

***Panaque nigrolineatus laurafabianae*, a new, commercially exploited subspecies of ornamental wood-eating pleco (Loricariidae: Hypostominae) from the Guaviare River basin in Colombia**

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Abstract

The suckermouth armored catfish genus *Panaque* contains seven valid species, including the Royal Pleco, *Panaque nigrolineatus*, which has long been popular as an ornamental aquarium fish and was originally described from the Apure River basin in Venezuela. We examine a phenotypically distinct population of *P. nigrolineatus* from the Guaviare River in southern Colombia at the southwesternmost corner of the Orinoco River basin. In contrast to typically boldly striped populations from closer to the type locality of *P. nigrolineatus*, the Guaviare River basin population is usually boldly spotted, earning them the common name Watermelon Pleco in the aquarium fish trade. Because of the commercial popularity of this distinctive color morph, it is heavily exploited for export to the global ornamental fish trade. We find that the Guaviare River *P. nigrolineatus laurafabianae* is not only distinct geographically and in color pattern, but is also morphometrically diagnosable from *P. nigrolineatus* individuals from outside the Guaviare River basin. However, relatively subtle phenotypic differences, invariance in nuclear DNA markers, < 0.5% divergence in mitochondrial DNA markers 16S, cytb, and ND2, and the non-monophyly of Guaviare River populations prevent us from robustly inferring species-level distinctiveness of the Watermelon Pleco. We therefore propose to recognize this population as a distinct subspecies.

Resumen

El género *Panaque* corrientemente con siete especies validas, incluye la cucha real *Panaque nigrolineatus*, que fue descrita para la cuenca del río Apure en Venezuela y durante muchos años ha sido popular como pez ornamental. En este estudio, examinamos una población fenotípicamente distinta de *P. nigrolineatus* del río Guaviare, en el sur de Colombia, en el extremo suroeste de la cuenca del río Orinoco. En contraste con los individuos de *P. nigrolineatus sensu stricto* que tienen el cuerpo típicamente cubierto de rayas, los individuos provenientes de la cuenca del río Guaviare tienen el cuerpo cubierto por puntos por lo que se conocen con el nombre común de cucha real de punto o full punto en el comercio de peces ornamentales. Debido a la popularidad comercial de este patrón de coloración, las poblaciones del río Guaviare son fuertemente explotados para su exportación al comercio global de peces ornamentales. Encontramos que *P. nigrolineatus laurafabianae* del río Guaviare no solo es distinta geográficamente y por el patrón de coloración, sino que también es diagnosticable morfométricamente de los individuos de *P. nigrolineatus* externos a la cuenca del río Guaviare. Por lo tanto proponemos reconocer a la población del río Guaviare como una subespecie distinta, ya que las diferencias fenotípicas relativamente sutiles y complicadas, sumadas a la evidencia genética conflictiva, nos impiden proponer que esta población sea una especie diferente.

Key words: Taxonomy, Neotropics, Orinoco, coloration, wood-eating, ornamental aquarium fishes

Introduction

The Neotropical wood-eating catfish genus *Panaque* Eigenmann & Eigenmann (1889) is monophyletic (Armbruster 2004, 2008; Lujan *et al.* 2015, 2017) and comprises seven valid species that are allopatrically distributed across the Amazon, Orinoco, Magdalena, and Lake Maracaibo basins in South America. Four species of *Panaque* are recognized from the Amazon basin: *P. armbrusteri* Lujan, Hidalgo & Stewart (2010) from southern tributaries of the lower Amazon, *P. bathyphilus* Lujan & Chamon (2008) from central and southwestern tributaries of the upper Amazon, *P. schaeferi* Lujan, Hidalgo & Stewart (2010) from main channel habitats throughout the Amazon River and its western tributaries, and *P. titan* Lujan, Hidalgo & Stewart (2010) from the lower Napo River. Only one species each is currently recognized from the Orinoco, Magdalena and Lake Maracaibo basins: *P. nigrolineatus* (Peters, 1877) from throughout the western Orinoco River basin, *P. cochliodon* (Steindachner, 1879) from main channels of the Magdalena River basin, and *P. suttonorum* Schultz (1944) from southern tributaries of the Lake Maracaibo basin.

Species of *Panaque* are externally diagnosed from all but three other genera in the suckermouth armored catfish family Loricariidae by having relatively few (<25) teeth per jaw ramus that are short, robust, and rigid with single broad, spoon-shaped cusps (vs. generally elongate, gracile, and flexible teeth with flattened, acute cusps) and by having upper and lower jaw teeth arranged in contralateral rows that form an acute angle relative to each other. The only other loricariid genera that share all of these oral characteristics are *Panaqolus* and species of the *Hypostomus cochliodon* group. These species with spoon-shaped teeth specialize on diets consisting largely of wood particles scraped from dead submerged logs (Lujan *et al.* 2011). *Panaque* can be diagnosed from the *H. cochliodon* group by having clusters of evertible cheek odontodes at the posteroventral corners of the head (vs. evertible cheek odontodes absent), and from *Panaqolus* by having larger adult body sizes (>15 cm SL), a hyaline caudal-fin window in juveniles of most species (excluding *Panaque cochliodon* and *P. suttonorum*; vs. uniformly opaque, banded, or spotted caudal fin in juveniles and adults), and body coloration consisting of a uniformly dark gray or black base color with or without black spots or longitudinal brown stripes (vs. black base color with white, blue, brown or gold spots or vertical to oblique bands). Additional internal osteological and DNA sequence data strongly support the monophyly of each of these groups (Armbruster 2004, 2008; Lujan *et al.* 2015, 2017). A fourth genus, *Pseudoqolus*, has similarly few (4–6) teeth per jaw ramus that are short, robust, and rigid with broad cusps; however, *Pseudoqolus* is endemic to the upper Maroni River basin in French Guiana where *Panaque* does not occur and its teeth are typically bicuspid (vs. unicuspid in the genera above).

Within *Panaque*, species are most easily distinguished by geographic range and combinations of body coloration, morphology of the caudal-fin and mouth, and counts of teeth and odontodes (Lujan *et al.* 2010). *Panaque cochliodon* and *P. suttonorum* have uniformly gray to black bodies, blue or blueish-gray eyes, and lunate caudal fins, with *P. cochliodon* having a generally darker body and more intensely blue eye. Four species (*P. armbrusteri*, *P. bathyphilus*, *P. nigrolineatus*, and *P. titan*) have varying degrees of longitudinal striping, with *P. armbrusteri* and *P. nigrolineatus* being the most boldly and uniformly striped species, and *P. bathyphilus* and *P. titan* having more faded and/or irregularly broken striping. *Panaque armbrusteri* is distinguished from *P. nigrolineatus* by having more premaxillary and dentary teeth at all body sizes, whereas *Panaque titan* is distinguished from all other striped species by its larger (>390 mm SL) more robust head and body. All of the striped species have truncate caudal fins except *Panaque bathyphilus*, which is distinguished from all congeners by having the dorsal and ventral caudal-fin spine elongated as filaments. Only one species, *Panaque schaeferi*, is heavily spotted as an adult, having a pale gray to brown base color with body and fins covered in evenly distributed round black spots similar in size to the eye.

