



Taxonomic review of the typical long-snouted species of *Corydoras* (Siluriformes: Callichthyidae) from the río de La Plata basin

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The typical long-snouted species of *Corydoras* from the río de La Plata basin were reviewed herein, and the previously proposed synonymy of *Corydoras ellisae* was corroborated. *Corydoras areio* and *C. aurofrenatus* are diagnosed from their congeners, excluding those in lineage 1, by the following features: temporal sensory canal in sphenotic with two pores; upper tooth plate of branchial arch with three or four series of teeth; fleshy flap at mouth corner. *Corydoras areio* differs from all lineage 1 congeners by having infraorbital 2 with relatively wider posterior laminar expansion; absence of large patches of black pigmentation on the body and absence of conspicuous concentration of dark brown or black chromatophores on anterior portion of the dorsal fin; and presence of blotches on flanks not aligned in longitudinal series. *Corydoras aurofrenatus* differs from all lineage 1 congeners by having ventral surface of head and trunk densely covered by small, not coalescent platelets; middle portion of flank with two or three dark brown or black patches (below the dorsal-fin, below the adipose-fin base, and on the caudal peduncle base, diffuse and variably present), patches decreasing in size posteriorly; poorly developed fleshy flap at the corner of mouth; anteroventral portion of cleithrum exposed.

Keywords: Corydoradinae, *Corydoras diphyes*, *Corydoras ellisae*, Osteology, río Paraguay basin.

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As espécies típicas de focinho longo de *Corydoras* da bacia do rio de La Plata foram revisadas, e a sinonímia proposta anteriormente de *Corydoras ellisae* foi corroborada. *Corydoras areio* e *C. aurofrenatus* são diagnosticadas de seus congêneres, excluindo aquelas da linhagem 1, pelas seguintes características: canal sensorial temporal no esfenótico com dois poros; placa dentária superior do arco branquial com três ou quatro séries de dentes; aba carnosa no canto da boca. *Corydoras areio* difere de todos os congêneres da linhagem 1 pelo infraorbital 2 com expansão laminar posterior relativamente mais ampla; ausência de grandes manchas de pigmentação preta no corpo e ausência de concentração conspicua de cromatóforos marrom-escuros ou pretos na porção anterior da nadadeira dorsal; presença de manchas laterais não alinhadas em série longitudinal. *Corydoras aurofrenatus* difere de todas as congêneres da linhagem 1 pela superfície ventral da cabeça e do tronco densamente coberta por pequenas plaquetas não coalescentes; porção média lateral com duas ou três manchas marrom-escuras ou pretas (abaixo da nadadeira dorsal, abaixo da base da nadadeira adiposa, e na base do pedúnculo caudal, difusa e variavelmente presente), manchas diminuindo de tamanho posteriormente; aba carnosa pouco desenvolvida no canto da boca; porção anteroventral do cleitro exposta.

Palavras-chave: Bacia do rio Paraguai, Corydoradinae, *Corydoras diphyes*, *Corydoras ellisae*, Osteologia.

INTRODUCTION

Callichthyidae is composed of armoured catfishes with two longitudinal series of dermal plates on flanks, currently comprising more than 200 species (Reis, 2003; Fricke *et al.*, 2020). *Corydoras* Lacépède, 1803, its largest genus, currently contains 175 species, making it the most species-rich genus of Siluriformes (Tencatt *et al.*, 2019; Lima, Britto, 2020). Despite the efforts to better understand the taxonomy and interrelations of *Corydoras* (e.g. Eigenmann, Eigenmann, 1890; Ellis, 1913; Gosline, 1940; Nijssen, 1970; Nijssen, Isbrücker, 1967, 1980a, 1983, 1986; Britto, 2003; Alexandrou *et al.*, 2011), some species are still poorly known and remain like ghosts to science (Tencatt, Ohara, 2016a).

Eigenmann, Kennedy (1903) provided a revised catalogue of a fish collection from Paraguay sent to the Indiana University by Juan Anisits. This collection comprises a total of 750 specimens from many localities of Paraguay, including material collected by Carl Ternetz at Asuncion, and also from Descalvados, State of Mato Grosso, Brazil. In addition, the authors described several new species. One of them is *Corydoras aurofrenatus* Eigenmann & Kennedy, 1903, a typical long-snouted species from lineage 1 *sensu* Alexandrou *et al.* (2011) described based on a single specimen captured in Aguada, near arroyo Trementina, río Paraguay basin, Paraguay. Eigenmann, Kennedy (1903) mentioned that this species displays a very peculiar color pattern among *Corydoras* species, with “no color on sides, belly or breast” (p. 508), dorsal and caudal fins spotted and “a broad yellow band across the snout” (p. 508).

Corydoras species lacking any kind of conspicuous pigmentation on the body are very uncommon. Considering the río de La Plata basin, the only species sharing the

same unusual color pattern described for *C. aurofrenatus* is *C. polystictus* Regan, 1912, which can totally lack conspicuous blotches on the flanks (LFCT pers. obs.). Despite that, *C. polystictus* is a typical lineage 9 species *sensu* Alexandrou *et al.* (2011), and can be undoubtedly distinguished from *C. aurofrenatus* by having a short, rounded snout. Nevertheless, *C. aurofrenatus* is not often assigned to typical long-snouted specimens from the río de La Plata basin because they generally display conspicuous blotches on flanks, although with variable degree of pigmentation.

In the description of *Corydoras diphys* Axenrot & Kullander, 2003 and *Otocinclus mimulus* Axenrot & Kullander, 2003, the authors also discussed the presence of another *Corydoras* species in the arroyo Laguna Penayo, río Aquidabán drainage (same basin of the *C. aurofrenatus* type-locality), near Concepción, Paraguay. The authors mentioned that the examined specimens possess two blotches on flanks, the first just below the dorsal fin and the second just below the adipose fin, dorsal and caudal fin with transversal black bars, and the remaining parts of the body unspotted, which they attributed to *C. aurofrenatus* since some specimens may possess diffuse dark brown or black pigmentation on the flanks, fitting with the description of Eigenmann, Kennedy (1903).

The color pattern described for *Corydoras aurofrenatus* by Axenrot, Kullander (2003) is very similar to *C. ellisae* Gosline, 1940. The authors mentioned that the *C. aurofrenatus* material from many localities of Paraguay, deposited in the Natural History Museum from Stockholm (NRM), may display a diffuse pigmentation or even more conspicuous and larger blotches than described for *C. ellisae* by Ellis (1913). Axenrot, Kullander (2003) mentioned that these color pattern variations are possibly correlated with the habitat of each population, with lighter-colored specimens inhabiting open, sandy shores, whereas darker-colored specimens inhabit streams shaded by the riparian forest. Since the authors did not find any conspicuous morphological difference between the light and dark patterns, they proposed *C. ellisae* as a junior synonym of *C. aurofrenatus*. Despite the evidence provided by Axenrot, Kullander (2003), even the specimens with diffuse pigmentation are still identified as *C. ellisae*, and the synonymy proposed by them is still omitted in catalogues (*e.g.* Ferraris, 2007; Fricke *et al.*, 2020).

Corydoras areio Knaack, 2000 is the only other known lineage 1 species *sensu* Alexandrou *et al.* (2011) from the río de La Plata basin. The species is characterized by the presence of a dorsal series of four rounded or irregular dark brown or black blotches, one on each edge of the dorsal-fin base, the third on the adipose-fin base and the last one on the posterior-most portion of the caudal peduncle; small irregular patches of dark brown or black pigmentation on the flanks, generally restricted to the dorsolateral body plates; and a vertically elongated dark brown or black blotch on the distal lateral portion of the caudal peduncle. Despite the peculiar color pattern, which can promptly distinguish *C. areio* from all of its congeners, information on this species is basically restricted to its original description. Through the analysis of several specimens attributed to *C. areio*, *C. aurofrenatus* and also *C. ellisae*, it was possible to observe that part of the available material of the true *C. areio* has been misidentified as *C. aurofrenatus*. This can be explained due to the fact that some specimens of *C. areio* can present faded spots on the flanks, which makes its color pattern similar to that originally described for *C. aurofrenatus*. Therefore, it is clear that the identity of these species needs to be investigated further.

After the analysis of several specimens from the rio Paraguay basin in Brazil and

Paraguay, the synonymy proposed by Axenrot, Kullander (2003) was corroborated. Because the original descriptions of *C. areio* and *C. aurofrenatus* lack standard diagnoses and several morphological information (mainly concerning osteology), in addition to the difficulty in clearly distinguishing them, the aim of this study is to provide redescriptions for both species, allowing their clear recognition.

MATERIAL AND METHODS

Measurements were obtained using a precision digital calipers in tenth of millimeter. Morphometric and meristic data were taken following Reis (1997) with modifications of Tencatt *et al.* (2013). Morphometrics are reported as percentages of standard length (SL) and head length (HL). Homology of barbels follows Britto, Lima (2003). The specimens used for osteological analysis were cleared and stained (cs) following the protocol of Taylor, Van Dyke (1985). Osteological terminology was based on Reis (1998), except for the use of the parieto-supraoccipital instead of supraoccipital (Arratia, Gayet, 1995), compound pterotic instead of pterotic-supracleithrum (Aquino, Schaefer, 2002) 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) will be treated here as a part of the hyomandibula according to Vera-Alcaraz (2013). Vertebral counts include only free centra, with the compound caudal centra (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. In the descriptions, numbers between brackets represent the total number of specimens with those counts. Literature in which it was not possible to corroborate the species identification (through voucher specimens, drawings or photographs) were not included in the synonymic lists. The majority of the specimens examined herein were obtained in museums/ichthyological collections, and therefore no specific licenses were needed.

Institutional abbreviations. ANSP, The Academy of Natural Sciences, Philadelphia; BMNH, Natural History Museum, London; CPUFMT, Coleção de Peixes da Universidade Federal de Mato Grosso, Cuiabá; DZSJRP, Departamento de Zoologia e Botânica da Universidade Estadual Paulista “Júlio Mesquita Filho”, São José do Rio Preto; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels; LBP, Laboratório de Biologia e Genética de Peixes da Universidade Estadual Paulista “Júlio Mesquita Filho”, Botucatu; LIV, World Museum, Liverpool; MCP, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MCZ, Museum of Comparative Zoology of Harvard University, Cambridge; MHNG, Muséum d’Histoire Naturelle, Geneva; MNHN, Muséum National d’Histoire Naturelle, Paris; MNRJ, Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro; MPEG, Museu Paraense Emílio Goeldi, Belém; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; MTD F, Museum für Tierkunde; NMW, Naturhistorisches Museum, Vienna; NRM, Swedish Museum of Natural History, Stockholm; NUP, Coleção Ictiológica do Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura da Universidade Estadual de Maringá, Maringá; ROM, Royal

Ontario Museum, Toronto; USNM, National Museum of Natural History, Washington D.C.; ZMA/RMNH, Naturalis Biodiversity Center, Leiden; ZMB, Museum für Naturkunde, Berlin; ZUEC, Museu de Zoologia da Universidade Estadual de Campinas “Adão José Cardoso”, Campinas; ZUFMS-PIS, Coleção Zoológica de Referência da Universidade Federal de Mato Grosso do Sul, Campo Grande.

RESULTS

Corydoras areio Knaack, 2000

(Figs. 1, 2A, 3A, 4)

Corydoras areio Knaack, 2000:45, 47, 49, 51–53 (original description; type-locality: “Brasilien, Mato Grosso (östlich von Cuiaba), in Fließgewässern des Córreg. Areio-Systems” [= Brazil, Mato Grosso (east of Cuiabá), in the flowing waters of the córrego Areio basin]). —Reis, 2003:295 (listed). —Fuller, Evers, 2005:70 (photo in life; presence in the aquarium hobby; córrego Areio basin). —Britski *et al.*, 2007:154–155 (identification key; brief description). —Ferraris, 2007:113 (listed). *Corydoras aurofrenatus* (*non* Eigenmann, Kennedy, 1903). —Britto, 2003: 153 (*partim*; specimens from MZUSP 36720).



FIGURE 1 | *Corydoras areio*, holotype, MCP 28675 (ex-ZMB 33113), 48.8 mm SL, Brazil, Mato Grosso, tributaries of the córrego Areia. Dorsal (top), lateral (middle) and ventral (bottom) views. Photo by Diogo Araújo.

Diagnosis. *Corydoras areio* can be distinguished from its congeners, except for the species within lineage 1 *sensu* Alexandrou *et al.* (2011), by the presence of the following features: temporal sensory canal in sphenotic with two pores anteriorly to the branch that gives rise to infraorbital canal (*vs.* with a single pore), upper tooth plate of branchial arch with three or four series of teeth (*vs.* two series of teeth), area at the corner of the mouth, ventral to the maxillary barbel, with a fleshy flap (*vs.* fleshy flap absent). *Corydoras areio* can be distinguished from the species belonging to the lineage 1, except for *C. acutus* Cope, 1872, *C. cervinus* Rössel, 1962, *C. maculifer* Nijssen, Isbrücker, 1971, *C. oxyrhynchus* Nijssen, Isbrücker, 1967, *C. saramaccensis* Nijssen, 1970, *C. vittatus* Nijssen, 1971 and *C. zawadzki* Tencatt & Ohara, 2016, by the absence of large patches of black pigmentation on the body (*vs.* presence in the remaining congeners). *Corydoras areio* is diagnosed from *C. acutus*, *C. cervinus*, *C. maculifer*, *C. vittatus* and *C. zawadzki* by the presence of blotches on flanks not aligned in longitudinal series (*vs.* aligned in longitudinal series, sometimes forming continuous bands). *Corydoras areio* can still be distinguished from *C. vittatus* plus *C. saramaccensis* by the absence of a dark brown or black stripe transversally crossing the eye (*vs.* presence of such stripe, forming the typical mask-like blotch). *Corydoras areio* also differs from *C. cervinus* by having infraorbital 2 with relatively wider posterior laminar expansion (*vs.* infraorbital 2 with relatively narrower posterior laminar expansion). Finally, *C. areio* is diagnosed from *C. oxyrhynchus* by the absence of conspicuous concentration of dark brown or black chromatophores on anterior portion of dorsal fin, especially close to dorsal-fin spine insertion (*vs.* presence of such pattern).

