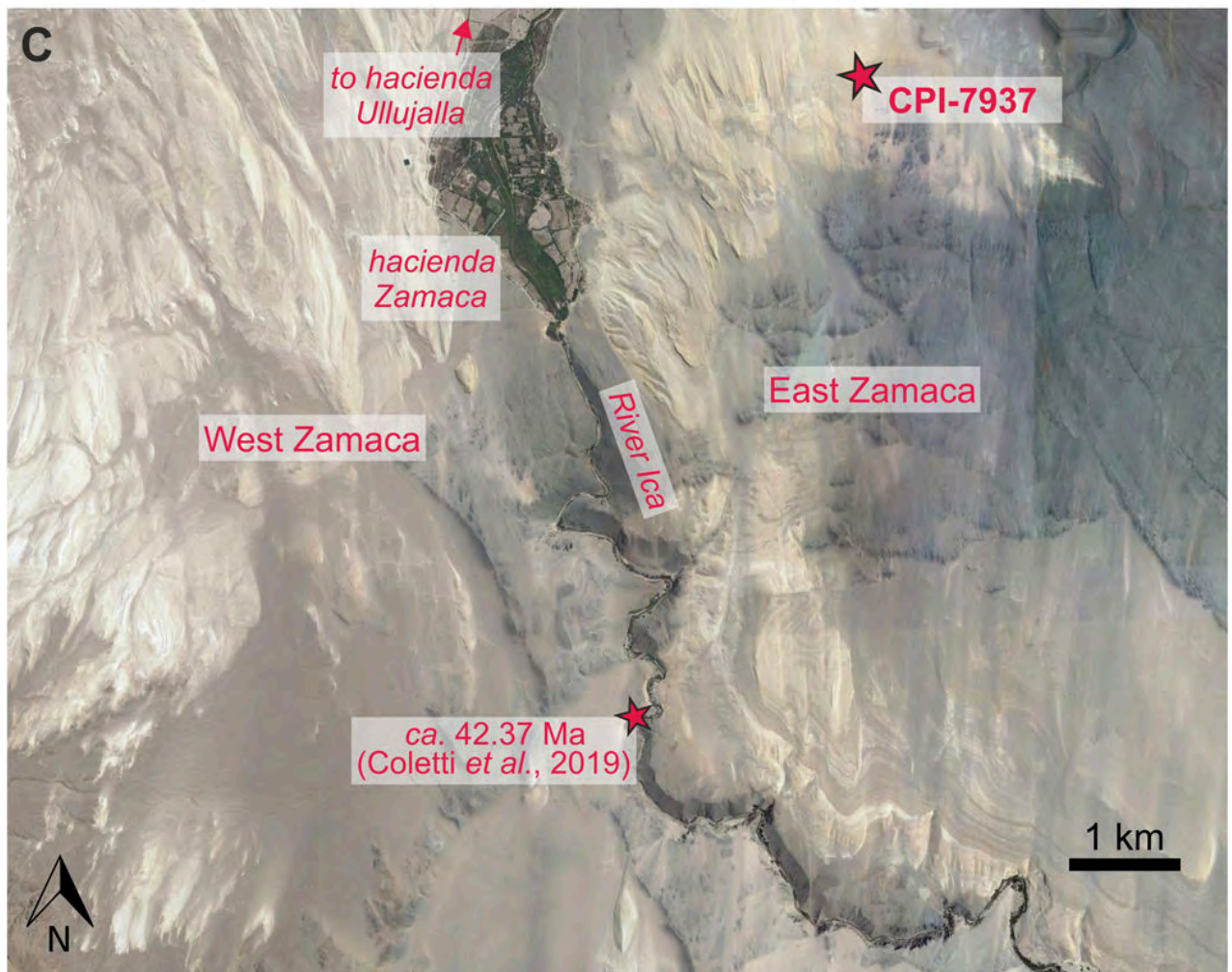
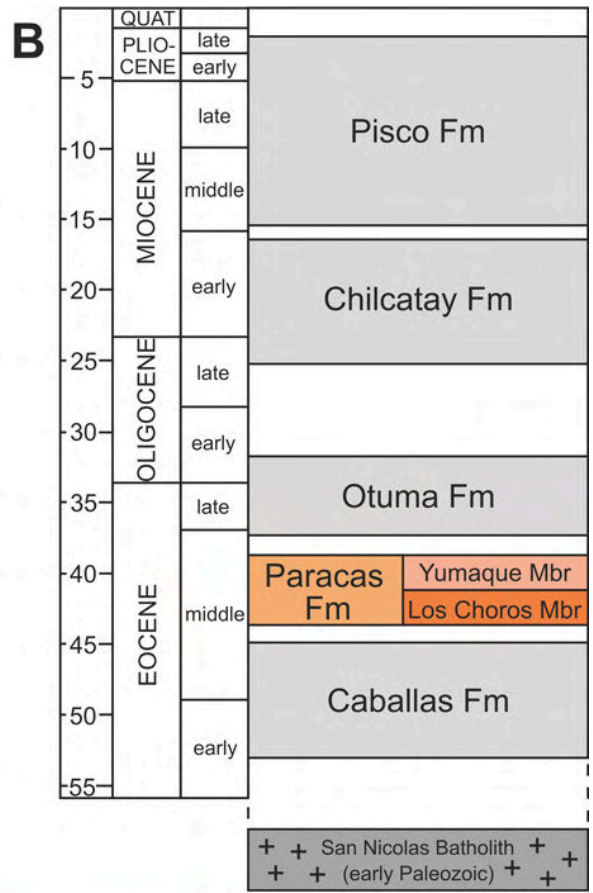
The portion of rostrum preserved in the main block (Fig. 2) is almost complete and dorsoventrally flattened, being *ca.* 12 mm thick along its entire length. Diagenetic compaction resulted in exaggerating the degree of dorsoventral flattening of the rostrum; indeed, the transverse section of the rostrum, which can be observed at the posterior end of the main block, shows that the internal rostral ducts (WUERINGER *et al.*, 2009, and references therein) have collapsed, so that no obvious cavities appear within the rostral cartilage. The rostrum gradually tapers towards its anterior-most tip, which appears to be almost complete. The transverse width of the rostral cartilage varies between *ca.* 60 mm (at the anterior end of the rostrum) and *ca.* 100 mm (at the posterior termination of the preserved portion of the rostrum). The ventral surface of the rostrum is gently convex to almost flat transversely and bears two distinct grooves trending the entire length of the preserved portion of the rostrum (Fig. 2). Each groove is just lateral to the midline (*i.e.*, paracentral *sensu* MILLER, 1974) and they are parallel with the lateral margins of the rostrum. In living sawfishes, the paracentral grooves [*sensu* CICIMURRI (2007), not to be confused with the 'ducts with ophthalmic & buccal nerves & rostral artery' of WUERINGER *et al.* (2009: Fig 4), which in turn coincide with the 'paracentral canals' of CICIMURRI (2007)] that are found on the dorsal and ventral surfaces of the rostrum host blood vessels (*i.e.*, veins; MILLER, 1974). The distance between the paracentral grooves changes gradually from 5.5 mm, measured at the anterior termination of the rostrum, to 14.5 mm (measured at the posterior end of the preserved portion of the rostrum). Lateral to the paracentral grooves, a series of rectangular cartilage projections emanate from the main body of the rostrum, and the edges of these form the alveoli where the rostral spines are located (Figs. 2,

