

Another piece to the *Hoplisoma paleatum* puzzle, with a discussion on the monophyly of *Hoplisoma*

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In this work, we revisited the taxonomy of *Hoplisoma paleatum*, a species with one of the most extensive taxonomic histories within the genus *Hoplisoma*. The analysis of the type-specimens of *H. microcephalus* and non-type specimens from Tres Arroyos, Argentina, led us to propose this species as a junior synonym of *H. paleatum*. Additionally, considering that the monophyly of *Hoplisoma* and generic placement of *H. paleatum* and its closest relatives were recently contested, a broad discussion on the systematics of the genus is provided herein. Considering the potential taxonomic instability related to the recent proposal of *Urkumayu*, and in light of the large dataset supporting a monophyletic *Hoplisoma*, we herein consider *Urkumayu* to represent a junior synonym of *Hoplisoma*, pending further analysis. A discussion on the taxonomic status of the species in *Urkumayu*, *H. steindachneri* and *H. osvaldoi* is also provided.

Keywords: Classification, Corydoradinae, *Hoplisoma microcephalus*, Systematics, *Urkumayu*.

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Neste trabalho, revisitamos a taxonomia de *H. paleatum*, uma espécie com uma das histórias taxonômicas mais extensas dentro do gênero. A análise dos espécimes-tipo de *H. microcephalus* e de espécimes não-tipo de Tres Arroyos, Argentina, nos levou a propor esta espécie como sinônimo júnior de *H. paleatum*. Adicionalmente, considerando que o monofilismo de *Hoplisoma* e a alocação genérica de *H. paleatum* e suas espécies correlatas mais próximas foram recentemente contestados, uma ampla discussão sobre a sistemática do gênero é fornecida aqui. Considerando a potencial instabilidade taxonômica relacionada a recente proposta de *Urkumayu*, em contraste com o amplo conjunto de dados que apoiam *Hoplisoma* monofilético, consideramos que *Urkumayu* represente um sinônimo júnior de *Hoplisoma*, pendente de análise mais aprofundada. Uma discussão sobre o status taxonômico das espécies em *Urkumayu*, *H. steindachneri* e *H. osvaldoi* é apresentada.

Palavras-chave: Classificação, Corydoradinae, *Hoplisoma microcephalus*, Sistemática, *Urkumayu*.

INTRODUCTION

The Callichthyidae are armored catfishes widely distributed in the Neotropical region, from Panama to Argentina. They inhabit all large drainages of the cis-Andean portion of South America, in addition to some trans-Andean basins of Panama and Colombia (Reis, 2003). Representatives of the family occupy a variety of habitats, including the channels of large rivers, small streams, lakes, lagoons, marshes, and ephemeral water bodies (Tencatt, 2022). Morphologically, the Callichthyidae can be distinguished from other Siluriformes by the presence of two longitudinal series of dermal plates on the flanks (Reis, 1998, 2003). The composition and arrangement of these plates creates a strong but flexible anti-predator armor shield (Lowe *et al.*, 2021). Currently, the family includes ~230 valid species in two subfamilies, Callichthyinae and Corydoradinae, with five and seven valid genera, respectively (Dias *et al.*, 2024; Fricke *et al.*, 2025). Callichthyinae is composed by small- to medium-sized species with long maxillary barbels (reaching or passing the pectoral-fin origin). These species are commonly captured for food, or used as live bait, and some species are exported for the aquarium trade (Tencatt, 2022). Corydoradinae comprises small-sized species with short maxillary barbels (not reaching the pectoral-fin origin), most of them highly appreciated in the aquarium hobby (Tencatt, 2022). Callichthyinae is currently represented by 17 species, while Corydoradinae is much more diverse, with 210 species.

Over ~135 years, many researchers have studied the taxonomy of the Corydoradinae catfishes (*e.g.*, Eigenmann, Eigenmann, 1890; Ellis, 1913; Gosline, 1940; Nijssen, 1970; Nijssen, Isbrücker, 1967, 1980, 1983, 1986; Britto, 1998, 2003; Britto, Castro, 2002; Britto, Reis, 2005; Britto *et al.*, 2005, 2007, 2009, 2016; Tencatt *et al.*, 2013, 2025a,b) and their phylogenetic interrelationships (*e.g.*, Britto, 2003; Alexandrou *et al.*, 2011; Marburger *et al.*, 2018; Dias *et al.*, 2024). One of the most relevant turning points in Corydoradinae systematics is arguably the morphology-based phylogenetic hypothesis

by Britto (2003), demonstrating the non-monophyly of *Corydoras* (similar to Reis, 1998), which was later corroborated by molecular analyses (e.g., Alexandrou *et al.*, 2011; Marburger *et al.*, 2018). In summary, Britto's (2003) work resulted in the revalidation of *Scleromystax*, the synonymization of *Brochis* under *Corydoras*, and the establishment of nine clades, with most species attributed to *Corydoras* within a large polytomy.

In 2004 the first molecular phylogeny of Callichthyidae was published and showed, for the first time the polyphyly of the theretofore recognized *Corydoras* (Shimabukuro-Dias *et al.*, 2004). Later, Alexandrou *et al.* (2011), revisited the systematics of Corydoradinae based on molecular data. This study identified nine lineages based on nuclear and mitochondrial DNA, but the authors recognized the limitations of the data generated at that time, which resulted in low statistical support for several important points of the phylogeny. Accordingly, they did not propose taxonomic changes in the group. The recognition of these nine lineages was nonetheless widely followed in subsequent taxonomic papers and diagnoses of *Corydoras sensu lato* (i.e., species within lineages 1, 4, 5, 6, 7, 8 and 9) (e.g., Tencatt *et al.*, 2013, 2016; 2019, 2020, 2021, 2022a, 2023a,b, 2024a,b; Tencatt, Pavanelli, 2015; Tencatt, Britto, 2016; Tencatt, Evers, 2016; Tencatt, Ohara, 2016a,b; Bono *et al.*, 2019; Bentley *et al.*, 2021). Although subsequent works provided morphological diagnoses for almost all of these lineages (see Tencatt *et al.*, 2023b:23), no diagnosis between the species of the lineages 6 and 9 have been provided to date (see Tencatt, Ohara, 2016a; Tencatt *et al.*, 2022a, 2023b).

Marburger *et al.* (2018) showed for the first time a close relationship between the species of lineages 6 and 9 in a nuclear-based phylogenetic hypothesis (pyRAD). This result was later corroborated with basis on ultraconserved elements (UCEs) by Dias (2022), which brings a new phylogeny with strong support for almost all internal nodes, confirming the monophyletic nature of the group composed by the species within both lineages 6 and 9 *sensu* Alexandrou *et al.* (2011). Considering the convergence of results of both morphological and molecular data, Dias *et al.* (2024) proposed a new phylogenetic hypothesis based on a phylogenomic analysis using nuclear markers (UCEs), providing morphological features gathered in the last two decades to support each major clade/genus. In that paper, the authors provided a new classification of Corydoradinae, establishing the monophyly of *Corydoras* with strong support and resurrecting *Brochis*, *Gastrodermus*, *Hoplisoma*, and *Osteogaster*.

Later, Alonso *et al.* (2025) published a phylogenetic hypothesis based on both molecular and morphological data, combining the molecular matrix of Alexandrou *et al.* (2011) with the morphological matrix of Britto (2003), and adding data for six species, namely: *Hoplisoma gladysae*, *H. longipinne*, *H. micracanthus*, *H. osvaldoi*, *H. paleatum* (already analyzed in Britto, 2003), and *H. petracinii*. Regarding the molecular dataset, the authors added one single gene sequence, the cytochrome b, of the six aforementioned species in their matrix, while Alexandrou *et al.*'s (2011) dataset included four additional gene sequences (mitochondrial ribosomal 12S and 16S, and NADH dehydrogenase 4, and the nuclear recombination activating 1 gene - RAG1). The most controversial decision in Alonso *et al.* (2025) surely refers to the proposal of a new genus, *Urkumayu*, changing the monophyletic status of *Hoplisoma sensu* Dias *et al.* (2024) to polyphyletic. The authors did not propose a genus to accommodate the species of the “*H. paleatum* group”, possibly due to the lack of morphologic synapomorphies or even diagnostic features to support generic status. Similarly, the authors kept *H. flaveolum*, the sister

group of *Urkumayu*, in *Hoplisoma*, a decision that was not further explained besides stating that the divergence among them (i.e., *H. flaveolum* and *Urkumayu*) is possibly linked to regional biogeographic aspects. According to Alonso *et al.* (2025), *Hoplisoma sensu* Dias *et al.* (2024) would have three distinct lineages, not exclusively related: “*H. flaveolum*”, the “*paleatum* group”, and *Hoplisoma sensu stricto*.

Hoplisoma sensu Dias *et al.* (2024) is currently the most species-rich genus within Corydoradinae, and also of Callichthyidae, with about 90 valid species. The species of *Hoplisoma* can be recognized by sharing the following non-exclusive features: (I) mesethmoid moderate in size, (II) posterior margin of both dorsal- and pectoral-fin spines typically with all or nearly all serrations directed towards the tip of the spine or perpendicularly directed, (III) posterior laminar expansion of infraorbital 2 ranging from strongly reduced to relatively well developed, typically not in contact with pterotic-extrascapular, (IV) single cranial fontanel, and (V) a combination of ground color of body pale yellow, brownish yellow or grayish yellow, typically with small dark spots at least in some part of the body and/or more than one large, dark blotch/stripe on body (Dias *et al.*, 2024; Tencatt *et al.*, 2025a).

Perhaps one of the most complex taxonomic histories among *Hoplisoma* species (and Corydoradinae as a whole) is that of *H. paleatum* (Jenyns, 1842), a species collected by Charles Darwin during his circumnavigation voyage (1831 to 1836) on HMS Beagle. Tencatt *et al.* (2016) presented a redescription and taxonomic review of *H. paleatum*. Although the authors were able to recognize several populations corresponding to the lectotype and some paralectotypes of *H. paleatum*, they highlighted the necessity for further investigations of populations attributed to *H. longipinne* (Knaack, 2007) and *H. microcephalus* (Regan, 1912). According to Tencatt *et al.* (2016), several populations from the rio Paraná basin in Brazil, rio Uruguay basin in Brazil and Uruguay, and also from coastal drainages from Southern Brazil and Uruguay likely represent populations of *H. longipinne*, which can be promptly distinguished from *H. paleatum* by features related to pectoral-fin spine serrations, and color pattern of dorsal and pectoral fins.

When compared to *H. longipinne*, *H. microcephalus* is clearly more similar in morphology to *H. paleatum*, having been regarded as conspecific by Nijssen, Isbrücker (1980). According to Regan's (1912) original description, *H. microcephalus* displays a very similar color pattern to *H. paleatum*, basically presenting one distinctive feature, four to five oblong dark blotches longitudinally aligned on midline of flank (*vs.* three dark blotches). Based on high resolution photographs of *H. microcephalus*'s lectotype, Tencatt *et al.* (2016) were able to confirm the presence of a series of four large, distinct, strongly faded brown blotches along its flank midline. Although Tencatt *et al.* (2016) have reported the presence of smaller blotches on midline of flank in *H. paleatum* and *H. longipinne*, which they refer to as “fragmented blotches”, this was not considered by them as equivalent to the larger blotches of the lectotype of *H. microcephalus*. In the diagnosis of *H. paleatum* presented by Tencatt *et al.* (2016), it was mentioned that *H. microcephalus* shares one of its main diagnostic features, the perpendicularly directed serrations on the posterior margin of the pectoral-fin spine, however, this statement was based only on the analysis of some Argentinian specimens identified by them as “*Corydoras cf. microcephalus*” (= *Hoplisoma cf. microcephalus sensu* Dias *et al.* (2024)). Despite the number of blotches in the longitudinal series along midline of flank represents the only diagnostic feature presented by Tencatt *et al.* (2016) to split *H. microcephalus* from *H. paleatum*, the authors decided to consider *H. microcephalus* as valid until further analysis.

In 2017, the first author was able to analyze the lectotype and paralectotypes of *C. microcephalus*, which confirmed the presence of the color pattern described by Regan (1912) and also of the same serration pattern on the posterior margin of the pectoral-fin spine observed by Tencatt *et al.* (2016) in *H. paleatum* and *H. cf. microcephalus*, in all type-specimens. Additionally, the paralectotypes of *H. paleatum*, which were examined only through photography by Tencatt *et al.* (2016), could also be personally checked. Since the three key diagnostic features of *H. paleatum* are present in *H. microcephalus*, plus *H. cf. microcephalus*, and considering the variations in color pattern of the flank midline observed in these three taxa, it seems reasonable to conclude that they constitute a single, though slightly variable, species. Considering this, the diagnosis and the synonymic list of *H. paleatum* provided by Tencatt *et al.* (2016) become outdated. Therefore, the aim of this study is to provide a new diagnosis for *H. paleatum*, updating its synonymic list and geographical distribution. High resolution photographs of the whole type-series of *H. microcephalus* and of the paralectotypes of *H. paleatum*, that were not presented by Tencatt *et al.* (2016), are provided herein. Additionally, considering that the generic placement of *H. paleatum* and its close relatives, as well as the monophyly of *Hoplisoma*, were recently questioned by Alonso *et al.* (2025), a broad discussion on this subject is provided.

MATERIAL AND METHODS

This work follows the classification proposed in Dias *et al.* (2024). The specific epithets of *Hoplisoma micracanthus* and *H. microcephalus* were not declined as they are considered compound nouns and not adjectives (*i.e.*, *micracanthus*, from the Greek *mikrós*, meaning small, and *ákantha*, meaning thorn = “small spine”, not “small-spined”; and *microcephalus*, from the Greek *mikrós*, meaning small, and *kephalé*, meaning head = “small head”, not “small-headed”). Measurements were obtained using digital caliper to the nearest tenth of millimeter. Morphometric and meristic data were taken following Tencatt *et al.* (2022b) and Reis (1997), respectively. Morphometrics are reported as percent of standard length (SL) or as percent of head length (HL). Terminology of barbels follows Britto, Lima (2003). For the osteological analysis, some specimens were cleared and stained (CS) according to the protocol of Taylor, Van Dyke (1985). Osteological terminology was based on Reis (1998), with the exception of parieto-supraoccipital instead of supraoccipital (Arratia, Gayet, 1995), pterotic-extrascapular instead of pterotic-supracleithrum (Slobodian, Pastana, 2018), and scapulocoracoid instead of coracoid (Lundberg, 1970). Nomenclature of the latero-sensory canals and preopercular pores are according to Schaefer, Aquino (2000) and Schaefer (1988), respectively. The supra-preopercle *sensu* Huysentruyt, Adriaens (2005) was treated here as a part of the hyomandibula according to Vera-Alcaraz (2013). Vertebral counts include only free centra, with the compound caudal centrum (preural 1+ ural 1) counted as a single element. The last two dorsal-fin rays were counted as distinct elements. Pharyngeal teeth were counted in both sides of the branchial arches. To determine the development degree of the anterior laminar expansion of infraorbital 1 in relation to the nasal capsule, the specimen was positioned to maintain the largest diameter of the nasal capsule horizontally. The width of the frontal bone was obtained at the same point as the least interorbital width. In the photos illustrating CS specimens, the apparent size of some structures may eventually be altered

by the perspective from which the photo was taken, especially regarding structures in different planes. In the description, numbers in parentheses represent the total number of specimens with those counts. Regarding color pattern description, the longitudinal markings on the body are referred to as stripes, whereas the transversal markings on the head and trunk are referred to as bars; the transversal markings on fins are referred to as bands. The synonymic list includes only the literature from which it was possible to confirm the identification of *H. paleatum* through examination of voucher specimens, drawings or photographs. Institutional abbreviations follow Sabaj (2023).

The morphological arguments presented in the discussion are based on previous datasets (e.g., Britto, 1998, 2003; Britto, Castro, 2002; Britto, Reis, 2005; Britto *et al.*, 2005, 2007, 2009, 2016; Tencatt *et al.*, 2013, 2014a,b, 2016, 2019, 2020, 2021, 2022a,b, 2023a,b, 2024a,b, 2025a,b; Tencatt, Pavanelli, 2015; Tencatt, Britto, 2016; Tencatt, Evers, 2016, Tencatt, Ohara, 2016a,b; Espíndola *et al.*, 2018; Bono *et al.*, 2019; Bentley *et al.*, 2021), of which the material examined represents approximately 71% of the diversity of the group. Additionally, comparative data of *H. habrosum* (Weitzman, 1960), *H. reynoldsi* (Myers & Weitzman, 1960), and *H. steindachneri* (Isbrücker & Nijssen, 1973) were obtained through their original descriptions and/or high-resolution photographs of their type-specimens, some of which are available in Morris *et al.* (2006). This study is based solely on museum specimens, and therefore no collecting permits were needed.

RESULTS

Hoplisoma paleatum (Jenyns, 1842)

(Figs. 1–2; Tab. 1)

- Callichthys paleatus* Jenyns, 1842 (in Jenyns, 1840–42):113–14 (original description; type-locality: unknown, original label lost [most likely the Laguna del Potrero, Maldonado, Uruguay (Calviño, 2020)]).
- Corydoras marmoratus* Steindachner, 1879b:26–28 (*partim*; pl. V, fig. 1). —Nijssen, Isbrücker, 1980:203, 204 (designation of the lectotype; listed as a synonym of *Corydoras paleatus*; fig. 18).
- Corydoras paleatus* Eigenmann & Eigenmann, 1890:466, 471, 472 (identification key; brief description). —Nijssen, Isbrücker, 1980:203, 204 (designation of the lectotype; brief comments on the synonymic list; fig. 18). —Reis, 2003:301 (listed). —Casciotta *et al.*, 2005:77, 167, 232, fig. 88. —Ferraris, 2007:122 (listed). —Almirón *et al.*, 2008:124. —Almirón *et al.*, 2015:29, 150, 151. —Tencatt *et al.*, 2016:e150089 (redescription). —Calviño, 2020:61 (discussion on the type-locality; photos in life).
- Corydoras microcephalus* Regan, 1912:211 (original description; type-locality: La Plata). —Nijssen, Isbrücker, 1980:204 (designation of the lectotype; listed as a synonym of *Corydoras paleatus*). —Tencatt *et al.*, 2016:e150089 (revalidation; morphological comparison with *Corydoras paleatus*).
- Corydoras longipinnis* (non Knaack, 2007). —Knaack, 2007:36, 39 (*partim*; allotype; figs. 5–7, 12, 43).
- Corydoras* cf. *paleatus*. —Calviño, Alonso, 2009:207 (fig. 5).
- Corydoras* cf. *microcephalus*. —Tencatt *et al.*, 2016:e150089 (morphological analysis; listed as comparative material).
- Hoplisoma paleatum* (Jenyns, 1842). —Dias *et al.*, 2024:11 (phylogeny; allocation in *Hoplisoma*; wrongly spelled as “*paleatus*”). —Alonso *et al.*, 2025:11 (phylogeny; member of the “*Hoplisoma*” *paleatum* clade).

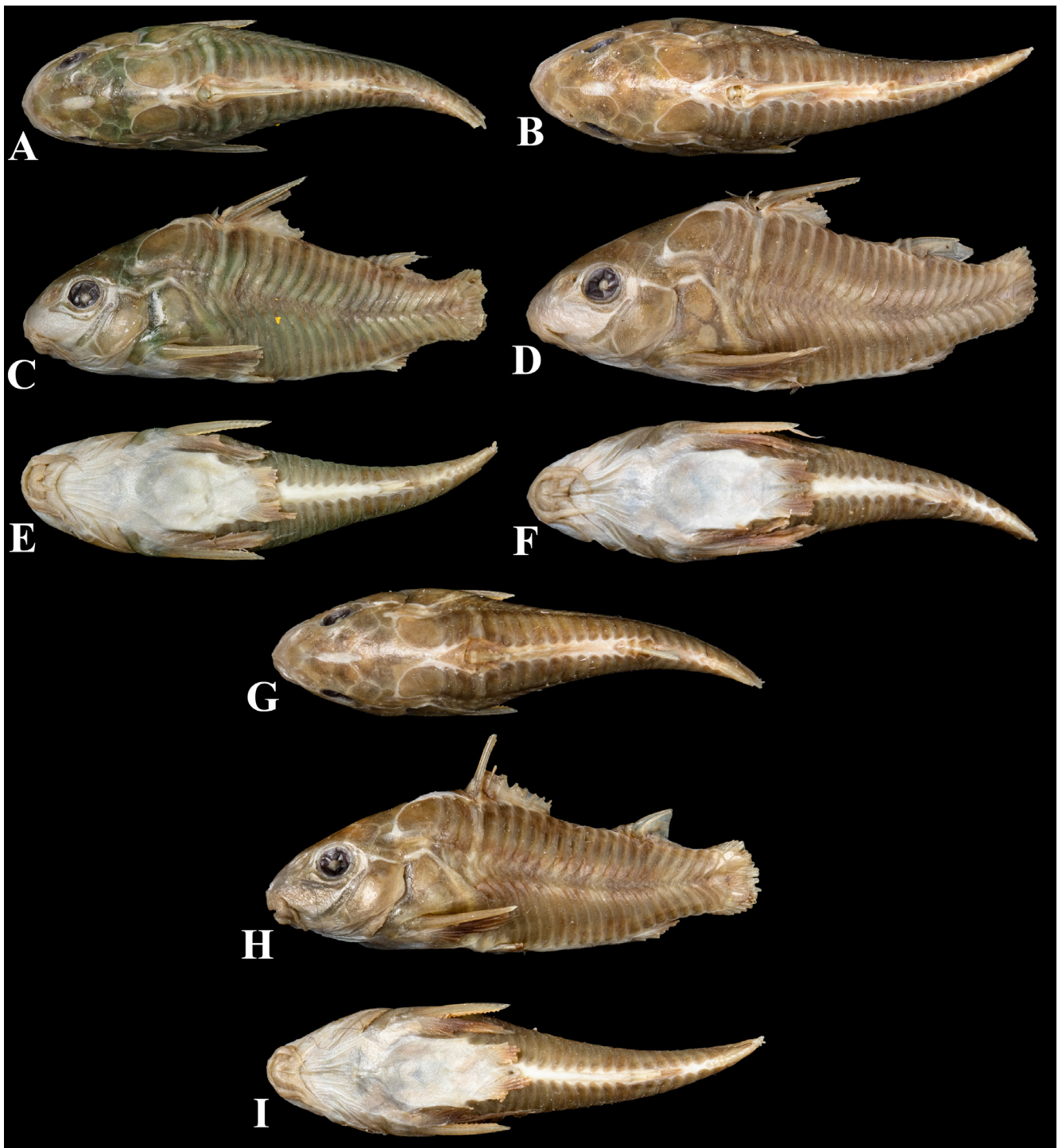


FIGURE 1 | *Hoplisoma paleatum* type-series, showing the (A, C, E) lectotype (BMNH 1917.7.14.18, 30.0 mm SL), and two paralectotypes (BMNH 1917.7.14.19 and 19a). Paralectotype depicted in (B, D, F) with 28.7 mm SL, and in (G–I) with 26.6 mm SL. Photos (A–B, G), (C–D, H), and (E–F, I) showing specimens in dorsal, lateral and ventral views, respectively. Photos by Kevin Webb.

