

Panaque changae, a new species of catfish (Siluriformes: Loricariidae) from eastern Peru

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Panaque changae, new species, from the ríos Itaya and Momon in the vicinity of Iquitos (eastern Peru) is a member of the *P. dentex* species group, and it differs from all but *P. gnomus* and *P. maccus* by the presence of dark bars on the trunk and bands on the fins. *Panaque changae* differs from *P. gnomus* by trunk bars angled in a posterodorsal to anteroventral direction (vs. angled in an anterodorsal to posteroventral direction), a larger pectoral-spine length to pelvic-dorsal length ratio (d10-d4) (119-149 % vs. 92-106), and a larger pelvic-spine length to pelvic-dorsal length ratio (102-132 % vs. 85-102). *Panaque changae* differs from *P. maccus* by having the light interspaces as wide or wider than the dark bars and bands (vs. light interspaces much thinner), 6-12 trunk bars (vs. 3-7), adipose fin usually with 2 bands (vs. usually 1). In addition, numerous collections have been obtained of *P. maccus* since its description, and a revised distribution map is provided.

Se describe *Panaque changae* de los ríos Itaya y Momon del este de Perú en el área de Iquitos. *Panaque changae* es un miembro del grupo de especies *P. dentex*, y se puede diferenciar de todas las otras especies de este grupo, excepto *P. gnomus* y *P. maccus*, por la presencia de bandas oscuras en el tronco y bandas en las aletas. *Panaque changae* se puede diferenciar de *P. gnomus* por el ángulo de la dirección posterodorsal a anteroventral de las bandas del tronco (contra el ángulo de la dirección anterodorsal a posteroventral), una proporción más grande de la longitud de espina-péctoral a la longitud pélvica-dorsal (119-149 % contra 92-106), y una proporción más grande de la longitud de espina-pélvica a la longitud pélvica-dorsal (102-132 % contra 85-102). *Panaque changae* se diferencia de *P. maccus* teniendo los espacios intermedios entre las bandas oscuras de la misma medida que las bandas oscuras o más anchos (contra los espacios intermedios entre las bandas oscuras siendo mucho más delgados que las bandas oscuras), 6-12 bandas en el tronco (contra 3-7), la aleta adiposa con usualmente 2 bandas (contra usualmente 1). Además, se han obtenido colecciones numerosas de *P. maccus* desde su descripción y un mapa con las revisiones de su distribución está incluido.

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Introduction

Panaque Eigenmann & Eigenmann is a small genus (nine described species) of the family Loricariidae (the suckermouth armored catfishes) found in the río Amazonas, río Orinoco, río Magdalena, and Lago Maracaibo basins. *Panaque*, along with the unrelated loricariid *Cochliodon* Heckel, represent the only known fishes that consume wood (Schaefer & Stewart, 1993; Nelson et al., 1999). *Panaque* and *Cochliodon* share large, spoon-shaped teeth and highly angled jaws which allow them to chisel small pieces of wood for consumption. It is currently unknown whether *Panaque* and *Cochliodon* have the ability to digest the wood or if they are consuming it solely for the bacteria, algae, and fungus growing on and through the wood.

Panaque is considered to be closely related to *Peckoltia* A. de Miranda Ribeiro (Schaefer, 1986; Schaefer & Stewart, 1993; Armbruster, 1997) and *Scobinancistrus* Isbrücker & Nijssen (Armbruster, 1997). *Panaque* differs from *Peckoltia* and *Scobinancistrus* mainly in the presence of spoon-shaped teeth. The teeth in *Scobinancistrus* are similar to the teeth of *Panaque*, but they are elongated (Armbruster, 1997). *Scobinancistrus* shares with *Panaque* the presence of tall ridges on the hyomandibula and preopercle, a characteristic listed as a synapomorphy for *Panaque* in Schaefer & Stewart (1993). Schaefer & Stewart (1993) also list the presence of an elongate, narrow metapterygoid channel as a synapomorphy for *Panaque*. *Scobinancistrus* lacks the lateral wall of the pterygoid channel (Armbruster, 1997) and, hence, the state is not homologous with that seen in *Panaque*.

Panaque changae is found in the río Itaya and río Nanay drainages near Iquitos, Peru, and it has become very popular in the aquarium trade, due to its bright and complex coloration (Fig. 1). Although *Panaque* has not been fully revised, Schaefer & Stewart (1993) provide a revision of the miniature *Panaque* (the *P. dentex* species group). *Panaque changae* is clearly a member of the *P. dentex* group based upon the osteological synapomorphies provided in Schaefer & Stewart (1993) and Armbruster (1997), but differs from congeners in coloration. In this paper, we describe *Panaque changae* as new, compare it to other members of the *P. dentex* group (particularly *P. gnomus* Schaefer & Stewart and *P. maccus* Schaefer & Stewart), provide a revised key to the species of the *P. dentex*

group, and provide an updated distribution for *P. maccus*.

