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A historical vertebrate collection from the Middle Miocene of the Peruvian Amazon

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Abstract

The Miocene aquatic and terrestrial fossil record from western Amazonia constitute a clear evidence of the palaeoenvironmental diversity that prevailed in the area, prior to the establishment of the Amazon River drainage. During the Miocene, the region was characterized by a freshwater megawetland basin, influenced by episodic shallow-marine incursions. A fossil vertebrate collection from the middle Miocene strata of the Pebas Formation is here studied and described. This historical collection was recovered in 1912 along the banks of the Itaya River (Iquitos, Peru), during a scientific expedition led by two scientists of the University of Zurich, Hans Bluntschli and Bernhard Peyer. Our findings include a total of 34 taxa, including stingrays, bony fishes, turtles, snakes, crocodylians, and lizards. Fishes are the most abundant group in the assemblage (~23 taxa), including the first fossil record of the freshwater serrasalmids *Serrasalmus*, and *Mylossoma*, and the hemiodontid *Hemiodus* for the Pebas system, with the latter representing the first fossil to be discovered for the entire Hemiodontidae. The presence of a representative of Colubroidea in the middle Miocene of Iquitos supports the hypothesis of arrival and dispersal of these snakes into South America earlier than previously expected. This fossil assemblage sheds light on the palaeoenvironments, and the geographical/temporal range of several aquatic/terrestrial lineages inhabiting the Amazonian region.

Keywords: South America, Middle Miocene, Pebas Formation, Fishes, Reptiles, Palaeoenvironments

Introduction

More than a century ago, two scientists of the University of Zurich, Dr. Hans Bluntschli (1877–1962) and Dr. Bernhard Peyer (1885–1963), left for a scientific expedition to the Pampas region in Argentina and the Amazon region of Brazil and Peru. The expedition, which was supported by a federal travel grant (Strauss, 1962), aimed at collecting hitherto poorly known animals, plants, and fossils for scientific study from these regions, with focus on mammals, especially primates. The expedition took place in

1912 (between February and November), with important discoveries, and a substantial amount of collected zoological, botanical, geological, palaeontological, and anthropological specimens (Bluntschli, 1923). After their return to Europe, Bluntschli became professor and director at the Senckenberg Anatomical Institute in Frankfurt, Germany, in 1914, then professor in 1915, and later was offered a professorship at the Anatomical Institute of the University of Bern in 1933 (Greif und Schmutz, 1995). Peyer habilitated at the University of Zurich in 1918 and became professor in 1930 at the Zoological Institute, as well as first ordinarius of Palaeontology and Comparative Anatomy in 1943 (Fischer, 1963). In the years after their return from South America, most of the collections from the Pampas and Amazonian regions were distributed among various institutions and museums in Europe

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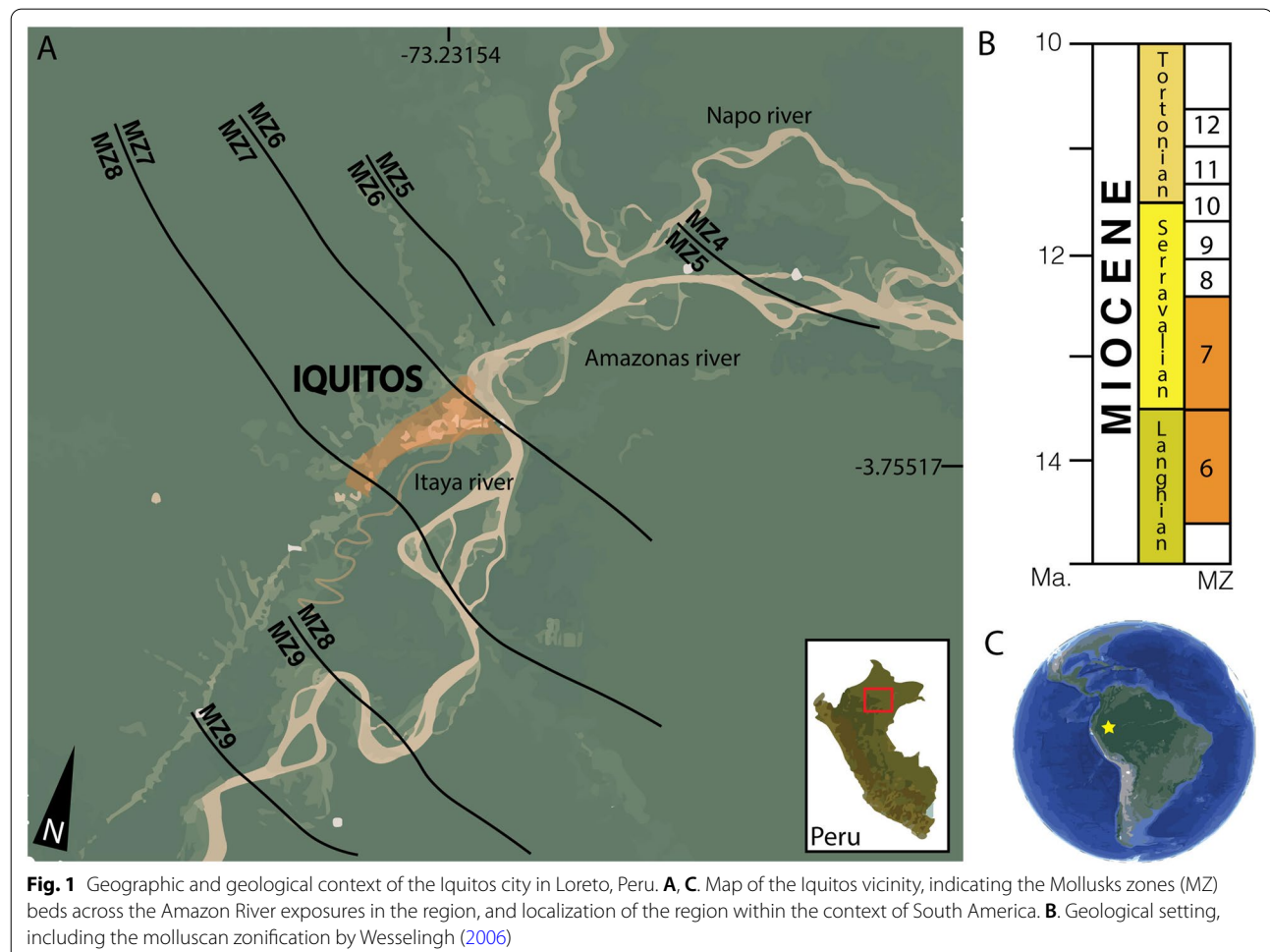
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including Berlin, Frankfurt, Vienna, and Zurich, but parts were also kept for future studies in the ‘custody’ of the two scientists (Bluntschli, 1923).

In the banks of the Itaya River in Iquitos ($03^{\circ}44'37''\text{S}$, $073^{\circ}15'4''\text{W}$), Department of Loreto (Fig. 1), Bluntschli and Peyer collected the fossil invertebrate and vertebrate assemblages from the Peruvian Amazon. Those were brought to Zurich during the summer of 1913, being sorted (glass tubes and boxes containing the fossil invertebrates/vertebrates were identified with papers of different colours according the fossiliferous sites/layers, see Fig. 2B, C), preserved, and assigned with a preliminary taxonomy (de Greve, 1938). The entire specimens were housed in the collections, which are now part of the Palaeontological Institute and Museum of the University of Zurich (PIMUZ). Peyer (1929, 1937) preliminarily mentioned and illustrated a premaxillary bone of a characiform (later referenced and figured again in Peyer, 1968), and few isolated loricariid teeth in the collection from Iquitos. Posteriorly, de Greve (1938) studied the fossil mollusks assemblage in detail. Since that time, no other

work or research has been carried out on the Iquitos vertebrate assemblage housed in Zurich. The outcrops in the surrounding of Iquitos from where the fossil assemblages were collected (de Greve, 1938) are recognized as belonging to the Miocene Pebas Formation (see Wesselingh et al., 2002, Fig. 17).

The Pebas Formation (Fm.), equivalent to the Brazilian Solimões Fm. (see Cozzuol, 2006), crops out in western and central Amazonia, and their wide depositional range and fossil record in Brazil, Colombia, Ecuador and Peru have supported the existence of a megawetland system in the region during the Miocene (e.g., Hoorn and Wesselingh, 2010; Hoorn et al., 2010; Gross et al., 2011; Salas-Gismondi et al., 2015; Jaramillo et al., 2017; Linhares et al., 2017; Alvim et al., 2021, and references therein). Abundant aquatic and terrestrial vertebrate taxa including elasmobranchs, bony fishes, turtles, lizards, snakes and mammals, have been also reported from several Pebasian intervals (e.g., Monsch, 1998; Antoine et al., 2007, 2016; Pujos et al., 2009; Salas-Gismondi, 2006, 2015, 2016; Hoorn and



specimens, more than 2000 elements correspond to fish fragments, poorly preserved and not diagnostic (Table 2).

The images of micro-specimens were captured with a Leica MZ16F multifocal stereomicroscope and a scanning electronic microscope (JEOL JSM-6010). General descriptions of the most complete and diagnostic cranial/postcranial elements are presented. Taxonomic identification involved an extensive bibliographic review and comparisons with fossil and extant specimens housed in: Brazil [Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA); Museu de Zoologia da Universidade Estadual de Londrina (MZUEL); Museu de Zoologia da Universidade de São Paulo (MZUSP)], Colombia [Museo Geológico José Royo y Gómez, Servicio Geológico Colombiano, Bogotá (IGM); Collection (Vigías del Patrimonio Paleontológico la Tatacoa) in the Natural History Museum la Tatacoa, La Victoria], France [Muséum National d'Histoire Naturelle, Paris (MNHN)], Switzerland [Natural History Museum of Basel (NMB); Palaeontological Institute and Museum of the University of Zurich (PIMUZ)], USA [Academy of Natural Sciences of Drexel University, Philadelphia (ANSP)], and Venezuela [Palaeontological collection of the Alcaldía Bolivariana de Urumaco, Falcón State; Museo de Biología de la Universidad del Zulia (MBLUZ); Museo de Historia Natural La Salle (MHNLS), Fundación La Salle de Ciencias Naturales, Caracas].

Additional institutions mentioned in the text: ING-EOMINAS, Instituto de Geología y Minería, Bogotá, Colombia; MTKD, Museum für Tierkunde Dresden, Germany; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA; ZM, Zoological Museum of the University of Zurich, Zurich, Switzerland.

Localities. According to de Greve (1938), the fossil collection from Iquitos comes from six different layers which are referred to in Table 1. The layers I, III, IV and VI were associated to the same outcrop section in the

Telefunkenstation (telegraph station) site (de Greve, 1938), while layers II and V cropped up in other two different sites along the banks of the Itaya River. So far, no vertebrate specimens in the Iquitos collection has been associated either with layer V. Two other layers, including one from the lignite bank, and one of indeterminate location from Itaya (Table 1), were not referred to by de Greve (1938). From these we could not find any invertebrate/vertebrate remains associated to the layer of indeterminate location from Itaya. In contrast, from the lignite bank layer, labelled as Telefunkenstation (blue in Table 1), which is referred to here for the first time as “layer VII”, abundant fish remains, and coprolites are identified (Table 2). According to de Greve (1938), there was a bone-bed layer between the two main lignite layers at the Telefunkenstation site, which was characterized by abundant bone splinters and fish remains. The lignite bank layer VII contains abundant fish remains and bone fragments that could suggest a match with the bone-bed layer referred to by de Greve (1938). Although some specimens in the collection do not have precise information about the layer from which they come from (referred to in Table 2 as indeterminate locality), their taphonomic and preservation conditions could suggest that these specimens likely were collected in any of the layers that cropped up in the Telefunkenstation site.

Geological settings

The Pebas Formation is a lithostratigraphic unit exposed in the northeast of Peru, ranging from earliest Miocene (23 Ma) to early late Miocene age (10.5 Ma). Most of the Pebas Fm. is formed by a succession of grey or blue clays, occasionally interrupted by unconsolidated sands, mollusk shell beds and fossiliferous lignite layers (Roddaz et al., 2005; Salas-Gismondi et al., 2015). These strata were deposited during a series of flooding events, which affected most of the Amazonian

Table 1 Layers where the fossil invertebrates and vertebrates from Iquitos were collected during Bluntschli/Peyer expedition of 1912

Layers	Original text in German	Text translated into English	Assigned colour
I	Thone am Itaya-Ufer bei der Telefunkenstation	Clays on the banks of the Itaya at the Telefunken station	Gelb/yellow
II	Ansiedelung Soledad, Itaya-Ufer	Settlement Soledad, Itaya shore	Rot/red
III	Obere Bank der Lignitbank bei der Telefunkenstation	Upper horizon of the lignite layer at the Telefunken station	Braun/brown
IV	Untere Bank der Lignitbank bei der Telefunkenstation	Lower horizon of the lignite layer at the Telefunken station	Schwarz/black
V	Itaya-Ufer beim Puesto des Chinesen	Itaya shore at the Puesto of the Chinese	Grün/green
VI	Thone 15 cm oberhalb der Lignitbank bei der Telefunkenstation	Clays 15 cm above the lignite layer at the Telefunken station	Violett/violet
Further identified layers			
	Thone, unbestimmt (Itaya)	Clays, indeterminate (Itaya)	Rosa/pink
VII ^a	Lignitbank Telefunkenstation	Lignite bank, Telefunken station	Blau/blue

^a Referred for the first time herein

Table 2 Vertebrate palaeodiversity from Iquitos assemblage

Taxonomy	No. Ts		Species	Layer numbers and colours									
	Higher ranking	Family	Genus	No. Ts	No. Tt	I	II	III	IV	V	VI	VII	Pink
Chondrichthyes													
Myliobatiformes		Myliobatidae/Rhinopteridae	<i>Myliobatis/Rhinoptera</i>	1	1		X						
		Potamotrygonidae	<i>Potamotrygon</i>	2	1	X							
		Potamotrygonidae	<i>Potamotrygon</i>	2	1	X							
		Potamotrygonidae	Indet	1		X							
Osteichthyes													
Characiformes		?Bryconidae/Characidae	Indet	1	1	X							
		Cynodontidae	Indet	9	1	X		X					
		Erythrinidae	cf. <i>Hoplias</i>	2	1							X	
		Hemiodontidae	<i>Hemiodus</i>	4	1	X							
		Serrasalminae	<i>Colossoma</i>	3	1			X				X	X?
		Serrasalminae	cf. <i>Mylossoma</i>	1	1	X							
		Serrasalminae	"pacu" or "Myleus" clades	25		X		X	X			X	
		Serrasalminae	cf. <i>Serrasalmus</i>	2	1	X							
Cichliformes		Cichlidae	Indet	2	1	X							
Perciformes		?Sciaenidae ^a	Indet. ^a	20	4	X					X		
		Indet	Indet	101		X							
?Cichliformes or Perciformes		Indet	Indet	33		X	X	X	X			X	
Siluriformes		Ariidae ^a	Indet. ^a	2	1	X					X		
		Callichthyidae	Indet	3	1	X		X					
		Doradidae	Indet	1	1	X							
		Doradidae	Indet	1	1	X							
		Doradidae	Indet	6		X							
		Loricariidae	Indet	25	1	X							
		Loricariidae	Indet	1	1	X							
		Loricariidae	Indet	3		X							
		Pimelodidae	Indet	1	1	X							
		Indet	Indet	44		X		X				X	
Osteoglossiformes		?Osteoglossoidae	Indet	42	1	X							
<i>incertae sedis</i>		?†Aregoliathidae	?† <i>Aregoliath</i>	1	1	X							
Indet		Indet	Indet	2297	>2	X	X	X	X			X	X
Reptilia													
Testudines		Chelidae	<i>Chelus</i>	1	1								X
		Podocnemididae	Indet	14	1			X	X				X

