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From the inside out: a new species of armoured catfish *Corydoras* with the description of poorly-explored character sources (Teleostei, Siluriformes, Callichthyidae)

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A new species of the armoured catfish genus *Corydoras* is described from the Xingu–Tapajos ecoregion, Brazilian Amazon. The new species can be distinguished from its congeners by having the following combination of features: short mesethmoid, with anterior tip poorly developed, smaller than 50% of bone length; posterior margin of pectoral spine with serrations directed towards spine tip or perpendicularly oriented; infraorbital 2 only in contact with sphenotic; ventral laminar expansion of infraorbital 1 poorly or moderately developed; flank midline covered by small dark brown or black saddles with similar size to remaining markings on body; relatively larger, scarcer and more sparsely distributed dark brown or black spots on body; absence of stripe on flank midline; caudal fin with conspicuous dark brown or black spots along its entire surface; slender body; and strongly narrow frontals. A more comprehensive description of poorly-explored internal character sources, such as the gross morphology of the brain, Weberian apparatus and swimbladder capsule elements is presented.

Key words: Brazilian Amazon; Corydoradinae; *Corydoras* sp. C22; gross brain morphology; taxonomy; Xingu–Tapajos ecoregion.

INTRODUCTION

There are currently approximately 180 valid species of the armoured catfish genus *Corydoras* Lacépède 1803, which correspond to 85% of species in the subfamily Corydoradinae (Eschmeyer *et al.,* 2017). *Corydoras* species are widely distributed throughout cis-Andean South America in diverse habitats such as shallow marginal areas of rivers, pools and smaller tributaries (Reis, 2003). Although several new *Corydoras* species have been described in recent decades, many taxa are still undescribed (Füller

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& Evers, 2005). According to Britto (2003), *Corydoras* can be readily recognized and supported by the following synapomorphies: complex vertebra compact in shape; posterior expansion of ceratobranchial 3 with a notch; dorsal lamina on anguloarticular triangular in shape; medial expansion of scapulocoracoid exposed. Alexandrou *et al.* (2011) generated a molecular hypothesis for *Corydoras* and recognized nine distinctive lineages.

The Xingu and Tapajos ecoregions (*sensu* Abell *et al.,* 2008) are adjacent tributaries to the Amazon River and possess a substantial number of endemic fish species (Buckup *et al.,* 2011). Four species of *Corydoras* have been described from the Xingu–Tapajos ecoregion (*sensu* Buckup *et al.,* 2011): *Corydoras xinguensis* Nijssen 1972, from the Rio Xingu basin and *Corydoras bifasciatus* Nijssen 1972, *Corydoras ornatus* Nijssen & Isbrücker 1976 and the relatively recent *Corydoras apiaka* Espíndola, Spencer, Rocha & Britto 2014 from the Rio Tapajós basin.

Examination of *Corydoras* specimens from this region revealed an undescribed, roughly spotted and saddled *Corydoras* sp., recorded from relatively few localities in both the Rio Xingu and Rio Tapajós basins (excluding the lower Rio Tapajós basin; see Discussion), which is formally described herein. Considering the broad geographic distribution of the new species, both basins are herein treated as a single ecoregion, following Buckup *et al.* (2011).

Historically, some anatomical structures, particularly soft tissue structures, have been poorly-explored in systematic studies. Datovo & Vari (2014), summarizing Wiley & Johnson (2010), revealed that within 180 major groups of Teleostei, 6% of synapomorphies are based on myology, 5% on splanchnology and 1% on neurology. Of the last, the first attempts to understand the neural-complex date back to the beginning of the 20th century, but only from the mid-1990s has neuroanatomy been used in systematic works on Antarctic fishes (Eastman & Lannoo, 1995, 2001, 2003, 2008, 2011) and more recently on Neotropical groups (Albert, 2001; Pupo, 2011; Abrahão & Shibatta, 2015; Pupo, 2015; Pereira & Castro, 2016). Likewise with other structures, such as the swimbladder capsule and Weberian apparatus, many studies were provided in the 19th century (Birindelli *et al.,* 2012) and there has more recently been renewed interested in describing them (Birindelli *et al.,* 2009, 2012; Birindelli & Shibatta, 2011). Sometimes, this anatomy is superficially included in taxonomic studies in which osteology was described. Thus, descriptions of the gross brain morphology, swimbladder capsule and Weberian apparatus of the new species are provided herein to broaden knowledge about these character sources and provide a reference for future systematic analyses of the Callichthyidae and of catfish morphology as a whole.

MATERIAL AND METHODS

Morphometric measurements were taken from the left side of specimens whenever possible and were recorded to the nearest 0·1 mm. Morphometric and meristic measurements follow Reis (1997), with modifications by Tencatt *et al.* (2013). Morphometrics are reported as percents of standard length (L_S) and head length (L_H). Teeth and vertebral counts were made from cleared-and-stained (c&s) specimens prepared according to Taylor & van Dyke (1985). Vertebral counts include only free centra, with the compound caudal centra (preural 1 + ural 1) counted as a single element. Lateral plate counts include all dorso-lateral and ventro-lateral plates, except for the small, irregular plates on the caudal peduncle. In the description, numbers in parentheses following each count represent total of specimens with that respective value and an asterisk indicates data for the holotype. Nomenclature of latero-sensory canals follows Schaefer & Aquino

(2000) and that of pre-opercular pores follows Schaefer (1988). Osteological terminology follows Reis (1998), except for parieto-supraoccipital is used instead of supraoccipital (Arratia & Gayet, 1995), compound pterotic is used instead of pterotic-supracleithrum (Aquino & Schaefer, 2002) and scapulocoracoid is used instead of coracoid (Lundberg, 1970). The supra-preopercle (*sensu* Huysentruyt & Adriaens, 2005) was herein treated as a part of the hyomandibula according to Vera-Alcaraz (2013). The Weberian complex vertebra was considered to include vertebrae 2–4 following Fink & Fink (1981). The Weberian apparatus is restricted to the tripus and concha scaphium, as described for Callichthyidae (Chardon, 1968). Homology of barbels follows Britto & Lima (2003).

Six specimens were dissected for brain description. The dissection protocol followed Abrahão & Pupo (2014). Nomenclature of brain subunits follows Meek & Nieuwenhuys (1998). Figures of the c&s-bone structures and brain topography were made using a Leica DFC 450 digital camera attached to a Leica M205C auto-stacking multifocus stereomicroscope, with the help of Leica application suite 4.8 software to obtain an all-in-focus image (www.leica-microsystems.com). Subsequently, all images were improved using the Pixelmator 3.6 software (www.pixelmator.com). The map was generated using Quantum GIS 2.8.2 software (www.quantum-gis.en.lo4d.com).

Institutional abbreviations follow Sabaj (2016): AI, Asociación Ictiológica, Museo de La Plata, La Plata, Argentina; ANSP, The Academy of Natural Sciences, Philadelphia, PA, U.S.A.; BMNH, Natural History Museum, London, U.K.; LBP, Laboratório de Biologia e Genética de Peixes, Departamento de Morfologia, Universidade Estadual Paulista 'Júlio de Mesquita Filho', Campus de Botucatu, Brazil; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A.; MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; NRM, Naturhistoriska Riksmuseet, Department of Vertebrate Zoology, Stockholm, Sweden; NUP, Coleção Ictiológica do Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia), Universidade Estadual de Maringá, Maringá, Brazil; ROM, Royal Ontario Museum, Department of Natural History, Toronto, Canada; ZUFMS-PIS, Coleção Zoológica de Referência (fishes) da Universidade Federal de Mato Grosso do Sul, Campo Grande, Brazil.

RESULTS

CORYDORAS BENATTII, SP. NOV.

(Figs 1–3 and Table I)

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Corydoras sp. 4. Castilhos & Buckup, 2011: 241 (species list). *Corydoras* sp. C22. Evers, 1994: 755, Fig. 2 (species catalogue). Glaser *et al.,* 1996: 92 (photos, species catalogue). Evers & Schäfer, 2004: 11, 12 (photos, species catalogue). Füller & Evers, 2005: 281, 285, 294 (species catalogue). *Corydoras* sp. aff. C22. Glaser *et al.,* 1996: 90 (photos, species catalogue).

Holotype

MZUSP 121671, 25·4 mm L_S, Brazil, Mato Grosso, between Canarana and Gaúcha do Norte, Rio Culuene, a tributary to the Rio Xingu, 13° 30′ 52″ S; 53° 05′ 34″ W; 19 October 2004, O. Oyakawa, J. Birindelli & C. Nolasco.

Paratypes

All from Brazil, Rio Xingu basin: MNRJ 35425 (6, 22·3–30·9 mm L_S), Pará, Cumaru do Norte, Rio Trairão (Rio Fresco subdrainage), tributary to Rio da Ponte, 15 km S; of

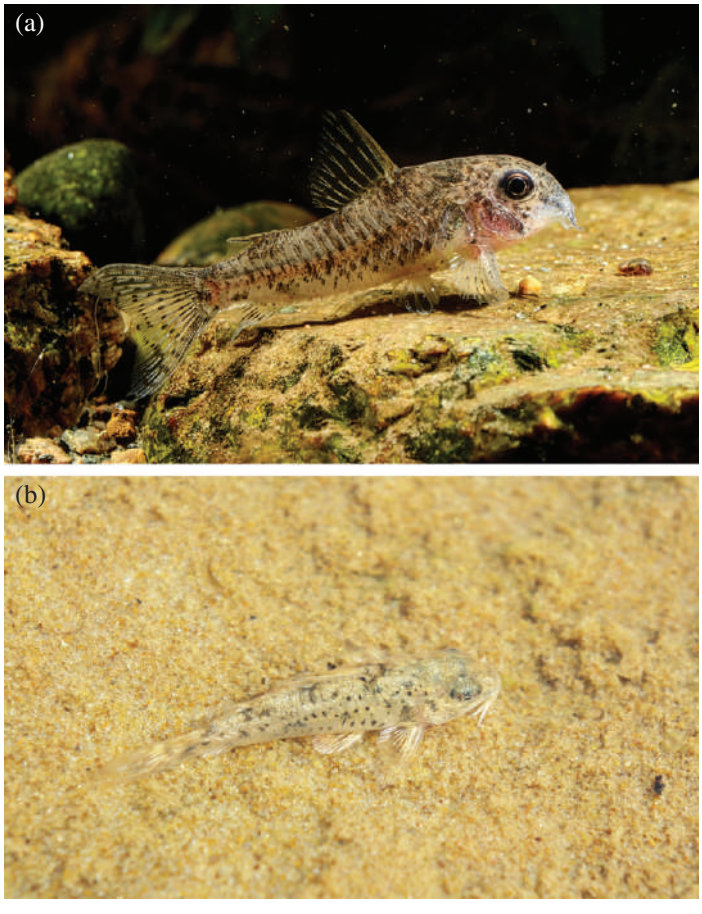

FIG. 1. *Corydoras benattii* sp. nov. in (a) aquarium and (b) natural habitat, uncatalogued specimens, both near Altamira, lower Rio Xingu Basin, 3° 37′ 20″ S; 51° 49′ 13″ W and 3° 35′ 2·4″ S; 51° 49′ 22·8″ W, respectively.

