Rev. Mus. Argentino Cienc. Nat., n.s.
27(2): 000-000, 2025
ISSN 1514-5158 (impresa)
ISSN 1853-0400 (en línea)

New species of the highly diversified *Hoplias malabaricus* group (Characiformes - Erythrinidae) from la Plata basin: another brick in the wall

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Abstract: With 13 species, the genus *Hoplias* contains more than 75% of the diversity of the family Erythrinidae. However, cytogenetic and molecular studies strongly suggest the existence of an outstanding cryptic diversity in this genus, with more than 20 likely new species only for the *H. malabaricus* group. Here, we described a new species for this group, including specimens from a wide geographic coverage within La Plata Basin: Iguazu River and Urugua-í Reservoir in Argentina and upper Parana River in Brazil. Traditional taxonomic and molecular analyses were performed. The new species is diagnosed by the following combination of characters: 15–17 predorsal scales, 38–41 lateral-line scales, 10–11 premaxillary teeth; 8–10 plate-like denticulate rakers in ceratobranchial, 39–41 vertebrae, pectoral-fin length (16.24–19.58 % SL), orbital diameter (13.15–20.06 % HL), the last vertical scale row in the caudal fin forming a straight line and the last portion of the ascending process of the premaxilla with a marked ridge. A key for the species of the *H. malabaricus* group is provided. This work contributes to the inventory of biological diversity of the study region but also aims to accurately identify species belonging to a group with complex taxonomy.

Key words: Taxonomy, Neotropics, COI, Iguazu River, Parana River, *Hoplias guri*

Resumen: Nueva especie del altamente diversificado grupo *Hoplias malabaricus* (Characiformes - Erythrinidae) de la cuenca del Plata: otro ladrillo en la pared. Con 13 especies, el género *Hoplias* contiene más del 75% de la diversidad de la familia Erythrinidae. Sin embargo, los estudios citogenéticos y moleculares sugieren fuertemente la existencia de una diversidad críptica sobresaliente en este género, con más de 20 nuevas especies probables solo para el grupo *H. malabaricus*. Aquí, describimos una nueva especie para este grupo que incluye especímenes de una amplia cobertura geográfica dentro de la Cuenca del Plata: el río Iguazú y embalse de Urugua-í en Argentina y el alto Río Paraná en Brasil. Se realizaron análisis taxonómicos y moleculares tradicionales. La nueva especie se diagnostica por la siguiente combinación de caracteres: 15–17 escamas predorsales, 38–41 escamas de la línea lateral, 10–11 dientes premaxilares; 8–10 branquiespinas dentadas en forma de placa en ceratobranquial, 39–41 vértebras, longitud de la aleta pectoral (16,24–19,58 % SL), diámetro orbital (13,15–20,06 % HL), la última fila de escamas verticales en la aleta caudal formando una línea recta y la última porción del proceso ascendente de la premaxila con una cresta marcada. Se proporciona una clave para las especies del grupo *H. malabaricus*. Este trabajo contribuye al inventario de la diversidad biológica de la región de estudio pero también aporta a la precisión en la identificación de especies pertenecientes a un grupo con taxonomía compleja.

Palabras clave: Taxonomía, Neotrópico, COI, Río Iguazú, Río Paraná, *Hoplias guri*

INTRODUCTION

With 63 families and more than 6,400 species, the freshwater fish fauna of the Neotropical Region is the richest of the World (Reis & Helfman, 2024). Irrespective of that, numerous taxa have been described in recent decades (Nelson, 2016) and current diversity is estimated to exceed 9,000 species (Reis *et al*., 2016). In this region, the La Plata Basin hosts an exceptional diversity of fish, surpassed only by the Amazon and Orinoco Rivers (Albert & Reis, 2011).

The Erythrinidae Family is widely distributed along the Neotropical region and comprises only three genera (Oyakawa, 2003). The *Hoplias* genus, with 13 species contains more than 75% of its members (Toledo-Pizza *et al*., 2024). Species in the *Hoplias* genus have historically been arranged in different groups, with the *H. malabaricus* group being the most species-rich. Furthermore, cytogenetic (Bertollo *et al*., 2000; Perin *et al*., 2024) and molecular (Cardoso *et al*., 2018; Guimarães *et al*., 2022) evidence strongly suggest the existence of an outstanding cryptic diversity in this group. Species of this group are differentiated by the presence of tooth plates on basihyal and basibranchials and the medial margins of contralateral dentaries converging to the mandibular symphysis in a V-shape (Oyakawa, 1990).

Hoplias malabaricus sensu stricto was formerly reported from its type locality in Suriname to the lower La Plata River in Argentina (Ringuelet *et al*., 1967). Indeed, *H. malabaricus* was the only species of the *H. malabaricus* group recorded in the La Plata River basin until the recent taxonomic descriptions of *H. mbigua* (Azpelicueta *et al*., 2015), *H. misionera* (Rosso *et al*., 2016) and *H. argentinensis* (Rosso *et al*., 2018). Moreover, the recent molecular evidence suggests that *H. malabaricus sensu stricto* does not inhabit the La Plata River Basin (Cardoso *et al*., 2018; Guimarães *et al*., 2022).

In previous molecular studies, the algorithm known as the Barcode Index Number (BIN) perfectly recovered the molecular identity of many taxonomic species of *Hoplias* and suggested an astonishing 22 mitochondrial lineages for the *H. malabaricus* group with only five of them belonging to taxonomic species (Guimarães *et al*., 2022). In this work, one of these putative species labeled with the BIN AAB1733 and with known occurrence in the La Plata River Basin was selected herein for a formal taxonomic description.

MATERIAL AND METHODS

The specimens examined come from a wide geographical area, including several aquatic environments from very distant locations within the La Plata Basin: Iguazu River and Urugua-í Reservoir in Argentina and the upper Paraná River in Brazil. Sampling permissions (Instituto Misionero de Biodiversidad) were obtained for field sampling in the Iguazu and Urugua-í systems. During field campaigns, fish handling followed international ethical guidelines (Barker *et al*., 2022). The revised specimen from the Upper Parana River is housed in the Museum of Natural History of Geneva (MHNG).

Body measurements and counts were performed on the left side of the body following Fink and Weitzman (1974) and modifications incorporated by Mattox *et al*. (2006), Rosso *et al*. (2018), and Guimarães *et al*. (2021). Overall, the complete number of measurements (22) and counts (35) followed Guimarães *et al*. (2021). Values for the holotype are denoted with an asterisk.

Institutional abbreviations where the examined material is deposited are as follows: BMNH: Natural History Museum, London, U.K.; CFA-IC: Fundación de História Natural Félix de Azara, Universidad Maimónides, Buenos Aires, Argentina; CI-FML: Fundación Miguel Lillo, San Miguel de Tucumán, Argentina; LBP: Laboratório de Biologia e Genética de Peixes, Departamento de Morfologia, Instituto de Biociências, Universidade Estadual Paulista "Júlio de Mesquita Filho", Campus de Botucatu, São Paulo, Brazil; LGEP: Laboratorio de Genética Evolutiva-Peces, Posadas, Argentina; MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina. MHNN: Museum d'Histoire Naturelle de Neuchâtel, Neuchâtel, Switzerland; MLP: Museo de La Plata, Instituto de Limnologia, La Plata, Argentina; MNHN: Muséum National d›Histoire Naturelle, Systématique et Évolution, Laboratoire d›Ichthyologie Générale et Appliquée, Paris, France; UFOPA: Universidade Federal do Oeste do Pará, Coleção Ictiológica, Instituto de Ciências e Tecnologia das Águas, Santarém, Brazil; UNMDP: Instituto de Investigaciones Marinas y Costeras, Universidad Nacional de Mar del Plata, Argentina; ZMB: Museumfür Naturkunde, Leibniz-Institutfür Evolutions und Biodiversitätsforschung, Berlin, Germany. Institutional abbreviations follow Fricke and Eschmeyer (2025).