In addition to being ecologically distinctive trophic specialists (Lujan *et al.* 2011, 2012), many species and populations of *Panaque* are exploited for the global trade in ornamental aquarium fishes, where they are highly valued for their bold color patterns, distinctive morphologies and large body sizes. Aquarists and ornamental fish collectors are particularly drawn to fishes with unusual color patterns, which places hobbyists at the forefront of taxonomic discovery, especially for popular and widespread loricariid genera such as *Panaque* (Lujan *et al.* 2017). To minimize conflict between scientific nomenclature and names that aquarists use to track distinctive, potentially undescribed color morphs, populations, or species of Loricariidae, aquarium fish hobbyists have developed an alphanumeric coding system known as L-numbers (*i.e.*, Loricariidae numbers; Stawikowski 1988; Dignall 2014). One such L-number that has been perceived to be either an undescribed species or geographic color variant of *Panaque nigrolineatus* is L330, also commonly called the Watermelon Pleco (Fig. 1). In contrast to the more uniformly striped body coloration of *P. nigrolineatus sensu stricto* (Fig. 1A), which was originally described from the Apure

River basin in Venezuela, representatives of the L330 morph usually have the head, abdomen and trunk covered in light gray-green spots on a dark gray to black base (Fig. 1B). This phenotypic distinctiveness, combined with the distribution of L330 color morphs exclusively in Colombia's upper Guaviare River basin, at the far southwestern corner of the Orinoco River basin, have been interpreted as evidence that the L330 Watermelon Pleco is a distinct evolutionary lineage deserving of taxonomic recognition (Ortega-Lara *et al.* 2015).

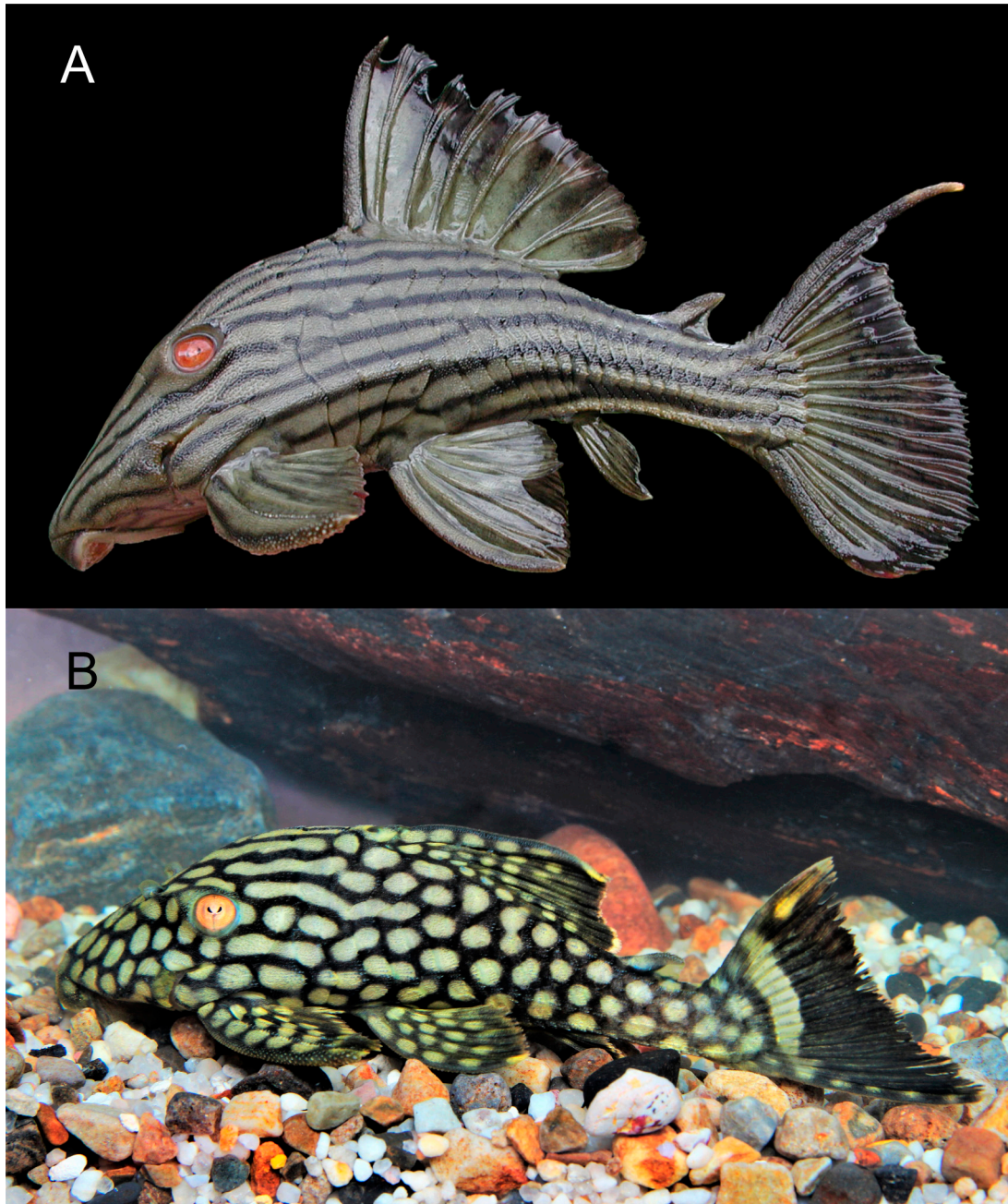


FIG. 1. A) Specimen of *Panaque nigrolineatus nigrolineatus* (AUM 39281) from the Parucito River, a tributary of the Ventuari River in southern Venezuela. Photographed at the collecting site by NKL. B) Uncatalogued specimen of the L330 or Watermelon Pleco color morph described herein as *Panaque nigrolineatus laurafabianae* new subspecies, from the Ariari River, a tributary of the Guaviare River in southern Colombia. Photographed by AOL at an ornamental fish warehouse in Villavicencio, Colombia.

Despite being common in the commercial aquarium fish trade, specimens of L330 are rare in scientific collections. In the most recent taxonomic revision of the genus *Panaque*, Lujan *et al.* (2010) examined over 140 *Panaque* specimens from 15 North and South American fish collections, including 33 specimens of *P. nigrolineatus*. Of these, the authors recorded only a single specimen (IAVHP 5588) that was from the Guaviare River and exhibited the L330 spotted color pattern. Lujan *et al.* (2010) therefore treated the L330 color morph as conspecific with *P. nigrolineatus*.

However, in a recent molecular phylogenetic analysis of the genus, Lujan *et al.* (2017) found a single L330 specimen to be sister to a well-supported clade comprising two *P. nigrolineatus sensu stricto* specimens – one from the Apure River in Venezuela (near the type locality) and one from the Meta River in Colombia, in between the Apure and Guaviare river basins. Lujan *et al.* (2017) found that nuclear DNA sequences at the markers MyH6, RAG1 and RAG2 were invariant across all three Orinoco River populations, yet modest variation in the mitochondrial genes 16S and cytb yielded strong support for the L330 morphotype being sister to a clade containing individuals from the Apure and Meta rivers. Thus, the L330 color morph was treated therein as an undescribed species.

One reason why specimens of L330 have historically been rare in collections is that, until recently, almost their entire geographic range fell within territory occupied by armed guerilla groups who excluded scientists under threat of violence. However, recent peace agreements have made it easier to safely conduct field work in much of the Guaviare River basin, so that fresh specimens, tissues, and DNA data of the spotted L330 color morph can now be collected for scientific research. This newly available material and associated morphological and genetic data, combined with recent phylogenetic analyses of the genus (Lujan *et al.* 2017) and interviews of ornamental fishermen that confirm the geographic distribution of L330 provide the basis and motivation for this study's reexamination of evidence supporting taxonomic recognition of the L330 phenotype.

