

New species of *Cyphocharax* (Ostariophysi: Characiformes: Curimatidae) from Suriname and French Guiana and a discussion of curimatid diversity on the Guiana Shield

by

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ABSTRACT. - *Cyphocharax biocellatus*, a species of curimatid characiform apparently endemic to the Marowijne River/ Fleuve Maroni system in Suriname and French Guiana, and the Mana River basin in French Guiana is described as new. The new species is diagnosed from congeners based on meristic and morphometric features and details of pigmentation of the body and dorsal and caudal fins. The description of the new species brings the total number of *Cyphocharax* species in the drainages overlying the Guiana Shield to 14, with eight species occurring in the northern-flowing river systems of the Guianas. As such, the Guianas demonstrate the highest species-level diversity within *Cyphocharax* among comparably-sized areas within the range of the genus. The pronounced diversity of the genus *Cyphocharax* and the family Curimatidae at the level of the Maroni basin, the Guianas and the rivers systems draining the Guiana Shield is discussed.

RÉSUMÉ. - Description d'une nouvelle espèce de *Cyphocharax* (Ostariophysi: Characiformes: Curimatidae) du Suriname et de Guyane française avec une discussion sur la diversité des Curimatidés du bouclier guyanais.

Dans cet article, nous décrivons une nouvelle espèce de curimatidé (Characiformes), *Cyphocharax biocellatus*, apparemment endémique des bassins versants de la Mana et du Maroni (Marowijne River), ce dernier étant situé à la frontière de la Guyane française et du Surinam. Sa diagnose est basée sur des caractères méristiques et morphométriques, ainsi que sur les détails de la pigmentation du corps et des nageoires dorsale et anale. La description de cette nouvelle espèce porte à 14 le nombre de *Cyphocharax* présents dans les cours d'eau du bouclier guyanais, dont huit d'entre eux inféodés aux réseaux hydrographiques du nord des Guyanes. Ainsi, dans l'aire de distribution de *Cyphocharax*, les Guyanes possèdent la plus forte diversité spécifique en comparaison d'autres régions de taille similaire. La grande diversité au sein du genre *Cyphocharax* et de la famille des Curimatidae observée au niveau du Maroni, des Guyanes et des réseaux hydrographiques du bouclier guyanais, est discutée.

Key words. - Curimatidae - *Cyphocharax biocellatus* - South America - Guiana Shield - Biodiversity - New species.

The Curimatidae is a family of slightly more than 100 species (Vari, 2003; Lucinda and Vari, 2009; Vari *et al.*, 2010) broadly distributed across the rivers and streams of the lowlands and lower elevation regions of South America and southern Central America. Curimatids are characterized by numerous dramatic modifications of the jaws, gill arches, digestive tract, periphyton and associated systems, which allow members of the family to exploit microdetritus, flocculent organic matter, and filamentous algae. The ability to utilize these abundant food sources may account for the numerous species and often extensive populations of many curimatid species across the vast range of the family. With 35 species (Vari, 1989a, 1989b; Vari and Blackledge, 1996; Vari *et al.*, 2010), *Cyphocharax* Fowler (1906) is by far the

most speciose of the eight genera in that family (Vari, 2003). *Cyphocharax* is notably diverse in the rivers of the Guiana Shield which are home to 13 species of the genus recognized in the recent literature, eight of which occur in the Atlantic versant drainages of the Guianas (Vari, 2009; results herein).

Thirty-five species of the Curimatidae, nearly one-half of which (17) are species of *Cyphocharax*, have been described as new to science in the last quarter century. Nonetheless, ichthyological explorations continue to reveal previously unknown species of the family and genus from many regions (e.g., Lucinda and Vari, 2009; Vari *et al.* 2010; pers. obs.), a phenomenon general for the Neotropical ichthyofauna (Vari and Malabarba, 1998). In keeping with that trend, ichthyological surveys in the rivers eastern of Suriname and west-

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ern French Guiana yielded a previously unknown species of *Cyphocharax* which we describe as new herein, raising the total of species of the genus on the Guiana shield to fourteen.

