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A review of *Dicrossus foirni* and *Dicrossus warzeli*, two species of cichlid fishes from the Amazon River basin in Brazil (Teleostei: Cichlidae)

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Abstract

Dicrossus warzeli and *D. foirni* were described with focus on within-species colour pattern variation and aquarium observations. Validity of the two species is confirmed on the basis of wild specimens of *D. warzeli* from the lower Rio Tapajós between Itaituba (São Luis do Tapajós) and Cururu, and of *D. foirni* from tributaries of the middle Rio Negro (Rio Marauiá and Rio Padauari). A phylogenetic assessment using colour pattern and fin shape shows that *D. foirni* and *D. warzeli* are sister species, and form the sister group of *D. filamentosus* from the Rio Negro and Rio Orinoco basins and *D. maculatus* from the central Amazon basin.

Zusammenfassung

Beschrieben wurden *Dicrossus warzeli* und *D. foirni* mit dem Schwerpunkt auf den innerartlichen Varianten im Farbmuster und auf der Grundlage von Aquarienbeobachtungen. Die Gültigkeit der beiden Arten wird auf der Basis von Exemplaren aus der Natur bestätigt: *D. warzeli* vom unteren Rio Tapajós zwischen Itaituba (São Luis do Tapajós) und Cururu sowie *D. foirni* von den Zuflüssen des mittleren Rio Negro (Rio Marauiá and Rio Padauari). Phylogenetische Untersuchungen der Farbmuster und der Flossenformen ergaben, dass es sich bei *D. foirni* und *D. warzeli* um Schwesterarten handelt, die eine Schwestergruppe zu *D. filamentosus* von den Becken des Rio Negro und des Rio Orinoco und *D. maculatus* vom zentralen Amazonasbecken bilden.

Résumé

Dicrossus warzeli et *D. foirni* ont été décrits surtout sur base des différences de patron de coloration et d'observations en aquarium. La validité des deux espèces est confirmée sur base de spécimens sauvages de *D. warzeli* du bas Rio Tapajós entre Itaituba (São Luis de Tapajós) et Cururu, et de *D. foirni* de tributaires du moyen Rio Negro (Rio Marauia et Rio Padauari). Un examen phylogénétique recourant au patron de coloration et à la forme des nageoires montre que *D. foirni* et *D. warzeli* sont des espèces soeurs et font partie du groupe comprenant *D. filamentosus* des bassins du Rio Negro et du Rio Orinoco et *D. maculatus* du bassin de l'Amazone central.

Sommario

Dicrossus warzeli e *D. foirni* sono stati descritti focalizzando l'attenzione sulle variazioni intraspecifiche della colorazione e basandosi su osservazioni in acquario. La validità delle due specie è confermata dall'esame di esemplari di *D. warzeli* raccolti nel Rio Tapajós inferiore tra Itaituba (São Luis do Tapajós) e Cururu e di *D. foirni* dagli affluenti del Rio Negro medio (Rio Marauiá e Rio Padauari). Uno studio filogenetico che impiega la livrea e la forma delle pinne mostra che *D. foirni* e *D. warzeli* sono specie sorelle, che rappresentano il gruppo fratello di *D. filamentosus* dei bacini del l Rio Negro e del Rio Orinoco e di *D. maculatus* del bacino centrale del Rio delle Amazzoni.

INTRODUCTION

The South American cichlid genus *Dicrossus* Steindachner (1875), was long synonymised with *Crenicara* Steindachner, 1875, but recognized as a subgenus of *Crenicara* by Kullander (1990) and later treated as a full genus by most authors (e.g. Kullander 2003). *Dicrossus* includes the valid species *D. filamentosus* (Ladiges, 1958), from the Orinoco and Negro drainages (Kullander 1978), *D. maculatus* Steindachner, 1875, from the central Amazon basin (Kullander 2003) and *D. gladicauda* Schindler & Staeck, 2008, from the Orinoco basin. *Crenicara praetoriusi* Weise (in Praetorius 1935) and its homonym *C. praetoriusi* Ahl, 1936, are synonyms of *D. maculatus* (Kullander 2003). Most recently two more species were described based largely on aquarium material, viz. *D. foirni* Römer, Hahn & Vergara, 2010, from the middle Rio Negro, and *D. warzeli* Römer, Hahn & Vergara, 2010, from the lower Rio Tapajós. These had already been recognized by Kul-

lander (1990), who referred to two undescribed species of *Dicrossus*, but without providing any details. The two species have meanwhile entered the ornamental fish trade in Europe and North America and are well covered in hobby literature (Stawikowski & Werner 2004). Their formal descriptions are also mainly geared toward the ornamental fish hobby. Because Römer et al. (2010) relied mainly on aquarium observations, and did not engage in taxonomic or other analysis, it is pertinent to report on observations made from wild caught specimens with reliable locality information, which is the objective of this paper.

MATERIAL AND METHODS

Measurements and counts were taken as described by Kullander (1980, 1986). Specimen lengths are given as standard length (SL), measured from the tip of the upper jaw to the middle of the base of the caudal fin. Scales in a longitudinal row (E1 row scales) are counted in the row immediately dorsal to that containing the lower lateral line. Colour marking terminology follows Kullander (1980, 1986), except that a maximum complement of the pattern of blotches is referred to as follows and as in Fig. 1.

Horizontal rows of blotches are referred to as rows H1–H4. H1 includes the dark blotch at the nape and four blotches along the dorsal fin base; H2 begins immediately above the lateral line origin and continues on the dorsal margin of the caudal peduncle and caudal fin base; H3 starts immediately below the upper lateral line origin and includes the superior spot at the base of the caudal fin; H4 includes blotches immediately below H3, and ends with the lower spot at the base of the caudal fin. In *Crenicara*, *Dicrossus maculatus* and *D. filamentosus*, the blotches in rows H1-2 and H3-4 are contiguous vertically so that only two horizontal blotch rows are present in these species. In *D. warzeli* rows H1 and H2 also form contiguous markings below the dorsal fin, so that only three rows of blotches are clearly distinguishable.

Vertical rows of blotches are referred to as V1-V9: V1 is represented by the blotch anteriorly on the nape; V2 includes the blotch around the dorsal fin origin, and the first blotch in row H2; V3 includes the second blotch close to the dorsal fin base, the H2 blotch below and the first blotch in row H3. In *D. warzeli* and *D. foirni* the H1+2/V3 blotch is particularly prominent; V4-5 include the blotches in a forward-slanting row below the dorsal fin base; V6 descends from the end of the dorsal fin base; V7 descends anteriorly on the caudal peduncle; V8 has the dorsal blotch at the base of the caudal fin dorsally; V9 includes only the one or two markings at the middle of the base of the caudal fin.

Vertebral counts include the last half-centrum and were taken from radiographs made on Kodak X-omat V film using a Philips MG-105 low voltage X-ray unit. Morphometric data were managed and analysed using PASW Statistics 18 (SPSS 2009), except that the principal component analysis (PCA) of measurements was made using a separate procedure for component shearing, partialing out multivariate size residues from the second and further components as described by Humphries et al. (1981). The PCA analysis was made with log-transformed measurement data to tenth of a millimetre in a covariance matrix, and without rotation. Pelvic fin length was excluded from the PCA because of the strong sexual dimorphism in the length of the pelvic fin. Only wild specimens preserved in the field were used for measurements and counts. Comparative measurement data were taken from Kullander (1978) for *Dicrossus filamentosus*, Kullander

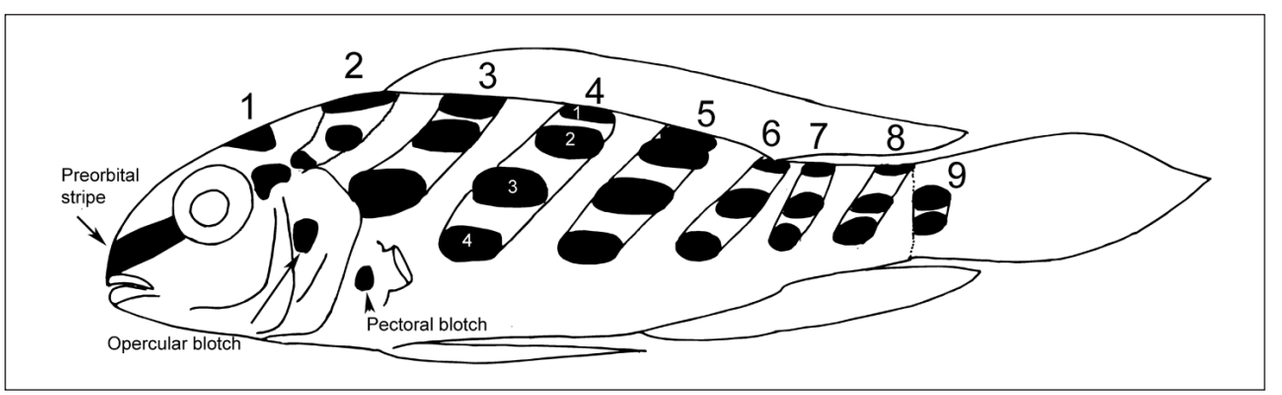

Fig. 1. Schematic representation of vertically (black numbers) and horizontally arranged markings in species of *Dicrossus*.

(1986) for *Crenicara punctulatum* (Günther, 1863), and Kullander & Staeck (1990) for *Crenicara latruncularium* Kullander & Staeck, 1990.

The phylogenetic analysis includes seven parsimony-informative morphological characters (Table 1). It was made with PAUP* 4 (Swofford 2002), using the exhaustive parsimony algorithm and default settings. WinClada (Nixon 2002) and NONA (Goloboff 1993) were used in concert to visualize character state transformations on the parsimony tree.

Specimens studied are deposited in the following institutions: CAS, California Academy of Sciences, San Francisco; FMNH, Field Museum of Natural History, Chicago; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; IRSNB, Institut royal des Sciences naturelles de Belgique, Bruxelles; MBUCV-V, Museo de Biología, Universidad Central de Venezuela, Caracas; MZUSP, Museu de Zoología da Universidade de São Paulo, São Paulo; NRM, Swedish Museum of Natural History, Stockholm; USNM, United States National Museum, Smithsonian Institution, Washington, D.C.; and ZSM, Zoologische Staatssammlung, München.