Material and Methods

Meristic and morphometric data were collected using the methodology and landmarks of Armbruster (2003) as modified by Lujan *et al.* (2010), with the exclusion of the following three measurements: length of the dorsal-fin spine, length of the dorsal unbranched caudal-fin ray, and length of the maxillary barbel. A total of 42 linear measurements were made with a digital caliper precise to 0.1 mm. Thirty morphometric variables are presented as percentages of standard length (SL) and 11 as percentages of head length (HL). Infraorbital plate numbers follow Schaefer (1987), and circumorbital plate and trunk plate row names follow Schaefer (1997). Institutional abbreviations follow Sabaj (2016).

A principal component analysis (PCA) of new log-transformed morphometric data combined with data from Lujan *et al.* (2010) was used to assess morphometric variation among specimens of seven species or populations of *Panaque* (excluding only *P. bathyphilus*). To test for morphometric differences between populations within *P. nigrolineatus*, we used a discriminant function analysis (DFA). Both analyses were conducted using the software PAST v3.15 (Hammer *et al.* 2001).

Given the known invariance in three nuclear DNA markers (MyH6, RAG1, RAG2) across populations of *Panaque* from the Apure, Meta and Guaviare river basins (Lujan *et al.*, 2017), we examined DNA sequence variation across portions of three mitochondrial markers (16S: 561 bp, cytb: 1050 bp, ND2: 907 bp). In addition to the data presented in Lujan *et al.* (2017), we generated new 16S sequences for two new Guaviare River individuals and one new Meta River individual, and we generated new ND2 sequences for one Meta River individual and three Guaviare River individuals following the methods of Lujan *et al.* (2019). Variation in 16S sequences was examined across a total of six *Panaque nigrolineatus* individuals (three from the Guaviare River basin, two from the Meta River basin, and one from the Apure River basin), cytb variation across a total of three individuals (one each from the Guaviare, Meta and Apure river basins), and ND2 variation across a total of four individuals (two from the Guaviare and two from the Meta). Because our results yielded mismatches between genetic and phenotypic patterns that could have resulted from laboratory error, yet we were unable to check for such error because of the availability of only single individuals from each site, we report only aggregate patterns of variance across all samples and not individual sequence data or phylogenetic relationships inferred therefrom.

Finally, ten years of data on the number of wild-caught *Panaque* individuals exported from Colombia for the ornamental fish trade were gathered from the Colombian National Authority of Fisheries and Aquaculture (AUNAP) and are reported here.

Results

Panaque nigrolineatus laurafabianae, new subspecies

Holotype.—IMCN 8223, 319.0 mm SL, Colombia, Meta Department, Granada Municipality, Guaviare-Orinoco River basin, Ariari River near town of Puerto Caldas, 3°28'45"N, 73°42'58"W, 5 December 2012, G. Zamora.

Paratypes.—All specimens Colombia, Meta Department, Granada Municipality, Guaviare-Orinoco River basin, Ariari River: IMCN 8224, 10, 169.0–293.3 mm SL, same data as holotype. ROM 104126, 2, 310–320 mm SL, near town of Puerto Caldas, 3°31'06"N, 73°42'27"W, 10 January 2013, purchased from local fisherman. IMCN 8227, 1, 128.36 mm SL, near town of Puerto Caldas, 27 September 2015, purchased from local fisherman. IAVHP 5588, 1, 158.5 mm SL, Ariari River at the golden bridge, Puerto Caldas inspection station, 20 March 2009, EMBRIOPEZ.



FIG. 2. Holotype of *Panaque nigrolineatus laurafabianae*, new subspecies, IMCN 8223, 319.0 mm SL, Colombia, Meta Department, Granada Municipality, Guaviare-Orinoco River basin, Ariari River near town of Puerto Caldas, 3°28'45"N, 73°42'58"W, 5 December 2012. Scale bar = 5 cm.

Non-type material.—All specimens Colombia, Meta Department, Villavicencio Municipality, originating from the Ariari River but collected from the regional ornamental fish warehouse: IMCN 8228, 11, 105.9–229.6 mm SL, 1 April 2013, Alizandro Villalba. IMCN 6321, 3, not measured, August 2013. IMCN 6322, 4, not measured, September 2013. IMCN 6600, 5, not measured, June 2014. IMCN 6679, 40, not measured, August 2014. IMCN 6682, 20, not measured, July 2014.

Diagnosis.—Most *Panaque nigrolineatus laurafabianae* individuals can be diagnosed from congeners by having live coloration consisting of greenish yellow spots over a brown to black base across the entire head and body (Figs. 1B, 2) or, when stripes are present on the head and flanks, spots or vermiculations cover at least the abdomen (Figs. 2, 3B; vs. body uniformly colored or with black spots on a light gray to brown base in *P. cochliodon*, *P. suttonorum* and *P. schaeferi*, or with alternating longitudinal dark brown to black stripes on a light brown to gray base in *P. armbrusteri*, *P. titan*, and other *P. nigrolineatus*); from *P. armbrusteri*, *P. cochliodon* and *P. suttonorum* by having the adpressed pectoral-fin spine reaching to or beyond the anus (vs. reaching point between the pelvic-fin insertion and the anus); from *P. cochliodon* and *P. armbrusteri* by having the supraoccipital rounded but not elevated above predorsal plates as a hump (vs. supraoccipital raised as a hump); from *P. cochliodon* and *P. suttonorum* by having the eyes colored red or brown (vs. blue or blueish) and by juveniles smaller than 105 mm SL having a hyaline window at the base of the caudal fin (Fig. 1B; vs. juveniles with uniformly gray caudal fin); from *P. armbrusteri* and *P. titan* by having the margin of the caudal fin in adults lunate (vs. truncate); from *P. armbrusteri* by having the interpremaxillary and intermandibular tooth row angles invariant from juveniles to adults (vs. angles increasing with body size); and from *P. titan* by having the postorbital region flat, flush with the ventral margin of the pterotic, without a bump (vs. postorbital region bulged beyond ventral margin of pterotic).

Panaque nigrolineatus laurafabianae is generally distinguishable from *P. nigrolineatus nigrolineatus* by color pattern and by having an elongated patch of papillae located in parallel with and internal (medial) to each premaxillary and dentary tooth row (Fig. 3). However, throughout the range of *Panaque nigrolineatus*, there is variation in both coloration and the presence and size of the patch of papillae internal to tooth rows such that some individuals within the Guaviare basin may lack these characteristics and some individuals outside of the Guaviare basin may have these characteristics.