Description. Morphometric data are presented in Tab. 1. Head compressed with convex dorsal profile, roughly triangular in dorsal view. Snout conical conspicuously pointed. Head profile slightly concave from tip of snout to anterior nares, ascending straight to slightly convex from this point to anterior portion of parieto-supraoccipital; slightly convex from this point to tip of posterior process of parieto-supraoccipital. Profile slightly convex along dorsal-fin base. Postdorsal-fin body profile concave to adipose-fin spine, concave from this point to caudal-fin base. Ventral profile of body nearly straight from isthmus to pectoral girdle, and slightly convex from this point until pelvic girdle. Profile nearly straight from pelvic girdle to base of first anal-fin ray, roughly concave until caudal-fin base. Body roughly elliptical in cross section at pectoral girdle, gradually becoming more compressed toward caudal fin.

Eye rounded, located dorsolaterally on head. Orbit delimited anteriorly by lateral ethmoid, anterodorsally by frontal, posterodorsally by sphenotic, posteriorly by infraorbital 2, and ventrally by infraorbital 1. Anterior and posterior nares close to each other, only separated by flap of skin. Anterior naris tubular. Posterior naris close to anterodorsal margin of orbit, separated from it by distance similar to naris diameter. Mouth small, subterminal, width nearly equal to bony orbit diameter. Maxillary barbel long in size, reaching anteroventral limit of gill opening. Outer mental barbel slightly longer than maxillary barbel. Area at corner of mouth, ventral to maxillary barbel, with reduced fleshy flap. Inner mental barbel fleshy, base of each counterpart slightly separated from each other. Small rounded papillae covering entire surface of all barbels, upper and lower lips, snout and isthmus.

Mesethmoid long with anterior tip well developed, larger than 50% of bone length

(see Britto, 2003:123, character 1, state 0; fig. 1A), and posterior portion relatively narrow, entirely covered by thin layer of skin. Middle portion of mesethmoid with well-developed lateroventral process; region of process with width similar to width of posterior portion of mesethmoid. Nasal capsule delimited anterodorsally by mesethmoid, anteriorly and ventrally by lateral ethmoid, and posteriorly and dorsally by frontal. Nasal slender, laterally curved, inner margin laminar, and mesial border contacting frontal and mesethmoid. Lateral ethmoid conspicuously expanded anteriorly, with anterodorsal expansion contacting only mesethmoid, and anteroventral expansion connected to lateroventral process of mesethmoid. Frontal elongated, strongly narrow, width clearly smaller than half of its entire length; anterior projection short, size smaller than nasal length. Frontal fontanel large, conspicuously slender, posterior tip extension markedly entering anterior margin of parieto-supraoccipital. Sphenotic somewhat trapezoid, contacting parieto-supraoccipital dorsally, compound pterotic posteriorly, second infraorbital ventrally and frontal anteriorly (Fig. 2A). Compound pterotic roughly pipe-shaped, with posteriormost portion contacting first lateral-line ossicle, posteroventral margin contacting cleithrum, and anteroventral margin contacting opercle and infraorbital 2, and posterior expansion almost entirely covering lateral opening of swimbladder capsule, leaving slender area on its dorsal margin covered only by thick layer of skin (Fig. 2A). Parieto-supraoccipital wide, posterior process long and contacting nuchal plate and region of contact between posterior process and nuchal plate covered by thick layer of skin.

Two laminar infraorbitals with minute odontodes. Infraorbital 1 large, ventral laminar expansion ranging from moderately- to well developed; anterior portion with well-developed laminar expansion, reaching to or slightly surpassing anterior margin of nasal capsule; inner laminar expansion strongly reduced (Fig. 2A). Infraorbital 2 small, widened, with posterior laminar expansion well developed, and posteroventral margin contacting posterodorsal ridge of hyomandibula, posterodorsal edge contacting sphenotic and compound pterotic; inner laminar expansion poorly developed (Fig. 2A). Posterodorsal ridge of hyomandibula close to its articulation with opercle conspicuously slender, exposed, reduced and bearing small odontodes. Dorsal ridge of hyomandibula between compound pterotic and opercle covered by thick layer of skin. Interopercle covered by thin layer of skin, subtriangular, anterior projection well-developed. Preopercle relatively slender, elongated, minute odontodes sparse on external surface. Opercle dorsoventrally elongated, width equal to or smaller than half of entire length; free margin slightly convex, without serrations and covered by small odontodes.

Four branchiostegal rays decreasing in size posteriorly. Hypobranchial 2 somewhat triangular, tip ossified and directed towards anterior portion, posterior margin cartilaginous, and ossified portion conspicuously well developed, its size three times or more than cartilaginous portion. Five ceratobranchials with expansions increasing posteriorly; ceratobranchial 1 generally with strongly reduced process on anterior margin of mesial portion; ceratobranchial 3 with continuous laminar expansion on postero-lateral margin; ceratobranchial 5 toothed on posterodorsal surface, with 22 to 26 (2) teeth aligned in one row. Four epibranchials with similar size; epibranchial 2 slightly larger than others, with small pointed process on laminar expansion of posterior margin; epibranchial 3 with mesially-curved uncinat process on laminar expansion of posterior margin. Two wide pharyngobranchials (3 and 4), pharyngobranchial 3 with

triangular laminar expansion variably notched on posterior margin. Upper tooth plate oval, 42 to 51(2) teeth roughly aligned in three or four rows on posteroventral surface.

Lateral-line canal reaching cephalic laterosensory system through compound pterotic, branching twice before reaching sphenotic: pterotic branch, with single pore, preoperculomandibular branch conspicuously reduced, with single pore opening close to postotic main canal, postotic main canal becoming widened just posterior to pterotic branch. Sensory canal continuing through compound pterotic, reaching sphenotic as temporal canal, which splits into two branches: one branch giving rise to infraorbital canal, other branch connecting to frontal through supraorbital canal, with one and two pores, respectively. Supraorbital canal branched, running through nasal bone. Epiphyseal branch relatively long, pore opening close to frontal fontanel. Nasal canal with two or three openings, first on posterior edge, second, when present, on posterolateral portion and generally fused with first pore, and third on anterior edge. Infraorbital canal running through entire infraorbital 2, extending to infraorbital 1 and opening into two pores. Preoperculomandibular branch giving rise to preoperculo-mandibular canal, which runs through entire preopercle with three openings, leading to pores 3, 4, and 5, respectively.

Dorsal fin subtriangular, located just posterior to third dorsolateral body plate. Dorsal-fin rays II,7 (1), II,8 (39), II,9 (1), posterior margin of dorsal-fin spine with seven to 10 poorly-developed serrations directed towards tip of spine, serrations arranged on distal half of posterior margin; small odontodes on anterior and lateral surfaces of spine. Nuchal plate well developed, almost entirely exposed, with minute odontodes. Spinelet short, spine moderately developed, adpressed distal tip slightly surpassing posterior origin of dorsal-fin base, and anterior margin with small odontodes. Pectoral fin roughly triangular, its origin just posterior to gill opening. Pectoral-fin rays I,9 (15), I,10 (26), posterior margin of pectoral spine with 16 to 17 with moderately- to well-developed conical serrations along its entire length, most serrations directed towards pectoral-fin origin, and some serrations perpendicularly directed or directed towards tip of spine; small odontodes on anterior, dorsal and ventral surfaces of spine (Fig. 3A). Anteroventral portion of cleithrum exposed; posterolateral portion of scapulocoracoid exposed; small odontodes on exposed areas. Pelvic fin oblong, located just below third ventrolateral body plate, and at vertical through first branched dorsal-fin ray. Pelvic-fin rays i,5. Adipose fin roughly triangular, separated from base of last dorsal-fin ray by generally six dorsolateral body plates. Anal fin subtriangular, located just posterior to 12th ventrolateral body plates, and at vertical through anterior margin of adipose-fin spine. Anal-fin rays ii,5 (3), i,7 (1), ii,6 (16). Caudal fin bilobed, markedly furcated, with dorsal lobe slightly larger than ventral lobe. Caudal-fin rays i,12,i, generally four dorsal and ventral procurent rays.

Two to four laterosensory canals on trunk. First ossicle tubular, second ossicle laminar and the remaining encased in third, fourth and fifth dorsolateral body plate, respectively. Body plates with minute odontodes scattered over exposed area, conspicuous line of odontodes confined on posterior margins. Dorsolateral body plates 23 (30), 24 (9). Ventrolateral body plates 20 (8), 21 (31). Dorsolateral body plates along dorsal-fin base 6. Dorsolateral body plates between adipose- and caudal-fin 7 (13), 8 (7). Preadipose platelets 1 (1), 2 (6), 3 (26), 4 (5), 5 (3). Small platelets covering base of caudal-fin rays. Small platelets disposed dorsally and ventrally between junctions of lateral plates on

posterior portion of caudal peduncle. Anterior margin of orbit, above the junction of frontal and lateral ethmoid, ventral margin of nasal capsule and dorsal surface of snout with small, irregular platelets bearing odontodes. Ventral surface of head and trunk densely covered by small irregular platelets bearing odontodes.

Vertebral count 22 (2). Ribs 5 (2), first pair conspicuously large, its middle portion closely connected to first ventrolateral body plate. Complex vertebra moderately developed.

TABLE 1 | Morphometric data of 20 non-type specimens of *Corydoras areio*, and of 30 non-type specimens of *Corydoras aurofrenatus*. SD = standard deviation.

	<i>Corydoras areio</i>		<i>Corydoras aurofrenatus</i>	
	Low-High	Mean±SD	Low-High	Mean±SD
Standard length (mm)	33.4–42.1	37.6±2.2	29.7–47.6	40.4±5.2
Percentages of standard length				
Depth of body	34.0–37.4	35.2±1.0	32.1–37.8	35.0±1.5
Predorsal distance	46.9–51.9	49.4±1.2	45.9–50.8	48.3±1.1
Prepelvic distance	46.9–50.0	48.2±0.9	45.4–50.3	47.6±1.2
Preanal distance	78.2–82.4	80.8±1.2	76.9–82.5	79.7±1.6
Preadipose distance	80.7–85.8	83.3±1.3	80.2–84.8	82.1±1.2
Length of dorsal spine	19.6–23.2	21.2±1.0	18.2–23.9	20.9±1.4
Length of pectoral spine	20.5–26.7	23.3±1.8	19.1–24.0	21.8±1.3
Length of adipose-fin spine	8.1–11.6	9.2±0.8	7.4–11.4	9.4±1.0
Depth of caudal peduncle	13.1–14.6	14.0±0.4	12.8–15.4	14.0±0.7
Length of dorsal-fin base	16.2–18.7	17.6±0.7	15.4–20.6	18.1±1.1
Dorsal to adipose distance	17.7–21.7	19.6±0.9	15.9–21.6	18.6±1.5
Maximum cleithral width	24.5–26.2	25.4±0.5	23.3–27.0	25.3±1.1
Head length	40.3–44.5	42.2±1.1	38.4–43.4	41.4±1.3
Length of maxillary barbel	18.9–23.6	21.0±1.4	13.2–22.4	18.9±2.4
Percentages of head length				
Head depth	72.7–81.9	77.4±1.9	69.8–82.8	77.7±2.8
Least interorbital distance	21.8–25.2	23.4±1.0	21.7–26.9	24.3±1.2
Horizontal orbit diameter	20.9–23.2	22.0±0.7	18.3–22.5	20.2±1.3
Snout length	39.1–48.7	45.0±2.4	38.6–45.6	42.7±1.9
Least internarial distance	9.3–14.7	12.6±1.4	8.3–13.0	10.9±1.5

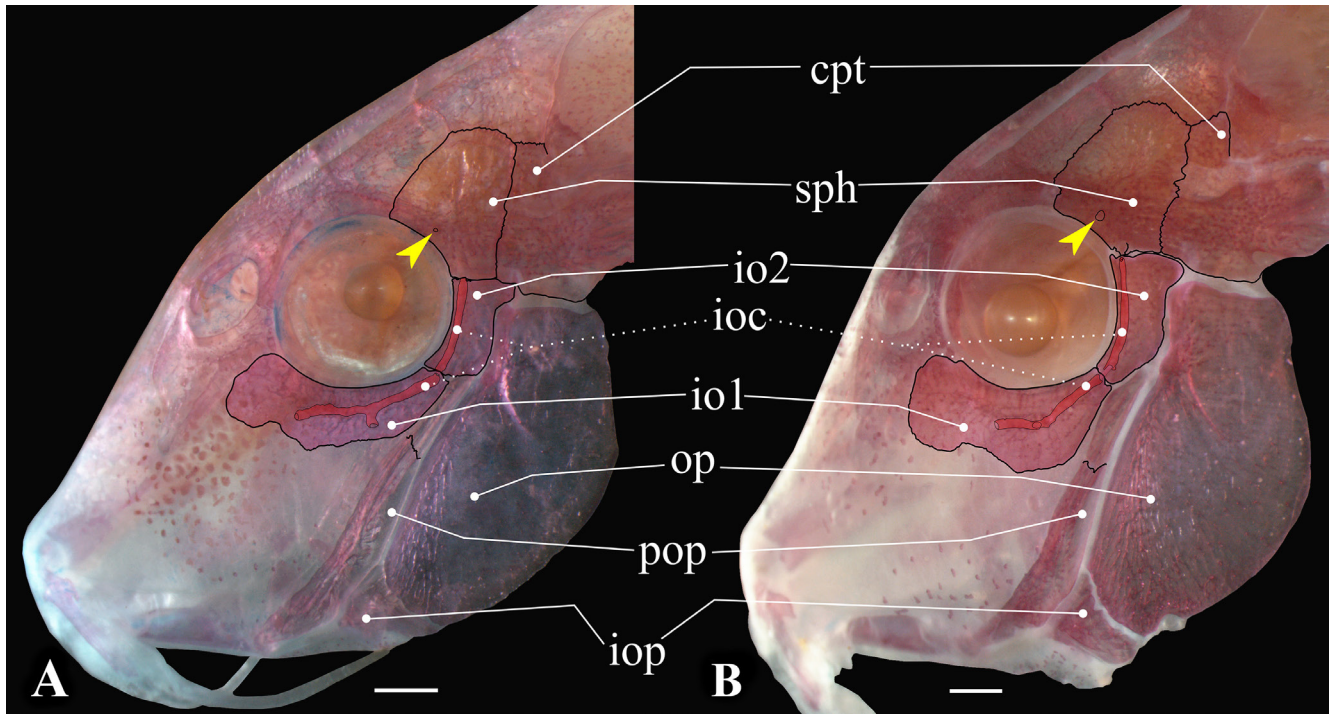


FIGURE 2 | Lateral view of the head of cleared-and-stained specimens of (A) *Corydoras areio*, ZUFMS-PIS 1314, 38.7 mm SL, and (B) *Corydoras aurofrenatus*, NUP 16191, 41.6 mm SL. The black lines represent the limits of the bones. Yellow arrows indicate additional pore on the sphenotic bone. Abbreviations: cpt: compound pterotic. Scale bars = 1.0 mm, io1: infraorbital 1, io2: infraorbital 2, ioc: infraorbital canal, iop: interopercle; op: opercle, pop: preopercle, sph: sphenotic.



