Redescription of the Guiana Shield Darter Species Characidium crandellii and C. declivirostre (Crenuchidae) with Descriptions of Two New Species

Authors: Armbruster, Jonathan W., Lujan, Nathan K., and Bloom, Devin D.

Source: Ichthyology & Herpetology, 109(1) : 102-122

Published By: The American Society of Ichthyologists and Herpetologists

URL: https://doi.org/10.1643/i2019299

Ichthyology & Herpetology 109, No. 1, 2021, 102–122

Redescription of the Guiana Shield Darter Species *Characidium crandellii* and *C. declivirostre* (Crenuchidae) with Descriptions of Two New Species

Jonathan W. Armbruster[1], Nathan K. Lujan[2], and Devin D. Bloom[3]

Based on collections made in the western Guiana Shield over the last 21 years, *Characidium crandellii* and *C. declivirostre* are redescribed and two similar species are described from Guyana. These species all have enlarged paired fins with three to four rays thickened ventrally on the pectoral fin and two rays thickened on the pelvic fin. The species can be separated from all other *Characidium* and *Melanocharacidium* by having the venter unscaled from the isthmus to the pelvic origin. *Characidium crandellii* is found in the Essequibo and Takutu River systems and in an isolated population above Tencua Falls in the Ventuari River and the upper Paragua River (Orinoco River basin). *Characidium declivirostre* is found throughout the right-bank, shield tributaries of the Orinoco River system and in the upper Negro River. *Characidium duplicatum*, new species, appears to be rare but widely distributed in the Essequibo River system. *Characidium wangyapoik*, new species, is only known from the upper Ireng River, Branco River basin, along the border between Brazil and Guyana.

CHARACIDIUM is the most species-rich genus (70 species, Fricke et al., 2019) in the South American darter family Crenuchidae (Characiformes); it consists of small (generally less than 8 cm SL; although a 10.7 cm specimen is described here), benthic fishes found in rivers and streams throughout most of tropical South America and southern Panama. To date, the most extensive phylogenetic analysis of *Characidium* was Buckup (1993a), who developed a matrix of 64 morphological characters observed across a broad diversity of *Characidium* and its relatives. His analysis of this matrix found support for a clade comprising *Characidium crandellii* and *C. declivirostre* (Clade C3), both of which were described by Steindachner (1915). The sister relationship between these species was supported by three unique and two homoplastic synapomorphies: 1) scaleless area of isthmus extending posteroventrally between pectoral fins to pelvics (unique); 2) branchiostegal membranes united across the isthmus (unique); 3) dermal flaps around anterior and posterior nares independent but touching each other distally (unique); 4) posterior process of coracoid reduced to squarish protuberance (homoplastic); 5) basicaudal spot secondarily absent (homoplastic). Additionally, the species have thickened pads of tissue on the ventral side of the anterior pectoral and pelvic-fin rays (Fig. 1; Conway et al., 2012).

After nearly two decades collecting in rivers of the western Guiana Shield in Venezuela and Guyana, we have amassed over 300 specimens assignable to *C. crandellii*, *C. declivirostre*, and two undescribed, similar species (from the Ireng and Essequibo River basins), providing the justification and basis for this first taxonomic revision of the rheophilic *Characidium* of the Guiana Shield.

MATERIALS AND METHODS

In species location information, the total number of specimens analyzed (*C. crandellii* and *C. declivirostre*) or total number of specimens in the lot (new species) is indicated, followed in parentheses by the number used in standard morphometric (mo), meristic (me), geometric morphometric (gm), and cleared and stained (cs) analyses. Size ranges in mm standard length (SL) are for specimens analyzed (*C. crandellii* and *C. declivirostre*) or all specimens (types of new species).

Species were identified through a combination of standard morphometrics and meristics, geometric morphometrics, examination of color patterns, and geographic range. Taxonomic assessment began by first dividing each of the four identified morphotypes into separate basins and/or localities, and evaluating whether finer-scale taxonomic divisions were recognizable.

Standard morphometrics and meristics.—Measurements and meristics were preferentially taken on the left side of specimens (unless damaged) according to Buckup (1993b) using digital Mitutoyo calipers accurate to 0.1 mm. All raw count and measurement data are provided as supplemental material (see Data Accessibility).

Geometric morphometrics.—We photographed the right side of specimens in lateral view with a Canon Eos Rebel T3i digital camera with a 100 mm macro lens and an LED-illuminated light box. Specimens were mounted so that their flanks were parallel with the camera lens. Fifteen landmarks were placed on the photographs using Stereomorph (Olsen and Westneat, 2015; Fig. 2A). Stereomorph creates individual files for each specimen, and these are combined into a single tps file in R (R Core Team, 2013) using the writeLMToTPS command. The tps file was entered into MorphoJ (Klingenberg, 2011), a generalized Procrustes analysis (GPA) was performed, the data were checked for outliers (one improperly digitized specimen was removed), and a covariance matrix created, all using the Preliminaries menu of MorphoJ. We performed a PCA on the data to examine morphological

[1] Department of Biological Sciences, 101 Life Sciences Building, Auburn, Alabama 36849; Email: armbrjw@auburn.edu. Send reprint requests to this address.
[2] Department of Ichthyology, American Museum of Natural History, New York, New York 10024.
[3] Department of Biological Sciences and Institute of the Environment and Sustainability, Western Michigan University, Kalamazoo, Michigan 49008.
Submitted: 9 October 2019. Accepted: 16 September 2020. Associate Editor: R. E. Reis.
 DOI: 10.1643/i2019299 Published online: 29 March 2021

Fig. 1. Thickened, keratinized pads on the undersurface of the anterior pectoral-fin rays of (A) *Characidium wangyapoik*, new species, CSBD F-3615, holotype, and (B) *C. crandellii*, AUM 67142. Photos by N. K. Lujan.

differences between populations (Fig. 2B–D). Specimens in the PCA were initially separated and compared according to locality and morphotype. We additionally duplicated the analyses in geomorph (Adams et al., 2020) and ran an allometric correction using the procD.allometry command, but we do not present this analysis as it did not alter the results. Landmarks were defined as follows: 1) snout tip, 2) anterior edge of nares, 3) posterior edge of maxilla, 4) anterior margin of orbit along longest axis, 5) posterior margin of orbit along longest axis, 6) end of supraoccipital, 7) posteriormost extent of opercle, 8) insertion of first unbranched pectoral-fin ray, 9) insertion of first unbranched dorsal-fin ray, 10) insertion of last dorsal-fin ray, 11) insertion of first unbranched pelvic-fin ray, 12) anterior edge of adipose fin, 13) insertion of first unbranched anal-fin ray, 14) insertion of posteriormost anal-fin ray, and 15) end of caudal peduncle at lateral line. Photographs and tps files of AUM specimens examined are available via the AUM fish collection catalog search page available at http://aumnh.auburn.edu.

RESULTS

We initially identified four morphotypes based on a combination of color pattern, meristics, and fin positions (see descriptions): one containing primary types and topotypes of *C. declivirostre*, one that was similar to type material of *C. crandellii*, one from the upper Ireng River that did not match any described species (described herein as *C. wangyapoik*, new species), and one that was patchily distributed throughout the Essequibo River system that also did not match any described species (described herein as *C. duplicatum*, new species). Separating the morphotypes by location did not reveal any differences in the geometric morphometric PCA, and all that is retained in Figure 2 are the basins for *C. crandellii* to demonstrate that the PCA was insufficient in finding differences between these populations and the type specimens.

The PCA showed extensive overlap between *Characidium declivirostre, C. duplicatum*, new species, and *C. wangyapoik*, new species, and slight overlap between *Characidium declivirostre* and *C. wangyapoik*, new species, with *C. crandellii*. PC1 (Fig. 2B) explained 37.0% of variation focused on differences in mouth position, dorsal-fin size, fin positioning, and angle of the ventral portion of the body posterior to the anal fin. *Characidium crandellii* was mostly separated from the other species along PC1, and this species tends to have the snout downturned, a longer dorsal-fin base, and the anal-fin base (between landmarks 14 and 15) forming a smaller angle than in other species and landmark 15 (end of caudal peduncle) more ventral (this is particularly true when compared to the largest *C. wangyapoik*, new species). In *C. wangyapoik,* new species, the angle of the ventral portion of the body posterior to the anal fin is more steeply angled, particularly in larger specimens, and the tip of the snout is more elevated. PC2 (Fig. 2C) explained 18.5% of the variation focused on differences in head length and anteroposterior position of the eye, with *C. duplicatum*, new species, and some *C. crandellii* having the highest values (longer head, more posteriorly positioned eye).

There is considerable allometry in eye size and other head measurements. Smaller individuals have relatively larger eyes when the ratio of orbital diameter vs. head length is plotted against SL (Fig. 3). This difference is also apparent when comparing Figures 4 and 5 of a larger vs. a smaller specimen of *C. crandellii*. An allometric correction on the geometric morphometric data did not significantly change the results, so only the standard PCA is presented.

Characidium crandellii Steindachner, 1915
Figures 1B, 4–6

Characidium crandellii Steindachner 1915: 32, Rio Miang, tributary Cotingo, Tacutu; Boa Vista, Rio Branco, Brazil.

Specimens examined.—Brazil: syntypes: NMW 62673, 5 (2gm), 69260, 2 (1gm), Amazon River basin, Rio Miang, tributary Cotingo, Tacutu; Boa Vista, Rio Branco, Brazil.

Guyana: AUM 28034, 3 (0mo/me, 3 gm), 26.8–33.3 mm SL, Potaro-Siparuni, Essequibo River basin, Potaro River, Tumatumari cataract, S bank below old hydroelectric plant, 5.36333, –59.00111; AUM 28139, 1 (0), 24.4 mm SL, Potaro-Siparuni, Essequibo River basin, Potaro River, Waratuk cataract, 5.25889, –59.40028; AUM 28184, 1 (1mo/me, 1gm), 37.1 mm SL, Potaro-Siparuni, Essequibo River basin, Potaro River and tributaries, at Tukeit cataract, 4.99889,

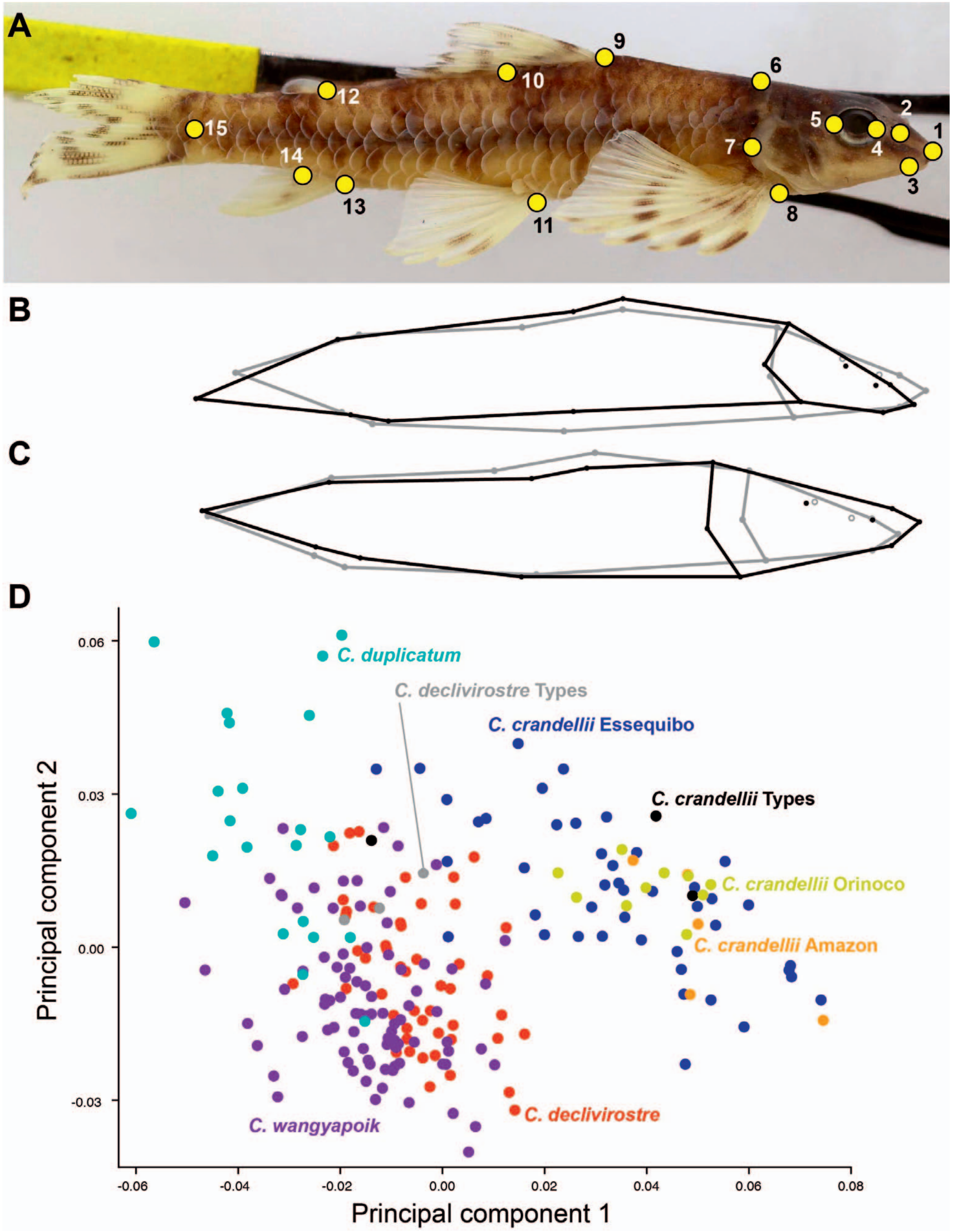

Fig. 2. (A) Landmarks used in geometric morphometrics. Specimens were propped to maintain bodies orthogonal to the lens (*Characidium declivirostre*, AUM 36674, 44.0 mm SL); photo by J. W. Armbruster. (B) Wireframes of changes along PC1; gray is average shape and black is a shape that corresponds to a shape with +0.1 Procrustes units. (C) Wireframes of changes along PC2 colored as in B. (D) Results of PCA of geometric morphometrics; specimens of *C. crandellii* are split by basin with a syntype (Amazon basin) indicated in black.

