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middle Miocene freshwater ichthyofauna
from the Tatacoa Desert, Colombia

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in Juan D. CARRILLO (ed.),
Neotropical palaeontology:
the Miocene La Venta biome

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New clues on the palaeodiversity of the middle Miocene freshwater ichthyofauna from the Tatacoa Desert, Colombia

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ABSTRACT

The middle Miocene rocks of the Honda Group (La Victoria and Villavieja formations) in the Tatacoa Desert, Upper Magdalena River Valley, Colombia, possess one of the best studied continental faunas of the Neotropics, ranging in age from *c.* 16 to *c.* 10.5 Ma. The fossil record of the region shows a high diversity of fishes, crocodylians, snakes, lizards, turtles, and aquatic/terrestrial mammals. Here we present a new overview of the freshwater fish palaeodiversity and its biostratigraphic context. The new data includes the description of a new fossil catfish †*Sciades maldonadonis* n. sp., the putative first fossil record of the cichlids *Astronotus* and *Cichla*, the first report for the region of the thorny catfish *Oxydoras*, and taxonomical comments on some taxa previously reported for this stratigraphic unit. With a palaeodiversity tentatively represented by at least 23 taxa of chondrichthyans and bony fishes, the Honda Group preserves one of the most diverse Miocene freshwater fish fauna so far known from the Neotropics. The taxonomical and biogeographical affinities of the fossil fish assemblage, with extant taxa in the Orinoco and Amazonas river systems, sustain the hypotheses of drainages flowing from western Amazonia into the proto-Caribbean Sea. This middle Miocene fish assemblage also offers significant evidence for the evolutionary history of the Neotropical freshwater fishes and ancient environments.

KEY WORDS
Northwestern South America,
Neogene,
Neotropics,
rays,
bony fishes,
hydrographic systems
Orinoco-Amazonas,
new species.

RÉSUMÉ
Nouveaux indices sur la paléodiversité de l'ichtyofaune d'eau douce du Miocène moyen du désert de Tatacoa, Colombie.
Les roches du Miocène moyen du groupe Honda (formations de La Victoria et de Villavieja) dans le désert de Tatacoa, vallée supérieure du fleuve Magdalena, Colombie, possèdent l'une des faunes continentales les mieux étudiées des Néotropiques, dont l'âge varie entre environ 16 et environ 10,5 Ma. Les archives fossiles de la région montrent une grande diversité de poissons, crocodiliens, serpents, lézards, tortues, et de mammifères aquatiques/terrestres. Nous présentons ici un nouvel aperçu de la paléodiversité des poissons d'eau douce et de son contexte biostratigraphique. Les nouvelles données comprennent la description d'un nouveau poisson-chat fossile †*Sciades maldonadonis* n. sp., le premier enregistrement fossile présumé des cichlidés *Astronotus* et *Cichla*, le premier rapport pour la région du poisson-chat épineux *Oxydoras*, et des commentaires taxonomiques sur certains taxons précédemment rapportés pour cette unité stratigraphique. Avec une paléodiversité représentée provisoirement par au moins 23 taxons de chondrichtyens et de poissons osseux, le groupe Honda préserve l'une des faunes de poissons d'eau douce du Miocène les plus diversifiées connues à ce jour dans les pays néotropicaux. Les affinités taxonomiques et biogéographiques de l'assemblage de poissons fossiles, avec les taxons existants dans les systèmes fluviaux de l'Orénoque et de l'Amazonas, soutiennent les hypothèses de drainages s'écoulant de l'Amazonie occidentale vers la mer proto-caribéenne. Cet assemblage de poissons du Miocène moyen offre également des preuves significatives de l'histoire évolutive des poissons d'eau douce néotropicaux et des environnements anciens.

MOTS CLÉS
Nord-ouest de
l'Amérique du Sud,
Néogène,
Néotropiques,
raies,
poissons osseux,
systèmes hydrographiques
Orinoco-Amazonas,
espèce nouvelle.

RESUMEN
Nuevas evidencias sobre la paleodiversidad de la ictiofauna de agua dulce del Mioceno medio del desierto de la Tatacoa, Colombia.
Las rocas del Mioceno medio del Grupo Honda (formaciones La Victoria y Villavieja) en el Desierto de la Tatacoa, Valle Superior del Río Magdalena, Colombia, poseen una de las faunas continentales mejor estudiadas del Neotrópico, con edades comprendidas entre 16 y *c.* 10,5 Ma. El registro fósil de la región muestra una alta diversidad de peces, cocodrilos, serpientes, lagartos, tortugas y mamíferos acuáticos/terrestres. Aquí presentamos una nueva visión general de la paleodiversidad de peces de agua dulce y su contexto bioestratigráfico. Los nuevos datos incluyen la descripción de un nuevo bagre fósil †*Sciades maldonadonis* n. sp., el primer registro fósil de los cíclidos *Astronotus* y *Cichla*, el primer reporte para la región del bagre espinoso *Oxydoras*, como también comentarios taxonómicos sobre algunos taxones reportados previamente para esta unidad estratigráfica. Con una paleodiversidad representada tentativamente por unos 23 taxones de condrictios y peces óseos, el Grupo Honda conserva una de las faunas de peces de agua dulce más diversa conocida hasta ahora para el Mioceno del Neotrópico. Las afinidades taxonómicas y biogeográficas del conjunto de peces fósiles, con taxones existentes en los sistemas de los ríos Orinoco y Amazonas, sustentan las hipótesis de drenajes que fluyeron desde la Amazonía occidental hacia el proto-caribe. Este conjunto de peces del Mioceno medio también ofrece evidencia significativa de la historia evolutiva de los peces de agua dulce neotropicales y los ambientes antiguos.

PALABRAS CLAVE
Noroeste de América
del Sur,
Neógeno,
Neotrópico,
rayas,
peces óseos,
sistemas hidrográficos,
Orinoco-Amazonas,
nuevas especies.

INTRODUCTION

A wide range of fossil fishes, reptiles, amphibians, and aquatic mammals found in Miocene deposits from trans-Andean basins (west of the Andes) of Colombia and Venezuela (Kay *et al.* 1997; Aguilera 2004; Hsiou & Albino 2010; Lundberg *et al.* 2010; Sánchez-Villagra *et al.* 2010; Scheyer *et al.* 2013, 2019; Cadena & Jaramillo 2015; Moreno-Bernal *et al.* 2016; Aguirre-Fernández *et al.* 2017; Delfino & Sánchez-Villagra 2018; Ballen & Moreno-Bernal 2019; Cadena *et al.* 2020; Ballen *et al.* 2021a, b, and references therein), have been relevant to sustain the hypotheses of ancient fluvial drainages from western Amazonia in the direction to the proto-Caribbean Sea (Díaz de Gamero 1996; Hoorn *et al.* 2010; Aguilera

et al. 2013a). Cessation or reduction of these hydrographic systems had occurred by the late Miocene-Pliocene, possibly related to major hydrographic events resulting from the Northern Andes uplift (Jaramillo *et al.* 2010; Mora *et al.* 2010; Scheyer *et al.* 2013; Albert *et al.* 2018; Jaramillo 2018). The new isolation between western Amazonia and its northern peripheral drainages flowing to the proto-Caribbean Sea, created habitat partitioning that drove range contraction in many freshwater faunal communities (Lundberg *et al.* 1998; Lundberg *et al.* 2010; Scheyer *et al.* 2013; Cadena *et al.* 2020, Carrillo-Briceño *et al.* 2021a). Freshwater fishes were possibly one of the most affected groups (Lundberg *et al.* 1998, 2010). Many extant freshwater fish taxa today restricted to the Orinoco/Amazonas River systems (cis-Andean drainages), and the

fossil record in some trans-Andean Miocene localities supports this hypothesis of habitat fragmentation (see Lundberg *et al.* 2010; Aguilera *et al.* 2013a; Ballen *et al.* 2021a, b, Carrillo-Briceño *et al.* 2021a). These Neogene trans-Andean localities with freshwater fish assemblages include the middle Miocene-Pliocene deposits of the Castilletes and Ware formations in the Guajira Peninsula (Aguilera *et al.* 2013a; Ballen *et al.* 2021a, b), and the Honda Group in the Upper Magdalena River Valley (Lundberg 1997, 2005; Ballen & Moreno-Bernal 2019) in Colombia, and the early Miocene Castillo Formation (Fm) (Dahdul 2004; Núñez-Flores *et al.* 2017), middle Miocene-Pliocene Urumaco sequence (Lundberg *et al.* 1988, 2010; Lundberg & Aguilera 2003, Aguilera 2004; Sabaj Pérez *et al.* 2007; Aguilera & Machado-Allison 2013; Aguilera *et al.* 2013a; Carrillo-Briceño *et al.* 2021a), and late Miocene Caujarao Fm (Carrillo-Briceño *et al.* 2018), in northwestern Venezuela. Despite this, the region's fossil record of freshwater fishes remains scarce compared to the enormous extant diversity present in both trans-Andean and cis-Andean basins (Rodríguez-Olarte *et al.* 2009, 2011; van der Sleen & Albert 2018). Taphonomic processes may be one bias that explains the differences in diversity between fossil and modern communities and, in many cases, limits identifications to only high taxonomic levels. In addition, sedimentary environments and the nature of the biological remains lend a bias towards large, dense, and heavy fish bones, teeth, scales, and spines being preserved compared to small and delicate ones (see Bogan & Agnolin 2020).

The middle Miocene rocks of the Honda Group include one of the best-studied Neotropical freshwater and continental fossil assemblages, with a wide diversity of fishes, crocodylians, snakes, lizards, turtles, and mammals (Kay *et al.* 1997; Carrillo *et al.* 2015; Cadena *et al.* 2019, 2020; Defler 2019; Mora-Rojas *et al.* 2023). Fossil fishes from the Honda Group rocks have been reported since the first half of the 20th century (e.g., Royo y Gómez 1945; Savage 1951; Hoffstetter 1971; Bondesio & Pascual 1977; Lundberg & Chernoff 1992; Lundberg 1997, 2005; Lundberg *et al.* 1986, 2010; Ballen & Moreno-Bernal 2019). With a palaeodiversity totaling over 20 taxa (see Ballen & Moreno-Bernal 2019), these rocks preserve one of the more complete Miocene freshwater fish assemblages known in the region. Here we present new additions to the freshwater fish palaeodiversity of the middle Miocene from the La Victoria and Villavieja formations (Honda Group), at the La Venta site in the Upper Magdalena River Valley, Colombia (Fig. 1). This contribution includes the description of a new fossil catfish species, the first report for the region of other siluriform and cichliform taxa, and taxonomical comments on some taxa previously reported in these geological units. We also report only a small fraction of the total fossils collected during our field activities, because we are giving priority to taxa that for now can be cataloged as new species and/or first fossil record for the region, although some taxa described previously (Lundberg 1997), are also here

taxonomically revised. We present a taxonomic list of the other fossil fish remains from the Honda Group currently under study (Table 1; Appendix 1). Due to the taxonomic and biogeographic affinities of the fish assemblage of the Honda Group with extant and fossil taxa from the Orinoco and Amazonas River systems, the new data offers significant evidence for the evolutionary history of Neotropical freshwater fishes and ancient environments.

MATERIAL AND METHODS

REFERRED MATERIAL
Beginning in 2009 we conducted fieldwork in the Tatacoa Desert (La Venta Site) in the Upper Magdalena River Valley (Colombia). We surface collected abundant fossil fish specimens from the middle Miocene La Victoria and Villavieja formations. We also reviewed previously collected fossil specimens from the region, housed in the paleontological collections of the Fundación Vigías del Patrimonio Paleontológico de la Tatacoa (VPPLT) housed at the Museo de Historia Natural La Tatacoa and the Museo de La Tormenta, Huila Department, Colombia, the Instituto Geológico Minero/Museo Geológico Nacional José Royo y Gómez (IGM), and the Departamento de Ciencias Biológicas y Administración, Universidad de Los Andes (ULA), both in Bogotá. The specimens from "IGM" correspond to the historical collection created by Dr Royo y Gómez in 1945, and some specimens collected during the Duke expeditions in the late 1980s. The authors (AV, JDCB, OA, KH) and other collaborators collected the specimens from "ULA" and "VPPLT" during several field expeditions between 2009 and 2019.

The total of the fossil freshwater fishes from the Honda Group deposited in the above institutions, correspond to approximately 700 cranial and postcranial elements recovered from at least 71 localities of the middle Miocene of the La Victoria and Villavieja formations (Fig. 1; Table 1; Appendix 1).