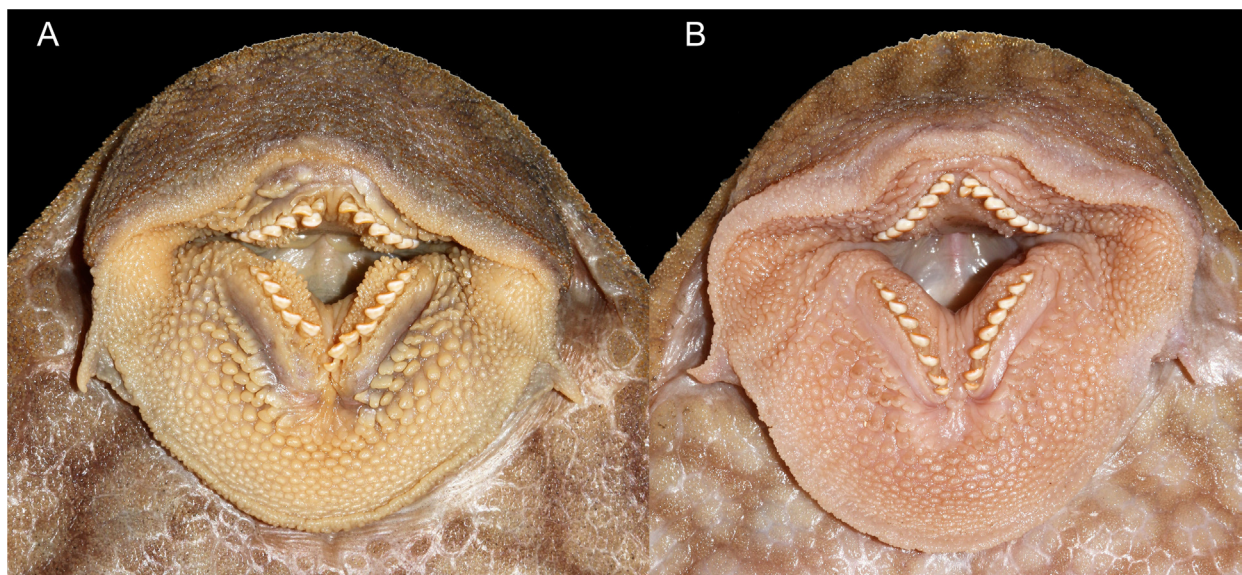


FIG. 3. Oral disks of (A) paratype of *Panaque nigrolineatus laurafabianae* new subspecies, IMCN8224, 267.90 mm SL, showing well-developed patches of papillae immediately interior (medial) to each premaxillary and dentary tooth row and (B) *P. nigrolineatus nigrolineatus*, IMCN 8226, 266.93 mm SL, with much smaller, more reduced patches.

Description.—Morphometrics and meristics in Tables 1 and 2. Largest specimen 320 mm SL. Body deep and robust. Dorsal profile straight and rising approximately 45° from the snout to middle of supraoccipital, slightly convex from there to nuchal plate. Body deepest at nuchal plate. Dorsal profile posterior of nuchal plate gently sloped downward and straight or shallowly convex to posterior insertion of adipose-fin spine, then sloping upward slightly to first dorsal procurent caudal-fin ray, upward slope increasing at first dorsal procurent 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 procurent caudal-fin ray; downward slope increasing slightly at first ventral procurent 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 (mode 80, range 47–91), evertible to approximately 90° from sagittal plane; longest odontode reaching anterior margin of third midventral plate. Eye large (orbit diameter 9.8–13.8% HL); orbit positioned at or dorsal to lateral midline at anterior margin of posterior third of head; orbit accentuated by conspicuous preorbital crest; 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 always present. Iris operculum present. Oral disk occupying approximately three-fourths of snout anterior of cleithrum. Interpremaxillary tooth row angle between 75° and 95°, intermandibular tooth row angle <90°.

Premaxillary tooth row flanked by one, two or three rows of quadrangular papillae; elongate patch of papillae located in parallel with and internal (medial) to each tooth row, with length approximately equal to that of tooth row; buccal papilla absent. All teeth unicuspid and spoon-shaped; lateralmost 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 spinelet prominent and *V*-shaped; dorsal-fin lock functional; posteriormost dorsal-fin ray not adnate. Pectoral-fin spine extending to vent 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 spine reaching point between anal-fin origin and first caudal ventral plate. First anal-fin pterygiophore exposed as plate; first unbranched ray ossified. Preadipose plate present, adipose-fin spine sloped at approximately 45°, spine straight or curved, bearing slightly enlarged odontodes along dorsal surface; adnate to caudal peduncle via fleshy membrane with straight or concave posterior margin. Caudal fin shallowly lunate with unbranched caudal-fin rays approximately even with branched rays, not elongated as filaments. Branched rays of all fins bearing odontodes.

Body widest at evertible cheek plates or cleithrum; anterior margin of cleithrum straight, posterior margin curved with a medial projection. Anteriormost five or six midventral plates strongly bent. Abdomen fully plated. Modest ventrolateral caudal-peduncle keel formed by angled ventral plates having medial rows of slightly enlarged odontodes.

Morphometric variation.—A principal component analysis of morphometrics from all species of *Panaque* except *Panaque bathyphilus* (Fig. 4) showed that *Panaque cochliodon* and *P. schaeferi* have distinctive body shapes that minimally overlap each other and other species. *Panaque armbrusteri* also occupied a distinctive, largely non-overlapping region of morphospace. However, all other species (*P. suttonorum*, *P. nigrolineatus sensu lato*, and *P. cf. titan*) showed broad overlap in their morphometrics. A discriminant analysis of just *P. nigrolineatus* individuals, including 11 *P. n. laurafabianae* and 47 *P. n. nigrolineatus*, correctly classified 100% of these specimens (Fig. 5). The most diagnostically important characteristics in this analysis were width and length of the mouth and length of premaxillary and mandibular tooth rows (Fig. 3).

Mitochondrial sequence variation.—Three examined mitochondrial gene regions (16S, cytb, ND2) showed less than 0.5% variation each when compared across *Panaque nigrolineatus* individuals from the Apure, Meta and Guaviare river basins. Six *Panaque nigrolineatus* individuals (three from the Guaviare River basin, two from the Meta River basin, one from the Apure River basin) had two variable sites across a 561 bp portion of the 16S gene (0.35% variation). Three individuals (one each from the Guaviare, Meta and Apure river basins) had five variable sites in a 1050 bp portion of the cytb gene (0.48% variance). And four individuals (two from the Guaviare, two from the Meta) had four variable sites across a 907 bp portion of the ND2 gene (0.44% variation). None of these gene regions supported monophyly either of individuals with the L330 phenotype or of individuals from the Guaviare River basin. However, because of the overall small sample sizes involved and our inability to test for laboratory errors due to the availability of only a single individual for a given site, we report only aggregate variance patterns and not individual sequences or interrelationships inferred from these sequences.

Coloration.—Head, body and abdomen of most adult specimens covered with greenish yellow spots no larger than eye diameter over a brown to black base (Figs. 1B, 2). Abdomen almost always with spots or vermiculations,

whereas dorsal pattern may be dominated by varying degrees of striping, from irregularly sinuous or broken longitudinal stripes to complete longitudinal stripes.

