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Illustrated identification key for Characidae (Characiformes) fishes from a protected area and vicinity, upper Rio Paraná, Brazil

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ABSTRACT

Characidae is the most diverse family of Neotropical ichthyofauna and has a conservative external morphology, making the identification process difficult without comparative material. Producing identification materials aimed at non-specialists is necessary to accelerate research on the ichthyofauna, contribute to its preservation, and assist in training human resources. This work aimed to elaborate an illustrated dichotomous identification key for the fish of this family around the protected area Biological Refuge of Santa Helena and adjacent rivers, upper Rio Paraná basin, Brazil-Paraguay border. This region was inventoried quarterly from November 2017 to November 2019, and additional collections occurred from 2019 to 2022. For the elaboration of the identification key, the fish were divided into increasingly less inclusive groups based on the presence, absence, or state of morphological characteristics. These characteristics were photographed under a stereoscopic microscope, and auxiliary figures for the identification key were provided. This work includes 26 species, including three notable additions to the region's existing identification guides: *Deuterodon luetkenii*, *Serrapinnus kriegi*, and *Psalidodon* sp. The latter represents a possible new species. It also discusses taxonomic issues and compares similar species.
Keywords: Ichthyofauna. Taxonomy. Itaipu reservoir.

Chave de identificação ilustrada para Characidae (Characiformes) de uma unidade de conservação e áreas adjacentes, bacia do alto Rio Paraná, Brasil

RESUMO

Characidae é a família mais diversa da ictiofauna Neotropical e apresenta morfologia externa conservadora, dificultando o processo de identificação sem material comparativo. A produção de materiais de identificação direcionados para não-especialistas é necessária para acelerar as pesquisas sobre a ictiofauna, contribuir para sua preservação e auxiliar no treinamento de recursos humanos. O objetivo deste trabalho foi elaborar uma chave de identificação dicotômica ilustrada para os peixes desta família do entorno da Unidade de Conservação Refúgio Biológico de Santa Helena e rios adjacentes, bacia do Alto rio Paraná, fronteira Brasil-Paraguai. Esta região foi inventariada trimestralmente entre novembro de 2017 e novembro de 2019, e coletas adicionais ocorreram entre 2019 e 2022. Para a elaboração da chave de identificação os peixes foram divididos em grupos cada vez menos inclusivos baseados na presença, ausência ou estado de características morfológicas. Estas características foram fotografadas em um microscópio estereoscópio e figuras auxiliares à chave de identificação são fornecidas. Este trabalho inclui 26 espécies, incluindo três

notáveis adições aos guias de identificação existentes para a região: *Deuterodon luetkenii*, *Serrapinnus kriegi* e *Psalidodon* sp. A última representa uma possível espécie nova. Também discute questões taxonômicas e compara espécies similares.
Palavras-chave: Ictiofauna. Taxonomia. Reservatório de Itaipu.

INTRODUCTION

The Characidae family comprises 1.252 species and represents little more than half of the species in the Characiformes order (FRICKE et al., 2023). Also, it is the most diverse family in Neotropical ichthyofauna (ALBERT et al., 2011). This immense diversity, combined with a conservative external morphology (MIRANDE, 2019), non-monophyletic genera defined with homoplastic characteristics (e.g., *Hyphessobrycon* Durbin, 1908; see ELÍAS et al., 2023), and many species yet to be described, makes identification at the species level demanding. This family lacks a comprehensive manual for identification. For this purpose, it is necessary to resort to the available taxonomic works carried out at the level of specific watersheds or, more rarely, to the few published reviews for subfamilies, genera, or species complexes (BUCKUP, 2021).

The Area of Relevant Ecological Interest (ARIE) known regionally as "Refúgio Biológico de Santa Helena" (hereafter, Biological Refuge of Santa Helena) is a protected area included on the east banks of the Itaipu reservoir, upper Rio Paraná basin, in the municipality of Santa Helena, Brazil. Its ichthyofauna was recently inventoried by Brandão et al., (2022). This work, together with other samplings in the surrounding rivers and streams, revealed the presence of three species of Characidae in addition to those reported by Ota et al., (2018), the last identification guide including the Itaipu reservoir, reinforcing that the richness of small-sized species in this region still needs taxonomic studies (PEREIRA et al., 2021). Besides that, some of the recorded species present significant taxonomic problems, such as *Psalidodon* aff. *paranae* (Eigenmann, 1914), the most abundant characid in streams east of the Itaipu reservoir (PEREIRA et al., 2021).

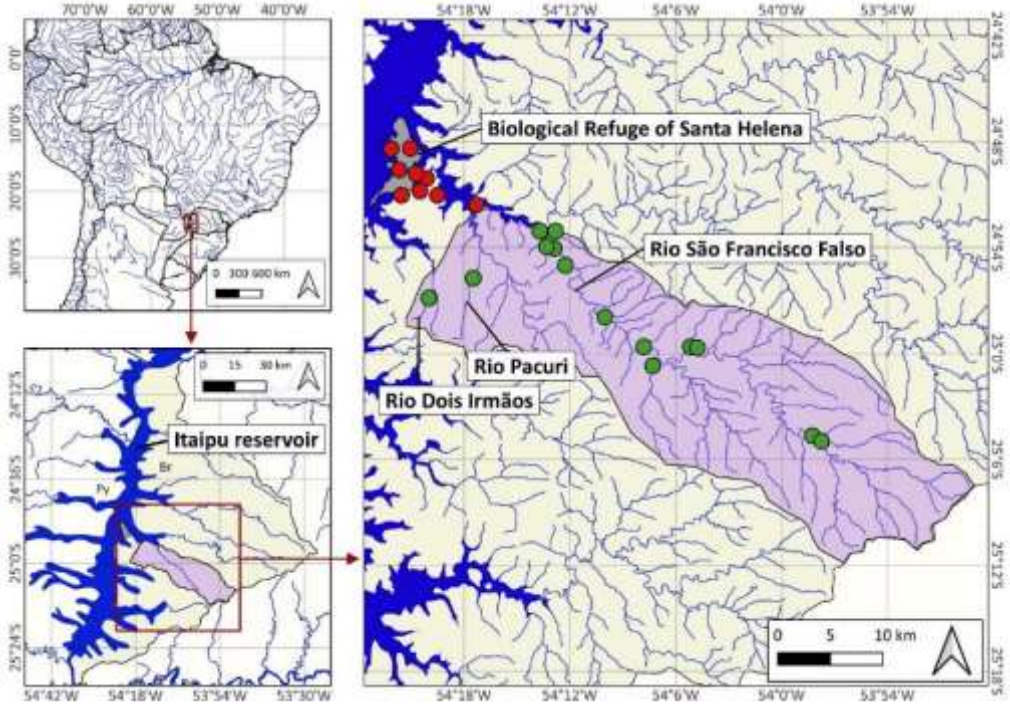
Producing identification materials aimed at non-specialists is necessary to accelerate research on the ichthyofauna, contribute to its preservation, and assist in training human resources (FISCHER, 2013). In this regard, photographs can significantly aid the interpretation of diagnostic characteristics when no comparative material is available during identification, especially considering the similar morphology between some species of characids. This work provides an illustrated dichotomous identification key for the Characidae fishes around the protected area Biological Refuge of Santa Helena

and adjacent Brazilian rivers, compares similar species, and discusses taxonomic issues associated with the species in the study region.

MATERIAL AND METHODS

The study region can be divided into two areas delimited based on the type of habitat (Figure 1). The first corresponds to the lentic waters in the vicinity of the Biological Refuge of Santa Helena in the Itaipu Reservoir, including the flooded portion of the Rio São Francisco Falso. The second corresponds to the semi-lotic and lotic waters of the Rio São Francisco Falso, Rio Pacuri, and Rio Dois Irmãos, tributaries of the Brazilian margin of the Itaipu reservoir.

Figure 1 – Location of the study region. Red dots represent the sampled locations in the vicinity of the Biological Refuge of Santa Helena (highlighted in grey), and the green dots represent the sampled locations in the adjacent Brazilian rivers (highlighted in lilac). Source: https://www.ibge.gov.br/. Datum: SIRGAS 2000.



The study region was sampled quarterly on the margins of the Biological Refuge of Santa Helena and the lower portion of the Rio São Francisco Falso from November 2017 to November 2019 (Sistema de Autorização e Informação em Biodiversidade (SISBIO) nº 57181 and Sistema Nacional de Gestão do Patrimônio Genético e Conhecimentos Tradicionais Associados (SisGen) nº A6AE3EF and nº A3242EO); additional expeditions were also carried out in the superior stretches of the Rio São

Francisco Falso, Rio Pacuri, and Rio Dois Irmãos from 2019 to 2022 (SISBIO nº 38532, SisGen nº AD02205 and nº A8ADC41). All the fishes were collected using active sampling with a sieve, dragging net, or cast net, except *Galeocharax gulo* (Cope, 1870), which was only collected using passive sampling with a set of gillnets with mesh sizes of 3 to 7 cm exposed for approximately 12 hours and *Oligosarcus paranensis* Menezes & Géry, 1983, which was collected with both active and passive sampling. The fishes were deposited in the Coleção Ictiológica da Universidade Tecnológica Federal do Paraná, Campus Santa Helena (CISH), and in the Coleção Ictiológica do Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (NUP).

For the elaboration of the identification key, the species were divided into increasingly less inclusive groups based on the presence, absence, or state of morphological characteristics, thus characterizing each step of the key. The morphologic characteristics were photographed under a stereo microscope Olympus SZ51 with a smartphone holder. The photos were shot on a Redmi Note 7 smartphone, and the figures were edited in the GIMP 2.10.32 software (THE GIMP DEVELOPMENT TEAM, 2022). Figures 2–4 are organized alphabetically by species names. Figures 6–11 are placed at the end of the Results and Discussion section and organized according to the steps of the identification key and the similarity of the photographed characteristics.

