


Science and hobby joining forces for the discovery of three new *Corydoras* (Siluriformes: Callichthyidae) from the rio Tapajós basin, Brazil, with comments on *Corydoras* sp. CW111

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An expedition crowdfunded by aquarists to a region of the Brazilian state of Pará drained by the Tapajós and Xingu river basins resulted in the capture of five species of *Corydoras* from the rio Jamanxim basin, a tributary to the rio Tapajós, of which three could be confirmed as new and described herein. The new species can be promptly diagnosed from their congeners by the combination of features related to color pattern and osteology. Considering the gathered information on color patterns and morphology plus field observations, the new species are considered to compose two distinct Müllerian mimicry rings, with two of them forming a mimetic pair, while the third one forms a pair with a fourth non-identified species captured in the same expedition. An identification key to the species of *Corydoras* from the rio Tapajós basin is also provided.

Keywords: Amazon basin, Corydoradinae, Osteology, Rio Jamanxim, Taxonomy.

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Uma expedição com financiamento coletivo por aquaristas a uma região do estado brasileiro do Pará, drenada pelas bacias dos rios Tapajós e Xingu, resultou na captura de cinco espécies de *Corydoras* da bacia do rio Jamanxim, um tributário do rio Tapajós, das quais três puderam ser confirmadas como novas e descritas aqui. As novas espécies podem ser prontamente diagnosticadas de suas congêneres por uma combinação de características relacionadas a padrão de colorido e osteologia. Considerando a informação reunida sobre padrões de coloração, morfologia e observações de campo, as espécies novas são consideradas como componentes de dois arcos de mimetismo Mülleriano distintos, com duas delas formando um par mimético, enquanto que a terceira forma par com uma quarta espécie, ainda não identificada, capturada na mesma expedição. Uma chave de identificação para as espécies de *Corydoras* da bacia do rio Tapajós também é fornecida.

Palavras-chave: Bacia amazônica, Corydoradinae, Osteologia, rio Jamanxim, Taxonomia.

INTRODUCTION

Callichthyidae is a family of Neotropical armored catfishes that can be promptly distinguished from other Siluriformes by having two longitudinal series of dermal plates on flanks (Reis, 1998, 2003). Currently, there are more than 220 valid species within Callichthyidae, and about 180 included in *Corydoras* Lacépède, 1803 (Fricke *et al.*, 2022), making it the most species-rich genus of the family and also of Siluriformes (Bentley *et al.*, 2021; Tencatt *et al.*, 2021). Although a series of comprehensive studies aiming to elucidate the taxonomy (*e.g.*, Eigenmann, Eigenmann, 1890; Ellis, 1913; Gosline, 1940; Nijssen, 1970; Nijssen, Isbrücker, 1967, 1980a, 1983, 1986) and phylogenetic relationships (*e.g.*, Britto, 2003; Alexandrou *et al.*, 2011) of the species within *Corydoras* have been made, the knowledge on these fields remains far from an elucidative scenario (Britto *et al.*, 2007; Tencatt, Ohara, 2016a).

Corydoras is widely distributed within cis-Andean South America, having more than the half of its representatives occurring in the Amazon basin (Britto, 2003; Tencatt, Ohara, 2016b). Jézéquel *et al.* (2020) reported 982 fish species for the rio Tapajós basin, six of which belonging to *Corydoras*: *C. apiaka* Espíndola, Spencer, Rocha & Britto, 2014, *C. benattii* Espíndola, Tencatt, Pupo, Villa-Verde & Britto, 2018, *C. bifasciatus* Nijssen, 1972, *C. hephaestus* Ohara, Tencatt & Britto, 2016, *C. ornatus* Nijssen & Isbrücker, 1976, and *C. rikbaktsa* Lima & Britto, 2020 (Dagosta, de Pinna, 2019; Lima, Britto, 2020).

However, the number of putative undescribed species recognized by the fishkeeping hobby said to be from this basin is considerably higher, with 20 coded species apparently occurring in the rio Tapajós basin (C86, C133, C145, C146, CW4, CW66, CW101, CW127, CW135, CW146, CW155, CW156, CW162, CW167, CW168, CW170, CW171, CW172, CW173, and CW174; see Tencatt, Evers (2016) for further information on the coding system in Corydoradinae), showing that the diversity of this genus in the rio Tapajós drainage is certainly underestimated.

As evidenced above, the intake of new species introduced into the aquarium hobby tends to be much higher than the number of species described by science. Aquarists played an important role in the scientific advances on Corydoradinae systematics, providing grants for museum visits, photographs in life, preserved specimens and tissue samples (I. J. H. Isbrücker, 2017; I. A. M. Fuller, 2017; H. G. Evers, 2017, pers. comm.; LFCT pers. obs.). Considering the discrepancy between the high number of putative undescribed species in the aquarium trade and the ones gathered by scientific ichthyological surveys, eventually absent in Natural History collections, a crowdfunding initiative was created by Ian Fuller, founder of the “*Corydoras World*” website, the Research Assistance Program (RAP), in which hobbyists can make donations to scientific projects related to Corydoradinae (see <https://www.corydorasworld.com/knowledgebase/research-assistance-programme>).

Currently, one of the most notorious species in the hobby is the “Zebrina” or “Vulcan” *Corydoras*, which was coded as CW111 and was believed to be from the rio Curuá, a tributary to the rio Xingu basin at the Serra do Cachimbo region. Despite its uniqueness and consequently high demand on the aquarium trade, few specimens are available in scientific collections. Therefore, the first author submitted a project to RAP in order to visit the region of the Serra do Cachimbo attempting to collect specimens of *Corydoras* CW111 for examination and formal description, accordingly. With the financial support provided by the RAP and by the Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), it was possible to perform an expedition to the region of the Serra do Cachimbo, starting from the surroundings of Sinop Municipality, Mato Grosso State, to the surroundings of Novo Progresso Municipality, Pará State, through the road BR-163, where some tributaries from both rio Xingu and rio Tapajós basins were sampled. In this expedition, five *Corydoras* species were found in tributaries draining to the rio Tapajós basin (rio Jamanxim and some of its tributaries): *C. apiaka* and four putative undescribed species, *Corydoras* spp. CW146, CW171, CW172, and CW173, all in the rio Tapajós basin, on the main channel of the rio Jamanxim and some of its tributaries. No specimen undoubtedly fitting CW111 color pattern was found neither in the rio Curuá or in any other tributary to the Xingu or to the Tapajós river basins.

After the analysis of the gathered material, it was possible to confirm the presence of three undescribed species, *Corydoras* sp. CW146, *Corydoras* sp. CW173, and *Corydoras* sp. CW172. Considering the available data, it was not possible to undoubtedly differ *Corydoras* sp. CW171 from *C. guianensis* Nijssen, 1970, which occurs in coastal rivers of French Guiana and Suriname (Reis, 2003). However, minor differences in snout shape and infraorbital morphology, as well as the considerable distance between their regions of occurrence, suggest that these populations may not be conspecific, and, for this reason, the population of the rio Tapajós basin will continue to be referred herein by its code until further analysis. Therefore, the aim of this study is to present the formal description of these three undescribed species of *Corydoras* from the rio Jamanxim basin, Pará State, Brazil. Additionally, an identification key to the valid species of *Corydoras* within the rio Tapajós drainage is provided.

MATERIAL AND METHODS

Measurements were obtained using digital calipers to the nearest tenth of millimeter. Morphometric and meristic data were taken following Reis (1997) with the modifications of Tencatt *et al.* (2013). Morphometrics are reported as proportions of standard length (SL) or 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), except for the use 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). 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 frontal bone was obtained at the same point as the least interorbital width. 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. In the description, numbers in parentheses represent the total number of specimens with those counts. Numbers with an asterisk refer to the counts of the holotype.

Institutional abbreviations follow Sabaj (2020), except for CITL, Coleção Ictiológica de Três Lagoas, Universidade Federal de Mato Grosso do Sul, Três Lagoas. The comparative material examined is the same as listed in Tencatt *et al.* (2021).

RESULTS

Corydoras thanatos, new species

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(Figs. 1–3; Tab. 1)

Corydoras CW146. —Lucanus, 2021:29 [AMAZONAS magazine, guide about *Corydoras* from Serra do Cachimbo].

Holotype. MNRJ 53287, 33.2 mm SL, Brazil, Pará State, Novo Progresso Municipality, stream with unknown name tributary to the rio Jamanxim, rio Tapajós basin, 08°23'06"S 55°19'43"W, 7 Jul 2019, M. R. Britto, W. M. Ohara and L. F. C. Tencatt.

Paratypes. All from Brazil, Pará State, Novo Progresso Municipality, rio Jamanxim basin, rio Tapajós drainage, collected by M. R. Britto, W. M. Ohara and L. F. C.

Tencatt. CITL 382, 32, 12.6–18.5 mm SL, rio Jamanxim, 08°23'01"S 55°19'08"W, 7–8 Jul 2019. INPA 59776, 2, 12.9–14.2 mm SL; NUP 23540, 1, 33.2 mm SL, stream with unknown name, 08°23'33"S 55°22'36"W, 7–8 Jul 2019. CITL 383, 7 of 9, 15.0–37.0 mm SL, 2 cs of 9, 30.0–33.8 mm SL; INPA 59777, 3, 29.0–33.3 mm SL; INPA 59778, 1, 21.9 mm SL; MZUSP 126860, 7, 21.5–32.3 mm SL, collected with the holotype.



FIGURE 1 | *Corydoras thanatos*, holotype, MNRJ 53287, 33.2 mm SL, Novo Progresso Municipality, Pará State, Brazil, stream with unknown name tributary to the rio Jamanxim, rio Tapajós basin.

Diagnosis. *Corydoras thanatos* can be distinguished from its congeners, except for the species from the lineages 6, 7 and 9 *sensu* Alexandrou *et al.* (2011) plus *C. diffluviatilis* Britto & Castro, 2002, *C. hastatus* Eigenmann & Eigenmann, 1888, and *C. pygmaeus* Knaack, 1966, by having posterior margin of pectoral-fin spine with most serrations directed towards the tip of the spine (*vs.* most serrations directed towards origin of spine); from *C. diffluviatilis* and *C. pygmaeus* it differs by the presence of contact between nuchal plate and posterior process of the parieto-supraoccipital (*vs.* absence of contact between nuchal plate and the posterior process of the parieto-supraoccipital); from *C. hastatus* by the absence of a large-sized dark blotch on caudal-fin base (*vs.* caudal-fin base region with a dark brown or black large blotch, roughly diamond-shaped or rhomboid, or arrow-shaped, typically bordered anteriorly and posteriorly by conspicuously light areas); it can be distinguished from the species within lineage 7 by having dark brown or black markings on fins, except for the pelvic fin (*vs.* all fins devoid of dark markings); it differs from the species within lineages 6 and 9, except for *C. coppenamesis* Nijssen, 1970, *C. lymnades* Tencatt, Vera-Alcaraz, Britto & Pavanelli, 2013, *C. garbei* Ihering, 1911, and *C. gossei* Nijssen, 1972, by having anterior laminar expansion of infraorbital 1 strongly well developed, conspicuously expanded towards the anteroventral portion of snout, significantly covering its lateral surface (*vs.* anterior laminar expansion of infraorbital 1 ranging from poorly to well developed, not conspicuously expanded towards the anteroventral portion of snout, leaving most of its lateral surface exposed); the new species differs from *C. gossei* by presenting dark brown or black markings on head (*vs.* presence of pale yellow to white blotches on head); from *C. lymnades* by having a robust body (*vs.* slender); from *C. coppenamesis*, *C. lymnades*, and *C. garbei* by having flank midline covered by small-sized dark brown or black blotches; flank midline variably with distinct longitudinal series of blotches, generally more evident on posterior half of flank (*vs.* flank midline with longitudinal dark brown or black stripe in *C. coppenamesis*; with a distinct series of longitudinally aligned moderate- to large-sized dark brown or black blotches in *C. lymnades* and *C. garbei*).