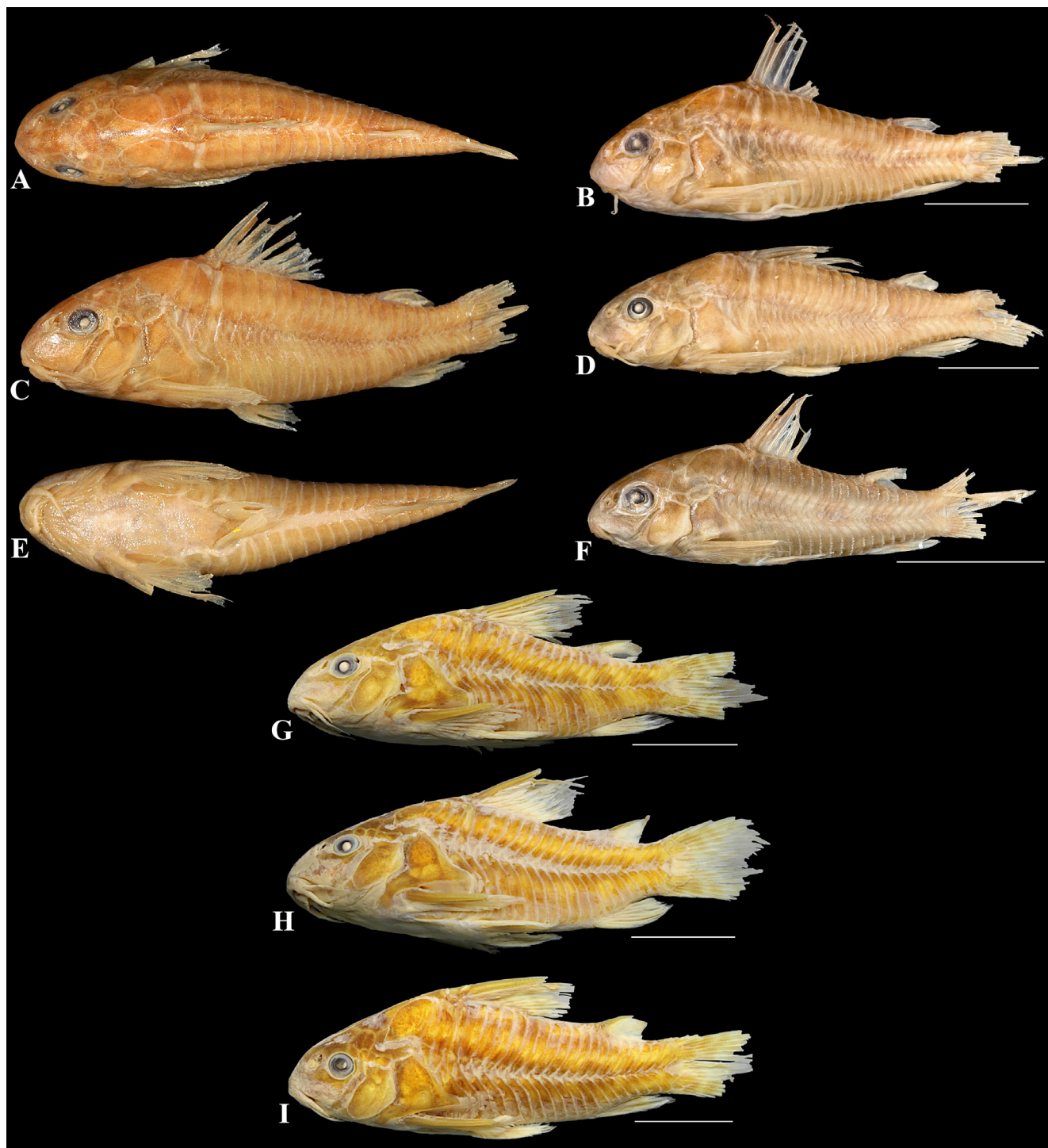


FIGURE 2 | Lectotype (BMNH 1890.3.12.4, 36.8 mm SL; **A, C, E**) and three paralectotypes of *Corydoras microcephalus* (BMNH 1890.3.12.5-6, 3, 23.7–38.0 mm SL; **B, D, F**), plus three non-type specimens of *H. paleatum* (MLP 3147; **G–I**) from the region of Tres Arroyos, Buenos Aires, Argentina. Photos (**A**), (**B, C, D, F, G–I**), and (**E**) showing specimens in dorsal, lateral and ventral views, respectively. Photos (**A, C, E**) by Mark Allen, and (**B, D, F**) by Kevin Webb.

TABLE 1 | Morphometric data of *Hoplisoma paleatum*, including the lectotypes of *Callichthys paleatus* (BMNH 1917.7.14.18) and *Corydoras microcephalus* (BMNH 1890.3.12.4), and 92 non-type specimens, comprising the data from Tencatt *et al.* (2016; 45 specimens) plus 47 specimens from the region of Tres Arroyos, Buenos Aires, Argentina. SD = Standard deviation.

	Lectotypes		Non-type specimens	
	<i>Callichthys paleatus</i>	<i>Corydoras microcephalus</i>	Low–High	Mean±SD
Standard length (mm)	30.0	36.8	28.0–44.0	34.5
Percent of standard length				
Depth of body	38.3	35.1	34.1–39.8	36.7±1.3
Predorsal distance	50.3	47.0	45.9–51.8	48.9±1.3
Prepelvic distance	51.3	48.4	46.3–51.3	48.2±1.2
Preal anal distance	82.7	84.0	74.9–84.0	78.6±1.7
Preadipose distance	87.7	83.2	78.0–85.6	83.0±1.4
Length of dorsal spine	23.0	19.3	19.3–31.2	27.1±2.0
Length of pectoral spine	27.0	22.8	21.5–31.4	26.3±1.9
Length of adipose-fin spine	8.0	10.6	6.8–11.0	8.8±1.0
Depth of caudal peduncle	14.0	13.9	11.6–18.2	14.9±1.3
Length of dorsal-fin base	18.3	17.7	15.1–19.6	17.4±0.9
Dorsal to adipose distance	22.0	22.3	15.7–22.3	18.9±1.6
Maximum cleithral width	29.7	28.5	25.9–30.0	27.7±0.9
Head length	43.0	40.8	39.8–45.1	42.2±1.1
Length of maxillary barbel	11.0	9.2	9.2–16.6	14.0±1.6
Percent of head length				
Head depth	83.7	83.3	75.9–85.4	81.0±2.2
Least interorbital distance	34.1	28.0	28.0–36.8	32.7±1.6
Horizontal orbit diameter	22.5	20.7	15.9–21.1	18.9±1.2
Snout length	32.6	30.7	30.7–37.0	34.3±1.3
Least internarial distance	16.2	12.7	12.7–18.4	14.8±1.2

Diagnosis. *Hoplisoma paleatum* can be distinguished from its congeners, except for *H. armatum* (Günther, 1868), *H. atropersonatum* (Weitzman & Nijssen, 1970), *H. loretoense* (Nijssen & Isbrücker, 1986), *H. osteocarus* (Böhlke, 1951), and *H. osvaldoi*, by typically having posterior margin of pectoral-fin spine only with perpendicularly directed serrations, with some specimens variably presenting some serrations smoothly bent towards the tip of the spine (*vs.* most serrations conspicuously antrorse, perpendicularly directed serrations, if present, generally scarce, bifid and/or restricted to the proximal or distal portion of the spine); it can be distinguished from *H. armatum*, *H. atropersonatum*, *H. loretoense* and *H. osteocarus* by having a longitudinal series of three to five moderate- to large-sized dark brown or black blotches along flank midline; some specimens with coalescent blotches, forming a wide and irregular stripe (*vs.* blotches on midline of flank, if present, conspicuously smaller and not forming a distinct longitudinal series or stripe); no non-overlapping features between *H. paleatum* and *H. osvaldoi* were found (see “Comparison with morphologically similar congeners” below). Considering the congeners with similar color pattern, *H. paleatum* can be distinguished from *H. cochui* (Myers & Weitzman, 1954), *H. diphyes* (Axenrot & Kullander, 2003), *H. flaveolum* (Ihering, 1911), *H. froehlichii* (Tencatt, Britto & Pavanelli, 2016), *H. gryphus* (Tencatt, Britto & Pavanelli, 2014), *H. habrosum*, *H. lacrimostigmata* (Tencatt, Britto & Pavanelli, 2014), *H. longipinne*, and *H. lymnades* (Tencatt, Vera-Alcaraz, Britto & Pavanelli, 2013) by having anterior portion of dorsal fin with conspicuous concentration of dark brown

or black chromatophores, not forming small dark markings (*vs.* with small dark brown or black markings); from *H. carlae* (Nijssen & Isbrücker, 1983) by having pectoral fin with conspicuous concentration of dark brown or black chromatophores, not forming small dark markings (*vs.* pectoral fin with small dark markings); from *H. reynoldsi*, *H. tukano* (Britto & Lima, 2003) and *H. weitzmani* (Nijssen, 1971) by the absence of a dark brown or black bar crossing the orbit (*vs.* such bar present, forming the typical mask-like blotch); from *H. gladysae*, *H. micracanthus*, *H. petracinii* by the contact between the parieto-supraoccipital and nuchal plate (*vs.* parieto-supraoccipital and nuchal plate not in contact); from *H. ehrhardti* (Steindachner, 1910) by the presence of conspicuous dark brown or black bands on caudal-fin lobes (*vs.* caudal-fin lobes typically hyaline or brownish; dark markings, if present, diffuse); from *H. steindachneri* by having a fold in the middle portion of the lower lip (*vs.* fold absent).

Geographical distribution. *Hoplisoma paleatum* is known from the lower rio Paraná basin in Argentina, coastal rivers from Southern Brazil, Rio Grande do Sul State, and Uruguay, rio de La Plata basin in Argentina and Uruguay, and rio Uruguay basin in Uruguay (Tencatt *et al.*, 2016). Following Calviño (2020), the type-locality is currently considered to be the Laguna del Potrero, Maldonado Department, Uruguay. Additionally, a new record from Argentina reported to be from Tres Arroyos, Buenos Aires Province, likely from the coastal drainage system, representing the southernmost limit of the distribution of *H. paleatum* (Fig. 3).

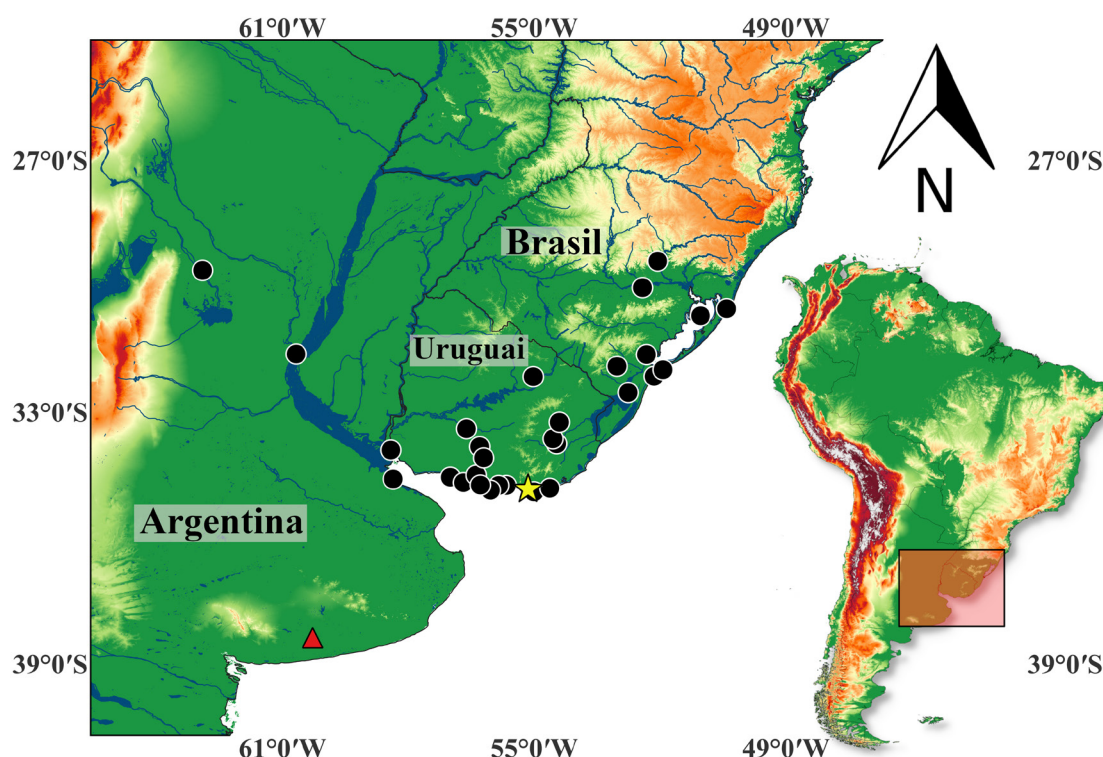


FIGURE 3 | Map showing the geographic distribution of *Hoplisoma paleatum*, with the yellow star representing its type-locality, the Laguna del Potrero, Uruguay, the red triangle represents the new record from the region of Tres Arroyos, Argentina, and the black circles represent remaining records within Argentinian, Brazilian and Uruguayan territories, following Tencatt *et al.* (2016). Each symbol may represent more than one locality.

Remarks. Morphologically, including morphometrical and osteological features, the population from the region of Tres Arroyos in Argentina (MLP 3147; Figs. 2G–I, 4–5; Tab. 1), is clearly compatible with the remaining populations of *H. paleatum* (see Tencatt *et al.*, 2016). Similarly, no meristic difference between the populations were found. Regarding color pattern, although they overlap in all aspects when comparing the different populations of *H. paleatum*, it is clear that the population from Tres Arroyos tend to present more numerous and smaller midline blotches (four or five), while most populations of *H. paleatum* tend to present three large midline blotches, with some specimens variably presenting up four or five smaller blotches (previously referred to as “fragmented blotches” in Tencatt *et al.*, 2016). In this context, we consider that a redescription of *H. paleatum* is currently unnecessary.

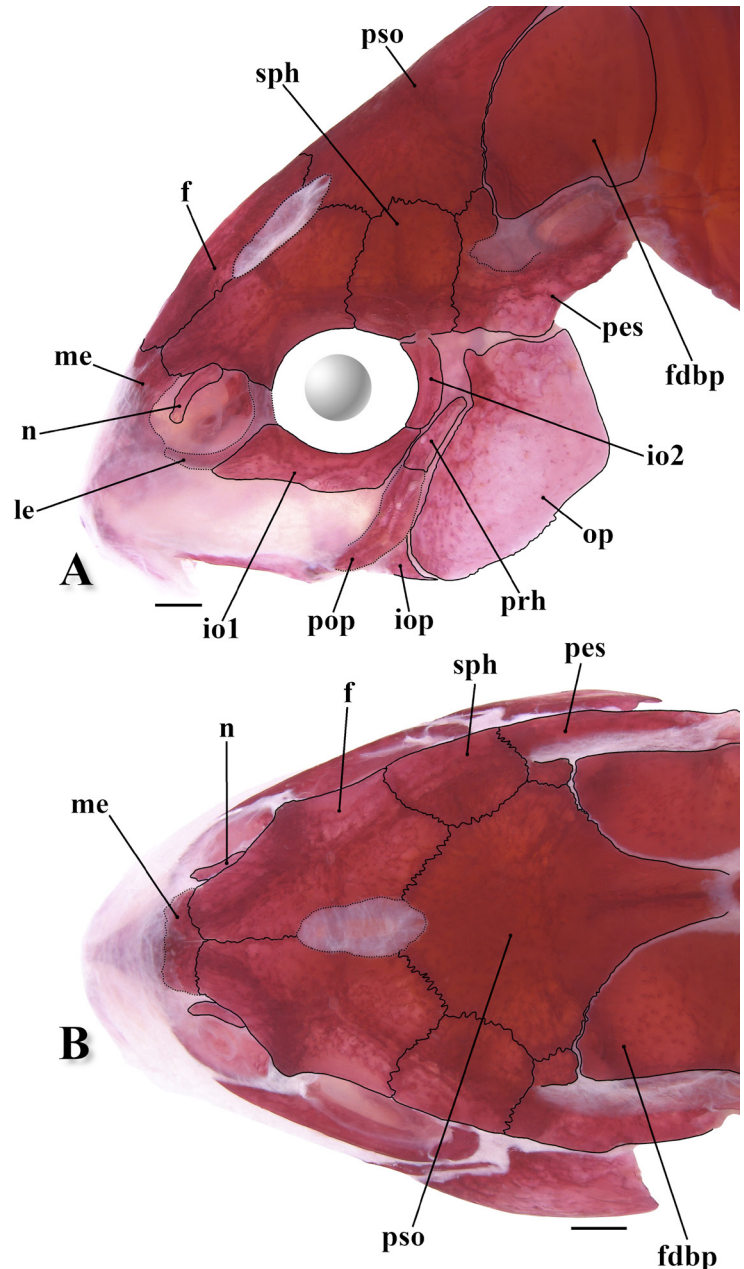


FIGURE 4 | Head osteological pattern in a CS specimen of *Hoplisoma paleatum* (MLP 3147, 34.6 mm SL), showing general morphology in lateral (A) and dorsal (B) views. Abbreviations: f: frontal, fdbp: first dorsolateral body plate, io1–2: infraorbital 1 and 2, iop: interopercle, le: lateral ethmoid, n: nasal, me: mesethmoid, op: opercle, pes: pterotic-extrascapular, pop: preopercle, prh: posterodorsal ridge of hyomandibula, pso: parieto-supraoccipital, sph: sphenotic. Scale bar = 1 mm.

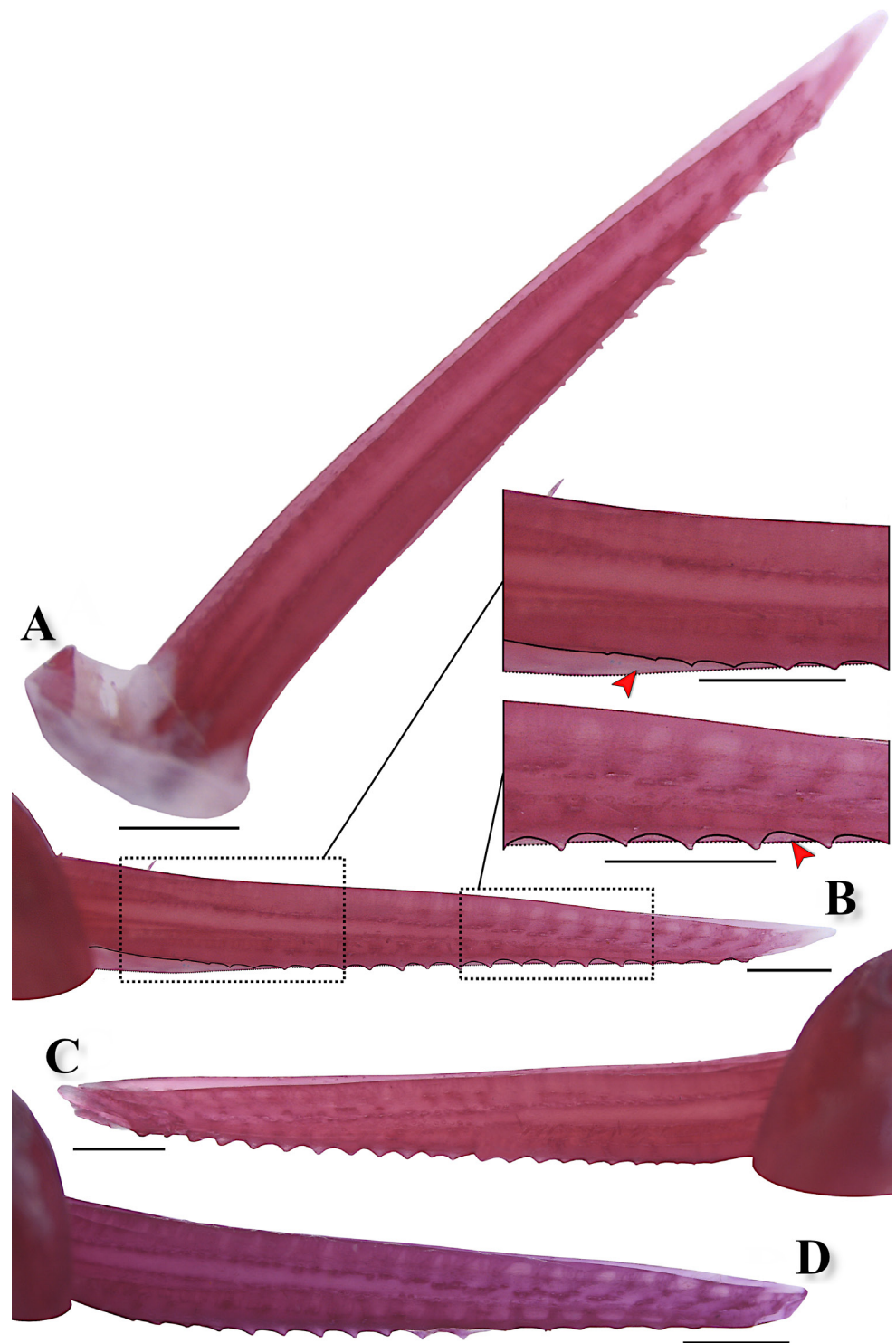


FIGURE 5 | Dorsal- and pectoral-fin spines of CS specimens of *Hoplisoma paleatum* (MLP 3147), showing their general morphology and serration pattern on posterior margin. Lateral view of the dorsal spine (**A**) and dorsal view of the right pectoral spine (**B**) of specimen with 34.6 mm SL, the left pectoral spine (**C**) of a specimen with 36.0 mm SL, and the right pectoral spine of a specimen with 34.5 mm SL. Black dotted lines in (**B**) delimiting the two regions shown in detail in the images just above to it, on the right; solid black lines delimiting the serrations in areas where they overlap with the posterior ventral laminar margin of the pectoral-fin, which is indicated by the red arrows. Scale bars = 1 mm.