FIGURE 3 | Pectoral-fin spine of cleared-and-stained specimens of *Corydoras areio*, ZUFMS-PIS 1314, 38.7 mm SL, and *Corydoras aurofrenatus*, NUP 16191, 38.2 mm SL, showing the well-developed conical serrations directed towards pectoral-spine origin, disposed along the posterior margin of the (A) right spine of *C. areio* (8.8 mm long) and of the (B) left spine of *C. aurofrenatus* (8.6 mm long). Yellow arrows indicate serrations that are directed towards tip of spine or perpendicularly directed.

Coloration in alcohol. Overall color of body in Fig. 1. Ground color of body yellow. Top of head dark brown. Region just above posterodorsal margin of orbit with nearly straight, horizontally elongated dark brown or black blotch, forming eyebrow-like marking, blotch slightly arched, following outline of orbit in some specimens, variably diffuse or absent. Dorsal surface of snout with conspicuous concentrations of dark brown or black chromatophores, variably forming rounded or irregular blotches generally diffuse. Ventral region of infraorbital 1 with conspicuous concentration of dark brown or black chromatophores, with pigmentation extending ventrally in anterior- and posterior-most infraorbital 1 edges in some specimens. Opercle with border and middle portion yellow, remaining area with conspicuous concentration of dark brown or black chromatophores. Cleithrum with conspicuous concentrations of dark brown or black chromatophores on its dorsolateral surface, variably forming irregular small blotches; blotches absent or diffuse in some specimens. Dorsal series of diffuse dark brown or black blotches, first on anterior portion of dorsal-fin base, second on posterior portion of dorsal-fin base, third on adipose-fin base and the last one on posterior portion of caudal peduncle. First blotch conspicuously circular, remaining blotches irregular or rounded. Dorsolateral body plates with relatively small rounded, irregular or elongated dark brown blotches. Ventrolateral body plates generally unspotted, dark brown rounded, irregular or elongated blotches close to midline of flank in some specimens. Last dorso- and ventrolateral body plates with conspicuous concentration of dark brown or black chromatophores, forming generally diffuse, irregular, transversally elongated blotch; some specimens with conspicuous blotch. Spots on flanks faded in few specimens. Dorsal-fin with conspicuous concentration of dark brown or black chromatophores, generally more evident on rays, forming small spots; some specimens with diffuse spots. Pectoral and pelvic fins with dark brown or black chromatophores, generally more concentrated on rays and not forming spots. Adipose fin with dark brown or black chromatophores, generally more concentrated on spine, especially on its distal two-thirds and ventral portion of its origin. Anal fin with conspicuous concentration of dark brown or black chromatophores, generally more evident on rays of its middle portion, forming small spots; spots roughly aligned transversally and generally diffuse. Middle portion of caudal-fin base with small and diffuse dark brown or black dot. Caudal fin with conspicuous concentrations of dark brown or black chromatophores, generally more evident on rays, forming blotches roughly aligned transversally in four to ten slender bars; diffuse bars in some specimens.

Coloration in life. Similar to color pattern of preserved specimens but with lighter ground color of body, and with greenish yellow iridescent coloration (Fig. 4). Eyebrow-like blotch generally more evident. Spots faded in some specimens.

Sexual dimorphism. The presence of lanceolate genital papilla is a common feature in males of all Corydoradinae species (see Nijssen, Isbrücker, 1980b; Britto, 2003). Additionally, the males present a fibrous tissue on pectoral spine, which is generally covered by hypertrophied odontodes, and also a segmented filament on the tip of the spine, as illustrated for *C. solox* Nijssen & Isbrücker, 1983 (see Nijssen, Isbrücker, 1983:81, fig. 10g).

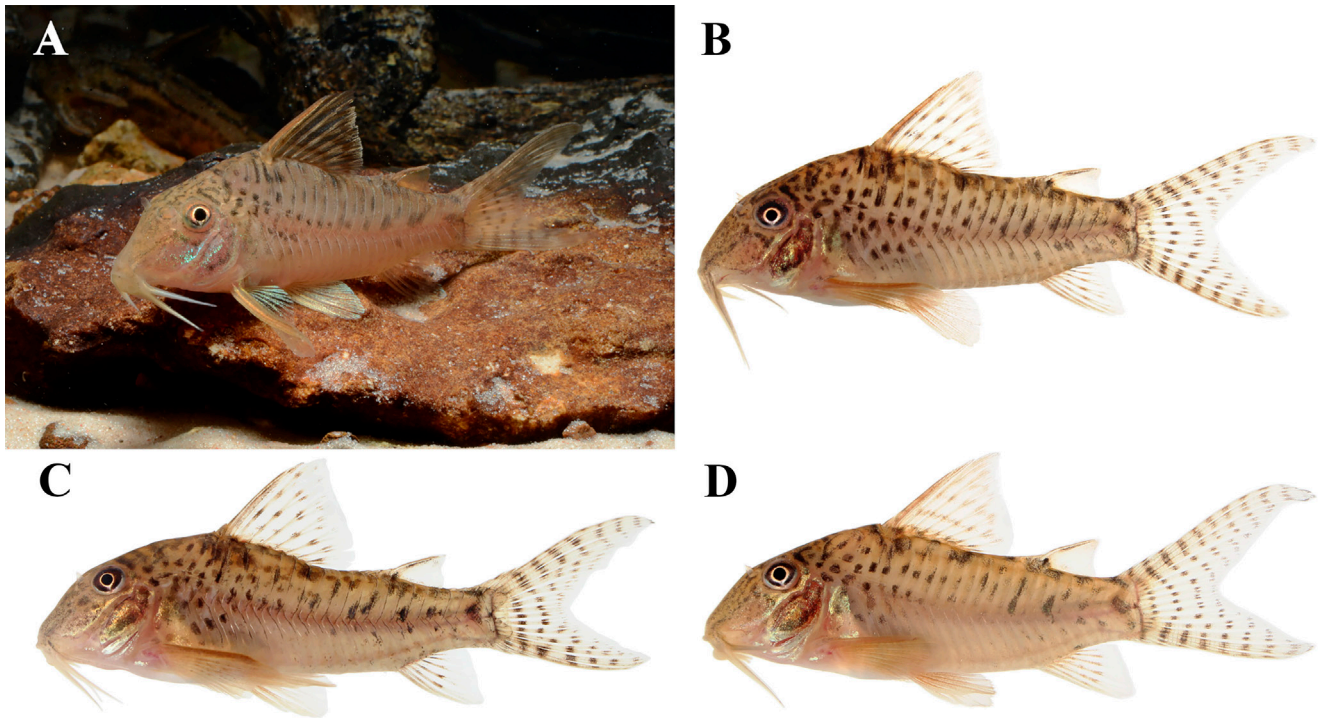


FIGURE 4 | Uncatalogued live specimens of *Corydoras areio*, from the ribeirão dos Veados (= córrego do Veado), rio Taquari basin, Mato Grosso do Sul, Brazil, showing the general color pattern in life of a specimen settled in a biotope aquarium (A), and the main variations observed within the species, (B) densely spotted, (C) moderately spotted, and (D) scarcely spotted. Photos by Hans-Georg Evers (A) and Heriberto Gimênes (B–D).

Geographical distribution. *Corydoras areio* is known from the rio Piquiri (rio Itiquira) and the ribeirão Parnaíba, tributaries of the rio São Lourenço basin, State of Mato Grosso, and also from the rio Negro (rio Taboco) and rio Taquari basins, State of Mato Grosso do Sul, Brazil (Fig. 5).

Ecological notes. In the rio Taboco and rio Taquari basins, *Corydoras areio* was generally found inhabiting small streams (Fig. 6), mainly associated with deep, lentic habitats during the day, ranging from about 50 cm to 1 m depth, with substrate predominantly composed of sand. During day, the species displays a more active behavior, swimming away at the sign of any movement, even from outside of the water. On the other hand, the species can be easily observed and captured in shallow beaches of streams (about 10 cm depth) during the night, where they stay nearly motionless. At the beaches of the ribeirão dos Veados (Fig. 6A), the species was observed in syntopy with *C. polystictus* and *Corydoras* aff. *polystictus*. The species was rarely captured in the main channel of the rio Taboco (Fig. 6B), where it is also associated with the sandy substrate of the river banks. In the rio Taboco basin, *C. areio* occurred in syntopy with *Corydoras* aff. *aeneus* (Gill, 1858). In most collecting sites, *C. areio* specimens were observed burying themselves in the sandy substrate, especially during capture attempts. Another interesting feature of *C. areio* observed in natural habitat is the presence of

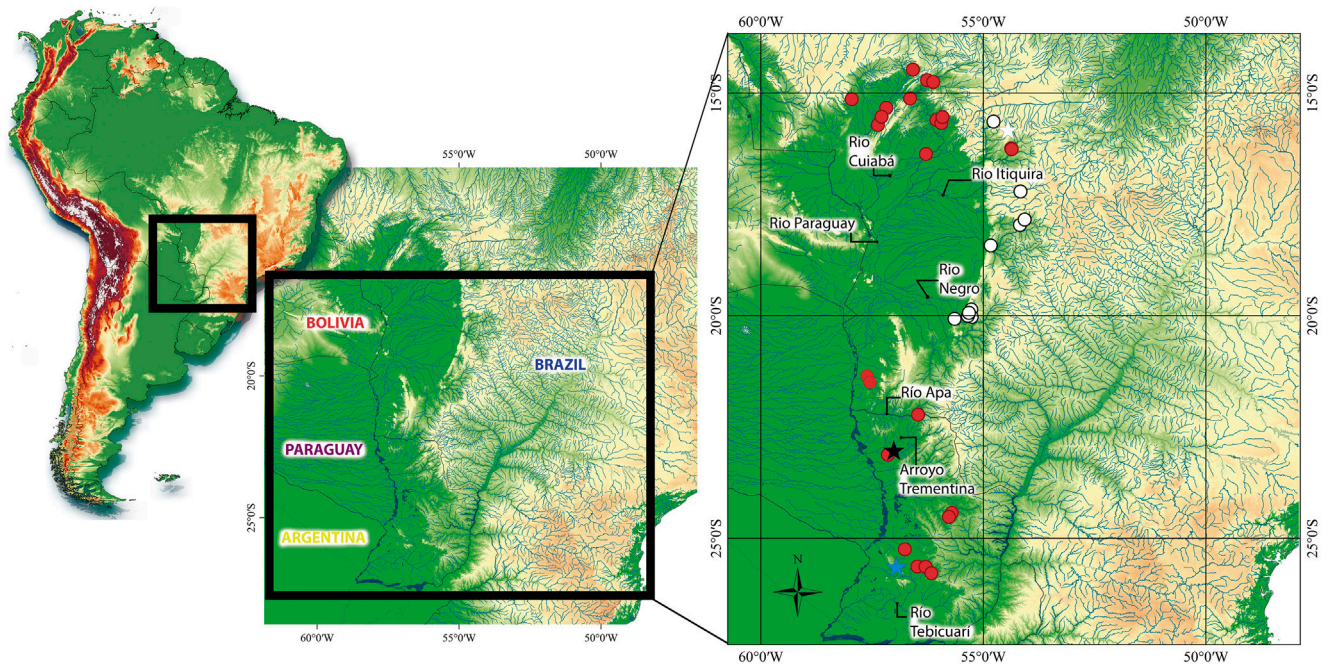


FIGURE 5 | Map of geographic distribution of *Corydoras areio* and *C. aurofrenatus* from the rio Paraguay basin, in Brazil and Paraguay, respectively: white star and white circles denote the possible type locality and non-type material of *C. areio*, respectively; black star and red circles denote the type locality and non-type material of *C. aurofrenatus*, respectively, blue star indicates the type locality of *Corydoras ellisae* (a junior synonym of *Corydoras aurofrenatus*). Each symbol may represent more than one locality.

translucid trunk in smaller specimens (up to 30.0 mm SL), which possibly enhances their camouflage on sand. Additionally, it was possible to observe signs of severe deforestation in the region of both river basins, basically for agricultural and cattle raising purposes, which reflects the high levels of siltation in most of the local water bodies (LFCT pers. obs.).

Remarks. An interesting point concerning *Corydoras areio* is its exact type-locality, since Knaack (2000) did not provide an exact locality, pointing that the species was captured in streams of the “Córr.” (surely an abbreviation for *córrego*) Areio, in the vicinity of Vila Nova, east of Cuiabá, Mato Grosso State, Brazil. According to Knaack (2000: 47–48), *C. areio* seems to be found in two streams that cross the road MT-373, one of them in the kilometer 8.5 and the other one in the kilometer 13.5, near the city of Poxoréo. Searches for “Vila Nova” in Mato Grosso only resulted in a small town at the margins of the rio das Garças, upper rio Araguaia basin, which seems unlikely to be related to the *C. areio* type-locality. Even though it was not possible to track these exact points, the *córrego* Areia basin, tributary from the rio Poxoréo, itself a tributary from rio Vermelho, where the rio São Lourenço flows seems the most plausible potential area for the type-locality, especially considering that the *córrego* Areia itself and some of its tributaries cross the road MT-373 close to the city of Poxoréo (in a range of about 10 kilometers). In a recent collecting trip led by LFCT, the *córrego* Areia was sampled where it crosses the road MT-130, less than 1 km from the urban area of Poxoréo, where no specimens of *C. areio* were captured. Despite this, considering the data provided



FIGURE 6 | The typical structure of habitats where *Corydoras areio* was more frequently observed, showing (A) the ribeirão dos Veados (= córrego do Veado), rio Taquari basin, and (B) the rio Taboco, rio Negro basin, both part of the rio Paraguay drainage in Mato Grosso do Sul, Brazil.

by Knaack (2000), it seems reasonable to consider the córrego Areia drainage around Poxoréo (15°50'41"S 54°26'44"W) as the type-locality of *C. areio*.

