New Corydoradine Catfish (Siluriformes: Callichthyidae) from the Upper Paraná and São Francisco: The Sister Group of *Brochis* and Most of *Corydoras* Species

MARCELO R. BRITTO AND RICARDO M. C. CASTRO

Corydoras difluviatilis, new species, is described from the upper rio Paraná and the upper rio São Francisco, Brazil. The new taxon differs from its congeners by three exclusive features: the posterior pectoral-spine serrations restricted to its proximal half, and the parapophyses of the fourth free vertebra reduced and separated from each other, not fused into a haemal arch. The new species has several plesiomorphic character states relative to the assemblage composed of *Brochis* and most *Corydoras* species, such as absence of contact between the supraoccipital and nuchal plate, reduction of the ossified portion of hypobranchial 2, and well-developed mesial expansions of the first and second infraorbitals, indicating its basalmost position within the genus.

Corydoras difluviatilis, espécie nova, é descrita para o alto rio Paraná e alto rio São Francisco. O novo táxon difere de suas congêneres por três caracteres exclusivos: o serrilhado posterior do espinho peitoral restrito à sua metade proximal, e as parapófises da quarta vértebra livre reduzidas e disjuntas, não fundidas em um arco hemal. A nova espécie apresenta vários estados plesiomórficos em relação ao grupo formado por *Brochis* e maioria das espécies de *Corydoras*, tais como ausência de contato entre o supra-occipital e a placa nucal, redução da porção ossificada do hipobranquial 2, e expansões mesiais do primeiro e segundo infraorbitais bem desenvolvidas, indicando sua posição basal dentro do gênero.

CORYDORAS Lacépède, 1803, is a broad assemblage, that currently including more than 140 species (Nijssen and Isbrücker, 1980a; Eschmeyer, 1998). The genus is widely distributed in South America from the rio Magdalena basin, in Colombia, to the rio de la Plata system, in Argentina, and occurs in a variety of environments. Species assigned to *Corydoras* display a broad diversity of body shapes, coloration, and behavior and have attracted the attention of numerous ichthyologists in the course of the extensive taxonomic history of the genus (e.g., Bloch, 1794; Gosline, 1940; Nijssen and Isbrücker, 1986).

Although *Corydoras* species are well known among aquarists and ichthyologists worldwide, little is known about their phylogenetic relationships. Historically, problems concerning the definition and limits of *Corydoras* began as early as the original description of the genus by Lacépède (1803), as noted by previous authors such as Valenciennes (1840, in Cuvier and Valenciennes), and Myers (1940). *Corydoras* has been diagnosed as a member of the subfamily Corydoradinae lacking the characters defining the remaining genera of the subfamily, that is, *Aspidoras* and *Brochis*. Reis (1998) proposed characters indicative of the monophyly of the group composed of *Corydoras* plus *Brochis* and implied that *Corydoras* is paraphyletic if *Brochis* is recognized. Britto (1997) indicated that a small group of *Corydoras*, composed of three valid and one undescribed species, is closer to *Aspidoras* than to *Brochis* and that successive groups of other *Corydoras* species, including the type-species of the genus, *Corydoras geoffroy* (Isbrücker, 1998), are closely related to *Brochis*.

According to the phylogenetic analysis of Britto (1997), the new *Corydoras* species described herein, exhibits features shared by the assemblage composed of *Brochis* and most *Corydoras* species, an assemblage defined in that study by narrow complex vertebral centrum and parapophysis, a notch on the posterior expansion of the third ceratobranchial, a triangular dorsal lamina on the anguloarticular, and exposed medial expansion of the coracoid. Britto (1997) indicated that the new species (identified in that study as *Corydoras* sp. n.) is the basalmost taxon of this assemblage, showing several features that are plesiomorphic relative to its members.

In a study of a fish community from the rio Pardo, upper rio Paraná system, Castro and Casatti (1997) tentatively identified as *Corydoras* aff. *cochui* the new species described herein. Examination of *Corydoras* sampled in various Bra-

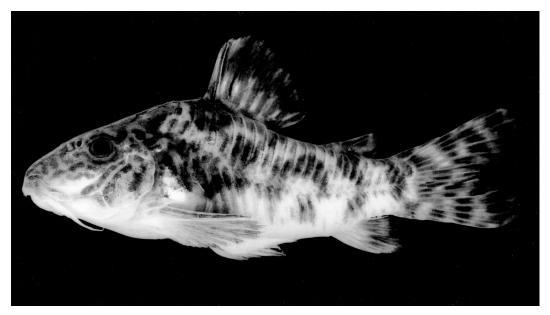


Fig. 1. Corydoras difluviatilis, holotype, MZUSP 75268, 39.8 mm, female. Photo by R. Castro.

zilian fish collections and additional collecting efforts revealed that the distribution of the new species extends into the upper rio São Francisco. *Corydoras* diversity is low in this region, with only two species, *Corydoras garbei* (rio São Francisco) and *Corydoras flaveolus* (rio Paraná), known to date.

Despite its basal position, we decided to place the new taxon to the genus *Corydoras* rather than erecting a new one, to avoid the proliferation of new generic names.

MATERIALS AND METHODS

Morphometric and meristic data were taken according to Reis (1997), except for anal-spine length, which is absent in all corydoradines. Length of the ossified portion of pectoral spine was measured from the spine-pectoral girdle articulation to distal tip of spine. Measurements were obtained with 0.1 mm precision calipers. Teeth and vertebral counts were taken from cleared-and-stained (cs) specimens, prepared according to Taylor and Van Dyke (1985). Vertebral counts include only free centra, the compound caudal centra (preural 1 + ural 1) being counted as a single element. In the description, numbers in parentheses represent counts from the holotype. Nomenclature of latero-sensory canals follows Schaefer and Aquino (2000), that of preopercular pores follows Schaefer (1988), and osteological terminology follows Reis (1998). The usage of the term "Corydoras" along the text refers to those species closer to *Brochis* than to *Aspidoras*, as briefly explained in the introduction. The small assemblage closely related to *Aspidoras* is referred herein as "undescribed genus." Abbreviations of institutions follow Leviton et al. (1985), with the addition of DBAV.UERJ, Departamento de Biologia e Anatomia de Vertebrados, Universidade Estadual do Rio de Janeiro, Rio de Janeiro, Brazil, LIRP, Laboratório de Ictiologia de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, Brazil, and UFRJ, Laboratório de Ictiologia Geral e Aplicada da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

