Copeia 2010, No. 4, 676–704

Revision of *Panaque* (*Panaque*), with Descriptions of Three New Species from the Amazon Basin (Siluriformes, Loricariidae)

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The *Panaque nigrolineatus* group (subgenus *Panaque*) is revised; three nominal species—*P. cochliodon*, *P. nigrolineatus*, and *P. suttonorum*—are redescribed and three new species are described. *Panaque armbrusteri*, new species, is widespread in the Tapajós River and its tributaries in Brazil and is distinguished by having a supraoccipital hump, higher numbers of jaw teeth and an ontogenetic increase in interpremaxillary and intermandibular tooth-row angles, relatively short paired-fin spines, and dorsal margin of infraorbital six flared laterally. *Panaque schaeferi*, new species, is widespread in main-channel habitats of the upper Amazon (Solimões) River basin in Brazil and Peru; it is distinguished by having a coloration consisting of dark or faded black spots evenly distributed on a pale gray to brown base, and by its large adult body size (>570 mm SL). *Panaque titan*, new species, is distributed in larger, lowland to piedmont rivers of the Napo River basin in Ecuador, and is distinguished by having a postorbital pterotic region bulged beyond the ventral pterotic margin, coloration consisting of irregular and widely spaced dark gray to brown stripes on light brown to tan base, and large adult body size (>390 mm SL). A relatively large pterotic, indicative of an enlarged gas bladder and gas bladder capsule, and allometric increases in tooth number are hypothesized to be synapomorphies uniting members of the subgenus *Panaque*.

Se revisó el grupo *Panaque nigrolineatus* (subgénero *Panaque*); se redescriben tres especies nominales—*P. cochliodon*, *P. nigrolineatus*, and *P. suttonorum*—y tres nuevas especies son descritas. *Panaque armbrusteri* n. sp. tiene amplia distribución en el río Tapajós y sus tributarios en Brasil y se distingue por tener una joroba supraoccipital, un gran número de dientes mandibulares y un incremento ontogénico en el ángulo de la hilera de dientes interpremaxilares e intermandibulares, espinas de las aletas pares relativamente cortas, y el margen dorsal del sexto infraoccipital hinchado lateralmente. *Panaque schaeferi* n. sp. se distribuye ampliamente en hábitats del canal principal de la cuenca del río alto Amazonas (Solimões) en Brasil y Perú; se distingue por tener una coloración que consiste en puntos negros oscuros o descoloridos uniformemente distribuidos sobre un color gris pálido a marrón base, y por el gran tamaño corporal de los adultos (>570 mm SL). *Panaque titan* n. sp. presenta distribución más amplia, desde la llanura hasta los ríos de pie de monte de la cuenca del río Napo en Ecuador, y se distingue por tener una región pterótica postorbital hinchada detrás del margen ventral pterótico, coloración que consiste en rayas irregulares y ampliamente espaciadas de color negro a marrón sobre marrón claro a un color bronceado base, y tamaño grande del cuerpo en adultos (>390 mm SL). La presencia de un pterótico relativamente grande que es indicador de una agrandada vejiga gaseosa y su cápsula extendida, y el aumento allometrico del número de dientes suponen ser sinapomorfías que unen a los miembros del subgénero *Panaque*.

EIGENMANN and Eigenmann (1889) erected *Panaque* and designated *Chaetostomus nigrolineatus* Peters 1877 as the type species, with *Chaetostomus cochliodon* Steindachner 1879 and *Chaetostomus dentex* Günther 1868 as congeners. Characters given by Eigenmann and Eigenmann as diagnostic for *Panaque* include enlarged teeth with spoon-shaped cusps, teeth few in number, and erectile spines on the 'interopercle.' Loricariid erectile cheek spines present in *Panaque* are actually hypertrophied odontodes supported by specialized cheek plates (Schaefer, 1988) and everted via a specialized opercular mechanism (Geerinckx and Adriaens, 2006). *Panaque* shares this mechanism with other members of the tribe Ancistrini (Hypostominae), for which evertible cheek odontodes are an important synapomorphy (Armbruster, 2004). Since 1889, nine new species of *Panaque* have been described and considered valid (*P. albomaculatus*, *P. bathyphilus*, *P. changae*, *P. gnomus*, *P. maccus*, *P. nocturnus*, *P. purusiensis*, and *P. suttonorum*). A tenth species (*P. oculeus* Fowler 1943) has been described and subsequently removed to *Hypostomus* (subgenus *Cochliodon*; Isbrücker, 1980; Armbruster, 2003a).

Schaefer and Stewart (1993) diagnosed *Panaque* from all other Loricariidae via the following unique combination of characters: spoon-shaped, unicuspid teeth; straight, elongate cheek odontodes; an elongate metapterygoid channel; hyomandibular and preopercle with greatly expanded crest for origin of the adductor mandibulae and its derivatives; hypertrophy of the anterior and posterior transverse intrinsic premaxillary ligaments; and anteromedial premaxilla margin forming a notch; and from all other ancistrins via the derived absence of odontodes on the preopercle; a tall, nearly horizontal levator arcus palatini crest; and the levator muscle inserting into a distinct concavity on the lateral surface of the hyomandibular just anterior to the levator crest. Other characters given by Schaefer and Stewart (1993) as helpful in the identification of *Panaque* include quadrate condyle broad, maxilla sigmoid, opercle bar-shaped (illustrated and described as sickle-shaped by Armbruster [2004]), opercle not exposed laterally, posterolateral margin not expanded, with single hyomandibular point of articulation, and preopercle expanded dorsally.

Armbruster's (2004) phylogenetic study provided further support for the use of spoon-shaped teeth and a broad

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Submitted: 11 October 2009. Accepted: 21 July 2010. Associate Editor: R. E. Reis.
 DOI: 10.1643/CI-09-185

quadrate condyle as diagnostic synapomorphies for genus *Panaque*, and contributed two additional synapomorphies homoplasic within Loricariidae: hyomandibular with anterior margin sutured to posterior metapterygoid along entire length, lacking notch between the two, and lateral ethmoid with tall ridge.

Schaefer and Stewart (1993) hypothesized the existence of two clades within *Panaque*: a smaller bodied *P. dentex* clade (now comprised of *P. albomaculatus*, *P. bathyphilus*, *P. changae*, *P. dentex*, *P. maccus*, *P. nocturnus*, and *P. purusiensis*) and a larger bodied *P. nigrolineatus* clade (*P. cochliodon*, *P. nigrolineatus*, and *P. suttonorum*). Schaefer and Stewart (1993) diagnosed the *P. dentex* clade as having the following synapomorphies: dorsal margin of the fifth ceratobranchial with posterior elongate indentation (vs. lacking elongate indentation in all members of the *P. nigrolineatus* clade and other ancistrins), symplectic foramen of the preopercle greatly enlarged (vs. symplectic foramen relatively small in the *P. nigrolineatus* clade and other ancistrins), anterior preopercle–quadrate suture positioned well posterior relative to distance between the symplectic foramen and quadrate–anguloarticular condyle (vs. suture positioned well anterior toward the articular condyle in the *P. nigrolineatus* clade and other ancistrins), and preopercle with deep lateral groove located near the reflected lateral margin of the bone (vs. groove absent in the *P. nigrolineatus* clade and other ancistrins). Chockley and Armbruster (2002) reported an additional osteological synapomorphy for members of the *P. dentex* clade: elongate lateral projections born distally from ventral processes of the Weberian complex centrum (ventral processes mistakenly referred to as tripus, J. Armbruster, pers. comm.).

Armbruster's (2004) morphology-based phylogenetic analysis of nearly all ancistrin genera recovered a monophyletic *P. dentex* clade sister to a clade consisting of *P. nigrolineatus* and the loricariid genus *Scobinancistrus* (including two species: *S. aureatus* and *S. pariolispos*). Armbruster (2004) also reported an apparently autapomorphic enlargement of the gas bladder and gas bladder capsule in *P. nigrolineatus* (only pterotic wall of capsule visible externally). In a phylogenetic analysis of the cytochrome *b* gene, Hardman (2005) recovered *Panaque* as paraphyletic, but recovered a clade within *Panaque* consisting of *Panaque* sp. (*P. schaeferi*, new species, described herein) and *P. nigrolineatus*, both large-bodied species with large gas bladder capsules. Data presented herein (see Discussion) further suggest that an enlarged gas bladder and bladder capsule as well as ontogenetic increases in premaxillary and dentary tooth number may serve as morphological synapomorphies uniting members of a large-bodied *Panaque nigrolineatus* clade.

Isbrücker et al. (2001) assigned members of the smaller-bodied *P. dentex* clade to the new genus *Panaqolus*; however, Chockley and Armbruster (2002) placed *Panaqolus* in synonymy with *Panaque*, stating that erection of a new genus was unwarranted. Given the support now available for at least three clades within *Panaque*, we follow the taxonomy of Armbruster (2004), who recommended recognition of three subgenera: *Panaque* (*P. nigrolineatus* clade), *Panaqolus* (*P. dentex* clade), and *Scobinancistrus*. In this study, we report meristic and morphometric data collected from most specimens referable to subgenus *Panaque* in most major North and South American collections, including type specimens of *P. cochliodon*, *P. nigrolineatus*, and *P. suttonorum*. We redescribe these species based on available material, and describe three new species based on specimens from the Amazon Basin of Brazil, Ecuador, and Peru.

MATERIALS AND METHODS

Counts and measurements follow Armbruster (2003b), with the addition of seven landmarks: Landmarks 5′ and 6′ are defined as the dorsalmost border of respective right and left orbits, landmarks 8′ and 9′ as the ventromedialmost border of respective right and left cleithral sockets in which pectoral-fin spines insert, landmark 13′ as insertion of the right pelvic-fin spine, landmark 16′ as posterior base of the posteriormost dorsal-fin pterygiophore (landmark 16 of Armbruster [2003b] is located at the posterior margin of the fleshy dorsal-fin membrane extending posteriorly from the pterygiophore; J. Armbruster, pers. comm. to NKL), and landmark 18′ as the posteriormost insertion of the fleshy adipose-fin membrane. Tables 1 and 3 report morphometric data from specimens larger than 50 mm SL. Infraorbital plate numbers follow Schaefer (1987), and circumorbital plate and trunk plate row names follow Schaefer (1997). Interdorsal plates are those plates in the dorsal series that contact each other medially between the dorsal and adipose fins. Dorsal-fin spinelet is treated as a spine. Institutional abbreviations are as listed at http://www.asih.org/codons.pdf, with the addition of MUSM for Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru.

Panaque armbrusteri, new species

Figures 1–5; Tables 1, 2

Holotype.—MZUSP 95465, 344.7 mm SL, Brazil, Mato Grosso State, Tapajós River drainage, Teles Pires River, near the highway MT-416 ferry, 9°27′07″S, 56°30′46″W, 27 September 2007, L. M. Sousa and A. L. Netto-Ferreira.

Paratypes.—ANSP 182811, 2, 114.4, 280.9 mm SL, Brazil, Pará State, Tapajós River drainage, Jamanxim River near the town of Mil, 7°43′51″S, 55°16′36″W, 23 October 2007, J. L. Birindelli, L. M. Sousa, A. L. Netto-Ferreira, M. H. Sabaj Pérez, and N. K. Lujan. ANSP 182812, 1, 223.7 mm SL, Brazil, Mato Grosso State, Tapajós River drainage, right bank tributary of the Peixoto de Azevedo River, 10°17′14″S, 54°50′57″W, 17 October 2007, J. L. Birindelli, L. M. Sousa, A. L. Netto-Ferreira, M. H. Sabaj Pérez, and N. K. Lujan. AUM 50543, 1, 199.7 mm SL, Brazil, Mato Grosso State, Tapajós River drainage, right bank tributary of the Peixoto de Azevedo River, 10°17′14″S, 54°50′57″W, 17 October 2007, J. L. Birindelli, L. M. Sousa, A. L. Netto-Ferreira, M. H. Sabaj Pérez, and N. K. Lujan. MZUSP 92625, 1, 94.8 mm SL, Brazil, Pará State, Tapajós River drainage, Tapajós River near Itaituba and Pimental, 8 November 2006, purchased from fishermen. MZUSP 95889, 1, 303.8 mm SL, Brazil, Mato Grosso State, Tapajós River drainage, Teles Pires River, 11°03′44″S, 55°19′08″W, 26 September 2007, J. L. Birindelli and P. Hollanda Carvalho. MZUSP 96326, 1, 180.0 mm SL, Brazil, Mato Grosso State, Tapajós River drainage, right bank tributary of the Peixoto de Azevedo River, 10°17′14″S, 54°50′57″W, 17 October 2007, J. L. Birindelli, L. M. Sousa, A. L. Netto-Ferreira, M. H. Sabaj Pérez, and N. K. Lujan. MZUSP 96388, 6, 69.3–231.7 mm SL, Brazil, Pará State,

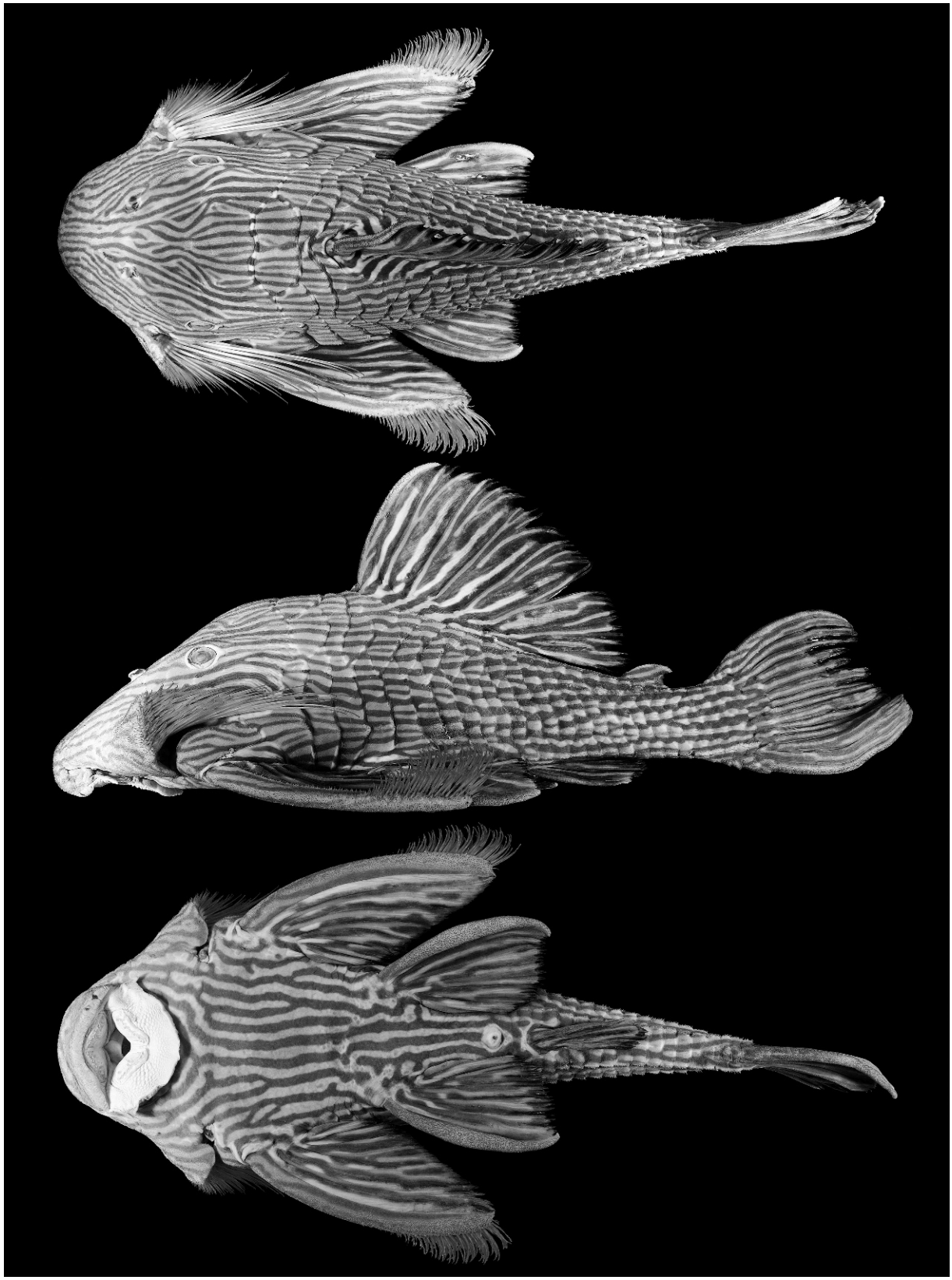

Fig. 1. Holotype of *Panaque armbrusteri*, new species, MZUSP 95465, 344.7 mm SL, Brazil, Mato Grosso State, Tapajós River drainage, Teles Pires River, near the highway MT-416 ferry, 9°27′07″S, 56°30′46″W, 27 September 2007 (photos by L. M. Sousa).

Tapajós River drainage, Jamanxim River near town of Mil, 7°43′51″S, 55°16′36″W, 23 October 2007, J. L. Birindelli, L. M. Sousa, A. L. Netto-Ferreira, M. H. Sabaj Pérez, and N. K. Lujan.

Diagnosis.—*Panaque armbrusteri* is diagnosed from all members of subgenus *Scobinancistrus* by having greater than seven dentary and premaxillary teeth (vs. three or four dentary and premaxillary teeth), by dentary and premaxil-

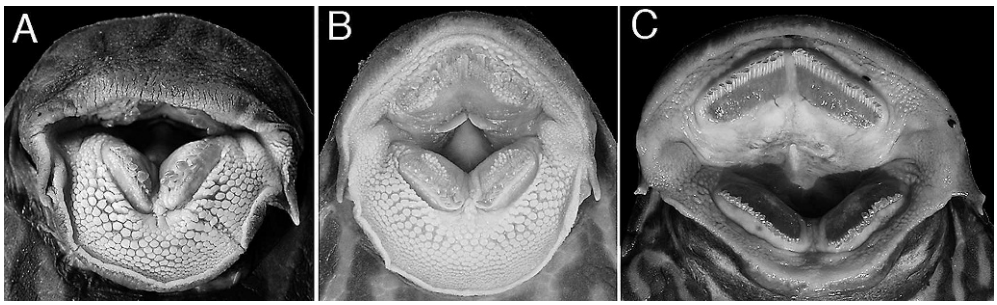

Fig. 2. Oral disks of *Panaque armbrusteri*, new species, paratypes (A) ANSP 182811, 114 mm SL, (B) MZUSP 96388, 172 mm SL, and non-type (C) MNRJ 34091, 323 mm SL, showing ontogenetic increase in interpremaxillary and intermandibular tooth row angles.

lary tooth cusps being unicuspid (vs. bicuspid), and by dentary and premaxillary tooth cusps being short and ladle- or spoon-shaped (vs. main tooth cusps being long and spatulate); and from all members of subgenus *Panaqolus* by having a body color pattern consisting of alternating dark brown to black and light brown to gray longitudinal stripes (vs. body color pattern consisting of spots or vertical and/or oblique bands), by individuals <114 mm SL having a hyaline caudal-fin window (vs. caudal fin uniformly opaque, banded, or spotted), and by reaching a maximum adult size of at least 345 mm SL (vs. <150 mm SL).