Table 2 (continued)

Taxonomy		No. Ts	No. Tt	Layer numbers and colours								
Higher ranking	Family	Genus	Species	I	II	III	IV	V	VI	VII	Pink	Indet
Squamata—Serpentes	Indet	† <i>Colombophis</i>	<i>portai</i>	1	1	X						
	Colubroidea	Indet	Indet	1	1		X					
Crocodylia—Alligatoridae	Caimaninae	† <i>Purussaurus</i>	sp.	14	1	X	X					X
	Caimaninae	cf. † <i>Gnatusuchus</i>	<i>pebasensis</i>	2	1	X	X					
	Caimaninae	Indet	Indet	23		X						
	Indet	Indet	Indet	15	X		X			X		
Crocodylia—Gavialidae	Gryposuchinae	Indet	Indet	4	1							X
Crocodylia	Indet	Indet	Indet	7		X	X					X
Reptilia (?lizard)	Indet	Indet	Indet	1	1	X						
Reptilia	Indet	Indet	Indet	5	X	X	X					
Indet. (Coprolites)	Indet	Indet	Indet	14						X		

Total number of specimens (No. Ts), Total estimated taxa (No. Tt)

^a Specimen under study. For more details, see Additional file 1. For the layer numbers and colours see Table 1

basin; thus, creating a large megawetland system that includes both fluvial deposits and marine incursions (Roddaz et al., 2005; Hoorn and Wesselingh, 2010; Hoorn et al., 2010, 2017; Gross et al., 2011; Higgings et al., 2011; Boonstra et al., 2015; Salas-Gismondi et al., 2015; Jaramillo et al., 2017; Linhares et al., 2017; Alvim et al., 2021). Environments recorded at the Pebas Fm. include fluvio-lacustrine, shallow lacustrine, lacustrine and mangrove-like areas, and the biostratigraphy of these depositional sequences has been based on pollen, ostracods, but mostly the abundant mollusk assemblages (Wesselingh et al., 2002, 2006, 2010; Wesselingh and Renema, 2009). The Pebas megawetland system had approximately more than one million km², and prior to the establishment of the modern Amazon River drainage, the basin drained towards the Caribbean (Hoorn et al., 2010; Salas-Gismondi et al., 2015; Wesselingh et al., 2002).

The layers here referred to (Table 1) were likely situated within the urban area or the vicinity of the city of Iquitos. However, because of the erosion both by the river and rain, but also due to the growth of the city in more than a century, an exact location of them is not possible. Based on the Molluscan Zones (MZ) proposed by Wesselingh et al., (2006), the city of Iquitos and its surroundings correspond to the MZ6 (15–14 Ma) and MZ7 (14–12 Ma) zones, respectively (Fig. 1B). The fossil record from this region indicates that several groups of vertebrates as fishes, aquatic turtles, and mammals were abundant in the Pebas system (Monsch, 1998; Cozzuol, 2006; Antoine et al., 2007, 2016; Pujos et al., 2009; Salas-Gismondi, 2006; Hoorn and Wesselingh, 2010; Lundberg et al., 2010; Bianucci et al., 2013; Tejada-Lara, 2015; Chabain et al., 2017; Pujos and Salas-Gismondi, 2020, and references therein).

Results

Around 2738 cranial, postcranial and coprolite specimens were identified from the layers I–IV, VI–VII. The total estimated taxa from fossil fauna studied here from Iquitos (Pebas Fm.) includes at least three chondrichthyans, 23 actinopterygians, two testudines, two squamates, three crocodylians, one lizard taxon, plus other indeterminate remains that do not belong to mammals or birds. As referred to above in the “Material and methods” section, from the total fossil vertebrate specimens, more than 2000 elements correspond to fish remain fragments, which are poorly preserved and not diagnostic (Table 2; Additional file 1).

Chondrichthyes

Six isolated teeth of Myliobatiformes rays represent this group from the Iquitos fauna. PIMUZ A/I 5016 comes from site II (Table 2) and it corresponds to a lateral-file tooth of indeterminate jaw position, of relatively hexagonal contour, and longer (4.36 mm) than broad with a high crown and well-defined root grooves (Fig. 3A1–A3). The morphology of PIMUZ A/I 5016 matches with those lateral-files teeth of the eagle ray *Myliobatis* or the cownose rays *Rhinoptera* (see Herman et al., 2000). However, taxonomic identifications based on isolated lateral teeth in *Myliobatis* and *Rhinoptera* is a difficult task due to the large dental variation within both genera (e.g., Hovestadt and Hovestadt-Euler, 2013).

The remaining five micro-teeth assigned to potamotrygonid stingrays (Table 2) are of indeterminate jaw position, the biggest specimen being 1.5 mm wide and 2 mm high. The two specimens PIMUZ A/I 5052 (Fig. 3B1–C3) are assigned here to *Potamotrygon* aff. †*P. rajachloae* Chabain et al., 2017. As in the contemporaneous material from *P. rajachloae* (Chabain et al., 2017), sexual dimorphism is weakly pronounced, and all teeth from Iquitos possess a more or less developed cusp located on the transverse crest. PIMUZ A/I 5052 are small, characterized by a crown generally wider than high and dominating the root, a labial visor usually bifid in occlusal view (Fig. 3B2, C2). Enameloid is principally unornamented with a slight hollow on the labial face formed by its high marginal angles and its transverse crest. The labial face of the crown is concave between the labial visor, the marginal edges, and the salient transverse crest. The root is short, narrower than the crown but always massive in lateral view as in *P. rajachloae*. PIMUZ A/I 5052 are clearly close to those of *P. rajachloae* from Quebrada Cachiyacu section (Chabain et al., 2017, fig. 3A–O), however, the specimens from Iquitos are slightly distinguished in having more irregular enameloid with some micro-alveolar cupules observable on the labial face of cusp (Fig. 3B1–B2, C1–C2), justifying affiliation only. Individuals could reach approximately a similar size to *P. rajachloae* with 25 cm disc width based on extant tooth–body size relationship (Chabain et al., 2017).

The two specimens PIMUZ A/I 4819 (Fig. 3D1–E2) are assigned to †*P. canaanorum* Chabain et al., 2017, previously recorded in the Quebrada Cachiyacu section (Chabain et al., 2017). This taxon is characterized by small and elongated oval to hexagonal teeth, and a homogenous ornamented labial face of the crown (contrary to what occurs in larger coeval species †*Potamotrygon contaminensis* Chabain et al., 2017, and in *P. aff. rajachloae*), which shows mainly furrows and crests

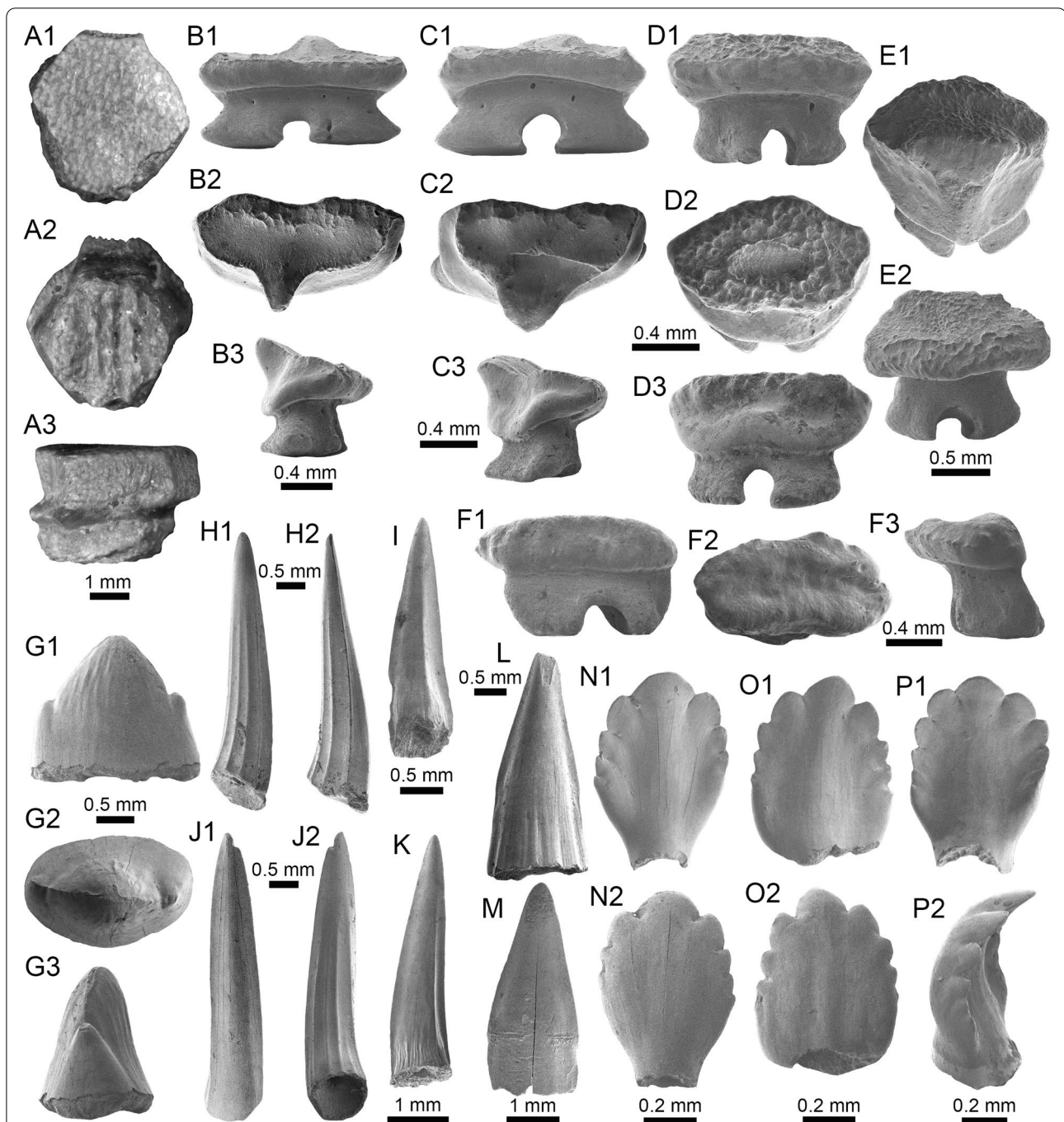


Fig. 3 Rays (Myliobatiformes) and Characiformes fishes from the Iquitos assemblage. **A1–A3** Lateral-file tooth of *Myliobatis* or *Rhinoptera* (PIMUZ A/I 5016). **B1–C3** *Potamotrygon* aff. †*P. rajachloae* teeth (PIMUZ A/I 5052). **D1–E2** †*Potamotrygon canaanorum* teeth (PIMUZ A/I 4819). **F1–F3** *Potamotrygonidae* indet. tooth (PIMUZ A/I 5053). **G1–G3** ?*Bryconidae* or *Characidae* tooth (PIMUZ A/I 4825). **H1–K** Canine (**H1–H2**, **J1–J2**) and lateral (**I**, **K**) *Cynodontidae* indet. teeth (PIMUZ A/I 4822 and 4823). **L–M** cf. *Hoplias* sp. teeth (PIMUZ A/I 4828). **N1–P2** *Hemiodus* sp. teeth (PIMUZ A/I 4829). Views: labial (**B1**, **C1**, **D1**, **E2**, **J1**, **M**, **N2**, **O2**), lingual (**D3**, **H1**, **J2**, **L**, **N1**, **O1**, **P1**), occlusal (**A1**, **B2**, **C2**, **D2**, **E1**, **G2**), lateral (**A3**, **B3**, **C3**, **G3**, **H2**, **I**, **K**, **P2**), basal (**A2**), and indet. (**G1**)

including in its central hollow. The lingual face is often marked by the development of a deep transverse and horizontal furrow, interrupted by a median vertical

crest in more anterior teeth (Fig. 3E1). Male teeth have more concave labial faces than female ones due to the presence of a cusp (unpreserved in Fig. 3E1–E2) and

a more salient labial visor, but less ornamented enameloid. This extinct species is pointing to a *ca.* 35 cm disc width based on extant tooth size–body size relationship (Chabain et al., 2017). The specimen PIMUZ A/I 5053 (Fig. 3F1–F3) though it could possibly belong to one of both species referred above, is referred herein as an indeterminate potamotrygonid only due to its poor state of preservation.

Actinopterygii

With at least 23 taxa, actinopterygians represent the most diverse and abundant group from the Iquitos fossil fauna, with records in almost all layers (Table 2; Additional file 1).

Characiformes

This is one of the most diverse group of bony fishes from the Iquitos fossil fauna (Table 2), with representatives of Cynodontidae, Erythrinidae, Hemiodontidae, and Serrasalminidae. The specimen PIMUZ A/I 4825 preserves only the crown, which is 2.15 mm in height and 2.49 mm in width with a basal oval shape. It is robust with a molariform-like shape, characterized by a well-developed main cusp and two accessory small lateral cusplets (Fig. 3G1–G3); vertical parallel folds are present on both the labial and lingual sides. PIMUZ A/I 4825 probably corresponds to a tooth of the premaxillary bone, with a morphology that resembles some extant Bryconidae (e.g., *Brycon* PIMUZ A/I 4884) and Characidae (e.g., *Creagrutus* PIMUZ A/I 4881). Due to the fragmentary condition of PIMUZ A/I 4825, the little knowledge about dental morphology of many extant Characiformes species, and the scarce comparative material, this specimen is kept here in open nomenclature.

Cynodontidae or “dogtooth characins” from the Iquitos fauna (Table 2) are represented by nine isolated dentary canine-like and lateral teeth (PIMUZ A/I 4822 and 4823) that do not exceed 5 mm in height (Fig. 3H1–K). The canine-like teeth are blade-like, labiolingually compressed, sharp and with well-developed cutting edges (Fig. 3H1–H2, J1–J2). Lateral teeth are sharp with well-developed cutting edges and smaller than the canine (Fig. 3I, K). These cynodontid teeth, especially the canine-like, are indistinguishable from those of small/medium size specimens of the three extant Cynodontinae genera (see van der Sleen and Albert, 2018) *Cynodon*, *Hydrolycus* (e.g., PIMUZ A/I 4878), and *Rhaphiodon* (e.g., PIMUZ A/I 4877–78), which make identification beyond family level not possible. In reference to the Erythrinidae specimens, only two isolated teeth (PIMUZ A/I 4828) of indeterminate position are identified here as *cf. Hoplias* sp. (Fig. 3L–M; Table 2). These teeth are up to 4 mm in height, straight with a

conical and pointed crown, distinctly sharp edges, and with a basal section with parallel sulcus. The specimens PIMUZ A/I 4828 from the Iquitos fauna are very similar to those recent and fossil teeth of *Hoplias* (e.g., Carrillo-Briceño et al., 2021).