Corydoras difluviatilis, n. sp. Figures 1–2

Holotype.—MZUSP 75268, female, 39.8 mm SL; Brazil: São Paulo, Município de Santa Rita do

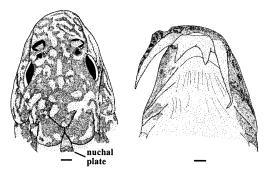


Fig. 2. Dorsal (left) and ventral (right) view of head of *Corydoras difluviatilis*, paratype, MCP 20815, 36.9 mm. Scale bar = 1 mm.

Passa Quatro, Parque Estadual de Vassununga, Gleba Pé-do-Gigante, córrego Paulicéia, tributary of rio Pardo, rio Paraná system, 21°38'S, 47°38'W, K. Ferreira, 25 August 2000.

Paratypes.—106, 6 cs, 13.2–47.3 mm SL. Brazil: rio Paraná system: São Paulo: collected with the holotype; MZUSP 75269, 33.0 mm SL, LIRP 816, 42.0 mm SL. Município de São Simão, headwaters of ribeirão Tamanduá (ribeirão Assombração), rio Pardo basin, 21°30'S, 47°34'W, E. Obara et al., 15 January 1989; LIRP 333, 41.9 mm SL. Município de Cajuru, Fazenda Santa Carlota, ribeirão sem nome or Barra Branca, rio Pardo basin, 21°16'S, 47°21'W, A. Zanata and M. Santos, 24 March 1989; LIRP 171, 27.2 mm SL. Município de São Simão, headwaters of ribeirão Tamanduá (Assombração), rio Pardo basin, 21°30'S, 47°34'W, E. Obara et al., March 1989 to March 1990; LIRP 817, 31: 15.4-47.3 mm SL. Município de Cajuru, Fazenda Santa Carlota, ribeirão sem nome or Barra Branca, rio Pardo basin, 21°16'S, 47°21'W, R. Castro et al., 14 November 1993; LIRP 41, 2: 30.7-35.8 mm SL, MZUSP 49226, 4: 28.7-32.5 mm SL. Município de Rifaina, córrego do Fundão, rio Grande basin, C. Alves et al., 23 March 1995; MZUSP 51487, 5: 21.4-36.7 mm SL. Minas Gerais: Município de Unaí, córrego Suapara, tributary of rio São Marcos, rio Paranaíba basin, 16°23'S, 47°16'W, M. Britto et al., 02 February 1998; MCP 20815, 3: 31.5-38.9 mm SL, MZUSP 52909, 38.2 mm SL, MZUSP 52910, 38.2 mm SL, UFRJ 4655, 31.8 mm SL, UMMZ 234253, 2: 32.7-42.0 mm SL. Município de Nova Ponte, ribeirão Reserva do Jacó, tributary of rio Araguari, F. Vieira et al., October 1995; MZUSP 51496, 5: 29.0-34.5 mm SL. Município de Sacramento, córrego Borá, rio Grande basin, 19°52'S, 47°26'W, C. Alves et al., 19 December 1994; MZUSP 51485, 2: 30.2-34.4 mm SL. Goiás: Município de Catalão, serra do Facão, córrego Jovenço Alves, tributary of ribeirão São Domingos, tributary of rio São Marcos, rio Paranaíba basin, 18°05'S, 47°42'W, C. Figueiredo et al., 24 September 1999; MNRJ 19735, 37.7 mm SL, MNRJ 19736, 2: 13.2-19.3 mm SL. Município de Catalão, serra do Facão, córrego do Barreiro at Fazenda Barreiro, tributary of rio São Marcos, rio Paranaíba basin, 17°55'S, 47°40'W, C. Figueiredo and F. Bockmann, 24 September 1999; MNRJ 19737, 12, 3 cs: 30.1-38.8 mm SL. Município de Campo Alegre de Goiás, serra do Facão, ribeirão Pirapitinga at Fazenda Pirapitinga, tributary of rio São Marcos, rio Paranaíba basin, 17°48'S, 47°41'W, C. Figueiredo et al., 26 September 1999; MNRJ 19738, 6: 27.5-42.4 mm SL, MNRJ 19739, 41.8 mm SL. Município de Catalão, serra do Facão, ribeirão Buracão at Fazenda Sr. Zé Martins, tributary of rio São Marcos, rio Paranaíba basin, 17°55'S, 47°41'W, F. Bockmann et al., 17 September 1999; MNRJ 19909, 6: 18.4-39.9 mm SL. Município de Catalão, serra do Facão, ribeirão do Segredo, tributary of rio São Marcos, rio Paranaíba basin, 17°51'S, 47°40'W, F. Bockmann and C. Figueiredo, 18 November 1999; MNRJ 19910, 13, 3 cs: 29.0-38.9 mm SL. Município de Catalão, serra do Facão, ribeirão Pires, tributary of rio São Marcos, rio Paranaíba basin, 17°59'S, 47°43'W, F. Bockmann et al., 20 November 1999; MNRJ 19911, 35.5 mm SL. Município de Catalão, serra do Facão, córrego da Prata, tributary of rio São Marcos, rio Paranaíba basin, 17°47'S, 47°35'W, F. Bockmann et al., 21 November 1999; MNRJ 19912, 2: 23.3-28.9 mm SL, MNRJ 19913, 36.9 mm SL.

Nontype material.—8, 3 cs, 32.3–41.7 mm SL. LIRP 748, 33.1 mm SL; MNRJ 16169, 4: 35.5– 41.7 mm SL; UFRJ 4656, 3 cs: 32.3–37.2 mm SL.