Comparative material: *Dicrossus filamentosus*: Colombia, Rio Orinoco basin: FMNH 92861 (82), Rio Meta drainage, Río Manacacías. J. Thomerson et al., 1 Apr 1974; NRM 11245 (3), Rio Inírida drainage, Caño Bocón, near Las Palmeras, Puerto Nariño. T. Hongslo, 2 Jun 1972; NRM 11246 (2), same data as NRM 11245 but date 5–6 Jun 1972; NRM 11248 (5), same data as NRM 11245 but date 4 Jun 1972; NRM 11249 (1), Rio Inírida drainage, Puerto Inírida area. T. Hongslo, 24 May-13 Jun 1972; NRM 27545 (11), Rio Vita drainage, Caño Alisal, a few km S of Puerto Carreño. T. Hongslo, 6 Mar 1985; NRM 27546 (14) and NRM 37065 (1), Rio Vichada drainage, Rio Guarrojo where emptying in Rio Vichada, Finca Boca de Guarrojo. T. Hongslo, 8 Mar 1972; NRM 27547 (1), Rio Inírida drainage, Puerto Inírida, Barrio de Indígenas, Caño Conejo and flooded areas. T. Hongslo, 11 Jul 1976. Venezuela, Rio Orinoco basin: CAS SU 63548 (1), Atabapo, San Fernando. C. Ternetz, 8 Apr 1925. Venezuela, Rio Negro basin: MBUCV-V 4837 (5), Rio Parguaza, 12 Mar 1967; NRM 27542 (1), Rio Casiquiare, caño tributary to Rio Pasimoni. T. Hongslo, 13 Feb 1981; NRM 27543 (4), San Carlos and Rio Pasimoni (3 different samples mixed up). T. Hongslo, Feb 1981; NRM 27544 (1), Caño Adabo [=Caño Mayabo?]. T. Hongslo, 4 Feb 1981; USNM 269302 (2), Caño Manu tributary of Casiquiare Canal c. 250 m upstream of Solano. R. P. Vari et al., 7 Dec 1984; USNM 269310 (5), small caño off Caño Urami, just upriver of Sta Lucía. R. P. Vari et al., 6 Dec 1984; USNM 269319 (1), Caño Chola where crossed by road from San Carlos de Rio Negro to Solano. R. P. Vari et al., 5 Dec 1984. Brazil, Rio Negro basin: CAS 14659 (3), Praya Bulufú, Rio Itu, ca 80 km upstream from Rio Negro. M.R. Brittan, 26 Apr 1964; CAS 34953 (1), Rio Jufari, at 'Santa Fé', a small fishing camp ca 20 km upstream from Parica & Campinho. M.R. Brittan, 20 Apr 1964; CAS 34954 (6), Igarapé Duyá, a creek tributary to Rio Itú about 160 km up from Rio Negro. M. R. Brittan, 26 Apr 196; INPA uncat. (8), Igarapé da "Cachoeira", Rio Unini. Equipe Ictiologica do INPA, 28 Dec 1976; MZUSP 28182 (8), Rio Negro, Ilha Cumuri, near Rio Arirará, lago. M. Goulding, 1 Feb 1980; MZUSP 28191 (29), Rio Negro, Paraná na Ilha de Tamaquaré. M. Goulding, 7 Feb 1980; MZUSP 28197 (4), Rio Arirará, near mouth. M. Goulding, 1 Feb 1980; MZUSP 28205 (829), Rio Urubaxi, swamp near mouth. M. Goulding, 3-11 Feb 1980; MZUSP 28212 (3), Rio Negro, central lake near Daraá. M. Goulding, 17 Feb 1980; NRM 19438 (2), Rio Negro junction with Rio Urubaxi. M. Goulding, Feb 1987; NRM 19439 (1), Rio Negro junction with Rio Ererê. M. Goulding, Feb 1987.

Dicrossus maculatus: Brazil, Rio Tapajós drainage: MZUSP 8421 (7), Alter do Chão, Igarapé Jacundá. EPA, 23 Dec 1967; MZUSP 8454 (44), Alter do Chão, Igarapé Jacundá. EPA, 23 Dec 1967; MZUSP 8502 (17), Santarém, igarapé left bank margin of Rio Mapiri. EPA, 25 Dec 1967; MZUSP 38297 (126), Igarapé Jacaré on right bank of Rio Tapajós, near Boím. EPA, 27 Oct 1970; NRM 14851 (3), Santarém. A. Werner, 1988; NRM 16469 (10), Lago Jacundá at Alter do Chão. B. Kilian & I. Seidel, 12 Oct 1991; NRM 18528 (5), Rio Arapiuns, one third of way Vila de Cachoeira – Vila Brasil, island with sand shore. R. Stawikowski et al., 5 Oct 1992; NRM 18684 (1), Rio Arapiuns, 1 h by boat downstream mouth of Rio Aruã, small fazenda at right shore. R. Stawikowski et al., 4 Oct 1992; NRM 19497 (6) and NRM 37117 (2), Lago Jacundá at Alter do Chão. B. Kilian & C. Seidel, 12 Oct 1991; NRM 30923 (5), right bank of lower part of igarapé tributary to R. Tapajós bordering city upstream. S. O. Kullander, 27 Sep 1980; NRM 30924 (3), same data as 30923 but date 28 Sep 1980; NRM 31957 (5), Rio Tapajós at mouth, right bank, bay off Lago Piranha, near Alter do Chão,

laguna. T. B. Andersen, 23 Sep 1994. Brazil, Rio Maués drainage: MZUSP 7369 (1) Rio Maués, município Maués, Igarapé Limãozinho. EPA, 4 Dec 1967. Brazil, Rio Amazonas drainage: MZUSP 7814 (9), Parintins, igarapé of Lago Ze Açú. EPA, 11-12 Dec 1967; USNM 120404, (2), Lago Ze Açú. Thayer Expedition, 1866. Brazil, Rio Trombetas drainage: MZUSP 8225 (17), Rio Trombetas, Oriximiná, Igarapé Jacupá. EPA, 17 Dec 1967.

Dicrossus cf. *maculatus:* NRM 37547 (1), Brazil, Rio Madeira drainage: Rio Traíra where crossing Road BR-230. U. Werner et al., 29 Jul 1996.

Type material of *D. warzeli* and *D. foirni* was not re-examined. The present material comes in part from the same or nearly the same localities and the validity and identity of the species are not in question. The respective holotypes could not be examined because they had not been received at the repository, MZUSP, by December 2010 (O. Oyakawa, pers. comm., 6 December 2010).

Dicrossus warzeli Römer, Hahn & Vergara, 2010

(Figs 2-6; Tables I-II)

Material examined: All from Brazil, State of Pará, Rio Tapajós drainage. IRSNB 784, 1 female, 28.5 mm SL, arm of Rio Cururu below the Franciscan mission of Cururu. J. P. Gosse & Léopold III, 21 Nov 1964; MZUSP 25423. 49, 12.9-50.0 mm SL (9 measured, 26.3-50.0 mm SL), Pimental village, right bank of Rio Tapajós, mouth of Igarapé Pimental (PARNA), J. C. de Oliveira, 15-31 Jul 1979; MZUSP 32740. 4, 16.8-24.0 mm SL. Road Jacareacanga-Itaituba, rocky stretch in stream. M. Goulding, 10 Aug 1984; MZUSP uncat. 1 female, 20.5 mm SL. Pederneiras, below Itaituba, pool in pedral, M. Goulding, 24 Oct 1983; NRM 32146. 1 male, 52.8 mm SL, 1 female, 39.7. mm SL, mouth of Igarapé near Pimentel; kept in aquarium, F. Warzel, 1995; NRM 35579. 1 female, 43.3 mm SL. Rio Tapajós about 5 km upstream of São Luis do Tapajós, small bay, F. Warzel et al., 30 Aug 1995; NRM 41431, 2 females, 24.4-29.5 mm SL, Rio Tapajós about 10 km upstream of São Luis do Tapajós, small river, F. Warzel, 1998; ZSM 25358. 1 juvenile, 20.8 mm SL. 100 km E of Jacareacanga, H. Bleher, Sep 1974.

Diagnosis: Similar to *Dicrossus foirni*, but distinguished from all other species of *Dicrossus* by colour pattern consisting of nine vertical rows of blotches on side and caudal fin base, four horizontal rows (H1-4) of blotches anteriorly on side,

Fig. 2. *Dicrossus warzeli*, MZUSP 25423, adult female, 37.8 mm SL. Brazil, Pará Rio Tapajós drainage, mouth of Igarapé Pimental. Photo by S. O. Kullander

Fig. 3. *Dicrossus warzeli*, MZUSP 25423, adult male, 50.0 mm SL. Brazil, Pará, Rio Tapajós drainage, mouth of Igarapé Pimental. Photo by S. O. Kullander

Table I. Character matrix for phylogenetic analysis of *Dicrossus*. Characters and states: 1, Dorsal blotch: 0 absent;1 present; 2, Pectoral blotch: 0 absent; 1 present; 3, Blotch rows V6–7: 0 separate; 1 combined; 4, Blotch rows H3–4: 0 single; 1 separate; 5, Caudal fin: 0 rounded; 1 lanceolate; 2 lyreate; 6, Pelvic fin in males: 0 short; 1 filamentous; 7, Caudal fin colour pattern: 0 vertical stripes present; 1 vertical stripes absent.

Character	1	2	3	4	5	6	7
Crenicara punctulatum	0	0	0	0	0	0	0
Crenicara latruncularium	0	0	0	0	0	0	0
Dicrossus filamentosus	0	0	1	0	2	1	0
Dicrossus maculatus	0	0	1	0	1	1	0
Dicrossus warzeli	1	1	0	1	1	1	1
Dicrossus foirni	1	1	0	1	1	0	1

three posteriorly (H2-4), and caudal fin base with two small dark blotches (H3-4). In *D. maculatus*, *D. filamentosus*, and *D. gladicauda* only two rows of large blotches along side, single large dark spot at caudal fin base and also usually only eight vertical markings. Blotches along middle of side (rows H3-4) appearing as short horizontal stripes each extending over several scales whereas in *D. foirni* blotches in rows H3 and H4 typically composed of two smaller contiguous blotches.

Description: Based primarily on adults from MZUSP 25423. General aspect and colour pattern illustrated in Figs 2-5. Measurement data summarised in Table II.

Elongate, moderately compressed laterally, body depth slightly decreasing caudad. Dorsal outline only slightly curved, not much elevated above caudal peduncle. Ventral outline slightly curved. Head short, deep, laterally compressed. Predorsal contour straight, very slightly inclined, nape wide, somewhat depressed; dorsal outline of snout steeply inclined. Orbit large, positioned at about middle of head length, in upper half of head.

Preopercle with 24-46 short, pointed, well differentiated projections along the posterior margin and corner. Pterotic with 1-8 short, variably developed, more or less pointed projections from posterior margin. Supracleithrum dorsally with 4-11 pointed, usually well differentiated projections along the posterior margin; usually each projection with one point, but projections with two points occur.

Cephalic lateralis system comprising lachrymal with four pores; short, tubular first postlachrymal infraorbital with terminal pores, followed by long, tubular, curved infraorbital with median and terminal pores; short, tubular dermosphenotic with terminal pores; three pterotic pores, each shared with dermosphenotic, preorbital and lateral extrascapular; posttemporal with posterior external pore and internal opening to lateral extrascapular; medial extrascapular with terminal pores, ventral pore shared with lateral extrascapular; four dentary pores, posteriormost toward anguloarticular from which lateralis canal absent; six preopercular pores; three supraorbital pores; terminal nasal pores; and simple coronalis pore.

Scales in E1 row 25 (in 6), 26 (4). Scales on sides and abdomen relatively large, strongly ctenoid. Cheek posteriorly with 2 (1), 3 (8), 4 (1) rows of small cycloid scales, anteriorly naked; posterior to orbit one row of ctenoid scales. Scales absent from preopercle. Opercle with 3 rows of ctenoid scales. Subopercle with 2 rows of cycloid scales. Interopercle with 1 minute cycloid scale. Scales absent from pectoral fin base. Predorsal scales 9 (1), 10 (3), 11 (6) in midline row, slightly irregularly

Fig. 4. *Dicrossus warzeli*, NRM 41431, female, 29.5 mm SL. Brazil, Rio Tapajós about 10 km upstream of São Luis do Tapajós. Photo by S. O. Kullander

Table II. Standard length (in millimeters) and proportional measurements in percents of standard length of *Dicrossus warzeli* (IRSNB 784, MZUSP 25423). SD, standard deviation. Regression line parameters, a (intercept), b (slope), and r (Pearson's correlation coefficient) are calculated from measurements expressed in millimeters.