Panaque armbrusteri is diagnosed from all other *P.* (*Panaque*) by having adults with interpremaxillary and intermandibular tooth row angles >100° (Fig. 2; vs. adults with acute interpremaxillary and intermandibular tooth row angles) and by having more premaxillary and dentary teeth at equivalent body sizes (Fig. 3); from all but *P. suttonorum* by having pelvic-fin spine terminating between anterior and posterior insertion of anal fin when adpressed (vs. terminating at or beyond posterior insertion of anal fin when adpressed); from all but *P. titan* by having dorsal half of infraorbital six strongly flared laterally (Figs. 5, 6; vs. infraorbital six vertical and straight or only slightly flared laterally at dorsalmost margin); from all but *P. cochliodon* by having supraoccipital raised as a hump (Fig. 5; vs. supraoccipital smoothly rounded); from *P. nigrolineatus*, *P. schaeferi*, and *P. titan* by having pectoral-fin spine terminating between pelvic-fin insertion and anus when adpressed ventral to pelvic fin (vs. pectoral-fin spine terminating at or coequal with anus); from *P. cochliodon*, *P. nigrolineatus*, and *P. suttonorum* by adults having truncate caudal fin (vs. caudal fin lunate or forked); from *P. cochliodon*, *P. suttonorum*, and *P. schaeferi* by having body color consisting of alternating dark brown to black and light brown to gray longitudinal stripes (vs. body color uniformly dark gray to black or with dark or faded black spots on pale gray to brown base color); from *P. cochliodon* and *P. suttonorum* by having red to brown eye color (vs. blue or bluish eye), and by juveniles up to approximately 114 mm SL having a hyaline anterior caudal-fin window (vs. juveniles with caudal fins uniformly opaque); from *P. nigrolineatus* by having dark longitudinal body stripes frequently wider than light stripes (vs. light longitudinal body stripes frequently wider); from *P. schaeferi* by having maximum body size of approximately 350 mm SL (vs. approximately 600 mm SL); and from *P. titan* by postorbital pterotic region being flush with ventral pterotic margin (Fig. 5; vs. postorbital pterotic region bulged beyond ventral pterotic margin, Fig. 6).

Panaque armbrusteri is further diagnosed from *P. cochliodon* and *P. schaeferi* by having greater predorsal length (48.7–54.9% SL vs. 42.5–48.3), by having greater head length (39.9–46.7% SL vs. 35.3–40.9), and by having shorter postanal length (26.2–31.3% SL vs. 31.9–36.0); from *P. cochliodon* by having greater head–pectoral length (29.5–32.6% SL vs. 26.5–29.2), by having lesser adipose–upper caudal depth (10.4–13.8% SL vs. 14.6–19.3), by having lesser caudal peduncle–dorsal caudal ray distance (17.7–32.8% SL vs. 36.9–46.7), by having lesser adipose–lower caudal depth (17.5–21.0% SL vs. 21.3–24.0), and by having greater snout length (69.1–74.5% HL vs. 64.3–68.0); from *P. titan* by having greater barbel length (3.4–5.8% HL vs. 1.4–2.3), and by having greater dentary tooth cup length (11.5–16.1% HL vs. 9.7–10.5); and from *P. schaeferi* by having greater mouth width (34.8–47.3% HL vs. 26.0–39.2).

Description.—Morphometrics in Table 1. Largest specimen 345 mm SL. Body deep and stout. Dorsal profile of snout rising at approximately 35°, straight to anterior margin of supraoccipital; upward slope increasing slightly at anterior edge of supraoccipital and approaching horizontal at posterior edge of supraoccipital, forming modest supraoccipital hump (Fig. 5); dorsal profile sloped slightly upward, slightly downward, or horizontal from supraoccipital to nuchal plate. Body depth greatest at nuchal plate, at posterior margin of supraoccipital, or coequal at both. Dorsal profile posterior of nuchal plate sloped gently downward and straight to posterior insertion of adipose-fin membrane, then horizontal or sloping upward slightly to first dorsal procurrent caudal-fin ray, upward slope increasing sharply at first dorsal procurrent caudal-fin ray. Ventral profile straight and horizontal from snout to anal-fin insertion, sloped slightly upward along anal-fin insertion, slightly concave or straight from anal-fin insertion to first ventral procurrent caudal-fin ray; downward slope increasing slightly at first ventral procurrent caudal-fin ray.

Entire snout, dorsal and lateral surfaces of trunk armored with plates bearing small odontodes; dorsal, middorsal, and lateral median plates posterior of dorsal-fin spine and all midventral and ventral plates with enlarged odontodes arranged either as row down plate midline (Fig. 7) or as posteromedial cluster. Cheek plates bearing moderately to highly hypertrophied, distally hooked odontodes (mean 53, range 17–90, holotype = 90) evertible to approximately 90° from sagittal plane; longest odontodes extending to posterior margin of fourth midventral plate. Eye large (orbit diameter 12.2–20.2% HL); orbit positioned at or dorsal to

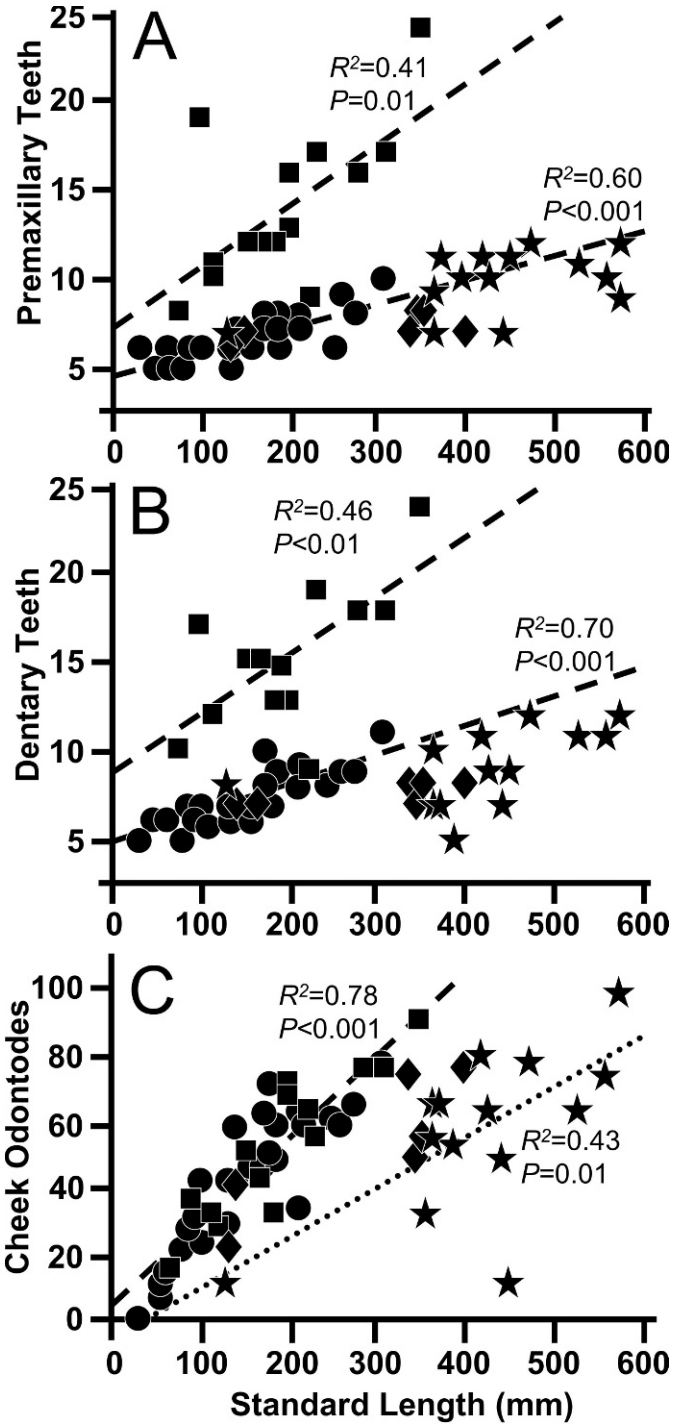

Fig. 3. (A) Premaxillary and (B) dentary tooth number and (C) cheek odontode number versus standard length of *Panaque nigrolineatus* (circles), *P. armbrusteri*, new species (squares), *P. titan*, new species (diamonds), and *P. schaeferi*, new species (stars). Significant relationships between premaxillary and dentary tooth number and standard length of *P. armbrusteri* and *P. nigrolineatus* described by respective upper and lower dashed lines in (A) and (B). Significant relationships between cheek odontode number and standard length of *P. nigrolineatus* and *P. schaeferi* described by respective dashed and dotted lines in (C).

lateral midline at anterior margin of posterior third of head; orbit accentuated by projecting laterally slightly from head and by preorbital crest extending posteriorly from midline below naris (Figs. 5, 6); dorsal margin of infraorbital plate six flared laterally (Figs. 5, 6); roof of orbit horizontally flat, laterally projected as supraorbital shelf formed by sphenotic with expanded and horizontal ventral half; supraorbital shelf accentuated by steep upward slope from dorsal half of sphenotic to supraoccipital; supraorbital shelf continued posteriorly into pterotic; postorbital pterotic region not bulged beyond ventral pterotic margin. Orbit sloped ventrolaterally at approximately 20° from sagittal plane in anterior view. Postorbital notch (Fig. 5) present or absent. Iris operculum present.

Oral disk occupying approximately two-thirds to three-fourths of snout anterior of cleithrum. Interpremaxillary and intermandiblar tooth row angle ontogenetically variable, from just under 90° in small- to medium-sized specimens (<250 mm SL) up to approximately 120° in large specimens (>250 mm SL). Premaxillary teeth eight to 24 (mode 12, holotype = 24); dentary teeth nine to 24 (mode 15, holotype = 24). Rows of short, branched, fimbriate papillae immediately internal to each tooth row; single flattened and semicircular flange-like papilla at posteromedial corner of each premaxilla in more narrowly jawed specimens, or single low undulating fold-like papilla contiguous across top of both premaxillae in more broadly jawed specimens; buccal papilla absent. All teeth unicuspid and spoon-shaped; proximalmost one to two teeth smaller than other teeth. Maxillary barbel short and attached to lower lip along most of length; ventral surface of labial disk with hemispherical or semicircular papillae decreasing in size distally and toward rictus; posterior margin of labial disk lacking fimbriae.

Dorsal fin II,7; dorsal-fin spinelet prominent and V-shaped; dorsal-fin lock functional; posteriormost dorsal-fin ray free from body. Pectoral fin I,6; pectoral-fin spine extending to approximately halfway between posterior insertion of pelvic fin and anus when adpressed ventral to pelvic fin; posterodorsal and anterior surfaces of spine with slightly enlarged odontodes, anterior odontodes increasing in size and areal extent distally; distal pectoral-fin spine odontodes moderately to highly hypertrophied. Pelvic fin I,5; pelvic-fin spine extending to middle or posterior insertion of anal fin when adpressed. Anal fin I,4; first pterygiophore exposed as plate; first unbranched ray ossified. Adipose-fin spine sloped at approximately 40° and slightly curved along entire length or more strongly curved proximally; bearing slightly enlarged odontodes along dorsal surface; adnate to caudal peduncle via fleshy membrane with straight or concave posterior margin. Caudal fin I,14,I; dorsal procurrent caudal-fin rays four or five (mode five); ventral procurrent caudal-fin rays three to five (mode five); caudal fin truncate. Branched rays of all fins bearing small odontodes.

Body broadest at evertible cheek plates or cleithrum; cleithrum tapering to point posteriorly. Lateral median plates 25 or 26 (mode 25), middorsal plates 23–25 (mode 24), midventral plates 24–26 (mode 25); anteriormost four or five midventral plates strongly bent. Caudal peduncle plate rows five. One azygous preadipose plate; interdorsal plate rows three to five (mode five). Abdomen fully plated. Ventrolateral caudal-peduncle keel formed by somewhat strongly angled ventral plates bearing rows of slightly enlarged odontodes medially.

Color.—Body and fin spines boldly patterned with alternating dark brown to black and light brown to gray longitudi-

Fig. 4. Paratype of *Panaque armbrusteri*, new species, MZUSP 96326, 180 mm SL, Brazil, Mato Grosso State, Tapajós River drainage, right bank tributary of the Peixoto de Azevedo River, 10°17′14″S, 54°50′57″W, 17 October 2007 (photographed alive).

nal stripes (Fig. 4); stripes largely contiguous from snout to caudal-fin insertion although irregular branching, termination, interruption, or joining of stripes may occur, especially on ventrum and around posterior part of head; stripe width uniform and coequal or darker stripes slightly wider than lighter stripes; stripes faded but present in preserved specimens. Paired, dorsal, adipose, and anal fins striped as body with rays of paired fins usually lighter colored and membranes usually darker colored; caudal fin with stripes, spots, or uniformly colored, sometimes having yellow-orange posterior margin (Fig. 4). Eyes dark gray to black in preserved specimens, orange to red in life. Juveniles with square, trapezoidal, or irregularly shaped anterior hyaline caudal-fin window surrounded by uniformly dark brown spines and posterior margin; dark brown posterior margin expanding anteriorly and hyaline region reducing in area with increasing body size so that caudal fin is entirely opaque in adults. Largest specimen observed with hyaline caudal-fin window present 114 mm SL (MZUSP 96388).

Fig. 5. Posterior head and anterior trunk region of paratype of *Panaque armbrusteri*, new species, ANSP 182812, 224 mm SL, illustrating supraoccipital hump, pterotic lacking postorbital bulge, and the dorsal half of infraorbital six flared laterally. Scale bar = 11 mm.

Ontogenetic variation.—*Panaque armbrusteri* appears to undergo an ontogenetic increase in interpremaxillary and intermandibular tooth row angles that is unique within *Panaque* and most other Loricariidae. Juveniles less than 172 mm SL have left and right tooth rows angled at approximately 90° relative to each other, similar to that observed in all body sizes of all other *Panaque* (*Panaque*) species. A single 172 mm SL specimen of *P. armbrusteri* (MZUSP 96388) has left and right tooth rows angled at approximately 100° relative to each other, and all specimens greater than approximately 200 mm SL have left and right tooth rows angled at approximately 120° relative to each other.

Distribution.—The type series of *Panaque armbrusteri* has been restricted to the Tapajós River and its tributaries (Fig. 8, squares); however, we are aware of several potentially conspecific populations from the Xingú, Tocantins, and Araguaia rivers to the east (Fig. 8, circles with "×"; also Eigenmann and Eigenmann, 1889, 1890; Buckup et al.,

Table 1. Selected Morphometric Characters for New Species of *Panaque* (*Panaque*). Interlandmarks (ILM) are the two points between which measurements were taken (from Armbruster, 2003b and defined in Materials and Methods).

		P. armbrusteri, new species					*P. schaeferi*, new species					*P. titan*, new species				
ILM	Measurement	Holotype	*n*	Mean	Min	Max	Holotype	*n*	Mean	Min	Max	Holotype	*n*	Mean	Min	Max
1–20	Standard length	344.7	14	190.7	69.3	344.7	576.0	16	432.5	128.7	600.0	394.0	6	283.3	133.9	394.0
							Percents of standard length									
1–10	Predorsal length	48.7	14	51.4	48.7	54.9	47.5	14	45.5	42.5	47.9	51.6	6	50.7	49.2	51.7
1–7	Head length	39.9	14	43.3	39.9	46.7	38.4	14	37.8	35.3	40.0	43.9	6	44.1	42.6	47.1
7–10	Head–dorsal length	8.9	14	8.7	6.7	10.4	9.8	14	8.2	7.0	9.8	8.1	6	7.7	6.6	9.4
8–9	Cleithral width	33.8	14	33.8	31.9	36.5	38.2	14	34.9	31.8	38.5	37.0	6	35.4	34.4	37.0
8′–9′	Cleithral width ventral	28.6	14	26.9	22.6	29.3	31.3	14	27.4	25.1	31.9	28.8	6	27.1	25.5	28.8
1–12	Head–pectoral length	30.6	14	31.3	29.5	32.6	30.8	14	27.8	25.5	30.8	31.2	6	29.4	28.3	31.2
12–13	Thorax length	20.9	14	22.5	20.8	25.4	19.1	14	21.5	19.1	23.1	25.0	5	24.6	23.8	25.9
12–29	Pectoral-spine length	37.0	13	35.8	30.0	43.2	41.9	14	41.1	34.8	44.0	42.5	6	41.6	38.1	46.3
13–14	Abdominal length	22.8	14	22.9	21.9	24.4	24.1	14	23.9	23.0	25.4	24.1	6	24.3	23.4	25.2
13–30	Pelvic-spine length	25.6	14	26.1	22.7	29.2	26.3	13	27.6	25.5	30.0	24.3	6	25.5	24.3	28.3
13–13′	Pelvic girdle width	16.9	14	18.6	16.9	19.9	18.2	14	17.4	15.9	18.8	19.0	6	18.8	18.2	19.7
14–15	Postanal length	31.3	14	29.0	26.2	31.3	31.9	14	33.5	31.9	35.3	28.2	6	27.7	26.0	28.5
14–31	Anal-fin spine length	15.3	14	14.9	11.0	18.2	16.5	13	17.6	15.7	20.0	—	4	14.9	14.3	15.4
10–12	Dorsal–pectoral depth	34.0	14	34.4	32.6	37.7	34.5	14	32.9	31.0	34.5	38.1	6	36.3	34.1	38.4
10–11	Dorsal-spine length	21.7	11	27.7	21.7	32.6	28.4	7	30.8	28.0	34.1	29.1	3	29.7	28.1	32.0
10–13	Dorsal–pelvic depth	27.9	14	29.5	26.1	31.7	31.1	14	27.6	25.4	31.1	32.1	6	30.2	29.1	32.1
10–16	Dorsal-fin base length	27.9	14	29.1	27.9	31.7	28.0	14	27.3	25.5	28.6	29.0	6	27.7	24.8	29.6
10–16′	Dorsal-fin base length′	24.8	14	25.3	23.8	27.4	25.7	14	24.6	23.2	25.7	26.6	6	25.4	23.8	26.6
16–17	Dorsal–adipose distance	13.3	13	12.4	10.6	15.0	15.8	14	15.6	14.3	17.3	13.3	6	12.8	11.4	14.5
16′–17	Dorsal–adipose distance′	15.7	13	15.3	12.7	17.8	18.8	14	18.7	16.9	20.8	15.3	6	15.7	15.2	16.9
17–18	Adipose-spine length	6.0	13	6.5	5.5	7.6	7.6	13	7.7	6.7	8.4	6.6	6	7.0	6.6	7.8
17–19	Adipose–upper caudal distance	13.1	13	12.2	10.4	13.8	13.0	14	15.2	12.4	17.3	12.0	6	11.7	10.6	12.4
17–18′	Adipose height	2.4	13	4.1	2.4	5.0	3.0	12	3.9	1.8	5.8	4.1	6	4.7	4.1	5.7
15–19	Caudal peduncle depth	12.0	14	12.3	10.9	13.7	12.4	14	11.6	10.2	13.1	12.0	6	11.6	11.2	12.0
20–32	Caudal peduncle–middle caudal ray	19.6	12	21.3	16.0	24.5	20.2	13	20.1	15.6	23.5	19.9	6	19.6	13.8	22.4
20–33	Caudal peduncle–dorsal caudal spine	21.0	9	25.2	17.7	32.8	30.2	2	30.8	30.2	31.5	20.3	3	21.2	20.2	23.2
15–17	Adipose–lower caudal depth	19.9	13	19.6	17.5	21.0	20.0	14	21.1	19.1	22.8	18.9	6	18.3	16.8	19.1
14–17	Adipose–anal depth	19.1	13	18.8	17.9	19.7	21.0	14	20.2	19.0	21.6	19.9	6	18.9	18.2	19.9
14–16	Dorsal–anal depth	15.9	14	16.8	15.7	18.0	17.8	14	16.6	15.1	17.8	17.5	6	17.6	17.1	18.7
14–16′	Dorsal–anal depth′	16.3	14	17.7	16.3	19.2	19.1	14	17.6	16.1	19.1	18.6	6	18.9	17.9	20.4
13–16	Pelvic–dorsal depth	29.7	14	30.9	29.0	32.7	29.9	14	29.8	28.4	31.3	30.4	6	30.9	29.1	32.3
13–16′	Pelvic–dorsal depth′	28.3	14	28.9	27.4	30.0	29.2	14	28.0	26.7	29.5	29.8	6	27.8	20.2	30.2

Table 1. Continued.