MATERIALS AND METHODS

Museum abbreviations follow Leviton *et al.* (1985) with the addition of the NZCS, National Zoological Collection of Suriname, Paramaribo. Counts and measurements follow Vari (1992a). Measurements were point-to-point linear distances taken using digital callipers with a precision of 0.1 mm. In the description, the number of examined specimens with a particular count is provided in parentheses with the value of the holotype in square brackets. Vertebral counts are from specimens examined by radiography. Abbreviations in the text are head length (HL) and standard length (SL). A series of smaller specimens from the Maroni River basin in French Guiana were not included in the type series due to their distinctly smaller body sizes than those of the holotype and paratypes.

CYPHOCHARAX BIOCELLATUS, NEW SPECIES

(Fig. 1; Tab. I)

Holotype. - ANSP 189146, 62.8 mm SL; Suriname, Sipalawini, Litani River at mouth and confluence with Marowini River, just upstream from settlement of Konya Kondre, 03°17'24"N, 054°04'38"W, J. Lundberg, M. Sabaj, P. Willink, and J. Mol, 21 Apr. 2007.

Paratypes. - NZCS F 6828-6829, 2 specimens, 44.3-45.8 mm SL; Suriname, Oelemari River, 71 km upstream of confluence with Litani River 03°06'28"N, 54°32'46"W, P.E. Ouboter and S. Sahdew, 1 May 1998. MNHN 2010-0006, 1 specimen, 69.2 mm SL; French Guiana, confluence of Coumarou crique with Mana River, 2 km upstream of Saut Ananas, 04°07'20"N, 53°32'09"W, P.-Y. Le Bail, P. Planquette and P. Keith, 19 Sept. 1995.

Non-type specimens. - MNHN 2010-0028, 45 specimens, 18.8-36.5 mm SL; USNM 396055, 10 specimens, 29.9-33.2 mm SL; French Guiana, Maroni River drainage, Grand Inini, Saut Batardeau, 03°36'04"N, 53°49'01"W, P.-Y. Le Bail, P. Keith and M. Jégu, 29 September 1997.

Diagnosis

Cyphocharax biocellatus is distinguished from all congeners by the possession in all but the smallest examined specimens of a midlateral spot of dark pigmentation in the region ventral to the dorsal fin, with the spot when present ranging in intensity from a diffuse concentration of dark chromatophores in smaller specimens to a distinct black spot in the larger examined individuals [versus the presence of 3 to 6 larger midlateral spots extending posteriorly onto the caudal peduncle in *C. punctatus* Vari & Nijssen, 1986, and *C. vanderi* (Britski, 1980), a series of smaller dark spots on each lateral line scale in *C. pantostictos* Vari & Barriga, 1990, and the absence of dark spots along the midlateral surface of the body in the area under the dorsal fin in all remaining species of *Cyphocharax*]. Pigmentation features which further distinguish *Cyphocharax biocellatus* from many congeners include the presence of a dark, midlateral somewhat longitudinally-ovoid spot on the posterior portion of the caudal peduncle and scales overlying the basal portions of the middle caudal-fin rays [versus the absence of dark pigmentation on the midlateral surface of the caudal peduncle in *C. abramoides* (Kner, 1859), *C. aspilos* Vari, 1992, *C. festivus* Vari, 1992, *C. leucostictus* (Eigenmann & Eigenmann, 1889), *C. magdalenae* (Steindachner, 1878), *C. microcephalus* (Eigenmann & Eigenmann, 1889), *C. multilineatus* (Myers, 1927), *C. nigripinnis* Vari, 1992, *C. notatus* (Steindachner, 1908), *C. platanus* (Günther, 1880), *C. plumbeus* (Eigenmann & Eigenmann, 1889), *C. stilbolepis*, Vari, 1992, and *C. vexillapinnus* Vari, 1992, the possession of a longitudinally-elongate midlateral stripe on the caudal peduncle and sometimes the entirety of the middle caudal-fin rays in *C. gilbert* (Quoy & Gaimard, 1824), *C. laticlavus* Vari & Blackledge, 1986, *C. nagelii* (Steindachner, 1881), and *C. pantostictos* or the vertically-elongate spot in *C. meniscoporus* Vari, 1992], the

