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Original article

Cenozoic batoids from Contamana (Peruvian Amazonia) with focus on freshwater potamotrygonins and their paleoenvironmental significance[☆]



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ARTICLE INFO

Article history:

Received 4 July 2017

Accepted 4 October 2017

Available online 10 October 2017

Keywords:

Potamotrygoninae
 Batoida
 Chondrichthyes
 Peruvian Amazonia
 Cenozoic
 Paleocology
 Paleoenvironment

ABSTRACT

Among the ichthyofaunal remains collected in the Tertiary deposits of Peruvian Amazonia, elasmobranchs show an unexpected richness of rays, consisting primarily of mostly potamotrygonins (river stingrays), but also pristids (sawfishes) and rhinopterids (cownose rays). Among the Potamotrygoninae subfamily and in addition to the middle Eocene *Potamotrygon ucayalensis* found in oldest levels, three new fossil species of *Potamotrygon*, namely *P. contamanensis* nov. sp., *P. canaanorum* nov. sp., and *P. rajachloae* nov. sp. are described from late Oligocene-late Miocene deposits along the Quebrada Cachiyacu, near Contamana, Peru. These new fossils fill a substantial gap in the sporadic fossil record of this exclusive freshwater elasmobranch subfamily, native to South America, thereby highlighting their ancient biological and ecological diversity. In the absence of sharks, the occurrence of obligate freshwater potamotrygonins, along with additional marine to brackish batoids from nine successive fossiliferous levels, supports the predominance of fluvio-lacustrine environments in that region throughout the considered period, with a peak of marine influence around the middle-late Miocene transition, as recorded in other areas of Western Amazonia.

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1. Introduction

Among Potamotrygonidae that now include the marine sister subfamily Styracurinae (Carvalho et al., 2016a), the subfamily Potamotrygoninae (river stingrays, here termed potamotrygonins) is the most diverse group of obligate freshwater stingrays within living batoids, with four genera and about thirty species distributed in all major river basins of the Amazon and Orinoco basins (Rosa et al., 2010; Lasso et al., 2014; Fig. 1). The subfamily Potamotrygoninae has been successively revised in a systematic perspective (Müller and Henle, 1841; Garman, 1913; Rosa, 1985). More recently, Carvalho et al. (2004) have summarized many aspects of potamotrygonin taxonomy, general biology and

distribution. Since that time, additional new species have been described (e.g., Deynat, 2006; Rosa et al., 2008; Carvalho and Lovejoy, 2011; Carvalho and Ragno, 2011; Loboda and Carvalho, 2013; Fontenelle et al., 2014; Carvalho, 2016; Carvalho and Araújo, 2016; Silva & Carvalho, 2016). Today, 32 nominal species (White et al., 2016) are recognized within four genera: *Paratrygon* Duméril, 1865 (Orinoco and Amazon basins), *Potamotrygon* Garman, 1877 (including ~27 species in both basins), *Plesiotrygon* Rosa et al., 1987 (Amazon basin), and *Heliotrygon* Carvalho and Lovejoy, 2011 (Amazon basin). Carvalho and Lovejoy (2011) have discussed the phylogenetic relationships among potamotrygonin genera (see also Fontenelle and Carvalho, 2016). With the exception of the puzzling *Plesiotrygon* (Marques, 2000; Toffoli et al., 2008; Carvalho and Lovejoy, 2011; Carvalho and Ragno, 2011), there is virtually no controversy regarding the generic assignment of potamotrygonin species. Yet, the intra-generic relationships and species boundaries within the genus *Potamotrygon* are sometimes problematic, and

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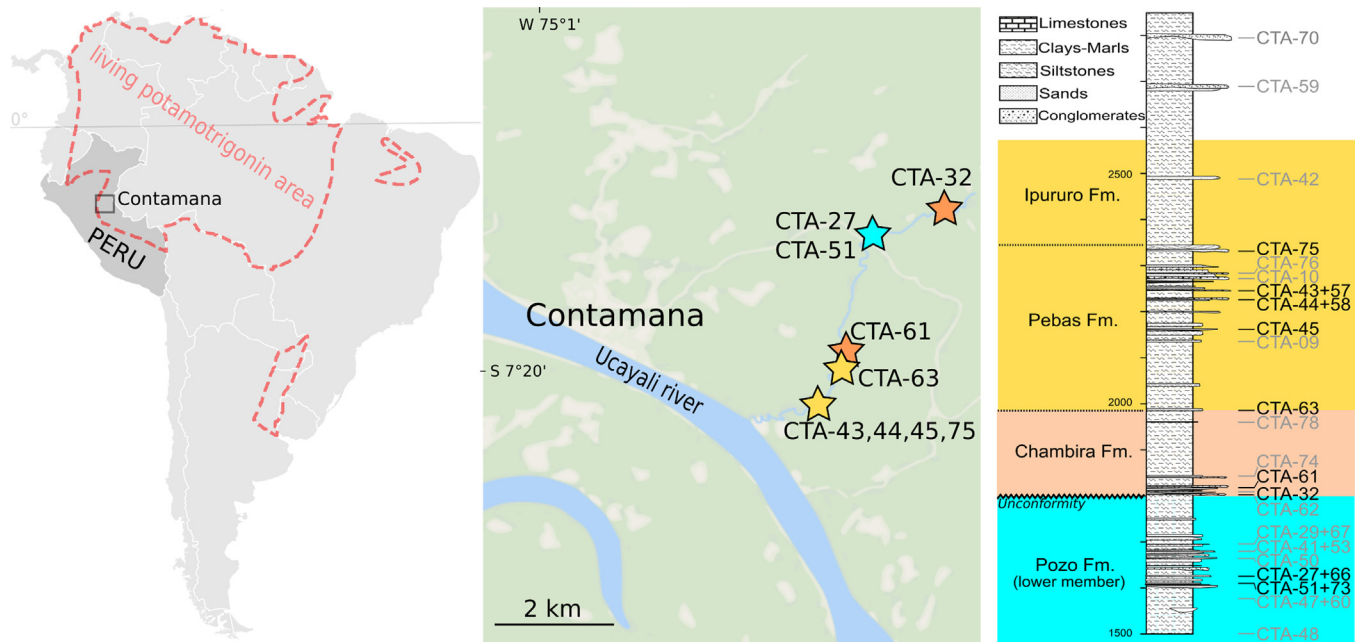


Fig. 1. Location map of Contamana area, Loreto, Peruvian Amazonia, with a focus on fossil elasmobranch-yielding localities (CTA-) along the Quebrada Cachiayacu section. Blue star: middle Eocene localities (Pozo Fm.; CTA-27 and 51), close to the Maquía Anticline core; orange stars: late Oligocene localities (Chambira Fm.; CTA-32 and 61), on both sides of the Maquía Anticline; yellow stars: Miocene localities (Pebas Fm. and lower part of Ipururo Fm.; CTA-43, 44, 45, 63, and 75), in the southwestern flank of the Maquía Anticline. For more details on these localities, see Antoine et al. (2016).

they remain subject of debates (Toffoli et al., 2008; Garcia et al., 2016) despite several recent re-examinations of type species (Carvalho, 2016; Silva and Carvalho, 2016).

Without any consensus on the phylogenetic relationships of *Potamotrygon* species, tooth morphologies of extant *Potamotrygoninae* have so far remained poorly studied. A preliminary review suggested the existence of at least five dental groups, a diversity which testifies to the extreme dental variation range observed in living potamotrygonin specimens (Adnet et al., 2014). These are most likely tied to the wide range of their feeding habits, with exclusive fish eaters (e.g., *Paratrygon* spp.), insect feeders (e.g., *Potamotrygon orbignyi* (Castelnau, 1855) and *Potamotrygon signata* Garman, 1913) possessing slender cusped teeth, and durophagous species (e.g., *Potamotrygon leopoldi* Castex and Castello, 1970) possessing imbricated teeth with flatter crown. It is worth noting that the living species with the most varied feeding habits and habitats, *Potamotrygon motoro*, displays the highest dental variability observed (from globular to cuspidate teeth) even though it has been assumed that these different dental morphologies would belong to several mimetic but distinct species (e.g., Loboda, 2010; Loboda and Carvalho, 2013) or populations (Lasso et al., 2014) with specialized and distinct feeding habits (Adnet et al., 2014). The tooth morphology of *Potamotrygoninae* is very close to that of the marine *Styracurinae*, which include the formal Caribbean *Himantura schmardae* Werner, 1904 and *H. pacifica* Beebe and Tee-Van, 1941 (now considered as belonging to the genus *Styracura* Carvalho et al., 2016), and with which they probably shared a close common ancestor (Lovejoy, 1996; McEachran et al., 1996; Marques, 2000; Aschliman et al., 2012; Naylor et al., 2012).

From a paleontological perspective, a comprehensive survey of the Cenozoic deposits exposed near Contamana, in Peruvian Amazonia, has allowed for the discovery of 34 Cenozoic localities, mostly along the Quebrada Cachiayacu (Fig. 1). These fossil assemblages include vertebrate remains, molluscs, arthropods, plants, microfossils, and nanofossils ranging from the early Paleocene up to the late Miocene (Antoine et al., 2016). Among the > 200 animal species preliminarily identified in this area,

about ten are referable to Chondrichthyes (sharks, rays, and chimaeras), with a vast majority of river stingrays (Antoine et al., 2016), i.e. *Potamotrygoninae sensu* Carvalho et al., 2016, formerly recognized as *Potamotrygonidae* (e.g., Adnet et al., 2014). Interestingly, the earliest potamotrygonin from South America, *Potamotrygon ucayalensis* Adnet et al., 2014, was reported from a late middle Eocene locality in the Contamana section (CTA-27, Pozo Fm., ~41 Ma; Antoine et al., 2012, 2016; Adnet et al., 2014). With the exception of this species, the fossil record of potamotrygonins in South America is virtually unknown, with only few isolated teeth or dermal denticles from the late middle and late Miocene deposits of the Magdalena basin, Colombia (Lundberg, 1997), the Paraná basin in Argentina (Larrazet, 1886 with invalid taxa such as *Raja agassizii*, *Dynobatis paranensis*, and *Dynobatis rectangularis*; Deynat and Brito, 1994; Brito and Deynat, 2004), and the Acre-Solimões basins (Monsch, 1998; Lundberg et al., 2010). The teeth have been unidentified due to the lack of knowledge on potamotrygonin dental patterns, or considered as being similar to those of the living species *Potamotrygon motoro* (e.g., Deynat and Brito, 1994). In contrast, numerous fossil freshwater rays have been described in the Paleocene-Eocene deposits of North America (Carvalho et al., 2004; Wroblewski, 2004; Cook et al., 2014), thereby testifying to a potentially wider origination area for the *Potamotrygonidae* (Adnet et al., 2014). However, North American freshwater rays become extinct after Middle Eocene times, thus restricting the comparison with their South American counterparts.

In this paper, we describe new fossil remains of potamotrygonins discovered from the Quebrada Cachiayacu section near Contamana, in deposits ranging from the late Oligocene to the early late Miocene (Chambira and Pebas formations; Antoine et al., 2016). We also provide a short survey of the batoid record from the same section (late middle Eocene-late Miocene, i.e., including also localities from the Pozo Fm.).

2. Material and methods

Near Contamana, potamotrygonin remains occur throughout the Eocene-Miocene section (Fig. 1), but they principally originate

from the fossil-rich levels of CTA-27 (Poza Fm., late middle Eocene), CTA-32 and CTA-61 (Chambira Fm., late Oligocene), as well as CTA-44 top and CTA-43 (Pebas Fm., late middle and early late Miocene, respectively). Except for the Pebas Fm. localities (CTA-43, 44, 45, and 75) that document rapid changes from lake, estuarine embayment to coastal plain with marginal marine affinities, all other fossiliferous localities attest to the occurrence of channelized fluvial settings, representative of Proto-Amazonian freshwater ecosystems (Tejada-Lara et al., 2015; Salas-Gismondini et al., 2015, 2016; Antoine et al., 2016; Boivin et al., 2017). Any information concerning the geological settings (e.g., sedimentology, estimated ages, paleontological content, and inferred paleoenvironments) are available in the review by Antoine et al. (2016).