In Fig. 1B we placed 58 fossiliferous localities in the stratigraphic section (when it was possible to identify the stratigraphic position) of the 71 localities of the Honda Group that have provided fossil fish records. Appendix 1 and Appendix 2 include all referred localities. For Fig. 1B, we used the mapping of Montes *et al.* (2021) and the graphical correlations of Mora-Rojas *et al.* (2023) as references. Additionally, Appendix 2 includes the geographic coordinates and stratigraphic position of localities.

The 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), and Museu de Paleontologia da Universidade Federal do Acre], France [Muséum national d'Histoire naturelle, Paris (MNHN)], Switzerland [Natural History Museum of Basel (NMB);
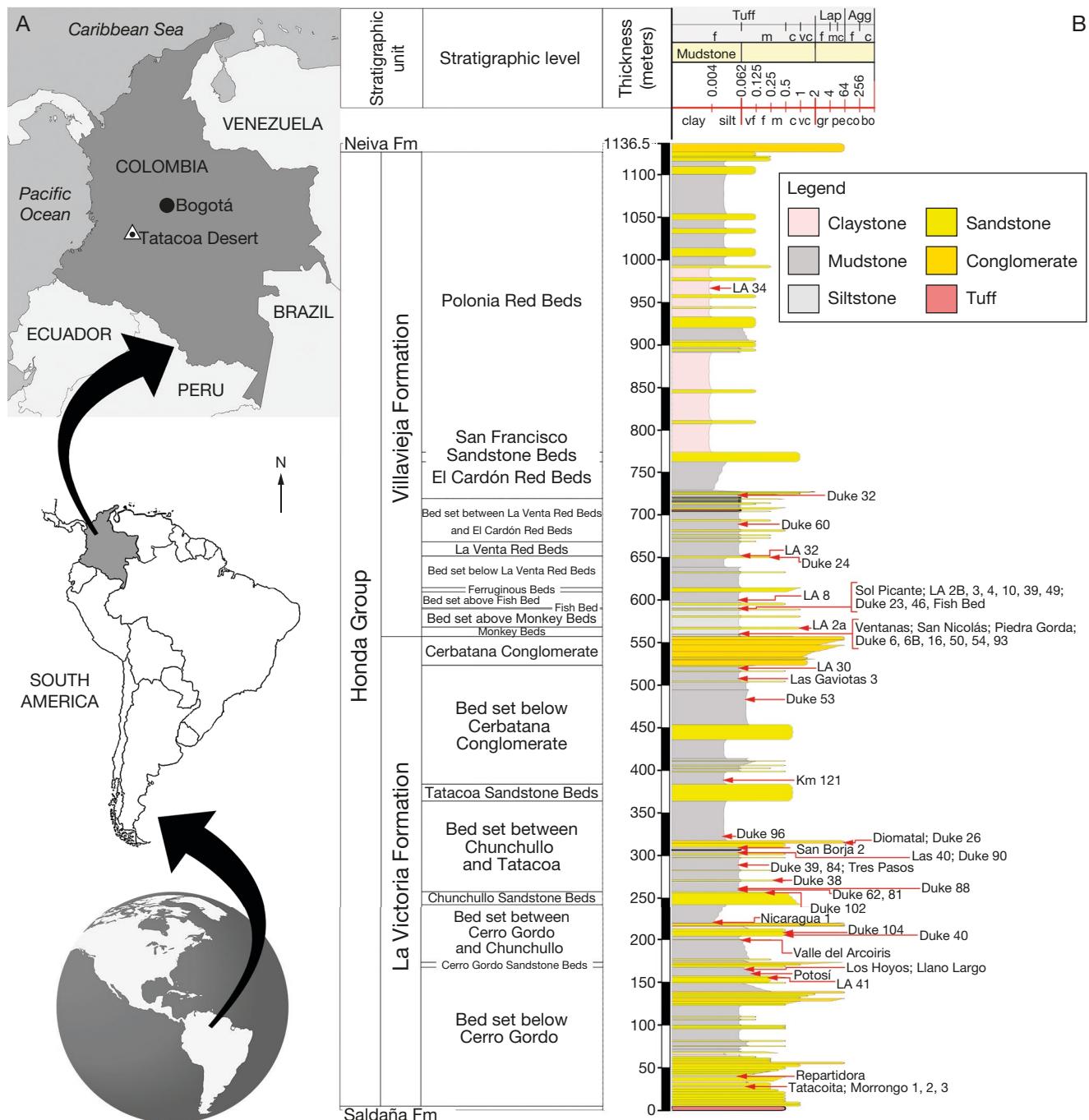
Fig. 1. — Geographical position (**A**) of the Honda Group's stratigraphic section (**B**) at La Venta site placed in the Upper Magdalena River Valley, Colombia. For details on the localities' geographic coordinates and stratigraphic position, please see Appendix 2.

Palaeontological Institute and Museum of the University of Zurich (PIMUZ)], USA [Academy of Natural Sciences of Drexel University, Philadelphia (ANSP)], and Venezuela [Universidad Experimental Francisco de Miranda (UNEFM); Museo de Ciencias de Caracas (MCNC); Museo de Biología de la Universidad del Zulia (MBLUZ); Museo de Historia Natural La Salle (MHNLS), Fundación La Salle de Ciencias Naturales, Caracas; Colección Paleontológica de la Alcaldía Bolivariana de Urumaco, Falcón State; Universidad Simón Bolívar (USB)].

GEOLOGICAL SETTING

The La Victoria Formation (younger than 16 Ma and older than 12.58 Ma) and Villavieja Formation (younger than 12.58 Ma and older than 10.52 Ma) constitute the Honda Group in the La Tatacoa area (Villarroel *et al.* 1996; Guerrero 1997; Montes *et al.* 2021; Mora-Rojas *et al.* 2023) (Fig. 1B). Mainly volcaniclastic sandstones and reddish-brown and greenish mudstones characterize the La Victoria Fm, with the mudstone layers very rich in fossil vertebrates (Guerrero 1997). Traditionally, the La

TABLE 1. — Fish palaeodiversity of the Honda Group: new reports (×), previous reports by Lundberg 1997 (×*) and Ballen & Moreno-Bernal 2019 (×**).

Higher ranking	Genus	Species	Honda Group La Victoria Fm	Villavieja Fm	indet. Fm
CHONDRICHTHYES					
Myliobatiformes			–	–	–
Potamotrygonidae	cf. *Potamotrygon*	sp.	×	×*	–
	Indet.	Indet.	×	×, ×*	–
OSTEICHTHYES					
Dipnoi					
Lepidosirenidae	*Lepidosiren*	*paradoxa*	×, ×*	×, ×*	–
Characiformes			–	–	–
Anostomidae	cf. *Leporinus*	sp.	×*	×*	–
Characidae	cf. Tetragonopterinae	indet.	–	×*	–
Erythrinidae	*Hoplias*	sp.	–	–	?×*
Cynodontidae	*Hydrolycus*	sp.	×*	×*	–
	cf. *Hydrolycus*	sp.	×	×	–
	indet.	indet.	–	–	×
Serrasalmidae	*Colossoma*	*macropomum*	–	×*	–
	?*Colossoma* or ?*Piaractus*	sp.	×	×	–
	?*Pristobrycon/Pygocentrus/Serrasalmus*	sp.	–	×*	–
Cichliformes			–	–	–
Cichlidae	cf. *Astronotus*	sp.	×	–	–
	cf. *Cichla*	sp.	×	–	–
	indet.	indet.	×	×*	–
Siluriformes			–	–	–
Ariidae	*Sciades*	†*maldonadonis* n. sp.	×	–	–
	indet.	indet.	–	×*	×
Callichthyidae	*Hoplosternum*	sp.	×, ×*	×*	–
	Indet. (Morphotype 1)	indet.	×	–	–
Doradidae	*Oxydoras*	sp.	–	×	–
	indet. (Morphotype 1)	sp.	×	×	–
	indet.	indet.	×	×*	–
Loricariidae	cf. *Acanthicus*	sp.	×	×, ×*	–
	cf. *Hypostomus*	sp.	×*	×*	–
	indet.	indet.	×	×, ×*	–
Pimelodidae	*Brachyplatystoma*	cf. *vaillantii*	–	×*	–
	Brachyplatystoma	†*promagdalena*	–	×*	–
	Brachyplatystoma	sp.	×, ×*	×, ×*	–
	Phractocephalus	sp.	×	×, ×*	–
	cf. *Pimelodus*	sp.	×	×, ×*	–
	indet.	indet.	×	–	–
Osteoglossiformes			–	–	–
Arapaimidae	*Arapaima*	sp.	–	×*	–
	indet.		×	×	–
incertae sedis					
†Acregoliathidae	†*Acregoliath*	*rancii*	×**	×	–
Osteichthyes indet.	indet.	indet.	×	–	–

Victoria Fm has been considered as a unit resulted from the accumulation of meandering rivers, except for the upper part (Stratigraphic level Cerbatana Conglomerate Beds), which resulted from the accumulation of braided streams influenced by debris flow events (Villarroel *et al.* 1996; Guerrero 1997; Mora-Rojas *et al.* 2023). However, for the base of the La Victoria Fm, recent studies suggest that sedimentary accumulation could occur in distal alluvial fan environments (Mora-Rojas *et al.* 2023). The overlaying Villavieja Fm is characterized by gray, green, and conspicuous red mudstones interbedded with volcaniclastic sandstones, accumulated in meandering streams and rivers (stratigraphic levels from Monkey Beds to San Francisco Sandstone Beds), which may coexist with lake or swamp deposits (e.g., Fish Bed stratigraphic level) (Villarroel *et al.* 1996; Guerrero 1997; Mora-Rojas *et al.* 2023). The upper portion of the Villavieja Fm includes the mudstones and sandstone beds from Polonia Red Beds, possibly accumulated in an anastomosed river (Villarroel *et al.* 1996; Guerrero 1997) (Appendix 2). Finally, upper contact from the Villavieja Fm represents a discordance with the overlying conglomeratic Neiva Formation (Guerrero 1997).

Flynn *et al.* (1997) suggested that the accumulation of the Honda Group could have happened between 13.5 and 11.6 Ma approximately (but see Guerrero 1997; Anderson *et al.* 2016). New dating samples extend the lapse, including an age from *c.* 16 to *c.* 10.5 Ma for the Honda Group (Mora-Rojas *et al.* 2023).

NEW REPORTS
AND TAXONOMICAL COMMENTS

Class CHONDRICHTHYES Huxley, 1880
Order MYLIOBATIFORMES Compagno, 1973
Family POTAMOTRYGONIDAE Garman, 1877
Genus *Potamotrygon* Garman, 1877

TYPE SPECIES. — *Trygon histrix* Müller & Henle, 1841 (type species by original designation; Garman 1877).

cf. *Potamotrygon* sp.
(Fig. 2A1, A2)

EXAMINED BODY PART. — Isolated teeth.

NOTES
Specimens figured by Lundberg 1997: fig. 5.1

Potamotrygonidae indet.
(Fig. 2B1-G2).

EXAMINED BODY PARTS. — Bucklers and caudal spines.

MATERIAL EXAMINED. — Museo de La Tormenta, two isolated teeth (VPPLT 10000, 10001); Museo de Historia Natural La Tatacoa, 13 isolated dermal bucklers (VPPLT-668, 805, 1226 [no. 2], 1239, 1245 [no. 2], 1415, 1440, 1444, 1452 [no. 2], 1481), and four isolated caudal spines (VPPLT-042, 1425, 1430, 1485).

LOCALITIES. — **La Victoria Fm.** Diomatal-Museo La Tormenta (VPPLT-1481, 1485); Morrongo 1 (VPPLT-1415, 1452), Morrongo 2: (VPPLT-805, 1226, 1239, 1245, 1430, 1440); Km-121 (VPPLT-042, 1425, 1444). — **Indeterminate Fm**. Santa Barbara 2 (VPPLT-668) (see Fig. 1; Appendix 1). The two isolated teeth (VPPLT 10000 and VPPLT 10001) do not have precise information about their locality (presumably Diomatal-Museo La Tormenta).