3.A). All the preserved alveoli still host the corresponding rostral spines, so that each side of the rostrum exhibits 17 rostral spines (see description below). The alveoli of the right and left sides are slightly staggered, rather than directly opposing each other, the extent of unalignment changing significantly along the length of the preserved portion of the rostrum. The spacing between adjacent alveoli, measured at the base of the free portions of the rostral spines (*i.e.*, along the lateral margin of the rostrum), varies between 12-13 mm (close to the tip of the snout) and 18-19 mm (at the posterior end of the preserved portion of the rostrum). The second block of cartilage is not informative in terms of rostral cartilage morphology.

Similar to some of the fossilised sawfish rostra described by LERICHE (1905), CASIER (1949), CICIMURRI (2007), and CARRILLO-BRICEÑO *et al.* (2015), the external surface of CPI-7937 locally displays a fibrous texture. Some fragments of rostral cartilage from the second block (e.g., Fig. 3.B) display the preservation of the individual tesseræ that, in chondrichthyan fishes, form the coat of prismatic cartilage surrounding the external surface of the rostrum [see e.g. CICIMURRI (2007) and CARRILLO-BRICEÑO *et al.* (2015, 2019) for a reference on the prismatic cartilage of sawfishes]. These tesseræ are rounded-polygonal to almost star-shaped and have a mean diameter of *ca.* 0.7-0.8 mm. More than one layer of prismatic cartilage seems to be present. As highlighted elsewhere (WUERINGER *et al.*, 2011, and references therein), in extant sawfishes, the ampullae of LORENZINI pass the rostral cartilage through hollow tubules that might get preserved in fossilised rostra. Differing from what was observed by CARRILLO-BRICEÑO *et al.* (2015) for some phosphatised rostra from the Neogene of Venezuela, however, no trace of the ampullae of LORENZINI could be detected along the external surface of CPI-7937.