The morphometric and meristic data were obtained according to Fink and Weitzman (1974), except for the count of scale series below the lateral line, which was counted as the number of scale series between the lateral line scale series and the pelvic-fin origin. Measurements are presented as percentages of standard length (SL) or head length (HL) for subunits of the head. Unbranched rays are expressed in lowercase Roman numerals, and branched rays in Arabic numerals. In the results and discussion, the measurements and counts are followed by the expression "(n = x)", where x represents the number of specimens analyzed, or by the respective reference when data were obtained from the literature. Information on non-native species is according to Reis et al., (2020) (but see the Results and Discussion for details). The classification of the subfamilies follows Mirande (2019).

RESULTS AND DISCUSSION

A total of 26 Characidae species were found in both areas, distributed in 17 genera and five subfamilies (Table 1; Figures 2–4). *Galeocharax gulo*, *Serrapinnus kriegi*

(Schindler, 1937), *Hyphessobrycon moniliger* Moreira, Lima & Costa, 2002, *Moenkhausia gracilima* Eigenmann, 1908, *Psalidodon* aff. *fasciatus* (Cuvier, 1819), and *Knodus moenkhausii* (Eigenmann & Kennedy, 1903) were exclusively captured in the vicinity of the Biological Refuge of Santa Helena, while *Deuterodon luetkenii* (Boulenger, 1887), *Oligosarcus paranensis*, *Oligosarcus pintoi* Campus, 1945, *Psalidodon* aff. *paranae*, *Psalidodon* sp., *Bryconamericus exodon* Eigenmann, 1907, *Bryconamericus* cf. *iheringii* (Boulenger, 1887), and *Piabina argentea* Reinhardt, 1867 were captured exclusively in the tributaries of the reservoir.

Table 1 – List of Characidae species vouchers in the vicinity of the Biological Refuge of Santa Helena (Reservoir) and adjacent Brazilian rivers (Tributaries), upper Rio Paraná basin, Brazil. - = absent.

Classification	**Origin**	**Voucher**	
		Reservoir	**Tributaries**
APHYOCHARACINAE			
Aphyocharax sp.	Native	CISH 260A	CISH 129A
CHARACINAE			
Galeocharax gulo (Cope, 1870)	Possibly non-native	CISH 51O	-
Roeboides descalvadensis Fowler, 1932	Possibly native	CISH 124A	CISH 307A
CHEIRODONTINAE			
Serrapinnus kriegi (Schindler, 1937)	Undetermined	NUP 23068	-
Serrapinnus notomelas (Eigenmann, 1915)	Native	CISH 230A	CISH 253O
STETHAPRIONINAE			
Astyanax lacustris (Lütken, 1875)	Native	CISH 340O	CISH 240O
Deuterodon luetkenii (Boulenger, 1887)	Native	-	NUP 23114
Hemigrammus ora Zarske, Le Bail & Géry, 2006	Non-native	CISH 74A	CISH 65A
Hyphessobrycon eques (Steindachner, 1882)	Non-native	CISH 286A	CISH 108A
Hyphessobrycon moniliger Moreira, Lima & Costa, 2002	Non-native	NUP 23063	-
Moenkhausia bonita Benine, Castro & Sabino, 2004	Native	CISH 27A	CISH 56A
Moenkhausia forestii Benine, Mariguela & Oliveira, 2009	Possibly native	CISH 28A	CISH 280A
Moenkhausia gracilima Eigenmann, 1908	Non-native	CISH 347A	-
Oligosarcus paranensis Menezes & Géry, 1983	Possibly native	-	CISH

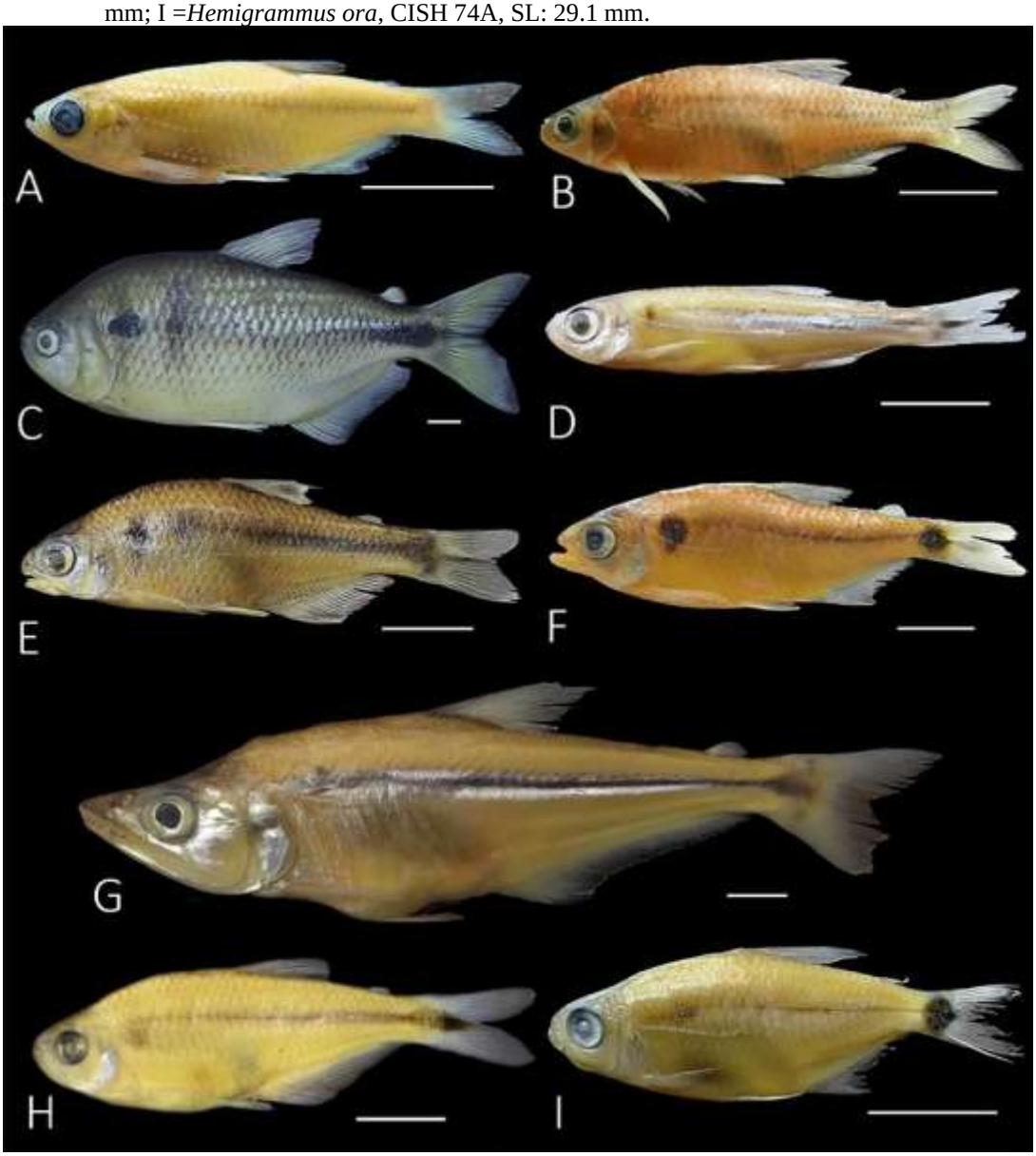
			139TB
Oligosarcus pintoi Campos, 1945	Possibly non-native		CISH 341O
Psalidodon aff. *fasciatus* (Cuvier, 1819)	Native	NUP 23043	-
Psalidodon aff. *paranae* (Eigenmann, 1914)	Native	-	CISH 306O
Psalidodon sp.	Undetermined	-	CISH 303O
Psellogrammus kennedyi (Eigenmann, 1903)	Possibly native	CISH 19A	CISH 90A
STEVARDIINAE			
Bryconamericus exodon Eigenmann, 1907	Possibly native	-	CISH 313O
Bryconamericus cf. *iheringii* (Boulenger, 1887)	Native	-	CISH 239O
Diapoma guarani (Mahnert & Géry, 1987)	Possibly native	CISH 416A	CISH 279A
Knodus moenkhausii (Eigenmann & Kennedy, 1903)	Native	CISH 343A	-
Piabarchus stramineus (Eigenmann, 1908)	Native	NUP 23087	CISH 310O
Piabina argentea Reinhardt, 1867	Native	-	CISH 307O

The study region is below the former biogeographic barrier formed by the Sete Quedas waterfalls that separated two ichthyofaunistic provinces, the upper Rio Paraná basin and Parano-Platense (lower Rio Paraná) (BONETTO, 1986). This barrier was suppressed in 1982 with the formation of the Itaipu reservoir, causing a mixture of species and a mass invasion towards the upper Rio Paraná above the falls (JÚLIO-JÚNIOR et al., 2009). The study region is not initially included in the upper Rio Paraná basin, and the present work follows Reis et al., (2020) regarding native species to reflect the original biogeographic pattern.