–59.53889; AUM 35582, 7 (2mo, 1me), 26.4–29.1 mm SL, Cuyuni-Mazaruni (Region 7), Mazaruni River basin, Whitewater Creek 6.8 km SW Bartica, 6.378, –58.67374; AUM 36957, 12 (1mo/me, 8gm), 25.1–45.2 mm SL, Upper Demerara-Berbice (Region 10), Essequibo River basin, Essequibo River at Kurukupari, E bank, 4.66149, –58.67519; AUM 36958, 7 (0) 20.0–23.6 mm SL, Upper Takutu-Upper Essequibo (Region 9), Amazon River basin, Pirara River, tributary of the Ireng River, 3.5 km NNW Pirara, 3.6487, –59.68897; AUM 36959, 1 (1mo/me, 1gm), 34.6 mm SL, Upper Takutu-Upper Essequibo (Region 9), Amazon River basin, Moco-Moco River at Moco-Moco Hydro Power Station 18.8 km SE Lethem, 3.29672, –59.64466; AUM 36960, 5 (2mo/me, 2gm), 47.4–48.6 mm SL, Upper Demerara-Berbice (Region 10), Essequibo River basin, Essequibo River at Kurukupari, E bank, 4.66149, –58.67519; AUM 45273, 1 (0), 30.0 mm SL, Potaro-Siparuni (Region 8), Essequibo River

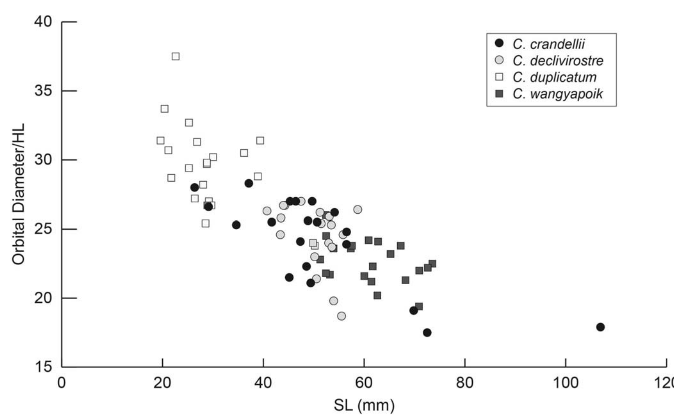

Fig. 3. Plot of the ratio of orbital diameter to head length versus standard length for all measured specimens of fast-water *Characidium* of the Guiana Shield showing allometry in eye size.

Fig. 4. Dorsal, lateral, and ventral views of *Characidium crandellii* in life, potential nuptial male, AUM 67142, 106.9 mm SL; Ireng River population. Photos by N. K. Lujan.

basin, Essequibo River, side channel in rapids, 4.4215, –58.48623; AUM 45348, 1 (0), 23.7 mm SL, Potaro-Siparuni (Region 8), Essequibo River basin, Essequibo River, side channel in rapids, 4.4215, –58.48623; AUM 45371, 4 (0mo/me, 4gm), 23.8–27.0 mm SL, Potaro-Siparuni (Region 8), Essequibo River basin, Essequibo River, side channel in rapids, 4.4215, –58.48623; AUM 62834, 1 (0), Potaro-Siparuni (Region 8), Essequibo River basin, Kuribrong River, in rapids at Grass Shoals, 5.40791, –59.53179; AUM 62874, 7 (0mo, 4me, 4gm), 37.2–43.8 mm SL, Potaro-Siparuni (Region 8), Essequibo River basin, Kuribrong River, at Ram Sheep Rapids, 5.44236, –59.50201; AUM 62889, 1 (0), Potaro-Siparuni (Region 8), Essequibo River basin, Grass Falls Creek [Kiwikparu Creek], just upstream from mouth of Kuribrong River, 5.4065, –59.53361; AUM 62898, 76 (8mo, 6me, 24gm, 6cs), 41.7–56.5 mm SL, Potaro-Siparuni (Region 8), Essequibo River basin, Grass Falls Creek [Kiwikparu Creek], near top of falls, 5.40532, –59.5439; AUM 63165, 2 (0), 23.1–24.3 mm SL, Upper Takutu-Upper Essequibo (Region 9), Amazon River basin, Ireng River, 6.9 km WSW Karasabai, 4.01957,

Fig. 5. Dorsal and lateral views of *Characidium crandellii* in life, common coloration, AUM 62874, 57.0 mm SL; Kuribrong River population. Photos by J. W. Armbruster.

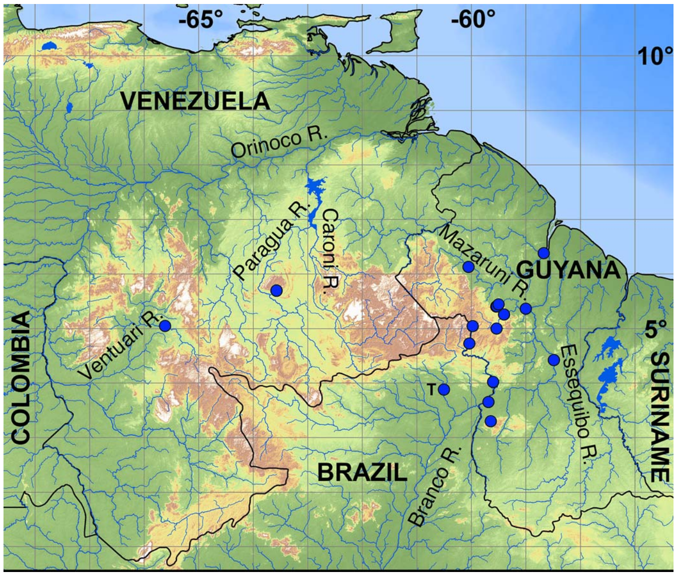

Fig. 6. Distribution of *Characidium crandellii*, type locality indicated with T.

–59.6017; AUM 67037, 3 (2mo, 3me, 3gm, 1cs), 47.4–72.5 mm SL, Potaro-Siparuni (Region 8), Amazon River basin, Ireng River, at Orinduik Falls, between upper and lower falls, 4.72536, –60.03852, 2 January 2016; AUM 67142, 1 (1mo, 1me, 1gm), 106.9 mm SL, Potaro-Siparuni (Region 8), Amazon River basin, Ireng River, shoals at mouth of Monkey Creek, Kaibarupai, 5.04398, –59.97717, 9 January 2016; ROM 91332, 3 (0), Potaro-Siparuni (Region 8), Essequibo River basin, Sheetrock Creek at crossing of Wailang-Powis tractor trail, 5.47473, –59.43770; ROM 91410, 1 (0), Potaro-Siparuni (Region 8), Essequibo River basin, Mikobe Creek approximately 0.5 km upstream from mouth, at rapids beyond first rapid blocking upstream boat movement, 5.41396, –59.47025, October 201; ROM 110044, 2 (0), Potaro-Siparuni (Region 8), Essequibo River basin, Sheetrock Creek at crossing of road between Wailang and Mona Falls, 5.47494, –59.43769; ROM 101902, 1 (0), Cuyuni-Mazaruni (Region 7), Mazaruni River basin, no common locality given, 6.13585, –60.0745.

Venezuela: AUM 39466, 1 (1mo, 1me, 1gm), 49.4 mm SL, Amazonas, Orinoco River basin, Río Ventuari, above Salto Tencua, 58 km ESE of San Juan de Manapiare, 5.04777, –65.61583; AMNH 91171, 21 (0mo/me, 10gm), Bolivar, Orinoco River basin, Río Carapo, at third rapids above camp

Table 1. Morphometrics for *Characidium crandellii* and *C. declivirostre* (*n* = 20 each).

Measurement	*Characidium crandellii*				*Characidium declivirostre*			
	Avg.	SD	Min.	Max.	Avg.	SD	Min.	Max.
Standard length (SL; mm)	50.8		26.4	106.9	50.2		40.7	58.7
%SL								
Head length (HL)	22.7	1.2	19.9	25.1	22.6	1.0	20.9	25.2
Prepectoral distance	18.0	1.4	15.2	21.6	18.9	1.3	17.2	21.6
Prepelvic distance	54.1	1.2	52.4	56.9	55.5	0.9	53.9	57.5
Preanal distance	75.0	1.1	72.9	76.6	78.4	1.0	76.9	80.6
Anal–apex distance	91.5	1.2	89.4	94.0	95.6	1.2	93.9	97.8
Body width	14.4	0.8	12.9	15.4	14.8	0.6	13.6	16.1
Body depth at dorsal-fin origin	15.5	1.5	12.7	17.6	16.1	1.7	13.4	19.1
Body depth at anal-fin origin	12.2	1.1	10.5	14.5	12.0	0.7	10.7	13.3
Least caudal peduncle depth	8.3	0.5	7.6	9.6	8.3	0.6	6.7	9.7
First pectoral-fin ray length	16.5	1.1	15.1	18.8	16.3	1.2	13.7	18.1
Greatest pectoral fin distance	30.0	1.6	27.7	33.8	32.5	1.7	29.1	36.3
%HL								
Snout length	32.6	2.5	28.7	39.2	36.0	2.1	32.9	39.3
Snout-maxillary tip distance	20.8	2.2	16.1	25.8	20.8	2.8	15.6	27.8
Anterior nostril–orbit	11.6	1.5	8.0	13.5	13.9	2.3	8.9	16.8
Posterior nostril–orbit	5.5	0.6	4.1	6.6	6.3	0.9	4.3	7.8
Cheek depth	17.2	2.4	14.1	23.0	18.4	3.8	11.0	25.4
Orbital diameter	24.2	3.3	17.5	28.3	24.5	2.3	18.7	27.0
Interorbital distance	24.4	2.3	21.6	30.9	21.7	2.3	17.3	27.2

along left bank, 5.71333, –63.53333 (coordinates per Armbruster and Taphorn, 2013).

Diagnosis.—*Characidium crandellii* can be distinguished from all crenuchids except *C. declivirostre, C. duplicatum*, new species, and *C. wangyapoik*, new species, by having the venter without scales from the isthmus to the pelvic girdle (vs. maximally to pectoral-fin insertion) and from most species of *Characidium* by having a very large pectoral fin with the first four unbranched pectoral-fin rays thickened, and the first pectoral-fin ray bent at an oblique angle (vs. pectoral-fin rays not thickened and first ray either straight or slightly convex). *Characidium crandellii* can be distinguished from *C. declivirostre*, *C. duplicatum*, new species, and *C. wangyapoik*, new species, by having the dorsal fin strongly falcate or concave (vs. largely rectangular with slightly convex edge); dorsal fin with a terminal hyaline band followed by a wide, dark band approximately 25% or greater the width of the fin, another wide hyaline band ~50% of the width of the fin, and a basal, dark band with all dark colors present on rays and membranes (vs. two or more thin dark bands much less than 25% of fin width, spots forming bands present only on fin rays); by having the pectoral fin either uniformly dark or with a lighter middle (vs. having spots forming two or more bands), by having the adipose fin inserted directly above insertion of the posteriormost anal-fin ray or slightly behind (vs. over the middle of the anal-fin base), by having 12 circumpeduncular scales (vs. 10), having dentary and premaxillary teeth wide and tri- to pentacuspid (central cusp longest; vs. teeth narrow and peg-like, and maximally tricuspid with only the central cusp well developed), by many teeth (>5) in the posterior dentary row (vs. usually zero but up to two total); and by an anal–apex length/SL ratio of 89.4–94.0 (vs. 93.9–100.3); from *C. declivirostre* and *C. wangyapoik*, new species, by having four branched pectoral-fin rays (vs. 3) and a preanal length/SL ratio of 72.9–76.6 (vs. 76.9–82.3); and from *C. duplicatum*, new species, by having one anterior branched pelvic-fin ray and ray count of i,6,i (vs. two, and ray count of ii,5,i). In addition, infraorbitals 3–4 are reduced to just ossification around the infraorbital canal in *C. crandellii*, while there is some laminar bone dorsal and ventral to the canal in *C. declivirostre, C. duplicatum*, new species, and *C. wangyapoik*, new species.