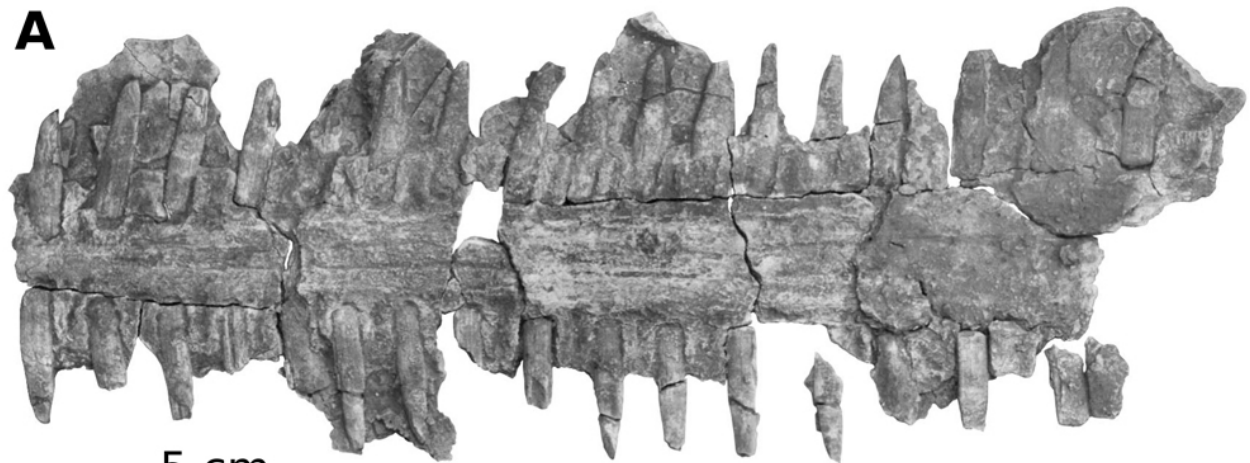
Rostral spines. All the preserved rostral spines (Figs. 2.A, 3.A, 4) are rather thick dorsoventrally, moderately elongated mediolaterally, and slightly curved ventrally, with convex anterior and sub-straight posterior margins. As a result of functional wear, the distal parts of the rostral spines are thinner than the proximal ones. In the best-preserved rostral spines, the anterior margin is regularly rounded, whereas the posterior margin invariably bears a rather deep mediolateral groove, so that its transverse sections would appear as C-shaped (*i.e.*, concave backwards) (Figs. 3.A, 4.B, 4.D). However, this posterior furrow is only partly developed, carving indeed only the distal halves of the rostral spines of CPI-7937 – a condition that recalls that observed in the extant species *Pristis clavata* GARMAN, 1906 (FARIA *et al.*, 2013; WHITTY *et al.*, 2014). The dorsal and ven-

► **Figure 1:** Geographical and stratigraphic background of the collection site of the fossil sawfish specimen CPI-7937. A) Location of the southern Peruvian East Pisco Basin along the Pacific Coasts of South America. B) Schematic stratigraphic log of the East Pisco Basin sedimentary succession. C) Close-up of the Zamaca area (Google Earth image, © 2018 DigitalGlobe). The smaller star indicates the location of the stratigraphic section studied by COLETTI *et al.* (2019); the larger star indicates the collection site of CPI-7937.





