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SOUTH AMERICAN FRESHWATER NEEDLEFISHES OF THE GENUS *POTAMORRHAPHIS* (BELONIFORMES: BELONIDAE)

Bruce B. Collette

Abstract.—*Potamorrhaphis* and *Belonion* share several specialized characters: round caudal fin; few large pharyngeal teeth; pectoral-fin rays reduced to eight or fewer; elongate nasal barbel; and an association of the expanded first neural spine with the supraoccipital crests and exoccipital flange which is unique to these two genera. *Potamorrhaphis* has a long caudal section of its body and many caudal vertebrae and dorsal- and anal-fin rays. Three species are recognized: *P. eigenmanni* Miranda Ribeiro, *P. guianensis* (Schomburgk), and *P. petersi* Collette. They show increasing numbers of dorsal- and anal-fin rays, vertebrae, and predorsal scales from *P. eigenmanni* to *P. guianensis* to *P. petersi*. They form a similar series from south to north with *P. eigenmanni* concentrated in the Paraguay-Paraná system, *P. guianensis* throughout the Amazon and the Guianas, and *P. petersi* in the upper Orinoco. Apparently, *P. eigenmanni* invaded the Amazon through the Mato Grosso into the Upper Río Madeira in Bolivia and Brazil. Similarly, *P. petersi* seems to have moved through the Río Casiquiare into the upper Rio Negro. Geographic variation in meristic and morphometric characters was studied in the three species. Four populations of *P. petersi* differ only in mean number of total vertebrae. There is variation in meristic characters within and between major populations of *P. guianensis* (Orinoco, Guianas, and Amazon). Generally, counts are low in the Orinoco, intermediate in the Guianas, and high in the Amazon. These three populations differ significantly in P_1–P_2 and P_2–C distances, pelvic fin length, interorbital width, and head width. In *P. eigenmanni,* there is a general pattern of decreasing counts from the Mamoré, to the Guaporé and Beni (all tributaries of the upper Madeira) and finally to the Paraguay. The means for all seven meristic characters for the combined Madeira populations are significantly different statistically from those in the Paraguay. The Paraguay and Madeira populations also differ significantly in seven of 12 morphometric characters. Recognition of *P. eigenmanni* confirms the number of species in the family Belonidae as 32 and the known neotropical species as nine in four genera: *Potamorrhaphis* (3), *Belonion* (2), *Pseudotylosurus* (2), and *Strongylura* (2).

This paper completes the review of the genus *Potamorrhaphis* begun with the description of *P. petersi* (Collette, 1974a). A third species in the genus, *P. eigenmanni,* is validated herein from the Paraguay-Paraná river system and the upper Río Madeira in Bolivia and Brazil.

Methods and Materials

The methods used are similar to those described in previous papers in this series (Collette 1966, Collette 1974a–c). Body length (BL) is substituted for stan-

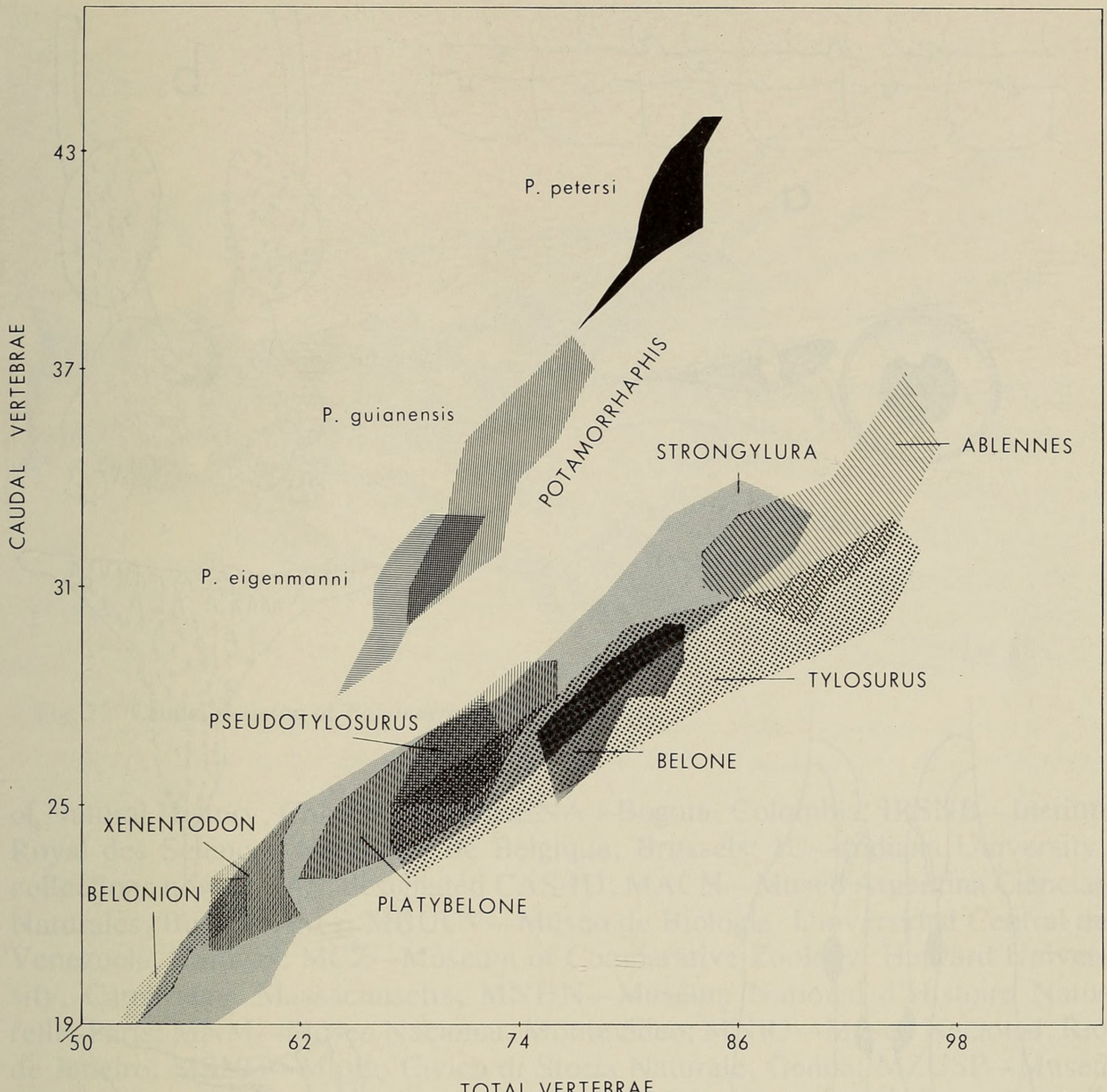

Fig. 1. Relationship of caudal to total vertebrae in the 3 species of *Potamorrhaphis* and the other genera of Belonidae.