Description. Morphometric data in Tab. 1. Head laterally compressed with convex dorsal profile, roughly triangular in dorsal view. Snout short, rounded. Head profile convex from tip of snout to anterior nares, ascending nearly straight or slightly convex from this point to dorsal-fin origin; interorbital region slightly concave in some specimens. Profile slightly convex along dorsal-fin base. Postdorsal-fin body profile slightly concave to adipose-fin spine, concave from this point to caudal-fin base. Ventral profile of body nearly straight or slightly convex from isthmus to pectoral girdle, and slightly convex from this point until pelvic girdle. Profile nearly straight or slightly convex from pelvic girdle to base of first anal-fin ray, ascending abruptly 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, posteroventrally by infraorbital 2, and anteroventrally 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 similar to bony orbit diameter. Maxillary

barbel moderate in size, not reaching anteroventral limit of gill opening. Outer mental barbel slightly longer than maxillary barbel. 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 moderate in size, with anterior tip poorly developed, smaller than 50% of bone length (see Britto, 2003:123, character 1, state 1; fig. 1B); posterior portion wide, partially exposed and bearing small odontodes. Nasal capsule delimited posteriorly and dorsally by frontal, anteriorly by mesethmoid, and ventrally and posteriorly by lateral ethmoid. Nasal relatively wide, laterally curved, inner margin with relatively well-developed laminar expansion contacting frontal and mesethmoid; outer margin with poorly-developed laminar expansion typically contacting lateral ethmoid. Lateral ethmoid moderately expanded anteriorly, with anterodorsal expansion contacting nasal, and anterior margin contacting posterior portion of mesethmoid. Frontal elongated, narrow, width less than half of entire length; anterior projection short, size clearly smaller than nasal length. Frontal fontanel large, slender, and somewhat ellipsoid; posterior tip extension slightly surpassing anterior margin of parieto-supraoccipital. Sphenotic somewhat trapezoid, contacting parieto-supraoccipital dorsally, pterotic-extrascapular posteriorly, second infraorbital posteroventrally and frontal anteriorly (Fig. 2A). Pterotic-extrascapular roughly pipe-shaped, with posteriormost portion contacting first lateral-line ossicle, posteroventral margin contacting cleithrum, and anteroventral margin contacting opercle and variably 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. Parieto-supraoccipital wide, posterior process long and contacting nuchal plate; region of contact between posterior process and nuchal plate covered by thick layer of skin.

Two laminar infraorbitals with minute odontodes. Infraorbital 1 conspicuously large, ventral laminar expansion generally strongly well developed; some specimens with well-developed expansion; anterior portion with strongly well-developed laminar expansion, surpassing anterior margin of nasal capsule; inner laminar expansion moderately developed (Fig. 2A). Infraorbital 2 small, relatively slender, with posterior laminar expansion ranging from moderately to well developed; posteroventral margin contacting posterodorsal ridge of hyomandibula, posterodorsal edge contacting sphenotic and generally pterotic-extrascapular; posterodorsal edge not in contact with pterotic-extrascapular in some specimens; inner laminar expansion ranging from poorly- to moderately developed (Fig. 2A). Posterodorsal ridge of hyomandibula close to its articulation with opercle relatively slender, exposed, and bearing small odontodes. Dorsal ridge of hyomandibula between pterotic-extrascapular and opercle exposed and bearing odontodes. Interopercle partially covered by thick layer of skin, with posterior portion exposed and bearing odontodes; subtriangular, anterior projection ranging from moderately to well developed. Preopercle elongated, relatively slender; minute odontodes on external surface. Opercle dorsoventrally elongated; relatively compact in shape, with width equal to or slightly larger than half of its entire length; free margin slightly convex, without serrations and covered by small odontodes.

Four branchiostegal rays decreasing in size posteriorly. Hypobranchial 1 deep; hypobranchial 2 somewhat triangular, tip ossified and directed towards anterior portion, posterior margin cartilaginous; ossified portion well developed, its size

about twice cartilaginous portion. Five ceratobranchials with expansions increasing posteriorly; ceratobranchial 1 with small process on anterior margin of mesial portion; ceratobranchial 3 with continuous laminar expansion on postero-lateral margin; ceratobranchial 5 toothed on posterodorsal surface, with 42 to 45(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 small roughly triangular laminar expansion on posterior margin; rounded expansion in some specimens. Upper tooth plate roughly oval, 48 to 58(2) teeth aligned in two rows on posteroventral surface; rows closely aligned.

Lateral-line canal reaching cephalic laterosensory system through pterotic-extrascapular, branching twice before reaching sphenotic: pterotic branch, with single pore, preoperculomandibular branch conspicuously reduced, with single pore opening at postotic main canal; postotic main canal widens just posterior to pterotic branch. Sensory canal continuing through pterotic-extrascapula, 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, both with single pore. Supraorbital canal branched, running through nasal bone. Epiphyseal branch conspicuously reduced; pore opening close to supraorbital main canal, directed towards frontal fontanel. Nasal canal with three openings, first on posterior edge, second 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 or three 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 second or third dorsolateral body plate. Dorsal-fin rays II,8*(20), posterior margin of dorsal-fin spine with 20 to 24 ranging from strongly reduced to poorly-developed serrations; most serrations directed towards tip of spine; some serrations variably perpendicularly directed; serrations absent close to origin of spine; small odontodes on anterior and lateral surfaces of spine (Fig. 2B). Nuchal plate moderately developed, almost entirely exposed, with minute odontodes. Spinelet short; spine typically well developed, with adpressed distal tip surpassing posterior origin of dorsal-fin base. Pectoral fin roughly triangular, its origin just posterior to gill opening. Pectoral-fin rays I,6,i(1), I,7*(3), I,7,i(12), I,8(3) or I,9(1), posterior margin of pectoral spine with 25 to 28 poorly- to moderately-developed serrations along almost its entire length, absent close to origin of spine; most serrations directed towards tip of spine; some serrations perpendicularly directed; small odontodes on anterior, dorsal and ventral surfaces of spine (Fig. 2C). Anteroventral portion of cleithrum exposed; posterolateral portion of scapulocoracoid moderately developed, exposed, with anterior portion slightly expanded anteriorly, not in contact with anteroventral portion of cleithrum; exposed areas bearing small odontodes. Opening of axillary gland *sensu* Kiehl *et al.* (2006) located just posterior to pectoral-fin spine base. Pelvic fin oblong, located just below first or second ventrolateral body plate, and at vertical through dorsal-fin spine or first branched dorsal-fin ray. Pelvic-fin rays i,5*(20). Adipose fin roughly triangular, separated from base of last dorsal-fin ray by six or seven dorsolateral body

plates. Anal fin subtriangular, located just posterior to 12th or 13th ventrolateral body plates, and at vertical through adipose-fin spine base or region of preadipose platelets. Anal-fin rays i,4,ii(1), ii,5(16), i,6*(2) or ii,5,i(1). Caudal fin bilobed, with dorsal and ventral lobes similar in size or dorsal lobe slightly larger than ventral lobe. Caudal-fin rays i,11,i(1) or i,12,i*(19), generally four or five dorsal and ventral procurent rays.

Two laterosensory canals on trunk; first ossicle tubular, second ossicle laminar, both bearing small odontodes. Body plates with minute odontodes scattered over exposed area, with conspicuous line of odontodes confined to posterior margins. Dorsolateral body plates 22(1) or 23*(19). Ventrolateral body plates 20*(17) or 21(3). Dorsolateral body plates along dorsal-fin base 6*(20). Dorsolateral body plates between adipose- and caudal-fin 6(1), 7*(16) or 8(3). Preadipose platelets 2(9) or 3*(11). Ventral surface of trunk between posteroventral margin of cleithrum and pelvic-fin origin laterally delimited only by first ventrolateral body plate; ventral portion of first ventrolateral body plate ranging from slightly to moderately expanded anteriorly. Small platelets covering base of caudal-fin rays. Small platelets disposed dorsally and ventrally between junctions of

TABLE 1 | Morphometric data of the holotype and 19 paratypes of *Corydoras thanatos*. SD = Standard deviation.

	Holotype	Low-High	Mean±SD
Standard length (mm)	33.2	16.0–37.0	27.1
Percent of standard length			
Depth of body	42.5	37.8–42.7	39.9±1.4
Predorsal distance	54.5	49.8–54.5	52.5±1.1
Prepelvic distance	50.3	47.2–51.9	49.2±1.0
Preanal distance	85.2	80.9–87.0	84.0±1.6
Preadipose distance	89.2	84.7–89.7	87.4±1.4
Length of dorsal spine	32.2	25.1–34.2	29.8±2.7
Length of pectoral spine	31.0	26.3–32.3	29.7±1.7
Length of adipose-fin spine	8.1	6.9–10.1	9.1±0.9
Depth of caudal peduncle	17.5	15.4–18.8	16.6±0.8
Length of dorsal-fin base	18.7	16.9–21.3	18.7±1.2
Dorsal to adipose distance	20.2	16.5–22.0	19.9±1.5
Maximum cleithral width	30.1	27.5–31.1	29.3±1.0
Head length	48.2	43.4–48.2	45.9±1.1
Length of maxillary barbel	12.3	9.3–14.7	12.4±1.3
Percent of head length			
Head depth	81.9	77.5–84.1	80.8±2.0
Least interorbital distance	31.9	29.1–32.9	31.1±0.8
Horizontal orbit diameter	20.6	19.7–25.9	22.0±2.1
Snout length	36.9	34.2–42.7	38.0±2.0
Least internarial distance	17.5	15.7–19.2	17.6±1.0

lateral plates on posterior portion of caudal peduncle. Anterior margin of orbit, above region of junction between frontal and lateral ethmoid, region around nasal capsule, on region above lateral ethmoid, and dorsal, lateral and variably ventrolateral portions of snout with small- to relatively large-sized platelets bearing odontodes; platelets on snout conspicuously more concentrated above mesethmoid. Ventral surface of trunk with numerous small- to relatively large-sized irregular platelets bearing odontodes; region around pectoral-fin origin typically with larger platelets.

Vertebral count 21(2); ribs 5(2); first pair conspicuously large, its middle portion closely connected to first ventrolateral body plate; its tip connected to anterior external process of basipterygium. Parapophysis of complex vertebra well developed.

Color in alcohol. Overall color of body in Fig. 1. Ground color of body pale- to brownish yellow or beige. Top of head dark brown; dark area typically extending mesially towards posterior tip of parieto-supraoccipital as thin longitudinal line. Dorsal and lateral surface of head with conspicuous concentrations of dark brown or black chromatophores, forming rounded, irregular or striated, diffuse blotches in some specimens. Lateral surface of cleithrum with conspicuous concentrations of dark brown or black chromatophores, forming rounded, irregular or vermiculated, blotches in some specimens; blotches, when present, diffuse or slightly more marked than blotches on head. Dorsolateral body plates with conspicuous concentration of dark brown or black chromatophores, typically forming rounded, irregular or vertically elongated conspicuous dark blotches; diffuse in some specimens. Ventrolateral body plates, except for region around pelvic-fin origin, with conspicuous concentration of dark brown

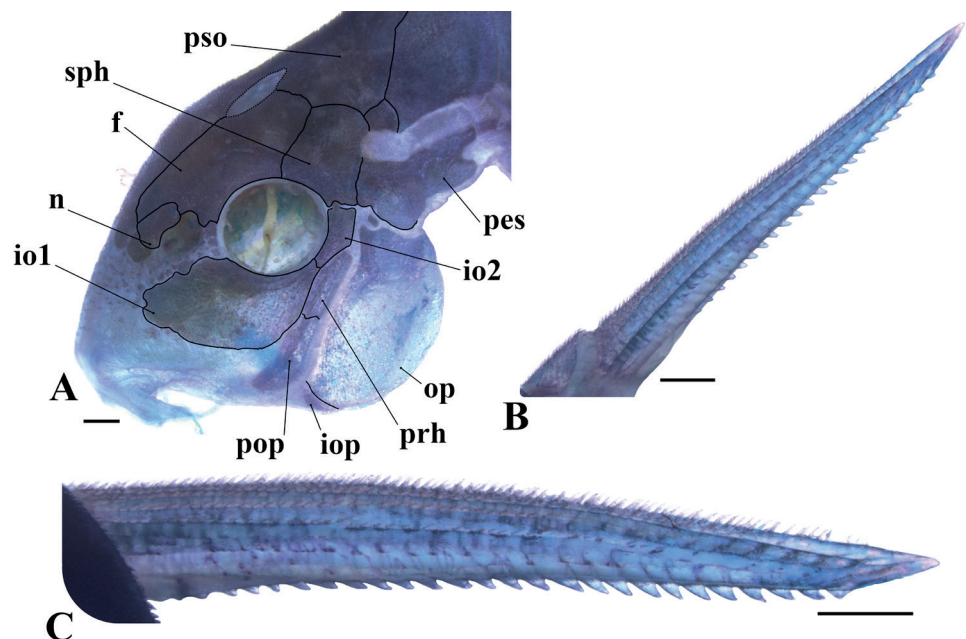


FIGURE 2 | Lateral view of the head (A), lateral view of the dorsal-fin spine (B) and dorsal view of the left pectoral-fin spine (C) in cs paratype of *Corydoras thanatos*, CITL 383, 33.8 mm SL. Abbreviations: f: frontal, io1-2: infraorbital 1 and 2, iop: interopercle, n: nasal, op: opercle, pes: pterotic-extrascapular, pop: preopercle, prh: posterodorsal ridge of hyomandibula, pso: parieto-supraoccipital, sph: sphenotic. Scale bars = 1 mm.