Methods

Measurements follow Schaefer & Stewart (1993) with the addition of two measurements from Boeseman (1968): cleithral width and dorsal-spine length. Distances not named in Schaefer & Stewart (1993) are followed by the landmarks from Schaefer & Stewart (1993) in parentheses. All measurements were made to the nearest 0.1 mm with the use of digital calipers. Counts follow Schaefer & Stewart (1993) and Schaefer (1997). Names of lateral plate rows follow Schaefer (1997) except that the mid-dorsal row is referred to as the suprmedian row and the mid-ventral row is referred to as the infrmedian row. This was done because mid-dorsal and mid-ventral generally refer to areas at the dorsalmost and ventralmost areas of an animal, respectively, and not elements on the lateral aspect of an animal; thus, Schaefer's (1997) terminology is confusing.

All measurements were log-transformed and a principal components analysis was performed using a covariance matrix in JMP in (ver. 4.0.3, SAS Institute Inc. 2000). No meristic characters were used in the principal components analysis. The following abbreviations were used: SL, standard length; HL, head length; DW, oral disk width; and CS, cleared and stained.

Specimens for osteological study were cleared and stained according to procedures modified from Taylor & Van Dyke (1985). Drawings were prepared with the aid of a camera lucida attached to a Leica MZ8 stereomicroscope. Institutional abbreviations are as listed in Leviton et al. (1985) with the addition of MUSM for Museu de Historia Natural de la Universidad Nacional Mayor de San Marcos Lima, Peru.

Key to the *Panaque dentex* species group (modified from Schaefer & Stewart, 1993)

1. - Head and body without alternating dark and light bars, trunk typically without three light brown saddles between dorsal and caudal fins; large overall adult size, typically greater than 90 mm SL. 2

- Head and body with alternating dark and light bars or trunk with three light brown saddles between dorsal and caudal fins; small overall adult body size, typically less than 90 mm SL.
..... 4
- 2 - Head, trunk and fins with small, round, light-colored spots (yellow in life); two platelets between ventral supraoccipital and dorsal pterotic margins; 4-5 premaxillary and 3-5 mandibular teeth per ramus; maxillary barbels short, approximately 15 % disk width (upper río Amazonas, río Ucayali, río Napo, and río Marañón drainages).
..... *P. albomaculatus*
- Head, trunk, and fins without light-colored spots; three or more platelets between the ventral supraoccipital and dorsal pterotic margins; 5-7 premaxillary teeth and 6-7 mandibular teeth per ramus; maxillary barbels elongate, approximately 20-40 % of disk width.
..... 3
- 3 - Small eye, 12.7-13.1 % HL; short trunk, 21.5-23.4 % SL; deep caudal peduncle, 12.7-13.4 % SL (río Purus drainage).
..... *P. purusiensis*
- Large eye, 13.7-15.9 % HL; elongate trunk, 23.5-26.5 % SL; shallow caudal peduncle, 10.5-11.6 % SL (upper río Amazonas, río Ucayali, río Napo, and río Marañón drainages).
..... *P. nocturnus*
- 4 - Fins without alternating light and dark bands (upper río Amazonas, río Ucayali, río Napo, and río Marañón drainages).
..... *P. dentex*
- Fins with alternating light and dark bands.
..... 5
- 5 - Bars angled in an anterodorsal to posteroventral direction on trunk (upper río Amazonas, río Ucayali, río Napo and río Marañón drainages).
..... *P. gnomus*
- Bars angled in a posterodorsal to anteroventral direction on trunk.
..... 6
- 6 - Dark bars on trunk and bands on dorsal fin much wider than light interspaces; trunk with 3-7 (mode=4) dark bars; adipose fin usually with 1 (rarely 2) dark bands; adipose fin dark (río Orinoco drainage).
..... *P. maccus*
- Dark bars on trunk and bands on dorsal fin as wide as or thinner than light interspaces; trunk with 6-12 (mode=8) dark bars; adipose with 1-2 (usually 2) dark bands; adipose fin light (río Nanay and río Itaya drainages).
..... *P. changae*

***Panaque changae*, new species**

(Fig. 1)

Holotype. MUSM 17107, 59.1 mm SL; Peru: Loreto: río Itaya, río Amazonas drainage, 11 km SSW center of Iquitos at bearing 39°, 3°49'47.6"S 73°18'2.9"W; 28 July 1997; J. W. Armbruster, M. H. Sabaj, R. E. Weitzell, R. L. Powell, M. Littman & L. Isuiza.