The new fossil material consists of isolated teeth and dermal denticles (including some dermal bucklers). They were all collected by *in situ* wet-screening of sediments (180–850 kg in each locality, for a total weight exceeding 4 tons), with a 0.4-mm to 2-mm mesh (see Antoine et al., 2016 for further information). All the figured material is permanently housed in the collections of the Vertebrate Paleontology Department of the “Museo de Historia Natural – Universidad Nacional Mayor San Marcos” (MUSM), in Lima, Peru.

The dental description and systematics of Potamotrygonidae follow the terminology of Cappetta (2012) and recent work of Carvalho et al. (2016), respectively. Comparisons with living potamotrygonins (e.g., *Paratrygon*, *Plesiotrygon*, and *Potamotrygon* spp.) were performed thanks to the material housed in the “Institut des Sciences de l’Evolution de Montpellier”, France, in the “Muséum National d’Histoire Naturelle” in Paris, France, and in the Elasmobranch Research Belgium, as previously detailed in Adnet et al. (2014).

3. Systematic paleontology

Class Chondrichthyes Huxley, 1880
 Subclass Elasmobranchii Bonaparte, 1838
 Order Myliobatiformes Compagno, 1973
 Superfamily Dasyatoidea Whitley, 1940
 Family Potamotrygonidae Garman, 1877
 Subfamily Potamotrygoninae Garman, 1877
 Genus *Potamotrygon* Garman, 1877

Remarks: On morphological grounds, three non-overlapping clusters of specimens can be distinguished in the Oligocene-Miocene localities of the Quebrada Cachiyacu section (Fig. 1). They will be described here as documenting three new species assigned to *Potamotrygon*.

Potamotrygon contamanensis nov. sp.

Fig. 2

Derivation of the name: The species name derives from the city of Contamana, in the vicinity of which all the specimens described were unearthed.

Holotype: MUSM 3542, an anterior tooth from a female specimen (Fig. 2(A–D)).

Type locality: CTA-43 locality, nearby Contamana, Loreto Department, Peru.

Type horizon: Top of the Pebas Fm., earliest late Miocene (ca. 11 Ma; Antoine et al., 2016; Marivaux et al., 2016a).

Material: 537 isolated teeth and dermal denticles including the figured specimens MUSM 3542–3554.

Stratigraphic and geographic range: Late Oligocene (CTA-61; Antoine et al., 2016; Marivaux et al., 2016b) to late Miocene (CTA-75; Antoine et al., 2016) in the Ucayali basin, Peruvian Amazonia. Possibly found also in the latest Miocene of Acre, Brazilian Amazonia (Brito and Deynat, 2004: fig. 1B–D).

Diagnosis: A *Potamotrygon* species characterized by a strong monognathic heterodonty between the lateral teeth (large and globular) and the most anterior and posterior teeth. The teeth share a crown where the central tip of the labial visor is extremely thick and projected labially, designing a characteristic bulge in lateral view. On the occlusal side of the crown, enameloid ornamentation is strong and mainly marked by numerous alveoli and granules concentrated on the central part of the labial face. The root is particularly thick, with a short labial face and two massive and rounded lobes in labial and lingual views.

Description: Teeth are generally higher than wide (height = 1–4 mm), depending on dental files. Like in almost all dasyatoids, including other potamotrygonids, inferred sexual dimorphism consists of a marked dental heterodonty with male teeth having a main cusp located on the transverse crest (Fig. 2(E–L)) and female teeth being comparatively larger and without cusps (Fig. 2(A–D, M–O, Q–T)).

The holotype is an anterior tooth from an adult female specimen. Higher (3 mm) than wide (2 mm), this tooth displays very thick crown and root. The crown has a slight concavity on the lingual face split by a median ridge (Fig. 2(A)). This lingual face is rectangular in outline due to the straight marginal sides and because of a lingual visor that is not projected lingually (Fig. 2(A)). The transverse crest separating the lingual from the labial faces is generally smooth because of wear (Fig. 2(A, B)). The labial face is flat or slightly rounded (Fig. 2(B)); it has a strong granuliform ornamentation (Fig. 2(C)). The labial visor is thick and labially bent, forming a strong bulge near the apex (Fig. 2(B)). The resulting occlusal face is diamond-shaped in occlusal view (Fig. 2(C)). The holaulacorhize root displays two root lobes stretched out and separated by a large and deep groove, with a nutritive foramen located in its lingual part. In labial view, the crown-root junction is well marked and highlighted by several small foramina. In basal view, the basal faces of the root lobes are rounded and they form two symmetrical semi-circles (Fig. 2(D)). In other anterior teeth of females, the bulge of the labial visor can be more angular but always thick (Fig. 2(N)). The lingual extension of the root lobes is not always pronounced. The number of foramina at the crown-root junction on the labial face of the root is variable (0 to 6; Fig. 2(O)). The largest lateral teeth of females (e.g., Fig. 2(M)) are twice as large as anterior teeth, as observed on teeth of some extant *Potamotrygon* (De Araújo, 1998; Rosa et al., 2010; Cappetta, 2012; Loboda and Carvalho, 2013); the lingual face lacks a median vertical crest, and it is united and slightly more concave than on anterior teeth (Fig. 2(M)). The root lobes, in lingual view, are smaller and pointed out (Fig. 2(M, Q)). In teeth showing an advanced stage of wear, the ornamentation is restricted to some marks (Fig. 2(Q)).

Compared to female teeth, the male teeth exhibit a prominent central cusp, which is bent lingually from the transverse crest (Fig. 2(F, I, K)). The concavity observable on the lingual face of female teeth is thus accentuated by the presence of this protruding cusp (Fig. 2(K)). In some teeth, the marginal edges are straighter and the crown outline is thus triangular in occlusal view (Fig. 2(L)).

Juvenile teeth do not have any strong ornamentation as observable in adults (Fig. 2(U–X)). They have a cusp more or less developed on the transverse crest, depending on sex. With wear, this bulge appears as a triangular smooth platform bearing a small depression on its labial face. Juvenile teeth are almost translucent compared to adult teeth, probably due to a thinner enameloid layer.

Remarks: *Potamotrygon contamanensis* nov. sp. is primarily distinguishable from all other morphotypes recovered in similar Contamanan assemblages in having high and globular teeth. It is in particular distinguishable from the coeval species *P. rajachloae* nov. sp. by its larger size, and in exhibiting a

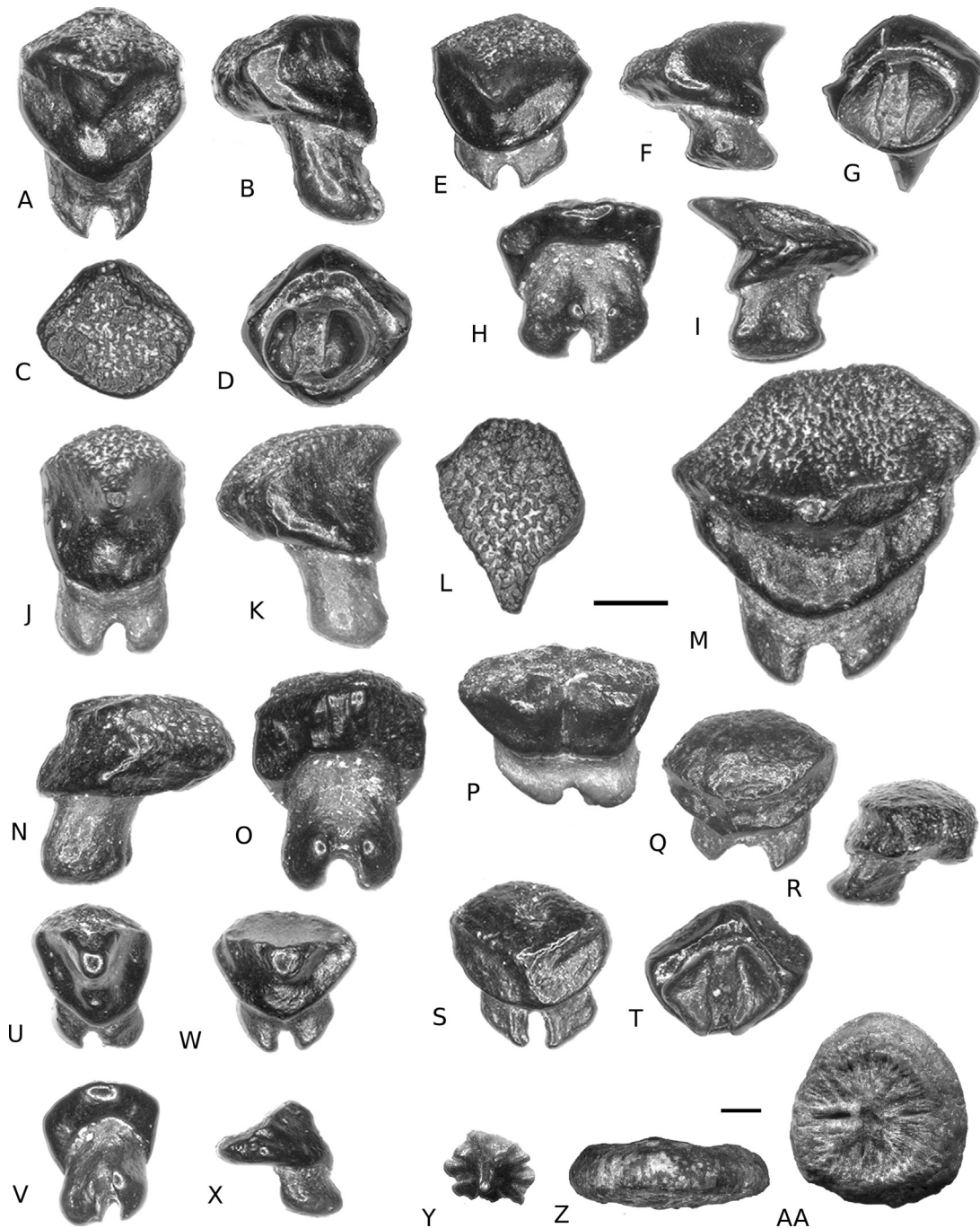


Fig. 2. *Potamotrygon contamanensis* nov. sp. **A–D.** Holotype, MUSM 3542: anterior tooth (female) in lingual (A), profile (B), occlusal (C), and basal (D) views. **E–G.** MUSM 3543: antero-lateral tooth (male) in lingual (E), profile (F), and basal (G) views. **H, I.** MUSM 3544: lateral tooth (male) in labial (H) and profile (I) views. **J–L.** MUSM 3545: anterior tooth (male) in lingual (J), profile (K), and occlusal (L) views. **M.** MUSM 3546: lateral tooth (female) in lingual view. **N, O.** MUSM 3547: anterior tooth (female) in profile (N) and labial (O) views. **P.** MUSM 3548: pathologic morphology in lingual view. **Q, R.** MUSM 3549: lateral tooth (female) in lingual (Q) and profile (R) views. **S, T.** MUSM 3550: antero-lateral tooth (female) in lingual (S) and basal (T) views. **U, V.** MUSM 3551: juvenile tooth (male) in lingual (U) and labial (V) views. **W, X.** MUSM 3552: juvenile tooth (female) in lingual (W) and profile (X) views. **Y–AA.** Dermal denticles; Y: MUSM 3554, skin denticle in apical view; Z, AA: MUSM 3553, skin buckler in profile (Z) and apical (AA) views. Scale bars: 1 mm (A–X), 2 mm (Y–AA).

strongly ornamented enameloid. Distinction with the co-occurring species *P. canaanorum* nov. sp. is more tenuous, but the ornamentation in *P. contamanensis* nov. sp. is more granuliform than furrowed. Moreover, roots in *P. contamanensis* nov. sp. are less angular (with rounded lobes in lingual and profile views) than in the two other species.