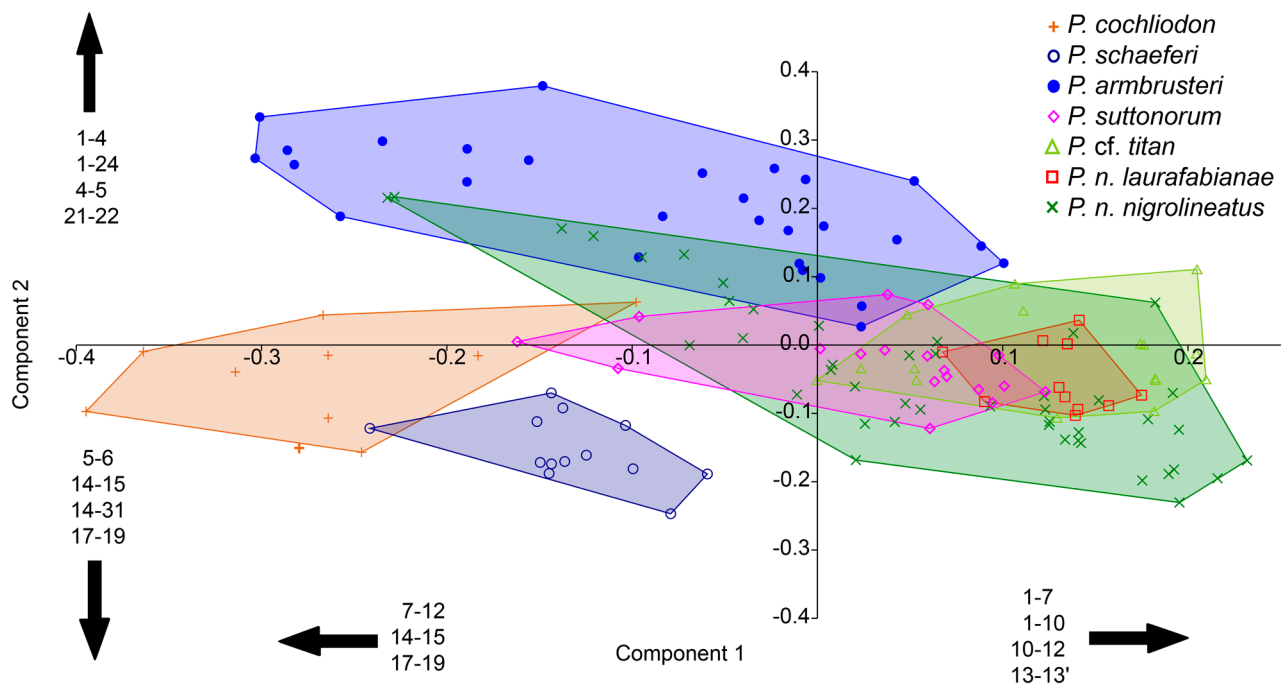


FIG. 4. Results of principal component analysis of morphometric data from all species of *Panaque* except *Panaque bathyphilus*. Variables that contributed most to Component 1 were: head depth (ILM: 7–12), postanal length (14–15), adipose–upper caudal distance (17–19), head length (1–7), predorsal length (1–10), dorsal–pectoral distance (10–12), pelvic girdle width (13–13'). Variables that contributed most to Component 2 were: snout length (1–4), mouth length (1–24), orbit diameter (4–5), mouth width (21–22), interorbital width (5–6), postanal length (14–15), anal–fin spine length (14–31), adipose–upper caudal distance (17–19) (Table 1). Data analyzed were those collected for this study plus those from Lujan et al. (2010).

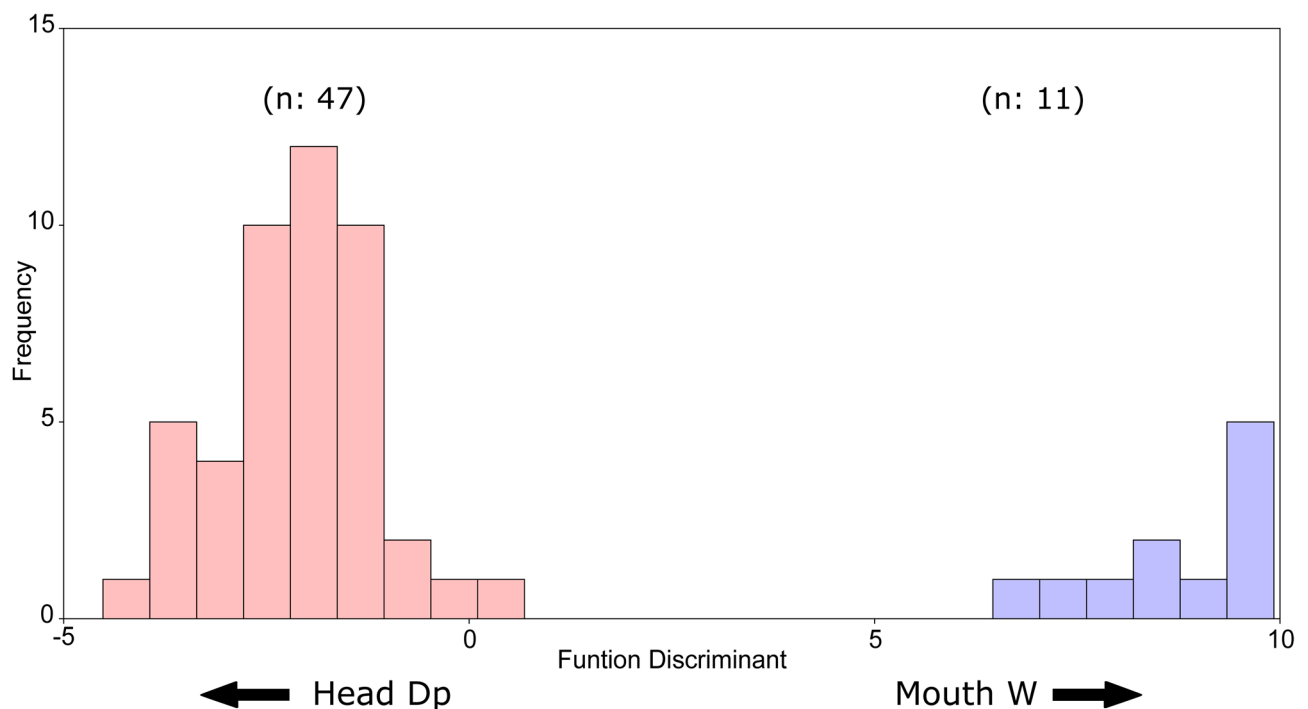


FIG. 5. Results of a discriminant function analysis of morphometrics of *Panaque nigrolineatus nigrolineatus* (red) and *P. nigrolineatus laurafabianae* (blue). All individuals in the analysis were correctly classified. Variables that contributed most to the discrimination were depth of the head and width of the mouth.

Fin spines have same color pattern as body. Color patterns faded but still apparent in alcohol-preserved specimens. Fin rays and membranes with spots as on body or uniformly dark brown, posterior margins generally lacking hyaline regions, tips of caudal-fin spines light white or tan, not elongated as filaments. Juveniles with caudal fin hyaline except for spines and posterior margin; dark brown posterior margin expanding anteriorly and hyaline region shrinking with increasing body size so that caudal fin is entirely opaque in adults. Smallest specimen observed without hyaline caudal-fin window 111.5 mm SL (IMCN 8228). Eyes dark gray to black in preserved specimens, orange to red in life.

Distribution.—Restricted to Andean headwaters of the Guaviare River, which joins the Inírida and Atabapo rivers close to where the latter enters the right bank of the upper Orinoco River in southern Venezuela. Most individuals in this study were collected from the Ariari River near the city of Granada, Meta Municipality, Colombia (Fig. 6); however, ornamental fishermen also collect this species from near the villages of Puerto Santander, Puerto Lleras, Puerto Caldas and from the Guaviare River proper in San José del Guaviare Municipality.

Etymology.—The subspecies epithet *laurafabianae* honors Laura Fabiana Ortega Lucumi, only daughter of the first author, in recognition of the time with her father that she has lost to ichthyological research and for her understanding of the importance of this work.