Another curious subject regarding the *C. areio* original description refers to the institution where the holotype and nine paratypes were deposited, which was not mentioned in detail, having the catalogue number as the only available information, BZM 33113 and BZM 33136, respectively. A search in the databases available in Sabaj (2019) and Fricke, Eschmeyer (2020) revealed no match for the acronym "BZM". However, Knaack himself (1966: 364) provided further information on "BZM" as follows: "Das Material, welches der Neubeschreibung von Eigenmann und Ward [1907] zu Grunde lag, wurde von Anisits in Paraguay eigesammelt und davon Paratypen auch dem Berliner Zoologischen Museum überlassen (Asuncion, Pilcomayo, BZM Nr. 17249; Matto Grosso, Corumba, BZM Nr. 17258)" (= The material on which the new description by Eigenmann, Ward (in Eigenmann *et al.*, 1907) was based was collected by Anisits in Paraguay, and the paratypes were also given to the Berlin Zoological Museum (Asunción, Pilcomayo, BZM 17249; Mato Grosso, Corumbá, BZM 17258)). Therefore, it seems reasonable to conclude that Knaack created "BZM" for "Berliner Zoologischen Museum", not knowing that the "Zoologischen Museum" in Berlin (a former name of the Museum für Naturkunde) was recognized by the acronym "ZMB" (see Sabaj, 2019).

Although Knaack (2000:47) planned to send the type series of *C. areio* to a fish collection in São Paulo (possibly MZUSP): "Es ist vorgesehen den Holotyp und weiteres Typenmaterial dem Museum Sao Paulo zu übergeben" (= It is planned to hand over the holotype and other type material to the São Paulo Museum), the holotype and paratypes were repatriated in 2001 through their deposit at the MCP, in Rio Grande do Sul, Brazil, under the catalog numbers MCP 28675 and MCP 28676, respectively. Additionally, four topotypes were also donated by the ZMB (MCP 28677) (Carlos A. S. Lucena, 2020, pers. comm.).

Material examined. All from Brazil, rio Paraguay basin. Mato Grosso: MNRJ 20694, 2, 27.0–41.5 mm SL, Dom Aquino, ribeirão Parnaíba, tributary of the rio São Lourenço, 15°44'22"S 54°56'44"W, F. A. G. Melo, P. A. Buckup & M. R. S. Melo, 18 Feb 2000. MZUSP 36720, 6, 27.7–37.1 mm SL, Itiquira, rio Piquiri, Porto Chinelo, Fazenda Santo Antônio do Paraíso, J. H. B. Medeiros & J. C. Oliveira, 17–20 Oct 1980. MZUSP 75231, 2, 26.1–36.5 mm SL, Itiquira, rio Piquiri e Itiquira, Fazenda Santo Antônio do Paraíso, J. C. Oliveira & J. H. B. Medeiros. Mato Grosso do Sul: MNRJ 51964, 5, 34.2–40.1 mm SL, Pedro Gomes, unnamed stream tributary from the córrego do Lobo, rio Taquari basin 17°50'22"S 54°04'19"W, L. F. C. Tencatt, M. N. Souza & M. Santos, 28 Nov 2018. MZUSP 59364, 3, 22.9–25.0 mm SL, Aquidauana, rio Taboco, rio Negro basin, 20°04'18"S 55°38'47"W, A. Machado-Allison, B. Chernoff, O. Froehlich & A. Catella. ZUFMS 1105, 5, 33.7–44.4 mm SL, Corguinho, córrego São João (= córrego Periquito), rio Taboco basin, 19°56'11"S 55°19'28"W, O. Froehlich, M. R. Cavallaro, D. Silva, L. S. Inocêncio & A. Brum, 11 Oct 2001. ZUFMS 1314, 15, 34.4–41.9 mm SL, 2 cs, 38.1–38.7 mm SL, Corguinho, córrego São João (= córrego Periquito), rio Taboco basin, 19°56'11"S 55°19'28"W, O. Froehlich, M. R. Cavallaro, J. Sedenho, D. Silva, M. V. Costa & F. L.G. Leal, 2 Jun 2001. ZUFMS 3899, 3, 25.8–36.9 mm SL, Corguinho, córrego São João (= córrego Periquito), rio Taboco basin, 19°56'12"S 55°19'27"W,

L. F. C. Tencatt, B. F. Santos & R. L. Santos, 18 Jul 2014. ZUFMS 4134, 2, 27.6–30.7 mm SL, Aquidauana, rio Taboco, rio Negro basin, 20°00'15"S 55°20'53"W, L. F. C. Tencatt, B. F. Santos & T. R. F. Sinani, 4 Dec 2014. ZUFMS 4135, 1, 34.3 mm SL, Aquidauana, rio Taboco, rio Negro basin, 20°00'15"S 55°20'53"W, L. F. C. Tencatt, B. F. Santos & T. R. F. Sinani, 19 Jan 2015. ZUFMS 4136, 1, 36.0 mm SL, Aquidauana, córrego Mundo Novo (= córrego Grande), rio Taboco basin, 20°01'45"S 55°15'43"W, L. F. C. Tencatt, B. F. Santos & T. R. F. Sinani, 4 Dec 2014. ZUFMS 4137, 13, 30.2–40.8 mm SL, Corguinho, córrego Bandeira, rio Taboco basin, 19°51'45"S 55°16'16"W, L. F. C. Tencatt, B. F. Santos, F. Severo-Neto & T. R. F. Sinani, 20 Apr 2015. ZUFMS 5951, 7, 30.3–42.3 mm SL, Corguinho, córrego Bandeira, rio Taboco basin, 19°51'45"S 55°16'16"W, L. F. C. Tencatt, B. F. Santos, F. Severo-Neto & T. R. F. Sinani, 20 Apr 2015. ZUFMS 5965, 1, 36.9 mm SL, Corguinho, córrego São João (= córrego Periquito), rio Taboco basin, 19°56'12"S 55°19'27"W, L. F. C. Tencatt, B. F. Santos & R. L. Santos, 18 Jul 2014. ZUFMS 6379, 3, 37.7–40.8 mm SL, Pedro Gomes, unnamed stream, rio Taquari basin, 17°57'39"S 54°10'39"W, L. F. C. Tencatt, M. N. Souza & M. Santos, 28 Nov 2018. ZUFMS 6380, 1, 32.4 mm SL, Coxim, ribeirão dos Veados (= córrego do Veados), rio Taquari basin, 18°25'21"S 54°50'04"W, L. F. C. Tencatt, H. Gimênes Jr., R. Rech & R. Mochi, 16 May 2018. ZUFMS 6381, 5, 32.4–36.3 mm SL, Pedro Gomes, unnamed stream tributary from the córrego do Lobo, rio Taquari basin 17°50'22"S 54°04'19"W, L. F. C. Tencatt, M. N. Souza & M. Santos, 28 Nov 2018.

Corydoras aurofrenatus Eigenmann & Kennedy, 1903

(Figs. 2B, 3B, 7, 8, 9, 11A)

Corydoras aurofrenatus Eigenmann, Kennedy, 1903:506–508 (original description; type-locality: Aguada near arroyo Trementina, Paraguay). —Nijssen, Isbrücker, 1980a:215, 217, table X (listed; member of the “*Corydoras acutus* group”; morphometric data of the holotype). —Axenrot, Kullander, 2003:262, (occurrence in the río Paraguay basin; discussion on color pattern variations; proposed as senior synonym of *Corydoras ellisae*). —Reis, 2003:295 (listed). —Fuller, Evers, 2005:74 (photo in life of an alleged topotype; presence in the aquarium hobby). —Ferraris, 2007:113 (listed). —Tencatt, Pavanelli, 2015:294 (listed as comparative material). —Tencatt, Britto, 2016: e150062 (listed as comparative material). —Tencatt, Evers, 2016:e150019 (listed as comparative material). —Tencatt, Ohara, 2016a:438 (listed as comparative material). —Tencatt, Ohara, 2016b:e150063 (listed as comparative material). —Tencatt *et al.*, 2016:e150089 (relation with *Corydoras paleatus* taxonomic history; diagnosis from *Corydoras froehlichii*; listed as comparative material). —Espíndola *et al.*, 2018:(listed as comparative material). —Tencatt *et al.*, 2019:468 (listed as comparative material).

Corydoras flaveolus (non Ihering, 1911). —Ellis, 1913:398, 407, Pl. XXVIII fig. 1 (identification key; catalogue).

Corydoras ellisae Gosline, 1940:13, 17, 18 (original description; type-locality: arroyo Poná, Sapucay, Paraguay; identification key). —Axenrot, Kullander, 2003:262, (occurrence in the río Paraguay basin; proposed as junior synonym of *Corydoras aurofrenatus*). —Reis, 2003:297 (listed). Fuller, Evers, 2005:119 (photo in life;

presence in the aquarium hobby). —Britski *et al.*, 2007:154–155 (identification key; brief description). —Ferraris, 2007:116 (listed). —Tencatt *et al.*, 2013:263 (listed as comparative material). —Tencatt *et al.*, 2014a:96 (listed as comparative material). —Tencatt *et al.*, 2014b:78 (listed as comparative material). —Tencatt *et al.*, 2016:e150089 (diagnosis from *Corydoras froehlichii*).



FIGURE 7 | *Corydoras aurofrenatus*, holotype, CAS 20661, 40.9 mm SL, Paraguay, Aguada, near arroyo Trementina. Dorsal (top), lateral (middle) and ventral (bottom) views. Copyright © California Academy of Sciences, with all rights reserved.

Diagnosis. *Corydoras aurofrenatus* can be distinguished from its congeners, except for the species within lineage 1, by the presence of the following features: temporal sensory canal in sphenotic with two pores anterior to the branch that gives rise to infraorbital canal (*vs.* with a single pore), upper tooth plate of branchial arch with three to four series of teeth (*vs.* two series of teeth), area at the corner of the mouth, ventral to maxillary barbel, with a fleshy flap (*vs.* fleshy flap absent). *Corydoras aurofrenatus* can be distinguished from the species of the lineage 1, except for *C. acutus*, *C. areio*, *C. cervinus*, *C. coriatae* Burgess, 1997, *C. desana* Lima & Sazima, 2017, *C. filamentosus* Nijssen & Isbrücker, 1983, *C. fowleri* Böhlke, 1950, *C. geoffroy* Lacépède, 1803, *C. maculifer*, *C. negro* Knaack, 2004, *C. ourastigma* Nijssen, 1972, *C. oxyrhynchus*, *C. sarareensis* Dinkelmeyer, 1995, *C. semiaquilus* Weitzman, 1964, *C. septentrionalis* Gosline, 1940, *C. simulatus* Weitzman & Nijssen, 1970, *C. solox*, *C. stenocephalus* Eigenmann & Allen, 1942, *C. treitlii* Steindachner, 1906 and *C. zawadzki* by the absence of a dark brown or black stripe transversally crossing the eye (*vs.* presence of such stripe, forming the typical mask-like blotch). *Corydoras aurofrenatus* is diagnosed from *C. coriatae*, *C. fowleri* and *C. semiaquilus* by having ventral surface of head and trunk densely covered by small, not coalescent platelets (*vs.* ventral surface of head and trunk covered by relatively large, coalescent platelets). *Corydoras aurofrenatus* can be promptly distinguished from *C. acutus*, *C. areio*, *C. cervinus*, *C. desana*, *C. filamentosus*, *C. geoffroy*, *C. maculifer*, *C. negro*, *C. ourastigma*, *C. oxyrhynchus*, *C. sarareensis*, *C. septentrionalis*, *C. simulatus*, *C. solox*, *C. stenocephalus*, *C. treitlii* and *C. zawadzki* by the color pattern of the middle portion of its flank, composed by two or three dark brown or black patches, with first one below dorsal-fin, second one below adipose-fin base and third one, if present, diffuse, and on caudal peduncle base, patches decreasing in size posteriorly (*vs.* covered by small, rounded black spots, with a longitudinal dark brown or black stripe along midline of flank; stripe variably fragmented and generally more evident on posterior half of flanks in *C. acutus*, *C. filamentosus* and *C. vittatus*; covered by numerous, small, rounded, irregular or elongated, dark brown or black spots aligned in both longitudinal rows along flanks and in vertical rows on lateral body plates in *C. cervinus* and females of *C. sarareensis*; covered by small, rounded, irregular or elongated, dark brown or black spots roughly aligned in longitudinal rows; spots variably fused, forming slender longitudinal stripes in *C. maculifer*; with longitudinal series of small, rounded or irregular black spots; series of spots just below midline of flank variably fused, forming a slender longitudinal black stripe; region just above midline of flank with wider longitudinal black stripe in *C. zawadzki*; with conspicuous concentration of dark brown or black chromatophores on dorsolateral body plates; variably, dorsolateral body plates entirely or almost entirely covered by intensely dark brown or black coloration; region of ventrolateral body plates close to flank midline with irregular dark brown or black spots or conspicuous concentration of dark brown or black chromatophores in *C. geoffroy*, *C. negro*, *C. stenocephalus*, *C. solox* and *C. treitlii*; with two dark brown or black blotches, first one larger and vertically elongated, below dorsal fin, and second one smaller, roughly rectangular or rounded, on base of caudal peduncle; region between the two blotches with smaller and variably diffuse dark brown or black markings in *C. desana*; generally with two dark brown or black patches, first one larger, extending from the region just anterior to dorsal fin to region close to adipose-fin anterior origin; first patch more intensely pigmented below dorsal fin, becoming diffuse posteriorly; and second one smaller, on

base of caudal peduncle; patches fused in some specimens, forming a single large patch on flanks in *C. septentrionalis*; generally with two dark brown or black patches, first one below dorsal fin and second one on posterior portion of caudal peduncle; first patch generally larger than second one, variably smaller, diffuse or even absent; second patch generally smaller than first one, vertically elongated; region between the two patches with scattered dark brown or black chromatophores in *C. simulatus*; with conspicuous concentrations of dark brown or black chromatophores on anterior half of flank, forming rounded, irregular or vertically elongated blotches; presence of fused blotches, forming a large patch below dorsal fin in some specimens; posterior half of flank with rounded or irregular blotches roughly aligned in longitudinal rows; blotches variably more intensely pigmented close to flank midline in males of *C. sarareensis*; with dark brown or black, small, irregular or rounded blotches on dorsolateral body plates and on ventrolateral body plates on region close to flank midline; blotches on dorsolateral body plates on the posterior half of the flanks larger in *C. areio*; anterior portion of flanks with small, rounded or irregular, dark brown or black spots, and a large, oblong, dark brown or black patch on caudal peduncle in *C. ourastigma*; diffuse dark brown or black chromatophores scattered all over the body; chromatophores conspicuously concentrated along with posterior margin of lateral body plates in *C. oxyrhynchus*). Additionally, *Corydoras aurofrenatus* can be distinguished from *C. septentrionalis* by the presence of a poorly developed fleshy flap of skin at the corner of the mouth (*vs.* moderately to well developed, forming a barbel-like structure). *Corydoras aurofrenatus* is further distinguished from *C. negro* by the presence of short opercular membrane, leaving anteroventral portion of cleithrum exposed (*vs.* long, covering anteroventral portion of cleithrum).