Compared with other known fossil species, the dental morphology of *P. contamanensis* nov. sp. is clearly different from that of the late middle Eocene *P. ucayalensis* (Adnet et al., 2014) and

from that of the Paleocene-Eocene North American *Dasyatoida* recovered in freshwater-brackish deposits (Benson, 1998; Carvalho et al., 2004; Wroblewski, 2004; Cook et al., 2014) in having a more globular crown shape. There is some resemblance between the tooth ornamentation of *P. contamanensis* nov. sp. and that of the early Paleocene *Dasyatis puercensis* (Williamson et Lucas, 1993) from New Mexico; however, teeth of *P. contamanensis* nov. sp. have a higher lingual face, the root lobes are smaller, and there is always a concavity on the labial visor. Otherwise, the

dental pattern of this new species (and of some large unidentified bucklers; e.g., Fig. 2(Z, AA)) is strongly reminiscent to that of isolated teeth of unnamed potamotrygonins from the late Miocene of Acre, Brazil, as illustrated by Brito and Deynat (2004: fig. 1B–D).

Although there is so far no general consensus regarding the taxonomy of *Potamotrygon*, which has prohibited a clear understanding of the emergence of the tooth morphology characterizing living species, it is worth noting the striking resemblance with some large-figured specimens attributed to *P. motoro* (e.g., Adnet et al., 2014: Fig. 3.10–13), as those illustrated in Cappetta (2012: fig. 151 fig. 15, J) or with drawings of Loboda and Carvalho (2013: fig. 8). All these figured specimens share a similar strong monognathic heterodonty (with large lateral files in females), a similar large dental size, as well as robust roots. Nevertheless, teeth of *P. contamanensis* nov. sp. remain distinct from those of recent

P. motoro in having a lingual face with a more rhombic shape and a stronger ornamentation that vanishes before the labial face of the crown. A first-order correlation between body and tooth sizes in the closest living species available in our collections (e.g., *P. motoro*) suggests that the largest individuals of *P. contamanensis* nov. sp. may have reached a disc width of ca. 60 cm.

Potamotrygon rajachloae nov. sp.
Fig. 3(A–O)

Derivation of the name: The name is composed by “raja”, the Latin word for ray, and “chloae”, deriving from the name Chloé, in memory of the first author’s friend who passed away during the writing process.

Holotype: MUSM 3555, an anterior tooth from a male specimen (Fig. 3(D–F)).

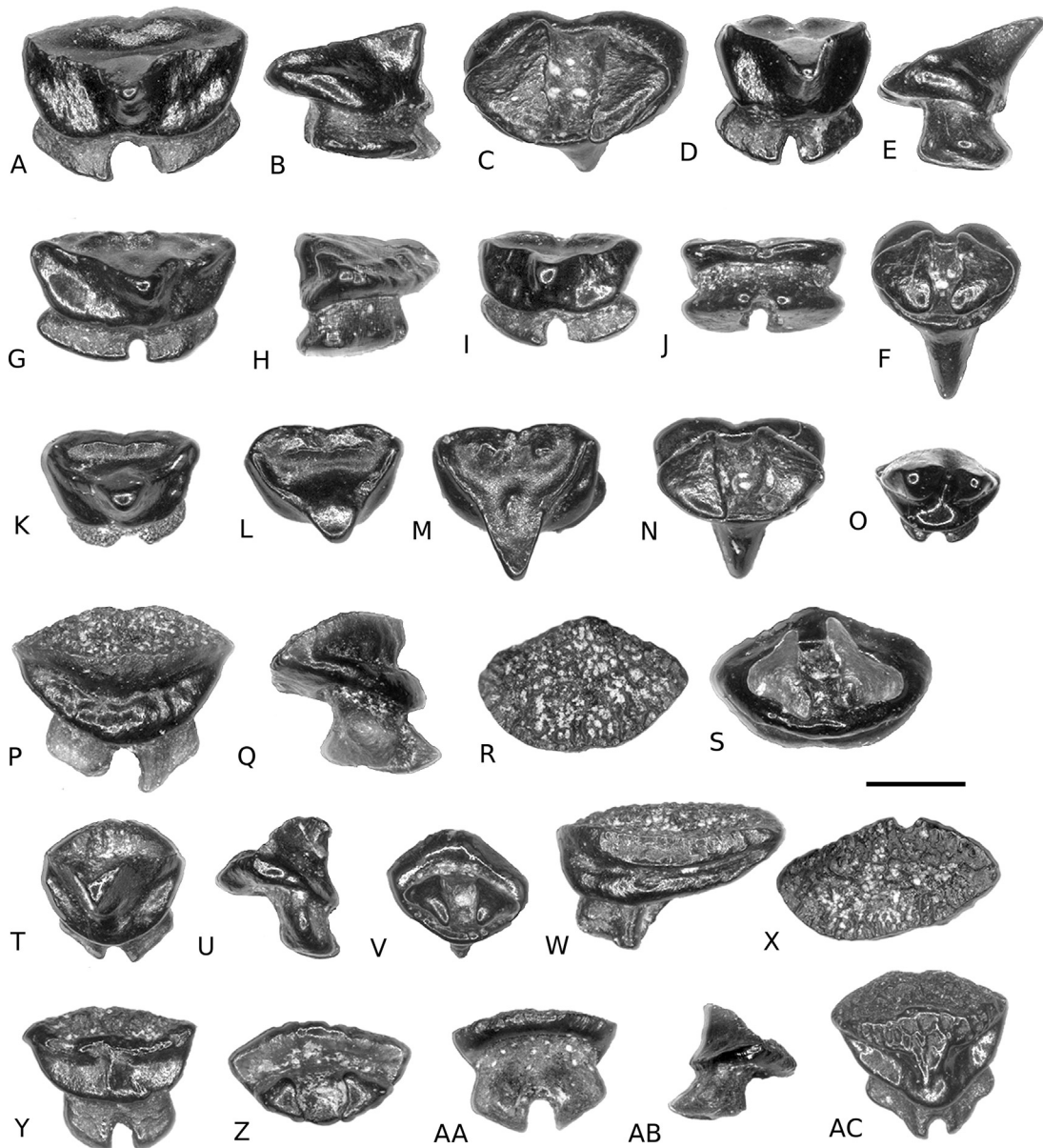


Fig. 3. A–O. *Potamotrygon rajachloae* nov. sp. A–C: MUSM 3556, lateral tooth (female) in lingual (A), profile (B), and basal (C) views; D–F: Holotype, MUSM 3555, anterior tooth (male) in lingual (D), profile (E), and basal (F) views; G, H: MUSM 3557, lateral tooth (female) in lingual (G) and profile (H) views; I, J: MUSM 3558, lateral tooth (female) in lingual (I) and labial (J) views; K, L: MUSM 3559, anterior tooth (female) in lingual (K) and occlusal (L) views; M, N: MUSM 3560, anterior tooth (male) in occlusal (M) and basal (N) views; O: MUSM 3561, pathologic morphology in lingual view. **P–AC.** *Potamotrygon canaanorum* nov. sp. P–S: Holotype, MUSM 3562, lateral tooth (female) in lingual (P), profile (Q), occlusal (R), and basal (S) views; T–V: MUSM 3563, anterior tooth (male) in lingual (T), profile (U), and basal (V) views; W, X: MUSM 3564, lateral tooth (female) in lingual (W) and occlusal (X) views; Y, Z: MUSM 3565, anterior tooth (female) in lingual (Y) and basal (Z) views; AA, AB: MUSM 3566, lateral tooth (male) in labial (AA) and profile (AB) views; AC: MUSM 3567, anterior tooth (female) in lingual view. Scale bar: 1 mm.

Type locality: CTA-43 locality, nearby Contamana, Loreto Department, Peru.

Type horizon: Top of the Pebas Fm., earliest late Miocene (ca. 11 Ma; Antoine et al., 2016; Marivaux et al., 2016a).

Material: 173 isolated teeth including the figured specimens MUSM 3555–3561.

Stratigraphic and geographic range: Late Oligocene (CTA-61; Antoine et al., 2016; Boivin et al., 2017) to late Miocene (CTA-75; Antoine et al., 2016) in the Ucayali basin, Peruvian Amazonia.

Diagnosis: A *Potamotrygon* species characterized by jaws with a weak dental heterodonty. Teeth are small; they share a crown enameloid that is entirely smooth, with a slight hollow on the labial face formed by its high marginal angles and its transverse crest. The labial visor is usually bifid (more or less marked) and both marginal edges are convex. Sexual dimorphism is weakly pronounced and teeth of both genders possess a more or less developed cusp located on the transverse crest. As such, it differs from the majority of dasyatoids in which it is usually absent on female teeth.

Description: Minute teeth (1 mm high), characterized by a crown generally wider than high, and dominating the root. There is no marked character indicating sexual dimorphism except difference in global size (male being smaller than female). The holotype is an anterior minute tooth of an adult male (Fig. 3(D–F)). The crown enameloid is exclusively smooth. This tooth possesses a prominent cusp implanted on the transverse crest and lingually bent (Fig. 3(E)). The tooth crown possesses a bifid labial visor that widely overlaps the root (Fig. 3(E)). The rest of the labial face of the crown is concave between the labial visor, the marginal edges and the salient transverse crest (Fig. 3(D)). The lingual face is more or less rectangular in shape in lingual view (Fig. 3(D)), and slightly concave between the angular marginal edges and median cusp (Fig. 3(D, E)). The root is short, narrower than the crown but massive in lateral view (Fig. 3(E)). In basal view, the two-root lobes are triangular in shape, roughly symmetric and poorly developed; they surround a shallow and narrow nutritive groove with a central foramen (Fig. 3(F)). The lingual face of the root possesses additional foramina at the crown-root junction. In other male teeth, the hollow highlighting the labial visor of the crown (Fig. 3(M)) is more or less deep, depending on the position of teeth in jaw. From the available material, it seems that this species had a weak monognathic heterodonty.

Female teeth differ from those of males in being 50% larger (Fig. 3(A–C, G–H)). The labial visor is sometimes less bifid than in males (Fig. 3(A–C, G–H)) and more rounded in lateral view (Fig. 3(H)). Bumps are sometimes observed on the labial face, between the central part and the labial visor of the labial face (e.g., Fig. 3(G)) that can fuse in a salient crest (e.g., Fig. 3(K, L)), thereby attenuating the depth of the labial visor hollow. The roots are as wide as in males but shorter (Fig. 3(B, H)). In basal view, the root lobe morphology is the same as in males: triangular, nearly symmetric and weakly developed (Fig. 3(C)).

Teeth of immature individuals are very similar in shape to those of adults; only their size – and sometimes a more pronounced transparency of their enameloid – differentiate them from the latter. As for *P. contamanensis* nov. sp., it was possible to associate several teeth of *P. rajachloae* nov. sp. with dental pathologies, corresponding to teeth with two cusps merging from a same root (Fig. 3(O)). These pathologies often result from previous injuries on dental tissues, associated with hard object diets (e.g., shells; Becker et al., 2000).