Diagnosis.—Corydoras difluviatilis is distinguished from all other Corydoradinae, by the following unique features: serrations of posterior border of pectoral spine restricted to proximal half of spine (vs serrations absent or along entire border of spine), and parapophyses of fourth free vertebra reduced (vs parapophyses well developed), separated from each other, and not fused into haemal arch (vs contacting each other and fused into haemal arch).

The following characters are primitive for the Callichthyidae but are also useful to diagnose the new species among *Corydoras*: absence of contact between supraoccipital and nuchal plate (vs contact present), reduction of ossified portion of hypobranchial 2 (vs well developed), and mesial expansion on first and second infraorbitals well developed (vs reduced).

Corydoras difluviatilis superficially resembles *C. garbei* in color pattern, and both species are putatively sympatric in the rio São Francisco system. *Corydoras difluviatilis* is distinguished from *C. garbei* by a relatively pointed snout (vs rounded), odontodes present on infraorbitals and opercle (vs absent), presence of a large round patch of orange pigmentation on lower region of cleithrum (vs dark brown coloration), and fewer ribs (6–7 vs 8).

Description.—Morphometric data presented in Table 1. Head compressed with slightly convex dorsal profile; roughly triangular in dorsal view (Fig. 2). Snout nearly straight, blunt in small specimens. Dorsal profile of body convex from tip of supraoccipital process to origin of dorsal

	Holotype MZUSP 75268	Paratypes $(n = 48)$	
		Mean	Range
Standard length (mm)	39.8	36.4	28.7-47.3
Percentage of standard length			
Depth of body	37.9	37.2	33.5-44.4
Predorsal distance	52.2	51.3	45.2-57.6
Prepelvic distance	52.1	48.6	43.9-54.3
Preanal distance	82.7	80.7	76.0-87.9
Preadipose distance	86.6	85.2	81.4-88.6
Length of dorsal spine	19.2	19.7	14.0-24.4
Length of pectoral spine	20.9	22.3	17.4-26.4
Length of adipose fin spine	8.7	9.4	5.9-11.7
Depth of caudal peduncle	15.3	15.1	13.0-18.3
Dorsal to adipose distance	20.3	21.0	17.1-26.6
Length of dorsal fin base	21.5	19.2	16.8-21.5
Maximum cleithral width	16.4	13.0	9.1-17.0
Head length	42.4	42.1	38.2-46.0
Length of longer barbel	16.6	14.5	5.2 - 20.0
Percentage of head length			
Head depth	82.5	81.6	77.4-88.8
Least interorbital distance	31.4	31.6	27.8-40.3
Horizontal orbit diameter	18.6	18.8	15.8-23.2
Snout length	42.5	40.5	35.7-45.1
Least internareal distance	22.4	19.4	16.2-23.9

TABLE 1. MORPHOMETRIC DATA FOR THE HOLOTYPE AND SELECTED PARATYPES OF Corydoras difluviatilis.

fin; slightly concave from this point to posteriormost dorsal fin ray. Some specimens with wholly convex profile from supraoccipital process to last dorsal fin ray. Postdorsal fin body profile slightly concave. Ventral profile of body nearly straight from isthmus to anal fin origin, slightly convex along region of pectoral and pelvic girdles. Profile from first anal fin ray to caudal fin base markedly concave. Body roughly cylindrical in cross section at pectoral girdle, gradually becoming more compressed toward caudal fin.

Eye round, located laterally on head; orbit delimited dorsally by frontal and sphenotic, ventrally by infraorbitals. Anterior and posterior nares proximal, only separated by flap of skin. Anterior naris tubular. Posterior naris close to anterodorsal margin of orbit, separated from it by distance equal to or smaller than naris diameter. Mouth small, subterminal, width nearly equal to bony orbit length. Two pairs of long maxillary barbels, usually reaching anteroventral limit of gill opening (Fig. 2). Some specimens with short barbels, not reaching gill openings. Ventral maxillary barbel slightly longer than dorsal barbel. One pair of fleshy mental barbels. Small rounded papillae covering entire surface of all barbels, upper and lower lips, and isthmus. Gill membranes united to isthmus. Four branchiostegal rays covered by thick layer of skin; distal two rays united at their tips by branchiostegal cartilage. Teeth on upper pharyngeal tooth plate 33. Teeth on fifth ceratobranchial 29.

Nasal, frontal, sphenotic, pterotic-supracleithrum, and supraoccipital visible externally, all covered by thin layer of skin and bearing minute scattered odontodes. Frontal fontanel elongate, ellipsoid in shape; posterior tip extending into supraoccipital anteriorly, covered by thin layer of skin. Nasal slender, slightly curved laterally, mesial border contacting frontal. Frontal quadrangular; anterior expansion in contact with nasal bone, posterior portion contacting sphenotic and supraoccipital. Sphenotic trapezoid in shape, contacting supraoccipital dorsally, pterotic-supracleithrum posteriorly, second infraorbital ventrally. Pterotic-supracleithrum rectangular, with slender posterior expansion contacting first dorsal body plate and first lateral line ossicle. Ventral margin of pterotic-supracleithrum contacting infraorbital 2 and cleithrum. Supraoccipital quadrangular with pointed posterior process, separated from nuchal plate by narrow space bridged by integument (Fig. 2).

Two infraorbital bones, externally visible, covered by thin layer of skin bearing minute odontodes directly attached to infraorbitals. First infraorbital with anterior expansion; second infraorbital with small, conspicuous posterior process contacting pterotic-supracleithrum. Opercle exposed, compact in shape, with angular free border. Preopercle, externally visible, slender and covered by thin layer of skin. Opercle and preopercle with minute odontodes. Interopercle triangular, covered by thin layer of skin.