or black chromatophores, typically forming rounded, irregular or vertically elongated conspicuous dark blotches; diffuse in some specimens; region around pelvic-fin origin with dark brown or black chromatophores but typically not forming any conspicuous pattern; ventral portion of ventrolateral body plates between pelvic-fin origin to area just anterior to anal-fin origin variably with sparse dark brown or black chromatophores. Flank midline variably with distinct longitudinal series of dark brown or black blotches, generally more evident on posterior half of flank. Blotches on flanks ranging from small to moderate in size. Posterior margin of body plates typically with dark brown or black chromatophores, variably forming thin dark lines along border of plates. Dorsal-fin with conspicuous concentrations of dark brown or black chromatophores, forming small dark blotches; blotches roughly longitudinally or obliquely aligned in some specimens, variably fused with each other and forming stripes; some specimens with less evident blotches on posterior portion of fin. Pectoral fin with conspicuous concentrations of dark brown or black chromatophores, forming small, irregular dark spots; spots roughly transversally aligned in some specimens; variably diffuse. Pelvic fin with sparse dark brown or black chromatophores, not forming spots. Adipose fin with dark brown or black chromatophores, generally more numerous and concentrated on spine and on region of membrane close to spine, typically forming single dark patch. Anal fin with conspicuous concentrations of dark brown or black chromatophores, generally more evident along its base, middle portion, and/or posterior portion, forming dark blotches roughly aligned transversally; blotches diffuse and/or not aligned in some specimens. Caudal fin with conspicuous concentrations of dark brown or black chromatophores, mainly on rays, forming dark blotches roughly aligned transversally in three to six slender bars; some specimens with less evident blotches on posterior portion of fin.

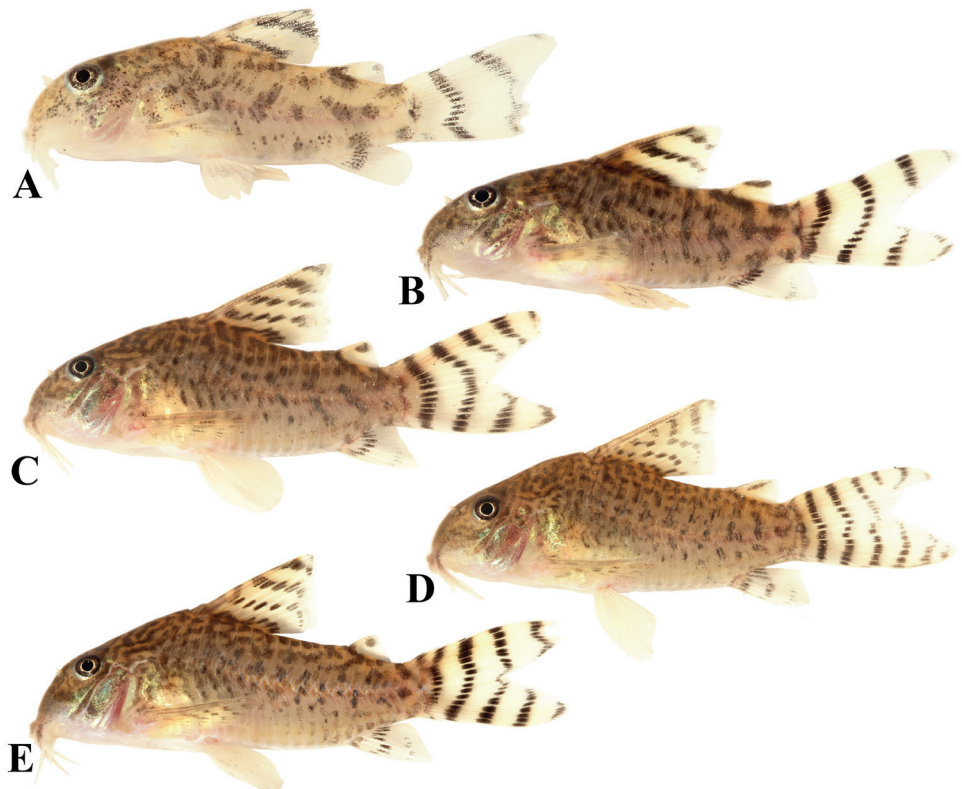


FIGURE 3 | Paratypes of *Corydoras thanatos* photographed alive, showing general color pattern and morphology in lateral view in (A) INPA 59776, 14.2 mm SL, (B) INPA 59778, 21.9 mm SL, (C) INPA 59777, 29.0 mm SL, (D) INPA 59777, 30.0 mm SL, and (E) INPA 59777, 33.3 mm SL, all from tributaries to the rio Jamanxim, rio Tapajós basin.

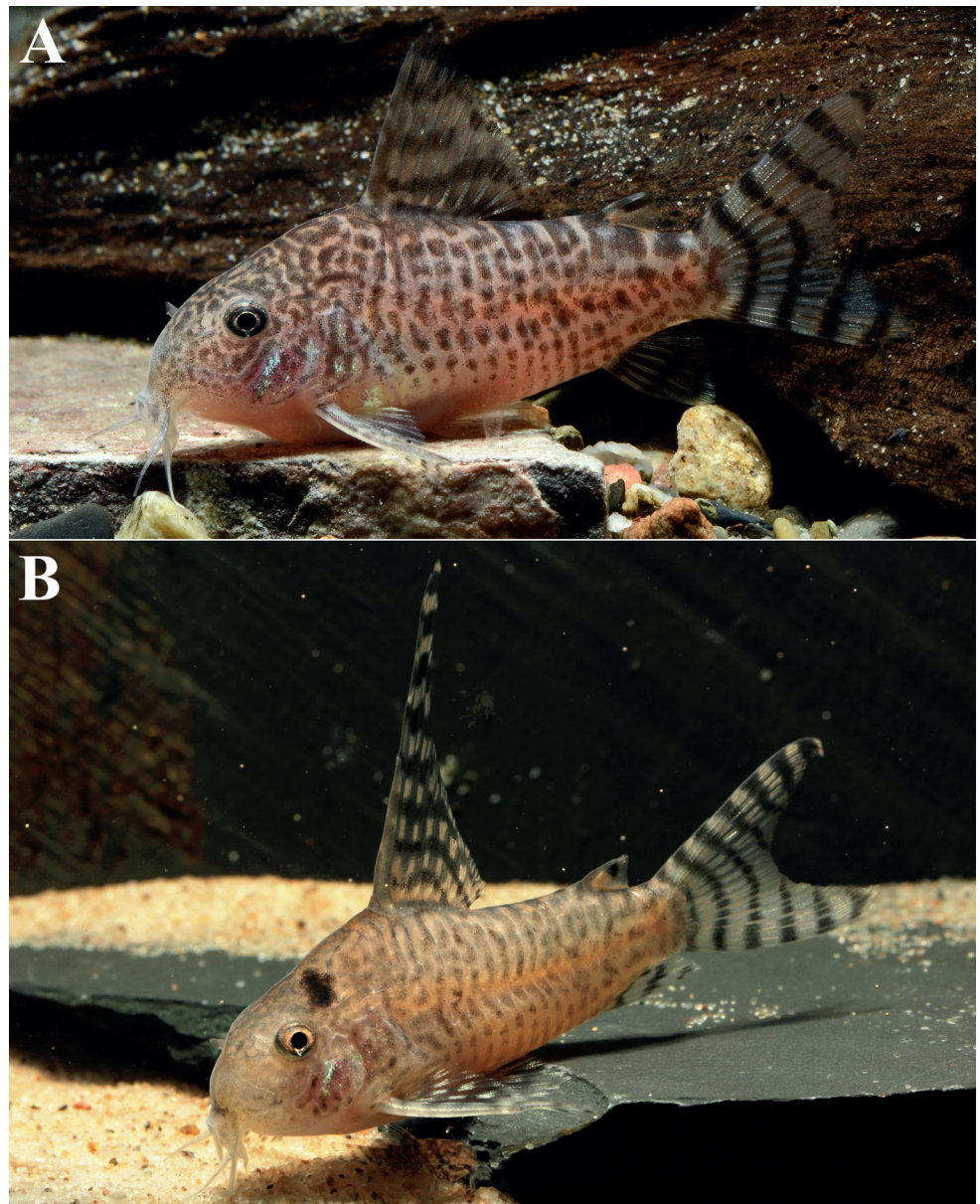


FIGURE 4 | Uncatalogued aquarium specimens of *Corydoras thanatos* photographed alive, showing general color pattern and morphology of (A) a female specimen, and (B) a dimorphic male specimen. Photos by Hans Evers.

Color in life. Similar to color pattern of preserved specimens, but with light ground color of body, and with greenish yellow iridescent coloration (Figs. 3–4).

Sexual dimorphism. As well-documented in Corydoradinae (see Nijssen, Isbrücker, 1980b; Britto, 2003; Spadella *et al.*, 2017), male specimens of *C. thanatos* present a genital papilla, which is somewhat tubular in shape. Aquarium male specimens eventually display a conspicuous elongation of the first and second dorsal-fin branched rays (Fig. 4B).

Geographical distribution. *Corydoras thanatos* is currently known from the main channel of the rio Jamanxim and two of its tributaries, both with unknown names, rio Tapajós basin, Novo Progresso Municipality, Pará State, Brazil (Fig. 5).