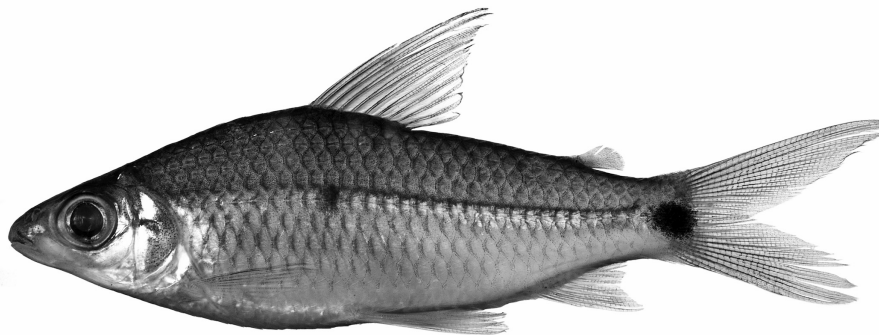


Figure 1. - *Cyphocharax biocellatus*, holotype, ANSP 189146, 62.8 mm SL; Suriname, Sipalawini, Litani River at mouth and confluence with Marowini River, just upstream from settlement of Konya Kondre, 03°17'24"N, 054°04'38"W.

Table I. - Morphometrics of holotype and paratypes of *Cyphocharax biocellatus*, new species. Range and mean include holotype and paratypes.

	Holotype	Range	Mean
Standard length (mm)	62.8	44.3-69.2	-
Percent of SL			
Greatest body depth	33.9	32.3-32.7	33.2
Snout to dorsal-fin origin	49.9	48.0-52.8	50.2
Snout to pectoral-fin origin	33.3	28.8-32.2	31.9
Snout to pelvic-fin origin	53.4	51.0-53.2	52.7
Snout to anal-fin origin	80.7	77.0-79.7	78.7
Snout to anus	76.9	75.9-77.7	76.7
Dorsal-fin origin to hypural joint	57.5	55.6-57.1	56.2
Dorsal-fin origin to anal-fin origin	45.3	39.9-46.0	44.1
Dorsal-fin origin to pelvic-fin insertion	38.1	33.5-39.1	37
Dorsal-fin origin to pectoral-fin insertion	33.3	28.8-32.2	31.6
Caudal-peduncle depth	12.3	11.3-12.4	12.1
Pectoral-fin length	18.3	18.3-18.8	18.5
Pelvic-fin length	22.7	21.0-22.4	21.7
Dorsal-fin length	30.8	27.7-28.5	28.9
Head length	27.4	25.4-28.2	26.1
Percent of HL			
Snout length	31.1	29.4-33.3	31.9
Orbital diameter	38.8	36.6-37.9	37.6
Postorbital length	37.4	36.7-38.3	37.9
Interorbital width	41.4	37.8-41.2	38.6

absence of a series of dark stripes running between the scale rows [versus the presence of such pigmentation in *C. helleri* (Steindachner, 1910)], the lack of a patch of dark pigmentation on the dorsal fin (versus the presence of such pigmentation in *C. notatus* and *C. vexillapinnus*), the hyaline or lightly speckled adipose fin (versus the black distal portions of that fin in *C. nigripinnis*). *Cyphocharax biocellatus* can be further distinguished meristically from various other congeners in the number of lateral line scales [29 to 31 versus 27 in *C. vanderi* and 27 or 28 in *C. gangamon* Vari, 1992, or 32 to 97 in *C. abramoides*, *C. aspilos*, *C. gilbert*, *C. leucostictus*, *C. magdalenae*, *C. nagelii*, *C. nigripinnis*, *C. platanus*, *C. santacatarinae* (Fernández-Yépez, 1948), *C. stilbolepis*, and *C. voga* (Hensel, 1870)], the number of scales above the lateral line (5 versus 6-11 in *C. leucostictus*, *C. nagelii*, *C. platanus*, and *C. stilbolepis* and 24-30 in *C. abramoides*), the number of scales below the lateral line (4 or 5 versus 7 to 10 in *C. nagelii*, *C. platanus*, and *C. stilbolepis* and 20-25 in *C. abramoides*), and the number of vertebrae [31 or 32 versus 28 to 30 in *C. gangamon* and *C. saladensis* (Meinken, 1933) and 33 to 35 in *C. nagelii*, *C. platanus*, and *C. voga*]. Information below is suitable to further discriminate *C. biocellatus* morphometrically from various congeners (for comparative data see Vari, 1989b; Vari and Blackledge, 1996; Vari *et al.*, 2010).