Tissue samples collected from the type material of the new species, as well as additional samples of *H. argentinensis* and *H. mbigua* from the Iguazú River and the Urugua-í reservoir (Paraná River), were incorporated in the molecular analyses. Genetic analyses were conducted using the Cytochrome c oxidase subunit I (COI) gene as a molecular marker. DNA extraction, amplification and sequencing followed Cardoso *et al*. (2018). The sequences were aligned and visually inspected using Bioedit (Hall, 1999). New sequences were deposited in GenBank under access numbers PV032011-25.

We applied the Barcode Index Number (BIN) approach (Ratnasingham & Hebert, 2013) for species delimitation to identify species based on DNA barcode of the new sequences. The BIN is an online tool implemented in the BOLD System Workbench (www.boldsystems.org). According to the preliminary results of Cardoso *et al*. (2018) and Guimarães *et al*. (2022), the BIN AAB1733 is an undescribed species of *Hoplias* from the Paraná River Basin. All available sequences corresponding to that BIN were retrieved from public repositories. All these sequences belong to specimens that are considered as referred members of the species described here (Supplementary Table 1). The aim of this was to further support the molecular identity and relationships of the new species and to better characterize its geographic distribution. The intra-BIN-AAB1733 distance and the distance to the nearest neighbor (both *p*-distance) were obtained from BOLD System Workbench.

In addition, several sequences from most of the species already described for the *H. malabaricus* group (*H. argentinensis*, *H. mbigua*, *H. auri, H. malabaricus*, *H. microlepis*, *H. misionera*) were used, including sequences from their holotypes or topotype specimens (collected in the basin containing the type locality) for most of these species. Sequences of *H. lacerdae* and *H. australis* were used as outgroups. Overall, a total dataset of 86 sequences was used (GenBank accession numbers presented in the molecular tree). The best-fitting molecular evolution model and the phylogenetic analyses were conducted using the IQ-TREE algorithm (Nguyen *et al*., 2015) on the W-IQ-TREE web server (Trifinopoulos *et al*., 2016). Nodal support was calculated with 1000 replicates of ultrafast bootstrap.

RESULTS

Hoplias guri sp. nov.

Zoobank Registration Number. urn:lsid:zoobank.org:pub:045D8EA3-2B7C-489A-A12B-99A53AD41115

Holotype. MACN-Ict 13259 shallow lake tributary of San Antonio River, Iguazu River Basin, alongside Rute 25, near Prefectura Andresito, 25° 35.563' S; 53° 59.686› W, Misiones, (Fig. 1).

Paratypes. ARGENTINA, Misiones Province: Same locality as holotype. CFA-IC-4435, Coll. Meluso, JM and Bogan, S., 2-5-2015; **UNMDP 5271**, Coll. Rosso, JJ and Bogan, S. 11-04-2023; **MACN-Ict 13260**, Coll. Rosso, JJ and Bogan, S. 11-04-2023; **CFA-IC- 13201,** Coll. Rosso, JJ and Bogan, S. 11-04-2023; **UNMDP 5285**, Coll. Rosso, JJ and Bogan, S. 12-04-2023; **CFA-IC- 13202**, Coll. Rosso, JJ and Bogan, S. 12-04-2023. **Embalse Urugua-í, Camping Club Alto Paraná,** 25° 51´ 11.13´´ S, 54°, 32´49.59´´ W. **MACN Ict-9634** (Fig. 2), Coll. Cardoso Y.P., Casciotta J. and Almirón A., 24-04-2010; **UNMDP-5348**, Coll. Rosso, JJ and Bogan, S. 13-04-2023; **MNHN-IC-2025-0033**, Coll. Rosso, JJ and Bogan, S. 13-04-2023; **CFA-IC- 13203,** Coll. Rosso, JJ and Bogan, S. 13-04-2023; **BRAZIL**, Unnamed stream tributary of Tiete River, at the road Biritiba Mirim-Casa Grande, Upper Paraná River, -24.5758 S; -46.0175 W, **MHNG 2587.5,** Coll. Montoya-Burgos, J.I., Reis, R.E., Pezzi J. and Pereira, E.H.L. 13-01-1997.

Allocation to species group. The presence of medial margins of dentaries converging towards the mandibular symphysis in a V or Y shape, four pores in the mandibular sensory canal and the presence of tooth plates on basyhial and basibranchial bones assign this new species to the *H. malabaricus* group.

Diagnosis. *Hoplias guri* is diagnosed by the following combination of characters: 15–17 predorsal scales, 38–41 lateral-line scales, 10–11 premaxillary teeth; 8–10 plate-like denticulate rakers in ceratobranchial, 39–41 vertebrae, pectoral-fin length (16.24–19.58 % SL), orbital diameter (13.15–20.06 % HL), the last row of vertical scales in the caudal fin forming a straight line and the posterior angular end of the ascending process of the premaxilla with a marked ridge.

The number of predorsal scales differentiates *H. guri* from *H. teres*, *H. argentinensis* and *H. microlepis* (15–17 vs. 18 (one paratype) ; 17–19 and 17–19 respectively). Lateral-line scales discriminate *H. guri* from *H. mbigua, H. argentinensis* and *H. microlepis* (38–41 vs 41 or more). Premaxillary teeth, separates *H. guri* from *H. auri* (10–11 vs 10 or less). The number of plate-like denticulate rakers in ceratobranchial bone distinguishes *H. guri* from *H. mbigua*, *H. misionera* and *H. argentinensis* (8–10 vs. 10 or more). The low number of vertebrae count discriminates this species from *H. mbigua*, *H. microlepis*, *H. teres* and *H. argentinensis* (39–41 vs. 42–44 vertebrae). A longer pectoral-fin length discriminates *Hoplias guri* (mean 18.12, 16.24–19.58 %SL) from both *H. auri* (mean 16.85, 15.85–19.01 %SL) and *H. malabaricus* (mean 16.89, 15.91–17.80 % SL). A smaller orbital diameter distinguishes the new species (mean 16.13, 13.15–20.06 %SL) from *H. auri* (mean 17.28,

Table 1. Morphometric data of *Hoplias guri*, new species. Standard and total lengths in mm; values 1-14 in percents of standard length; values 15-22 in percents of head length. SD, standard deviation; n, number of specimens; min, minimum; max, maximum. All ranges include the holotype.

		Holotype	n	Mean	min	MAX	SD
	Total length	325	12	275.17	137	515	123.21
	Standard length	262	12	222.67	108	417	100.35
1	Body depth	23.93	11	22.49	20.37	24.80	1.29
2	Head length	32.06	12	31.05	29.88	33.33	1.19
3	Pectoral-fin length	19.58	12	18.12	16.24	19.58	0.92
4	Pelvic-fin length	19.73	12	18.83	17.36	19.95	0.76
5	Anal-fin length	19.47	12	18.78	17.31	20.74	0.98
6	Dorsal-fin length	32.06	12	30.95	28.42	33.78	1.74
7	Dorsal-fin base length	18.05	12	17.76	15.87	19.73	1.13
8	Anal-fin base length	9.12	12	8.97	7.69	10.75	0.84
9	Pre-Pectoral length	30.42	12	29.35	27.84	30.83	0.90
10	Pre-Pelvic length	56.64	10	54.65	52.58	56.64	1.29
11	Pre-Dorsal length	49.81	11	49.80	47.37	52.52	1.62
12	Pre-Anal length	83.82	11	79.92	75.25	83.82	2.85
13	Caudal peduncle depth	14.05	10	13.66	12.18	14.72	0.74
14	Caudal peduncle length	12.37	11	12.45	10.41	13.89	0.98
15	Head depth	48.09	10	51.75	48.09	56.99	3.32
16	Snout length	25.48	12	24.34	21.25	27.78	2.00
17	Snout width	22.02	11	22.44	19.50	24.83	1.56
18	Snout depth	17.86	11	18.45	15.88	21.59	1.74
19	Pre-nasal distance	15.12	12	14.86	13.29	17.32	1.54
20	Orbital diameter	14.17	12	16.13	13.15	20.06	2.26
21	Interorbital width	26.43	11	26.37	22.01	32.05	2.87
22	Upper jaw length	52.14	11	52.18	48.45	58.70	2.89

Supplementary information Table S1. Detailed information on cytochrome C-oxidase subunit 1 (COI-I) of the new species and its sympatric species used for the Maximum Likelihood tree and BIN determination.