Ecological notes. The new species was observed to inhabit from main channel of the rio Jamanxim to its small tributary streams (Fig. 6). In the rio Jamanxim, it was mostly associated with the margins of the river, where juvenile specimens were observed shoaling together with juvenile and adult specimens of *C. hypnos* in the sandy shores,

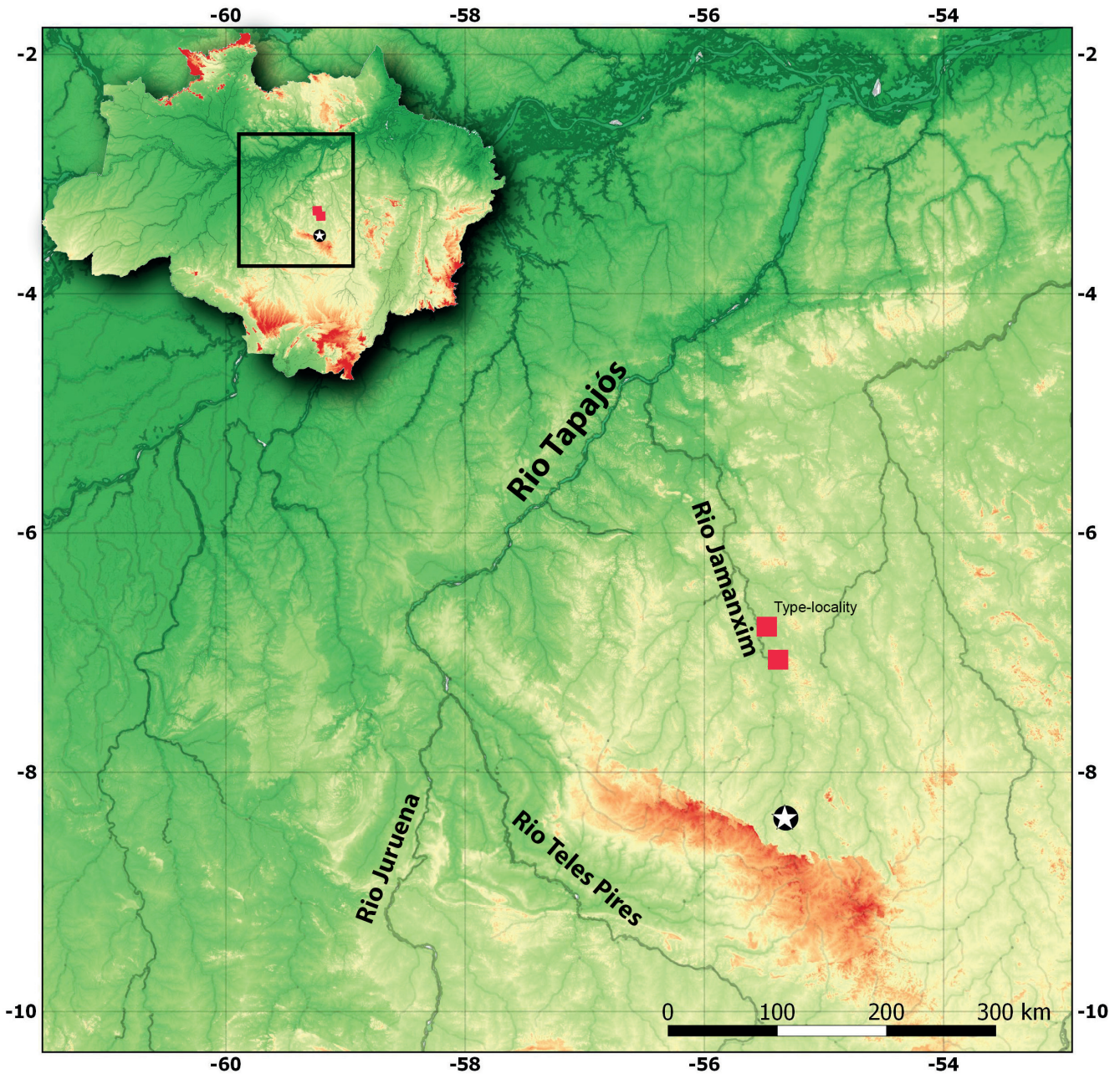


FIGURE 5 | Map of the rio Tapajós and adjoining areas, showing the geographical distribution of *Corydoras thanatos* (black circle), *C. hypnos* (white star), and *C. psamathos* (red squares). Each symbol may represent more than one locality.

both species in relatively high abundance. In the small streams, adult and juvenile specimens were found shoaling together with juvenile and adult specimens of *C. hypnos*, generally in sites with submerged branches, leaf litter, and sandy and/or fine gravel substrate. In these streams, *C. thanatos* was found in higher numbers than *C. hypnos*. Although not shoaling together, the new species was found in syntopy with *Corydoras* sp. CW171 in these streams. In all sampled sites, the new species was mostly observed and captured at night.



FIGURE 6 | Natural habitat of *Corydoras thanatos* and *C. hypnos*, showing (A) the rio Jamanxim, type locality of *C. hypnos*, and one of its tributaries (B), type locality of *C. thanatos*, rio Tapajós basin in Pará State, Brazil.

Etymology. The specific epithet “*thanatos*” refers to Thanatos (from the Greek θάνατος, *thánatos*, which means “death”), the Greek god or personification of death, and the twin brother of Hypnos, the god/personification of sleep. The name makes an allusion to the fact that even though both *C. thanatos* and *C. hypnos* may present some similarities (in color pattern), they are completely different in other aspects (general morphological pattern). A noun in apposition.

Conservation status. *Corydoras thanatos* is currently known from its type locality and two additional records in its surroundings. However, these records are in the border of a conservation unit, the Floresta Nacional do Jamanxim, and no threat to the species as a whole is currently suspected. According to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Subcommittee, 2019), *Corydoras thanatos* can be classified as Least Concern (LC).

Corydoras hypnos, new species

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(Figs. 7-9; Tab. 2)

Holotype. MNRJ 53288, 31.7 mm SL, Brazil, Pará State, Novo Progresso Municipality, rio Jamanxim, a tributary to the rio Tapajós, 08° 23'00”S 55° 19'08”W, 8 Jul 2019, M. R. Britto, W. M. Ohara and L. F. C. Tencatt.

Paratypes. All from Brazil, Pará State, Novo Progresso Municipality, rio Jamanxim basin, rio Tapajós drainage, collected by M. R. Britto, W. M. Ohara and L. F. C. Tencatt. CITL 384, 2, 20.9–26.3 mm SL, stream with unknown name, 08° 23'06”S 55° 19'43”W, 7 Jul 2019. INPA 59775, 3, 22.2–27.2 mm SL, same locality as holotype, 7 Jul 2019. INPA 59774, 2, 22.6–28.2 mm SL, same locality as holotype, 11 Jul 2019. CITL 385, 11 of 13, 17.6–25.7 mm SL, 2 cs of 13, 26.6–32.0 mm SL; MZUSP 126861, 12, 13.2–24.7 mm SL; NUP 23541, 11, 18.9–26.1 mm SL, collected with the holotype.

Diagnosis. *Corydoras hypnos* can be distinguished from its congeners, except for the species from the lineages 6, 7 and 9 *sensu* Alexandrou *et al.* (2011) plus *C. diffluiatilis*, *C. hastatus*, and *C. pygmaeus*, by having posterior margin of pectoral-fin spine with most serrations directed towards the tip of the spine (*vs.* most serrations directed towards origin of spine); from *C. diffluiatilis* and *C. pygmaeus* it differs by the presence of contact between nuchal plate and posterior process of the parieto-supraoccipital (*vs.* absence of contact between nuchal plate and the posterior process of the parieto-supraoccipital); from *C. hastatus* by the absence of a large-sized dark blotch on caudal-fin base (*vs.* caudal-fin base region with a dark brown or black large blotch, roughly diamond-shaped or rhomboid, or arrow-shaped, typically bordered anteriorly and posteriorly by conspicuously light areas); it can be distinguished from the species within lineage 7 by having dark brown or black markings on fins, except for the pectoral and pelvic fins (*vs.* fins devoid of conspicuous dark markings); it differs from the species within lineages 6



FIGURE 7 | *Corydoras hypnos*, holotype, MNRJ 53288, 31.7 mm SL, Brazil, Pará State, Novo Progresso Municipality, rio Jamanxim, a tributary to the rio Tapajós basin.

and 9, except for *C. benattii*, *C. eversi* Tencatt & Britto, 2016, *C. froehlichii* Tencatt, Britto & Pavanelli, 2016, *C. granti* Tencatt, Lima & Britto, 2019, *C. gryphus* Tencatt, Britto & Pavanelli, 2014, *C. psamathos*, and *C. thanatos*, by having dorsal surface of snout with numerous platelets bearing odontodes (*vs.* dorsal surface of snout lacking platelets); from *C. benattii* and *C. froehlichii* by having moderately- to relatively well-developed and smoothly rounded snout (*vs.* conspicuously short and rounded snout); from *C. eversi* and *C. granti*, it can be distinguished by having ventral surface of trunk only with small-sized, non-coalescent platelets (*vs.* ventral surface of trunk entirely or partially covered by moderate- to relatively large-sized, coalescent platelets); from *C. gryphus* by having midline of flank with longitudinal series of dark brown or black blotches, when present, diffuse (*vs.* midline of flank with a longitudinal series of four to six conspicuous dark

brown or black blotches), and mesethmoid partially exposed (*vs.* entirely covered by thick layer of skin); from *C. psamathos* by the presence of conspicuous dark brown or black markings at least in dorsal and caudal fins (*vs.* absence of conspicuous dark brown or black markings on body; dark markings, when present, diffuse); from *C. thanatos* by having anterior laminar expansion moderately developed, poorly expanded towards the anteroventral portion of snout, leaving most of its lateral surface exposed (*vs.* anterior laminar expansion of infraorbital 1 strongly well developed, conspicuously expanded towards the anteroventral portion of snout, significantly covering its lateral surface).

Description. Morphometric data in Tab. 2. Head laterally compressed with convex dorsal profile, roughly triangular in dorsal view. Snout ranging from moderately to relatively well developed and smoothly rounded. Head profile convex from tip of snout to anterior nares; ascending nearly straight or slightly convex from this point to dorsal-fin origin; region of frontal or parieto-supraoccipital slightly concave in some specimens. Profile slightly convex along dorsal-fin base. Postdorsal-fin body profile slightly concave to adipose-fin spine, slightly concave from this point to caudal-fin base. Ventral profile of body nearly straight or slightly convex from isthmus to pectoral girdle, and slightly convex from this point until pelvic girdle. Profile nearly straight or slightly convex from pelvic girdle to base of first anal-fin ray, ascending slightly 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, posteroventrally by infraorbital 2, and anteroventrally 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 similar to bony orbit diameter. Maxillary barbel ranging from short to moderate in size, not reaching to anteroventral limit of gill opening. Outer mental barbel slightly longer than maxillary barbel. 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 moderate in size, with anterior tip poorly developed, slightly smaller than 50% of bone length (see Britto, 2003:123, character 1, state 1; fig. 1B); posterior portion wide, partially exposed and bearing small odontodes. Nasal capsule delimited posteriorly and dorsally by frontal, anteriorly by mesethmoid, and ventrally and posteriorly by lateral ethmoid. Nasal slender, laterally curved, inner margin with poorly- to moderately-developed laminar expansion generally contacting frontal and mesethmoid; variably close but not in direct contact with mesethmoid; outer margin with poorly-developed to strongly reduced laminar expansion. Lateral ethmoid slightly expanded anteriorly, with anterodorsal expansion relatively distant from nasal, and anterior margin contacting posterior portion of mesethmoid. Frontal elongated, narrow, width less than half of entire length; anterior projection short, size smaller than nasal length. Frontal fontanel large, slender, and somewhat ellipsoid; posterior tip extension slightly surpassing anterior margin of parieto-supraoccipital. Sphenotic somewhat trapezoid, contacting parieto-supraoccipital dorsally, pterotic-extrascapular posteriorly, second infraorbital posteroventrally and frontal anteriorly (Fig. 8A).

Pterotic-extrascapular roughly pipe-shaped, with posteriormost portion contacting first lateral-line ossicle, posteroventral margin contacting cleithrum, and anteroventral margin contacting opercle; posterior expansion almost entirely covering lateral opening of swimbladder capsule, leaving slender area on its dorsal margin covered only by thick layer of skin. Parieto-supraoccipital wide, posterior process long and contacting nuchal plate; 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 poorly to moderately developed; anterior portion with laminar expansion moderately developed, reaching to middle portion of nasal capsule; inner laminar expansion poorly developed (Fig. 8A). Infraorbital 2 small, slender, with posterior laminar expansion ranging from strongly reduced to poorly developed; posteroventral margin contacting posterodorsal ridge of hyomandibula, posterodorsal edge contacting only sphenotic; inner laminar expansion ranging from strongly reduced to poorly developed (Fig. 8A). Posterodorsal ridge of hyomandibula close to its articulation with opercle relatively slender, exposed, and bearing small odontodes. Dorsal ridge of hyomandibula between pterotic-extrascapular and opercle typically covered by thin skin layer. Interopercle entirely covered by thick layer of skin or almost entirely covered by thick layer of skin, with posterior portion exposed, and typically bearing small odontodes; subtriangular, anterior projection moderately developed. Preopercle elongated, relatively slender; minute odontodes on external surface. Opercle dorsoventrally elongated, with width slightly smaller or similar to half of its entire length; free margin slightly convex, without serrations and covered by small odontodes.

Four branchiostegal rays decreasing in size posteriorly. Hypobranchial 1 deep; hypobranchial 2 somewhat triangular, tip ossified and directed towards anterior portion, posterior margin cartilaginous; ossified portion well developed, its size about twice or triple of cartilaginous portion. Five ceratobranchials with expansions increasing posteriorly; ceratobranchial 1 with small process on anterior margin of mesial portion; ceratobranchial 3 notched on postero-lateral margin; variably with continuous laminar expansion on postero-lateral margin; ceratobranchial 5 toothed on posterodorsal surface, with 34 to 37(3) 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 smoothly rounded to nearly straight laminar expansion on posterior margin. Upper tooth plate roughly oval, 40 to 53(3) teeth aligned in two rows on posteroventral surface; rows closely aligned.