Description

Morphometric data presented in table 1. Body somewhat compressed and moderately elongate; elongation more pronounced in larger specimens. Dorsal profile of head convex from margin of upper lip to vertical situated slightly posterior of anterior nares, straight from that point to posterior terminus of supraoccipital spine. Dorsal profile of body slightly convex from tip of supraoccipital spine to dorsal-fin origin; straight to slightly convex and posteroventrally slanted from base of last dorsal-fin ray to origin of adipose fin and then very slightly concave to insertion of anteriormost dorsal procurent ray. Dorsal surface of body somewhat flattened medially anterior to dorsal fin and transversely rounded posterior to fin. Ventral profile of head very slightly convex to nearly straight from margin of lower lip to isthmus. Ventral profile of body slightly convex from isthmus to pelvic-fin insertion, nearly straight from that point to rear of anal-fin base and then slightly concave to insertion of anteriormost ventral procurent ray. Prepelvic region somewhat flattened transversely. Postpelvic region of body transversely rounded.

Dorsal fin pointed, with distal margin straight to slightly concave and last unbranched and first branched rays longest. Longest dorsal-fin ray approximately four times length of ultimate ray. Pectoral-fin profile pointed. Tip of adressed pectoral fin falls two scales short of vertical through pelvic-fin insertion. Pelvic fin profile pointed. Tip of adressed pelvic fin falls one scale short of anus in smaller paratypes and reaches that opening in holotype and largest paratype. Caudal fin forked with tips of lobes somewhat pointed. Adipose fin well developed. Anal fin emarginate with first branched ray longest and about 2.5 times length of ultimate ray. Tip of adressed anal fin falls two scales short of insertion of ventralmost caudal-fin ray.

Head profile pointed overall, but rounded anterior to vertical through posterior nostril. Upper jaw very slightly longer than lower jaw with mouth effectively terminal. Nares very close; anterior circular, posterior crescent-shaped with aperture closed by thin flap of skin separating nares. Adipose eyelid moderately developed and extending posteriorly onto anterodorsal portion of opercle. Central aperture of adipose eyelid round across size range of examined specimens.

All scales of lateral line pored with primary laterosensory canal straight. Pored lateral line scales from supracleithrum to hypural joint 29 (1), 30 (2) or 31 (1) [30]. Pored scales on basal portions of caudal fin posterior of hypural joint 3 (4) [3]. Scales in transverse series from dorsal-fin origin to lateral line not including median scale 5 (4) [5]. Scales in transverse series from anal-fin origin to lateral line not including

median scale 4 (1) or 5 (3) [4]. Scales between anus and anal-fin origin 1 (4) [1]. Middorsal series of scales from rear of supraoccipital spine to dorsal-fin origin 10 (2), 11 (1) or 13 (1) [11]. Caudal fin lacking adherent scales continuing posteriorly onto each lobe of fin.

Dorsal-fin rays iii,9 (4) [iii,9]; with first ray very short. Anal-fin rays iii,7 (4) [iii,7]; with first ray very short. Pelvic-fin rays i,8 (3) or i,9 (1) [i,8]. Pectoral-fin rays 13 (2) or 14 (2) [13]. Total vertebrae 31 (3) or 32 (1) [31].

Coloration in alcohol

Ground coloration of holotype and largest paratype (MNHN 2010-006; both specimens distinctly larger than other paratypes and all non-type specimens) ranging from pale (paratype) to somewhat dusky (holotype). Snout and dorsal portion of remainder of head of holotype dark, with scattered dark chromatophores on dorsal two-thirds of opercle, upper and lower lips and ventral surface of lower jaw. Pigmentation much lighter in largest paratype, albeit with scattered melanophores throughout these areas. Distinct, deep-lying, dark midlateral stripe masked by guanine extending from immediately posterior of head (holotype) or under middle of dorsal fin (largest paratype) to end of caudal peduncle. Distinct, vertically-ovoid, dark spot overlying dusky midlateral stripe in region under anterior portion of dorsal fin. Spot extends approximately one and one-half scales vertically and two scales longitudinally. Second slightly smaller and more posteriorly positioned dark spot present on right side of paratype, but absent on other side of that specimen, and both sides of body of holotype and other paratypes. Posterior margin of scales bordered by small dark chromatophores and forming overall faint reticulate pattern on lateral and dorsolateral surfaces of body in larger paratype. Holotype darker overall than other specimens with reticulate pattern more obvious and extending further ventrally to horizontal running approximately through base of pectoral fin. Posterior portion of caudal peduncle overlain by intensely dark, very slightly longitudinally-elongate dark spot with irregular margins that extends posteriorly onto basal portions of middle caudal-fin rays. Fin rays of dorsal and anal fins outlined by small, dark chromatophores, with chromatophores overlying rays to varying degrees. Adipose fin speckled with small dark chromatophores; more obviously so in holotype. Anal, pectoral, and pelvic fins hyaline or with few scattered melanophores.