Description. Morphometric data presented in Tab. 1. Head compressed with convex dorsal profile, roughly triangular in dorsal view. Snout conical, conspicuously pointed. Head profile slightly concave from tip of snout to anterior nares, ascending slightly convex from this point to tip of posterior process of parieto-supraoccipital. Profile slightly convex along dorsal-fin base. Postdorsal-fin body profile concave to adipose-fin spine; concave from this point to caudal-fin base. Ventral profile of body nearly straight from isthmus to pectoral girdle, and slightly convex from this point until pelvic girdle. Profile nearly straight from pelvic girdle to base of first anal-fin ray, concave from this point until caudal-fin base. Body roughly elliptical in cross section at pectoral girdle, gradually becoming more compressed toward caudal fin.

Eye rounded, located dorsolaterally on head. Orbit delimited anteriorly by lateral ethmoid, anterodorsally by frontal, posterodorsally by sphenotic, posteriorly by infraorbital 2, and ventrally by infraorbital 1. Anterior and posterior nares close to each other, only separated by flap of skin. Anterior naris tubular. Posterior naris close to anterodorsal margin of orbit, separated from it by distance similar to naris diameter. Mouth small, subterminal, width nearly equal to bony orbit diameter. Maxillary barbel long in size, reaching anteroventral limit of gill opening. Outer mental barbel slightly longer than maxillary barbel. Area at corner of mouth, ventral to maxillary barbel, with reduced fleshy flap. Inner mental barbel fleshy, base of each counterpart slightly separated from each other. Small rounded papillae covering entire surface of all barbels, upper and lower lips, snout and isthmus.

Mesethmoid long, anterior tip well developed, larger than 50% of the bone length (see Britto, 2003: 123, character 1, state 0; fig. 1A), posterior portion relatively narrow, entirely covered by thin layer of skin. Middle portion of mesethmoid with well-developed lateroventral process; region of process with width slightly larger than width of posterior portion of mesethmoid. Nasal capsule delimited anterodorsally by mesethmoid, anteriorly and ventrally by lateral ethmoid, and posteriorly and dorsally by frontal. Nasal slender, curved laterally, inner margin laminar, with mesial border contacting frontal and mesethmoid, variably contacting only frontal. Lateral ethmoid conspicuously expanded anteriorly, with anterodorsal expansion contacting only mesethmoid, and anteroventral expansion connected to lateroventral process of mesethmoid. Frontal elongated, strongly narrow, width clearly smaller than half of its entire length; anterior projection short, size smaller than nasal length. Frontal fontanel large, conspicuously slender, posterior tip extension markedly entering anterior margin of parieto-supraoccipital. Sphenotic somewhat trapezoid, contacting parieto-supraoccipital dorsally, compound pterotic posteriorly, infraorbital 2 ventrally and frontal anteriorly (Fig. 2B). Compound pterotic roughly pipe-shaped, with posteriormost portion contacting first lateral-line ossicle, posteroventral margin contacting cleithrum, and anteroventral margin contacting opercle and infraorbital 2, posterior expansion almost entirely covering lateral opening of swimbladder capsule, leaving slender area on its dorsal margin covered only by thick layer of skin (Fig. 2B). Parieto-supraoccipital wide, posterior process long and contacting nuchal plate, and region of contact between posterior process and nuchal plate exposed.

Two laminar infraorbitals with minute odontodes. Infraorbital 1 large, ventral laminar expansion ranging from moderately- to well developed; anterior portion with laminar expansion ranging from moderately developed, almost reaching to anterior margin of nasal capsule, to well developed, slightly surpassing anterior margin of nasal capsule; inner laminar expansion strongly reduced (Fig. 2B). Infraorbital 2 small, widened, with posterior laminar expansion well developed, posteroventral margin contacting posterodorsal ridge of hyomandibula, posterodorsal edge contacting sphenotic and compound pterotic; inner laminar expansion moderately developed (Fig. 2B). Posterodorsal ridge of hyomandibula close to its articulation with opercle slender, exposed, reduced and bearing small odontodes. Dorsal ridge of hyomandibula between compound pterotic and opercle covered by thick layer of skin. Interopercle covered by thin layer of skin, subtriangular, anterior projection well-developed. Preopercle relatively slender, elongated, minute odontodes sparse on external surface. Opercle dorsoventrally elongated, width equal or smaller than half of entire length, free margin slightly convex, without serrations and covered by small odontodes.

Four branchiostegal rays decreasing in size posteriorly. Hypobranchial 2 somewhat triangular, tip ossified and directed towards anterior portion, posterior margin cartilaginous, ossified portion moderately to well developed, ranging from slightly larger to more than twice size of cartilaginous portion. Five ceratobranchials with expansions increasing posteriorly; ceratobranchial 1 with small process on anterior margin of mesial portion; ceratobranchial 3 notched on posterolateral margin, variably with continuous laminar expansion; ceratobranchial 5 toothed on posterodorsal surface, with 22 to 28 (2) teeth aligned in one row. Four epibranchials with similar size. Epibranchial 2 slightly larger than others, with small pointed process on laminar expansion of posterior

margin. Epibranchial 3 with triangular uncinat process on laminar expansion of posterior margin, process variably trapezoid. Two wide pharyngobranchials (3 and 4). Pharyngobranchial 3 with triangular laminar expansion, variably notched, on posterior margin. Upper tooth plate oval, 34 to 53 (3) teeth roughly aligned in three or four rows on posteroventral surface. Lateral-line canal reaching cephalic laterosensory system through compound pterotic, branching twice before reaching sphenotic: pterotic branch, with single pore. Preoperculomandibular branch conspicuously reduced, with single pore opening close to postotic main canal. Postotic main canal becoming widened just posterior to pterotic branch. Sensory canal continuing through compound pterotic, reaching sphenotic as temporal canal, which splits into two branches: one branch giving rise to infraorbital canal, other branch connecting to frontal through supraorbital canal, with one and two pores, respectively. Supraorbital canal branched, running through nasal bone. Epiphyseal branch relatively long, pore opening close to frontal fontanel. Nasal canal with three openings, first on posterior edge, second, on posterolateral portion generally fused with first pore, and third on anterior edge. Infraorbital canal running through entire second infraorbital, extending to infraorbital 1 and opening into two pores. Preoperculomandibular branch giving rise to preoperculo-mandibular canal, which runs through entire preopercle with three openings, leading to pores 3, 4, and 5, respectively.

Dorsal fin subtriangular, located just posterior to third dorsolateral body plate. Dorsal-fin rays II,7 (1), II,8 (26), II,9 (3), posterior margin of dorsal-fin spine with four to seven poorly-developed serrations directed towards tip of spine, serrations arranged on distal half of its posterior margin; small odontodes on anterior and lateral surfaces of spine. Nuchal plate well developed, exposed, with minute odontodes. Spinelet short, spine moderately developed, adpressed distal tip slightly surpassing posterior origin of dorsal-fin base, and anterior margin with small odontodes. Pectoral fin roughly triangular, its origin just posterior to gill opening. Pectoral-fin rays I,9 (15), I,10 (14), posterior margin of pectoral spine with 13 to 21 moderately- to well-developed conical serrations along its entire length, most serrations directed towards pectoral-spine origin, and some serrations perpendicularly directed; small odontodes on anterior, dorsal and ventral surfaces of spine (Fig. 3B). Anteroventral portion of cleithrum exposed; posterolateral portion of scapulocoracoid exposed; minute odontodes sparse on exposed areas. Pelvic fin oblong, located just below third ventrolateral body plate, and at vertical through first branched dorsal-fin ray. Pelvic-fin rays i,5. Adipose fin roughly triangular, separated from base of last dorsal-fin ray by generally six dorsolateral body plates. Anal fin subtriangular, located just posterior to 12th ventrolateral body plates, and at vertical through anterior margin of adipose-fin spine. Anal-fin rays ii,5 (1), ii,6 (24). Caudal fin bilobed, markedly furcated, with dorsal lobe slightly larger than ventral lobe. Caudal-fin rays i,12,i, generally four dorsal and ventral procurent rays.

Four to five laterosensory canals on trunk. First ossicle tubular, second ossicle laminar, and remaining lateral-line canals, when present, encased in third, fourth and fifth dorsolateral body plates, respectively. Body plates with minute odontodes scattered over exposed area, a conspicuous line of odontodes confined on posterior margins. Dorsolateral body plates 22 (1), 23 (19), 24 (10), 25 (4). Ventrolateral body plates 20 (14), 21 (11), 22 (9). Dorsolateral body plates along dorsal-fin base 5 (1), 6 (24), 7 (10). Dorsolateral body plates between adipose- and caudal-fin 7 (10), 8 (12), 9 (3). Preadipose

platelets 2 (2), 3 (20), 4 (8), 5 (3). Small platelets covering base of caudal-fin rays. Small platelets disposed dorsally and ventrally between junctions of lateral plates on posterior portion of caudal peduncle. Anterior margin of orbit, above junction of frontal and lateral ethmoid, anterior and ventral margins of nasal capsule, and dorsal surface of snout with small, irregular platelets bearing odontodes. Ventral surface of head and trunk densely covered by small irregular platelets bearing odontodes.

Vertebral count 22 (2). Ribs 5 (2), first pair conspicuously large, its middle portion closely connected to first ventrolateral body plate. Complex vertebra moderately developed.

Color in alcohol. Overall color of body in Fig. 8. Ground color of body yellow or brownish yellow. Top of head and snout dark brown. Dorsal surface of snout with conspicuous concentration of dark brown or black chromatophores, not forming blotches. Ventral region of infraorbital 1 with conspicuous concentration of dark brown or black chromatophores, with pigmentation extending ventrally in anterior- and posterior-most infraorbital 1 edges in some specimens. Opercle with border and middle portion yellow or brownish yellow, remaining area conspicuous concentration of dark brown or black chromatophores. Cleithrum with conspicuous concentration of dark brown or black chromatophores on its dorsolateral surface, generally more evident on middle portion. Dorsal series of diffuse dark brown or black blotches, first on anterior portion of dorsal-fin base, second on posterior portion of dorsal-fin base, third on adipose-fin base and last one on posterior portion of caudal peduncle. Middle portion of flanks with two or three dark brown or black patches, first below dorsal-fin base, second below adipose-fin base and third, if present, diffuse, on caudal peduncle base. Patches decreasing in size posteriorly, presence of darker patches with scarce and diffuse black pigmentation between them, generally restricted to dorsolateral-body plates, in some specimens; patches diffuse in some specimens. Dorsal-fin rays with conspicuous concentration of dark brown or black chromatophores, generally more evident on rays, forming small spots; diffuse spots in some specimens. Pectoral, pelvic and anal fins with dark brown or black chromatophores, generally more concentrated on rays and not forming spots; anal fin variably with small diffuse spots roughly aligned transversally on its middle portion. Adipose fin with dark brown or black chromatophores, generally more concentrated on spine, especially on its distal two-thirds and ventral portion of its origin, and on posterodorsal portion of membrane. Middle portion of caudal-fin base variably with small and diffuse dark brown or black dot. Caudal fin with conspicuous concentrations of dark brown or black chromatophores, generally more evident on rays, forming blotches roughly aligned transversally in five to eight slender transversal bars.

Color in life. Similar to the color pattern of preserved specimens, but ground color of body light and with greenish yellow iridescent coloration. Additionally, region just above posterodorsal margin of orbit with nearly straight, horizontally elongated dark brown or black blotch, forming eyebrow-like marking; blotch slightly arched, following outline of orbit in some specimens (Fig. 9).

Sexual dimorphism. Same as described for *Corydoras areio*.