DESCRIPTION
The indeterminate potamotrygonid isolated teeth described and illustrated by Lundberg (1997: fig. 5.1), plus another group of teeth were observed but not photographed or described in detail by one of the authors (JDCB) during a visit to the Academy of Natural Sciences of Drexel University, Philadelphia (ANSP), where they are temporarily housed. A detailed description of at least five of the isolated teeth housed in the ANSP is presented by Lundberg (1997). Most of these specimens in the ANSP, as well as two other isolated teeth reported here from the Museo de La Tormenta (Fig. 2A1, A2), are smaller than 3 mm wide and are characterized by a crown that is higher than the root with a middle transverse crest that separates the labial and lingual sides. The labial side of the crown is coarsely ornamented in specimens that do not show a wear pattern. In some cuspidate teeth, the crest is lingually elongated and forms a distinctive triangular cusp. The root is a typical holaucorhize type with two rounded and basal flattened lobes (see Fig. 2A1-A2; Lundberg 1997: fig. 5.1).

The dermal bucklers are up to 3.5 mm in diameter and circular and semi-circular in shape (Fig. 2B1-F). Three specimens are fused

bucklers (up to 33 mm in length) of ovoidal/or irregular shape (e.g., Fig. 2C, E). The bucklers are characterized by an erected curved crown with a central and small tip. Abundant ridges and deep furrows from the base of the central tip to the basal edges of the buckler ornament the crown. In some specimens, abundant rounded and micro like-bucklers (up to 2 mm in diameter) are present in the crown (Fig. 2B1-B2, D-F). Of the four caudal spines, only two specimens are relatively complete (58 and 64 mm in length). All the caudal spines preserve their denticles at the lateral margins, the central ridge, and the central groove on the ventral and dorsal sides, respectively (Fig. 2G1-G2).

REMARKS
The only previous reports of stingrays from the Honda Group include the few isolated teeth (from the Fish Bed layer) and the fragmented caudal spines reported as indeterminate potamotrygonids by Lundberg (1997). The teeth described by Lundberg (1997), and the two isolated teeth reported here (Fig. 2A1-A2), have morphological features that more closely resemble those teeth of the extant and fossil *Potamotrygon* species than other genera within the Potamotrygonidae (see Adnet *et al.* 2014; Carrillo-Briceño *et al.* 2021a). It is best to assign these specimens from the Honda Group to cf. *Potamotrygon*, and we believe that new specimens and future detailed studies are necessary for more accurate taxonomic assignments.

The preservation of the caudal spines does not allow an assignment beyond Potamotrygonidae. The dermal bucklers are recorded here for the first time from the Honda Group. These dermal bucklers are similar in size and morphology to those of fossil potamotrygonids from the late Miocene of Argentina and Brazil (Brito & Deynat 2004), as well as some extant *Potamotrygon* species (Deynat & Brito 1994). In accordance with Brito & Deynat (2004), we believe that the dermal bucklers from the Honda Group can be tentatively identified as indeterminate potamotrygonids; although the chances that these belong to *Potamotrygon* are very high (see Deynat & Brito 1994). Still there is poor knowledge of the broader dermal elements and dental patterns among the more than 35 potamotrygonid species (four genera) from different South American river basins. These stingrays inhabit a wide range of environments, including lakes, still waters, and flowing rivers, commonly associated on sandy substrates (Lasso *et al.* 2014; van der Sleen & Albert 2018).

Class ACTINOPTERI Cope, 1871

REMARKS
For nomenclature priority of Actinopteri instead of Actinopterygii Klein, 1885, see Schwarzhans *et al.* 2020.

Order CICHLIFORMES Betancur-R *et al.*, 2013
Family CICHLIDAE Bonaparte, 1835
Genus *Astronotus* Swainson, 1839

TYPE SPECIES. — *Lobotes ocellatus* Agassiz, 1831 (type species by original designation; Swainson 1839).

FIG. 2. — Stingrays (**A1**-**G2**) and cichlids (**H1**-**L2**) from the Honda Group: **A1, A2**, cf. *Potamotrygon* sp. tooth (VPPLT 10000); **B1**-**F**, isolated dermal bucklers; **B1, B2**, VPPLT-1415; **C, E**, VPPLT-1245; **D**, VPPLT-1126; **F**, VPPLT-1239; **G1, G2**, isolated caudal spines (VPPLT-42) of Potamotrygonidae indet.; **H1**-**H4**, left dentary of cf. *Astronotus* sp. (VPPLT-668A); **I1, I2**, left dentary of the extant *Astronotus ocellatus* (Agassiz, 1831) (ANSP s/n); **J1**-**J3**, left dentary of cf. *Cichla* sp. (VPPLT-668B); **K1**-**K3**, left dentary of the extant *Cichla* Bloch & Schneider, 1801 (PIMUZ A/I 4897); **L1, L2**, indet. cichlid anal spine (VPPLT-1164). Views: **L1**, anterior; **B, C**-**G1, H3, I2, J3, K3**, dorsal; **A1**, labial; **A2**, lingual-lateral; **H1, I1, J2, K1**-**K2**, left lateral; **L2**, lateral; **B2**, profile; **H4, J1**, right lateral; **G2, H2**, ventral. Scale bars: A, 0.5 mm; B, 1 cm; C, E, I1, J, K2, 5 mm; D, H, 7 mm; F, K1, L, 6 mm; G, K3, 4 mm; I2, 3 mm.

cf. *Astronotus* sp.
(Fig. 2H1-H4).

MATERIAL EXAMINED. — Isolated dentary bone (VPPLT-668A)

LOCALITY. — **La Victoria Fm**. Tatacoita (see Fig. 1B; Appendix 1).

DESCRIPTION
VPPLT-668A is a short and high left dentary bone, 22 mm in length and missing the posterior part of the mandibular sensory canal and the coronoid process (Fig. 2H1-H4). The dorsal margin is well preserved, but all teeth are missing. There are approximately six circular tooth implantation rows, with the first three from the outer border best defined (Fig. 2H3). Enlarged bases characterize the outer tooth row, reaching up to twice the diameter of those bases of the other inner rows. The external face of the dentary has three well-developed foramina on the bony mandibular canal. The largest one is oval in shape (Fig. 2H1) and corresponds with the foramen "f.5" referred by Casciotta & Arratia (1993). In the ventral section of the dentary, abundant small foramina can be observed.

REMARKS
Our comparison (based on osteological collections and literature review) suggests that VPPLT-668A is clearly different from other medium/large sizes South American cichlids such as *Acaronia* Myers, 1940, *Aequidens* Eigenmann & Bray, 1894, *Caquetaia* Fowler, 1945, *Cichla* Bloch & Schneider, 1801, *Cichlasoma* Swainson, 1839, *Crenicichla* Heckel, 1840, *Geophagus* Heckel, 1840, *Retroculus* Eigenmann & Bray, 1894, *Satanoperca* Günther, 1862, *Symphysodon* Heckel, 1840, and *Uaru* Heckel, 1840. The dentary shape and the pattern and size of the tooth implantation rows in VPPLT-668A resemble the jaw morphology of *Astronotus* (see Fig. 2I1-I2). These are features that are "apparently" observed only in this genus; although this should be confirmed in the future with more detailed studies on cranial elements of the South American cichlids. Our osteological comparisons with specimens of *Astronotus* were restricted to *Astronotus ocellatus* (Agassiz, 1831). The genus *Astronotus* is represented by three extant species, *Astronotus ocellatus*, *Astronotus crassipinnis* (Heckel, 1840), and *Astronotus mikoljii* (Pérez-Lozano *et al.* 2022). The natural distribution of *Astronotus* includes the Amazon, Orinoco, upper Paraná, and French Guiana basins (Pérez-Lozano *et al.* 2022), with habitat preference of quiet shallow waters (van der Sleen & Albert 2018). Due to the state of preservation of VPPLT-668A, and the absence of more specimens with other diagnostic characters, we are unable to classify this fossil beyond cf. *Astronotus* sp. The presence of cf. *Astronotus* in the middle Miocene of the Honda Group represents the first fossil record for the genus.

Neotropical cichlids, with at least 44 genera, constitute the third most speciose group of freshwater fishes in South America (van der Sleen & Albert 2018). Despite the high species richness, few studies based on comparative descriptions of cranial elements (e.g., dentaries, maxillary, and premaxillary bones) have been carried out (e.g., Casciotta & Arratia 1993). One of the problems added to the study of isolated fossil cichlid dentaries is that the morphology of dentary bone is similar among Neotropical cichlids (Casciotta & Arratia 1993). Nevertheless, morphological features can allow some tentative assignments as long as the comparisons are supported by diversity in comparative osteological material.

Genus *Cichla* Bloch & Schneider, 1801

TYPE SPECIES. — *Cichla ocellaris* Bloch & Schneider, 1801 (type species by original designation).

cf. *Cichla* sp.
(Fig. 2J1-J3).

MATERIAL EXAMINED. — Isolated dentary bone (VPPLT-668B).

LOCALITY. — **La Victoria Fm**. Tatacoita (see Fig. 1B; Appendix 1).

DESCRIPTION
VPPLT-668B is an incomplete dentary bone of 16 mm in length, missing the posterior part of the mandibular sensory canal and the coronoid process (Fig. 2J1-J2). The external face of the dentary preserves four well-developed foramina on the bony mandibular canal, the two smallest being located close to the dentary symphysis. All teeth are missing, and the preserved dorsal margin is characterized by six to seven circular tooth implantations rows of small size.

REMARKS
VPPLT-668B is easily distinguishable from VPPLT-668A assigned to cf. *Astronotus*. Our osteological comparisons suggest a close resemblance between VPPLT-668B and the dentaries of extant *Cichla* species (Fig. 2K1-K3) than with those of *Crenicichla* or other medium/large sizes South American cichlids. Although VPPLT-668B is incomplete, its dentary shape and the pattern and size of the tooth implantations rows resemble the jaw morphology of *Cichla* species. However, due to the state of preservation of VPPLT-668B and the absence of more specimens, for now, we prefer to refer to this fossil as cf. *Cichla* sp. The genus *Cichla*, contains the largest cichlid of South America, and is represented by at least 15 species from the Amazon and Orinoco basins, as well as rivers of the Guianas (Froese & Pauly 2022). The extant species have a wide range of habitat preferences, including rivers and floodplain lakes (van der Sleen & Albert 2018). The presence of cf. *Cichla* in the middle Miocene of the Honda Group represents the first fossil record for the genus.

From the Honda Group, Lundberg (1997) reported three premaxillaries, three dentaries, and two anguloarticular bones in fragmentary condition as indeterminate cichlids from the Fish Bed locality, suggesting a lack of morphological characters and relation to modern cichlids. Future work with more detailed anatomical comparisons on the specimens that Lundberg (1997) reported could support or contrast these assignments. Other new cichlid material reported herein includes an isolated anal spine (VPPLT-1164) coming from the Km 121 locality (Appendix 1). The spine is 18 mm in

length, robust and elongated, with a sharp end at the apical section, and typical of the anal region (Fig. 2L1-L2); nevertheless, taxonomic identification based on isolated spines is not possible.

Order SILURIFORMES *sensu* Grande (1987)
Family Ariidae *Bleeker*, 1862a

Genus *Sciades* Müller & Troschel, 1849

Type species. — *Sciades emphysetus* Müller & Troschel, 1849 (type species by original designation).

†*Sciades maldonadonis* n. sp.
(Fig. 3A1-A3)

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Diagnosis. — The combination of extremely depressed lapillus otolith, regularly clam-shaped outline, sharp antero-medial projection, strongly arched dorsal margin anteriorly and oblique-straight posteriorly distinguish †*Sciades maldonadonis* n. sp. from extant *Sciades* species, extinct brackish and freshwater species (e.g., †*Cantarius* Aguilera *et al.*, 2013b), and extant South American freshwater species (*Chinchaysuyoa* Marceniuk *et al.*, 2019a, and *Paragenidens* Marceniuk *et al.*, 2019a).

Type material. — Holotype VPPLT-832. A complete lapillus otolith (Fig. 3A1-A3), preserved length 20.94 mm, width 16.84 mm, thickness 7.08 mm.

Type locality. — **La Victoria Fm**. Morrongo 1 (see Fig. 1B; Appendix 1).

Derivation of name. — The species is named in honor of Dr Javier Alejandro Maldonado-Ocampo (1977-†2019), renowned Colombian ichthyologist who passed away on 2 March 2019 during an expedition to the Río Vaupés in Colombia. Javier dedicated more than twenty years to the study and conservation of the freshwater fish fauna of Colombia, including the Andes, Orinoco and Amazon basins.