dard length because many specimens have broken beaks and because upper jaw length is markedly allometric in some needlefishes. BL is defined as the distance from the posterior margin of the opercular membrane to the caudal base. Vertebral counts were made from radiographs, and counts of dorsal- and anal-fin rays made from the specimens were checked against the radiographs. Analyses of variance (ANOVA) were conducted on the frequency distributions for each of seven meristic characters to test for intraspecific differences. When an ANOVA was significant ($P < 0.05$), a Student Newman-Keuls Multiple Range Test (SNK) was performed to ascertain which means differed significantly from others. Twelve measurements (listed in Table 12) were made in addition to body length. Analysis of covariance (ANCOVA) was performed on regressions of body parts on body length to test for intraspecific and interspecific differences. If the F value for regression was significant at the 0.05 level, the F value for slopes was examined.

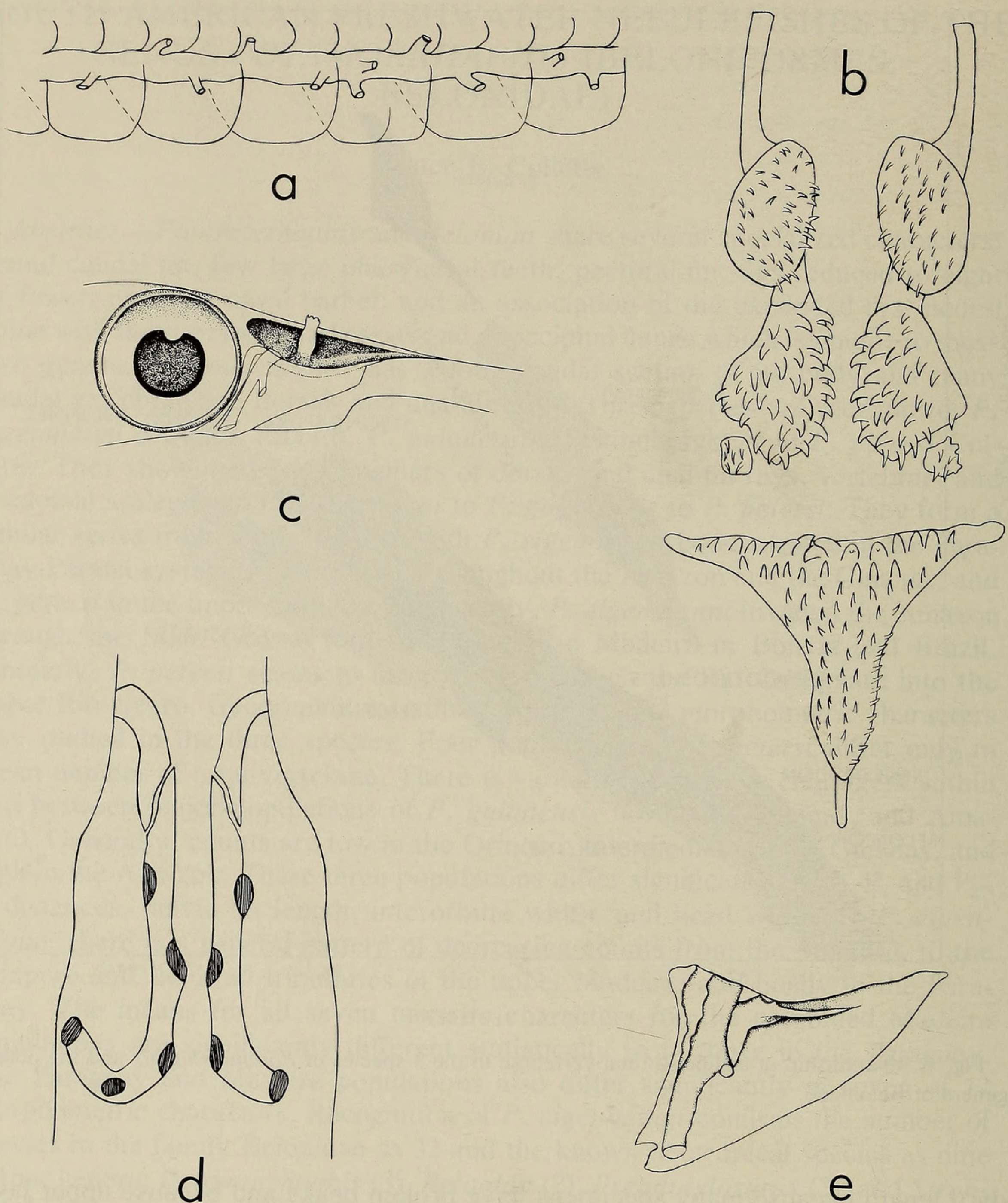

Fig. 2. *Potamorrhaphis guianensis*: a, Lateral line canals on anterior part of body; b, Pharyngeal dentition; c, Nasal fossa and nasal barbel; d, Interorbital canal; e, Preorbital bone and canal.

If this was significant, the Newman-Keuls Multiple Range Test was performed (Q value) to see which means differed significantly from others. If the F value for regressions was significant and the F value for slopes was not significant, the F value for intercepts was examined. If this was significant, the SNK was performed as for the slopes.