Four isolated broken premaxillary teeth (PIMUZ A/I 4829) (Fig. 3N1–P2; Table 2) represent Hemiodontidae. These teeth do not exceed 0.8 mm in height, and only the crown is preserved. Tooth base is small, pedunculated, and oval in cross-section. The crown is oval-shaped and bilaterally symmetrical; with the cutting edge being rounded and occupying two-thirds of the lateral margin and extended proximally for more than half of lateral border. Up to nine diamond-shaped cusps with rounded or pointed cutting edge are observed. These cusps tend to get smaller gradually as they descend laterally, being the central cusps the largest and located of the tooth apex (e.g., Fig. 3N1, O1, P1). The tooth is compressed, with lingual face distinctly concave and labial face distinctly convex. The size, shape, and morphology of the specimens comprising PIMUZ A/I 4829 are consistent with those of *Hemiodus* (see also Scharcansky and Lucena, 2008). The latter genus is diagnosed among other Hemiodontidae by having multicuspid teeth on premaxillary and maxilla bones, and no teeth on the dentary bone (Langeani, 1999, 2003). *Hemiodus* is the most diverse genus of Hemiodontidae with at least 23 extant valid species (Nogueira et al., 2020). The specimens PIMUZ A/I 4829 are also slightly similar to those described by Roberts (1974) for *Saccodon*, a trans-Andean parodontid that exhibits dental polymorphism in which some specimens have some teeth that resemble those of *Hemiodus* (Roberts, 1974). Nevertheless, given the rarity of these polymorphic specimens, and their distribution, it is unlikely that the fossil specimens PIMUZ A/I 4829 described herein belong to *Saccodon* instead of *Hemiodus*. Like closely related families (Parodontidae and Anostomidae; see Roberts, 1975), hemiodontid teeth seem to preserve relatively well and are unique enough for confident identification. The specimens PIMUZ A/I 4829 assigned here to *Hemiodus* sp. represent the first fossil record of Hemiodontidae.

Colossoma, *cf. Mylossoma* sp., and indeterminate “pacu” and “piranha-like” clades (Table 2), represents the serrasalmids (Serrasalminidae) from the Iquitos fauna. Specimen PIMUZ A/I 4810 is a large right premaxillary bone of 44.5 mm in length with five molariform-like teeth, of which four and two teeth are from the outer and inner row, respectively (Fig. 4A1–A2). The contact and no gap between the first inner and first outer teeth in the premaxillary bone is a diagnostic element to differentiate the genus *Colossoma* from *Piaractus* (van der Sleen

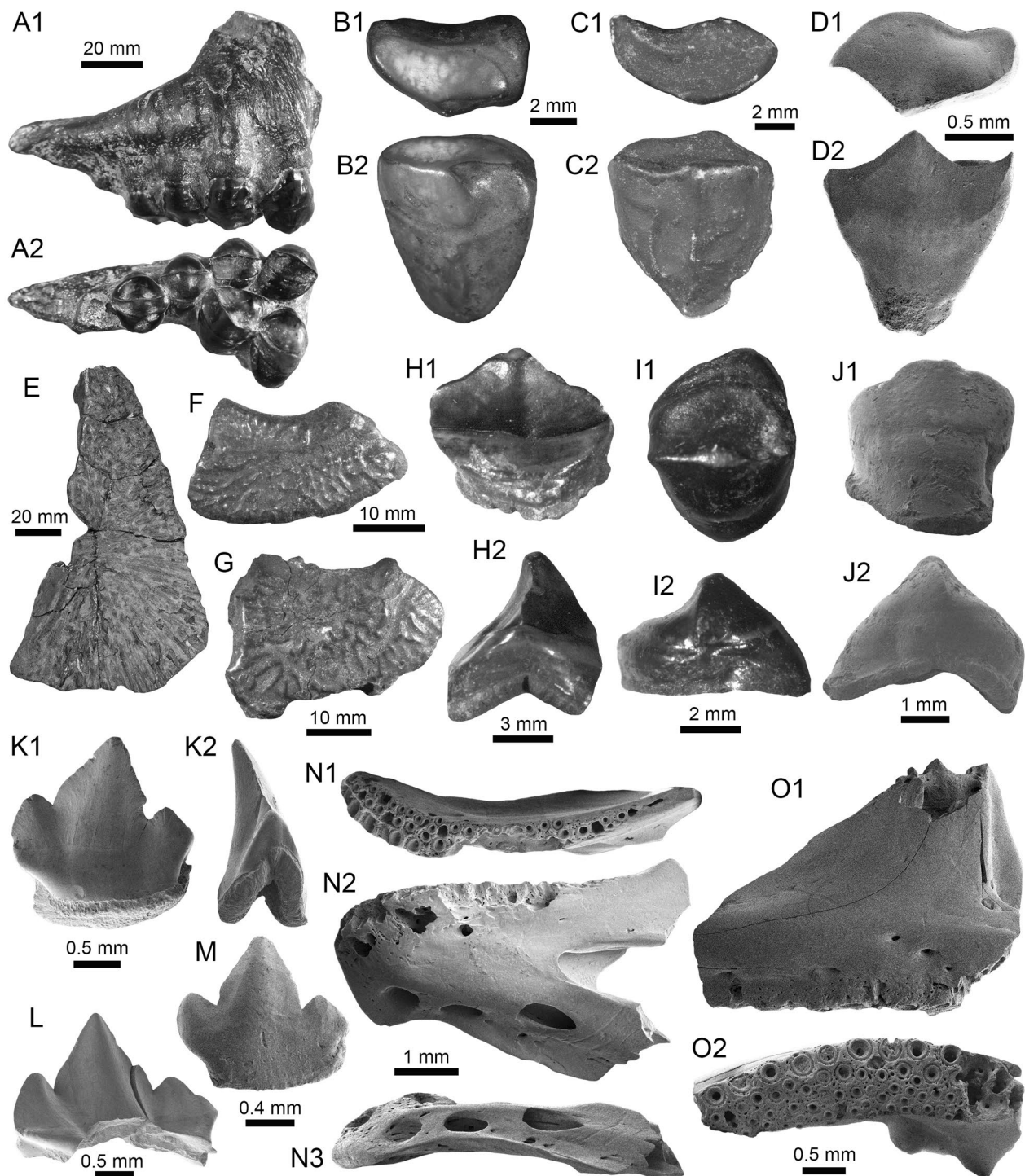


Fig. 4 Characiformes and Cichliformes fishes from the Iquitos assemblage. **A1–C2** Right premaxillary (**A1–A2**: PIMUZ A/I 4810), and symphyseal teeth (**B1–B2**: PIMUZ A/I 4812; **C1–C2**: PIMUZ A/I 4813A) of *Colossoma* cf. *C. macropomum*. **D1–D2** Symphyseal mandibular tooth of cf. *Mylossoma* sp. (PIMUZ A/I 4818). **E–J2** left operculum (**E**: PIMUZ A/I 4811), circumorbital (**F**) and frontal? (**G**) bones (PIMUZ A/I 5009), and molariform-like teeth of indet. “pacu” or “*Myleus*” clades (**H1–H2**: PIMUZ A/I 4813B; **I1–I2**: PIMUZ A/I 5008; **J1–J2**: PIMUZ A/I 4814). **K1–L** cf. *Serrasalmus* sp. teeth (PIMUZ A/I 4826). **M** Recent tooth of *Serrasalmus neveriensis* (PIMUZ A/I 5058). **N1–O2** Left dentary (**N1–N3**: PIMUZ A/I 4979), and right premaxilla (**O1–O2**: PIMUZ A/I 4981) of indet. cichlids. Views: dorsal (**G**), labial (**B2, C2, D2, J1, K1, M**), lingual (**H1, L**), lateral (**F, H2, I2, J2, K2**), left lateral (**E, N2**), right lateral (**A1, O1**), occlusal (**B1, C1, D1, I1, N1**), and ventral (**A2, N3, O2**)

and Albert, 2018, fig. 3a, b, pp. 176). PIMUZ A/I 4810 was preliminarily reported as *Myletes* by Peyer (1937), and Peyer (1968: p. 107) noted later that the genus was “replaced by the three genera: *Colosoma*, *Metynnis* and *Mylossoma*”. The diagnostic concavity in the lingual face of symphyseal mandibular teeth, in which the elevation of the distal edge is different among *Colossoma*, *Piaractus* and *Mylossoma* (see Dahdul, 2004; Aguilera and Machado-Allison, 2013; Carrillo-Briceño et al., 2021), allows the assignment of the two left symphyseal teeth PIMUZ A/I 4812 (10.9 mm in height; Fig. 4B1–B2) and PIMUZ A/I 4813A (10.9 mm in height; Fig. 4C1–C2) to *Colossoma*. PIMUZ A/I 4810, 4812 and 4813A, are indistinguishable from premaxillary bone and symphyseal teeth of the only extant species *Colossoma macropomum* Cuvier, 1818; in this regard, we assigned the above-mentioned fossil specimens to *Colossoma* cf. *C. macropomum*. It is important note that the tooth PIMUZ A/I 4813A is a cast, not knowing the current repository of the original specimens. On the basis of the diagnosis for symphyseal mandibular teeth determination in *Colossoma*, *Piaractus* and *Mylossoma* (Dahdul, 2004; Aguilera and Machado-Allison, 2013; Carrillo-Briceño et al., 2021), the left tooth PIMUZ A/I 4818 (7.1 mm in height; Fig. 4D1–D2.) is tentatively assigned to cf. *Mylossoma* sp.

Other cranial remains include a left operculum (PIMUZ A/I 4811; Fig. 4E), three broken cranial bones (PIMUZ A/I 5009; Fig. 4F–G), and 21 molariform-like teeth with a transverse high crest, from both outer and inner rows (PIMUZ A/I 4813B–4817 and 5008; Fig. 4H1–J2). Specimens such as the operculum (PIMUZ A/I 4811) and large molariform-like teeth likely belong to *Colossoma*. However, as has been referred by Carrillo-Briceño et al. (2021), “pacu clade” species have a combination of molariform-like teeth adapted for crushing hard foods that look very similar and difficult to distinguish among *Colossoma*, *Piaractus*, and *Mylossoma*, especially when the determination is based on isolated elements. Isolated cranial bones of the large *Colossoma* and *Piaractus* species appear to be indistinguishable. In reference to the small molariform-like, we neither allocate these isolated teeth to generic level nor discard that they could belong to more than on taxon within the “pacu” or “*Myleus*” clades (Thompson et al., 2014). The greatest difficulty in using dental morphology as a taxonomic character in fossil serrasalmids within the “pacu” or “*Myleus*” clades is the lack of comparative information on extant representatives and the considerable dental variation among extant species (see Ballen et al., 2021).

Two isolated lower symphyseal teeth PIMUZ A/I 4826 that do not exceed 1.96 mm in height represent the

“Piranha-like” group. Both specimens (Fig. 4K1–L) are labiolingually compressed, characterized by a central triangular sharp cusp, and two lateral and low triangular-rounded cusplets separated by a notch. The central cups and lateral cusplets are covered by smooth enamel and are characterized by a very sharp and no serrated cutting edge. Extant piranhas are represented by the genera *Catoprion*, *Pygocentrus*, *Pristobrycon*, *Pygopristis*, and *Serrasalmus* (Thompson et al., 2014; van der Sleen and Albert, 2018). Tooth morphology in *Catoprion* and *Pygopristis* is very different from that of the specimens PIMUZ A/I 4826 (see Kolmann et al., 2018; van der Sleen and Albert, 2018). Compressed teeth with a triangular cusp and sharp cutting edges characterize *Pygocentrus*, *Pristobrycon*, and *Serrasalmus* (Lundberg, 1997; van der Sleen and Albert, 2018). In our comparisons, we have observed that the fossil specimens PIMUZ A/I 4826 more closely resembles lower symphyseal *Serrasalmus* teeth than those of *Pygocentrus* and *Pristobrycon* (see Fig. 4M). We tentatively assign the specimens PIMUZ A/I 4826 to cf. *Serrasalmus* sp.

Cichliformes

The specimen PIMUZ A/I 4979 (Fig. 4N1–N3) is an incomplete left dentary bone coming from the layer I (Table 1). The dentary is short and high with 5.2 mm in length, missing the coronoid process and the posterior part of the mandibular sensory canal. On the external face, at least three well-developed foramina on the bony mandibular canal are preserved (Fig. 4N2). The dorsal margin is covered by circular tooth implantations in three well-defined inner rows, the outer one being characterized by enlarged bases, about three times in diameter of those of the ones of the in inner rows (Fig. 4N1). After characids and loricariids, the Neotropical cichlids with at least 44 genera, constitute the third speciose group of freshwater fishes in South America (van der Sleen and Albert, 2018). Despite this and with some exceptions (e.g., Casciotta and Arratia, 1993), studies and detailed comparative descriptions of cranial elements of cichlids from South America are scarce. Added to this, the morphology of the lower jaws is very similar among Neotropical cichlids (Casciotta and Arratia, 1993), which makes identifying fossil cichlids difficult especially when determinations are based only on isolated and fragmented materials; although some morphological features of the skull elements could allow some tentative assignments (e.g., Lundberg, 1997). With the scarce comparative material that we have been able to study, it is possible to rule out that PIMUZ A/I 4979 is a representative of the *Astronotus*, *Cichla*, *Crenicichla*, *Caquetaia*, or *Pterophyllum* genera. Although PIMUZ A/I 4979 has certain similarities to *Aequidens*, we tentatively assign it to Cichlidae,

and future determinations will require better comparative material. A fragmented right premaxillary bone of 4.41 mm of length (PIMUZ A/I 4981), preserving the base of the ascending arm, and part of the alveolar arm of bone (Fig. 4O1), which is covered by circular tooth implantations in four well-defined rows (Fig. 4O2), is referred here also as an indeterminate cichlid.

Perciformes

At least four sciaenid (Sciaenidae) taxa are preliminary reported here from the Iquitos fauna (Table 1; Additional file 1). These extinct sciaenids are represented exclusively by well-preserved otoliths ($n=20$), and these are currently under study. From the layer I, 101 indeterminate isolated micro-pharyngeal teeth were identified here as belonging to indeterminate perciforms (PIMUZ A/I 4824; Fig. 5D1–E2). Fossil Sciaenidae croaker and Ariidae marine catfish otoliths were previously recorded in the Western Amazon by Monsch (1998), however, the precise stratigraphic provenience of otoliths at the Solimões and/or Pebas formations is not clear.

