Copeia 2013, No. 3, 454–463

Description of a New, Narrowly Endemic South American Darter (Characiformes: Crenuchidae) from the Central Guiana Shield Highlands of Guyana

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Characidium amaila, **new species, is described from rapids of the upper Kuribrong River (Potaro–Essequibo drainage) upstream of Amaila Falls. It is diagnosed from most other species of *Characidium* by lacking scales on the isthmus and chest, and by having 8–13 premaxillary teeth, the first four pectoral-fin rays noticeably thickened, 34–36 lateral line scales, and branchiostegal membranes that are free from each other across the isthmus. *Characidium amaila* is further distinguished by its large adult body size (max. = 85.5 mm SL), and by having a tan body base color with a dark midlateral stripe that originates on the upper lip and continues posteriorly to the base of the middle caudal-fin rays, a gray to dark-black dorsum with two horizontal rows of small light spots formed by aligned light-colored scale centers, a dark humeral spot, up to 15 irregular black bars that extend from dorsum to lower sides, a light opercular margin, and fins that are uniformly dusky. Several cranial, vertebral, and swim bladder characteristics also support distinctiveness of the new species.**

Characidium amaila **es descrita de los rápidos de el alto río Kuribrong (cuenca del Potaro–Essequibo) aguas arriba de las Cascadas de Amaila. Se distingue de la mayoría de las otras especies de *Characidium* por la ausencia de escamas en el istmo y el pecho, y por tener 8–13 dientes premaxilares, por poseer los primeros cuatro radios de la aleta pectoral notablemente ensanchados, 34–36 escamas en la línea lateral, y por tener las membranas de los radios branquiostegales separadas del istmo. *Characidium amaila* se distingue además por el gran tamaño del adulto (max. = 85.5 mm SL) y por tener el cuerpo de color base café claro con una banda medio lateral que se origina en el labio superior y continúa posteriormente hasta la base de los radios medios de la aleta caudal; el dorso gris a negro con dos hileras horizontales de pequeños puntos claros formados por la alineación de los centros más claros de las escamas; una mancha humeral oscura; hasta quince barras negras irregulares que se extienden del dorso a la parte inferior de los flancos; el margen del opérculo de color más claro y aletas uniformemente grisáceas. Varios caracteres craneales, de las vertebras y de la vejiga natatoria apoyan el diagnostico de esta especie nueva.**

THE Kuribrong River is a remote north (left) bank tributary of the Potaro River in the Essequibo River drainage of western Guyana. Headwaters of the Kuribrong River, including its entire Amaila River tributary, drain a plateau with an average elevation of approximately 450 meters above sea level (masl) that is nested within the Guiana Shield's Pakaraima Mountain range (average elevation = approx. 1000 masl; Lujan and Armbruster, 2011). The Kuribrong and Amaila Rivers join each other immediately upstream of Amaila Falls, where their combined discharge exits the Guiana Shield in a steep descent to the coastal plain, itself an area of low topographic relief with an average elevation of less than 80 masl. During recent biodiversity surveys to identify potential environmental impacts of a hydroelectric dam being planned for the Kuribrong River immediately upstream of Amaila Falls, the first author and colleagues intensively sampled five major rapids habitats in the upper Kuribrong watershed and collected 170 specimens of an apparently endemic species identifiable to the genus *Characidium* Reinhardt, 1866 (family Crenuchidae, subfamily Characidiinae) but not assignable to any known species.

The genus *Characidium* was defined by Buckup (1993a, 1993b) as a monophyletic group that currently includes 53 valid species geographically restricted to tropical South America and southern Panama (Eschmeyer, 2012). *Characidium* are relatively small-bodied (<100 mm SL), invertivorous fishes that occupy the benthic zone in flowing, often swift-water, habitats. The genus is similar to the more extensively studied North American darters (Percidae: Etheostomatini), from which they derive their common name. Buckup (1993a) revised select lineages within Characidiinae and (1993b) presented a morphology-based hypothesis of interspecific relationships within Characidiinae that remains in use today. Buckup (1992, 1993b) proposed a clade within *Characidium* consisting of *C. fasciatum* (type species for the genus), *C. boavistae*, *C. bolivianum*, *C. gomesi*, and *C. purpuratum*. Diagnostic characters given for the *C. fasciatum* group included six internal and external traits: 1) scales absent from the chest and area surrounding the pectoral-fin base (Buckup, 1992:1068); 2) pterosphenoid foramen for ophthalmic nerve centrally located (vs. ventrolaterally located in the plesiomorphic condition; Buckup, 1992:1068); 3) foramen largely flat and lacking a bony crest (vs. foramen with tubular form derived from encircling bony crests; Buckup, 1992:1068); 4) foramen exceptionally large, allowing ventral view of the brain cavity (vs. small, not

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Submitted: 25 February 2013. Accepted: 23 March 2013. Associate Editor: R. E. Reis.
 DOI: 10.1643/CI-12-079