Cumaru do Norte, 7° 56′ 34·3″ S; 50° 47′ 48·7″ W; 9 October 2008, P. Buckup, J. Birindelli, C. Chamon, J. Gomes, J. Maldonado, C. Zawadski, F. Jerep, F. Carvalho & L. Fries. MNRJ 35426 (6, 21·2–28·0 mm L_S), Pará, São Felix do Xingu, Igarapé Manguari (km 28), an affluent to Rio Fresco basin, 6° 35′ 41·8″ S; 51° 48′ 48·5″ W; 12 October 2008, M. Britto, C. Chamon, J. Maldonado, F. Jerep, C. Zawadski. MNRJ 35427 (4, 19·0–22·7 mm L_S), Pará, Altamira, Page Beach, Rio Xingu upstream to Altamira and Igarapé Panela, 3° 14′ 07·9″ S; 52° 13′ 21·2″ W; 25 September 2008, P. Buckup, J. Birindelli, L. Fries, F. Carvalho, V. Felzman. MNRJ 50710 (2, 23·7–24·2 mm L_S); MZUSP 87015 (20, 16·1–29·1 mm L_S, 2 c&s, 22·1–27·4 mm L_S), NUP 19106 (1, 23·0 mm L_S); ZUFMS-PIS 5352 (1, 23·1 mm L_S), collected with the holotype. MZUSP 111582 (31, 14·3–28·8 mm L_S), Pará, Altamira, black water stream tributary to Rio Xingu, near Espelho Falls, 3° 42′ 32″ S; 52° 27′ 11″ W; 17 November 2011, O. Oyakawa, J. Birindelli, C. Moreira, A. Akama, L. Sousa & H. Varela. MZUSP 111700 (443, 14·3–27·0 mm L_S), Pará, Altamira, Rio Xingu at Pajé Beach, 3° 14′ 12″ S; 52°

FIG. 2. *Corydoras benattii* sp. nov., MZUSP 121671, holotype, 25·4 mm standard length, Brazil, Mato Grosso, Canarana–Gaúcha do Norte, Rio Culuene, tributary to Rio Xingu Basin.

13′ 21″ W; 8 November 2011, O. Oyakawa, J. Birindelli, C. Moreira, A. Akama, L. Sousa & H. Varela.

Non-types

All from Brazil, Rio Tapajós basin: MNRJ 35424 (1, 12·5–28·9 mm L_S, 16 c&s, 14·2–24·3 mm L_S), Mato Grosso, Guarantã do Norte, Strege Balneary, Braço Rio Norte, tributary to right margin of Rio Peixoto de Azevedo, a tributary to Rio Teles Pires, 9° 56′ 56″ S; 55° 2′ 9″ W; 2 October 2008, P. Buckup, J. Maldonado, J. Birindelli, C. Chamon & V. Felzman. MZUSP 116758 (5, 17·1–23·3 mm L_S), Pará, beach at Rio Cururu, 8° 53′ 42″ S; 57° 14′ 27″ W; 6 December 2005, A. Datovo,

FIG. 3. Juvenile specimen of *Corydoras benattii* sp. nov., MNRJ 35424, 12·5 mm standard length, Brazil, Mato Grosso, Guarantã do Norte, Rio Braço Norte, right bank tributary of the Rio Peixoto de Azevedo. Scale bar = 1·0 mm.

M. Carvalho & M. Rodrigues. MZUSP 116768 (1, 24·2 mm L_S), Pará, Rio Cururu, 8° 52′ 27″ S; 57° 15′ 9″ W; 6 December 2005, A. Datovo, M. Carvalho & M. Rodrigues. MZUSP 96764 (64, 15·3–28·7 mm L_S), Mato Grosso, Rio Peixoto de Azevedo, a tributary to Rio Teles Pires, 10° 17′ 14″ S; 54° 50′ 57″ W; 17 October 2007, J. Birindelli, L. Sousa, A. Netto-Ferreira, M. Sabaj-Pérez & N. Lujan. MZUSP 96584 (27, 17·8–26·8 mm L_S), Mato Grosso, Rio Peixoto de Azevedo, a tributary to Rio Teles Pires, 10° 13′ 14″ S; 54° 58′ 02″ W; 16 October 2007, J. Birindelli, L. Sousa, A. Netto-Ferreira, M. Sabaj-Pérez & N. Lujan. MZUSP 116653 (1, 21·2 mm L_S), Mato Grosso, Paranaíta, Rio São Benedito, a tributary to Rio Teles Pires, 9° 07′ 00″ S; 57° 00′ 35″ W; 12 January 2015, W. Ohara.

Diagnosis

Corydoras benattii can be distinguished from its congeners, with the exception of species from lineages 4, 5, 6, 7 and 9 *sensu* Alexandrou *et al.* (2011), by having a short mesethmoid with anterior tip poorly developed, smaller than 50% of bone length (*v.* mesethmoid long, with anterior tip well developed, larger than 50% of bone length), resulting in a blunt, short snout. From the species of lineages 4 and 5, with the exception of *Corydoras hastatus* Eigenmann & Eigenmann 1888 and *Corydoras pygmaeus* Knaack 1966, by having the posterior margin of the pectoral spine with serrations directed towards the spine tip or perpendicularly oriented (Fig. 4; *v.* directed towards spine origin); from *C. hastatus* and *C. pygmaeus* by having infraorbital 2 only in contact with sphenotic (Fig. 5; *v.* contacting sphenotic and compound pterotic). It differs from the species of lineage 7 by having the ventral laminar expansion of infraorbital 1 poorly or moderately developed (Fig. 5; *v.* well or very well developed). The new species can be distinguished from the species of lineage 6 and 9, with the exception of *Corydoras albolineatus* Knaack 2004, *Corydoras armatus* (Günther 1868), *Corydoras breei* Isbrücker & Nijssen 1992, *Corydoras loretoensis* Nijssen & Isbrücker 1986, *Corydoras osteocarus* Böhlke 1951, *Corydoras potaroensis* Myers 1927 and *C. xinguensis*, by having the flank midline covered by small dark brown or black saddles similar in size to remaining markings on the body (*v.* flank midline with longitudinal series of

TABLE I. Morphometric data of the holotype (MZUSP 121671) and 56 paratypes (MNRJ 50710, 2; MZUSP 87015, 14; MZUSP 111582, 10; MZUSP 111700, 30) of *Corydoras benattii* sp. nov.

	Holotype	Paratypes	Mean	S.D.
Standard length (L_S, mm)	25·4	21·1–29·1	25·6	1·8
Head length (L_H, mm)	12·0	8·6–13·5	11·0	0·9
% L_S				
Depth of body	33·7	30·0–35·7	34·3	1·6
Predorsal distance	48·7	45·3–50·2	49·8	1·8
Prepelvic distance	45·3	44·7–46·2	47·3	1·4
Preanal distance	77·3	75·4–79·8	80·5	1·8
Preadipose distance	77·7	75·4–84·4	81·8	1·7
Length of dorsal spine	31·0	21·7–29·6	27·2	2·5
Length of pectoral spine	32·1	24·3–29·1	30·3	2·4
Length of adipose-fin spine	9·6	7·7–9·5	10·9	1·3
Depth of caudal peduncle	15·6	14·0–16·1	15·6	0·8
Dorsal to adipose distance	17·6	16·0–22·7	19·9	1·6
Length of dorsal-fin base	16·5	16·6–20·8	19·5	1·5
Maximum cleithral width	10·7	6·7–10·5	9·2	1·1
Head length	47·4	33·6–43·4	43·2	2·3
Length of longer barbel	14·5	7·9–16·3	14·7	2·2
% L_H				
Head depth	66·9	65·0–78·7	74·9	4·5
Least interorbital distance	25·6	18·8–27·7	26·8	2·0
Horizontal orbit diameter	19·7	17·0–24·3	21·7	2·5
Snout length	32·8	29·2–40·6	34·4	2·5
Least internareal distance	16·5	14·3–21·5	18·2	2·2

large, dark brown or black blotches, clearly larger than remaining markings on body; or conspicuous longitudinal dark brown or black stripe). It differs from *C. albolineatus*, *C. loretoensis*, *C. osteocarus* and *C. potaroensis* by having caudal fin with conspicuous dark brown or black spots along its entire surface (*vs*. hyaline or with dark brown or black spots only on its proximal third in *C. loretoensis*; entirely hyaline in remaining species); from *C. armatus* and *C. xinguensis* by having clearly slender body (*v*. clearly robust).

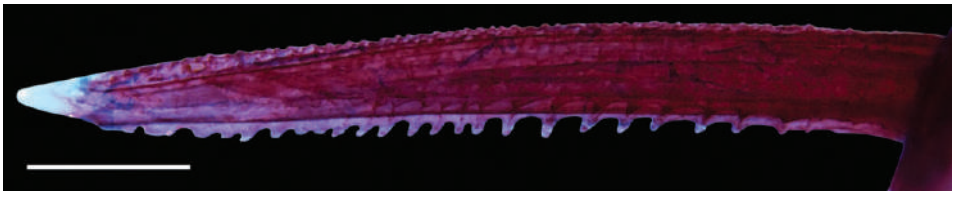

FIG. 4. Pectoral-fin spine of a cleared-and-stained specimen of *Corydoras benattii* sp. nov., MZUZP 87015, paratype, 22·1 mm standard length, showing serrations directed towards tip of spine or perpendicularly oriented on posterior margins of the right pectoral-fin spine (7·5 mm length). Scale bar = 1·0 mm.