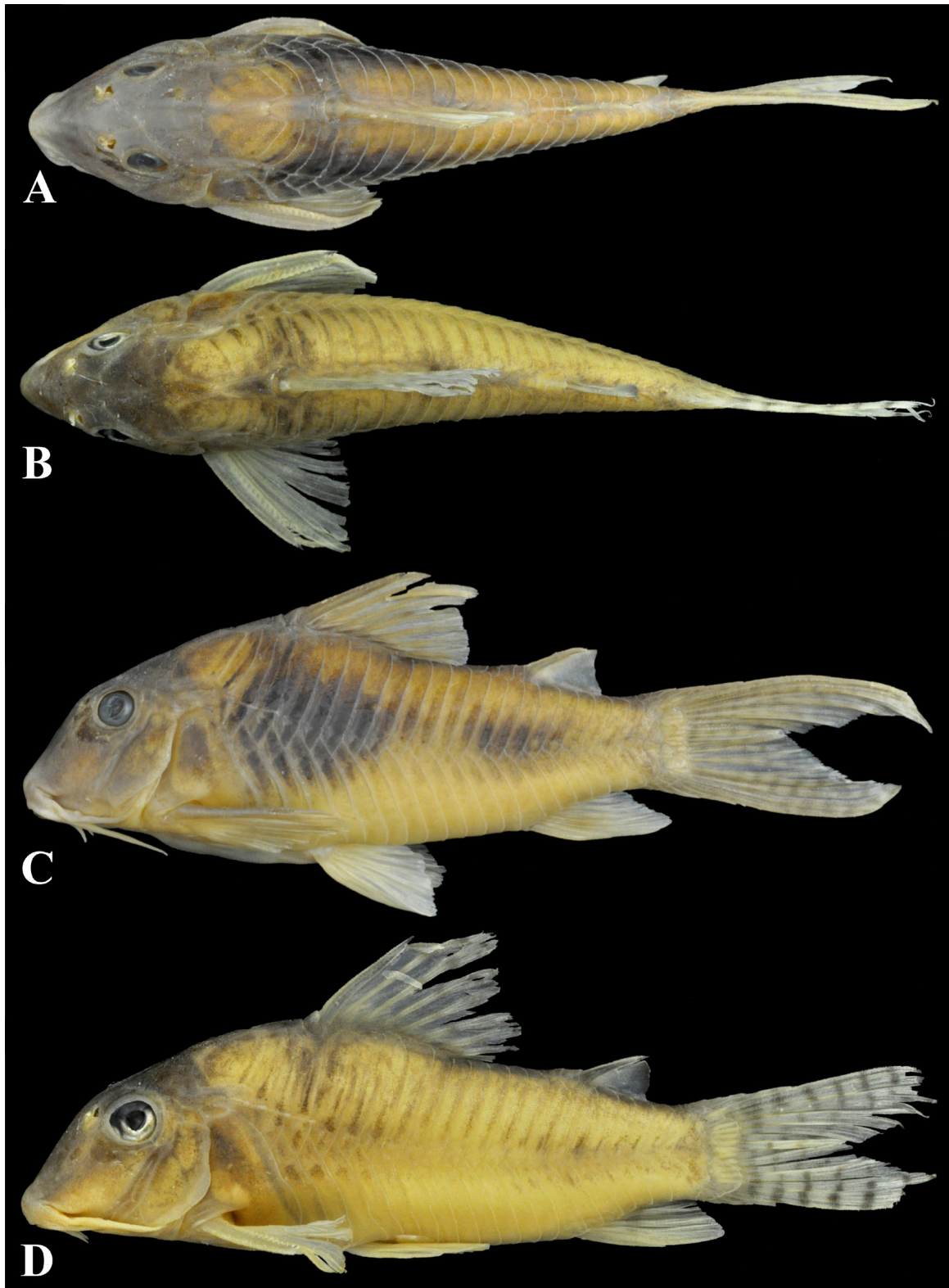


FIGURE 8 | Color pattern variation in preserved specimens of *Corydoras aurofrenatus*, showing the intensely pigmented pattern, NUP 16191, 45.8 mm SL, Brazil, Mato Grosso, Rosário do Oeste, córrego Cancela, in dorsal (A) and lateral (C) views, and the diffuse pattern, NRM 23529, 44.6 mm SL, Paraguay, Concepción, arroyo Laguna Penayo, in dorsal (B) and lateral (D) views.

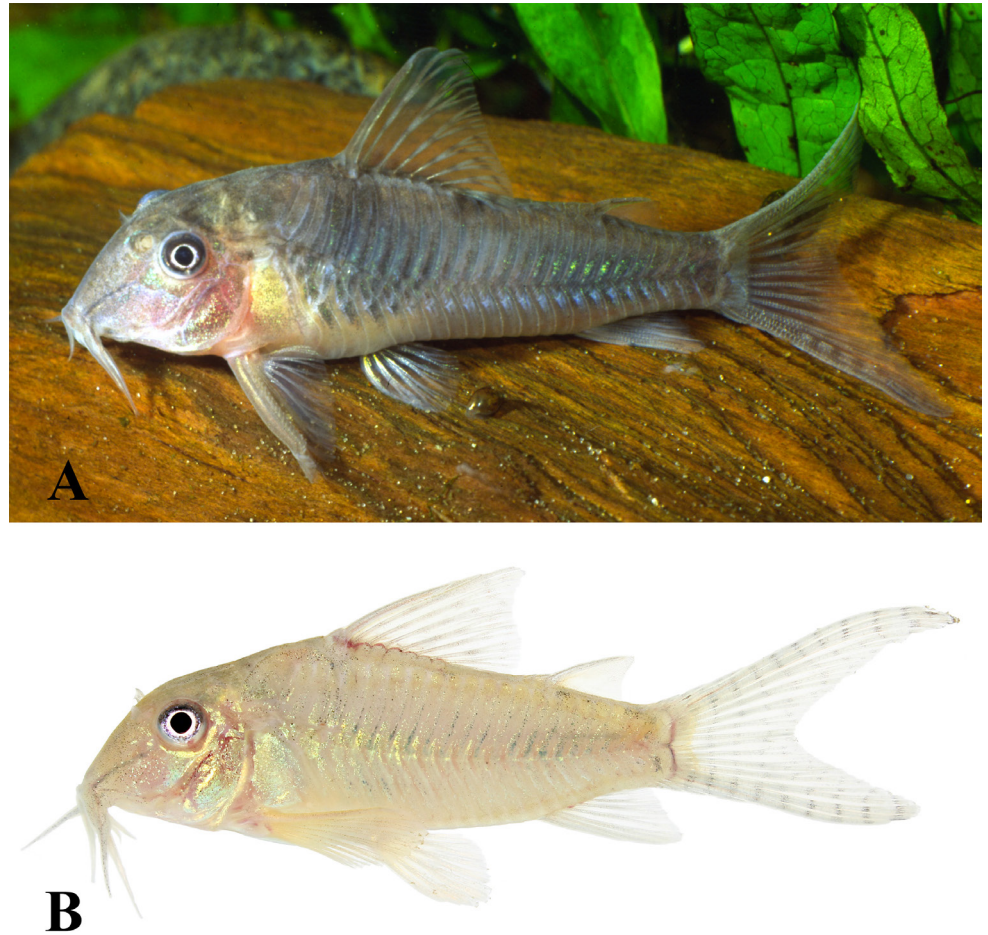


FIGURE 9 | Uncatalogued live specimens of *Corydoras aurofrenatus*, showing (A) a specimen with conspicuous blotches on flanks, said to be from “Paraguay”, and (B) a specimen with diffuse pigmentation on flanks, from the rio Amonguijá, Mato Grosso do Sul, Brazil. Photo by Hans-Georg Evers and Heriberto Gimênes, respectively.

Geographical distribution. *Corydoras aurofrenatus* is known from several tributaries of the rio Paraguay basin in Brazil and Paraguay (Fig. 5).

Ecological notes. During collecting trips for the Proyecto Vertebrados del Paraguay (1992–1999) conducted by the NRM and the Museo Nacional de Historia Natural del Paraguay (MNHNP), *C. aurofrenatus* was captured from small streams to the main channel of rivers within Paraguayan territory. The arroyo Laguna Penayo (Fig. 10A) is a stream with about 20 m width and 0.5 m deep, very slight to stagnant current, turbid water, and substrate composed mainly by clay. An unnamed stream tributary from the río Apa (Fig. 10B) with about 25m width and 1 m deep, stagnant current, dark brown, very turbid water, and substrate composed by sand, rocks and trunks. The río Araguay-Guazú (Fig. 10C) is relatively small river with about 35 m width and 1 m deep, moderate current, turbid water, and substrate composed mainly

by sand. The río Jejuí-Guazú (Fig. 10D) is a small river with brown semitransparent water, and substrate composed mainly by sand, gravel and leaf heaps. A small, unnamed stream tributary from the río Paraguay (Fig. 10E) with light brown water, and substrate composed mainly by sand. Most sites presented some degree of anthropogenic impact. Habitat information summarized herein is available at the NRM online database (<http://artedi.nrm.se/nrmfish/>).

Remarks. In a revisionary study for Callichthyidae, Ellis (1913) mentioned the presence of *C. flaveolus* Ihering, 1911 (described from the rio Tietê basin) in the río Paraguay basin, at Sapucay, Paraguay. In the illustration of one of the examined specimens (Ellis, 1913:Pl. XXVIII, fig. 1), it is possible to observe that the specimen presents a long and conical snout, contrary to *C. flaveolus*, which displays a short and rounded snout (Tencatt *et al.*, 2014a:93, fig. 4). Ellis's (1913) confusion is probably due to the comparison between *C. aurofrenatus* and *C. flaveolus* made by Ihering (1911:386), which stated that his new species is morphologically similar to *C. aurofrenatus*, from which it differs by its color pattern. Gosline (1940) also conducted a review on Callichthyidae, in which he described *Corydoras ellisae* based on that material identified as *C. flaveolus* by Ellis (1913:407, pl. 28, fig. 1). Gosline (1940) mentioned that *C. ellisae* and the other new species described therein (*C. septentrionalis*) are remarkably similar but regarded them as different species by some morphological features and geographic distribution (Gosline, 1940:18). As previously discussed by Axenrot, Kullander (2003), there is no unequivocal way to distinguish *C. aurofrenatus* from *C. ellisae*, which led the authors to consider them conspecific. A synonymy corroborated herein in a broader analysis.

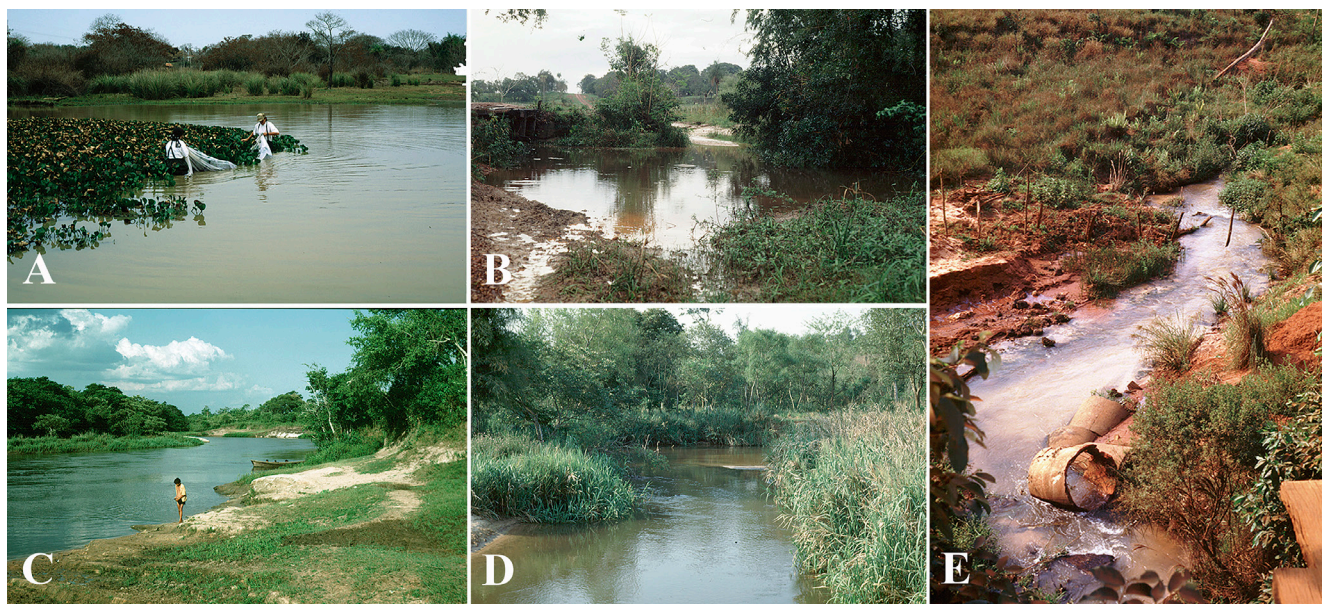


FIGURE 10 | Habitats in which *Corydoras aurofrenatus* was found during the Proyecto Vertebrados del Paraguay, in Paraguay, showing (A) the arroyo Laguna Penayo, (B) an unnamed stream tributary from the río Apa, (C) the río Araguay-Guazú, (D) the río Jejuí-Guazú, and (E) a small, unnamed stream tributary from the río Paraguay.

Some fish catalogs (e.g. Menni, 2004; Liotta, 2005; Arias *et al.*, 2013; Mirande, Koerber, 2015; Fricke *et al.*, 2020) recorded *C. aurofrenatus* from Argentina and Bolivia. However, it was not possible to confirm these records in any way (e.g. analysis of voucher specimens, drawings or photos). Although they are possibly correct, we consider only checked information to assign species distribution.

Material examined. All from the rio Paraguay basin: **Brazil.** Mato Grosso: CPUFMT 243, 4, 18.4–27.9 mm SL, Alto Paraguai, córrego Estorda, 14°28'19"S 56°34'57"W, S. Silva, 6 Sep 2008. CPUFMT 1635, 2, 31.3–43.6 mm SL, Poxoréo, córrego Lajeado, 16°15'38"S 54°21'52"W, V. Oliveira, 5 Sep 2009. CPUFMT 1697, 1, 43.3 mm SL, Poxoréo, córrego Macaco, 16°14'37"S 54°22'29"W, V. Oliveira, 22 Aug 2010. CPUFMT 1702, 4, 15.0–51.6 mm SL, Poxoréo, córrego Macaco, 16°14'37"S 54°22'29"W, V. Oliveira, 31 May 2011. CPUFMT 1709, 1, 41.7 mm SL, Poxoréo, córrego Lajeado, 16°15'38"S 54°21'52"W, V. Oliveira, 25 Aug 2010. CPUFMT 1997, 1, 41.6 mm SL, Porto Estrela, unnamed stream, córrego Salobro basin, 15°31'55"S 57°17'17"W, T. Arnhold, 15 Jan 2012. CPUFMT 2303, 9, 31.0–48.3 mm SL, Cuiabá, córrego Aricazinho, 15°32'21"S 55°55'05"W, L. Pereira, 25 Oct 2013. CPUFMT 2323, 2, 35.1–42.7 mm SL, Cuiabá, córrego Aricazinho, 15°32'21"S 55°55'05"W, L. Pereira. CPUFMT 2324, 1, 20.5 mm SL, Cuiabá, córrego Aricazinho, 15°32'21"S 55°55'05"W, L. Pereira. CPUFMT 2344, 9, 25.6–34.8 mm SL, córrego Aricazinho, 15°32'21"S 55°55'05"W, L. Pereira, 16 Feb 2014. CPUFMT 2362, 12, 28.9 mm SL, 43.1 mm SL, Cuiabá, córrego Aricazinho, 15°32'21"S 55°55'05"W, L. Pereira, 12 Apr 2014. CPUFMT 2381, 1, 37.9 mm SL, Cuiabá, córrego Aricazinho, 15°32'21"S 55°55'05"W, L. Pereira, 29 Jun 2014. CPUFMT 3575, 2, 29.9–32.8 mm SL, Nossa Senhora do Livramento, Baía dos Coqueiros (córrego Landi), 16°22'12"S 56°17'24"W, F. Machado, 28 Nov 1990. MNRJ 20541, 4, 28.8–38.5 mm SL, Cuiabá, small tributary of the rio Aricá-Açu, BR364, East from Cuiabá, 15°40'21"S 55°56'37"W, F. A. G. Melo, P. A. Buckup & M. R. S. Melo, 18 Feb 2000. MNRJ 31382, 1, 44.6 mm SL, Chapada dos Guimarães, a stream in the Santa Cruz neighborhood, rio Coxipó basin, 15°36'20"S 56°03'07"W, M. N. Mehana, L. Centofante & D. Krinski, 21 Feb 2007. MZUSP 44283, 1, 30.3 mm SL, Rosário Oeste, ribeirão Chiqueirão, 15°07'15"S 56°38'45"W, Expedition MZUSP/USNM/MCP/UFMT staff, 10 Aug 1991. MZUSP 44336, 2, 36.0–43.0 mm SL, Porto Estrela, unnamed stream, 15°19'35"S 57°11'34"W, Expedition MZUSP/USNM/MCP/UFMT staff, 11 Aug 1991. MZUSP 44351, 3, 37.6–47.2 mm SL, Porto Estrela, córrego Cachoeirinha, 15°44'28"S 57°19'56"W, Expedition MZUSP/USNM/MCP/UFMT staff, 11 Aug 1991. MZUSP 91053, 5, 16.2–30.5 mm SL, Salto do Céu, córrego dos Veados, 15°08'10"S 57°57'28"W, H. A. Britski, O. Froehlich, A. Catella & F. Marques. NUP 3239, 7, 25.3–45.3 mm SL, Rosário Oeste, córrego Forquilha, 14°44'58"S 56°07'39"W, Nupélia staff, 15 Jun 2001. NUP 10227, 1, 17.6 mm SL, Nobres, córrego Cancela, 14°42'31"S 56°15'52"W, Nupélia staff, 12 Dec 2002. NUP 16191, 33, 20.1–53.8 mm SL, 2 cs, 38.2–41.6 mm SL, Rosário Oeste, córrego Cancela, Nupélia staff, 15 Jan 2001. Mato Grosso do Sul: ZUFMS 5353, 4, 14.2–23.4 mm SL, Porto Murtinho, córrego Rapadura, rio Tarumã basin, 21°29'47"S 57°32'42"W, F. Severo-Neto, 28 Mar 2017. ZUFMS 5704, 2, 22.6–27.5 mm SL, Porto Murtinho, córrego Tererê, rio Tererê basin, 21°21'23"S 57°36'45"W, F. Severo-Neto, D. A. Lopes & T. T. M. Taveira, 20 May 2018. **Paraguay.** Amambay: NRM 30085, 1, 49.7 mm SL,