Description
The lapillus otolith is clam-shaped with a semi-circular outline, very depressed dorso-ventrally, and with a sharp antero-medial projection (Fig. 3A1, A2). The dorsal margin is strongly arched anteriorly and oblique-straight posteriorly. The ventral margin is strongly arched. The posterior margin forms an obtuse angle. The lateral profile is slightly biconvex. The pseudocauda and the mesial inward curvature are not well preserved. The umbo is located in the center of the dorsal surface. The lapillus length to width ratio: 1.2. Lapillus length to thickness ratio: 3.0.

Remarks
VPPLT-832 is characterized by a typical Ariidae otolith morphology. The recognition of †*Sciades maldonadonis* n. sp. as a member of *Sciades* is based on its otolith morphology, which is characterized by the combination of extremely depressed dorso-ventral shape and by the dorsal margin being strongly arched anteriorly, and oblique-straight posteriorly. This allows it to be differentiated from the other *Sciades* species (for comparative proposes see Aguilera *et al.* 2020: figs. 4.49-4.60; 6.9-6.12).

Marceniuk *et al.* (2017) reviewed the genus *Sciades* and showed a strong morphological relationship between nominal genera *Sciades* and *Ariopsis* Gill, 1861. More than seven extant *Sciades* species are currently recognized (Froese & Pauly 2022). The age of diversification of modern species of *Sciades* is older than 9 Ma (including *Sciades dowii* Gill, 1863, from the Pacific), and the age of the Atlantic *Sciades* species is *c.* 6.7 Ma (4-8 Ma) (Betancur-R. 2009). †*Sciades maldonadonis* n. sp. came from a freshwater palaeoenvironment in the middle Miocene rocks of the Honda Group, associated with a wide diversity of freshwater fishes, crocodylians, snakes, lizards, turtles, and mammals (e.g., Kay *et al.* 1997; Carrillo *et al.* 2015; Cadena *et al.* 2019, 2020; Defler 2019). The ancestral form of freshwater catfish Ariidae otolith-based species from the western Amazon included †*Cantarius nolfi* Aguilera, Moraes-Santos, Costa, Ohe, Jaramillo & Nogueira, 2013b, and †*Cantarius ohei* Schwarzhans, Aguilera, Scheyer & Carrillo-Briceño, 2022, recorded from the Miocene Pebas wetland system at the Pebas Formation (Carrillo-Briceño *et al.* 2021b; Schwarzhans *et al.* 2022). In North, Central, and South America, six extant ariid species are primarily freshwater, including *Chinchaysuyoa labiata* Boulenger, 1898, *Chinchaysuyoa ortegai* Marceniuk, Marchena, Oliveira & Betancur-R, 2019a, *Paragenidens grandoculis* Steindachner, 1877, *Paragenidens nelsoni* Evermann & Goldsborough, 1902, *Paragenidens izabalensis* Hubbs & Miller, 1960, and *Paragenidens usumacintae* Betancur-R & Willink, 2007 (Marceniuk & Menezes 2007; Marceniuk *et al.* 2019a, b). On the other hand, fossil skull-based species of †*Sciades latissimum* Aguilera & Marceniuk, 2018, and †*Sciades peregrinus* Aguilera & Marceniuk, 2018 without preserved internal otolith, were described from the late Miocene Urumaco Fm, Venezuela, characterized by palaeoenvironments associated to a large palaeo-hydrographic system of the Orinoco/Amazonas discharging into the proto-Caribbean Sea (Aguilera *et al.* 2020).

Other ariid remains from the Honda Group include two isolated dorsal-spine fragments ornamented by rugose tuberculations, from the Duke 24 (see Lundberg 1997) and Mini Desierto localities (VPPLT-1108; Figs 1B, 3B1-B3). Sedimentary characteristics and the associated fauna from the Honda Group support that VPPLT-832 and the indeterminate ariid spines were from a freshwater palaeoenvironment.

Family Doradidae Bleeker, 1858
Genus *Oxydoras* Kner, 1855

Type species. — *Oxydoras kneri* Bleeker, 1862a (type species by original designation).

Oxydoras sp.
(Fig. 3C1-C3).

Material examined. — Incomplete neurocranium (ULA-1316).

Locality. — **Villavieja Fm**. LA-3 (fish bed) (see Fig. 1B; Appendix 1).

DESCRIPTION

ULA-1316 is an incomplete neurocranium of 51 mm in length, preserving only the anterior section of the skull (Fig. 3C1-C3), and is assigned here to *Oxydoras*. It preserves a complete mesethmoid bone clearly observable in both dorsal and ventral views. It has an elongate arrow-shape with a bifid anterior tip, and a convex profile in lateral view (Fig. 3C1). In dorsal view, the anterior section of both right and left frontals and both right and left lateral ethmoids are articulated to the mesethmoid; the most proximal section of the anterior cranial fontanelle is also preserved (Fig. 3C1). The ornamentation of the skull is not well defined, possibly as a result of erosion. In ventral view, the mesethmoid, vomer, remnants of what appear to be lateral ethmoids, and the parasphenoid are preserved (Fig. 3C2). The vomer has an arrow-shaped anterior section and seems to have reduced anterolateral processes; its posterior section is elongated and narrow, being enclosed in the anterior bifid tip of the parasphenoid.

REMARKS

ULA-1316 possess a mesethmoid bone similar to those present in living and fossil representatives of *Oxydoras*, which can be differentiated from the mesethmoid bones of any other living (Birindelli 2014) or fossil (see Lundberg *et al.* 2010) species of doradid. The thorny catfish *Oxydoras* is represented by three extant species, *Oxydoras niger* (Valenciennes *in* Humboldt & Valenciennes, 1821), *Oxydoras kneri* Bleeker, 1862a, and *Oxydoras sifontesi* Fernández-Yépez, 1968, from the Amazon, Essequibo, Orinoco and Paraná basins. These species occur over mud in streams and lakes, but are also present in large rivers (Froese & Pauly 2022). The only fossil of *Oxydoras* known to date corresponds to an isolated mesethmoid bone from the Miocene of Peru illustrated by Lundberg *et al.* (2010). Although ULA-1316 resembles the skull of the extant *O. niger* (see Birindelli 2014; Prestes-Carneiro *et al.* 2019), and/or the other two living species *O. kneri* and *O. sifontesi*, its incomplete and poor state of preservation make it difficult to associate this fossil specimen with any of these extant species. The skulls of the extant species of *Oxydoras* usually present well-defined ornamentation (see Birindelli 2014: fig. 25); in the case of ULA-1316, the ornamentation pattern is not well-defined or is absent, possibly as a consequence associated with taphonomic processes or erosion of the fossil during its exposure in the outcrop. Due to that, ULA-1316 is tentatively assigned to *Oxydoras* sp. This fossil specimen from the middle Miocene of the Honda Group, and the isolated mesethmoid bone from the Miocene (Lundberg *et al.* 2010), are to date the only known fossils of *Oxydoras*.

Family PIMELODIDAE *sensu* Lundberg & Littmann (2003)

Genus *Phractocephalus* Agassiz, 1829

TYPE SPECIES. — *Phractocephalus bicolor* Agassiz, 1829, by monotypy, a junior objective synonym of *Silurus hemioliopterus* Bloch & Schneider, 1801.

Phractocephalus sp.
(Fig. 3D-M).

MATERIAL EXAMINED. — Fourteen skull fragments (IGM-87-314, -2221-f-a, -2382-b (no. 2), and VPPLT-223, 421(no. 2), 422 (no. 2), 742, 1128, 1272, 1282, 1432); a pectoral girdle (IGM-s/n), and 12 pectoral/dorsal fragmented spines (IGM-2285-c, ULA-44, and VPPLT-043 (no. 4), 417, 473, 474, 1092, 1478, 1482).

LOCALITIES. — **La Victoria Fm**. Diomatal-Museo La Tormenta (VPPLT-1478, 1-482); Km-121 (VPPLT-043, 223, 742, 1128, 1432); Tatacoita (VPPLT-417, 421, 422, 470, 473, 474, 1092); San Nicolás (VPPLT-1272, 1282). — **Villavieja Fm**. Duke 46 (IGM-87-314); LA 2 (ULA-44). — **Indeterminate Fm**. Alrededor del Campamento de la Venta, Villa vieja (IGM-2382-h); Norte del Punto 16 (IGM-2221-h-a); NW del Campamento de la Venta, Villavieja (IGM-2285-c) (see Fig. 1B; Appendix 1).

DESCRIPTION

The dorsal surface of the skull, including the sphenotic, pterotic, and parieto-supraoccipital bones, has well-developed dorsal ornamentation characterized by dense, deep, and rounded pits surrounded by a thick and tall crest arranged in a mosaic (Fig. 3D-I). The ornamentation in the frontal and the parieto-supraoccipital bones are characterized by elongated and parallel pits delimited by a stronger crest. These ornamentation patterns of elongated and parallel pits, gutter-like, are slightly interrupted at the middle part by changes in the ornamentation pattern that consist of disperse oval pits (Fig. 3D). The postero-lateral laminar projections of the parieto-supraoccipital bone form a thick and strong arch on both sides. The external surface is densely ornamented with small pits irregularly arranged. However, the entire bone expansion is not complete, and the distal smooth edge is not preserved (Fig. 3E-F). The ornamentation on the pterotic bone shows a pattern of parallel alignment of the pits. The largest pits are arranged in the medial region, and the minor ones are aligned in the outermost region of the bone (Fig. 3G). The sphenotic has a stronger anastomosing ridge on the dorsal surface (Fig. 3H). The pectoral girdle is robust with the posterior process of the cleithrum expanded in a thick laminar bone in a triangular-shape. The outer surface is densely ornamented with a series of