Lateral-line canal reaching cephalic laterosensory system through pterotic-extrascapular, branching twice before reaching sphenotic: pterotic branch, with single pore, preoperculomandibular branch conspicuously reduced, with single pore opening at postotic main canal; postotic main canal widens just posterior to pterotic branch. Sensory canal continuing through pterotic-extrascapular, 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, both with single pore. Supraorbital canal branched, running through nasal bone. Epiphyseal branch conspicuously reduced; pore opening close to supraorbital main canal, directed towards 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 infraorbital 2, extending to infraorbital 1 and opening into two or three pores. Preoperculo-mandibular branch giving rise to preoperculo-mandibular canal, which runs through entire preopercle with three openings, leading to pores 3, 4, and 5, respectively; pore 3 variably opening at posterodorsal ridge of hyomandibula.

Dorsal fin subtriangular, located just posterior to second or third dorsolateral body plate. Dorsal-fin rays II,8*(19), II,9(1), posterior margin of dorsal-fin spine with 16 to 17 strongly reduced to poorly-developed serrations; most serrations directed towards tip of spine; some serrations variably perpendicularly directed; serrations absent close to origin of spine; small odontodes on anterior and lateral surfaces of spine (Fig. 8B). Nuchal plate moderately developed, almost entirely exposed, with minute odontodes. Spinelet short; spine moderately developed, with adpressed distal tip slightly surpassing posterior origin of dorsal-fin base. Pectoral fin roughly triangular, its origin just posterior to gill opening. Pectoral-fin rays I,7(3), I,7,i(1) or I,8*(16), posterior margin of pectoral spine with 20 to 32 strongly reduced to moderately-developed serrations along its entire length; most serrations directed towards tip of spine; some serrations perpendicularly directed or directed towards origin of spine; serrations variably bifid; small odontodes on anterior, dorsal and ventral surfaces of spine (Fig. 8C). Anteroventral portion of cleithrum exposed; posterolateral portion of scapulocoracoid moderately developed, exposed, with anterior portion slightly expanded anteriorly, not in contact with anteroventral portion of cleithrum; exposed areas bearing small odontodes. Opening of axillary gland *sensu* Kiehl *et al.* (2006) located just posterior to pectoral-fin spine base. Pelvic fin oblong, located just below first or second ventrolateral body plate, and at vertical through first branched dorsal-fin ray. Pelvic-fin rays i,5*(20). Adipose fin roughly triangular, separated from base of last dorsal-fin ray by generally six dorsolateral body plates. Anal fin subtriangular, typically located just posterior to 12th ventrolateral body plates, and at vertical through adipose-fin spine base or region of preadipose platelets. Anal-fin rays ii,5(19) or ii,6(1). Caudal fin bilobed, with dorsal and ventral lobes similar in size or dorsal lobe slightly larger than ventral lobe. Caudal-fin rays i,12,i*(20), generally four or five dorsal and ventral procurrent rays.

Typically, three laterosensory canals on trunk; first ossicle tubular, second ossicle laminar, both bearing small odontodes; third, encased in third dorsolateral body plates. Body plates with minute odontodes scattered over exposed area, with conspicuous line of odontodes confined to posterior margins. Dorsolateral body plates 23(17) or 24*(3). Ventrolateral body plates 20(13) or 21*(7). Dorsolateral body plates along dorsal-fin base 6*(18) or 7(2). Dorsolateral body plates between adipose- and caudal-fin 7(18) or 8*(2). Preadipose platelets 3*(6) or 4(14). Ventral surface of trunk between posteroventral margin of cleithrum and pelvic-fin origin laterally delimited only by first ventrolateral body plate; ventral portion of first ventrolateral body plate slightly expanded anteriorly. 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 region of junction between frontal and lateral ethmoid, ventral margin of nasal capsule, above lateral ethmoid, and dorsal surface of snout with numerous small- to relatively large-sized platelets bearing odontodes; platelets on anterior margin of orbit and ventral margin of nasal capsule typically larger and

coalescent. Ventral surface of trunk with scarce to relatively numerous small-sized irregular platelets bearing odontodes; platelets more concentrated anteriorly and/or around pectoral-fin base.

Vertebral count 21(3); ribs 5(3); first pair conspicuously large, its middle portion closely connected to first ventrolateral body plate; its tip connected to anterior external process of basipterygium. Parapophysis of complex vertebra well developed.

TABLE 2 | Morphometric data of the holotype and 19 paratypes of *Corydoras hypnos*. SD = Standard deviation.

	Holotype	Low-High	Mean±SD
Standard length (mm)	31.7	20.8–31.7	23.4
Percent of standard length			
Depth of body	32.2	30.9–35.4	33.1±1.1
Predorsal distance	47.9	47.5–51.2	48.9±0.9
Prepelvic distance	46.4	45.1–49.8	47.0±1.0
Preanal distance	80.1	79.3–83.1	81.0±0.9
Preadipose distance	82.6	81.6–86.0	83.5±1.2
Length of dorsal spine	31.2	29.1–33.8	31.4±1.2
Length of pectoral spine	27.8	25.9–29.1	27.7±1.2
Length of adipose-fin spine	7.6	7.6–9.2	8.4±0.5
Depth of caudal peduncle	14.5	14.3–15.9	15.1±0.4
Length of dorsal-fin base	18.9	16.4–20.9	18.3±0.9
Dorsal to adipose distance	18.0	16.9–20.5	19.0±1.0
Maximum cleithral width	25.2	24.3–26.5	25.2±0.6
Head length	43.2	42.1–45.0	43.8±0.8
Length of maxillary barbel	9.1	7.5–12.1	9.6±1.2
Percent of head length			
Head depth	72.3	67.7–76.9	71.1±2.3
Least interorbital distance	24.1	23.1–25.6	24.5±0.8
Horizontal orbit diameter	24.1	24.1–28.0	26.5±1.0
Snout length	37.2	34.4–39.5	36.9±1.2
Least internarial distance	13.9	11.8–15.4	13.7±1.0

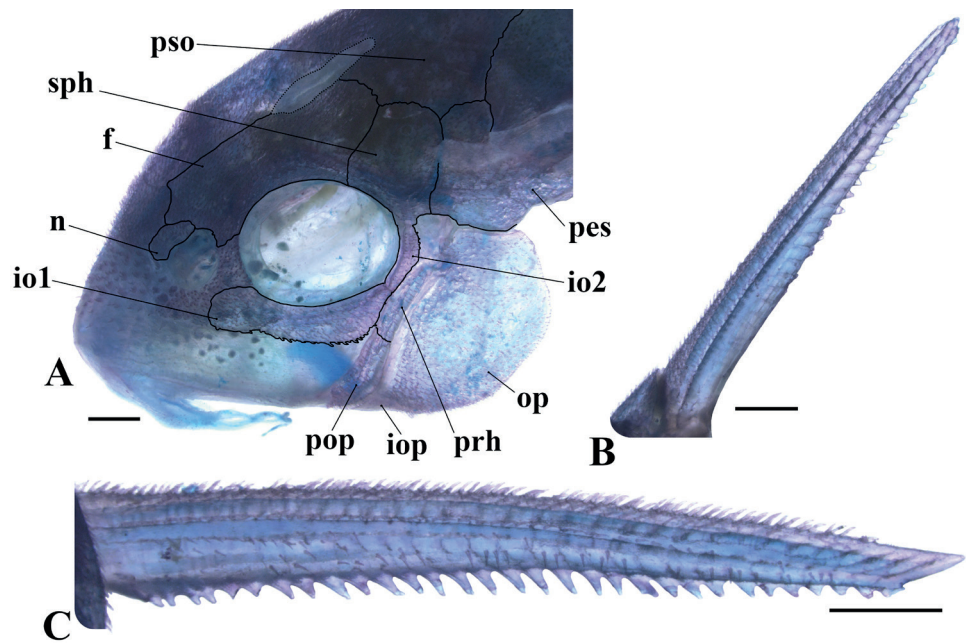


FIGURE 8 | Lateral view of the head (A), lateral view of the dorsal-fin spine (B) and dorsal view of the left pectoral-fin spine (C) in cs paratype of *Corydoras hypnos*, CITL 385, 32.0 mm SL. Abbreviations: f: frontal, io1-2: infraorbital 1 and 2, iop: interopercle, n: nasal, op: opercle, pes: pterotic-extrascapular, pop: preopercle, prh: posterodorsal ridge of hyomandibula, pso: parieto-supraoccipital, sph: sphenotic. Scale bars = 1 mm.

Color in alcohol. Overall color of body in Fig. 7. Ground color of body pale to brownish yellow or beige. Top of head dark brown; dark area typically extending mesially towards posterior tip of parieto-supraoccipital as thin longitudinal line. Dorsal and lateral surface of head, and lateral surface of cleithrum covered by dark brown or black chromatophores, typically not forming blotches; diffuse stripe from anteroventral portion of eye to upper lip lateral area in some specimens. Dorsolateral body plates with conspicuous concentration of dark brown or black chromatophores, typically forming rounded, irregular or vertically elongated diffuse dark blotches. Ventrolateral body plates, except for ventral portion of plates between pelvic-fin origin to area just anterior to anal-fin origin, with conspicuous concentration of dark brown or black chromatophores, typically forming rounded, irregular or vertically elongated diffuse dark blotches; ventral portion of plates between pelvic-fin origin to area just anterior to anal-fin origin, especially around pelvic-fin origin, typically with sparse dark brown or black chromatophores, not forming any conspicuous pattern. Midline of flank generally with distinct longitudinal series of typically diffuse dark brown or black blotches, generally more evident on posterior half of flank. Blotches on flanks ranging from small to moderate in size; strongly faded in some specimens. Dorsal portion of body with conspicuous concentration of dark brown or black chromatophores at anterior and posterior origins of dorsal fin, adipose-fin base, and caudal-fin base, variably forming longitudinal series of four typically diffuse dark brown or black blotches. Posterior margin of body plates typically with dark brown or black chromatophores, variably forming

thin dark lines along border of plates. Dorsal-fin with conspicuous concentrations of dark brown or black chromatophores, forming small dark blotches; blotches roughly longitudinally or obliquely aligned in some specimens, variably fused with each other and forming stripes; blotches diffuse in some specimens. Pectoral and pelvic fins with sparse dark brown or black chromatophores, generally more concentrated on rays and not forming dark spots. Adipose fin with dark brown or black chromatophores, generally more numerous and concentrated on spine and on posterior portion of membrane, typically forming single dark patch; diffuse patch in some specimens. Anal fin with conspicuous concentrations of dark brown or black chromatophores, generally more evident on its anterior half, typically forming diffuse or conspicuous dark blotches roughly aligned transversally; blotches fused with each other, forming dark stripe in some specimens. Caudal fin with conspicuous concentrations of dark brown or black chromatophores, mainly on rays, forming dark blotches roughly aligned transversally in two to five slender bars; some specimens with diffuse blotches/bars.

Color in life. Similar to color pattern of preserved specimens, but with light ground color of body and slightly more evident stripe from anteroventral portion of eye to upper lip lateral area. Body covered by greenish yellow iridescent coloration (Fig. 9). Aquarium specimens were observed to present dorsal and lateral surface of head plus lateral surface of cleithrum with irregular, rounded or vermiculated, conspicuous dark brown or black blotches, and conspicuous blotches on body. Some specimens with ground color of body greyish yellow (Fig. 10).