	N	Min	Max	Mean	SD	r	a	b
Standard length (mm)	10	26.3	50.0	34.4	7.54			
Head length	10	29.4	30.9	29.9	0.48	0.998	0.403	0.287
Snout length	10	5.3	8.0	6.2	0.71	0.972	-1.151	0.097
Body depth	10	26.0	30.9	28.5	1.61	0.985	2.13	0.22
Orbital diameter	10	11.8	13.6	12.9	0.49	0.988	0.713	0.107
Head width	10	13.6	16.8	15.4	0.84	0.977	1.267	0.116
Interorbital width	10	6.6	7.9	7.3	0.46	0.961	0.56	0.056
Preorbital depth	10	2.6	4.0	3.2	0.37	0.968	-0.514	0.048
Caudal-peduncle depth	10	11.2	13.6	12.5	0.65	0.970	0.76	0.102
Caudal-peduncle length	10	15.9	17.5	16.7	0.56	0.990	-0.116	0.171
Pectoral fin length	10	25.9	29.1	27.6	0.86	0.995	-0.416	0.289
Pelvic fin length	10	25.1	37.6	27.1	3.73	0.930	-5.486	0.436
Last dorsal fin spine length	10	14.1	15.9	15.0	0.46	0.991	0.315	0.141

Fig. 5. *Dicrossus warzeli*, NRM 32146, male, 52.8 mm SL, in aquarium. Photo by F. Warzel.

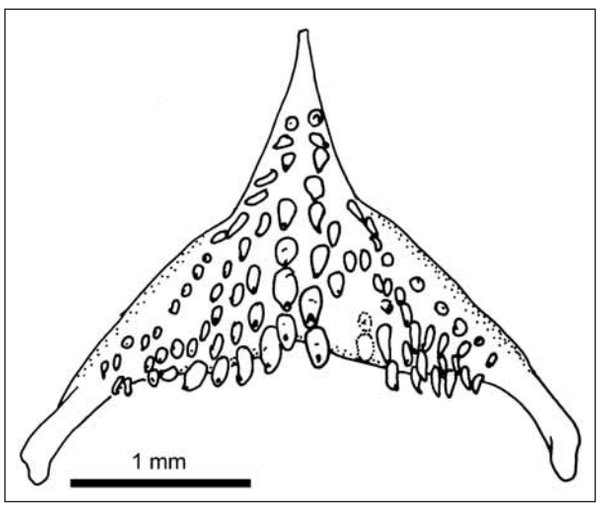

Fig. 6. *Dicrossus warzeli*. Lower pharyngeal tooth plate in occlusal view. MZUSP 25423, 36.8 mm SL.

arranged, all ctenoid. Prepelvic scales very small, cycloid except those between pelvic fin bases. Chest scales ctenoid, slightly smaller than flank scales. Circumpeduncular scales 16, comprising 7 above and 7 below lateral line scales. Scales between dorsal fin and lateral line 2½ anteriorly, ½–1 posteriorly. Lateral line scales 16/8 (2), 16/9 (2), 16/10 (1), 17/9 (1), 18/8 (1), 18/9 (3); both upper and lower with 1-5 pored scales terminally or subterminally at open ends. Lateral lines separated by two scale rows, non-overlapping. Lateral line scale at middle of caudal fin base present or absent. Scales absent from dorsal, anal, pelvic and pectoral fins; narrow basal band of ctenoid scales on caudal fin, up to about ¼ of fin length.

Dorsal fin rays XIV,8 (3), XIV,9 (1), XV,7 (4), XV,8 (5), XVI,7 (1). Dorsal fin origin above posterior margin of opercle; first spine short, spine

length increasing to 5th or 6th, from which subequal in length, last 1-2 spines slightly longer. Dorsal fin lappets short, truncate or rounded. Soft dorsal fin in females with 3rd or 4th ray longest, forming short point reaching to above caudal fin base; in large males, 5th ray prolonged, reaching slightly beyond caudal fin base.

Anal fin rays III,6 (1), III,7 (12), III,8 (1). Anal fin in females with 4th and 5th rays of about equal length forming short point, not extending to caudal fin base; in large males 5th ray prolonged, reaching slightly beyond caudal fin base. Pectoral fin rays 12 (7), 13 (3). Pectoral fin rounded, fifth ray longest, reaching posterior to vertical from vent, or first anal fin spine. Pelvic fin in females pointed, first and second rays of about equal length, forming pointed tip, reaching to genital papilla; in males first ray prolonged, filamentous, reaching at most to middle of caudal fin base. Caudal fin subtruncate in young, rounded in females, lanceolate in large males.

Teeth caniniform; in outer row hemiseries in upper jaw, 9 (2), 11 (2), 22 (1, 23 (2), 24 (2), 27 (1), number increasing with size; in outer row hemiseries in lower jaw 16 (1), 19 (4), 20 (1), 22 (2), 23 (1), 24 (1). In juveniles premaxilla anteriorly with three rows of small teeth, outer row teeth slightly larger; teeth absent from horizontal arm: lower jaw with one row laterally and broad band of teeth anteriorly. In adults premaxilla with 2-4 rows posteriorly on horizontal arm, reduced to 1-2 rows anteriorly and expanding to wide band of about 4-5 rows anteriorly; 4-5 teeth in outer row on each side of symphysis slightly larger than other teeth. Lower jaw with one row laterally; wide band of 3-4 rows of teeth anteriorly; anterior 5 on each side in outer row slightly larger than other teeth.

Lower pharyngeal tooth-plate examined in one specimen (MZUSP 25423, 36.8 mm SL), slightly wider than long (Fig. 6). Teeth in about 5 rows; 7 teeth along middle, about 17 along posterior margin, but at least one tooth missing; teeth compressed, along margins and anteriorly slender, unicuspid; mediad and caudad slightly coarser and longer, bicuspid, with strong posterior, antrorse cusp, and minor anterior blunt or pointed cusp subdistally.

Gill rakers externally on first gill arch, 1 in angle or associated distally on epibranchial, 4 (7), 5 (3) on ceratobranchial. Microbranchiospines absent. Supraneurals 1 (14). Vertebrae 13+14=27 (13), 13+15=28 (1).

Colouration in preservative: Ground colour yellowish white. Snout pale grey. Broad dark

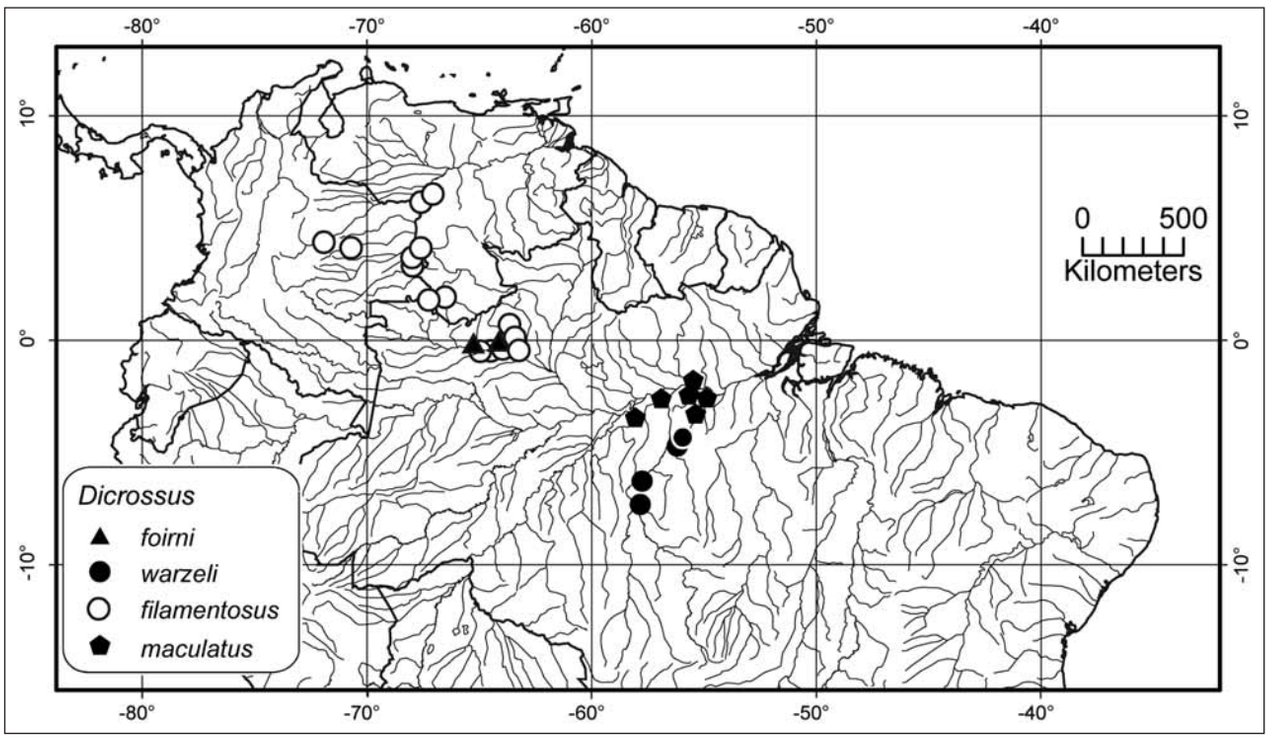

Fig. 7. Collecting localities of species of *Dicrossus*. A symbol may cover several localities.

grey preorbital stripe across upper part of lachrymal and across snout tip. Upper and lower lip folds anteriorly dark grey. Contrasting pigment-free wide area across sides of lips and lower part of lachrymal. Cheek sparsely pigmented. Two dark grey to black blotches dorsally on inner surface of opercle showing through bone. Horizontally elongate dark blotch at and posterior to dorsal tip of preopercle. Dark brown blotch on pectoral fin peduncle. Dark brown blotch at dorsal margin of pectoral fin base and dorsal portion of inner surface of pectoral fin base. Three horizontal rows of dark brown markings along dorsum and side (H1+2, H3, H4). Uppermost row composed of one blotch (V1 row) across nape slightly posterior to orbits; second blotch (V2 row) at origin of dorsal fin, extending to lateral line scales; third blotch (V3 row) below anterior third of dorsal fin, extending to lateral line scales; fourth blotch (V4 row) below posterior part of dorsal fin, extending to lateral line scales; fifth blotch (V5 row) immediately below soft dorsal fin; two small blotches (V6-7 rows), or one slightly longer blotch immediately posterior to dorsal fin base; one small blotch (V8 row) dorsally on caudal peduncle immediately anterior to caudal fin. Each of second through fifth blotches sometimes also divided into one dark blotch close to dorsal fin and another on lateral line scales separated by lighter brown colour between them. Middle row of dark brown blotches running onto E1 scales, comprising four distinct, elongate blotches (V3-6 rows) approximately positioned below interspaces of second to sixth blotches in upper row; posteriorly two rounded or single elongate blotch (V7-8 rows) on caudal peduncle. Lower row (H4) of blotches running posterior to pectoral fin base, composed of three elongate blotches (V4-6) approximately positioned below interspaces of first to fourth blotches in middle (H3) row; posteriorly two round or elongate blotches (V7-8 rows) on caudal peduncle. Dark brown blotch ventrally between vent and anal fin, continuing narrowly along anterior base of anal fin.