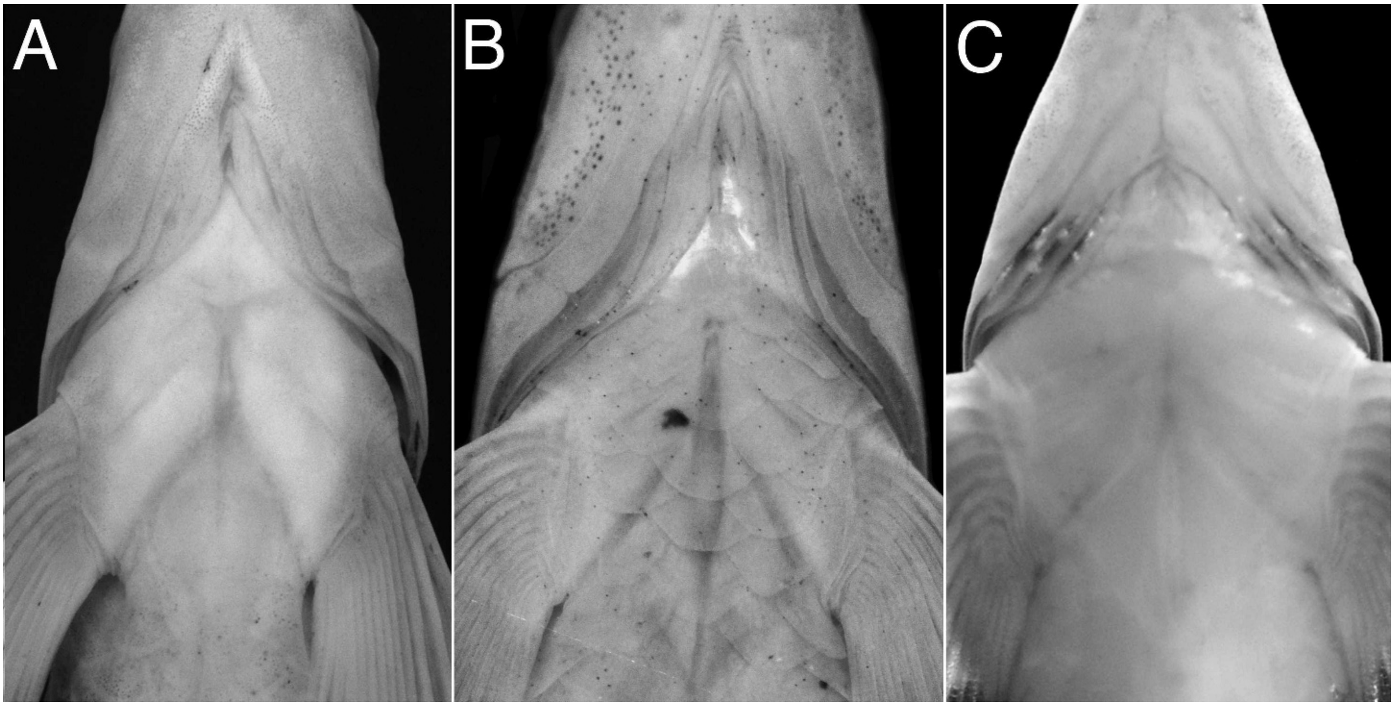

Fig. 1. (A) Unscaled breast and free branchiostegals of *Characidium amaila*, CSBD 1655 (holotype), compared with (B) the scaled breast and free branchiostegals of *C. zebra*, AUM 36637, and (C) the unscaled breast and united branchiostegals of *C. declivirostre*, AUM 54207.

allowing view of brain cavity; Buckup, 1992:1068, 1993b:331); 5) second vertebral centrum with pair of ventral processes extending anteroventrally along the connective tissue surrounding the dorsal aorta and the anterior wall of the swim bladder (Buckup, 1992:1068, 1993b:331); and 6) swim bladder with posterior chamber smaller than anterior chamber (Buckup, 1992:1068).

In this paper, we examine these and other characters in specimens of *Characidium* collected from the upper Kuribrong River, we place each character in a differential diagnosis that distinguishes this species from all other species of *Characidium,* and we describe the new species as *Characidium amaila*.

MATERIALS AND METHODS

A total of 157 specimens from the upper Kuribrong were examined, 83 of which were examined morphometrically and meristically. Morphometrics and meristics used in the description follow Buckup (1993a). Straight-line measurements and counts of bilateral structures were taken on the left side when possible under a stereomicroscope using a Mitutoyo digital caliper precise to 0.1 mm. Meristic counts listed in the text are followed by the total number of individuals having each count (in parentheses) and/or an asterisk indicating the value of the holotype. The complex ural centrum was treated as a single vertebra for meristic purposes. Color descriptions follow Buckup and Reis (1997) where ‘stripe’ refers to horizontal and ‘bar’ refers to vertical marks on the body or fins. Institutional abbreviations are as listed at http://www.asih.org/node/204. One specimen was cleared and stained according to methods described by Taylor and Van Dyke (1985). Morphometric data were analyzed statistically using JMP statistical software (v5.0.1a) for Mac OS X. Comparative data for the southeastern Brazilian species *Characidium alipioi*, *C. fasciatum, C. gomesi, C. japuhybense*, *C. grajahuensis*, *C. lauroi*, *C. timbuiense*, and *C. vidali* were gathered from original descriptions or, in the case of *C. fasciatum*, the redescription by Buckup (1992).

Characidium amaila, new species

Figures 1, 2; Table 1

Holotype.—CSBD 1655, 70.6 mm SL, Guyana, Region 8, Kuribrong River drainage, a tributary of the Potaro/Essequibo River system, confluence of the Amaila and Kuribrong rivers immediately above Amaila Falls (Rapids 1), 5°22′33″N, 59°33′1″W, N. Lujan, B. Noonan, G. Savory, K. Andrew, 23 March 2011.

Paratypes.—All from Guyana, Region 8, upper Potaro–Kuribrong River drainage, Essequibo River Basin:

ANSP 182814 (ex ROM 91366, see locality data below), 5, 44.1–57.0 mm SL; AUM 56867 (ex ROM 91366, see locality data below), 5, 43.0–61.3 mm SL; ROM 89838, 12, 33.3–73.1 mm SL, Kuribrong River at rapids about 15 minutes upstream from camp (Rapids 3), 5°20′15″N, 59°33′58″W, N. Lujan, A. Khan, G. Savory, K. Andrew, 12 March 2011; ROM 89857, 1, 44.6 mm SL, Kuribrong River at Rapids 3, 5°20′15″N, 59°33′58″W, N. Lujan, F. Lima, T. Pessali, T. Teixera, 16 March 2011; ROM 89894, 8, 32.2–85.5 mm SL, Kuribrong River at Rapids 3, 5°20′15″N, 59°33′58″W, N. Lujan, F. Lima, T. Pessali, T. Teixera, 19–20 March 2011; ROM 89905, 5, 30.3–68.9 mm SL, Kuribrong River at Rapids 2, 5°21′6″N, 59°32′44″W, N. Lujan, F. Lima, T. Pessali, T. Teixera, 21 March 2011; ROM 89912, 1, 80.8 mm SL, same data as holotype; ROM 91366, 106, 34.1–62.0 mm SL, large unnamed right (east) bank tributary (‘‘Tributary 4’’) of upper Kuribrong River at Rapids 5, 5°18′50″N, 59°33′5″W, 450 masl, N. Lujan, D. Abraham, D. Stoby, D. Gordon, 23 October 2011; ROM 91394, 8, 48.0–79.6 mm SL, upper Kuribrong River at Rapids 4, 5°16′19″N, 59°42′9″W, N. Lujan, D. Abraham, D. Stoby, D. Gordon, 19 October

Fig. 2. (A) Paratype of *Characidium amaila*, ROM 89838, 73.1 mm SL (live photo by NKL); (B) holotype of *Characidium amaila*, CSBD 1655, 70.6 mm SL, Guyana, Region 8, Kuribrong River drainage, a tributary of the Potaro/Essequibo River system, Amaila River at rapids immediately above Amaila Falls.

2011; ROM 91401, 3, 57.1–75.0 mm SL, upper Kuribrong River at Rapids 3, 5°20′27″N, 59°33′53″W, 450 masl, N. Lujan, D. Abraham, D. Stoby, D. Gordon, 24 October 2011; ROM 91490, 11, 58.0–72.4 mm SL, upper Kuribrong river Rapids 4, 5°16′31″N, 59°42′4″W, N. Lujan, D. Abraham, D. Stoby, D. Gordon, 25 October 2011; ROM 91501, 1, 76.9 mm SL, Amaila River at top of Amaila Falls (Amaila River mouth; Rapids 1), 5°22′33″N, 59°32′50″W, N. Lujan, D. Abraham, D. Stoby, D. Gordon, M. Benjamen, 26 October 2011.