In this sense, some non-native species to the upper Rio Paraná basin (above the Sete Quedas waterfalls) are possibly native in the study region of this work because they presumably have a natural geographic distribution below the Sete Quedas waterfalls. It is the case of *Bryconamericus exodon*, *Diapoma guarani* (Mahnert & Géry, 1987), *Moenkhausia forestii* Benine, Mariguela & Oliveira, 2009, *Psellogrammus kennedyi* (Eigenmann, 1903), and *Roeboides descalvadensis* Fowler, 1932. For example, *Deuterodon luetkenii* was considered as native based on the NUP 2621 record from 1989 in a stream in Santa Helena, Brazil. The fish pass Canal da Piracema would only be inaugurated in 2002 (MAKRAKIS et al., 2007), which means that this species already inhabited the tributaries of the Itaipu reservoir before the connection with the downstream

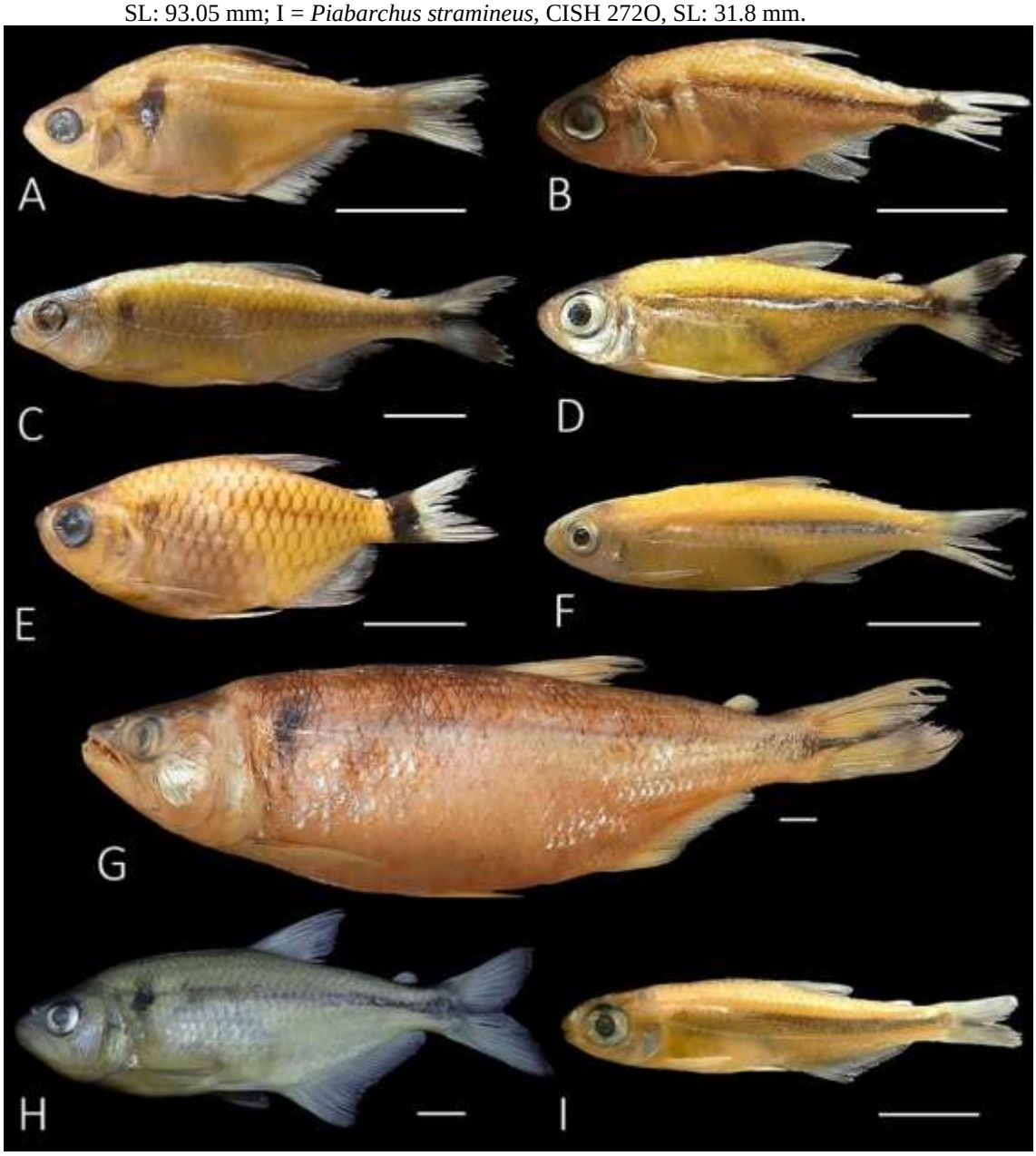
portion established by the Canal da Piracema. The origin of *Serrapinnus kriegi* is uncertain as it was only recently recorded (BRANDÃO et al., 2022). This species is currently found in several Upper Paraná River basin locations and may have multiple origins (KAMPFERT et al., 2023). Specific studies using molecular markers can shed light on this issue.

Figure 2 – Characidae species from the surroundings of the Biological Refuge of Santa Helena and adjacent Brazilian rivers. Scale bar = 10 mm. A = *Aphyocharax anisitsi*, CISH 254A, SL: 22.8 mm; B = *Aphyocharax* sp., CISH 260A, SL: 33.8 mm; C = *Astyanax lacustris*, CISH 340O, SL: 120.90 mm D = *Bryconamericus exodon*, CISH 313O, SL: 35 mm; E = *Bryconamericus* cf. *iheringii*, CISH 271O, SL: 55.8 mm; F = *Deuterodon luetkenii*, CISH 260O, SL: 40 mm; G = *Galeocharax gulo*, CISH 51O, SL: 141.2 mm; H = *Diapoma guarani*, CISH 412A, SL: 31.2 mm; I =*Hemigrammus ora*, CISH 74A, SL: 29.1 mm.



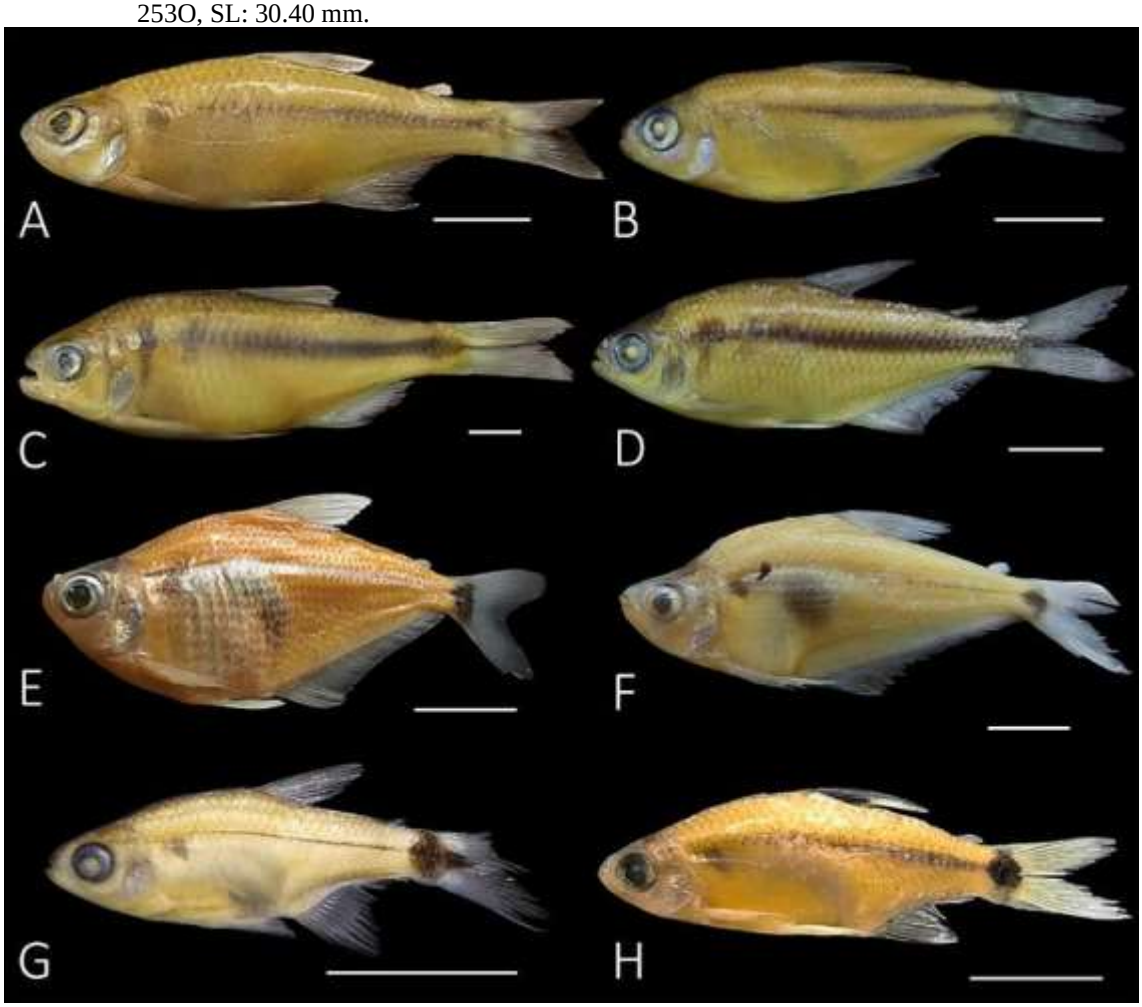
On the other hand, *Oligosarcus pintoi* was considered possibly non-native due to the absence of previous records below the Sete Quedas waterfalls, even after the construction of the Itaipu dam (see RIBEIRO; MENEZES, 2015; WENDT et al., 2019; REIS et al. 2020). This paper presents the first published record of this species for the Itaipu reservoir region and may indicate that the species reached this region only recently.

Figure 3 – Characidae species from the surroundings of the Biological Refuge of Santa Helena and adjacent Brazilian rivers. Scale bar = 10 mm. A = *Hyphessobrycon eques*, CISH 286A, SL: 22.2 mm; B = *Hyphessobrycon moniliger*, NUP 23063, CP: 27.2 mm; C = *Knodus moenkhausii*, CISH 343A, SL: 44.1 mm; D = *Moenkhausia bonita*, CISH 39A, SL: 29.2 mm; E = *Moenkhausia forestii*, CISH 280A, SL: 31.2 mm; F = *Moenkhausia gracilima*, CISH 347A, SL: 30.1 mm; G = *Oligosarcus paranensis*, CISH 139TB, SL: 205 mm; H = *Oligosarcus pintoi*, CISH 341O, SL: 93.05 mm; I = *Piabarchus stramineus*, CISH 272O, SL: 31.8 mm.



Regarding *O. paranensis*, it was not precisely possible to establish whether the species is native below Sete Quedas waterfalls. Some paratypes used in the original description of this species by Menezes and Géry, (1983) come from tributaries of the Rio Paraná below Setes Quedas waterfalls collected before damming by Itaipu (National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A. (USNM) 228081; Muséum National d'Histoire Naturelle, Paris, France (MNHN) 1982-1111-12;

Figure 4 – Characidae species from the surroundings of the Biological Refuge of Santa Helena and adjacent Brazilian rivers. Scale bar = 10 mm. A = *Piabina argentea*, CISH 287O, SL: 55.1 mm; B = *Psalidodon* aff. *fasciatus* NUP 23043, SL: 37.66 mm; C = *Psalidodon* aff. *paranae*, CISH 306O, SL: 88.3 mm; D = *Psalidodon* sp., CISH 303O, SL: 47,46 mm; E = *Psellogrammus kennedyi*, CISH 19A, SL: 38.1 mm; F = *Roeboides descalvadensis*, CISH 307A, SL: 55.60 mm; G = *Serrapinnus kriegi*, CISH 326O, SL: 20 mm; H = *Serrapinnus notomelas*, CISH 253O, SL: 30.40 mm.



Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP) 21085, 21747, 21768-771, 21774-81). Even so, later works mention the species as endemic above the Sete Quedas waterfalls (MENEZES, 1987; RIBEIRO; MENEZES,

2015) and Reis et al., (2020) do not mention any record of the species for the Lower Paraná ecoregion (below the Sete Quedas waterfalls). The species is listed in this work as possibly native due to material collected by the Companhia de Tecnologia de Saneamento Ambiental de São Paulo (CETESB) in 1980 and used in the description of the species.

Characidae has a conservative external morphology; most morphological characteristics with phylogenetic value are osteological (MIRANDE, 2019). However, through a geographic approach, it is possible to establish good diagnostic characters between sympatric species that are easy to visualize, such as those used in this work (Table 2). In addition, all features were photographed, allowing for a better understanding of the key (FISCHER, 2013).

The identification guide published by Ota et al., (2018) includes 38 species of characids, of which 23 was captured in the study area, in addition to three other species: *Deuterodon luetkenii*, *Psalidodon* sp., and *Serrapinnus kriegi*. The smallest number of species in the present paper is expected since the work by Ota et al., (2018) also includes the floodplain of the upper Rio Paraná. On the other hand, the additional records reinforce that the richness of small-sized species in the Itaipu reservoir and its tributaries is underestimated (PEREIRA et al., 2021). Therefore, new survey efforts in the Itaipu reservoir and tributaries should emphasize small species. Also, the present identification key can be used for identifying the stream fish fauna of the tributaries of the Itaipu reservoir, as we recorded all the ten Characidae species reported by Pereira et al., (2021) plus other 16 species. However, due to the great diversity of the family Characidae, caution is needed when using identification keys, and we recommend confirming the determination in the specialized literature for each taxon.

Many of the original descriptions made in the 19th and 20th centuries are currently digitized and freely available (COPE, 1870; LÜTKEN, 1875; STEINDACHNER, 1882; BOULENGER, 1887; EIGENMANN; KENNEDY, 1903; ELLIS, 1911; EIGENMANN, 1908; EIGENMANN, 1915; EIGENMANN; MYERS, 1929; FOWLER, 1932; MENEZES; GÉRY, 1983; MAHNERT; GÉRY, 1987). More recent descriptions are also available online (e.g., MOREIRA et al., 2002; BENINE et al., 2004; BENINE et al., 2009; ZARSKE et al., 2006). Besides the original descriptions, other valuable papers in the identification of the species presented in this research are Jerep et al., (2011) for *Hemigrammus ora* Zarske, Le Bail & Géry, 2006; Miquelarena et al., (2008),Serra et al., (2018) and Kampfert et al., (2023) for *Serrapinnus kriegi*; Venegas-Ríos et al., (2019)

and Lima et al., (2020) for *Moenkhausia bonita* Benine, Castro & Sabino, 2004; Serra and Langeani (2006) for *Bryconamericus exodon*; Lucena and Soares (2016) for *Astyanax lacustris* (Lütken, 1875); Giovannetti et al., (2017) for *Galeocharax gulo*; Lucena (2007) for *Roeboides descalvadensis*; Almirón and Casciotta (1999) for *Diapoma guarani*; Menezes (1987) and Ribeiro and Menezes (2015) for *Oligosarcus paranensis* and *O. pintoi*. Some unpublished doctoral theses and master dissertations are also helpful for morphological comparisons of some of the species in the study area: Tavares (2007), Oliveira (2011), and Oliveira (2017) for *Psalidodon* spp.; Weiss (2013) for *Deuterodon luetkenii*; and Santos (2016) for *Piabina argentea* and other species of the Stevardiinae subfamily from the upper Rio Paraná.

Some species presented in the key belong to taxonomic groups with very similar morphology, such as *Moenkhausia forestii*, which has a coloration pattern similar to two other congeners found in the upper Rio Paraná basin: *M. sanctaefilomenae* (Steindachner, 1907) and *M. australis* Eigenmman, 1908. However, only *M. forestii* has been collected in the study area. This species can be distinguished from the ones mentioned above by presenting incomplete lateral line (vs. complete or interrupted in *M. australe*) and having five rows of scales between the dorsal fin origin and lateral line and four between the lateral line and pelvic fin origin (vs. four and three, respectively, in *M. sanctaefilomenae*) (BENINE et al., 2009).

Furthermore, Reis et al., (2020) mentioned three other species of this genus with color patterns similar to each other from the Lower Paraná ecoregion (bellow Sete Quedas waterfall): *M. bonita*, *M.* aff. *intermedia* Eigenmann, 1908, and *M. dichroura* (Kner, 1858). Only the first was collected in the study area. *Moenkhausia bonita* differs from *M. intermedia* and *M. dichroura* by having 6 to 8 gill rakers on the upper limb and 11 to 15 on the lower limb of the first gill arch (vs. 9-12 gill rakers on the upper limp and 18-22 on the lower limb in both *M. intermedia* and *M. dichoura)* (VANEGAS-RÍOS et al., 2019). This feature was confirmed in four cleared and stained specimens having 7 gill rakers on the upper limb and 13 or 14 on the lower limb. Additionally, the morphological data of *M.* aff. *intermedia* published by Graça and Pavanelli (2007) states that this species has ten dorsal fin rays instead of 11 in *M. bonita* (OTA et al., 2018). All analyzed fish have ii,9 (n = 30) dorsal fin rays. Moreover, *M. bonita* presents a black or silvery mid-lateral stripe, becoming wider after the vertical on the dorsal fin origin and forming an intense black blotch on the caudal peduncle (vs. silvery mid-lateral stripe widening

anteriorly to the dorsal fin origin in *M. dichroura* and *M. intermedia*; faint or absent blotch on the caudal peduncle) (LIMA et al., 2020).

Aphyocharax dentatus Eigenmann & Kennedy, 1903 is native to the Paraguay-Paraná system below Sete Quedas waterfalls (OTA et al., 2018; Reis et al., 2020) but was not recorded in this work. This species is very similar to *Aphyocharax* sp. in color and shape but can be differentiated by presenting the posterior end of the maxilla reaching the transverse line that passes through the middle of the orbit (vs. posterior end of the maxilla not reaching the transverse line that passes through the middle of the orbit in *Aphyocharax* sp.) (OTA et al., 2018).

Other species with very similar morphology are *Serrapinnus kriegi* and *Serrapinnus calliurus* (Boulenger, 1900). The former was captured in the present work, but only the latter was reported by Ota et al., (2018) and Reis et al., (2020). These species can be easily distinguished in life due to a black spot on the posteroventral region of the abdomen in *S. kriegi*, which is absent in *S. calliurus* (see the figures 1 and 2 in SERRA et al., 2018). However, this pigmentation is not on the scales or skin. It is on the outer surface of the peritoneum, below the musculature (Figure 8F). This pigmentation is usually preserved after fixation. However, some fish can present this spot as inconspicuous or absent (UJ, 1987) due to the opaque yellowish coloration of the body after the fixation. Therefore, *S. kriegi* can additionally be distinguished from *S. calliurus* by the ventral procurrent caudal fin rays with the distal tip curved anteriorly in females and immature males (vs. ventral procurrent caudal fin rays straight or slightly curved posteriorly in *S. calliurus* females) (MIQUELARENA et al., 2008; ALMIRÓN et al., 2015).

Deuterodon luetkenii can be distinguished from the other species in the study area by the sharp comma-shaped humeral blotch (Figure 11G). However, at the same time, it can be confused with *Deuterodon ribeirae* (Eigenmann, 1911), a species present in the Ribeira do Iguape basin and coastal basins of the South Atlantic Forest (WEISS, 2013; REIS et al., 2020) very similar to *D. luetkenii*. Both are currently valid species, but they possibly represent a problem of synonymy (WEISS, 2013), and we maintained the identification as *D. luetkenii* due to the presence of an incomplete lateral line (vs. complete lateral line in *D. ribeirae*) (OLIVEIRA, 2011; WEISS, 2013). *Hyphessobrycon moniliger* can also have a slight comma-shaped humeral blotch. Nevertheless, this species can also be differentiated by the number of cusps in the larger premaxillary teeth (7 or 8

in *D. luetkenii* and 5 in *M. moniliger*) and by the sexual dimorphic format of the anal fin in *H. moniliger* males (MOREIRA et al., 2002).

Hemigrammus ora was described by Zarske et al., (2006) and reanalyzed by Jerep et al., (2011). The latter authors expanded their geographical distribution and commented on some morphological variations among the fish of lowland rivers of French Guiana, studied by Zarske et al., (2006), and of the lower Amazon tributaries, upper Rio Xingu, and Rio Tocantins-Araguaia basins, analyzed by them. This species is non-native to the Rio Paraná basin and has been collected since 2011 in the upper Rio Paraná floodplain (OTA et al., 2018). The fish collected in this study agrees with the diagnosis of this species but has scales perforated by the lateral line in the caudal peduncle, a characteristic not mentioned before. The analyzed fish have a lateral line with 10–15 (n = 15) scales in the anterior portion plus 1-3 (n = 15) in the caudal peduncle (Figure 11E). A deep comparison between populations of *H. ora* from the Rio Paraná and other basins previously studied is not the focus of this paper. However, we strongly recommend it for new studies.

Boulenger (1887) described *Bryconamericus iheringii* from the Laguna dos Patos system (São Lourenço do Sul, Rio Grande do Sul State, Brazil). Studies in the upper Rio Paraná basin consider a very similar species, endemic to this basin, yet to be described (e.g., OTA et al., 2018; REIS et al., 2020; AZEVEDO-SANTOS et al., 2020; PEDROSO et al., 2024). We found high morphological variability regarding this species within the study region. For this reason, we kept the "cf." particle. This species was collected by us only in the reservoir's tributaries, and it is necessary to investigate whether the probable endemic species from above Sete Quedas waterfalls colonized the reservoir tributaries after suppressing this biogeographic barrier.