Fins hyaline or lightly pigmented. Indistinct dark blotch anteriorly on dorsal fin. Black blotch basally between sixth to ninth dorsal fin spines, more or less confluent with third blotch in upper row of lateral blotches. Dark brown, elongate, posteriorly narrower blotches (V9 row) on caudal fin base posterior to middle and lower rows (H3-4) of lateral blotches.

Live colouration: Live colour photos of aquarium specimens provided by F. Warzel (Fig. 5) and published by Warzel (1996), Stawikowski & Werner (2004: 71) and Römer et al. (2010) show males with almost white ground colour, pale grey lateral blotches, and black preorbital, opercular and pectoral blotches. Dorsal fin and posterodorsal margin of caudal fin with narrow blue iridescent submarginal stripe. Gill cover with distinct golden sheen, continued along side between blotch rows H3 and H4. Golden sheen and blue submarginal stripe in caudal fin apparently absent in females, and also submarginal stripe in dorsal fin less distinct. Breeding female with pale red pelvic fins, and when spawning blotches in row H3 forming continuous stripe, blotches in row H4 absent. The striped pattern was illustrated for a male in an aquarium by Römer et al. (2010: fig. 19).

Distribution and biology: Streams along the Rio Tapajós between Itaituba and Cururu (Fig. 7). Habitats were reported by Warzel (1996) as clear-water streams with leaf litter. Warzel (1996) and Stawikowski & Werner (2004: 71) reported on a single spawning in captivity, suggesting a maternal substrate brooder. Römer et al. (2010) only had specimens from near São Luis do Tapajós, collected by Warzel.

Dicrossus foirni Römer, Hahn & Vergara, 2010

(Figs 8-13; Tables I, III)

Material examined: All from Brazil, State of Amazonas, Rio Negro drainage. MZUSP 28220, 5 males, 18.3-27.1 mm SL, 3 females, 21.8-24.6 mm SL, Rio Marauiá, beach near the mouth, M. Goulding, 13 Oct 1979; NRM 12016. 2 males, 51.9-56.3 mm SL, aquarium import, F. Warzel, 1990; NRM 13279, 13, 15.3-36.3 mm SL; locality not precisely given, likely Rio Preto at mouth into Rio Padauari, W. Windisch, 14 Nov 1990; NRM 19490. 3 males, 43.3-48.7 mm SL, 1 female, 32.4 mm SL, Arquipélago das Anavilhanas, floodwaters 2-3 miles south-east of Santo Antonio, kept in aquarium, G. Grant, 2 Apr 1984.

Diagnosis: Similar to *Dicrossus warzeli*, but distinguished from all other species of *Dicrossus* by colour pattern consisting of nine vertical rows of blotches on side and caudal fin base, four horizontal rows (H1-4) of blotches anteriorly on side, three posteriorly (rows H2-4) and caudal fin base with two small dark blotches (rows H3-4). In *D. maculatus* and *D. filamentosus* only two rows of large blotches present along side and single large dark spot at caudal fin base; also usually only eight vertical

markings. Anterior blotches in rows H3 and H4 typically composed of two smaller contiguous blotches whereas in *D. warzeli* blotches along middle of side (rows H3-4) appearing as short horizontal stripes each extending over several scales.

Description: Based on MZUSP 28220, complemented with information from larger specimens NRM 12016 and NRM 19490. General aspect and colour pattern is illustrated in Figs 8-12. Measurement data are summarised in Table III.

Elongate, moderately compressed laterally, body depth slightly decreasing caudad. Dorsal outline only slightly curved, not much elevated above level of caudal peduncle. Ventral outline slightly curved. Head short, deep, laterally compressed. Predorsal contour straight, very little inclined (about 30°), nape wide,

Fig. 8. *Dicrossus foirni*, MZUSP 28220, young male, 27.1 mm SL. Brazil, Amazonas, Rio Negro drainage, Rio Marauiá. Photo by S. O. Kullander

Fig. 9. *Dicrossus foirni*, NRM 12016, adult male, 56.4 mm SL. Aquarium import. Photo by S. O. Kullander

Fig. 10. *Dicrossus foirni*, NRM 119490, adult male, 48.7 mm SL. Brazil, Amazonas, Rio Negro drainage, aquarium fish stated to be from the Arquipélago das Anavilhanas. Photo by S. O. Kullander

Table III. Standard length (in millimeters) and proportional measurements in percents of standard length of *Dicrossus foirni* (MZUSP 28220). SD, standard deviation. Regression line parameters, a (intercept), b (slope), and r (Pearson's correlation coefficient) are calculated from measurements expressed in millimeters; shown when $p<0.05$.

	N	Min	Max	Mean	SD	r	a	b
Standard length (mm)	8	18.3	27.1	23.9	2.74			
Head length	8	28.0	31.7	29.7	1.10	0.928	2.337	0.2
Snout length	8	4.5	5.8	5.2	0.45	0.483	-0.045	0.054
Body depth	8	27.6	29.3	28.4	0.50	0.961	0.08	0.28
Orbital diameter	8	12.8	14.8	13.4	0.61	0.968	1.034	0.091
Head width	8	15.3	16.9	15.7	0.54	0.978	0.627	0.131
Interorbital width	8	7.0	7.8	7.3	0.30	0.817	0.423	0.055
Preorbital depth	8	2.7	3.1	2.9	0.15	0.942	-0.207	0.038
Caudal-peduncle depth	8	10.4	12.0	11.6	0.51	0.985	-0.642	0.143
Caudal-peduncle length	8	17.3	19.5	18.8	0.70	0.803	0.492	0.167
Pectoral fin length	7	26.0	28.9	27.5	0.91	0.888	0.601	0.251
Pelvic fin length	8	24.4	26.2	25.3	0.54	0.952	0.387	0.236
Last dorsal fin spine length	8	13.7	16.5	15.6	0.93	0.888	-1.101	0.202

somewhat depressed; dorsal outline of snout steeply inclined (60-90°). Orbit large, positioned chiefly in anterior half of head, in upper half of head.

Preopercle with 22-26 short, pointed, well differentiated projections along posterior margin and corner. Pterotic with 3-6 short, pointed projections from posterior margin. Supracleithrum dorsally with 5-6 pointed, well differentiated projections along posterior margin.

Cephalic lateralis system comprising lachrymal with four pores; short, tubular first postlachrymal infraorbital with terminal pores, followed by long, tubular, curved infraorbital with median and terminal pores; short, tubular dermosphenotic with terminal pores; three pterotic pores, each shared with dermosphenotic, preorbital and lateral extrascapular; posttemporal with posterior external pore and internal opening to lateral extrascapular; medial extrascapular with terminal pores, ventral pore shared with lateral extrascapular; four dentary pores, posteriormost toward anguloarticular from which lateralis canal absent; six preopercular pores; three supraorbital pores; terminal nasal pores; and simple coronalis pore.

Scales in E1 row 25 (in 5). Scales on sides and abdomen relatively large, strongly ctenoid. Cheek almost completely covered with 3 (1), 4 (6), 5 (1) rows of small ctenoid scales; posterior to orbit one row of ctenoid scales. Scales absent from preopercle. Opercle with 3 rows of ctenoid scales. Subopercle with 2 rows of ctenoid scales. Interopercle with 1-2 minute ctenoid scales. Scales absent from pectoral fin base. Predorsal scales 9 (1), 10 (4), 11 (2) in midline row, slightly irregularly arranged, all ctenoid. Prepelvic scales slightly smaller than flank scales, and cycloid. Chest scales ctenoid, very slightly smaller than flank scales. Circumpeduncular scales 16, comprising 7 above and 7 below lateral line scales. Scales between dorsal fin and lateral line 3 anteriorly, 1½ posteriorly. Upper lateral line scales 16 (7), lower lat-

Fig. 11. *Dicrossus foirni*, male, in aquarium. Specimen not preserved. Photo by F. Warzel.

Fig. 12. *Dicrossus foirni*, female, in aquarium. Specimen not preserved. Photo by F. Warzel.

eral line scales 7(1), 9 (3); both upper and lower lateral line including 1-4 pored scales terminally or subterminally at open ends. Lateral lines separated by two scale rows, non-overlapping. Lateral line scale at middle of caudal fin base present or absent. Scales absent from dorsal, anal, pelvic, and pectoral fins; narrow basal band of ctenoid scales on caudal fin, up to about ¼ of fin length.

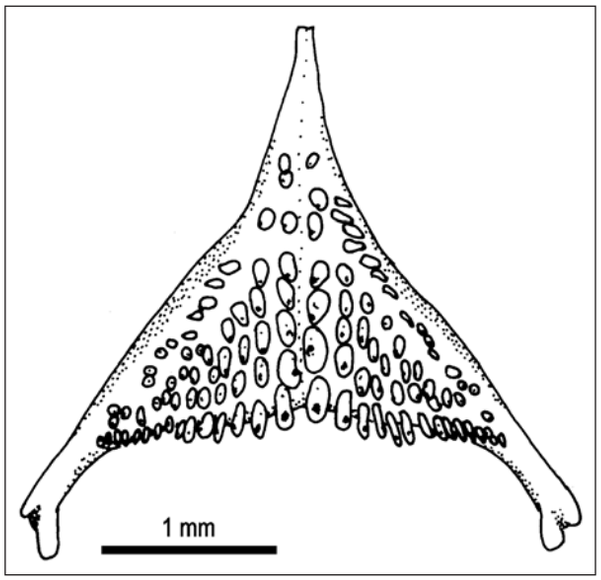

Fig. 13. *Dicrossus foirni*. Lower pharyngeal tooth plate in occlusal view. NRM 19490, 44.5 mm SL.

Dorsal fin rays XV,7 (2), XV,8 (11), XVI,7 (1). Dorsal fin origin above posterior margin of opercle; first spine short, spine length increasing to fifth or sixth, succeeding spines in small specimens subequal in length, last 1-2 spines slightly longer, in large specimens slightly increasing or subequal in length from eighth spine, last 2 spines distinctly longer than preceding. Dorsal fin lappets short, truncate or rounded. Soft dorsal fin in young specimens with third or fourth ray longest, forming short point reaching to above caudal fin base or slightly shorter; in large males, fifth ray prolonged, reaching to about 1/3 of caudal fin.

Anal fin rays III,7 (12), III,8 (2). Anal fin in young specimens with fourth and fifth rays of about equal length forming short point, not extending to caudal fin base; in large males fifth ray prolonged, reaching at most about 1/3 of caudal fin. Pectoral fin rays 12 (1), 13 (7). Pectoral fin rounded, fifth ray longest, reaching posterior to vertical from midway between genital papilla and first anal fin spine. Pelvic fin in young specimens pointed, first and second rays of about equal length, forming pointed tip, reaching almost to anal fin base; in large males first ray prolonged, inner branch of first ray longest, filamentous, reaching at most to base of third anal fin spine. Caudal fin subtruncate in young, lanceolate in large males, two middle rays longest.