ILM	Measurement	*P. armbrusteri*, new species					*P. schaeferi*, new species					*P. titan*, new species				
		Holotype	*n*	Mean	Min	Max	Holotype	*n*	Mean	Min	Max	Holotype	*n*	Mean	Min	Max
		Percents of head length														
5–7	Head–eye length	36.0	14	36.2	33.7	40.4	40.9	14	41.6	39.5	44.1	44.7	6	41.5	37.8	44.7
4–5	Orbit diameter	12.5	14	14.7	12.2	20.2	12.9	14	10.8	8.1	15.9	9.7	6	11.5	9.3	16.2
1–4	Snout length	72.5	14	72.5	69.1	74.5	64.8	14	66.8	63.5	70.5	69.6	6	70.1	68.2	73.8
2–3	Internares width	19.4	14	18.5	16.8	20.7	15.5	14	16.4	13.7	17.7	17.6	6	18.8	17.4	19.9
5–6	Interorbital width	56.1	14	56.1	52.5	61.3	54.8	14	56.1	53.6	61.3	60.6	6	60.7	58.7	65.2
5′–6′	Dorsal interorbital width	53.6	14	50.7	43.1	56.1	45.8	14	49.5	45.8	53.8	56.2	6	57.0	54.2	61.8
7–12	Head depth	74.7	14	69.7	66.4	74.7	77.9	14	76.2	71.0	80.5	76.7	6	72.8	68.4	76.7
1–24	Mouth length	45.6	14	45.2	37.6	51.3	30.5	14	34.7	30.5	44.6	36.5	6	35.2	33.2	36.5
21–22	Mouth width	45.8	14	41.2	34.8	47.3	27.2	14	29.3	26.0	39.2	28.9	6	27.2	25.2	28.9
22–23	Barbel length	5.3	14	4.4	3.4	5.8	3.1	11	3.9	3.1	5.2	2.3	5	1.7	1.4	2.3
25–26	Dentary tooth cup length	15.2	14	13.4	11.5	16.1	11.7	14	11.1	8.7	13.0	10.4	5	10.1	9.7	10.5
27–28	Premaxillary tooth cup length	13.9	14	12.8	9.1	15.9	11.3	14	11.1	9.3	12.8	8.8	6	9.5	8.8	11.6

2007; Nonogaki et al., 2007). These populations are currently under study by others and have been excluded here.

Etymology.—Patronym honoring Jonathan W. Armbruster, ichthyologist, Associate Professor, and Curator of Fishes at the Auburn University Museum Fish Collection, for his many contributions to the field of ichthyology, and to our understanding of the Loricariidae in particular. A noun in apposition.

Panaque cochliodon **(Steindachner, 1879)**

Figures 9, 10A; Tables 2, 3

Chaetostomus cochliodon Steindachner, 1879a:194–195 [type locality: Cauca River, Colombia]. Steindachner, 1879b:187 [description].

Chaetostomus cochliodon (sive *gibbosus*) Steindachner, 1880:63–65, plate 4 [description, synonymy, figure].

Panaque cochliodon (Steindachner).—Eigenmann and Eigenmann, 1889:44 [synonymy]. Isbrücker, 1980:74 [synonymy]. Burgess, 1989:437 [synonymy, distribution]. Isbrücker, 2001:26, 30 [synonymy]. Fisch-Muller, 2003:414 [synonymy, distribution, common names]. Maldonado-Ocampo et al., 2005:158, 159, map 151, figure 149 [synonymy, common names, ecology, distribution]. Ferraris, 2007:278 [type catalog].

Panaque gibbosus (Steindachner).—Eigenmann, 1920:30 [distribution]. Schultz, 1944:311 [differentiation from *P. suttonorum*].

Syntypes.—NMW 47297, 1, 229 mm SL, Colombia, Magdalena River drainage, Cauca River. NMW 47298, 1, 139.8 mm SL, Colombia, Magdalena River drainage, Cauca River.

Non-type material.—CAS 77239, 4, 109.3–189.9 mm SL, Colombia, Cundinamarca Department, Magdalena River, 1 February 1912, C. Eigenmann. FMNH 55168, 1, 270.0 mm SL, Colombia, Bolivar Department, Magdalena River drainage, lower Magdalena Basin near Soplaviento, 10°15′N, 75°10′W, 1912, C. Eigenmann et al. FMNH 58542, 2, 172.9, 198.7 mm SL, Colombia, Cundinamarca Department, Magdalena River drainage, Apulo, 1912, M. Gonzales. MPUJ 3293, 1, 282.6 mm SL, Colombia, Santander Department, Magdalena River drainage, Magdalena River at Barrancabermeja, 24 January 1950, B. Diez S.

Diagnosis.—*Panaque cochliodon* is diagnosed from all members of subgenus *Scobinancistrus* by having greater than five dentary and premaxillary teeth (vs. three or four dentary and premaxillary teeth), by dentary and premaxillary tooth cusps being unicuspid (vs. bicuspid), and by dentary and premaxillary tooth cusps being short and ladle- or spoon-shaped (vs. main tooth cusps being long and spatulate); and from all members of subgenus *Panaqolus* by having a blue eye (vs. black, gray, or brown) and by reaching a maximum adult size of at least 283 mm SL (vs. <150 mm SL).

Panaque cochliodon is diagnosed from all other *P.* (*Panaque*) except *P. suttonorum* by having uniformly dark gray to black body color (vs. body patterned with spots or stripes), by having a blue eye (vs. red, brown, or gray), and by juveniles having a uniformly opaque caudal fin (vs. juveniles up to approximately 145 mm SL with hyaline, anterior caudal-fin window); from all but *P. armbrusteri* by having supraoccipital raised beyond contours of head as a hump (Fig. 5; vs.

Table 2. Characteristics Interspecifically Variable within *Panaque* (*Panaque*). See text and other figures for descriptions and illustrations of characteristics.

Characteristic	*P. armbrusteri*, new species	*P. cochliodon*	*P. nigrolineatus*	*P. schaeferi*, new species	*P. suttonorum*	*P. titan*, new species
Supraoccipital hump	present	present	absent	absent	absent	absent
Postorbital pterotic bulge	absent	absent	absent	absent	absent	present
Infraorbital six	flared outward dorsally	vertical, not flared dorsally	vertical, not flared (or only slightly flared at dorsalmost margin)	vertical, not flared dorsally	vertical, not flared dorsally	flared outward dorsally
Eye color	red to brown	blue	red to brown	brown to gray	bluish	brown
Interpremaxillary tooth row angle	ontogenetically variable; approximately 90–120°	slightly under to slightly over 90°	slightly under 90°	slightly under 90°	slightly under 90°	slightly under 90°
Maxillary barbel	long	short	short	long	long	short
Trunk plate odontode formation	cluster or row	cluster	cluster or row	row or rows	cluster or row	row or rows
Posterior reach of pectoral-fin spine	halfway between pelvic-fin base and anus	halfway between pelvic-fin base and anus	coequal with anus	coequal with anus	halfway between pelvic-fin base and anus	coequal with anus
Posterior reach of pelvic-fin spine	between anterior and posterior insertion of anal fin	beyond posterior insertion of anal fin	to or slightly beyond posterior insertion of anal fin	to posterior insertion of anal fin	between anterior and posterior insertion of anal fin	to anterior or middle of anal-fin insertion
Adult caudal fin shape	truncate	lunate	lunate	lunate or truncate	lunate or forked	truncate
Juvenile caudal-fin hyaline window	present to 114 mm SL	absent	present to 135 mm SL	present to 129 mm SL	absent	present to 145 mm SL
Head and body color	alternating dark brown to black and light brown to gray longitudinal stripes; stripes coequal in width or dark stripes wider	uniformly dark gray to black	alternating dark brown to black and light brown to gray longitudinal stripes; stripes coequal in width or light stripes wider	distinctly dark black or faded black spots evenly distributed on pale gray to brown base color	uniformly dark gray to black	irregular, widely spaced dark gray to brown stripes and spots on light brown to tan base color; abdomens with spots, stripes, and/or loops
Maximum known size	345 mm SL	283 mm SL	306 mm SL	600 mm SL	278 mm SL	394 mm SL

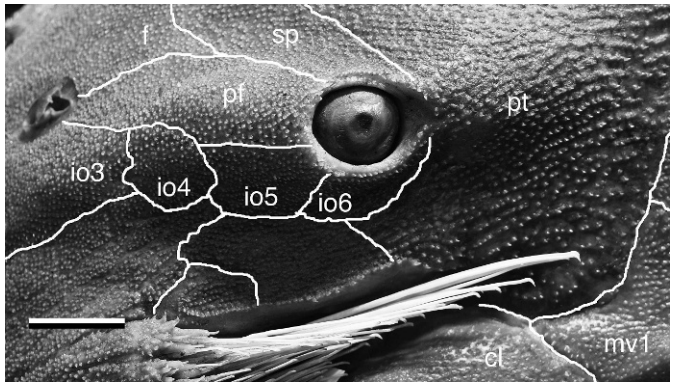

Fig. 6. Circumorbital plates and bones of holotype of *Panaque titan*, new species, MEPN 9507, 394 mm SL, illustrating 1) preorbital crest composed ventrally of infraorbital plates three to five and dorsally of prefrontal plate, 2) postorbital bulge, and 3) dorsal margin of infraorbital six flared laterally. Abbreviations: cl, cleithrum; f, frontal, io3–io6, infraorbitals three through six; mv1, midventral plate one; pf, prefrontal plate; pt, pterotic; sp, sphenotic. Scale bar = 17 mm.

supraoccipital smoothly rounded); from all but *P. nigrolineatus* by having pelvic-fin spine terminating beyond posterior insertion of anal fin when adpressed (vs. pelvic-fin spine terminating at or before posterior insertion of anal fin); from *P. nigrolineatus*, *P. schaeferi*, and *P. titan* by having pectoral-fin spine terminating halfway between pelvic-fin base and anus when adpressed ventral to pelvic fin (vs. pectoral-fin spine terminating at anus); from *P. schaeferi* and *P. titan* by having enlarged odontodes on trunk plates arranged as clusters (vs. as row or rows, Fig. 7) and by having a maximum adult body size of approximately 300 mm SL (vs. approximately 400 mm SL or greater); from *P. armbrusteri* and *P. titan* by having a vertical and flat infraorbital six (vs. dorsal margin of infraorbital six strongly flared laterally, Figs. 5, 6), and by adults having a lunate caudal fin (vs. truncate); from *P. armbrusteri* by having adults with acute interpremaxillary and intermandibular tooth row angles (vs. adults with interpremaxillary and intermandibular tooth row angles >100°, Fig. 2); and from *P. titan* by postorbital pterotic region being flush with ventral pterotic margin (Fig. 5; vs. postorbital pterotic region bulged beyond ventral pterotic margin, Fig. 6).

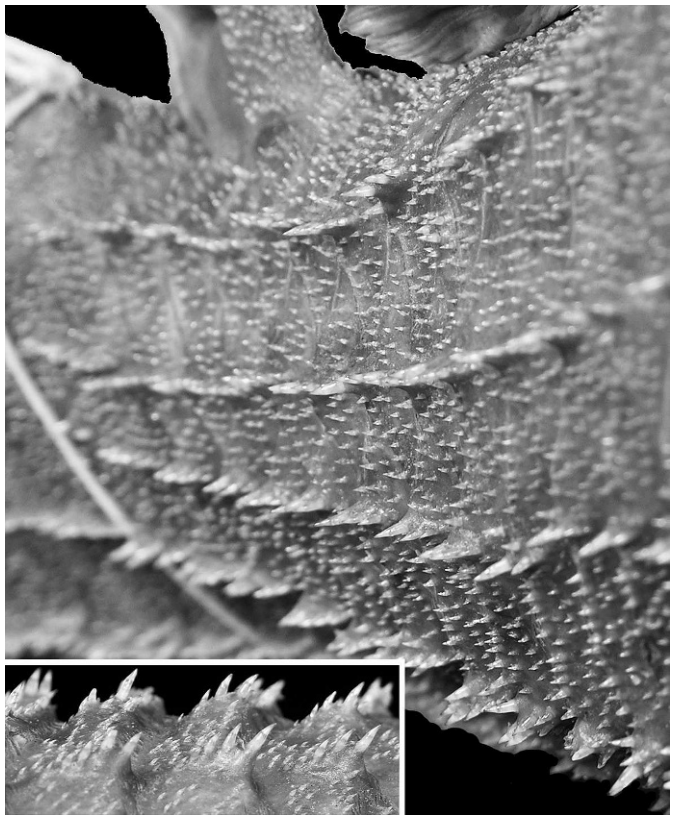

Fig. 7. Anterolateral view of dorsal, middorsal, lateral median, and midventral caudal peduncle plates of holotype of *Panaque titan*, new species, MEPN 9507, 394 mm SL, illustrating enlarged trunk plate odontodes arranged as a row or rows. Inset view of enlarged odontode rows in dorsal view.

Panaque cochliodon is further diagnosed from *P. armbrusteri*, *P. nigrolineatus*, and *P. titan* by having a lesser predorsal length (45.4–48.3% SL vs. 48.7–54.9) and a greater postanal length (32.5–36.0% SL vs. 26.0–31.3); from *P. armbrusteri*, *P. suttonorum*, and *P. titan* by having a greater adipose to lower caudal depth (21.3–24.0% SL vs. 16.8–21.0); from *P. armbrusteri* and *P. titan* by having a greater caudal peduncle to tip of dorsal caudal ray distance (36.9–46.7% SL vs. 17.7–32.8); from *P. nigrolineatus* and *P. titan* by having a shorter head length (37.3–40.9% SL vs. 41.2–47.1), by having a narrower cleithral width (29.3–33.1% SL vs. 33.8–38.6), and by having a shallower dorsal–pectoral depth (29.6–32.8% SL vs. 33.2–40.4); from *P. schaeferi* and *P. titan* by having a narrower ventral cleithral width (22.8–24.8% SL vs. 25.1–31.9); from *P. schaeferi* by having a shallower adipose–anal depth (17.1–18.9% SL vs. 19.0–21.6); from *P. armbrusteri* by having a shorter head–pectoral length (26.5–29.2% SL vs. 29.5–32.6); and from *P. titan* by having a narrower pelvic-girdle width (16.9–18.0% SL vs. 18.2–19.7), by having a shallower dorsal–pelvic depth (29.6–32.8% SL vs. 29.1–32.1), by having a shallower dorsal–anal depth (14.4–16.6% SL vs. 17.1–18.7), by having a narrower internares width (12.7–17.1% HL vs. 17.4–19.9), by having a wider mouth (31.5–37.8% HL vs. 25.2–28.9), and by having a longer maxillary barbel (2.9–5.9% HL vs. 1.4–2.3).

Description.—Morphometrics in Table 1. Largest specimen 283 mm SL. Body deep and relatively laterally compressed as compared to other *Panaque* (*Panaque*). Snout elongate, dorsal profile rising at approximately 35° to anterior margin of supraoccipital; profile of supraoccipital rising more steeply, then approaching horizontal posteriorly to form modest supraoccipital hump; profile of predorsal plates sloped slightly upward to nuchal plate. Body depth greatest at nuchal plate, only slightly greater at nuchal plate than at posterior of supraoccipital. Dorsal profile posterior of nuchal plate sloped downward approximately 20° below horizontal and slightly concave to posterior insertion of adipose-fin membrane, then approximately horizontal and straight back to first dorsal procurrent caudal-fin ray; dorsal profile rising sharply at first dorsal procurrent caudal-fin ray. Ventral profile straight and horizontal from snout to pelvic-fin insertion, sloped slightly upward to posteriormost reach of adpressed anal fin, then slightly downward to first ventral procurrent caudal-fin ray; downward slope increasing slightly at first ventral procurrent caudal-fin ray.