Identifying the *Psalidodon* Eigenmann, 1911 species without comparative material is a challenging task. The correct identification of fish collected in this basin is hampered by the significant interspecific morphological overlap and the known existence of formally undescribed species. *Psalidodon* aff. *paranae* differs from *P. paranae* (type-locality: Castro, Rio Tibagi drainage, Brazil, restricted by Garutti and Britski, 2000 apud Bertaco and Lucena, 2006) in the number of scales on the lateral line (35 to 37 (n = 21) vs. 38 to 40 in *P. paranae*) (TAGLIACOLLO et al., 2011). Furthermore, the population of *Psalidodon* aff. *paranae* in the present study differs from that described in Ota et al., (2018) because it has a lower number of scales on the lateral line (35 to 37 (n = 21) vs.

38 to 39 in Ota et al., (2018) and a greater number of scales between the lateral line and the origin of the dorsal fin (6, 6+½ or 7 vs. 5 or 5+½ in OTA et al., 2018). For this reason, we decided to keep the identification of this species as *Psalidodon* aff. *paranae* until its taxonomic identity can be determined precisely, preferably through a combination of morphological, cytogenetic, and molecular tools.

Psalidodon fasciatus is restricted to the Rio São Francisco basin and differs from *Psalidodon* aff. *fasciatus* by an elongation in the dorsal fin into a filament in mature males (elongation in the dorsal fin into a filament absent in *P.* aff. *fasciatus*) (MELO; BUCKUP, 2006). Although there is cytogenetic and molecular evidence of the existence of different lineages of this complex in the La Plata basin (GAVAZZONI et al., 2022), there is a lack of morphological data available in the literature that allows the diagnosis of these lineages. No species of this complex is formally described for the upper Rio Paraná basin. The fish analyzed in the present study slightly differs from that described by Ota et al., (2018) by presenting more scales on lateral line (38–40 (n=7) vs. 34–36) and fewer pelvic-fin rays (i,6 (n=1) or i,7 (n=6) vs. i,8). However, just seven specimens of this species were captured, all in the surroundings of the Biological Refuge of Santa Helena, so more specimens are necessary to assess the morphology of the population.

The *Psalidodon* sp. is part of the *Psalidodon* aff. *fasciatus* species complex, as defined by Melo and Buckup (2006). Further research is needed to clarify its taxonomic status, integrating morphological and genetic data. In this study, we tentatively identify it based on the following provisional diagnosis: it can be distinguished from all other congeners in the upper Rio Paraná by possessing a complete lateral line. (vs. incomplete in *Psalidodon anisitsi* (Eigenmann, 1907)), a second humeral blotch (vs. second humeral blotch absent in *P.* aff. *fasciatus*, *P. paranae*, and *P. schubarti* (Britski, 1964)), and dark midlateral stripe, composed by melanophores, beginning immediately behind the upper margin of the opercle (see Figure 9D) (vs. beginning after first humeral blotch in *P. bifasciatus*, *P. bockmanni* (Vari & Castro, 2007), *Psalidodon rioparanaibanus* Alves, Oliveira, Pasa & Kavalco, 2020, and *P.* aff. *paranae*). In life, the lateral band is iridescent blueish to greenish in lateral view but becomes black in oblique view; pectoral and dorsal fins are yellowish; pelvic, anal, and caudal fins are yellow-orange to reddish; dorsal portion of the eye is red; the mouth is yellow (Figure 5).

Figure 5 – Color in life of *Psalidodon* sp., CISH 303O, SL: 47.46 mm. Scale bar = 10 mm.

Table 2 – Dichotomous illustrated identification key for Characidae species around of the Biological Refuge of Santa Helena and adjacent Brazilian rivers, upper Rio Paraná basin, Brazil.

1	Ctenoid scales (Figure 6A) →	*Galeocharax gulo* (Figure 3G)
-	Cycloid scales (Figure 6B) →	2
2	Anal fin with at least 35 branched rays; dorsal profile very convex between the tip of the supraoccipital and origin of the dorsal fin in adults (Figure 6C) →	3
-	Anal fin with less than 35 branched rays; dorsal profile straight or slightly convex between the tip of the supraoccipital and origin of the dorsal fin in adults (Figure 6D) →	4
3	Caudal peduncle blotch horizontally elongated (Figure 6E); presence of teeth outside the mouth in adults (Figure 6F) →	*Roeboides descalvadensis* (Figure 4F)
-	Caudal peduncle blotch vertically elongated (Figure 6G); teeth arranged only inside the mouth (Figure 6H) →	*Psellogrammus kennedyi* (Figure 4E)
4	Maxilla with teeth along its entire length (Figure 7A); palate with teeth (Figure 7B) →	5
-	Maxilla with teeth restricted to the proximal half or absent, sometimes more visible under diascopic lighting (Figure 7C); palate without teeth →	6
5	Lateral line with 47–55 pored scales (see the pored scales represented in Figure 8I) →	*Oligosarcus paranensis* (Figure 3G)
-	Lateral line with 36–40 scales (see the pored scales represented in Figure 8I) →	*Oligosarcus pintoi* (Figure 3H)
6	One tooth row in premaxilla (Figure 7D) →	7
-	Two or three teeth row in premaxilla (Figures 7E–H) →	10
7	Pseudotympanum present, more visible under a stereo microscope with transmitted illumination (Figure 8A) →	8
-	Pseudotympanum absent (Figure 8B) →	9

8	Dorsal fin with intense black pigmentation at the anterior and basal portion (Figure 8C); abdomen without a black spot on the posteroventral region (Figure 8D) →	*Serrapinnus notomelas* (Figure 4H)
-	Hyaline dorsal fin with dispersed melanophores (Figure 8E); black spot on the posteroventral region of the abdomen (always conspicuous in unfixed specimens and sometimes inconspicuous in fixed specimens) (Figure 8F) →	*Serrapinnus kriegi* (Figure 4G)
9	Humeral blotch absent (Figure 8G) →	*Aphyocharax anisitsi* (Figure 2A)
-	Diffuse humeral blotch present (Figure 8H) →	*Aphyocharax* sp. (Figure 2B)
10	Incomplete lateral line (Figure 8I) →	21
-	Complete lateral line (similar to Figure 8I, but all scales in this series have the lateral line canal) →	11
11	Five teeth in the inner row of the premaxilla →	12
-	Four teeth in the inner row of the premaxilla →	17
12	Caudal fin with scales covering at least the first third of lobes (more visible with the caudal fin obliquely positioned, then the scales will reflect the light, as Figure 8J shows) →	16
-	Caudal fin scaleless, except on the base (Figure 9A) →	13
13	Humeral blotch horizontally elongated, vertical projection absent (Figure 9B); maxilla without teeth, rarely one tooth is present→	*Astyanax lacustris* (Figure 2C)
-	Humeral blotch vertically elongated (Figure 9C, D), some individuals present the superior portion of humeral blotch horizontally elongated but with a conspicuous vertical projection; maxilla with at least one tooth →	14
14	Humeral blotch not followed by any concentration of melanophores other than the lateral band (Figure 9C) →	*Psalidodon* aff. *fasciatus* (Figure 4B)
-	Humeral blotch followed by a second diffuse humeral spot, sometimes inconspicuous (Figure 8D) →	15
15	Anal fin base short, usually smaller than 26% of SL (Figure 9E); longitudinal band on flanks beginning after a less pigmentated area posterior to the first humeral spot →	*Psalidodon* aff. *paranae* (Figure 4C)
-	Anal fin base long, usually greater than 26% of SL (Figure 9F); longitudinal band on flanks beginning just after the head →	*Psalidodon* sp. (Figure 4D)
16	Humeral blotch absent (Figure 9G); caudal fin with equally pigmented lobes (Figure 9H) →	*Moenkhausia bonita* (Figure 3D)
-	Humeral blotch inconspicuous (only a few scattered melanophores) (Figure 10A); caudal fin with the upper lobe more pigmented than the lower lobe (Figure 10B) →	*Moenkhausia gracilima* (Figure 3F)

17	Caudal fin with scales covering at least the first third of lobes (more visible with the caudal fin obliquely positioned, then the scales will reflect the light, as Figure 8J shows) →	*Knodus moenkhausii* (Figure 3C)
-	Caudal fin scaleless, except on its base (Figure 9A) →	18
18	Three rows of teeth in the premaxilla (varying arrangement as shown in Figures 7E, F); the lower jaw is set to further back than the upper jaw (mandibular retrognathia) (Figure 10C) →	*Piabina argentea* (Figure 4A)
-	Two rows of teeth in the premaxilla; the outer row can be misaligned or aligned but does not form a third row (Figs 7G, H, respectively); the lower jaw is aligned with the upper jaw, even when the mouth is subterminal (Figure 10D) →	19
19	Outer premaxillary tooth row with non-aligned teeth (Figure 7G) →	20
-	Outer premaxillary tooth row with aligned teeth (Figure 7H) →	*Bryconamericus* cf. *iheringii* (Figure 2E)
20	Absent or inconspicuous humeral blotch (only a few scattered melanophores) (Figure 10E) →	*Piabarchus stramineus* (Figure 3I)
-	Conspicuous humeral blotch (Figure 10F) →	*Bryconamericus exodon* (Figure 2D)
21	Dorsal fin with conspicuous dark pigmentation, with any evident pattern (Figures 10G, H) →	22
-	Dorsal fin hyaline, with chromatophores dispersed but not forming an evident pattern (Figure 11A) →	23
22	Dorsal fin almost completely dark-pigmented (Figure 10G); caudal peduncle blotch absent (Figure 11B) →	*Hyphessobrycon eques* (Figure 3A)
-	Dark pigmentation in the dorsal fin is present in the basal and posterodistal portion but more concentrated in the last-mentioned region (Figure 10H); caudal peduncle blotch is present but more evident on median caudal fin rays (Figure 11C) →	*Diapoma guarani* (Figure 2H)
23	Black vertical band covering the posterior portion of the caudal peduncle and first third of the caudal fin, preceded by a lighter area (Figure 11D) →	*Moenkhausia forestii* (Figure 3E)
-	Caudal peduncle blotch oval or diamond-shaped, horizontally elongated (Figure 11E, left picture) →	24
24	Humeral blotch restricted to the region above the lateral line (Figure 11F) →	*Hemigrammus ora* (Figure 2I)
-	Humeral blotch vertically surpassing the lateral line (Figure 11G, H) →	25
25	Humeral blotch conspicuously darker than the adjacent pigmentation (Figure 11G); largest premaxillary teeth with six, seven or eight cusps →	*Deuterodon luetkenii* (Figure 2F)