Description.—Measurements (Table 1) and meristics (reported below) based on 20 specimens. Dorsal profile of body convex arc from tip of snout to posterior end of dorsal fin (highest point of arc at dorsal-fin origin); body then relatively straight and angled ventrally to adipose fin, then shallowly concave to caudal fin. Ventral profile straight to anal fin, then concave arc to caudal fin. Body depth greatest at dorsal-fin origin and least at middle of caudal peduncle. Body oval in cross section anteriorly with ventral surface flattened and oval with dorsal and ventral surfaces somewhat flattened on caudal peduncle. Eye diameter 45.8–97.3% snout length, decreasing with SL (Fig. 3); oval, angled with anterior vertex ventral to posterior vertex; dorsal rim of orbit slightly higher than interorbital surface. Snout broadly rounded. Gill membranes united across isthmus. Tubercles absent.

Scales cycloid, mostly smooth, some with numerous (~20–30) weak, parallel striae. Lateral line complete with anterior segments within each scale occupying approximately one-third length of each scale and pores visible laterally, vs. posterior segments occupying less than one-quarter length of each scale and pores covered by previous scale; 30 (2), 31 (3), 32 (8), 33 (6), or 36 (1) lateral-line scales; lateral-line scales distinctly smaller anteriorly; naked area located between anterior lateral-line scales and pectoral-fin base; lateral line continues onto scales covering caudal base. 4 (12) or 5 (8) scales above lateral line, 1 (2) or 2 (18) scales below lateral line, 12 circumpeduncular scales. Scales covering anterior 20% of caudal fin. 8 (2), 9 (6), 10 (9), or 11 (3) predorsal scales. Venter unscaled on isthmus and posteriorly to about 2 scales before pelvic-fin origin.

Dorsal fin with 2 unbranched and 8 (9) or 9 (11) branched rays (ii,8–9); first unbranched ray about half length of second; first branched ray longest with shortest ray in middle making fin falcate. Pectoral fin with 4 unbranched and 11 (11) or 12 (9) branched rays (iv,11–12); unbranched rays and first unbranched ray with thick pads of tissue anteriorly; first unbranched ray strongly bent in middle to form oblique angle; first branched ray longest and last shortest; pectoral fin oriented obliquely on body with insertion of posteriormost fin ray located posterodorsally to origin. Pelvic fin with 1 leading unbranched ray, 6 branched rays, and 1 posterior unbranched ray (i,6,i); first branched ray longest; 2 or 3 pelvic axillary scales present with complex covering about half of pelvic-fin base. Anal fin with 2 unbranched rays and 5 (4) or 6 (16) branched rays (ii,5–6); first unbranched ray approximately one-third length of second, closely adhered; fin falcate with first unbranched ray longest and last shortest. Caudal fin with 1 unbranched and 9 (17) or 10 (3) branched rays in upper lobe and 7 (6), 8 (12), or 9 (2) branched and 1 unbranched ray in lower lobe (i,9–10,7–9,i); forked with upper and lower lobes equal. Adipose fin present with base centered on vertical over last ray of anal fin. Rays of paired, dorsal, and anal fins with thick flaps of skin dorsally (paired fins) and laterally (dorsal and anal fins) that overlap successive rays in folded fin; flaps widest and longest anteriorly, decreasing in size and width posteriorly and usually absent on posterior rays.

Teeth tri- to pentacuspid, wide with edges sharp. 5 (3), 6 (6), 7 (8), or 8 (3) premaxillary teeth. 5 (1), 6 (1), 7 (4), 8 (3), 9 (5), 10 (2), 11 (2), or 12 (2) teeth in outer dentary row. Inner dentary row made up of many small, unicuspid teeth. Ectopterygoid with 2 rows of approximately 8–10 minute teeth per row.

Branchiostegal rays 4; 1 ray attached to posterior ceratohyal; 3 rays attached to anterior ceratohyal. Gill rakers 3–5 on dorsal limb, 1 on angle, 7–8 on ventral limb of anterior branchial arch. One supraorbital present; moderately crescent shaped with ventral edge almost straight; from dorsal midpoint of orbit to dorsal ~1/4–1/3 anterior scleral ossicle; one individual had the posterior portion of each supraorbital present as three separate ossifications in addition to main anterior ossification. All elements of infraorbital series, except infraorbital 1, without laminar component; infraorbitals 3–4 no more than ossification around canal. Parietal branch of supraorbital sensory canal extending to middle or about 3/4 of parietal. Parietal fontanel variable from tiny triangle at posterior borders of parietals to narrow opening at posterior borders of parietals that widens in posterior ~1/3 of parietals then narrows to contact with frontals. Frontal foramina above supraorbital canal 4, wide, circular.

Total number of vertebrae 35 (2), 36 (2), 37 (2). Vertebral centra 2+3 fused, without ventral processes. Rib of centrum 4 distally expanded, extending anteriorly toward lateral process of centrum 2. Posterior chamber of swim bladder absent. Supraneurals between neural spine of fourth centrum and anterior dorsal-fin pterygiophore 4 (4), 5 (1). Epurals 2. Uroneural present, about 60% as long as urostyle.

Coloration in life.—(Figs. 4, 5) Background color generally light tan on body to yellow on fins occasionally with some green iridescence. Background color of largest specimen (AUM 67142) golden with gold filling lighter areas of fins and gold present on ventral surface (although lighter) from anterior of the pelvic fins to caudal peduncle. Dark midlateral stripe generally present from opercle to caudal fin; scales within stripe darkest in their centers making stripe appear to be made out of chevrons with distal portions of some of these chevrons bleeding into scales above and below (darker above than below); stripe widens to large spot on caudal peduncle. About seven dorsal saddles present, first two in nuchal area, third below anterior portion of dorsal fin, fourth and fifth in interdorsal area, and sixth and seventh between adipose and caudal fin. Scales in lighter areas between saddles have posterior halves dark with darker colors dorsally. Irregular blotches present below lateral stripe and often contiguous with dorsal saddles. Light areas of body rich tan above midlateral stripe and pale yellow below; tan above stripe fades to pale yellow posteriorly. Head with mottled dark patch above roof of cranium, dark line behind the eye, dark line leading from near snout tip to posterior of eye, mottling dorsally on the snout with pale yellow spot located anterodorsally to eye, and lighter areas of the cheek and opercle speckled with melanophores. All fins gray at distal margins and yellow proximally; gray and yellow portions bleed into one another along fin rays. Membranes and some parts of rays between gray and yellow regions dark; most intense dark marks on dorsal fin, ventral portion of caudal fin, and at bases of pectoral and adipose fins. Unbranched pectoral and pelvic rays (and less so following branched rays) with darkest colors centrally along rays and increasing distally, with anterior margins gray and posterior margins yellow. Ventrally, colors more muted; thickened, unbranched and anterior branched rays of pectoral and pelvic fins light gray. Dark areas located at bases of all fins. Largest specimen (AUM 67142) differs from this general pattern in that light areas golden and dark areas more intense, lateral stripe absent, and iris brick red (vs. reddish but mottled with black).

Coloration in alcohol.—Similar to color in life, but dark areas more intense and wider and light areas light gray or tan.

Distribution.—*Characidium crandellii* has been found mostly in the upper Branco River (Amazon River) basins of Brazil and Guyana and the middle and lower Essequibo River of Guyana (Fig. 6). The type locality is a tributary of the Cotinga River (tributary of the Takutu/Branco) in the vicinity of Boa Vista (Fig. 6). We have examined two collections of the species from the Orinoco River basin. One specimen is from above Tencua Falls (Salto Tencua), the first major barrier to navigation and a major faunal break between the middle and upper Ventuari River (Lujan et al., 2018), and the other collection is from south of Tepuy Guaiquinima in the Paragua/Caroni River basin, also above a series of rapids, including Uraima Falls located just north of the tepui. The Tencua specimen differs from other *C. crandellii sensu stricto* by having a series of small, vertical spots below the midline and just posterior to the pectoral fin and only the faint remnant of a lateral stripe. The Río Paragua specimens appear more similar to the specimens from the Amazon and Essequibo than to the Tencua specimen.

Remarks.—One specimen from the Ireng River (AUM 67142; 106.9 mm SL; Fig. 4) is the largest specimen of *Characidium* ever examined and far larger than any other specimens. Its

Fig. 7. Dorsal, lateral, and ventral views of *Characidium declivirostre* in life, AUM 56680, 55.5 mm SL; Raudales Danto, Río Cuao, Amazonas, Venezuela. Photos by N. K. Lujan.

golden color seems to suggest that it is a nuptial male, but we did not confirm with dissection because the specimen is unique.

Characidium declivirostre Steindachner, 1915

Figures 2A, 7–9

Characidium declivirostre Steindachner 1915: 31, Río Coquenan, tributary of Río Caroni, Venezuela.

Melanocharacidium pectorale (sic).—Conway et al., 2012: figs. 6C, D, H, and J, and other mentions [fin pad description].

Specimens examined.—Venezuela: AMNH 91168, 1 (0), Bolivar, Orinoco River basin, Río Carapo, at first rapids along right bank, 5.69750, –63.54167 (coordinates per Armbruster and Taphorn, 2013); AMNH 91169, 4 (0), Bolivar, Orinoco River basin, Río Carapo, at third rapids above camp along left bank, 5.71333, –63.53333 (coordinates per Armbruster and Taphorn, 2013); AMNH 91170, 17 (0), Río Paragua, at

Fig. 8. Dorsal, lateral, and ventral views of a specimen of *Characidium declivirostre* from the same stream as the type locality, AUM 36625, 50.1 mm SL. Scale = 1 cm. Photos by J. W. Armbruster.

Gusano Rapids, ca. 1–1.5 hours upriver from Río Carapo mouth, ~5.5037, –63.5941 (coordinates placed at first large rapids complex upstream of Río Carapo, 1 March 1990; AMNH 232950, 8 (0), Amazonas, Orinoco River basin, Río Cuao at Guacamaya Raudal, 13 km upstream from Raudal del Danto, 5.12861, –67.52556; AMNH 232982, 2 (0), Amazonas, Orinoco River basin, Río Cuao at Raudal Piapoco, 21.5 km upstream from Raudal del Danto, 5.18250, –67.51361; AMNH 233000, 26 (0), Amazonas, Orinoco River basin, Río Cuao, Raudal Cielo, west side of Isla del Cielo, 15 minutes by foot from SAS-01-04 basecamp, 7 March 2001; AMNH 233025, 1 (0), Amazonas, Orinoco River basin, Río Cuao at Raudal Pauji, W side of Isla del Cielo, ca. 10 minutes by boat downstream from SAS-01-04 basecamp, 5.14861, –67.53639; AMNH 233084, 14 (0), Amazonas, Orinoco River basin, Caño Pawa ca. 30 minutes by foot upstream from mouth into Río Cuao, ca. 30 minutes downstream from Puerto Nuevo, 5.29194. –67.32889; AUM 22310, 1 (0), Bolivar, Orinoco River basin, Río Chaviripa, at base of falls, ca. 2 km SE Caicara-Puerto Ayacucho Rd., 7.11389, –66.47306; AUM 22318, 1 (0mo/me, 1gm), 34.9 mm SL, Bolivar, Orinoco River basin, Tributary of Río Caripo, ca. 16 km ESE Los Pijiguaos, Caicara-Puerto Ayacucho Rd., 6.57361, –66.93417; AUM 36625, 4 (3mo/me, 4gm), 43.4–50.2 mm SL, Bolivar, Orinoco River basin, Río San Ignacio, km 258, 5.01015, –61.13694; AUM 36638, 8 (3mo/3me, 4gm), 37.0–56.2 mm