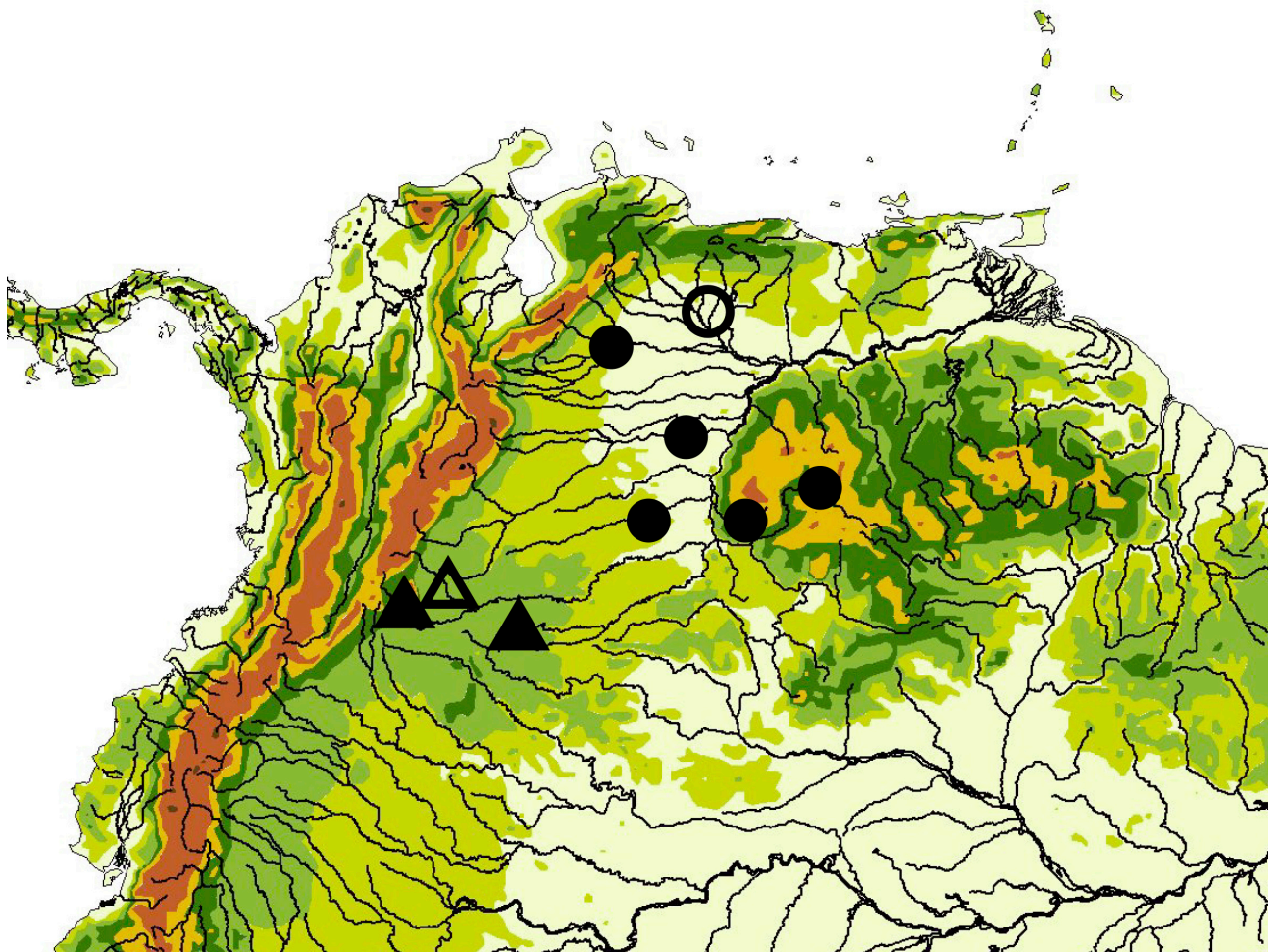


FIG. 6. Known distributions of *Panaque nigrolineatus* subspecies in northwestern South America: *P. n. laurafabianae* (triangles) and *P. n. nigrolineatus* (circles). Open symbols indicate type locality.

Remarks on the commercial exploitation of *Panaque* in Colombia

Over one hundred species are exported from Colombia to the international trade in ornamental aquarium fishes (Ortega-Lara *et al.* 2015). Ornamental fish exporters recognize three forms of striped or patterned *Panaque* among

these species: *P. nigrolineatus nigrolineatus*, which has the common names Royal Pleco or Lined Royal Pleco and is collected from the Meta and Orinoco rivers; *P. cf. titan*, which has the common names Green Pleco, Royal Pleco or Broken Line Pleco and comes from the Caqueta River, a tributary of the Amazon basin (Ortega-Lara & Ríos 2015), and *P. nigrolineatus laurafabianae*, which has the common name Spotted Royal Pleco, Watermelon Pleco, or L330 and was legally codified as species number 336 in Resolution No. 1924 (2015) of the Colombian legislature.

Species of *Panaque* are among the most valuable of Colombia's ornamental fish exports, selling for between US\$10 and >\$150 wholesale (equivalent to US\$30 to >\$450 retail) each depending on species, size and quality. Thus, wild *Panaque* populations are under commercial fishing pressure throughout much of their range. For this reason, the Colombian Ministry of Agriculture and Rural Development set an annual export quota of 180,000 specimens for all three species and subspecies of *Panaque* and all exporters combined (Resolution 000301, 2011) – a value that remained unchanged until 2018 (Resolution 0428, 2017). Since 1999, *P. nigrolineatus nigrolineatus* has been the most exploited of the three Colombian *Panaque* taxa and *P. nigrolineatus laurafabianae* has been the least (Fig. 7). Since 2011, total numbers of *Panaque* exported from Colombia have declined and, in recent years, respective exports of both *nigrolineatus* subspecies have equalized (Fig. 7). There are two possible explanations for these shifts: The first is that management measures taken by Colombian fisheries authorities have worked as intended to reduce exploitation of these species, whereas the second is that exports of these species are being under-reported, which would raise concerns about whether fish stocks are being sustainably managed. Formal description of *P. nigrolineatus laurafabianae* as a distinct subspecies is an important step toward the improved conservation of this population, the designation of legal protections and more precise statistical tracking of its harvest and export.