Comparison with morphologically similar congeners. According to Alonso *et al.* (2025), *H. osvaldoi* can be distinguished from its congeners by having the following features: (I) a subsquare dorsal fin, and (II) a unique coloration in adults consisting of hyaline pelvic fins; grey basal and median portion of pectoral fin rays and its spine, hyaline membrane; light brown rays with dark grey portions and hyaline membrane in caudal fin, forming 4 to 5 discontinuous irregular bands; hyaline dorsal fin membrane, except light brown base and dark grey anterior portion; brown spine and light brown rays with grey blotches in pectoral fin; three dark grey subsquare spots on medial portion of flanks, decreasing in size posteriorly; four black blotches on body dorsal portion (including an irregularly-shaped blotch at predorsal plate [= nuchal plate] and base of dorsal fin spine); speckled small irregular roundish dark blotches on dorsal surface of head; and a bow-shaped black spot anterior to supraoccipital process.

Regarding dorsal-fin general shape, we observed no conspicuous differences between *H. osvaldoi* and *H. paleatum*, which present an overall subtriangular shape (Fig. 6). Typically, the dorsal-fin shape is analyzed considering its adducted position, with the spine forming an angle of about 45° relative to the longitudinal axis of the body, and at least the last two branched rays parallel to this axis (*i.e.*, in an intermediate position between totally abducted and totally addressed; see Figs. 7A, C, E, 8C, J). However, the general dorsal-fin shape can be interpreted as subsquare when considering specimens with fully abducted/open fin (Figs. 7D, 8D). Therefore, it is possible that the differences found by Alonso *et al.* (2025) resulted from the comparison between specimens with fully abducted fin with those with fins in intermediate position, not representing a real difference between the two aforementioned species. Although reported as unique, the color pattern of *H. osvaldoi* presents clear similarities with that of *H. paleatum* (Fig. 9). In both species, the dorsal fin presents dark anterior portion, with small, dark blotches on remaining areas. Regarding the pectoral fin, the authors reported two contrasting color patterns (see Alonso *et al.*, 2025:13, subitem 3, and p. 14, subitem 6), first stating that such fin is unspotted, presenting hyaline membrane, with spine and proximal and middle portions of soft rays dark, and then that the spine is brown and soft rays are light brown with dark blotches. Nonetheless, the pectoral fin is unspotted in both, with proximal and median portions typically dark, with chromatophores clearly more concentrated on rays but also present on membranes.

The color pattern of the caudal fin in *H. osvaldoi* and *H. paleatum* is also clearly similar, with four to five irregular dark bands in the first, and three to five in the latter. Regarding the series of blotches along midline of flank, Alonso *et al.* (2025) reported the presence of three dark blotches, decreasing in size posteriorly. In *H. paleatum*, the midline of flank typically displays three blotches, with some specimens presenting four or five blotches. Indeed, the midline blotches in these species variably decrease in size posteriorly, but some specimens lack such pattern, including *H. osvaldoi*, as it is possible see in the photo of the holotype (Alonso *et al.*, 2025:13, fig. 1), which presents the second blotch clearly larger than the first one. The dorsal series of four blotches along dorsum and a roughly bow-shaped blotch on dorsal portion of head are also shared by both species (Fig. 9).

Additionally, Alonso *et al.* (2025) stated that *H. osvaldoi* can be distinguished from *H. paleatum* by having the following features: (I) the presence of odontodes on infraorbitals 1 and 2, preopercle and interopercle (*vs.* absence); (II) the presence of a process on the



FIGURE 6 | General morphology of *Hoplisoma paleatum* (NRM 54230, 53.5 mm SL) and of three paratypes of *H. osvaldoi* (MNRJ 55045), showing their general morphology and color pattern in lateral view (A). Specimen (B) with 33.9 mm SL (left side of the body), (C) with 36.7 mm SL (left side of the body), and (D) with 30.8 mm SL (right side of the body, mirrored image).

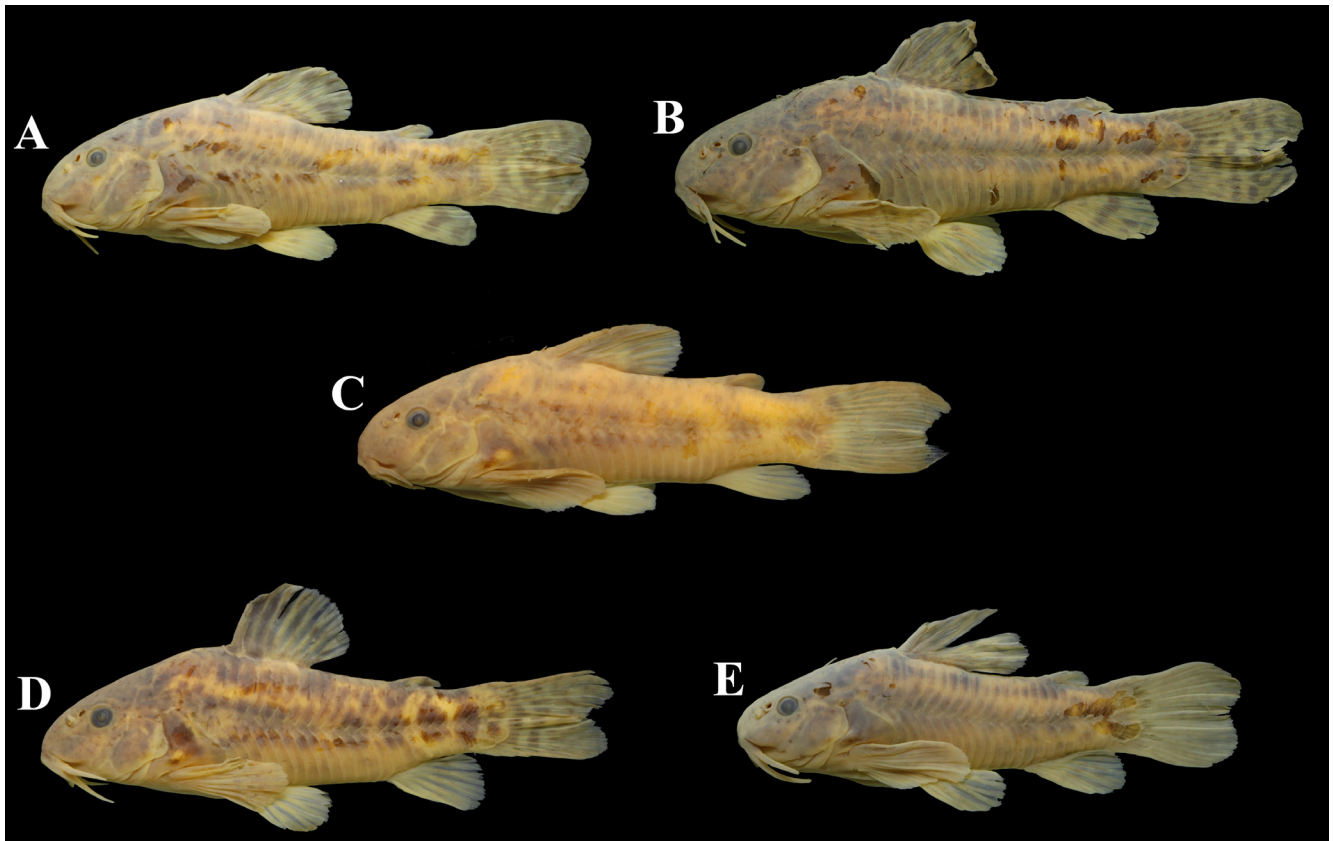


FIGURE 7 | General morphology and color pattern of (A, 32.0 mm SL; B, 32.2 mm SL) *Hoplisoma gladysae* (CI-FML 7262), (C) *H. micracanthus* (CI-FML 7114, 30.1 mm SL), and (D, 33.3 mm SL; E, 25.3 mm SL) *H. petracinii* (CI-FML 7260) in lateral view.

posterior expansion of epibranchial 2 (*vs.* absence; Britto, 2003: Fig. 10); (III) eight serrations on the distal third of pectoral-fin spine posterior margin (*vs.* 16–24 along its entire length); (IV) flap on pectoral-fin spine covering basal third posterior margin (*vs.* flap covering basal half); (V) 1–5 small serrations in distal portion of dorsal spine (*vs.* 8–11); (VI) absence of dark grey blotches on ventral portion of lateral scutes above anal fin or immediately anterior to it (*vs.* present); (VII) a shorter horizontal orbit diameter 16.3 ± 1.7 (*vs.* 20.6 ± 1.5 % SL); (VIII) presence of only three prominent, large lateral subsquare dark grey blotches on the flanks, distinctly separated by golden clear spaces (*vs.* three to six dark grey blotches, tending to merge in some individuals into a lateral stripe, and separated by brownish spaces with dark grey markings). The authors also stated that “all the examined specimens of *H. osvaldoi* have two small platelets just dorsal to infraorbital 1, lateral to lateral ethmoid, absent in *H. paleatum*, and small platelets bearing odontodes distributed in the belly that are absent in all examined CS specimens of *H. paleatum* from the type-locality but present in one of the specimens from Buenos Aires province, Argentina” (Alonso *et al.*, 2025).

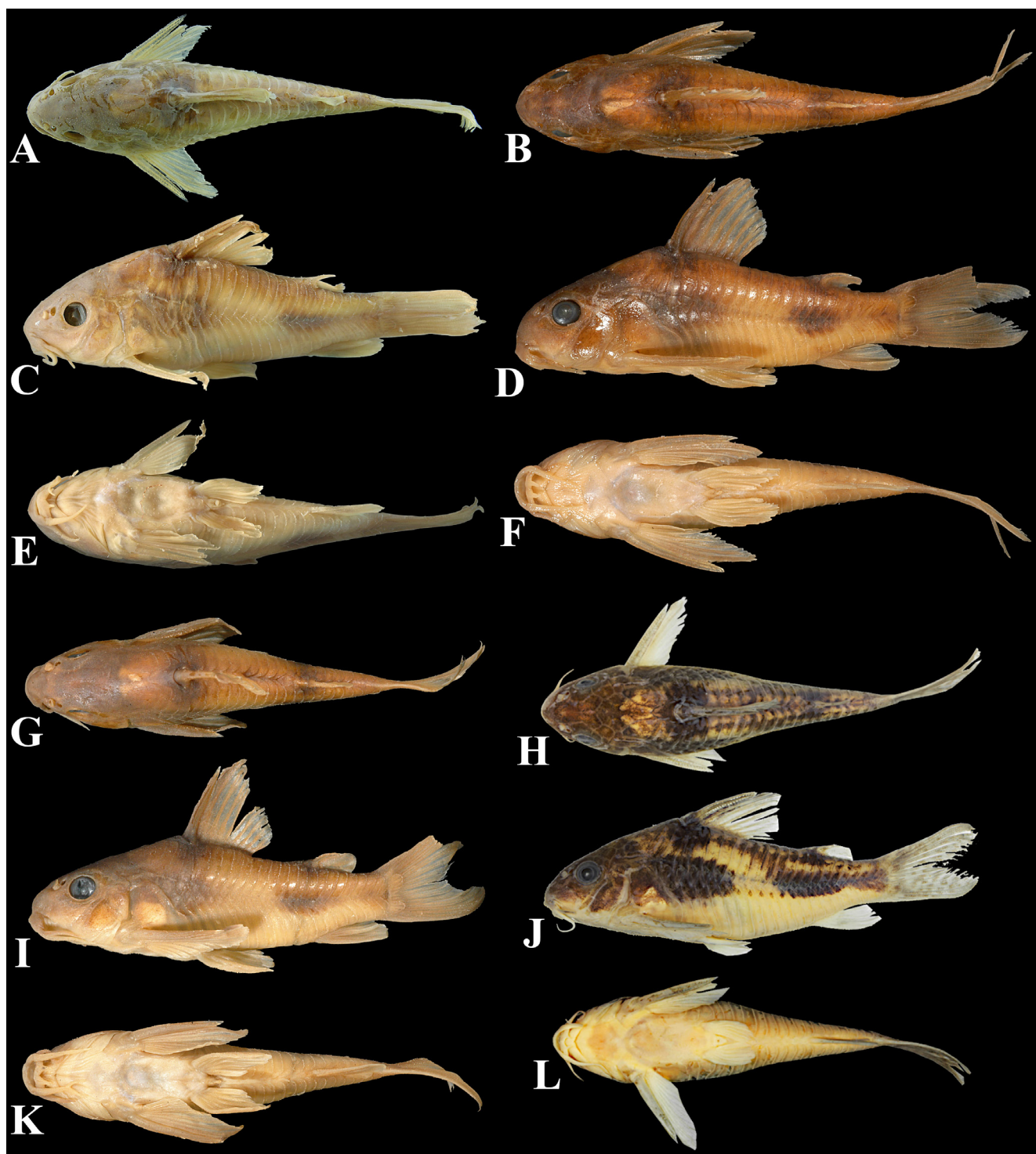


FIGURE 8 | General morphology and color pattern of *Hoplisoma ehrhardti*, showing the (A, C, E) lectotype, NMW 61104, 42.5 mm SL, (B, D, F, G, I, K) two paralectotypes, ZSM 4813, 17983 (both referred as “ZSM 4813, 17983” in Morris *et al.*, 2006), unmeasured, and (H, J, L) a non-type specimen, UFRGS 20938, 47.6 mm SL. Photos (A–B, G–H), (C–D, I–J), and (E–F, K–L) in dorsal, lateral and ventral views, respectively. Photos (A, C, E) by Anja Palandacic and Alexander Naseka, (B, D, F, G, I, K) by Natasha Khardina, and (H, J, L) by Gabriel Deprá.

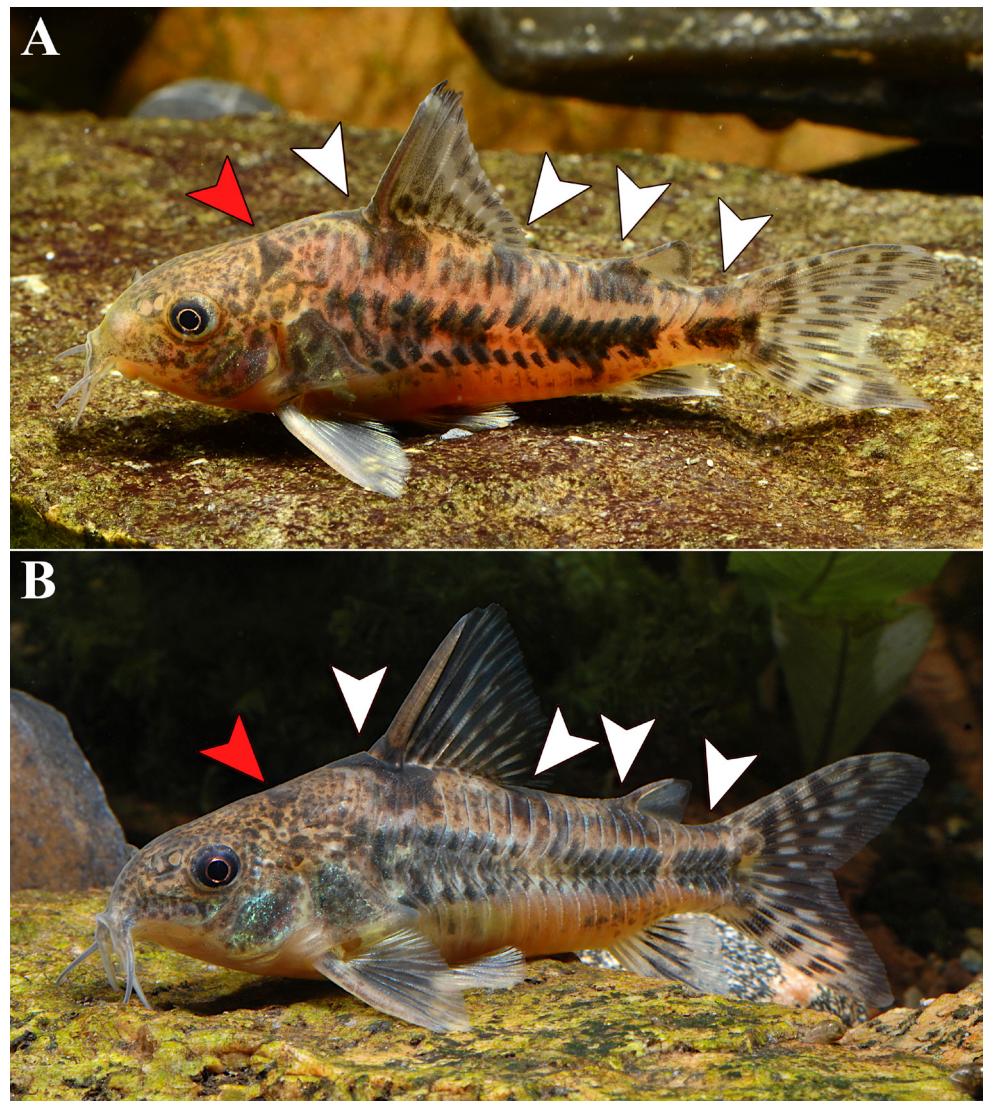


FIGURE 9 | Uncatalogued aquarium specimens of *Hoplisoma paleatum*, showing the general color pattern in life. Red arrows indicate the bow-shaped dark blotch on the top of the head, and white arrows indicate the blotches longitudinally aligned on dorsum. Specimen in (A) from the Laguna del Diario, and in (B) from Montevideo, Salinas, both from Uruguay. Photos by Hans Evers.

Regarding the presence of odontodes on both infraorbitals (1 and 2), preopercle and interopercle, both species possess odontodes on these bones (and in all the remaining exposed bony structures, which is typical of all Corydoradinae; see Discussion), as already stated by Tencatt *et al.* (2016), except for the interopercle, in which this feature was not checked. Nonetheless, the analysis of specimens of *H. paleatum* allowed us to confirm the presence of odontodes also on the exposed portions of the interopercle. Similarly, Alonso *et al.* (2025) did not assign this specific information provided in Tencatt *et al.* (2016) regarding the statement that *H. paleatum* lacks a process on the posterior expansion of epibranchial 2 (putative diagnostic feature II), already mentioned to be present by those authors (see Tencatt *et al.*, 2016; Fig. 10A).

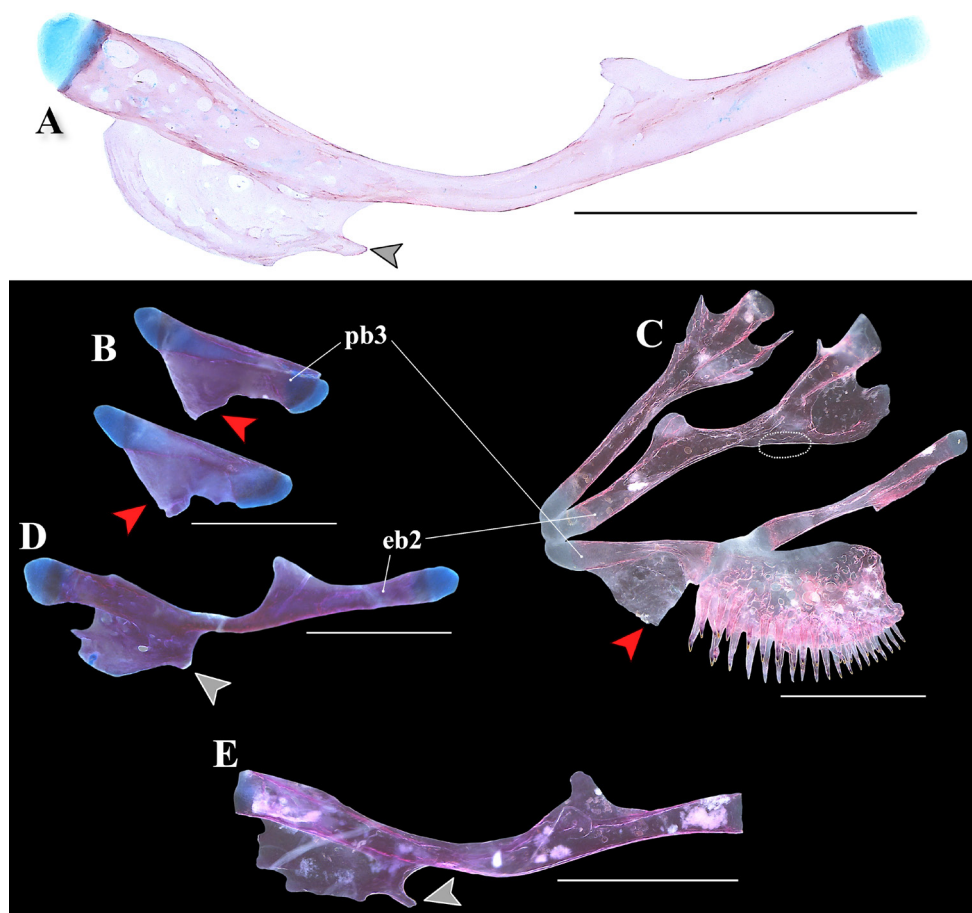


FIGURE 10 | Bones of the branchial arches in CS specimens of *Hoplisoma paleatum* (A), UFRGS 1722, 37.6 mm SL, showing the dorsal surface of its left epibranchial 2; *H. gladysae*, CI-FML 7110, unmeasured specimen, showing (B) the dorsal surface of the right (top right) and the ventral surface of the left (bottom left) pharyngobranchial 3, and the dorsal surface of the left epibranchial 2 (D); *H. micracanthus*, CI-FML 7111, 30.0 mm SL, showing the ventral surface of the left pharyngobranchial 3 and epibranchial 2 (C); and *H. flaveolum*, LBP 14596, unmeasured specimen, showing the dorsal surface of its left epibranchial 2 (E). Abbreviations: eb2: epibranchial 2, pb3: pharyngobranchial 3. Grey arrows indicate the small pointed process on posterior expansion of epibranchial 2, and red arrows indicate the triangular expansion on posterior portion of pharyngobranchial 3. Scale bars = 1 mm.