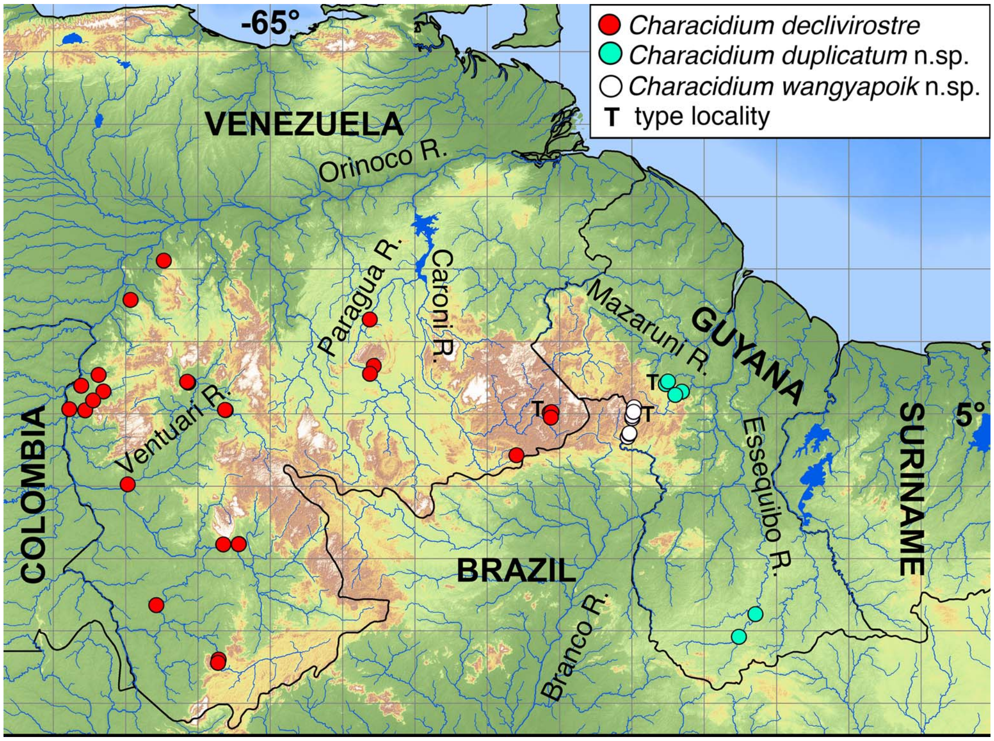

Fig. 9. Distributions of *Characidium declivirostre*, *C. duplicatum*, new species, and *C. wangyapoik*, new species. Type localities indicated by T's (approximated for *C. declivirostre*).

SL, Bolivar, Orinoco River basin, tributary to Río Yuruani, km 255, 5.01888, –61.11447; AUM 36660, 2 (0), 41.7–45.7 mm SL, Bolivar, Orinoco River basin, Río Samey, 57.5 km WSW of Santa Elena, 6 km S. of El Piaje, on foot path, 4.42296, –61.59586; AUM 36674, 7 (2mo/me, 7gm), 33.0–47.5 mm SL, Bolivar, Orinoco River basin, Río Mapuari, km 268, 38 km N of Santa Elena, 4.94401, –61.12099; AUM 37137, 2 (0), 29.6–32.7 mm SL, Bolivar, Orinoco River basin, Río Paragua, 66.9 km SSW of La Paragua, at Uraima Falls, 6.30117, –63.62427; AUM 39296, 5 (0), 19.1–20.5 mm SL, Amazonas, Orinoco River basin, Río Manapiare, 14.5 km NW of San Juan de Manapiare, 5.42863, –66.13616; AUM 39468, 2 (0mo/me, 2gm), 34.5–36.3 mm SL, Amazonas, Orinoco River basin, Río Ventuari, above Salto Tencua, 58 km ESE of San Juan de Manapiare, 5.04777, –65.61583; AUM 39539, 1 (0mo/me, 1gm), 38.6 mm SL, Amazonas, Orinoco River basin, Río Ventuari, at Raudales Tencua, 56 km ESE of San Juan de Manapiare, 5.04968, –65.62722; AUM 39601, 1 (0), Amazonas, Orinoco River basin, Río Manapiare, 17 km NW of San Juan de Manapiare, 5.44198, –66.1507; AUM 40191, 44 (6mo/me, 20gm, 4cs), 18.4–57.2 mm SL, Amazonas, Orinoco River basin, tributary to Orinoco, 30 km S of Puerto Ayacucho, 5.38659, –67.61556; AUM 43381, 3 (0mo/me, 1gm), 58.4 mm SL, Amazonas, Orinoco River basin, Río Iguapo, 12.6 km ENE of La Esmeralda, 3.19988, –65.43582, 7 March 2005; AUM 43461, 1 (0), Amazonas, Orinoco River basin, Río Casiquiare, bedrock in stream, 73 km NE of San Carlos de Río Negro, 2.35258, –66.57521; AUM 43497, 6 (0), Amazonas, Amazon River basin, Río Siapa, raudales, 154 km E of San Carlos de Río Negro, 1.60339, –65.71587; AUM 43519, 1 (1mo/me, 1gm), 58.7 mm SL, Amazonas, Amazon River basin, Caño Aracamoní, 156 km ESE of San Carlos de Río Negro, 1.55669, –65.72533; AUM 43924, 11 (0), Amazonas, Orinoco River basin, Río Iguapo, 12.8 km ENE of Esmeralda, 3.19544, –65.43908; AUM 43943, 1 (0), Amazonas, Orinoco River basin, Caño Tama Tama, 31 km WNW of Esmeralda, 3.21294, –65.82502; AUM 44072, 1 (0), Amazonas, Orinoco River basin, Río Orinoco, Punto de Maraya, 80.8 km E of San Fernando de Atabapo, Isla Maraya, 4.02303, –66.97189; AUM 53418, 1 (0mo/me, 1gm), 53.9 mm SL, Amazonas, Orinoco River basin, Cano Pasa, 98 km S of the Puerto Ayacucho airport, 5.06119, –67.77957; AUM 54195, 1 (0), Amazonas, Orinoco River basin, Río Cataniapo, at Gavilan community, 5.54902, –67.38808; AUM 54207, 26 (0), Amazonas, Orinoco River basin, Río Cataniapo, at Sardi community, 5.53375, –67.37395; AUM 56680, 27 (5mo/me, 11gm, 2cs), 50.5–55.5 mm SL, Amazonas, Orinoco River basin, Río Cuao, at Raudales Danto, 69.3 km S of Puerto Ayacucho, 5.04409, –67.56045; AUM 56762, 2 (0), Amazonas, Orinoco River basin, Caño Soromoni, 11.8 km WNW of La Esmeralda, 3.1938, –65.65197; NMW 62442, 4 (3gm), syntypes, Orinoco River basin, Río Coquenan, tributary of Río Caroni.

Diagnosis.—*Characidium declivirostre* can be distinguished from all crenuchids except *C. crandellii, C. duplicatum*, new species, and *C. wangyapoik*, new species, by having venter without scales from isthmus to pelvic girdle (vs. maximally to insertion of posteriormost pectoral-fin ray) and from most species of *Characidium* by having a very large pectoral fin with first three, unbranched pectoral-fin rays thickened, and first pectoral-fin ray bent at an oblique angle (vs. pectoral-fin rays not thickened and first ray either straight or slightly curved). *Characidium declivirostre* differs from *C. crandellii* and *C. duplicatum*, new species, by having three unbranched pectoral rays (vs. four); from *C. crandellii* by having ten circumpeduncular scales (vs. 12), by having two or more thin dark bands consisting of spots on rays in the dorsal and pectoral fins (vs. a median wide dark band with pigment concentrated on membranes in the dorsal fin and the pectoral fin either entirely dark or dark with a lighter middle), by having an almost square dorsal fin with slightly concave distal edge (vs. falcate), by having the adipose fin above the middle of the anal-fin base (vs. anterior edge of the adipose fin above or behind a vertical through the insertion of the posterior most anal-fin ray), by having dentary and premaxillary teeth narrow and peg-like, and maximally tricuspid with only the central cusp well developed (vs. wide and tri- to pentacuspid, central cusp longest), by having zero to two (total) teeth in the second dentary row (vs. 8 or more), by a preanal length/SL ratio of 76.9–80.6% (vs. 72.9–76.6%), and an anal–apex length/SL ratio of 93.9–97.8% (vs. 89.4–94.0%); from *C. duplicatum*, new species, by having one leading unbranched pelvic ray (vs. two); and from *C. wangyapoik*, new species, by having the ventral portion of the flanks with less than ten almost square blotches (vs. 10 or more narrow bars), by having lateral-line canals at least 33% of scale length and pores not covered by preceding scales (vs. lateral-line canals very short in scale, less than 25%, and pores covered by preceding scales).

Description.—Measurements (Table 1) and meristics (reported below) based on 20 specimens. Dorsal profile of body forms convex arc from tip of snout to adipose fin (slight change in conformation at insertion of posteriormost dorsal-fin ray) then concave arc to caudal fin. Ventral profile straight to anal fin, then concave arc to caudal fin. Body depth greatest at dorsal-fin origin and least at middle of caudal peduncle. Body oval in cross section anteriorly (flattened ventrally) and oval with dorsal and ventral surfaces somewhat flattened on caudal peduncle. Eye 57.6–78.8% snout length, decreasing in size with SL (Fig. 3), oval, angled with anterior vertex ventral to posterior vertex; dorsal rim of orbit slightly higher than interorbital surface. Snout pointed. Gill membranes united across isthmus. Tubercles present in both sexes, distributed dorsally on head and anterodorsal scales.

Scales cycloid, generally flat with about 6 striae in first postdorsal scale. Lateral line complete with canal in scales running approximately 33% of scales and pores visible laterally just posterior to previous scales; 30 (1), 31 (13), 32 (3), 33 (2), or 35 (1) lateral-line scales; lateral-line scales distinctly smaller anteriorly; naked area between anterior lateral-line scales and pectoral-fin base; lateral line continues onto scales covering caudal base. 3 (3) or 4 (17) scales above lateral line and 2 scales below lateral line, 10 circumpeduncular scales. Scales covering anterior 20% of caudal fin. 8 (10), 9 (9), or 10 (1) predorsal scales. Venter unscaled on isthmus and posteriorly to about two to three scales anterior to pelvic-fin origin.

Dorsal fin with 2 unbranched and 9 branched rays (ii,9); first unbranched ray about one-half length of second, closely adhered; first branched ray longest and last shortest; fin roughly rectangular. Pectoral fin with 3 unbranched and 9 (1), 10 (17), or 11 (2) branched rays (iii,9–11); unbranched rays and first branched ray with thick pads of tissue anteriorly; first unbranched ray forming curve; first branched ray longest and last shortest; pectoral fin oriented obliquely on body with insertion of posteriormost ray located posterodorsally to origin. Pelvic fin with 1 leading unbranched ray, 6 branched rays, and 1 posterior unbranched ray (i,6,i); first branched ray longest; 2 to 3 pelvic axillary scales present with complex covering approximately half of pelvic-fin base. Anal fin with 2 unbranched rays and 5 (15) or 6 (5) branched rays (ii,5–6); first unbranched ray approximately one-third length of second, closely adhered; fin margin almost straight with second unbranched or first branched ray longest; anal fin fits into space made available by steep, concave profile of venter starting at anal-fin origin. Caudal fin with 1 unbranched and 9 branched rays in upper lobe and 7 (1) or 8 (19) branched and one unbranched ray in lower lobe (i,9,7–8,i); forked with upper and lower lobes coequal. Adipose fin present with base centered on vertical through middle of anal-fin base. Rays of paired, dorsal, and anal fins with thick flaps of skin dorsally (paired fins) and laterally (dorsal and anal fins) that overlap successive rays of adpressed fin; flaps widest and longest anteriorly, decreasing in size and width posteriorly and often absent on middle and posterior rays.

Teeth tricuspid, narrow and peg-like with median cusp round and lateral cusps poorly developed. 5 (1), 6 (9), 7 (3), 8 (4), 9 (2), or 10 (1) premaxillary teeth. 6 (2), 7 (1), 8 (6), 9 (3), 10 (3), 11 (1), or 12 (4) teeth in outer dentary row. Inner dentary row made up of many small, unicuspid teeth; teeth may be absent or not readily visible in smaller specimens. Ectopterygoid usually with 2 rows of approximately 10 (lateral) and 5–10 (medial) minute teeth, some specimens having only lateral row.

Branchiostegal rays 4, 1 attached to posterior ceratohyal, 3 attached to anterior ceratohyal. Gill rakers 1–3 on dorsal limb, 1 on angle, 6–7 on ventral limb of anterior branchial arch. 1 supraorbital present; crescent shaped; from dorsal midpoint of orbit to dorsal 1/3 of anterior scleral ossicle. All elements of infraorbital series, except infraorbital 1, without laminar component. Parietal branch of supraorbital sensory canal extending to middle of parietal. Parietal fontanel reduced to tiny triangle at posterior borders of parietals. Frontal foramina above supraorbital canal 3 wide, circular.

Total number of vertebrae 33 (1), 34 (1), 35 (2), 36 (2). Vertebral centra 2–4 fused, without ventral processes. Rib of centrum 4 distally expanded, extending anteriorly toward lateral process of centrum 2. Posterior chamber of swim bladder extremely reduced, about length of one vertebral centrum. Supraneurals between neural spine of fourth centrum and anterior dorsal-fin pterygiophore 4 (3), 5 (3). Epurals 2 (1), 3 (5). Uroneural present, about 50% as long as urostyle.