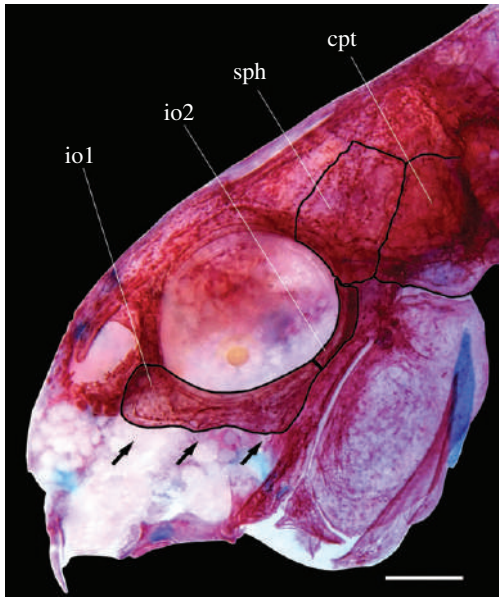

FIG. 5. Lateral view of the head of a cleared-and-stained specimen of *Corydoras benattii* sp. nov., MZUSP 87015, paratype, 22·1 mm standard length, showing infraorbital 2 (io2) only in contact with sphenotic (sph). A moderately ventral laminar expansion of infraorbital 1 (io1; ↑). cpt, Compound pterotic. Scale bar = 1·0 mm.

Corydoras benattii can be distinguished from *C. breei* by having the following combination of features: absence of conspicuous concentration of dark brown or black blotches along flank midline, forming longitudinal stripe (*v.* stripe variably present, fragmented in some specimens) and by slightly larger, scarcer and clearly more distant dark brown or black irregular spots on flanks (*v.* flanks densely covered by closely-spaced roundish dark brown or black spots). *Corydoras benattii* differs from *C. apiaka* by having strongly narrow frontals (*v.* relatively narrow but clearly thicker; see Britto, 2003:126, character 6, states 2 and 1, respectively).

Description

Measurements of holotype and paratypes in Table I. Head compressed (Fig. 2); roughly triangular in dorsal view. Rounded snout profile from upper lip to horizontal through anterior nares; bluntly round in juveniles (Fig. 3). Head profile slightly convex from upper lip to tip of parieto-supraoccipital expansion. Moderate ascent of dorsal profile nearly straight from nares to base of dorsal spine. Body concave from last dorsal-fin ray to base of adipose-fin spine; straight to slightly concave from that point to caudal-fin base. Ventral profile of body straight from isthmus to pelvic-fin origin, convex from that point to caudal-fin base. Body approximately triangular in cross section at pectoral girdle, gradually becoming more compressed toward caudal fin.

Eyes rounded, dorso-lateral on head; orbit bordered dorsally by frontal, lateral ethmoid and sphenotic, ventrally by infraorbitals. Anterior and posterior nares very close, only detached by flap of skin. Anterior naris tubular; fleshy flap. Posterior naris close to antero-dorsal margin of orbit, separated from orbit by distance slightly smaller

than naris diameter. Mouth small, subterminal; width nearly equal to bony orbit diameter. Maxillary barbel moderately developed, not reaching antero-ventral limit of gill opening. Outer mental barbel slightly larger than maxillary barbel. Inner mental barbel fleshy, with base close to its counterpart. Small rounded papillae scattered over entire surface of all barbels, upper and lower lips, snout and isthmus. Gill membranes united to isthmus.

Posterior portion of mesethmoid, frontal, sphenotic, compound pterotic and parieto-supraoccipital externally visible, covered by thin layer of skin and bearing minute scattered odontodes. Long frontal fontanel, ellipsoid, sheltered by thin layer of skin; posterior portion extending into parieto-supraoccipital. Nasal slender, curved laterally, mesial border contacting mesethmoid and frontal. Frontal rectangular; anterior expansion in contact with nasal bone, posterior portion bordered by sphenotic and parieto-supraoccipital. Posterior area of mesethmoid wide. Sphenotic somewhat trapezoidal in shape, contacting parieto-supraoccipital dorsally, compound pterotic posteriorly, second infraorbital ventrally and frontal anteriorly. Compound pterotic roughly pipe-shaped, with posterior expansion limited by first lateral-line ossicle. Ventral margin of compound pterotic coffined by opercle and cleithrum. Parieto-supraoccipital wide, posterior process well developed, contacting nuchal plate.

Two laminar infraorbitals with minute odontodes; infraorbital 1 large, ventral laminar expansion ranging from poorly to relatively well developed; anterior portion with moderately to well developed expansion, reaching to or slightly surpassing middle portion of nasal capsule; inner laminar expansion poorly developed (Fig. 5). Infraorbital 2 small, slender; with posterior laminar expansion from poorly to moderately developed; inner laminar expansion generally poorly developed; postero-ventral margin contacting postero-dorsal ridge of hyomandibula; dorsal tip contacting only sphenotic (Fig. 5). Postero-dorsal ridge of hyomandibula close to its articulation with opercle oblong; exposed, relatively slender; dorsal ridge of hyomandibula between compound pterotic and opercle exposed or covered by thinner to thicker layer of skin in some specimens; exposed areas bearing small odontodes. Interopercle entirely covered by thick layer of skin; posterior portion exposed in some specimens; somewhat triangular, anterior projection moderately developed. Preopercle relatively slender, elongated, minute odontodes sparse on external surface. Opercle slender in shape, width equal to or slightly smaller than half of its length; free margin convex; postero-dorsal region with smoothly concave area in some specimens; without serrations and covered by small odontodes; some portions of bony distal margin irregular in some specimens.

Four branchiostegal rays decreasing in size posteriorly. Hypobranchial 2 somewhat triangular, tip ossified and directed towards anterior portion, posterior margin cartilaginous; ossified portion well developed, about twice size of cartilaginous portion. Five ceratobranchials with increasing posterior expansions; ceratobranchial 1 with small process on anterior margin of mesial portion; ceratobranchial 3 notched on postero-lateral margin; ceratobranchial 5 toothed on postero-dorsal surface, 26–37(5) teeth aligned in one row. Four epibranchials with comparable size; epibranchial 2 slightly larger than others, with small pointed process on laminar expansion of posterior margin; epibranchial 3 with curved mesially uncinate process on laminar expansion of posterior margin. Two wide pharyngobranchials (3 and 4); pharyngobranchial 3 with irregular laminar expansion on posterior margin. Upper tooth plate oval; 27–44(5) teeth aligned in two rows on postero-ventral surface.

Trunk lateral line with two or three latero-sensory canals; two anteriormost canals reduced to small ossicles; first ossicle tubular, second ossicle laminar; third lateral-line canal, if present, encased in third dorso-lateral body plate. Lateral-line canal confined on neurocranium through compound pterotic, branching twice before entering sphenotic; pterotic and preoperculo-mandibular branches, each with single pore. Sensory canal passes along compound pterotic, through sphenotic as temporal canal, then splits into two branches: one branch rises to infraorbital canal, another branch passes through frontal and supraorbital canal. Single supraorbital canal, along nasal bone. Epiphyseal pore opening at supraorbital main canal. Nasal canal with three openings, first on posterior edge, second on postero-lateral portion and third on anterior edge; second pore generally fused with first pore. Infraorbital canal through entire infraorbital 2, extended to infraorbital 1 and opening into two or three pores. Preoperculo-mandibular branch emerges into preoperculo-mandibular canal, along entire preopercle with three openings (pores 3, 4 and 5, respectively).

Body plates with minute odontodes restricted to posterior margins. Nuchal plate exposed. Posterior extremity of cleithrum along vertical through dorsal-fin spinelet. Cleithrum and mesial process of scapulocoracoid exposed. Body plates not delimited by counterparts ventrally, instead, narrow naked area. Dorso-lateral body plates 22(21) or 23*(75); ventro-lateral body plates 20(12) or 21*(85); dorso-lateral body plates along dorsal-fin base six(18) or seven*(79); dorso-lateral body plates from adipose fin to caudal-fin base seven*(77) or eight(20); pre-adipose platelets two(16), three*(69), or four(12); small platelets positioned dorsally and ventrally between junctions of lateral plates on posterior portion of caudal peduncle. Anterior margin of orbit, above region of junction of frontal with lateral ethmoid, region of lateral ethmoid in ventral margin of nasal capsule and region of mesethmoid generally with small platelets; ventro-lateral portion of snout with platelets in some specimens. Ventral surface of trunk with scarce small and irregular platelets, generally restricted to pectoral girdle area; this area naked in some specimens.

Dorsal fin roughly triangular, located just posterior to second dorso-lateral body plate. Dorsal spine shorter than first branched ray. Anterior border of dorsal spine with odontodes; posterior border with 10–24 minute serrations. Dorsal-fin rays II,7(15) or II,8*(82). Adipose fin roughly triangular, separated from base of last dorsal-fin ray by six dorso-lateral body plates in all specimens. Anal fin roughly triangular, located just posterior to 13th ventro-lateral body plate and at vertical through anterior margin of adipose-fin spine. Anal fin with eight rays in all specimens, ii,5,i or ii,6*. Pectoral fin triangular, its origin located just posterior to gill opening. Ossified portion of pectoral spine shorter than first branched ray. Distal tip of spine with minute, segmented, unossified portion. Pectoral spine with 15–27 relatively small serrations along almost entire posterior border (Fig. 4). Pectoral serrations more developed than those of dorsal spine; directed towards tip of spine; presence of perpendicularly directed and bifid serrations in some specimens (Fig. 4). Pectoral-fin rays I,7 in all specimens. Pelvic fin ellipsoid, at horizontal position just below first ventro-lateral body plate and at vertical through first branched dorsal-fin ray. Pelvic-fin rays i,5 in all specimens. Caudal fin forked; upper lobe slightly longer. Principal caudal-fin rays i,6/6,i in all specimens, with generally four dorsal and ventral procurrent rays. All fins with minute odontodes scattered over all rays. Vertebral count 21(5); ribs five(4) or six(1), first pair conspicuously larger than others.