Paratypes. 5 specimens. SIU 29928, 1, 47.0 mm SL; same data as holotype. – AUM 29929, 1, 83.5 mm SL; INHS 42419, 2, 55.9-57.7 mm SL; MUSM 17108, 1, 39.4 mm SL; same locality as holotype; 6 Aug 1997; J. W. Armbruster, M. H. Sabaj, R. E. Weitzell, R. L. Powell, M. W. Littman, L. Isuiza & C. C. Guardia.

Additional material (non-types). 10 specimens. AUM 28908, 8 (2 CS), 32.9-83.8 mm SL; Peru: Iquitos: río Momon, río Nanay-río Amazonas drainage, ca. 8 hours by boat from Iquitos; río Momon aquarium collectors, 8 Aug 1997.

Diagnosis. The presence of dark bars on the trunk and bands on the fins alternating with light interspaces distinguishes *P. changae* from all other *Panaque*, except *P. maccus* and *P. gnomus*. *Panaque changae* can be distinguished from *P. gnomus* by the posterodorsal to anteroventral orientation of bars on the trunk (vs. anterodorsal to posteroventral), the ratio of pectoral-spine length to pelvic-dorsal distance (d4-10) (119-149 % vs. 92-106) and the ratio of pelvic-spine length to pelvic-dorsal distance (102-132 % vs. 85-102). *Panaque changae* typically has more dark bars on its trunk than *P. maccus* (6-12, mode=8 vs. 3-7, mode=4), more dark bands on its adipose fin (1-2, usually 2

Table 1. Selected morphometric features of *Panaque changae*, *P. gnomus*, and *P. maccus*.

	<i>P. changae</i>				<i>P. gnomus</i>			<i>P. maccus</i>		
	holotype	n	range	mean±SD	n	range	mean±SD	n	range	mean±SD
Standard length (mm)	59.1	16	32.9-84.1	59.7±18.6	10	51.3-69.3	56.9±5.0	33	23.3-86.2	55.1±16.2
% standard length										
Body depth	23.3	16	18.0-26.9	22.7±2.7	10	23.8-30.3	26.8±2.3	33	17.2-29.7	24.3±2.4
Caudal peduncle depth (d7-8)	11.4	12	10.5-12.6	11.5±0.5	10	12.3-13.8	13.2±0.5	29	9.8-13.3	11.3±0.7
Caudal peduncle length (d7-9)	26.2	12	23.8-28.1	26.0±1.2	10	24.2-27.2	25.7±1.1	29	23.0-27.2	25.1±1.0
Head length (d1-2)	38.3	12	35.7-39.3	37.7±1.0	10	36.9-41.2	38.6±1.3	29	36.5-41.7	38.5±1.4
% head length										
Orbit length (d19-20)	18.5	12	16.8-19.0	18.0±0.6	10	16.2-18.5	17.5±0.8	29	13.7-18.5	16.9±1.1
Interorbital distance (d13-19)	45.4	12	41.6-51.2	46.5±2.8	10	45.9-51.5	48.8±2.1	29	40.0-49.9	43.9±2.4
Internasal distance (d17-18)	20.2	12	19.2-23.3	20.7±1.4	10	19.2-23.8	21.1±1.6	29	19.0-24.9	21.4±1.3
Oral disk width (DW: d27-29)	40.2	12	36.0-43.7	40.1±2.5	10	37.1-47.0	43.2±2.7	29	36.0-52.1	42.6±3.3
Max. barbel length (d27-28)	12.2	12	11.1-18.5	14.8±1.9	10	8.0-11.9	10.3±1.2	29	7.1-17.3	12.3±2.7
% oral disk width										
Oral disk length (d1-30)	114.7	12	100.9-128.3	111.3±8.6	10	85.1-103.4	95.0±6.2	29	92.5-120.6	105.5±6.6
Premax. tooth row length (d23-24)	30.6	12	20.6-35.1	29.9±4.2	10	29.7-35.8	31.1±1.8	29	23.9-36.9	30.3±3.4
Mand. Tooth row length (d25-26)	37.9	12	31.4-43.6	36.5±3.0	10	27.5-39.4	33.9±3.8	29	30.9-41.3	34.8±2.7
% pelvic-dorsal length (d10-4)										
Pectoral Spine (d11-14)	129.5	12	119.3-148.9	129.5±9.6	10	92.1-106.3	99.6±5.0	29	94.1-128.1	111.7±6.8
Pelvic Spine (d10-15)	114.5	12	102.3-132.0	111.8±10.0	9	84.8-102.4	95.4±5.8	28	81.0-113.5	97.3±6.8
Meristics										
Lateral Plates	24	12	23-24	23.5±0.5	10	23	–	27	23-24	23.6±0.5
Dorsal procurrent caudal rays	4	12	4-5	4.2±0.4	10	4-5	4.7±0.5	27	4-5	4.9±0.3
Ventral procurrent caudal rays	3	12	3	–	10	3	–	27	3	–
Marginal caudal plates	8	12	7-8	7.9±0.3	10	7-8	7.4±0.5	27	7-8	7.9±0.3
Dorsal to adipose plates	4	12	4	–	10	4	–	29	4	–
Post-pterotic plates	2	12	2	–	10	2	–	29	2	–
Left premaxillary teeth	5	12	2-6	4.8±1.1	10	0-6	4.3±1.8	29	4-8	4.9±0.9
Right premaxillary teeth	5	12	4-6	5.0±0.9	10	2-6	4.8±1.3	29	3-7	4.9±1.0
Left mandibular teeth	6	12	3-7	5.2±1.1	10	4-7	6.3±1.0	29	4-9	5.6±1.1
Right mandibular teeth	5	12	4-7	5.5±1.2	10	6-8	7.0±0.5	29	5-9	5.7±1.0