Coloration in life.—(Fig. 7) Base color tan with very slight yellow tinge (particularly on head and fins). Dorsal surface with six saddles considerably darker than light intervening regions (light regions from head to dorsal fin have spots centrally [dorsoventrally] and distally [anteroposteriorly] located on scales); first dorsal saddle located on nape, second anterior to dorsal-fin origin, third directly under dorsal fin, fourth in interdorsal region, fifth posterior to adipose-fin base, and sixth at end of caudal peduncle and continuing on to scales covering base of caudal fin. Faint lateral stripe made of spotted scales present along lateral line (spots always located along center lines, but may be posterior on scale (anterior body), central on scales (middle body), or anterior on scales (posterior body); lateral stripe covers lateral-line scales and one row above. Approximately 8 roughly square blotches located below lateral line (usually 2–2.5 scale rows wide, but some blotches smaller, particularly in smaller specimens). These blotches terminate in lateral stripe. Faint, iridescent yellow-green area noticeable above pectoral-fin base.

Head mottled with dark patches on tan to yellow background. Dark patch located on center of opercle, patch fading anteriorly; posterodorsal corner of opercle tan. Large, diffuse, dark blotches present below and behind eye. Wide stripe present from eye to snout. Dark bands present between orbits and down snout. Amount of melanin on head variable, some individuals with large light gray to yellow patches and some almost entirely dark gray.

Dorsal fin with alternating dark and light bands; bands better developed anteriorly. Distal band dark, pigment concentrated on rays. Second band gray (membranes) and tan (rays). Third band black, pigment concentrated on membranes. Fourth band wide gray (membranes) and tan (rays) band. Fifth (most proximal) band black, band covering rays and membranes. Pectoral fin with yellow to gray base color with dark spots centered on rays in two to three distal and one basal band; bands irregular; some spots bleeding onto membranes; ventrally, pectoral-fin colors more diffuse, generally gray with fleshy pads of unbranched and first branched rays almost white. Pelvic fin colored similarly to pectoral with single median band including melanophores on interradial membranes, and diffuse dark band at base of fin. Anal fin as pelvic fin, but no basal band, and band much wider anteriorly. Adipose fin yellow to gray proximally and dark distally with dark color confluent with saddle below it. Base color of caudal fin dark with pigment particularly concentrated at branching points of lepidotrichia; 2 yellow spots present at base (just above and below midline); dorsal and ventral spots may bleed into one another across center; rest of fin with large yellow blotches.

Coloration in alcohol.—(Fig. 8) As in life but yellows and grays change to tan to light brown, spots on scales less distinct and numerous, and iridescence absent. Juveniles colored similarly to adults, but may have more and narrower ventral blotches, generally lighter in color overall. Some populations considerably lighter with greater contrast between light and dark areas, narrower bands, and smaller spots on fins.

Distribution.—(Fig. 9) *Characidium declivirostre* is known from throughout the Orinoco River basin and the upper Negro River basin. The type locality is the Río Coquenán (also spelled Kukenan), a tributary of the upper Caroni River in Venezuela, We collected and examined material from near this locality (AUM 37137). Its range likely also includes left-bank clear or blackwater tributaries of the Orinoco River in Colombia and rivers draining the southern slope of the western Guiana Shield in Brazil. Our collections of this species were mostly from bedrock shoals in medium to large-sized streams.

Remarks.—In their investigation of the microanatomy of paired-fin pads in ostariophysan fishes, Conway et al. (2012: figs. 6C, D, H, and J) described the pectoral- and pelvic-fin pads of this species (AUM 40191, misidentified therein as *Melanocharacidium pectorale*). The pads were described as Type I pads where the epidermis is thickened without contribution from the subepidermal layers. They found the epidermis to be thicker ventrally than dorsally (60 vs. 30 μm), the subdermal layer thicker dorsally than ventrally (30 vs. 10 μm), keratinized unculi present on the ventral surfaces of the fin-ray pads, and alarm substance cells and mucocytes present and common on dorsal and ventral surfaces except the ventral surfaces of the pads.

***Characidium duplicatum*, new species**

urn:lsid:zoobank.org:act:11B1C6B7-9273-4C91-959A-31FDF3C0797B
Figure 10

Leptocharacidium sp.—Hardman et al., 2002: 235 [locality record].

Holotype.—CSBD F-3614 (ex AUM 62835), 1 (1mo/me, 1gm), 39.4 mm SL, Guyana, Region 8 (Potaro-Siparuni), Potaro-Essequibo River basin, Kuribrong River, in rapids at Grass Shoals, 05.40791, –059.53179, J. W. Armbruster, D. C. Werneke, E. A. Liverpool, D. P. Fernandes, D. C. Taphorn, 12 March 2014.

Paratypes.—Guyana: AUM 28124, 1 (1mo/me), 25.2 mm SL, Potaro-Siparuni (Region 8), Essequibo River basin, Potaro River, Amatuk cataract and beach just below cataract, 5.30389, –59.31111, L. M. Page, J. W. Armbruster, M. H. Sabaj, M. Hardman, J. H. Knouft, W. S. Prince, 25 October 1998; AUM 28135, 5 (5mo/me, 5gm, 1cs), 19.6–22.6 mm SL, Potaro-Siparuni (Region 8), Essequibo River basin, Potaro River, Waratuk cataract, 5.25889, –59.40028, L. M. Page, J. W. Armbruster, M. H. Sabaj, M. Hardman, J. H. Knouft, W. S. Prince, 26 October 1998; AUM 62835, 1 (1mo/me, 1gm), 38.9 mm SL, Potaro-Siparuni (Region 8), Essequibo River basin, Kuribrong River, in rapids at Grass Shoals, 5.40791, –59.53179, J. W. Armbruster, D. C. Werneke, E. A. Liverpool, D. P. Fernandes, D. C. Taphorn, 12 March 2014; AUM 72308, 1 (0mo, 1me, 1gm), 29.9 mm SL, Potaro-Siparuni (Region 8), Essequibo River basin, Kuribrong River, at Ram Sheep Rapids, 5.44236, –59.50201, D. C. Taphorn, J. W. Armbruster, D. C. Werneke, E. A. Liverpool, D. P. Fernandes, M. Benjamin, 13 March 2014; ROM 61496, 13 (5mo/me, 7gm), 19.5–28.9 mm SL, Potaro-Siparuni (Region 8), Essequibo River basin, Potaro River, Amatuk Falls, side channel of Potaro River near portage, 5.30421, –59.31051, E. Holm, 2 October 1990; ROM 110060, 1 (1mo/me, 1 gm), 36.2 mm SL, Potaro-Siparuni (Region 8), Essequibo River basin, Sheetrock Creek at crossing of road between Wailang and Mona Falls, 5.47494, –59.43769, N. K. Lujan, E. Liverpool, D. Gordon, M. Benjamen, L. Ziccardi, O. Williams, 29 April 2013.

Other specimens examined.—Guyana: AUM 38991, 1 (1mo/me, 1gm), 25.2 mm SL, Upper Takutu-Upper Essequibo (Region 9), Essequibo River basin, Essequibo River at Kassi-Attae Rapids, 5.5 km SE mouth of Kuyuwini River, 2.22654, –58.29379, J. W. Armbruster, M. H. Sabaj, M. Hardman, D. Arjoon, N. K. Lujan, L. S. de Souza, 10 November 2003; AUM 39024, 7 (6mo, 7me, 6gm, 1cs), 25.0–30.0 mm SL, Upper Takutu-Upper Essequibo (Region 9), Essequibo River basin, Essequibo River at Yukanopito Falls, 44.5 km SW mouth of Kuyuwini River, 1.91461, –58.52046, J. W. Armbruster, M. H. Sabaj, M. Hardman, D. Arjoon, N. K. Lujan, L. S. de Souza, 9 November 2003.

Diagnosis.—*Characidium duplicatum* can be distinguished from all other crenuchids except *Leptocharacidium* by having two anterior unbranched pelvic rays, and from all crenuchids except *C. crandellii, C. declivirostre,* and *C. wangyapoik*, new species, by having venter without scales from the isthmus to

Fig. 10. Lateral view (top) of *Characidium duplicatum*, new species, in life and dorsal, lateral, and ventral views after preservation, CSBD F-3614, holotype, 39.4 mm SL. Photos by J. W. Armbruster.

Table 2. Morphometrics for *Characidium duplicatum*, new species ($n = 20$), and *C. wangyapoik*, new species ($n = 21$).

	Characidium duplicatum				*Characidium wangyapoik*			
Measurement	Avg.	SD	Min.	Max.	Avg.	SD	Min.	Max.
Standard length (SL; mm)	27.8		19.6	39.4	61.4		51.3	73.6
%SL								
Head length (HL)	25.5	1.7	22.6	28.6	21.7	0.9	20.0	22.8
Prepectoral distance	22.5	1.8	19.8	26.3	18.5	0.9	16.7	19.9
Prepelvic distance	58.2	2.0	53.5	61.1	54.4	1.1	52.0	56.4
Preanal distance	77.6	2.5	72.8	83.1	79.4	1.4	77.4	82.3
Anal–apex distance	98.5	7.5	94.5	129.5	97.3	1.7	94.6	100.3
Body width	16.0	1.0	14.5	18.7	15.1	0.6	14.2	16.6
Body depth at dorsal-fin origin	16.0	1.6	13.2	18.6	18.7	1.0	16.5	20.0
Body depth at anal-fin origin	11.6	1.0	9.1	13.2	14.3	1.1	13.0	17.6
Least caudal peduncle depth	8.2	1.0	6.3	10.9	9.1	0.5	7.9	10.0
First pectoral-fin ray length	19.5	1.7	16.3	23.3	16.7	1.2	14.8	19.1
Greatest pectoral fin distance	35.0	1.9	31.0	37.8	33.3	2.0	28.9	36.8
%HL								
Snout length	33.0	2.9	26.5	40.0	38.6	2.2	33.9	44.2
Snout-maxillary tip distance	20.9	2.4	17.4	26.4	23.1	1.8	19.6	25.9
Anterior nostril–orbit	14.1	1.5	10.3	16.8	16.7	1.3	14.4	19.2
Posterior nostril–orbit	6.8	1.6	4.4	10.9	6.7	1.0	4.6	9.1
Cheek depth	21.1	2.6	16.5	29.0	25.0	2.3	21.6	29.6
Orbital diameter	29.8	2.8	25.4	37.5	22.6	1.5	19.4	26.0
Interorbital distance	18.9	2.5	13.5	22.3	21.9	1.6	17.9	24.1

pelvic girdle (vs. maximally to posteriormost pectoral-fin ray insertion), and from most species of *Characidium* by having a very large pectoral fin with first four unbranched pectoral-fin rays thickened, and first pectoral-fin ray bent at oblique angle (vs. pectoral-fin rays not thickened and first ray either straight or slightly convex). *Characidium duplicatum* further differs from *C. declivirostre* and *C. wangyapoik*, new species, by having four unbranched pectoral-fin rays (vs. three); from *C. crandellii* by having nine branched pectoral-fin rays (vs. 10–11); pelvic fin ii,5,i (vs. i,6,i), by having ten circumpeduncular scales (vs. 12), by having two or more thin dark bands consisting of spots on dorsal- and pectoral-fin rays (vs. a median wide dark band with pigment concentrated on dorsal- and pectoral-fin membranes, membranes either entirely dark or lighter at center), by having an almost square dorsal fin with slightly concave distal margin (vs. falcate), by having adipose fin above middle of anal-fin base (vs. origin of adipose fin above or behind vertical through posteriormost anal-fin ray insertion), by having dentary and premaxillary teeth narrow, peg-like, maximally tricuspid with only central cusp well developed (vs. wide and tri- to pentacuspid, central cusp longest), by having no teeth in the second dentary row (vs. 8 or more), and by an anal–apex length/SL ratio of 94.5–100.0% (vs. 89.4–94.0%). In addition, the anterior border of the pectoral girdle is convex such that it is deepest at the midline in *C. duplicatum*, while the anterior border is slightly notched (deepest lateral of midline) in *C. declivirostre* and *C. wangyapoik*, new species, and deeply notched in *C. crandellii*.

Description.—Measurements based on 20 specimens (Table 2); meristics based on 23 specimens. Dorsal profile of body convex arc from tip of snout to posterior end of supraoccipital, then beginning steeper and longer concave arc from supraoccipital to end of dorsal fin (highest point of arc at dorsal-fin origin); body then relatively straight and angled ventrally to end of caudal peduncle. Ventral profile straight to end of pelvic base, rises slightly to anal fin, then concave arc to caudal fin. Body deepest at dorsal-fin origin and shallowest at middle of caudal peduncle. Body oval in cross section anteriorly and oval with dorsal and ventral surfaces somewhat flattened on caudal peduncle. Eye diameter 78.8–118.0% snout length, decreasing in size with SL (Fig. 3), oval, angled with anterior vertex ventral to posterior vertex; dorsal rim of orbit significantly higher than interorbital surface. Snout broadly rounded. Gill membranes united across isthmus, but width of membrane greater in larger specimens. Tubercles absent.