13.94–20.84 %SL) and *H. malabaricus* (mean 19.43, 17.01–22.12 % SL). The last vertical scale row in the caudal fin distinguishes *H. guri* from *H. misionera* (forming a straight line vs. forming a marked curve). The posterior angular end of the ascending process of the premaxilla differentiates *H. guri* (with a marked ridge) from *H. malabaricus* (with a smooth surface of head without ridges).

Description. Morphometric features of *H. guri* are shown in Table 1. Body shape subcylindrical. Anterior profile of head angular in lateral view. Dorsal profile of head straight. Dorsal surface of head with a notorious ridge at the posterior angular end of the ascending process of the premaxilla in contact with the mesetmoid medially and the nasal bone laterally (Fig. 3). The greatest body depth in the middle of the body, at the origin of dorsal fin. Last vertical series of scales around caudal peduncle nearly straight. Medial margins of contralateral dentaries converging to the mandibular symphysis in a V or Y-shaped angle. Larger lower jaw larger with fleshy lips. Posterior nostril without fleshy flap and equidistant to anterior nostril and anterior margin of orbit. Eyes of *H. guri* exceed the orbit ring and in dorsal view the dark sclera is easily remarkable (Fig. 3). Single premaxillary tooth row with 10*–11 teeth. First two medial teeth large, followed by four to five smaller teeth, and other two large canines. One to three small teeth behind the last largest premaxillary canine. Maxillary teeth 42–48 (47*); first 4–6* increasing progressively in size. Dentary external series with 4–5 small teeth followed by two large canines. Posteriorly, a series of 4–6 small teeth followed by 7–10 teeth arranged in a repetitive series of one large and 1–3 small conic teeth. Dorsal-fin rays ii,11–12* or iii,11. Anal-fin rays ii,8. Pectoral-fin rays i,10–13*. Total pelvic-fin rays i,7*–8. Caudal-fin rays i,11–15*,i. Predorsal scales 15–17 (16*) (Fig. 4). Lateral line with 38–41 (39*) perforated

Fig. 1. *Hoplias guri*, new species, MACN-Ict 13259, holotype, 262 mm SL, Comandante Andresito, Misiones, Argentina. **A**, Preserved specimen. **B**, Recently collected specimen. **C**, X-ray image.

scales, plus 2*–3 non-perforated scales beneath the opercle membrane. Longitudinal series of scales between dorsal-fin origin and lateral line 5*–6; between lateral line and pelvic-fin origin 4*–5. Longitudinal series of scales around caudal peduncle, 20* (one specimen with 21). First epibranchial with 9–13 (11*) plate-like denticulate gill rakers. One raker on cartilage. Ceratobranchial with 4*–6 elongated rakers followed by 8–10* small plate-like rakers. Latero-sensory canal along ventral surface of dentary with 4 pores. Six laterosensory pores in preopercle. Latero-sensory canal along infraorbitals with 11*–13 pores. Infraorbital 5 with no pores. Ten* to 12 pores in laterosensory system of dorsal surface of head. The following combination of pores in supraopercle-extra-escapular bones: 0–2 or 1–1*. Total vertebrae count 39–41* (n=9).

Color in life. Body dark olive dorsally, fading downwards with a distinct yellowish-white belly. Five to six dark chevron-shaped lateral markings facing posteriorly. Dark rounded spot on the dorsal half of the caudal peduncle in contact with the upper branch of last lateral chevron blotch. Head with chromatophores forming dark spots or irregular marks and dark bands posteriorly oriented from the orbital ring along the second and third infraorbitals (Fig. 5). Some specimens showed a third band in infraorbital four or six. Infraorbitals and opercle green to iridescent gold. A dark rounded spot on the dorsal half of opercle more noticeable in smaller individuals. Ventral surface of dentaries grey to dark with irregularly-distributed light stripes. Some individuals from Urugua-í reservoir have paler dentaries. Pectoral and pelvic fins orange-yellow with a series of dark spots. Dorsal, anal and caudal fins have dark spots more visible on the rays and interradial membranes, forming bands.

Color In alcohol. Body dark brown dorsally. Chevron-shaped lateral blotches and a rounded spot on the peduncle more conspicuous. A dark

Fig. 2. *Hoplias guri*, new species, MACN-Ict 9634, paratype, 197 mm SL, Urugua-í Reservoir, Misiones, Argentina; **A**, lateral; **B**, dorsal and **C**, ventral views.

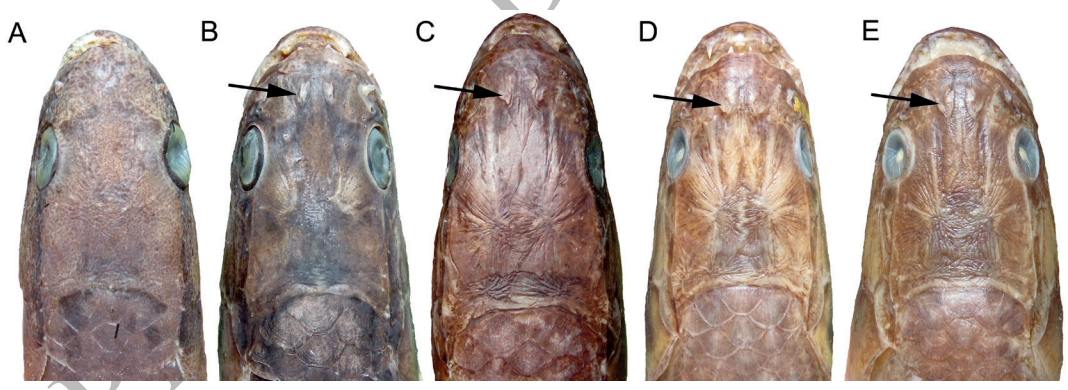

Fig. 3. Dorsal surface of head in species of the *Hoplias malabaricus* group. **A**, *H. malabaricus* MNHN 2003-2529, 148 mm SL; **B**, *H. guri* UNMDP 5349, 162 mm SL; **C**, *H. auri* UNMDP 5205, 194 mm SL; **D**, *H. misionera* UNMDP 3327, 171 mm SL; **E**, *H. argentinensis* UNMDP 502, 170 mm SL. Arrow indicates the notorious ridge in the posterior angular end of the ascending process of the premaxilla in all species but *H. malabaricus*.

lateral stripe, more conspicuous in smaller (< 220 mm SL) individuals. Spots and markings on the head still visible, but paler. Infraorbital bands less conspicuous or absent. Second infraorbital band, noticeable. A dark ring on the sclera of the eyes visible dorsally.