Remarks: In many living and fossil dasyatoids, the mesio-distally compressed cusped teeth are often distinctive of male when female and juvenile teeth, proportionally bigger or smaller, respectively, lack any cusp (Cappetta, 2012). In material belonging to the new species, all teeth have a more or less developed cusp on

the transverse crest despite the difference of tooth size. We thus suppose that the wide teeth with a small cusp (Fig. 3(A, B, G–J)) belonged to females. Conversely, the narrower teeth with a lengthened cusp and a bifid labial visor (Fig. 3(D–F, M, N)) are considered as belonging to males. *Potamotrygon rajachloae* nov. sp. is particularly well distinguished from *P. contamanensis* nov. sp. and *P. canaanorum* nov. sp. in having teeth without any ornamentation of their enameloid, and in bearing a small and bifid labial visor. Such tooth morphology is strikingly unusual among fossil dasyatoids known to date. However, teeth with entirely smooth enameloid are observable in some living Potamotrygoninae (e.g., *Potamotrygon henlei* (Castelnaud, 1855) or *P. yepezi* Castex and Castello, 1970; Adnet et al., 2014) as well as some marine dasyatoids (Lovejoy, 1996; Rocco et al., 2007; Naylor et al., 2012). The weak sexual heterodonty is another diagnostic criterion, particularly interesting since very few recent dasyatoids have this peculiarity (e.g., marine pelagic *Pteroplatytrygon violacea* and some species of *Potamotrygon* such as *P. magdalenae* (Duméril, 1865), *P. schroederi* Fernández-Yépez, 1958, *P. tigrina* Carvalho, Sabaj Pérez et Lovejoy, 2011, and *P. yepezi* Castex and Castello, 1970; Stepanek and Kriwet, 2015). However, none of these aforementioned species possesses the same combination of characters, i.e., the presence of a hollow on the labial face, a bifid visor, and an entire smooth enameloid. In terms of body size dimensions, the diameter of the individuals could reach approximately a 25 cm disc width based on extant tooth size–body size relationship.

Potamotrygon canaanorum nov. sp.

Fig. 3(P–AC)

Derivation of the name: The species name derives from the Canaan de Cachiyacu Shipiba Native Community, for their kindness during the successive fieldtrips to the Quebrada Cachiyacu.

Holotype: MUSM 3415, a lateral tooth from an adult female specimen (Fig. 3(P–S)).

Type locality: CTA-43 locality, nearby Contamana, Loreto Department, Peru.

Type horizon: Top of the Pebas Fm., earliest late Miocene (ca. 11 Ma; Antoine et al., 2016; Marivaux et al., 2016a).

Stratigraphic and geographic range: Late Oligocene (CTA-32; Antoine et al., 2016; Boivin et al., 2017) to late Miocene (CTA-75; Antoine et al., 2016) in the Ucayali basin, Peruvian Amazonia.

Material: 156 isolated teeth, including the figured specimens MUSM 3415–3420.

Diagnosis: A *Potamotrygon* species characterized by small teeth, laterally elongated with a homogenous ornamented labial face of crown, which shows mainly furrows, crests and sometimes granules, including in its central hollow. The lingual face is often marked by the development of a deep transverse and horizontal furrow, more or less interrupted by a median vertical crest. The wide root lobes, triangular in basal view, are lingually projected; they can exceed the width of the lingual face of the crown.

Description: Teeth are relatively small, not exceeding 2 mm in width; they tend to be wider than high. The crown overhangs the root in size. Sexual dimorphism is marked by the presence in male teeth of a cusp on the transversal crest (Fig. 3(T, AB)), which is replaced in female teeth by a transversal crest delimiting a labial face with a strongly ornamented enameloid (Fig. 3(P, W, AC)).

The holotype is an antero-lateral adult female tooth, wider than high, with a crown overlapping the root in occlusal and basal views (Fig. 3(R, S)). The labial face of the crown is flat to slightly concave near the salient labial visor, which largely overhangs the root in lateral view (Fig. 3(Q)). Its surface, oval to hexagonal in shape in occlusal view (Fig. 3(R)), is fully ornamented with furrows and crests (Fig. 3(R)). The transverse crest delimiting the labial from the

lingual faces is slightly curved toward the lingual part (Fig. 3(P, Q)). Contrary to the labial face, the lingual face is smooth and slightly bulging on its basal part. It is also concave with a deep horizontal and transversal furrow, which separates the transverse crest and the lingual visor (Fig. 3(P, Q)). Its marginal edges are sub-angular (Fig. 3(P, Q)). The root lobes are wider than long, flaring laterally except near the median nutritive groove in lingual view (Fig. 3(P)). In basal view, the lobes appear asymmetric with a pronounced triangular shape (Fig. 3(S)). The nutritive groove is wide and deep, with a large central nutritive foramen (Fig. 3(S)). In lateral view, the lingual projections of the root lobes go beyond the lingual face of the crown (Fig. 3(Q)).

The lateral teeth of females can be very wide with an elongate labial face in occlusal view (Fig. 3(W, X)), thereby determining a crushed-form for the tooth (Fig. 3(W, X)). Conversely, the more anterior teeth are as wide as high (Fig. 3(Y, Z, AC)). Their lingual faces sometimes present a median vertical crest with or without enameloid ornamentation (Fig. 3(Y, AC)). In this context, the lingual visor is comparatively sharper, determining a triangular outline to this face in lingual view (Fig. 3(AC)).

Male teeth are often smaller than female teeth but they have a similar morphology, except for the presence in males of a cusp directed upward on the transverse crest (Fig. 3(T, U, AB)). Furthermore, male teeth have more concave labial faces due to the presence of a cusp (Fig. 3(T)), a less ornamented enameloid, and a more salient labial visor (Fig. 3(U, AB)). Teeth of young specimens are morphologically similar to those of adult forms, but they lack a strong enameloid ornamentation. For *Potamotrygon canaanorum* nov. sp. as for *P. rajachloae* nov. sp., translucent teeth probably testify to the immature developmental stage of enameloid in young individuals.

Remarks: Teeth of *Potamotrygon canaanorum* nov. sp. possess a strong enameloid ornamentation, similar to those of *P. contamanensis* nov. sp. However, this ornamentation is relatively homogenous and well developed on the whole surface of the labial face, contrary to what occurs in the latter species. The shape of the labial visor is rounded instead of being labially deflected as observed on teeth of *P. contamanensis* nov. sp. and *P. ucayalensis* (at least in anterior files) or often bifid in *P. rajachloae* nov. sp. In addition, the labial face of the crown is slightly concave, as in *P. rajachloae* nov. sp. or *P. ucayalensis*, and contrary to *P. contamanensis* nov. sp. The root is wide with short rectangular root lobes, and with flat triangular basal faces as observed in *P. rajachloae* nov. sp. and, to a lesser extent, in *P. ucayalensis*. Compared with the other species recovered in the Quebrada Cachiyacu section (and ranging from the late middle Eocene to the late Miocene), the overall dental morphology of this new species appears to be somewhat intermediate between *P. ucayalensis* (restricted to Eocene localities of the Pozo Fm.) and *P. contamanensis* nov. sp. or *P. rajachloae* nov. sp. (late Oligocene-late Miocene). In *P. canaanorum* nov. sp., the elongated oval to hexagonal teeth and the development of deep transversal furrows on the lateral part of the lingual face, combined with the salient development of the labial visor in female teeth seem to indicate that tooth files must have been at least partially embedded in staggered rows forming a tooth plate, as in representatives of the living *P. leopoldi*, which does not necessarily support close phylogenetic relationships, as the former species shows a mixture of characters observable in several other living species of *Potamotrygon*. For instance, a similar ornamentation is found in modern *P. motoro* (despite the differences previously evocated) whereas short and wide roots are observable in *P. magdalenae* or *P. dumerili*. The tooth size is intermediate between that of other co-occurring species (*P. contamanensis* nov. sp. and *P. rajachloae* nov. sp.), pointing to a ca. 35 cm disc width based on extant tooth size–body size relationship.

4. Discussion

4.1. High diversity of fossil freshwater potamotrygonins

The temporal distribution of fossil elasmobranchs in the Quebrada Cachiyacu section is represented in Fig. 4. *Potamotrygon ucayalensis* is so far the only species known in the late middle Eocene deposits of the Pozo Fm. (CTA-51 and CTA-27 localities). *Potamotrygon canaanorum* nov. sp., *P. contamanensis* nov. sp., and *P. rajachloae* nov. sp. have overlapping ranges, from the late Oligocene CTA-32 (*P. canaanorum* nov. sp.) and CTA-61 localities (*P. contamanensis* nov. sp. and *P. rajachloae* nov. sp.) up to the late Miocene CTA-75 locality. They are either absent or poorly documented in intermediate levels, such as CTA-63 and CTA-45 localities from the lower part of the Pebas Fm., in which only a few unidentified potamotrygonin teeth have been collected so far. The low number and poor state of preservation of the concerned specimens discard any taxonomic assignment at the species level, but this record testifies to the continuous occurrence of potamotrygonins in the early-middle Miocene of the Contamana area. From molecular data, Lovejoy (1996), Lovejoy et al. (1998), and Marques (2000) estimated that the split between the Potamotrygoninae and their marine sister group (Styracurinae) occurred around the early-middle Miocene. These authors underlined the key role of marine incursions and especially those occurring during the early-middle Miocene in South American lowlands (Räsänen et al., 1995; Lundberg et al., 1998, 2010). In absence of any fossil record for potamotrygonins predating Neogene times before Adnet et al. (2014), the hypothesis that Miocene marine incursions would have triggered the emergence of this freshwater subfamily from marine precursors made sense. Brito and Deynat (2004) and Carvalho et al. (2004) further suggested the role of pre-Miocene transgressions as triggering a vicariant event. Later on, Bloom and Lovejoy (2011) hypothesized several scenarii regarding marine-derived lineages in South America (including potamotrygonins), advocating several pathways of marine incursions at different epochs (late Cretaceous, late Eocene, and early-middle Miocene). More recently, Louterbach et al. (2014) reported a (late) Paleocene marine incursion in the southern Amazonian foreland basin (Madre de Dios, Peru), associated with an early pulse of the Andean uplift. The latter incursion may have played a critical role in the Neotropical biodiversity dynamics in favoring biogeographical isolation and promoting speciation of freshwater organisms from marine ancestors. The continuous presence of representatives of *Potamotrygon* in freshwater deposits of Western Amazonia since the middle Eocene-late Oligocene (Antoine et al., 2016) is consistent with the earliest split ages proposed (i.e., late Cretaceous and Paleocene; Adnet et al., 2014), thereby indicating that the emergence of potamotrygonins may have occurred earlier than during the middle Eocene. Whatever the precise timing of origination, hypotheses about the historical biogeography of potamotrygonids shall necessarily include not only a robust phylogeny of the group based on revised living species, but also strong fossil evidence and a well constrained geological-climatic history (Rosa et al., 2010; Lasso et al., 2014; Carvalho et al., 2004).