Scales cycloid with approximately 10 parallel striae in first postdorsal scale. Lateral line complete with canal in most scales occupying approximately 33–50% of scales and pores exposed just posterior to previous scale (some scales with pore at or near posterior end of scale); 28 (1), 29 (10), 30 (3), or 31 (3) lateral-line scales; lateral-line scales distinctly smaller anteriorly; naked area between anterior lateral-line scales and pectoral-fin base; lateral line continues onto scales covering caudal-fin base. 4 scales above lateral line and 1 (3) or 2 (14) scales below lateral line, 10 circumpeduncular scales. Scales covering anterior 20% of caudal fin. 8 (5), 9 (9), 10 (2), or 11 (1) predorsal scales. Venter unscaled on isthmus and posteriorly to approximately 2 scales before pelvic-fin origin.

Dorsal fin with 2 unbranched and 8 (1), 9 (20) or 10 (2) branched rays (ii,8–10); first unbranched ray slightly less than one-half length of second, closely adhered; first branched ray longest and antepenultimate shortest, making fin slightly concave. Pectoral fin with 4 unbranched and 8 (2), 9 (19), or 10 (2) branched rays (iv,8–10); unbranched rays with thick pads of tissue anteriorly; first unbranched ray strongly curved posteriorly; fourth unbranched ray longest and last branched ray shortest; pectoral fin oriented obliquely on body with posteriormost insertion located dorsal to origin. Pelvic fin with 2 leading unbranched rays, 5 branched rays, and 1 posterior unbranched ray (ii,5,i); second branched ray longest; 2 to 3 pelvic axillary scales present with complex covering ~half of pelvic-fin base. Anal fin with 2 unbranched rays and 3 (1) or 5 (22) branched rays (ii,3 or 5); first unbranched ray less than 1/3 length of second, closely adhered; fin slightly falcate with second branched ray longest, first unbranched ray considerably shorter, rays then becoming shorter to last; anal fin fits into concavity made by steep, concave margin of ventral profile starting at anal-fin origin. Caudal fin with 1 unbranched and 10 (22) branched rays in upper lobe and 9 (22) branched and 1 unbranched ray in lower lobe (i,10,9,i; one specimen had caudal fin too damaged to count rays); forked with upper and lower lobes equal. Adipose fin present with base centered on vertical over middle of anal-fin base. Rays of paired, dorsal, and anal fins with thick flaps of skin dorsally (paired fins) and laterally (dorsal and anal fins) that overlap successive rays of adpressed fin; flaps widest and longest anteriorly, decreasing in size and width posteriorly, sometimes absent on posterior rays.

Teeth tricuspid, narrow and peg-like with median cusp round and lateral cusps poorly developed. 5 (3), 6 (14), or 7 (6) premaxillary teeth. 3 (1), 5 (4), 6 (6), 7 (10), 8 (1), or 9 (1) teeth in outer dentary row. No teeth observed on inner dentary row. Ectopterygoid with single row of approximately 10 minute teeth.

Branchiostegal rays 4; 1 ray attached to posterior ceratohyal; 3 rays attached to anterior ceratohyal. Gill rakers 1–3 on dorsal limb, 1 on angle, 3–5 on ventral limb of anterior branchial arch. One supraorbital present; approximately crescent shaped with ventral side almost straight; from dorsal midpoint of orbit to dorsal ~1/3 of anterior scleral ossicle. All elements of infraorbital series, except infraorbital 1, without laminar component. Parietal branch of supraorbital sensory canal extending to middle of parietal. Parietal fontanel absent; however, parietals do not meet along midline, perhaps due to small size of cleared and stained specimens. Frontal foramina above supraorbital canal 3 wide, circular.

Total number of vertebrae 33 (2). Vertebral centra 2–4 fused, without ventral processes. Rib of centrum 4 distally expanded, extending anteriorly toward lateral process of centrum 2. Swim bladder was not examined. Supraneurals between neural spine of fourth centrum and anterior dorsal-fin pterygiophore 4(2). Epurals 3(2). Uroneural present, about 3/4 as long as urostyle.

Color in life.—(Fig. 10) Body with yellow base color dorsally fading to gray ventrally. Dorsal surface covered with eight dark saddles, first on posterior of head, three between head and dorsal-fin origin (middle band lighter), one under dorsal fin, one between dorsal and adipose fins, one beginning under posterior half of adipose and continuing on caudal peduncle, and one at end of the caudal peduncle. Lighter spaces between saddles with yellow pigment covered by brown dorsally. Lateral stripe faintly visible, formed by scales in stripe with spot of color that leaves anterior edges of scales yellow-gray. Scales with spots covering all except anterior edge of scales present in all regions of body; spots more distinct on caudal peduncle. Several long wide blotches below lateral line with those between posteriormost pectoral-fin ray insertion and anal-fin origin most distinct. Dorsal fin with two distalmost bands formed from spots on rays with interspaces on rays yellow and fin membranes gray; proximal band of dorsal fin similar to others, but anterior end of band with large spot that covers both rays and membranes. Pectoral fin with three bands consisting of spots on branched rays; unbranched rays with central column of black surrounded by gray; interradial membranes gray; large dark spot present above most of pectoral fin and yellow spot present just above pectoral-fin origin; anterior base of pectoral fin to opercle gray with some patches of black melanophores. Pelvic fin colored similar to dorsal fin but with two bands; base of pelvic fin yellow. Anal fin with one medial dark band made of spots centered on rays and bleeding into interradial membranes; rest of anal fin gray. Adipose fin with yellow-gray base and dark tip contiguous with dorsal saddles below. Caudal fin with mostly gray membranes and alternating dark and yellow patches; dark patches longer than yellow patches on central rays and distally on all rays; dorsal- and ventral-most three or four rays with two to three large yellow spots surrounded by black; yellows and blacks fading distally. Head mostly mottled with black and dusky yellow; black interorbital bar present, continuing ventrally along anterior border of eye; large, dark crescent anterior of eye with small connection to interorbital bar; large black spot below eye that widens and fades ventrally; large dark spot on opercle, preopercle, and posterior infraorbitals. Some iridescent green and yellow spots present posterior to eye.

Color in alcohol.—(Fig. 10) Similar to life except with iridescence absent and grays and yellows converted to tan. Holotype and specimen collected with it (AUM 62835) considerably darker than all other specimens.

Distribution.—(Fig. 9) Found throughout the Essequibo River basin, but has been rarely encountered during our surveys. Most locations are in the lower Potaro and Kuribrong, but two localities are in the upper Essequibo upstream of the mouth of the Kuyuwini River.

Remarks.—Because *Characidium duplicatum* is distributed in both the lower and upper Essequibo with no collections in between, we excluded the upper Essequibo localities from the type series to be more certain that the types contain a single species.

Although similar to *Characidium declivirostre* in color pattern, *C. duplicatum* has extra unbranched pectoral and leading pelvic rays. The fourth unbranched pectoral and second unbranched pelvic rays are more similar in appearance to the first unbranched rays than to other branched rays, suggesting that the extra unbranched fin rays were gained via conversion of anterior branched rays. This is further supported by the fact that the pectoral and pelvic fins have the same total number of rays (usually 13 and 8, respectively) in *C. duplicatum* and *C. declivirostre*. The fourth unbranched pectoral ray and second unbranched pelvic rays are also the longest in their respective fins, while the first branched ray is the longest in *C. declivirostre* and *C. wangyapoik*, new species. The only other crenuchid with two unbranched pelvic rays is *Leptocharacidium omospilus*.

Etymology.—*Duplicatum* is Latin for double and is a neuter adjective. In reference to the presence of two unbranched anal-fin rays.

Fig. 11. Dorsal, lateral, and ventral views of *Characidium wangyapoik*, new species, in life, CSBD F-3615, holotype, 72.6 mm SL. Photos by N. K. Lujan.

***Characidium wangyapoik*, new species**
urn:lsid:zoobank.org:act:1EBB34BE-431E-4D03-A343-6E8132EE810C
Figures 1A, 11–12

Characidium n. sp. 'Ireng'.—Lujan et al., 2020: 1216 [locality information].

Holotype.—CSBD F-3615 (ex AUM 67118), 1 (1mo/me, 1gm), 72.6 mm SL, Guyana (border with Brazil), Potaro-Siparuni (Region 8), Amazon River basin, Ireng River, first shoal upriver from split with Sukwabi Creek, 5.07711, –59.97423, N. K. Lujan, J. W. Armbruster, D. C. Werneke, M. Ram, 8 January 2016.

Paratypes.—All specimens Guyana (border with Brazil), Potaro-Siparuni (Region 8), Amazon River basin, Ireng River basin (known as the Rio Mau in Brazil): ANSP 207526, 3 (1mo/me, 3gm), 42.6–56.8 mm SL, AUM 67036, 26 (5mo/me, 26gm, 4cs), 22.0–59.9 mm SL, CSBD F-3616, 3 (1mo/me, 3gm), 37.7–52.2 mm SL, INPA ICT-059496, 3 (0mo/me, 3gm), 52.6–54.6 mm SL, ROM 111286, 3 (0mo/me, 3gm), 47.7–53.8 mm SL, Ireng River, at Orinduik Falls, between upper and lower falls, 4.72536, –60.03852, D. C. Werneke, J. W. Armbruster, N. K. Lujan, M. Ram, 2 January 2016; AUM 67046, 16 (0), 17.8–46.4 mm SL, Ireng River, below lower Orinduik Falls, 4.71898, –60.03507, N. K. Lujan, J. W. Armbruster, D. C. Werneke, M. Ram, 3 January 2016; AUM 67068, 18 (0), 25.2–43.5 mm SL, Ireng River, at Branana Rapids, shoals downstream of Orinduik Falls, 4.67585, –60.06046, D. C. Werneke, J. W. Armbruster, D. I. Brooks, M. Ram, 4 January 2016; AUM 67076, 4 (0), 36.0–40.4 mm SL, Ireng River, at Orinduik Falls, between upper and lower falls, 4.72536, –60.03852, D. C. Werneke, J. W. Armbruster, D. I. Brooks, M. Ram, N. K. Lujan, 4 January 2016; AUM 67077, 20 (0mo/me, 13gm), 31.8–51.9 mm SL, Ireng River, at Orinduik Falls, around halfway between upper and lower falls, 4.72176, –60.03703, D. C. Werneke, J. W. Armbruster, D. I. Brooks, M. Ram, N. K. Lujan, 4 January 2016; AUM 67094, 1 (0), 30.2 mm SL, Ireng River, just above Orinduik Falls, 4.72798, –60.03597, N. K. Lujan, J. W. Armbruster, D. C. Werneke, D. I. Brooks, M. Ram, 5 January 2016; AUM 67118, 14 (4mo/me, 7gm, 2cs), 49.4–76.1 mm SL, INPA ICT-

Fig. 12. Dorsal, lateral, and ventral views of *Characidium wangyapoik*, new species, after preservation, CSBD F-3615, holotype, 72.6 mm SL; Kuribrong River population. Photos by J. W. Armbruster.

059497, 2 (1mo/me, 2gm), 60.6–62.6 mm SL, first shoal upriver from split with Sukwabi Creek, 5.07711, –59.97423, N. K. Lujan, J. W. Armbruster, D. C. Werneke, M. Ram, 8 January 2016; AUM 67143, 6 (0mo/me, 6gm), 44.8–67.7 mm SL, Ireng River, shoals at mouth of Monkey Creek, Kaibarupai, 5.04398, –59.97717, N. K. Lujan, J. W. Armbruster, D. C. Werneke, 9 January 2016; AUM 67181, 9 (3mo/me, 9gm), 49.1–68.8 mm SL, ROM 111287, 2 (2mo/me, 2gm), 60.6–61.3 mm SL, Ireng River, shoals at mouth of Monkey Creek, Kaibarupai, 5.04398, –59.97717, J. W. Armbruster, N. K. Lujan, D. I. Brooks, 12 January 2016; AUM 67189, 2 (0mo/me, 2gm), Sukwabi Creek, East Fork, downstream of Wotowanda Falls, 5.08867, –59.96952, J. W. Armbruster, N. K. Lujan, D. I. Brooks, D. C. Werneke, P. Peters, R. Daniel, local fishermen, 13 January 2016; AUM 67196, 12 (0mo/me, 11gm), 28.1–67.9 mm SL, Ireng River, downstream of Kaibarupai, 5.02404, –59.97763, D. C. Werneke, J. W. Armbruster, N. K. Lujan, M. Ram, D. I. Brooks, 14 January 2016; AUM 67199, 2 (0), 19.7–23.2 mm SL, Ireng River, at Sand Hill shoals, 4.96554, –59.99411, D. C. Werneke, J. W. Armbruster, N. K. Lujan, M. Ram, D. I. Brooks, 14 January 2016; AUM 67204, 12 (5mo/me), 17.1–72.0 mm SL, Ireng River, at Waipa Landing, 4.93345, –59.99514, D. C. Werneke, J. W. Armbruster, N. K. Lujan, M. Ram, D. I. Brooks, 14 January 2016.