Distribution. *Hoplias guri* is known from the Iguazu River Basin and the Urugua-i Reservoir in Argentina and one tributary of the Tiete River in the upper Paraná Basin, Brazil. All localities of occurrence in the Iguazu and Urugua-i Reservoir are situated above the respective waterfalls. Molecular evidence based on mitochondrial marker COI suggests that *H. guri* also inhabits other localities in the upper Paraná (Itaipu Reservoir) and Iguazu (Brazil) rivers, as well as in Paraiba

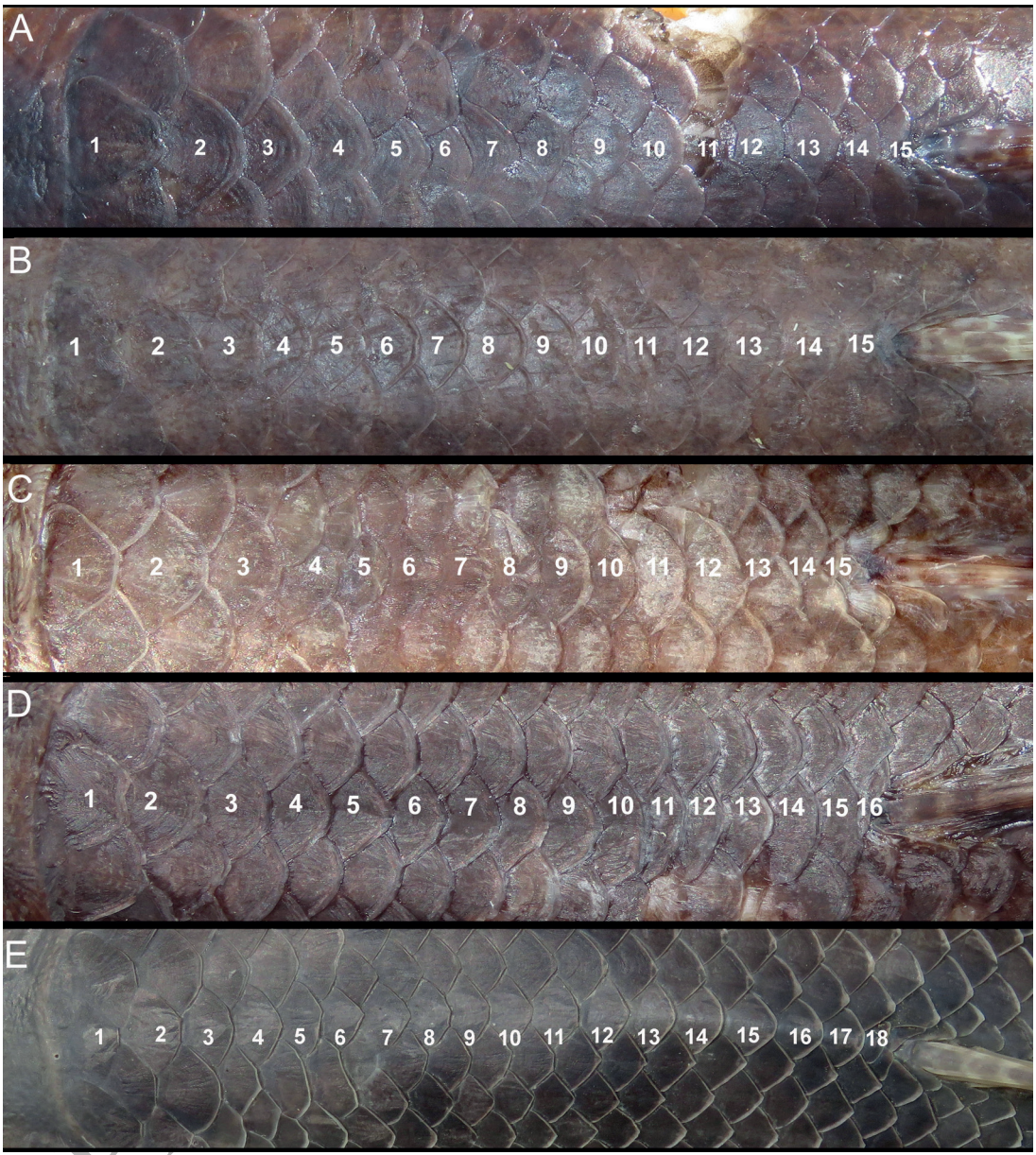

Fig. 4. Pre-dorsal scales in species of the *Hoplias malabaricus* group: **A**, *H. guri* UNMDP 5349, 162 mm SL; **B**, *H. malabaricus* MNHN 2003-2529, 148 mm SL; **C**, *H. misionera* UNMDP 3327, 171 mm SL; **D,** *H. auri* UNMDP 5204, 245 mm SL; **E**, *H. argentinensis* CFA-IC-4364, 188 mm SL.

do Sul and other Atlantic drainages (Fig. 6). In the Iguazu River and the Parana Basin, *H. guri* is sympatric with *H. argentinensis* (Dagosta *et al.*, 2024), *H. mbigua* (Dos Reis *et al.*, 2020), *H. misionera* (Mezzaroba *et al.*, 2021) *and H. intermedius* (Oyakawa and Mattox, 2009).

Etymology. This species is dedicated to all those children (*nguri* in guarani), who, like the one in the folk song (*Guri Pescador*) of Osiris Rodriguez Castillo, have grown up dreaming for a huge bite of a thraira. To all our loved sons and daughters: Julián Bogan, Julia and Clara Iucci, Joaquín and Manuel Rosso, Iñaki, Clara and Juan Blas Díaz de Astarloa.