Potamotrygonins seem to be already well-established in the late Oligocene-Miocene deposits in Peruvian Amazonia, with at least three coeval species with different tooth patterns among *Potamotrygon* at Contamana, and unidentified potamotrygonins mentioned in the late middle Miocene La Venta fauna (Colombia; Lundberg et al., 2010) and Fitzcarrald local fauna (eastern Peru; Antoine et al., 2007; Tejada-Lara et al., 2015). Such a high species diversity of potamotrygonins recorded in a restricted area is also observed today (Lucinda et al., 2007; Oddone et al., 2012; Carvalho, 2016; Carvalho and Araújo, 2016). Living representatives of

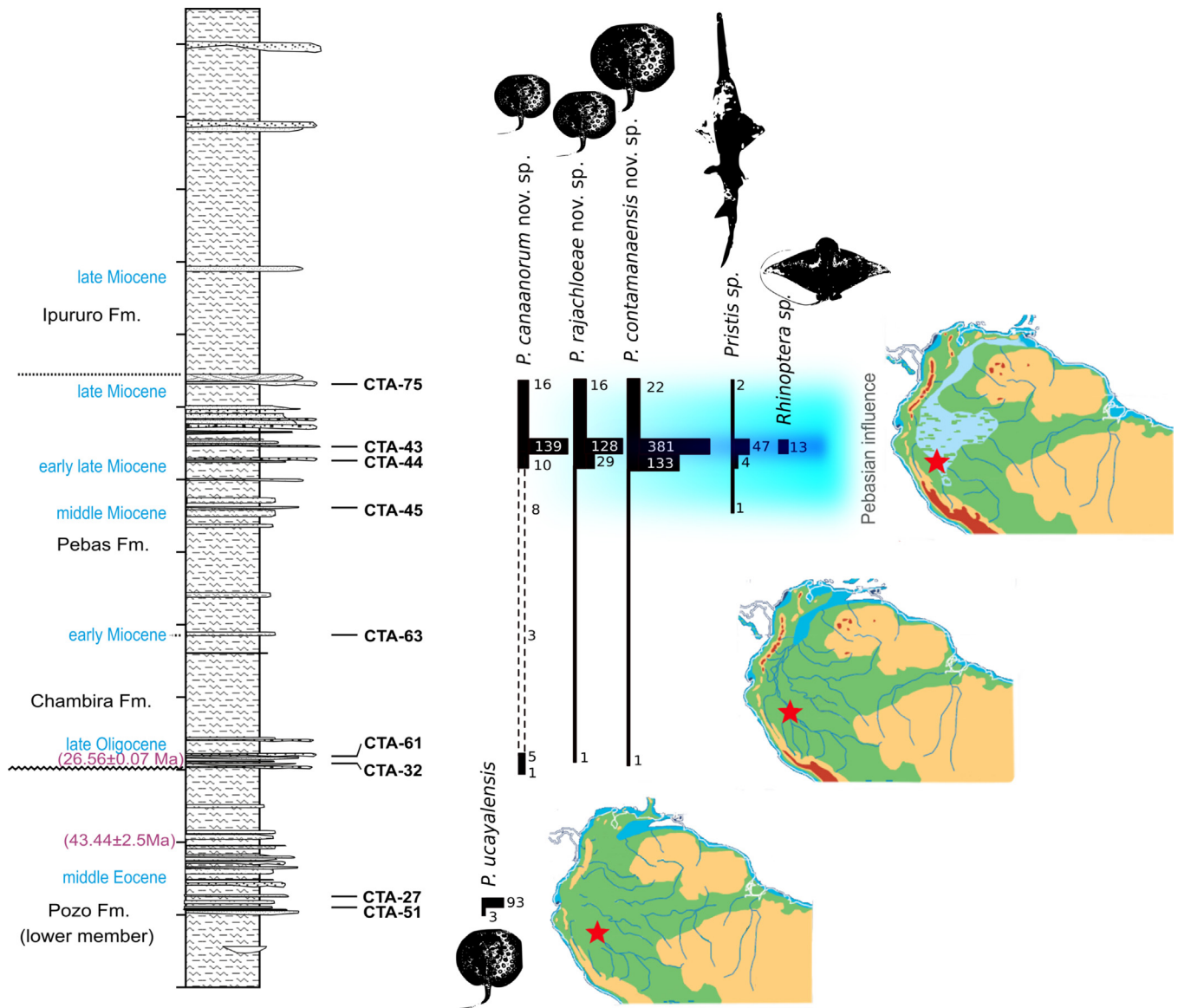


Fig. 4. Time occurrence of batoid taxa along the Quebrada Cachiyacu section in Contamana. Horizontal bars (with number of teeth) is indicative of fossil abundance. Past environmental maps show the location of the Contamana area (star) (simplified from Hoorn et al., 2010).

potamotrygonins are usually found in diverse micro-habitats of freshwater environments (Carvalho, 2016), such as beach sands, flooded forests, small creeks with mud or stone bottoms, and lakes. They perfectly embody niche partitioning observed in close freshwater species as a mean to limit individual competition for strained food resources in lakes and rivers compared to the marine realm. Moreover, adults of some potamotrygonin species are known to predate mainly fishes, worms and crustaceans, while their juveniles eat smaller preys such as aquatic insects (Lasso et al., 1997). If the three coeval species really inhabited the same fluvial and lacustrine subsystem, the hypothesis of an ecological specialisation regarding diet could be advanced based on their dental morphologies. The dental morphology of *P. contamanaensis* nov. sp. and *P. canaanorum* nov. sp. (e.g., strong enameloid crown and/or marked ornamentation of crushing surface, and partially embedded in staggered rows forming a tooth plate) could be indicative of a durophagous (malacophagous) diet, as is the case in living species such as *P. motoro* or *P. leopoldi*, which display a similar tooth pattern. Compared to females, males of *P. contamanaensis* nov. sp. and *P. canaanorum* nov. sp. potentially

had access to more varied feeding resources, in having smaller cusped teeth (Feduccia and Slaughter, 1974). However, these cusped teeth might have been present only during the breeding season, as the cusp is primarily used to grasp the back of the female during the mating, as observed in many living dasyatoids (McEachran, 1977; McCourt and Kerstitch, 1980; Kajiura and Tricas, 1996; Rangel et al., 2014, 2016), thereby involving a slight change in tooth morphology with ontogeny as reported in some modern potamotrygonins (Garrone Neto, 2010). Interestingly, Miocene potamotrygonin-yielding deposits of the Quebrada Cachiyacu section also yield a variety of mollusc shells (bivalves and snails; Antoine et al., 2016) and freshwater caimanine crocodyliforms with globular teeth, interpreted as mollusc-feeders (Salas-Gismondi et al., 2015; Antoine et al., 2016). Such assemblages are a diagnostic element of the long-lasting Pebas Mega-Wetland System that the Contamana area was part of during the late early-early late Miocene interval (Wesselingh et al., 2006; Hoorn et al., 2010; Boonstra et al., 2015; Antoine et al., 2016; Fig. 1). Conversely, the minute teeth of *P. rajachloae* nov. sp., with a long smoothed cusp in both genders, rather match the dental

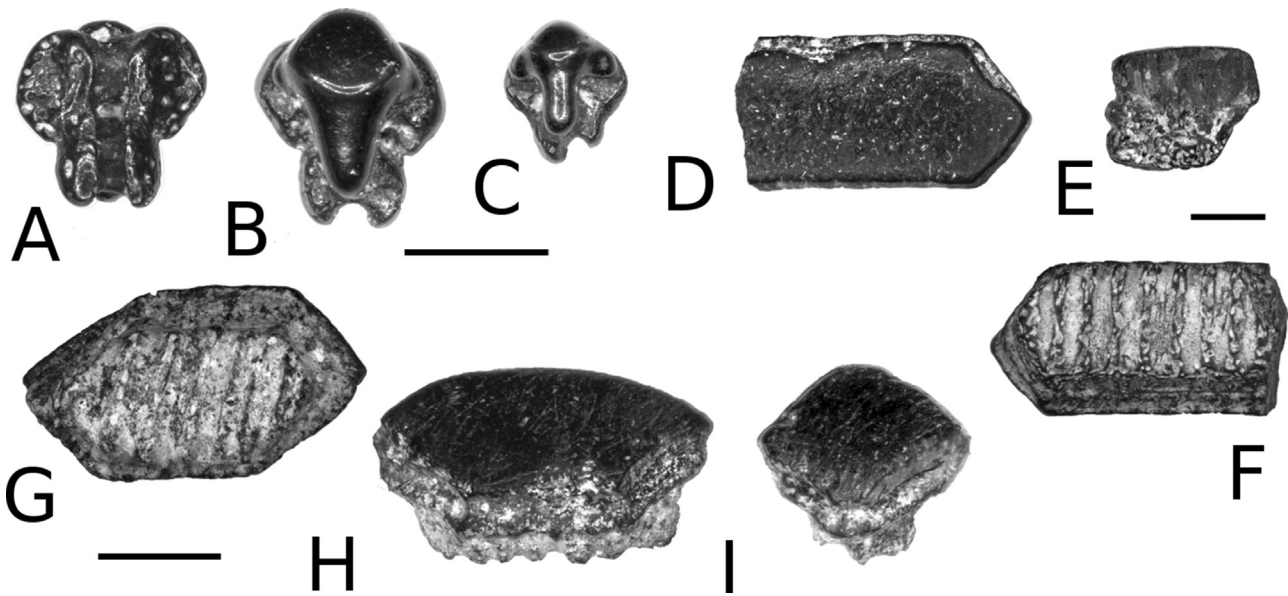


Fig. 5. A–C. Oral teeth of sawfish *Pristis* sp. A, B: MUSM 3568, adult tooth in basal (A) and lingual (B) views; C: MUSM 3569, juvenile tooth twice as small than adult, in lingual view. D–F. Oral teeth of *Rhinoptera* sp. D–F: MUSM 3570, median tooth in occlusal (D), profile (E), and basal (F) views; G, H: MUSM 3571, lateral tooth in basal (G) and lingual (H) views; I: MUSM 3572, more lateral tooth, in lingual (I) view. Scale bars: 1 mm (A–C), 2 mm (D–F, G–I).

patterns observed in fish-eaters or specialized insect-feeders, as in the living *P. orbignyi* (Lasso et al., 1997, 2014). Moreover, the presence of three co-occurring potamotrygonin species of distinct body size strengthens support for the hypothesis of ecological and/or environmental segregation, as observed today in some living potamotrygonins (Almeida et al., 2010; Garrone Netto and Uieda, 2012; Carvalho, 2016).

4.2. Marine influence within the Pebas Mega-Wetland System

At Contamana, fossils of two other batoid families were excavated in association with potamotrygonins, but in lower numbers. They consist of > 60 isolated teeth of Pristidae Bonaparte, 1838 (sawfish), which occur from CTA-45 (early-middle Miocene) up to CTA-75 (late Miocene), as well as few teeth of Rhinopteridae Jordan and Evermann, 1896 (cownose rays), recovered only at CTA-43 (early late Miocene; Fig. 5). The material assigned to Pristidae is referred to as *Pristis* sp. It includes minute oral teeth (Fig. 5(A–C)) and rostral denticles of both young and adult individuals (Antoine et al., 2016; fig. 10Y). Specimens of Rhinopteridae are preliminary attributed to *Rhinoptera* sp. (Fig. 5(D–I)) and consist of typical hexagonal teeth in median to lateral files (contrary to *Myliobatis* spp.), which constitute the usual jaw plate as already figured in Antoine et al. (2016; fig. 10V–X). In Amazonia, rare fossils of pristids were already recovered in late Miocene of the Acre-Solimões basins (Monsch, 1998; Lundberg et al., 2010) and in deposits corresponding to an older (Paleocene) marine incursion in the Madre de Dios (Louterbach et al., 2014). Concerning the rhinopterids, distinctively shaped hexagonal and flat-crowned teeth (*Myliobatis* and/or *Rhinoptera*; Lundberg et al., 2010) seem to be locally common in the Miocene faunas of northwestern Amazonia (Monsch, 1998; Lundberg et al., 2010). These new occurrences, associated with the marine incursion in the Pebas Mega-Wetland System, confirm the existence of at least two distinct Cenozoic marine incursions as far as in southern Amazonia.