Trunk lateral line with 3-4 laterosensory canals; two anteriormost canals reduced to small ossicles, remaining canals encased in dorsolateral body plates. Lateral line canal entering neurocranium through pterotic-supracleithrum, splitting into two branches before entering sphenotic: pterotic and preoperculomandibular, each with single pore. Sensory canal continuing through pterotic-supracleithrum, entering sphenotic as temporal canal, which splits into two branches. One branch giving rise to infraorbital canal, and other branch entering frontal through supraorbital canal. Supraorbital canal with two branches: epiphyseal, which opens in frontal bone, and nasal canal. Nasal canal with single opening at each end. Infraorbital canal running through entire second infraorbital, extending to infraorbital 1 and opening into two pores. Preoperculomandibular branch gives rise to preoperculomandibular canal, which runs through entire preopercle with three openings, leading to pores 3, 4, and 5, respectively.

Body plates with minute odontodes restricted to posterior margins. Nuchal plate partially covered by skin anteriorly. Cleithrum and medial process of coracoid exposed. Minute odontodes scattered over area between coracoids. Dorsolateral body plates 24–25 (24); ventrolateral body plates 21–22 (21); dorsolateral body plates along dorsal fin base 5–7 (7); dorsolateral body plates from adipose fin to caudal fin base 7–9 (7); preadipose platelets 3–5 (3). Parapophyses of fourth free vertebra reduced, separate from each other, and not fused into haemal arch. Precaudal vertebrae 10; caudal vertebrae 12; 6–7 pairs of ribs, first pair conspicuously larger than others.

Dorsal fin rounded; its origin just posterior to third dorsolateral body plate. Dorsal spine shorter than first 3–4 branched rays. Anterior and posterior borders of dorsal spine smooth. Dorsal fin rays I,6–8 (I,8). Adipose fin rounded; its origin separated from base of last dorsal fin ray by 7–8 dorsolateral body plates. Anal fin ovoid; its origin located just posterior to 12th to 13th ventrolateral body plates, coinciding with a vertical through posterior margin of second or third preadipose platelet. Anal fin rays ii,5– 7,i (ii,5,i). Pectoral fin triangular; its origin lo-

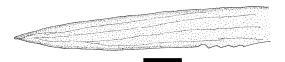


Fig. 3. Left pectoral spine of *Corydoras difluviatilis*, UFRJ 4656, 37.2 mm SL. Odontodes and head of spine not depicted. Scale bar = 1 mm.

cated just posterior to gill opening. Ossified portion of pectoral spine shorter than first three branched rays. Distal tip of spine with small-segmented unossified portion, extending less than one-third length of spine. Posterior border of pectoral spine with weak serrations restricted to proximal third to one-half (Fig. 3). Pectoral fin rays I,8,i. Pelvic fin ellipsoid; its origin just below second ventrolateral body plate, at vertical through base of first or second branched dorsal fin ray. Pelvic fin rays i,5. Caudal fin bilobed; upper lobe slightly longer. Principal caudal fin rays i,6/6,i; upper procurrent caudal fin rays 3-5; lower procurrent caudal fin rays 3-4. All fins with minute odontodes scattered over all rays.

Color in alcohol.-Ground coloration of head light brown to yellowish. Small dark brown blotches scattered over dorsal and lateral surface of head and snout forming reticulate pattern. Some specimens with more sparse pigmentation. Anterior naris with series of minute brown chromatophores more concentrated at margin. Thin dark brown ring surrounding orbit. Sphenotic and supraoccipital with dark brown blotch in some individuals. Dorsal maxillary barbel light brown, with minute scattered dark brown dots on dorsal surface. Ventral maxillary and mental barbels unpigmented. Preopercular region with irregular elongate brown blotch divided in two small blotches in some specimens. Opercle with three irregular dark brown blotches surrounded by series of brown chromatophores. Largest blotch close to junction with neurocranium; remaining blotches close to midportion of anterior and posterior margins of opercle, respectively. One individual (MCP 20815) with blotches arranged in three irregular parallel stripes. Ventral and lower sides of head yellowish, with some scattered chromatophores, mainly on anterior isthmus and branchiostegal membranes.

Ground color of trunk light brown. Large dark brown blotch on dorsal limit of cleithrum and posterior region of pterotic-supracleithrum. Large round orange to light red patch on lower region of cleithrum just dorsal to pectoral spine insertion. Series of large irregular dark brown blotches on dorsal and lateral surfaces of body from anteriormost lateral plates to caudal peduncle. Ventrolateral blotches more elongate than remaining marks. Some specimens with dorsal, midlateral, and ventrolateral blotches united. Minute dark brown dots scattered over entire surface of trunk, more concentrated on posterior border of each lateral body plate. Ventral surfaces of body yellowish.

Ground color of all dorsal fin elements light brown; interradial membranes hyaline; two or three series of small dark brown blotches restricted to dorsal fin rays. Some specimens with scattered chromatophores on distal portion of dorsal fin membrane; one to four series of dark brown spots restricted to anal fin rays. Ground color of anal fin rays light brown. Interradial anal fin membranes with scattered dark brown chromatophores on base of fin; remainder of fin membranes hyaline. Adipose fin spine brown. Adipose fin membrane with dark brown blotch. Pectoral spine brown. Five to seven series of small dark brown blotches restricted to pectoral fin rays, not extending onto membranes. Ground color of all pectoral fin rays yellowish to light brown; interradial membranes hyaline. Base of pectoral fin with scattered dark brown chromatophores. Pelvic fin with rays overlaid by minute dark brown blotches, interradial membranes hyaline. Some specimens with pectoral and pelvic fins entirely hyaline. Ground color of caudal fin rays light brown; caudal fin membranes hyaline. Caudal fin with five to seven series of small, dark brown blotches restricted to rays and forming poorly defined vertical bands.

Sexual dimorphism.—Genital papilla is dimorphic in Corydoradinae (Nijssen and Isbrücker, 1980b:135; Britto, 1997). As in the remaining members of Corydoradinae, males of *Corydoras difluviatilis* possess a lanceolate genital papilla. Specimens' examination revealed that the sex ratio is nearly 1:1.

Distribution.—Upper rio Paranaíba and upper rio Grande basins, rio Paraná system, and rio Jequitaí, rio Preto, and headwaters of rio da Prata, São Francisco system (Fig. 4), in the States of Goiás, Minas Gerais and São Paulo, Brazil.