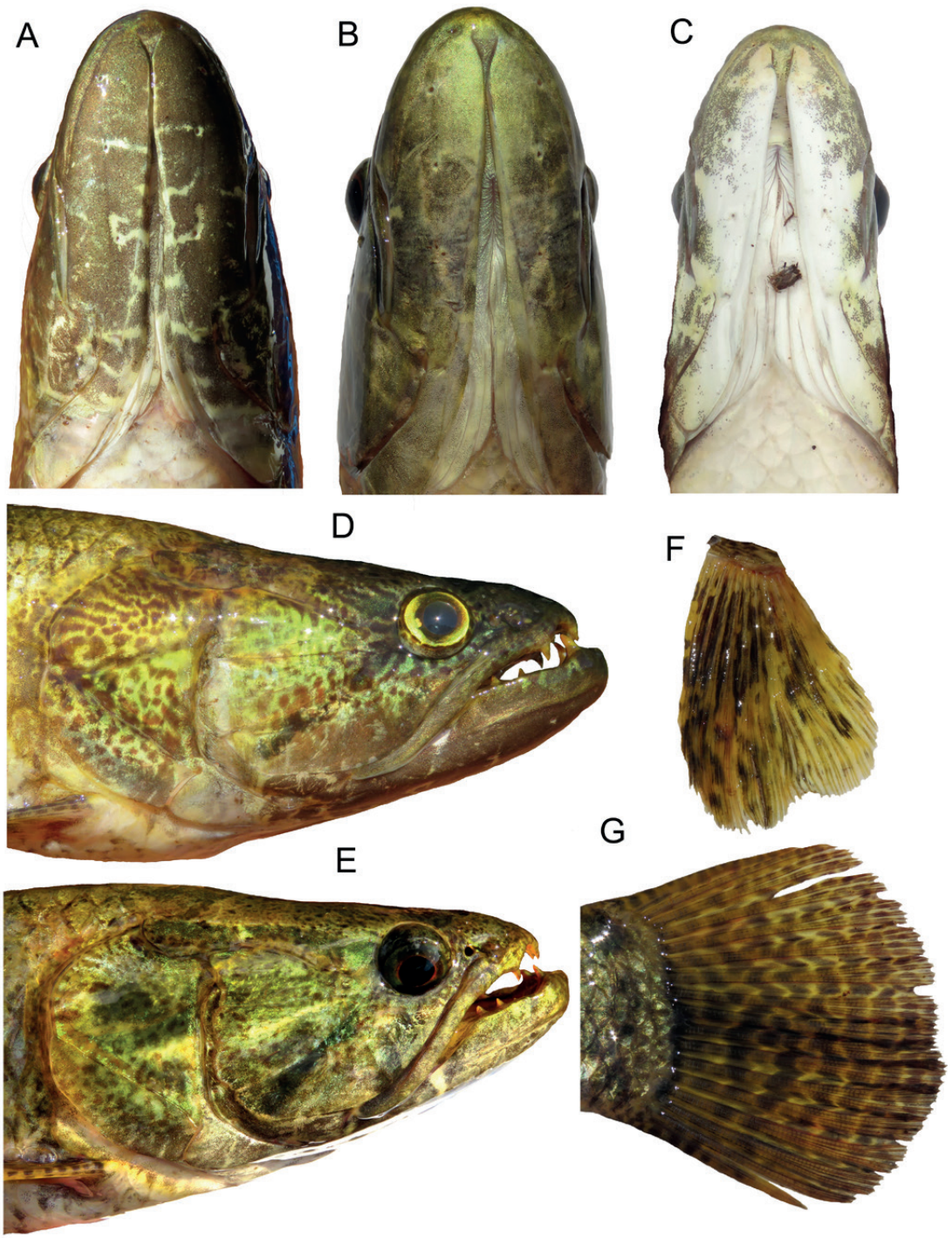

Fig. 5. Colour in life of *Hoplias guri*, new species. **A-C**: different patterns of colouration of ventral surface of dentaries. **A**, MACN-Ict 13259, 262 mm SL; **B**, UNMDP 5271, 202 mm SL; **C**, MNHN-IC-2025-0033, 162 mm SL. **DE:** lateral view of head. **D**, MACN-Ict 13259, 262 mm SL; **E**, UNMDP 5271, 202 mm SL. **F**, pectoral UNMDP 5285, 417 mm SL and **G**, caudal UNMDP 5348, 190 mm SL, fins.

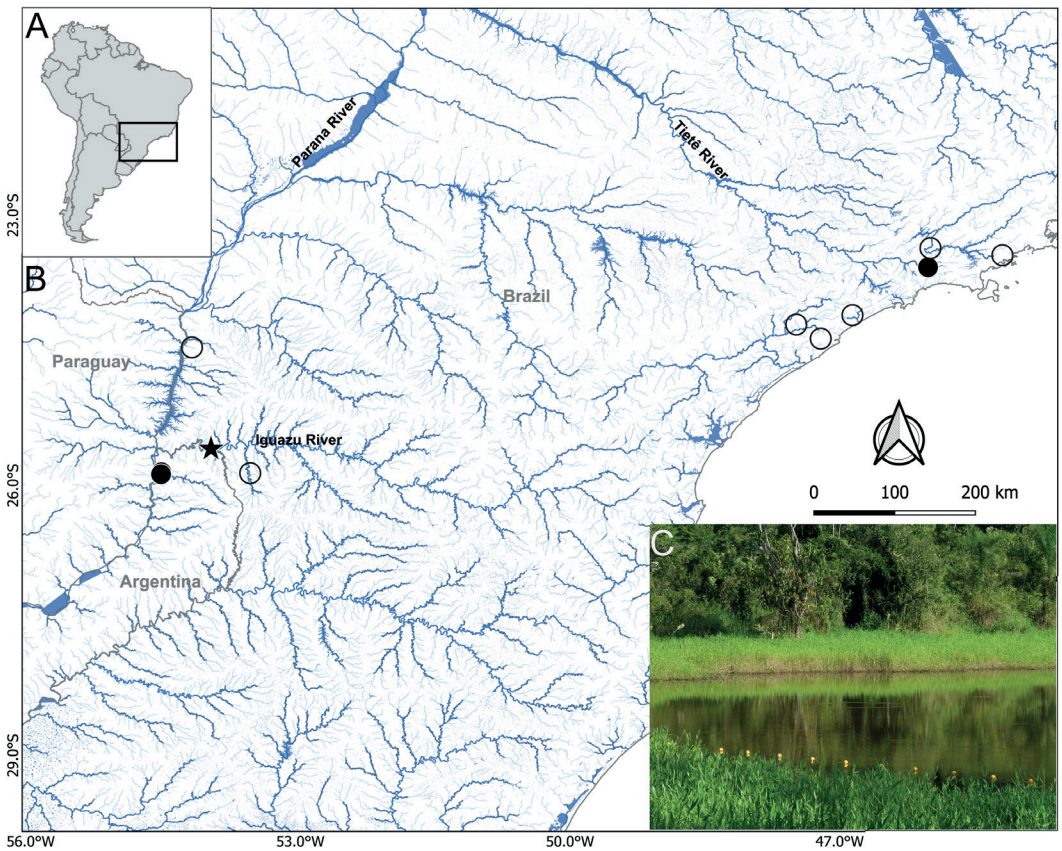

Fig. 6. Geographic distribution of *Hoplias guri*, new species. **A,** Geographic context at the continental scale. **B,** Occurrence sites of type material (black circles); type locality is denoted with a black star. Localities where only molecular data is available for referred specimens (white circles). **C,** Small Lake tributary of San Antonio River, Iguazu Basin, alongside rute 25, near Prefectura Naval Argentina, Comandante Andresito, Misiones.

Key to the species of the *Hoplias malabaricus* group

1a Last vertical series of scales on caudal-fin base curved ..... *Hoplias misionera*

1b Last vertical series of scales on caudal-fin base nearly straight 2

2a Thirty-seven to 40 scales on the lateral line, 38–41 vertebrae (low count group *sensu* Rosso *et al.*, 2018) 3

2b Forty to 46 scales on the lateral line, 42–43 vertebrae (high count group *sensu* Rosso *et al.*, 2018) 5

3a Dorsal surface of head smooth, without any notorious ridge ..... *H. malabaricus*

3b A marked ridge in the ascending process of premaxilla (Fig. 3) 4

4a Premaxillary teeth 8–10, pectoral fin-length (mean 16.85, 15.85–19.01 %SL), orbital diameter (mean 17.28, 13.94–20.84 %SL) .... *H. auri* (Amazon Basin)

4b Premaxillary teeth 10–11, pectoral fin-length (mean 18.30, 16.85–19.58 %SL), orbital diameter (mean 15.70, 13.15–20.06 .... *H. guri* sp nov. (Paraná Basin)

5a Twenty-two to 24 scales around caudal peduncle ..... *H. microlepis*

5b Twenty scales around caudal peduncle 6

6a Five distinctive transverse bands in the lower jaw, dorsal profile of head concave .... *H. mbigua*

6b No distinctive transverse bands in the lower jaw, dorsal profile of head straight 7

7a Forty-one to 44 scales on the lateral line, snout width less than 25% of head length .... *H. argentinensis*

7b Forty or 41 scales on the lateral line, snout width more than 29% of head length .... *H. teres*