Cranial and postcranial remains, most of them in fragmentary condition, have some certain morphological features that resemble those present in both cichlids and perciforms; nevertheless, an assignment to either of the two groups for now is not feasible. The specimens include two incomplete right lower dentaries (PIMUZ A/I 5013 and 5014; Fig. 5A1–B3) and 31 dorsal and anal fin-spines (PIMUZ A/I 4970, 4982, 4987 and 4991; Fig. 5C1–C2).

Siluriformes

At least seven taxa of the Ariidae, Callichthyidae, Doradidae, Loricariidae, and Pimelodidae families represent the Siluriformes or catfishes from the Iquitos fossil fauna (Table 2). Isolated and in most cases fragmented cranial and postcranial bones, teeth and an odontodes, are the most common siluriform remains from the Iquitos fauna; nevertheless, two isolated otoliths (PIMUZ A/I 4998 and 5001; Table 2) are identified tentatively as at least one taxon of Ariidae catfishes. Like the other otoliths referred to in the section above, these two specimens are also under study.

Three fragmented pectoral fin-spines (PIMUZ A/I 4975 and 4984) represent specimens assigned here to Callichthyidae (Fig. 5F–G2). In all the spines, the articular process is missing, and only a portion of the shaft is preserved, the largest specimen being no longer than 7 mm in length. The shaft is ovoid in section, with the anterior and anterodorsal edges ornamented by small circular odontode bases, while the posterior edge bears sharp triangular denticles inclined toward the proximal direction of the spine (Fig. 5F–G1). Dorsal fin-spines anteriorly and anterodorsally ornamented by small odontodes

and well-developed posterior dentitions are typical of Callichthyidae (see Lundberg, 1997). Due to the poor preservation state and absence of diagnostic characters in PIMUZ A/I 4975 and 4984, a taxonomic assignment beyond Callichthyidae is not possible.

Doradidae, also known as thorny catfishes, are represented in the Iquitos assemblage by two skull fragments and five isolate pectoral fin-spines assigned here to indeterminate doradids (Table 2). PIMUZ A/I 5051 (morphotype “1”) is a partial left cleithrum, including exclusively the middle of the posterior cleithral process (Fig. 5H1–H3). The fossil is approximately 5.6 mm in length and 1.7 mm in height. The lateral face bears four longitudinal ridges, two dorsal-most ridges converging posteriorly, and three dorsal-most ridges with inconspicuous spines, with 14, eight and four spines (respectively, from ventral to dorsal ridge) are also present. Weak ridges (without spines) characterize the median face. Doradidae and Auchenipteridae are the only South American freshwater catfishes with elongated posterior cleithral process (Birindelli, 2014). Among Doradidae, Astrodoradinae, *Acanthodoras* and *Agamyxis* have spines and ridges on the lateral face of the posterior cleithral processes (Higuchi et al., 2007), a condition similar to that present in PIMUZ A/I 5051. PIMUZ A/I 4973 (morphotype “2”) is also a partial left cleithrum (Fig. 5I1–I3) including the lateral portion (but not the median shelf), the bulge associated to the pectoral fin-spine base, and the posterior cleithral process, except the posterior tip. PIMUZ A/I 4973 is 4.6 mm in length, and 1.6 mm in height; a smooth lateral face, with no distinct ridge or spine, and with posterior and dorsal processes completely leveled. The median face is also smooth, with a distinct median process forming part of a socket for the pectoral-fin base. There is no clear match between PIMUZ A/I 5051 and PIMUZ A/I 4973 with extant species or genera of Doradidae, possibly due to the poorly state of preservation and fragmentation of the fossils, or because they could belong to extinct taxa. Most species of Doradidae have ridges or spines on the lateral face of the posterior cleithral process, whereas others have deep, rectangular processes, and all have the dorsal process covered by the posttemporal–supracleithrum and unlevelled with the ventral and posterior portion. Fossils that constitute the posterior cleithral process were previously described for Doradidae (Sabaj et al., 2007; Aguilera et al., 2013; Carrillo-Briceño et al., 2021), but not for Auchenipteridae. In reference to the isolate pectoral fin-spines, the most complete one is PIMUZ A/I 5050, which is from the left position and of approximately 23 mm in length (Fig. 5J). PIMUZ A/I 5050 has a robust shaft, which is well ossified, flattened dorso-ventrally, and with both dorsal

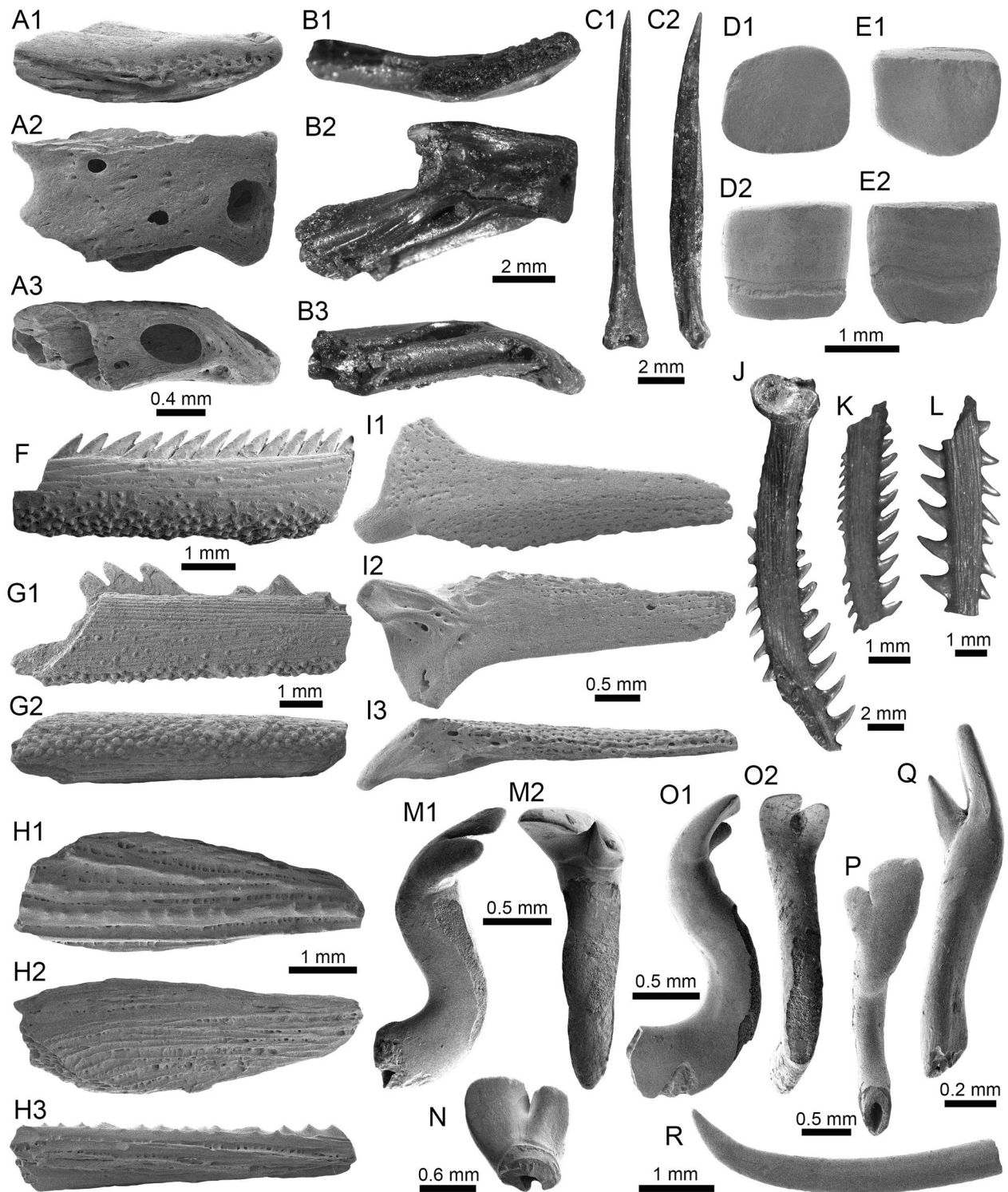


Fig. 5 Perciformes and Siluriformes fishes from the Iquitos assemblage. **A1–C2** Right lower dentaries (**A1–A3**: PIMUZ A/I 5013; **B1–B3**: PIMUZ A/I 5014), and dorsal fin-spine (**C1–C2**: PIMUZ A/I 4982) of cichlids or perciforms. **D1–E2** Pharyngeal teeth of indet. perciforms (PIMUZ A/I 4824). **F–G2** Pectoral fin-spines of Callichthyidae indet. (**F**: PIMUZ A/I 4975; **G1–G2**: PIMUZ A/I 4984). **H1–L** Partial left cleithrum (**H1–H3**: morphotype “1”, PIMUZ A/I 5051; **I1–I3**: morphotype “2”, PIMUZ A/I 4973), and pectoral fin-spines (**J**: PIMUZ A/I 5050; **K–L**: PIMUZ A/I 5049) of Doradidae indet. **M1–R** Teeth (**M1–P**: morphotype “1”, PIMUZ A/I 4965A; **Q**: morphotype “2”, PIMUZ A/I 4965B), and odontode (**R**: PIMUZ A/I 4827) of Loricariidae indet. Views: anterior (**C1**, **G2**), dorsal (**J**), dorsolateral (**H1**, **I1**), labial (**P**), lingual (**M2**, **N**, **O2**), lateral (**H3**, **I3**, **M1**, **O1**, **Q**), left lateral (**C2**), right lateral (**A2**, **B2**), occlusal (**A1**, **B1**, **D1**, **E1**), ventral (**A3**, **B3**, **H2**, **I2**), and indet. (**D2**, **E2**, **F**, **G1**, **K**, **L**, **R**)

and ventral surfaces bearing coarse parallel grooves. The anterior edge is characterized by triangular and sharp denticles inclined in the distal direction, while denticles of the posterior edge are bigger and inclined toward the proximal direction of the spine. The dorsal process is well preserved, and it is semi-circular and wide in shape; the anterior process and ventral process are missing. The other four pectoral fin-spines (PIMUZ A/I 5049; Fig. 5K–L), are in fragmentary condition, preserving only part of the shaft, which bears triangular and sharp denticles in the anterior (inclined in the distal direction) and posterior (inclined toward the proximal direction) edges. Due to the fragmentary condition of the three above-referred spines, added to the poor knowledge of intraspecific spine variation in thorny catfishes, determinations beyond Doradidae are not possible. Although all the specimens referred here as doradids come from the same layer I (Table 2), it is a difficult task to assume whether the spines could belong to one of the morphotypes or to another, third doradid taxon.

Isolated teeth, an odontode and body armour plates represent the indeterminate Loricariidae from the Iquitos fauna. In a sample of 26 teeth, at least two morphotypes are recognized. The morphotype “1” (PIMUZ A/I 4965A; Fig. 5M1–P) is the most common ($n=25$), with complete and fragmented teeth. A curved “S”-like shape, preserving part of the base, shaft and crown characterizes the complete teeth. The crown is rounded, curved, smooth and asymmetrically bicuspid, with the median lobe longer and bigger than the lateral one. These teeth were referred to indeterminate loricariids by Peyer (1937). The single tooth referred as morphotype “2” (PIMUZ A/I 4965B; Fig. 5Q), preserves only the shaft and the smooth asymmetric bicuspid crown, with triangular-like lobes, which are more stylized triangular than those of morphotype “1”. Dental diversity and variation in loricariids is wide and little studied (Geerinckx et al., 2007, and references therein), which makes the generic determination of the specimens from the Iquitos fauna difficult; nevertheless, both morphotypes suggest the presence of at least two loricariid taxa. The odontode (PIMUZ A/I 4827) is elongated with a sharp tip and 3.6 mm in length (Fig. 5R). The two body armour plates (PIMUZ A/I 5048) of indeterminate position are small, fragmented and poorly preserved, bearing a slightly rough ornamentation.

Pimelodidae from the Iquitos fauna is represented by one complete left pectoral fin-spine (PIMUZ A/I 4974), reaching 12.9 mm in length and missing only the tip (Fig. 6A1–A5). PIMUZ A/I 4974 is slightly curved with a flattened dorso-ventrally shaft, which is characterized by coarse parallel grooves in both ventral and dorsal surfaces. The anterior edge is characterized by triangular and sharp denticles inclined in the distal direction,

while denticles of the posterior edge are bigger and inclined toward the proximal direction of the spine. The dorsal process is well preserved, robust and somewhat rectangular (Fig. 6A5); the articular groove is triangular in outline, and the anterior and ventral process are preserved (Fig. 6A3–A5). PIMUZ A/I 4974 is clearly different from other pimelodid pectoral fin-spines of the genera *Brachyplatystoma*, *Cheirocerus*, *Perrunichthys*, *Phractocephalus*, *Pimelodina*, *Pimelodus*, *Platynemichthys*, *Pseudoplatystoma*, and *Sorubim*. PIMUZ A/I 4974 is relatively similar to those pectoral fin-spines of *Platysilurus* (see Vanscoy et al., 2015, Fig. 1); nevertheless, our review did not include all the extant representatives of Pimelodidae, an immense and varied group that includes possibly more than 109 species in 30 genera (van der Sleen and Albert, 2018). In this regard, PIMUZ A/I 4974 is tentatively assigned here to an indeterminate pimeloid.

Forty-four isolated dorsal and pectoral fin-spines (PIMUZ A/I 4971, 4972, 4983, 4986, and 4988) are referred here as indeterminate Siluriformes (Fig. 6B1–F). These dorsal and pectoral catfish fin-spines are in a poor fragmentary condition, most of them with a marked degree of erosion preventing the recognition of diagnostic elements that allow taxonomic identification even at the family level.