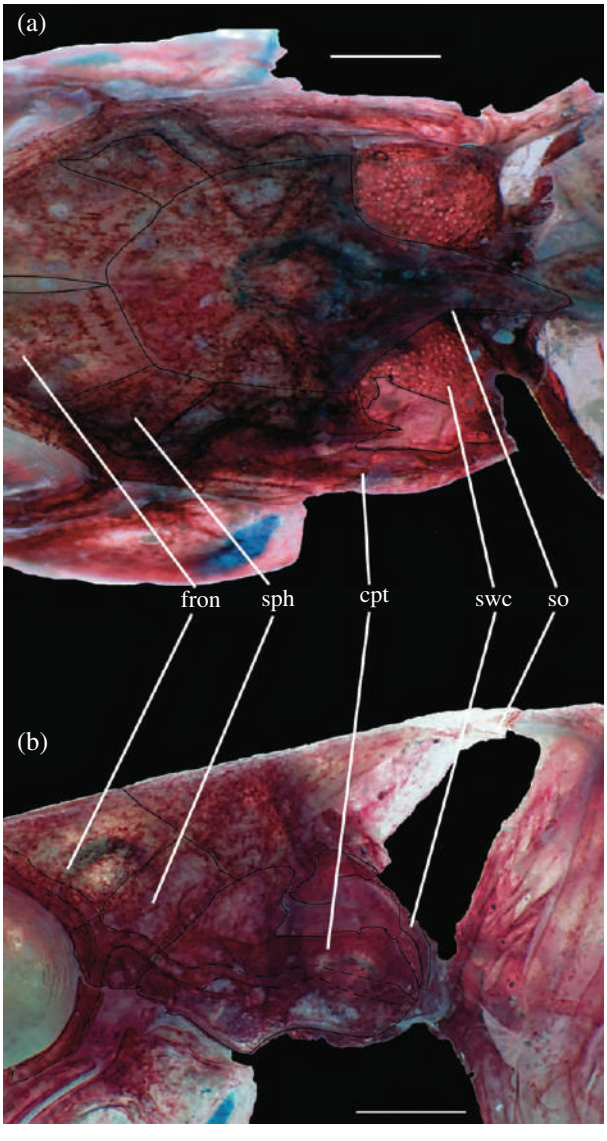

FIG. 6. Mid-posterior part of head of cleared-and-stained specimen of (a) dorsal, (b) lateral views of *Corydoras benattii* sp. nov., MZUSP 87015, paratype, 22·1 mm standard length, showing swimbladder capsule (swc) and associated structures. Traced lines indicate the cephalic lateral line canal. fron, Frontal; sph, sphenotic; cpt, compound pterotic; so, parieto-supraoccipital. Scale bar = 1·0 mm.

Weberian apparatus and swimbladder capsule

Complex vertebra relatively compact. Swimbladder capsule bullae-like with dorsal elevation (Fig. 6). Lateral opening circular, similar diameter to proximal portion and partially occluded by compound pterotic. Cleithrum near to swimbladder capsule lateral opening. Transverse canal between bullae and near medial portion of swimbladder capsule. Swimbladder capsule posterior portion free from bone elements. Ventral

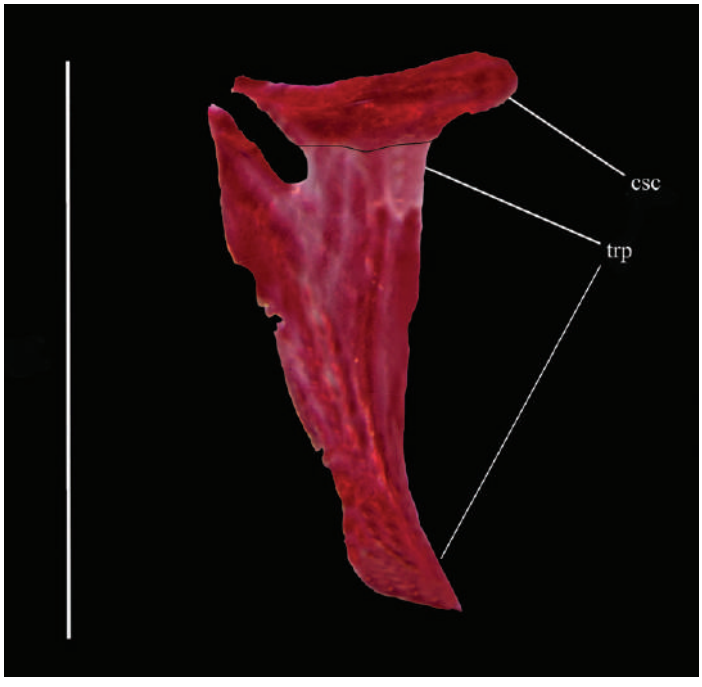

FIG. 7. Weberian apparatus of cleared-and-stained specimen of *Corydoras benattii* sp. nov., MZUSP 87015, paratype, 27·4 mm standard length. csc, Concha scaphium; tr, tripus. Scale bar = 0·5 mm.

suture of swimbladder capsule and basioccipital diagonal to transverse canal between bullae foramina; ventral suture limited by transverse canal between bullae suture and basioccipital. Transverse canal between bullae larger than complex vertebra width. Pneumatic duct absent. Transverse canal between bullae foramina under swimbladder capsule, near medial portion and distant from complex vertebra. Support bone process from aortic canal sheath robust. Ventral apophysis under both swimbladder capsule and complex vertebra; anterior to transverse canal and among bullae, complex vertebra and bone process support of aortic canal sheath. Sixth vertebra articulated with fifth vertebra. Fifth and sixth vertebra parapophyses fused. Weberian apparatus inside complex vertebra; concha scaphium connected to endolymphatic sinus; tripus proximal portion connected to concha scaphium (Fig. 7); tripus distal portion with thin expansion, nearly straight angle and connected to swimbladder through capsule foramen.

Gross brain morphology

Lobus vagi expanded in size with roughly spherical format (Fig. 8). Subunit larger than corpus cerebelli, but smaller than tectum mesencephali and with anterior tip rounded and above posterior portion of lobus facialis (Fig. 9). Bilateral lobus facialis detached to medial margin of fourth ventricle and discontinuous to lobus vagi. Subunit ventrally positioned and almost completely covered by corpus cerebelli, with postero-lateral tip exposed in dorsal view. Subunit roughly divided in three regions: medial (smallest); intermediate; and lateral (largest). Latter extended and with lateral area above lobus vestibulolateralis. Corpus cerebelli roughly spherical

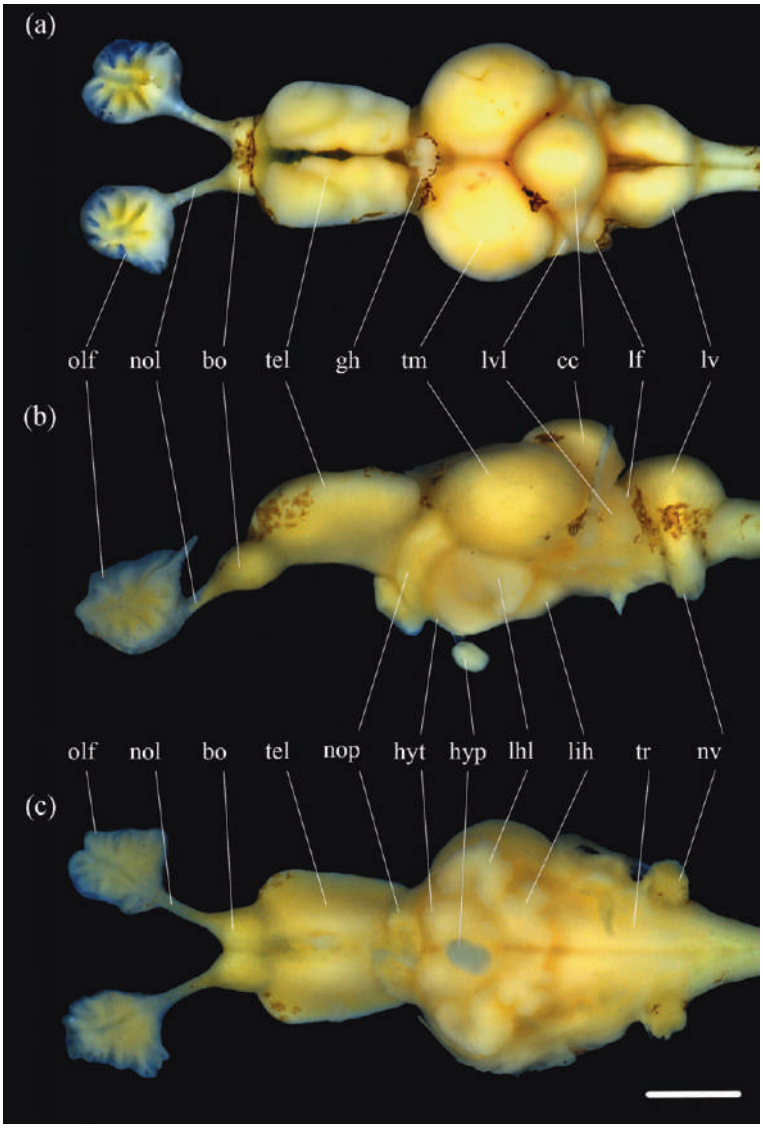

FIG. 8. (a) Dorsal, (b) lateral and (c) ventral views of the brain and associated olfactory organ of *Corydoras benattii* sp. nov., MNRJ 35424, 27·5 mm standard length. bo, Bulbus olfactorius; cc, corpus cerebelli; gh, ganglion habenulae; hyp, hypophysis; hyt, hypothalamus; lf, lobus facialis; lhl, lobus hypothalami lateralis; lih, lobus inferior hypothalami; lv, lobus vagi; lvl, lobus vestibulolateralis; nol, nervus olfactorius; nop, nervus opticus; nv, nervus vagi; olf, olfactory organ; tel., telencephalon; tm, tectum mesencephali; tr, tegmentum rhombencephali. Scale bar = 1·0 mm.