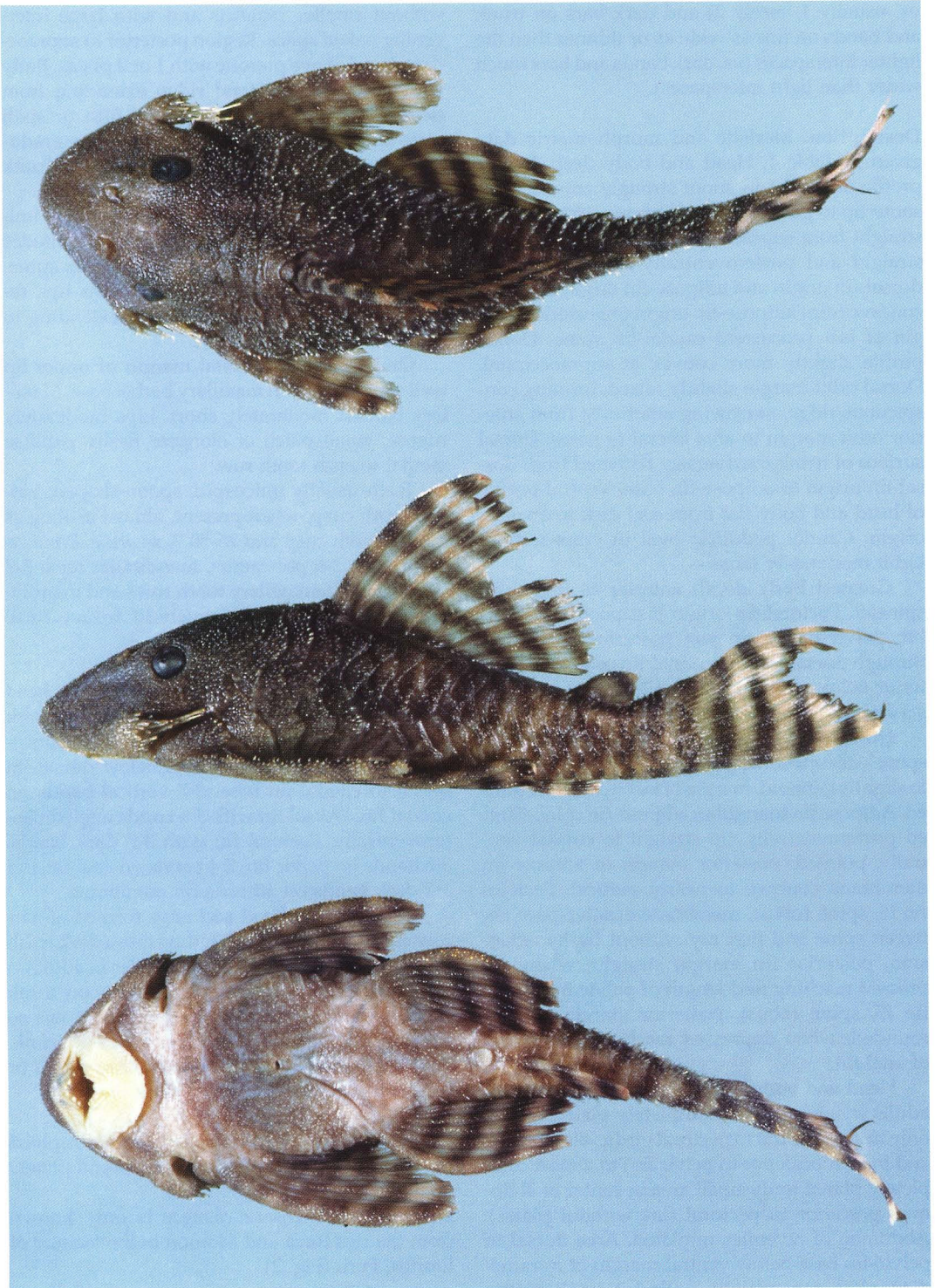


Fig. 1. *Panaque changae*, AUM 28908, 83.8 mm SL; Peru: Rio Momon (photographs: J. W. Armbruster).

vs. usually 1, rarely 2) and dark bars on trunk and bands on fins as wide as or thinner than the lighter interspaces (vs. dark bands and bars much wider than light interspaces).