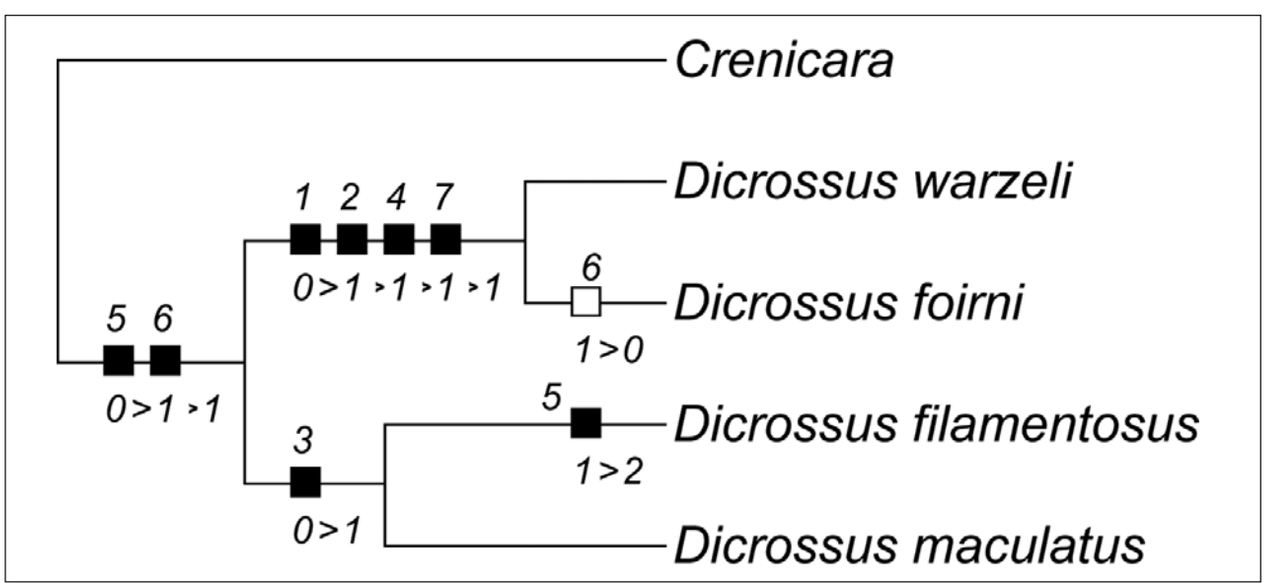

Fig 14. Single most parsimonious tree showing interrelationships of species of *Dicrossus*, with *Crenicara punctulatum* and *C. latruncularium* as outgroup. Consistency index = 0.8889, homoplasy index = 0.1111, retention index = 0.8750, rescaled consistency index = 0.7778. Black squares represent synapomorphies, open squares homoplasy. Numbers above squares are character numbers (Table I), and numbers below show optimized character state transformations.

Table IV. Standard length (in millimeters) and proportional measurements in percents of standard length of *Dicrossus maculatus* (MZUSP 38297). SD, standard deviation. Regression line parameters, a (intercept), b (slope), and r (Pearson's correlation coefficient) are calculated from measurements expressed in millimeters.

	N	Min	Max	Mean	SD	r	a	b
Standard length (mm)	10	30.4	47.2	38.8	6.22			
Head length	10	27.7	30.3	29.3	0.78	0.990	1.183	0.262
Snout length	10	5.9	7.6	6.6	0.64	0.982	-1.354	0.102
Body depth	10	26.1	28.7	27.7	0.84	0.982	0.85	0.255
Orbital diameter	10	10.8	12.8	11.7	0.70	0.995	1.566	0.076
Head width	10	14.2	16.1	14.8	0.63	0.993	1.288	0.114
Interorbital width	10	8.0	8.7	8.3	0.26	0.981	0.01	0.083
Preorbital depth	10	2.8	4.0	3.5	0.44	0.989	-0.94	0.06
Caudal-peduncle depth	10	12.4	13.2	12.7	0.30	0.990	0.36	0.118
Caudal-peduncle length	10	15.9	18.4	17.0	0.83	0.952	1.086	0.142
Pectoral fin length	10	24.4	27.8	26.1	1.02	0.966	0.237	0.254
Pelvic fin length	10	26.4	63.2	36.4	11.17	0.822	-17.689	0.83
Last dorsal fin spine length	10	15.2	18.0	16.4	0.89	0.947	-0.613	0.18

Teeth caniniform. In Marauiá specimens teeth in outer row hemiseries in upper jaw, 7 (2), 8 (3), 9 (1); in outer row hemiseries in lower jaw 18 (1), 19 (2), 20 (1), 21 (1). Premaxilla anteriorly with three rows of small teeth, outer row teeth slightly larger; teeth absent from horizontal arm: lower jaw with one row laterally and broad band of teeth anteriorly. In larger specimens (NRM 19490) premaxilla with 2-3 rows posteriorly on horizontal arm, reduced to 1 row anteriorly and expanding to wide band of about 2-3 rows anteriorly; 4-5 teeth in outer row on each side of symphysis slightly larger than other teeth. Lower jaw with one row laterally; anteriorly wide band 3-4 rows of teeth anteriorly; outer row teeth slightly larger compared to inner teeth, but not enlarged anteriorly. Specimen 32.4 mm SL (NRM 19490) has 13 teeth anteriorly on premaxilla, 8 teeth posteriorly, separated by distinct gap.

Lower pharyngeal tooth plate examined in one specimen (NRM 19490, 44.5 mm SL), only slightly wider than long (Fig. 13). Teeth in about 5 rows; 7-8 plus one emerging tooth along middle, 29 along posterior margin; compressed, along margins and anteriorly slender, unicuspid; mediad and caudad slightly coarser and longer, bicuspid, with strong posterior, antrorse cusp and minor anterior blunt cusp subdistally.

Gill rakers externally on first gill-arch, one in angle or associated with distal end of epibranchial, 4 (5), 5 (3) ceratobranchial. Microbranchiospines absent. Supraneurals 1 (14). Vertebrae 13+14=27 (13), 13+15=28 (1).

Colouration in preservative: Marauiá specimens with ground colour yellowish white, dark markings pale brown. Snout pale grey. Broad dark preorbital stripe across snout tip. Wide unpig-

Fig. 15. *Dicrossus maculatus*, MZUSP 38297, male, 47.2 mm SL. Brazil, Pará, Igarapé Jacaré on right bank of Rio Tapajós, near Boím. Photo by S. O. Kullander

Table V. Standard length (in millimetres) and proportional measurements in percents of standard length of *Dicrossus filamentosus* (data from Kullander 1979; Orinoco drainage specimens). SD, standard deviation. Regression line parameters, a (intercept), b (slope), and r (Pearson's correlation coefficient) are calculated from measurements expressed in millimetres.

	N	Min	Max	Mean	SD	r	a	b
Standard length (mm)	28	20.8	38.4	29.5	4.90			
Head length	28	27.5	31.0	29.4	0.88	0.983	-0.026	0.295
Snout length	28	4.8	7.3	5.9	0.56	0.962	-0.824	0.087
Body depth	28	23.8	29.3	26.6	1.16	0.972	0.970	0.232
Orbital diameter	28	12.2	14.0	13.0	0.51	0.986	0.661	0.107
Head width	28	13.2	15.8	14.2	0.65	0.980	0.851	0.113
Interorbital width	28	6.6	8.0	7.3	0.37	0.977	-0.343	0.085
Preorbital depth	28	2.1	3.9	2.7	0.39	0.894	-0.447	0.430
Caudal-peduncle depth	28	10.7	12.9	11.8	0.51	0.965	0.172	0.112
Caudal-peduncle length	28	15.7	18.8	16.9	0.73	0.971	-0.382	0.182
Pectoral fin length	26	20.4	26.6	24.0	1.50	0.968	-1.371	0.288
Pelvic fin length	28	21.9	56.8	28.9	10.55	0.888	-16.903	0.875
Last dorsal fin spine length	24	9.5	12.3	11.1	0.85	0.962	-0.886	0.141

mented band across lachrymal and sides of upper and lower lip. Distinct darker brown blotch on inner surface of opercle showing through bone. Pigmentation absent from cheek. Small dark blotch immediately posterior to orbit. Diffuse dark blotch on pectoral peduncle. Four horizontal rows of dark brown markings along dorsum and sides (rows H1-H4). Uppermost row comprising dark blotch anteriorly on scaled nape (V1 row), another around base of anterior dorsal spines (V2 row), three dark blotches (V3-5 rows) in sequence close to dorsal fin base, last blotch extending to about upper lateral line scales, one (V6 row) at end of dorsal fin base and one blotch (V7 row) dorsally on caudal peduncle. Row H2 including three dark blotches (V2-4 rows) dorsally on side, first blotch above origin of lateral line, the other two bisected by lateral line and confluent with blotches along dorsal fin base. Row H3 including dark blotch (V3 row) below origin of upper lateral line, followed by three blotches (V4-6 rows) each comprising two smaller, partly confluent dark blotches in sequence and one more rounded or elongate simple blotch (V7 row). Below that blotch row, row (H4) of three blotches (V4-6 rows) including partly confluent dark blotches and simple blotch (V7 row) extending vertically into H3 blotch row above. Oval dark blotch posteriorly on side of caudal peduncle representing confluent V8 row blotches from rows H3 and H4. Dark brown blotch ventrally between vent and anal fin. Fins lightly pigmented. Dark blotches (V9 row) above and below middle of caudal fin base.

Large adult males in NRM 12016 differing above all in fin colour pattern (Fig. 9). Dorsal fin with dark brown blotch basally between sixth and ninth spines, continuous with intensified dark brown

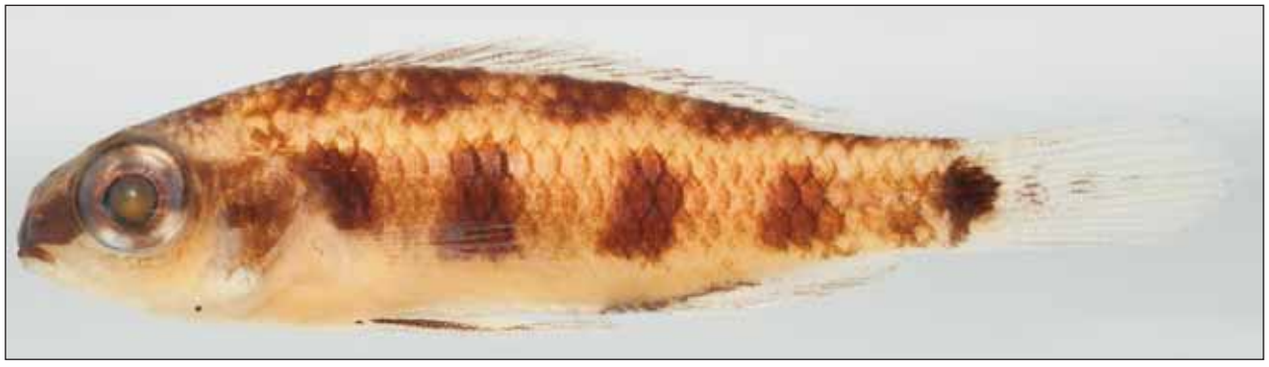

Fig. 16. *Dicrossus maculatus*, MZUSP 38297, female, 30.0 mm SL. Brazil, Pará, Igarapé Jacaré on right bank of Rio Tapajós, near Boím. Photo by S. O. Kullander

Table VI. Loadings of principal components I-III from pooled morphological dataset of *Crenicara latruncularium* (N=10), *C. punctulatum* (N=42), *Dicrossus filamentosus* (N=23), *D. foirni* (N=7), *D. maculatus* (N=10) and *C. warzeli* (N=10). Highest loadings indicated in boldface.