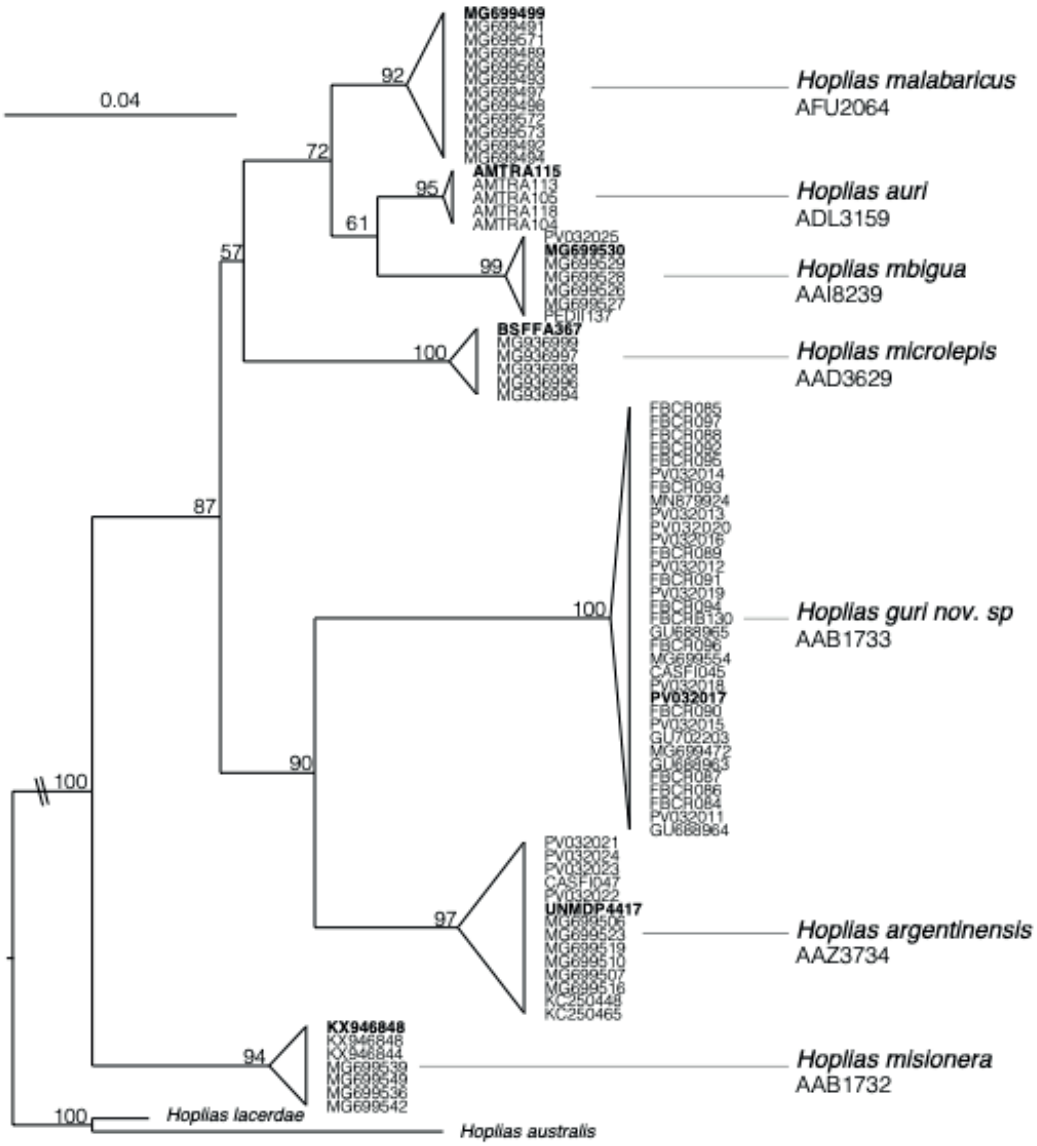

Fig. 7. Maximum likelihood tree based on COI mitochondrial marker of *Hoplias guri* and related species of the *H. malabaricus* group. All the sequences labelled with Genbank or BOLD iD accession numbers. The holotype or a topotype of each species are remarked. Values in branches indicate the bootstrap values

Material Examined:

Hoplias aimara: French Guiana: MNHN A-9968 (dry mount), 1, 770 mm SL, holotype; Cayenne. ***Hoplias argentinensis***: All from Argentina. Holotype: UNMDP 4417, 302 mm SL. Santa Fe Province: Río Paraná Basin: Río Coronda, J. J. Rosso, E. Mabragaña & M. González-Castro, 3 Dec 2015. Paratypes: Buenos Aires Province: UNMDP 492, 1, 410 mm SL; UNMDP 502, 1, 170 mm SL; UNMDP 503, 1, 145 mm SL; and UNMDP 504, 1, 159 mm SL; Ascensión: Río Paraná Basin: Río Rojas; J. J. Rosso *et al.*, 10 Dec 2010. CFA-IC 3825, 1, 215 mm SL; Junín: Laguna Gómez; J. R. Miranda *et al.*, 30 Sep 2014. CFA-IC 4364, 2, 125–188 mm SL; Río de La Plata, Punta Indio wetlands; S. Bogan, 22 Mar 2015. CFA-IC 4355, 1, 140 mm SL; Río Paraná Basin, Cañada Arias; S. Bogan, 21 Mar 2015. CFA-IC 1741, 1, 138 mm SL; Arroyo El Destino; L. Protogino *et al.*, 19 Jan 2007. CFA-IC 2452, 1, 105 mm SL; Río Paraná; J. M. Meluso & S. Bogan, 4 Feb 2013. CFA-IC 4665, 1, 315 mm SL; Río de La Plata; J. Meluso *et al.*, 6