Description. Meristic and morphometric data given in Table 1. Head and body deep. Dorsal profile of head and snout strongly convex from snout tip to posterior tip of supraoccipital, nearly straight from supraoccipital to dorsal-fin origin, straight and posteroventrally slanted between dorsal-fin origin and adipose-fin origin, strongly concave from adipose-fin origin to posterior margin of last procurrent caudal-fin spine. Dorsal profile slightly more convex at supraoccipital. Dorsal orbit margin slightly raised, forming conspicuous ridge, narrowing anteriorly, from anterior orbit margin to area lateral to nares. Dorsal surface of trunk transversely flattened from dorsal-fin origin to adipose-fin base. Ventral profile of head and body flat from oral disk to anal-fin origin. Caudal peduncle oval in cross-section. Orbit moderately large.

Greatest body depth anterior to dorsal-fin spinelet. Pectoral-fin origin just posterior to orbit, pelvic-fin origin just posterior to vertical through dorsal-fin origin, anal-fin origin just posterior below vertical through origin of last dorsal-fin ray.

Dorsal fin II7, spinelet V-shaped, dorsal-fin spine lock functional, posterior fin margin straight to slightly sigmoid, margin of last two rays rounded. Adipose fin triangular; adipose-fin spine slanted posteroventrally, tip straight to curved ventrally, pointed; posterior margin of adipose-fin membrane concave to nearly vertical. Pectoral fin I6, spine robust, membrane of interspace between spine and first ray without fleshy extension, posterior fin margin straight, when depressed reaching mid-length of pelvic fin. Pelvic fin I5, spine robust, posterior margin slightly rounded, when depressed reaching mid-length of anal fin.

Head and body entirely plated. Abdomen of adults ranging from incompletely plated (plates only in skin ventral to pectoral girdle, along sides, and in skin posterior to pelvic fin) to almost completely plated (only small area in center of abdomen posterior to pectoral fins without plates). Abdomen of juveniles unplated. Area dorsal to pelvic-fin base below ventral margin of inframedian plate row usually with 1-3 small plates,

without smaller platelets and with large intervening naked space. Region posterior to supraoccipital and above pterotic with 1 or 2 plates. Body with pronounced lateral ridge extending from cleithrum to posterior margin of fifth or sixth plate of the inframedian plate row; ridge gradually decreasing in prominence posteriorly. Trunk without elevated ridges.

Head and body covered by odontodes of uniform size and distribution. Enlarged odontodes on anterodorsal border of pectoral-fin spine. Cheek odontodes hypertrophied with tips recurved laterally, longest odontode extending to posterior cleithrum margin.

Oral disk round, distal margin of upper lip well separated from maxillary barbel base. Maxillary barbels moderately short. Lips moderately rugose, small patch of elongate fleshy papillae medial to each tooth row.

Teeth usually unicuspid, spoon-shaped. Lateral tooth cusp, when present, almost as long as medial tooth cusp and 25-50 % as wide. Premaxillary teeth 2-6 per ramus, mandibular teeth 3-7 per ramus. Premaxillary tooth rows and mandibular rows angled approximately 30° from vertical midline.

Color in alcohol. Base coloration on body, head and fins light gray to tan. Trunk with 6-12 dark gray broad narrow bars, running posterodorsally to anteroventrally from area below dorsal-fin origin to caudal-fin base. 3-7 vertical bands on caudal fin. Dorsal fin with 3-6 bands angled posteroventrally. Pectoral fin with 3-7 dark bands, 3-6 bands on pelvic fin, 2-4 bands on anal fin and 1-2 dark bands on adipose-fin membrane.

Coloration on head and nape formed of narrow vermiculations, often fading into a dark wash in adults. Sometimes 3-4 faint saddles in addition to lateral bars on trunk. Vertical bars on trunk typically split ventrally as individual grows so that larger individuals have more bars on trunk. Abdomen and ventral surface of head white or with sinuous interconnecting dark lines.

Sexual dimorphism. Males with hypertrophied odontodes on posterior margin of lateral plates.