	I	II	Sheared II	III	Sheared III
Standard length	0.237	-0.186	-0.154	0.106	0.106
Head length	0.219	-0.177	-0.148	0.040	0.040
Snout length	0.289	**-0.747**	**-0.701**	-0.024	-0.024
Body depth	0.321	0.327	0.361	0.291	0.291
Orbital diameter	0.186	-0.02	0.003	0.161	0.161
Head width	0.243	0.082	0.111	-0.003	-0.003
Interorbital width	0.300	0.035	0.070	0.134	0.134
Preorbital depth	0.456	0.238	0.289	0.213	0.213
Caudal-peduncle depth	0.284	0.051	0.085	0.129	0.129
Caudal-peduncle length	0.211	**-0.357**	**-0.327**	-0.103	-0.103
Pectoral fin length	0.305	0.196	0.23	-0.076	-0.076
Last dorsal fin spine length	0.316	0.190	0.225	**-0.883**	**-0.883**
Eigenvalue	2.7364	0.0435	N/A	0.0129	N/A
Cumulative Variance	97.4%	98.9%	N/A	99.4%	N/A

blotch immediately adjacent to fin base. Posteriorly, dark brown small spot between every spine, on soft portion extending dorsally as vertical bars. Close to middle of height of fin, row of interradial dark brown spots on spinous portion. Narrow unpigmented submarginal stripe along length of fin, distally pale brown lappets and margin of soft portion. Pelvic fin white. Anal fin smoky, with faint dark blotch basally on each membrane along fin base, posteriorly extending as seven short vertical bars along posterior margin of fin. Caudal fin with two separate brown spots basally, rest smoky; upper corner hyaline with short oblique row of black spots followed distally by continuous black stripe, unpigmented stripe, and narrow dark margin. Males in NRM 19490 with about 10 narrow, faint vertical bars anteriorly on side, below lateral line (Fig. 10).

Live colouration: Images of living specimens provided by F. Warzel (Figs 11-12) and others published in aquarium literature (e.g. Windisch 1992; Stawikowski & Werner 2004) show specimens with pale grey or dull white ground colour, and dark grey to black markings. Dorsal fin of males with red margin, including narrow blue submarginal stripe, and dorsoposterior margin of caudal fin likewise margined with red, with pale blue submarginal stripe. Same dorsal fin pattern in females, but much paler. On some images, dorsal, caudal and anal fins of males deep red. Pale grey vertical bars across anterior sides as in Fig. 10 variably expressed. Breeding females with red pelvic and anal fins and dark blotches apparently forming continuous stripe along middle of side (Windisch 1992).

Distribution and biology: Rio Negro drainage,

Fig. 17. *Dicrossus filamentosus*, NRM 11245, male, 37.7 mm SL. Colombia, Guainía, Caño Bocón. Photo by S. O. Kullander

Table VII. Loadings of principal components I-III from pooled morphological dataset of *Dicrossus filamentosus* (N=23), *D. foirni* (N=7), *D. maculatus* (N=10) and *C. warzeli* (N=10). Highest loadings indicated in boldface.

	I	II	Sheared II	III	Sheared III
Standard length	0.253	-0.203	-0.189	-0.069	-0.076
Head length	0.247	-0.188	-0.174	-0.056	-0.063
Snout length	0.369	**-0.411**	**-0.390**	0.033	0.022
Body depth	0.242	-0.002	0.011	-0.099	-0.107
Orbital diameter	0.193	-0.207	-0.196	-0.099	-0.105
Head width	0.231	0.053	0.065	-0.110	-0.117
Interorbital width	0.292	-0.12	-0.104	-0.332	-0.34
Preorbital depth	0.400	0.046	0.068	**0.865**	**0.852**
Caudal-peduncle depth	0.272	-0.069	-0.054	**-0.267**	**-0.274**
Caudal-peduncle length	0.240	-0.077	-0.063	-0.056	-0.063
Pectoral fin length	0.290	0.135	0.151	-0.081	-0.090
Last dorsal fin spine length	0.359	**0.814**	**0.831**	-0.144	-0.155
Eigenvalue	0.6915	0.0263	N/A	0.0085	N/A
Cumulative Variance	93.0%	96.5%	N/A	97.7%	N/A

the mouth of the Rio Marauiá and the lower Rio Padauari on the middle Rio Negro (Fig. 7). The lower Marauiá is within the black-water inundation zone of the Rio Negro. Windisch (1992) reported the sampling site in the Rio Padauari as being a fast flowing stream full of tree and leaf litter, having turbid water with a temperature of 26-27°C. Windisch (1992) provided a detailed description of attempts to breed the species in captivity. When finally successful, the female apparently took on all the brood care and the male and other fishes were removed from the aquarium. Tomey's (1983) report of this species from Peru is apparently mistaken with regard to the locality (cf. also Stawikowski & Werner 2004: 69), and the locality information for the aquarium specimens NRM 19490 is probably not correct. Römer et al. (2010) only had specimens from the Rio Preto.

Remarks: The material available of *D. foirni* is relatively limited, and wild-caught specimens are relatively small, comprising immature males and potentially mature females, not showing pronounced sexual dimorphism. All large specimens are from aquarium sources, some with imprecise or dubious locality information and one sample is in a poor state of preservation. Those samples are helpful, however, because they include adult males which help to improve the diagnosis and provide more characters for phylogenetic assessment.

Interrelationships of species of *Dicrossus*

Colour pattern and fin shape characters show that *D. maculatus* and *D. filamentosus* are sister species, and form the sister group to a clade composed of *D. foirni* and *D. warzeli* (Fig. 14).

Morphometric analysis of species of *Dicrossus*

Principal component analysis of pooled measure-

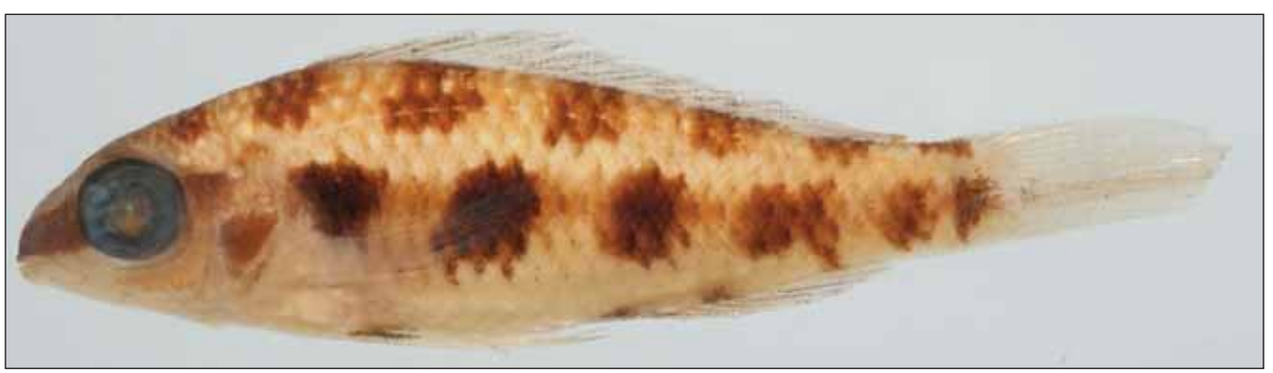

Fig. 18. *Dicrossus filamentosus*, NRM 11245, female, 32.4 mm SL. Colombia, Guainía, Caño Bocón. Photo by S. O. Kullander

Table VIII. Loadings of principal components I-III from pooled morphological dataset of *Dicrossus filamentosus* (N=23), *D. foirni* (N=7), *D. maculatus* (N=10) and *C. warzeli* (N=10), and data from Römer et al. (2010) for *D. foirni* (N=7) and *D. warzeli* (N=9). Highest loadings indicated in boldface.

	I	II	Sheared II	III	Sheared III
Standard length	0.246	-0.080	-0.089	0.124	0.117
Head length	0.241	-0.140	-0.149	0.085	0.078
Snout length	0.391	**-0.345**	**-0.359**	0.353	0.341
Body depth	0.283	-0.138	-0.149	-0.153	-0.161
Orbital diameter	0.188	-0.112	-0.119	0.193	0.187
Head width	0.249	-0.084	-0.093	-0.17	-0.177
Interorbital width	0.293	-0.100	-0.111	0.199	0.19
Preorbital depth	0.403	-0.089	-0.103	**-0.787**	**-0.799**
Caudal-peduncle depth	0.268	-0.051	-0.061	0.018	0.009
Caudal-peduncle length	0.218	0.063	0.055	0.101	0.094
Pectoral fin length	0.274	0.171	0.161	0.304	0.295
Last dorsal fin spine length	0.330	**0.873**	**0.860**	0.026	0.016
Eigenvalue	1.0475	0.0295	N/A	0.0111	N/A
Cumulative Variance	93.8%	96.4%	N/A	97.4%	N/A

ment data from *D. warzeli*, *D. foirni*, *D. maculatus*, *D. filamentosus*, *Crenicara punctulatum* and *C. latruncularium* separate *Crenicara* and *Dicrossus*, but also nearly separate *D. filamentosus* along the sheared PC II axis reflecting snout length, body depth and caudal peduncle length (Fig. 19A, Table 6). Within *Dicrossus*, *D. filamentosus* comes out separate from a cluster containing the other species, based on snout length and length of the last dorsal fin spine (Fig. 19B, Table VII). Adding data of Römer et al. (2010) to the PCA produced a more scattered distribution of scores, with their specimens of *D. warzeli* and *D. foirni* closer to *D. filamentosus* than to the other species of *Dicrossus* (Fig. 19C, Table VIII). Plotting PC III against PC I or PC II did not provide recognizable clusters. Variation in PC III within *Dicrossus* (Table VI) thus seems to reflect individual variation in preorbital depth and caudal peduncle depth, in particular within *D. filamentosus*.

Key to species of *Dicrossus*

1a. A single row of 5-6 blotches along middle of side 2
1b. Two parallel horizontal rows of small dark spots or several narrow dark vertical bars along middle of side 4
2a. Five blotches along middle of side, 12-13 pectoral-fin rays, caudal fin in males lanceolate with middle rays longest ..... *D. maculatus*
2b. Five or 6 blotches along middle of side, 10-11 pectoral-fin rays, caudal fin in males with prolonged rays in dorsal and ventral lobes, or only in dorsal lobe 3
3a. Caudal fin in males with prolonged rays in dorsal lobe..... *D. gladicauda*
3b. Caudal fin in males lyreate with prolonged rays in both dorsal and ventral lobes .... *D. filamentosus*
4a. Two parallel rows of elongate blotches along middle of side.....*D. warzeli*
4b. Anterior side with narrow vertical bars, or two parallel rows of small round blotches, usually grouped in pairs..... *D. foirni*

DISCUSSION

Dicrossus is the sister group of *Crenicara* as suggested by molecular (López-Fernández et al. 2010) and morphological (Kullander 1998) phylogenetic analyses, which also place these two genera in the subfamily Geophaginae (recognized at tribe level by López-Fernández et al. (2010)). *Crenicara* includes two valid species, viz., *C. punctulatum*, widely distributed in the Amazon drainage and also recorded from the Essequibo drainage (Kullander 1986) and *C. latruncularium* from the Bolivian Amazon (Kullander 2003). Kullander (1998) recognized the tribe Crenicaratini for *Crenicara*, *Dicrossus*, *Biotoecus* Steindachner and *Mazarunia* Kullander, diagnosed by a combination of character states, none unique to the Crenicaratini. *Mazarunia* was not included in that phylogenetic analysis due to lack of suitable material, but referred to Crenicaratini using characters provided

by Kullander (1990). The only species of *Mazarunia, M. mazarunii*, known then from only two specimens, has not been collected anywhere else than in the upper Mazaruni River in Guyana. Molecular phylogenetic analyses meanwhile suggest that *Mazarunia* may be more related to *Guianacara* Kullander & Nijssen than to *Crenicara* and *Dicrossus* (López-Fernández et al. 2010), and *Biotoecus* more related to *Crenicichla* (López-Fernández et al. 2005) or *Acarichthys* (López-Fernández et al. 2010).