Regarding the putative diagnostic feature III, the analysis of two CS paratypes of *H. osvaldoi* revealed a quite different number and disposition of the pectoral-fin spine serrations, ranging from 14 to 16 serrations, disposed in most of the posterior margin of the spine (contrary to the eight serrations restricted to the distal third of pectoral spine), with serrations absent only close to the origin of the spine, like in *H. paleatum* (and most Corydoradinae) (Fig. 11). Interestingly, the pectoral spine depicted by Alonso *et al.* (2025:15, fig. 4C) bear 13 serrations on its posterior margin, with eight of them larger and with similar size, inserted on distal portion of the spine, and five smaller serrations decreasing in size towards the origin of the spine, similar to the pattern observed in one of the paratypes examined herein (MNRJ 55043, 38.8 mm SL; Figs. 11A–B). Moreover, one of the paratypes (MNRJ 55043, 33.8 mm SL) presents perpendicularly directed

serrations on the posterior margin of the pectoral spine (Figs. 11C–D), a condition also found in *H. paleatum* (see Tencatt *et al.*, 2016). Therefore, considering that both number and disposition of serrations on pectoral-fin spine overlap between *H. osvaldoi* and *H. paleatum*, we also discard such feature as diagnostic.

Regarding feature IV, the authors mention the presence of a flap on pectoral-fin spine, which covers the basal third of posterior margin in *H. osvaldoi* and basal half in *H. paleatum*. Considering that the authors did not describe the structure further than “flap”, we checked both ethanol-preserved and CS specimens of both species in order to find any structure similar to a flap. Although without any indication, there is a structure with laminar aspect on pectoral-fin spine posterior margin, which is depicted in Alonso *et al.*'s (2025) fig. 4C, which likely represents such flap. However, our analysis did not reveal the depicted structure in both species (see Figs. 5B–D, 11), and no difference

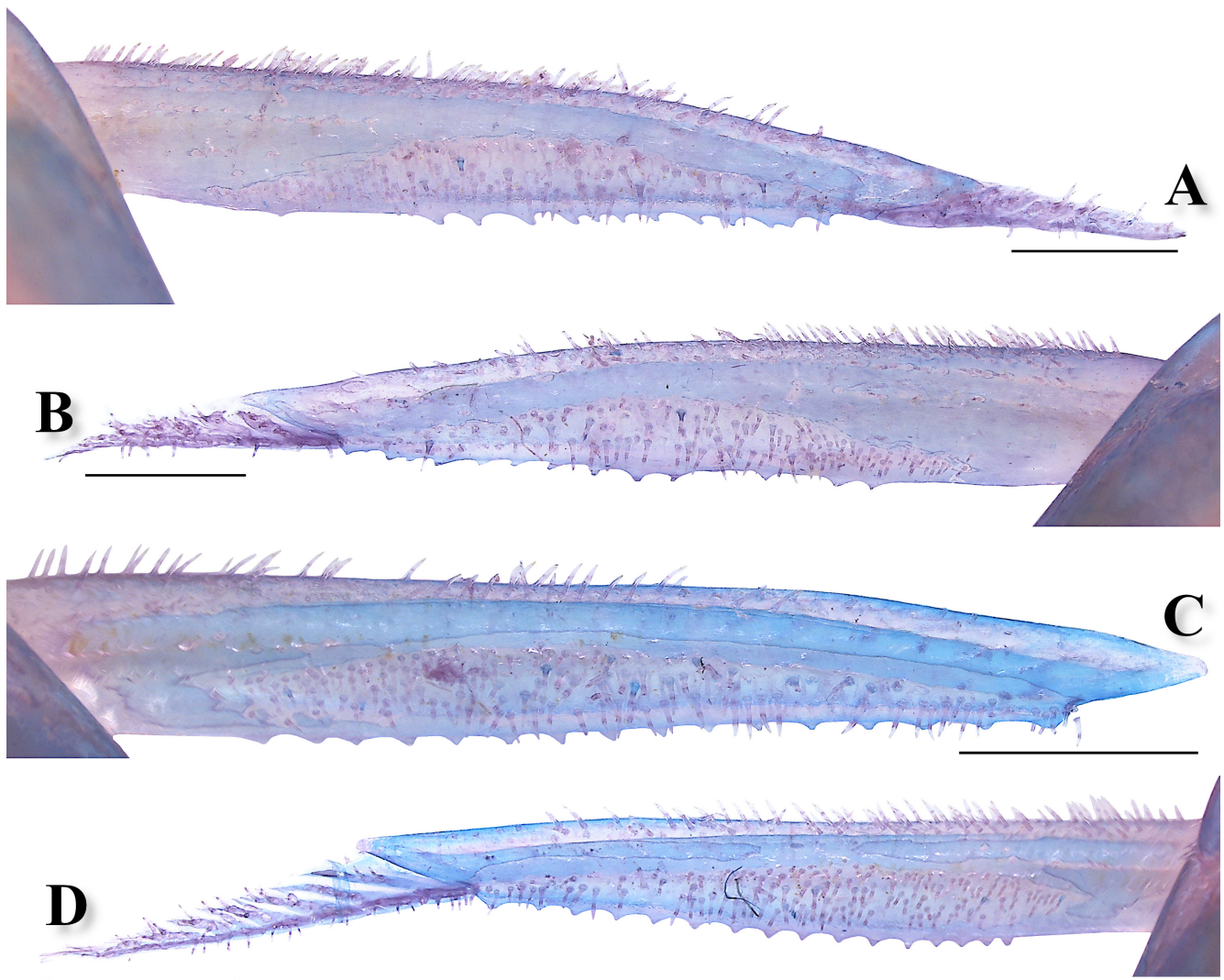


FIGURE 11 | Pectoral-fin spines of CS paratypes of *Hoplisoma osvaldoi* (MNRJ 55043), showing their general morphology and serration pattern on posterior margin in dorsal view. Right (A) and left (B) pectoral spine in paratype with 38.8 mm SL, and right (C) and left (D) pectoral spine in paratype with 33.8 mm SL. Scale bars = 1 mm.

on the posterior margin of the pectoral-fin spine was found. A possible explanation on the interpretation of such flap is related to the morphology of the spine itself. In many Corydoradinae species, including both *H. osvaldoi* and *H. paleatum*, both dorsal and pectoral spines present a groove along their posterior margin, which gives a roughly C-shaped form to the spine in cross section, forming a dorsal and a ventral laminar posterior margin of the pectoral spine (or left and right lateral laminar margins in the case of the dorsal-fin spine).

Traditionally, the pectoral spine is examined in dorsal view, with the posterior margin/serrations in ventral position (e.g., Figs. 5B–D, 11). In this case, if the spine is slightly inclined anteriorly (i.e., bent forward), the posterior ventral laminar margin of the pectoral-fin spine becomes visible, appearing to be project posteriorly. Considering that no flap (bony or fleshy) was observed herein, as well as no difference on the posterior margin of proximal portion of pectoral-fin spine was found, it is possible that the posterior ventral laminar margin of the pectoral fin spine, when visually projected posteriorly, led the authors to interpret it as a flap. If we are correct, the size of this expansion will appear to be smaller or larger depending on how inclined the spine is when examined in dorsal view. When visible dorsally, the posterior ventral laminar margin of the pectoral-fin spine is generally removed during the photo editing (Figs. 5C–D) as it makes it difficult to clearly see the serrations in photographs, especially when they are poorly developed (Fig. 5B). In any case, the posterior ventral laminar margin is not only present in the proximal portion of the spine, but along its posterior margin (see the detail in Fig. 5B).

Relative to feature V, Alonso *et al.* (2025) stated that the posterior margin of the dorsal-fin spine bears one to five small serrations, which are restricted to spines' distal portion, while *H. paleatum* presents eight to eleven. As previously mentioned by Tencatt *et al.* (2016), the posterior margin of the dorsal-fin spine present “five to nine serrations, only in distal portion of spine; serrations smoothly directed towards dorsal-spine tip; serrations absent in some specimens.”. Moreover, the examination of the two CS paratypes of *H. osvaldoi* (MNRJ 55043) revealed that one of the specimens present three serrations restricted to distal third of the spine, while the other one present ten serrations disposed on the two distal thirds of the spine (Fig. 12). As aforementioned, the posterior margin of the dorsal-fin spine presents a groove, in which the serrations are inserted, making it more difficult to visualize them, especially the smaller ones, which is a possible explanation for the difference in number and disposition of dorsal-fin spine serrations found by us. Anyway, the overlap between both species makes it clear that such feature cannot be considered as diagnostic.

The putative diagnostic feature VI refers to color pattern, with *H. osvaldoi* lacking “dark grey blotches on ventral portion of lateral scutes above anal fin or immediately anterior to it”, which would be present in *H. paleatum*. The analysis of some paratypes indeed revealed that, in such region, some specimens may present scattered dark brown or black chromatophores but no conspicuous blotches were found. Nonetheless, some specimens of *H. paleatum* present only scattered dark chromatophores in this region, lacking conspicuous dark blotches, as showed in previous articles (e.g., Knaack, 2007:39, fig. 5; the allotype of *H. longipinne*, which is considered herein as conspecific with *H. paleatum* following Tencatt *et al.*, 2016); Calviño, Alonso (2009:207, fig. 5; following Tencatt *et al.*, 2016); Tencatt *et al.* (2016; see fig. 2); and Calviño (2020:71, fig. 4)).

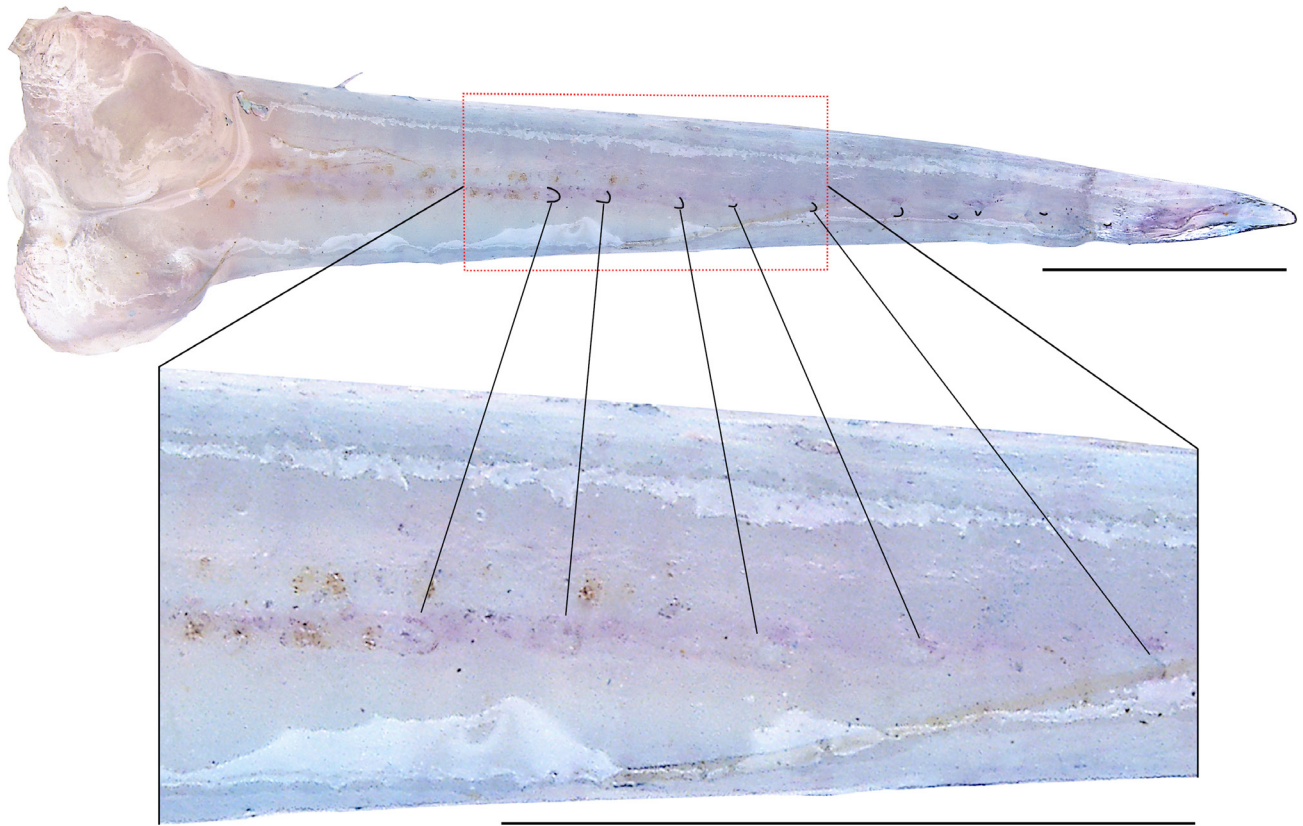


FIGURE 12 | Dorsal-fin spine of a CS paratype of *Hoplisoma osvaldoi* (MNRJ 55043, 38.8 mm SL), showing the serration pattern on its posterior margin. Solid lines on top image outlining the tip of serrations; red dotted square delimiting the area detailed in the bottom image. Scale bars = 1 mm.

Considering that this less mottled color pattern is also present in *H. paleatum*, such feature turns ineffective to distinguish this species from *H. osvaldoi*. The next feature (VII) refers to the horizontal orbit diameter, which presents a mean value of 16.3 ± 1.7 in *H. osvaldoi* and 20.6 ± 1.5 % of SL in *H. paleatum*, an information on the latter obtained in Tencatt *et al.* (2016; see tab. 1). First, the horizontal orbit diameter is always analyzed as percent of head length (HL), and not standard length (SL). Second, such features (having a smaller/larger structure) should be analyzed considering the range of the species, and not only the mean value, as the idea is to prove that there is no overlap between species.

According to Alonso *et al.* (2025:16, tab. 2), the horizontal orbit diameter ranges from 12.3 to 19.0% of HL in *H. osvaldoi*, whereas in *H. paleatum* it ranges from 15.9 to 24.0% of HL (Tencatt *et al.*, 2016; this study, see Tab. 1). Again, the overlap between both species makes such feature ineffective to distinguish them. Similarly to the size of the dorsal- and pectoral-fin spines (see Remarks section), the relative size of the eye (horizontal orbit diameter) can be influenced by the size/age of the analyzed specimens, as the allometric growth of the eye can vary (or not) throughout fish development (*e.g.*, Contreras-Tapia *et al.*, 2024; Xiang *et al.*, 2025), tending to be proportionally larger in juvenile specimens of Corydoradinae (LFCT, pers. obs.). The potential difference in relative eye size when comparing individuals of different sizes/ages reinforces the importance of considering the entire range of the analyzed species rather than just considering mean values.

The putative diagnostic feature VIII refers to the color pattern of the midline of flank, which is characterized to present “only three prominent, large lateral subsquare dark grey blotches on the flanks, distinctly separated by golden clear spaces” in *H. osvaldoi*, while it presents “three to six dark grey blotches, tending to merge in some individuals into a lateral stripe, and separated by brownish spaces with dark grey markings” in *H. paleatum*. However, similarly to the discussed regarding feature VI, specimens of *H. paleatum* variably present a “light color pattern”, i.e., with less small dark markings on flanks (see Knaack, 2007:39, fig. 5; Tencatt *et al.*, 2016, “Color in alcohol” section). The metallic golden sheen between the midlateral blotches mentioned by Alonso *et al.* (2025) is formed by the greenish yellow iridescent coloration, which is actually present all over the body of living specimens. Using the reflection of this coloration is tricky as this is typically variable, becoming more evident (or not) or more yellow or green depending on the illumination (e.g., intensity, angle of incidence, use flash). As aforementioned, our analysis also showed that *H. paleatum* presents three to five moderate- to large-sized dark brown or black blotches along the flank midline (none of the examined specimens presented six), which can variably merge and form a wide and irregular stripe. Nonetheless, the presence of dark markings between the three large dark blotches along the midline of flank were also observed in *H. osvaldoi* paratypes (Figs. 6B–C), having three large, dark blotches along midline of flank, which is the typical condition of *H. paleatum*, though variably presenting more blotches in some specimens.

Finally, Alonso *et al.* (2025) bring unnumbered additional features that would distinguish *H. osvaldoi* from *H. paleatum*, which are: the presence of two small platelets just dorsal to infraorbital 1, lateral to lateral ethmoid, in *H. osvaldoi* (vs. absent in *H. paleatum*), and “small platelets bearing odontodes distributed in the belly that are absent in all examined CS specimens of *H. paleatum* from the type-locality but present in one of the specimens from Buenos Aires province, Argentina”. As for other features, Tencatt *et al.* (2016) already reported the presence of these small platelets on anterior margin of orbit, especially above junction of frontal and lateral ethmoid, in *H. paleatum*. The same for the small platelets on ventral surface of trunk, of which the presence was the condition found in all examined specimens of *H. paleatum* (see Tencatt *et al.*, 2016). Nevertheless, we do not discard the absence of small platelets in ventral surface of trunk in some specimens of *H. paleatum*, as reported by Alonso *et al.* (2025), but this is surely not the typical condition of the species.

Alonso *et al.* (2025:14) provided additional features that would differ *H. osvaldoi* from both *H. longipinne* and *H. paleatum*, as follows: 1) hyaline pelvic fins in adult specimens (vs. usually bearing a conspicuous basal black blotch in *H. paleatum* and small black blotches on rays in *H. longipinne*), 2) hyaline membrane and light grey middle and basal portion of rays in pectoral fin (vs. with a basal wide dark grey blotch in *H. paleatum* and small blotches over the rays in *H. longipinne*), 3) a shorter dorsal-fin spine 16.0 ± 1.7 (vs. 23.1 ± 2.9 in *H. paleatum* and 25.4 ± 0.7 in *H. longipinne*), 4) a shorter pectoral fin spine 20.5 ± 2.1 (vs. 25.9 ± 2.3 in *H. paleatum* and 30.2 ± 1.2 in *H. longipinne*). Herein we will focus only on the comparison between *H. osvaldoi* and *H. paleatum*, leaving *H. longipinne* out of the discussion as we consider this species clearly different from the first two, especially considering the color pattern of the dorsal and pectoral fins (see Diagnosis; Tencatt *et al.*, 2016). The pelvic fin in the paratypes of *H. osvaldoi* tend to have few dark brown or black chromatophores in larger specimens, while some

of the smaller specimens (not necessarily juveniles) may present conspicuously more concentrated dark chromatophores. In any case, the presence of hyaline pelvic fin in *H. paleatum* was already mentioned in the taxonomic review of the species (see Tencatt *et al.*, 2016). As aforementioned, we were not able to find any conspicuous difference in the color pattern of the pectoral fin between *H. osvaldoi* and *H. paleatum*, as in the latter the proximal and middle portions of fin are also darkened, with distal portion hyaline, with some specimens variably presenting hyaline pectoral fin (Tencatt *et al.*, 2016). Moreover, the analysis of paratypes of *H. osvaldoi* revealed that some specimens also present dark brown or black chromatophores on membranes, and not only rays.

The difference of dorsal- and pectoral-fin spines size was also proposed only considering the mean values. According to Alonso *et al.* (2025:16, tab. 2), the dorsal-fin spine in *H. osvaldoi* ranges from 13.1 to 19.4% of SL, and the pectoral-fin spine from 15.2 to 25.1% of SL, whereas in *H. paleatum* they range from 17.1 to 31.2% of SL and 19.5 to 31.4% of SL, respectively (Tencatt *et al.*, 2016; this study, see Tab. 1). Therefore, regarding both spines, the overlap between both species makes these features ineffectively diagnostic. Furthermore, it is important to mention that differences in the size of the dorsal- and pectoral-fin spines can be biased by the sex ratio of the analyzed material, especially when considering only mean values, as larger spines tend to be secondary sex characters in males of some species (e.g., *H. longipinne* and *H. tukano*). In summary, all the putative diagnostic features, including the two allegedly autapomorphic features (i.e., presence of odontodes on the interopercle and serrations on the posterior margin of the pectoral-fin spine restricted to its distal half) proposed by Alonso *et al.* (2025) appear to be insufficient to distinguish *H. osvaldoi* from *H. paleatum*, either because they do not correspond with the material examined herein or by Tencatt *et al.* (2016), or by the presence of overlaps between both species. In this context, our analysis suggests that *H. osvaldoi* likely represents a population of *H. paleatum*. However, no extensive review searching for putative diagnostic features was carried out herein and, though of uncertain validity, we opted to revisit the taxonomy of this species in a more in-depth revisionary and integrative future analysis, comparing *H. osvaldoi* with the several populations of *H. paleatum*, and only then make a decision regarding the validity of this taxon.

Regarding its doubtful taxonomic status, another species putatively close related to the *H. paleatum* group is *H. steindachneri*. This species was described by Isbrücker, Nijssen (1973) from Paranaguá, in the coastal region of the Paraná State, southern Brazil, based on two specimens collected in 1923. At the time that the species was described, the type specimens of *H. steindachneri* were about 50 years old, and most of the color pattern was faded. However, Isbrücker, Nijssen (1973:6) were able to see traces of a color pattern similar to that of *H. paleatum* and its close relatives (i.e., a dorsal and midline longitudinal series of dark brown or black blotches). However, different from the typical pattern of the group, in which at least three large midline dark blotches are present, the authors reported the presence of only two, one below dorsal fin and another below adipose fin (considering the reference of count of plates provided in the original description). Isbrücker, Nijssen (1973:6, fig. 5a) also reported the absence of a labial fold (i.e., lower lip strongly reduced) and the presence of dark markings on caudal fin.