and smaller than tectum mesencephali and lobus vagi. Subunit in contact with tectum mesencephali and positioned in central part of brain above lobus facialis. Tectum mesencephali largest subunit of brain in dorsal view; bilateral dome located on dorsal surface of tegmentum mesencephali. Nervus opticus more than three times thicker than nervus olfactorius. Hypothalamus most conspicuous external subunit

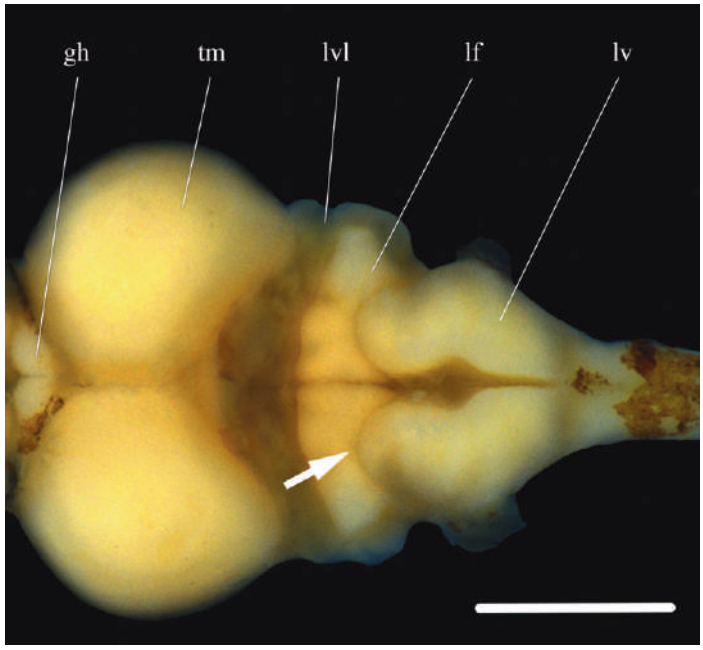

FIG. 9. Posterior half of brain of *Corydoras benattii* sp. nov., MNRJ 35424, 31·52 mm standard length, without corpus cerebelli, showing the lobus facialis (lf) in dorsal view. Arrow indicates the anteriormost margin of the lobus vagi (lv) above the posterior region of the lobus facialis. gh, Ganglion habenulae; lvl, lobus vestibulolateralis; tm, tectum mesencephali. Scale bar = 1·0 mm.

in ventral view and posteriorly positioned to chiasma opticum, ventral to tectum mesencephali and truncus cerebri. Subunit divided in hypothalamus itself, lobus lateralis hypothalami and lobus inferior hypothalami. Latter with invagination located in posterior margin. Hypophysis spherical and anteriorly anchored to lobus inferior hypothalami and above hypothalamus. Telencephalon located on dorsal surface of brain as bilaterally-elongated structure, posterior to bulbus olfactorius and anterior to tectum mesencephali; anterior area somewhat wider in dorsal view and lateral margin almost straight. Bulbus olfactorius sessile and spherical, with posterior area ventrally positioned on anterior tip of telencephalon. Nervus tractus olfactorius absent. Olfactory organ circular with <15 lamellae and connected to bulbus olfactorius *via* nervus olfactorius. Posterior lamellae with small flap toward dorsal surface and larger than anterior lamellae. Nervus olfactorius length about twice of bulbus olfactorius diameter.

Colour in alcohol

Overall colour pattern in Fig. 2. Ground colour of body light or brownish yellow, with top of head dark brown. Dorsal and lateral portions of head with scattered small roundish or irregular dark-brown or black spots. Region between antero-ventral margin of infraorbital 1 and lateral portion of mouth and between postero-ventral portion of infraorbital 1 and antero-ventral portion of opercle with concentration of dark brown or black chromatophores in some specimens. Upper lip, maxillary barbel, opercle and cleithrum generally with dark brown or black chromatophores. Dorso and ventro-lateral body plates with dark brown or black chromatophores,

generally forming small roundish or irregular spots; region around pelvic-fin origin lacking chromatophores; dorso-lateral body plates on regions of anterior and posterior portion of dorsal-fin base, adipose-fin base and caudal-fin base with more concentrated chromatophores in some specimens. Midline of flank with somewhat aligned dark-brown or black blotches, forming longitudinal series; slightly larger than remaining blotches on flanks. Dorsal fin covered by dark brown or black small roundish or irregular spots; spine covered by dark-brown or black chromatophores. Pectoral fin with sparse dark-brown or black chromatophores, generally more evident on spine; hyaline in some specimens. Pelvic fin hyaline. Adipose fin with dark-brown or black chromatophores, generally more concentrated on spine; membrane hyaline in some specimens. Anal fin with dark-brown or black chromatophores, generally restricted to proximal portion. Middle portion of caudal-fin base generally with small dark-brown or black spot; diffuse in some specimens; Caudal fin covered by small dark-brown or black spots, forming up to seven slender transverse bars.

Colour in life

Based on field observations, photographs and aquarium specimens. Similar to preserved specimens but with ground colour of body greyish yellow. Region between antero-ventral margin of infraorbital 1 and lateral portion of mouth and between postero-ventral portion of infraorbital 1 and antero-ventral portion of opercle generally with conspicuously concentrated dark-brown or black chromatophores. Body covered by greenish yellow iridescent coloration (Fig. 1).

Sexual dimorphism

Males have urogenital papilla, as is usual for corydoradine catfishes (Nijssen & Isbrücker, 1980; Britto, 2003).

Geographical distribution

Corydoras benattii occurs in both the Rio Xingu and Rio Tapajós basins, Brazilian Amazon (Fig. 10). In the Rio Xingu basin, it is known in Mato Grosso State from tributaries to the Rio Culuene, a clearwater tributary of the upper Rio Xingu (type locality) and in Pará State from the Rio Fresco sub drainage (Rio Trairão and Igarapé Manguari), middle Rio Xingu and from the lower Rio Xingu basin near Altamira. In the Rio Tapajós basin, it occurs in the Rio Peixoto de Azevedo, a tributary to the Rio Teles Pires, Mato Grosso and from Rio Cururu, a tributary to the Rio São Manuel, Pará.

Habitat notes

Specimens of *Corydoras benattii* were found in lotic habitats in the Rio Culuene, Rio Xingu basin and Rio Braço Norte, tributary to Rio Peixoto de Azevedo, Rio Tapajós basin (Fig. 11). Both localities have muddy-brown water with clay and sandy substrata. Most specimens were captured in the small forest streams of black or clearwater, or in marginal ponds.

Specimens from the Rio Braço Norte were caught on 2 October 2008, around 1100 hours, with air temperature 32° C and from water with the following

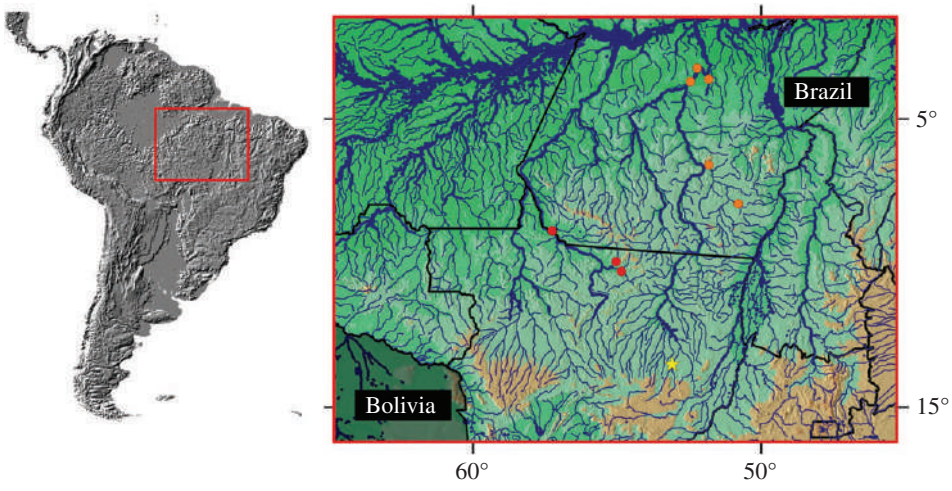

FIG. 10. Geographic distribution of *Corydoras benattii* sp. nov. Type locality in Rio Culuene, a tributary of the upper Xingu Basin, Mato Grosso (☆), and paratype localities in middle and lower Rio Xingu, Pará State (●). Non-type localities in Rio Tapajós basin, Mato Grosso and Pará states (●).

physic-chemical variables: pH 6·52, conductivity 0·092 μS cm^{-1} and water temperature 30·1° C.

Etymology

The specific name, *benattii*, honours the late Laert Benatti for his humanitarian work, providing fresh water from artesian wells to poor communities in Brazil. Case is genitive.

Remarks

As mentioned by Tencatt & Evers (2016), the Corydoradinae are very popular in the aquarium hobby, being kept and reproduced for many decades by hobbyists around the world. Some species in the ornamental fish trade are recognized for the difficulty in determining their taxonomic status among those already described. To avoid the creation of nomina nuda by using trade names, Evers (1993) implemented a code system for putative new species, giving each of them a C-number (where C stands for Corydoradinae) published in the Die Aquarien- und Terrarienzeitschrift (DATZ) German aquarist magazine. After the C-number coding was finished with by DATZ magazine with C159, this labelling system was taken over by the *Corydoras World* website (www.corydorasworld.com) and changed to a CW-number coding (where CW stands for *Corydoras World*), which restarted the count to include the many new morphotypes known in the aquarium trade.

Corydoras benattii is already known in the hobby under the code C22 (Evers, 1994; Glaser *et al.,* 1996; Evers & Schäfer, 2004; Füller & Evers, 2005). Specimens of *C. benattii* captured in the Rio Itata, a tributary to the Rio Xingu near Altamira, Pará have been spawned and reared under aquarium conditions by H. Evers, who provided photos of its fry with 1 and 4 weeks of life (Fig. 12), showing colour pattern variation during initial stages of growth.