A



5 cm

B

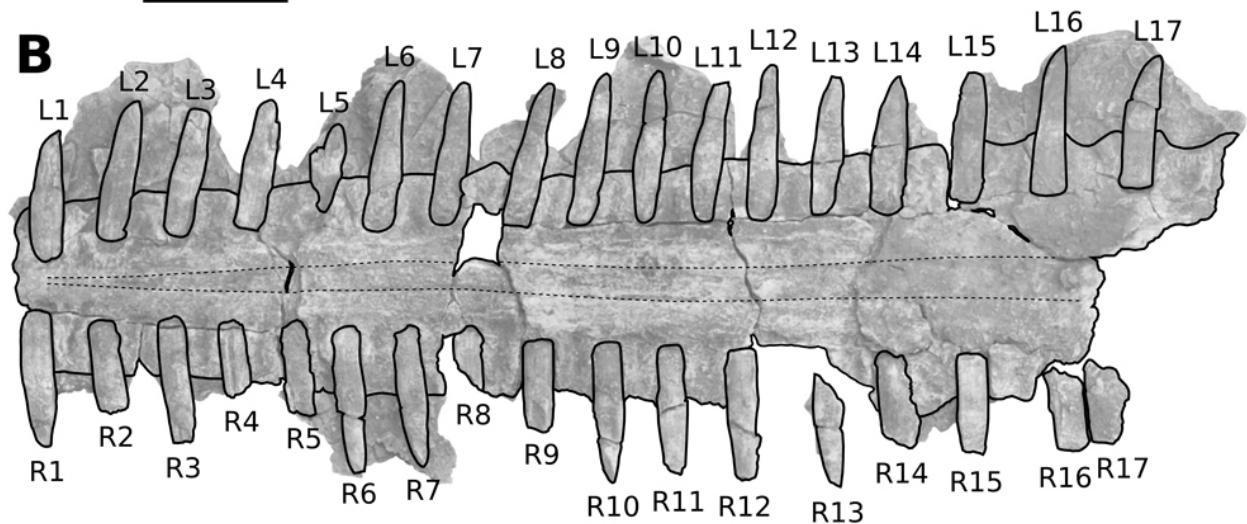
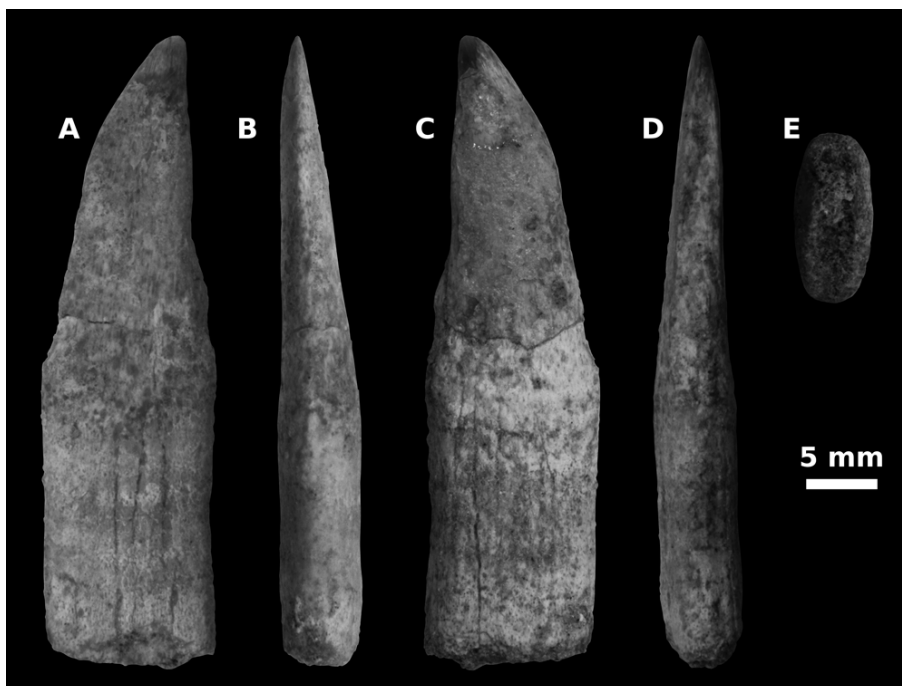
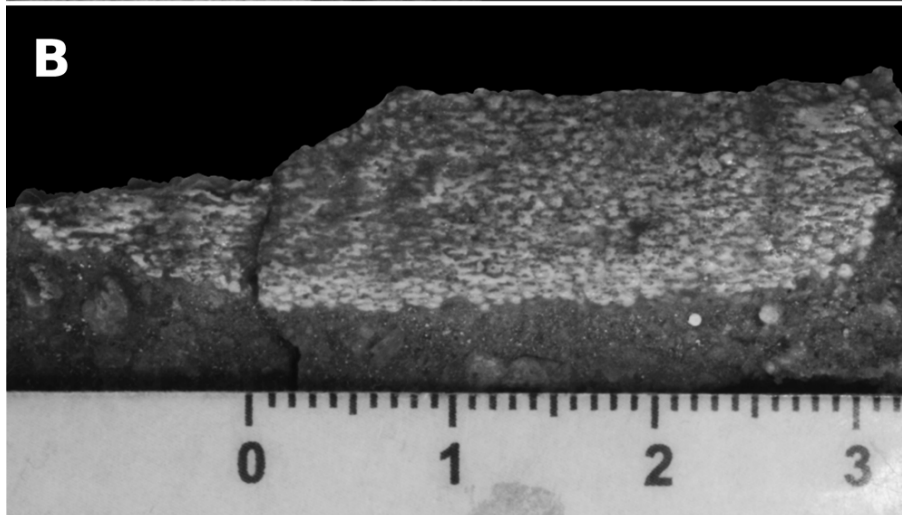
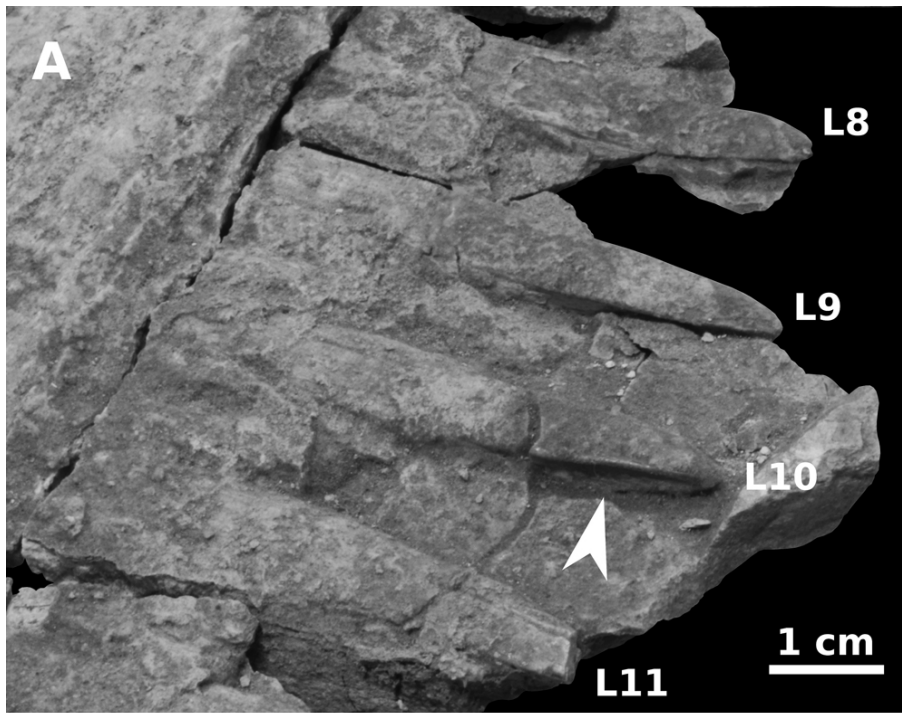