The analysis of photographs of the holotype of *H. steindachneri* (NMW 1504; Fig. 13) revealed that the anterior portion of the dorsal fin, between the spine and second

branched ray, are slightly darker than remaining portions of fin, something that can also be observed in the photograph provided by Isbrücker, Nijssen (1973:3, fig. 3). Additionally, it was possible to check the serrations on the posterior margin of the left pectoral-fin spine, which are mostly antrorse, as illustrated by Isbrücker, Nijssen (1973:5, fig. 4b). In this region, there is at least one species sharing most of these features with *H. steindachneri*, *H. ehrhardti* (Fig. 11). Although typically lacking dark markings on caudal fin, some specimens of *H. ehrhardti* variably display diffuse dark markings (Figs. 11H, J, L). Regarding the dark markings on caudal fin, it is uncertain, though likely, if the diffuse dark coloration observed in the holotype (see Isbrücker, Nijssen, 1973:3, fig. 3; Fig. 13) is due to the long preservation period of the holotype or not, something that could also explain the observation of only two midlateral dark blotches in the long-preserved holotype.



FIGURE 13 | Holotype of *Hoplisoma steindachneri* (NMW 1504), showing its general morphology and color pattern in dorsal (top), lateral (middle) and ventral (bottom) views. Scale bars = 10 mm.

Interestingly, the analysis of photographs of some of the type specimens of *H. ehrhardti*, including the lectotype (NMW 61104; Figs. 8A, C, E) and two paralectotypes (ZSM 4813, 17983; Figs. 8B, D, F, G, I, K), revealed that the third midlateral blotch, the one on the posterior portion of the caudal peduncle, is almost imperceptible, while the anterior two are still evident, though faded when compared to recently preserved specimens. Still regarding *H. ehrhardti* type specimens, the photographs also show that the anterior portion of the dorsal fin is also darkened in the lectotype and one of the paralectotypes (Figs. 8C–D), a feature shared with both *H. paleatum* and *H. steindachneri*. Interestingly, Isbrücker, Nijssen (1973) reported the presence of small dark blotches on the dorsal fin of *H. steindachneri*, which can be confirmed by a photo of the holotype (see p. 3, fig. 3), a feature shared with *H. paleatum* but not *H. ehrhardti*. Additionally, the lower lip in one of the paralectotypes of *H. ehrhardti* is reduced (Fig. 11C), similar to that depicted by Isbrücker, Nijssen (1973:6, fig. 5a). A poorly-developed lower lip was also observed in some specimens of *H. paleatum* (see Tencatt *et al.*, 2016, fig. 2), but, like in *H. ehrhardti* (Fig. 8C), comparatively more developed than in *H. steindachneri* (Fig. 13).

In summary most of the features related to morphology and color pattern shows that *H. steindachneri* seems slightly more similar to *H. paleatum* than to *H. ehrhardti*, though also sharing some features with the latter. Curiously, in the region where *H. steindachneri* occurs (coastal region of the Paraná State), only *H. ehrhardti* and a morphotype of *H. longipinne* occur (LFCT, pers. obs.), while *H. paleatum* is restricted to southernmost drainages (considering only the Brazilian territory), with the northernmost records in the Rio Grande do Sul State, Brazil (Tencatt *et al.*, 2016; Fig. 3). Anyway, considering the currently available information, which is scarce, allied to the fact that there are still some diagnostic features between the three species, it seems reasonable to still consider *H. steindachneri* as a valid species until further analysis.

Morphological delimitation of closely-related groups. The phylogenetic hypothesis of Alonso *et al.* (2025) recovered a clade composed by *Urkumayu* plus *H. flaveolum* as the sister group of the *H. paleatum* group. According to these authors, *Urkumayu* can be distinguished from the remaining genera within Corydoradinae by having the following combination of characters: (I) supraoccipital and nuchal plate not in contact, (II) posterior expansion of pharyngobranchial triangular, and (III) ossified portion of pectoral spine strongly reduced. Although present in the three species of *Urkumayu*, this diagnosis fails to distinguish the new genus from the remaining genera of Corydoradinae as these three characters are simultaneously present in representatives of at least three other genera: *Aspidoras* (all species), *Brochis* (*B. diffluviatilis*), and *Osteogaster* (*O. hephaestus*). Regarding the differential diagnosis of the new genus, some of the additional features assigned by authors are inconsistent with the currently available data, which will be addressed herein. According to the authors, *Urkumayu* can be distinguished from *Corydoradinae* plus *Hoplisoma* and *Osteogaster* by having the posterior expansion of pharyngobranchial (presumably the pharyngobranchial 3) triangular (*vs.* concave or rounded). However, the presence of a posterior triangular expansion on the pharyngobranchial 3 is arguably the most common condition not only within Corydoradinae but in Callichthyidae as a whole, being present in all genera (see Britto, 2003; Tencatt *et al.*, 2013, 2014b, 2016, 2019, 2020, 2021, 2022a,b, 2023a,b, 2024a,b, 2025a,b; Tencatt, Pavanelli, 2015; Ohara *et al.*, 2016; Tencatt, Ohara, 2016a,b; Bono

et al., 2019; see Figs. 10B–C). Additionally, intraspecific variation is also possible, with some specimens presenting posterior expansion on pharyngobranchial 3 triangular, while others display a rounded or irregular expansion, such as in *H. osvaldoi*.

Regarding the opercle, Alonso *et al.* (2025) stated that the new genus can be distinguished from *Corydoras* plus *Gastrodermus* by having a compact opercle (*vs.* elongated). Even though *Corydoras* indeed presents a relatively slender opercle, the opercle in *Gastrodermus* (and in most genera within Corydoradinae) can also be relatively compact (*e.g.*, Bono *et al.*, 2019), as aforementioned. The authors also mentioned the presence of “external arm of basipterygium falciform (*vs.* laminar)” to differentiate *Urkumayu* from *Gastrodermus* plus *Aspidoras*, *Osteogaster*, and *Scleromystax*. The condition described by Britto (2003:141, fig. 22C) is relatively uncommon within Corydoradinae, being typically reported for *Hoplisoma*, such as *H. colossus* (see Tencatt *et al.*, 2023b:12, fig. 7) and *H. flaveolum* (Tencatt *et al.*, 2014b:94, fig. 5b). The falciform external arm of the basipterygium is characterized by being clearly expanded posteriorly, with a conspicuous notch on its anterolateral portion, where the first rib passes through (LFCT, pers. obs.). Many Corydoradinae, including at least *H. gladysae* and *H. micracanthus*, have an intermediary condition between the typical falciform state described above and the laminar state in Britto (2003:141, fig. 22, A, B, D), in which the external arm is somewhat expanded posteriorly but lacks a conspicuous notch on its anterolateral portion (Fig. 14). The typical laminar state, in which the external arm is poorly expanded laterally and posteriorly, and has a more rounded shape, is present in representatives of all genera within Corydoradinae (as well as in Callichthyinae). In addition to the discovery of this intermediary condition, a high degree of intraspecific variation was observed in some species (*e.g.*, *Hoplisoma noxium* Tencatt, Ohara, Carvalho, Grant & Britto, 2025 and *H. tenebrosus* Tencatt, Ohara, Carvalho, Grant & Britto, 2025 and *Osteogaster oharai* Tencatt, Carvalho, Silva & Britto, 2025), apparently linked to sex (LFCT, pers. obs.). Therefore, although potentially useful at species level, the sharing of the aforementioned intermediary condition by most Corydoradinae makes this character not as reliable at genus level, at least the way it was originally proposed by Britto (2003).

Alonso *et al.* (2025) pointed that *Urkumayu* could be distinguished from *Aspidoras* by having the anterior projection of frontal bone short (*vs.* long), which is inaccurate as such expansion is extremely variable, even intraspecifically, ranging from short to long (Tencatt *et al.*, 2022). The authors also pointed that a compact complex vertebra (*vs.* slender) differs *Urkumayu* from *Aspidoras*. However, the information provided by the authors is not fully accurate, as the presence of three different states were reported by Tencatt *et al.* (2022a), showing that the parapophysis of the complex vertebra in *Aspidoras* can be poorly developed (= slender), moderately developed, and well developed (= compact). Moreover, the analysis of CS specimens of *H. micracanthus* and *H. gladysae* revealed that the parapophysis of the complex vertebra ranges from poorly- to moderately developed (*i.e.*, horizontally oblong, typically not expanded anteriorly, or slightly expanded anteriorly) (Fig. 15), with no specimen displaying a well-developed parapophysis (*i.e.*, compact, conspicuously expanded anteriorly, with subtriangular shape) (see Tencatt *et al.*, 2022b:18, fig. 8A). Still regarding *Aspidoras*, the authors stated the “medial expansion of coracoid exposed” in *Urkumayu* as a diagnostic feature. Although not expanded mesially and with different degrees of development,

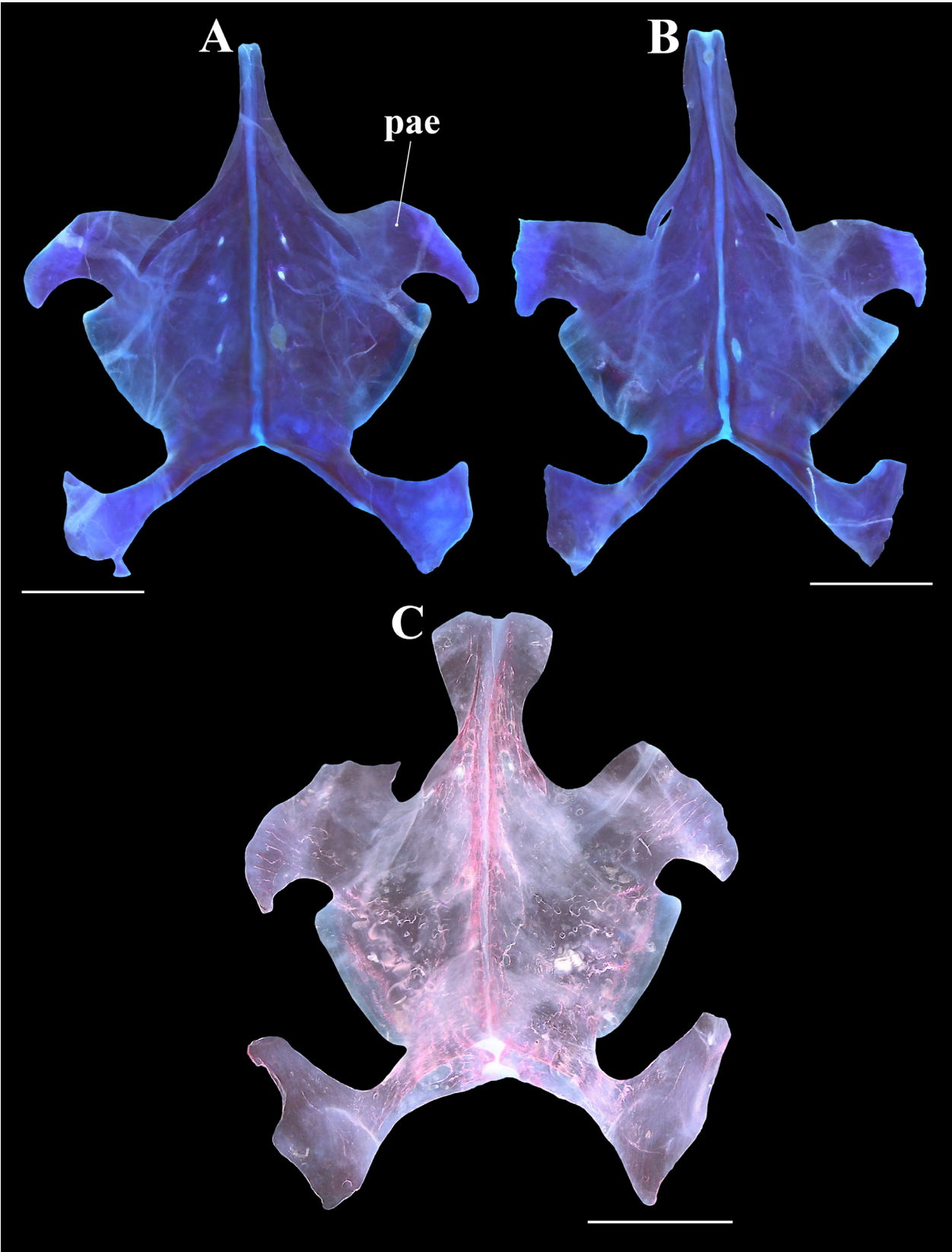


FIGURE 14 | Pelvic girdle in CS specimens of (A–B) *Hoplisoma gladysae* (CI-FML 7110, unmeasured), and (C) *H. micracanthus* (CI-FML 7111, 30.0 mm SL), showing the general morphology of its dorsal surface, especially of the anterior external process of basipterygium (pae). Scale bars = 1 mm.



FIGURE 15 | Ventral view of the complex vertebra in a CS specimen of *Hoplisoma micracanthus* (CI-FML 7111, 30.0 mm SL), showing a moderately-developed parapophysis (pcv). Dotted black line indicating the anterior border of the parapophysis. Scale bar = 1 mm.

this structure, referred to as posterolateral portion of scapulocoracoid in the more recent literature, is exposed in all Corydoradinae, making this character, the way it was proposed (see Britto, 2003), not diagnostic for the group.

Regarding *Osteogaster*, Alonso *et al.* (2025) additionally used the presence of a posterior expansion of ceratobranchial 3 continuous (*vs.* with a notch), and posterior margin of ischiac process (presumably the dorsal one) smooth (*vs.* with a narrow expansion). As stated in the recent literature, the presence of a notched or continuous posterior expansion of ceratobranchial 3 can be often variable, with some specimens presenting both states (comparing left and right side of branchial arches), such as observed for *H. micracanthus* (CI-FML 7111). Additionally, the presence of an intermediary condition between those states was also observed. The intraspecific variation allied with the presence of an intermediary state was possibly the main reason that led Vera-Alcaraz (2013:134) to omit such character from his analysis, a reasonable decision in our view. Similarly, the posterior margin of the dorsal ischiac process range from poorly expanded posteriorly and smooth/rounded (*e.g.*, *C. caramater* and *C. iiap*) to conspicuously expanded posteriorly and roughly triangular/pointed (referred as “narrow expansion” by Britto (2003)) (*e.g.*, *O. maclurei*), with many species presenting an intermediary condition between these states (*e.g.*, *Hoplisoma noxium* and *H. tenebrosum*, and *Osteogaster oharai*).

Hoplisoma flaveolum, a species from the upper rio Paraná basin in Brazil, is the sister group of *Urkumayu*. This clade is supported by the following three morphological synapomorphies: “(I) the lack of odontodes on infraorbitals (14:0), (II) lack of a dorsally oriented process on posterior expansion of epibranchial 2 (27:1), and (III) the lack of odontodes on preopercle (36:0)” (Alonso *et al.*, 2025). As aforementioned, the presence of odontodes on exposed bony structures is common to all Corydoradinae, which is the case in *H. flaveolum* and *Urkumayu* (Fig. 16). First, the authors seem to confuse the characters in Britto (2003), mentioning character 14 for feature (I), 27 for (II), and 36 for (III), whereas these characters should be 13, 26, and 35, respectively. Contrary to the species attributed to *Urkumayu*, in which the odontodes on exposed portions of cranium are scarcer (Figs. 16A–B, 17D), the infraorbital 1 and 2, preopercle, as well as the remaining exposed bones, of *H. flaveolum* are densely covered by odontodes (Fig. 16C). Moreover, all specimens of *H. flaveolum* examined herein displays a small pointed process on posterior expansion of epibranchial 2, directed towards the pharyngobranchials (3 and 4), a condition also found in *H. gladysae*, type species of *Urkumayu* (Figs. 10D–E). Regardless of the problems with the taxonomic status of the holotype of *H. flaveolum*, which seems to represent one of the numerous morphotypes currently identified as *B. difluviatilis* (see Tencatt, 2015), the species identified as *H. flaveolum* by Britto (2003) and Alexandrou *et al.* (2011), and consequently the same on Alonso *et al.* (2025), present conspicuously different morphology from the species proposed as members of *Urkumayu* (see Tencatt *et al.*, 2014a,b; Figs. 17A–C).

In addition to the aforementioned features, the species currently recognized as *H. flaveolum* also presents ossified portion of both dorsal- and pectoral-fin spines well developed, and parieto-supraoccipital and nuchal plate contacting each other, which clearly rules out any possibility of considering it as a member of their new genus, according to the definition proposed. At the same time, no diagnostic feature (at genus level) between the species attributed to *H. flaveolum*, the species from the *H. paleatum* group, and the species within *Hoplisoma sensu stricto* was found so far. As for the holotype of *H. flaveolum*, the specimen presents all of the key diagnostic features of *B. difluviatilis*, which are: (I) absence of contact between the parieto-supraoccipital and the nuchal plate, (II) posterior margin of dorsal-fin spine smooth, (III) posterior margin of pectoral-fin spine with poorly-developed serrations restricted to proximal portion of spine, (IV) infraorbital 1 with well-developed ventral laminar expansion, (V) infraorbital 2 with well-developed posterior laminar expansion, contacting pterotic-extrascapular by means of a roughly triangular secondary posterodorsal expansion, (VI) middle portion of posterior laminar expansion of infraorbital 2 with roughly triangular process, (VII) anterodorsal edge of infraorbital 2 expanded anteriorly, and (VIII) roughly straight and more prominent snout. In any case, both the holotype and specimens attributed to *H. flaveolum* in previous studies (*e.g.*, Britto, 2003; Alexandrou *et al.*, 2011; Tencatt *et al.*, 2013, 2014a,b, 2016; Dias *et al.*, 2024) conspicuously differ from the species proposed as members of *Urkumayu*.

Synapomorphies of *Urkumayu*. According to Alonso *et al.* (2025), the putative synapomorphies of *Urkumayu* are: “(I) absence of contact between the supraoccipital and the nuchal plate (11:0), (II) opercle compact, not vertically elongated (42:1), (III) absence of odontodes on opercle (44:1), and (IV) strongly reduced ossified portion

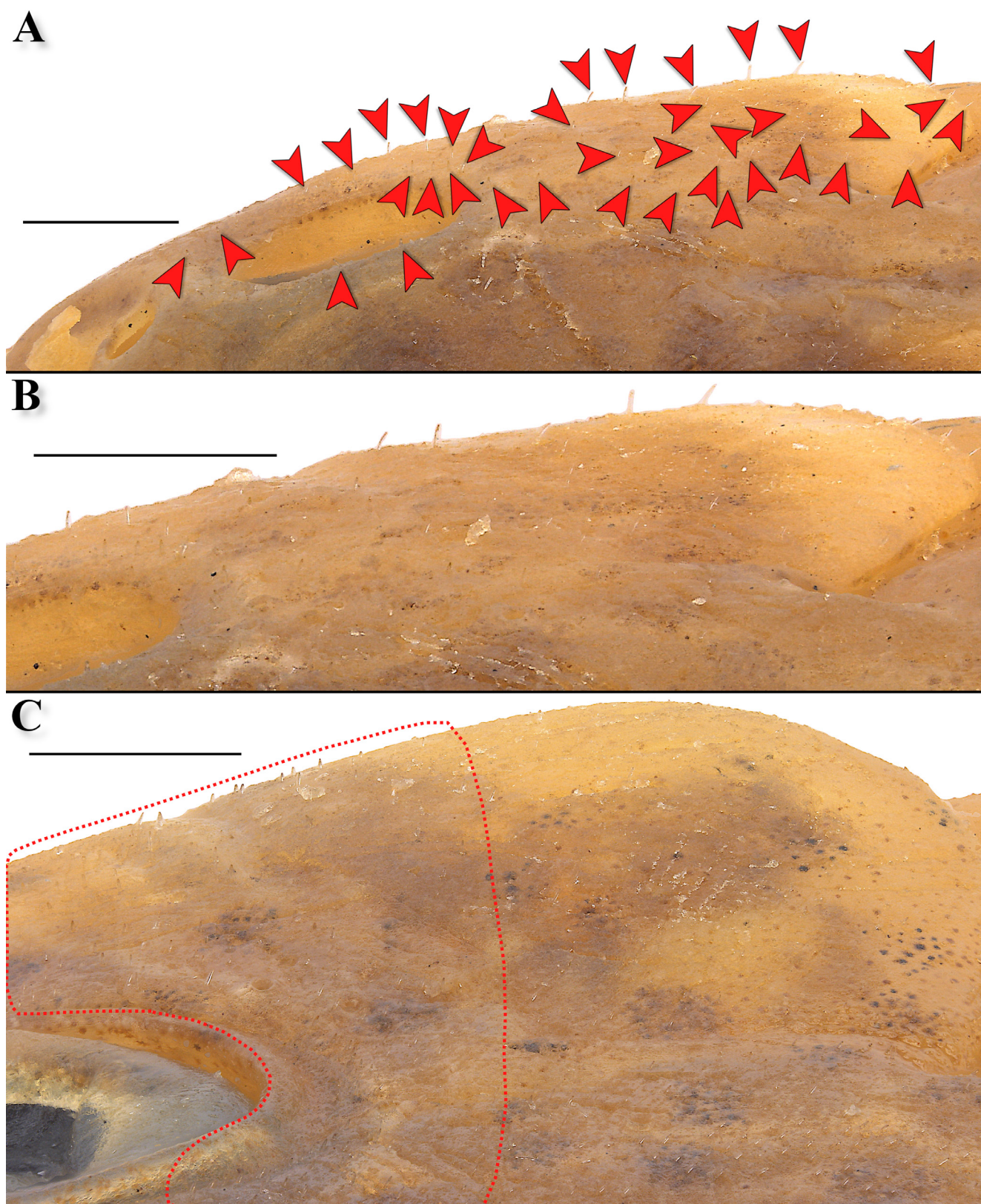


FIGURE 16 | Detail of the head of (A–B) *Hoplisoma micracanthus* (CI-FML 7111, 26.6 mm SL), and (C) *H. flaveolum* (LBP 14596, 37.4 mm SL). Red arrows in (A) represent the odontodes on cranial exposed bones; photo (B) is the zoomed and unmarked version of photo (A); red dotted lines in (C) indicate the area covered by numerous odontodes, including infraorbital 1 and 2, and preopercle, as well as interopercle, opercle, pterotic-extrascapular, preopercle, posterodorsal ridge of hyomandibula, and sphenotic. Scale bars = 1 mm.

of pectoral spine (66:2)". The absence of contact between the posterior process of the supraoccipital and the nuchal plate is a relatively common condition within Corydoradinae, being present in representatives of most genera within Callichthyidae, as follows: Callichthyinae (all species), *Aspidoras* (all species, but variable in *A. belenos*), *Brochis* (*B. difluviatilis*), *Gastrodermus* (*G. pygmaeus*, *G. pauciradiatus*, in most specimens of *G. undulatus*, and apparently in *G. latus*), *Osteogaster* (*O. melanotaenia*, *O. maclurei*, and *O. hephaestus*), and *Scleromystax* (all species).