Osteoglossiformes (?Osteoglossoides)

At least 42 well-preserved squamules or fragments of reticulated scales (PIMUZ A/I 5054) are reported from the layer I (Table 2). These squamules are small and flat, with a quadrangular, rhombic, polygonal, or irregular shape (Fig. 6H–M). The ornamentation of the external surface of the squamules, which depend on their position on the scales (e.g., anterior, lateral or posterior field), is characterized by a granular ornamentation or circuli (Fig. 6H–J). The inner surface is concave (Fig. 6K–L), with lateral margins or walls that exhibit horizontal lamination (Fig. 6M). Like the inner surface in the squamules from of the Palaeocene of Belgium (see Taverne et al., 2007), the squamules from Iquitos are characterized by an internal smooth face (Fig. 6K–L), sometimes with large and widely spaced tubercles bearing a small hole in their apex. Osteoglossiformes, also known as “bony tongues”, are heavily ossified teleosts whose scales frequently offer a reticular pattern formed by small squamules, which are separated from each other by very narrow grooves (Gayet and Meunier, 1983; Taverne et al., 2007). This reticular pattern with squamules appears to be typical of Osteoglossoides (Zhang and Wilson, 2017). Osteoglossids are a diverse group that includes the Arapaimidae (*Arapaima* and *Heterotis*) and Osteoglossidae (*Osteoglossum* and *Scleropages*), with a distribution in Africa, Southeast

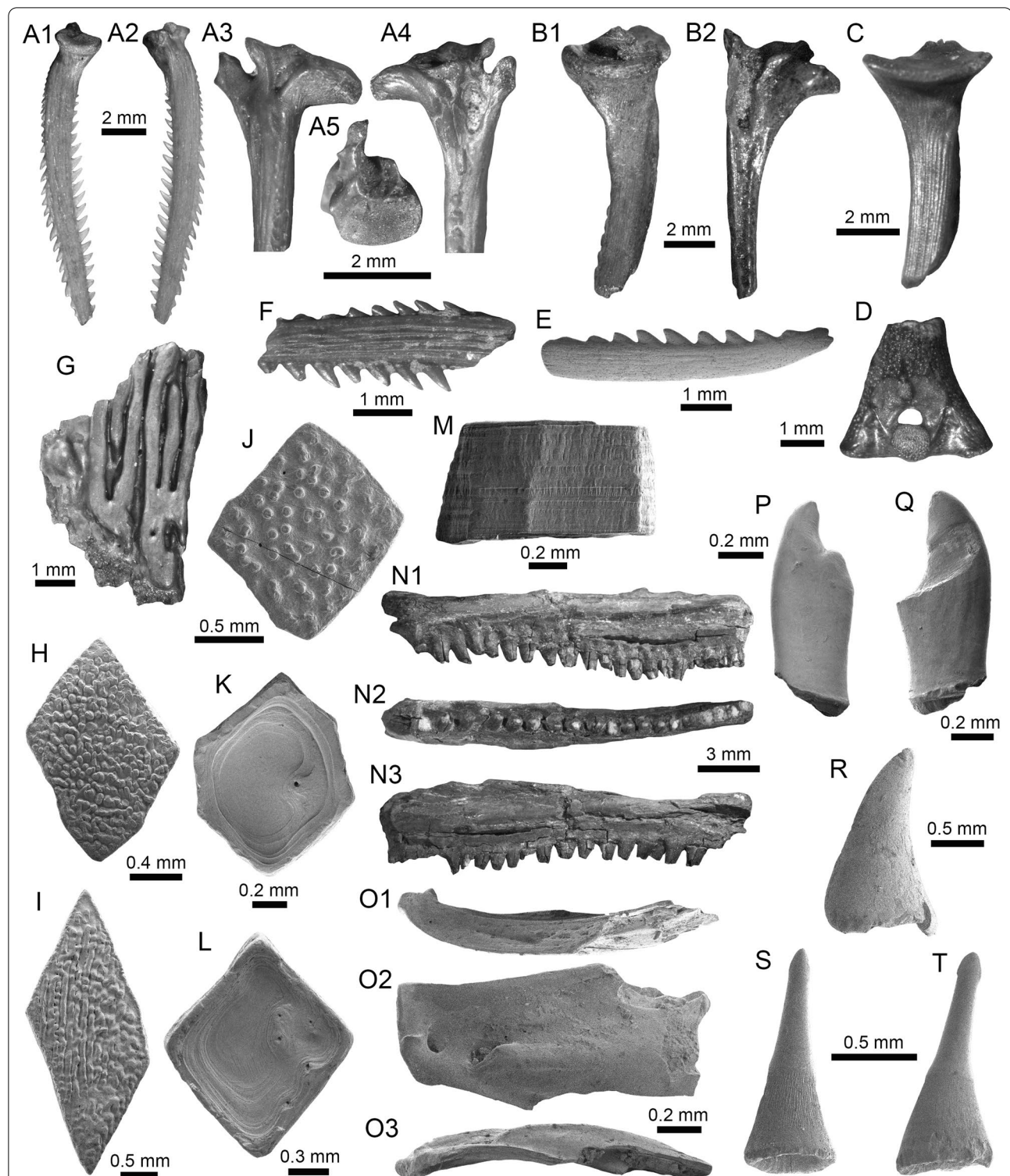


Fig. 6 Siluriformes, Osteoglossiformes and other bony fishes from the Iquitos assemblage. **A1–A5** Left pectoral fin-spine of *Pimelodidae* indet. (PIMUZ A/I 4974). **B1–B2** Dorsal (**D**: PIMUZ A/I 4971; **E**: PIMUZ A/I 4983) and pectoral fin-spines (**B1–B2**: PIMUZ A/I 4986; **C, F**: PIMUZ A/I 4971) of *Siluriformes* indet. **G** Fragment of a posterior field scale assigned to ?†*Acregoliath* sp. (PIMUZ A/I 5047). **H–M**. Squamules of ?*Osteoglossoides* (PIMUZ A/I 5054). **N1–T** Maxilla (**N1–N3**: PIMUZ A/I 4599), dentary (**O1–O2**: PIMUZ A/I 4980), pharyngeal and other teeth (**P–T**: PIMUZ A/I 4964) of indet. actinopterygians. Views: anterior (**A3, D**), dorsal (**A1, B1, C, O1**), external surface (**G–J**), internal surface (**K–L**), lateral (**M**), left lateral (**N1, O2**), right lateral (**N3**), posterior (**A4, B2**), proximal (**A5**), ventral (**A2, N2, O3**), and indet. (**E, F, P–T**)

Asia, Australia, and South America (Hilton and Lavoué, 2018); *Arapaima* and *Osteoglossum* being restricted to the latter continent (van der Sleen and Albert, 2018). In all the osteoglossids, the scales are large, cycloid and reticulated, with a network of furrows that define the squamules (Hilton and Lavoué, 2018). In osteoglossids, squamules with an inner surface lacking concavities are characteristic of *Arapaima* (Prasad, 1987; Otero and Gayet, 2001). Isolated squamules have been successfully used to identify extinct osteoglossid taxa (e.g., Prasad, 1987; Otero and Gayet, 2001; Taverne et al., 2007; Zhang and Wilson, 2017). The squamules from Iquitos resemble those from scales of extant and fossil *Heterotis*, *Osteoglossum* and *Scleropages* (Otero and Gayet, 2001; Taverne et al., 2007; Zhang and Wilson, 2017), and due to the geographical region, it is not unreasonable to think these squamules from Iquitos could belong to *Osteoglossum*. Nevertheless, future fossil osteological evidence is necessary to support this.

Incertae sedis Teleostei (?†Acregoliathidae)

PIMUZ A/I 5047 is a fragment (7.25 mm in length) of the posterior field (exposed area) of the scale (Fig. 6G). A glassy and birefringent tissue represented by longitudinal, subparallel, and coarse ribs characterizes the ornamentation of the posterior field in PIMUZ A/I 5047. It is similar to the ornamentation present in the scales of †*Acregoliath rancii* Richter, 1989, from the middle and late Miocene of Colombia (see Ballen and Moreno-Bernal, 2020, fig. 3) and Brazil (Richter, 1989, fig. 3). According to Ballen and Moreno-Bernal (2020), scales of *A. rancii* also present ridges interleaved by aligned tubercles; a small tubercle is preserved also in PIMUZ A/I 5047. *Acregoliath rancii* is one of the most enigmatic extinct freshwater taxa from Neogene of South America, and its scarce fossil records from the Miocene of Brazil (Richter, 1989), Colombia (Ballen and Moreno-Bernal, 2020) and Peru (Tejada-Lara et al., 2015), is represented exclusively by isolated scales. PIMUZ A/I 5047 is assigned here tentatively to ?*Acregoliath* sp., although it should not be ruled out that our specimen belongs to an Arapaimidae.

Indeterminate Actinopterygii

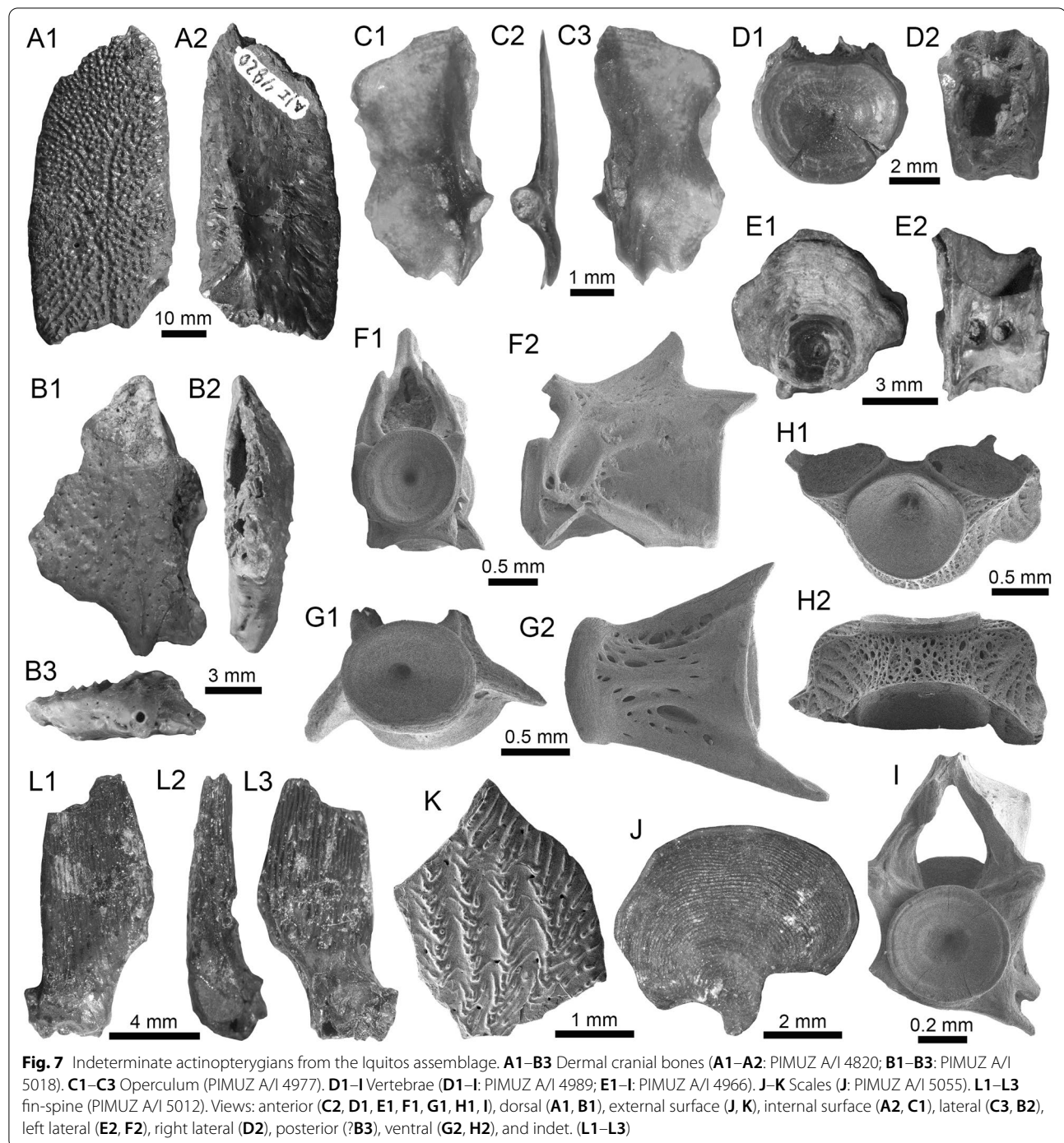
The sample includes an assortment of bony fish remains (Table 2), represented by cranial and postcranial elements such as maxillae and dentaries (PIMUZ A/I 4599 and 4980; Fig. 6N1–O3), teeth (PIMUZ A/I 4962, 4964, and 5015; Fig. 6P–T), other skull bones (PIMUZ A/I 4820, 4821, 5018, and 5019; Fig. 7A1–C3), fin-spines/rays (e.g., PIMUZ A/I 5012; Fig. 7L1–L3), and vertebrae (PIMUZ A/I 4966; Fig. 7D1–I). The sample also includes

a great quantity (more than 2000) of no diagnostic fragmented and poorly preserved bones and micro-fragmented scales (PIMUZ A/I 4963, 4967, 4968, 4976, 4977, 4978, 4985, 4989, 5010, 5011, 5017, 5020, and 5055) (Additional file 1).

PIMUZ A/I 4820 (Fig. 7A1–A2), 5018 (Fig. 7B1–B3), and 5019, are dermal cranial bones, being characterized by strong rugose ornamentation, and the presence of what appears to be lateral-line canals and openings (Fig. 7A1–B3). These dermal cranial bones do not match with any other bony fish taxa described in the above sections, and they are currently under study. One hundred and eight isolated vertebrae (PIMUZ A/I 4966) were identified here from the layer I (Table 2). Well-preserved and incomplete or poor preserved vertebrae are present in the sample PIMUZ A/I 4966. It is important to mention that PIMUZ A/I 4966 includes a large number of micro vertebrae (<3 mm in length) that likely could belong to juvenile specimens, or other small-sized species different from the taxa that can be recognized for the Iquitos fauna. Mainly due to the scarcity of extant comparative material, a more detailed taxonomic identification of these vertebrae currently is not possible. In reference to the specimens referred here to as fragmented bones and micro-fragmented scales (Fig. 7J), these are in such a poor state that they do not allow any assignment beyond indeterminate Actinopterygii. A great quantity of scale fragments with characteristic ornamentation patterns shown in Fig. 7K (PIMUZ A/I 4978) are abundant in the samples coming from the layers I, III, IV and VII.