There are many reports of sharks in Miocene deposits along the tropical South American and Caribbean coasts (e.g., Lundberg et al., 2010; Aguilera Socorro et al., 2011; Carrillo-Briceño et al., 2016)

down to the Brazilian Amazonian basin (e.g., Monsch, 1998; Costa et al., 2009) and in the in-land Solimões Fm. (Brazil; Lundberg et al., 2010). In contrast, there is no fossil shark in Miocene deposits of the Contamana section despite evidence of marine influence (Antoine et al., 2016). The dominance of batoids and/or the absence of sharks in modern elasmobranch assemblages is usually indicative of estuarine environments. Pristidae and Rhinopteridae are both marine groups of batoids but include many euryhaline species (e.g., the living “freshwater sawfish” *Pristis microdon* Latham, 1794). For instance, most of the living pristids are known to frequently inhabit brackish river deltas and to penetrate far into rivers and major lakes (Thorson, 1976, 1982; Peverell, 2005). Rhinopteridae (e.g., *Rhinoptera*) are more marine-dependent but they frequently invade bays and river deltas for feeding and pupping during the warm seasons (Collins et al., 2007, 2008; Goodman et al., 2011), even if their occurrences in brackish waters remind occasional compared to euryhaline pristids (Martin, 2005).

During the early Miocene (Fig. 4), the ancient fluvial system recorded in the Chambira Fm. was progressively replaced by lakes, swamps, tidal channels, and marginal marine embayments typical of the Pebas Mega-Wetland System (PMWS; Wesselingh et al., 2006; Hoorn et al., 2010, 2011). The influence of seawater was noticed in many localities where the Pebas Fm. is exposed (Boonstra et al., 2015). In the Contamana area, located in the southwestern tip of the PMWS (Fig. 4), the stratigraphical section measured in the Quebrada Cachiyacu provides evidence for a rapid shift in the environmental conditions, notably at the CTA-44 locality which records deposits ranging from lake shore, coastal plain with marginal marine affinities to channelized estuarine embayment. Fossil evidence attesting to marine affinities (including foraminifera, mesohaline ostracods, dinoflagellates, urchins, and oysters; Antoine et al., 2016) was recorded in the CTA-44 locality and in the coeval CTA-58 and CTA-77 localities. The presence of euryhaline pristids (with both young and adult specimens) recorded from the laminated blue siltites of CTA-45 (level located below CTA-44; Fig. 4) up to CTA-75 (level situated above CTA-43; Fig. 4), indicate the existence of sustainable brackish conditions in Contamana, with a marine influence peak recorded in CTA-44 (middle-late Miocene transition) and CTA-43

(early late Miocene). In addition, the co-occurrence of some cownose rays in CTA-43 implies a true connection with the northern marine realm, as evidenced by the higher batoid diversity in the Acre fauna (Lundberg et al., 2010). Such scenario for penetration of these rays from the Caribbean Sea far into the Amazonian mega-wetland would be consistent with a real inshore marine environment.

However, regardless of a sampling artefact, the absence of shark (contrary to what is recorded in the late Miocene deposits of Solimões basin, Brazilian Amazonia; Lundberg et al., 2010) indicates that the Contamana area was peripheral to these marine incursions. In this region, the river/lake systems likely prevailed, as attested by the presence of numerous freshwater potamotrygonins and freshwater ray-finned fishes recorded in the same levels of the Pebas Fm. (Antoine et al., 2016). At the time of the Pebas deposition the Contamana area probably consisted in a mosaic of aquatic environments including lakes, swamps and fluvial belts, and emerged land with a tropical rainforest. Similar mosaic environments are recorded in the northern Marañon basin (Wesselingh et al., 2006), that also experienced a maximal tidal influence during early late Miocene times, when a marine connection is clearly evidenced (Roddaz et al., 2010).

5. Conclusion

The oldest South American potamotrygonin, *Potamotrygon ucayalensis* Adnet et al., 2014, was previously reported from middle Eocene deposits of the Contamana region, in Peruvian Amazonia. The discovery of three new freshwater potamotrygonin species in the same area, from deposits dating from the late Oligocene to the late Miocene, substantially improves the fossil record of that group in South America, and more particularly in western Amazonian lowlands where they are conspicuous ichthyofaunal elements today. The long temporal record of potamotrygonins along the Quebrada Cachiyacu section in the Contamana area confirms that freshwater environments were prevailing there during most Cenozoic times, as further attested by the associated ichthyofauna, fully dominated by characiforms (Antoine et al., 2016). However, the co-occurrence of some marine batoid taxa (Rhinopteridae and Pristidae), known for their tolerance to brackish waters, attests to a diffuse marine influence in the southern tip of the Pebas Mega-Wetland System (PMWS) by late early-early late Miocene times. From an environmental perspective, batoids indicate a rapid transition from a river system including exclusively potamotrygonins during the late middle Eocene-early Miocene interval, towards a brackish-marine environment marked by two successive pulses of saline inputs during the middle-late Miocene: a moderate one with the arrival of sawfish (Pristidae) by late early-middle Miocene (CTA-45), followed by a stronger pulse with the arrival of cownose rays (Rhinopteridae) in the early late Miocene (CTA-43). This fully agrees with what is largely observed in the PMWS around 12–10 Ma (Hoorn, 1993; Wesselingh et al., 2002; Hoorn et al., 2010; Boonstra et al., 2015). The brackish influence had an impact until the late Miocene (CTA-75). If the low diversity of marine elasmobranchs (including the absence of shark) testifies for a limited marine influence during the middle-late Miocene in Contamana, the local variations of the sea level induced by Andean tectonics and eustasy triggered environmental modifications and drastically modified lowland river systems. This probably factored into the evolutionary differentiation of freshwater fishes (Lundberg et al., 1998, 2010; Albert and Reis, 2011). Such hypothesis could be applied to freshwater potamotrygonins, considering that middle Miocene marine incursions involved freshwater habitat fragmentation and triggered speciation. However, the strong dental disparity observed between the three

co-occurring potamotrygonin species described here seems to indicate that such ecological radiation started before the Miocene marine incursions, which is further highlighted by the early occurrence of the modern genus *Potamotrygon* in western Amazonian lowlands by Eocene times.

Acknowledgements

We thank everybody from the Canaan Shipibo Native Community near Contamana city (Loreto Department, Peruvian Amazonia), the IRD-PeruPetro Convention Program, and Maple Gas Peru S.A. for access to the field. Many thanks to Manuel and Manuel, for their long standing help in the forest during the field seasons. We also thank T. Cook, P. Brito and M.R. Carvalho for their criticisms and suggestions on the manuscript. The 2011–2016 field expeditions of this project were supported by the CNRS (ISE-M Paleontology Department, Montpellier, France), the Leakey Foundation, the National Geographic Foundation, and the ANR PALASIAFRICA (ANR-08-JCJC-0017, ANR-ERC). Previous field seasons of this project in the Contamana area were granted by the CNRS “Eclipse 2”, CNRS “Paleo2”, and Toulouse University “SPAM” programs to P.O.A. This work was supported by an “Investissements d’Avenir” grant managed by the French ANR (CEBA, ANR-10-LABX-25-01). This work is also in the framework of two cooperative programs, ECOS-FonCyt (2015–2017) and CoopIntEER CNRS-CONICET (2015–2016). This is ISEM publication n° 2017-243 SUD.

References

- Adnet, S., Salas-Gismondi, R., Antoine, P.-O., 2014. Comparisons of dental morphology in river stingrays (Chondrichthyes: Potamotrygonidae) with new fossils from the middle Eocene of Peruvian Amazonia rekindle debate on their evolution. *Naturwissenschaften* 101, 33–45.
- Aguilera Socorro, O.A., Ramos, M.I.F., Paes, E.T., Costa, S.A.R.F., Sánchez-Villagra, M.R., 2011. The Neogene tropical America fish assemblage and the paleobiogeography of the Caribbean region. *Swiss Journal of Palaeontology* 130, 217–240.
- Albert, J.S., Reis, R.E., 2011. *Historical biogeography of Neotropical freshwater fishes*. University of California Press, Berkeley, Los Angeles.
- Almeida, M.P., Lins, P.M.O., Charvet-Almeida, P., Barthem, R.B., 2010. Diet of the freshwater stingray *Potamotrygon motoro* (Chondrichthyes: Potamotrygonidae) on Marajo Island (Para Brazil). *Brazilian Journal of Biology* 70, 155–162.
- Antoine, P.-O., Salas-Gismondi, R., Baby, P., Benammi, M., Brusset, S., De Franceschi, D., Espurt, N., Goillot, C., Pujos, F., Tejada, J., Urbina, M., 2007. The middle Miocene (Laventan) Fitzcarrald fauna Amazonian Peru. In: Díaz-Martínez, I., Rábano, (Eds.), *Proceedings of the 4th European Meeting on the Palaeontology and Stratigraphy of Latin America Cuadernos del Museo Geominero* (8). Madrid, Instituto Geológico y Minero de España, pp. 19–24.
- Antoine, P.-O., Marivaux, L., Croft, D.A., Billet, G., Ganerod, M., Jaramillo, C., Martin, T., Orliac, M.J., Tejada, J., Altamirano, A.J., Duranthon, F., Fanjat, G., Rousse, S., Salas-Gismondi, R., 2012. Middle Eocene rodents from Peruvian Amazonia reveal the pattern and timing of caviomorph origins and biogeography. *Proceedings of the Royal Society B: Biological Sciences* 279, 1319–1326.
- Antoine, P.-O., Abello, M.A., Adnet, S., Altamirano Sierra, A.J., Baby, P., Billet, G., Boivin, M., Calderón, Y., Candela, A., Chabain, J., Corfu, F., Croft, D.A., Ganerod, M., Jaramillo, C., Klaus, S., Marivaux, L., Navarrete, R.E., Orliac, M.J., Parra, F., Pérez, M.E., Pujos, F., Rage, J.-C., Ravel, A., Robinet, C., Roddaz, M., Tejada-Lara, J.V., Vélez-Juarbe, J., Wesselingh, F.P., Salas-Gismondi, R., 2016. A 60-million-year Cenozoic history of western Amazonian ecosystems in Contamana, eastern Peru. *Gondwana Research* 31, 30–59.
- Araújo, M.L.G., 1998. Biología Reproductiva e Pesca de *Potamotrygon* sp. C (Chondrichthyes - Potamotrygonidae), no médio Rio Negro, Amazonas. M. Sc. Thesis, Manaus, Instituto Nacional de Pesquisas da Amazônia and Universidade do Amazonas, 171 p. (unpubl.).
- Aschliman, N.C., Nishida, M., Miya, M., Inoue, J.G., Rosana, K.M., Naylor, G.J.P., 2012. Body plan convergence in the evolution of skates and rays (Chondrichthyes: Batoidea). *Molecular Phylogenetics and Evolution* 63, 28–42.
- Beebe, W., Tee-Van, J., 1941. Eastern Pacific expeditions of the New York Zoological Society. XXVIII. Fishes from the tropical eastern Pacific. [From Cedros Island, Lower California, south to the Galápagos Islands and northern Peru]. Part 3. Rays Mantas and Chimaeras. *Zoologica, Scientific Contributions of the New York Zoological Society* 26 (3), 245–280.
- Becker, M.A., Chamberlain, J.A., Stoffer, P.W., 2000. Pathologic tooth deformities in modern and fossil chondrichthians: a consequence of feeding-related injury. *Lethaia* 33, 103–118.
- Benson, R.N., 1998. Geology and paleontology of the lower Miocene Pollack Farm Fossil Site Delaware. *Delaware Geological Survey Special Publication* 21, 1–191.