FIG. 3. — Siluriforms from the Honda Group: **A1-A3**, complete lapillus otolith (Holotype) of †*Sciades maldonadonis* n. sp. (VPPLT-832) from the Honda Group. **B1-B3**, dorsal spine fragment of Ariidae indet. (VPPLT-1108); **C1-C3**, incomplete neurocranium of *Oxydoras* sp. (ULA-1316); **D-M**, *Phractocephalus* sp.; **D**, parieto-supraoccipital frontal fragment (VPPLT-1272); **E**, **F**, parieto-supraoccipital bone fragments; **E**, VPPLT-1128; **F**, VPPLT-223; **G**, pterotic fragment (VPPLT-442); **H**, sphenotic fragment, VPPLT-421; **I**, indeterminate fragments, VPPLT-742; **J**, right pectoral girdle (IGM-s/n°); **K-M**, pectoral spines fragments; **K**, **M**, VPPLT-043; **L**, ULA-44; **N-P**, *Hoplosternum* sp.; **N**, **O**, parieto-supraoccipital; **N**, VPPLT-1453; **O**, ULA-829; **P**, left pectoral-fin spine, VPPLT-1250; **Q-T**, Doradidae indet.; **Q**, **R**, parieto-supraoccipital; **Q**, VPPLT-921; **R**, ULA-2997; **S**, **T**, fragmented pectoral-fin spines; **S**, VPPLT-43; **T**, VPPLT-1442; **U1**, **U2**, cf. *Acanthicus* sp., pectoral-fin spine, VPPLT-469; **V1**, **V2**, cf. *Hypostomus* sp., left pectoral-fin spine, VPPLT-504; **W**, **X**, Loricariidae indet.; **W**, skull fragment, VPPLT-1375; **X**, portion of a caudal fin, ULA-2413. Views: **B1**, **U1**, **V2**, anterior; **C1**, **D-I**, **N-R**, **V1**, dorsal; **A1**, dorsal face; **C3**, left lateral; **A3**, **X**, lateral; **B2**, **U2**, posterior; **B3**, **J**, right lateral; **C2**, ventral; **A2**, ventral face; **K-M**, **S-T**, **W**, indet. Abbreviations: **acf**, anterior cranial fontanel; **ad**, anterior dentations; **adp-cl**, anterior dorsal process of
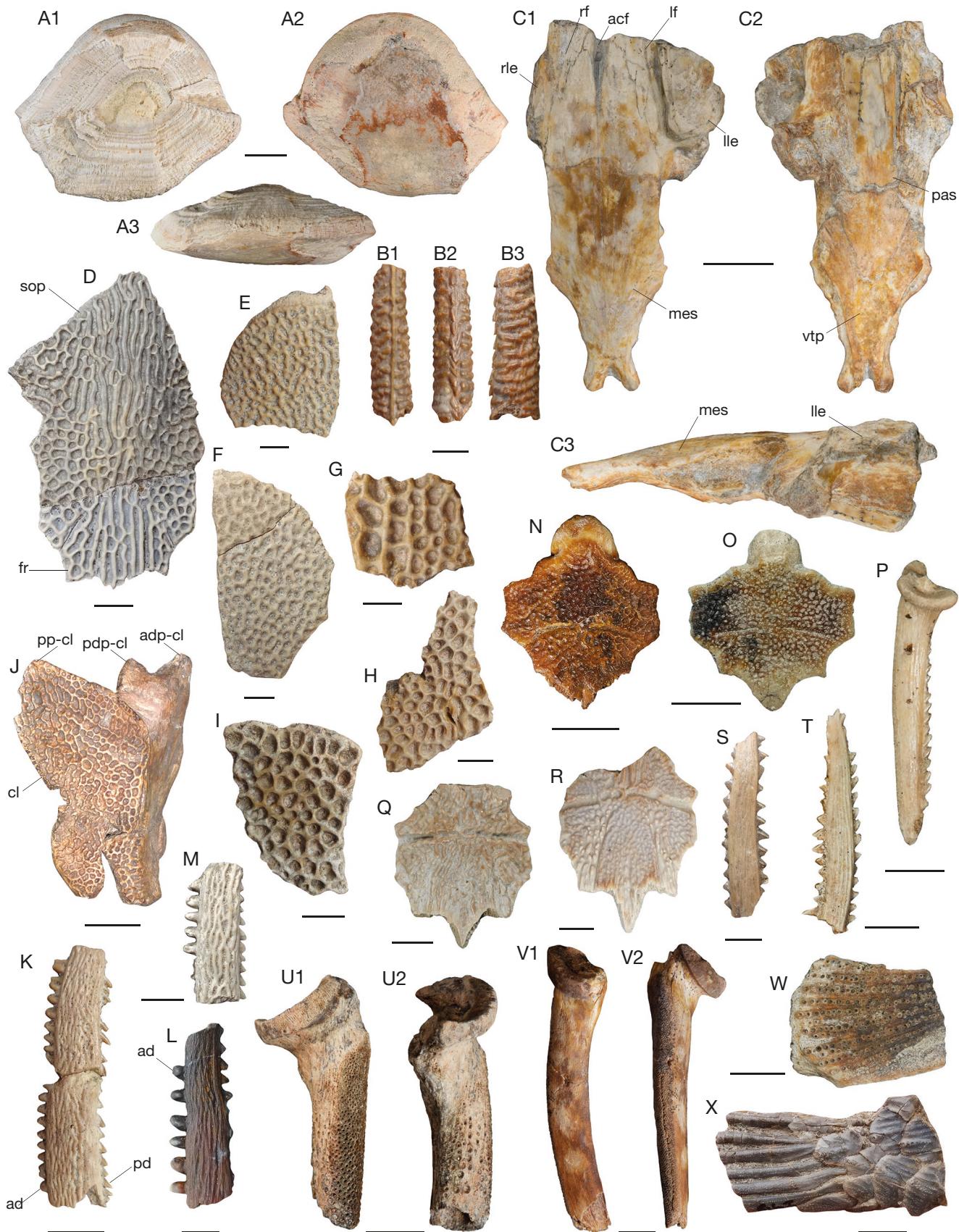
cleithrum; **cl**, cleithrum; **fr**, frontal; **lf**, left frontal; **lle**, left lateral ethmoid; **mes**, mesethmoid; **pas**, parasphenoid; **pd**, posterior dentations; **pdp-cl**, posterior dorsal process of cleithrum; **pp-cl**, posterior process of cleithrum; **rf**, right frontal; **rle**, right lateral ethmoid; **sop**, parieto-supraoccipital; **vtp**, vomeral tooth plate. Scale bars: A, N, V, 6 mm; B, E, F, L, O, Q-S, W, X, 5 mm; C, D, H, I, K, 10 mm; G, 7 mm; J, 20 mm; M, 8 mm; P, 3 mm; T, 4 mm; U, 9 mm.

pits arranged in oblique rows in most of the upper area, and pits in a random distribution on the lower area. Both, the anterior dorsal process and posterior dorsal process of the cleithrum are robust (Fig. 3J). The ornamentation in the pectoral spines form elongated, crossed and irregular crest without rounded or ovoid pits. The anterior edge has small acute spines oriented posteriorly and on the posterior edge the small spines are robust, and obtuse without a well-defined orientation (Fig. 3K-M).

REMARKS
Phractocephalus is represented by the single extant species *P. hemioliopterus*. The fossil record of the genus includes †*Phractocephalus nassi* Lundberg & Aguilera, 2003, from the late Miocene Urumaco Fm in Venezuela, †*Phractocephalus acreornatus* Aguilera *et al.*, 2008, from the late Miocene Solimões Fm in Brazil, and †*Phractocephalus yaguaron* Bogan & Agnolin, 2019, from late Miocene Ituzaingó Formation, Argentina. †*Phractocephalus ivy* Azpelicueta & Cione, 2016, from late the Miocene of Argentina was recently referred to the extant genus *Steindachneridion* Eigenmann & Eigenmann, 1919 (see Bogan & Agnolín 2019). The skull bones of *Phractocephalus* from the Honda Group can be distinguished from those of extinct species by the stronger ornamentation pattern, density, and depth of the circular pits surrounded by thick crest arranged in a mosaic-like pattern vs. less skull ornamentation in †*P. acreornatus* and †*P. nassi*. Skull bones in †*P. yaguaron* are strongly ornamented with reticulating ridges and subcircular pits (see Azpelicueta & Cione 2016; Bogan & Agnolín 2019), a pattern that is relatively different from the specimens from the Honda Group, where ornamentation, especially in frontal and the parieto-supraoccipital bones, show continuous elongated and parallel pits (see Fig. 3D-F). Lundberg (1997) described a partial mesethmoid bone and a fragmented pectoral-spine (Lundberg 1997: fig. 5.9A) from the Fish Bed locality as extant *P. hemioliopterus*; nevertheless, these materials were later referred to as too incomplete to assess their species status (Lundberg & Aguilera 2003). The ornamental pattern on specimens from the Honda Group shows clear differences from the skull ornamentation in the extant *P. hemioliopterus* (e.g., see skulls illustrated in Lundberg & Aguilera 2003; Aguilera *et al.* 2008; Bogan & Agnolín 2019). Based on the skull and pectoral/dorsal spine ornamentation, the *Phractocephalus* specimens from the Honda group is most closely related to †*P. nassi*. Nevertheless, by the fragmentary conditions of bones and the absence of well-preserved diagnostic elements to support an accurate diagnosis and description, we tentatively use an open nomenclature for the *Phractocephalus* specimens from the Honda Group.

Phractocephalus hemioliopterus occurs in a broad range of habitats, from large rivers to flooded forests and lakes, with a wide distribution in the Orinoco and the Amazon (van der Sleen & Albert 2018). Recently, a reticulate nuchal plate attributed to *Phractocephalus* sp. was recorded from the middle Miocene Castilletes Formation in the Guajira Peninsula, northern Colombia (Ballen *et al.* 2021a), and

this report, together with the other fossil *Phractocephalus* from northwestern Venezuela (Lundberg & Aguilera 2003) suggests a broader distribution of the genus during the Miocene and support ancient connections between trans-Andean and cis-Andean drainages.

Other siluriforms taxa reported herein (Table 1) and in previous works (e.g., Lundberg 1997, 2005) for the Honda Group include *Hoplosternum* Gill, 1858 (Fig. 3N-P), the loricariids cf. *Acanthicus* Agassiz, 1829 (Fig. 3U1-U2), and cf. *Hypostomus* Lacépède, 1803 (Fig. 3V1-V2), and the pimelodids *Brachyplatystoma* (Fig. 4A1-B2), and *Pimelodus* Lacépède, 1803 (Fig. 4C). The goliath catfish †*Brachyplatystoma promagdalena* Lundberg, 2005, was described from the Fish Bed layer. Tentatively we designate the siluriforms as the most diverse fish group of the Honda Group (Fig. 5). Other bony fishes reported from the Honda Group (see Table 1) includes cynodontids or "dogtooth characins" (Fig. 4E1-F2), "piranha-like" and "pacu" serrasalmids (Fig. 4G1-M), dipnoids (Fig. 4D1-D2), and osteoglossiforms (Fig. 4N1-N2).

DISCUSSION AND CONCLUSIONS

The fishes reported here from the Honda Group tentatively includes at least 23 taxa of chondrichthyans and bony fishes (see Table 1; Figs 5, 6; also see Ballen & Moreno-Bernal 2019, fig. 2). Chondrichthyans are the least diverse fish group from the Honda Group, represented exclusively by a single taxon of the stingray cf. *Potamotrygon*. In contrast, bony fishes, with a minimum of 22 taxa (fourteen families) of dipnoids, characiforms, cichlids, siluriforms, and osteoglossiforms (Table 1), represent the most diverse group of fishes in the sequence (see Fig. 5). Catfishes are well recorded throughout the entire stratigraphic sequence of the La Victoria and Villavieja formations (Appendix 1; Fig. 6). The presence of †*Sciades maldonadonis* n. sp., *Oxydoras* sp. and two taxa under study of armored (indet. callichthyid as Morphotype 1, Table 1) and thorny catfishes (indet. doradid as Morphotype 1, Table 1), raise the palaeodiversity of siluriforms in the Honda Group to at least five families and 11 taxa, which would tentatively lead us to designate this group of fishes as the most diverse of the Honda Group (Fig. 5). The siluriforms paleodiversity is followed by the characiforms (six taxa) and cichlids (two taxa) (Fig. 5A). With the exception of a few taxa of characids, cichlids, and siluriforms (see Table 1), the rest of the taxa represented at family and generic levels have a stratigraphic record in the Honda Group that include both La Victoria and the Villavieja formations (Fig. 5B).