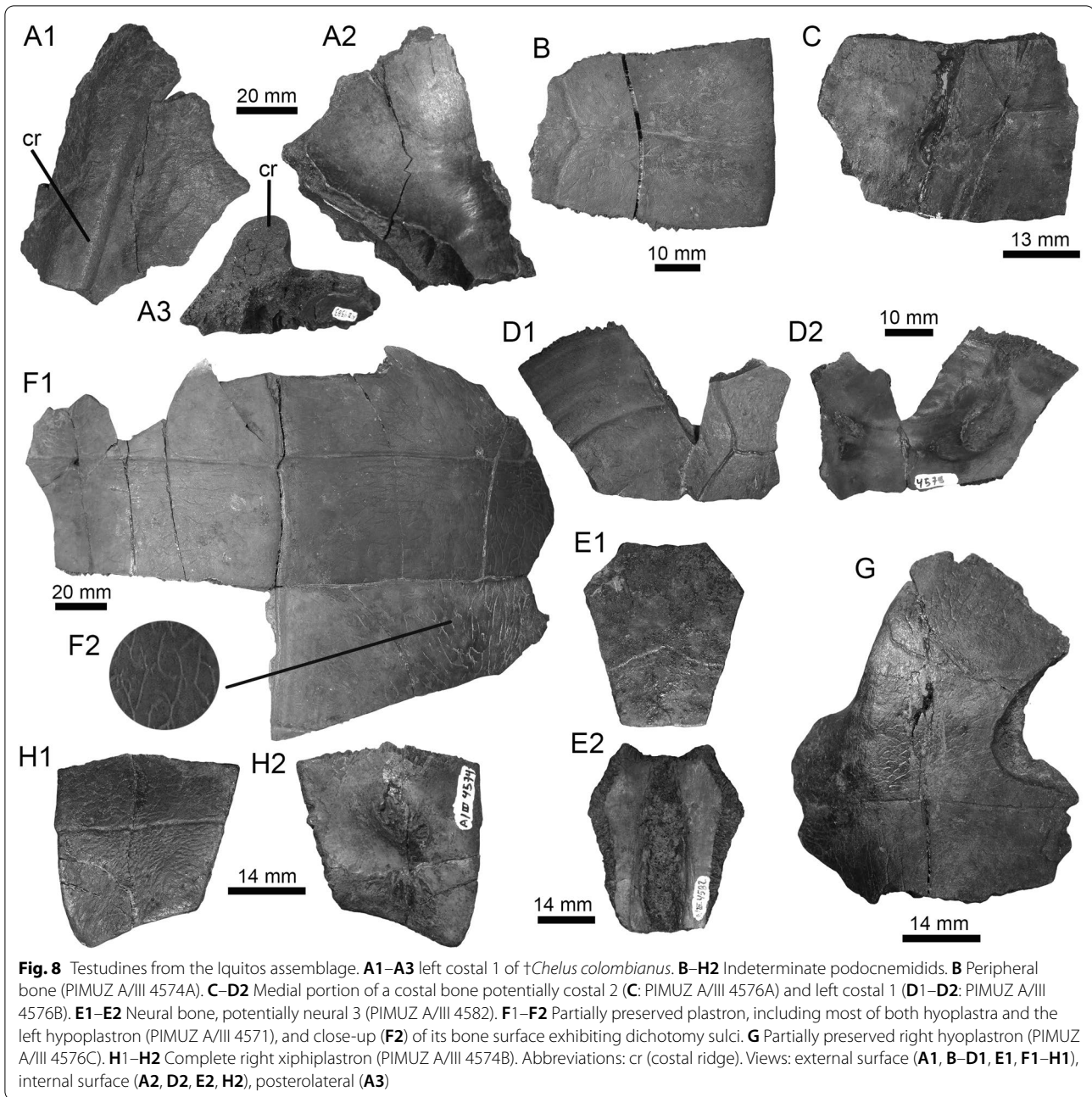
Testudines

The carapace fragment PIMUZ A/III 4583 (Fig. 8A1–A3; Additional file 2) of an unknown locality (Table 2) (likely associate to one of the “Telefunkenstation” layers), and which is a nearly complete left costal 1, is assigned here to the extinct turtle †*Chelus colombianus* Wood, 1976. The specimen exhibits on its external surface a well-defined and nearly continuous costal ridge (Fig. 8A1). In internal view (Fig. 8A2) the axillary buttress scar is narrow and crosses the entire costal from its anterolateral to its posterior edges and it is evident continues onto the costal 2. In posterolateral view (Fig. 8A3); the costal ridge is high, thick and dorsally convex. Our attribution to *C. colombianus* is based on the specimen exhibiting a suture of the axillary buttress extending onto costal 2 instead of being restricted to costal 1, as is the condition in the extant representative of the genus (Cadena and Jaramillo, 2015; Ferreira et al., 2016). This carapacial bone could represent a moderate-to-large individual of at least 40 cm.



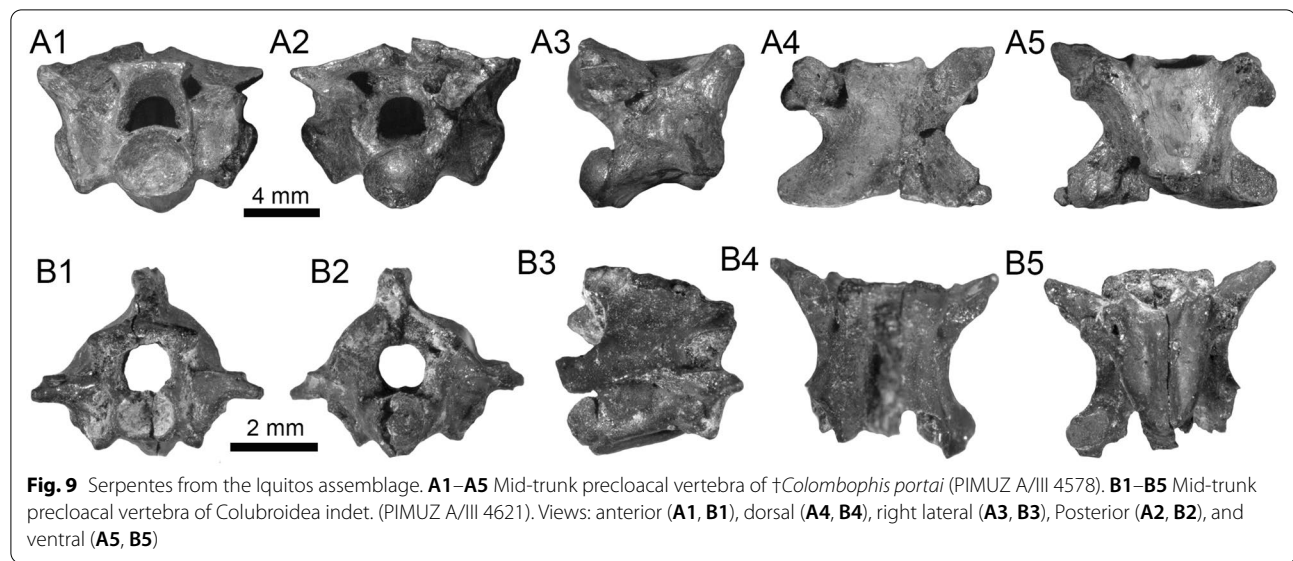
Other carapace and plastron fragments ($n=14$) assigned here to indeterminate podocnemidids are also present in the Iquitos assemblage (Table 2; Additional file 3). Carapace remains include an isolated peripheral bone from the posterior margin, potentially peripheral 10 or 11 (PIMUZ A/III 4574A, Fig. 8B), a medial portion of a costal bone (PIMUZ A/III 4576A, Fig. 8C), a

left costal 1 missing most of its lateral and anteromedial portions (PIMUZ A/III 4576B, Fig. 8D1–D2), and a completely preserved neural bone (PIMUZ A/III 4582, Fig. 8E1–E2). Plastron remains are represented by a partially preserved specimen including most of both hyoplastra and the left hypoplastron (PIMUZ A/III 4571, Fig. 8F1), a partially preserved right hyoplastron



missing some portions of its lateral and medial regions (PIMUZ A/III 4576C, Fig. 8G), a complete right xiphiplastron (PIMUZ A/III 4574B, Fig. 8H1–H2), and an indeterminate plastron bone fragment (PIMUZ A/III 4581). The sample also includes four other indeterminate shell fragments (PIMUZ A/III 4576D–G, 4577). All carapacial bones could represent moderate-to-large individuals of at least 80–120 cm in length. In all the aspects of bones shape, sutures, sulci and sculpturing pattern, the above-referred specimens resemble the

carapace of extant and extinct podocnemidids (see Carvalho et al., 2002; Gaffney et al., 2011; Cadena, 2015). The exception could be the position of some of the scutes, as indicated by the sulci, as is the case PIMUZ A/III 4571, which exhibits a humeropectoral sulcus that did not reach the epiplastron–hyoplastron sutural level. This could be a particular feature of this individual, and more complete material should be found to validate if this was a general condition in the podocnemidids turtles from this locality.



Serpentes

Two isolated snake vertebrae from the layers III (PIMUZ A/III 4578) and IV (PIMUZ A/III 4621) (Table 2) represent the sample. PIMUZ A/III 4578 corresponds to a well-preserved mid-trunk precloacal vertebra, only lacking the neural spine and the left prezygapophysis and with a centrum length of 6.3 mm (Fig. 9A1–A5). PIMUZ A/III 4578 is assigned here to †*Colombophis portai* Hoffstetter and Rage, 1977. In the specimen, the neural arch is broad, displaying a long prezygapophysis in anterior view. The prezygapophysis is slender, long, and strongly inclined dorsolaterally, reaching the level of the dorsal margin of the zygosphen. The zygosphen is moderately thick and shows a straight dorsal margin, and in its dorsal margin is slightly elevated in the mid-portion. The neural canal is small, high, and triangular. The cotyle is nearly circular. There is no evidence of the paracotylar foramen. The paradiapophyses are relatively reduced, not surpassing the cotyle's ventral margin. The dia- and parapophyseal surfaces are weakly separated; the diapophysis is slightly convex, and the parapophysis is somewhat concave. The neural arch is flattened in the posterior view. The posterodorsal notch of the neural arch is rather well marked. The postzygapophyses are elongated and strongly inclined dorsolaterally. The condyle is nearly circular. Ventral to the condyle, the haemal keel can be seen as a posterior prominence. In ventral view, the centrum is triangular; its ventral face is broadly rounded anteriorly, very short, and wide. PIMUZ A/III 4578 shows shallow subcentral grooves from the cotyle's ventrolateral margin until mid-length of the centrum, limiting anterolaterally the haemal keel, which narrows posteriorly. There is a single small subcentral foramen, anteriorly located of

the haemal keel. The subcentral ridges are well marked in all its extension. The condylar surface is exposed in ventral view, where the precondylar constriction is moderately marked. Although the neural spine is lacking, it is restricted to the neural arch's posterior edge in the lateral view. The centrum is inclined posteroventrally, where it distally bears a relatively prominent haemal keel. The posterodorsal notch of the neural arch is well-marked but not deep. The prezygapophyses' articular facets are comparatively slender, longer than broad in the dorsal view. The main axis is strongly anteriorly orientated—a small and sharp-edged prezygapophyseal process projects beyond the right prezygapophysis articular facet. The interzygapophyseal constriction is well-marked and very short between the pre- and postzygapophysis on each side. The anterior margin of the zygosphen is slightly concave.

Colombophis is an enigmatic alethinophidian snake and a very well-known fossil squamate from Neogene deposits from northern South America (Hsiou et al., 2010). The genus *Colombophis* is represented by the two species †*Colombophis spinosus* Hsiou et al., 2010, and *C. portai*, with a fossil record that includes the middle Miocene of Colombia and late Miocene of Venezuela and Brazil (Hoffstetter and Rage, 1977; Hecht and LaDuke, 1997; Head et al., 2006). The specimen PIMUZ A/III 4578 described herein from Iquitos shows vertebral features seen in the morphology of *C. portai*. These morphological vertebral characteristics are distinct from the *C. spinosus* by its mid-trunk vertebrae longer than broad, with a very low neural spine, resembling a tubercle and circular in outline in dorsal view; thin-to-moderate zygosphen; anterolaterally orientated prezygapophyses; and

undivided paradiapophyses (see Hsiou et al., 2010). This last feature is weakly developed in specimen PIMUZ A/III 4578 from the Iquitos assemblage and could indicate a new vertebral intraspecific variation for *C. portai*.

The second specimen PIMUZ A/III 4621 is assigned here to an indeterminate Colubroidea, and it corresponds to an incomplete mid-trunk precloacal vertebra, lacking the neural arch's posterior distal, left paradiapophysis, and the right postzygapophysis and with a centrum length of 3.2 mm (Fig. 9B1–B5). In the anterior view, the zygosphenes shows the dorsal edge is slightly arched, broad, and thick. The zygosphenes is thick and wider than the cotyle. The neural canal has a pentagon-like shape, and it is practically the same diameter as the cotyle. The cotyle is rounded and broken near the mid-portion of the element. The prezygapophyses are horizontalized with a robust and prominent prezygapophyseal process. The paradiapophyses are oriented laterally, with both articular facets differentiated; the diapophyseal articular facet has a strongly projecting convex edge. The parapophyseal articular facet is concave (only observed on the left side). Below the parapophyseal area, there are small parapophyseal process anteriorly oriented. In posterior view, the neural arch is vaulted, showing a high neural spine. The zyganchtrum is small and shallow and internally bears a large zyganchtral foramen (only seen on the right side). Only the right postzygapophysis is preserved, and it is horizontally oriented. The condyle has rounded in shape, and as seen in the cotyle, is also broken near its mid-portion. The neural spine is fragmented in all dorsal margins; however, it increases anteroposteriorly in height. Lateral foramina are present on the mid-portion of the vertebra. A marked precondylar constriction characterizes the posterior region of the centrum. A flattened haemal keel is present on the mid-precloacal vertebra's ventral surface, rising from the ventral margin of the cotyle and extending anteroposteriorly to reach the precondylar constriction. In the dorsal view, the prezygapophyses are tightly oriented anterolaterally, with the articular facets of the prezygapophyses showing oval-shaped and long and robust prezygapophyseal processes. The anterior edge of the zygosphenes is broken. The interzygapophyseal constriction is well marked and deep. The centrum

is elongated and narrow, relatively wider anteriorly in the ventral view, with well-defined subcentral ridges. The haemal keel is well-developed on the whole ventral surface of the centra. It originates at the ventral edge of the cotyle and is slightly prominent and slender. There is a pair of small subcentral foramina, one foramen on each side of the haemal keel. Only the right postzygapophyses is preserved and show a small articular facet with an oval form, posterolaterally orientated.

The Colubroidea is a monophyletic group of snakes (Figueroa et al., 2016; Zaher et al., 2009), and a very speciose group of caenophidian snakes with an overall fossil record since the Palaeogene (Burbrink et al., 2020; Rage, 1984). Based only on vertebral morphology, colubroids are traditionally identified by the following combination of characters: delicate vertebrae, longer than wide; thin zygosphenes, neural spine thin and slender; paradiapophyses differentiated; paracotylar foramina usually present; and prezygapophyseal processes well developed (Rage, 1984; Holman, 2000; Albino and Montalvo, 2006; Hsiou and Albino, 2010). A few Neogene South American records of colubroidean snakes have been reported, mainly from the late Miocene of Argentinean Patagonia and Brazilian Amazonia (Albino and Brizuela, 2014; Hsiou and Albino, 2010). The specimen PIMUZ A/III 4621 from the Iquitos assemblage (middle Miocene) represents the oldest records of South American colubroidean snakes.