Diagnosis.—*Characidium amaila* is diagnosed from all other *Characidium* except *C. alipioi*, *C. crandellii*, *C. declivirostre*, *C. grajahuensis*, *C. japuhybense*, *C. lauroi*, *C. timbuiense*, *C. vidali*, and members of the *C. fasciatum* clade by lacking scales on the isthmus and on the chest (the area between and around the pectoral-fin bases; Fig. 1); it is diagnosed from *C. crandellii*, *C. declivirostre*, *C. japuhybense*, *C. lauroi*, and all members of the *C. fasciatum* clade except *C. fasciatum* by having 9–15 (allometrically increasing) narrow vertical bars extending from dorsum to below the lateral line (Fig. 2; vs. bars absent or, if present, numbering 8 or fewer; Fig. 3); from *C. fasciatum* (known from the Tietê and São Francisco river drainages), *C. timbuiense* (known from coastal streams of SE Brazil), and *C. vidali* (known from coastal drainages of Rio de Janeiro, Brazil) by having bars with an irregular zigzag pattern or an offset arrangement of dorsal and ventral halves, dorsal portions of bars narrower than ventral or bar margins parallel, and bars extending ventrally at least three to four scale rows below lateral line (Fig. 2; vs. vertical bars wider near dorsum and reaching ventrally to lateral line or up to two scale rows below); from *C. alipioi* (known from the Paraíba do Sul River), *C. fasciatum*, *C. gomesi* (known from the upper Paraná River basin), *C. japuhybense* (known from coastal streams of SE Brazil), *C. lauroi* (known from the Paraíba do Sul River), and *C. timbuiense* by having more premaxillary teeth (8–13 vs. 7 or fewer); from *C. declivirostre* (known from Orinoco and N Amazon drainages), *C. gomesi*, *C. grajahuensis* (known from coastal streams of Rio de Janeiro, Brazil), and *C. vidali* by having the caudal fin dusky with a gradually increasing concentration of darker pigment toward the bases of the middle caudal-fin rays (vs. a distinct chevron pattern located subdistally on the caudal fin in *C. gomesi*, and vertically aligned spots in *C. declivirostre*, *C. grajahuensis*, and *C. vidali*); from *C. boavistae*, *C. bolivianum* (described from the upper Río Beni system, Bolivia), and *C. fasciatum* by having the first four pectoral-fin rays noticeably thickened (vs. first three or fewer rays thickened); from *C. boavistae* and *C. purpuratum* by having more lateral-line scales (34–36 vs. 32 or fewer); from *C. crandellii* and *C. declivirostre* by having branchiostegal membranes free from each other across the isthmus (Fig. 1A; vs. membranes united across the isthmus; Fig. 1C); from sexually mature

Table 1. Morphometric Data from *Characidium amaila* (*n* = 83).

	Holotype	Mean	Min	Max	SD
Total length (mm)	89.2	70	41.5	102.2	14.3
Standard length (mm)	70.6	56.8	34	85.5	11.9
Percentage of SL					
Head length	24.5	25.2	23.3	27.6	1
Prepectoral distance	22.3	22.4	20.1	25	1.1
Predorsal distance	47.4	46.6	43.4	49	1.3
Prepelvic distance	49.9	49.6	46.8	52.8	1.2
Preanal distance	74.5	73.4	70.8	76.9	1.2
Anal-apex distance	96.4	93	89.1	98.8	1.7
Body width	13.5	12.5	10.4	14.6	0.9
Body depth at dorsal-fin origin	24.5	23.4	18.1	26.7	1.8
Body depth at anal-fin origin	20.5	18.3	14.3	21.4	1.3
Least caudal peduncle depth	12.8	12.4	10.2	14	0.7
Percentage of HL					
Snout length	25.4	25.6	23.1	29.1	1.5
Snout-maxillary tip	22.2	21	17.2	23.7	1.6
Anterior nostril-orbit	10.5	10.1	7.7	12.4	0.9
Posterior nostril-orbit	7.7	6.7	4.9	8.9	0.9
Cheek	12.8	11.7	8.6	16.1	1.5
Orbital diameter	22.9	25.8	19.8	30.6	2.8
Interorbital distance	23.8	23.3	17	27.6	2.1

C. purpuratum and *C. boavistae* by lacking any transition to dark purple body color without vertical bars; and from *C. bolivianum* by having the longest dorsal-fin ray much shorter in length than the maximum body depth (vs. ''height of dorsal in some cases equaling the depth of the body'' [Pearson, 1924:32]).

Internally, *Characidium amaila* is diagnosed from all other members of the *C. fasciatum* clade by having the pterosphenoid foramen for ophthalmic nerve centrally located on pterosphenoid (vs. ventrolaterally located), foramen small and canal-like (Fig. 4; vs. large and flat), by lacking pair of ventral processes on second vertebral centrum (Fig. 4; vs. processes present and extending anteroventrally along the connective tissue underlying the Weberian apparatus), and by having the posterior chamber of the swimbladder much longer than the anterior chamber (vs. smaller than anterior chamber; Fig. 5).

Description.—Morphometric data in Table 1. Body large for crenuchids (max. = 85.5 mm SL), laterally compressed with dorsal profile rising and shallowly convex from snout to supraoccipital and from supraoccipital to dorsal-fin origin, slight indentation where epaxial musculature meets cranium, profile convex and declining along dorsal-fin base and then horizontal and straight or slightly convex from posterior dorsal-fin insertion through adipose-fin base to base of caudal fin; ventral profile straight and horizontal or sloped downward to back of head, horizontal and convex from pectoral-fin origin to anal-fin origin, then rising and shallowly convex from anal-fin origin to caudal-fin base. Greatest body depth at or just anterior to dorsal-fin origin. Snout sharp with apex at horizontal through ventral margin of orbit. Maxilla not greatly elongate, reaching vertical between anterior and posterior nares. Orbit circular to obliquely oval, shorter than snout length; dorsal margin of orbit reaching but not surpassing dorsal profile; iris asymmetrically ovoid, anteroventrally directed. Cheek large, with depth equal to or greater than orbit diameter. Nares distinctly separate, posterior naris closer to anterior naris than to orbit; margin of anterior naris raised, forming circular rim; dermal flaps absent from both anterior and posterior naris.

Dorsal-fin rays totaling 10(2), 11*(79), or 12(2): ii8(2), ii9*(73), iii8(5), iii9(2); anal-fin rays totaling 8*: ii6*(83); pectoral-fin rays totaling 12*(83): iv8*(83); pelvic-fin rays totaling 8*(82) or 9(1): i-6-i*(70), ii-5-i (12), iii-4-i(1); principal caudal-fin rays in dorsal lobe 10*(83), in ventral lobe 9*(83). First four pectoral-fin rays and first one to three pelvic-fin rays thickened ventrally as histologically described by Conway et al. (2012). Adipose fin well developed with origin at vertical through posterior insertion of anal fin. All fins lacking sexually dimorphic hooks.