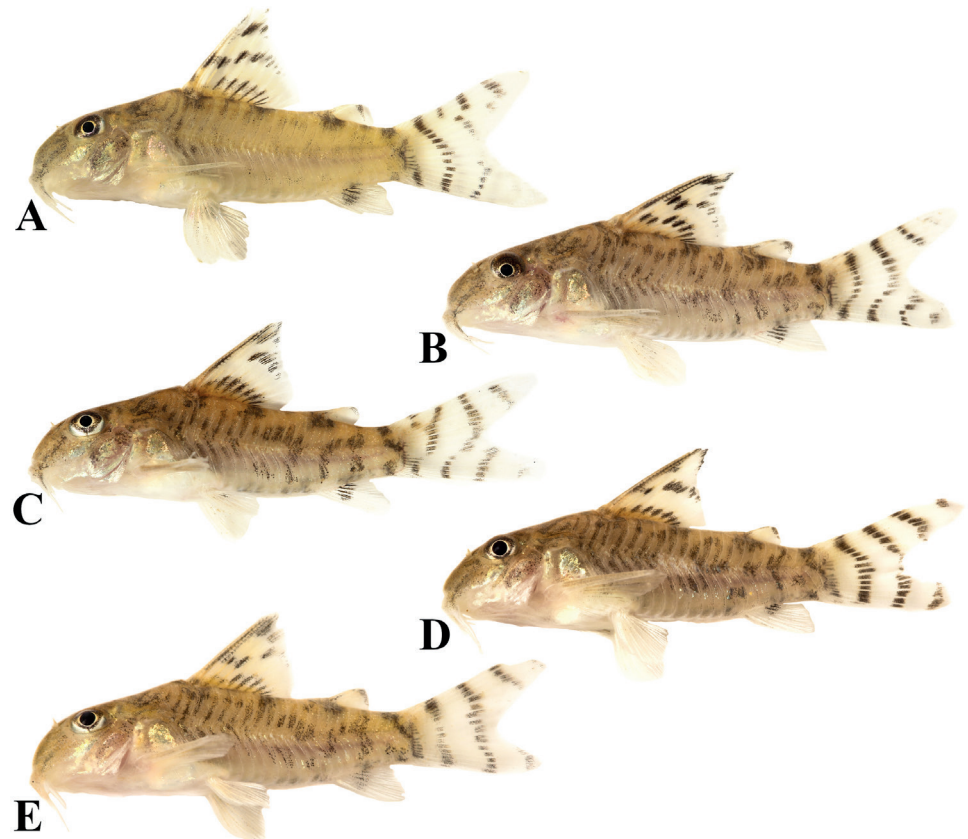


FIGURE 9 | Paratypes of *Corydoras hypnos* photographed alive, showing general color pattern and morphology in lateral view in (A) INPA 59775, 26.2 mm SL, (B) INPA 59775, 27.2 mm SL, (C) INPA 59775, 22.2 mm SL, (D) INPA 59774, 28.2 mm SL, and (E) INPA 59774, 22.6 mm SL, all from the rio Jamanxim, rio Tapajós basin, Pará State, Brazil.

FIGURE 10 | Uncatalogued aquarium specimens of *Corydoras hypnos* photographed alive, showing general morphology and color pattern of (A) a specimen with brownish yellow ground color of body, and (B) and two specimens with greyish yellow ground color of body. Photos by Robert McLure (A) and Oliver Lucanus (B).



Sexual dimorphism. Similar to the described for *Corydoras thanatos*, except by the absence of elongated dorsal fin in males, which was not observed so far in both wild caught or aquarium specimens.

Geographical distribution. *Corydoras hypnos* is currently known from the rio Jamanxim and one of its tributaries, with unknown name, rio Tapajós basin, Novo Progresso Municipality, Pará State, Brazil (Fig. 5).

Ecological notes. Specimens of *Corydoras hypnos* were always observed by the authors in syntopy and shoaling together with *C. thanatos*, information on its natural history and habitat notes can be found in the “Ecological notes” section of *C. thanatos*.

Etymology. The specific epithet “*hypnos*” refers to Hypnos (from the Greek Ὕπνος, Ὕπνος, which means “sleep”), the Greek god or personification of sleep, and the twin brother of Thanatos, the god/personification of death. The name makes an allusion to the fact that even though both *C. hypnos* and *C. thanatos* may present some similarities (in color pattern), they are completely different in other aspects (general morphological pattern). A noun in apposition.

Conservation status. *Corydoras hypnos* is currently known from its type locality and an additional record in its surroundings. However, both records are in the border of a conservation unit, the Floresta Nacional do Jamanxim, and no threat to the species as a whole is currently suspected. According to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Subcommittee, 2019), *Corydoras hypnos* can be classified as Least Concern (LC).

Corydoras psamathos, new species

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(Figs. 11-13; Tab. 3)

Holotype. MNRJ 53289, 29.4 mm SL, Brazil, Pará State, Novo Progresso Municipality, Igarapé Santa Júlia, a tributary to the rio Jamanxim, rio Tapajós basin, 06°45'38"S 55°28'44"W, 10 Jul 2019, M. R. Britto, W. M. Ohara and L. F. C. Tencatt.

Paratypes. All from Brazil, Pará State, Novo Progresso Municipality, rio Jamanxim basin, rio Tapajós drainage, collected by M. R. Britto, W. M. Ohara and L. F. C. Tencatt. CITL 386, 3, 18.1–21.8 mm SL; INPA 59772, 1, 23.7 mm SL, rio Jamanxim, 07°03'52"S 55°26'28"W, 9 Jul 2019. CITL 387, 9 of 12, 19.3–29.6 mm SL, 3 cs of 12, 22.0–28.6 mm SL; INPA 59773, 2, 29.3–30.2 mm SL; MZUSP 126862, 10, 19.6–27.8 mm SL; NUP 23542, 10, 18.7–26.9 mm SL, collected with holotype.

Diagnosis. *Corydoras psamathos* can be distinguished from its congeners, except for the species from the lineages 6, 7 and 9 *sensu* Alexandrou *et al.* (2011) plus *C. diffluviatilis*, *C. hastatus* and *C. pygmaeus*, by having posterior margin of pectoral-fin spine with most serrations directed towards the tip of the spine (*vs.* most serrations directed towards origin of spine); from *C. diffluviatilis* and *C. pygmaeus* it differs by the presence of contact between nuchal plate and posterior process of the parieto-supraoccipital (*vs.* absence of contact between nuchal plate and the posterior process of the parieto-supraoccipital); from *C. hastatus* by the absence of a large-sized dark blotch on caudal-fin base (*vs.* caudal-fin base region with a dark brown or black large blotch, roughly diamond-shaped or rhomboid, or arrow-shaped, typically bordered anteriorly and posteriorly by conspicuously light areas); from the species within lineage 7, it differs by having posterodorsal edge of infraorbital 2 only in contact with sphenotic (*vs.* in contact with sphenotic and pterotic-extrascapular); from the species of lineages 6 and 9, except for *C. concolor* Weitzman, 1961, *C. esperanzae* Castro, 1987, *C. guianensis*, *C. polystictus* Regan, 1912, and *C. sanchesi* Nijssen & Isbrücker, 1967, by the absence of conspicuous dark brown or black markings on body; dark markings, when present, diffuse (*vs.* presence of conspicuous small- to large- sized dark brown or black markings in at least some region of the body); from *C. concolor*, *C. esperanzae*, *C. guianensis*, *C. polystictus*, and *C. sanchesi* by having posterior laminar expansion of infraorbital 2 strongly reduced, nearly imperceptible in some specimens (*vs.* posterior laminar expansion at least poorly developed, but clearly more developed and perceptible), by the slender body (*vs.* more robust), and by the narrower frontal bone (*vs.* wider). The new species can be further



FIGURE 11 | *Corydoras psamathos*, holotype, MNRJ 53289, 29.4 mm SL, Novo Progresso Municipality, Pará State, Brazil, igarapé Santa Júlia, a tributary to the rio Jamanxim, rio Tapajós basin.

distinguished from *C. concolor* and *C. esperanzae* by the presence of ventral surface of trunk only with small-sized, irregular platelets (*vs.* ventral surface of trunk entirely or almost entirely covered by larger coalescent platelets); from *C. sanchesi* by having anterior portion of dorsal fin with scattered dark brown or black chromatophores, not forming any conspicuous pattern (*vs.* anterior portion of dorsal fin typically with a conspicuous concentration of dark brown or black chromatophores, forming a dark patch); from *C. polystictus* by presenting dorsal surface of snout with numerous platelets bearing odontodes (*vs.* dorsal surface of snout lacking platelets).

Description. Morphometric data in Tab. 3. Head laterally compressed with convex dorsal profile, roughly triangular in dorsal view. Snout ranging from relatively short to moderately developed and generally smoothly rounded; slightly more rounded in some specimens. Head profile convex from tip of snout to anterior nares; ascending nearly straight or slightly convex from this point to dorsal-fin origin; region of frontal fontanel slightly concave in some specimens. Profile slightly convex along dorsal-fin base. Postdorsal-fin body profile slightly concave to adipose-fin spine, slightly concave from this point to caudal-fin base. Ventral profile of body nearly straight or slightly convex from isthmus to pectoral girdle, and slightly convex from this point until pelvic girdle. Profile nearly straight or slightly convex from pelvic girdle to base of first anal-fin ray, ascending slightly 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, posteroventrally by infraorbital 2, and anteroventrally 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 similar to bony orbit diameter. Maxillary barbel ranging from short to moderate in size, not reaching to anteroventral limit of gill opening. Outer mental barbel slightly longer than maxillary barbel. 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 moderate in size, with anterior tip poorly developed, slightly smaller than 50% of bone length (see Britto, 2003:123, character 1, state 1; fig. 1B); posterior portion wide, partially exposed and bearing small odontodes. Nasal capsule delimited posteriorly and dorsally by frontal, anteriorly by mesethmoid, and ventrally and posteriorly by lateral ethmoid. Nasal slender, laterally curved, inner margin with poorly- to moderately-developed laminar expansion generally contacting frontal and mesethmoid; variably close but not in direct contact with mesethmoid; outer margin typically with strongly reduced laminar expansion. Lateral ethmoid slightly expanded anteriorly, with anterodorsal expansion relatively distant from nasal, and anterior margin contacting posterior portion of mesethmoid. Frontal elongated, narrow, width less than half of entire length; anterior projection short, size smaller than nasal length. Frontal fontanel large, slender, and somewhat ellipsoid; posterior tip extension slightly surpassing anterior margin of parieto-supraoccipital. Sphenotic somewhat trapezoid, contacting parieto-supraoccipital dorsally, pterotic-extrascapular posteriorly, second infraorbital posteroventrally and frontal anteriorly (Fig. 12A). Pterotic-extrascapular roughly pipe-shaped, with posteriormost portion contacting first lateral-line ossicle, posteroventral margin contacting cleithrum, and anteroventral margin contacting opercle; posterior expansion almost entirely covering lateral opening of swimbladder capsule, leaving slender area on its dorsal margin covered only by thick layer of skin. Parieto-supraoccipital wide, posterior process long and contacting nuchal plate; 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 poorly to moderately developed; anterior portion with laminar expansion moderately developed, reaching to middle portion of nasal capsule;

inner laminar expansion poorly developed (Fig. 12A). Infraorbital 2 small, slender, with posterior laminar expansion strongly reduced, nearly imperceptible in some specimens; posteroventral margin contacting posterodorsal ridge of hyomandibula, posterodorsal edge contacting only sphenotic; inner laminar expansion ranging from strongly reduced to poorly developed (Fig. 12A). Posterodorsal ridge of hyomandibula close to its articulation with opercle relatively slender, exposed, and bearing small odontodes. Dorsal ridge of hyomandibula between pterotic-extrascapular and opercle typically covered by thick skin layer. Interopercle entirely covered by thick layer of skin; subtriangular, anterior projection ranging from moderately developed to relatively well developed. Preopercle elongated, relatively slender; minute odontodes on external surface. Opercle dorsoventrally elongated, with width similar to half of its entire length; free margin slightly convex, without serrations and covered by small odontodes.

Four branchiostegal rays decreasing in size posteriorly. Hypobranchial 1 deep; hypobranchial 2 somewhat triangular, tip ossified and directed towards anterior portion, posterior margin cartilaginous; ossified portion ranging from strongly reduced, with only region of tip ossified, to well developed, its size about twice of cartilaginous portion. Five ceratobranchials with expansions increasing posteriorly; ceratobranchial 1 with small process on anterior margin of mesial portion; ceratobranchial 3 typically notched on postero-lateral margin; ceratobranchial 5 toothed on posterodorsal surface, with 28 to 38(3) 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 uncinuate process on laminar expansion of posterior margin. Two wide pharyngobranchials (3 and 4); pharyngobranchial 3 with slightly triangular to smoothly rounded laminar expansion on posterior margin. Upper tooth plate roughly oval, 34 to 43(3) teeth aligned in two rows on posteroventral surface; rows closely aligned.