FIG. 11. Habitats of *Corydoras benattii* sp. nov. in (a) Rio Culuene, Xingu Basin, 13° 30′ 52″ S; 53° 05′ 34″ W, type locality, and (b) Strege Balneary, Rio Braço Norte, a tributary of the Rio Peixoto de Azevedo, Tapajós Basin, 9° 56′ 56″ S; 55° 2′ 9″ W, both in Mato Grosso State, Brazil.

DISCUSSION

The molecular phylogenetic hypothesis of Alexandrou *et al.* (2011) revealed nine lineages of Corydoradinae species. *Corydoras benattii* presents a general morphological pattern most similar to the species of lineage 9 *sensu* Alexandrou *et al.* (2011), with characteristics such as: the presence of a short mesethmoid; posterior margin of the pectoral-fin spine with serrations generally directed towards the tip of the spine; infraorbital 1 generally with moderately developed ventral laminar expansion; infraorbital 2 generally not contacting compound pterotic, as cited by Tencatt & Britto (2016) and Tencatt & Ohara (2016). Even though lineage 6 has a similar general morphological pattern as lineage 9, the assignment of *C. benattii* to lineage 6 is less plausible as all species of that clade exhibit a distinctive colour pattern on the midline

FIG. 12. Fry development of *Corydoras benattii* sp. nov. bred under aquarium conditions, showing the general morphological and colour patterns after (a) 1 and (b) 4 weeks post-hatch.

of the flank (Tencatt *et al.,* 2016) not observed in the new species. Additionally, regarding general morphological and colour patterns, the two species most similar to *C. benattii* (*i.e*., *C. loretoensis* and *C. osteocarus*) are among the members of lineage 9.

Regarding gross brain morphology, the increase in size of the lobus vagi among Siluriformes occurs in Callichthyidae and, probably independently, in other lineages [*e.g*. Claroteidade, Plotosidae, Loricariinae, *Conorhynchos conirostris* (Valenciennes 1840)] (Pupo, 2015). This area innervates chemical and mechanical taste buds present in the oropharyngeal cavity indicating an enhancement of the sense of taste (Butler & Hodos, 2005). Together with a large lobus facialis, which enervates taste buds on body, fins, lips and barbels, it seems likely that this species has an enhanced sense of taste. The tectum mesencephali size and the optic nerve (cranial nerve II) thickness represent an enhancement in the vision sense in *Corydoras*. Pupo (2011) noticed that some *Corydoras* species have a large tectum mesencephali and optic nerve gauge when compared to other Callichthyidae. *Corydoras benattii* has both features. Nevertheless, this paper is not intended to make precise phylogenetic inferences using these structures and those from the swimbladder capsule and Weberian apparatus, but to present a preliminary description to encourage further research.

According to Dagosta & de Pinna (2017), numerous teleost species occur in both the Rio Tapajós and Rio Xingu basins. These authors suggest that the lower Rio Tapajós basin is more ichthyologically similar to other Amazonian basins than to the remainder of the Xingu–Tapajos ecoregion. Notwithstanding, *Corydoras benattii* has not been recorded from the lower Rio Tapajós basin, which corroborates the Dagosta & de Pinna (2017) hypothesis. Although the Xingu–Tapajos ecoregion does not constitute a biogeographical unit (Dagosta & de Pinna, 2017), the Simpson's faunistic similarity indices between the Rio Xingu and Rio Tapajós basins is about 53·8% (Buckup *et al.,* 2011). It indicates the two regions share a similar biogeographical history.

Knowledge about the distribution of this new species brings additional information to help understand the historical biogeography of this enigmatic ecoregion.

ADDITIONAL SPECIMENS EXAMINED

Corydoras acutus Cope 1872: MNRJ 3985 (2, 47·1–54·8 mm L_S). *Corydoras adolfoi* Burgess 1982: MZUSP 26641 (holotype, 32·5 mm L_S). *Corydoras albolineatus* Knaack 2004: MNRJ 33864 (5, 21·7–27·2 mm L_S). *Corydoras ambiacus* Cope 1872: MCP 26178 (1, 42·5 mm L_S); MCP 26209 (10 of 19, 25·0–33·3 mm L_S); MZUSP 26053 (2, 41·8–47·2 mm L_S). *Corydoras apiaka* Espíndola, Spencer, Rocha & Britto 2014: MNRJ 40720 (holotype, 28·4 mm L_S); MNRJ 23334 (paratype, 1, 31·6 mm L_S). *Corydoras approuaguensis* Nijssen & Isbrücker 1983: MZUSP 27895–6 (paratypes, 2, 43·0–46·1 mm L_S). *Corydoras araguaiaensis* Sands 1990: MZUSP 87155 (4 of 33, 24·9–46·7 mm L_S, 2 c&s, 27·6–31·8 mm L_S); MZUSP 86248 (7, 36·2–54·6 mm L_S). *Corydoras areio* Knaack 2000: ZUFMS-PIS 1314 (15, 34·4–41·9 mm L_S, 2 c&s, 38·1–38·5 mm L_S). *Corydoras armatus* (Günther 1868): MNRJ 38436 (12, 28·5–40·9 mm L_S); MZUSP 49567 (1, 45·3 mm L_S). *Corydoras aurofrenatus* Eigenmann & Kennedy 1903: NRM 23529 (10 of 33, 31·4–45·7 mm L_S). *Corydoras cervinus* Rössel 1962: MNRJ 33867 (1, 44·6 mm L_S). *Corydoras bifasciatus* Nijssen 1972: MZUSP 38976 (paratypes, 16, 23·6–30·0 mm L_S). *Corydoras blochi* Nijssen 1971: MZUSP 8580 (paratypes, 3, 31·0–42·6 mm L_S). *Corydoras bondi* Gosline 1940: ROM 66202 (7 of 134, 33·8–39·9 mm L_S, 3 c&s, 36·7–38·6 mm L_S). *Corydoras brevirostris* Fraser-Brunner 1947: LBP 3080 (10, 23·8–27·7 mm L_S, 3 c&s, 25·8–27·9 mm L_S). *Corydoras britskii* (Nijssen & Isbrücker 1983): ZUFMS-PIS 862 (12, 72·0–78·0 mm L_S). *Corydoras brittoi* Tencatt & Ohara 2016: MNRJ 43316 (holotype, 38·1 mm L_S). *Corydoras carlae* Nijssen & Isbrücker 1983: NUP 711 (1, 47·9 mm L_S); NUP 4425 (1 c&s, 45·0 mm L_S). *Corydoras cochui* Myers & Weitzman 1954: MZUSP 35838 (4 of 6, 16·1–18·5 mm L_S); MZUSP 89055 (6, 18·7–23·6 mm L_S). *Corydoras condiscipulus* Nijssen & Isbrücker, 1980: MZUSP 38957 (paratypes, 7, 34·1–40·3 mm L_S). *Corydoras coppenamensis* Nijssen 1970: MZUSP 13995-99 (paratypes, 5, 29·31–37·60 mm L_S). *Corydoras crimmeni* Grant 1997: MZUSP 52490 (holotype, 36·1 mm L_S). *Corydoras davidsandsi* Black 1987: MZUSP 110066 (4 of 40, 36·0–41·9 mm L_S, 2 c&s, 40·9–42·1 mm L_S). *Corydoras difluviatilis* Britto & Castro 2002: MZUSP 75268 (holotype, 39·8 mm L_S). *Corydoras diphyes* Axenrot & Kullander 2003: ANSP 169756 (2, 40·7–43·1 mm L_S). *Corydoras ehrhardti* Steindachner 1910: NUP 11255 (15, 36·5–46·8 mm L_S). *Corydoras elegans* Steindachner 1876: MZUSP 26017 (6, 25·9–28·3 mm L_S). *Corydoras ephippifer* Nijssen 1972: MZUSP 31605 (2, 44·9–49·1 mm L_S). *Corydoras eques* Steindachner 1876: MCZ 8204 (4 of 12, 37·6–44·4 mm L_S). *Corydoras eversi* Tencatt & Britto, 2016: MNRJ 43195 (holotype, 44·5 mm L_S). *Corydoras flaveolus* Ihering 1911: MZUSP 424 (holotype, 33·4 mm L_S); MZUSP 111174 (7, 24·2–37·5 mm L_S). *Corydoras fowleri* Böhlke 1950: LBP 12462 (9, 44·3–59·9 mm L_S, 1 c&s, 50·4 mm L_S). *Corydoras garbei* Ihering 1911: MNRJ 18089 (14, 19·2–25·3 mm L_S, 2 c&s, 25·9–27·4 mm L_S). *Corydoras geoffroy* Lacépède 1803: MZUSP 38984 (paratypes, 2, 38·7–45·2 mm L_S). *Corydoras gossei* Nijssen 1972: MZUSP 38977 (paratypes, 6, 48·4–53·4 mm L_S). *Corydoras griseus* Holly 1940: MZUSP 108896 (4 of 13, 31·5–36·2 mm L_S, 2 c&s, 30·6–34·5 mm L_S). *Corydoras guapore* Knaack 1961: ZUFMS-PIS 4000 (5,