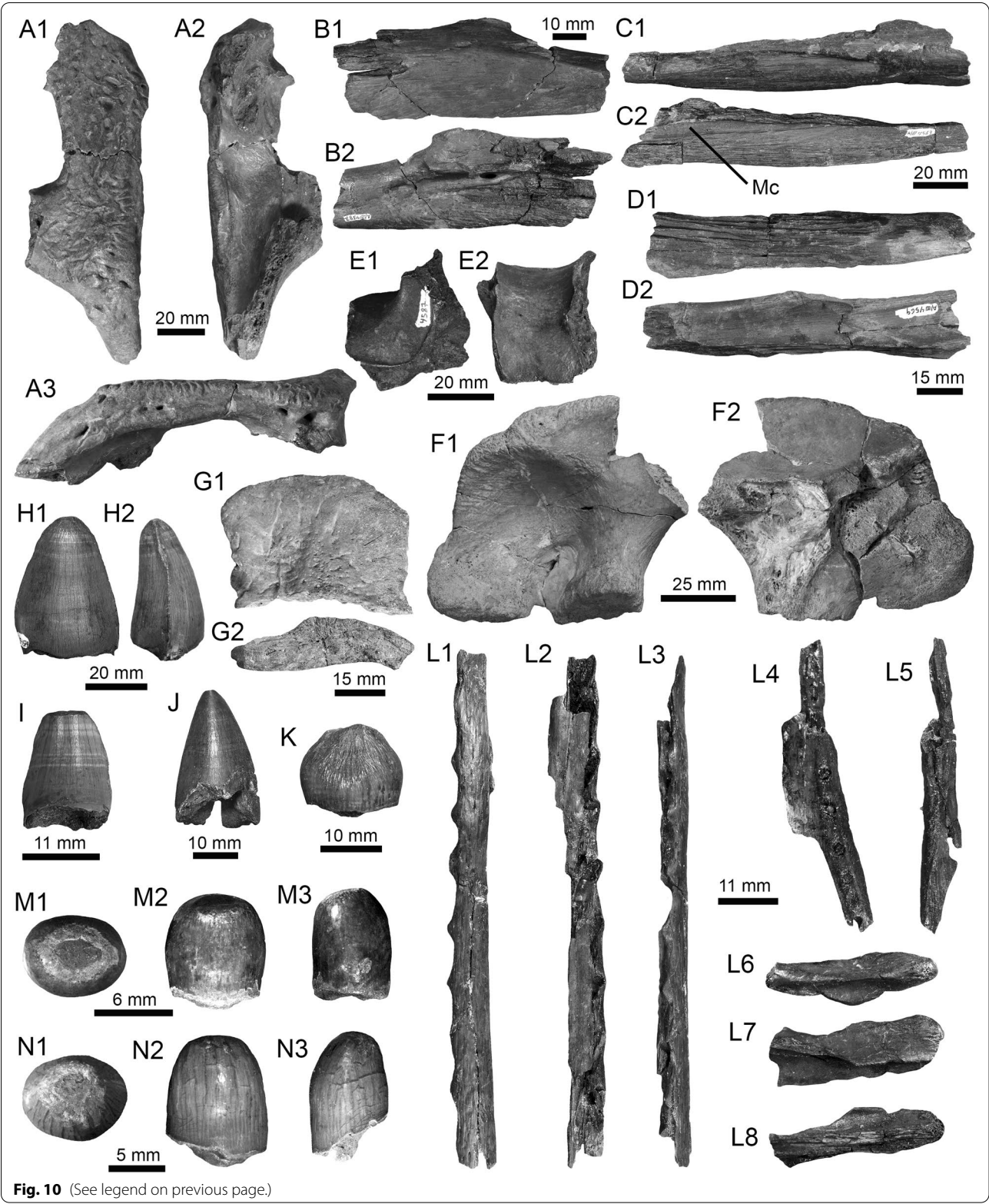
Crocodylia

The crocodylian sample includes mostly isolated teeth, but also a few identifiable skull bones and postcranial elements. Most of the elements pertain to caimanines (Alligatoridae) or gryposuchines (Gavialidae), whereas other fragments cannot be identified beyond Crocodylia indet. (Table 2; Additional file 1).

Most prominent among the sample are several bones assignable to *Purussaurus* sp., including a partial right skull roof preserving the postorbital shelf and the squamosal (PIMUZ A/III 4567; Fig. 10A1–A3), a proximal part of a right quadrate (PIMUZ A/III 4587; Fig. 10B1–B2), the central part of a right angular preserving the lower margin of the foramen intermandibularis caudalis and a strongly

(See figure on next page.)

Fig. 10 Crocodylia from the Iquitos assemblage. **A1–K** Partial right skull roof (**A1–A3**: PIMUZ A/III 4567), proximal part of a right quadrate (**B1–B2**: PIMUZ A/III 4587), central part of a right angular (**C1–C2**: PIMUZ A/III 4569), posterocentral portion of a dentary (**D1–D2**: PIMUZ A/III 4569), anterior part of a left surangular (**E1–E2**: PIMUZ A/III 4587), partially preserved left ilium (**F1–F2**: PIMUZ A/III 4568), partial dorsal osteoderm (**G1–G2**: PIMUZ A/III 4587), and teeth (**H1–H2**: PIMUZ A/III 4579; **I**: PIMUZ A/III 4573; **J–K**: PIMUZ A/III 4584) of *Purussaurus* sp. **L1–L8** Juvenile gryposuchine Gavialidae (PIMUZ A/III 4575). **L1–L3** Mid-region of a right dentary. **L4–L5** Part of the maxilla. **L6–L8** Posterior part of an articular. **M1–N3** Globular teeth (**M1–M3**: PIMUZ A/III 4591; **N1–N3**: PIMUZ A/III 4592) tentatively identified to *Gnatusuchus pebasensis*. Abbreviations: Mc (Meckel's canal). Views: anterodorsal (**E2**), dorsal (**A1**, **G1**, **L2**, **L6**), cross sectional (**G2**), labial (**H1**, **N2**), lingual (**I–J**, **M2**), lateral (**E1**, **H2**, **L8**, **M3**, **N3**), left lateral (**B1**, **C1**, **D1**, **F1**, **L5**), right lateral (**A3**, **L3**), medial (**B2**, **C2**, **D2**, **F2**, **L7**), occlusal (**M1**, **N1**), ventral (**A2**, **L1**, **L4**), and indet. (**K**)



striated attachment area for the dentary (PIMUZ A/III 4569; Fig. 10D1–D2), the posteroventral portion of a dentary (PIMUZ A/III 4569; Fig. 10C1–C2) preserving only a thin portion of the Meckel's groove medially, the anterior part of a left surangular (PIMUZ A/III 4587; Fig. 10E1–E2) preserving articulation facets for the coronoid and dentary medially, as well as the mid-dorsal margin of the external mandibular fenestra. In addition, two further indeterminate fragments pertaining either to the cranium or to the postcranium were found (PIMUZ A/III 4569 and 4587). Despite their fragmentary nature, all these bones were found close-by in the same layer, are of similar large size and do not show duplicate elements, so we treat them as belonging to a single individual herein.

A partially preserved left ilium (PIMUZ A/III 4568; Fig. 10F1–F2) was identified as belonging to a juvenile *Purussaurus* sp. based on the Pi-shaped separation of three medial articulation sites for three sacral vertebrae, a feature so far known only to occur in the giant caiman *Purussaurus* among Crocodylia (Scheyer et al., 2019). The specimen has a height of 7 cm, but due to the largely broken off postacetabular process its length, as preserved, is only 10 cm. The remaining specimens identified as *Purussaurus* sp. include a dense partial dorsal osteoderm (PIMUZ A/III 4572; Fig. 10G1–G2) with a low keel and few shallow vascular grooves dorsally and a cross-hatching striation on the ventral surface, as well as a few large teeth (Fig. 10H1–K) with more or less conical shape and anterior and posterior carinae and a large globular tooth with a strongly wrinkled enamel crown (PIMUZ A/III 4573, 4579 and 4584). Globular teeth are found in the posterior part of the skull and mandible, whereas the higher carinated teeth are situated in the anterior snout region in *Purussaurus* (e.g., Langston, 1965; Aguilera et al., 2006; Scheyer and Delfino, 2016). While the crowns of PIMUZ A/III 4579 and 4584 are complete, the two specimens of PIMUZ A/III 4573 show considerable damage.

Three associated fragments (Fig. 10L1–L8) are interpreted to belong to a single individual of a small early juvenile–gryposuchine gavialid (PIMUZ A/III 4575). The largest fragment, 11.6 cm long, is from the mid-region of a right dentary of the lower jaw, showing remnants of 10 alveoli but no preserved teeth (Fig. 10L1–L3). The bone is straight showing a long medial suture and the lateral margin is slightly festooned (where the alveoli meet the bone margin). The second bone fragment is the posterior part of an articular preserving an elongated and slightly upturned retroarticular process (3.3 cm in length) with a sharp crest that extends anteriorly about 1 cm of the retroarticular process and then smoothens anteriorly into a less acute ridge (Fig. 10L6–L8). Ventromedially the specimen

shows a well-defined groove and laterally an articulation facet for the surangular (and potentially the angular). The third specimen (6.3 cm in length) comprises a posterior part of the maxilla with nine partially preserved alveoli, and a short, sutured part with the palatine medially (Fig. 10L4–L5). Posteriorly the anterior margin of the suborbital fenestra is preserved and the 5th alveolus from posterior still carries a small pointed tooth.

Of the isolated teeth, two small globular teeth (Fig. 10M1–N3) showing distal wear (PIMUZ A/III 4591 and 4592) are tentatively identified to belong to the shovel-snouted caiman +*Gnatusuchus pebasensis* Salas-Gismondi et al., 2015. Three pointy, slender and strongly curved teeth (PIMUZ A/III 4580), all are longer than 2 cm and showing dorso-ventrally striations but lacking carinae (Fig. 11A1–B), are identified as pertaining to gryposuchine gavialids herein. The remaining teeth (Fig. 11C1–D2) are only identified as belonging to Caimaninae indet. (PIMUZ A/III 4588, 4589, 4593 and 4595) or Crocodylia indet. (PIMUZ A/III 4596).

Other postcranial elements are only identified as pertaining to Crocodylia indet. Of those, we identified a small right femur (PIMUZ A/III 4585) preserving most of the diaphyseal shaft but lacking the proximal and distal ends (Fig. 11E1–E2), and a fragment of a posterior thoracic rib (PIMUZ A/III 4586; Fig. 11F1–F2).

Other vertebrate remains

The sample includes a micro-caudal vertebra of rectangular shape (PIMUZ A/III 4618) of a probable lizard (Fig. 11G1–G3), an ungual phalanx (PIMUZ A/III 4598, Fig. 11J1–J2), and two complete (PIMUZ A/III 4619, Fig. 11H1–H2), a partial phalanx (PIMUZ A/III 4617, Fig. 11I), respectively (Table 2). These phalanges could potentially belong to crocodylians or turtles. Two isolated vertebrae (PIMUZ A/III 4597) are referred here to Reptilia indet., but with uncertain position and taxonomy (Fig. 11K1–L2). In addition, the two isolated caudal vertebrae illustrated in Fig. 11K1–L2, also resemble the vertebrae of the most distal part of the tail of some lizard taxa (e.g., Etheridge, 1967).

Fourteen complete/fragmented coprolites (PIMUZ A/III 4570) are reported from layer VII (Fig. 11M1–R), the largest specimen being 34 mm in length. The most complete specimens have a cylindrical-elongate shape, with rounded to oval (Fig. 11M1–M2), or with pointed ends (Fig. 11N); like some coprolite morphotypes described from the late Miocene Urumaco Formation (Dentzien-Dias et al., 2018). Most of the coprolites from Iquitos are characterized by a smooth surface, some specimens are segmented (Fig. 11R), while others preserve longitudinal

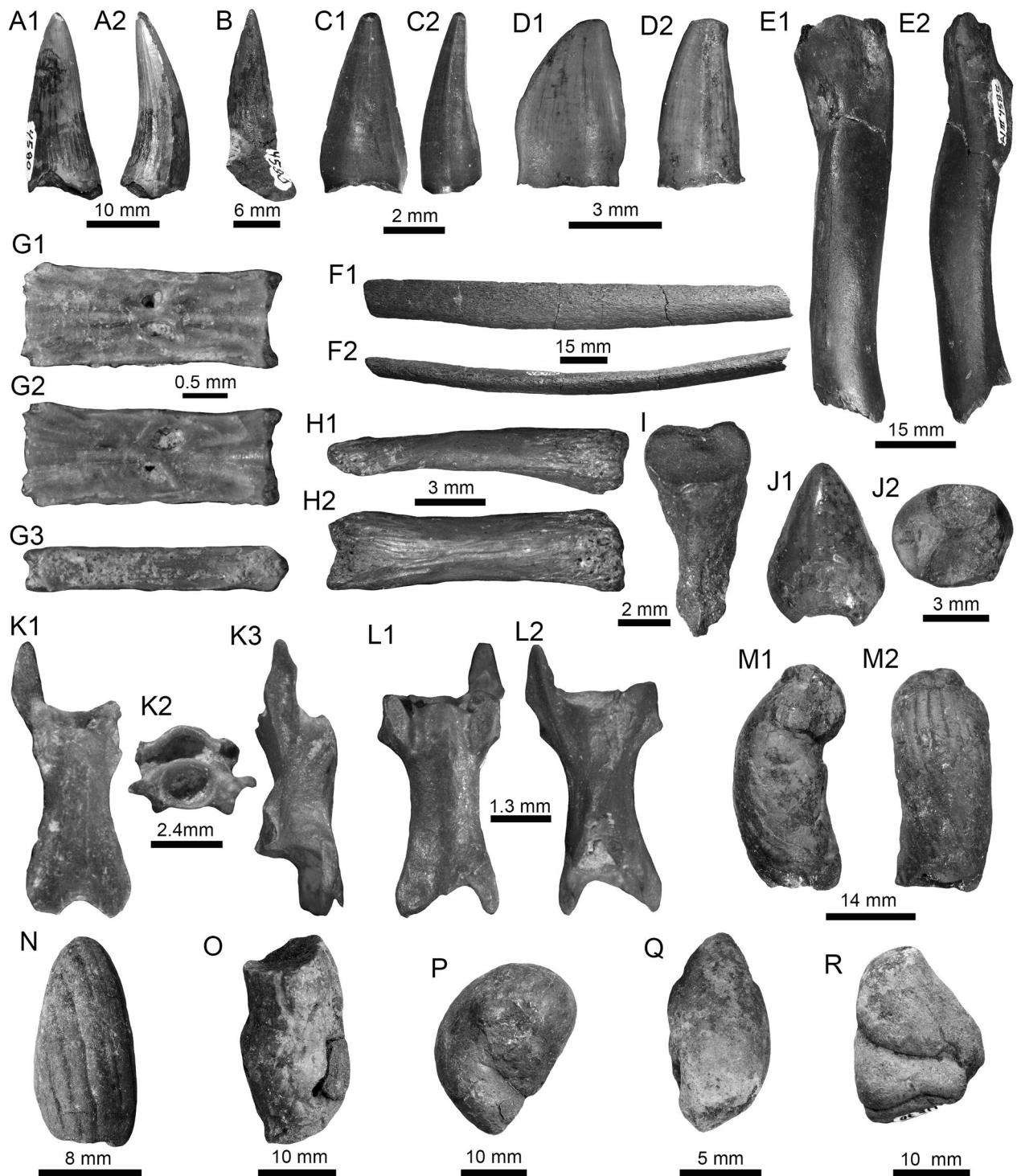


Fig. 11 Crocodylia and other indeterminate vertebrate remains and coprolites from the Iquitos assemblage. **A1–B** Gryposuchine gavialid teeth (PIMUZ A/III 4580). **C1–D** Crocodylia indet. teeth (**C1–C3**: PIMUZ A/III 4588; **D1–D2**: PIMUZ A/III 4593). **E1–E2** Right femur (PIMUZ A/III 4585). **F1–F2** Fragment of a posterior thoracic rib (PIMUZ A/III 4586). **G1–G3** Caudal vertebra of probable lizard (PIMUZ A/III 4618). **H1–J** Complete (**H1–H2**: PIMUZ A/III 4619), partial (**I**: PIMUZ A/III 4617), and an ungual (**J1–J2**: PIMUZ A/III 4598) phalanges. **K1–L2** Reptilian vertebrae of uncertain taxonomy (PIMUZ A/III 4597). **M1–R** coprolites (PIMUZ A/III 4570). Views: dorsal (**F2**, **H2**, **I**, **J1**, **K1**, **L1**), labial (**D1**), lingual (**A1**, **B**, **C1**), lateral (**A2**, **C2**, **D2**, **E1**), left lateral (**H1**, **K3**), posterior (**E2**, **J2**, **K2**), ventral (**L2**), and indet. (**F1**, **G1–G3**, **K1–P**)

striations (Fig. 11M1–N). These coprolites probably came from different producers, not ruling out crocodiles and turtles among these.