Lateral-line canal reaching cephalic laterosensory system through pterotic-extrascapular, branching twice before reaching sphenotic: pterotic branch, with single pore, preoperculomandibular branch conspicuously reduced, with single pore opening at postotic main canal; postotic main canal widens just posterior to pterotic branch. Sensory canal continuing through pterotic-extrascapular, 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, both with single pore. Supraorbital canal branched, running through nasal bone. Epiphyseal branch conspicuously reduced; pore opening close to supraorbital main canal, directed towards frontal fontanel. Nasal canal typically 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 infraorbital 2, extending to infraorbital 1 and generally 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, generally located just posterior to second dorsolateral body plate. Dorsal-fin rays II,7*(1) or II,8(19), posterior margin of dorsal-fin spine with 10 to 16 strongly reduced to poorly-developed serrations; most serrations directed towards tip of spine; some serrations variably perpendicularly directed; serrations absent close to origin of spine; small odontodes on anterior and lateral surfaces of spine (Fig. 12B).

Nuchal plate moderately developed, almost entirely exposed, with minute odontodes. Spinelet short; spine moderately developed, with adpressed distal tip slightly surpassing posterior origin of dorsal-fin base. Pectoral fin roughly triangular, its origin just posterior to gill opening. Pectoral-fin rays I,7*(5), I,7,I(3) or I,8(12), posterior margin of pectoral spine with 17 to 26 strongly reduced to moderately-developed serrations along its entire length; most serrations directed towards tip of spine; some serrations perpendicularly directed; small odontodes on anterior, dorsal and ventral surfaces of spine (Fig. 12C). Anteroventral portion of cleithrum exposed; posterolateral portion of scapulocoracoid moderately developed, exposed, with anterior portion slightly expanded anteriorly, not in contact with anteroventral portion of cleithrum; exposed areas bearing small odontodes. Opening of axillary gland *sensu* Kiehl *et al.* (2006) located just posterior to pectoral-fin spine base. Pelvic fin oblong, located just below first or second ventrolateral body plate, and at vertical through first branched dorsal-fin ray. Pelvic-fin rays I,5*(20). Adipose fin roughly triangular, separated from base of last dorsal-fin ray by generally six dorsolateral body plates. Anal fin subtriangular, typically located just posterior to 12th or 13th ventrolateral body plates, and at vertical through adipose-fin spine base. Anal-fin rays ii,5(18), ii,5,i*(1), ii,7(1). Caudal fin bilobed, with dorsal and ventral lobes similar in size or dorsal lobe slightly larger than ventral lobe. Caudal-fin rays I,12,i*(20), generally five dorsal and ventral procurrent rays.

Typically, three laterosensory canals on trunk; first ossicle tubular, second ossicle laminar, both bearing small odontodes; third, encased in third dorsolateral body plates. Body plates with minute odontodes scattered over exposed area, with conspicuous line of odontodes confined to posterior margins. Dorsolateral body plates 23(2), 24*(15) or 25(3). Ventrolateral body plates 21(15) or 22*(5). Dorsolateral body plates along dorsal-fin base 6*(17) or 7(3). Dorsolateral body plates between adipose- and caudal-fin 7(2), 8*(17) or 9(1). Preadipose platelets 3*(14) or 4(6). Ventral surface of trunk between posteroventral margin of cleithrum and pelvic-fin origin laterally delimited only by first ventrolateral body plate; ventral portion of first ventrolateral body plate slightly expanded anteriorly. 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 region of junction between frontal and lateral ethmoid, ventral margin of nasal capsule, above lateral ethmoid, and dorsal surface of snout with numerous small- to relatively large-sized platelets bearing odontodes; platelets on anterior margin of orbit and ventral margin of nasal capsule typically larger and coalescent. Ventral surface of trunk with scarce small-sized irregular platelets bearing odontodes; platelets more concentrated anteriorly and/or around pectoral-fin base.

Vertebral count 22(3); ribs 5(3); first pair conspicuously large, its middle portion closely connected to first ventrolateral body plate; its tip connected to anterior external process of basipterygium. Parapophysis of complex vertebra well developed.

Color in alcohol. Overall color of body in Fig. 11. Ground color of body pale to brownish yellow or beige. Top of head dark brown; dark area typically extending mesially towards posterior tip of parieto-supraoccipital as thin longitudinal line. Dorsal and lateral surface of head and lateral surface of cleithrum with conspicuous concentrations of dark brown or black chromatophores, typically not forming blotches;

TABLE 3 | Morphometric data of the holotype and 19 paratypes of *Corydoras psamathos*. SD = Standard deviation.

	Holotype	Low–High	Mean±SD
Standard length (mm)	29.4	19.9–29.6	24.1
Percent of standard length			
Depth of body	34.7	31.7–35.3	33.7±1.1
Predorsal distance	49.7	47.6–50.7	49.3±0.9
Prepelvic distance	46.3	45.7–48.1	46.9±0.7
Preanal distance	82.3	78.8–83.6	81.4±1.3
Preadipose distance	84.0	81.3–86.6	84.0±1.4
Length of dorsal spine	30.3	27.4–35.3	30.8±2.1
Length of pectoral spine	27.9	25.6–31.1	28.1±1.5
Length of adipose-fin spine	9.5	7.2–10.1	8.9±0.8
Depth of caudal peduncle	15.3	14.4–16.2	15.4±0.5
Length of dorsal-fin base	18.0	16.5–20.0	17.9±1.0
Dorsal to adipose distance	18.7	15.2–21.3	18.8±1.4
Maximum cleithral width	26.2	24.5–26.6	25.7±0.6
Head length	43.9	42.6–45.2	43.7±0.7
Length of maxillary barbel	9.5	8.2–12.3	10.4±1.1
Percent of head length			
Head depth	72.9	68.1–75.9	72.0±2.6
Least interorbital distance	24.0	23.4–27.1	25.3±1.0
Horizontal orbit diameter	25.6	23.4–28.4	26.0±1.4
Snout length	36.4	34.1–40.9	37.6±1.7
Least internarial distance	14.0	12.8–16.1	14.6±0.8

top of head with diffuse irregular dark blotches in some specimens; diffuse stripe from anteroventral portion of eye to upper lip lateral area typically present. Dorsolateral body plates with conspicuous concentration of dark brown or black chromatophores, typically not forming dark blotches; diffuse rounded, irregular or vertically elongated dark blotches in some specimens; dorsal portion of plates with slightly more concentrated chromatophores on anterior and posterior origins of dorsal fin, adipose-fin base, and caudal-fin base in some specimens. Ventrolateral body plates, except for ventral portion of plates between pelvic-fin origin to area just anterior to anal-fin origin, with conspicuous concentration of dark brown or black chromatophores, typically not forming dark blotches; diffuse rounded, irregular or vertically elongated dark blotches in some specimens; ventral portion of plates between pelvic-fin origin to area just anterior to anal-fin origin, especially around pelvic-fin origin, typically with sparse dark brown or black chromatophores, not forming any distinctive pattern. Midline of

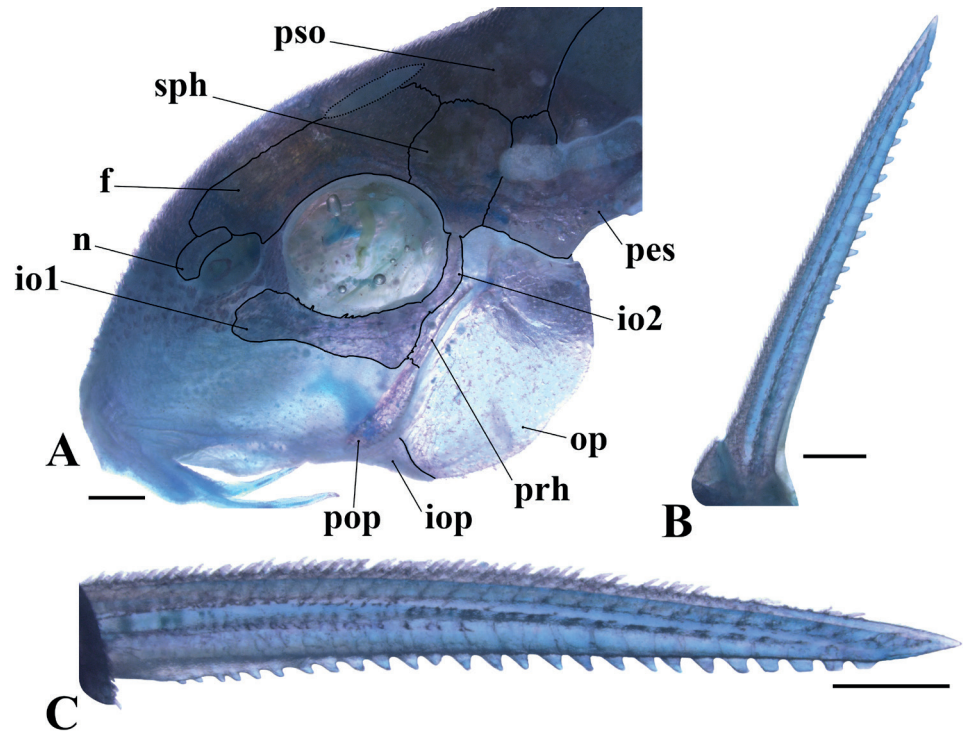


FIGURE 12 | Lateral view of the head (A), lateral view of the dorsal-fin spine (B) and dorsal view of the left pectoral-fin spine (C) in cs paratype of *Corydoras psamathos*, CITL 387, 28.6 mm SL. Abbreviations: f: frontal, io1–2: infraorbital 1 and 2, iop: interopercle, n: nasal, op: opercle, pes: pterotic-extrascapular, pop: preopercle, prh: posterodorsal ridge of hyomandibula, pso: parieto-supraoccipital, sph: sphenotic. Scale bars = 1 mm.

flank with distinct longitudinal series of diffuse dark brown or black blotches, more evident on posterior half of flank in single juvenile specimen (18.4 mm SL). Blotches on flanks typically small. Posterior margin of body plates typically with dark brown or black chromatophores, variably forming thin dark lines along border of plates. Dorsal-fin with dark brown or black chromatophores, especially on rays, generally not forming evident blotches; forming strongly faded to diffuse small dark blotches in some specimens; chromatophores typically more numerous and concentrated on dorsal half of first branched-ray region, including membranes, and along dorsal-fin proximal portion. Pectoral, pelvic, and anal fins with sparse to relatively numerous dark brown or black chromatophores, especially on rays, typically not forming dark spots; chromatophores on anal fin more concentrated on its proximal half. Adipose fin with conspicuous concentrations of dark brown or black chromatophores on spine; dark brown or black chromatophores on membrane typically more numerous and concentrated on its posterior margin and/or along its proximal portion, not forming any conspicuous pattern. Caudal fin with dark brown or black chromatophores, mainly on rays, typically forming closely-spaced, strongly faded to diffuse dark blotches; some specimens with blotches roughly aligned transversally in up to nine slender and closely-spaced rows of blotches; some specimens with non-aligned blotches; dark blotches variably absent.

Color in life. Similar to color pattern of preserved specimens, but with light ground color of body and slightly more evident stripe from anteroventral portion of eye to upper lip lateral area. Body covered by greenish yellow iridescent coloration (Fig. 13). Some aquarium specimens with greyish-white ground color of body (Fig. 14).

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

Geographical distribution. *Corydoras psamathos* is currently known from the main channel of the rio Jamanxim and one of its tributaries, the igarapé Santa Júlia, rio Tapajós basin Novo Progresso Municipality, Pará State, Brazil (Fig. 5).