Two smaller paratypes and all of non-type specimens with overall coloration light to very light brown. Scattered, small, dark chromatophores present on dorsal and dorsolateral portions of head. Ventrolateral and ventral portions of head without dark pigmentation other than for some dark chromatophores on ventral surface of lower lip. Irregular, slightly dusky patch formed of separate dark chromatophores located on midlateral surface of body anterior to midlateral

stripe and under anterior portion of dorsal fin in all examined specimens above approximately 28 mm SL. Patch situated in position of distinct dark spot in larger holotype and largest paratype. Spot variably obvious, but typically quite distinct from more posterior midlateral pigmentation. Scattered dark chromatophores in smaller specimens forming barely apparent dusky midlateral stripe on body. Stripe most evident posterior of vertical through base of ultimate dorsal-fin ray. Posterior margin of scales on lateral and dorsolateral surfaces of body with some small dark chromatophores and forming faint reticulate pattern. Smallest examined specimens without pigmentation at base of middle caudal-fin rays, but posterior portion of caudal peduncle and basal sections of middle caudal-fin rays in most specimens overlain by patch of discrete dark chromatophores that form dusky, somewhat horizontally elongate ovoid spot. Dorsal, pectoral and pelvic fins with scattered dark chromatophores on fin membranes.

Coloration in life (based on photograph in Planquette *et al.*, 1996: 123; species identified therein as *Cyphocharax punctatus*)

Ground coloration light brown with distinct dark reticulation pattern obvious along scale margins of dorsal and dorsolateral portions of body. Guanine well developed on scales of anterior portion of dorsolateral region of body and on portion of body ventral of lateral line. Guanine also very obvious on opercle, infraorbitals, and ventrolateral and ventral portions of head. Iris silvery. Dorsal and caudal fins with yellowish tint, more so on basal portion of caudal fin. Two prominent dark spots obvious on midlateral surface of body, one in region under dorsal fin and second on base of middle caudal-fin rays.

Habitat and ecology

The holotype was captured in a side channel of the Litani River that isolated a small, elongate, forested island. Upstream portions of the channel were dominated by shallow cataracts over a bedrock substrate strewn with boulders and cobble whereas the downstream portion of channel was a small, shallow (less than 2 m deep) backwater over a sand substrate. Margins of the channel included shallow pockets of slackwater habitat, often with submerged vegetation and shaded by overhanging bank vegetation extending into the water. The holotype was the only specimen of the Curimatidae captured during three days of collecting at that location which otherwise yielded near 60 species of fishes. It is possible that this is a marginal habitat for the species. The paratype from the Mana River system was caught in an overall similar habitat in a 10 meter wide, shallow (0.50 m deep) tributary to the main river in an area with relatively rapid water flow (around 1m/s). The substrate was principally sand with some rocky bars and large pieces of dead wood. As was the case with the holotype, it was the only specimen of the

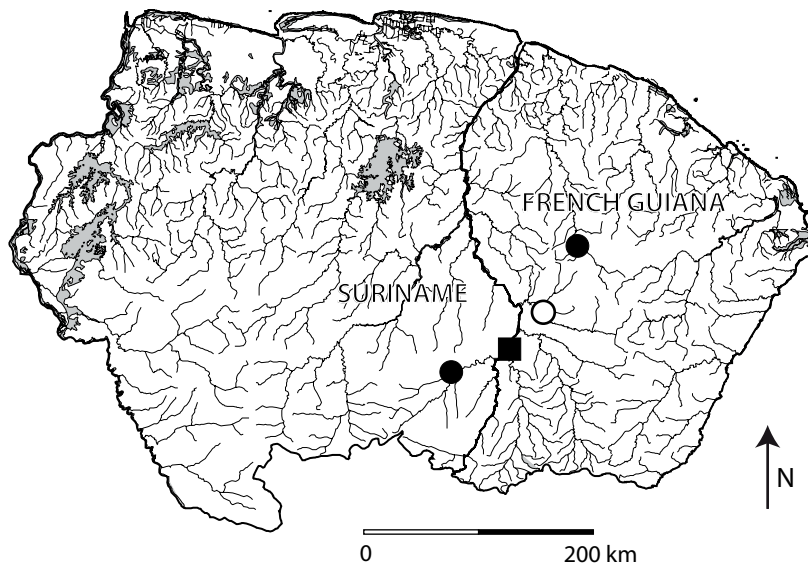


Figure 2. - Map of French Guiana and eastern Suriname showing known localities for *Cyphocharax biocellatus* (filled in square = holotype locality; dots = paratype localities; circle = non-type locality).