Similarly, following the interpretation of Britto (2003) on his character 42, the opercle in Corydoradinae can be long (*i.e.*, length about twice its width) or compact (*i.e.*, width slightly smaller than length). However, the analysis of material has showed that there are nuances in the morphology of the opercle that make these two character-states little explanatory the way they were proposed, especially considering that intraspecific variation was also observed (*e.g.*, *B. arcuata* and *H. granti*, which variably present relatively slender or compact opercle; see Tencatt *et al.*, 2019:457, 463). The opercle in Corydoradinae is always dorsoventrally elongated (*i.e.*, its total length is always larger than its width), with some species presenting a relatively slender opercle, characterized by having its width smaller than or equal to half of its entire length, which is the common condition in *Corydoras* (*e.g.*, Tencatt *et al.*, 2020, 2021, 2024a,b), and in some *Brochis* (*e.g.*, Tencatt, Ohara 2016a, Bentley *et al.*, 2021), *Gastrodermus* (*e.g.*, Tencatt, Pavanelli, 2015), *Hoplisoma* (*e.g.*, Tencatt *et al.*, 2016, 2022a, 2023b). Other species present a relatively compact opercle, with width larger than half of entire length, like in *Aspidoras* (see Britto, 2003; Tencatt *et al.*, 2022a), some *Brochis* (Britto, 2003), some *Gastrodermus* (Bono *et al.*, 2019), some *Hoplisoma* (Britto, 2003; Tencatt *et al.*, 2016, 2022a), and in *Osteogaster* (Britto, 2003; Ohara *et al.*, 2016; Tencatt *et al.*, 2023a). However, in species/groups with relatively compact opercle, the width may be slightly or clearly larger than half of its entire length, something observed even when comparing the species composing *Urkumayu* (Figs. 7, 17A–B).

Regarding the absence of odontodes on the opercle (and on other cranial bones), this character was analyzed by Britto (2003) exclusively on CS specimens, whose preparation process tends to damage such structures, which are typically fragile in Corydoradinae, and, by this reason, some species were erroneously coded as lacking odontodes on the opercle and other cranial bones. Additionally, it is clear that specimen size and sex are also important factors for the presence, number and/or degree of development of odontodes in Corydoradinae. In this case, only through the examination of fully grown non-CS specimens of both sexes an unambiguous analysis of such structures is possible. As extensively published in previous articles (*e.g.*, Britto, Reis, 2005; Tencatt *et al.*, 2013, 2014a,b, 2016, 2019, 2020, 2021, 2022a,b, 2023a,b, 2024a,b; Tencatt, Pavanelli, 2015; Britto *et al.*, 2016; Tencatt, Britto, 2016; Tencatt, Evers, 2016; Tencatt, Ohara, 2016a,b; Espíndola *et al.*, 2018; Bono *et al.*, 2019), all exposed cranial bones (*i.e.*, covered by a thin layer of skin) in representatives of all genera within Corydoradinae bear odontodes. As expected, the analysis of specimens included by Alonso *et al.* (2025) in *Urkumayu* also revealed the presence of odontodes on the opercle (and on other cranial bones), though typically scarce when compared to other species (Figs. 16A–B).

The fourth synapomorphic feature refers to the strongly reduced ossified portion of the pectoral spine. First, it is important to mention that the analysis of the species attributed to *Urkumayu* revealed that the degree of development of both dorsal- and

pectoral-fin spines is variable, with specimens presenting comparatively smaller or larger spines. Nonetheless, although less common within Corydoradinae, some species from other genera also share this feature, such as *Aspidoras* (all species), *Brochis* (i.e., *B. diffluvialis*), and *Osteogaster* (i.e., *O. hephaestus*). In all of these cases, the species have a series of features that suggest them as paedomorphic, such as a poorly-developed ossified portion in both dorsal- and pectoral-fin spines, and absence of contact between the parieto-supraoccipital and nuchal plate (except for *A. belenos*), both indicated as synapomorphies of *Urkumayu*. Therefore, in most major clades within Corydoradinae (except *Corydoras*), species sharing the same reductive features of *Urkumayu* can be found, and in none of these cases were these species regarded as belonging to a different genus from other closely-related species.

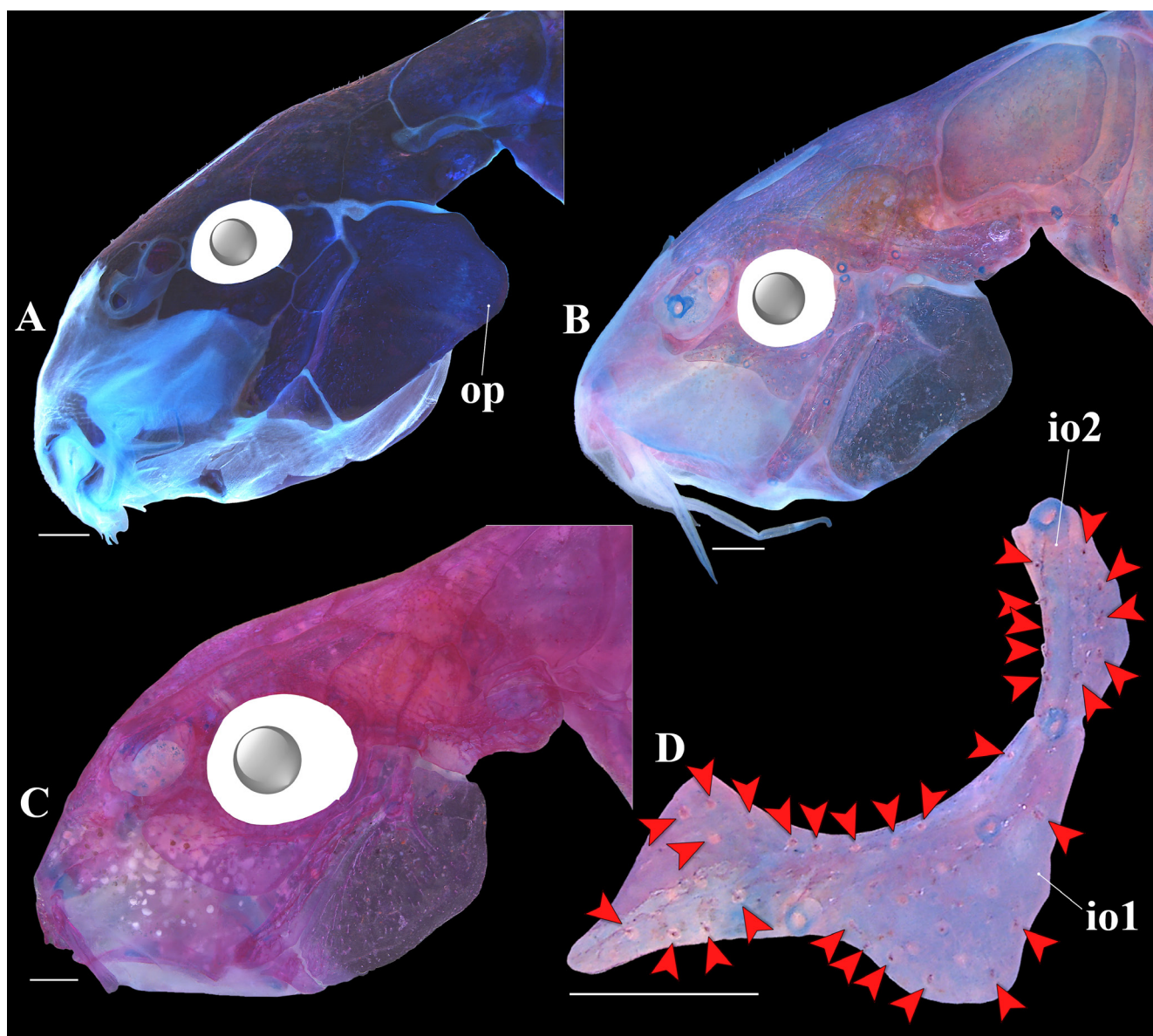


FIGURE 17 | Head osteological pattern in CS specimens of (A) *Hoplisoma gladysae* (CI-FML 7110, unmeasured), (B) *H. micracanthus* (CI-FML 7111, 30.0 mm SL), and (C) *H. flaveolum* (LBP 14596, 33.7 mm SL). Detail of the infraorbital series of *H. micracanthus* (CI-FML 7111, 30.0 mm SL) in (D). Abbreviations: io1–2: infraorbital 1 and 2, op: opercle. Red arrows in (D) indicate the odontodes in both infraorbital 1 and 2. Scale bars = 1 mm.

Taxonomic status of the species in *Urkumayu*. The analysis of the species allocated to *Urkumayu* by Alonso *et al.* (2025) suggest that the limits between these three species are currently diffuse. According to Calviño, Alonso (2009), *H. gladysae* (type-species of *Urkumayu*) can be distinguished from *H. micracanthus* by having fewer dorsolateral body plates (23 *vs.* 25), shorter dorsal-fin spine (mean = 9.2% *vs.* 13.9% in SL), approximately straight dorsal profile of head from the eye to the parieto-supraoccipital process (*vs.* dorsal profile of head convex), presence of dots or dark brown blotches on pectoral, pelvic and anal fins (*vs.* absence of dark markings), and by the brown ground color of the body with small dark blotches on the flanks and dorsal region (*vs.* four to six big subsquare blotches on the middle area of flanks). Besides the lectotype (BMNH 1897.1.27.8), six paralectotypes (BMNH 1897.1.27.9–14), and two additional species labeled as “syntypes” (BMNH 1906.5.31.40–41) but not included in Nijssen, Isbrücker (1980), six non-type specimens of *H. micracanthus* were examined for these features (*i.e.*, CI-FML 7114, 2, 24.0–30.1 mm SL; CI-FML 7111, 4, 24.2–33.0 mm SL).

Regarding *H. micracanthus*, the lectotype, three specimens from CI-FML 7111, and one specimen from CI-FML 7114, the number of dorsolateral body plates is indeed 25. In one specimen of each CI-FML 7111 and CI-FML 7114, the count of dorsolateral body plates was 24. Interestingly, the count of dorsolateral body plates in five specimens of *H. gladysae* (CI-FML 7262, 5, 26.4–34.6 mm SL) demonstrated to be relatively variable, with specimens presenting 24 (1), 25 (3), and 26 (1) dorsolateral body plates. Considering the variation range of dorsal-fin spine found in our specimens, it is also possible to observe an overlap between *H. micracanthus* (12.4 to 16.9% in SL, with 14.8% in the lectotype) and *H. gladysae* (10.3 to 12.9% in SL), even though there is a tendency for the latter to have relatively smaller dorsal-fin spine. Relative to the dorsal profile of body, no difference between the two species was noticed as the dorsal profile ranged from nearly straight to slightly convex in both species (Fig. 7). Regarding the two remaining putatively diagnostic features, the specimens of *H. gladysae* indeed tend to present a more mottled pattern, whereas *H. micracanthus* typically displays a less mottled pattern (Fig. 7). However, both species present a longitudinal series of relatively large, quadrangular dark blotches along midline of flank (Fig. 7), something that can be seen even in the holotype of *H. gladysae* (see Calviño, Alonso, 2009:201, fig. 1). The osteological comparison performed herein did not reveal any potential diagnostic feature. Therefore, the only putatively diagnostic feature refers to the presence of small, diffuse dark blotches on pectoral and variably pelvic fins, in *H. gladysae* (*vs.* pectoral and pelvic fins devoid of small, dark blotches). The anal fin, on the other hand, may variably present small, diffuse dark makings.

Regarding *H. petracinii*, Calviño, Alonso (2009) stated that this species can be distinguished from *H. gladysae* by the following features: longer dorsal-fin spine (12.6 to 19.6% in SL *vs.* 7.6 to 10.6% in SL), longer pectoral-fin spine (16.6 to 19.6% in SL *vs.* 11.9 to 17.4% in SL), caudal-fin shape a bit more emarginated (*vs.* slightly emarginated), triangular-shaped dorsal fin (*vs.* rounded), and by the color pattern of flanks and caudal fin. The authors also provided ways to distinguish *H. petracinii* from *H. micracanthus*, as follows: lower modal number of dorsolateral body plates in *H. petracinii* (23 *vs.* 25 in *H. micracanthus*), triangular dorsal-fin shape (*vs.* rounded rectangular), first dorsal-fin soft ray branched (*vs.* not always branched), and five to seven small, diffuse dark blotches (*vs.* four to six large blotches).

The dorsal-fin spine in our specimens of *H. petracinii* ranged from 9.3 to 17.3% in SL, whereas it ranged from 10.3% to 12.9% in SL in *H. gladysae*, and 12.4 to 16.9% in SL in *H. micracanthus*. Pectoral-fin spine size in *H. petracinii* ranged from 16.6 to 19.8% in SL, ranging from 14.2 to 18.1% in SL in *H. gladysae*, and 15.2 to 20.1% in SL in *H. micracanthus*. Considering our data, both features (*i.e.*, size of dorsal- and pectoral-fin spines) cannot be considered diagnostic, as they clearly overlap among the three congeners. Furthermore, the relative size of the dorsal- and pectoral-fin spines must be used with caution, as it may be influenced by the sex of the analyzed individuals, showing an artificial difference between set of specimens with sex ratio discrepancy (see Remarks section). Relative to caudal-fin shape, we also observed some degree of intraspecific variation, with some specimens presenting more markedly truncated fin while others present slightly more developed caudal-fin lobes, and no conspicuous difference was found when comparing the three species (Fig. 7). Similar to the findings related to *H. osvaldoi*, the dorsal-fin shape, which was suggested as diagnostic, seems basically the same in the three species, displaying an overall subtriangular shape, with rounded posterior margin. As aforementioned (see Comparison with morphologically similar congeners section), the position of the dorsal fin (depending on the way the specimen was preserved) interferes the interpretation of its general shape in lateral view. Therefore, it is possible that the differences found by Calviño, Alonso (2009) resulted from the comparison between specimens with fully abducted fin with those with fins in intermediate position. Still on the dorsal fin, the authors stated that *H. petracinii* always present first dorsal-fin soft ray branched (not always branched in *H. micracanthus*), which in itself is not diagnostic, since the authors themselves indicate an overlap. In any case, the first dorsal-fin soft ray is always branched in all of our 11 specimens.

Calviño, Alonso (2009) mentioned differences in color pattern between *H. petracinii* and *H. gladysae*, without specifying such differences (see p. 213). Interestingly, the color of *H. petracinii* seems to be intermediary between those of *H. gladysae* and *H. micracanthus*, sharing with the first the presence of small, diffuse dark blotches on the pectoral fin, and anterior portion of dorsal fin with a conspicuous dark patch with the latter. In *H. gladysae*, the anterior portion of dorsal fin also presents a conspicuous concentration of dark brown or black chromatophores but they generally form a diffuse dark patch (*vs.* more evident in *H. micracanthus* and *H. petracinii*). The pelvic fin in *H. petracinii* tend to be devoid of small dark spots, but dark markings were variably observed. The size and of dark blotches along midline of flank also overlaps between species, ranging from moderate to large in size (Fig. 7). The number of blotches ranged from four to six in *H. gladysae*, three to five in *H. micracanthus*, and four to six in *H. petracinii*. The blotches are conspicuous in the three species, including in *H. petracinii* (not diffuse, as stated by Calviño, Alonso (2009)), which can be seen in the photo of the holotype provided in the original description (see p. 203, fig. 2).

Finally, the number of dorsolateral body plates in our specimens of *H. petracinii* is quite variable, with specimens presenting 23(1), 24(5), 25(3), 26(1), and 27(1) plates on dorsal series (*vs.* 24(1), 25(3), and 26(1) in *H. gladysae*; 24(2), and 25(5) in *H. micracanthus*), showing that this feature is clearly not diagnostic. In summary, the only differences found among *H. micracanthus* and *H. petracinii* is the presence of small, diffuse dark blotches on the pectoral fin of the latter, which is shared with *H. gladysae* (*vs.* pectoral fin devoid of small, dark spots in the first). Besides the color pattern of pectoral and pelvic fins, the

only difference between *H. micracanthus* and *H. gladysae* is the presence of an evident dark patch on anterior portion of dorsal fin and a less mottled pattern of dark markings on flanks in the first, both features shared with *H. petracinii* (*vs.* dark pigmentation on anterior portion of dorsal fin diffuse, and more mottled pattern on flanks). As discussed above, most of the putatively diagnostic features presented in the original description are not functionally diagnostic (*i.e.*, the features overlap), leaving only a few subtle differences in the color pattern to support the validity of the three species. However, it is important to mention that, regarding morphology/color pattern, *H. micracanthus* and *H. gladysae* seem to represent two extreme forms, with *H. petracinii* as an intermediate morphotype between them. Interestingly, the geographic distribution of these species also shows the same pattern, with *H. micracanthus* and *H. gladysae* occurring in extreme positions (though geographically close to each other), and *H. petracinii* in between them (Calviño, Alonso, 2009:208, fig. 6).

Material examined. In addition to the material listed in Tencatt *et al.* (2016), the following material was examined: *Hoplisoma paleatum*: BMNH 1917.7.14.19 and 19a, 2, 26.6–28.7 mm SL, paralectotypes of *Callichthys paleatus*. BMNH 1890.3.12.4, lectotype of *Corydoras microcephalus*, 36.8 mm SL. BMNH 1890.3.12.5–6, 3, 23.7–38.0 mm SL, paralectotypes of *Corydoras microcephalus*. MLP 3147, 44, 28.0–44.0 mm SL, 3 CS, 34.5–36.0 mm SL.

DISCUSSION

Tencatt *et al.* (2016) stated that it was only possible to examine *H. microcephalus* through photographs of its lectotype, which along with the data provided in the original description by Regan (1912) was their main source of information regarding color pattern, whereas their osteological data was obtained from poorly-preserved specimens provisionally identified as *Hoplisoma* cf. *microcephalus*, collected in Buenos Aires Province near Tres Arroyos, Argentina. As aforementioned, the three most important features to recognize *H. paleatum* are related to the color patterns of both the dorsal and pectoral fins, and to the uncommon pattern of pectoral-fin spine serrations (see Tencatt *et al.*, 2016). Though Regan's (1912:212) description of the color pattern of dorsal and pectoral fins matches the pattern observed in *H. paleatum* and *Hoplisoma* cf. *microcephalus*, it was not possible to undoubtedly confirm this through the photograph of the lectotype of *H. microcephalus*, since both fins are damaged and with strongly faded color pattern (Figs. 2A, C, E). Additionally, Regan (1912) made no mention to the serration pattern on pectoral-fin spine posterior margin, which also cannot be checked in the available photograph of the lectotype (Figs. 2A, C, E). Therefore, the available data by that time did not allow the authors to clearly delimit *H. microcephalus* and, consequently, recognize it as a synonym of *H. paleatum*.

One year after the publication of the revisionary study by Tencatt *et al.* (2016), the first author was able to personally examine the whole type-series of both *H. paleatum* and *C. microcephalus* at the BMNH fish collection, of which only both lectotypes were examined by MRB in Tencatt *et al.* (2016). With the new data gathered with the examination of these specimens, it was possible to confirm that the color pattern of

both dorsal and pectoral fins, as well as the serration pattern of the posterior margin of pectoral-fin spine (see Tencatt *et al.*, 2016:8, fig. 4a; Figs. 5B–D), of *H. microcephalus* are compatible with those of *H. paleatum*. Regarding the color pattern of flank midline in *H. paleatum*, Tencatt *et al.* (2016) pointed out some variations, with the most common condition characterized by the presence of three clearly distinct, large, longitudinally aligned dark brown or black blotches, which can be more longitudinally elongated in some specimens, forming even larger blotches. In other cases, these blotches can be fused to each other, forming a wide and irregular stripe. Interestingly, other congeners with a distinct longitudinal series of blotches along midline of flank share the aforementioned variable pattern of *H. paleatum*, such as *H. diphys* (see Axenrot, Kullander, 2003:259, fig. 5) and *H. habrosum*.

The authors also observed the presence of closely-spaced and unusually smaller blotches along midline of flank, which they hypothesized to be formed by the presence of a transversal lack of pigmentation in a “regularly-sized blotch” (= with the size observed for most specimens), fragmenting it in two smaller blotches. This makes sense when considering that if it was possible to merge both smaller blotches, they would form a regularly-sized blotch as observed in most specimens. They also reported the presence of these fragmented blotches for *H. longipinne*, as can be seen in the original description (see Knaack, 2007:41, fig. 9). When comparing the flank midline pattern observed in their examined material of *H. paleatum* to that of the lectotype of *H. microcephalus*, Tencatt *et al.* (2016) considered the “fragmented blotches” as a single blotch, though split into two smaller pieces, and thus counting them as a single element instead of two. Following this logic, the authors used the number of these regularly-sized blotches between *H. paleatum* (three) and *H. microcephalus*’s lectotype (four) as their main argument to consider the later as a valid species. However, even considering that the authors are correct regarding the origin of the so called “fragmented blotches”, it makes more sense to count the midlateral blotches based on what is observed in each specimen. In this case, some of the *H. paleatum* specimens examined by Tencatt *et al.* (2016) present, in fact, four midlateral blotches, overlapping with what is observed in *C. microcephalus*, and no diagnostic feature between the two species is left.