Diagnosis.—*Characidium wangyapoik* can be distinguished from all crenuchids except *C. crandellii, C. declivirostre,* and *C. duplicatum* by having venter without scales from the isthmus to the pelvic girdle (vs. maximally to pectoral insertion) and from most species of *Characidium* by having a very large pectoral fin with first three unbranched pectoral-fin rays thickened and first pectoral-fin ray bent at an oblique angle (vs. pectoral-fin rays not thickened and first pectoral-fin ray either straight or slightly convex). *Characidium wangyapoik* differs from *C. crandellii, C. declivirostre,* and *C. duplicatum* by having at least the ventral region of flank with thin bars becoming contiguous across body at larger sizes (vs. ventral area with almost square blotches), having lateral-line canal in most of scales very short (~25% of scale length), and having canal pores covered by preceding scales (vs. canal at least 33% of scale length and pores not covered by preceding scales); from *C. crandellii* by having 10 circumpeduncular scales (vs. 12), having two or more thin dark bands consisting of spots on rays in dorsal and pectoral fins (vs. a median wide dark band with pigment concentrated on membranes in dorsal fin and pectoral fin either entirely dark or dark with lighter middle), having an almost square dorsal fin with slightly concave distal margin (vs. falcate), having adipose fin located above middle of anal-fin base (vs. anterior edge of adipose fin at or behind vertical through posteriormost anal-fin insertion), by having dentary and premaxillary teeth narrow, peg-like, and maximally tricuspid with only central cusp well developed (vs. wide and tri- to pentacuspid, central cusp longest), by having zero to two (total) teeth in second dentary row (vs. 8 or more); by a preanal length/SL ratio of 77.4–82.3% (vs. 72.9–76.6%), and anal–apex length/SL ratio of 94.6–100.3% (vs. 89.4–94.0%); from *C. declivirostre* by having the flanks with 10 or more narrow bars (vs. less than 10 almost square blotches); and from *C. duplicatum* by having one leading unbranched pelvic ray (vs. two). *Characidium wangyapoik* is most similar in color to *C. amaila* from the upper Kuribrong River, but it has bands in the dorsal and pectoral fins (vs. no bands in *C. amaila*) and the unbranched pectoral-fin rays are greatly thickened (vs. only slightly thickened).

Description.—Measurements based on 21 specimens (Table 2); meristics based on 20 specimens (reported below). Dorsal profile of body forms convex arc from tip of snout to posterior end of supraoccipital, then becomes steeper and longer convex arc from supraoccipital to end of dorsal fin (highest point of arc at dorsal-fin origin); dorsal profile relatively straight and ventrally angled from dorsal fin to adipose fin, then forming concave arc to caudal fin. Ventral profile straight to anal fin, then forming concave arc to caudal fin. Body depth greatest at dorsal origin and least at middle of caudal peduncle. Body oval in cross section anteriorly (flattened ventrally) and oval with dorsal and ventral surfaces somewhat flattened on caudal peduncle. Eye diameter 52.5–69.0% snout length, decreasing in size with SL (Fig. 3), oval, angled with anterior vertex ventral to posterior vertex; dorsal rim of orbit slightly higher than interorbital surface. Snout broadly rounded. Gill membranes united across isthmus. Tubercles present in both sexes dorsally on head and anterodorsal scales.

Scales cycloid with most scales having 10–30 short, parallel striae (most on first postdorsal scale). Lateral line complete with canal occupying approximately 1/4 of scale length and pores covered by previous scales; 30 (1), 31 (4), 32 (12), or 33 (3) lateral-line scales; lateral-line scales distinctly smaller anteriorly; naked area between anterior lateral-line scales and pectoral-fin base; lateral line continues onto scales covering caudal base. 4 scales above lateral line and 2 scales below lateral line; 10 circumpeduncular scales. Scales covering anterior 1/5 of caudal fin. 7 (2), 8 (14), or 9 (4) predorsal scales. Venter unscaled on isthmus and posteriorly to 4 to 5 scales anterior to pelvic-fin origin.

Dorsal fin with 2 unbranched and 8 (1) or 9 (19) branched rays (ii,8–9); first unbranched ray about 1/3 length of second; first unbranched ray longest and last shortest; fin roughly rectangular. Pectoral fin with 3 unbranched and 10 (19) or 11 (1) branched rays (iii,10–11); unbranched rays and first branched ray with thick pads of tissue anteriorly; first unbranched ray strongly curved; first branched ray longest and last shortest; pectoral fin oriented obliquely on body with posteriormost insertion located posterodorsally to origin. Pelvic fin with 1 leading unbranched ray, 6 (19) or 7 (1) branched rays, and 1 posterior unbranched ray (i,6–7,i); first branched ray longest; 2 to 3 pelvic axillary scales present with complex covering ~half of pelvic-fin base. Anal fin with 2 unbranched rays and 5 branched rays (ii,5); first unbranched ray slightly less than 1/3 length of second, closely adhered; fin margin curved with second unbranched ray longest and last branched ray shortest. Caudal fin with 1 unbranched and 8 (4) or 9 (16) branched rays in upper lobe and 8 (16), or 9 (4) branched and 1 unbranched ray in lower lobe (i,8–9,8–9,i); forked with upper and lower lobes coequal. Adipose fin present with base centered on vertical through middle of anal-fin base. Rays of paired, dorsal, and anal fins with thick flaps of skin dorsally (paired fins) and laterally (dorsal and anal fins) that overlap successive rays in adpressed fins; flaps widest and longest anteriorly, decreasing in size and width posteriorly, flaps usually absent on posterior rays.

Teeth tricuspid, narrow and peg-like with median cusp round and lateral cusps poorly developed. 6 (4), 7 (12), or 8 (4) premaxillary teeth. 9 (3), 10 (6), 11 (6), 12 (4), or 14 (1) teeth in outer dentary row. Inner dentary row comprising many small, unicuspid teeth; teeth may be poorly visible or absent in smaller specimens. Ectopterygoid with two rows of approximately 10 (lateral) and 5–10 (medial) minute teeth.

Branchiostegal rays 4; 1 ray attached to posterior ceratohyal; 3 rays attached to anterior ceratohyal. Gill rakers 2–3 on dorsal limb, 1 on angle, 6–7 on ventral limb of anterior branchial arch. One supraorbital present; crescent shaped; from dorsal midpoint of orbit to dorsal ~1/4 of anterior scleral ossicle. All elements of infraorbital series, except infraorbital 1, without laminar component. Parietal branch of supraorbital sensory canal extending less than 1/4 into parietal. Parietal fontanel reduced to tiny triangle at posterior borders of parietals, almost absent in some; smallest specimens with gap between parietals. Frontal foramina above supraorbital canal 3–4 with some posterior foramina sometimes combined, wide, circular.

Total number of vertebrae 33 (3). Vertebral centra 2–4 fused, without ventral processes. Rib of centrum 4 distally expanded, extending anteriorly toward lateral process of centrum 2. Posterior chamber of swim bladder extremely reduced, about length of one vertebral centrum. Supraneurals between neural spine of fourth centrum and anterior dorsal-fin pterygiophore 4 (4), 5 (1). Epurals 3 (5). Uroneural present, about 1/2 as long as urostyle.

Coloration in life.—(Fig. 11) Base color tan with slight yellow tinge (particularly on head, fins, and dorsally). Dorsal surface with many (~10) diffuse saddles that seem to subdivide in larger specimens. Faint stripe present along lateral line. Numerous narrow bars below lateral line (1–1.5 scale rows wide). These may extend above lateral line and join with dorsal saddles (particularly in larger specimens). Color generally concentrated on scales with each scale having lighter edges, but either anterior or posterior edges may be light. Ventral surface gray with ventral bars almost meeting midventrally. Iridescent yellow-green stripe noticeable in some specimens between midlateral stripe and dorsal surface;

stripe located below dark pigment and fades at insertion of posteriormost dorsal-fin ray.

Head with dorsal saddle that extends to near ventral margin of opercle (posterior margin of opercle gray to yellow). Large dark blotches present below and behind eye. Wide stripe present from eye to snout. Dark bands present between orbits and down snout. Amount of melanin on head varies, some individuals with large gray to yellow patches and some almost entirely dark. Iridescent green spot present in some specimens located dorsal to postorbital dark spot.

Dorsal fin with dark distal margin, gray band that changes to yellow proximally, then black band made of spots on rays that covers ~1/4 width of fin (interradial membranes gray along band), then narrow gray to yellow band, and finally proximal black band made of roughly triangular spots with longest edges along anterior margins of rays and sloping posteroventrally to posterior margin of rays (interradial membranes gray to yellow); all bands more diffuse anteriorly. Pectoral fin with gray distal margin changing to yellow proximally; dark spots present in two bands distally; distalmost dark band with spots only on rays, but some spots bleed onto membranes in proximal band; dark band at base of pectoral fin may be present; pectoral-fin colors more diffuse ventrally, generally gray with fleshy pads of unbranched and first branched rays almost white. Pelvic fin colored similarly to pectoral with single median band that includes melanophores on interradial membranes and band at base of fin. Anal fin as pelvic fin, but no basal band. Adipose fin yellow to gray proximally and dark distally with dark color confluent with saddle below it. Base color of caudal fin dark with pigment concentrated at junctions of lepidotrichia; two yellow spots present at base (just above and just below midline), single median spot located along midline just after proximal spots, rest of fin with large yellow blotches proximally and large gray blotches distally (gray blotches may fade into base color).

Coloration in alcohol.—(Fig. 12) As in life but yellows and grays become tan and iridescence is lost.

Distribution.—(Fig. 9) *Characidium wangyapoik* is only known from the upper Ireng River basin (Amazon River) along the Brazil/Guyana border (known as the Rio Mau in Brazil). Specimens were collected from below Orinduik Falls to the upper falls on the Ireng and its equal tributary, the Sukwabi River, but not above the Uluk Tuwuk or Wotawanda falls of the upper Ireng and Sukwabi Rivers (see Lujan et al., 2020, for a more detailed map and description of this area).

Etymology.—*Wangyapoik* is the Patamona word for the species, and it is used as a noun in apposition. *Wang* means 'honey' and *yapoik* means 'seated,' perhaps in reference to the yellowish color. The Patamona also refer to the species by the English common name of "fallsfish."

KEY TO SPECIES OF THE FAST-WATER *CHARACIDIUM* OF THE GUIANA SHIELD

1a. Twelve circumpeduncular scales. Dorsal fin falcate with a medial dark band and terminal white band (Figs. 4, 5). Origin of adipose fin centered at vertical above insertion of posteriormost anal-fin ray (Figs. 4, 5). Pectoral fin uniformly dark or peripherally dark with lighter center. Proximal dentary and premaxillary teeth wide and tri- to pentacuspid (central cusp longest) .... ***Characidium crandellii***

1b. Ten circumpeduncular scales. Dorsal fin only slightly concave along distal margin and with two or more thin dark bands (Figs. 7, 8, 10–12). Origin of adipose fin at vertical over center of anal-fin base or more anterior. Pectoral fin light with at least one (usually two or three) dark bands made of separate elongate spots (Figs. 7, 8, 10–12). Proximal dentary and premaxillary teeth narrow, peg-like, tricuspid, but only central cusp conspicuous 2

2a. Pelvic fin with two unbranched rays. Pectoral fin with four unbranched rays (Fig. 1B) .... ***C. duplicatum*, new species**

2b. Pelvic fin with one unbranched ray. Pectoral fin with three unbranched rays (Fig. 1A) 3

3a. Dorsal coloration consisting of prominent saddles that extend to a faint midlateral stripe that may appear as a series of blotches (stripe most prominent in preserved specimens). No accessory bars between saddles. Ventral portion of sides with few, rectangular to square blotches that do not extend dorsal to midlateral stripe (Figs. 7, 8) .... ***C. declivirostre***

3b. Dorsal saddles not prominent in adults, and usually confluent with thin bands from below midlateral stripe, which is usually demarcated by a faint stripe made of zig-zag lines with the stripe most prominent in smaller individuals. Thin bars also present in lighter interspaces between saddles, some of which extend below midlateral stripe (Figs. 11, 12). Ventral portion of sides with numerous narrow bars that extend above midlateral stripe (in juveniles, only some bars may continue dorsal to midlateral stripe; Figs. 11, 12) .... ***C. wangyapoik*, new species**

DISCUSSION

Like their North American namesakes (Welsh and Perry, 1998), South American darters seem to partition benthic habitats by water speed and associated sediment types; with some species inhabiting slow-flowing, sandy habitats, or even backwaters, while others occur largely on bedrock in fast-flowing water (Leitão and Buckup, 2014). Benthic, rheophilic fishes have many adaptations to maintain position in swift currents (Lujan and Conway, 2015). One such adaptation in darters and various similar fishes in streams throughout the world (Conway et al., 2012; Lujan and Conway, 2015) is having large, angled pectoral fins that generate downforce from water flowing over them. These fins often have ventral pads of tissue that help to resist abrasion and increase adhesion via microscopic keratinous structures known as unculi. In their review of paired-fin pads across the Ostariophysi, Conway et al. (2012) examined *C. declivirostre* (misidentified as *Melanocharacidium pectorale*) and described it as having Type I pads (thickening of the epidermis with no contribution from subepidermal layers) on the first three pectoral-fin rays and first two pelvic-fin rays. The epidermis was thicker ventrally, the subdermis thicker dorsally, unicellular, rearward-facing unculi present on the ventral surfaces of the pads, and alarm substance cells and mucocytes present and common dorsally and present ventrally only on areas without the pads.