Entire snout, dorsal and lateral surfaces of trunk armored with plates bearing small odontodes; each dorsal, middorsal, and lateral median trunk plate posterior of dorsal-fin spine and all midventral and ventral trunk plates with postero-

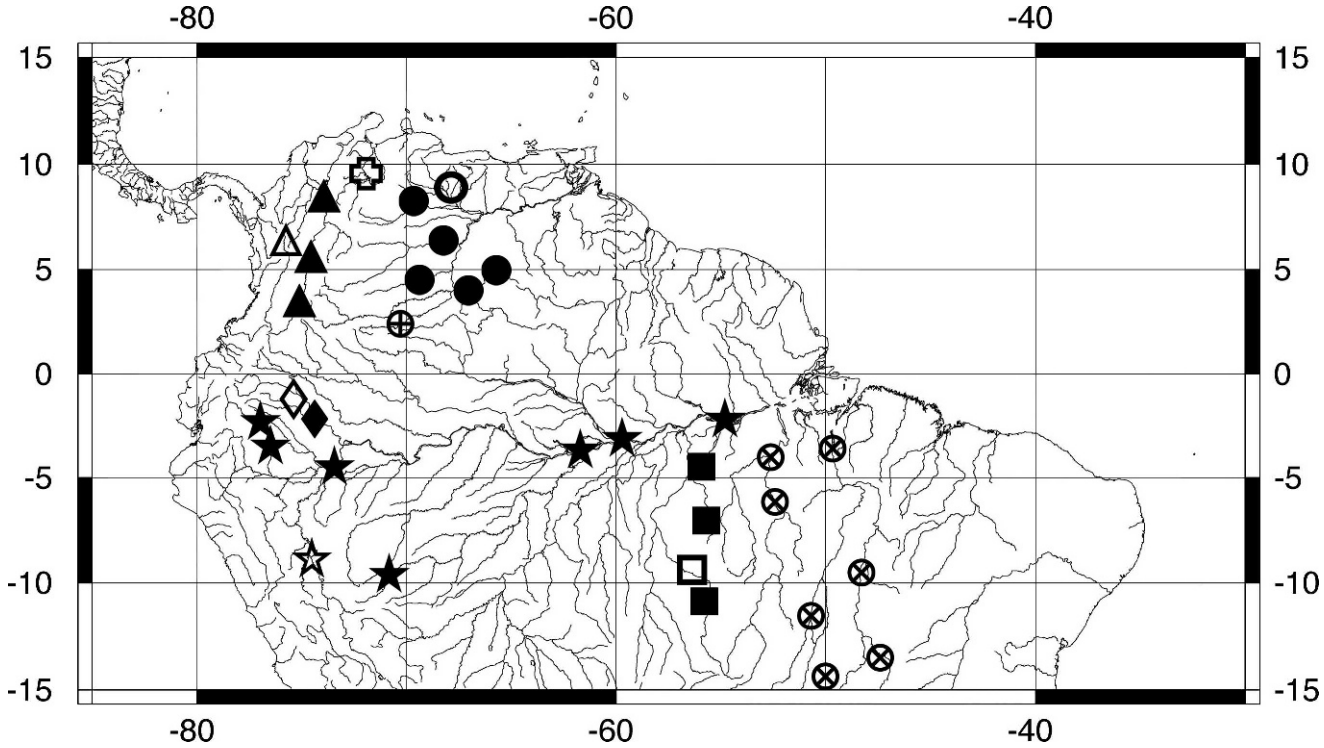

Fig. 8. Distribution of *Panaque* (*Panaque*) species. *P. armbrusteri* (squares), *P. cochliodon* (triangles), *P. nigrolineatus* (open and filled circles), *P. schaeferi* (stars), *P. suttonorum* (cross), *P. titan* (diamonds), and congeneric populations that we are aware of but either did not examine in this study or that we suspect may represent additional, undescribed species: *Panaque* cf. *nigrolineatus* (circle with "+"), and *Panaque* cf. *armbrusteri* (circles with "×"). Symbols may represent more than one locality. Open symbols indicate type localities.

medial cluster of slightly enlarged odontodes. Cheek plates bearing minimally to highly hypertrophied, distally hooked odontodes (mean 34, range 22–38) evertible to approximately 90° from sagittal plane; longest odontodes extending just past posterior margin of first midventral plate. Eye small (orbit diameter 9.3–12.9% HL); orbit positioned along lateral midline at anterior margin of posterior third of head; orbit accentuated by modest preorbital crest (Figs. 5, 6); interobital plate six vertical, not flared dorsally; postorbital pterotic region flush with ventral pterotic margin. Orbit sloped ventrolaterally at approximately 30° from sagittal plane in anterior view. Postorbital notch present or absent. Iris operculum not observed.

Oral disk occupying approximately two-thirds to three-fourths of snout anterior of cleithrum. Interpremaxillary tooth row angle slightly variable, from just under to just over 90°; premaxillary teeth six to 15 (mode six). Intermandibular tooth row angle acute; dentary teeth six to 18 (mode seven). Rows of short, branched, fimbriate papillae immediately internal to each tooth row; single semicircular flange-like papilla at posteromedial corner of each premaxilla; buccal papilla absent. All teeth unicuspid and spoon-shaped; proximalmost one or two teeth smaller than others. Maxillary barbel short, attached to lower lip along most of length; ventral surface of labial disk with hemispherical papillae decreasing in size distally and toward rictus; posterior margin of labial disk lacking fimbriae.

Dorsal fin II,7; dorsal-fin spinelet prominent and V-shaped; dorsal-fin lock functional; posteriormost dorsal-fin ray free from body. Pectoral fin I,6; pectoral-fin spine extending approximately halfway between posterior insertion of pelvic fin and anus when adpressed ventral to pelvic fin; posterodorsal and anterior surfaces of spine with slightly enlarged odontodes; anterior odontodes increasing in size and areal extent distally. Pelvic fin I,5; pelvic-fin spine extending beyond posterior insertion of anal fin when adpressed. Anal fin I,4; first pterygiophore exposed as plate; first unbranched ray ossified. Adipose-fin spine sloped at approximately 30° and slightly curved along entire length; bearing slightly enlarged odontodes along dorsal surface; adnate to caudal peduncle via fleshy membrane with concave posterior margin. Caudal fin I,14,I; dorsal procurrent caudal-fin rays five or six (mode five), ventral procurrent caudal-fin rays four to six (mode four); caudal fin symmetrically lunate or asymmetrically lunate with ventral lobe slightly larger than dorsal lobe; caudal-fin spines extended posteriorly beyond rays as short filaments; dorsal caudal-fin spine terminating coequally with or slightly anterior to ventral caudal-fin spine. Branched rays of all fins bearing small odontodes.

Body broadest at cleithrum; cleithrum tapering to point or rounded posteriorly. Lateral median plates 25–27 (mode 26), middorsal plates 23–25 (mode 24), midventral plates 25 or 26 (mode 25); anteriormost five or six midventral plates strongly bent. Caudal peduncle plate rows five. One azygous preadipose plate; interdorsal plate rows five or six (mode six). Abdomen fully plated. Modest ventrolateral caudal-peduncle keel formed by somewhat strongly angled ventral plates bearing rows of slightly enlarged odontodes medially.

Color.—All available preserved specimens uniformly pale and bleached. Live specimens not observed. Maldonado-Ocampo et al. (2005:fig. 149) illustrate *Panaque cochliodon* as being uniformly dark gray to black in color with a blue eye.

Fig. 9. Syntype of *Chaetostomus cochliodon*, NMW 47297, 229 mm SL, Cauca River, Colombia (photos by J. W. Armbruster).

Distribution.—Endemic to the Magdalena and Cauca River basins, Colombia (Fig. 8).

Remarks.—*Panaque cochliodon* and *P. suttonorum* are similar in gross morphology and color, both having lunate caudal fins and a uniformly dark gray to black body color with blue or bluish eyes. Given their similar appearance and the overall similarity of fish faunas in the Magdalena and Maracaibo Basins (Pérez and Taphorn, 1993; Galvis et al., 1997), they are likely sister species.

Panaque nigrolineatus (Peters, 1877)

Figures 3, 10B, 11; Tables 2, 3

Chaetostomus nigrolineatus Peters, 1877:471, figure [type locality: Calabozo, Venezuela].

Panaque nigrolineatus (Peters).—Eigenmann and Eigenmann, 1889:44 [synonymy]. Isbrücker, 1980:75 [synonymy]. Burgess, 1989:437 [synonymy, distribution]. Montoya-Burgos et al., 1998:367 [molecular phylogenetic relationships]. Isbrücker, 2001:26, 30 [synonymy]. Fisch-Muller, 2003:415 [synonymy, distribution, common names]. Armbruster, 2004:23, 25, 29, 45, 48, 73 [osteology, phylogenetic relationships]. Hardman, 2005:710 [phylogenetic relationships]. Sanabria-Ochoa et al., 2007:215, fig. 261a–c [synonymy, common names, description, ecology, distribution]. Ferraris, 2007:278 [type catalog]. Armbruster, 2008:47 [phylogenetic relationships].

Syntypes.—ZMB 10046, 1, 303 mm SL, Venezuela, Guárico State, Apure River drainage, Guárico River at Calabozo. ZMB 10047, 1, 158 mm SL, Venezuela, Guárico State, Apure River drainage, Guárico River at Calabozo.

Non-type material.—ANSP 128682, 1, 56.9 mm SL, Colombia, Meta Department, Meta River drainage, Negro River, downstream from main Villavicencio-Puerto Lopez highway at La Balsa, W side of river, 4°04′N, 73°04′W, 29 February 1972, J. Böhlke, D. Foster, N. Foster, and D. Smith. ANSP 128686, 1, 88.8 mm SL, Colombia, Meta Department, Meta River drainage, Negro River, downstream from main Villavicencio-Puerto Lopez highway at La Balsa, E side of river, 4°04′N, 73°04′W, 1 March 1972, J. Böhlke, N. Foster, and D. Smith. ANSP 131654, 2, 102.7, 133.9 mm SL, Colombia,

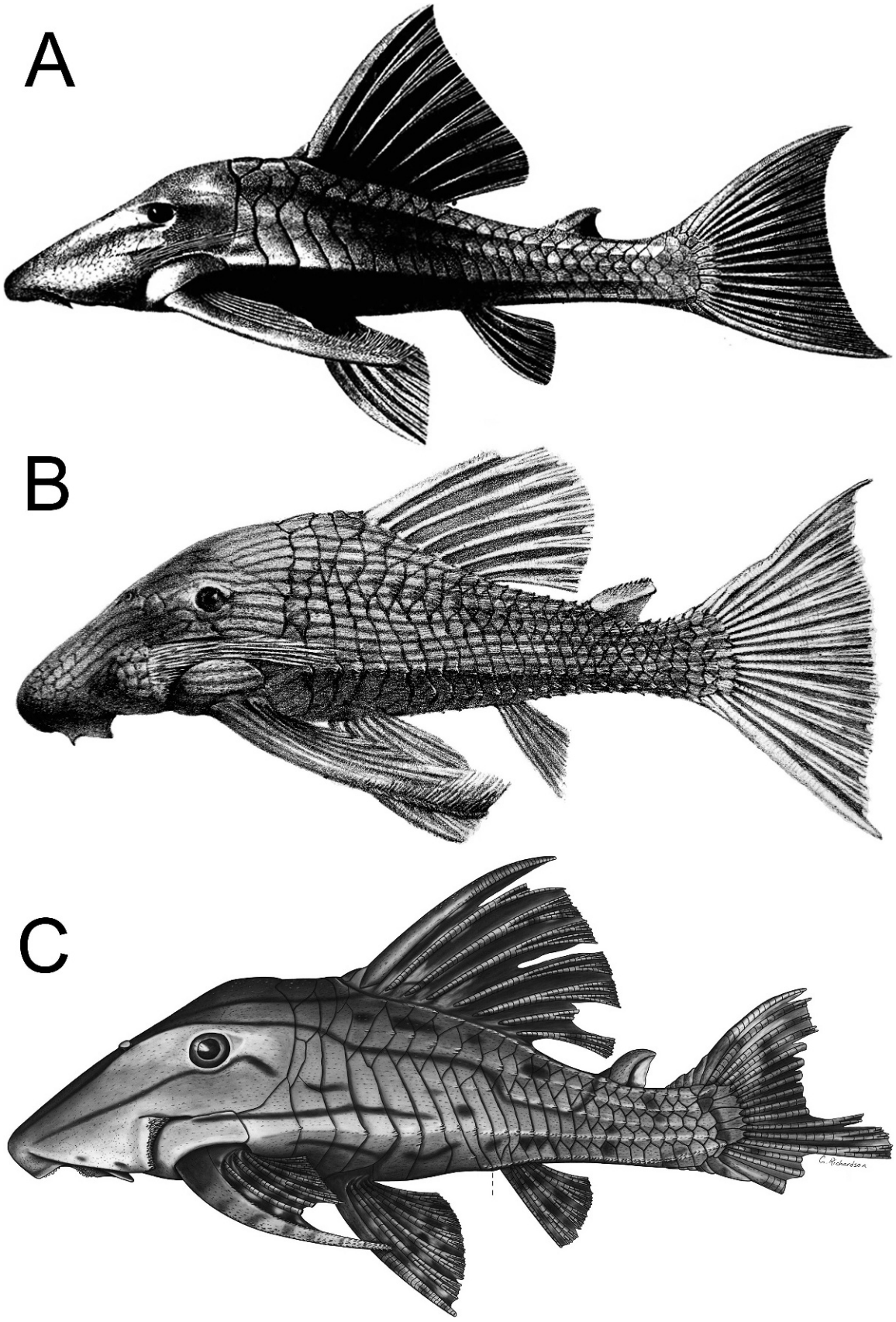

Fig. 10. Illustrations of (A) *Panaque cochliodon* (reproduced from Steindachner, 1880:pl. 4, modified by flipping horizontally); (B) *P. nigrolineatus* (reproduced from Peters, 1877:556); and (C) paratype of *Panaque titan*, new species, FMNH 97591, 145.1 mm SL (original illustration by C. Richardson).

Meta Department, Meta River drainage, Metica River, approximately 3 km SE of Hacienda Mozambique, 20 March 1975, J. Böhlke, W. Saul, and L. Fuiman. ANSP 162456, 1, 260.0 mm SL, Venezuela, Apure State, Meta River drainage, Meta River approximately 40 minutes upstream from confluence of Orinoco River, 06°18′N, 67°37′W, 27 November 1985, B. Chernoff, W. Saul, and R. Royero. ANSP 162759, 1, 245.0 mm SL, Venezuela, Amazonas State, Orinoco River drainage, Iguapo River about 1 hour beyond mouth, 13 March 1987, H. Lopez, J. Fernandez, O. Castillo, M. Antonio, and J. Moreno. AUM 22813, 2, 98.2, 132.2 mm SL, Venezuela, Portuguesa State, Apure River drainage, Portuguesa River just downstream of Guanarito, north shore across from beach, 8°42′N, 69°12′W, 1 January 2000, J. Armbruster, M. Hardman, J. Evans, and J. Thomas. AUM 39281, 1, 139.5 mm SL, Venezuela, Amazonas State, Ventuari River drainage, Parucito River at Salomon rapids, 2.7 km NE of San Juan de Manapiare, 5°20′N, 66°02′W, 16 April 2004, N. Lujan, D. Werneke, and O. Leon. AUM 39546, 1, 181.5 mm SL, Venezuela, Amazonas State, Ventuari River drainage, Asita River, 33 km ESE of San Juan de Manapiare, 5°09′N, 65°48′W, 23 April 2004, N. Lujan, D. Werneke, and O. Leon. AUM 39903, 1, 169.8 mm SL, Venezuela, Apure State, Apure River drainage, Arauca River, 100 meters from the mouth of the Cañafistola, 7°32′N, 67°31′W, 6 November 1997, Arana. AUM 42727, 1, 306.0 mm SL, Venezuela, Amazonas State, Orinoco River drainage, Orinoco River at Pasaganado, 38 km N of San Fernando de Atabapo, 4°23′N, 67°46′W, 1 March 2005, N. Lujan, D. Werneke, M. Sabaj, M. Arce, and T. Wesley. CAS 36575, 1, 178.9 mm SL, Colombia, Meta Department, Guaviare River drainage, small tributary to the Ariari River, near town of Granada, January 1974, H. Heinrich. FMNH 100165, 1, 176.4 mm SL, Venezuela, Guárico State, Apure River drainage, Apure River above and below bridge, 12 December 1988, B. Chernoff and O. Castillo. FMNH 103540, 1, 90.2 mm SL, Venezuela, Barinas State, Apure River drainage, Anaro River, 10 minutes from mouth in Suripa River, 10 January 1991, A. Machado, B. Chernoff, and R. Royero. FMNH 105999, 1, 157.7 mm SL, Venezuela, Barinas State, Apure River drainage, Suripa River, approximately 15 minutes above pump station, 13 January 1991, A. Machado, B. Chernoff, R. Royero, and F. Gill. IAVHP 1963, 1, 172.7 mm SL, Colombia, Casanare Department, Tauramena County, Meta River drainage, Chitamena River, 2 May 1996, J. Jimenez. IAVHP 3925, 1, 87.7 mm SL, Colombia, Casanare Department, Meta River drainage, Tocaría River, 3 March 1998, V. Ortiz. IAVHP 3926, 1, 211.9 mm SL, Colombia, Casanare Department, Meta River drainage, Cusiana River, 30 May 1999, V. Ortiz. IAVHP 3927, 1, 213.5 mm SL, Colombia, Casanare Department, Meta River drainage, Cusiana River, 10 February 2000, V. Ortiz. IAVHP 4717, 1, 274.0 mm SL, Colombia, Arauca Department, Arauquita County, Arauca River drainage, Aquas Limón River, 2 November 1993, G. Castaño. IAVHP 5123, 1, 60.3 mm SL, Colombia, Meta Department, Granada County, Guaviare River drainage, Urichare Creek, gauge 5, Port Caldas inspection, 3°25′N, 73°40′W, 5 February 2009, EMBRIOPEZ. IAVHP 5588, 1, 158.5 mm SL, Colombia, Meta Department, Granada County, Guaviare River drainage, Ariari River bridge of gold, Port Caldas inspection, 20 March 2009, EMBRIOPEZ. INHS 28992, 1, 57.3 mm SL, Venezuela, Cojedes State, Apure River drainage, San Carlos River, WNW of Las Vegas, 9°33′N, 68°38′W, 9 January 1993, J. W. Armbruster, D. C. Taphorn, L. M. Page, K. S. Cummings, C. A. Mayer, P. A. Ceas, C. A. Laird, and M. H. Sabaj. INHS 32033, 1, 53.7 mm SL, Venezuela, Cojedes State, Apure River drainage, San Carlos River, Hondo Creek, 5 km S of Las Vegas, 14 January 1994, J. W. Armbruster, M. H. Sabaj, K. S. Cummings, and C. A. Mayer. INHS 35688, 1, 214.0 mm SL, Venezuela, Portuguesa State, Apure River drainage, Portuguesa River, 3 km NE of El Barriero, 9°03′N, 69°29′W, 1 January 1995, P. A. Ceas, J. W. Armbruster, M. H. Sabaj, C. A. Laird, S. M. Phelps, F. T. Burbrink, and M. L. Manrique. INHS 60238, 1, 31.6 mm SL, Cojedes State, Apure River drainage, Pao River, W of La Yeguera, at Hwy 13 bridge, 9°32′N, 68°06′W, 22 December 1990, L. M. Page, P. A. Ceas, M. E. Retzer, and A. Barbarino.

Diagnosis.—*Panaque nigrolineatus* is diagnosed from all members of subgenus *Scobinancistrus* by having greater than five dentary and premaxillary teeth (vs. three or four dentary and premaxillary teeth), by dentary and premaxillary tooth cusps being unicuspid (vs. bicuspid), and by dentary and premaxillary tooth cusps being short and ladle- or spoon-shaped (vs. main tooth cusps being long and spatulate); and from all members of subgenus *Panaqolus* by having a body color pattern consisting of alternating dark brown to black and light brown to gray longitudinal stripes (vs. body color pattern consisting of spots or vertical and/or oblique bands), by individuals <135 mm SL having a hyaline caudal-fin window (vs. caudal fin uniformly opaque, banded, or spotted), and by reaching a maximum adult size of at least 306 mm SL (vs. <150 mm SL).