-	Humeral blotch not conspicuously darker than the adjacent pigmentation (Figure 11H); largest premaxillary teeth with five cusps →	*Hyphessobrycon moniliger* (Figure 3B)

Figure 6 – Visual resources for the identification key. A = Ctenoid scales, *Galeocharax gulo*, CISH 51O, SL: 141.2 mm; = B = Cycloid scales, *Astyanax lacustris*, CISH 340O, SL: 120.90 mm; C Predorsal profile of *Roeboides descalvadensis*, CISH 307A, SL: 53.6 mm; D = Predorsal profile of *Knodus moenkhausii*, CISH 343A, SL: 44.9 mm; E = Caudal peduncle spot of *Roeboides descalvadensis*, CISH 307A, SL: 55.8 mm; F = dorsal view of the mouth of *Roeboides descalvadensis* showing the mamiliform teeth outside, CISH 307A, SL: 55.8 mm; G = caudal peduncle spot of *Psellogrammus kennedyi*, CISH 19A, SL: 38.85 mm; H = obliquely lateral view of the mouth of *Psellogrammus kennedyi*, CISH 19A, SL: 39.1 mm.

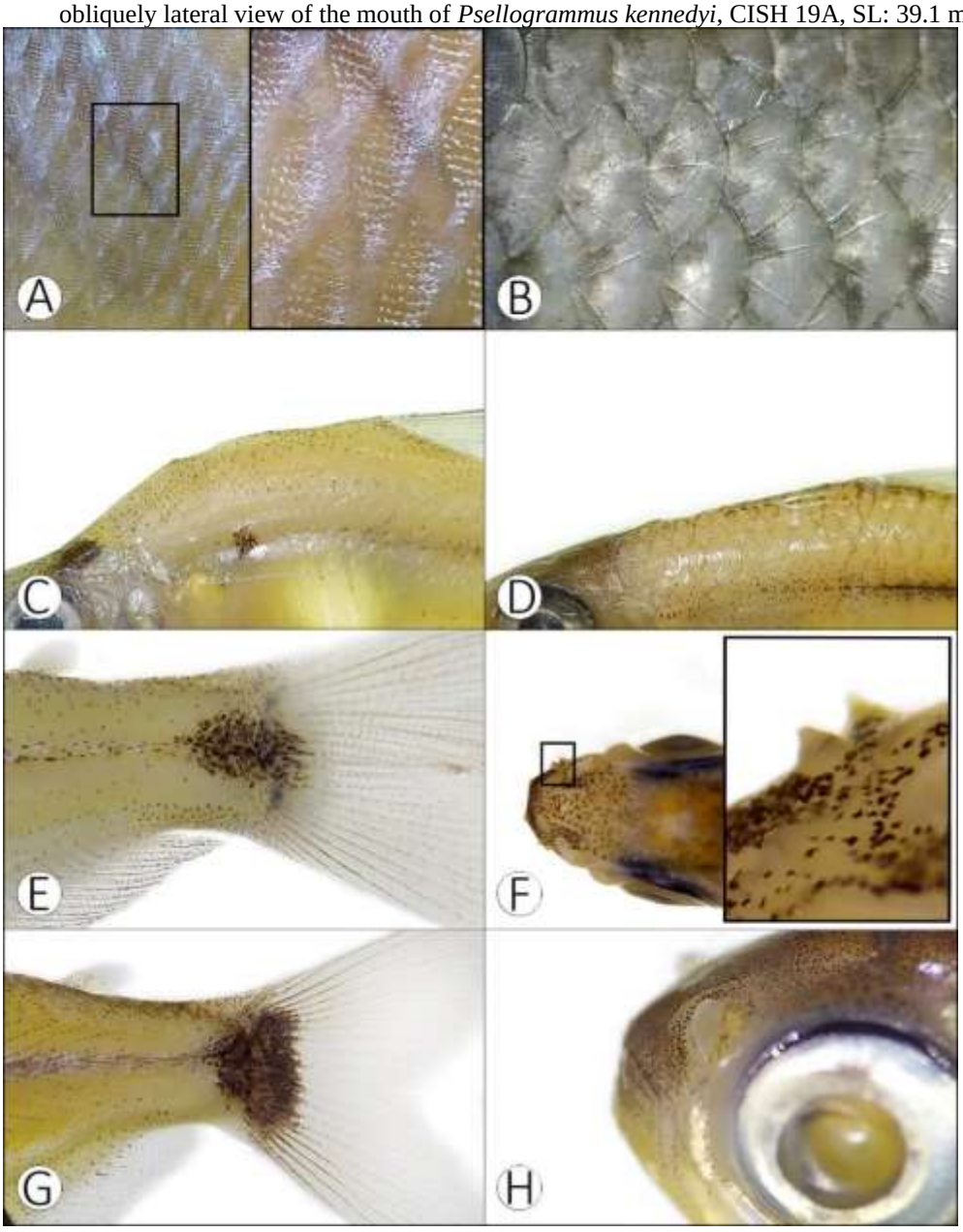


Figure 7 – Visual resources for the identification key. A = lateral view of the maxilla of *Oligosarcus paranensis*, CISH 139TB, SL: 208 mm; B = Internal oblique view of the superior part of the mouth of *Oligosarcus paranensis*, highlighting the palate teeth, CISH 139TB, SL: 208 mm; C = Internal lateral view of the maxilla of *Piabarchus stramineus* with transmitted illumination, highlighting the maxillary teeth outlined, CISH 310O, SL: 56.26 mm; D = Ventral view of the premaxilla of *Aphyocharax* sp., CISH 260A, SL: 37.8 mm; E = Ventral view of the premaxilla of *Piabina argentea*, CISH 307O, SL: 68.9 mm; F = Ventral view of the premaxilla of *Piabina argentea*, CISH 307O, SL: 74.4 mm; G = Ventral view of the premaxilla of *Piabarchus stramineus*, CISH 310O, SL: 63.4 mm; H = Ventral view of the premaxilla of *Bryconamericus* cf. *iheringii*, CISH: 239O, SL: 55.2 mm.