Etymology.—difluviatilis, "from two rivers, "is derived from the Latin *di,* meaning "two," and *fluviatilis,* meaning "from the river." In allusion to the occurrence of the new species in two major drainage basins of the Neotropics.

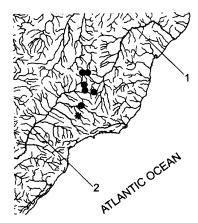


Fig. 4. Map of southeastern South America, showing the distribution of *Corydoras difluviatilis* (circles). Type locality indicated by an asterisk. (1) Rio São Francisco system; (2) Rio Paraná system.

Biological notes.—Corydoras difluviatilis is found in small, shallow first to third order streams (cf. Strahler, 1957), in well-forested areas or savannah-like "cerrado," with clear water, and bottom composed mostly of very fine sand (Obara and Mendes, 1990; Castro and Casatti, 1997).

The type-locality is located in a second-order stretch of the córrego Paulicéia that is approximately 3 km downriver from its source (at 608 m height), running through "cerrado" vegetation. The stream is approximately 1.5 m wide, 0.2-0.8 m deep, with a sandy bottom and submerged leaf litter, twigs, and small logs. During the collection of the holotype, the air and water temperatures were 25.4 C and 19.3 C, respectively, the pH 6.68, dissolved oxygen 8.3 mg/l, conductivity 90 µS/cm, current velocity 0.25 m/ s, and horizontal water transparency 270 cm. A detailed description of one collection site of the new species was presented in Castro and Casatti (1997:table 1, figs. 2-4), who also described stomach contents of two specimens (31.6-36.2 mm SL). Obara and Mendes (1990) studied stomach contents of 32 specimens (16.1-45.6 mm SL) collected over a year and found in a sequence of decreasing importance: aquatic insects (mostly Diptera and Trichoptera larvae), algae (only diatoms), thecamoebas, aquatic Arachnida, debris of vascular plants, and terrestrial insect fragments, showing the feeding behavior of a typical benthic substrate speculator ("grubbers" of Sazima, 1986), probing the substrate with snout and barbels while moving in search of food items. Based on snorkeling observations of the new species in its natural environment, those authors described its activity period as diurnal, with individuals always alone

or in pairs. Underwater observations by K. Ferreira (pers. comm.) similarly indicated that individuals of the new species were always actively feeding, either alone or in pairs, around noontime.

DISCUSSION

Castro and Casatti (1997) identified the new *Corydoras* species as *C.* aff. *cochui*; however, *C. difluviatilis* shares neither morphological similarities with nor the distributional patterns of *C. cochui*. As mentioned above, *Corydoras difluviatilis* is most similar to *C. garbei*, although several characters distinguish the two species (see Diagnosis).

Corydoras difluviatilis differs from all members of the Corydoradinae by three unique features: the parapophyses of the fourth free vertebra reduced, and separated from each other, not fused into a haemal arch, and the serrations along the posterior border of the pectoral spine being restricted to the proximal half of the spine (Fig. 3).

In representatives of the Corydoradinae, the parapophyses of each precaudal vertebra increase in size posteriorly, with the third free vertebra already showing well-developed parapophyses. In members of the subfamily other than *C. difluviatilis*, the first haemal arch, formed by fusion of parapophyses, is either present on the third or on the fourth vertebra. *Corydoras difluviatilis* has the first haemal arch present only on the fifth free vertebra.

The development of the pectoral spine serrations varies considerably among members of the Corydoradinae. Representatives of *Aspidoras* and some species of *Corydoras* have well-developed serrations on the pectoral spine, whereas in other *Corydoras* species the serrations are weak or absent. Pectoral spine serrations are often schematically illustrated in the Corydoradinae descriptions (e.g., Nijssen and Isbrücker, 1976:fig. 15; 1986:figs. 19–20, 31, 44); however, none of these noted variations on the serrations matching the condition in *C. difluviatilis*.

Corydoras difluviatilis exhibits several plesiomorphic features compared to the assemblage composed of *Brochis* and *Corydoras* species (Britto, 1997; Reis, 1998), such as the lack of contact between the supraoccipital and the nuchal plate (Fig. 2). In *Aspidoras*, the undescribed genus and the subfamily Callichthyinae, the posterior process of the supraoccipital is short and separated from the nuchal plate by one to three pairs of dorsolateral body plates (Britto, 2000: fig. 2). *Corydoras* and *Brochis* species, in contrast, typically have the posterior process of the supraoccipital well developed and fully contacting the nuchal plate, with the tips of the bones sometimes overlapping. In *C. difluviatilis*, the posterior process of the supraoccipital although well developed, does not contact the nuchal plate, leaving a small gap between these bones, which is covered by fleshy skin.

Other primitive character states shown by *C. difluviatilis* are the small degree of ossification of the second hypobranchial, a condition shared with other representatives of the Loricarioidea (Schaefer, 1987:fig. 8; de Pinna, 1992: fig. 6), and the large mesial expansions on the first and second infraorbitals, also present in the subfamily Callichthyinae, the undescribed genus and *Aspidoras* (Reis, 1998:fig. 12A–F).

The basal placement of C. difluviatilis within the assemblage composed of Corydoras and Brochis has important implications for understanding the relationships within this group. Current phylogenetic knowledge of Callichthyidae (Reis, 1998) reveals that several character states, which represent synapomorphies for the family (e.g., arrangement of body plates, articulation between infraorbital 1 and lateral ethmoid, articulation between infraorbital 2 and sphenotic, lateral projection and muscle insertion of the dentary, processes of the basipterygium) show some degree of variation among its members. Since no outgroups show these conditions, these variations are not decisively informative about relationships in less inclusive clades of the family, denying comparisons about homology. The description of the new taxon and its hypothesized relationship with other members of the Corydoradinae may help to elucidate the direction of change in some of these characters and, indirectly, contribute to improving phylogenetic resolution within the subfamily. Besides, the inclusion of new taxa in phylogenetic analyses, mainly those in basal positions, bringing an amount of new characters and conflicting hypotheses about character-state interpretations, may overturn previous phylogenetic schemes, acting as a pivot in resolution of state ambiguity and polarization (de Pinna, 1992; Schaefer, 1998).