The fish palaeodiversity of the Honda Group could be underestimated as a direct consequence of taphonomic processes (not yet studied in La Venta site), imprecise taxonomic identifications and/or sampling biases. The latter is clearly related to the scarce study of micro vertebrate remains due to the lack of extensive screen-washing of sediments and other techniques of searching for small and delicate specimens along the Honda Group's sedimentary succession. Consequently, future studies must consider methods to standardize taxa diversity to ensure a homogeneous sampling effort. Despite
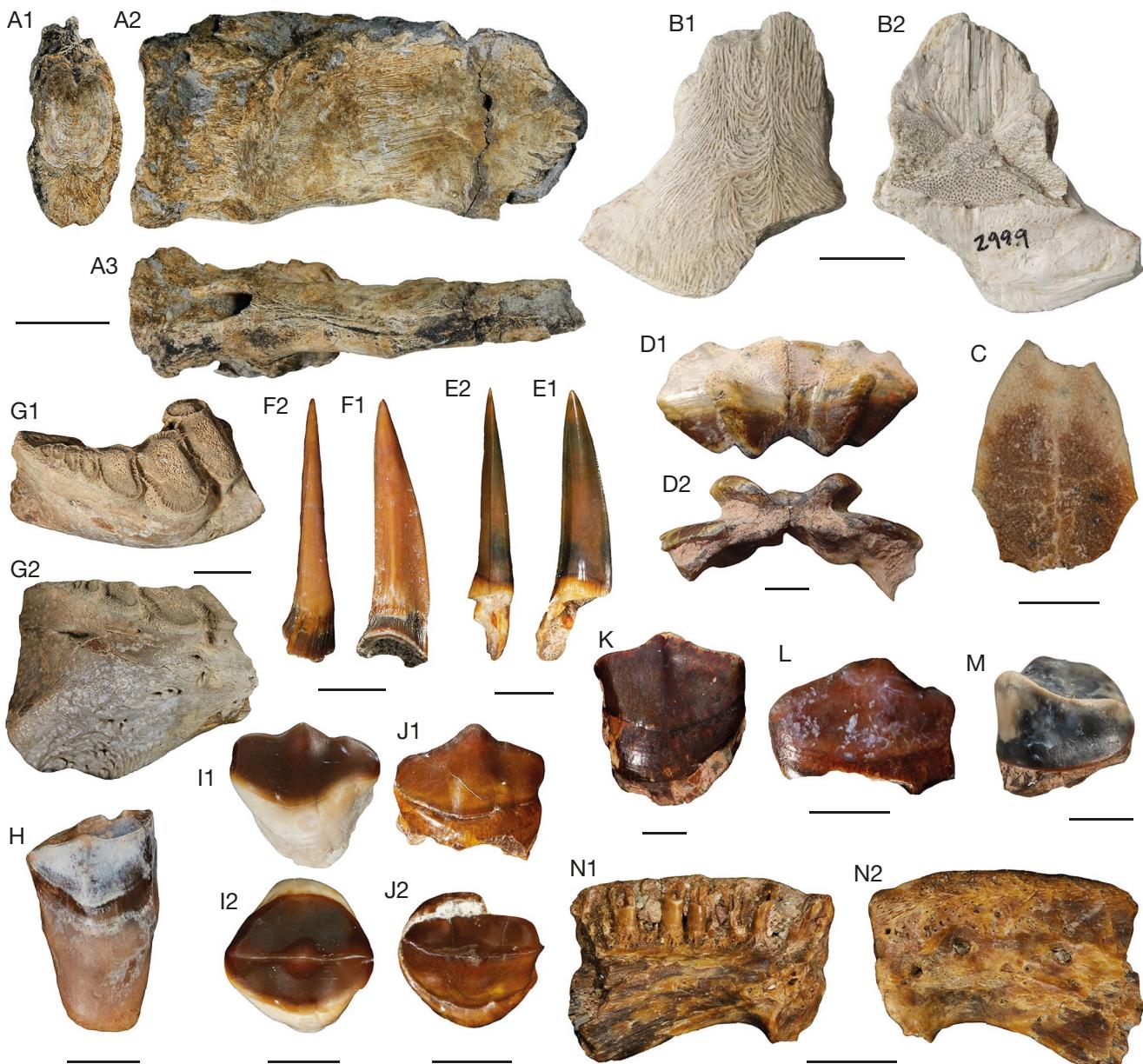
Fig. 4. — Siluriforms, Dipnoi, characiforms, and osteoglossiforms from the Honda Group: **A1**-**B2**, *Brachyplatystoma* sp.; **A1**-**A3**, weberian complex, VPPLT-1451; **B1**, **B2**, mesethmoid, ULA-2999; **C**, *Pimelodus* sp., parieto-supraoccipital, VPPLT-479; **D1**, **D2**, *Lepidosiren paradoxa* Fitzinger, 1837, prearticular toothplate, VP-PLT-1356; **E1**-**F2**, cf. *Hydrolycus* sp., isolated teeth; **E1**, **E2**, VPPLT-428; **F1**, **F2**, VPPLT-1140; **G1**-**M**, ?*Colossoma* or ?*Piaractus* spp.; **G1**, **G2**, right dentary fragment, VPPLT-925; **H**-**M**, isolated teeth; **H**, VPPLT-1453; **I1**, **I2**, VPPLT-1422; **J1**, **J2**, VPPLT-671; **K**, VPPLT-1107; **L**, VPPLT-1105; **M**, VPPLT-813; **N1**, **N2**, Arapaimidae indet., left dentary fragment, VPPLT-1371. Views: **A1**, **D1**, anterior; **B1**, **C**, **G1**, dorsal; **A2**, **N2**, left lateral; **H**, **I1**, **J1**, **K**-**M**, labial; **E2**, **F2**, lateral; **E1**, **F1**, lingual; **D2**, **I2**, **J2**, occlusal; **G2**, **N1**, right lateral; **A3**, **B2**, ventral. Scale bars: A, 40 mm; B, 10 mm; C, 6 mm; D, J, N, 5 mm; E, H, K, 3 mm; F, I, L, 4 mm; G, 7 mm; M, 2 mm.

this, the stratigraphic intervals with higher diversity coincide with fine-grained sediments accumulated in meandering rivers and possible distal alluvial fan palaeoenvironments (Figs 1; 6).

The Honda Group, followed by the Pebas Fm (see Carrillo-Briceño *et al.* 2021b; Schwarzhans *et al.* 2022), preserves one of the most diverse middle Miocene continental bony fish faunas so far known from the Neotropics. For an overview of the Neotropical freshwater fish palaeodiversity see Ballen *et al.* (2021a: table S1).

The record of †*Sciades maldonadonis* n. sp. in the La Victoria Fm (Morrongo 1 locality; Figs 1B, 6) is stratigraphically

significative. Its report for the middle Miocene expands the biochron, and the biogeographic range of the genus, with a fossil record known exclusively from the late Miocene Urumaco Fm (Aguilera & Marceniuk 2018). The specimen referred here to *Oxydoras* sp. from the Honda Group and the isolated mesethmoid bone from the Utuquina Valley near Pucallpa (Miocene of Peru) reported by Lundberg *et al.* (2010), are to date the only known fossils of thorny catfish *Oxydoras*. The newly recognized cichlids cf. *Astronotus* sp. and cf. *Cichla* sp. from the La Victoria Fm (Table 1; Appendix 1), together with †*Cichlasoma bluntschlii* Schwarzhans *et al.*, 2022, from the Pebas Fm, represent the only neotropical cichlid fossil taxa
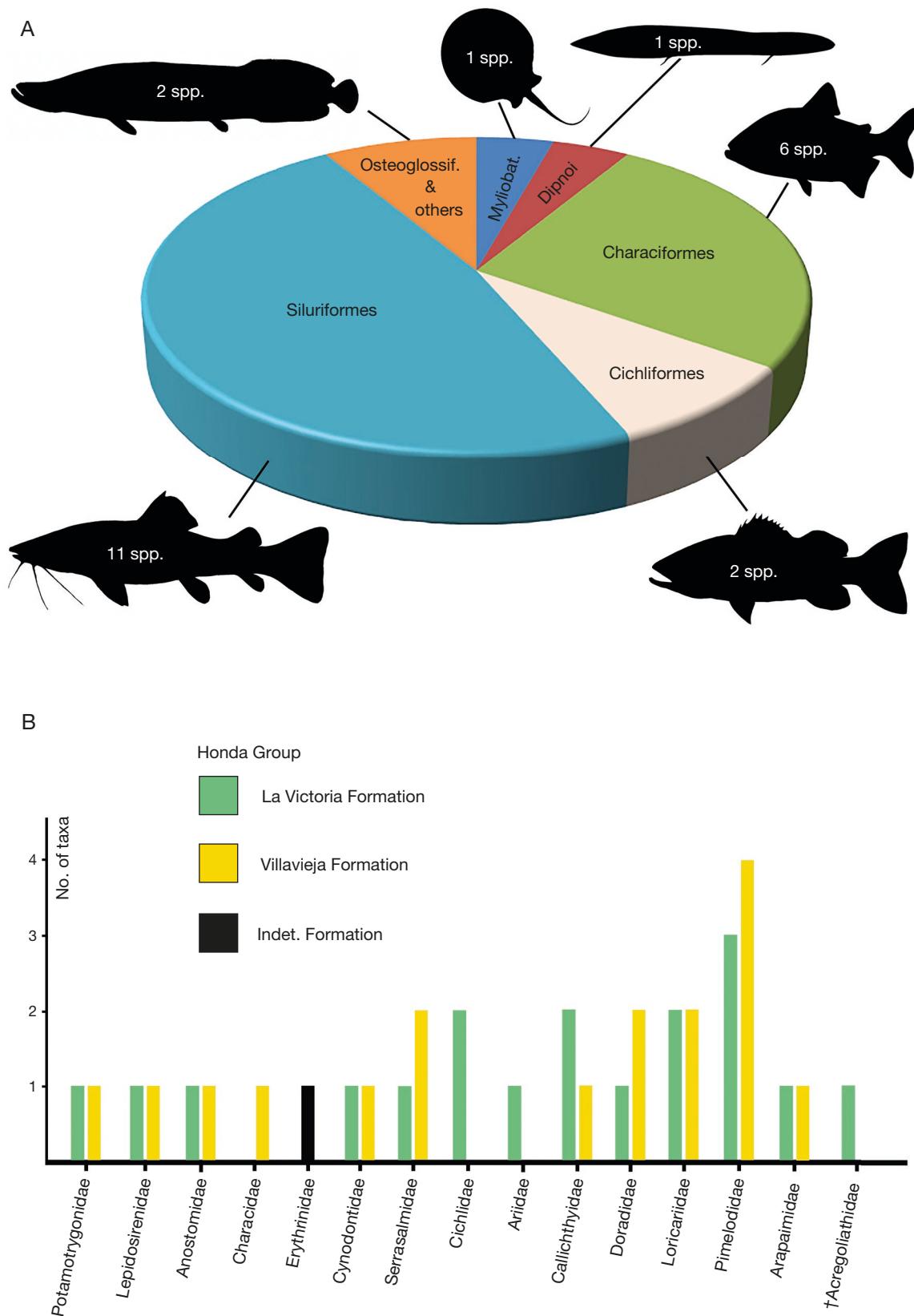
FIG. 5. — Fish palaeodiversity from the middle Miocene Honda Group: **A**, overall taxa reported in the Honda group by orders, "Osteoglossiformes & others" include *Arapaima* Müller, 1843 and †*Acregoliath* Richter, 1989; **B**, total number of taxa by families and geological unit. The total number of taxa is based on Table 1 and Appendix 1.

known so far. Other fossil cichlids from the Neotropics are scarce and correspond to isolated and indeterminate remains (Lundberg 1997; Moreno *et al.* 2015; Carrillo-Briceño *et al.* 2021a, b). This indicates the immense bias in the fossil record of neotropical cichlids, a group currently represented by at least 44 genera and more than 290 species, constituting the third most speciose group of freshwater fishes in South America (see van der Sleen & Albert 2018). The fossil record of †*Sciades maldonadonis* n. sp., *Oxydoras* sp., cf. *Astronotus* sp., and cf. *Cichla* sp. in the Honda Group can thus offer fossil calibration points for these taxa into the middle Miocene.

All the fossil bony fish taxa so far reported for the Honda Group have living representatives, which currently inhabit both the trans- and cis-Andean basin (see Lundberg *et al.* 2010; Rodríguez-Olarte *et al.* 2009; van der Sleen & Albert 2018). The exception is †*Acregoliath rancii* Richter, 1989, which is one of the most enigmatic extinct freshwater taxa from the Neogene of South America, and whose description was based exclusively on isolated scales from the late Miocene of Brazil (Richter 1989). Ballen & Moreno-Bernal (2019) reported †*A. rancii* in La Victoria Fm based on a few isolated scales. In Table 1 and Appendix 1, we are reporting new records of bony-tongued fishes. These specimens are represented mainly by isolated cranial (e.g., Fig. 4N1-N2) and postcranial remains. Bony-tongued fishes were known in the Honda Group exclusively from a single record assigned to *Arapaima* Müller, 1843, by Lundberg & Chernoff (1992). The new Bony-tongued fishes remains, as well as those *Lepidosiren* Fitzinger, 1837, indet. callichthyid and thorny catfishes (referred as "Morphotype 1" in Table 1) are reported here in a general way because they are currently under study. For example, our preliminarily review suggests that *Lepidosiren* (see Appendix 1) is an abundant taxon in the Honda Group. We have registered more than 200 isolated toothplates (counting specimens reported by Lundberg 1997), including a complete and articulated skull collected by us in 2019, representing almost a third of the fossil fish specimens that we have totaled. No other site in the Neotropics exhibits as abundant a fossil record of Cenozoic lungfishes as the Honda Group. Additionally, *Lepidosiren* represents the most continuous register of fossil fish along the sedimentary succession of Honda Group, spanning rocks older than *c.* 16 Ma according to the most recent age model (Mora-Rojas *et al.* 2023).

The presence of cf. *Potamotrygon* sp. in the Honda Group increases the geographical distribution of these stingrays during the middle Miocene, whose record for this time was restricted to what would be today the Peruvian Amazon (Chabain *et al.* 2017; Carrillo-Briceño *et al.* 2021b). Nowadays, more than 35 living potamotrygonid species (four genera) are recognized from different South American river basins (Lasso *et al.* 2014; van der Sleen & Albert 2018), and only *Potamotrygon* inhabit trans-Andean basins with at least two species, one restricted to the Magdalena and Atrato rivers (Colombia), and the other Lake Maracaibo basins (Lasso *et al.* 2014). Fossil potamotrygonids from the Urumaco region in Venezuela (Carrillo-Briceño *et al.* 2021a), including possible potamotrygonid teeth erroneously identified as Dasyatidae indet. by Carrillo-Briceño *et al.* (2015) suggest that these freshwater

stingrays had wider geographic distribution in the region at the end of the Cenozoic. It is not unreasonable to think that after the termination of the ancient fluvial drainages from western Amazonia in the direction of the proto-Caribbean Sea (see Aguilera *et al.* 2013a), that the freshwater stingrays that inhabited the region during the deposition of the Honda Group basin could have given rise to the two extant trans-Andean *Potamotrygon* species inhabiting the Magdalena and Atrato rivers.