Figure 2: CPI-7937, partial rostrum of *Pristis* sp. from the Paracas Formation of southern Peru. A) The well-preserved anterior portion of the rostrum, preserving 34 associated rostral spines, in ventral view. B) Corresponding line drawing. Labels L1 to L17 refer to the left row of rostral spines; labels R1 to R17 refer to the right row of rostral spines. The dashed lines indicate the trend of the paracentral grooves (*sensu* CICIMURRI, 2007) that, in extant pristids, contain veins.

tral surfaces of the rostral spines (Fig. 4.A, 4.C) are gently ornamented by weak, sub-straight radial striae, especially in their basal halves, and show no trace of transversely oriented growth folds. As typical of pristid rostral spines, the proximal parasagittal surface exhibits a porous texture that originates by the presence of a plethora of very small-sized nutrient foramina (HERMAN *et al.*, 1997; MARSILI, 2006) (Fig. 4.E). Differing from other fossil (*e.g.*, COLLARETA *et al.*, 2017b) and extant (*e.g.*, NEVATTE *et al.*, 2017) rostral spines of sawfish, no obliquely-oriented shallow incisions that might evoke the abrasive action of water laden with sediment flowing at the sides of the rostrum could be detected on the rostra spines of CPI-7937.

From the tip of the snout backwards, the right rostral spines preserved in the main block are here indicated as R1 (the anterior-most one) to R17 (the 17th one); similarly, the left rostral spines are indicated as L1 to L17. Considering the complete rostral spines only, their mediolateral length varies between 46 mm (in L15) and 55.5 mm (in L9); overall, no clear trends in rostral spine length are observed moving from the tip of the snout backwards. Similarly, the values of maximum anteroposterior width of these rostral spi-

nes are quite invariant, ranging between 10 mm to 12 mm, whereas their values of maximum dorsoventral thickness equal about one-seventh of the corresponding values of mediolateral length. Whereas the medial halves of the anterior-most rostral spines are located medial to the lateral margins of the rostrum, only about one-third of the total mediolateral length of the rostral spines R15 to R17 and L15 to L17 is located in the corresponding alveoli (Fig. 2). Considering that 17 rostral spines are present on each side of the portion of rostrum preserved in the main block, and 16 additional rostral spines are preserved in the second block, a minimum rostral spine count (*i.e.*, number of spines on each side of the rostrum) of 25 can be reconstructed for CPI-7937. Such an estimate is consistent with the values observed in most extant pristids (Table 1), but distinguishes CPI-7937 from *Pristis pristis* (LINNAEUS, 1758), here regarded as including also *Pristis 'microdon'* LATHAM, 1794, and *Pristis 'peroteti'* MÜLLER & HENLE, 1841 (FARIA *et al.*, 2013), which exhibits smaller rostral spine counts (WHITTY *et al.*, 2014: tab. 1; LANGE *et al.*, 2015: tab. 1; SEITZ & HOOVER, 2017: tab. 1).



◀ **Figure 3:** Details of CPI-7937, partial rostrum of *Pristis* sp. from the Paracas Formation of southern Peru. A) Left posterolateral view of the ventral part of rostrum that hosts the rostral spines L8 to L11. The arrowhead indicates the distinctly grooved posterior margin of L10. B) Fragment of fossilised cartilage displaying the individual tesserae that, in chondrichthyan fishes, form the coat of prismatic cartilage that surrounds the external surface of the rostrum. Note that the tessellated structure of the cartilage is seemingly slightly obliterated by an overlying patina of consolidant that could not be removed before taking the photograph.

◀ **Figure 4:** Close-up of a detached right rostral spine (position unknown but posterior to R17) belonging to CPI-7937, partial rostrum of *Pristis* sp. from the Paracas Formation of southern Peru. A) Dorsal view. B) Anterior view. C) Ventral view. D) Posterior view. E) Mesial view. Note the worn-down aspect of the lateral half of the rostral spine (panels B and D) and the presence of an only partially developed groove running along its posterior margin (panel D). Measurements of the figured rostral spine are the following: maximum dorsoventral thickness – 6.5 mm; maximum anteroposterior width – 11.5 mm; mediolateral length – 42.5 mm.



Table 1: Rostral spine count for CPI-7937, the partial rostrum of *Pristis* sp. described herein, compared with extant and extinct pristid species. The three Venezuelan specimens (AMU-CURS-023, AMU-CURS-235, and AMU-CURS-237) come from the middle to upper Miocene Urumaco Formation and have been described in detail by CARRILLO-BRICEÑO *et al.* (2015). Data from FARRÉS (2003), CARRILLO-BRICEÑO *et al.* (2015: tab. 1), and the present work.