Abbreviations used for the institutions cited herein are as follows: AMNH—American Museum of Natural History, New York; ANSP—Academy of Natural Sciences, Philadelphia; BMNH—British Museum (Natural History), London; CAS—California Academy of Sciences, San Francisco; FMNH—Field Museum

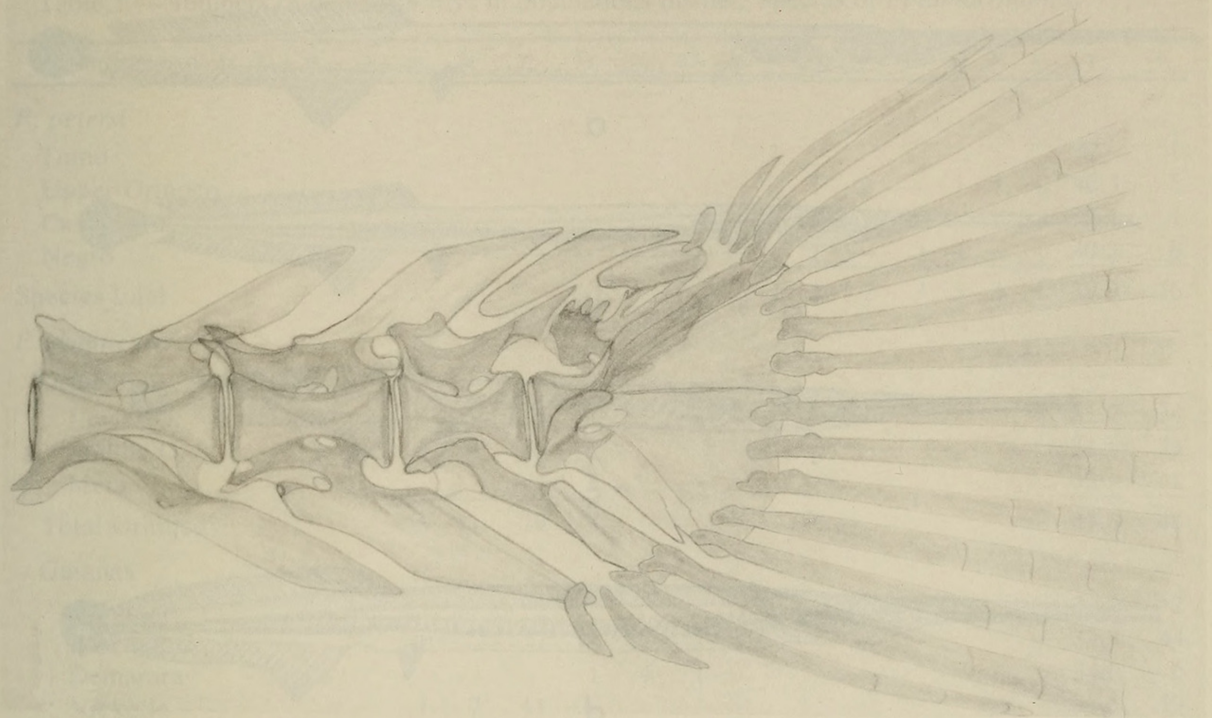

Fig. 3. Caudal skeleton of *Potamorrhaphis guianensis.*

of Natural History, Chicago; INDERENA—Bogotá, Colombia; IRSNB—Institut Royal des Sciences Naturelles de Belgique, Brussels; IU—Indiana University, collections now at CAS, designated CAS-IU; MACN—Museo Argentina Ciencias Naturales, Buenos Aires; MBUCV—Museo de Biología, Universidad Central de Venezuela, Caracas; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNHN—Muséum National d'Histoire Naturelle, Paris; MNM—Museo Nacional, Montevideo; MNRJ—Museu Nacional, Rio de Janeiro; MSNG—Museo Civico di Storia Naturale, Genoa; MZUSP—Museu de Zoologia, Universidade do São Paulo; NHMV—Naturhistorisches Museum, Vienna; RMNH—Rijksmuseum van Natuurlijke Historie, Leiden; SMF—Senckenberg Museum, Frankfurt am Main; SU—Stanford University, collections now at CAS, designated CAS-SU; UAIC—University of Alabama Ichthyological Collections, University, Alabama; UMMZ—University of Michigan Museum of Zoology, Ann Arbor; USNM—National Museum of Natural History, Washington, D.C.; ZMA—Zoological Museum, Amsterdam; ZMH—Zoological Museum, Hamburg.

Potamorrhaphis Günther

Belone (*Potamorrhaphis*) Günther, 1866:256 (original description; type-species *B.* (*P.*) *taeniata* Günther by subsequent designation of Jordan & Fordice 1887: 359, =*Belone guianensis* Schomburgk).

Pomatorrhaphis.—Bleeker, 1871:43 (misspelling of *Potamorrhaphis* although considered as an available name by Whitley, 1970:243).

Potomarrhaphis.—Fowler, 1914:277 (misspelling of *Potamorrhaphis*).

Potamorhaphis.—von Ihering, 1940:621 (misspelling of *Potamorrhaphis*).

Potamorhamphus.—Bănărescu, 1970:321 (misspelling of *Potamorrhaphis*).