- Bloom, D.D., Lovejoy, N.R., 2011. The biogeography of marine incursions in South America. In: Albert, J.S., Reis, R.E. (Eds.), *Historical biogeography of neotropical freshwater fishes*. University of California Press, Berkeley, Los Angeles.
- Boivin, M., Marivaux, L., Candela, A.M., Orliac, M.J., Pujos, F., Salas-Gismondi, R., Tejada-Lara, J.V., Antoine, P.-O., 2017. Late Oligocene caviomorph rodents from Contamana, Peruvian Amazonia. *Special Papers in Palaeontology* 3, 69–109.
- Bonaparte, C.L., 1838. *Selachorum tabula analytica*. *Nuovi Annali della Scienza Naturali Bologna* 1 (2), 195–214.
- Boonstra, M., Ramos, M.I.F., Lammertsma, E.I., Antoine, P.-O., Hoorn, C., 2015. Marine connections of Amazonia: Evidence from foraminifera and dinoflagellate cysts (early to middle Miocene, Colombia/Peru). *Palaeogeography, Palaeoclimatology, Palaeoecology* 417, 176–194.
- Brito, P.M., Deynat, P.P., 2004. Freshwater stingrays from the Miocene of South America with comments on the rise of potamotrygonids (Batoids, Myliobatiformes). In: Arratia, G., Wilson, M.V.H., Coutier, R. (Eds.), *Recent Advances in the Origin and Early Radiation of Vertebrates*. Verlag Dr. Friedrich Pfeil, München, pp. 575–582.
- Cappetta, H., 2012. *Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii: Teeth*. *Handbook of Paleichthyology*. Verlag Dr. Friedrich Pfeil, Stuttgart-New York, 3E.
- Carrillo-Briceño, J.D., Argyriou, T., Zapata, V., Kindlimann, R., Jaramillo, C., 2016. A new early Miocene (Aquitania) Elasmobranchii assemblage from the la Guajira Peninsula Colombia. *Ameghiniana* 53, 77–99.
- Collins, A.B., Heupel, M.R., Motta, P.J., 2007. Residence and movement patterns of cownose rays *Rhinoptera bonasus* within a south-west Florida estuary. *Journal of Fish Biology* 71, 1159–1178.
- Collins, A.B., Heupel, M.R., Simpfendorfer, C.A., 2008. Spatial distribution and long-term movement patterns of cownose rays *Rhinoptera bonasus* within an estuarine river. *Estuaries and Coasts* 31, 1174–1183.
- Cook, T.D., Eaton, J.G., Newbrey, M.G., Wilson, M.V.H., 2014. A new genus and species of freshwater stingray (Myliobatiformes, Dasyatoidea) from the latest middle Eocene of Utah, U.S.A. *Journal of Paleontology* 88, 497–503.
- Costa, S.A.R.F., Richter, M., Mann de Toledo, P., de Santos, H.M.M.A., 2009. Shark teeth from Pirabas Formation (Lower Miocene), northeastern Amazonia, Brazil. *Boletim do Museu Paraense Emílio Goeldi Ciências Naturais* 4, 221–230.
- Carvalho de, M.R., 2016. Description of two extraordinary new species of freshwater stingrays of the genus *Potamotrygon* endemic to the rio Tapajós basin Brazil (Chondrichthyes: Potamotrygonidae), with notes on other Tapajós stingrays. *Zootaxa* 4167, 1–63.
- Carvalho de, M.R., Maisey, J.G., Grande, L., 2004. Freshwater stingrays of the green river Formation of Wyoming (early Eocene), with the description of a new genus and species and an analysis of its phylogenetic relationships (Chondrichthyes: Myliobatiformes). *Bulletin of the American Museum of Natural History* 284, 1–136.
- Carvalho de, M.R., Ragno, M.P., 2011. An unusual, dwarf new species of Neotropical freshwater stingray, *Plesiomyron nana* sp. nov., from the upper and mid Amazon basin: the second species of *Plesiomyron* (Chondrichthyes: Potamotrygonidae). *Papeis Avulsos de Zoologia* 51, 101–138.
- Carvalho de, M.R., Lovejoy, N., 2011. Morphology and phylogenetic relationships of a remarkable new genus and two new species of Neotropical freshwater stingrays from the Amazon basin (Chondrichthyes: Potamotrygonidae). *Zootaxa* 2776, 48–83.
- Carvalho de, M.R., Loboda, T.S., Da Silva, J., 2016. A new subfamily, Styrcurinae, and new genus, *Styrcura*, for *Himantura schmarda* (Werner, 1904) and *Himantura pacifica* (Beebe and Tee-Van, 1941) (Chondrichthyes: Myliobatiformes). *Zootaxa* 4175, 201–221.
- Carvalho de, M.R., Araújo, M.L.G., 2016. A new species of Neotropical freshwater stingray (Chondrichthyes: Potamotrygonidae) from the Rio Negro, Amazonas Brazil: the smallest species of *Potamotrygon*. *Zootaxa* 4107, 566–586.
- Castelnau, F.L., 1855. Poissons, in: Animaux nouveaux ou rares recueillis pendant l'expédition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro à Lima, et de Lima au Paraná; exécutée par ordre du gouvernement Français pendant les années 1843 à 1847. Part 7, *Zoology* 2, i–xii + 1–112.
- Castex, M.N., Castello, H.P., 1970. *Potamotrygon leopoldi*, a new species of freshwater sting-ray for the Xingú River, Brazil (Chondrichthyes Potamotrygonidae). *Acta Scientifica, Universidad del Salvador* 10, 1–16.
- Compagno, L.J.V., 1973. Interrelationships of living elasmobranchs. *Zoological Journal of the Linnean Society* 53 (Suppl. 1), 15–61.
- Deynat, P., 2006. *Potamotrygon marinae* n. sp., une nouvelle espèce de raies d'eau douce de Guyane (Myliobatiformes Potamotrygonidae). *Comptes Rendus Biologies* 329, 483–493.
- Deynat, P., Brito, P.M., 1994. Révision des tubercules cutanés de raies (Chondrichthyes, Batoidea) du bassin du Paraná. Tertiaire d'Amérique du Sud. *Annales de Paléontologie* 80, 237–251.
- Duméril, A., 1865. Histoire naturelle des poissons ou ichthyologie générale. Elasmobranches plagiostomes et holocéphales ou chimères. Librairie Encyclopédique de Roret, Paris, 720 p.
- Feduccia, A., Slaughter, B.H., 1974. Sexual dimorphism in skates (Rajidae) and its possible role in differential niche utilization. *Evolution* 28, 164–168.
- Fernández-Yépez, A., 1958. Nueva raya para la ciencia: *Potamotrygon schroederi* n. sp., 2–3. *Boletín del Museo de Ciencias Naturales, Caracas, Venezuela*, pp. 8–11.
- Fontenelle, J.P., Da Silva, J.P., Carvalho de, M.R., 2014. *Potamotrygon limai*, sp. nov., a new species of freshwater stingray from the upper Madeira River system, Amazon basin (Chondrichthyes: Potamotrygonidae). *Zootaxa* 3765, 249–268.
- Fontenelle, J.P., Carvalho de, M.R., 2016. Systematic implications of brain morphology in potamotrygonidae (Chondrichthyes: Myliobatiformes). *Journal of Morphology* 277, 252–263.
- García, D.A., Lasso, C.A., Morales, M., Caballero, S.J., 2016. Molecular systematics of the freshwater stingrays (myliobatiformes: potamotrygonidae) of the Amazon, Orinoco, Magdalena, Esequibo, Caribbean, and Maracaibo basins (Colombia - Venezuela): evidence from three mitochondrial genes. *Mitochondrial DNA part A - DNA Mapping, Sequencing, and Analysis* 27, 4479–4491.
- Garman, S., 1877. On the pelvis and external sexual organs of selachians, with special references to new genera *Potamotrygon* and *Disceus* (with descriptions). *Proceedings of the Boston Society of Natural History* 19, 197–215.
- Garman, S., 1913. *The plagiostoma Memoirs of the Museum of Comparative Zoology at Harvard College* 36, 528 p.
- Garrone Neto, D., 2010. Considerações sobre a reprodução de duas espécies de raia (Myliobatiformes, Potamotrygonidae) na região do Alto Rio Paraná Sudeste do Brasil. *Pan-American Journal of Aquatic Sciences* 5, 101–111.
- Garrone Neto, D., Uieda, V.S., 2012. Activity and habitat use of two species of stingrays (Myliobatiformes: Potamotrygonidae) in the upper Paraná River basin Southeastern Brazil. *Neotropical Ichthyology* 10, 81–88.
- Goodman, M.A., Conn, P.B., Fitzpatrick, E., 2011. Seasonal occurrence of cownose rays (*Rhinoptera bonasus*) in North Carolina's estuarine and coastal waters. *Estuaries and Coasts* 34, 640–651.
- Hoorn, M.C., 1993. Marine incursions and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: results of a palynostratigraphic study. *Palaeogeography, Palaeoclimatology, Palaeoecology* 109, 1–55.
- Hoorn, C., Wesselingh, F.P., Hovikoski, J., Guerrero, J., 2011. The development of the Amazonian Mega-Wetland (Miocene; Brazil, Colombia, Peru, Bolivia). In: Hoorn, C., Wesselingh, F.P. (Eds.), *Amazonia: Landscape and Species Evolution*. Oxford, Wiley-Blackwell Publishing Ltd, pp. 123–142.
- Hoorn, C., Wesselingh, F.P., ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Sanmartin, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, C., Riff, D., Negri, F.R., Hooghiemstra, H., Lundberg, J., Stadler, T., Sarkinen, T., Antonelli, A., 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* 330, 927–931.
- Huxley, T.H., 1880. *A Manual of the Anatomy of Vertebrated Animals*. D. Appleton & Company, New York, 431 p.
- Jordan, D.S., Evermann, B.W., 1896. The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama Part I. *Bulletin of the United States National Museum* 47, 1–1240.
- Kajiura, S.M., Tricas, T.C., 1996. Seasonal dynamics of dental sexual dimorphism in the Atlantic stingray *Dasyatis sabina*. *Journal of Experimental Biology* 199, 2297–2306.
- Latham, J., 1794. An essay on the various species of Sawfish. *Transactions of the Linnean Society of London* 2, 273–282.
- Lasso, C.A., Rial, A.B., Lasso-Alcalá, O., 1997. Notes on the biology of the freshwater stingrays *Paratrygon aiereba* (Müller and Henle, 1841) and *Potamotrygon orbignyi* (Castelnau, 1855) (Chondrichthyes: Potamotrygonidae) in the Venezuelan Llanos. *Aqua, International Journal of Ichthyology* 2, 39–52.
- Lasso, C.A., Rosa, R.S., Sánchez-Duarte, P., Morales-Betancourt, M.A., Agudelo-Córdoba, E., 2014. Rayas de agua dulce (Potamotrygonidae) de Suramérica. Parte I. Colombia, Venezuela, Ecuador, Perú, Brasil, Guyana, Surinam y Guayana Francesa: diversidad, bioecología, uso y conservación. In: Carlos, A., Lasso, C.A. et al. (eds.), *Serie Recursos Hidrobiológicos y Pesqueros Continentales de Colombia, IX - Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá*, 368 p.
- Larrazet, M., 1886. Des pièces de la peau de quelques Sélaciens fossiles. *Bulletin de la Société Géologique Française* 3, 255–277.
- Loboda, T.S., 2010. Revisão taxonômica e morfológica de *Potamotrygon motoro* (Müller and Henle, 1841) na bacia Amazônica (Chondrichthyes: Myliobatiformes: Potamotrygonidae). M.Sc.Thesis. Instituto de Biociências da Universidade de São Paulo, 305 (unpubl.).
- Loboda, T.S., Carvalho de, M.R., 2013. Systematic revision of the *Potamotrygon motoro* (Müller and Henle, 1841) species complex in the Paraná-Paraguay basin, with description of two new ocellated species (Chondrichthyes: Myliobatiformes: Potamotrygonidae). *Neotropical Ichthyology* 11, 693–737.
- Louterbach, M., Roddaz, M., Bailleul, J., Antoine, P.-O., Adnet, S., Kim, J.H., van Soelen, E., Parra, F., Gérard, J., Calderon, Y., Gagnaison, C., Sinninghe Damsté, J.S., Baby, P., 2014. Evidences for a Paleocene marine incursion in southern Amazonia (Madre de Dios Sub-Andean Zone, Peru). *Palaeogeography, Palaeoclimatology, Palaeoecology* 414, 451–471.
- Lovejoy, N.R., 1996. Systematics of myliobatoid elasmobranchs: with emphasis on the phylogeny and historical biogeography of Neotropical freshwater stingrays (Potamotrygonidae: Rajiformes). *Zoological Journal of the Linnean Society* 117, 207–257.
- Lovejoy, N.R., Bermingham, E., Martin, A.P., 1998. Marine incursion into South America. *Nature* 396, 421–422.
- Lucinda, P.H.F., Freitas, I.S., Soares, A.B., Marques, E.E., Agostinho, C.S., Oliveira de, R.J., 2007. Fish, Lajeado Reservoir, rio Tocantins drainage State of Tocantins, Brazil. *Check List* 3 (2), 70–83.
- Lundberg, J.G., 1997. Freshwater fishes and their paleobiotic implications. In: Kay, R.F., Madden, R.H., Cifelli, R.L., Flynn, J.J. (Eds.), *Vertebrate Paleontology in the Neotropics: the Miocene Fauna of La Venta, Colombia*. Smithsonian Inst. Press, Washington D.C., pp. 67–91.
- Lundberg, J.G., Marshall, L.G., Guerrero, J., Horton, B., Malabarba, M.C.S.L., Wesselingh, F.P., 1998. The stage of Neotropical fish diversification: a history of tropical South American rivers. In: Malabarba, L.R., et al. (Eds.), *Phylogeny and Classification of Neotropical Fishes*. Edipucrs, Porto Alegre, pp. 13–48.