Distribution. *Panaque changae* is only known from the ríos Itaya and Momon in the vicinity of Iquitos, Peru (Fig. 2)

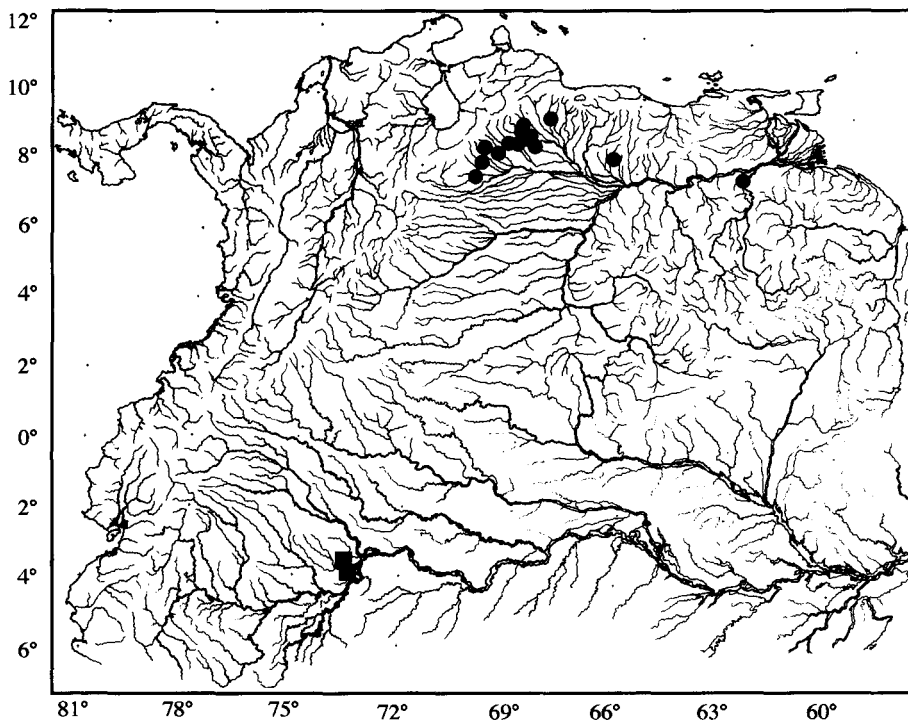


Fig. 2. Distribution of *Panaque changae* (■) and *P. maccus* (●).

Etymology. Named for Fonchii Chang of MUSM, who died recently in a tragic collecting accident in the Amazon, in honor of her contributions to the study of loriciariids and her specific interest in this species.

Discussion

In our review of Schaefer & Stewart (1993), we determined that the ratios of internasal distance/HL and oral disk length/DW reported therein cannot be correct. In Schaefer & Stewart (1993), the internasal distance/HL ratio is 36.5-44.8 % for all species combined (vs. 19.2-23.4 in *P. changae*), and the oral disk length/DW ratio is 37.3-49.8 % (vs. 100.9-128.3) despite the fact that *P. changae* appears to not differ this significantly from the other species based on cursory observation. Comparing independent measurements of other species of the *P. dentex* group to those in Schaefer & Stewart (1993), we found that the internasal distance/HL and oral disk length/DW ratios are similar to those of *P. changae* indicating

that there was an error in the reporting of these values by Schaefer & Stewart (1993). Based on the values determined in this study, we surmise that Schaefer & Stewart's internasal distance/HL actually represents internasal distance/interorbital distance and oral disk length/DW actually represents oral disk length/HL. Table 1 reflects the correct ratios for internasal distance/HL and oral disk length/DW, and these values should not be compared to the values listed in Schaefer & Stewart (1993).

Panaque changae was determined to have all of the synapomorphies of the *P. dentex* group listed in Schaefer & Stewart (1993): dorsal margin of fifth ceratobranchial with posterior indentation, symplectic foramen greatly enlarged laterally, anterior preopercle-quadrates suture positioned posteriorly when viewed laterally, and preopercle with a deep lateral groove posterolaterally. In addition, all of the members of the *P. dentex* group examined have an elongate, lateral process on the tripus (Fig. 3). This characteristic was not found in any other member of the Ancistrinae and can tentatively be considered a

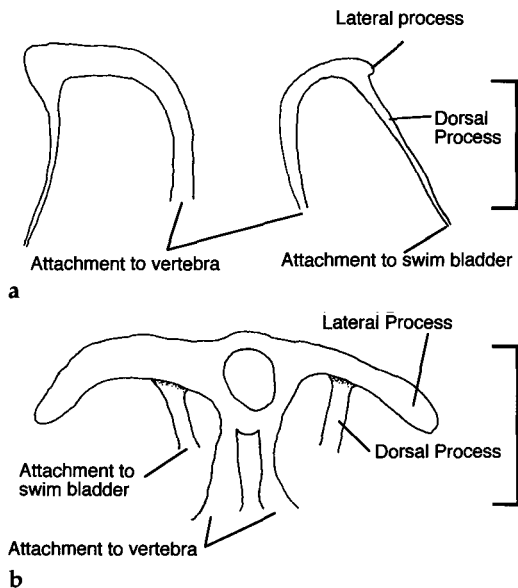


Fig. 3. Left and right tripuses of the Weberian apparatus, antero-ventral view. **a**, *Aphanotorulus unicolor*, USNM 319355; **b**, *Panaque maccus*, INHS 29862. Scale bars: 1 mm.

synapomorphy for the *P. dentex* group (*P. dentex*, *P. gnomus*, and *P. purusiensis* were not examined in this study).