Bella Vista, unnamed stream tributary from the río Apa, A. M. C. Silfvergrip *et al.*, 14 Jun 1994. Caaguazú: NRM 45022, 2, 11.9–14.3 mm SL, río Tebicuary, where it crosses the road Cnel. Oviedo – Villarica, Åhlander *et al.*, 12 Nov 1999. Canindeyú: NRM 31506, 6, 21.2–46.4 mm SL, unnamed stream, S. O. Kullander *et al.*, 12 Oct 1994. NRM 32591, 10 of 19, 32.0–47.6 mm SL, río Jejuí-Guazú, 76 km on the road leading to Curuguaty, S. O. Kullander *et al.*, 11 Oct 1994. Concepción: NRM 23529, 10 of 33, 31.4–45.7 mm SL, Paso Barreto, arroyo Laguna Penayo where it crosses the road Concepción–Paso Barreto, S. O. Kullander *et al.*, 20 Aug 1993. Cordillera: NRM 42315, 1, 36.9 mm SL, arroyo Yhaguy, where it crosses Ruta 2 at about Km 83, E. Åhlander *et al.*, 21 Mar 1998. Guairá: NRM 42361, 1, 43.6 mm SL, arroyo Guazú at road bridge in Carlos Fannel, Åhlander *et al.*, 27 Mar 1998. NRM 42703, 2, 28.4–30.5 mm SL, río Tebicuary, where it crosses the road Mauricio J. Troche – Independencia, Åhlander *et al.*, 27 Mar 1998. ZMB 16911, 1, 26.7 mm SL, Villa Rica (= Villarrica), Anisits. ZMB 17046, 1, 45.0 mm SL, Villa Rica (= Villarrica), Anisits. Paraguari: MTD F 26329, 1, 42.6 mm SL, Sapucay (= Sapucaí), arroyo Poná, 25° 43'55"S 57° 12'28"W, A. Zarske, 1 Oct 1997. MTD F 26330, 1, 39.4 mm SL, Sapucay (= Sapucaí), arroyo Poná, 25° 43'55"S 57° 12'28"W, A. Zarske, 1 Oct 1997. ZMB 33323, 1, 42.5 mm SL, Sapucay (= Sapucaí), arroyo Poná, J. Knaack, 21 April 2001. ZMB 33324, 1, 40.0 mm SL, Sapucay (= Sapucaí), arroyo Poná, J. Knaack, 21 Apr 2001.

DISCUSSION

The only two typical long-snouted species from the lineage 1 *sensu* Alexandrou *et al.* (2011) that occurs in the río Paraguay basin are *C. areio* and *C. aurofrenatus*. However, there are at least other two species in the río de La Plata basin, *C. britskii* (Nijssen & Isbrücker, 1983) and *Corydoras* cf. *splendens* (Castelnau, 1855), both lineage 8 species *sensu* Alexandrou *et al.* (2011), sharing the presence of a long and pointed snout with *C. areio* and *C. aurofrenatus*. Despite the presence of a long mesethmoid, which gives to the aforementioned species from both lineages an externally similar long and pointed snout, this condition is not the same, especially regarding the posterior portion of the mesethmoid, which is smaller and narrower in *C. areio* and *C. aurofrenatus* (*vs.* larger and wider in *C. britskii* and *Corydoras* cf. *splendens*). Additionally, *C. areio* and *C. aurofrenatus* can be clearly distinguished from *C. britskii* and *Corydoras* cf. *splendens* by the presence of conical serrations on the posterior margin of the pectoral-fin spine (*vs.* laminar serrations), posterior margin of the dorsal-fin spine with serrations directed towards the tip of the spine (*vs.* directed towards the origin of the spine), absence of a bony plate contacting the anteroventral portion of infraorbital 1 (*vs.* presence of such bony plate), and smaller number of branched dorsal-fin rays (seven to nine *vs.* 10 to 19).

The most similar congeners to *C. aurofrenatus* are *C. septentrionalis*, from the río Pinã, Venezuela, *C. stenocephalus*, from the río Ucayali basin, Peru and *C. negro*, from the río Negro, río Blanco system, upper río Itenez (= Guaporé) basin, Bolivia (see Gosline, 1940; Nijssen, Isbrücker, 1986; Knaack, 2004). Despite the similarity between these four species, the color patterns of their flanks present clear differences (see *C. aurofrenatus* "Diagnosis"). In *C. aurofrenatus* it is possible to observe the presence of conspicuous concentrations of dark brown or black chromatophores, forming two or three distinct

patches decreasing in size along the middle portion of the flank, first one below the dorsal fin, second one below the adipose fin, and third one, if present, diffuse on the posterior portion of the caudal peduncle. Even the specimens of *C. aurofrenatus* with diffuse coloration present black chromatophores in the three aforementioned regions, thus, the only difference between the two morphotypes is the intensity of the dark brown or black coloration. In all aforementioned congeners, no distinct dark brown or black patch below the adipose fin was observed.

One of the most similar congeners to *C. aurofrenatus* is *C. negro*, which is reinforced by its frequent misidentification as *C. aurofrenatus* in different fish collections around the world (SAS pers. obs.). The confusion in distinguishing both species is probably due to the incipient information regarding the identity of *C. negro*, which is basically restricted to its original description. Additionally, material of this species in museums and fish collections is scarce, as Knaack (2004:81) deposited only 10 of the 167 available specimens in regular collections, keeping 157 specimens as paratypes in his private collection, which seems to have been lost (see Tencatt, Pavanelli, 2015:293). The relatively small distance between type localities of both species may have also contributed to this problem, since Paraguay and Bolivia are neighbor countries. Beyond the difference in color pattern presented in the diagnosis, *C. negro* also presents an apparently uncommon feature in Corydoradinae, a well-developed opercular membrane, covering the anteroventral portion of the cleithrum, contrary to *C. aurofrenatus*, which presents a poorly-developed opercular membrane, leaving the anteroventral portion of the cleithrum exposed (Fig. 11).

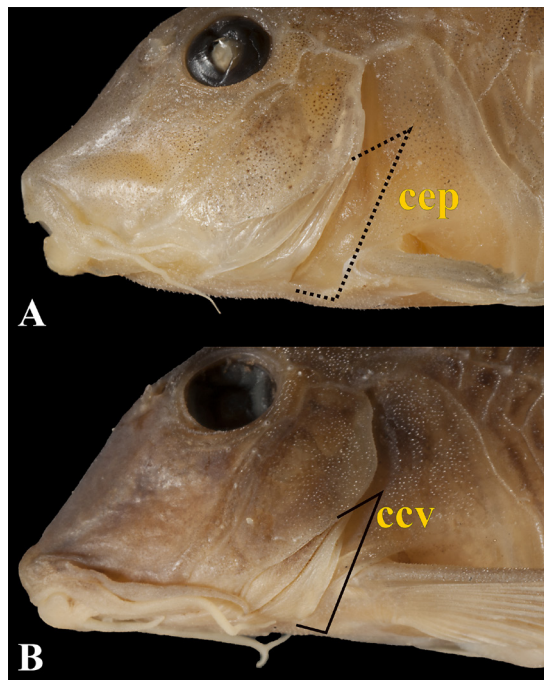


FIGURE 11 | Lateral view of the head of (A) *Corydoras aurofrenatus* (non-type specimen, MTD F 19127, 46.9 mm standard length) and (B) *Corydoras negro* (holotype, MTD F 28472, 41.8 mm standard length), showing the short opercular membrane of *C. aurofrenatus*, with anteroventral portion of cleithrum exposed (cep), and the long opercular membrane of *C. negro*, with anteroventral portion of cleithrum covered (ccv) by it.

Corydoras areio is a very peculiar species known only from the upper rio Paraguay basin, Brazil. Its most similar congeners are *C. cervinus* and *C. sararensis*, both from the rio Guaporé basin in Brazil, from which it can be promptly distinguished by its color pattern. *Corydoras areio* has rounded, irregular or elongated, dark brown or black blotches on the flanks, generally restricted to the region of the dorsolateral body plates, contrary to *C. cervinus* and females of *C. sararensis*, which have numerous, small, rounded, irregular or elongated, dark brown or black spots aligned in both longitudinal rows along the flanks and also in vertical rows on the lateral body plates. Additionally, *C. areio* presents a transversally elongated brown blotch at the end of the caudal peduncle, which is absent in *C. cervinus* and females of *C. sararensis*. Male specimens of *C. sararensis* are readily distinguished from *C. areio* by having dark brown or black rounded, irregular and elongated blotches on the snout, forming a marbled or striated pattern (*vs.* conspicuous concentrations of dark brown or black chromatophores on the snout, variably forming rounded or irregular blotches, not forming a marbled or striated pattern, and blotches generally diffuse).

Alexandrou *et al.* (2011) performed an extensive phylogenetic hypothesis based on molecular data, which revealed nine different lineages of species. The typical long-snouted species, which includes *C. areio* and *C. aurofrenatus*, compose the lineage 1 clade, which appears as the sister-group of all other Corydoradinae. Despite the clear evidence of the paraphyly of *Corydoras* found by Alexandrou *et al.* (2011), their study does not propose any changes in the classification of the Corydoradinae. However, since *C. geoffroy*, the type-species of *Corydoras*, is a member of the lineage 1 clade (see Alexandrou *et al.*, 2011: suppl. fig. 2), it is probable that both *C. areio* and *C. aurofrenatus* remain in *Corydoras* after the proposal of a new classification in order to reflect monophyletic groups within the Corydoradinae.

Comparative material examined. *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 adolfoi*: MZUSP 26641, holotype of *Corydoras adolfoi* Burgess, 1982, 32.5 mm SL. *Corydoras aeneus*: USNM 1116, lectotype of *Hoplosoma aeneum* Gill, 1858, 38.2 mm SL. *Corydoras amapaensis*: IRSNB 476, holotype of *Corydoras amapaensis* Nijssen, 1972, 55.5 mm SL; IRSNB 477, 2, 47.3–48.4 mm SL, paratypes; IRSNB 478, 1, 62.3 mm SL, paratype; IRSNB 479, 3, 25.2–46.4 mm SL, paratypes; IRSNB 480, 1, 34.4 mm SL, paratype; IRSNB 481, 1, 43.4 mm SL, paratype; IRSNB 482, 2, 40.6–42.2 mm SL, paratypes; IRSNB 483, 2, 41.9–54.5 mm SL, paratypes; IRSNB 484, 4, 42.2–45.9 mm SL, paratypes; USNM 205865, 1, 46.0 mm SL, paratype; ZMA 110600, 4, 30.1–55.9 mm SL, paratypes. *Corydoras ambiacus*: ANSP 8291, holotype of *Corydoras ambiacus* Cope, 1872, 40.4 mm SL; MZUSP 26053, 2, 41.8–47.2 mm SL. *Corydoras amphibelus*: ANSP 8290, holotype of *Corydoras amphibelus* Cope, 1872, 26.4 mm SL. *Corydoras approuaguensis*: IRSNB 696, 2, 45.7–52.2 mm SL, paratypes of *C. approuaguensis* Nijssen & Isbrücker, 1983; MZUSP 27895–6, 2, 43.0–46.1 mm SL, paratypes. *Corydoras araguaiaensis*: MZUSP 87155, 33, 24.9–46.7 mm SL, 2 cs, 27.6–31.8 mm SL. *Corydoras arcuatus*: BMNH 1939.3.3.1, holotype of *Corydoras arcuatus* Elwin, 1938, 43.3 mm SL. *Corydoras armatus*: BMNH 1867.6.13.51, lectotype of *Callichthys armatus* Günther, 1868, 42.1 mm SL. *Corydoras atropersonatus*: USNM 204359, holotype of *Corydoras atropersonatus* Weitzman, Nijssen, 1970, 37.1 mm SL. *Corydoras bifasciatus*: MZUSP