Curimatidae captured at that location, with the Characidae, Anostomidae and Crenuchidae being the most prominent members of the ichthyofauna at that location.

Distribution

Cyphocharax biocellatus is known from the Marowijne River/Maroni River system in eastern Suriname and western French Guiana, and the Mana basin in French Guiana (Fig. 2).

Etymology

The specific name, *biocellatus*, from the Latin *bi*, two, and *ocellatus*, having little eyes, is in reference to the two small dark spots on the lateral surface of the body in the species, one under the dorsal fin and the second on the middle of the caudal peduncle.

Generic placement

As now defined, *Cyphocharax* is delimited by its possession of the synapomorphies for a quadrotomy formed by that genus, *Curimatella* Eigenmann & Eigenmann, *Pseudocurimata* Fernández-Yépez, and *Steindachnerina* Fowler in combination with the absence of the synapomorphies diagnostic for each of the latter three genera (Vari, 1989a, 1991, 1992a, 1992b). The absence of identified derived features common to the species of *Cyphocharax* leaves open the possibility that the closest relatives of *C. biocellatus* (and perhaps some of its nominal congeners) are one of *Curimatella*, *Pseudocurimata*, and *Steindachnerina* rather than the other species now assigned to *Cyphocharax*. Nonetheless, *C. biocellatus* lacks the externally obvious synapomorphies characteristic of *Pseudocurimata* (Vari, 1989a: 58; 1989b: 8), *Steindachnerina* (Vari, 1989a: 58; 1991: 23) and *Curimatella* (Vari, 1989a: 58; 1992b: 4) and in the absence of those

derived characters is assigned to *Cyphocharax* following present taxonomic practice.

Comparisons

The features noted in the Diagnosis serve to generally distinguish *Cyphocharax biocellatus* from all of its congeners; however, the ichthyofauna of the northerly-flowing rivers of the Guianas includes an overall distinct and proportionally speciose subset of the Curimatidae (see Diversity below). Seven other members of the genus (*C. festivus*, *C. gouldingi*, *C. helleri*, *C. leucostictus*, *C. microcephalus*, *C. punctatus*, and *C. spilurus*) are known to inhabit the rivers of Guyana, Suriname, and French Guiana. Pigmentation serves to readily delimit *C. biocellatus* from its congeners in those areas. The series of multiple longitudinal stripes along the body in *C. helleri* readily distinguishes that species from *C. biocellatus* in which such pigmentation is lacking. The absence of a dark spot at the rear of the caudal peduncle and basal portions of the middle caudal-fin rays in *C. festivus* and *C. leucostictus* similarly differentiates those species from *C. biocellatus*, which is characterized by that pigmentation pattern. *Cyphocharax microcephalus*, *C. gouldingi* and *C. spilurus* lack the dark spot under the dorsal fin that is characteristic of *C. biocellatus*. *Cyphocharax punctatus* has multiple additional midlateral dark spots on the body in addition to those under the dorsal fin and at the rear of the caudal peduncle (see Vari and Nijssen, 1986: pl. 1 for variation), with these spots quite dark in specimens of *C. punctatus* of a size at which the single midlateral spot in *C. biocellatus* is obscure. Various meristic and morphometric features further serve to distinguish *C. biocellatus* from the other members of the genus in the Guianas. The species most similar to *C. biocellatus* in terms of overall form is *C. spilurus* which also shares a variably intense patch of dark pigmentation at the base of the caudal

fin. The species differ most obviously in the presence of the midlateral spot under the dorsal fin in *C. biocellatus* which is present even in the smallest examined specimens as a diffuse, but discrete patch of dark chromatophores which is more intense than the pigmentation of the midlateral stripe extending posteriorly from that area. No such pigmentation is apparent in examined specimens of *C. spilurus*.