Based on the fossil record of aquatic vertebrates (Kay *et al.* 1997; Carrillo *et al.* 2015; Cadena *et al.* 2019, 2020; Defler 2019, and references therein), it is indisputable that the Honda Group accumulated in a purely continental environment. A variety of aquatic palaeoenvironments (see Fig. 6), characterized by meandering, braided, and anastomosing rivers, and alluvial fans have been proposed for the Honda Group (Villarroel *et al.* 1996; Guerrero 1997; Mora-Rojas *et al.* 2023). The palaeoichthyofauna from the Honda Group (Table 1), have a typical tropical-freshwater composition, with extant representatives that 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 & Albert 2018). This supports the great variety of freshwater environments proposed for the sequence (Fig. 6). Even the presence of extinct and enigmatic *Acregoliath* in the Honda Group (Ballen & Moreno-Bernal 2019), supports purely freshwater environments, since this taxon has been recorded exclusively from freshwater palaeoenvironments (Richter 1989; Carrillo-Briceño *et al.* 2021b).

The presence of †*Sciades maldonadonis* n. sp. in the La Victoria Fm (Fig. 6) supports our hypothesis that this species of catfish was a freshwater species, as it has been referenced for other fossil and living ariid catfish species (see Schwarzhans *et al.* 2022). The extant *S. dowii* from the Pacific side inhabits rivers and brackish waters from Panama to Ecuador (Froese & Pauly 2022). So far, the only two known fossil species of *Sciades* (*S. latissimum* and *S. peregrinus*) come from the late Miocene rocks of the Urumaco Fm, a unit that has been associated with a wide variety of palaeoenvironments influenced by a large palaeo-hydrographic system of the Orinoco/Amazonas discharging into the proto-Caribbean (Aguilera *et al.* 2020). In the same region of Urumaco, but in more recent sediments from the late Pliocene, remains assigned to cf. *Sciades* were also reported from freshwater palaeoenvironments (Carrillo-Briceño *et al.* 2021a).

Taxa like the lungfish *Lepidosiren*, the characiform *Hydrolycus* Müller & Troschel, 1844, *Colossoma* Eigenmann & Kennedy, 1903, some piranha-like taxa (see Lundberg 1997), the cichlids *Astronotus* and *Cichla*, the siluriforms *Oxydoras*, *Brachyplatystoma* Bleeker, 1862b, *Phractocephalus*, and the bony-tongued *Arapaima*, have extant representatives inhabiting exclusively cis-Andean drainages (see van der Sleen & Albert 2018). These above-mentioned taxa and other taxa of large groups, such as characiforms and siluriforms were common among the hydrographic systems of the Miocene in South America (see Lundberg 1997, 2005; Lundberg *et al.* 1988, 2010; Lundberg & Aguilera 2003, Sabaj Pérez *et al.* 2007; Aguilera *et al.*

FIG. 6. — Biostratigraphy of the freshwater fishes from the Honda group and palaeoenvironments. The fish fossil record is based on localities presented in Fig. 1B and Appendix 1. Palaeoenvironments: **1**, anastomosing river interpreted by Guerrero (1997), diagram based on Li & Zhang (2017); **2**, small meandering stream interpreted by Guerrero (1997) or a sand-bed meandering river interpreted by Mora-Rojas *et al.* (2023); **3**, braided river interpreted by Villarroel *et al.* (1996) and Guerrero (1997), influenced by debris flows and catastrophic flood events (Mora-Rojas *et al.* [2023]), diagram based on Nichols (2009); **4**, meandering river interpreted by Guerrero (1997) or a gravel-sand meandering fluvial system interpreted by Mora-Rojas *et al.* (2023); **5**, possible distal facies of an alluvial fan or a terminal fan in the distributary zone, suggested by Mora-Rojas *et al.* (2023), diagram based on Peterson (1981).
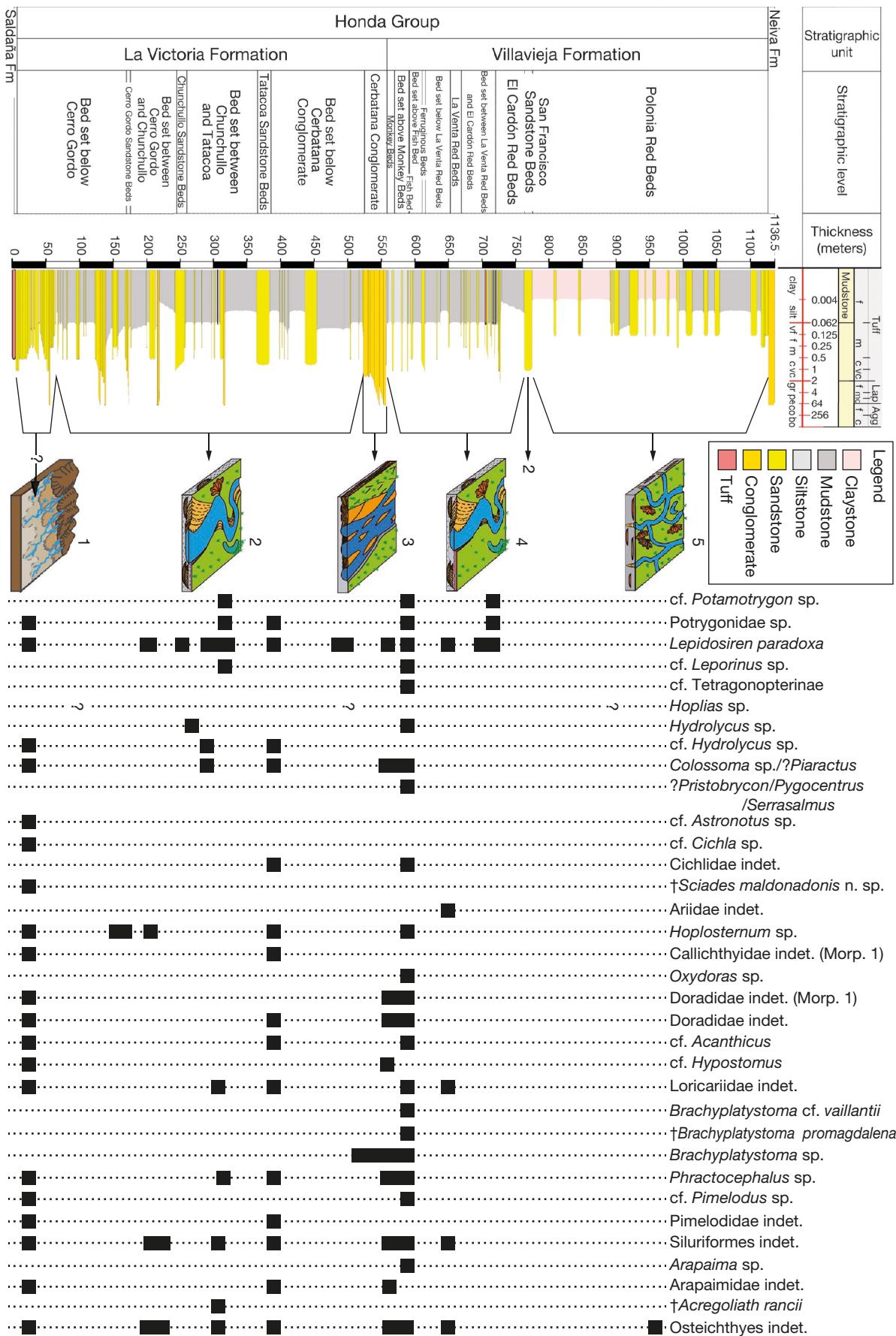
2008; 2013a; Azpelicueta & Cione 2016; Ballen *et al.* 2021a; Carrillo-Briceño *et al.* 2021a, b; Schwarzhans *et al.* 2022, and references therein). The presence of modern-day cis-Andean taxa in the Honda Group supports the hydrographic connection with western Amazonia drainages, possibly between *c.* 16 and 10.5 Ma (see Mora-Rojas *et al.* 2023). According to Ballen *et al.* (2021a), the similarity between "La Venta" (Honda Group) and Rio Acre (cis-Andean basin) fish faunas during the late Miocene further indicates that the northern Andean uplift was not a complete barrier at least until *c.* 11 Ma.

After the middle Miocene (*c.* 13 Ma) important changes occurred in the palaeogeographic landscape (Anderson *et al.* 2016; Montes *et al.* 2021). The extreme environmental changes likely occurred during the configuration of the western Amazonia (Pebas and the posterior Acre systems), and northern peripheral drainages that flowed to the proto-Caribbean, as a consequence of the Andean tectonic uplift. The isolation of the new trans-Andean hydrographic basins had a considerable impact on the fish communities, resulting in habitat size reduction, which led to the extinction or extirpation of many groups.

Although the fish palaeodiversity from the Honda Group is affected by a bias in the fossil record, it provides novel data about palaeodiversity and the geographical/temporal range of several lineages inhabiting the region at that time.

Declaration of competing interest

The authors declare that they have no conflict of interest that could influence the work reported in this contribution.

Acknowledgements

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APPENDIX 1. — Fish palaeodiversity of the Honda Group and the record by locality. Symbols: ×, this work; ×, Lunberg 1997 fossils; ×, Ballen & Moreno-Bernal 2019; **C/T**, Chunchu/Tatac.

OSTEICHTHYES / **CHONDRICHTHYES**

Higher ranking — Genus — Species:

- Osteichthyes indet. — indet.
- incertae sedis / †Acregoliathidae — †Acregoliath — rancii
- Arapaimidae — Arapaima — sp.
- Osteoglossiformes — indet. — indet.
- Pimelodidae — cf. Pimelodus — sp.
- Pimelodidae — indet. — indet.
- Phractocephalus — sp.
- Brachyplatystoma — sp.
- Brachyplatystoma — †promagdalena
- Brachyplatystoma — sp.
- Pimelodidae — indet. — indet.
- Loricariidae — cf. Hypostomus — sp.
- cf. Acanthicus — sp.
- Loricariidae — indet. — indet.
- Doradidae — (Morphotype 1) — sp.
- Oxydoras — sp.
- Doradidae — indet. (Morphotype 1) — indet.
- Callichthyidae — Hoplosternum — sp.
- Callichthyidae — indet. — indet.
- Ariidae — Sciades — †maldonadonis n. sp.
- Siluriformes — indet. — indet.
- Cichlidae — cf. Astronotus — sp.
- cf. Cichla — sp.
- Cichlidae — indet. — indet.
- Serrasalmidae — ?Pristobrycon/Serrasalmus — sp.
- ?Piaractus / ?Colossoma or — sp.
- Colossoma — macropomum
- Serrasalmidae — indet. — indet.
- Cynodontidae — cf. Hydrolycus — sp.
- Erythrinidae — Hoplias — sp.
- Characidae — cf. Tetragonopterinae indet.
- Anostomidae — cf. Leporinus — sp.
- Characiformes — indet.
- Lepidosirenidae — Lepidosiren — paradoxa
- Lepidosireniformes — indet.
- Potamotrygonidae — cf. Potamotrygon — sp.
- Myliobatiformes — indet.

with stratigraphic position

No.	Locality
1	Morrongo 1
2	Morrongo 2
3	Morrongo 3
4	Tatacoita
5	Repartidora
6	LA 41
7	Potosí
8	Los Hoyos
9	Llano Largo
10	Valle del Arcoiris
11	Duke 40
12	Duke 104
13	Nicaragua 1
14	Duke 102
15	Duke 62
16	Duke 81
17	Duke 88
18	Duke 38
19	Duke 39
20	Duke 84
21	Tres Pasos
22	Intrm. beds C/T
23	Las 40
24	Duke 90
25	San Borja 2
26	Diomatal, Museo T
27	Duke 26
28	Duke 96
29	Km 121
30	Duke 53
31	Las Gaviotas 3
32	LA 30
33	Cervatana beds?
34	Duke 6
35	Duke 6B
36	Duke 50
37	Duke 54
38	Duke 93
39	Ventanas
40	San Nicolás
41	Piedra Gorda
42	LA 2a
43	Sol Picante
44	Fish bed
45	LA 2B
46	LA 3
47	LA 4
48	LA 10
49	LA 39
50	LA 49
51	Duke 23
52	Duke 46
53	LA 8
54	Duke 24
55	LA 32
56	Duke 60
57	Duke 32
58	LA 34

without strat. position

No.	Locality
59	San Juanito
60	Santa Barbara 2
61	Alrd. Camp. La Venta
62	Cerro Gordo
63	Duke 16
64	Norte Punto 16
65	Las Mesitas
66	NW camp la Venta
67	San Francisco
68	Villa v. by purchase
69	Camino de Doche . V
70	Minidesierto
71	unknown locality

Appendix 2. — Geographic and stratigraphic details of the fossiliferous localities presented in Appendix 1 and Fig. 1B.