Fast-water specialist fishes seem to be particularly diverse in rivers draining the Guiana Shield, which are naturally low in sediment, have abundant bedrock shoals and rapids, and a complex history of geological uplift and erosion (Lujan and Armbruster, 2011; Lujan et al., 2013; Lehmberg et al., 2018). *Characidium crandellii* was described from the Branco River, a tributary of the Negro River, and *C. declivirostre* was described from the Caroni River, a tributary of the Orinoco River. Although the type localities of the two species are relatively close in linear distance (south and north of the Pakaraima Mountains near the Brazil/Venezuela border), they are quite far from each other in terms of the modern Orinoco and Negro River channels, which only connect via the Casiquiare Canal. However, a hypothesized paleo-river, the proto-Berbice, may have once united these type localities in a single river basin that drained into the Caribbean Sea through the current mouth of the Berbice River as recently as the Pleistocene (McConnell, 1959; Gibbs and Barron, 1983; Lujan and Armbruster, 2011). This paleo-river likely contributed to the disjunct distributions of species or species groups distributed throughout the highlands of the western Guiana Shield (Lujan et al., 2018). *Characidium crandellii* is an excellent example of such taxa, along with the loricariid species *Ancistrus saudades* (Souza et al., 2019) and the genus *Exastilithoxus* (Lujan et al., 2018) whose disjunct distributions suggest that some portion of the upper Ventuari River above Tencua Falls and upper courses of other south bank Orinoco tributaries such as the Paragua River once flowed in the opposite direction, forming headwaters of the proto-Berbice. A series of transcurrent faults run approximately east-west in Bolivar and Amazonas, Venezuela. Although these faults formed in the early Precambrian, they were rejuvenated in the late Mesozoic (de Loczy, 1973; Gibbs and Barron, 1983). Fish distributions suggest a recent switch of the upper courses of south bank Orinoco tributaries from the proto-Berbice perhaps due to tilting along these transcurrent faults. It is notable that despite fairly heavy sampling of south-bank Orinoco tributaries, *C. crandellii* is only found in the headwaters of those tributaries that have been proposed to have switched between the proto-Berbice and Orinoco. The Ventuari specimen of *C. crandellii* looks a little different than other specimens suggesting that isolation may be leading to speciation; however, one specimen is not enough to draw conclusions, and the Paragua specimens appear identical to other specimens in the range. All Orinoco specimens have shapes that fall within the main cluster of *C. crandellii* (Fig. 3). A more thorough test of the proto-Berbice hypothesis for these species' distributions will require material from intervening sites in the Uraricoera River drainage in northernmost Brazil—a river that remains largely unsampled by ichthyologists.

Buckup (1993b) described two species of *Melanocharacidium* that have a similar coloration and morphology to *C. crandellii, C. declivirostre, C. duplicatum*, and *C. wangyapoik*: *M. depressum* and *M. pectorale* (clade Me2 in Buckup, 1993a). These species of *Melanocharacidium* have the anterior pectoral- and pelvic-fin rays less thickened than that of the aforementioned *Characidium*, and they have a venter lacking scales from the isthmus to just posterior of the pectoral-fin base (vs. nearly to pelvic-fin origin). Buckup (1993a, 1993b) diagnosed *Melanocharacidium* based on several characteristics including loss of the supraorbital, presence of three supraneurals, and the supracleithrum posteriorly arched. *Characidium crandellii, C. declivirostre, C. duplicatum*, and *C. wangyapoik* lack all of the synapomorphies of *Melanocharacidium* with the exception of a lack of maxillary teeth, which was homoplastic in Buckup's analysis (Buckup included *C. crandellii* and *C. declivirostre* in his analysis, and we confirmed his characters in our specimens and the new species).

In addition, Buckup (1993a, 1993b) recognized a convergence between *C. declivirostre* and *M. depressum* and *M. pectorale* in fusion of the vertebrae of the Weberian apparatus, with *M. depressum* and *M. pectorale* having all four vertebrae fused and *C. declivirostre* having the third and fourth and maybe the second fused (we confirmed that vertebrae 2–4 are fused). *Characidium duplicatum* and *C. wangyapoik* also share the fusion of vertebrae 2–4 with *C. declivirostre*. In addition, Buckup describes the presence of a ventral lamellar process of the homolog of the pleural rib of vertebra 4 extending below the tripus to articulate with the homolog of the lateral process of vertebra 2 to form an osseus wall covering the anterior wall of the swim bladder as characters to diagnose the clade of *M. depressum* + *M. pectorale*. *Characidium declivirostre, C. duplicatum*, and *C. wangyapoik* also appear to have the osseus wall, and this was very similar to what we saw in a specimen of *M. pectorale* (AUM 40995).

DATA ACCESSIBILITY

Supplemental material is available at https://www.ichthyologyandherpetology.org/i2019299. ZooBank publication urn:lsid:zoobank.org:pub:24A53251-5BE2-4F5E-8666-9CBA2AA644A5.

ACKNOWLEDGMENTS

We would like to thank O. Leon Mata, *in memoriam* (Curator of Fishes, Museo de Ciencias Naturales de la UNELLEZ, Guanare, Venezuela) and D. Taphorn (UNELLEZ) for facilitating field work in Venezuela, and E. Liverpool (University of Guyana), O. Williams (Guyana Ministry of Indigenous Peoples' Affairs), D. Taphorn (UNELLEZ), L. Page (University of Florida), A. Williams (World Wildlife Fund Guianas), C. Hutchinson (WWF Guianas), and D. Fernandes (Guyana Protected Areas Commission) for facilitating field work in Guyana. We especially thank the Patamona community of Kaibarupai for hosting our expedition to the upper Ireng River and sharing their knowledge and skills in the field. We also thank the collection managers E. Holm (ROM), M. Burridge (ROM), D. Stacey (ROM), M. Sabaj (ANSP), B. Brown (*in memoriam*, AMNH), and R. Arrindell (AMNH) for facilitating visits to their collections and sharing specimens via loans. We especially thank all of the people who aided us in the field and deposited specimens in collections including: D. Abraham, C. Allison, M. Arce, D. Arjoon, J. Baskin, M. Benjamin, R. Betancur, J. Birindelli, T. Carvalho, C. Chin, J. Correia, R. Daniel, L. de Souza, K. Dookram, J. Evans, D. Fernandes, C. Ferraris, D. Gordon, M. Grant, M. Hardman, J. Hartsell, D. Hemraj, J. Knouft, E. Liverpool, H. López-Fernández, S. Lord, A. Luna, V. Meza, T. Pera, P. Peters, W. Prince, F. Provenzano, M. Ram, E. Richmond, R. Royero-I., M. Sabaj, S. Schaefer, D. Taphorn, J. Thomas, M. Thomas, D.

Werneke, T. Wesley, A. Yarumore, and L. Ziccardi. This project was supported by NSF grants DEB-0107751 and DEB-0315963, National Geographic CRE grants to JWA and NKL (8721-09), and a Coypu Foundation grant to NKL and JWA and funding from the WWF-Guianas and the Inter-American Development Bank. Salary support for NKL was provided by a Gerstner Fellowship from the American Museum of Natural History.

LITERATURE CITED

Adams, D. C., M. L. Collyer, and A. Kaliontzopoulou. 2020. Geomorph: software for geometric morphometric analyses. R package version 3.2.1. https://cran.r-project.org/package=geomorph

Armbruster, J. W., and D. C. Taphorn. 2013. Description of *Neblinichthys peniculatus*, a new species of loricariid catfish from the Río Paragua. Neotropical Ichthyology 11:65–72.

Buckup, P. A. 1993a. Phylogenetic interrelationships and reductive evolution in Neotropical characidiin fishes (Characiformes, Ostariophysi). Cladistics 9:305–341.

Buckup, P. A. 1993b. Review of the characidiin fishes (Teleostei: Characiformes), with descriptions of four new genera and ten new species. Ichthyological Exploration of Freshwaters 4:97–154.

Conway, K. W., N. K. Lujan, J. G. Lundberg, R. L. Mayden, and D. S. Siegel. 2012. Microanatomy of the paired-fin pads of ostariophysan fishes (Teleostei: Ostariophysi). Journal of Morphology 273:1127–1149.

De Loczy, L. 1973. Some problems of the tectonic framework of the Guiana Shield with special regard for the Roraima Formation. Geologische Rundschau 62:318–342.

Fricke, R., W. N. Eschmeyer, and R. van der Laan (Eds.). 2019. Eschmeyer's Catalog of Fishes: Genera, Species, References. (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp). Electronic version accessed 5 September 2019.

Gibbs, A. K., and C. N. Barron. 1993. The Geology of the Guiana Shield. Oxford University Press, New York.

Hardman, M., L. M. Page, M. H. Sabaj, J. W. Armbruster, and J. H. Knouft. 2002. A comparison of fish surveys made in 1908 and 1998 of the Potaro, Essequibo, Demerara, and coastal river drainages of Guyana. Ichthyological Exploration of Freshwaters 13:225–238.

Klingenberg, C. P. 2011. MorphoJ: an integrated software package for geometric morphometrics. Molecular Ecology Resources 11:353–357.

Lehmberg, E. S., A. A. Elbassiouny, D. D. Bloom, H. López-Fernández, W. G. Crampton, and N. R. Lovejoy. 2018. Fish biogeography in the "Lost World" of the Guiana Shield: phylogeography of the weakly electric knifefish *Gymnotus carapo* (Teleostei: Gymnotidae). Journal of Biogeography 45:815–825.

Leitão, R. P., and P. A. Buckup. 2014. A new species of *Characidium* (Characiformes: Crenuchidae) from coastal basins of Serra do Mar, southeastern Brazil. Copeia 2014:14–22.

Lujan, N. K., H. Agudelo-Zamora, D. C. Taphorn, P. N. Booth, and H. López-Fernández. 2013. Aescription of a new, narrowly endemic South American darter (Characiformes: Crenuchidae) from the Central Guiana Shield Highlands of Guyana. Copeia 2013:454–463.

Lujan, N. K., and J. W. Armbruster. 2011. The Guiana Shield, p. 211–224. *In:* Historical Biogeography of Neotropical Freshwater Fishes. J. Albert and R. Reis (eds.). University of California Press, Berkeley.

Lujan, N. K., J. W. Armbruster, and N. R. Lovejoy. 2018. Multilocus phylogeny, diagnosis and generic revision of the Guiana Shield endemic suckermouth armored catfish tribe Lithoxini (Loricariidae: Hypostominae). Zoological Journal of the Linnean Society 184:1169–1186.

Lujan, N. K., J. W. Armbruster, D. C. Werneke, T. Franco Teixeira, and N. R. Lovejoy. 2020. Phylogeny and biogeography of the Brazilian-Guiana Shield endemic *Corymbophanes* clade of armoured catfishes (Loricariidae). Zoological Journal of the Linnean Society 188:1213–1235.

Lujan, N. K., and K. W. Conway. 2015. Life in the fastlane: a review of rheophily in freshwater fishes, p. 107–136. *In*: Extremophile Fishes. M. Plath, R. Riesch, and M. Tobler (eds.). Springer International Publishing, Switzerland.

McConnell, R. B. 1959. Fossils in the North Savannas and their significance in the search for oil in British Guiana. Timehri: The Journal of the Royal Agricultural and Commercial Society of British Guiana 38:65–85.

Olsen, A. M., and M. W. Westneat. 2015. StereoMorph: an R package for the collection of 3D landmarks and curves using a stereo camera set-up. Methods in Ecology and Evolution 6:351–356.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Steindachner, F. 1915. Beiträge zur Kenntniss der Flufische Südamerikas. V. Denkschriften der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse 93:15–106.

Welsh, S. A., and S. A. Perry. 1998. Habitat partitioning in a community of darters in the Elk River, West Virginia. Environmental Biology of Fishes 51:411–419.