<i>Anoxypristis cuspidata</i> (living species)	16-33
<i>Anoxypristis osonensis</i> (Eocene, Spain)	21
<i>Pristis pristis</i> (living species)	14-24
<i>Pristis clavata</i> (living species)	18-27
<i>Pristis zijsron</i> (living species)	23-37
<i>Pristis pectinata</i> (living species)	20-30
<i>Pristis atlanticus</i> (Miocene, Portugal)	~20
<i>Pristis</i> sp. (AMU-CURS-023: Miocene, Venezuela)	23/24
<i>Pristis</i> sp. (AMU-CURS-235: Miocene, Venezuela)	23
<i>Pristis</i> sp. (AMU-CURS-237: Miocene, Venezuela)	>20
<i>Pristis</i> sp. (CPI-7937: Eocene, Peru)	≥25

Systematic identification. Based on the presence of grooves along the posterior margins of the best-preserved rostral spines, CPI-7937 is unambiguously attributed to the genus *Pristis* (e.g., BOURDON, 1999; COMPAGNO & LAST, 1999; WUERINGER *et al.*, 2009; CAPPETTA, 2012; WELTEN *et al.*, 2015; CAPPETTA & CASE, 2016). An unambiguous species-level determination of CPI-7937 would need a detailed revision of several extinct nominal species currently attributed to the genus *Pristis* (at least 29, according to CAPPETTA & CASE, 2016), which is beyond the scope of the present paper. Interestingly, however, CPI-7937 clearly differs from the widespread Eocene species *Pristis lathami* GALEOTTI, 1837 (a possible wastebasket taxon; CAPPETTA & CASE, 2016) by exhibiting relatively stout rostral spines, whose posterior margins bear only partially developed grooves.

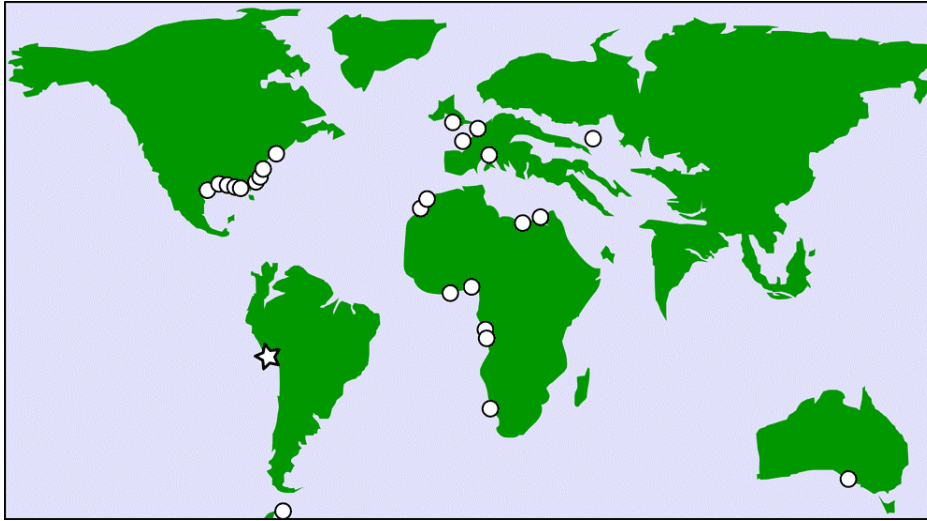
Remarks on the preservation state. CPI-7937 displays a high degree of preservation. As such, it represents a significant addition to the long list of remarkably preserved vertebrate fossils from the East Pisco Basin, which include articulated skeletons of sharks (COLLARETA *et al.*, 2017c), phosphatised baleen plates and bristles of mysticete whales (BRAND *et al.*, 2004; ESPERANTE *et al.*, 2008, 2015; GIONCADA *et al.*, 2016; MARX *et al.*, 2017), stomach contents and regurgitations of cetaceans (COLLARETA *et al.*, 2015, LAMBERT *et al.*, 2015), and even seabird feathers that preserve colour-imparting melanosome morphologies (CLARKE *et al.*, 2010). In the well-studied upper Miocene portion of the Pisco Formation, recent research has shown that many finely preserved fossil vertebrates occur in dolomite concretions, which seem to have formed very early during diagenesis (e.g., GARIBOLDI *et al.*, 2015; GIONCADA *et al.*, 2016, 2018a). In rarer cases, finely preserved vertebrate specimens appear to be enclosed in an apatite-rich volume of sediment delimited by an evident manganiferous boundary, which might also reflect precipitation of early diagenetic minerals around the skeleton (GIONCADA *et al.*, 2018b). The silty sediment that entombs the Zamaca fossil sawfish, however, does not ap-

pear to have been modified by early diagenetic cementation, at least macroscopically. This observation allows for associating CPI-7937 with a small-sized mysticete specimen, exhibiting strongly mineralised (*i.e.*, phosphatised) baleen plates, from silty deposits of the Pisco Formation exposed at Cerro Ballena (MARX *et al.*, 2017). In that case, strong mineralisation of the keratinous baleen material was likely made possible thanks to the retention of a relatively permeable, unconsolidated sediment through the first phases of diagenesis, which ultimately allowed the phosphatisation processes to protract for a long time (MARX *et al.*, 2017; GIONCADA *et al.*, 2018b). A similar scenario might be evoked for explaining the high degree of preservation shown by CPI-7937. Support of this interpretation comes from observing that the internal rostral ducts have collapsed, which implies that the rostral cartilage underwent diagenetic compaction before mineralisation could occur.