Grant (2018) raised interesting questions regarding the identity of *Callichthys punctatus* Valenciennes, 1834 (genus erroneously spelled as “*Callichthis*” in the original description) and of other taxa related to *H. paleatum* (e.g., *Corydoras maculatus* Steindachner, 1879 and *Corydoras marmoratus* Steindachner, 1879), also pointing some possible errors in previous articles, including the one by Tencatt *et al.* (2016), which will be discussed herein. One of the important contributions of Grant’s (2018) article is to correct the publication date of *C. punctatus* Valenciennes to 1834 (publication date of the plate in which the holotype was illustrated; see Sherborn, Griffin, 1934:131) and not 1840 as wrongly stated by Tencatt *et al.* (2016), as well as the publication order of Steindachner’s works, with *C. maculatus* coming before *C. marmoratus* (Steindachner, 1879a,b, respectively), and not the contrary as stated by Tencatt *et al.* (2016). Additionally, Grant (2018) provided his view on the identity of *C. punctatus* Valenciennes, 1834, *C. maculatus*, *C. marmoratus*, *Silurus quadricostatus* Larrañaga, 1923, and *Silurus septemradiatus* Larrañaga, 1923, which were mostly contrary to the ones of Tencatt *et al.* (2016). In summary, Grant (2018) considered *C. maculatus* as a replacement name for *C. punctatus* Valenciennes, 1834; *C. marmoratus* as likely to be a replacement name for *C. punctatus* Valenciennes, 1834; and

due to the lack of information in the original descriptions, no known type-specimens, and of other siluriforms (including Callichthyinae) being present in Uruguay, that *S. quadricostatus* and *S. septemradiatus* to be *nomina dubia*.

It is important to mention that Grant (2018), considering the available knowledge at the time, started from the assumption that the species within lineage 6, where *H. paleatum* belongs following Alexandrou *et al.* (2011), are not congeneric with the species of the lineage 9, the group in which *H. punctatum* (Bloch, 1794) (originally described as *Cataphractus punctatus*) belongs. In this context, Grant (2018) considered that *C. punctatus* (Bloch, 1794) would be placed in *Hoplisoma*, the available name for the species within lineage 9, whereas *C. punctatus* (Valenciennes, 1834) would be placed in new genus as no generic name is available for the species from lineage 6. Therefore, in this scenario, the name *C. punctatus* (Valenciennes, 1834) should be considered as valid, not needing any replacements names. In addition to that, Grant (2018) considered *C. punctatus* Valenciennes, 1834 conspecific with *H. paleatum*, which makes it its senior-synonym. As the holotype (the specimen illustrated by d'Orbigny; see d'Orbigny, 1847) is considered lost (see Nijssen, Isbrücker, 1980:204), the author considered two main arguments to come to that conclusion, origin/type-locality (said to be from Montevideo, Uruguay) and the color pattern depicted in d'Orbigny's drawing. Finally, Grant (2018) proposed that *C. punctatus* Valenciennes, 1834 would be a *nomen oblitum*, with *C. paleatus* as a *nomen protectum* as the valid name in accordance with article 23.9 of the International Code of Zoological Nomenclature (ICZN).

Although the work of Alonso *et al.* (2025) corroborates Grant's (2018) assumption on the generic placement of *C. punctatus* (Valenciennes, 1834), and, consequently, of *Hoplisoma paleatum sensu* Dias *et al.* (2024), robust molecular (Marburger *et al.*, 2018; Dias *et al.*, 2024) and morphological (Tencatt, Ohara, 2016a; Lima, Britto, 2020; Tencatt *et al.*, 2022a, 2023b; Dias *et al.*, 2024) evidence point to an opposite direction. As aforementioned, a monophyletic group composed by the species of both lineages 6 and 9 *sensu* Alexandrou *et al.* (2011) was demonstrated with basis on molecular (restriction-site-associated DNA, RAD; see Marburger *et al.*, 2018: 6, fig. 2, and UCEs; see Dias, 2022; Dias *et al.*, 2024), and reinforced by morphological diagnosis (Dias *et al.*, 2024). Therefore, in the light of the findings of Marburger *et al.* (2018) and Dias *et al.* (2024), the whole discussion on the generic placement of *H. paleatum* becomes unnecessary as both *C. punctatus* (Bloch, 1794) and *C. punctatus* (Valenciennes, 1834) would be members of the same monophyletic clade, making them secondary homonyms.

As aforementioned, the two recent phylogenetic hypotheses, *i.e.*, of Dias *et al.* (2024) and Alonso *et al.* (2025), conspicuously diverge regarding the taxonomic status of *Hoplisoma*, mainly the *H. paleatum* group and *H. flaveolum*. Considering the potential taxonomic instability resulted from the decisions of Alonso *et al.* (2025), which goes far beyond the taxonomic status of *H. paleatum*, we bring a discussion about the concerns in their approach and its implications. In the Introduction section, Alonso *et al.* (2025:11) pointed out that the findings of Dias *et al.* (2024) were not congruent with the results of Britto (2003), Alexandrou *et al.* (2011) and Marburger *et al.* (2018). Regarding the work of Marburger *et al.* (2018), the authors apparently considered the fossil-calibrated mtDNA tree based on Alexandrou *et al.*'s (2011) dataset (see Marburger *et al.*, 2018:4, fig. 1) as the only result of this study. In this case, it is obvious that such analysis would show the very same topology of Alexandrou *et al.* (2011). However, Marburger *et al.* (2018)

also used RAD markers to construct a nuclear-based phylogeny using pyRAD (see p. 6, fig. 2; electronic supplementary material, figures S2a and S2b), which showed, for the first time and with strong support for all branches, that the species of the lineages 6 and 9 *sensu* Alexandrou *et al.* (2011) form a monophyletic clade. Moreover, considering the major clades, the whole topology shown in Marburger *et al.* (2018: 6, fig. 2) is basically the same as the one presented in Dias *et al.* (2025:4, fig. 1). Therefore, contrary to the stated by Alonso *et al.* (2025:11), the results of Marburger *et al.*'s (2018) pyRAD phylogenetic analysis are congruent with the findings of Dias *et al.* (2024). There is no mention to the pyRAD phylogenetic analysis by Alonso *et al.* (2025). Regarding Britto's (2003) work, the comparison between his results and the results of more recent studies (*i.e.*, Alexandrou *et al.*, 2011; Marburger *et al.*, 2018; Dias *et al.*, 2024; Alonso *et al.*, 2025) is quite limited, as most of the interrelations within Corydoradinae found by him are, except for the *Aspidoras* and *Scleromystax* clades, remarkably different from all subsequent studies, including Alonso *et al.* (2025).

Even though Dias *et al.* (2024) did not include the species within *Urkumayu* in their work, they analyzed representatives of the so-called lineage 6 *sensu* Alexandrou *et al.* (2011), which is basically the *H. paleatum* clade in Alonso *et al.* (2025) plus *H. flaveolum*, which appeared within another clade sister to *Urkumayu* in Alonso *et al.* (2025). In Dias *et al.* (2024), six species of the *H. paleatum* group *sensu* Alonso *et al.* (2025) were included in their phylogenetic analysis, namely: *H. diphyes*, *H. ehrhardti*, *H. nattereri*, *H. paleatum*, *H. reynoldsi*, and *H. tukano*, as well as *H. flaveolum*. Therefore, considering that these species were recovered within the same clade along with the remaining *Hoplisoma* species, it is quite possible that the species in *Urkumayu*, especially due to their close relation with *H. flaveolum*, would also be more closely related to *Hoplisoma* than with any other genera within Corydoradinae. If that is case, this would be another case of small lineages with reductive features within major clades, as in *Brochis*, *Gastrodermus* and *Osteogaster*.

Regardless of the morphological inconsistencies related to the synapomorphies and/or diagnostic features widely discussed above, the most controversial aspect of Alonso *et al.*'s (2025) work refers to the creation of *Urkumayu* while leaving both *H. flaveolum*, the sister group of the new genus, and the species of the *H. paleatum* group as "*Hoplisoma*", even though these species were recovered in a completely different clade from the *Hoplisoma sensu stricto*. For instance, according to Alonso *et al.* (2025), *Hoplisoma sensu stricto* is more closely-related to *Brochis* and *Osteogaster*, two conspicuously different genera from *Hoplisoma*, than with the species regarded as "*Hoplisoma*". According to those authors, this was done by the following reasoning: regarding *H. flaveolum*, no explanation was offered besides stating "The divergence among these (= *Urkumayu* and *H. flaveolum*) is likely linked to the historical fragmentation of hydrographic basins in northwestern La Plata in the Andean region"; regarding the *H. paleatum* group: "Nevertheless, to prevail the taxonomic stability, we opted for not describing a new genus yet for the "*Hoplisoma*" *paleatum* clade, before new analyses solve the divergences found between our work and Dias *et al.* (2024).".

However, considering their own argument (*i.e.*, taxonomic stability), and the fact that, as stated by Alonso *et al.* (2025), the divergences between their work and the one of Dias *et al.* (2024), especially regarding *Hoplisoma*, are still unsolved, the creation of a new genus seems premature based on the currently available information. First, it is

important to mention that no synapomorphy was found for the *H. paleatum* group nor a diagnosis is currently available for this group. Additionally, the features proposed as synapomorphies for the clade *Urkumayu* plus *H. flaveolum* were shown to be either not present, such as the absence of odontodes on infraorbital 1 and 2 and on preopercle, since these three bones actually bear odontodes not only in *Urkumayu* but in all of the remaining Corydoradinae (Figs. 16, 17D), or variable, as the case of the process on the posterior expansion of epibranchial 2 (Figs. 10C–E) (see Morphological delimitation of closely-related groups section). Therefore, no morphological synapomorphies currently support the clade *Urkumayu* plus *H. flaveolum*, and no morphological diagnosis differing this clade from the remaining clades within Corydoradinae is available. Most importantly, there is currently no morphologic diagnosis to differentiate *H. flaveolum* or the species in the *H. paleatum* group from the remaining *Hoplisoma*.

In this context, and following Alonso *et al.*'s (2025) own argument towards taxonomic stability, the reasoning for not proposing a new genus for *H. flaveolum* and for the *H. paleatum* group could be equally used to avoid the creation of *Urkumayu*. The core of our argumentation relies on the fact that picking any small clade, even though it is diagnosable or has putative synapomorphies should not be sufficient, by itself, to justify the creation of new names, especially when this decision results in the creation of non-monophyletic groups, while no alternative to establish the monophyly of these resultant groups are presented. In our view, such an approach is potentially harmful to the taxonomic stability of the group. For instance, in all Corydoradinae major clades/ genera, it is possible to find smaller clades composed of species sharing exclusive features when compared to the remaining closely-related species. In this way, setting a precedent like this can generate a scenario favorable to the multiplication of names without any commitment to the implications of such actions (*i.e.*, the creation of non-monophyletic groups). If the taxonomic stability was indeed considered, the best approach would be creating two new genera, one for the clade *Urkumayu* plus *H. flaveolum*, and another genus for the *H. paleatum* group. However, the authors opted to create a new genus only for *H. gladysae*, *H. micracanthus*, and *H. petracinii*, which necessarily demands the creation of an additional generic name just for *H. flaveolum*, as this species conspicuously differs from the species in *Urkumayu*. As aforementioned, the potential taxonomic instability in this approach (*i.e.*, creating *Urkumayu* while leaving *H. flaveolum* and the species of the *H. paleatum* as “*Hoplisoma*”) becomes even more evident due to impossibility of morphologically differing, at genus level, *H. flaveolum* and the species of the *H. paleatum* group from the remaining *Hoplisoma* (see Tencatt, Ohara, 2016a; Lima, Britto, 2020; Tencatt *et al.*, 2022a, 2023b). For instance, one of the implications of such an approach is that, according to Alonso *et al.* (2025), *H. albolineatum*, *H. flaveolum* and *H. polystictum* (Fig. 18) must be allocated in three different genera in order to reestablish the monophyly of *Hoplisoma*.

Another relevant concern regarding the work of Alonso *et al.* (2025) refers to the use Britto's (2003) dataset in novel studies without sufficient scrutiny. The problems in some of the characters in Britto (2003) and/or their respective interpretation were evidenced in the last decade (*e.g.*, Tencatt *et al.*, 2013, 2014a,b, 2016, 2019, 2020, 2021, 2022a,b, 2023a,b, 2024a,b; Tencatt, Pavanelli, 2015; Britto *et al.*, 2016; Tencatt, Britto, 2016; Tencatt, Evers, 2016; Tencatt, Ohara, 2016a,b; Espíndola *et al.*, 2018; Bono *et al.*, 2019), especially in more recent studies (Tencatt *et al.*, 2025a,b), in which the

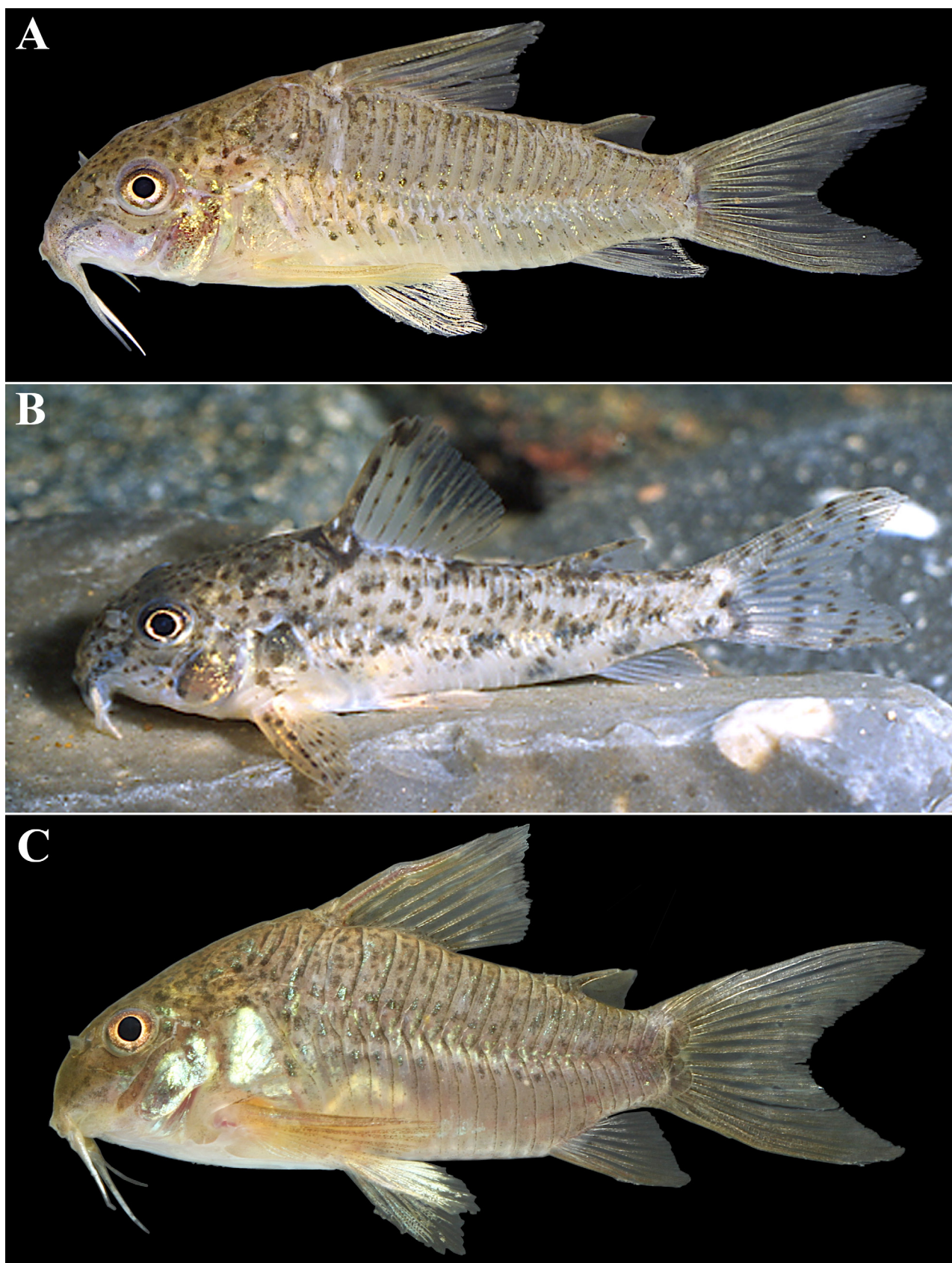


FIGURE 18 | Uncatalogued, unmeasured living specimens of *Hoplisoma albolineatus* (A), the species currently identified as *H. flaveolum* (B), and *H. polystictum* (C), showing their general morphology and color pattern in lateral view. Photos (A, C) by LFCT, and (B) by Hans Evers.

necessity of reevaluating the characters in Britto (2003) is highlighted. Considering these advances, it is already available in the literature that some of the features pointed as synapomorphies in Alonso *et al.* (2025), especially regarding the presence/absence of odontodes and the morphology of some of the bones of the branchial arches, are not phylogenetically informative at genus level, as most of the features related these structures are widely shared within Corydoradinae.

Regardless of the problems with some characters in Britto (2003), Alonso *et al.* (2025) carried out their analyses having access to 13 Corydoradinae species, whereas Britto (2003) examined 94 species (coding 60 of them in his data matrix). Adding up the material examined listed in Calviño, Alonso (2009), Alonso *et al.* (2018) and the supplementary file “S1”, 13 species were examined by them, as follows: *C. aurofrenatus*, *G. hastatus*, *G. undulatus*, *H. carlae*, *H. ehrhardti*, *H. gladyssae*, *H. longipinne*, *H. micracanthus*, *H. osvaldoi*, *H. paleatum* (three morphotypes), *H. petracinii*, *H. polystictum*, and *O. aenea* (two morphotypes), presenting about 5% of the current diversity of the group. The mention to Bono *et al.* (2019) is unclear as the examined material referred in that paper (see p. 20), *i.e.*, the examined material listed in Espíndola *et al.* (2018) plus type-specimens of *G. elegans*, *G. gracilis* and *G. nanus*, comprises the personal comparative material of LFCT, never having been examined by any of the other authors in Alonso *et al.* (2025), except for some specimens of *G. undulatus* from Argentina used in the redescription of this species. Nonetheless, the problems in part of the characters in Britto (2003) (*e.g.*, characters related to odontodes, branchial arches, mesethmoid, and pelvic girdle) could be observed with their examined material.

In this context, the approach of Alonso *et al.* (2025) regarding the creation of *Urkumayu* and its implications raises another important question: should we use an outdated dataset that have been proved to present important flaws in the name of performing an integrative methodology? Aside from the close relation between *Aspidoras* and *Scleromystax*, Britto's (2003) phylogenetic hypothesis failed to recover most of the well-defined clades found by posterior studies (Alexandrou *et al.*, 2011; Marburger *et al.*, 2018; Dias *et al.*, 2024), retaining a large polytomy. For example, except for the close relationship between *G. hastatus* and *G. pygmaeus*, Britto's (2003) phylogenetic hypothesis did not recover the species of *Gastrodermus* within the same clade, even though this is one of the most morphologically well-defined genera of Corydoradinae. As extensively explored in this article, the taxonomic studies published in the last decade revealed that some of the diverging groupings found in Britto (2003) when compared to the posterior studies are likely due to problems in some of his characters allied to the absence of informative characters in his analysis (*e.g.*, the serration pattern of both dorsal- and pectoral-fin spines).

Considering the problems related to Britto's (2003) dataset, Dias *et al.* (2024) purposely did not include it in their analysis. Nonetheless, the classification provided by Dias *et al.* (2024) includes only monophyletic genera, all supported by morphological diagnoses. Furthermore, studies such as Jarvis *et al.* (2015) demonstrate that Ultraconserved Elements (UCEs) methodology is significantly more efficient for phylogenetic reconstruction than traditional multilocus approaches. The UCEs methodology has proven highly effective in generating robust and well-resolved phylogenies, particularly in Neotropical freshwater fishes (Chakrabarty *et al.*, 2017; Roxo *et al.*, 2019; Ochoa *et al.*, 2020; Alda *et al.*, 2021; Silva *et al.*, 2021a,b, 2024; Melo *et al.*, 2022; Souza *et al.*, 2022; Nogueira

et al., 2023; Dias *et al.*, 2024; Melo *et al.*, 2024). Among its advantages are the relative ease of identifying homologous regions and low data saturation. Since these elements are distributed throughout the genome, they can be treated as independent loci in phylogenetic analyses, making them particularly valuable for tree-building methods that elucidate relationships among species (Knowles, 2009). Additionally, the increased number of loci (1500–2000 loci) significantly enhances the accuracy of the analyses. This approach allows for a much larger number of loci compared to multilocus sequencing, resulting in phylogenetic trees with high statistical support, based on thousands of genes (500 to 750 thousand characters for phylogenetic tree construction), when compared with five genes in multilocus approach.

Moreover, the difference between the UCE phylogeny from Dias *et al.* (2024) and multilocus phylogeny from Alonso *et al.* (2025) may be reflecting the historical mitochondrial introgression within Corydoradinae (see Taylor, 2024). Mitochondrial introgressions events are reported in the literature in populations with rapid radiation like *Hoplisoma*, and between sympatric species complex when the limit of each species was interrupted by hybridization (Laine *et al.*, 2023). Another possible explanation for the difference between both phylogenies refers to an incomplete lineage sorting. Due to its fourfold smaller effective population size, the haploid mtDNA is expected to ‘sort’ far more rapidly than the diploid nuclear DNA, leading to scenario where the nuclear genes are closely related, while the mtDNA is divergent and reciprocally monophyletic (Taylor, 2024). A broader discussion on the differences between mitochondrial- and nuclear-based phylogenies, highlighting the advantages of the latter over the former, can be found in Taylor (2024).

In summary, considering the lack of morphologic synapomorphies (see Alonso *et al.*, 2025:19) or even a morphological diagnosis for the *H. paleatum* group and also for the clade *Urkumayu* plus *H. flaveolum* (see Morphological delimitation of closely-related groups section), allied to the fact that Alonso *et al.* (2025) did not provide any alternative to reestablish the monophyly of *Hoplisoma*, an approach that can potentially result in taxonomic instability to the group, we suggest that the most reasonable decision at this time is to consider *Urkumayu* as a junior synonym of *Hoplisoma* until further analysis. In the light of the arguments exposed in this article, we consider that the same reasoning provided by Alonso *et al.* (2025) for not creating a new genus for the species of the *H. paleatum* group (*i.e.*, the necessity to solve the divergences found between their work and Dias *et al.*, 2024 in order “to prevail the taxonomic stability”) can also be applied for *Urkumayu*, especially when considering that its sister group, *H. flaveolum*, was recovered within *Hoplisoma* by Dias *et al.* (2024).