Ecological notes. The new species was observed to inhabit the rio Jamanxim and at least one of its tributaries, the igarapé Santa Júlia. In the rio Jamanxim, it was mostly associated with the margins of the river, where juvenile and adult specimens were observed in the shallow (up to about 20 cm deep) sandy shores with slow water flow. In the igarapé Santa Júlia (Fig. 15), juvenile and adult specimens were also observed associated in marginal shallow (up to about 20 cm deep) portions, with more

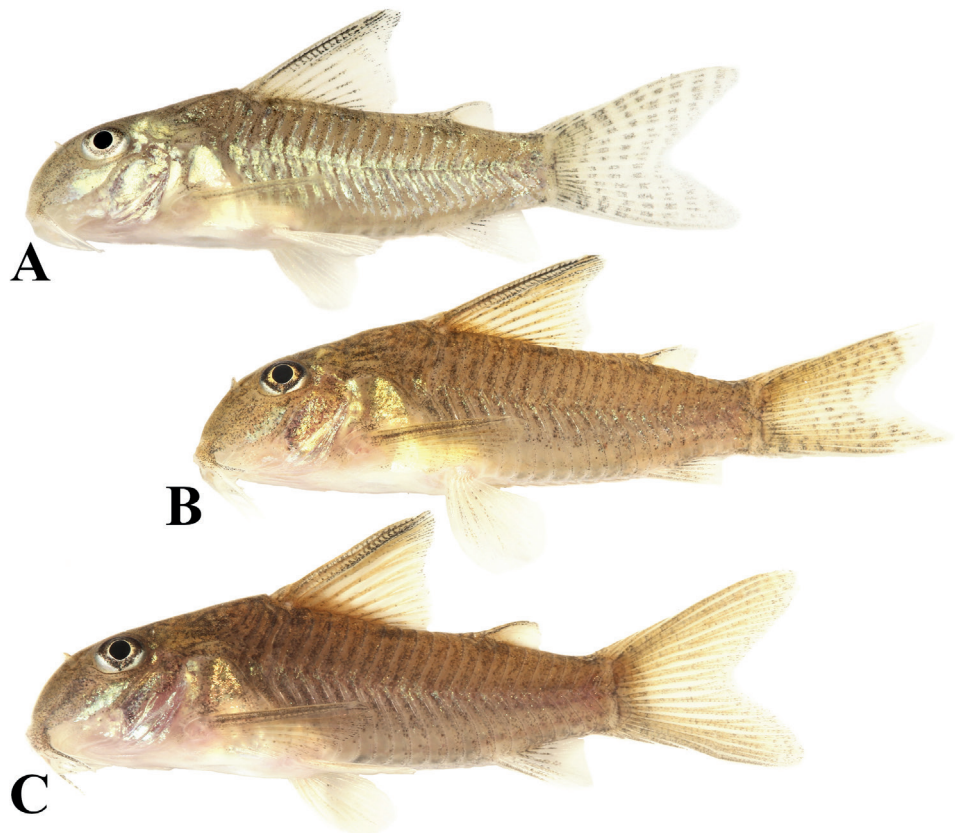


FIGURE 13 | Paratypes of *Corydoras psamathos* photographed alive, showing general color pattern and morphology in lateral view in (A) INPA 59772, 23.7 mm SL, (B) INPA 59773, 30.2 mm SL, and (C) INPA 59773, 29.3 mm SL. Specimen (A) is from the rio Jamanxim, and specimens (B–C) are from the igarapé Santa Júlia, rio Tapajós basin.



FIGURE 14 | Uncatalogued aquarium specimen of *Corydoras psamathos* photographed alive. Photo by Takayuki Shimizu.

complex substrate, mainly composed by sand, fine gravel and larger rocks. In this site, both juvenile and adult specimens of *C. psamathos* were observed shoaling together with juvenile specimens of *Corydoras* sp. CW171, being the new species clearly more abundant. Additionally, *C. apiaka* was observed syntopically with the new species and *Corydoras* sp. CW171 in the igarapé Santa Júlia. In both sampled sites, the new species was mostly captured at night.

Etymology. The specific epithet “*psamathos*” refers to Psamathos Psamathides, the oldest wizard among the Psamathists, the sand sorcerers, a fictional character created by J. R. R. Tolkien in his book *Roverandom*. The name derives from the Greek *psammos*, which means sand. The name alludes to the sand-dwelling behavior of the new species. A noun in apposition.

Conservation status. *Corydoras psamathos* is currently known from its type locality and an additional record from the same region. Although the region is severely impacted by anthropic action, no threat to the species as a whole is currently suspected. According to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Subcommittee, 2019), *Corydoras psamathos* can be classified as Least Concern (LC).



FIGURE 15 | Type locality of *Corydoras psamathos*, the igarapé Santa Júlia, a tributary to the rio Jamanxim, rio Tapajós basin in Pará State, Brazil.

Identification key to the valid species of *Corydoras* from the rio Tapajós basin

- 1a. Posterior margin of pectoral-fin spine with most serrations directed towards the origin of the spine 2
- 1b. Posterior margin of pectoral-fin spine with most serrations directed towards the tip of the spine..... 3
- 2a. Two relatively wide, dark brown or black, longitudinal stripes on flanks *C. bifasciatus*
- 2b. Three or four slender, dark brown or black, longitudinal stripes on flanks *C. ornatus*
- 3a. Body devoid of conspicuous dark brown or black blotches 4
- 3b. Body with conspicuous dark brown or black blotches 5
- 4a. Posterior process of the parieto-supraoccipital not in contact with the nuchal plate
C. hephaestus
- 4b. Posterior process of the parieto-supraoccipital in contact with the nuchal plate *C. psamathos*

- 5a. Broad, dark vertical bar at the level of eye present, occupying top of head, opercle, posterior portion of infraorbital 1 and entire infraorbital 2, and preopercle *C. rikbaktsa*
- 5b. Dark vertical bar at the level of eye absent..... 6
- 6a. Anterior laminar expansion of infraorbital 1 strongly well developed, conspicuously expanded towards the anteroventral portion of snout, significantly covering its lateral surface..... *C. thanatos*
- 6b. Anterior laminar expansion of infraorbital 1 ranging from moderately to well developed, not conspicuously expanded towards the anteroventral portion of snout, leaving most of its lateral surface uncovered..... 7
- 7a. Body depth 36.9–42.6% of SL; least interorbital distance (13.8–17.3% of HL) *C. apiaka*
- 7b. Body depth 30.0–35.7% of SL; least interorbital distance (18.8–27.7% of HL)..... 8
- 8a. Body with conspicuous dark brown or black markings *C. benattii*
- 8b. Body lacking conspicuous dark brown or black markings; dark markings, when present, diffuse *C. hypnos*

DISCUSSION

The presence of syntopic species sharing similar color patterns but distinct morphology has been widely reported for *Corydoras* (e.g., Nijssen, Isbrücker, 1980a,c; Britto, 2003; Britto *et al.*, 2009; Alexandrou *et al.*, 2011; Tencatt *et al.*, 2013, 2019, 2021; Tencatt, Pavanelli, 2015; Tencatt, Britto, 2016; Tencatt, Ohara, 2016a,b; Lima, Sazima, 2017), having almost certainly played an important role in the evolution of the group (Tencatt *et al.*, 2021). These convergent color patterns were generally reported as cases of Müllerian mimicry (Alexandrou *et al.*, 2011), with a single mention to the Batesian mode of mimicry (Lima, Sazima, 2017). During the fieldwork, it was possible to observe *C. thanatos* and *C. hypnos*, which share similar color patterns but clearly different general morphological patterns, shoaling together in some sites. The same was observed between *C. psamathos* and *Corydoras* sp. CW171. Considering that the four species present the defensive tripod formed by their pungent dorsal and pectoral spines (Fine, Ladich, 2003), allied to the presence of axillary glands *sensu* Kiehl *et al.* (2006), all of them can be considered as unpalatable. Therefore, it seems reasonable to conclude that these pairs of species compose two Müllerian mimicry rings (see Alexandrou *et al.*, 2011).

The Serra do Cachimbo is one of the highest elevations of the Brazilian Shield, located on the southernmost border of the Amazon basin. The mountain chain can reach 500 meters above the sea level and forms an arc, running from Southeast to Northwest dividing the headwaters of the middle rio Xingu basin to the East (rio Curuá basin) and the middle rio Tapajós basin to the West (headwaters of the rio Jamanxim basin and tributaries of the rio Teles Pires) (Goulding *et al.*, 2003). Goulding *et al.* (2003) identified the Serra do Cachimbo as an area with high endemism, a theory proven in following years by the description of a relatively high number of fish species reported as endemic to this region (e.g., Lima, Birindelli, 2006; Birindelli, Britski, 2009; Birindelli *et al.*, 2009; Sousa *et al.*, 2010; Netto-Ferreira, 2012; Netto-Ferreira *et al.*, 2013; Datovo, 2014;

Varella, Sabaj Pérez, 2014; Varella, Britzke, 2016; Garcia-Ayala *et al.*, 2017; Oyakawa *et al.*, 2018). Even though the specimens analyzed herein were not captured in the Serra do Cachimbo itself, they were recorded from an area in its surroundings (especially *C. thanatos* and *C. hypnos*), in the upper portion of the rio Jamaxim, which drains part of the Serra do Cachimbo. This explains the reason why the three new species together with *Corydoras* sp. CW111 and CW171 are called the “Serra do Cachimbo *Corydoras*” in the aquarium trade (see Lucanus, 2021).

Until recently, the area was relatively poorly sampled, but four major scientific expeditions were carried out in the early twenty-first century (for more details about those expeditions, see Birindelli *et al.*, 2009). One of them was the PIPE Expedition, funded by the US National Science Foundation project “All Catfish Species Inventory” (DEB-0315963 PI José Birindelli), the first scientific endeavor to the Cachimbo that shared its results on the internet. In this way, photos of live specimens were published in a report-like website in 2008 (http://silurus.acnatsci.org/ACSI/field/Pipe_Expedition/Home.html), making the species of the region known around the world. Some species depicted on the website immediately got the attention of fish-keeping hobbyists around the world, such as *Apistogramma* sp. “gigas” (later described as *Apistogramma kullanderi* Varella & Sabaj Pérez, 2014) and *Corydoras* sp. “bonita” (= *Corydoras* sp. CW111), both reported from the rio Curuá.

The demand for these species by aquarists made exporters focus their efforts on catching these fishes in the Serra do Cachimbo region. Fishermen from several places in Brazil (as well as from Colombia and Peru) traveled to the area and extensively seined the tributaries of the rio Curuá in order to capture the new fishes. *Apistogramma kullanderi* and *A. eleutheria* Varella & Britzke, 2016 were exported in great numbers, mainly to Asia, but also to Europe and North America, and have been successfully bred in captivity (O. Lucanus, 2022, pers. comm.; LMS pers. obs.). However, the impact of so many individuals being removed from wild populations of species with restrict geographical distribution is yet to be fully understood. In a recent expedition to the rio Curuá tributaries at the Serra do Cachimbo, very few specimens of *A. kullanderi* were spotted during field observations (O. Lucanus, 2022, pers. comm.), and the habitat was considerably impacted by fishing activity (*e.g.*, clearly overturned substrate, and disposed collection gear), in addition to the habitat degradation on the surroundings caused by the paving works of the BR-163 road, which runs close to these sites.

The absence of *Corydoras* CW111 in the most recent survey efforts, as well as reports from several fishermen of the scarcity of this species, brings a real concern. Is this species naturally rare, or was it overfished to supply the ornamental trade? Perhaps both factors combined. The capture of wild fishes to supply the ornamental fish trade is an activity that can be beneficial to both local human populations and ecosystems if made in a sustainable way (see Evers *et al.*, 2019; Sousa *et al.*, 2021). However, the over-exploitation of a species caused by the ornamental trade can lead to a series of negative impacts (Dey, 2016; Evers *et al.*, 2019; Sousa *et al.*, 2021), especially in the case of narrowly endemic species with naturally low abundance, which are often already affected by the local environmental degradation itself. This delicate balance between allowing local people to profit from native species found in their region, and affording an alternative income stream to the much more destructive practices (*e.g.*, gold mining, logging, industrial agriculture) (for a broader discussion on this theme, see Evers *et*

al., 2019), and the potential damage to some species with small and/or geographically restricted populations, especially in the fragile headwater streams of the Xingu and Tapajós basins, is a difficult and elusive problem that requires further study and input from all stakeholders.

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The authors declare no competing interests.

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