Kullander (1990) provided a number of synapomorphies for *Crenicara* and *Dicrossus*. The strongly decurved snout, subinferior mouth, and transverse anterior lower jaw dental arcade, are shared with *Mazarunia*, as is also a laminar expansion of epibranchial 1 associated with the pharyngobranchiad 2 arm (character 7 in Kullander 1998). The reduced everted fold of the lower lip is unique to *Crenicara* and *Dicrossus*. Kullander (1990) also listed a pattern of small dark spots on the snout as unique for *Crenicara* and *Dicrossus*, but I cannot verify this character state in *D. foirni* or *D. warzeli*. The loss of the second dentary lateralis canal opening, however, remains a synapomorphy of *Crenicara* and *Dicrossus* (character 46 in Kullander 1998). Other characters are shared with other small cichlids, such as teeth present along the entire alveolar arm of the premaxilla, absence of tooth plates on ceratobranchial 4, absence of accessory lateral lines on caudal fin and infraorbitals reduced to three (the middle with terminal and a lateral opening). The short dermal splint of the palatine shaft is shared only with *Cichla* Schneider and *Hemichromis* Gill (character 50 in Kullander 1998). *Dicrossus* was diagnosed from *Crenicara* only by the loss of the anguloarticular lateralis canal, a character state present also in *D. foirni* and *D. warzeli*, but shared also with some other small cichlids, including *Mazarunia*.

The morphometric analysis herein shows that *Crenicara* and *Dicrossus* are distinct (Fig. 19A), especially in the longer snout, deeper body and shorter caudal peduncle in *Crenicara* (cf. proportional data in Kullander (1986) and Kullander & Staeck (1990)), but also that *D. filamentosus* is distinct from the other species of *Dicrossus*.

Species of *Dicrossus* and *Crenicara* also share an unusual colour pattern inspiring the common name of checkerboard cichlids in the aquarium trade. The checkerboard pattern is produced by the two horizontal rows of dark blotches in *D. maculatus* (Figs 15-16) and *D. filamentosus* (Figs 17-18), and young *C. latruncularium* and *C. punctulatum* which are arranged so that the blotches on each row are positioned opposite the interspaces of the other row, and the two rows are separated by a conspicuous narrow light horizontal stripe. In these species there is a singe rounded dark blotch on the caudal fin base. *Dicrossus warzeli* and *D. foirni* deviate from this pattern because instead of having a single row of large dark blotches along the middle of the side, they have two rows of smaller blotches, and at the caudal fin base there are two small dark blotches separated by a light horizontal stripe.

Based on the condition in *D. warzeli* and *D. foirni*, the blotch pattern can be viewed as four horizontal rows of dark blotches, numbered H1-4, and nine vertical rows of blotches, including the blotch at the caudal fin base (V1-9) (Fig. 1). Each blotch can be referred to by these coordinates, e.g., H2/V3 is the third blotch in the second row. Nearly all other South American cichlids have a colour pattern consisting of vertical bars at some or all life stages, usually about eight. In those species the bars have a straight vertical or slightly caudoventrad inclination. In *Dicrossus* and *Crenicara*, however, the blotches are grouped into anteroventrad slanting series. Also unusual among South American cichlids is the absence of a particularly dark and prominent midlateral blotch.

In *D. maculatus* there are only eight vertical groups of markings, apparently due to fusion of V6 and V7, blotch H3+4/V8 is usually minute and indistinct and V9 appears as a single dark blotch. In *D. filamentosus* there are variably five or six dark blotches on the body in row H3+4, and when six, the fifth is very small, also suggestive of a variable fusion and separation of V6 and V7.

The shape of the blotches in rows H3-4 shows considerable variation within *Dicrossus*. Large, squarish blotches are shared by *D. filamentosus*, *D. maculatus* and species of *Crenicara*, whereas the patterns in *D. warzeli* and *D. foirni* are species-specific. In *D. warzeli*, H3 and H4 blotches are horizontally elongate. In *D. foirni* the H3/V4-5 and H4/V4-5 blotches appear as pairs of smaller blotches, that of H3/V7 is absent or weak whereas H4/V7 extends dorsad into the H3 row and H3-4/V8 usually appear as a single dark blotch. In large males of *D. foirni*, there is usually also a series of dark vertical bars, unique in the genus for this species, and formed from components of the H3 and H4 blotch rows.

Dicrossus foirni, *D. warzeli*, *D. maculatus* and *D. filamentosus* are very similar in morphometry (Tables II-V) and meristics. There is overlap in the number of scale rows on the cheek, but *D. filamentosus* and *D. maculatus* have fewer rows (1-3, usually 1-2, and 2-3, respectively) than *D. foirni* (3-5, usually 4), and *D. warzeli* (3-4, usually 3). *Dicrossus filamentosus* has 10-11 pectoral fin rays (Kullander 1979), whereas the other species have 12-13. In *D. filamentosus* the dorsal spines are gradated in length, first increasing then decreasing in length to a relatively short last spine, whereas in the other species, the posterior decrease is minor, resulting in a proportionally longer last dorsal fin spine (13.7-18.0% SL) compared to *D. filamentosus* (9.5-12.3% SL). *Dicrossus maculatus* has a slightly wider interorbital distance than the other species (8.0-8.7% SL vs. 6.6-8.0% SL). A principal compo-

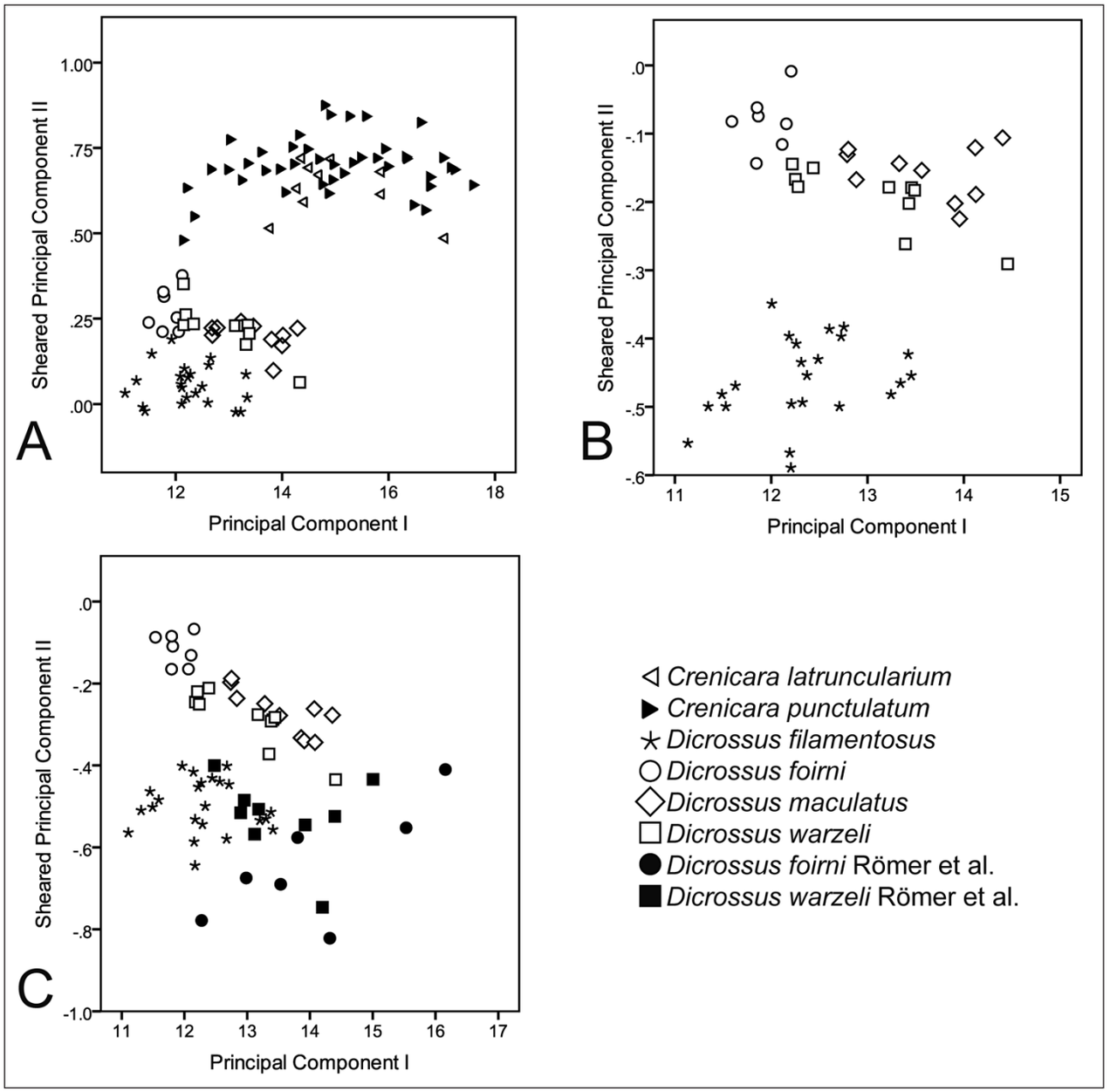

Fig. 19. Principal component analysis of *Crenicara* and *Dicrossus*. Plot of scores of sheared component II on component I for A. pooled data from species of *Crenicara* and *Dicrossus*; B. pooled data from species of *Dicrossus*; C. pooled data from species of *Dicrossus* with the addition of data from Römer et al. (2010) for *D. foirni* and *D. warzeli*.