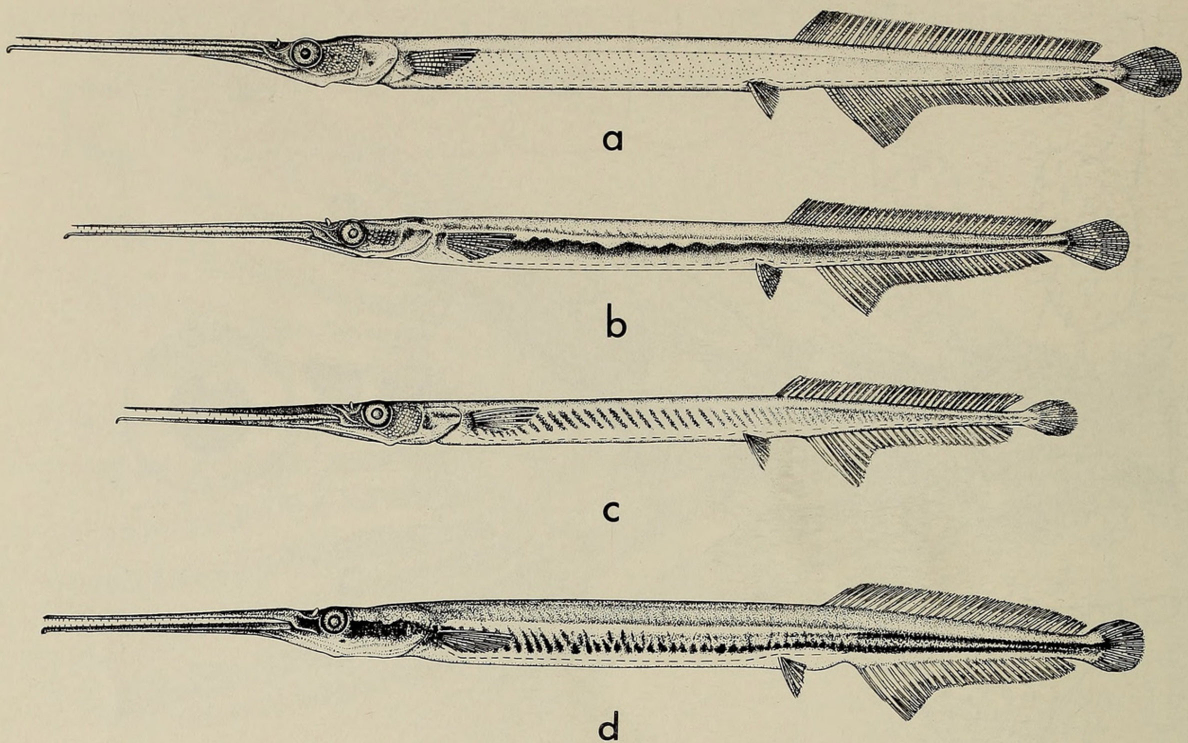

Fig. 4. Three species of *Potamorrhaphis*: a, *P. petersi,* Upper Río Orinoco, 134 mm BL, AMNH 9619; b, *P. guianensis,* Río Meta, Orinoco, 119 mm BL, ANSP 116533; c, *P. guianensis,* Río Urubu, Amazon, 108 mm BL, USNM 179527; d, *P. eigenmanni,* Río Paraguay, 123 mm BL, UMMZ 207901.

Potamoraphis.—Damon, 1971:8 (misspelling of *Potamorrhaphis*).
Potamorraphis.—Stone, 1976:24–25 (misspelling of *Potamorrhaphis*).
Potamorrhamphis.—Travers, 1981:857, 863 (misspelling of *Potamorrhaphis*).

A number of papers referred only to *Potamorrhaphis,* presumably on the presumption that the genus was monotypic and contained only *P. guianensis.* These are: Regan 1911:331 (74 vertebrae), 332 (in key, pharyngeal dentition); Nichols and Breder 1928:439 (*Potamorrhaphis* a specialized freshwater offshoot of *Strongylura* with a convex caudal fin); Fernández Yépez 1948:142 (position of dorsal fin relative to anal fin), 143 (figure), 144 (in key); Collette and Berry 1965:389 (generic characters); Géry 1969:843 (range), 845 (fig. 5); Astakhov 1980:191 (among freshwater genera), 192 (reference to Collette 1966).

Diagnosis.—Posterior part of body elongate compared to anterior, 28–44 caudal vertebrae constituting 43–52% of 64–85 total vertebrae (compared to 34–42% in other Belonidae, Fig. 1). Dorsal and anal fins very long, with 27–43 and 24–39 rays respectively. Dorsal-fin rays more numerous than in any other needlefish (except for slight overlap with *Tylosurus acus melanotus,* 24–27). Body lateral line with both dorsally and ventrally directed short secondary tubes (Fig. 2a). *Pseudotylosurus* also has dorsal and ventral secondary canals (Collette 1974b: fig. 2) but these are much longer than in *Potamorrhaphis.* Other belonids have the secondary canals directed ventrally (Parin and Astakhov 1982:fig. 12). Pectoral-fin rays usually 7–8 (5–6 in *Belonion*; 8–11, usually 9–10 in *Pseudotylosurus*; 9–15 in other belonid genera). Principal caudal-fin rays reduced from usual 7+8 to 5+6, branched rays reduced from 6+7 to 4+5 (Fig. 3).

Other differentiating characters include: anterior projection of the flattened first neural spine fitting between prominent flanges of the exoccipital and the paired

Table 1.—Numbers of dorsal-fin rays in populations of the 3 species of *Potamorrhaphis*.

Species	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	$\bar{x}$	n
P. petersi																			
Tomo											1							37	1
Upper Orinoco												1	2	—	1	1	1	40.3	6
Casiquiare												1						38	1
Negro												1	—	3	4			40.3	8
Species total											1	3	2	3	5	1	1	39.9	16
P. guianensis																			
Orinoco																			
Lower O.				1	7	15	1											31.7	24
Middle O.				4	4	14	1											31.5	23
Meta							1											33	1
Total Orinoco				5	11	29	3											31.6	48
Guianas																			
Kaituma						2												32.0	2
Essequibo						7	18	17	2									33.3	44
Demarara							1	4	1									34.0	6
Nickerie				1	7	11												31.5	19
Saramacca					1	1	2											32.3	4
Suriname					5	22	8	—	1									32.2	36
Maroni						4	2	1										32.6	7
Mana						1												32	1
Total Guianas				1	13	48	31	22	4									32.6	119
Amazon																			
Solimões			4	9	20	14	5	5										31.4	57
Negro							2	3	7	6								34.9	18
Middle A.					1	2	5	1										32.7	9
Lower A			1	8	9	31	25	14	8									32.5	96
Xingu						3	4	2										32.9	9
Araguia						1	1											32.5	2
Tocantins						1	1											32.5	2
Pará					1	10	13	11	—	1								33.1	36
Total Amazon			5	17	31	62	56	36	15	7								32.5	229
Species total			5	23	55	139	90	58	19	7								32.8	396
P. eigenmanni																			
Madeira																			
Madeira							1											33	1
Mamoré			1	1	5	2	1											31.1	10
Beni		6	8	1														28.7	15
Guaporé		2	4	15	11	1												30.2	33
Total Madeira		8	13	17	16	3	2											30.0	59
Paraguay	2	17	32	12	2	1												29.0	66
Species total	2	25	45	29	18	4	2											29.4	125

supraoccipital crests as in *Belonion*; 3 pairs of upper pharyngeal tooth plates (Fig. 2b) as in most other Belonidae (except *Belonion* and *Xenentodon*) but the third pair (UP_5) greatly reduced; lower pharyngeal bone (fused fifth ceratobranchials) triangular (Fig. 2b), not elongate as in *Pseudotylosurus* and *Xenentodon*; nasal

Table 2.—Numbers of anal-fin rays in populations of the 3 species of *Potamorrhaphis*.