To determine the effects of standard length on the principal components, the first three principal components were plotted against standard length. Principle component 1 was highly correlated with standard length and the result was a straight line. Plots of principal components 2 and 3 against standard length resulted in a cloud of points with no relationship to standard length indicating that principal components 2 and 3 represent relative size and not absolute size. Principle component 2 was affected most strongly and positively by caudal width and head-dorsal length (d2-3), and anal-dorsal length (d4-9); and negatively by maxillary barbel length, caudal length, anal-spine length. Principle component 3 was affected most strongly and positively by caudal peduncle length, thorax length, and anal-dorsal length; and negatively by maxillary barbel length, mouth length, and dentary length. The plot of principal component 2 vs. principal component 3 provides almost complete separation of *P. changae* from all other species of the *P. dentex* group examined (Fig. 4) suggesting that *P. changae*

varies significantly in shape from the other species.

Based on recently collected specimens, the range of *P. maccus* is significantly increased (Fig. 2). Specimens are now also known from throughout the Eastern Orinoco of Venezuela and from Guarico state in central Venezuela.

Recently, Isbrücker et al. (2001) proposed the genus name *Panoqolus* for the *Panaque dentex* species group. As *Panaque*, with the *P. dentex* species group included, is a small, well-diagnosed, and easily identifiable genus, we feel that the recognition of a new genus for the *P. dentex* species group is unwarranted. Therefore, we treat *Panoqolus* as a junior synonym of *Panaque*.

Comparative material. *Panaque albomaculatus*: FMNH 96951, 1 CS, not measured; Peru: Amazonas: Caterpiza.

P. dentex: Ecuador: río Napo drainage: FMNH 97593, 1, 41.0 mm SL; Estero Samonayacu, about 3.5 km SW of the bridge over río Napo along road from Coca to río Tiputini, Napo, 0°29'24"S 76°57'36"W. – FMNH 97594, 1, 34.2 mm SL; río Verde Jivino, at and below bridge on road between Coca and lago Agria, about 1.4 km south of turnoff to Shushufindi, Napo, 0°10'54"S 76°50'36"W. – FMNH 97595, 2, 66.7–72.4 mm SL; quebrada Apoalla, tributary to lower río Shushufindi, Napo, 0°17'S 76°27'W. – FMNH 97596, 3, 72.4–77.5 mm SL; lower río Bobonaza at Chicherata, about 25 km upstream from mouth of río Pastaza, 2°23'S 76°39'W. Peru: FMNH 96952, 1, 72.5 mm SL; Amazonas: Caterpiza.

P. gnomus: Ecuador: Pastaza: río Napo drainage: FMNH 70860, holotype, 56.2 mm SL; FMNH 97597, 3 paratypes, 51.3–59.3 mm SL; Cusuimi, on río Cusuimi, about 150 km SE of Puyo, 300 m. – FMNH 97332, 3, 53.0–59.4; Cusuimi, río Cusuimi, about 150 km SE of Puyo. – FMNH 97598, 2 paratypes, 55.0–55.1 mm SL; Río Bobonaza, at Sarayacu. Peru: FMNH 96950, 1 paratype, 69.3 mm SL; Amazonas: río Cenepa, río Marañón drainage, vicinity of Huampami.

P. maccus: Venezuela: río Orinoco basin: AUM 17527, 1, 58.9 mm SL; caño Maraca, caño Igues-río Portuguesa drainage, Guanare, 8°49'39"N 69°20'42"W. – AUM 22109, 1, 36.1 mm SL; río Portuguesa, río Apure drainage, at Highway 5 bridge, Portuguesa, 9.0818°N 69.68159°W. – AUM 22665, 4, 25.7–86.2 mm SL; INHS 55704, 3, 53.6–82.7 mm SL; caño Mamón, río Portuguesa – río Apure drainage, in El Mamón, 24 km E Guanare, Portuguesa, 9°4'18"N 69°30'54"W. – INHS 28285, 3, 17.0–49.4 mm SL; tributary to río Suripa, río Apure drainage, 36 km NE La Pedrera on Ruta 5, Barinas. – INHS 28709, 1, 59.8 mm SL; río Santo Domingo, río Apure drainage, in Torunos hacienda La Isla, Barinas, 8°30.54'N 70°5.05'W. – INHS 28993, 3, 31.6–55.8 mm SL; río San Carlos, río Portuguesa-río Apure drainage, WNW Las Vegas, Cojedes, 9°33'40"N 68°38'89"W. – INHS 29862, 4 (2 CS), 23.3–60.5 mm SL; Cano Yaure, tributary to río Suri-