Scales cycloid. Lateral line complete; pored lateral-line scales 34*(39), 35(39), 36(5). Scales above lateral line 4*(83), below 2*(82) or 3(1). Predorsal scales 9(2), 10(10), 11*(67), 12(4). Circumpeduncular scales 12*(83). Isthmus and area between and posterior to pectoral-fin bases lacking scales. Caudal fin with sheath of two or three scales at base. Posteriormost scale in series on dorsal and ventral caudal-fin lobes larger than rest. Scales with radii only, lacking circuli from apical field.

Teeth typically conic but sometimes weakly tricuspid with central cusp largest, posterior teeth often smaller, embedded in and obscured by skin. Premaxilla with 8(2), 9(1) 10(30), 11*(17), 12(29), or 13(3) teeth, size decreasing laterally. Maxilla lacking teeth. Dentary with outer row of 9(2), 10(7), 11(7), 12(11), 13*(17), 14(31), 15(3), or 16(2) teeth, size decreasing laterally, and inner row of tiny teeth more numerous than those in outer row (not counted). Teeth absent from ectopterygoid and mesopterygoid. Gill rakers on ventral lobe of first gill arch numbering nine in most specimens with first two small and rudimentary. Branchiostegal rays four, not connected across the isthmus (Fig. 1A). Vertebrae of single cleared-and-stained specimen (ROM 89894) = 35.

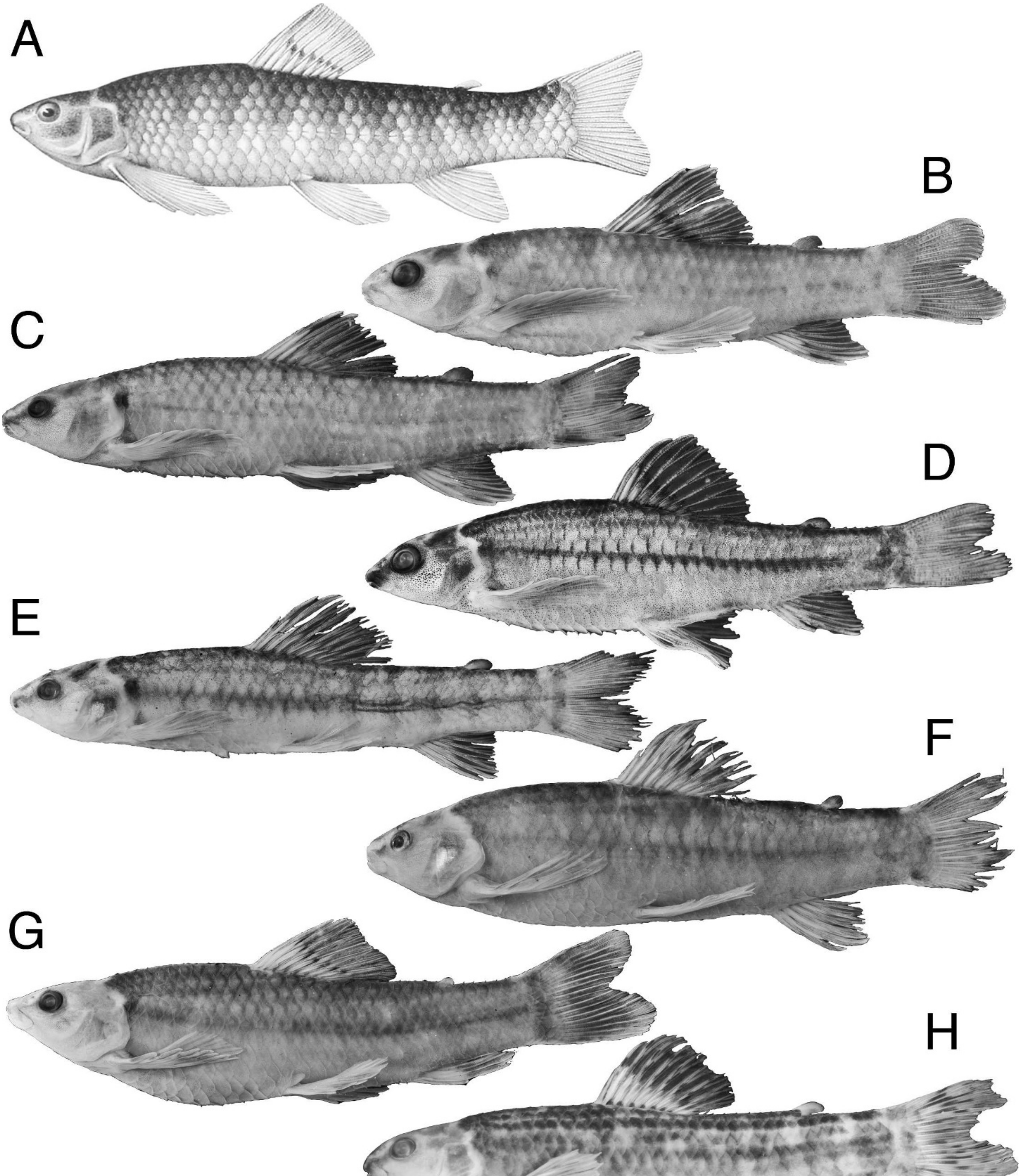

Fig. 3. Shape and color pattern variation across *Characidium fasciatum* group species: (A) *C. boavistae*, syntype, Branco drainage, northern Brazil (from Steindachner, 1915); (B) *C. boavistae*, AUM 37985, Kumu Creek, Takutu-Branco drainage, Guyana; (C) *C. boavistae*, Chururu River, Apure River drainage, Venezuela; (D) *C.* cf. *boavistae*, AUM 50720, Gran Creek, Maroni drainage, Suriname; (E) *C. purpuratum* (male), AUM 46741, Marañon R., Peru; (F) *C. purpuratum* (female), AUM 46793, Utcubamba River, Marañon drainage, Peru; (G) AUM 51233, *C.* cf. *bolivianum*, unnamed tributary of the Inambari River, Madre de Dios drainage, Peru; (H) *C. gomesi*, MZUSP 110229, Pardo River, Paraná River drainage, Brazil.