Species	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	$\bar{x}$	n
P. petersi																		
Tomo									1								32	1
Upper Orinoco											2	1	—	—	2	1	36.3	6
Casiquiare											1						34	1
Negro											1	1	3	3			36	8
Species total									1	—	4	2	3	3	2	1	35.8	16
P. guianensis																		
Orinoco																		
Lower O.			2	11	9	2											27.5	24
Middle O.			2	5	13	2	1										27.8	23
Meta					1												28	1
Total Orinoco			4	16	23	4	1										27.6	48
Guianas																		
Kaituma					1	1											28.5	2
Essequibo				2	19	16	7										28.6	44
Demarara					2	1	2	1									29.3	6
Nickerie				10	8	1											27.5	19
Saramacca					3	—	1										28.5	4
Suriname			1	8	19	6	1										27.9	35
Maroni				1	4	2											28.1	7
Mana				1													27	1
Total Guianas			1	22	56	27	11	1									28.2	118
Amazon																		
Solimões			11	22	14	9	1										27.4	57
Negro					2	2	6	7	1								30.2	18
Middle A.					5	4											28.4	9
Lower A.		1	9	23	42	12	8	1									27.9	96
Xingu					3	3	3										29.0	9
Araguia						2											29.0	2
Tocantins					2												28.0	2
Pará				1	10	13	10	1									29.0	35
Total Amazon		1	20	46	78	45	28	9	1								28.2	228
Species total		1	25	84	157	76	40	10	1								28.1	394
P. eigenmanni																		
Madeira																		
Madeira					1												28	1
Mamoré		1	1	—	8												27.5	10
Beni	2	10	3														25.1	15
Guaporé		4	16	10	3												26.4	33
Total Madeira	2	15	20	10	12												26.3	59
Paraguay	7	31	21	5	—	1											25.4	65
Species total	9	46	41	15	12	1											25.8	124

barbel elongate, projecting out of nasal fossa (Fig. 2c) as in *Belonion* and *Xenentodon*; caudal fin rounded as in other freshwater genera; caudal peduncle compressed, with no trace of a lateral keel; supraorbital canal simple, with 4 pores on each side (Fig. 2d), and without any secondary canals such as are present in most other belonid genera (Parin and Astakhov 1982:fig. 4).

Table 3.—Numbers of pectoral-fin rays in the 3 species of *Potamorrhaphis*.

Species	6	7	8	$\bar{x}$	n
P. petersi					
Tomo		1		7	1
Upper Orinoco		5	1	7.2	6
Casiquiare			1	8	1
Negro	1	7		6.9	8
Species total	1	13	2	7.1	16
P. guianensis					
Orinoco					
Lower O.		11		7.0	11
Middle O.		23	1	7.0	24
Meta		1		7.0	1
Total Orinoco		35	1	7.0	36
Guianas					
Kaituma		2		7.0	2
Essequibo		6	25	7.8	31
Demarara			6	8.0	6
Nickerie		10	2	7.2	12
Saramacca		4		7.0	4
Suriname		3	18	7.9	21
Maroni		3	1	7.3	4
Mana		1		7	1
Total Guianas		29	52	7.6	81
Amazon					
Solimões	1	44	6	7.1	51
Negro		15	1	7.1	16
Middle A.		6		7.0	6
Lower A.		57	21	7.3	78
Xingu	1	9		6.9	10
Araguia		2		7.0	2
Tocantins		2		7.0	2
Pará		13	12	7.5	25
Total Amazon	2	148	40	7.2	190
Species total	2	212	93	7.3	307
P. eigenmanni					
Madeira					
Madeira			1	8	1
Mamoré		2	8	7.8	10
Beni		5	5	7.5	10
Guaporé		4		7.0	4
Total Madeira		11	14	7.6	25
Paraguay		49	10	7.2	59
Species total		60	24	7.3	84

Description.—Dorsal-fin rays 27–43; anal-fin rays 24–39; pectoral-fin rays 7 or 8, rarely 6. Precaudal vertebrae 35–42; caudal vertebrae 28–44; total vertebrae 64–85. Predorsal scales 77–143. Vomerine teeth absent. Gill rakers absent. Two gonads present, right about as long as left, left/right = 0.810–1.176, no sexual dimorphism in ratio. No posterior lobe in dorsal fin of juveniles. Juvenile "halfbeak" stage either absent or upper jaw grows to near tip of lower jar by an early stage (by 35 mm BL). Anterior rays of anal fin longer than posterior rays and forming a distinct lobe. Branchiostegal rays 10–11. Preorbital canal with short, ventrally directed branch midway along its anterior margin (Fig. 2e).

Potamorrhaphis petersi Collette
Fig. 4a

Potamorrhaphis guianensis (not of Schomburgk, 1843) Mago Leccia, 1971:9 (Río Casiquiare, Venezuela).

Potamorrhaphis petersi Collette, 1974a:34–38, figs. 1a, 2 (original description; Upper Río Orinoco and Rio Negro). Cala, 1977:13 (listed, Colombian Orinoco).

Diagnosis:—Most similar to *P. guianensis* from which it differs most markedly in higher numbers of dorsal- and anal-fin rays, vertebrae, and predorsal scales (Tables 1–7).

Types.—*Potamorrhaphis petersi* Collette, 1974. Holotype: USNM 210546 (162 mm); Colombia, Laguna Coco NE of Puerto Inírida, pool near junction Río Guaviare and Río Inírida; 17 Jan 1972; P. Cala. D 39; A 34; P_1 8–7; vertebrae 40 + 40 = 80; predorsal scales 130; P_1–P_2 distance 73.0 mm; P_2–C distance 85.3 mm. Paratypes: 7 specimens, USNM 210547; AMNH 9619; MNHN 87-655-6 and USNM 210861; MBUCV-V-6132; and CAS 27587 (see Collette 1974a:38 and Material Examined).

Geographic variation.—The four populations of *P. petersi* examined differ in only one meristic character, total number of vertebrae. The means for the Tomo (77.0), Casiquiare (80.0), and Río Orinoco plus Rio Negro (82.3 and 82.8) are significantly different. There are no significant morphometric differences between any of the populations.

Material examined.—RÍO ORINOCO: 8 specimens (97.5–162) from 5 collections. USNM 210546 (1, 162) Colombia, Laguna Coco NE of Puerto Inírida, pool near junction of Río Guaviare and Río Inírida; 17 Jan 1972; P. Cala; holotype of *P. petersi*. USNM 210547 (1, 137), same data as holotype. INDERENA G. A. P-0066 (1, 111), Colombia, Río Tomo near entrance into Río Orinoco. AMNH 9619 (1, 133) Venezuela, Cãno Pescado, 8 km N of Esmeralda; 9 Mar 1929; G. H. Tate. MNHN 87-655-6 (2, 97.5–123) and USNM 210861 (1, 108) Venezuela, Amazonas, Río Atabapo at San Francisco de Atabapo; Oct 1886; J. Chaffanjon. MBUCV-V-6132 (1, 124), Venezuela, Amazonas, Caño Beripamoni, tributary of Río Casiquiare; 29 Jan 1969; F. Mago Leccia, J. Moscó, A. Machado.