Panaque nigrolineatus is diagnosed from *P. armbrusteri*, *P. cochliodon*, and *P. suttonorum* by having pectoral-fin spine terminating at anus (vs. halfway between pelvic-fin insertion and anus); from *P. armbrusteri*, *P. suttonorum*, and *P. titan* by having pelvic-fin spine terminating at or slightly beyond posterior insertion of anal fin (vs. between anterior and posterior insertion of anal fin); from *P. cochliodon*, *P. suttonorum*, and *P. schaeferi* by having body color consisting of alternating dark brown to black and light brown to gray longitudinal stripes (vs. body color uniformly dark gray to black or consisting of dark or faded black spots on pale gray to brown base color); from *P. cochliodon* and *P. armbrusteri* by supraoccipital being smoothly rounded (vs. supraoccipital raised as a hump, Fig. 5); from *P. armbrusteri* and *P. titan* by infraorbital six being vertical and straight or only slightly flared along dorsalmost margin (vs. dorsal half of infraorbital six strongly flared laterally, Figs. 5, 6); from *P. cochliodon* and *P. suttonorum* by having red to brown eyes (vs. blue or bluish); from *P. cochliodon* and *P. suttonorum* by juveniles up to approximately 135 mm SL having an anterior, hyaline caudal-fin window (vs. juvenile caudal fin uniformly opaque); from *P. schaeferi* and *P. titan* by having a maximum body size of approximately 300 mm SL (vs. approximately 400 mm SL or greater); from *P. armbrusteri* and *P. titan* by adults having a lunate caudal fin (vs. truncate); from *P. armbrusteri* by having fewer premaxillary and dentary teeth at equivalent body sizes (Fig. 3), by adults having acute interpremaxillary and intermandibular tooth row angles (vs. adult interpremaxillary and intermandibular tooth row angles >100°, Fig. 2), and by having light longitudinal body stripes frequently wider than dark longitudinal body stripes (Fig. 10B; vs. dark stripes frequently wider, Fig. 4); and from *P. titan* by having postorbital pterotic region flush with ventral pterotic margin (vs. postorbital pterotic region bulged beyond ventral pterotic margin, Fig. 6).

Table 3. Selected Morphometric Characters for Species of *Panaque* (*Panaque*) Redescribed Herein. Interlandmarks (ILM) are the two points between which measurements were taken (from Armbruster, 2003b and defined in Materials and Methods).

		P. cochliodon				*P. nigrolineatus*				*P. suttonorum*			
ILM	Measurement	*n*	Mean	Min	Max	*n*	Mean	Min	Max	*n*	Mean	Min	Max
1–20	Standard length	9	184.3	109.3	282.58	28	153.0	53.7	306.0	5	221.7	123.0	278.0
							Percents of standard length						
1–10	Predorsal length	9	46.7	45.4	48.3	28	51.7	48.7	54.9	5	46.4	38.1	50.3
1–7	Head length	9	39.0	37.3	40.9	28	43.4	41.2	46.2	5	39.9	31.8	44.4
7–10	Head–dorsal length	9	8.3	7.2	10.4	28	8.6	7.2	10.6	5	7.5	6.2	8.9
8–9	Cleithral width	9	31.3	29.3	33.1	28	35.5	33.8	38.6	5	31.4	29.3	33.5
8′–9′	Cleithral width ventral	9	23.7	22.8	24.8	28	26.3	23.0	28.2	5	25.1	22.2	27.2
1–12	Head–pectoral length	9	27.8	26.5	29.2	28	29.7	27.4	31.7	5	28.5	24.7	30.9
12–13	Thorax length	9	22.2	21.0	24.2	28	23.9	22.1	25.7	5	22.8	20.9	24.8
12–29	Pectoral-spine length	9	35.7	33.8	37.7	28	38.9	30.6	45.9	4	36.2	32.1	39.9
13–14	Abdominal length	8	22.2	20.6	23.7	27	23.3	20.9	25.5	5	24.2	23.7	25.2
13–30	Pelvic-spine length	9	26.7	23.9	28.5	28	26.7	22.9	29.6	5	25.2	23.9	26.1
13–13′	Pelvic girdle width	8	17.4	16.9	18.0	27	18.8	15.5	21.0	5	17.9	17.2	18.8
14–15	Postanal length	9	33.7	32.5	36.0	28	29.1	26.2	31.2	5	30.0	26.8	36.0
14–31	Anal-fin spine length	9	16.5	14.6	18.3	28	16.1	13.4	19.3	4	15.2	13.8	17.0
10–12	Dorsal–pectoral depth	9	31.2	29.6	32.8	28	35.9	33.2	40.4	5	32.2	27.7	35.3
10–11	Dorsal-spine length	6	34.1	28.6	38.4	15	32.5	28.2	35.2	4	30.9	27.9	38.6
10–13	Dorsal–pelvic depth	9	26.1	24.9	28.4	27	29.7	26.4	33.4	5	27.2	24.9	28.8
10–16	Dorsal-fin base length	9	25.8	24.6	28.0	28	27.1	25.1	30.4	5	26.7	25.1	30.5
10–16′	Dorsal-fin base length′	9	22.8	21.3	24.8	28	24.1	22.6	27.8	5	24.7	23.1	30.3
16–17	Dorsal–adipose distance	9	13.7	11.9	16.6	28	12.6	10.3	15.1	5	16.5	14.8	19.3
16′–17	Dorsal–adipose distance′	9	16.7	14.3	18.9	28	15.2	12.3	17.9	5	18.2	15.0	20.8
17–18	Adipose-spine length	8	7.9	7.2	8.5	27	8.2	6.6	9.6	5	6.6	6.1	7.9
17–19	Adipose–upper caudal distance	9	16.6	14.6	19.3	28	14.3	10.9	17.9	5	13.8	11.8	16.3
17–18′	Adipose height	9	3.1	2.1	3.8	26	4.5	3.0	5.9	5	4.2	2.7	5.4
15–19	Caudal peduncle depth	9	11.0	10.5	11.8	28	11.1	10.0	12.7	5	11.2	10.8	12.3
20–32	Caudal peduncle–middle caudal ray	9	20.0	18.5	21.2	28	20.9	16.5	23.7	4	20.5	19.3	21.1
20–33	Caudal peduncle–dorsal caudal spine	6	41.6	36.9	46.7	9	33.1	21.6	49.4	0	–	–	–
15–17	Adipose–lower caudal depth	9	22.3	21.3	24.0	28	20.7	17.8	24.2	5	19.3	18.3	21.0
14–17	Adipose–anal depth	9	18.1	17.1	18.9	28	17.6	16.1	19.8	5	19.4	18.3	21.7
14–16	Dorsal–anal depth	9	15.5	14.4	16.6	28	16.8	15.2	18.6	5	16.5	15.9	17.1
14–16′	Dorsal–anal depth′	9	16.4	14.7	17.9	28	18.2	17.0	20.0	5	17.5	16.6	18.2
13–16	Pelvic–dorsal depth	9	27.6	24.4	30.8	27	30.1	27.0	33.8	5	29.6	28.5	30.8
13–16′	Pelvic–dorsal depth′	9	26.3	24.6	28.7	27	28.6	25.4	32.5	5	28.7	27.4	30.3

Table 3. Continued.

ILM	Measurement	*P. cochliodon*				*P. nigrolineatus*				*P. suttonorum*			
		n	Mean	Min	Max	*n*	Mean	Min	Max	*n*	Mean	Min	Max
		Percents of head length											
5–7	Head–eye length	9	42.9	38.2	45.6	28	42.5	35.0	46.3	5	43.0	41.4	44.9
4–5	Orbit diameter	9	11.0	9.3	12.9	28	14.1	9.9	19.3	5	12.3	10.3	16.7
1–4	Snout length	9	66.5	64.3	68.0	28	68.3	16.3	73.1	5	66.7	65.0	69.4
2–3	Internares width	9	15.2	12.7	17.1	28	18.5	16.1	22.3	5	22.4	16.4	31.2
5–6	Interorbital width	9	57.1	52.4	62.1	28	63.4	58.1	67.5	5	60.0	53.9	65.5
5′–6′	Dorsal interorbital width	9	51.1	48.4	55.1	28	58.4	52.8	62.7	5	54.9	53.3	57.2
7–12	Head depth	9	70.4	67.3	73.4	28	72.5	68.2	77.3	5	72.5	68.3	78.2
1–24	Mouth length	8	39.9	34.4	44.2	28	36.5	31.7	43.7	5	39.5	32.9	48.3
21–22	Mouth width	8	34.3	31.5	37.8	28	30.7	22.2	39.5	5	33.7	28.4	42.1
22–23	Barbel length	8	3.6	2.9	5.9	25	2.7	1.6	3.6	5	4.6	3.1	7.2
25–26	Dentary tooth cup length	9	11.5	9.6	12.9	28	11.5	8.3	14.0	5	11.7	9.8	14.1
27–28	Premaxillary tooth cup length	9	10.4	8.7	11.8	28	9.6	7.6	12.1	5	11.1	8.1	14.1

Panaque nigrolineatus is further diagnosed from *P. cochliodon* and *P. schaeferi* by having a greater predorsal length (48.7–54.9% SL vs. 42.5–48.3), by having a longer head length (41.2–46.2% SL vs. 35.3–40.9), and by having a lesser postanal length (26.2–31.2% SL vs. 31.9–36.0); and from *P. cochliodon* and *P. suttonorum* by having a wider cleithral width (33.8–38.6% SL vs. 29.3–33.5).

Description.—Morphometrics in Table 1. Largest specimen 303 mm SL. Body deep and stout. Dorsal profile of snout rising at approximately 35° to middle of supraoccipital; dorsal profile approaching horizontal and flat or shallowly convex from middle of supraoccipital back to nuchal plate. Body depth greatest at nuchal plate. Dorsal profile posterior of nuchal plate sloped gently downward and straight or shallowly convex to posterior insertion of adipose-fin membrane, then sloping upward slightly to first dorsal procurrent caudal-fin ray, upward slope increasing at first dorsal procurrent caudal-fin ray. Ventral profile straight and horizontal from snout to pelvic-fin insertion, sloped upward to posteriormost insertion of anal fin, then straight back to first ventral procurrent caudal-fin ray; downward slope increasing slightly at first ventral procurrent caudal-fin ray.

Entire snout, dorsal and lateral surfaces of trunk armored with plates bearing small odontodes; each dorsal, middorsal, and lateral median trunk plate posterior of dorsal-fin spine and all midventral and ventral plates with posteromedial cluster or medial row of slightly enlarged odontodes. Cheek plates bearing minimally to highly hypertrophied, distally hooked odontodes (mean 40, range 24–60), evertible to approximately 90° from sagittal plane; longest odontodes extending just beyond anterior margin of third midventral plate. Eye large (orbit diameter 10.5–16.5% HL); orbit positioned at or dorsal to lateral midline at anterior margin of posterior third of head; orbit accentuated by modest preorbital crest (Figs. 5, 6); infraorbital plate six vertical and not flared or slightly flared only at dorsalmost margin; postorbital pterotic region flush with ventral pterotic margin; orbit sloped ventrolaterally at approximately 30° from sagittal plane in anterior view. Postorbital notch present or absent. Iris operculum present.

Oral disk occupying approximately three-fourths of snout anterior of cleithrum. Interpremaxillary tooth row angle just under 90°; premaxillary teeth six to nine (mode seven). Intermandibular tooth row angle acute; dentary teeth seven to nine (mode seven). Rows of short, branched, fimbriate papillae immediately internal to each tooth row; single semicircular flange-like papilla at posteromedial corner of each premaxilla; buccal papilla absent. All teeth unicuspid and spoon-shaped; proximalmost one to two teeth smaller than others. Maxillary barbel short and attached to lower lip along most of length; ventral surface of labial disk with hemispherical or semicircular papillae decreasing in size distally and toward rictus; posterior margin of labial disk lacking fimbriae.

Dorsal fin II,7; dorsal-fin spinelet prominent and V-shaped; dorsal-fin lock functional; posteriormost dorsal-fin ray free from body. Pectoral fin I,6; pectoral-fin spine extending to anus when adpressed ventral to pelvic fin; posterodorsal and anterior surfaces of spine with slightly enlarged odontodes, anterior odontodes increasing in size and areal extent distally; distal pectoral-fin spine odontodes moderately to highly hypertrophied. Pelvic fin I,5; pelvic-fin spine extending to or slightly beyond posterior insertion of

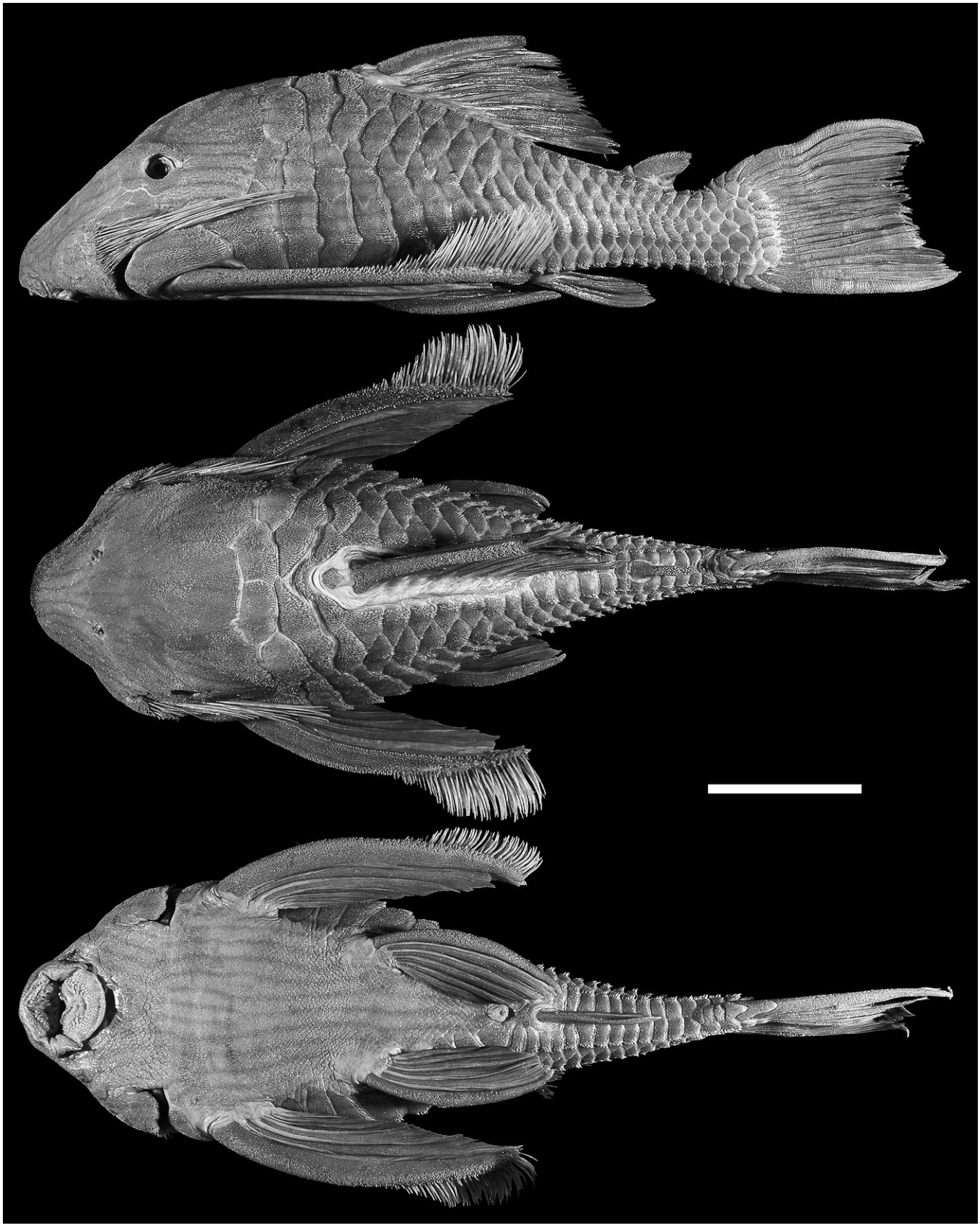

Fig. 11. Syntype of *Chaetostomus nigrolineatus*, ZMB 10046, 303 mm SL, Calabozo, Venezuela (photos by M. Allen). Scale bar = 60 mm.

anal fin when adpressed. Anal fin I,4; first anal-fin pterygiophore exposed as plate; first unbranched ray ossified. Adipose-fin spine sloped at approximately 35° and slightly curved along entire length or more strongly curved distally; bearing slightly enlarged odontodes along dorsal surface; adnate to caudal peduncle via fleshy membrane with straight posterior margin. Caudal fin I,14,I; dorsal procurrent caudal-fin rays four or five (mode five); ventral

procurrent caudal-fin rays four or five (mode four); caudal fin shallowly lunate with or without caudal-fin spines elongated as short filaments. Branched rays of all fins bearing small odontodes.

Body broadest at evertible cheek plates or cleithrum; cleithrum squared, rounded or tapering to point posteriorly. Lateral median plates 25 or 26 (mode 25), middorsal plates 23 or 24 (mode 24), midventral plates 24 or 25 (mode 25); anteriormost five or six midventral plates strongly bent. Caudal peduncle plate rows five. One azygous preadipose plate; interdorsal plate rows five or six (mode six). Abdomen fully plated. Modest ventrolateral caudal-peduncle keel formed by somewhat strongly angled ventral plates bearing rows of slightly enlarged odontodes medially.

Coloration.—Adult body and fin spines boldly patterned with alternating dark brown to black and light brown to gray longitudinal stripes; stripes largely contiguous from snout to caudal-fin insertion although irregular branching, termination, interruption, or joining of stripes may occur, especially on ventrum and around posterior of head; stripe width uniform and coequal or lighter stripes slightly wider than darker stripes; stripes faded but present in preserved specimens.

Paired- and dorsal-fin rays and membranes striped as body or uniformly dark brown; rayed fins with or without light white or tan posterior margin. Tips of caudal-fin spines light white or tan if elongated as filaments. Juveniles with caudal fin hyaline except for dark brown spines and posterior margin; dark brown posterior margin expanding anteriorly and hyaline region reducing with increasing body size so that caudal fin is entirely opaque in adults. Largest specimen observed with hyaline caudal-fin window present 134.5 mm SL (ANSP 131654). Eyes dark gray to black in preserved specimens, dark gray or orange to red in life.

Distribution.—Widespread in the Orinoco River basin, although collections are more common from western whitewater tributaries (e.g., Apure and Meta Rivers; see Coloration above for note regarding *P. nigrolineatus* from the Guaviare River in Colombia). Specimens have also been collected in the upper Orinoco mainstem and in the upper reaches of the Ventuari River, an eastern, Guiana Shield tributary of the upper Orinoco. To date, several surveys of the Casiquiare and its tributaries by the first author and by Winemiller et al. (2008) have not yielded *Panaque nigrolineatus*, and previous reports of this species from southeastern tributaries of the Amazon basin are probably misidentifications (Eigenmann and Eigenmann, 1889, 1890; Buckup et al., 2007; Nonogaki et al., 2007).