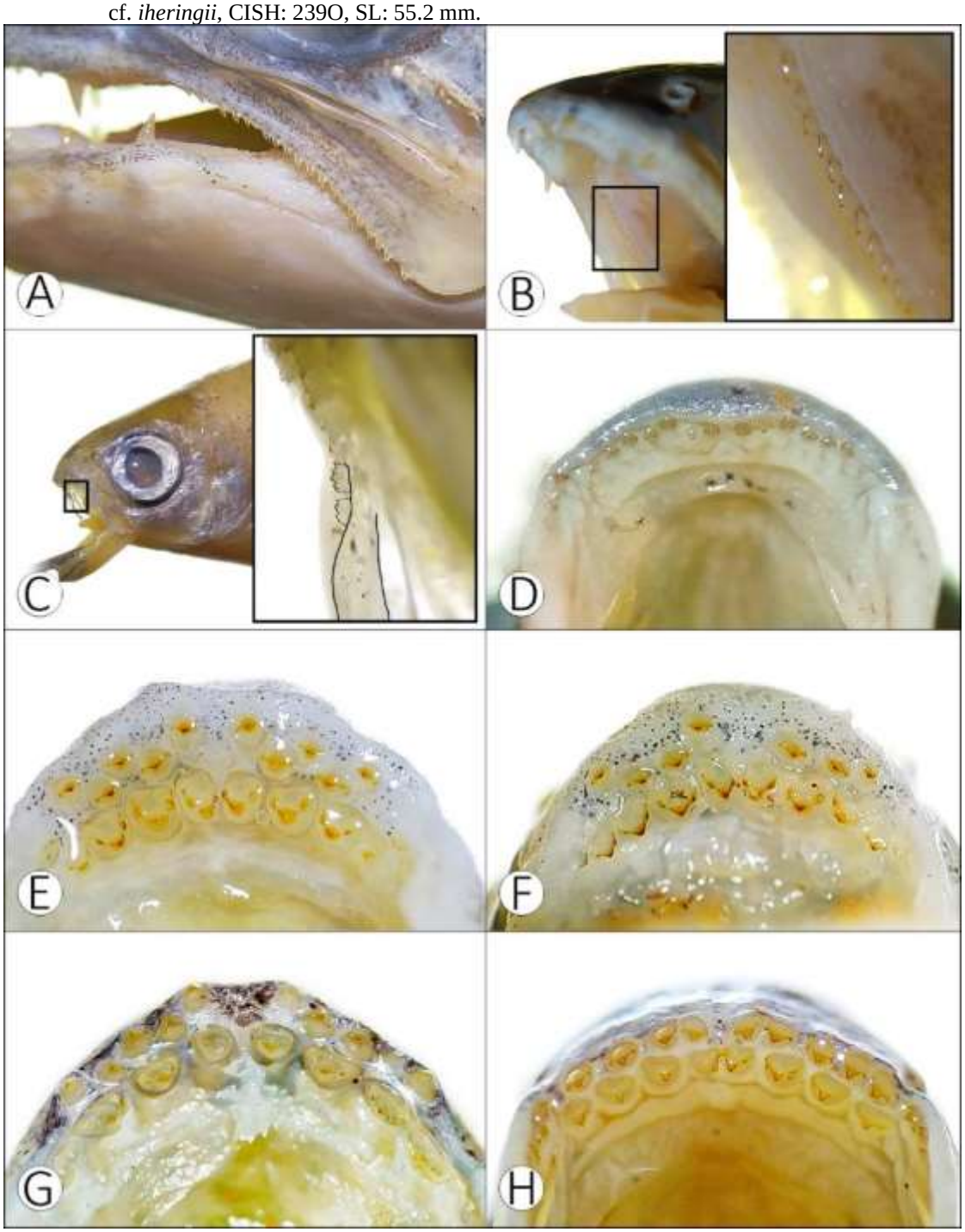


Figure 8 – Visual resources for the identification key. A = Lateral view of the head and humeral region of *Serrapinnus notomelas* with transmitted illumination, the circle indicates the pseudotympatum CISH 70O, SL: 32 mm; B = Lateral view of the head and humeral region of *Aphyocharax* sp. with transmitted illumination, the circle indicates the absence of pseudotympanum CISH 260A, SL: 37.8 mm; C = Lateral view of the dorsal fin of *Serrapinnus notomelas*, CISH 253O, SL: 31.1 mm; D = Lateral view of the posteroventral region of the abdomen of *Serrapinnus notomelas*, CISH 253O, SL: 32 mm; E = Lateral view of the dorsal fin of *Serrapinnus kriegi*, NUP 23068, SL: 19.5 mm; F = Lateral view of the posteroventral region of the abdomen of *Serrapinnus kriegi*, NUP 23068, SL: 19.5 mm; G = Lateral view of *Aphyocharax anisitsi*, highlighting the humeral region, CISH 254A, SL: 22.8 mm; H Lateral view of *Aphyocharax* sp. CISH 260A, SL: 37.8 mm, highlighting the humeral region; I = Lateral line of *Moenkhausia forestii*, scales with the lateral line canal outlined, CISH 280A, SL: 30.5 mm; J = Oblique view of the lower lobe of the caudal fin of *Moenkhausia forestii*, the scaled region indicated by square brackets, CISH 280A, SL: 30.5 mm.

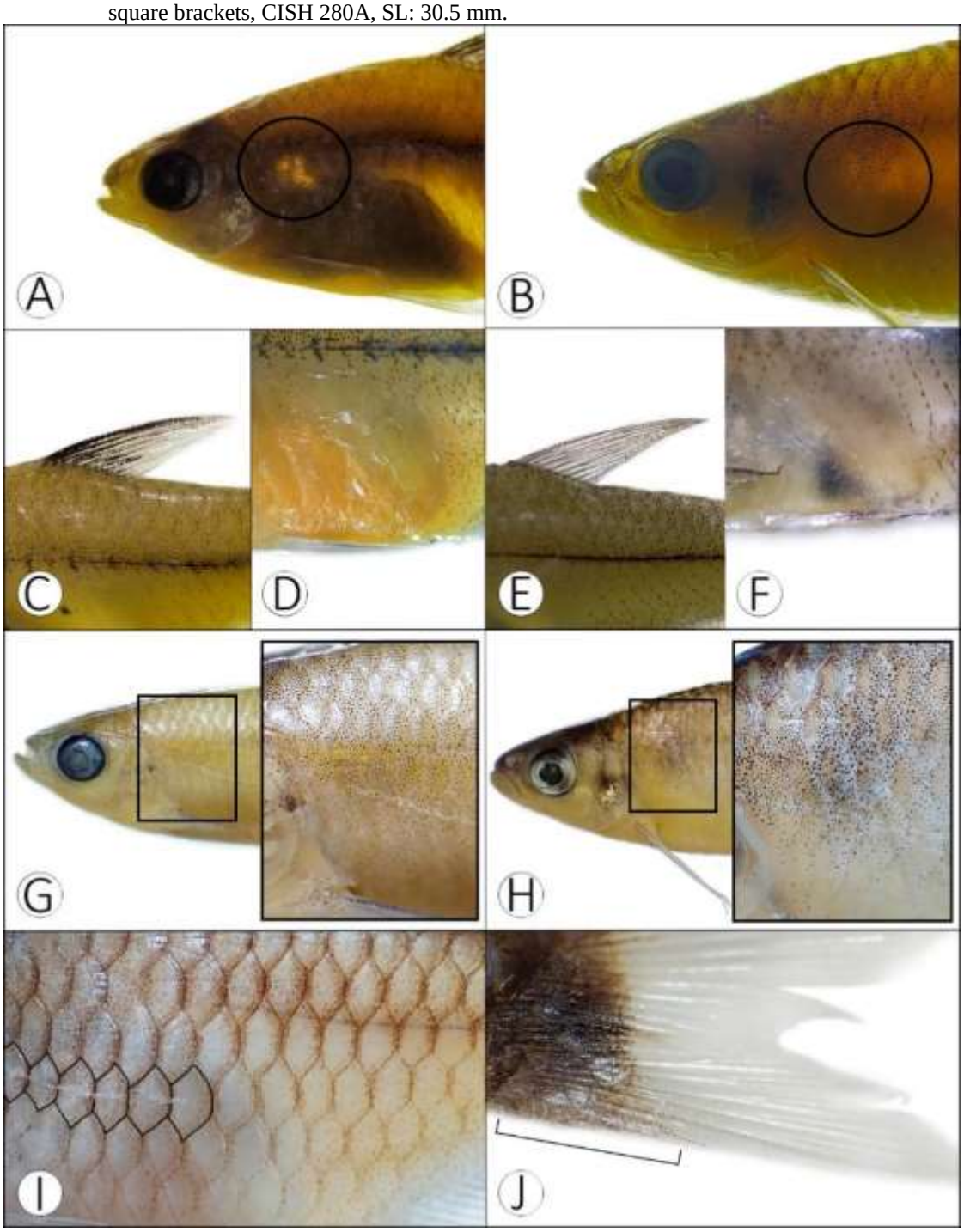


Figure 9 – Visual resources for the identification key. A = Obliquely view of the caudal fin of *Piabarchus stramineus*, the square brackets indicate a non-scaled region, CISH 182A, SL: 33.4 mm; B = Lateral view of *Astyanax lacustris*, highlighting the humeral spot, CISH 199A, SL: 49.4 mm; C = Lateral view of *Psalidodon* aff. *fasciatus*, highlighting the humeral region, NUP 23043, SL: 37.43 mm; D = Lateral view of *Psalidodon* sp., CISH 303O, SL: 47.46, highlighting the humeral region, CISH 334O, SL: 74.43 mm; E = Lateral view of the anal fin of *Psalidodon* aff. *paranae*, CISH 306O, SL: 88.3 mm; F = Lateral view of the anal fin of *Psalidodon* sp., CISH 226O, SL: 82.10 mm; G = Lateral view of *Moenkhausia bonita*, highlighting the humeral region, CISH 39A, SL: 29.2 mm; H = Lateral view of the caudal fin of *Moenkhausia bonita*, CISH 39A, SL: 29.2 mm.

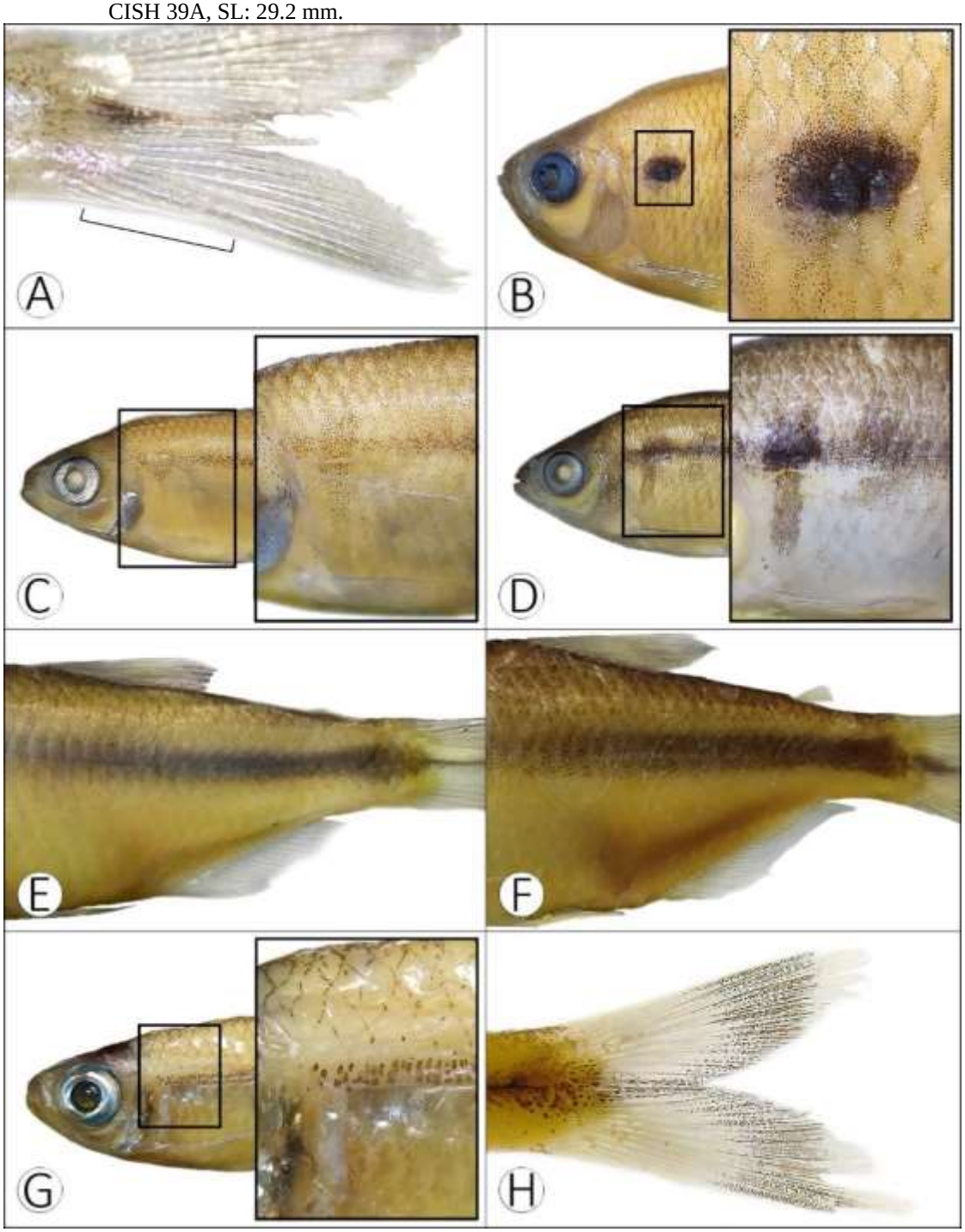


Figure 10 – Visual resources for the identification key. A = Lateral view of *Moenkhausia gracilima*, highlighting the humeral region CISH 347A, SL: 28.8 mm; B = Lateral view of the caudal fin of *Moenkhausia gracilima*, highlighting the humeral region, CISH 347A, SL: 27.6 mm; C = Lateral view of the head of *Piabina argentea*, CISH 307O SL: 64.46 mm; D = Lateral view of the head of *Bryconamericu*s cf. *iheringii*, CISH 239O SL: 59.20 mm; E = Lateral view of *Piabarchus stramineus*, highlighting the humeral region, CISH 310O, SL: 63.2 mm; F = Lateral view of *Bryconamericus exodon*, highlighting the humeral region CISH 313O, SL: 34.8 mm; G = Lateral view of the dorsal fin of *Hyphessobrycon eques*, CISH 286A, SL: 21.6 mm; H = Lateral view of the dorsal fin of *Diapoma guarani*, CISH 412A, SL: 30.41 mm.