Diversity

As we note under Comparisons, the description of *Cyphocharax biocellatus* brings to eight the number of species of the genus known from the rivers of the Guianas, with four of these species present in the Maroni River basin. Both totals are striking given the proportionally limited expanses represented by the Guianas and the Maroni River system within the total range of the Curimatidae. The eight species from the Guianas, nonetheless, represent a minority of the species of the Curimatidae occurring in those countries, which are inhabited by 19 species of the family (Vari, 2009: 26) in the genera *Curimata* (3 species), *Curimatella* (2 species), *Curimatopsis* (1 species), *Cyphocharax* (8 species including *C. biocellatus*), *Psectrogaster* (2 species), and *Steindachnerina* (3 species).

Such diversity is particularly notable when you consider that the totality of the range occupied by the Curimatidae across the vast expanse from the Pacific slopes of Costa Rica and Panama through the Atlantic, Pacific, and Caribbean versants of South America as far south as Argentina is home to 102 species of the family. The slightly less than 500,000 km² occupied by Guiana, Suriname and French Guiana thus are home to approximately 19% of the recognized diversity within the Curimatidae despite comprising only 4% of the approximately 12,500,000 km² occupied by that family. This diversity is disproportionately 4.5 times that expected based solely on the area of those countries. More generally, this pattern of higher than expected numbers of species correlates with the pronounced diversity of the Curimatidae across the river systems of the Guiana Shield which drain the three Guianas and adjoining portions of Brazil and Venezuela (see Funk and Kelloff, 2009: Fig. 1). These drainages are home to 36 curimatid species or approximately 36% of the species in the family (Vari, 2009: 26, plus *Cyphocharax gouldingi* from the Oyapock River system along the French Guiana-Brazilian border). Again this is a higher number than might otherwise be expected based solely on land area, since the circa 1.9 million km² of the Guiana Shield (Funk and Kelloff, 2009: 2) represent approximately 15% of the region occupied by the family.

The causes of the general pronounced diversity of the Guiana Shield ichthyofauna (see Vari and Ferraris, 2009) including the Curimatidae remain undetermined although Vari and Ferraris (2009) and other authors (e.g., Lujan and Armbruster, in press) have noted a number of potential con-

tributory factors including the ancient nature of the underlying formation, multiple instances of stream capture, incomplete separation of water basins, diversity of water types and the range of stream forms. Evaluation of the relative contribution of most of these potential factors to curimatid diversity is difficult at best and more likely impossible, but the ancient nature of the formation underlying the Guiana Shield and the long term stability of that formation parallels the apparent long evolutionary history of the Curimatidae.

Members of the Curimatidae in the rivers of Guiana, Suriname, and French Guyana and of the Guiana Shield extend across the phylogenetic range of the family from the basal genus *Curimatopsis* through to members of *Cyphocharax*, *Curimatella* and *Steindachnerina*, which together with the trans-Andean genus *Pseudocurimata* form a crown cluster within the family (Vari, 1989a). The only curimatid genera absent from the three Guianas in particular and the Guyana Shield in general are *Potamorhina*, a genus inhabiting portions of the Amazon, Maracaibo, Orinoco and Río de La Plata systems and *Pseudocurimata*, an endemic of several river systems of trans-Andean Colombia, Ecuador and Peru. Both of these genera are among the least speciose in the Curimatidae.

Notwithstanding the sparse nature of the fossil record of the Curimatidae, it is informative as to the likely age of multiple subunits within the family. Two fossil species of *Cyphocharax* are known from the eastern Brazilian Tremembé formation of Oligocene-Miocene age, thereby documenting the existence of this relatively derived genus (Vari, 1989a: Fig. 44a) within the Curimatidae at least 23 million years ago (Malabarba and Malabarba, 2010: 320, 324). Ancestors of *Cyphocharax*, all more encompassing lineages with the family, and more basal curimatid genera living on the rivers of the Shield (*Psectrogaster*, *Curimata* and *Curimatopsis* in sequentially more basal sequence) of necessity are of older ages, albeit with the timing of the earlier divergence events within the family unknown. As one of the more stable regions within the range of the Curimatidae, the Shield would have served both as a refuge and likely as a centre of diversification for diverse lineages within the Curimatidae in the period prior to 23 million years ago. As such the long term stability of the Shield was undoubtedly a factor, perhaps a significant one, in the high diversity of the family in the river systems of the region.

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