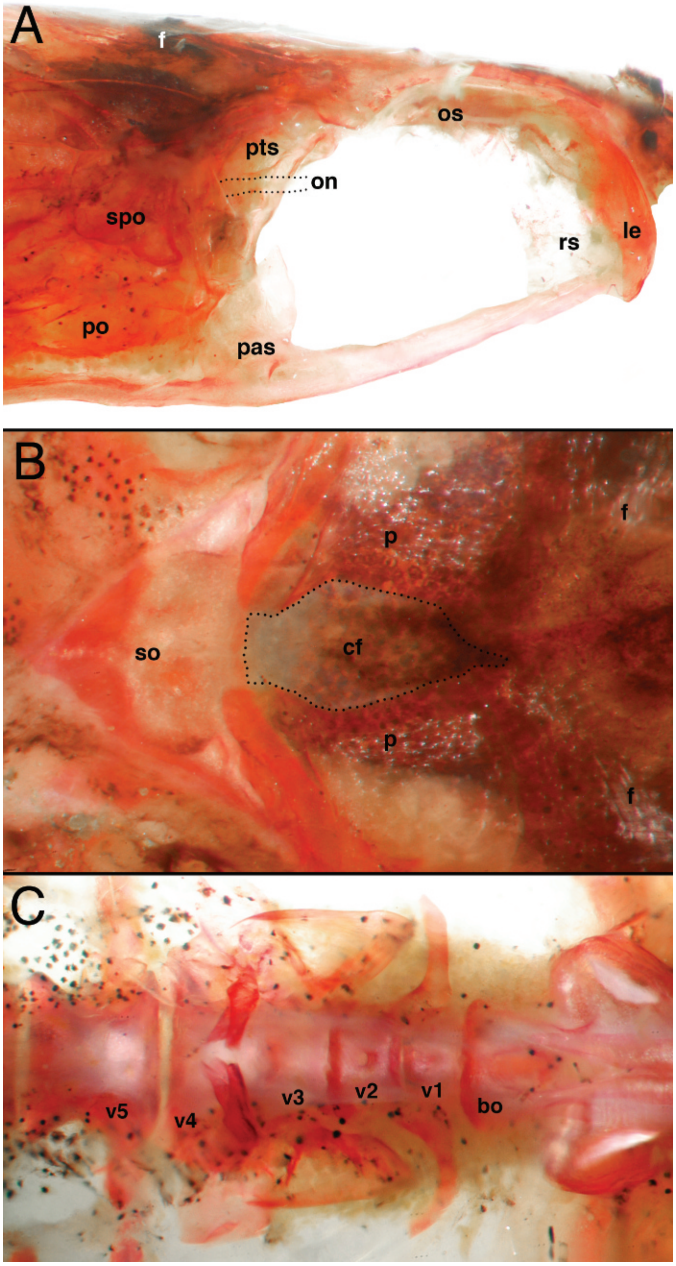

Fig. 4. Paratype of *Characidium amaila* (ROM 89894), in (A) lateral view of the right side of the neurocranium, (B) dorsal view of the posterior neurocranium, and (C) ventral view of the anterior vertebrae and posterior neurocranium. Abbreviations: bo, basioccipital; cf, cranial fontanelle; f, frontal; le, lateral ethmoid; on, superficial ophthalmic nerve (path after exiting pterosphenoid foramen indicated by dotted lines); os, orbitosphenoid; p, parietal; pas, parasphenoid; po, prootic; pts, pterosphenoid; rs, rhinosphenoid; so, supraoccipital; spo, sphenotic; v1–v5, vertebrae one through five.

Supraorbital bone present and anteroposteriorly ovoid, with medial and posterior margins contacting frontal, gap between supraorbital and lateral ethmoid. Parietal branch of supraorbital canal present. Pterosphenoid foramen for ophthalmic nerve centrally located on pterosphenoid, foramen small and canal-like (Fig. 4A). Cranial fontanel border formed anteriorly by frontals, laterally by parietals, and posteriorly by supraoccipital with incomplete closure of post-parietal bars (Fig. 4C). Second vertebral centrum lacking pair of ventral processes (Fig. 4C). Swimbladder with

Fig. 5. Swimbladder of paratype ROM 91490 (58.1 mm SL) in ventral view, with dotted lines showing the relative position of the body wall (white), opercula (green), and basioccipital (blue). Anterior to left, scale bar = 5 mm.

posterior chamber much longer than anterior chamber (Fig. 5).

Coloration in life.—Base color pale yellow or green with dorsum either uniformly dark gray to black or composed of three closely spaced dark stripes; broad dark mid-lateral stripe typically present (sometimes faded), anteriorly contiguous from snout through orbit (eye stripe) to back of head; series of irregular indistinct vertical bars extending from dorsum to ventrum, bars visible even if lateral stripe faded; ventrum pale. Fins yellowish, darker distally, with dark rays but otherwise lacking patterns (Fig. 2). Embedded spot near bases of middle caudal-fin rays typically inconspicuous in live individuals.

Coloration in alcohol.—Tan base color; dorsum dark overall, broken into three closely spaced stripes from head to posterior insertion of dorsal fin, two stripes between dorsal fin and adipose fin, and single stripe from adipose fin to caudal fin; light pigment between dorsal stripes limited to centers of scales forming dorsalmost one or two scale rows. Broad dark mid-lateral stripe originating on upper lip and continuing posteriorly across snout, eye, infraorbitals, and upper opercle, absent from posterior opercular margin, united with darker humeral spot and continuing caudally through pored lateral line scales (breadth approximately ½ height of single scale) to terminate at base of middle caudal-fin rays. All stripes overlain by 7–15 (allometrically increasing in number) irregular vertical bars. Embedded spot near bases of middle caudal-fin rays (characteristic of most species of *Characidium* including *C. fasciatum* clade) faded but usually present.

Dorsal fin dusky gray with transparent membranes and rays with tiny melanophores, rays darker than membranes, distal half of fin darker overall forming diffuse wide band. Adipose fin with white center and black edges. Caudal fin with concentrations of pigment near base of each lobe, sometimes with wide dusky marginal band. Anal-fin rays creamy white proximally, membranes darker gray, tips of first few rays often contrastingly white; second unbranched ray thickened with shaft often whitish, contrasting with surrounding dusky portion of fin. Pelvic fin lighter proximally and darker distally, thickened first rays with dark central portion outlined with white. Pectoral fin with first four rays dusky gray, thickened, and highlighted by white margins.

Ecology.—Habitat for *Characidium amaila* consists of shallow sandstone bedrock rapids with abundant attached