Remarks.—Individuals from the upper Guaviare River in Colombia (Fig. 8:circle with ''+'') with coloration shifting from stripes as juveniles to irregularly shaped light brown to gray spots on dark brown to black base color as adults. This color morph is common in the ornamental fish trade, but we examined only one catalogued specimen from this region (IAVHP 5588) and more material is needed to determine if these populations are conspecific with *Panaque nigrolineatus*.

***Panaque schaeferi*, new species**
Figures 12, 13; Tables 1, 2

Panaque sp.—Hardman, 2005 [molecular phylogeny].

Holotype.—MUSM 27500, 1, 576 mm SL, Peru, Ucayali Department, Padre Abad Province, Aguaytia River drainage, Santa Ana River, Cordillera Azul National Park, 8°29′51″S, 75°33′36″W, 250 m elevation, December 2006.

Paratypes.—INPA 28845, 5, 368–475 mm SL, Brazil, Amazonas State, Itacoatiara County, Amazonas River, below Paraná do Ramos and above Ponta Grossa, September 1980, A. de Souza. INPA 28846, 2, 364, 365 mm SL, Brazil, Amazonas State, Purus River, June 1982, A. de Souza. MEPN 3012, 1, 600 mm SL, Ecuador, Pastaza Province, Pastaza River drainage, Bobonaza River upstream of Morete village, 02°22′13″S, 76°39′12″W, 13 February 1958, G. Herrera and R. Olalla. MEPN 3013, 1, 475 mm SL, same locality as MEPN 3012. INHS 55408, 1, 420 mm SL, Peru, Loreto Department, Amazonas River, opposite Iquitos, beach along east bank of east channel, 9 August 1999, M. H. Sabaj, J. G. Stewart, G. R. Moyer, and N. R. Lovejoy. MUSM 9999, 1, 128.7 mm SL, Peru, Ucayali Department, Purus River drainage, Caserio Grau, Curanja River, 9°58′S, 71°02′W, 7 September 1994, F. Chang and P. De Rham. MUSM 28505, 1, 559 mm SL, Peru, Ucayali Department, Padre Abad Province, Aguaytia River drainage, Santa Ana River, 8°32′27″S, 75°36′36″W, 255 m elevation, June 2007. MUSM 33333, 1, 452 mm SL, Peru, Ucayali Department, Padre Abad Province, Aguaytia River at Aguaytia City, 9°03′56″S, 75°29′55″W, August 2008. MUSM 33334, 1, 355 mm SL, Peru, Loreto Department, Alto Amazonas Province, Marañon River drainage, Pastaza River at Andoas, 2°50′01″S, 76°26′41″W, 23 August 2007, M. Velazquez.

Diagnosis.—*Panaque schaeferi* is diagnosed from all members of subgenus *Scobinancistrus* by having greater than four dentary and premaxillary teeth (vs. three or four dentary and premaxillary teeth), by dentary and premaxillary tooth cusps being unicuspid (vs. bicuspid), and by dentary and premaxillary tooth cusps being short and ladle- or spoon-shaped (vs. main tooth cusps being long and spatulate); and from all members of subgenus *Panaqolus* by having a body color pattern consisting of distinctly dark black or faded black spots evenly distributed on pale gray to brown base color or of irregular and indistinct, broken, and widely spaced darker brown stripes, spots, and vermiculations on a light brown to gray base color (vs. body color pattern consisting of small white spots on a dark black base or vertical and/or oblique bands), by individuals <129 mm SL having a hyaline caudal-fin window (vs. caudal-fin uniformly opaque, banded, or spotted), and by reaching a maximum adult size of at least 600 mm SL (vs. <150 mm SL).

Panaque schaeferi is diagnosed from all other *P.* (*Panaque*) by having body color consisting of distinctly dark or faded black spots distributed evenly on pale gray to brown base color (vs. body color uniformly dark gray to brown or with alternating dark and light gray, brown, or black longitudinal stripes), and by having a maximum adult body size of approximately 600 mm SL (vs. no greater than approximately 400 mm SL); from all but *P. nigrolineatus* by having pelvic-fin spine terminating at posterior insertion of anal fin (vs. posterior or anterior to posterior insertion of anal fin); from *P. armbrusteri*, *P. cochliodon*, and *P. suttonorum* by pectoral-fin spine terminating coequally with anus (vs. approximately halfway between pelvic-fin base and anus); from *P. cochliodon* and *P. suttonorum* by having brown to gray

Fig. 12. Holotype of *Panaque schaeferi*, new species, MUSM 27500, 576 mm SL, Peru, Ucayali Department, Padre Abad Province, Aguaytia River drainage, Santa Ana River, Cordillera Azul National Park, 08°29′51″S, 75°33′36″W, 250 m elevation, December 2006. Scale bar = 100 mm.

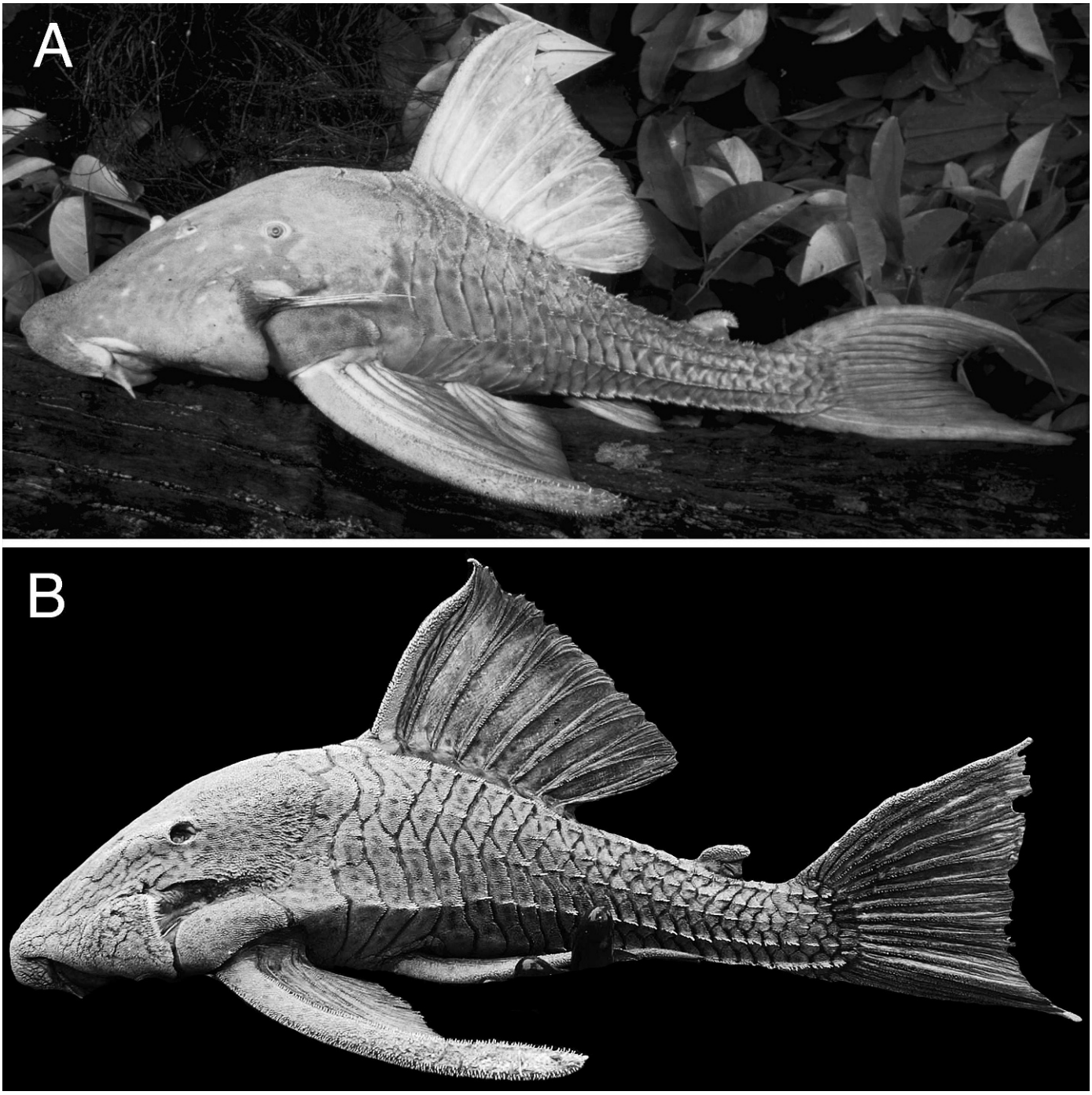

Fig. 13. (A) Uncatalogued specimen of *Panaque schaeferi*, new species, from the Amazon River main channel near Santarem, Brazil (photographed alive by M. Goulding); (B) paratype of *Panaque schaeferi*, new species, MUSM 28505, 559 mm SL, Ucayali, Peru.

eyes in live specimens (vs. blue or bluish eyes in live specimens), and by juveniles up to approximately 129 mm SL having a hyaline, anterior caudal-fin window (vs. caudal fin uniformly opaque); from *P. armbrusteri* and *P. cochliodon* by having a smoothly rounded supraoccipital (vs. supraoccipital raised as a hump, Fig. 5); from *P. armbrusteri* and *P. titan* by having infraorbital six vertical and straight (vs. dorsal half of infraorbital six strongly flared laterally, Figs. 5, 6); from *P. cochliodon* by having enlarged odontodes on trunk plates arranged as a row or rows (Fig. 7; vs. as a cluster); from *P. armbrusteri* by having fewer premaxillary and dentary teeth at equivalent body sizes (Fig. 3), by having adults with an acute interpremaxillary and intermandibular tooth row angles (vs. adults with interpremaxillary and intermandibular tooth row angles $>100^{\circ}$, Fig. 2); and from *P. titan* by having a postorbital pterotic region flush with ventral pterotic margin (Fig. 5; vs. postorbital pterotic region bulged beyond ventral pterotic margin, Fig. 6).

Panaque schaeferi is further diagnosed from *P. armbrusteri*, *P. nigrolineatus*, and *P. titan* by having a shorter predorsal length (42.5–47.9% SL vs. 48.7–54.9) and by having a greater postanal length (31.9–35.3% SL vs. 26.0–31.3); from *P. nigrolineatus* and *P. titan* by having a shorter head length (35.3–40.0% SL vs. 41.2–47.1); from *P. cochliodon* by having a wider ventral cleithral width (25.1–31.9% SL vs. 22.8–24.8), by having a shorter caudal peduncle–tip of dorsal caudal ray

length (30.2–31.5% SL vs. 36.9–46.7), and by having a greater adipose–anal distance (19.0–21.6% SL vs. 17.1–18.9); and from *P. titan* by having a greater anal-fin spine length (15.7–20.0% SL vs. 14.3–15.4), by having a narrower dorsal infraorbital width (45.8–53.8% HL vs. 68.4–76.7), and by having a greater barbel length (3.1–5.2% HL vs. 1.4–2.3).

Description.—Morphometrics in Table 3. Largest specimen 600 mm SL. Body deep and stout. Dorsal profile of snout slightly convex and rising at approximately 35° to middle of supraoccipital, then sloped slightly upward and straight or slightly convex to nuchal plate. Body depth greatest at nuchal plate. Dorsal profile posterior of nuchal plate sloped gently downward and straight or shallowly concave to posterior insertion of adipose fin, then straight and horizontal back to first dorsal procurrent caudal-fin ray; dorsal profile sloping upward at first dorsal procurrent ray. Ventral profile straight and horizontal from snout to anal-fin insertion, sloped slightly upward along anal-fin insertion, then straight back to first ventral procurrent caudal-fin ray; sloped downward at first ventral procurrent caudal-fin ray.

Entire snout, dorsal and lateral surfaces of trunk armored with plates bearing small odontodes; each trunk plate except anteriomost five or six lateral median plates with enlarged odontodes arranged as row or rows along plate midline (Fig. 7). Cheek plates bearing moderately to highly hypertrophied, distally hooked odontodes (mean 55, range 11–100, holotype = 100) evertible to approximately 90° from sagittal plane; longest odontodes extending to posterior margin of second inframedian plate (second plate behind cleithrum). Eye size variable (orbit diameter 8.1–16.1% HL); orbit positioned along lateral midline at posterior margin of middle third of head; orbit nearly flush with head, preceded by low preorbital rise (Figs. 5, 6); infraorbital plate six vertical, not flared dorsally; postorbital pterotic region flush with ventral pterotic margin. Orbit sloped ventrolaterally at approximately 30° from sagittal plane in anterior view. Postorbital notch present. Iris operculum absent.

Oral disk occupying approximately three-fourths of snout anterior of cleithrum. Interpremaxillary tooth row angle just under 90°; premaxillary teeth five to 12 (mode seven, holotype = nine). Intermandibular tooth row angle approximately 45°; dentary teeth five to 12 (mode eight, holotype = 12). Rows of short branched, fimbriate papillae immediately internal to each tooth row; single low undulating fold-like papilla contiguous across top of both premaxillae; buccal papilla absent. All teeth unicuspid and spoon-shaped; proximalmost one or two teeth smaller than others. Maxillary barbel long (1.4–4.2% HL), attached to lower lip along approximately half of length; ventral surface of labial disk with hemispherical or semicircular papillae decreasing in size distally and toward rictus; posterior margin of labial disk lacking fimbriae.

Dorsal fin II,7; dorsal-fin spinelet prominent and V-shaped; dorsal-fin lock functional; posteriormost dorsal-fin ray free from body. Pectoral fin I,6; pectoral-fin spine terminating coequally with anus when adpressed; posterodorsal and anterior surfaces of spine with slightly enlarged odontodes, anterior odontodes increasing in size and areal extent distally; distal pectoral-fin spine odontodes moderately to highly hypertrophied. Pelvic fin I,5; pelvic-fin spine extending to posterior anal-fin insertion when adpressed. Anal fin I,4; first anal-fin pterygiophore exposed as plate; first unbranched ray ossified. Adipose-fin spine sloped at approximately 30° and slightly curved along entire length or more strongly curved proximally or distally; bearing slightly enlarged odontodes along dorsal surface; adnate to caudal peduncle via fleshy membrane with straight or concave posterior margin. Caudal fin I,14,I; dorsal procurrent caudal-fin rays four or five (mode five); ventral procurrent caudal-fin rays four to six (mode five); caudal fin lunate with or without ventral and dorsal caudal-fin spines elongated as short filaments, or caudal fin truncate. Branched rays of all fins bearing small odontodes.

Body broadest at evertible cheek plates or cleithrum; cleithrum rounded or tapering to point posteriorly. Lateral median plates 24–26 (mode 25), middorsal plates 23–25 (mode 24), midventral plates 23–26 (mode 24); anteriormost four or five midventral plates strongly bent. Caudal peduncle plate rows five. One azygous preadipose plate; interdorsal plate rows four to seven (mode five). Abdomen fully plated. Modest ventrolateral caudal-peduncle keel formed by somewhat strongly angled ventral plates bearing rows of slightly enlarged odontodes medially.

Color.—Adult body and abdomen with distinctly dark black or faded black spots evenly distributed on pale gray to brown base color (Figs. 12, 13). Spot diameter similar to, or approximately half orbit diameter; spotting density variable. Fins and fin spines either spotted as body or uniformly pale gray to brown.

Ontogenetic variation.—Juvenile coloration unknown with certainty. Based on single 128.7 mm SL juvenile specimen from the Purus River (MUSM 9999) tentatively assigned to *Panaque schaeferi*, juveniles are colored differently than adults: light brown to gray body base color with irregular and indistinct, broken, and widely spaced darker brown stripes, spots, and vermiculations; caudal fin with anterior hyaline window and dark brown posterior margin. Given that adults are lacking the hyaline caudal-fin window, it seems likely that *P. schaeferi* follows a similar pattern of juvenile caudal-fin coloration change described above for *P. nigrolineatus*.

Intraspecifc variation.—Adult caudal-fin shape (lunate or truncate) and body coloration (density and darkness of spotting) are variable across the examined specimens and are treated as intraspecifically variable within *Panaque schaeferi*. Specimens from the Ucayali River in Peru, for example, have smaller, darker, and more densely spaced spots than specimens from the mainstem of the Amazon in Brazil (Figs. 12, 13).

Distribution.—Widespread in the upper Amazon (Solimões) mainstem and its tributaries in Brazil, Ecuador, and Peru including the Purus, Ucayali/Urubamba, and Pastaza Rivers, and at least as far down the Amazon River mainstem as Santarem, Brazil (M. Goulding, pers. comm. to NKL; Fig. 8).

Habitat.—*Panaque schaeferi* appears to be largely limited to main channel habitats of white- and clearwater rivers. As with other members of subgenus *Panaque* (Saul, 1975; Nonogaki et al., 2007), *P. schaeferi* has been observed by one of us in association with coarse woody debris (Hidalgo et al., 2006). Goulding (pers. comm. to NKL) also reports

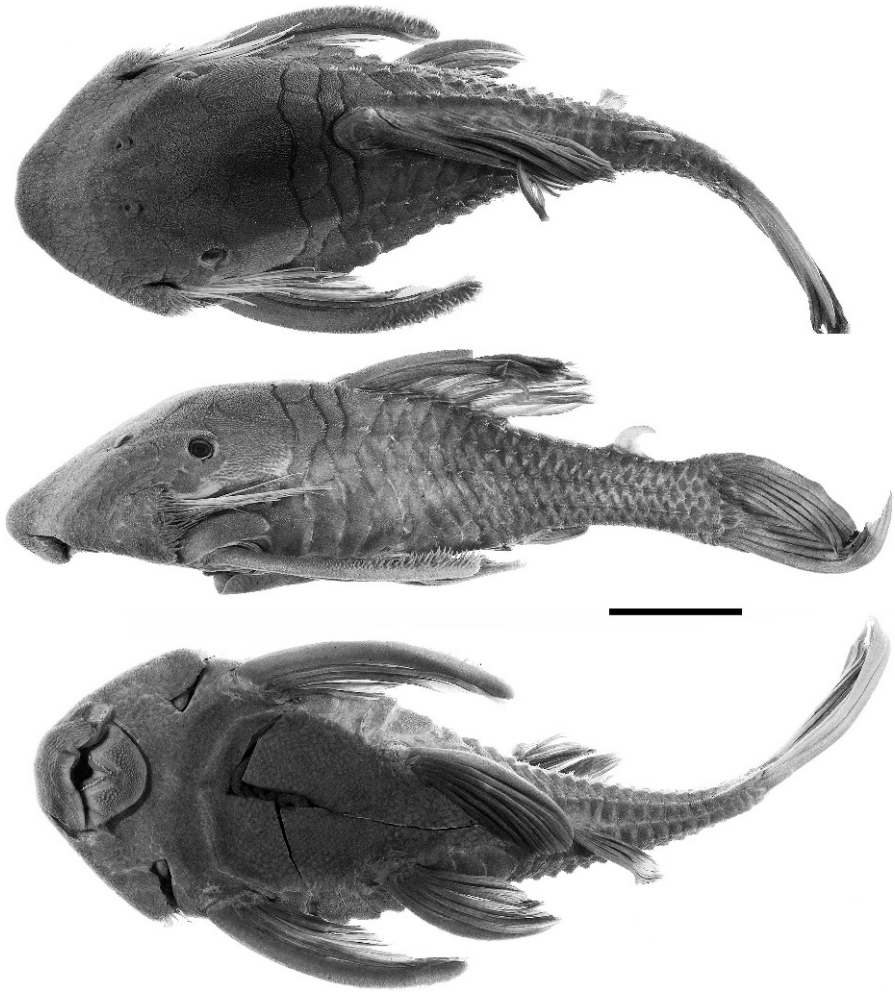

Fig. 14. Holotype of *Panaque suttoni*, USNM 121033, 278 mm SL, Negro River below Yasa River mouth, Maracaibo Lake basin, Venezuela (photos by S. Raredon). Scale bar = 50 mm.

that *P. schaeferi* are an occasional bycatch in commercial, deep-water gillnets targeting *Brachyplatystoma* spp. (Pimelodidae) in the main channel of the Amazon River.