RIO NEGRO, Brazil: 8 specimens (64.8–157) from 4 collections. CAS 27587 (1, 92.7) São Gabriel above Camanos; 1 Feb 1925; C. Ternetz. USNM 222571 (2, 137–145) Ilha de Buiú-acú-Tapuruquara; 6 Feb 1980; M. Goulding 959. USNM 222572 (4, 84.8–157), Ilha de Tamaquaré-Tapuruquara; 11 Oct 1979; M. Goulding 55. USNM 222573 (1, 152), mouth of Rio Urubaxi; 3 Feb 1980; M. Goulding.

Potamorrhaphis guianensis (Schomburgk)
Fig. 4b–c

Belone Guianensis Schomburgk, 1843:131–132, color pl. 1 (original description; Padauiri River, Guiana).

Table 4.—Numbers of precaudal vertebrae in the 3 species of *Potamorrhaphis*.

Species	35	36	37	38	39	40	41	42	$\bar{x}$	n
P. petersi										
Tomo					1				39	1
Upper Orinoco						3	3		40.5	6
Casiquiare						1			40	1
Negro					2	2	3	1	40.4	8
Species total					3	6	6	1	40.3	16
P. guianensis										
Orinoco										
Lower O.			1	2	8	7	1		39.3	19
Middle O.				2	11	10			39.3	23
Meta						1			40	1
Total Orinoco			1	4	19	18	1		39.3	43
Guianas										
Kaituma					2				39.0	2
Essequibo				12	7	2			38.5	21
Demarara					2				39.0	2
Nickerie			4	7	4				38.0	15
Suriname				1	15	9			39.3	25
Maroni				1					38	1
Total Guianas			4	21	30	11			38.7	66
Amazon										
Solimões			4	7	4	4			38.4	19
Negro					3	7	4		40.1	14
Middle A.				2	1				38.3	3
Lower A.			10	10	14	7			38.4	41
Xingu				3	6	1			38.8	10
Araguia					2				39.0	2
Tocantins				1	1				38.5	2
Pará				1	16	11			39.4	28
Total Amazon			14	24	47	30	4		38.9	119
Species total			19	49	96	59	5		38.9	228
P. eigenmanni										
Madeira										
Mamoré			4	5	1				37.7	10
Beni		1	9	4					37.2	14
Guaporé		3	17	10	2				37.3	32
Total Madeira		4	30	19	3				37.4	56
Paraguay	2	28	21	2					36.4	53
Species total	2	32	51	21	3				36.9	109

Belone scolopacina Valenciennes *in* Cuvier and Valenciennes, 1846:428–429 (original description; La Mana, Cayenne, French Guiana).

Tylosurus guianensis.—Müller and Troschel, 1848:626 (after Schomburgk).

Belone (*Potamorrhaphis*) *taeniata* Günther, 1866:256 (original description; Brazil).—Couto de Magalhães, 1931:149–150 (description, Amazon), fig. 76.—MacDonagh, 1938:189 (comparison of types with 8 *P. eigenmanni* from the Paraguay River by Dr. Trewavas, BMNH).

Table 5.—Numbers of caudal vertebrae in the 3 species of *Potamorrhaphis*.

Species	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	$\bar{x}$	n
P. petersi																			
Tomo											1							38	1
Upper Orinoco													3	—	—	1	2	41.8	6
Casiquiare													1					40	1
Negro														1	5	2		42.1	8
Species total											1	—	4	1	5	3	2	41.6	16
P. guianensis																			
Orinoco																			
Lower O.				1	6	10	2											32.7	19
Middle O.					6	10	5											33	21
Meta								1										35	1
Total Orinoco				1	12	20	7	1										32.9	41
Guianas																			
Kaituma						2												33.0	2
Essequibo						2	10	6	1									34.3	19
Demarara									1									36	1
Nickerie				3	3	8	1											32.5	15
Suriname					1	8	15	1										33.6	25
Maroni							1											34	1
Total Guianas				3	4	20	27	7	2									33.6	63
Amazon																			
Solimões				1	10	3	2	3										32.8	19
Negro								3	4	6	1							36.4	14
Middle A.							1	1										34.5	2
Lower A.			1	1	4	13	10	6	2	4								33.9	41
Xingu						2	3	4										34.2	9
Araguia								2										35.0	2
Tocantins						1	1											33.5	2
Pará						1	9	9	7									34.8	26
Total Amazon			1	2	14	20	26	28	13	10	1							34.3	115
Species total			1	6	30	60	60	36	15	10	1							33.8	219
P. eigenmanni																			
Madeira																			
Mamoré			1	—	3	5												32.3	9
Beni			8	4	1	1												30.6	14
Guaporé		1	6	11	11	2												31.2	31
Total Madeira		1	15	15	15	8												31.3	54
Paraguay	1	10	23	11	6	1												30.3	52
Species total	1	11	38	26	21	9												30.8	106

Potamorrhaphis taeniata.—Steindachner, 1876:96 (taken by Thayer Expedition at several Amazonian localities).

Potamorrhaphis guianensis.—Jordan, 1887:530 (reference to type-specimen of *Belone scolopacina*).—Jordan and Fordice, 1887:359–360 (synonymy, description, specimens from Itaituba, Brazil).—Eigenmann and Eigenmann, 1891:66 (synonymy).—A. de Miranda Ribeiro, 1915:I, 11–13 (description, 8 specimens from Rio Negro at Manaus). Fowler, 1919:6 (Peruvian Amazon and Rupununi River; *P. eigenmanni* considered a synonym).—Schultze, 1939: 101 (specimen in Munich Aquarium from Georgetown, British Guiana).—Fowler, 1940a:278 (synonymy; Ucayali River basin, Peru.—-Eigenmann and Allen, 1942:46 (lower Marañon), 48 (lower Ucayali) 58, in part (upper Amazon, Brazilian Amazon, Guianas), 381–382 (snyonymy, distribution).—Martin, 1954:3 (Venezuela, characters), 6 (in key).—Ringuelet and Arámburu, 1961:53 (listed.)—Mees, 1962:4 (recognized as separate monotypic genus).—Mees, 1964:314–315 (synonymy, description, range, *P. eigenmanni* considered a junior synonym).—Collette, 1966 (comparison with *Belonion*), tables 1–3 (numbers of vertebrae, pectoral fin rays, and branchiostegal rays), fig. 2A (pharyngeal teeth), fig. 6B (caudal skeleton), fig. 7B (interorbital canals).—Ovchynnyk, 1967:40 (Ecuador; distribution).—Ovchynnyk, 1968:260 (Ecuador, distribution).—Cressey and Collette, 1970:400 (presence of parasitic copepod, *Ergasilus orientalis* on Brazilian specimens), 416 (fig. 180, distribution).—Berghegger, 1970:199–203 (article on keeping *P. guianensis* in aquaria illustrated with photographs of juvenile *Xenentodon cancila* and with photographs of adult *Xenentodon* labelled as *P. guianensis,* see Foster 1973:84).—Mago Leccia, 1970:89 (listed, Venezuela).—Buen, 1972:160 (distribution, in part; photograph).—Hinegardner and Rosen, 1972:639 (DNA content; 24 haploid chromosomes).—Collette, 1974a (comparison of *P. petersi* with populations of *P. guianensis* from the Orinoco, Guianas, and lower Amazon), 37 (fig. 3, distribution of northern populations).—Kusaka, 1974:110 (fig. 161, description of urohyal of specimen from Guiana).—Böhlke and McCosker 1975:10 (Rio Tocantins near Tucuruí).—Cala, 1977:13 (Río Manacacías, tributary of R. Meta, Colombia).—Hubbs and Wisner, 1980:549 (reference to pharyngeal bones in Collette 1966).—Greenwood and Lauder, 1981: 221 (protractor pectoralis muscle present).—Parin and Astakhov, 1982:278 (reference to lateralis system from Collette 1966).