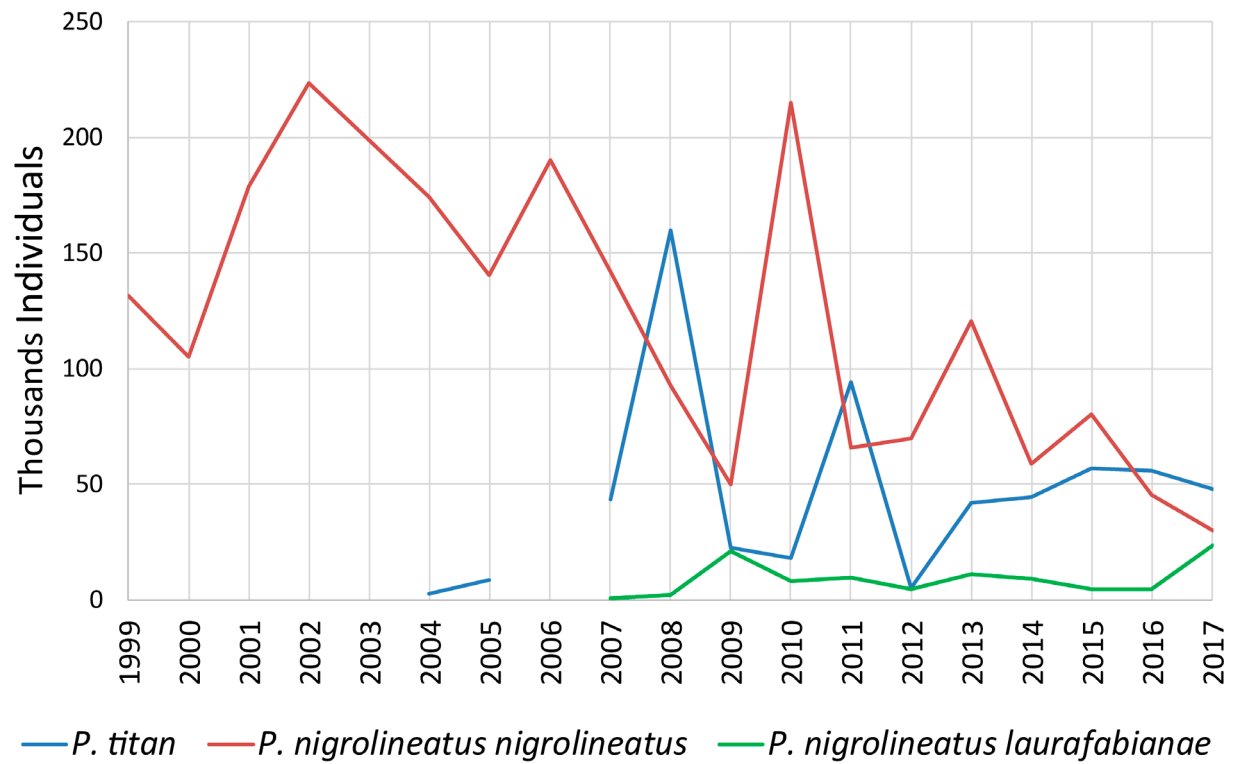


FIG. 7. Numbers of live *Panaque* individuals exported annually from Colombia between 1999 and 2017, based on fisheries statistics from the Colombian National Authority of Aquaculture and Fisheries (AUNAP).

TABLE 1. Selected morphometric characters for *P. nigrolineatus laurafabianae* new subspecies. Interlandmarks (ILM) are the two points between which measurements were taken (from Armbruster 2003, Lujan *et al.* 2010).

ILM	Measurement	Holotype	Paratypes n = 11			
			Mean	Min	Max	SD
1–20	Standard length	319.0	257.9	169.0	319.0	
	Percents of standard length					

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TABLE 1. (Continued)

ILM	Measurement	Holotype	Paratypes n = 11			
			Mean	Min	Max	SD
1–10	Predorsal L.	51.2	51.4	49.5	53.8	1.2
1–7	Head L.	43.1	43.3	42.4	44.8	0.9
7–10	Head-dorsal L.	9.2	8.9	7.3	9.7	0.7
8–9	Cleithral W.	35.5	36.0	34.9	37.2	0.7
8'–9'	Cleithral W. ventral	25.2	26.4	25.2	27.4	0.7
1–12	Head-pectoral L.	29.3	29.7	28.7	31.3	0.8
12–13	Thorax L.	24.3	23.1	21.6	24.3	1.0
12–29	Pectoral-spine L.	42.3	41.4	37.9	44.6	2.2
13–14	Abdominal L.	24.5	24.8	23.8	26.5	0.7
13–30	Pelvic-spine L.	25.8	25.2	23.5	27.6	1.3
13–13'	Pelvic girdle W	20.2	19.7	18.5	20.4	0.6
14–15	Postanal L.	31.4	30.2	28.7	31.5	1.0
14–31	Anal-fin spine L.	16.7	15.9	14.6	18.1	1.0
10–12	Dorsal-pectoral D.	35.9	35.7	34.3	37.0	0.8
10–13	Dorsal-pelvic D.	28.3	28.1	26.2	29.4	0.9
10–16	Dorsal-fin base L.	27.4	27.6	26.6	29.0	0.8
10–16'	Dorsal-fin base L.	26.3	25.6	24.4	26.5	0.7
16–17	Dorsal-adipose D.	13.5	13.4	11.7	14.3	0.7
16'–17	Dorsal-adipose D.	15.3	15.6	14.5	16.6	0.6
17–18	Adipose-spine L.	8.1	8.0	7.1	8.7	0.6
17–19	Adipose-up. caudal D.	13.7	13.7	12.9	15.2	0.7
17–18'	Adipose height	6.9	6.5	5.7	7.5	0.5
15–19	Caudal peduncle Dp.	14.0	14.0	13.4	15.0	0.5
20–32	Caudal peduncle - Middle C ray	22.5	20.8	17.6	23.1	1.8
15–17	Adipose-low. caudal D.	21.8	21.3	20.3	22.8	0.7
14–17	Adipose-anal D.	19.0	18.6	17.9	19.6	0.5
14–16	Dorsal-anal D.	16.6	16.6	14.3	17.6	0.9
14–16'	Dorsal-anal D.	17.1	17.7	17.1	18.2	0.3
13–16	Pelvic-dorsal D.	29.8	30.8	28.9	32.5	1.0
13–16'	Pelvic-dorsal D.	29.2	29.7	28.0	31.4	1.0
Percents of head length						
5–7	Head-eye L.	40.5	41.4	39.3	46.4	1.9
4–5	Orbit Dia.	10.8	11.8	9.8	13.8	1.4
1–4	Snout L.	68.7	69.5	67.2	71.4	1.5
2–3	Internares W.	16.1	16.3	15.1	17.4	0.8
5–6	Interorbital W.	58.4	60.0	57.9	62.4	1.4
5'–6'	Interorbital old	56.0	57.7	55.7	61.3	1.7
7–12	Head Dp.	63.8	62.7	59.6	65.9	2.2
1–24	Mouth L.	36.2	35.4	33.1	37.7	1.7
21–22	Mouth W.	31.9	30.4	25.9	33.6	2.4
25–26	Dentary tooth cup L.	12.2	13.0	11.1	15.0	1.1
27–28	Premax. tooth cup L.	11.5	11.9	10.8	14.3	1.0

TABLE 2. Selected meristic characters for *P. nigrolineatus laurafabianae* new subspecies and other species of *Panaque*.

Counts	<i>P. nigrolineatus laurafabianae</i> n.ssp.	Mode	<i>P. armbrusteri</i>	Mode	<i>P. titan</i>	Mode	<i>P. schaeferi</i>	Mode	<i>P. cochliodon</i>	Mode	<i>P. nigrolineatus nigrolineatus</i>	Mode	<i>P. suttonorum</i>	Mode
	n=11		n=32		n=5		n=17		n=12		n=48		n=19	
Interopercular odontodes	47 – 91	80	8 – 90	35	23 - 77	-	11 - 100	65	22 – 38	38	1 - 112	75	24 - 84	77
Premaxilar teeth	6 – 10	8	4 – 24	8	6 - 10	9	5 - 12	11	6 – 15	6	5 – 10	8	5 - 9	7
Dentary teeth	6 – 10	10	5 – 24	8	7 - 12	9	5 - 12	11	6 – 18	7	5 – 11	8	5 - 10	8
Dorsal–fin rays	II7	II7	II7	II7	II7	II7	II7	II7	II7	II7	II7	II7	II7	II7
Pectoral–fin rays	I6	I6	I6	I6	I6	I6	I6	I6	I6	I6	I6	I6	I6	I6
Pelvic–fin rays	I5	I5	I5	I5	I5	I5	I5	I5	I5	I5	I5	I5	I5	I5
Anal–fin rays	I4	I4	I4	I4	I4	I4	I4	I4	I4	I4	I4	I4	I4	I4
Caudal–fin rays	I14I	I14I	I14I	I14I	I14I	I14I	I14I	I14I	I14I	I14I	I14I	I14I	I14I	I14I
Median plates	24 - 25	25	25 – 26	26	24 – 25	25	24 - 26	25	24 - 26	25	24 – 26	25	24 - 28	25
Supramedian plates	24	24	23 – 25	24	23-25	23	23 - 25	24	22 - 25	25	22-25	24	24-26	24
Inframedian plates	23-25	24	24 - 26	25	24-25	24	23 - 26	25	24 - 26	25	24-26	25	25-27	25
Caudal peduncle plate rows	5	5	5	5	5	5	5	5	5	5	5	5	5	5
Preadipose plates	5	5	3 – 5	5	4 – 7	6	4 - 7	5	5 – 6	6	4 – 6	6	5 – 8	5