Jul 2015. MLP 6586, 1, 202 mm SL; Punta Lara; M. Galván & E. Martín, 27 Jun 1960. Entre Ríos Province: UNMDP 1279, 1, 240 mm SL; Embalse Salto Grande; J. J. Rosso & E. Mabragaña, 12 Sep 2011. UNMDP 1370, 1, 309 mm SL and UNMDP 1371, 1, 265 mm SL; Río Paraná-Guazú, Delta of Río Paraná; J. J. Rosso *et al.*, 7 Oct 2011. UNMDP 1595, 1, 98 mm SL; Arroyo Bergara; J. J. Rosso & E. Mabragaña, 9 Sep 2011. UNMDP 2452, 1, 202 mm SL and UNMDP 2453, 1, 203 mm SL; Río Paraná basin: Laguna El Pescado: J. J. Rosso & E. Mabragaña, 11 Nov 2012. UNMDP 2565, 1, 134 mm SL; Río Paraná Basin: Arroyo Nogoyá; J. J. Rosso & E. Mabragaña, 10 Nov 2012. UNMDP 2616, 1, 116 mm SL; Río Uruguay Basin: Arroyo Ayuí; J. J. Rosso & E. Mabragaña, 14 Nov 2012. CFA-IC-3480, 1, 116 mm SL; Arroyo Urquiza; A. Miquelarena *et al.*, 18 Nov 2005. CFA-IC 5812, 1, 190 mm SL; Arroyo El Tigre; H. Lopez *et al.*, 17 Aug 2010. Santa Fe Province: Río Paraná Basin: UNMDP 3867, 1, 177 mm SL; Arroyo Leyes; J. J. Rosso *et al.*, 25 Apr 2015. UNMDP 4416, 1, 342 mm SL; UNMDP 4423, 1, 239 mm SL; UNMDP 4425, 1, 203 mm SL; UNMDP 4426, 1, 206 mm SL; UNMDP 4427, 1, 314 mm SL; and UNMDP 4428, 1, 351 mm SL; Río Coronda: collected with the holotype. CFA-IC-3976, 1, 220 mm SL; Río Carcaraña; Y. P. Cardoso *et al.*, 24 Nov 2014. Cordoba Province: MLP 11302, 1, 87 mm SL; Río Primero, before Capilla de los Remedios; 24 Jul 1939. Santiago del Estero Province: CFA-IC 5537, 1, 134 mm SL; Embalse Tacañitas, J. Montoya-Burgos *et al.*, 8 Nov 2015. CFA-IC 5519, 2, 124– 165 mm SL; Río Dulce; J. Montoya-Burgos *et al.*, 8 Nov 2015. Tucumán Province: CFA-IC 5655, 1, 90 mm SL; Río Vipos; J. Montoya-Burgos *et al.*, 11 Nov 2015. Misiones Province: Río Uruguay Basin: CFA-IC-4414, 1, 165 mm SL; Arroyo Dorado; S. Bogan & J. M. Meluso, 4 May 2015. UNMDP 4837, 1, 176 mm SL; Arroyo Fortaleza; J. J. Rosso *et al.*, 8 Mar 2017. ***Hoplias auri***. Holotype: UFOPA - I 1353, 229 mm SL, Brazil, Pará State, Tapajos basin: Crepori River, Itaituba region, Creporizao District: Lago do Sr. Pena, 6° 50´ 1.3´´S, 56° 50´ 50.90´´W, L. Rodrigues, J. Santos, C. Silva, M. Brito, 21 July 2016. Paratypes All from Brazil, Pará State, Tapajos basin: Crepori River, Itaituba region, Creporizao Village: Lago do Sr. Pena, 6° 50´ 1.3´´S, 56° 50´ 50.90´´W, UFOPA - I 1353, 3, 159–202 mm SL, L. Rodrigues, J. Santos, C. Silva, M. Brito, 20–21 July 2016, UNMDP 5206, 1, 163 mm SL, L. Rodrigues, J. Santos, C. Silva, M. Brito, 20 July 2016, Lago Creporizao, 6° 49´ 11.56´´S, 56° 51´ 4.52´´W, L. Rodrigues, J. Santos, C. Silva, M. Brito, 21 July 2016, UFOPA - I 1355, 2, 153–154 mm SL, Igarapé da Sra. Maria Brito, 6° 49´ 12.50´´S, 56° 50´ 52.80´´W, L. Rodrigues, J. Santos, C. Silva, M. Brito, 20 July 2016: UFOPA - I 1354, 8, 138–321 mm SL, UNMDP 5204, 1, 245 mm SL, UNMDP 5205, 1, 194 mm SL, Igarapé Creporizao, 6° 49´ 09´´S, 56°51´ 31´´W, C. Duarte, 30 April 2008: INPA 32732, 2, 30.82–44.28 mm SL. ***Hoplias australis***: Argentina: Misiones: UNMDP 1991, 1, 43.9 mm SL; Río Uruguay Basin: Arroyo Ramos. UNMDP 2721, 1, 271 mm SL; UNMDP 2722, 1, 220 mm SL; UNMDP 2723, 1, 171 mm SL; and UNMDP 2724, 1, 166 mm SL; Río Yabotí Basin: Arroyo Oveja Negra. ***Hoplias curupira***: Brazil: Pará State: LBP 67349, 1, 153 mm SL; Itaituba: Rio Tapajos. ***Hoplias intermedius***: Brazil: Sergipe State: LBP 48702, 1, 231 mm SL; Gararu: Rio Sao Francisco.

Hoplias lacerdae: Argentina: Misiones: Río Uruguay Basin: UNMDP 570, 1, 346 mm SL; UNMDP 571, 1, 350 mm SL; and UNMDP 594, 1, 163 mm SL; Arroyo Ramos. UNMDP 2725, 1, 192 mm SL and UNMDP 2735, 1, 244 mm SL; Río Yabotí. ***Hoplias malabaricus***: ZMB 3515, 1, 167 mm SL; lectotype; South America, probably Suriname. ZMB 33059, 1, 69 mm SL; paralectotype; South America, probably Suriname. MHNN 773, 1, holotype of *Erythrinus macrodon*; Brazil: Bahia: Lake Almada; photograph and x-rays. MNHN 4409, 1, 108 mm SL; MNHN 4421, 3, 175–237 mm SL; MNHN A-9746, 1, 93 mm SL; MNHN A-9747, 1, 183 mm SL; and MNHN A-9748, 1, 245 mm SL; syntypes *of Macrodon tareira*; Brazil and French Guiana. USNM 1112, 1, 111 mm SL, syntype of *Macrodon ferox*; Trinidad Island; photographs and x-rays. ***Hoplias mbigua***: CI-FML 6763, 1, 224 mm SL, holotype; Argentina: Misiones: Río Paraná, Nemesio Parma. CI-FML 6764, 2, 224248 mm SL; collected with the holotype. LGE-P 314, 1, 237 mm SL and LGE-P 435, 1, 154 mm SL; Río Paraná, Garupá. LGE-P 316, 1, 229 mm SL; Río Paraná, mouth of Arroyo Yabebiry. LGE-P 317, 1, 302 mm SL; Río Paraná, Toma de Agua Eriday.

Hoplias microlepis: BMNH 1864.1.26.221, 1, 278 mm SL, lectotype; Panamá: Río Chagres. BMNH 1864.1.26.222, 1, 225 mm SL and BMNH 1864.1.26.309, 1, 176 mm SL, paralectotypes; Panamá: Río Chagres. BMNH.1860.6.16.128, 1, 293 mm SL; and BMNH.1860.6.16.154, 1, 124 mm SL, paralectotypes; Ecuador. LBP 18503, 1, 215 mm SL; Panamá: Atlantic Drainage: Río Llano Sucio. ***Hoplias misionera***: Argentina: UNMDP 574, 1, 164 mm SL, holotype; Misiones: Río Uruguay Basin: stream tributary to Río Acaraguá. UNMDP 1868, 1, 40 mm SL; UNMDP

1950, 1, 49 mm SL; and UNMDP 1951, 1, 50 mm SL; Formosa: Río Paraguay: Laguna Oca. UNMDP 1983, 1, 75 mm SL; Chaco: Río Paraná. UNMDP 3320, 1, 174 mm SL; UNMDP 3391, 1, 149 mm SL; and UNMDP 3392, 1, 104 mm SL; same locality as holotype. UNMDP 3321, 1, 142 mm SL; and UNMDP 3322, 1, 148 mm SL; Formosa: Río Paraguay: Riacho Saladillo. UNMDP 3327, 1, 171 mm SL; UNMDP 3328, 1, 146 mm SL; and UNMDP 3329, 1, 134 mm SL; Formosa: Río Paraguay: Riacho Salado. UNMDP 3371, 1, 154 mm SL; and UNMDP 3376, 1, 165 mm SL; Formosa: Río Paraguay: Riacho Mbiguá. Brazil: LBP 32184–32,186, 3, 77–155 mm SL; Sao Paulo: marginal lagoon: Paraná River. ***Hoplias teres***: MNHN-4377-1, 1, 121 mm SL and MNHN-4377-2, 1, 116 mm SL, syntypes; Venezuela: Lago Maracaibo.

Molecular analyses

Nine COI sequences were obtained for *Hoplias guri*, including localities on the Iguazú River and the Urugua-í Reservoir. All of these sequences were uniquely assigned to BIN AAB1733 in BOLD System Workbench. Three additional sequences were recovered from the type material derived from previously revised and sequenced specimens (Cardoso *et al*., 2018) including one locality in the upper Parana River, Brazil. Several public sequences (n=20) of unsurvey specimens matched this BIN, including localities in the upper Parana and Paraiba do Sul rivers. In addition, four sequences of *H. argentinensis* and one sequence of *H. mbigua* from individuals collected together with the *H. guri* type series were obtained and used. The distance of *H. guri* to the nearest neighbor (a specimen labeled with the BIN AAB3734 and corresponding to *H. argentinensis*) was 6.09% and the average intra-specific distance was 0.18%. The overall mean distance with the rest of the species in the *H. malabaricus* group was very similar to each other, ranging from 7.14 from *H. argentinensis* to 8.59 from *H. misionera* (Table 2).