Potomarrhaphis [sic] *guianensis.*—Fowler, 1914:277 (Rupununi R., British Guiana).

Potamorhaphis [sic] *guianensis.*—von Ihering, 1940:621 (Brazilian common name pirá-pucú).—Sterba, 1962:605 (description).

Tylosurus scolopacina.—Puyo, 1949:163 (description, in part, not reaching 768 mm in length; French Guiana).

Potamoraphis [sic] *guianensis.*—Damon, 1971:9 (description of aquarium specimens).

Potamorraphis [sic] *guianensis.*—Stone, 1976:24–25 (photos of aquarium specimens).

Potamorrhamphis [sic] *guianensis.*—Travers, 1981:857, 863 (interarcual cartilage absent).

Potamorrhaphis sp. Fyhn *et al.,* 1979: fig. 9, table 9, 60 (electrophoretic pattern of hemoglobin, 2 Amazonian specimens).

Misidentification.—Schultz (1949:74) reported *Potamorrhaphis guianensis* from the Río Apure in Venezuela. The specimen (UMMZ 146392) was reexamined and found to be *Pseudotylosurus microps* (Günther).

Diagnosis.—Intermediate in dorsal- and anal-fin rays, vertebrae, and predorsal scales between *P. petersi,* which has higher counts, and *P. eigenmanni,* which has lower counts (Tables 1–7).

Table 6.—Numbers of total vertebrae in populations of the 3 species of *Potamorrhaphis*.

Species	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	$\bar{x}$	n
P. petersi																								
Tomo														1									77	1
Upper Orinoco																	2	1	—	—	2	1	82.3	6
Casiquiare																	1						80	1
Negro																		1	3	1	3		82.8	8
Species total														1	—	—	3	2	3	1	5	1	82.1	16
P. guianensis																								
Orinoco																								
Lower O.						1	1	4	6	6	1												71.9	19
Middle O.								5	7	7	2												72.3	21
Meta												1											75.0	1
Total Orinoco						1	1	9	13	13	3	1											72.2	41
Guianas																								
Kaituma									2														72.0	2
Essequibo								2	6	8	3												72.6	19
Demarara												1											75	1
Nickerie						2	5	7	1														70.5	15
Suriname									9	14	1	1											72.8	25
Maroni									1														72.0	1
Total Guianas						2	5	9	19	22	4	2											72.2	63
Amazon																								
Solimões					1	3	3	3	3	5	1												71.2	19
Negro											2	—	4	6	2								76.4	14
Middle A.									1	1													72.5	2
Lower A.					1	2	5	8	8	5	6	1	4	1									72.3	41
Xingu									2	6	1												72.9	9
Araguia											2												74.0	2
Tocantins								1	—	1													72.0	2
Pará										4	13	7	2										74.3	26
Total Amazon					2	5	8	12	14	22	25	8	10	7	2								73.1	115
Species total					2	8	14	30	46	57	32	11	10	7	2								72.7	219

Table 6.—Continued.

Species	64	65	66	67	68	69	70	71	72	73	74	75		
P. eigenmanni														
Madeira														
Mamoré				1	—	—	6	1	1				70.0	9
Beni				6	5	2	1						67.9	14
Guaporé				5	12	6	7	1					68.6	31
Total Madeira				12	17	8	14	2	1				68.6	54
Paraguay	1	4	20	16	7	4							66.7	52
Species total	1	4	20	28	24	12	14	2	1				67.7	106

Table 7.—Numbers of predorsal scales in populations of the 3 species of *Potamorrhaphis* ($\bar{x}$ based on original frequency distributions).

Species	77	79	81	83	85	87	89	91	93	95	97	99	101	103	105	107
P. petersi																
P. guianensis																
Orinoco																
Lower O.										1	—	—	1	3	—	5
Middle O.										1	4	5	3	5	1	3
Meta																
Total Orinoco										2	4	5	4	8	1	8
Guianas																
Guyana							1	—	—	—	—	2	—	—	4	1
Nickerie					2	1	2	1	1	2	3					
Saramacca-Suriname									1	1	1	3	1	4	2	8
French Guiana							1	—	—	—	—	1	—	1	—	1
Total Guianas					2	1	4	1	2	3	4	6	1	5	6	10
Amazon																
Solimões												3	2	—	5	2
Negro											1	—	—	—	1	1
Lower Amazon											2	—	2	1	4	7
Pará												1	1	2	6	1
Total Amazon											3	4	5	3	16	11
Species total					2	1	4	1	2	5	11	15	10	16	23	29
P. eigenmanni																
Madeira																
Madeira													1			
Mamoré						1	—	1	—	—	2	2	1	1	1	—
Beni				1	1	—	1	—	3	—	1	1	—	—	1	
Guaporé						1	3	4	2	4	4	5	4	—	—	1
Total Madeira				1	1	2	4	5	5	4	7	8	6	1	2	1
Paraguay	2	1	3	2	3	5	6	7	6	8	1	3	2			
Species total	2	1	3	3	4	7	10	12	11	12	8	11	8	1	2	1

Types.—*Belone Guianensis* Schomburgk, 1843. No types known to be extant. Original description based on a specimen taken in the Padauiri River, British Guiana.