4. Discussion and conclusions

To our knowledge, the partial rostrum of *Pristis* sp. described herein from the middle Eocene Paracas Formation represents the geologically oldest fossil record of Pristidae from the Pacific Coast of South America and, seemingly, from the whole Pacific realm (Fig. 5). Furthermore, it consists of an exceptionally well preserved specimen that allows for the observation of anatomical structures that are unlikely to leave a fossil record, e.g., the paracentral grooves that extend along the ventral surface of the rostrum and the individual tesseræ that form the coat of prismatic cartilage surrounding the external surface of the rostrum. Therefore, our finding contributes to further qualify the sedimentary infill of the East Pisco Basin as a true Konservat-Lagerstätte, the outstanding fossil content of which is crucial for reconstructing the Cenozoic history of the cartilaginous fish faunas of Pacific South America (CARRILLO-BRICEÑO *et al.*, 2018). Not least, the discovery of CPI-7937 promotes the quest for well-preserved fossil chondrichthyans over the entire stratigraphic succession exposed in the Ica Desert.

Nowadays, sawfishes are absent from the coastal waters of southern Peru. However, in the East Pisco Basin, pristids are known as fossils from the Miocene strata of both the Chilcatay and the Pisco formations (BIANUCCI *et al.*, 2016b, 2018; LANDINI *et al.*, 2017a, 2017ba, 2019; DI CELMA *et al.*, 2018b, 2019; BOSIO *et al.*, 2020). Of all these Miocene occurrences, which consist of rostral spines only, those that can be confidently identified at the genus level are assigned to *Anoxypristis* (e.g., BIANUCCI *et al.*, 2018; BOSIO *et al.*, 2020). While extant *Anoxypristis* is confined to the Indo-western Pacific region, this genus had once a much wider distribution, largely overlapping that of *Pristis*, being indeed present in several Eocene to Pliocene sites of Africa, Asia, Europe, and North America (e.g., CAPPETTA, 2012, and references therein). The apparent replacement of *Pristis* by *Anoxypristis* recorded in the fossil record of the East Pisco Basin is thus difficult to



◀ **Figure 5:** Schematic palaeogeographic distribution map of the Eocene fossils of *Pristis* (circles) based on the occurrences reported by CAPPETTA (2012) and The Paleobiology Database (available online at <https://www.paleobiodb.org/>). The star indicates the southern Peruvian site where CPI-7937, the partial rostrum of *Pristis* sp. described herein, was found. Global palaeogeographic base map for the middle Eocene redrawn and modified after KOŠŤÁK *et al.* (2013: Fig. 10).

interpret and might be due to collection biases. Further investigations on the understudied chondrichthyan assemblages of the Palaeogene deposits of the East Pisco Basin might contribute to shed light on this issue.

The living species of *Anoxypristis* and *Pristis* are shallow-water nectobenthic fish that occupy restricted habitats close inshore or even in freshwater, commonly in muddy enclosed bays, in estuaries, off river mouths, surrounding large continental islands, and upstream in rivers and lakes (COMPAGNO & LAST, 1999). In particular, according to ALLEN (1982), *Pristis* spp. appear to prefer muddy substrates. These actualistic data are perfectly consistent with modern reconstructions of the bathymetric, physiographic, and sedimentological characteristics of the Yumaque depositional setting – an inshore, inner shelf palaeoenvironment, possibly connected with a series of semi-enclosed embayments, and characterised by a silty to silty-sandy seafloor (DUNBAR *et al.*, 1990; UHEN *et al.*, 2011).

In recent times, the palaeoclimatic significance of the Paracas Formation deposits has been the subject of some debate. UHEN *et al.* (2011) argued that the Paracas deposits represent a cool water depositional palaeoenvironment – a view that was previously proposed by DEVRIES *et al.* (2006). This hypothesis was based on *i*) the occurrence of some taxa of foraminifera (*e.g.*, the genera *Bolivina* ORBIGNY, 1839, *Nonion* MONTFORT, 1808, and *Uvigerina* ORBIGNY, 1826) and nannoplankton [*e.g.*, *Coccolithus pelagicus* (WALLICH, 1877)] that are currently associated with cool waters, and *ii*) the frequent observation of loose scales of clupeoid fishes (*i.e.*, anchovies and sardines), which correlates with relatively cool water environments in the Quaternary record of the Humboldt Current System off the Peruvian coast (UHEN *et al.*, 2011, and references therein). However, a recent re-examination of the actualistic data about the micro- and nannofossil taxa from the Yumaque deposits revealed a somewhat weak correlation with cool waters (COLETTI *et al.*, 2019), whereas the small-sized fish scales that are omnipresent in the same beds cannot be positively identified as belonging to any member of

Clupeoidea (personal observation by A.C.), a group of teleosts whose first unambiguous occurrence in the fossil record of the East Pisco Basin occurs in the upper Miocene strata of the Pisco Formation (COLLARETA *et al.*, 2015; LAMBERT *et al.*, 2015). Furthermore, considerations on the record of large benthic foraminifera from the Los Choros member, which includes abundant lepidocyclinids, as well as nummulitids and members of the extant genus *Amphistegina* ORBIGNY, 1826, provided a different interpretation of the Paracas depositional setting as a tropical palaeoenvironment (MORALES-REYNA *et al.*, 2010, 2013; COLETTI *et al.*, 2019). As mentioned above, pristids are currently known as tropical/subtropical fishes (*e.g.*, COMPAGNO & LAST, 1999; WUERINGER *et al.*, 2009; CAPPETTA, 2012; DULVY *et al.*, 2014); therefore, the present record of *Pristis* sp. from Zamaca further indicates that palaeoenvironmental conditions suitable for warm-water organisms characterised the East Pisco Basin during deposition of the Paracas strata.