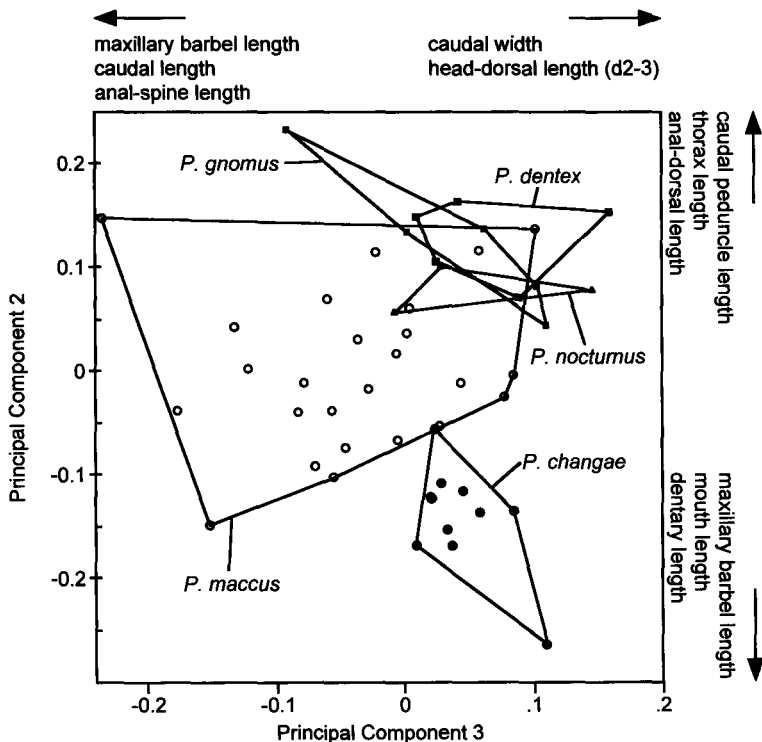


Fig. 4. Results of principal components analysis of species of the *Panaque dentex* group. The strongest loading characters and the directions of their loadings are indicated along the x and y axes.

pa, río Apure drainage, Yaure on Ruta 5, 36 km NE La Pedrera, Barinas, 7°42.05'N 71°17.77'W. – INHS 29906, 2 (1 CS), 42.5–55.2 mm SL; río Masparro, río Apure drainage, 5 km NW Libertad, Libertad to Barinas road, Barinas, 8°20.54'N 69°39.48'W. – INHS 31996, 1, 64.9 mm SL; río Guanare, río Apure drainage, Guanarito, Portuguesa. – INHS 32840, 1, 56.6 mm SL; caño Arenosa, río La Yuca – río Masparro drainage, 14 km N Barinas, Barinas, 8°46'14"N 70°15'30"W. – INHS 32862, 2, 63.3–67.5 mm SL; río La Yuca, río Masparro – río Apure drainage, 17 km N Barinas, Barinas, 8°46'N 70°15'W. – INHS 34312, 1, 47.6 mm SL; río Mocapra, Parque Nacional Aguaro-Guariquito, La Esperanza, Guarico, 8°16'39"N 66°44'21"W. – INHS 35690, 1, 63.8 mm SL; río Portuguesa, río Apure drainage, 3 km NE El Barriero, Portuguesa, 9°3'8"N 69°29'28"W. – INHS 69267, 1, 62.2 mm SL; caño Los Manires, río Apure drainage, on road to La Quebrada, 17 km E Guanare, Portuguesa, 9°8'40"N 69°32'00"W. – MCNG 18445, 5, 42.9–58.9 mm SL; río Caroní, small lateral arm near confluence of río Claro, Bolívar, 7°54'30"N 63°2'50"W.

P. nocturnus: Ecuador: río Napo drainage: FMNH 97599, 1 paratype, 120.8 mm SL; río Aguarico, near Destacamento militar Cuyabeno and confluence of río Cuyabeno – río Aguarico, Napo, 0°15'30"S 75°53'30"W. – FMNH 97600, 2 paratypes, 65.8–96.4 mm SL; lower río

Bobonaza, at Chicherota ca. 25 km upstream from mouth in río Pastaza, Pastaza, 2°23'S 75°39'W. Peru: FMNH 96955, 1 paratype, 136.8 mm SL; Amazonas: río Santiago at La Poza, río Marañón drainage, outside mouth of quebrada by airport.

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