- Lundberg, J.G., Sabaj Pérez, M.H., Dahdul, W.M., Aguilera, O.A., 2010. The Amazonian Neogene fish fauna. In: Hoorn, C., Wesselingh, F.P. (Eds.), *Amazonia: Landscape and Species Evolution*. Wiley-Blackwell Publishing Ltd, Oxford, pp. 281–301.
- Marivaux, L., Adnet, A., Altamirano-Sierra, A.J., Pujos, F., Ramdarshan, A., Salas-Gismondi, R., Tejada-Lara, J.V., Antoine, P.-O., 2016a. Dental remains of cebid platyrrhines from the earliest late Miocene of Western Amazonia Peru: macroevolutionary implications on the extant capuchin and marmoset lineages. *American Journal of Physical Anthropology* 161, 478–493.
- Marivaux, L., Adnet, A., Altamirano-Sierra, A.J., Boivin, M., Pujos, F., Ramdarshan, A., Salas-Gismondi, R., Tejada-Lara, J.V., Antoine, P.-O., 2016b. Neotropics provide insights into the emergence of New World monkeys: new dental evidence from the late Oligocene of Peruvian Amazonia. *Journal of Human Evolution* 97, 159–175.
- Marques, F.P.L., 2000. Evolution of Neotropical freshwater stingrays and their parasites: taking into account space and time Ph.D. Thesis, University of Toronto, 325 (unpubl.).
- Martin, R.A., 2005. Conservation of freshwater and euryhaline elasmobranchs. *Journal of the Marine Biological Association of the United Kingdom* 85, 1049–1073.
- McCourt, R.M., Kerstitch, A.N., 1980. Mating behavior and sexual dimorphism in dentition in the stingray *Urolophus concentricus*, from the Gulf of California. *Copeia* 1980, 900–901.
- McEachran, J.D., 1977. Reply to "Sexual dimorphism in Skates (Rajidae)". *Evolution* 31, 218–220.
- McEachran, J.D., Dunn, K.A., Miyake, T., 1996. Interrelationships of the batoid fishes (Chondrichthyes: Batoidei). In: Stiassny, M.L.J., Parenti, L.R., Johnson, G.D. (Eds.), *Interrelationships of fishes*. Academic Press, San Diego, London, pp. 63–84.
- Monsch, K.A., 1998. Miocene fish faunas from the northwestern Amazonia basin (Colombia, Peru, Brazil) with evidence of marine incursions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 143, 31–50.
- Müller, J., Henle, J., 1841. *Systematische Beschreibung der Plagiostomen*. Veit and Co, Berlin.
- Naylor, G.J.P., Caira, J.N., Jensen, K., Rosana, K.A.M., Straube, N., Lakner, C., 2012. Elasmobranch phylogeny: a mitochondrial estimate based on 595 species. In: Carrier, J.C., et al. (Eds.), *Biology of Sharks and their Relatives*. Edition 2. CRC Press, Boca Raton, Florida, pp. 31–56.
- Oddone, M.C., Velasco, G., Charvet, P., 2012. Record of the freshwater stingrays *Potamotrygon brachyura* and *P. motoro* (Chondrichthyes, Potamotrygonidae) in the lower Uruguay River South America. *Acta Amazonica* 42, 299–304.
- Peever, S., 2005. Distribution of sawfishes (Pristidae) in the Queensland Gulf of Carpentaria, Australia - with notes on sawfish ecology. *Environmental Biology of Fishes* 73, 391–402.
- Rangel, B.S., Rodrigues, S.S., Favaron, P.O., Amorim, A.F., Rici, R.E.G., 2014. Structure and dental sexual dimorphism in *Dasyatis hypostigma* (Santos and Carvalho, 2004) (Myliobatiformes, Dasyatidae), in: Méndez-Vilas, A. (Ed.), *Microscopy: Advances in Scientific Research and Education* 1, 89–94.
- Rangel, B.S., Santander-Neto, J., Rici, R.E.G., Lessa, R., 2016. Dental sexual dimorphism and morphology of *Urotrygon microphthalmum*. *Zoomorphology* 135, 367–374.
- Räsänen, M.E., Linna, A.M., Santos, J.C., Negri, F.R., 1995. Late Miocene tidal deposits in the Amazonian foreland basin. *Science* 269, 386–390.
- Rocco, L., Liguori, I., Costagliola, D., Morescalchi, M.A., Tinti, F., Stingo, V., 2007. Molecular and karyological aspect of batoidea (Chondrichthyes Elasmobranchii) phylogeny. *Gene* 389, 80–86.
- Roddaz, M., Hermoza, W., Mora, A., Baby, P., Parra, M., Christophoul, F., Brusset, S., Espurt, N., 2010. Cenozoic sedimentary evolution of the Amazonian foreland basin system. In: Hoorn, C., Wesselingh, F.P. (Eds.), *Amazonia: Landscape and Species Evolution*. Wiley-Blackwell Publishing Ltd, Oxford, UK, pp. 61–88.
- Rosa, R.S., 1985. A systematic revision of the South American freshwater stingrays (Chondrichthyes: Potamotrygonidae). Ph.D. Thesis, The College of William and Mary, Williamsburg, Virginia 523 (unpubl.).
- Rosa, R.S., Castello, H.P., Thorson, T.B., 1987. *Plesiotrygon iwamae*, a new genus and species of Neotropical freshwater stingray (Chondrichthyes: Potamotrygonidae). *Copeia* 1987, 447–458.
- Rosa, R.S., Carvalho de, M.R., de Almeida Wanderley, C., 2008. *Potamotrygon boesemani* (Chondrichthyes: Myliobatiformes: Potamotrygonidae), a new species of Neotropical freshwater stingray from Surinam. *Neotropical Ichthyology* 6, 1–8.
- Rosa, R.S., Charvet-Almeida, P., Quijada, C.C.D., 2010. Biology of the South American Potamotrygonid Stingrays. In: Carrier, J.C., et al. (Eds.), *Sharks and their Relatives II: Biodiversity, Adaptive Physiology, and Conservation*. Boca Roca, Florida, pp. 241–283.
- Salas-Gismondi, R., Flynn, J.J., Baby, P., Tejada-Lara, J.V., Wesselingh, F.P., Antoine, P.-O., 2015. A Miocene hyperdiverse crocodylian community reveals peculiar trophic dynamics in proto-Amazonian mega-wetlands. *Proceedings of the Royal Society of London, B* 282, 1–10.
- Salas-Gismondi, R., Flynn, J.J., Baby, P., Tejada-Lara, J.V., Claude, J., Antoine, P.-O., 2016. A new 13 million year old gavialoid crocodylian from Proto-Amazonian Mega-Wetlands reveals parallel evolutionary trends in skull shape linked to longirostry. *PLoS ONE* 11, e0152453.
- Silva da, J.P.C.B., Carvalho de, M.R., 2016. Systematics and morphology of *Potamotrygon orbignyi* (Castelnau, 1855) and allied forms (Chondrichthyes: Myliobatiformes: Potamotrygonidae). *Zootaxa* 3982, 1–82.
- Stepanek, R., Kriwet, J., 2015. Comparative morphology of the juvenile skeleton in freshwater stingrays with special focus on *Paratrygon aiereba* (Myliobatiformes: Potamotrygonidae). *Zoologischer Anzeiger - A Journal of Comparative Zoology* 255, 7–24.
- Tejada-Lara, J., Salas-Gismondi, R., Pujos, F., Baby, P., Benammi, M., Brusset, S., De Franceschi, D., Espurt, N., Urbina, M., Antoine, P.-O., 2015. Life in proto-Amazonia: middle Miocene mammals from the Fitzcarrald arch (Peruvian Amazonia). *Palaeontology* 58, 1–38.
- Thorson, T.B., 1976. Observations on the reproduction of the sawfish, *Pristis perotteti*, in Lake Nicaragua with recommendations for its conservation. In: Thorson, T.B. (Ed.), *Investigations of the Ichthyofauna of Nicaraguan Lakes*. University of Nebraska, Lincoln, pp. 641–650.
- Thorson, T.B., 1982. Life history implications of a tagging study of largetooth sawfish *Pristis perotteti*, in the Lake Nicaragua-Río San Juan System. *Environmental Biology of Fishes* 7, 207–228.
- Toffoli, D., Hrbek, T., Góes de Araújo, M.L., Pinto de Almeida, M., Charvet-Almeida, P., Farias, I.P., 2008. A test of the utility of DNA barcoding in the radiation of the freshwater stingray genus *Potamotrygon* (Potamotrygonidae Myliobatiformes). *Genetics and Molecular Biology* 31, 324–336.
- Werner, F., 1904. *Die Fische der zoologisch-vergleichend-anatomischen Sammlung der Wiener Universität*. I. Teil. Zoologische Jahrbücher, Abteilung für Systematik. Geographie und Biologie der Tiere 21 (3), 263–302.
- Wesselingh, F.P., Räsänen, M.E., Irion, G., Vonhof, H.B., Kaandorp, R., Renema, W., Romero Pittman, L., Gingras, M., 2002. Lake Pebas: a palaeoecological reconstruction of a Miocene, long-lived lake complex in western Amazonia. *Cainozoic Research* 1, 35–81.
- Wesselingh, F.P., Guerrero, J., Räsänen, M., Romero Pitmann, L., Vonhof, H., 2006. Landscape evolution and depositional processes in the Miocene Amazonian Pebas lake/wetland system: evidence from exploratory boreholes in northeastern Peru. *Scripta Geologica* 133, 323–361.
- Whitley, G.P., 1940. *The fishes of Australia*. Part 1. The sharks, rays, devil fishes and other primitive fishes of Australia and New Zealand. Royal Zoological Society of New South Wales, Sydney, 230 p.
- Williamson, T.E., Lucas, S.G., 1993. Freshwater selachians from the early Palaeocene of the San Juan basin north-western New Mexico USA. *The Tertiary Research Group* 14, 97–105.
- Wroblewski, A.F.-J., 2004. New selachian paleofaunas from "fluvial" deposits of the Ferris and Lower Hanna formations (Masstrichtian-Selandian: 66–58 Ma) Southern Wyoming. *Palaios* 19, 249–258.