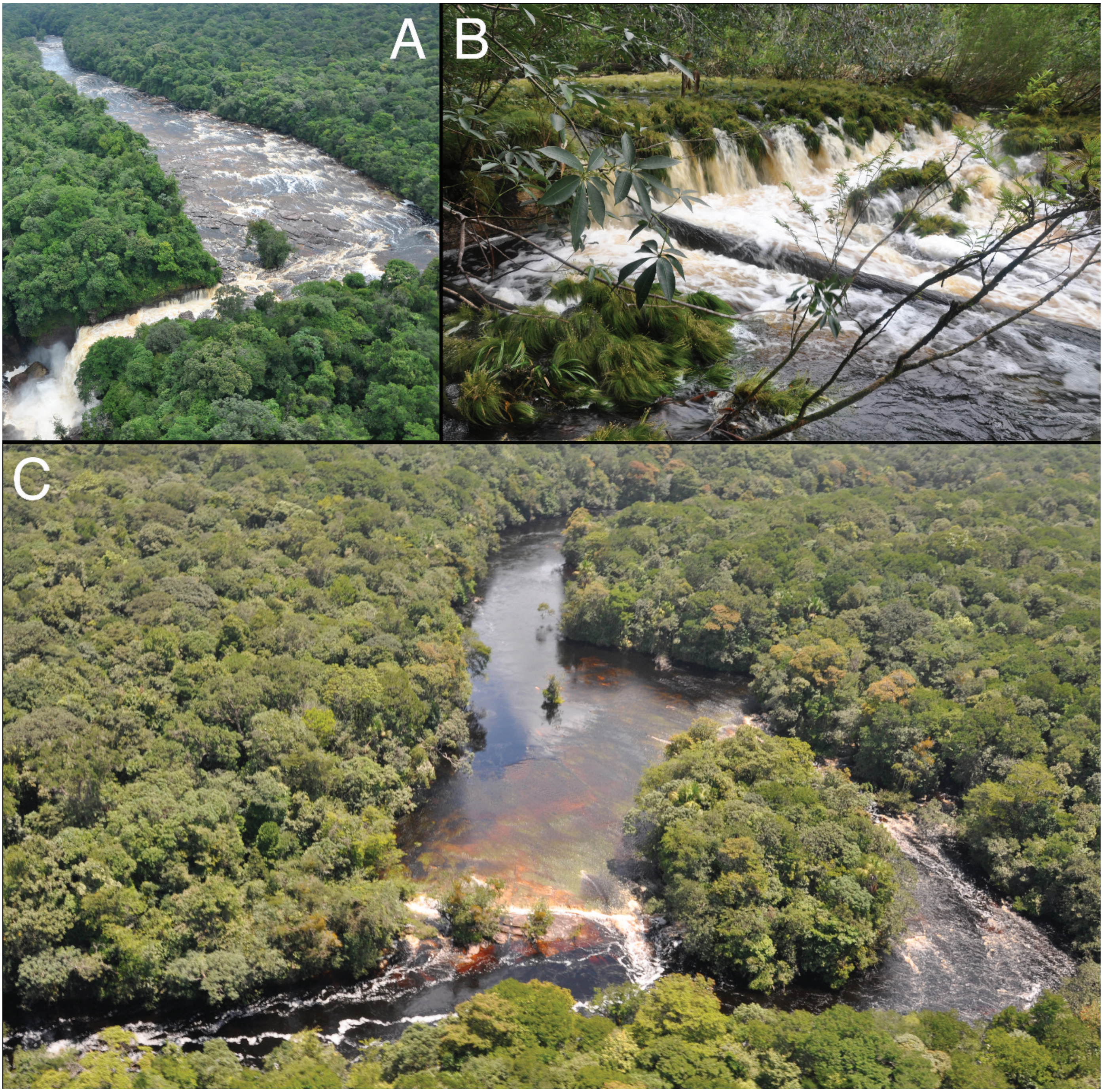

Fig. 6. Representative habitats of *Characidium amaila*: (A) Amaila Falls and the lowermost rapid (Rapid 1) in which *C. amaila* was collected; (B) Rapid 5, the uppermost habitat in which *C. amaila* was collected; (C) Rapid 3, just upstream of the uppermost limit of the planned reservoir.

macrophytes (Fig. 6), including a representative of the Podostemaceae, a representative of the Eriocaulaceae (*Rhondonanthus capillaceus*), and a third species with long grass-like leaves.

Distribution.—Specimens of *Characidium amaila* were collected from each of five separate rapids habitats encountered in the upper Kuribrong watershed; three of these habitats are clustered together in the lower portion of the upper Kuribrong River beginning immediately upstream of Amaila Falls (Fig. 7): Rapids 1 begins at the top of Amaila Falls (Fig. 6A) and extends upstream into the Kuribrong River for close to a kilometer; Rapids 2 is approximately 2 km upstream of the top of Rapids 1 and continues upstream for approximately 300 m; and Rapids 3 is approximately 2 km upstream of the top of Rapids 2 and continues upstream for approximately 200 m. In contrast, two other rapids habitats are highly disjunct within the upper Kuribrong watershed: Rapids 4 is located in the Kuribrong River main channel approximately 25 river km upstream of Rapids 3; and Rapids 5 is in an unnamed right (east) bank tributary of the Kuribrong River that is located approximately 5 river km upstream of the tributary's confluence with the Kuribrong (Fig. 7). The confluence itself is formed by a densely vegetated, shallow, slackwater swamp a short distance upstream of Rapids 3. Apparently robust

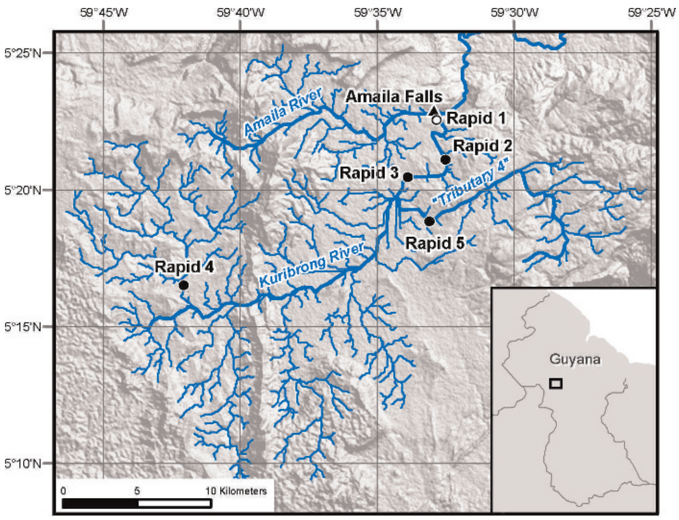

Fig. 7. Map showing localities of five rapids in the upper Kuribrong River watershed where *Characidium amaila* was collected. Open circle indicates the type locality.