Comparative material examined. *Aspidoras*: same as listed in Tencatt *et al.* (2022b). *Brochis*: *Brochis ambiacus*: ANSP 8291, holotype of *Corydoras ambiacus* Cope, 1872, 40.4 mm SL; MZUSP 26053, 2, 41.8–47.2 mm SL. *Brochis approuaguensis*: MZUSP 27895–6, 2, 43.0–46.1 mm SL, paratypes of *C. approuaguensis* Nijssen & Isbrücker, 1983. *Brochis arcuata*: BMNH 1939.3.3.1, holotype of *Corydoras arcuatus* Elwin, 1938, 43.3 mm SL. *Brochis bethanae*: MUSM 69403, holotype of *Corydoras bethanae* Bentley, Grant & Tencatt, 2021, 51.2 mm SL. *Brochis bifasciata*: MZUSP 38976, 16, 23.6–30.0 mm SL, paratypes of *Corydoras bifasciatus* Nijssen, 1972. *Brochis britskii*: ZUFMS-PIS 862, 12, 72.0–78.0 mm SL. *Brochis brittoi*: MNRJ 43316, holotype of *Corydoras brittoi* Tencatt & Ohara, 2016, 38.1 mm SL. *Brochis condiscipulus*: MZUSP 38957, 7, 34.1–40.3 mm SL, paratypes of *Corydoras condiscipulus* Nijssen & Isbrücker, 1980. *Brochis crimmeni*: MZUSP 52490, holotype of

Corydoras crimmeni Grant, 1997, 36.1 mm SL. *Brochis delphax*: LBP 9962, 24, 33.7–48.1 mm SL. *Brochis diffluvialis*: MZUSP 75268, holotype of *Corydoras diffluvialis* Britto & Castro, 2002, 39.8 mm SL. *Brochis ephippifer*: MZUSP 31605, 2, 44.9–49.1 mm SL. *Brochis garbei*: MNRJ 18089, 14, 19.2–25.3 mm SL, 2 CS, 25.9–27.4 mm SL. *Brochis haraldschultzi*: INPA 60255, 10 of 18, 38.6–49.6 mm SL. *Brochis heteromorphus*: USNM 204224, 2, 37.0–42.7 mm SL, paratypes of *Corydoras heteromorphus* Nijssen, 1970. *Brochis inolicana*: MZUSP 45717, holotype of *Corydoras inolicana* Burgess, 1993, 47.6 mm SL. *Brochis leopardus*: USNM 93305, lectotype of *Corydoras leopardus* Myers, 1933, 38.7 mm SL. *Brochis ornata*: USNM 216075, 1, 37.8 mm SL, paratype of *Corydoras ornatus* Nijssen & Isbrücker, 1976. *Brochis orphnopterus*: USNM 204361, holotype of *Corydoras orphnopterus* Weitzman & Nijssen, 1970, 55.9 mm SL. *Brochis pantanalensis*: NUP 10188, 1 CS, 46.4 mm SL; NUP 12593, 21, 38.7–51.2 mm SL. *Brochis pinheiroi*: MZUSP 48099, holotype of *Corydoras pinheiroi* Dinkelmeyer, 1995, 54.3 mm SL. *Brochis robineae*: MZUSP 27175, holotype of *Corydoras robineae* Burgess, 1983, 33.7 mm SL. *Brochis seussi*: MZUSP 49323, 10, 44.3–54.0 mm SL, paratypes of *Corydoras seussi* Dinkelmeyer, 1996. *Brochis splendens*: NUP 12990, 1, 43.7 mm SL; NUP 10195, 1 CS, 54.6 mm SL. *Brochis virginiae*: USNM 326186, 3, 31.6–33.5 mm SL, paratypes of *Corydoras virginiae* Burgess, 1993. *Corydoras*: *Corydoras acutus*: ANSP 113928, 1, 43.0 mm SL; MNRJ 3985, 2, 47.1–54.8 mm SL; USNM 305324, 10, 13.6–40.8 mm SL. *Corydoras amapaensis*: USNM 205865, 1, 46.0 mm SL, paratype of *Corydoras amapaensis* Nijssen, 1972. *Corydoras areio*: ZUFMS 1314, 15, 34.4–41.9 mm SL, 2 CS, 38.1–38.7 mm SL. *Corydoras aurofrenatus*: NUP 16191, 33, 20.1–53.8 mm SL, 2 CS, 38.2–41.6 mm SL. *Corydoras blochi*: MZUSP 8580, 3, 31.0–42.6 mm SL, paratypes of *Corydoras blochi* Nijssen, 1971. *Corydoras caramater*: MNRJ 54621, holotype of *Corydoras caramater* Tencatt, Couto, Santos & Sousa, 2024, 49.3 mm SL; CITL 929, 5 of 6, 35.7–45.3 mm SL, 1 of 6 CS, 45.3 mm SL, paratypes of *Corydoras caramater* Tencatt, Couto, Santos & Sousa, 2024. *Corydoras coriatae*: USNM 343866, 2, 53.2–57.1 mm SL, paratypes of *Corydoras coriatae* Burgess, 1997. *Corydoras desana*: ANSP 200804, 2, 29.5–43.4 mm SL, paratypes of *Corydoras desana* Lima & Sazima, 2017. *Corydoras filamentosus*: USNM 225536, holotype of *Corydoras filamentosus* Nijssen & Isbrücker, 1983, 30.2 mm SL. *Corydoras fowleri*: LBP 12462, 9, 44.3–59.9 mm SL, 1 CS, 50.4 mm SL. *Corydoras fulleri*: MUSM 69317, holotype of *Corydoras fulleri* Tencatt, Santos, Evers & Britto, 2021, 55.1 mm SL. *Corydoras geoffroy*: USNM 204222, 2, 54.5–55.4 mm SL, paratypes of *Corydoras octocirrus* Nijssen, 1970. *Corydoras iiap*: CIIAP 3906, holotype of *Corydoras iiap* Tencatt, Ruiz-Tafur, Chuctaya, 2024, 55.2 mm SL; MNRJ 55393, 5 of 7, 28.0–50.4 mm SL, 2 CS of 7, 41.5–50.4 mm SL, paratypes of *Corydoras iiap* Tencatt, Ruiz-Tafur, Chuctaya, 2024. *Corydoras maculifer*: NUP 8970, 2, 42.0–46.0 mm SL. *Corydoras ourastigma*: MZUSP 38950, 1, 23.0 mm SL, paratype of *Corydoras ourastigma* Nijssen, 1972. *Corydoras pastazensis*: USNM 177216, holotype of *Corydoras pastazensis* Weitzman, 1963, 46.2 mm SL. *Corydoras sarareensis*: MZUSP 48100, holotype of *Corydoras sarareensis* Dinkelmeyer, 1995, 40.9 mm SL. *Corydoras septentrionalis*: USNM 130634, 1, 42.3 mm SL, paratype of *Corydoras septentrionalis* Gosline, 1940; ZMA 112.288, 2, 37.8–46.3 mm SL, paratypes. *Corydoras simulatus*: USNM 197615, holotype of *Corydoras simulatus* Weitzman & Nijssen, 1970, 49.1 mm SL. *Corydoras spilurus*: BMNH 1926.3.2.738, lectotype of *Corydoras spilurus* Norman, 1926, 43.3 mm SL. *Corydoras stenocephalus*: MNRJ 3625, 3, 31.2–62.3 mm SL. *Corydoras treitlii*: NUP 16224, 3, 21.5–45.6 mm SL. *Corydoras zawadzskii*: MNRJ 45565, holotype of *Corydoras zawadzskii* Tencatt & Ohara, 2016, 48.7 mm SL; NUP 17824, 1 CS, 39.9 mm SL, paratype. *Gastrodermus*: *Gastrodermus elegans*: USNM 216716, 10, 36.3–43.3 mm SL, paralectotypes of *Corydoras elegans* Steindachner, 1876. *Gastrodermus gracilis*: USNM 216074, 1, 19.2 mm SL, paratype of *Corydoras gracilis* Nijssen & Isbrücker, 1976. *Gastrodermus guapore*: ZUFMS-PIS 4000, 5, 26.9–33.6 mm SL, 2 CS, 28.8–29.2 mm SL. *Gastrodermus hastatus*: NUP 6862, 116, 13.1–20.7 mm SL. *Gastrodermus napoensis*: USNM 270358, 2, 26.7–28.3 mm SL, paratypes of *Corydoras napoensis* Nijssen & Isbrücker, 1986. *Gastrodermus pauciradiatus*: INPA 34595, 5 of 22, 19.2–22.5 mm SL; MZUSP 109459, 5 of 22, 16.0–17.6 mm SL. *Gastrodermus pygmaeus*: ANSP 200357, 1, 16.1 mm SL. *Gastrodermus undulatus*: BMNH 1912.7.10.5, holotype of *Corydoras undulatus* Regan, 1912, 41.8 mm SL. *Hoplisoma*: *Hoplisoma adolfi*: MZUSP 26641, holotype of *Corydoras adolfi*

Burgess, 1982, 32.5 mm SL. *Hoplisoma albolineatum*: MNRJ 55942, 5 of 7, 20.3–29.7 mm SL, 2 CS of 7, 24.3–27.2 mm SL. *Hoplisoma amphibelum*: ANSP 8290, holotype of *Corydoras amphibelus* Cope, 1872, 26.4 mm SL. *Hoplisoma araguaiaense*: MZUSP 87155, 33 4, 24.9–46.7 mm SL, 2 CS, 27.6–31.8 mm SL. *Hoplisoma armatum*: BMNH 1867.6.13.51, lectotype of *Callichthys armatus* Günther, 1868, 42.1 mm SL. *Hoplisoma atropersonatum*: USNM 204359, holotype of *Corydoras atropersonatus* Weitzman, Nijssen, 1970, 37.1 mm SL. *Hoplisoma benattii*: MZUSP 121671, holotype of *Corydoras benattii* Espindola, Tencatt, Pupo, Villa-Verde & Britto, 2018, 25.4 mm SL. *Hoplisoma boehlkei*: ANSP 135912, 9, 21.4–26.7 mm SL; ANSP 148097, holotype of *Corydoras boehlkei* Nijssen & Isbrücker, 1982, 23.6 mm SL. *Hoplisoma bondi*: ROM 66202, 134, 33.8–39.9 mm SL, 3 CS, 36.7–38.6 mm SL. *Hoplisoma brevirostre*: BMNH 1946.10.10.1, holotype of *Corydoras melanistius brevirostris* Fraser-Brunner, 1947, 30.6 mm SL; LBP 3080, 10, 23.8–27.7 mm SL, 3 CS, 25.8–27.9 mm SL. *Hoplisoma burgessi*: USNM 288461, 2, 43.7–44.8 mm SL, paratypes of *Corydoras burgessi* Axelrod, 1987. *Hoplisoma carlae*: NUP 711, 1, 47.9 mm SL; NUP 4425, 1 CS, 45.0 mm SL. *Hoplisoma caudimaculatum*: INPA 60253, 10 of 24, 37.7–44.7 mm SL. *Hoplisoma colossus*: MNRJ 54421, holotype of *Corydoras colossus* Tencatt, Grant & Bentley, 2023, 44.5 mm SL; CITL 928, 1 of 3, 42.2 mm SL, 2 CS of 3, 43.1–48.4 mm SL, paratypes of *Corydoras colossus* Tencatt, Grant & Bentley, 2023. *Hoplisoma concolor*: ANSP 165646, 10 of 15, 18.4–44.2 mm SL. *Hoplisoma coppenamense*: USNM 202129, 5, 33.0–35.8 mm SL, paratypes of *Corydoras coppenamensis* Nijssen, 1970. *Hoplisoma davidsandsi*: MZUSP 110066, 40 4, 36.0–41.9 mm SL, 2 CS, 40.9–42.1 mm SL. *Hoplisoma diphyes*: ANSP 169756, 2, 40.7–43.1 mm SL. *Hoplisoma ehrhardti*: NUP 11255, 15, 36.5–46.8 mm SL. *Hoplisoma eversi*: MNRJ 43195, holotype of *Corydoras eversi* Tencatt & Britto, 2016, 44.5 mm SL. *Hoplisoma flaveolum*: LBP 14596, 12 of 15, 29.8–37.4 mm SL, 3 CS of 15, 33.2–34.0 mm SL; MZUSP 424, holotype of *Corydoras flaveolus* Ihering, 1911, 33.4 mm SL. *Hoplisoma gladysae*: CI-FML 7262, 5, 26.4–34.6 mm SL; CI-FML 7110, 4 CS, 27.3–32.4 mm SL. *Hoplisoma gossei*: MZUSP 38977, 6, 48.4–53.4 mm SL, paratypes of *Corydoras gossei* Nijssen, 1972. *Hoplisoma granti*: MNRJ 51193, holotype of *Corydoras granti* Tencatt, Lima & Britto, 2019, 48.4 mm SL. *Hoplisoma griseum*: MZUSP 108896, 13, 4, 31.5–36.2 mm SL, 2 CS, 30.6–34.5 mm SL. *Hoplisoma gryphus*: MNRJ 40770, holotype of *Corydoras gryphus* Tencatt, Britto & Pavanelli, 2014, 32.3 mm SL; NUP 14676, 3 CS, 27.7–32.4 mm SL, paratypes. *Hoplisoma guianense*: USNM 204218, 2, 26.0–32.0 mm SL, paratypes of *Corydoras guianensis* Nijssen, 1970. *Hoplisoma hypnos*: MNRJ 53288, holotype of *Corydoras hypnos* Tencatt, Ohara, Sousa & Britto, 2022, 31.7 mm SL. *Hoplisoma julii*: NUP 16225, 1, 46.8 mm SL. *Hoplisoma kanei*: MZUSP 52489, holotype of *Corydoras kanei* Grant, 1997, 36.6 mm SL. *Hoplisoma knaacki*: MUSM 52730, holotype of *Corydoras knaacki* Tencatt & Evers, 2016, 35.6 mm SL. *Hoplisoma lacrimostigmata*: MNRJ 40725, holotype of *Corydoras lacrimostigmata* Tencatt, Britto & Pavanelli, 2014, 31.8 mm SL; NUP 14657, 3 CS, 30.9–34.5 mm SL, paratypes. *Hoplisoma leucomelas*: ANSP 70509, holotype of *Corydoras caquetae* Fowler, 1943, 18.6 mm SL. *Hoplisoma longipinne*: AI 221, holotype of *Corydoras longipinnis* Knaack, 2007, 59.5 mm SL; NUP 14440, 2 CS, 29.9–33.4 mm SL. *Hoplisoma loretoense*: ANSP 121620, 32, 17.3–32.7 mm SL, paratypes of *Corydoras loretoensis* Nijssen & Isbrücker, 1986. *Hoplisoma loxozonum*: ANSP 150170, holotype of *Corydoras loxozonus* Nijssen & Isbrücker, 1983, 34.6 mm SL. *Hoplisoma lylnades*: MNRJ 15765, 6, 15.8–17.7 mm SL, 2 CS, 18.1–18.4 mm SL; MNRJ 40186, holotype of *Corydoras lylnades* Tencatt, Vera-Alcaraz, Britto & Pavanelli, 2013, 29.7 mm SL. *Hoplisoma melanistium*: BMNH 1864.1.21.86, lectotype of *Corydoras melanistius* Regan, 1912, 35.0 mm SL. *Hoplisoma metae*: ANSP 128611, 5, 30.7–36.4 mm SL. *Hoplisoma micracanthus*: BMNH 1897.1.27.8, lectotype of *Corydoras micracanthus* Regan, 1912, 33.7 mm SL; BMNH 1897.1.27.9–14, 6, 20.6–36.2 mm SL, paralectotypes of *Corydoras micracanthus* Regan, 1912; BMNH 1906.5.31.40–41, 2, 20.5 to 27.0 mm SL; CI-FML 7114, 2, 24.0–30.1 mm SL; CI-FML 7111, 4, 24.2–33.0 mm SL, 1 CS, 30.0 mm SL. *Hoplisoma multimaculatum*: MCP 29025, 2, 20.1–25.4 mm SL. *Hoplisoma nattereri*: MZUSP 110255, 31 4, 32.0–32.8 mm SL, 2 CS, 32.3–34.4 mm SL. *Hoplisoma oiapoquense*: USNM 205868, 2, 25.9–35.0 mm SL, paratypes of *Corydoras oiapoquensis* Nijssen, 1972. *Hoplisoma osteocarus*: ANSP 135734, 5, 23.8–34.7 mm SL; USNM 157367, 1, 25.1 mm SL, paratype of *Corydoras osteocarus* Böhlke,

1951. *Hoplisoma osvaldoi*: MNRJ 55043, 3, 30.4–34.5 mm SL, 2 CS, 33.8–38.8 mm SL, paratypes of *Hoplisoma osvaldoi* Alonso, Terán, Aguilera, Montes, Serra Alanís, Calviño, Vera-Alcaraz, Cardoso, Koerber & Mirande, 2024; MNRJ 55044, 5, 27.5–34.4 mm SL, paratypes of *Hoplisoma osvaldoi* Alonso, Terán, Aguilera, Montes, Serra Alanís, Calviño, Vera-Alcaraz, Cardoso, Koerber & Mirande, 2024; MNRJ 55045, 5, 30.8–43.1 mm SL, paratypes of *Hoplisoma osvaldoi* Alonso, Terán, Aguilera, Montes, Serra Alanís, Calviño, Vera-Alcaraz, Cardoso, Koerber & Mirande, 2024. *Hoplisoma panda*: BMNH 1969.7.15.8, holotype of *Corydoras panda* Nijssen & Isbrücker, 1971, 38.9 mm SL; ROM 55815, 6, 26.5–39.7 mm SL. *Hoplisoma parallelum*: MZUSP 45716, holotype of *Corydoras parallelus* Burgess, 1993, 47.4 mm SL. *Hoplisoma pavanelliae*: MNRJ 43317, holotype of *Corydoras pavanelliae* Tencatt & Ohara, 2016, 45.1 mm SL. *Hoplisoma petracinii*: CI-FML 7260, 11, 21.7–35.6 mm SL. *Hoplisoma polystictum*: BMNH 1895.5.17.62, lectotype, 27.5 mm SL. *Hoplisoma psamathos*: MNRJ 53289, holotype of *Corydoras psamathos* Tencatt, Ohara, Sousa & Britto, 2022, 29.4 mm SL. *Hoplisoma potaroense*: ROM 61526, 3 of 15, 35.0–44.8 mm SL, 2 CS, 32.6–35.1 mm SL. *Hoplisoma punctatum*: ZMB 3149, lectotype of *Cataphractus punctatus* Bloch, 1794, 41.7 mm SL. *Hoplisoma simile*: LBP 10648, 7, 21.4–34.3 mm SL. *Hoplisoma surinamense*: USNM 204223, 2, 29.1–34.3 mm SL, paratypes of *Corydoras surinamensis* Nijssen, 1970. *Hoplisoma thanatos*: MNRJ 53287, holotype of *Corydoras thanatos* Tencatt, Ohara, Sousa & Britto, 2022, 33.2 mm SL. *Hoplisoma trilineatum*: ANSP 8294, lectotype of *Corydoras trilineatus* Cope, 1872, 31.8 mm SL; MZUSP 30857, 25, 3, 40.9–44.1 mm SL, 2 CS, 44.2–43.8 mm SL. *Hoplisoma tukano*: MZUSP 82100, holotype of *Corydoras tukano* Britto & Lima, 2003, 40.9 mm SL. *Hoplisoma urucu*: MNRJ 32446, 4, 25.9–27.3 mm SL, paratypes of *Corydoras urucu* Britto, Wosiacki & Montag, 2009. *Hoplisoma weitzmani*: USNM 206018, 1, 38.5 mm SL, paratype of *Corydoras weitzmani* Nijssen, 1971. *Hoplisoma xinguense*: USNM 205870, 1, 27.9 mm SL, paratype of *Corydoras xinguensis* Nijssen, 1972. *Osteogaster*: *Osteogaster aenea*: USNM 1116, lectotype of *Hoplosoma aeneum* Gill, 1858, 38.2 mm SL; USNM 92819, 1, 49.5 mm SL, paralectotype; USNM 205649, 3, 32.7–44.9 mm SL, paralectotypes. *Osteogaster eques*: MCZ 8204, 4 of 12, 37.6–44.4 mm SL, paratypes of *Corydoras eques* Steindachner, 1876. *Osteogaster hephaestus*: MZUSP 119087, holotype of *Corydoras hephaestus* Ohara, Tencatt & Britto, 2016, 22.6 mm SL. *Osteogaster maclurei*: MUSM 70671, holotype of *Corydoras maclurei*, Tencatt, Gomes & Evers, 2023, 37.0 mm SL. *Osteogaster melanotaenia*: BMNH 1909.7.23.41, lectotype of *Corydoras melanotaenia* Regan, 1912, 38.3 mm SL; BMNH 1909.7.23.42, 1, 30.1 mm SL, paralectotype. *Osteogaster rabauti* (LaMonte, 1941): MNRJ 3626, holotype of *Corydoras myersi* Miranda Ribeiro, 1942, 46.0 mm SL; USNM 163252, 2, both 37.0 mm SL, paratypes of *Corydoras myersi* Miranda Ribeiro, 1942. *Osteogaster zygata* (Eigenmann & Allen, 1942): MZUSP 30858, 4 of 15, 41.7–47.3 mm SL. *Scleromystax*: *Scleromystax barbatus* (Quoy & Gaimard, 1824): UFRJ 4441, 1 CS, unmeasured, disarticulated specimen; UFRJ 4457, 2, unmeasured, disarticulated specimens. *Scleromystax lacerdai* (Hieronimus, 1995): MNRJ 26017, 4 CS of 17, 17.9–36.3 mm SL. *Scleromystax macropterus* (Regan, 1913): UFRJ 442, 2 CS, 34.4 mm SL (the other unmeasured, disarticulated specimen). *Scleromystax prionotos* (Nijssen & Isbrücker, 1980): UFRJ 4431, 1, unmeasured, disarticulated specimen. *Scleromystax salmacis* Britto & Reis, 2005: MCP 28729, 3 CS of 24, 23.9–45.6 mm SL.

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ETHICAL STATEMENT

Not applicable.

DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study are available within the article.

COMPETING INTERESTS

The authors declare no competing interests.

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