Collection name	Locality name	Latitude, longitude	Source	Formation	Strat. level (StL number)	Strat. pos. (m)	Comments
Tatacoa	Morrongo 1 Morrongo 2 Morrongo 3 Tatacoita	3.3442500, −75.111430 ◉ 3.3395500, −75.106860 ◉ 3.3389600, −75.10678 ◉ 3.3280500, −75.099620 ◉	Andrés Vanegas	La Victoria	Bed set below Cerro Gordo (StL 1)	28	Mudstone. We estimate the stratigraphical position using the Montes *et al.* (2021) cartography, and place it in the first mudstone bed of La Victoria Formation.
	La Repartidora 9	3.3911600, −75.164550 ◉	Andrés Vanegas	La Victoria	Bed set below Cerro Gordo (StL 1)	40	Approximate position. Using the cartography of Montes *et al.* (2021), it is in the Saldaña Formation, and consequently, it would be older than La Victoria. However, we consider that the mapping is misaligned.
Universidad de los Andes	LA 41	3.370111111, −75.14883333 ◉	Andrés Link	La Victoria	Bed set below Cerro Gordo (StL 1)	155.2	Below Cerro Gordo Sandstone Beds. We correlate this locality with the fossil locality La Repartidora (Cadena *et al.* 2020).
Tatacoa	Potosí	3.3707600, −75.146120 ◉	Andrés Vanegas	La Victoria	Bed set below Cerro Gordo (StL 1)	160	Founded in a siltstone
	Llano Largo Indet. Loc	3.3583500, −75.159370 ◉	Andrés Vanegas	La Victoria	Bed set below Cerro Gordo (StL 1)	165	We estimate the stratigraphical position using the Montes *et al.* (2021) cartography.
Universidad de los Andes	Los Hoyos	3.203722222, −75.11597222 ◉	Andrés Link	La Victoria	Bed set below Cerro Gordo (StL 1)	165	We estimate the stratigraphical position using the Montes *et al.* (2021) cartography.
Tatacoa	Valle del Arcoíris	3.3124200, −75.151070 ◉	Andrés Vanegas	La Victoria	Bed set between Cerro Gordo and Chunchullo (StL 3)	199.2	Siltstone. We correlate this locality with the Duke locality 85 (Guerrero 1997).
NA	Duke 40 Duke 104	3.337879787, −75.1454015 ◉ 3.310230377, −75.1456729 ◉	Guerrero (1997)	La Victoria	Bed set between Cerro Gordo and Chunchullo (StL 3)	205.1 208.1	–
Tatacoa	Nicaragua 1	3.3596600, −75.143180 ◉	Andrés Vanegas	La Victoria	Bed set between Cerro Gordo and Chunchullo (StL 3)	220	Founded in a siltstone. We correlate this locality with the Duke locality 91 (Guerrero 1997).
NA	Duke 102	3.308035356, −75.16374977 ◉	Guerrero (1997)	La Victoria	Chunchullo Sandstone Beds (StL 4)	256.2	
	Duke 62 Duke 81 Duke 88 Duke 38	3.299378083, −75.1579404 ◉ 3.298005195, −75.14228685 ◉ 3.325312238, −75.15345667 ◉ 3.322376449, −75.15190958 ◉	Guerrero (1997)	La Victoria	Bed set between Chunchullo and Tatacoa (StL 5)	259.6 259.6 261.3 271	–
Tatacoa	Tres Pasos	3.324444, −75.16361111 ◉	Andrés Vanegas	La Victoria	Bed set between Chunchullo and Tatacoa (StL 5)	288.7	Siltstone. We correlate this locality with the Duke locality 39 (Guerrero 1997)
NA NA	Duke 39 Duke 84	3.32303195, −75.15989242 ◉ 3.323103334, −75.15682291 ◉	Guerrero (1997)	La Victoria	Bed set between Chunchullo and Tatacoa (StL 5)	288.7	–
Tatacoa	Las 40 1	3.3376200, −75.178500 ◉	Andrés Vanegas	La Victoria	Bed set between Chunchullo and Tatacoa (StL 5)	303.3	Founded in a siltstone. We correlate this locality with the Duke locality 90 (Guerrero 1997).
NA	Duke 90	3.324745162, −75.16860125 ◉	Guerrero (1997)	La Victoria	Bed set between Chunchullo and Tatacoa (StL 5)	303.3	–
Tatacoa	San Borja 2 Diomatal – Museo La Tormenta	3.3375900, −75.186410 ◉ 3.2822200, −75.126670 ◉	Andrés Vanegas	La Victoria	Bed set between Chunchullo and Tatacoa (StL 5)	309 314.9	Founded in a siltstone We correlate this fossil locality with the Duke locality 26 (Guerrero 1997).
NA	Duke 26 Duke 96	3.278225733, −75.11075832 ◉ 3.240174744, −75.1136807 ◉	Guerrero (1997)	La Victoria	Bed set between Chunchullo and Tatacoa (StL 5)	314.9 322.3	– –

Appendix 2. — Continuation.

Collection name	Locality name	Latitude, longitude	Source	Formation	Strat. level (StL number)	Strat. pos. (m)	Comments
Tatacoa	Km 121	3.3247500, −75.182100 ◎	Andrés Vanegas	La Victoria	Bed set below Cerbatana Conglomerate (StL 7)	388.5	Sandstone. We correlate the stratigraphical position of this locality in the first sandstone bed of StL 7
NA	Duke 53	3.23127539, −75.12751111 ◎	Guerrero (1997)	La Victoria	Bed set below Cerbatana Conglomerate (StL 7)	483.2	–
Tatacoa	Las Gaviotas 3	3.3108000, −75.203220 ◎	Andrés Vanegas	La Victoria	Bed set below Cerbatana Conglomerate (StL 7)	507.7	Siltstone. We correlate this locality with the Duke locality 58 (Guerrero 1997)
Universidad de los Andes	LA 30	NA	Andrés Link	La Victoria	Bed set below Cerbatana Conglomerate (StL 7)	520	We estimate the stratigraphical position of this locality in the last mudstone bed of the Bed set below Cerbatana Conglomerate (StL 7)
Tatacoa	San Nicolás	3.2833300, −75.194440 ◎	Andrés Vanegas	La Victoria			Founded in a siltstone. For the stratigraphical position we correlate this locality with the Duke locality 22 (Guerrero 1997)
	Ventanas	3.2510800, −75.159130 ◎	Andrés Vanegas	La Victoria	Monkey Beds (StL 9)	560.4	–
	Piedra Gorda 3	3.2871000, −75.211360 ◎	Andrés Vanegas	Villavieja			Founded in a siltstone
IGM-Bogota	Duke 6B	3.255177747, −75.18768608 ◎	Guerrero (1997)	Villavieja	Monkey Beds (StL 9)	560.4	–
	Duke 16	NA	Guerrero (1997)	Villavieja	Monkey Beds (StL 9)	560.4	It lacks coordinates because Guerrero (1997) not placed it on a map and not provided coordinates. We use the stratigraphic position assigned by Mora-Rojas *et al.* (2023).
	Duke 50	3.222813132, −75.1383924 ◎	Guerrero (1997)	Villavieja	Monkey Beds (StL 9)	560.4	–
NA	Duke 6 Duke 54 Duke 93	3.254512045, −75.18478093 ◎ 3.287064496, −75.19438688 ◎ 3.251197278, −75.16628868 ◎	Guerrero (1997)	Villavieja Villavieja La Victoria	Monkey Beds (StL 9)	560.4	–
Universidad de los Andes	LA 2a	3.20075, −75.13816667 ◎	Andrés Link	Villavieja	Monkey Beds (StL 9)	567	Monkey beds. We estimate the stratigraphical position on the last sandstone bed of Monkey Beds.
Tatacoa	Sol Picante	3.2153000, −75.134600 ◎	Andrés Vanegas	Villavieja	Fish Bed (StL 11)	590	Mudstone. We correlate the stratigraphical position of this locality in the Fish Bed.
IGM-Bogota	Duke 46	3.244701349, −75.16835881 ◎	Guerrero (1997)	Villavieja	Fish Bed (StL 11)	590	–
	Fish Bed	NA		Villavieja	Fish Bed (StL 11)	590	It lacks coordinates. We correlate the stratigraphical position of this locality in the Fish Bed.
Universidad de los Andes	LA 2B	3.20191667, −75.138278 ◎					Fish beds. We correlate the stratigraphical position of this locality in the Fish Bed.
	LA 3	3.215833333, −75.13622222 ◎					We correlate the stratigraphical position of this locality in the Fish Bed.
	LA 4	3.214611111, −75.13513889 ◎	Andrés Link	Villavieja	Fish Bed (StL 11)	590	We correlate the stratigraphical position of this locality in the Fish Bed.
	LA 10 LA 39 LA 49	3.215277778, −75.13472222 ◎ 3.214611111, −75.135 ◎ 3.213833333, −75.14419444 ◎					Fish beds. We correlate the stratigraphical position of this locality in the Fish Bed.
NA	Duke 23	3.22675352, −75.14318939 ◎	Guerrero (1997)	Villavieja	Fish Bed (StL 11)	590	
Universidad de los Andes	LA 8 LA 8-A	3.210694444, −75.14005556 ◎ 3.213805556, −75.14227778 ◎	Andrés Link	Villavieja	Bed set above Fish Bed (StL 12)	600	Above fish beds

Appendix 2. — Continuation.

Collection name	Locality name	Latitude, longitude	Source	Formation	Strat. level (StL number)	Strat. pos. (m)	Comments
IGM-Bogota	Duke 24	3.226981948, −75.14752953 ◉	Guerrero (1997)	Villavieja	Bed set below La Venta Red Beds (StL 14)	650	
Universidad de los Andes	LA 32	3.235833333, −75.154535 ◉	Andrés Link	Villavieja	La Venta Red beds (StL 15)	652	Using the available cartographies (Guerrero 1997 and Montes *et al.* 2021), we placed this locality in the La Venta Red Beds.
IGM-Bogota	Duke 60	3.234317972, −75.16368097 ◉	Guerrero (1997)	Villavieja	Bed set between La Venta Red Beds and El Cardón Red Beds (StL 16)	689	
NA	Duke 32	3.229116324, −75.17404149 ◉	Guerrero (1997)	Villavieja	El Cardón Red Beds (StL 17)	722.8	
Universidad de los Andes	LA 34	3.169805556, −75.16475 ◉	Andrés Link	Villavieja	Polonia Red beds (StL 19)	967	Polonia Red beds. We correlate this locality with Duke localities 131 and 144.
Tatacoa	Santa Bárbara 2 Santa Bárbara 3 San Juanito	3.400833, −75.103611 ◉ 3.4011111, −75.105278 ◉ 3.410833, −75.102500 ◉	Andrés Vanegas	La Victoria	NA	NA	Founded in a siltstone. This locality is outside the mapping of Guerrero (1997) and Montes *et al.* (2021).
IGM-Bogota	Alrededor del campamento de la Venta	NA	Royo y Gómez (1945)	Villavieja?	NA	NA	It lacks coordinates because Royo y Gómez (1945) did not place it on a map and did not provide coordinates. Consequently, we lack additional information to assign it a stratigraphic position.
	Cerro Gordo	NA	idem	La Victoria?	NA	NA	idem
	Izquierda del Arroyo de la Venta al N. del punto 16	NA	idem	NA	NA	NA	idem
	Las Mesitas, Carretera de Baraya	NA	idem	NA	NA	NA	idem
	NW del Campamento de la Venta	NA	idem	NA	NA	NA	idem
	San Francisco, Camino de Doche	NA	idem	NA	NA	NA	idem
	Villavieja by purchase	NA		NA	NA	NA	idem