26·9–33·6 mm L_S, 2 c&s, 28·8–29·2 mm L_S). *Corydoras gryphus* Tencatt, Britto & Pavanelli 2014: MNRJ 40770 (holotype, 32·3 mm L_S); NUP 14676 (paratypes, 3 c&s, 27·7–32·4 mm L_S). *Corydoras haraldschultzi* Knaack 1962: MZUSP 94996 (299, 31·9–56·1 mm L_S). *Corydoras hastatus* Eigenmann & Eigenmann 1888: NUP 6862 (116, 13·1–20·7 mm L_S). *Corydoras hephaestus* Tencatt & Britto, 2016: MZUSP 119087 (holotype, 22·6 mm L_S). *Corydoras incolicana* Burgess 1993: MZUSP 45717 (holotype, 47·6 mm L_S). *Corydoras julii* Steindachner 1906: MNRJ 33869 (40, 21·2–28·6 mm L_S); MNRJ 33870 (4, 24·5–29·4 mm L_S); NUP 16225 (1, 46·8 mm L_S). *Corydoras kanei* Grant 1998: MZUSP 52489 (holotype, 36·6 mm L_S). *Corydoras knaacki* Tencatt & Evers 2016: MUSM 52730 (holotype, 35·6 mm L_S). *Corydoras lacrimostigmata* Tencatt, Britto & Pavanelli 2014: MNRJ 40725 (holotype, 31·8 mm L_S); NUP 14657 (paratypes, 3 c&s, 30·9–34·5 mm L_S). *Corydoras longipinnis* Knaack 2007: AI 221 (holotype, 59·5 mm L_S). NUP 14440 (2 c&s, 29·9–33·4 mm L_S). *Corydoras loretoensis* Nijssen & Isbrücker 1986: MNRJ 19960 (paratypes, 2, 32·2–34·2 mm L_S, 2 c&s, 31·0–31·2 mm L_S). *Corydoras lymnades* Tencatt, Vera-Alcaraz, Britto & Pavanelli 2013: MNRJ 15765 (6, 15·8–17·7 mm L_S, 2 c&s, 18·1–18·4 mm L_S). MNRJ 40186 (holotype, 29·7 mm L_S). *Corydoras maculifer* Nijssen & Isbrücker 1971: NUP 8970 (2, 42·0–46·0 mm L_S); MZUSP 89320 (1, 35·2 mm L_S). *Corydoras melanistius* Regan 1912: BMNH 1864·1·21·86, (lectotype, 35·0 mm L_S). *Corydoras melini* Lönnberg & Rendahl 1930: MZUSP 81163 (2, 37·0–45·0 mm L_S). *Corydoras multimaculatus* Steindachner 1907: MCP 29025 (2, 20·1–25·4 mm L_S); MNRJ 16118 (6, 19·9–24·5 mm L_S); MZUSP 40183 (13, 21·6–31·1 mm L_S). *Corydoras napoensis* Nijssen & Isbrücker 1986: MZUSP 26341 (paratype, 1, 27·8 mm L_S). *Corydoras nattereri* Steindachner 1876: MZUSP 110255 (4 of 31, 32·0–32·8 mm L_S, 2 c&s, 32·3–34·4 mm L_S). *Corydoras panda* Nijssen & Isbrücker 1971: ROM 55815 (6, 26·5–39·7 mm L_S). *Corydoras pantanalensis* Knaack 2001: NUP 10188 (1 c&s, 46·4 mm L_S); NUP 12593 (21, 38·7–51·2 mm L_S). *Corydoras parallelus* Burgess 1993: MZUSP 45716 (holotype, 47·4 mm L_S). *Corydoras pavanelliae* Tencatt & Ohara 2016: MNRJ 43317 (holotype, 45·1 mm L_S). *Corydoras pinheiroi* Dinkelmeyer 1995: MZUSP 48099 (holotype, 54·3 mm L_S). *Corydoras polystictus* Regan 1912: MNRJ 12418 (9, 13·1–24·2 mm L_S). *Corydoras potaroensis* Myers 1927: ROM 61526 (3 of 15, 35·0–44·8 mm L_S, 2 c&s, 32·6–35·1 mm L_S). *Corydoras pygmaeus* Knaack 1966: MZUSP 26344 (4, 13·5–20·0 mm L_S). *Corydoras reticulates* Fraser-Brunner 1938: MZUSP 28752 (3, 37·3–45·1 mm L_S). *Corydoras robineae* Burgess 1983: MZUSP 27175 (holotype, 33·7 mm L_S). *Corydoras sarareensis* Dinkelmeyer 1995: MZUSP 48100 (holotype, 40·9 mm L_S). *Corydoras septentrionalis* Gosline 1940: MZUSP 27953 (12, 28·7–41·9 mm L_S). *Corydoras seussi* Dinkelmeyer 1996: MZUSP 49323 (paratypes, 10, 44·3–54·0 mm L_S). *Corydoras similis* Hieronimus 1991: LBP 10648 (7, 21·4–34·3 mm L_S). *Corydoras splendens* (Castelnau 1855): NUP 12990 (1, 43·7 mm L_S); NUP 10195 (1 c&s, 54·6 mm L_S). *Corydoras stenocephalus* Eigenmann & Allen 1942: MNRJ 3625 (3, 31·2–62·3 mm L_S). *Corydoras sterbai* Knaack 1962: MZUSP 94998 (1, 39·9 mm L_S). *Corydoras treitlii* Steindachner 1906: NUP 16224 (3, 21·5–45·6 mm L_S). *Corydoras trilineatus* Cope 1872: MZUSP 30857 (3 of 25, 40·9–44·1 mm L_S, 2 c&s, 44·2–43·8 mm L_S). *Corydoras tukano* Britto & Lima, 2003: MZUSP 82100 (holotype, 40·9 mm L_S). *Corydoras xinguensis* Nijssen 1972: MNRJ 24871 (1, 48·0 mm L_S); MZUSP 38974 (paratype, 1, 31·8 mm L_S); MZUSP 38980 (paratype, 1, 24·7 mm L_S); MZUSP 116030, (2, 26·0–32·1 mm L_S); MZUSP 38987 (paratype, 1, 37·1 mm L_S). *Corydoras zawadzkii* Tencatt & Ohara 2016: MNRJ 45565

(holotype, 48·7 mm L_S); NUP 17824 (paratype, 1 c&s, 39·9 mm L_S). *Corydoras zygatus* Eigenmann & Allen 1942: MZUSP 30858 (4 of 15, 41·7–47·3 mm L_S).

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References

Abell, R., Thieme, M. L., Revenga, C., Bryer, M., Kottelat, M., Bogutskaya, N., Coad, B., Mandrak, N., Contreras-Balderas, S., Bussing, W., Stiassny, M. L. J., Skelton, P., Allen, G. R., Unmack, P., Naseka, A., Ng, R., Sindorf, N., Robertson, J., Armijo, E., Higgins, J. V., Heibel, T. J., Wikramanayake, E., Olson, D., Lópes, H. L., Reis, R. E., Lundberg, J. G., Sabaj-Pérez, M. H. & Petry, P. (2008). Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *Bioscience* **58,** 403–414. https://doi.org/10.1641/B580507

Abrahão, V. P. & Pupo, F. M. R. S. (2014). Técnica de dissecção do neurocrânio de Siluriformes para estudo do encéfalo. *Boletim Sociedade Brasileira Ictiologia* **112,** 21–26.

Abrahão, V. P. & Shibatta, O. A. (2015). Gross morphology of the brain of *Pseudopimelodus bufonius* (Valenciennes, 1840) (Siluriformes: Pseudopimelodidae). *Neotropical Ichthyology* **13,** 255–264. https://doi.org/10.1590/1982-0224-20130219

Albert, J. S. (2001). Species diversity and phylogenetic systematics of American knifefishes (Gymnotiformes, Teleostei). *Miscellaneous Publications of the Museum of Zoology* **190,** 1–127.

Alexandrou, M. A., Oliveira, C., Maillard, M., McGill, R. A. R., Newton, J., Creer, S. & Taylor, M. I. (2011). Competition and phylogeny determine community structure in Mullerian co-mimics. *Nature* **469,** 84–89. https://doi.org/10.1038/nature09660

Aquino, A. E. & Schaefer, S. A. (2002). The temporal region of the cranium of loricarioid catfishes (Teleostei: Siluriformes): morphological diversity and phylogenetic significance. *Zoologischer Anzeiger* **241,** 223–244. https://doi.org/10.1078/0044-5231-00071

Arratia, G. & Gayet, M. (1995). Sensory canals and related bones of Tertiary siluriform crania from Bolivia and North America and comparison with recent forms. *Journal of Vertebrate Paleontology* **15,** 482–505.

Birindelli, J. L. O. & Shibatta, O. A. (2011). Morphology of the gas bladder in bumblebee catfishes (Siluriformes, Pseudopimelodidae). *Journal of Morphology* **272,** 890–896. https://doi.org/10.1002/jmor.10961

Birindelli, J. L. O., Sousa, L. M. & Pérez, M. H. (2009). Morphology of the gas bladder in thorny catfishes (Siluriformes: Doradidae). *Proceeding of the Academy of Natural Sciences of Philadelphia* **158,** 261–296. https://doi.org/10.1635/053.158.0114

Birindelli, J. L. O., Akama, A. & Britski, H. A. (2012). Comparative morphology of the gas bladder in driftwood catfishes (Siluriformes: Auchenipteridae). *Journal of Morphology* **273,** 651–660. https://doi.org/10.1002/jmor.20012

Britto, M. R. (2003). Phylogeny of the subfamily Corydoradinae Hoedeman, 1952 (Siluriformes: Callichthyidae), with a definition of its genera. *Proceedings of the Academy of Natural Sciences of Philadelphia* **153,** 119–154. https://doi.org/10.1635/0097-3157(2003)153(0119:POTSCH)2.0.CO;2

Britto, M. R. & Lima, F. C. T. (2003). *Corydoras tukano*, a new species of corydoradine catfish from the Rio Tiquié, upper Rio Negro basin, Brazil (Ostariophysi: Siluriformes: Callichthyidae). *Neotropical Ichthyology* **1,** 83–91. https://doi.org/10.1590/S1679-62252003000200002

Buckup, P. A., Britto, M. R., Gomes, J. R., Birindelli, J. L. O., Lima, F. C. T., Maldonado-Ocampo, J. A., Zawadzki, C. H., Carvalho, F. R., Jerep, F. C., Chamon, C. C., Fries, L. C. C., Villa-Verde, L., Camargo, M., Souza-Lima, R., Bartolette, R. & Wingert, J. M. (2011). Inventário da ictiofauna da ecorregião aquática Xingu–Tapajós. In *Ecorregião Aquática Xingu-Tapajós* (Castilhos, Z. C. & Buckup, P. A., eds), pp. 163–174. Rio de Janeiro: CETEM/MCT.