In spite of the well-corroborated basal position of *C. difluviatilis*, relationships within the assemblage composed of *Brochis* and *Corydoras* are poorly resolved (Britto, 1997). Considering the current rudimentary knowledge of the phylogenetic relationships within the Corydoradinae (Reis, 1998), and the fact that the new species has a generalized appearance of a *Corydoras*, inclusion of the new species in a separate genus would lead to more confusion than clarification concerning taxon names. Thus, the more conservative course of action of the placement of the new species in *Corydoras* is the alternative favored here.

Comparative material examined.—Aspidoras albater MCP 15974, 5, 1 cs; MNRJ 12571, 26; MNRJ 12581, 45, 3 cs; A. belenos MCP 19294, 3 paratypes; MZUSP 51208, 3 paratypes; UFRJ 1206, 2 paratypes; UFRJ 3861, 3 paratypes, 2 cs; A. fuscoguttatus MCP 14253, 7; MCP 19401, 3 cs; MNRJ 12649, 11, 2 cs; MZUSP 35833, 2; A. lakoi MNRJ 5293, 4, 2 cs; A. menezesi MZUSP 49952, 2; Aspidoras microgalaeus MCP 19295, 4 paratypes; MZUSP 51209, holotype; MZUSP 51210, 4 paratypes; UFRJ 1247, 3 paratypes, 2 cs; UFRJ 1385, 2 paratypes; A. cf. pauciradiatus MZUSP 14634, 2; MZUSP 30841, 4; MZUSP 31282, 2; A. poecilus UFRJ 1473, 10, 1 cs; UFRJ 1693, 16; UFRJ 1818, 11; UFRJ 1823, 15, 2 cs; UFRJ 1925, 4; A. aff. poecilus MNRJ 997, 16; MNRJ 5233, 9; MNRJ 11716, 69; MNRJ 12779, 12, 3 cs; MNRJ 13045, 37; UFRJ 201, 12, 1 cs; UFRJ 2189, 7; A. rochai MCP 19402, 4 cs; MZUSP 24634, 4; A. spilotus MNRJ 8688, 4 paratypes, 2 cs; A. virgulatus MNRJ 4736, 14, 3 cs; UFRJ 1775, 17, 2 cs; Brochis britskii MZUSP 36382, 1; UFRJ 3850, 1 cs; B. multiradiatus MCP 16302, 1; MZUSP 26822, 1; MZUSP 31555, 1; B. splendens MCP 14261, 1 cs; MZUSP 30859, 4; MZUSP 42218, 1; NRM 13431, 4, 2 cs; Corydoras acutus USNM 305595, 4, 2 cs; C. adolfoi MZUSP 26641, holotype; C. aeneus INPA 3099, 3; MNRJ 5756, 4, 1 cs; UFRJ 95, 2; UFRJ 605, 1; UFRJ 3017, 6, 2 cs; UFRJ 3847, 15; UFRJ 3848, 8; UMMZ 169066, 15; UMMZ 205475, 8; C. agassizi MZUSP 15297, 3; NRM 28589, 4, 2 cs; C. amapaensis MZUSP 30842, 1; MZUSP 31553, 1; MZUSP 31606, 1; MZUSP 38979, 3 paratypes; C. ambiacus MZUSP 26016, 1; MZUSP 26053, 2; NRM 13397, 4, 2 cs; C. approuaguensis MZUSP 27895, paratype; MZUSP 27896, paratype; C. araguaiensis UFRJ 1332, 3, 1 cs; UFRJ 1427, 4, 1 cs; UFRJ 1458, 5, 1 cs; UFRJ 1474, 5, 1 cs; UFRJ 1536, 1; UFRJ 1945, 1; C. arcuatus NRM 13396, 4; USNM 317900, 4, 2 cs; C. atropersonatus NRM 28590, 4, 2 cs; C. aurofrenatus MZUSP 36720, 6; NRM 23528, 4, 2 cs; C. axelrodi USNM 246701, 4, 2 cs; C. baderi MZUSP 38986, (4 paratypes of C. oelemariensis); USNM 225587, 4, 2 cs; C. barbatus MNRJ 13723, 10, 2 cs; MNRJ 14843, 10, 2 cs; UFRJ 167, 10, 2 cs; UFRJ 591, 9, 1 cs; UFRJ 1649, 3; UFRJ 2151, 3; UFRJ 2268, 3; UFRJ 3204, 2; UFRJ 3344, 1; UFRJ 3374, 1; UFRJ 3379, 1; C. bicolor USNM 225580, 4, 2 cs; C. bifasciatus MZUSP 38976, 4 paratypes; C. blochi INPA 1289, 1; MZUSP 8580, 3 paratypes; C. vittatus UFRJ 3781, 6, 1 cs; C. bondi INPA 1288, 5, 2 cs; INPA 1639, 1; INPA 7797, 5; INPA 8133, 5, 2 cs; C. coppenamensis MZUSP