38976, 16, 23.6–30.0 mm SL, paratypes of *Corydoras bifasciatus* Nijssen, 1972. *Corydoras blochi*: MZUSP 8580, 3, 31.0–42.6 mm SL, paratypes of *Corydoras blochi* Nijssen, 1971. *Corydoras boehlkei*: ANSP 148097, holotype of *Corydoras boehlkei* Nijssen, Isbrücker, 1982, 23.6 mm SL. *Corydoras bondi*: ROM 66202, 134 7, 33.8–39.9 mm SL, 3 cs, 36.7–38.6 mm SL. *Corydoras brevirostris*: LBP 3080, 10, 23.8–27.7 mm SL, 3 cs, 25.8–27.9 mm SL. *Corydoras britskii*: ZUFMS-PIS 862, 12, 72.0–78.0 mm SL. *Corydoras brittoi*: MNRJ 43316, holotype of *Corydoras brittoi* Tencatt & Ohara, 2016, 38.1 mm SL. *Corydoras burgessi*: USNM 288461, 2, 43.7–44.8 mm SL, paratypes of *Corydoras burgessi* Axelrod, 1987. *Corydoras carlae*: NUP 711, 1, 47.9 mm SL; NUP 4425, 1 cs, 45.0 mm SL. *Corydoras cochui*: MZUSP 89055, 6, 18.7–23.6 mm SL; MZUSP 35838, 6 4, 16.1–18.5 mm SL. *Corydoras condiscipulus*: MZUSP 38957, 7, 34.1–40.3 mm SL, paratypes of *Corydoras condiscipulus* Nijssen & Isbrücker, 1980. *Corydoras coppenamensis*: USNM 202129, 5, 33.0–35.8 mm SL, paratypes of *Corydoras coppenamensis* Nijssen, 1970. *Corydoras coriatae*: USNM 343866, 2, 53.2–57.1 mm SL, paratypes of *Corydoras coriatae* Burgess, 1997. *Corydoras crimmeni*: MZUSP 52490, holotype of *Corydoras crimmeni* Grant, 1997, 36.1 mm SL. *Corydoras davidsandsi* Black, 1987: MZUSP 110066, 40 4, 36.0–41.9 mm SL, 2 cs specimens, 40.9–42.1 mm SL. *Corydoras desana*: ANSP 200804, 2, 29.5–43.4 mm SL, paratypes of *Corydoras desana* Lima & Sazima, 2017. *Corydoras difluviatilis*: MZUSP 75268, holotype of *Corydoras difluviatilis* Britto & Castro, 2002, 39.8 mm SL. *Corydoras diphyes*: ANSP 169756, 2, 40.7–43.1 mm SL. *Corydoras ehrhardti*: NUP 11255, 15, 36.5–46.8 mm SL. *Corydoras elegans*: USNM 216716, 10, 36.3–43.3 mm SL, paralectotypes of *Corydoras elegans* Steindachner, 1876. *Corydoras ephippifer*: MZUSP 31605, 2, 44.9–49.1 mm SL. *Corydoras eques*: MCZ 8204, 4 of 12, 37.6–44.4 mm SL, paratypes of *Corydoras eques* Steindachner, 1876. *Corydoras filamentosus*: USNM 225536, holotype of *Corydoras filamentosus* Nijssen & Isbrücker, 1983, 30.2 mm SL. *Corydoras flaveolus*: MZUSP 424, holotype of *Corydoras flaveolus* Ihering, 1911, 33.4 mm SL. *Corydoras fowleri*: LBP 12462, 9, 44.3–59.9 mm SL, 1 cs, 50.4 mm SL. *Corydoras garbei*: MNRJ 18089, 14, 19.2–25.3 mm SL, 2 cs, 25.9–27.4 mm SL. *Corydoras geoffroy*: USNM 204222, 2, 54.5–55.4 mm SL, paratypes of *Corydoras octocirrus* Nijssen, 1970. *Corydoras gossei*: MZUSP 38977, 6, 48.4–53.4 mm SL, paratypes of *Corydoras gossei* Nijssen, 1972. *Corydoras gracilis*: USNM 216074, 1, 19.2 mm SL, paratype of *Corydoras gracilis* Nijssen & Isbrücker, 1976. *Corydoras griseus*: MZUSP 108896, 13, 4, 31.5–36.2 mm SL, 2 cs, 30.6–34.5 mm SL. *Corydoras 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. *Corydoras guapore* Knaack, 1961: ZUFMS-PIS 4000, 5, 26.9–33.6 mm SL, 2 cs, 28.8–29.2 mm SL. *Corydoras guianensis*: USNM 204218, 2, 26.0–32.0 mm SL, paratypes of *Corydoras guianensis* Nijssen, 1970. *Corydoras hastatus*: NUP 6862, 116, 13.1–20.7 mm SL. *Corydoras heteromorphus*: USNM 204224, 2, 37.0–42.7 mm SL, paratypes of *Corydoras heteromorphus* Nijssen, 1970. *Corydoras inolicana*: MZUSP 45717, holotype of *Corydoras inolicana* Burgess, 1993, 47.6 mm SL. *Corydoras julii*: NUP 16225, 1, 46.8 mm SL. *Corydoras kanei*: MZUSP 52489, holotype of *Corydoras kanei* Grant, 1997, 36.6 mm SL. *Corydoras 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. *Corydoras leopardus*: USNM 93305, lectotype of *Corydoras leopardus* Myers, 1933, 38.7 mm SL. *Corydoras longipinnis*: AI 221, holotype of *Corydoras longipinnis* Knaack, 2007, 59.5 mm SL; NUP 14440, 2 cs, 29.9–33.4 mm SL. *Corydoras loretoensis*: ANSP 121620,

32, 17.3–32.7 mm SL, paratypes of *Corydoras loretoensis* Nijssen, Isbrücker, 1986. *Corydoras loxozonus*: ANSP 150170, holotype of *Corydoras loxozonus* Nijssen, Isbrücker, 1983, 34.6 mm SL. *Corydoras lychnades*: MNRJ 15765, 6, 15.8–17.7 mm SL, 2 cs, 18.1–18.4 mm SL; MNRJ 40186, holotype of *Corydoras lychnades* Tencatt, Vera-Alcaraz, Britto & Pavanelli, 2013, 29.7 mm SL. *Corydoras maculifer*: NUP 8970, 2, 42.0–46.0 mm SL; ZMA 110.681, 1, 22.9 mm SL, paratype. *Corydoras melanistius*: BMNH 1864.1.21.86, lectotype of *Corydoras melanistius* Regan, 1912, 35.0 mm SL. *Corydoras melanotaenia*: BMNH 1909.7.23.41, lectotype of *Corydoras melanotaenia* Regan, 1912, 38.3 mm SL. *Corydoras micracanthus*: BMNH 1897.1.27.8, lectotype of *Corydoras micracanthus* Regan, 1912, 33.7 mm SL. *Corydoras multimaculatus*: MCP 29025, 2, 20.1–25.4 mm SL. *Corydoras napoensis*: USNM 270358, 2, 26.7–28.3 mm SL, paratypes of *Corydoras napoensis* Nijssen & Isbrücker, 1986. *Corydoras narcissus*: ZMA 115.178, holotype of *Corydoras narcissus* Nijssen & Isbrücker, 1980, 65.9 mm SL. *Corydoras nattereri*: MZUSP 110255, 31 4, 32.0–32.8 mm SL, 2 cs, 32.3–34.4 mm SL. *Corydoras negro*: MTD F 28472, holotype, 41.8 mm SL; MTD F 28473, 1, 46.3 mm SL, paratype; ZMA 143.8337, 1, 38.5 mm SL, paratype; ZMA 143.934, 1, 43.1 mm SL, paratype; ZMB 33534, 1, 36.0 mm SL, paratype; ZMB 33535, 1, 41.9 mm SL, paratype; IRSNB 22143, 41 6, 43.0–48.7 mm SL; IRSNB 22149, 1, 53.3 mm SL; IRSNB 22150, 23 5, 41.0–47.0 mm SL; IRSNB 22153, 14 5, 30.9–56.3 mm SL; IRSNB 22154 15 5, 30.9–55.0 mm SL; IRSNB 22157, 10 9, 18.1–50.9 mm SL. *Corydoras oiapoquensis*: USNM 205868, 2, 25.9–35.0 mm SL, paratypes of *Corydoras oiapoquensis* Nijssen, 1972. *Corydoras ornatus*: USNM 216075, 1, 37.8 mm SL, paratype of *Corydoras ornatus* Nijssen & Isbrücker, 1976. *Corydoras orphnopterus*: USNM 204361, holotype of *Corydoras orphnopterus* Weitzman & Nijssen, 1970, 55.9 mm SL. *Corydoras osteocarus*: USNM 157367, 1, 25.1 mm SL, paratype of *Corydoras osteocarus* Böhlke, 1951. *Corydoras ourastigma*: IRSNB 498, holotype, 58.9 mm SL; MZUSP 38950, 1, 23.0 mm SL, paratype. *Corydoras oxyrhynchus*: RMNH 25329, holotype, 47.1 mm SL; RMNH 25330, 1, 50.4 mm SL, paratype; ZMA 104.640, 1, 46.5 mm SL, paratype. *Corydoras paleatus*: BMNH 1917.7.14.18, lectotype of *Callichthys paleatus* Jenyns, 1842, 30.0 mm SL; NRM 54230, 1, 53.5 mm SL. *Corydoras 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. *Corydoras pantanalensis*: NUP 10188, 1 cs, 46.4 mm SL; NUP 12593, 21, 38.7–51.2 mm SL. *Corydoras parallelus*: MZUSP 45716, holotype of *Corydoras parallelus* Burgess, 1993, 47.4 mm SL. *Corydoras pastazensis*: USNM 177216, holotype of *Corydoras pastazensis* Weitzman, 1963, 46.2 mm SL. *Corydoras pavanelliae*: MNRJ 43317, holotype of *Corydoras pavanelliae* Tencatt & Ohara, 2016, 45.1 mm SL. *Corydoras pinheiroi*: MZUSP 48099, holotype of *Corydoras pinheiroi* Dinkelmeyer, 1995, 54.3 mm SL. *Corydoras polystictus*: BMNH 1895.5.17.62, lectotype, 27.5 mm SL. *Corydoras potaroensis*: ROM 61526, 15 3, 35.0–44.8 mm SL, 2 cs, 32.6–35.1 mm SL. *Corydoras punctatus*: ZMB 3149, lectotype of *Cataphractus punctatus* Bloch, 1794, 41.7 mm SL. *Corydoras pygmaeus* Knaack, 1966: ANSP 200357, 1, 16.1 mm SL. *Corydoras robineae*: MZUSP 27175, holotype of *Corydoras robineae* Burgess, 1983, 33.7 mm SL. *Corydoras saramaccensis*: ZMA 106.018, holotype of *Corydoras saramaccensis* Nijssen, 1970, 50.4 mm SL; ZMA 105.563, 8, 35.5–44.2 mm SL, paratypes; ZMA 105.650, 1, 39.8 mm SL, paratype. *Corydoras sararensis*: MZUSP 48100, holotype of *Corydoras sararensis* Dinkelmeyer, 1995, 40.9 mm SL. *Corydoras septentrionalis*: USNM 130634, 1, 42.3 mm SL, paratype; ZMA 112.288, 2, 37.8–46.3 mm SL, paratypes.

Corydoras seussi: MZUSP 49323, 10, 44.3–54.0 mm SL, paratypes of *Corydoras seussi* Dinkelmeyer, 1996. *Corydoras similis*: LBP 10648, 7, 21.4–34.3 mm SL. *Corydoras simulatus*: USNM 197615, holotype, 49.1 mm SL; ZMA 110.384, 2, 44.5–45.8 mm SL, paratypes. *Corydoras solox*: ZMA 119.106, 4, 52.6–63.1 mm SL, paratypes. *Corydoras spilurus*: BMNH 1926.3.2.738, lectotype of *Corydoras spilurus* Norman, 1926, 43.3 mm SL. *Corydoras splendens*: NUP 12990, 1, 43.7 mm SL; NUP 10195, 1 cs, 54.6 mm SL. *Corydoras stenocephalus*: MNRJ 3625, 3, 31.2–62.3 mm SL. *Corydoras surinamensis*: USNM 204223, 2, 29.1–34.3 mm SL, paratypes of *Corydoras surinamensis* Nijssen, 1970. *Corydoras treitlii*: NMW 61103, lectotype, 42.6 mm SL; NMW 46797, 13, 35.8–45.9 mm SL, paralectotypes; NMW 46798, 9, 41.5–44.9 mm SL, paralectotypes; NMW 46799, 4, 41.5–45.5 mm SL, paralectotypes; NMW 46800, 6, 29.0–48.3 mm SL, paralectotypes; NMW 46798, 9, 41.5–44.9 mm SL, paralectotypes; NMW 46801, 14, 24.3–45.0 mm SL, paralectotypes; NMW 7035–48, 14, 31.3–46.7 mm SL, paralectotypes; NUP 16224, 3, 21.5–45.6 mm SL. *Corydoras trilineatus*: 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. *Corydoras tukano*: MZUSP 82100, holotype of *Corydoras tukano* Britto & Lima, 2003, 40.9 mm SL. *Corydoras undulatus*: BMNH 1912.7.10.5, holotype of *Corydoras undulatus* Regan, 1912, 41.8 mm SL. *Corydoras urucu*: ZUEC 14191, 9, 23.7–27.4 mm SL. *Corydoras virginiae*: USNM 326186, 3, 31.6–33.5 mm SL, paratypes of *Corydoras virginiae* Burgess, 1993. *Corydoras vittatus*: ZMA 109990, holotype of *Corydoras blochi vittatus* Nijssen, 1971, 40.3 mm SL; NMW 46803, 2, 35.4–39.7 mm SL, paratypes. *Corydoras weitzmani*: USNM 206018, 1, 38.5 mm SL, paratype of *Corydoras weitzmani* Nijssen, 1971. *Corydoras xinguensis*: USNM 205870, 1, 27.9 mm SL, paratype of *Corydoras xinguensis* Nijssen, 1972. *Corydoras zawadzki*: MNRJ 45565, holotype, 48.7 mm SL; NUP 17824, 1 cs, 39.9 mm SL, paratype. *Corydoras zygatus* Eigenmann & Allen, 1942: MZUSP 30858, 15 4, 41.7–47.3 mm SL.

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Luiz Fernando Caserta Tencatt: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

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Neotropical Ichthyology



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The authors declare no competing interests.

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