Etymology.—Patronym honoring Scott A. Schaefer, ichthyologist, Editor of *Copeia*, and Curator of Fishes at the American Museum of Natural History, for his many contributions to the field of ichthyology, and for his contributions to our understanding of the Loricarioidea in particular. A noun in apposition.

Panaque suttonorum Schultz, 1944

Figures 14, 15; Tables 2, 3

Panaque suttoni Schultz, 1944:308 (holotype: USNM 121033; Negro River below Yasa River mouth, Maracaibo Basin, Venezuela) [description]. Isbrücker, 1980:75 [synonymy]. Burgess, 1989:437 [distribution]. Galvis et al., 1997:95 [photo, common name].

Panaque suttonorum Schultz.—Isbrücker, 2001:26,30 [synonymy]. Fisch-Muller, 2003:415 [synonymy, distribution, common names]. Ferraris, 2007:278 [type catalog].

Holotype.—USNM 121033, 1, 278 mm SL, Venezuela, Zulia State, Santa Ana River drainage, Negro River below mouth of Yasa River, 2 March 1942, L. Schultz.

Paratypes.—USNM 121034, 1, paratype of *Panaque suttoni*, 223 mm SL, Venezuela, Trujillo State, Motatán River drainage, Motatán River at bridge 22 km N of Motatán, 17 March 1942, L. Schultz. USNM 121035, 1, 268 mm SL, Venezuela, Trujillo State, Motatán River drainage, Motatán River at bridge 22 km N of Motatán, 17 March 1942, L. Schultz. USNM 121075, 1, 123 mm SL, Venezuela, Zulia State, Santa Ana River drainage, Negro River below mouth of Yasa River, 2 March 1942, L. Schultz.

Non-type material.—IAVHP 3079, 1, 216 mm SL, Colombia, Norte de Santander Department, Caribe, Catatumbo River drainage, tributary of the Zulia River, 7°22′N, 72°39′W, 19 May 2008, J. D. Bogotá.

Diagnosis.—*Panaque suttonorum* is diagnosed from all members of subgenus *Scobinancistrus* by having greater than five dentary and premaxillary teeth (vs. three or four dentary and premaxillary teeth), by dentary and premaxillary tooth cusps being unicuspid (vs. bicuspid), and by dentary and premaxillary tooth cusps being short and ladle- or spoon-shaped (vs. main tooth cusps being long and spatulate); and from all members of subgenus *Panaqolus* by having a blue or bluish eye (vs. black, gray, or brown), and by reaching a maximum adult size of at least 278 mm SL (vs. <150 mm SL).

Fig. 15. Uncatalogued specimen of *Panaque suttonorum* from the Zulia River, Venezuela (photographed alive by D. Taphorn).

Panaque suttonorum is diagnosed from all other *P.* (*Panaque*) except *P. cochliodon* by having a uniformly dark gray to black body (vs. body patterned with spots or stripes), by having a blue or bluish eye (vs. red, brown, or gray eye), and by juveniles having a uniformly opaque caudal fin (vs. juveniles up to approximately 145 mm SL with hyaline, anterior caudal-fin window); from *P. cochliodon*, *P. nigrolineatus*, and *P. schaeferi* by having pelvic-fin spine terminating between anterior and posterior insertion of anal fin when adpressed (vs. pelvic-fin spine terminating at or slightly beyond insertion of anal fin); from *P. nigrolineatus*, *P. schaeferi*, and *P. titan* by having pectoral-fin spine terminating halfway between pelvic fin and anus when adpressed ventral to pelvic fin (vs. pectoral-fin spine terminating at or coequal with anus); from *P. armbrusteri* and *P. cochliodon* by supraoccipital being smoothly rounded (vs. supraoccipital raised as a hump, Fig. 6); from *P. schaeferi* and *P. titan* by having a maximum adult body size no greater than 300 mm SL (vs. approximately 400 mm SL or greater); from *P. armbrusteri* and *P. titan* by having a vertical and flat infraorbital six (vs. dorsal half of infraorbital six flared laterally; Figs. 5, 6), and by adults having a lunate or forked caudal fin (vs. truncate); from *P. armbrusteri* by adults having acute interpremaxillary and intermandibular tooth row angles (vs. adults with interpremaxillary and intermandibular tooth row angles >100°, Fig. 2); and from *P. titan* by postorbital pterotic region being flush with ventral pterotic margin (vs. postorbital pterotic region bulged beyond ventral pterotic margin, Fig. 6).

Panaque suttonorum is further diagnosed from *P. nigrolineatus* and *P. titan* by having a narrower cleithral width (29.3–33.5% SL vs. 33.8–38.6); from *P. cochliodon* by having a greater abdominal length (23.7–25.2% SL vs. 20.6–23.7); from *P. titan* by having a lesser dorsal–pelvic depth (24.9–28.8% SL vs. 29.1–32.1); from *P. titan* by having a greater dorsal–adipose distance (14.8–19.3% SL vs. 11.4–14.5); from *P. cochliodon* by having a lesser adipose–lower caudal depth (18.3–21.0% SL vs. 21.3–24.0); from *P. armbrusteri* by having a greater head–eye length (33.7–40.4% HL vs. 41.4–44.9); and from *P. titan* by having a greater barbel length (3.1–7.2% HL vs. 1.4–2.3).

Description.—Morphometrics in Table 3. Largest specimen 278 mm SL. Body deep and broad. Dorsal profile of snout rising at approximately 35° to middle of supraoccipital, then approaching horizontal back to nuchal plate. Body depth greatest at nuchal plate or approximately coequal with predorsal plates and posterior margin of supraoccipital. Dorsal profile posterior of nuchal plate sloped gently downward and approximately straight to posterior insertion of adipose-fin membrane, then sloping upward slightly to first dorsal procurrent caudal-fin ray, upward slope increasing at first dorsal procurrent caudal-fin ray. Ventral profile straight and horizontal from snout to pelvic-fin insertion, sloped slightly upward to posteriormost insertion of anal fin, then either straight or with distinct concavity back to first ventral procurrent caudal-fin ray; downward slope increasing slightly at first ventral procurrent caudal-fin ray.

Entire snout, dorsal and lateral surfaces of trunk armored with plates bearing small odontodes; each trunk plate with distinct posteromedial cluster or medial row of enlarged odontodes increasing in size posteriorly. Cheek plates bearing minimally to highly hypertrophied, distally hooked odontodes (mean 52, range 43–56, holotype = 56) evertible to approximately 90° from sagittal plane; longest odontodes extending to posterior margin of second midventral plate. Eye large (orbit diameter 10.3–16.7% HL); orbit positioned dorsal of lateral midline at anterior margin of posterior third of head; orbit accentuated by modest preorbital crest (Figs. 5, 6); infraorbital plate six vertical, not flared dorsally; postorbital pterotic region flush with ventral pterotic margin; orbit sloped ventrolaterally at approximately 45° from sagittal plane in anterior view. Postorbital notch present or absent. Iris operculum not observed in preserved specimens although present in live specimen (Fig. 15).

Oral disk occupying approximately two-thirds to three-fourths of snout anterior of cleithrum. Interpremaxillary tooth row angle approximately 45–90°; premaxillary teeth six to nine (mode seven, holotype = eight). Intermandibular tooth row angle acute; dentary teeth seven to nine (mode seven, holotype = nine). Rows of branched, fimbriate papillae immediately internal to each tooth row; single low unseparated fold-like papilla contiguous across top of

both premaxillae; buccal papilla absent. All teeth unicuspid and spoon-shaped; proximalmost one to two teeth smaller than other teeth. Maxillary barbel relatively long (2.8–5.1% HL), attached to lower lip along approximately half of length; ventral surface of labial disk with hemispherical or semicircular papillae decreasing in size distally and toward rictus; posterior margin of labial disk lacking fimbriae.

Dorsal fin II,7; dorsal-fin spinelet prominent and V-shaped; dorsal-fin lock functional; posteriormost dorsal-fin ray free from body. Pectoral fin I,6; pectoral-fin spine terminating approximately halfway between posterior insertion of pelvic fin and anus when adpressed ventral to pelvic fin; posterodorsal and anterior surfaces of spine with slightly enlarged odontodes, anterior odontodes increasing in size and areal extent distally; distal pectoral-fin spine odontodes moderately to highly hypertrophied. Pelvic fin I,5; pelvic-fin spine terminating between anterior and posterior insertion of anal fin when adpressed. Anal fin I,4; first pterygiophore exposed as plate; first unbranched ray ossified. Adipose-fin spine sloped at approximately 60° and slightly curved along entire length or more strongly curved distally; bearing slightly enlarged odontodes along dorsal surface; adnate to caudal peduncle via fleshy membrane with concave posterior margin. Caudal fin I,14,I; dorsal procurrent caudal-fin rays four or five (mode four); ventral procurrent caudal-fin rays four or five (mode five); caudal fin shallowly lunate or slightly forked. Branched rays of all fins bearing small odontodes.

Body broadest at evertible cheek plates; cleithrum tapering to point or rounded posteriorly. Lateral median plates 26–28 (mode 26), middorsal plates 24–26 (mode 24), midventral plates 25–27 (mode 25); anteriormost five or six midventral plates strongly bent. Caudal peduncle plate rows five. One azygous preadipose plate; interdorsal plate rows five to eight (mode six). Abdomen fully plated. Modest ventrolateral caudal-peduncle keel formed by somewhat strongly angled ventral plates bearing rows of slightly enlarged odontodes medially.

Color.—All paratypes uniformly pale and bleached. Holotype uniformly brown. Live specimen photographed by D. Taphorn (Fig. 15) uniformly dark gray to black with pale bluish eyes.

Distribution.—Endemic to the Lake Maracaibo basin in Venezuela and Colombia including the Catatumbo, Santa Ana, and Motatán River drainages.

Habitat.—Local fishermen interviewed in 2007 by D. Taphorn (UNELLEZ, pers. comm.) report that *Panaque suttonorum* are most frequently collected in slack water at the mouths of rivers where they join Lake Maracaibo.

Remarks.—Isbrücker (2001) recommended that since Schultz (1944:311) named this species after 'Dr. and Mrs. Frederick A. Sutton,' the singular species epithet *suttoni* should be pluralized to *suttonorum*.

Panaque titan, new species
Figures 6, 10C, 16; Tables 1, 2

Panaque nigrolineatus.—Saul, 1975 [ecology].

Holotype.—MEPN 9507, 1, 394.0 mm SL, Ecuador, Sucumbíos Province, Napo River drainage, Apoalla Creek, tributary of the lower Shushufindi River, 0°17′S, 76°27′W, 24 November 1983, D. Stewart, M. Ibarra, and R. Barriga.

Paratypes.—All Ecuador, Napo River drainage: FMNH 97589, 1, 334.0 mm SL, MEPN 3015, 1, 307 mm SL, Sucumbíos Province, Shushufindi River, lower reaches about 2 km upstream from mouth in Aguarico River, 0°17′30″S, 76°25′36″W, 24–25 November 1983, D. Stewart, M. Ibarra, and R. Barriga. FMNH 97591, 145.1 mm SL, Orellana Province, Napo River at Pompeya (night), north shore, 0°26′30″S, 76°38′12″W, 7 October 1981, D. Stewart, M. Ibarra, R. Barriga, and C. Uquillas. FMNH 118290, 1, 351.0 mm SL, Sucumbíos Province, Apoalla Creek, tributary of the lower Shushufindi River, 0°17′S, 76°27′W, 24 November 1983, D. Stewart, M. Ibarra, and R. Barriga. IAVHP 1620, 133.9 mm SL, Orellana Province, Napo River below mouth of Coca River, 7 March 1987, O. Pinto. KU 13907, 1, 342.0 mm SL, Sucumbíos Province, Aguarico River at Santa Cecilia, approx. 0°4′N, 76°59.5′W, 13 March 1967, W. G. Saul and G. Smith. MEPN 9508, 3, 134–154 mm SL, Orellana Province, Rio Yasuni at confluence with Rio Jatuncocha, gill net set along shore, 0°59′43″S, 75°26′00″W, 10 April 1998, D. Stewart and R. Barriga-Salazar. MEPN 3014, 1, 385 mm SL, Orellana Province, Yaunda Lake near San Jose de Payamino, approx. 0°30.5′S, 77°18′W, 21 December 1983, N. Irvine and D. Jipa.

Diagnosis.—*Panaque titan* is diagnosed from all members of subgenus *Scobinancistrus* by having greater than six dentary and premaxillary teeth (vs. three or four dentary and premaxillary teeth), by dentary and premaxillary tooth cusps being unicuspid (vs. bicuspid), and by dentary and premaxillary tooth cusps being short and ladle- or spoon-shaped (vs. main tooth cusps being long and spatulate); and from all members of subgenus *Panaqolus* by having a body color pattern consisting of irregular and widely spaced dark gray to brown stripes and spots on light brown to tan base color (vs. body color pattern consisting of white spots on a black base or vertical and/or oblique bands), by individuals <145 mm SL having a hyaline caudal-fin window (vs. caudal-fin uniformly opaque, banded, or spotted), and by reaching a maximum adult size of at least 394 mm SL (vs. <150 mm SL).

Panaque titan is diagnosed from all other *P.* (*Panaque*) by having postorbital region of the pterotic bulged beyond ventral pterotic region (Fig. 6; vs. postorbital pterotic region flush with ventral pterotic margin, Fig. 5). *Panaque titan* is diagnosed from all other *P.* (*Panaque*) but *P. armbrusteri* by dorsal half of infraorbital six being strongly flared laterally (Fig. 6; vs. infraorbital six being vertical and straight or only slightly flared laterally at dorsalmost margin), and by adult caudal fin being truncate (vs. lunate or forked); from *P. armbrusteri*, *P. cochliodon*, and *P. suttonorum* by having pectoral-fin spine terminating coequally with anus when adpressed ventral to pelvic fin (vs. pectoral-fin spine terminating between posteriormost pelvic-fin insertion and anus); from *P. cochliodon*, *P. nigrolineatus*, and *P. suttonorum* by maximum adult body size being approximately 400 mm SL (vs. maximum adult body size no greater than approximately 300 mm SL); from *P. cochliodon*, *P. schaeferi*, and *P. suttonorum* by having body color consisting of irregular and widely spaced dark gray to brown stripes and spots on light brown to tan base color (vs. body color uniformly dark gray to black or with distinct or faded black spots on pale gray to brown base color); from *P. armbrusteri* and *P. cochliodon* by supraoccipital being smoothly rounded (vs. supraoccipital raised as a hump); from *P. cochliodon* and

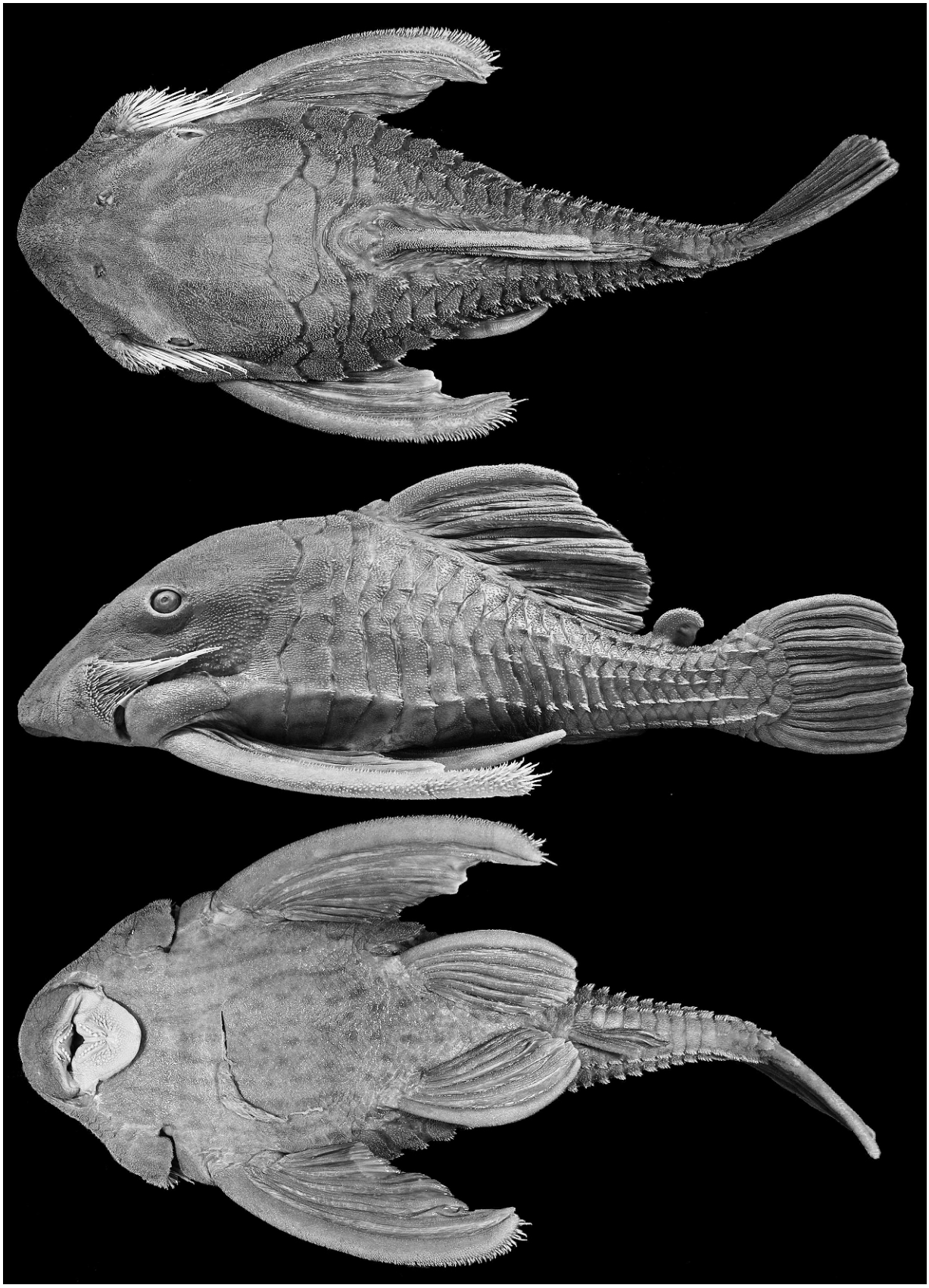

Fig. 16. Holotype of *Panaque titan*, new species, MEPN 9507, 394 mm SL, Ecuador, Sucumbíos Province, Napo River drainage, Apoalla Creek, tributary of the lower Shushufindi River, 0°17′S, 76°27′W, 24 November 1983.