The best model selected for the full set of analyzed sequences (n=86) wasTN+F+G4. Of a total 652 bp, 138 bp were parsimony-informative sites and 490 bp were constant sites. The resulting molecular tree (Fig. 7) shows that all species of *H. malabaricus* group, including the new species *H. guri*, are monophyletic (very strongly supported). All individuals that make up the type series of *H. guri* together with the sequences of the specimens referred from the upper Parana River were grouped into a single clade (AAB1733). This species is included in the *H. malabaricus* group, with its sister species being *H. argentinensis*. Interspecific relationships were only moderately supported.

DISCUSSION

Integrative taxonomy has contributed in recent years to unravel and describe a huge number of cryptic fish species (e.g. Cardoso *et al*., 2019; Faria *et al*., 2021; Guimarães *et al*., 2021), especially in taxa where traditional morphometry is very conservative between species, as is the case of the *H. malabaricus* group. In this work, we formally describe *Hoplias guri*, a lineage that based on molecular data had been previously reported as part of the *H. malabaricus* group (Pereira *et al*., 2011) and had been assumed as a putative new species based on DNA barcode distances (Cardoso *et al*. 2018). Here, a combination of morphological, morphometric, meristic and molecular evidence supports the evolutionary independence of *H. guri* as a single specific lineage. The interspecific COI divergence of *H. guri* with other species of the *H. malabaricus* group was greater than 7% which is consistent with previous divergence values observed among members of this group. The clustering of all individuals of the new species into a single BIN (AAB1733) and the monophyly of this group supported the barcode gap with strong molecular evidence. Furthermore, in a recent time-calibrated phylogeny based on ultra-conserved elements of the family Erythrindae, *H. guri* (individual LBPV38246, also used in our study) is postulated to have emerged around 4.6 Ma as a distinctive clade, very close to *H. argentinensis* (Conde-Saldaña *et al*., 2025), its closest relative detected here with the COI fragment.

The formal description of *H. guri* linked to a well-supported molecular lineage of the *H. malabaricus* group occurring in La Plata Basin, represents a significative contribution to the taxonomy of the Family Erythrinidae. In particular, field sampling efforts over the past 15 years in Argentina, have demonstrated a consistency between the diversity of molecular lineages and the taxonomic species associated to these lineages. This suggests that most (if not all) species of *Hoplias* inhabiting the freshwaters of lower La Plata River in Argentina had been well documented, revised and taxonomically characterized.

As observed in this study, the occurrence of three species of the genus *Hoplias* in the Iguazu River living in sympatry (*H. argentinensis*, *H.*

Table 2. Genetic divergences over sequence pairs between species of the *H. malabaricus* group. Analyses were conducted using the maximum likelihood model.

	H. guri	*H. argentinensis*	*H. mbigua*	*H. auri*	*H. microlepis*	*H. misionera*
H. argentinensis	0.0714					
H. mbigua	0.0787	0.0703				
H. auri	0.0748	0.0670	0.0360			
H. microlepis	0.0839	0.0681	0.0461	0.0572		
H. misionera	0.0859	0.0773	0.0686	0.0635	0.0830	
H. malabaricus	0.0718	0.0625	0.0449	0.0303	0.0580	0.0646

mbigua and *H. guri*) is a novelty for freshwaters of lower La Plata Basin. Moreover, recent studies (Dos Reis *et al*., 2020; Perin *et al*., 2024) show that *H. misionera* also inhabits the middle and lower Iguazu River. These authors suggested that this species had been introduced in this system as occurred with other allochthonous Neotropical fishes of the genera *Salminus*, *Brycon*, *Megaleporinus*, *Schizodon, Prochilodus,* among many others (Pini *et al*., 2021). Highly invasive species as *Ictalurus punctatus, Clarias gariepinus*, *Coptodon rendalli*, *Oreochromis niloticus* are also present in these waters (Mezzaroba *et al*., 2021). In this scenario, the conservation status of *H. guri* deserves some attention, as well as all the overall diversity of this region which is still largely underestimated (new species are described every year). Our results show a wide geographic distribution for *H. guri*, suggesting a significant area of occupancy throughout its geographic range. Furthermore, this species was collected in different types of aquatic habitats, including floodplain waters of the Iguazu River, reservoirs and tributaries of the upper Parana River, suggesting a good adaptability to different environmental drivers. Regardless, the occurrence in sympatry of three congeneric species (*H. argentinensis*, *H. mbigua* and *H. misionera*) along with highly invasive representatives of exotic fish fauna and other anthropogenic stressors, undoubtedly represents a potential threat to its conservation.

The use of public sequences to better describe the molecular identity of a new species also contributes to other relevant aspects. For instance, the actual geographic distribution of *H. guri* was better represented, including some of the extreme occurrences of its geographic range, in Paraiba do Sul and Atlantic drainages of Sao Paulo, Brazil (Pereira *et al*., 2011). On the other hand, Perin *et al*. (2024), incorporated sequences that now belong to the type material of *H. guri* in their analyses. Therefore, their results allow the inclusion of the Capanema River (Iguazu Basin) as another locality for this species, as well as characterizing its cytotype as belonging to the karyotype A1. The use of publicly available sequences assigned to the type material of taxonomic species is also useful in helping to resolve misidentifications. A small juvenile earlier identified as *H. mbigua* (LIC-444) in the Itaipu Reservoir (Pereira *et al*., 2021) has an associated COI sequence (MN879924) that perfectly matched with the molecular identity of *H. guri*.

The challenge in the taxonomic identification of specimens belonging to species of genus *Hoplias* has been widely postulated by several authors (Galindo *et al*. 2020; Mezzaroba *et al*. 2021; *Pereira et al*. 2021; Dos Reis *et al*. 2020; Dagosta *et al*. 2024). In this sense, the description of *H. guri* together with all the recent descriptions for the *H. malabaricus* group with type material associated with a robust molecular identity, represent an important benchmark to aim in this taxonomic challenge. Therefore, the larger number of monophyletic molecular lineages (BINs) identified for the genus *Hoplias* (Cardoso *et al*., 2018; Guimarães *et al*., 2022), but still without taxonomic identity, are very good candidates to describe new taxonomic species. For this reason, we strongly encourage colleagues from other regions to continue using these tools to discover and assess the enormous diversity of the *Hoplias* genus. Moreover, we firmly believe that collaborative research is key to keep adding more bricks to the great wall of knowledge of this complex taxonomic group.

Finally, this work not only contribute to the inventory of biological diversity in the study region but also aims to achieve precision (through the use of integrative approaches) in the identification of species belonging to a group with complex taxonomy. This certainly represents an important contribution to the conservation and management of the biodiversity in the La Plata Basin and neighboring drainages.

ACKNOWLEDGMENTS

The authors thank the authorities of the Instituto Misionero de Biodiversidad (IMIBIO) for the sampling permits and support during field expeditions. We also thank the authorities of Prefectura Naval Argentina and Prefecto Carlos Medina. Mr. Jorge Anfuso assisted during field sampling in the Urugua-í Reservoir. Special recognition to Dr. Carlos Capiel of the Instituto Radiologico Mar del Plata for his willingness to assist with X-rays and imaging. This research was supported by financial and logistic contributions of Fundación de Historia Natural Félix de Azara - Universidad Maimónides (Adrián Giacchino) and Research Projects conducted by Dr. Juan Martín Díaz de Astarloa (PICT-2018-00790) and Dra. Yamila P. Cardoso (PIBBA-0012, PICT-2021-0022). We would like to specially thank Juan Manuel Meluso, Tomás Favier Dubois, and Yolanda Davies. The authors also thank Reserva San Sebastián (Matias Romano) for the opportunity to work on their premises. Raphael Covain, from the Museum of Natural History of Ginebra, kindly provided material for the type series.

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Doi: 10.22179/REVMACN.27.915

Recibido: 15-II-2025
Aceptado: 03-IX-2025