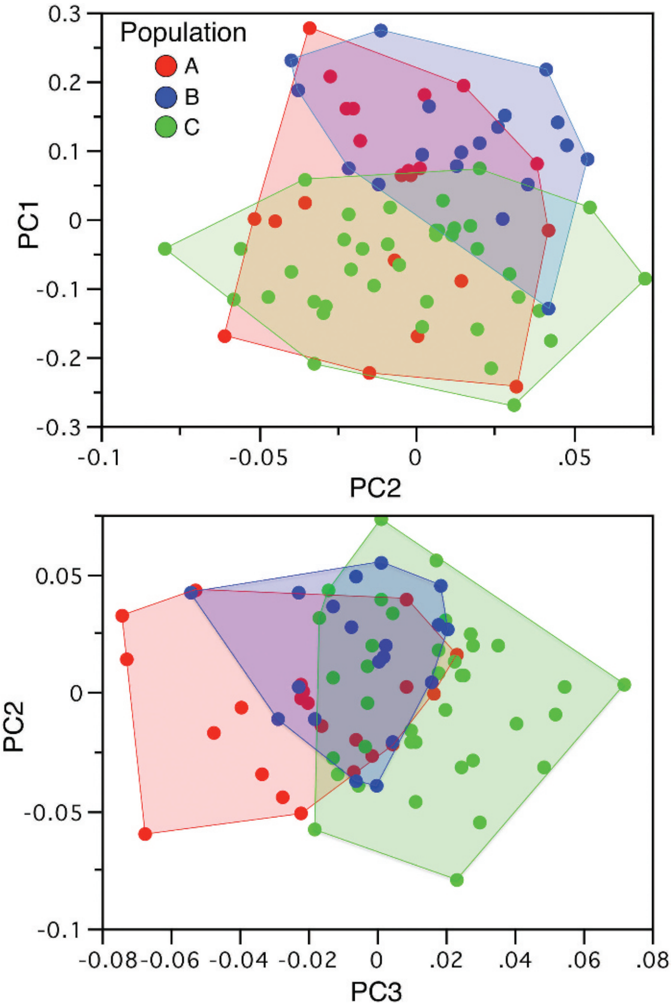

Fig. 8. Results of a principal components analysis of morphometric data from specimens of *Characidium amaila* collected from three disjunct rapids habitats within the upper Kuribrong River drainage.

populations of *C. amaila* were sampled at each of these rapids habitats but the species has not been encountered anywhere else in or out of the upper Kuribrong watershed.

Intraspecific variation.—We investigated the degree to which the surveyed populations might be morphologically distinguishable via a principal components analysis (PCA) of morphometric data. We conducted this analysis for two reasons: 1) the surveyed populations of *Characidium amaila* in the upper Kuribrong River are geographically isolated, and 2) a hydroelectic project that is under consideration may adversely affect the populations at Rapids 1 and to a lesser extent, the population at Rapids 2. Specimens from the closely spaced rapids 1–3 were grouped in the analysis as a single population (Population A, Fig. 8), whereas specimens from the more distantly located rapids 4 and 5 were treated independently as different populations (B and C respectively, Fig. 8). Results revealed partial differentiation of populations B and C on the first PC axis, and partial differentiation of populations A and C on the third PC axis. Despite the distribution across non-overlapping regions of morphospace of many specimens in each population, the high degree of overlap observed among all three populations supports our treatment of them as conspecific.

Etymology.—Named for Amaila Falls (Fig. 6A), a striking feature of the Guiana Shield escarpment in western Guyana that will have altered flow following completion of a dam that is now being planned. To be treated as a noun in apposition.

DISCUSSION

Based only on the easily observable absence of scales from its breast and its free branchiostegal rays (Fig. 1), *Characidium amaila* would group with either the well-defined and geographically widespread *C. fasciatum* group (*C. bolivianum*, *C. boavistae*, *C. fasciatum*, *C. gomesi*, and *C. purpuratum*) or with an assemblage of species restricted to southeastern Brazil, including *C. alipioi*, *C. japuhybense*, *C. grajahuensis*, *C. lauroi*, *C. timbuiense*, and *C. vidali*. Similarities between *C. amaila* and the *C. fasciatum* group largely end there, with *C. amaila* having the plesiomorphic condition for most other putatively derived internal characteristics of the *C. fasciatum* group. Although *C. amaila* has a foramen for the superficial ophthalmic nerve that is centrally located on the pterosphenoid, as in the *C. fasciatum* group, the *C. amaila* foramen differs by being small and canal-like. Also, *C. amaila* is missing ventral processes on the second vertebral centrum, and its posterior swim-bladder chamber is quite large (Figs. 4, 5; Buckup, 1993b). In each of these three characteristics, *C. amaila* appears to retain the plesiomorphic condition of *Characidium*.

Although a thorough test of the phylogenetic position of *C. amaila* must await a more extensive morphological and/or molecular data set, it is tempting to hypothesize based on the retention of several putatively plesiomorphic traits, that this species may represent a basal lineage within *Characidium*. Such a phylogenetic position and the narrowly endemic distribution of *C. amaila* above a waterfall on the Guiana Shield escarpment are both at least consistent with a pattern that is relatively common among fishes in drainages to the immediate north and south of the Kuribrong River (Lujan and Armbruster, 2011). Above Kaieteur Falls in the Potaro River to the south of the Kuribrong River, Eigenmann (1912) recorded *Lithogenes villosus*, the type species of a genus that has been recovered as sister to either all other Astroblepidae (Hardman, 2005; Armbruster, 2008) or all other Loricariidae (Schaefer, 2003). And isolated in the upper Mazaruni, above numerous cataracts and waterfalls, is a diverse assemblage of almost entirely endemic taxa in the families Cichlidae (*Mazarunia* spp.; López-Fernández et al., 2012), Crenuchidae (*Skiotocharax meizon*, Presswell et al., 2000), Lebiasinidae (*Lebiasina ardilai*; Netto-Ferreira et al., 2013; *Derhamia hoffmannorum*; Géry and Zarske, 2002), Loricariidae (*Neblinichthys* spp.; Taphorn et al., 2010; *Paulasquama callis*; Armbruster and Taphorn, 2011), and Parodontidae (*Apareidon agmatos*; Taphorn et al., 2008).

Regardless of the phylogenetic position of these taxa, available data make it clear that Guiana Shield rivers, particularly the upper parts of those rivers draining escarpments around the western lobe of the Guiana Shield, host a broad diversity of narrowly endemic fish species. In the Kuribrong River, these endemic taxa may be adversely affected by either the proposed hydroelectric project or the rapid expansion of artisanal and industrial-scale mining for placer deposits of gold and diamonds, which are both now abundant in the lower Kuribrong River. Indeed, one positive outcome of the proposed hydroelectric project at Amaila Falls is the commitment to add the entire upper Kuribrong River watershed to Kaieteur National Park, ostensibly protecting those habitats not directly impacted by the reservoir installation and operation, including at least three robust disjunct populations of *C. amaila*.

MATERIAL EXAMINED

Ammocryptocharax elegans: all Venezuela, Orinoco River drainage: ROM 88274, 1, Cuao River at Ceguera Rapids, 75 km S of Puerto Ayacucho, 4°59′52″N, 67°36′3″W; ROM 88368, 2, Caño Parhueña upstream of Route 12 bridge, ca. 35 km northeast of Puerto Ayacucho, 5°33′30″N, 67°24′13″W.

Ammocryptocharax vintonae: all Guyana, Region 8, Mazaruni River drainage: ROM 83665, 7, 61.8–90.1 mm SL, Kukui River at sandy/driftwood shore, 5°30′51″N, 60°24′46″W; ROM 83708, 8, 43.5–83.3 mm SL, Kukui River upstream around the camp on Philipai, 5°21′37″N, 60°22′18″W.