8950, 2 paratypes; C. cochui MZUSP 35838, 4; UFRJ 1760, 2, 1 cs; C. davidsandsi MZUSP 38633, paratype; MZUSP 38634, paratype; MZUSP 38635, paratype; C. ehrhardti UFR 2251, 4, 1 cs; UFRJ 3662, 3; C. elegans MZUSP 15299, 2; MZUSP 26017, 6; MZUSP 26342, 3; UFRJ 3782, 2, 1 cs; C. ellisae MCP 15517, 2 cs; UMMZ 206339, 4, 1 cs; C. ephippifer MZUSP 30844, 4, 2 cs; MZUSP 38948, 2 paratypes; C. eques USNM 317921, 4, 2 cs; C. flaveolus MZUSP 47925, 4, 2 cs; C. garbei MCP 16994, 4, 2 cs; MNRJ 1007, 35; MNRJ 6216, 41; MNRJ 5765, 9; MNRJ 15778, 6; MNRJ 15823, 12; MNRJ 16165, 2; MNRJ 16169, 4; MZUSP 40184, 4; MZUSP 57572, 1 ex; UFRJ 3064, 1; C. geoffroy (2 paratypes of C. octocirrus) MZUSP 38984; C. gossei MZUSP 38977, 4 paratypes; C. gracilis INPA 7759, 5, 2 cs; C. guapore UMMZ 204302, 7, 2 cs; C. habrosus USNM 220356, 4, 2 cs; C. hastatus MZUSP 35908, 4, 2 cs; UFR 384, 31, 5 cs; UFR 1909, 2; UFR 3654, 6 ex., 1 cs; UFRJ 3655, 5; UFRJ 3656, 2; UFRJ 3657, 4; UFRJ 3658, 3; UFRJ 3659, 3; UFRJ 3660, 3; UFRJ 3831, 5, 2 cs; C. heteromorphus MZUSP 9084, paratype; MZUSP 9085, 1; C. incolicana MZUSP 45717, holotype; C. julii UFRJ 3779, 59, 2 cs; C. leopardus MZUSP 22874, 1; C. leucomelas MCP 14249, 1 cs; UMMZ 204304, 5, 2 cs; C. loretoensis NRM 28562, 4 paratypes, 2 cs; C. macropterus UFRJ 202, 4, 2 cs; C. maculifer UFRJ 106, 28, 4 cs; C. melanistius INPA 4204, 1; INPA 6990, 5; INPA 7080, 2; INPA 8093, 1.; UFRJ 3177, 2, 1 cs; UFRJ 3780, 1; USNM 225582, 4, 2 cs; C. melanotaenia NRM 27872, 5, 1 cs; C. metae MZUSP 47926, 4; NRM 27873, 4, 2 cs; C. multimaculatus MNRJ 16103, 5; MNRJ 16118, 6; MZUSP 40183, 4; MZUSP 47405, 1; C. nanus NRM 13501, 4; NRM 28595, 4; USNM 218359, 4, 2 cs; C. napoensis MZUSP 26341, paratype; USNM 301949, 4, 2 cs; C. nattereri UFRJ 25, 8 ex.; UFRJ 31, 8; UFRJ 520, 26, 2 cs; UFRJ 565, 6, 1 cs; UFRJ 924, 3; UFRJ 928, 2; UFRJ 1085, 5; UFRJ 3692, 3; C. oiapoquensis MZUSP 38957, 4; C. ornatus INPA 4708, 1; MCP 14259, 2 cs; C. osteocarus INPA 7910, 2; INPA 7916, 5; INPA 8129, 5, 2 cs; C. ourastigma MZUSP 38960, 4 paratypes; C. paleatus DBAV.UERJ 232, 1; MCP 14835, 2 cs; MZUSP 27035, 4; MZUSP 41814, 2; C. panda MCP 14257, 2 cs; C. paralelus MZUSP 45716, holotype; C. pinheiroi MZUSP 48099, holotype; C. polystictus MZUSP 44454, 4, 2 cs; UFRJ 399, 22; UFRJ 3849, 20, 2 cs; UMMZ 205169, 20; C. prionotus UFRJ 3, 11, 2 cs; UFRJ 211, 8, 1 cs; UFRJ 521, 4, 1 cs; UFRJ 568, 2; UFRJ 1084, 1; UFRJ 1781, 2; C. punctatus INPA 7814, 5, 2 cs; MCP 16138, 2 cs; MZUSP 42507, 2; C. pygmaeus MZUSP 26344, 4; USNM 218355, 5, 2 cs; C. rabauti MCP 14258, 1 cs; MNRJ 3627 (6 paratypes of C. myersi); MZUSP 15300, 1; C. reticulatus MZUSP

28752, 3; USNM 317945, 4, 2 cs; C. robiniae MZUSP 27175, holotype; MZUSP 27176, paratype; MZUSP 27177, paratype; C. sanchesi USNM 203810, 2; C. sarareensis MZUSP 48100, holotype; C. schwartzi MZUSP 42506, 6; C. septentrionalis MZUSP 27953, 8, 2 cs; C. seussi MZUSP 49323, 5 paratypes; C. simulatus MZUSP 42514, 1; C. sodalis MZUSP 26817, 4 paratypes; C. stenocephalus MZUSP 25985, 3; USNM 264116, 4, 2 cs; C. sterbai UFRJ 4424, 1; C. trilineatus MZUSP 42510, 2; NRM 13398, 4; NRM 13492, 4; USNM 317949, 4, 2 cs; C. triseriatus MNRJ 8608, 4, 2 cs; C. undulatus MCP 13954, 2 cs; C. virginiae MZUSP 45715, holotype; C. xinguensis MCP 15633, 3 cs; MZUSP 36864, 4; MZUSP 38974, paratype; MZUSP 38980, paratype; MZUSP 38987, paratype; C. zygatus USNM 316823, 4, 2 cs; Corydoras sp.A UFRJ 4303, 2; UFRJ 4309, 8, 3 cs.

Acknowledgments

We are grateful to R. Benini, F. Bockmann, L. Casatti, F. Di Dário, K. Ferreira, F. Lima, N. Menezes, C. Moreira, M. de Pinna, A. Ribeiro, M. Toledo-Piza, and R. Vari for suggestions that improved the manuscript. We are also indebted to A. Aranda, P. Buckup, W. Costa, E. Ferreira, U. Gomes, S. Jewett, S. Kullander, L. Malabarba, A. Marques, D. Nelson, J. Pezzi, S. Raredon, R. Reis, H. Seccioso, S. Smith, R. Vari, and S. Weitzman for loan of material and to F. Bockmann for drawing the map. This work was supported by FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo) within the BIOTA/FA-PESP-the Virtual Biodiversity Institute Program (www.biotasp.org.br) through the Thematic Project "Fish diversity of the headwaters and streams of the upper Paraná River system in the State of São Paulo, Brazil" (FAPESP grant 98/05072-8) and by PRONEX Project "Conhecimento, conservação e utilização racional da diversidade da fauna de peixes do Brasil" (FI-NEP/CNPq grant 661058/1997-2). The first author received a grant from FAPESP (98/05447-1) and the second author is a Conselho Nacional de Desenvolvimento Científico e Tecnológico do Brasil researcher (grant 301309/91-4).