Discussion

The Pebas megawetland depositional system includes a vast geographical area that encompasses parts of different basins and geological units in Brazil (Solimões Fm.), Colombia (Pebas Fm.), and Peru (Pebas and Ipururo formations) (Monsch, 1998; Cozzuol, 2006; Hoorn and Wesselingh, 2010; Tejada-Lara, 2015). From these Pebasian units, diverse aquatic and continental vertebrates have been reported, including sharks, rays, bony fishes, turtles, crocodylians, snakes, lizards, birds, and aquatic and terrestrial mammals (e.g., Monsch, 1998; Cozzuol, 2006; Salas-Gismondi, 2006, 2015, 2016; Antoine et al., 2007, 2016; Pujos et al., 2009; Lundberg et al., 2010; Hoorn and Wesselingh, 2010; Bianucci et al., 2013; Tejada-Lara, 2015; Chabain et al., 2017; Marivaux et al., 2020; Pujos and Salas-Gismondi, 2020, and references therein). Aquatic/semi-aquatic vertebrates reported from the Pebas Fm. intervals that crop out in the Iquitos area and surroundings include cownose rays and stingrays, and several bony fishes (see Monsch, 1998, Tables 1, 2), a teiid lizard (Pujos et al., 2009), indeterminate turtles, and a hyperdiverse crocodylian community with at least seven species, plus one longirostrine gharial (Salas-Gismondi et al., 2015, 2016).

The new aquatic/terrestrial fauna described herein from the Pebas Fm. in the Iquitos area is represented by a palaeodiversity of at least 34 taxa of stingrays, bony fishes, turtles, snakes, crocodylians and lizards (Tables 1, 2; Additional file 1) that corroborates and expands previous reports. Iquitos and its surrounding can be mapped within the Molluscan Zones MZ6 (15–14 Ma) and MZ7 (14–12 Ma) as proposed by Wesselingh et al. (2006) (see Fig. 1B), which suggests a middle Miocene age for the vertebrate assemblages.

Bony fishes represent the most diverse group from the Iquitos assemblage, with at least 23 taxa (Table 2). This fish palaeodiversity is possibly underestimated, due to the large number of microscopic fish remains (e.g., isolated cranial and postcranial elements) that could not be identified. Bony fishes are well represented in most of the fossiliferous layers recognized in this work, the layer I being the most diverse (see Tables 1, 2; Additional file 1). From the new Iquitos assemblage, fishes such as characids, serrasalmids, cynodontids, erythrinids, perciforms, callichthyds, doradids, pimelodids, loricariids, other siluriforms, and the enigmatic †*Acregoliath* fish (Table 1), have also been reported for the Pebas Fm. in the Iquitos (Monsch, 1998, Table 2) and Contamana areas (Antoine et al., 2016), and other Pebasian intervals (Lundberg et al.,

2010; Tejada-Lara, 2015). For the first time *Mylossoma*, *Serrasalmus*, and *Hemiodus* are reported for the Pebas system. *Hemiodus* (Fig. 3N1–P2), represents the first fossil record for the taxon and Hemiodontidae, which can thus offer a new fossil calibration point for this group of freshwater fishes. In reference to the two potamotrygonid stingray taxa, and the eagle or cownose rays (*Myliobatis* or *Rhinoptera*) from the Iquitos assemblage, are solely reported from layers I, and II, respectively (Table 2). These rays have been also reported in other outcrops of the Pebas Fm. (Monch, 1998; Chabain et al., 2017).

The reptile fossil fauna (Table 2) includes at least two turtles, three crocodylians, two snakes, and one lizard of small size (Fig. 11G1–G3). The turtles are represented by the pleurodiran *Chelus colombianus*, an extinct species with a wide geographic distribution during the Miocene (Cadena and Jaramillo, 2015; Carrillo-Briceño et al., 2018; Ferreira et al., 2016; Riff et al., 2010), and abundant carapacial bones that could represent moderate-to-large podocnemidid individuals of up to 120 cm in length. Although podocnemidid turtles are abundantly represented in terms of fragments remains in the Pebas Fm. (Antoine et al., 2016), their generic and taxonomic identity still is unknown, in contrast with the podocnemidid palaeodiversity known from other Miocene units of Amazonia (Cadena et al., 2020; Riff et al., 2010).

Crocodylians from the Pebas Fm. are well known, especially from the Iquitos area, from where a hyperdiverse crocodylian community of seven crocodylians and a longirostrine gharial have been reported (Salas-Gismondi et al., 2015, 2016). The Caimaninae reported herein from Iquitos are in fragmentary conditions (Table 2), nevertheless, their diagnostic elements allow us to assign several specimens to caimanines with affinities to *Gnatusuchus pebasensis* and to *Purussaurus* sp. The size of the cranial elements referred to *Purussaurus* sp. suggest that this individual had a skull length around 40–50 cm, which lies in the size dimensions of the still small and probably juvenile specimen INGEOMINAS DHL-45 of †*Purussaurus neivensis* Mook, 1941 (Aguilera et al., 2006; Langston, 1965). In addition, the overall small size of the recovered ilium, compared to the much larger ones reported for †*Purussaurus mirandai* Aguilera et al., 2006 (Scheyer et al., 2019), indicates a juvenile ontogenetic stage of that individual as well. The cranial gharial remains also indicate a small individual, somewhat older than a yearling, as based on comparisons with hatchlings and juveniles of the extant *Gavialis gangeticus* Gmelin, 1789 (e.g., specimens ZM 125710, MTKD 4622; YPM HERR-008438 from Gold, 2011; Grigg and Kirshner, 2015).

Only two isolated snake vertebrae are reported here from the Iquitos assemblage, and these specimens provide a glimpse into the ophidian fauna and its evolution

in South America. The presence of *Colombophis portai* in the Pebas Fm. (Iquitos area), a species that has been associated with a semi-aquatic lifestyle (Hsiou et al., 2010), represents the first fossil record of this taxon in Peru, and the southernmost geographical distribution for the species during the middle Miocene. The fossil record of *C. portai* is known from the middle Miocene of Colombia, and late Miocene of Venezuela and Brazil (Hoffstetter and Rage, 1977; Hecht and LaDuke, 1997; Head et al., 2006; Hsiou et al., 2010). In reference to the isolated vertebra (PIMUZ A/III 4621, Fig. 9B1–B5) referred here as an indeterminate colubroid from the middle Miocene of Iquitos, it represents the oldest record of South American colubroidean snakes. Other fossil colubrids have been reported, exclusively from the late Miocene of Argentinean and Brazilian Amazonia (Albino and Brizuela, 2014; Hsiou and Albino, 2010). The presence of this middle Miocene colubroidean snakes in the Pebas system support the hypothesis of a Colubroidea dispersal earlier than previously estimated and prior to major continental events such as the uplifting of the Panama Isthmus and the Great American Faunal Interchange (Albino and Montalvo, 2006; Woodburne, 2010; Onary et al., 2018). Other snake remains of uncertain affinities have been also referred to from the Pebas Fm. in the Contamana area (Antoine et al., 2016), and other Pebasian intervals (Tejada-Lara, 2015), and future taxonomic works in these specimens could shed new light on the palaeodiversity of snakes in the region during the Pebas system time.

Palaeoenvironments

The molluscan fauna described by de Greve (1938), suggests a wide range of environments for the Pebas Fm. intervals in the Iquitos area (see Additional file 4). In reference to the vertebrate assemblage, most of the bony fishes reported here (Table 2; Additional file 1) are typical for a tropical freshwater composition. The habitat preferences of extant taxa related with fossil Characiformes (e.g., Characidae, Cynodontidae, *Hemiodus*, *Hoplias*, *Colossoma macropomum*, *Mylossoma*, *Serrasalmus*), Cichliformes (Cichlidae), Siluriformes (e.g., Callichthyidae, Doradidae, Loricariidae, Pimelodidae), and Osteoglossiformes (e.g., Arapaimidae, Osteoglossidae) inhabit a wide range of freshwater environments such as lakes, swamps, streams, rivers, ponds, seasonal floodplains and inundated forests (Lundberg et al., 2010; van der Sleen and Albert, 2018). The enigmatic and extinct *Aregoliath* fish has been also recorded exclusively from freshwater palaeoenvironments (Richter, 1989; Ballen and Moreno-Bernal, 2020). In contrast, the presence of other euryhaline species in the Iquitos assemblages, such as Ariidae catfishes support also estuarine environments,

although some marine and brackish species can migrate upstream (Marceniuk and Menezes, 2007; van der Sleen and Albert, 2018).

The Potamotrygonids reported herein from Iquitos (Table 2) come from the layer I, which associates the ichthyofauna assemblage to a freshwater environment. In the Contamana section (Chabain et al., 2017), the dominance of batoids and the absence of sharks, which are present in other Pebas Fm. intervals (see Monsch, 1998; Antoine et al., 2016), could be indicative of estuarine environments. The presence in the Iquitos assemblage of an eagle ray (*Myliobatis*) or cownose ray (*Rhinoptera*) (Table 2) could also support the presence of estuarine conditions. Living representatives of these batoids are associated to marine environments, but with the capacity to go in bays, river deltas, and other brackish waters (Collins et al., 2008). For example, some *Rhinoptera* species reproduce in the freshwater Maracaibo Lake (Lundberg et al., 2010).

The presence of the matamata turtle *Chelus colombianus* and other podocnemidids in the Iquitos assemblage supports the existence of freshwater environments (Cadena and Jaramillo, 2015; Trebbau and Pritchard, 2016; Carrillo-Briceño et al., 2021). For example, extant species of *Chelus* are associated mainly with slow-moving waters, swamps, and marshes (Trebbau and Pritchard, 2016).

In reference to the crocodylians, the habitat preferences of their extant relatives are freshwater lakes, marshes, swamps, mangroves, and flowing waters. For example, the habitat preferences of extant gharials are “slower pools of fast flowing river” (Grigg and Kirshner, 2015: p. 6) and those of caimanine alligatorids are freshwater lakes, marshes, swamps, mangroves, and flowing waters (Manolis and Stevenson, 2010). On the other hand, the giant *Purusaurus mirandai* and several extinct gryposuchine gharial species have been associated to freshwater/brackish environments in northern South America (Scheyer et al., 2013; Scheyer and Delfino, 2016). Based on the associated faunal components, it is plausible, however, to assume that the juvenile gharials, as indicated by the remains from Iquitos, were also raised in freshwater environments.

Conclusions

The fossil vertebrate assemblage studied herein from Iquitos, which includes 34 taxa suggests an unequivocal mixture of terrestrial, freshwater, and brackish depositional environments in the area during the middle Miocene (Fig. 12). It provides novel data about palaeodiversity and the geographical/temporal range of several lineages inhabiting the megawetland system that characterized the western Amazonia at that time.



Fig. 12 (Top) Life reconstruction of the Pebas Formation faunal assemblage during the middle Miocene. Artist: Jaime Chirinos. (Bottom) Key of the reconstruction. (1) Podocnemididae indet. (2) †*Chelus colombianus*. (3) Gryposuchinae (Gavialidae) indet. (4) Caimaninae indet. (5) †*Purussaurus* sp. (6) †*Colombophis portai*. (7) ?*Osteoglossoides* indet. (8) *Colossoma* cf. *C. macropomum*. (9) *Hemiodus* sp. (10, 15) Loricariidae ident. (11) Cynodontidae indet. (12) †*Potamotrygon canaanorum*. (13) Sciaenidae indet. (14) Doradidae indet. (16) cf. *Serrasalmus* sp. (17) Cichlidae indet

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13358-021-00239-7>.

Additional file 1: Vertebrate paleodiversity from Iquitos assemblage, with information about their layers and catalog numbers. For more details about layers, see Table 1.

Additional file 2: *†Chelus colombianus* from Iquitos (PIMUZ A/I 4583). Partially preserved right left costal 1 in external (A1–A2), internal (A3–A4), and posterolateral views (A5–A6). Abbreviations: as, axillary buttress scar; cr, costal ridge.

Additional file 3: Podocnemidid turtles from Iquitos. A1–A2. Peripheral bone (PIMUZ A/I 4574A). B1–B2. Medial portion of a costal bone potentially costal 2, and left costal 1 (C1–D2) (PIMUZ A/I 4576A). E1–E4. Neural bone, potentially neural 3 (PIMUZ A/I 4582). F1–F4. Partially preserved plastron, including most of both hyoplastra and the left hypoplastron (PIMUZ A/I 4571), and close-up (F2–F4) of its bone surface exhibiting dichotomy sulci. G1–G2. Partially preserved right hyoplastron (PIMUZ A/I 4576C). H1–H4. Complete right xiphiplastron (PIMUZ A/I 4574B). Abbreviations: Abd (abdominal scute), Ana (anal scute), as (axillary buttress scar), Fem (femoral scute), Hum (humeral scute), hyo (hyoplastron), hyp (hypoplastron), is (ischial scar), M (marginal scute), P (pleural scute), Pec (pectoral scute), ps (pubic scar), V (vertebral scute). Views: external surface (A1–C2, E1–E2, F1–H2), internal surface (D1–D2, E3–E4, H3–H4).

Additional file 4: Mollusca genera from the Iquitos area described by de Greve (1938). Taxonomical actualization, synonymy and habitat preferences based on Wesselingh et al. (2002).

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Authors' contributions

JDC-B and TMS conceived the study. The following authors performed the taxonomic work on the indicated taxa and drafted the description of those fossils: JDC-B, OA, SA and JLO. Birindelli (fishes), TMS (crocodilians), ASH (Squamata), Edwin-Alberto Cadena (turtles). JDC-B: processed, prepared fossils and took photographs. JDC-B, AB-P and TMS prepared figures and/or tables. JDC-B, TMS, OAA, AB-P, ASH, JLOB, SA and E-AC wrote partial drafts of the manuscript. JDC-B and TMS prepared the final draft, which was approved by all authors. All authors read and approved the final manuscript.

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Availability of data and materials

All the fossil specimens described here are freely available for study at the Palaeontological Institute and Museum of the University of Zurich, Switzerland. All data generated or analysed during this study are included in this published article [and its Additional files].

Declarations

Competing interests

The authors declare that they have no conflict of interest.

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