P. suttonorum by juveniles up to approximately 145 mm SL having a hyaline, anterior caudal-fin window (vs. juveniles with uniformly opaque caudal fin), and by having brown eye color (vs. blue or bluish); from *P. cochliodon* by having enlarged odontodes on trunk plates produced as row or rows (Fig. 7; vs. as clusters); and from *P. armbrusteri* by having fewer premaxillary and dentary teeth at equivalent body sizes (Fig. 3), and by adults having acute interpremaxillary and intermandibular tooth row angles (vs. adults with interpremaxillary and intermandibular tooth row angles >100°).

Panaque titan is further diagnosed from *P. armbrusteri*, *P. schaeferi*, and *P. suttonorum* by having a lesser barbel length (1.4–2.3% HL vs. 3.1–7.2); from *P. cochliodon* and *P. schaeferi* by having a greater predorsal length (49.2–51.7% SL vs. 42.5–48.3), by having a greater head length (42.6–47.1% SL vs. 35.3–40.9), and by having a lesser postanal length (26.0–28.5% SL vs. 31.9–36.0); from *P. cochliodon* and *P. suttonorum* by having a greater cleithral width (34.4–37.0% SL vs. 29.3–33.5), and by having a greater dorsal–pelvic depth (29.1–32.1% SL vs. 24.9–28.8); from *P. armbrusteri* and *P. cochliodon* by having a lesser mouth width (25.2–28.9% HL vs. 31.5–47.3); from *P. cochliodon* by having a greater ventral cleithral width (25.5–28.8% SL vs. 22.8–24.8), by having a greater pelvic girdle width (18.2–19.7% SL vs. 16.9–18.0), by having a greater dorsal–pectoral depth (34.1–38.4% SL vs. 29.6–32.8), by having a lesser adipose–upper caudal distance (10.6–12.4% SL vs. 14.6–19.3), by having a greater adipose height (4.1–5.7% SL vs. 2.1–3.8), by having a lesser adipose–lower caudal depth (16.8–19.1% SL vs. 21.3–24.0), by having a greater dorsal–anal depth (17.1–18.7% SL vs. 14.4–16.6), by having a greater snout length (68.2–73.8% HL vs. 64.3–68.0), and by having a greater internares width (17.4–19.9% HL vs. 12.7–17.1); from *P. armbrusteri* by having a lesser mouth length (33.2–36.5% HL vs. 37.6–51.3) and by having a lesser dentary tooth cup length (9.7–10.6% HL vs. 11.5–16.1); from *P. schaeferi* by having a greater thorax length (23.8–25.9% SL vs. 19.1–23.1) and by having a lesser anal-fin spine length (14.3–15.4% SL vs. 15.7–20.0); and from *P. suttonorum* by having a lesser dorsal–adipose distance (11.4–14.5% SL vs. 14.8–19.3).

Description.—Morphometrics in Table 3. Largest specimen 394 mm SL. Body deep and stout. Dorsal profile of snout straight and rising at approximately 35° to middle of supraoccipital, then sloped slightly upward and straight or slightly convex to nuchal plate; body depth greatest at nuchal plate. Dorsal profile posterior of nuchal plate sloped gently downward and straight or shallowly concave to anterior insertion of adipose fin, becoming horizontal across adipose-fin insertion and sloping upward at first dorsal procurrent caudal-fin ray. Ventral profile straight and horizontal from snout to anal-fin insertion, sloped slightly upward along anal-fin insertion, then straight and horizontal back to first ventral procurrent caudal-fin ray; sloped downward at first ventral procurrent caudal-fin ray.

Entire snout, dorsal and lateral surfaces of trunk armored with plates bearing small odontodes; each trunk plate except anteriormost four to seven lateral median plates, one to three middorsal plates, and one or two dorsal plates with enlarged odontodes arranged as row or rows along plate midline (Fig. 7). Cheek plates bearing moderately to highly hypertrophied, distally hooked odontodes (mean 60, range 42–77, holotype = 77) evertible to approximately 90° from sagittal plane; longest odontodes extending to posterior margin of cleithrum. Eye large (orbit diameter 9.3–13.8% HL); orbit positioned along lateral midline at anterior margin of posterior third of head in juveniles and at posterior margin of middle third of head in adults due to ontogenetic increase in relative size of pterotic; orbit accentuated by projecting slightly laterally from head contours and by preorbital crest (Fig. 6); dorsal half of infraorbital plate six sloped laterally (Fig. 6); roof of orbit laterally projected as supraorbital shelf formed by sphenotic with horizontal or shallowly sloped lateroventral half and more strongly sloped dorsomedial half; orbital ridge continuing posteriorly into pterotic as postorbital pterotic bulge raised above ventral pterotic margin (Fig. 6). Orbit sloped ventrolaterally at about 30° from sagittal plane in anterior view. Postorbital notch present (Fig. 6). Iris operculum present.

Oral disk occupying approximately three-fourths of snout anterior of cleithrum. Interpremaxillary tooth row angle just under 90°; premaxillary teeth seven or eight (mode seven, holotype = seven). Intermandibular tooth row angle acute; dentary teeth seven or eight (mode eight, holotype = eight). Rows of short, branched, fimbriate papillae immediately internal to each tooth row; single semicircular flange-like papilla at posteromedial corner of each premaxilla; buccal papilla absent. All teeth unicuspid and spoon-shaped; proximalmost one or two teeth smaller than others. Maxillary barbel short and attached to lower lip along most of length; ventral surface of labial disk with hemispherical or semicircular papillae decreasing in size distally and toward rictus; posterior margin of labial disk lacking fimbriae.

Dorsal fin II,7; dorsal-fin spinelet prominent and V-shaped; dorsal-fin lock functional; posteriormost dorsal-fin ray free from body. Pectoral fin I,6; pectoral-fin spine terminating coequally with anus when adpressed; posterodorsal and anterior surfaces of spine with slightly enlarged odontodes, anterior odontodes increasing in size and areal extent distally; distal pectoral-fin spine odontodes moderately to highly hypertrophied. Pelvic fin I,5; pelvic-fin spine terminating at anterior or middle of anal-fin insertion when adpressed. Anal fin I,4; first pterygiophore exposed as plate; first unbranched ray ossified. Adipose-fin spine oriented vertically or at approximately 60° and slightly curved along entire length or more strongly curved distally; bearing slightly enlarged odontodes along dorsal surface; adnate to caudal peduncle via fleshy membrane with straight or concave posterior margin. Caudal fin I,14,I; dorsal procurrent caudal-fin rays five; ventral procurrent caudal-fin rays five or six (mode five); caudal fin truncate. Branched rays of all fins bearing small odontodes.

Body broadest at evertible cheek plates or cleithrum; cleithrum squared, rounded or tapered to point posteriorly. Lateral median plates 24 or 25 (mode 25), middorsal plates 23–25 (mode 24), midventral plates 24 or 25 (mode 24); anteriormost five or six midventral plates strongly bent. Caudal peduncle plate rows five. One azygous preadipose plate; interdorsal plate rows six or seven (mode six). Abdomen fully plated. Modest ventrolateral caudal-peduncle keel formed by somewhat strongly angled ventral plates bearing rows of slightly enlarged odontodes medially.

Color.—Body, paired fins, dorsal fin, and anal fin with irregular and widely spaced dark gray to brown stripes and

spots on light brown to tan base color; abdomen with dark gray to brown spots, irregular widely spaced stripes, and/or loops on light brown to tan base color. Juveniles with caudal fin hyaline except for dark brown spines and posterior margin; dark brown posterior margin expanding anteriorly and hyaline region reducing with age and body size so that adult caudal fin is entirely opaque and dark brown. Largest specimen observed with hyaline caudal-fin window present 145.1 mm SL (Fig. 10C). A photo of the freshly collected Payamino River basin specimen (MEPN 3014) by N. Irvine shows a yellow-orange distal margin on the caudal fin reminiscent of that in *Panaque armbrusteri* (Fig. 4).

Distribution.—Known only from relatively large rivers in lowland and piedmont habitats of the Napo River basin, Ecuador.

Ecology.—Saul (1975:120) conducted an ecological study of the fishes in the Napo River in Ecuador and reported the following in regard to a single specimen of *Panaque titan*, new species (KU 13907; originally identified as *P. nigrolineatus*, ANSP 130587): ''taken in an inlet of the Río Aguarico in deep fast-moving water (1.0–2.5 m deep) where submerged trees, limbs, and logs formed a mass of snags. The bottom in this area was rock, giving way to a quietly flowing, sandy-bottomed pool. Stomach contents.—Plant debris (78 cc).'' Many of the other type specimens came from similarly deep waters, and those that were examined had mostly wood particles in their anterior gut.

Etymology.—From the Greek Titan, son or daughter of Uranus and Gaea, representing brute force and large size, masculine.

DISCUSSION

All members of subgenus *Panaque* are distinguished by having a pterotic that is much larger relative to head length (Figs. 1, 4, 5, 6, 9, 11, 13, 16) than most other loricariids we have examined (*Acanthicus*, *Megalancistrus*, *Otocinclus*, *Otothyris*, *Pseudotothyris*, and 'new genus 1' of Armbruster [2008] being exceptions). Although small sample sizes prevented us from examining the internal osteology of *Panaque* (*Panaque*) spp. other than *P. nigrolineatus*, the pterotic forms the external wall of the gas bladder capsule in all Loricariidae (Alexander, 1964), and an enlarged pterotic indicates congruent enlargement of this structure. Armbruster (2004) recovered an enlarged gas bladder and gas bladder capsule as autapomorphic for *P. nigrolineatus*, but this was the only member of subgenus *Panaque* he examined. Given the ubiquity of relatively large pterotics across subgenus *Panaque*, we hypothesize that this characteristic is more broadly synapomorphic for the subgenus. Also, all species of *P.* (*Panaque*) for which we had sufficient sample sizes to draw conclusions exhibit an allometric increase in numbers of upper and lower jaw teeth (Fig. 3). In contrast, Schaefer and Stewart (1993) observed an ontogenetic shift to fewer, larger, more unicuspid and spoon-shaped teeth in *P. (Panaqolus) maccus*, although the relationship was weak and may have been confounded by the inclusion of many aquarium-raised specimens. Likewise, unpublished analyses of the majority of *Peckoltia* spp. by the first author, using data from Armbruster (2008), showed mostly negative or insignificant relationships between SL and numbers of dentary and premaxillary teeth. Given the apparent ubiquity of ontogenetic increases in oral tooth number in *P.* (*Panaque*; Fig. 3) and the contrasting pattern observed in *Peckoltia* and subgenus *Panaqolus*, we hypothesize that this ontogenetic dentition trend is a second synapomorphy for subgenus *Panaque*.

Within subgenus *Panaque*, *P. armbrusteri* has the most teeth and exhibits the greatest increase in tooth number (Fig. 3). *Panaque armbrusteri* is also the only loricariid known to exhibit an ontogenetic increase in interpremaxillary and intermandibular tooth row angles (Fig. 2). Together, these ontogenetic trends contrast with prevailing evolutionary trends among wood-eating loricariids, and suggest that *P. armbrusteri* is one of the most specialized members of the subgenus. Indeed, ontogenetic shifts observed by Schaefer and Stewart (1993) in *P.* (*Panaqolus*) *maccus* more closely parallel evolutionary trends apparent in the most recent genus-level phylogenetic hypothesis for Loricariidae (Armbruster, 2008), which recovered genus *Panaque* as nested within a clade otherwise consisting entirely of *Peckoltia*, a genus characterized by greater numbers of smaller, more comb-shaped teeth than genus *Panaque* (Armbruster, 2008).

These same phylogenetic and ontogenetic trends toward fewer, more spoon-shaped teeth have also been observed in the *Hypostomus cochliodon*-group (Armbruster, 2003a). Both *Panaque* and the *H. cochliodon*-group specialize on a diet of wood (Saul, 1975; Schaefer and Stewart, 1993; Armbruster, 2003a, 2008; German, 2009), which allows most dental and oral osteological synapomorphies of genus *Panaque* to be viewed as evolutionarily adaptive. The spoon-shaped, unicuspid teeth of *Panaque* are similar in shape to the head of an adz, a tool designed specifically for gouging wood. The robust oral osteology of *Panaque,* including hyomandibular and preopercle with greatly expanded crest for origin of a hypertrophied adductor mandibulae, anteromedial premaxillary margin forming a notch to accommodate hypertrophied premaxillary ligaments, and a broad quadrate condyle for articulation with the mandible (Schaefer and Stewart, 1993) can all be interpreted as adaptations for producing and transmitting greater forces during feeding. Indeed, similarly reinforced jaws and hypertrophied musculature have been independently and repeatedly correlated with durophagous, surface gouging modes of feeding among coralivorous marine parrotfishes (Scaridae; Streelman et al., 2002). Given the apparently strongly selective trend toward decreased interpremaxillary and intermandibular tooth row angles accompanying these specializations, the divergence from this pattern observed in *P. armbrusteri* (Fig. 2) is ecomorphologically curious and deserving of further phylogenetic and ecological study.

With the inclusion of *Panaque titan*, which grows to at least 394 mm SL, and *P. schaeferi*, which grows to at least 600 mm SL, *Panaque* is one of the largest body-sized radiations within Loricariidae. Only the *Acanthicus*-clade of Armbruster (2008), which reaches sizes of up to 628 mm SL (*Acanthicus hystrix*, C. Chamon, MZUSP, pers. comm.) and is sister to the clade of *Panaque* + *Peckoltia* (Armbruster, 2008), is comparable. Both the *Acanthicus*-clade and genus *Panaque* also include species that are among the smallest Hypostominae: ''New genus 1'' of Armbruster (2008) is an undescribed member of the *Acanthicus*-clade that reaches a maximum known body size of 42 mm SL (Lujan, unpubl.), and *P. gnomus* reaches a maximum known body size of 71 mm SL (Schaefer and Stewart, 1993). Over eight-fold

variation in body size can therefore be observed within genus *Panaque*, versus approximately 14-fold variation in body size observable within the *Acanthicus*-clade. Although comparable length and weight data are not available for large specimens of *P. schaeferi* and *A. hystrix*, *P. schaeferi* has a much deeper body and larger head than *A. hystrix*, suggesting that *P. schaeferi* is heavier than *A. hystrix* at equivalent body lengths and is likely the largest loricariid species in terms of weight, if not also in terms of length.

The distribution of interspecifically variable morphological characteristics (Table 2) across *Panaque* (*Panaque*) suggests that this trans-Andean subgenus may be divided into separate trans- and cis-Andean clades: a northwestern South American trans-Andean clade comprised of *P. cochliodon* (Magdalena River basin) and *P. suttonorum* (Lake Maracaibo basin), and a cis-Andean clade including all remaining species distributed mostly across western and upper tributaries of the Orinoco River and western and southern tributaries of the Amazon River (Fig. 8). *Panaque cochliodon* and *P. suttonorum* are united by having blue or bluish eye color, a uniform head and body color, and by juveniles having a uniformly colored caudal fin lacking a hyaline window (Table 2). These species also have a relatively shallow body depth as compared to others (Tables 1, 3). All other *P.* (*Panaque*) species, in contrast, have more robust bodies, red, brown, or gray eye color, striped or spotted head and body coloration, and juveniles with a hyaline caudal-fin window (Table 2). Allopatric distribution of these putative clades on opposite sides of the Merida Andes suggests that origin of the *P.* (*Panaque*) lineage at least predates early major uplift of the Merida Andes in the Late Oligocene, approximately 28–23 million years ago (Villamil, 1999). The fossil record supports a younger minimum age for *Panaque* of 11.6–5.3 million years based on a single, robust pectoral-fin spine fragment recovered from the Late Miocene La Venta formation in Colombia and tentatively referred to *Panaque* (*Panaque*) by J. Lundberg (pers. comm. to NKL, fragment illustrated in Lundberg, 1997:fig. 5.13).

Despite the broad geographic ranges and highly distinctive morphologies of the new species described here, over 65 years have passed since the last new species of *Panaque* (*Panaque*) has been described. Specimens of *P.* (*Panaque*) remain scarce in collections and, at present, such scarcity permits us to only hint at further geographic, morphological, and, likely, taxonomic diversity (Fig. 8). There are large open areas on our map, reflecting, in part, the difficulty of collecting sedentary fishes that live among coarse woody debris and in deep river channels (Lujan and Chamon, 2008). We hope that our clarifications of species boundaries may assist with resolving the status of additional populations of *P.* (*Panaque*) mentioned both here and by various authors over the past 110 years, from Eigenmann and Eigenmann (1889, 1890) to Buckup et al. (2007) and Nonogaki et al. (2007).

ACKNOWLEDGMENTS

We gratefully acknowledge assistance of the following museums and museum staff in the loan of specimens and for their generosity in tracking down specimen data: M. Sabaj Pérez (ANSP), D. Werneke (AUM), D. Catania (CAS), M. Rogers and P. Willink (FMNH), M. Retzer (INHS), M. Rocha (INPA), A. Bentley (KU), K. Hartel and A. Williston (MCZ), R. Barriga-Salazar (MEPN), O. Oyakawa (MZUSP), and S. Raredon and J. Williams (USNM). NKL wishes to further thank J. Birindelli, L. Sousa, and A. Netto-Ferreira for facilitating his participation in Brazilian fieldwork yielding type specimens of *Panaque armbrusteri*, and K. Winemiller for providing a salary during the completion of this project. MH wishes to further thank J. David-Bogota and J. Maldonado (IAVHP), F. Lima and O. Oyakawa (MZUSP), and R. Leite, L. Rapp Py-Daniel, and A. Akama (INPA) for their hospitality and logistical support during his visits to these museums. This project represents part of Planetary Biodiversity Inventory: All Catfish Species (Siluriformes), a five-year grant through the U.S. National Science Foundation to describe all species of catfishes (NSF DEB-0315963) and NSF grant DEB-0107751 to J. Armbruster. In order to maintain the surprise to those honored, this manuscript went through the review process with pseudonyms and artificial etymologies for the new species described as *Panaque armbrusteri* and *P. schaeferi*.

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