LITERATURE CITED

- BLOCH, M. E. 1794. Allgemeine Naturgeschichte der ausländischen Fische 8:1–174.
- BRITTO, M. R. 1997. Filogenia da subfamília Corydoradinae (Siluriformes: Callichthyidae). Unpubl. master's thesis, Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil.
 - ------. 2000. Aspidoras depinnai (Siluriformes: Ca-

llichthyidae), a new species from northeastern Brazil. Copeia 2000:1048–1055.

- CASTRO, R. M. C., AND L. CASATTI. 1997. The fish fauna from a small forest stream of the upper Paraná River basin, southeastern Brazil. Ichthyol. Explor. Freshwaters 7:337–352.
- CUVIER, G., AND A. VALENCIENNES. 1840. Histoire naturelle des poissons. Tome quinzième. Suite du livre dix-septième. Siluroïdes. 15:i–xxxi, 1–540.
- ESCHMEYER, W. 1998. Catalog of fishes. 3 vols. California Academy of Sciences, San Francisco.
- GOSLINE, W. A. 1940. A revision of the Neotropical catfishes of the family Callichthyidae. Stanf. Ichthyol. Bull. 2:1–36.
- ISBRÜCKER, I. J. H. 1998. Corydoras geoffroy und Cataphractus punctatus. Revision der beiden zuerst entdecken Arten der Unterfamilie Corydoradinae (Actinopterygii, Siluriformes, Callichthyidae), Schluâ. Aquar. Terrar. Zeit. 52:38–43.
- LACÉPÈDE, B. G. E. 1803. Histoire Naturelle des poissons. P. Plassan, Paris 5:i–lxviii, 1–803.
- LEVINTON, A. E., R. H. GIBBS JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology. Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802–832.
- MYERS, G. S. 1940. A note on the status of the generic name *Corydoras*. Stanf. Ichthyol. Bull. 2:11–12.
- NIJSSEN, H., AND I. J. H. ISBRÜCKER. 1976. The South American plated catfish genus Aspidoras R. von Ihering, 1907, with descriptions of nine new species from Brazil (Pisces, Siluriformes, Callichthyidae). Bijr. Dierk. 46:107–131.
- , AND ——, 1980a. A review of the genus *Corydoras* Lacépède, 1803 (Pisces, Siluriformes, Callichthyidae). *Ibid.* 50:190–220.
- _____, AND _____. 1980b. Aspidoras virgulatus n. sp., a plated catfish from Espírito Santo, Brazil (Pisces, Siluriformes, Callichthyidae). Bull. Zool. Mus. Univ. Amsterdam 7:133–138.
- _____, AND _____. 1986. A review of the genus Corydoras from Peru and Ecuador (Pisces, Siluriformes, Callichthyidae). Stud. Neotrop. Faun. Environ. 21: 1–68.
- OBARA, E., AND L. MENDES. 1990. Aspectos da biologia dos peixes de um trecho da cabeceira do Ribeirão do Tamanduá, Bacia do Rio Pardo, SP. Unpubl. BSc. thesis, Faculdade de Filososfia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, São Paulo, Brazil.
- DE PINNA, M. C. C. 1992. A new subfamily of Trichomycteridae (Teleostei, Siluriformes), lower Loricarioid relationships, and a discussion on the impact of additional taxa for phylogenetic analysis. Zool. J. Linn. Soc. 106:175–229.
- REIS, R. E. 1997. Revision of the Neotropical genus *Hoplosternum* (Ostariophysi: Siluriformes: Callichthyidae) with the description of two new genera and three new species. Ichthyol. Explor. Freshwaters 7: 299–326.
- ——. 1998. Anatomy and phylogenetic analysis of the Neotropical callichthyid catfish (Ostariophysi, Siluriformes). Zool. J. Linn. Soc. 124:105–168.
- SAZIMA, I. 1986. Similarities in feeding behavior be-

tween some marine and freshwater fishes in two tropical communities. J. Fish Biol. 29:53–65.

SCHAEFER, S. A. 1987. Osteology of *Hypostomus plecostomus* (Linnaeus), with a phylogenetic analysis of the loricariid subfamilies (Pisces: Siluriformes). Contr. Sci., Nat. Hist. Mus. Los Angeles Co. 394:1– 31.

——. 1988. Homology and evolution of the opercular series in the loricarioid catfishes (Pisces: Siluroidei). J. Zool. Lond. 214:81–93.

. 1998. Conflict and resolution: impact of new taxa on phylogenetic studies of the Neotropical cascudinhos (Siluroidei: Loricariidae), p. 375–400. *In:* Phylogeny and classification of Neotropical fishes.
L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. S. Lucena, and C. A. S. Lucena (eds.). EDIPUCRS, Rio Grande do Sul, Brazil.

——, AND A. AQUINO. 2000. Postotic laterosensory canal and pterotic branch homology in catfishes. J. Morphol. 246:212–227.

- STRAHLER, A. N. 1957. Quantitative analyses of watershed geomorphology. Trans. Am. Geoph. Union 38:913–920.
- TAYLOR, R., AND C. C. VAN DYKE. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium 9:107–119.
- (MRB) MUSEU DE ZOOLOGIA DA UNIVERSIDADE DE SÃO PAULO, CX. POSTAL 42594, 04299–970 SÃO PAULO, SÃO PAULO, BRASIL; AND (RMCC) LABORATÓRIO DE ICTIOLOGIA DE RIBEIRÃO PRETO, FFCLRP, UNIVERSIDADE DE SÃO PAULO, AV. DOS BANDEIRANTES 3900, 14040–901, RI-BEIRÃO PRETO, SÃO PAULO, BRASIL. E-mail: (MRB) mrbritto@ib.usp.br. Send reprint requests to MRB. Submitted: 23 Oct. 2001. Accepted: 26 April 2002. Section editor: S. A. Schaefer.