Characidium boavistae: Guyana: AUM 37964, 1, Region 9, upper Takutu-Branco drainage, Moco-Moco Creek at Moco-Moco hydropower station, 18.8 km SE of Lethem, 3°17′48″N, 59°38′40″W; AUM 37985, 1, Region 9, Branco-Negro drainage, Kumu Creek 15.2 km SE Lethem, 3°15′34″N, 59°43′25″W; AUM 48541, 1, Region 9, upper Takutu-Branco-Negro-Amazonas drainage, Ireng River, S of Sunnyside, 3°42′54″N, 59°39′43″W. Venezuela: AUM 22212, 1, Táchira State, Uribante-Apure-Orinoco drainage, Chururú River in Chururú, 7°34′32″N, 72°0′6″W; MCNG 11817, 3, Portuguesa State, Apure River drainage, Moroturo River approx. 15 km above La Aparición, 9°31′00″N, 69°26′00″W; MCNG 36449, 29, Portuguesa State, Apure River drainage, Guache River in Balona at bridge, 9°26′35″N, –69°19′50″W.

Characidium cf. *boavistae*: all Suriname, Sipalawini District, Gran Kreek Region, Marowijne (Maroni) River drainage: AUM 50707, 1, creek (middle of three) flowing W from almost SW corner of Nassau Mountain, 2.75 km W Suralco Base Camp, Nassau Mountain, 4°49′13″N, 54°38′20″W; AUM 50708, 1, creek (middle of three) flowing W from almost SW corner of Nassau Mountain, 2.75 km W Suralco Base Camp, Nassau Mountain, 4°49′13″N, 54°38′20″W; AUM 50709, 1, creek (middle of three) flowing W from almost SW corner of Nassau Mountain, 2.75 km W Suralco Base Camp, Nassau Mountain, 4°49′13″N, 54°38′20″W; AUM 50710, 1, creek (middle of three) flowing W from almost SW corner of Nassau Mountain, 2.75 km W Suralco Base Camp, Nassau Mountain, 4°49′13″N, 54°38′20″W; AUM 50711, 1, creek (middle of three) flowing W from almost SW corner of Nassau Mountain, 2.75 km W Suralco Base Camp, Nassau Mountain, 4°49′13″N, 54°38′20″W; AUM 50712, 1, creek (middle of three) flowing W from almost SW corner of Nassau Mountain, 2.75 km W Suralco Base Camp, Nassau Mountain, 4°49′13″N, 54°38′20″W; AUM 50712, 6, creek (south of three) flowing W from almost SW corner of Nassau Mountain, 2.75 km W Suralco Base Camp, Nassau Mountain, 4°49′6″N, 54°38′23″W; AUM 50713, 1, creek (middle of three) flowing W from almost SW corner of Nassau Mountain, 2.75 km W Suralco Base Camp, Nassau Mountain, 4°49′13″N, 54°38′20″W; AUM 50714, 1, creek (middle of three) flowing W from almost SW corner of Nassau Mountain, 2.75 km W Suralco Base Camp, Nassau Mountain, 4°49′13″N, 54°38′20″W.

Characidium bolivianum: all Bolivia, Madeira River drainage: ROM 90335, 1, San Luis River at Comunidad Condor, 17°25′45″S, 64°7′58″W; ROM 90366, 7, Bermejo River at bridge on Samaipata-Santa Cruz road, 18°8′51″S, 63°41′52″W; ROM 90369, 2, San Pedrito River at bridge on Cochabamba-Villa Tunari road, 17°0′58″S, 65°39′7″W.

Characidium declivirostre: AUM 54207, 26, Venezuela, Amazonas State, Orinoco River drainage, Rio Cataniapo at community of Sardi, 5°32′01″N, 67°22′26″W; ROM 61496, 3, Guyana, Essequibo River drainage, Potaro River, Amatuk Falls, 5°17′59″N, 59°17′59″W; ROM 91332, 6, Guyana, Essequibo River drainage, Sheetrock Creek at crossing of Wailang-Powis tractor trail, 2°4′46″N, 56°2′58″W; ROM 91410, 1, Guyana, Essequibo River drainage, Mikobe Creek at rapids approx. 0.5 km from mouth, 2°2′48″N, 56°6′35″W.

Characidium gomesi: MZUSP 110229, 1, Brazil, São Paulo State, Rio Pardo at Cachoeira Véu de Noiva, 22°59′24″S, 48°25′40″W.

Characidium hasemani: all Guyana, Essequibo River drainage: ROM 61492, 1, Potaro River, Amatuk Falls, 5°17′59″N, 59°17′59″W; ROM 85882, 2, Rupununi River at Dadanawa, 2°49′54″N, 59°31′41″W.

Characidium purpuratum: all Peru: AUM 46741, 1, Amazonas Region, Condorcanqui Province, Marañon River, log riffle, 1.57 km ENE of Juan Velasco, Sta. Maria de Nieva, 4°35′22″S, 77°51′10″W; AUM 46775, 3, Amazonas Region, Condorcanqui Province, Marañon River at Imacita, 5°3′28″S, 78°20′6″W; AUM 46793, 4, Amazonas Region, Marañon River drainage, Utcubamba River, 23 km SE of Bagua Chica, 5°46′32″S, 78°22′28″W; AUM 51183, 1, Cusco, Quispicanchis, Araza-Inambari-Madre de Dios drainage, Nusiniscato River above confluence with Huactumberi River, 9.1 km N of Quincemil, 13°11′9″S, 70°37′7″W; AUM 51197, 1, Cusco, Quispicanchis, Araza-Inambari-Madre de Dios drainage, Araza River between Quincemil and Limonchayoc, 10.9 km WNW de Quincemil, 13°13′5″S, 70°43′16″W; AUM 51210, 1, Cusco, Quispicanchis, Inambari-Madre de Dios drainage, Araza River above mouth of the Nusiniscato River, 11.6 km ENE of Quincemil, 13°12′32″S, 70°32′40″W; AUM 51233, 1, Cusco, Quispicanchis, Araza-Inambari-Madre de Dios drainage, creek tributary to right bank of Araza River, 18.2 km NE of Quincemil, 13°10′31″S, 70°29′40″W.

Characidium zebra: Guyana: ROM 85947, 1, Rupununi River at Dadanawa; ROM 86171, 2, Sawariwau River, Takutu-Amazon drainage; ROM 86180, 1, Rupununi River near Yupukari, 3°34′34″N, 59°20′36″W. Venezuela: ROM 88367, 1, Ventuari River at rapids below Salto Tencua, 227 km ESE of Puerto Ayacucho, 5°3′2″N, 65°37′28″W.

ACKNOWLEDGMENTS

We gratefully acknowledge M. Melo for constructive comments on the manuscript, A. Khan, D. Abraham, G. Savory, K. Andrew, D. Stoby, D. Gordon, M. Benjamen, F. Lima, T. Pessali, T. Teixera, and B. Noonan for assistance collecting specimens, P. Maharaj and C. Bernard (University of Guyana) for assisting with specimen exportation, E. Holm and D. Stacey (Royal Ontario Museum) for curating and transporting specimens, the Guyana Environmental Protection Agency for collection and export permits, and Amaila Falls Hydro, Inc., for funding this research.

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