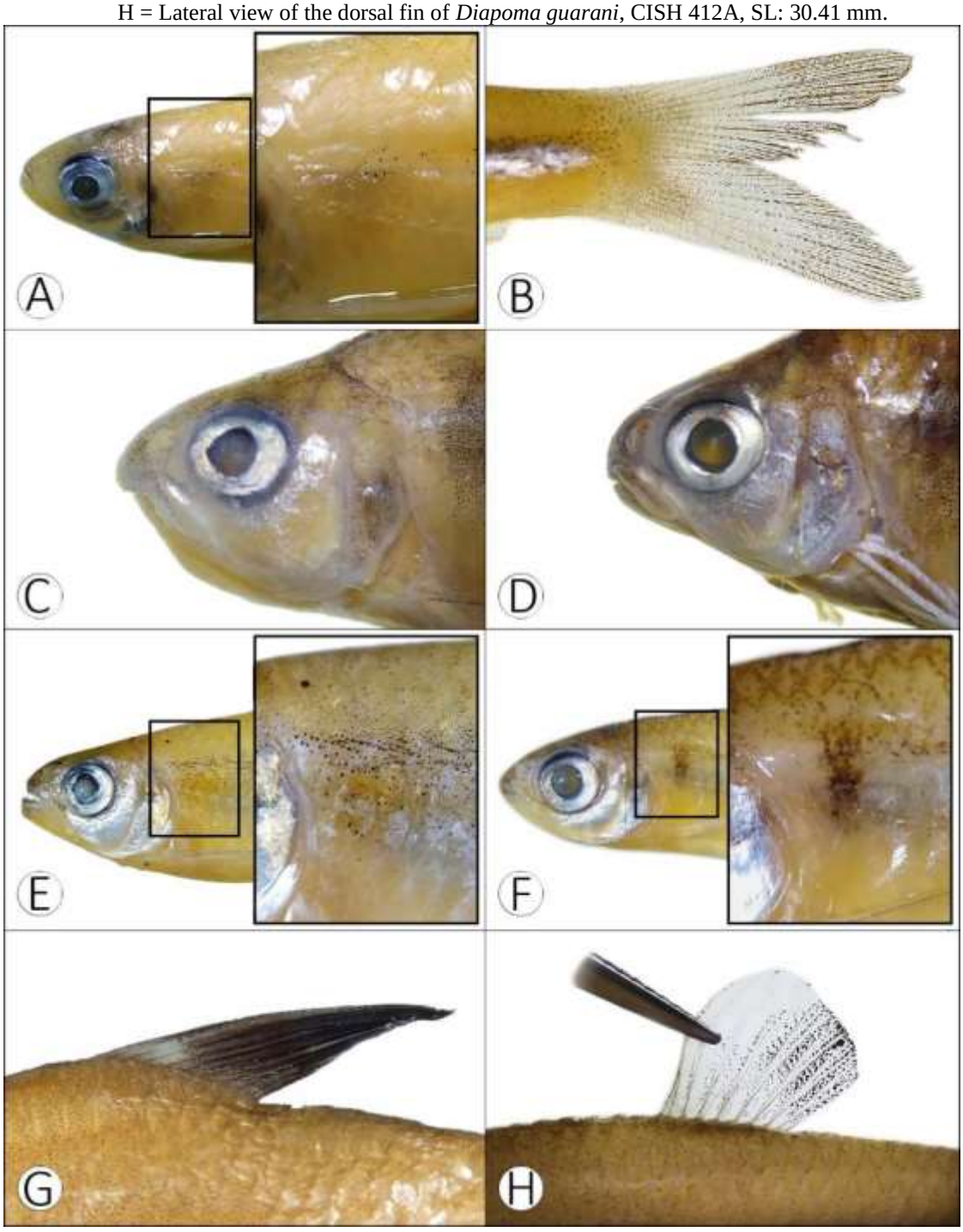
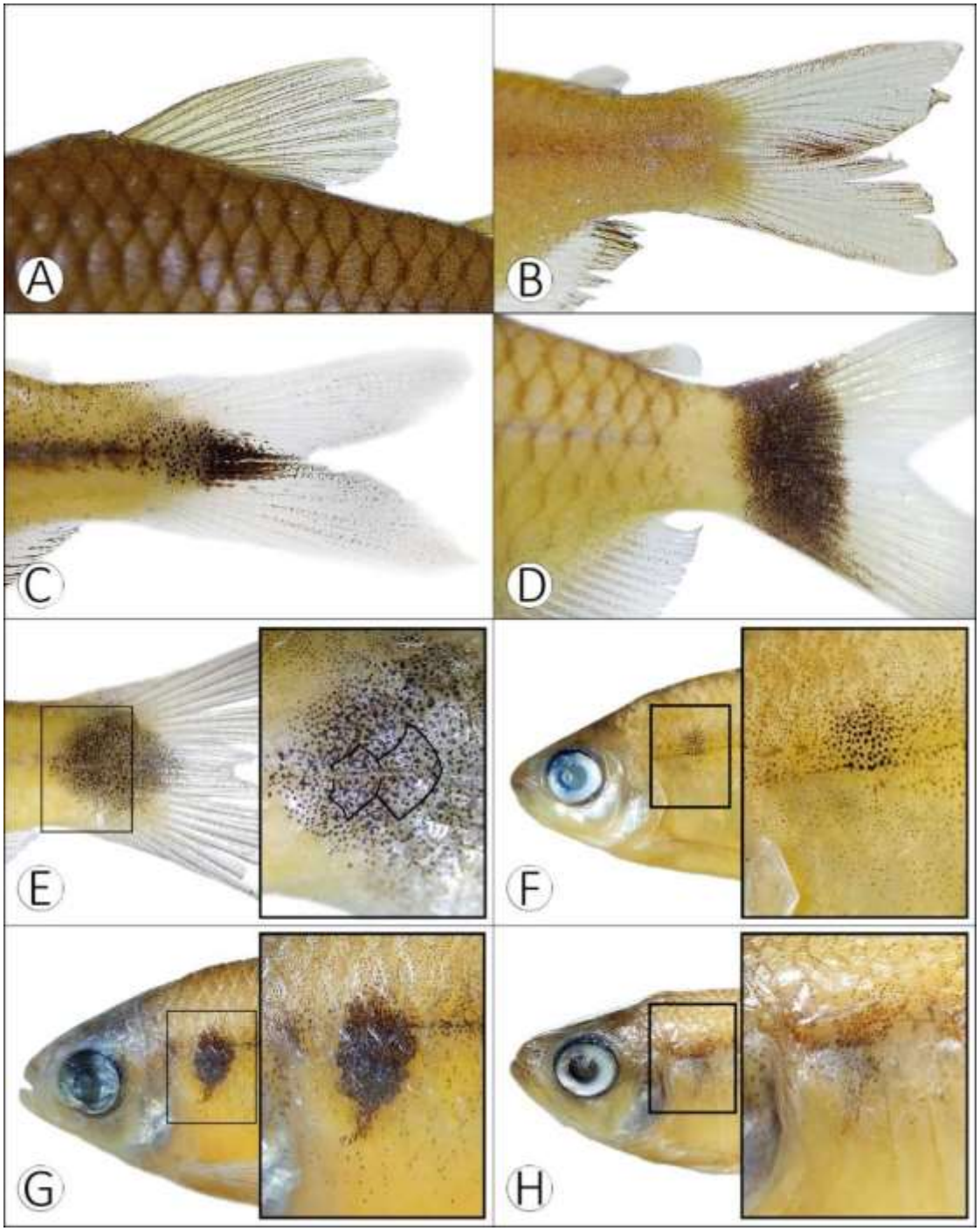


Figure 11 – Visual resources for the identification key. A = Lateral view of the dorsal fin of *Moenkhausia forestii*, CISH 280A, SL: 30.5 mm; B = Lateral view of the caudal peduncle of *Hyphessobrycon eques*, CISH 286A, SL: 22.2 mm; C = Lateral view of the caudal peduncle of *Diapoma guarani*, CISH 412A, SL: 32.76 mm; D = Lateral view of the caudal peduncle of *Moenkhausia forestii*, CISH 280A, SL: 30.5 mm; E = Lateral view of the caudal peduncle of *Hemigrammus ora*, highlighting the region with the presence of lateral line scales outlined, CISH 35A, SL: 31.81 mm; F = Lateral view of *Hemigrammus ora*, highlighting the humeral blotch, CISH 74A, SL: 29.6 mm; G = Lateral view of *Deuterodon luetkenii*, highlighting the humeral blotch, CISH 266O, SL: 43.65 mm; H = Lateral view of *Hyphessobrycon moniliger*, NUP 23063, SL: 27.2 mm.



FINAL CONSIDERATIONS

This paper provides an illustrated dichotomous identification key for 26 Characidae species around of the protected area Biological Refuge of Santa Helena and in the adjacent Brazilian rivers in the upper Rio Paraná basin, including three notable additions to the region's existing identification guides: *Deuterodon luetkenii*, *Serrapinnus kriegi*, and *Psalidodon* sp.

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