Although the large-tooth sawfish (*Pristis pristis*) might still inhabit tropical waters of northern Peru (DULVY *et al.*, 2014; MENDOZA *et al.*, 2017), and the fossil record of pristids from the East Pisco Basin spans from the middle Eocene to the late Miocene, sawfishes are currently absent from the cool, upwelling-influenced coastal waters of present-day southern Peru – an observation that might suggest warmer-than-today seawater temperatures for the Lutetian nearshore environments of southern Peru. This interpretation fits perfectly the global climatic scenario of the middle Eocene, which was characterized by high temperatures worldwide (*e.g.*, ZACHOS *et al.*, 2001). Furthermore, it is consistent with previous reconstructions of the palaeoceanographic conditions of the coastal sea of southern Peru, which in Eocene times was likely characterized by a weaker-than-today upwelling system driven by a sort of "proto-Humboldt" current; the latter would have comprised the eastern arm of the relatively warm Southern Pacific gyre rather than representing a cooler byproduct of the circum-Antarctic circulation (MARTY *et al.*, 1988). In this respect, it should be noted that the Lutetian records of



Pristis spp. even include an occurrence from the Seymour Island, Antarctica (KRIWET, 2005), which suggests that the warm climate regime of the middle Eocene might have been reflected in a phase of remarkable range expansion towards the high latitudes for pristid sawfishes worldwide.

That said, what happened to the southeastern Pacific pristids, leading to their eventual extirpation from the southern Peruvian latitudes? Recent research (CARRILLO-BRICEÑO *et al.*, 2018; PARTARRIEU *et al.*, 2018; VILLAFANA & RIVADENEIRA, 2018; VILLAFANA *et al.*, 2019) has investigated the role of physiological, ecological, and life-history traits, as well as the influence of environmental and historical factors in controlling the diversity and distribution of Pacific South American chondrichthyans in Neogene and Quaternary times, but sawfishes have not been specifically addressed by these studies. Nonetheless, some answers could come from observing that another iconic tropical cartilaginous fish, the extinct snaggletooth shark *Hemipristis serra* AGASSIZ, 1843, is thought to have contracted its range northwards as cool conditions took hold along the coasts of southern Peru, during a middle or late Miocene phase of a stronger Humboldt Current (BOSIO *et al.*, 2020). Similarly, the horn shark *Heterodontus* BLAINVILLE, 1816, seems to have been extirpated from most of its southeastern Pacific grounds following a series of regional changes, including seawater cooling due to coastal upwelling and advection of Subantarctic water masses, during the Plio-Pleistocene (PARTARRIEU *et al.*, 2018). A closer look at the habitat preferences of extant *Pristis* spp. could provide some further insights. Nowadays, pristids are regarded as highly imperilled fishes that are often associated with threatened seagrass meadows and mangrove forests (DULVY *et al.*, 2014), some of which represent crucial nursery grounds for these highly idiosyncratic rays (SIMPENDORFER, 2007). Present-day seagrasses are mostly known from tropical and subtropical environments; modern seagrass patches along the southeastern Pacific margin are limited to a few occurrences near Coquimbo, Chile (KUO, 2005, and references therein), but meadows might have been more widespread along the western coastline of South America in the past (PHILLIPS *et al.*, 1983). Mangrove forests are almost exclusively tropical habitats, their geographical spread being broadly delineated by the 20°C winter sea-temperature isotherm; in particular, South American Pacific mangroves are currently restricted to north of 5°32' S by the effect of the cold Humboldt Current (HOGARTH, 2015). However, the presence of mangrove fringes in the East Pisco Basin during the lower Palaeogene has been hypothesised on the basis of the molluscan assemblage of the Cuenca Member of the Caballas Formation (DEVRIES, 2017, 2018), which stratigraphically underlies the Paracas strata (DUNBAR *et al.*, 1990; DEVRIES, 1998). Besides lowering coastal seawater temperatures to the discomfort of pristids, a Neogene phase of a stronger Humboldt Current would definitively have had a deleterious effect on mangroves and,

possibly, on seagrasses as well, thus further compromising the fate of the South American Pacific sawfish communities via mechanisms of habitat loss and fragmentation. Therefore, in the light of the above considerations, the disappearance of pristids from the coastal waters off southern Peru could be interpreted as mainly reflecting the late Cenozoic trend of strengthening of the Humboldt Current, although the interplay of other environmental drivers (*e.g.*, tectono-eustatic factors leading to the emersion of the East Pisco Basin and other semi-enclosed shelf areas) might also have had a significant role in causing the regional extirpation of sawfishes.

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