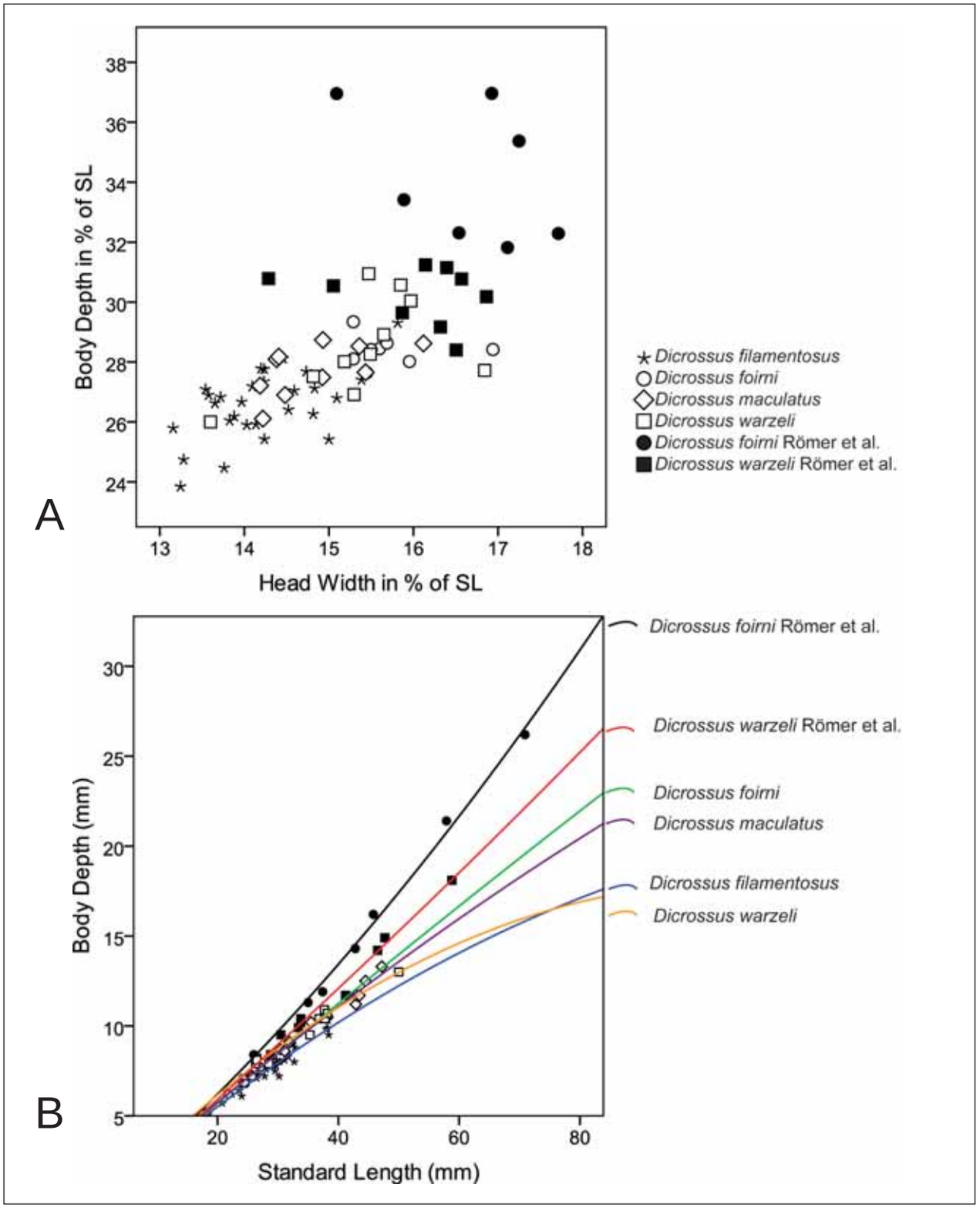

Fig. 20. Morphometry of *Dicrossus*: A. width of head in per cent of SL plotted against depth of body in per cent of SL; B. depth of body plotted against SL. Fit of quadratic regressions (r^2): *D. filamentosus*, 0.936; *D. foirni*, 0.975; *D. foirni* data from Römer et al. 2010, 0.995; *D. maculatus*, 0.963; *D. warzeli*, 0.969; *D. warzeli* data from Römer et al. 2010, 0.988.

nent analysis separates *D. filamentosus* from the other species of *Dicrossus* reflecting mainly the shorter last dorsal fin spine (Fig. 19B; Table VI).

Römer et al. (2010) diagnosed *D. foirni* by the general colour pattern and the "pointed rhombic caudal fin" in males (Römer et al. 2010: 125), said in the description to be "rhombic and pointed [in adult males], in medium-size males spatulate to rhombic, and rounded in smaller males" (Römer et al. 2010: 127). *Dicrossus warzeli* is also diagnosed by the colour pattern and the spatulate caudal fin of adult males (Römer et al. 2010: 129). They note, however, that the caudal fin is rhombic in some exceptionally large specimens (Römer et al. 2010: 130). They also point to differences in the colour pattern of aggressive males (sides with vertical bars in *D. foirni*, horizontal dark band in *C. warzeli)*, diagnostic tooth morphology and one morphometric difference (Römer et al. 2010: 137). The diagnostic tooth morphology is not explained. The morphometric difference consists of a non-overlapping head width to body depth ratio (Römer et al. 2010: fig. 20). From their measurements it appears that in specimens over 35 mm SL, *D. foirni* is slightly more deep-bodied than *D. warzeli*, and in specimens over 45 mm SL, *D. foirni* has a slightly wider head than *D. warzeli*. Figure 20A shows their data with the data from my measurements, confirming their calculations. However, the larger size of their specimens, especially of *D. foirni*, may be reflected here. Plotting body depth against standard length suggests both that their measurements of body depth lie somewhat higher (or they measure a shorter standard length) and that there is a slight positive size allometry in larger specimens of *D. foirni* for body depth, which is not observable in the other samples because specimens of those species are smaller, and the calculated regressions suggest isometry or even negative allometry (Fig. 20; Tables I-V).

Reanalysis of the measurements of *D. foirni* and *D. warzeli* in Römer et al. (2010: table 2) shows most variation to be in the length of the pelvic fin and in the length of the lower jaw among small specimens, but no conspicuous morphometric differences between species. Comparing identical measurements in the two datasets, specimens in Römer et al. (2010) tend to have deeper body, longer snout, and wider head, shorter last dorsal fin spine, and also somewhat more scattered data points contrasting with my dataset. A principal component analysis illustrates more difference between the two datasets than between the two species, as the data scores distribute more scattered, and separate from my measurements, clustering with *D. filamentosus* rather than with *D. foirni* or *D. warzeli*, and also more within than between species variation in the dataset of Römer et al. (Fig. 19C; Table VIII). This is partly a consequence of slightly larger size of some of Römer et al.'s (2010) specimens, but also must reflect differences in measurement precision and methodology. Major differences are in their interorbital width (7.3-9.0% SL vs. 6.6-7.9% in my specimens), pectoral fin length (20.3-27.3% SL vs. 25.9-29,1% in my specimens) in *D. warzeli* for which the two data sets have similar standard length range (28.8-58.8 mm vs. 26.3-50.0% in my specimens). The datasets for *D. foirni* represent different standard length ranges (26.0-70.9 mm SL vs. 18.3-27.1 mm SL in my specimens), and thus proportional data are not comparable.

Römer et al. (2010) did not provide information on vertebral number, pterotic or supracleithrum serrations, predorsal scales, circumpeduncular scales, cheek scale rows, tooth numbers, gill rakers, or pharyngeal jaws. Their counts of preopercular serrations are higher than mine, probably because of the larger size of the specimens, as the number is correlated with specimen length. Their count of E1 scales is one scale lower in *D. warzeli* (24-25 vs. 25-26), and with a wider range in *D. foirni* (24-26 vs. 25). Their pectoral fin count apparently is one ray less (11-12 vs. 12-13 in both *D. foirni* and *D. warzeli*.

Specimens of *D. gladicauda* have not been available for examination for this paper; Schindler & Staeck (2008) state that the only difference from *D. filamentosus* is the absence of prolonged fin-rays in the lower half of the caudal fin in adult males. For the purposes of diagnosis of other species of *Dicrossus*, *D. gladicauda* can apparently be equated with *D. filamentosus*, and consequently I did not add *D. gladicauda* to the phylogenetic analysis. The type locality of *D. gladicauda* is in the lower Rio Atabapo drainage, and aquarium specimens are said to be exported from the Rio Tomo, further north in the Orinoco basin (Schindler & Staeck 2008). Römer et al. (2010) listed specimens from the Rio Vichada. These localities are within the distribution area of *D. filamentosus*. It is possible that specimens from the Orinoco basin that I identified as *D. filamentosus* are actually *D. gladicauda* because adult males with well developed caudal fin streamers are absent from most samples. It also remains an option that caudal fin filament development in *D. filamentosus* is variable, and a revision using larger series of *Dicrossus* from

the Orinoco drainage is recommended to test the validity of *D. gladicauda*.

All species of *Dicrossus* have discrete, non-overlapping distributions (except perhaps *D. filamentosus* and *D. gladicauda). Dicrossus maculatus* and *D. warzeli* both occur in the Rio Tapajós, but *D. warzeli* is found only between Cururu and Itaituba, and *D. maculatus* is restricted to the lower Rio Tapajós, collected from Santarém upstream to Boím. The latter species is also known from the nearby lower Rio Trombetas, Rio Arapiuns, Rio Maués, and lago Ze Açú at Parintins. A specimen tentatively identified as *D. maculatus* is available from the lower Rio Madeira (NRM 37547). *Dicrossus filamentosus* was collected from the middle Rio Negro between about the Rio Urubaxi and the Rio Daraá, and in the upper Rio Orinoco drainage, including the Rio Casiquiare drainage (Fig. 7). The seemingly disjunct distribution probably reflects the concentration of collection efforts. Although the general distribution is shared with *D. foirni*, the two species are not found in the same localities, except that Römer (in Römer et al. 2010) reports them as syntopic in the Rio Preto. *Dicrossus gladicauda* is reported as the only species of *Dicrossus* at its type locality (Schindler & Staeck 2008), which is also within the general distribution of *D. filamentosus* in the Orinoco drainage.

The phylogenetic analysis, based on a set of diagnostic external characters (Fig. 14), points to two clades, each with two species. Interestingly, each clade has one species in the middle Rio Negro basin, and the other species in the Rio Tapajós/Central Amazon basin. *Dicrossus* is absent from the lower Rio Negro. This distribution pattern is partly explained by water conditions. *Dicrossus filamentosus* is primarily a black-water species (Stawikowski & Werner 2004: 65; Goulding et al. 1988). Information about *D. maculatus* is scant, but it seems to occur in various water conditions, but primarily clear-water conditions, as suggested by the collecting localities, personal observations and observations in Stawikowski & Werner (2004: 60). *Dicrossus foirni* seems to be a black-water species (cf. Windisch 1992), but *D. warzeli* is known only from clear-water conditions. Römer et al. (2010), based on various sources, consider *D. foirni* to occur in black-, clear- and white-water conditions.

Satanoperca lilith Kullander & Ferreira, 1988, in the middle and lower Rio Negro, Rio Uatumã, lower Rio Trombetas, Rio Aripuanã, and lower Rio Tapajós basins, and its sister species *S. daemon* Heckel, 1840, in the upper Rio Negro and Rio Orinoco basins (Kullander & Ferreira 1988), recaptures to some extent the distribution of *Dicrossus*, but with only two large species. *Symphysodon* duplicates to some extent the distribution of *Crenicara (S. aequifasciatus* Pellegrin, 1904, along the western Amazon floodplain) and *Dicrossus (S. discus* Heckel, 1840, in the Rio Negro, and Rio Maués basins) (Ready et al. 2006). Also *S. discus* and the *Satanoperca* species are found primarily in black- or clear-water habitats. *Aequidens epae* Kullander, 1995, has a known distribution similar to *Dicrossus warzeli*, collected only between São Luis do Tapajós and Jacareacanga (Kullander 1995). The genus *Aequidens* has a wide distribution in tropical South America, however, and no relationship analysis has yet been proposed for *A. epae*.

Although the white-water Amazon River itself is probably a barrier to dispersal for some black/clear-water species, especially because many black/clear-water species are found exclusively in northern or southern tributaries in the central Amazon, there evidently exists some dispersal. The distribution pattern of the species of *Dicrossus* may retrace ancient drainage conditions predating the reversal of the flow of the western Amazon itself in the late Miocene, with the cut through the Purús arch (cf. Lundberg et al. 1998: 40; Hoorn et al. 2010: 138). More habitat and distribution data for genera and species distributed along the Orinoco-Amazon-Tapajós will be instrumental for understanding this distribution pattern. Habitat information for *Dicrossus* species is also so far relatively sparse or anecdotal and needs improvement before physico-chemical distribution barriers can be considered.

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