Butler, A. B. & Hodos, W. (2005). *Comparative Vertebrate Neuroanatomy. Evolution and Adaptation*, 2nd edn. Hoboken, NJ: John Wiley & Sons.

Castilhos, Z. C. & Buckup, P. A. (2011). *Ecorregião Aquática Xingu-Tapajós*. Rio de Janeiro: CETEM/MCT.

Chardon, M. (1968). *Anatomie Comparée de L′ Appareil de Weber et des Structures Connexes chez les Siluriformes*, Serie In-8, Vol. 169. Tervuren: Annales du Musée Royale de l′ Afrique Centrale – Sciences Zoologiques.

Dagosta, F. C. P. & de Pinna, M. C. C. (2017). Biogeography of Amazonian fishes: deconstructing river basins as biogeographic units. *Neotropical Ichthyology* **15,** e170034. https://doi.org/10.1590/1982-0224-20170034

Datovo, A. & Vari, R. P. (2014). The adductor mandibulae muscle complex in lower teleostean fishes (Osteichthyes: Actinopterygii): comparative anatomy, synonymy and phylogenetic implications. *Zoological Journal of the Linnean Society* **171,** 554–622. https://doi.org/10.1111/zoj.12142

Eastman, J. T. & Lannoo, M. J. (1995). Diversification of brain morphology in Antarctic notothenioid fishes: basic descriptions and ecological considerations. *Journal of Morphology* **223,** 47–83. https://doi.org/10.1002/jmor.1052230107

Eastman, J. T. & Lannoo, M. J. (2001). Anatomy and histology of the brain and sense organs of the Antarctic eel cod *Muraenolepis microps* (Gadiformes; Muraenolepididae). *Journal of Morphology* **250,** 34–50. https://doi.org/10.1002/jmor.1057

Eastman, J. T. & Lannoo, M. J. (2003). Anatomy and histology of the brain and sense organs of the Antarctic plunderfish *Dolloidraco longedorsalis* (Perciformes: Notothenioidei: Artedidraconidae), with comments on the brain morphology of other artedidraconids and closely related harpagiferids. *Journal of Morphology* **255,** 358–377. https://doi.org/10.1002/jmor.10068

Eastman, J. T. & Lannoo, M. J. (2008). Brain and sense organ anatomy and histology of the Falkland Islands mullet, *Eleginops maclovinus* (Eleginopidae), the sister group of the Antarctic notothenioid fishes (Perciformes: Notothenioidei). *Journal of Morphology* **269,** 84–103. https://doi.org/10.1002/jmor.10571

Eastman, J. T. & Lannoo, M. J. (2011). Divergence of brain and retinal anatomy and histology in pelagic Antarctic notothenioid fishes of the sister taxa *Dissostichus* and *Pleuragramma*. *Journal of Morphology* **272,** 419–441. https://doi.org/10.1002/jmor.10926

Eschmeyer, W. N., Fricke, R. & van der Laan, R. (2017). *Catalog of Fishes: Genera, Species, References*. Available at http://research.calacademy.org/ichthyology/catalog/fishcatmain.asp/ (last accessed 4 October 2017).

Evers, H. G. (1993). C-Nummern für Panzerwelse. *Die Aquarien- und Terrarienzeitschrift* **46,** 755–758.

Evers, H. G. (1994). "Neue" Panzerwelse aus Brasilien. *Die Aquarien- und Terrarienzeitschrift* **12,** 755.

Evers, H. G. & Schäfer, F. (2004). *Corydoras: Alle C-Nummern / All C-Numbers*. Rodgau: Aqualog Animalbook GmbH.

Fink, S. V. & Fink, W. L. (1981). Interrelationships of ostariophysan fishes (Teleostei). *Zoological Journal of the Linnean Society* **72,** 297–353.

Füller, I. A. M. & Evers, H. G. (2005). *Identifying Corydoradinae Catfish: Aspidoras-Brochis-Corydoras-Scleromystax & C-numbers*. Worcester & Rodgau: Ian Füller Enterprises & Aqualog Animalbook GmbH.

Glaser, U., Schäfer, F. & Glaser, W. (1996). *All Corydoras*. Rodgau: Aqualog Animalbook GmbH.

Huysentruyt, F. & Adriaens, D. (2005). Descriptive osteology of *Corydoras aeneus* (Siluriformes: Callichthyidae). *Cybium* **29,** 261–273.

Lundberg, J. G. (1970). The evolutionary history of North American catfishes, family Ictaluridae. PhD Thesis, University of Michigan, Ann Arbor, Michigan, MI.

Meek, J. & Nieuwenhuys, R. (1998). Holosteans and teleosts. In *The Central Nervous System of Vertebrates*, Vol. 2 (Nieuwenhuys, R., Ten Donkelaar, H. J. & Nicholson, C., eds), pp. 759–937. Heidelberg: Springer.

Nijssen, H. & Isbrücker, I. J. H. (1980). A review of the genus *Corydoras* Lacépède, 1803 (Pisces, Siluriformes, Callichthyidae). *Bijdragentot de Dierkunde* **50,** 190–220.

Pereira, T. N. A. & Castro, R. M. C. (2016). The brain of *Brycon orbignyanus* (Valenciennes, 1850) (Teleostei: Characiformes: Bryconidae): gross morphology and phylogenetic considerations. *Neotropical Ichthyology* **14,** e150051. https://doi.org/10.1590/1982-0224-20150051

Pupo, F. M. R. S. (2011). Anatomia comparada da morfologia externa do sistema nervoso central da família Callichthyidae (Teleostei: Ostariophysi: Siluriformes) e suas implicações filogenéticas. MSc Thesis, Museu Nacional/UFRJ, Rio de Janeiro, Brazil. Available at http://objdig.ufrj.br/71/teses/782245.pdf/ (last accessed 4 October 2017).

Pupo, F. M. R. S. (2015). Anatomia comparada dos encéfalos dos Loricarioidea (Teleostei: Ostariophysi: Siluriformes) e suas implicações filogenéticas. PhD Thesis, Museu Nacional/UFRJ, Rio de Janeiro, Brazil. Available at http://objdig.ufrj.br/71/teses/828925.pdf/ (last accessed 4 October 2017).

Reis, R. E. (1997). Revision of the Neotropical catfish genus *Hoplosternum* (Ostariophysi: Siluriformes: Callichthyidae), with the description of two new genera and three new species. *Ichthyological Exploration of Freshwaters* **7,** 299–326.

Reis, R. E. (1998). Anatomy and phylogenetic analysis of the neotropical callichthyid catfishes (Ostariophysi, Siluriformes). *Zoological Journal of the Linnean Society* **124,** 105–168. https://doi.org/10.1006/zjls.1997.0127

Reis, R. E. (2003). Family Callichthyidae (Armored catfishes). In *Check List of the Freshwater Fishes of South and Central America* (Reis, R. E., Kullander, S. O. & Ferraris, C. J. Jr., eds), pp. 291–309. Porto Alegre: Edipucrs.

Sabaj, M. H. (2016). Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Version 6.5 (16 August 2016). In: American Society of Ichthyologists and Herpetologists, Washington, DC (Internet). Available at http://www.asih.org/sites/default/files/documents/symbolic_codes_for_collections_v6.5.pdf/ (last accessed 4 October 2017).

Schaefer, S. A. (1988). Homology and evolution of the opercular series in the loricarioid catfishes (Pisces: Siluroidei). *Journal of Zoology* **214,** 81–93. https://doi.org/10.1111/j.1469-7998.1988.tb04988.x

Schaefer, S. A. & Aquino, A. (2000). Postotic laterosensory canal and pterotic branch homology in catfishes. *Journal of Morphology* **246,** 212–227. https://doi.org/10.1002/1097-4687(200012)246:3<212::AID-JMOR5>3.0.CO;2-S

Taylor, W. R. & van Dyke, G. C. (1985). Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium* **9,** 107–119.

Tencatt, L. F. C. & Britto, M. R. (2016). A new *Corydoras* Lacépède, 1803 (Siluriformes: Callichthyidae) from the Rio Araguaia basin, Brazil, with comments about *Corydoras araguaiaensis* Sands, 1990. *Neotropical Ichthyology* **14,** e150062. https://doi.org/10.1590/1982-0224-20150062

Tencatt, L. F. C. & Evers, H. G. (2016). A new species of *Corydoras* Lacépède, 1803 (Siluriformes: Callichthyidae) from the Rio Madre de Dios basin, Peru. *Neotropical Ichthyology* **14,** 13–26. https://doi.org/10.1590/1982-0224-20150019

Tencatt, L. F. C. & Ohara, W. M. (2016). Two new species of *Corydoras* Lacépède, 1803 (Siluriformes: Callichthyidae) from the Rio Madeira basin, Brazil. *Neotropical Ichthyology* **14,** e150063. https://doi.org/10.1590/1982-0224-20150063

Tencatt, L. F. C., Vera-Alcaraz, H. S., Britto, M. R. & Pavanelli, C. S. (2013). A new *Corydoras* Lacépède, 1803 (Siluriformes: Callichthyidae) from the Rio São Francisco basin, Brazil. *Neotropical Ichthyology* **11,** 257–264.

Tencatt, L. F. C., Britto, M. R. & Pavanelli, C. S. (2016). Revisionary study of the armored catfish *Corydoras paleatus* (Jenyns, 1842) (Siluriformes: Callichthyidae) over 180 years

after its discovery by Darwin, with description of a new species. *Neotropical Ichthyology* **14,** 75–94. https://doi.org/10.1590/1982-0224-20150089

Vera-Alcaraz, H. S. (2013). Relações filogenéticas das espécies da família Callichthyidae (Ostariophysi, Siluriformes). PhD Thesis, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil. Available at http://repositorio.pucrs.br/dspace/bitstream/10923/5538/1/000451889-Texto%2bCompleto-0.pdf/ (last accessed 4 October 2017).

Wiley, E. O. & Johnson, G. D. (2010). A teleost classification based on monophyletic groups. In *Origin and Phylogenetic Interrelationships of Teleosts* (Nelson, J. S., Schultze, H. P. & Wilson, M. V. H., eds), pp. 123–182. München: Verlag Dr. Friedrich Pfeil.