Discussion

Although a principal component analysis of morphometric data from all *Panaque* species except *P. bathyphilus* showed complete overlap of *P. nigrolineatus laurafabianae* by *P. n. nigrolineatus* (Fig. 4), the first two axes of a discriminant analysis (DA) of morphometric data from 11 *P. nigrolineatus laurafabianae* and 47 *P. n. nigrolineatus* correctly classified 100% of these specimens (Fig. 5). Based on the combination of this morphometric pattern with the diagnosability of Guaviare River individuals based on color pattern and mandibular papilla morphology, we argue that the L330 Watermelon Pleco morphotype should be recognized as a distinct taxon. Such an official taxonomic recognition would not only be consistent with the data presented here, but would also provide a service to conservation biologists and managers who are working to protect these populations, which is an increasingly important goal of all taxonomic research (Thomson *et al.* 2018). However, despite the geographic and phenotypic distinctiveness of *Panaque nigrolineatus laurafabianae*, all examined individuals of *Panaque nigrolineatus sensu lato* are invariant in sequenced regions of the nuclear DNA markers MyH6, RAG1 and RAG2, and demonstrate very low (<0.5%) divergence in the mitochondrial DNA markers 16S, Cytb and ND2. Moreover, documented phenotypic variance among populations appears to be at least partially developmental, with these characteristics being gained or lost during transition from juvenile to adult. Although prevalence of distinctive phenotypic traits is great enough among individuals from the Guaviare basin that we think they justify recognition as a distinct taxon, we restrict our taxonomic hypothesis to that of a subspecies. We hope to continue exploring and expanding upon these data sets to better understand population structure throughout the entire broad range of *Panaque nigrolineatus*, but this requires additional field work. With the ongoing political turmoil in Venezuela, such field work is unlikely to occur in the near future, so we think it is appropriate to advance our taxonomic hypothesis now.

Restriction of *Panaque nigrolineatus laurafabianae* to the Guaviare River basin suggests that there is at least a partial barrier to gene flow that isolates this basin from the rest of the Orinoco; however, the precise location of this barrier is not obvious. The Guaviare River basin is a whitewater (Sioli 1964) tributary of the upper Orinoco River that carries high concentrations of nutrients and suspended solids that are eroded via its Andean headwaters. As the southwesternmost major tributary of the Orinoco River, the Guaviare River basin marks a transition zone between faunas of the Orinoco and Amazon rivers (Machado-Allison *et al.* 2010). *Panaque nigrolineatus* is also distributed across the Meta, Arauca, and Apure river basins to the north of the Guaviare, all of which are also whitewater rivers draining the Andes and llanos of the Arauca-Apure depression into the left-bank of the Orinoco (Galvis *et al.* 2007). Although *P. nigrolineatus* is also known from more clearwater right-bank tributaries of the upper Orinoco that drain the western margin of the Guiana Shield highlands (Fig. 6), the species is patchily distributed here and appears to be largely restricted to relatively whitewater streams within this landscape, such as the Manapiare and Parucito rivers, upper tributaries of the clearwater Ventuari River (Lujan *et al.* 2010).

Before major uplift of the Eastern Cordillera of the Colombian Andes, the Orinoco River flowed northward in a channel that remained adjacent to the proto-Andean foothills, but uplift of the Eastern Cordillera pushed the Orinoco eastward (Pindell *et al.* 1998; Galvis *et al.* 2007), thus disconnecting the Meta and Guaviare river basins despite the headwaters of these basins still being very close. Moreover, mouths of the Guaviare and Meta rivers became separated by the large Autures and Maipures rapids formed by large expanses of shallow, erosion-resistant bedrock that interrupts the Orinoco River main channel (Galvis *et al.* 2007; Lujan & Armbruster 2011). In this region, several black- and clearwater rivers, such as the Atabapo, upper Orinoco, Bitá, Tomo, Vichada, Cataniapo, and Sipapo-Cuaó (Machado-Allison *et al.* 2010; Lujan & Armbruster 2011) enter the Orinoco causing the pH and concentrations of nutrients and sediments to drop. This shift of the Orinoco River main channel from a whitewater to a more blackwater habitat lasts only a short distance until the Orinoco receives another large influx of sediment-laden water from the Meta River downstream. The effect of these rapid changes in the physicochemical characteristics of the Orinoco over a short distance, together with the presence of large rapids within the same stretch of blackwater, are factors that may contribute to the isolation of *Panaque nigrolineatus laurafabianae* from *P. nigrolineatus nigrolineatus*.

Comparative material.

Panaque nigrolineatus nigrolineatus: IMCN 5863, 4 not measured, Colombia, Meta Department, Villavicencio Municipality, October 2012, collected from regional ornamental fish warehouse, originating from the Metica River.

IMCN 6225, 1, not measured, Colombia, Meta Department, Villavicencio Municipality, October 2012, collected from regional ornamental fish warehouse. IMCN 8226, 19, 213.1–297.0 mm SL, Colombia, Meta Department, Puerto López Municipality, Orinoco River basin, Meta River drainage, Metica River near town of Puerto López, 4°02'45"N, 72°57'06"W, 24 January 2013, collected from regional fisherman. IMCN 8229, 4, not measured, Colombia, Meta Department, Villavicencio Municipality, 16 April 2013, collected from regional ornamental fish warehouse.

Panaque cochliodon: IMCN 0094, 1, 99.5 mm SL, Colombia, Valle Department, Cartago Municipality, Hoya del Alto Cauca, 1 October 1942, Cecil Miles. IMCN 8225, 2, not measured, Colombia, Antioquia Department, Puerto Berrío Municipality, Magdalena River basin, near town of Puerto Berrío, 15 March 2017, collected from regional fisherman.

Panaque suttonorum: IMCN 6330, 14, 88.59–293.78 mm SL, Colombia, Norte de Santander Department, Puerto Santander Municipality, Catatumbo River basin, Zulía River drainage, near town of Puerto Santander, 24 January 2013, collected from regional fisherman.

Panaque cf. titan: IMCN 6059, 1, not measured, Colombia, Amazonas Department, Leticia Municipality, August 2013, collected from regional ornamental fish warehouse, originating from the Tarapacá in Caquetá River. IMCN 5508–5512, 5, 238.0–470.0 mm SL, Colombia, Caquetá Department, La Tagua Municipality, Caquetá River basin, Caquetá River near town La Tagua. 25 October 2013, collected from regional fisherman. CZUT-IC 10866, 1, 486.0 mm SL, Colombia, Caquetá Department, La Tagua Municipality, Caquetá River basin, Caquetá River near town La Tagua. 25 October 2013, collected from regional fisherman. CZUT-IC 10867, 3, 157.8–424.0 mm SL, Colombia, Caquetá Department, La Tagua Municipality, Caquetá River basin, Caquetá River near town La Tagua. 25 October 2013, collected from regional fisherman.

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