Belone scolopacina Valenciennes, 1846. Holotype MNHN 833 (123 mm); French Guiana, Cayenne, Rio de la Mana; Leschenault and Doumerc. D 32; A 27; P_1 7-7; predorsal scales about 100; P_1–P_2 distance 59.2 mm; P_2–C distance 60.2 mm.

Belone (*Potamorrhaphis*) *taeniata* Günther, 1866. Lectotype: BMNH 1849.11.9: 59 (142 mm); Brazil, Pará, Capim River; purchased from Mr. Stevens; herein selected. D 32; A 30; P_1 8-8; vertebrae 38 + 36 = 74; predorsal scales about 110; P_1–P_2 distance 69.1 mm; P_2–C distance 69.9 mm. Paralectotypes: BMNH 1849.11.9: 60–61 (2, 130–153); same collection data.

Geographic variation.—Two sets of ANOVA comparisons were made for most of the meristic data in *P. guianensis*. First, comparisons were made among specimens from three sections of the Río Orinoco, among eight rivers in the Guianas,

Table 7.—Continued.

109	111	113	115	117	119	121	123	125	127	129	131	133	135	137	139	141	143	n	$\bar{x}$
1	—	—	—	—	2	—	—	—	2	2	1	2	2	—	1	1	1	15	130.5
4	2	3	—	1	—	—	—	—	—	—	1							21	109.4
1																		23	102.0
	1																	1	112
5	3	3	—	1	—	—	—	—	—	—	1							45	105.7
4	3	6	2	2	2	4	—	3										34	112.9
																		12	92.0
1	1	1																24	104.3
																		4	100.0
5	4	7	2	2	2	4	—	3										74	106.0
7	2	6	7	3	4	2	1	1	1	2	1	—	1					50	113.9
—	2	—	3	2	2													12	112.9
8	8	7	8	6	5	4	2	2	3									69	113.5
5	2	4	6	3	3	—	2	1	1									38	112.6
20	14	17	24	14	14	6	5	4	5	2	1	—	1					169	113.4
30	21	27	26	17	16	10	5	7	5	2	2	—	1					288	110.3
																		1	101
—	1																	10	99.5
																		9	93.4
1	—	1																30	97.4
1	1	1																50	97.2
																		49	90.6
1	1	1																99	93.9

and among eight tributaries or regions in the Amazon drainage (Tables 8–10). Comparisons were then made among the three major populations: Orinoco, Guianas, and Amazon (Table 11).

There is adequate material to compare *P. guianensis* from the lower Orinoco with the middle Orinoco (Caicara area). There is also one specimen from much further upstream, in the Río Meta. The specimen from the Río Meta had higher counts, except for the number of pectoral-fin rays. Differences were significant only for numbers of caudal and total vertebrae. Samples from the middle and lower Orinoco do not differ from each other but do have significantly lower counts than the specimen from the Río Meta (Table 8).

Material was available from eight rivers in the Guianas. From northwest to southeast they are the Katuma, Essequibo, and Demarara in Guyana; the Nickerie, Saramacca, and Suriname in Surinam, the Maroni (or Marowijne) on the Surinam-French Guiana border; the Mana River in French Guiana. In the Guia-

Table 8.—Comparison of means for meristic characters for 3 populations of *Potamorrhaphis guianensis* from the Orinoco River (* indicates mean is significantly different from adjacent mean by SNK, alpha = 0.05).

		Fin Rays			Vertebrae				Scales
Population	n	Dorsal	Anal	Pectoral	Precaudal	Caudal		Total	Predorsal
Lower	19–24	31.5	27.5	7.0	39.3	32.7	} *	71.9 } *	109.4
Middle	21–23	31.5	27.8	7.0	39.3	33.0	}	72.3 }	102.0
Meta	1	33	28	7	40	35*		75*	112

nas, specimens with the lowest counts were in the Nickerie River, sometimes joined with the Kaituma (Table 9). Specimens with the highest counts were in the Demarara River, sometimes joined with the Essequibo. Samples from the Saramacca, Suriname, Maroni, and Mana were generally intermediate between the groups with low and high counts. This pattern of meristic variation does not seem to conform to any simple geographic pattern.

The Amazon River was divided into eight areas or major tributaries. From upstream (west) to downstream (east), these are: Solimões (or upper Amazon: Colombia, Ecuador, Peru, and Brazil down to the confluence with the Rio Negro); middle Amazon (Manaus to Gurupá); Xingu; Araguaia; Tocantins; and the Pará region. Samples with the lowest counts in the Amazon drainage were from the Solimões (Table 10). The highest counts were generally in the Río Negro, sometimes joined by the Pará population. The Tocantins, lower Amazon, Xingu, and Araquaia populations were generally intermediate between the low and high counts. As in the Guianas, this pattern of meristic variation does not seem to conform to any simple geographic pattern, lowest and highest counts being from adjacent areas.

The three major populations of *P. guianensis* show a general pattern of low counts in the Orinoco, intermediate in the Guianas, and high in the Amazon drainage (Table 11). Populations in the Orinoco and Guianas were not significantly different in two characters (total vertebrae and predorsal scales) and those in the Guianas and Amazon were not significantly different in three characters (dorsal-

Table 9.—Comparison of means for meristic characters for 8 populations of *Potamorrhaphis guianensis* from the Guianas. (* indicates mean is significantly different from adjacent mean by SNK, alpha = 0.05. Means with the same superscript do not differ from each other but do differ from means with different superscripts).

		Fin rays			Vertebrae			Scales
Population	n	Dorsal	Anal	Pectoral	Precaudal	Caudal	Total	Predorsal
Nickerie	12–19	31.5 } *	27.5	7.2^{1}	38.0^{1}	32.5 }	70.5^{1}	92.0*
Kaituma	2	32.0 }	28.5	7.0^{2}	39.0^{2}	33.0 } *	72.0^{1}	—
Saramacca	0–4	32.3 }	28.5	7.0^{1}	—	— }	—	104.3 }
Suriname	21–36	32.2 } *	27.9	7.9^{3}	39.3^{2}	33.6 }	72.8^{2}	— } *
Maroni	1–7	32.6 }	28.1	7.3^{2}	38.0^{1}	34.1 }	72.0^{1}	100.0 }
Mana	0–1	32.0*	27.0	7.0^{2}	—	— } *	—	
Essequibo	19–44	33.3 }	28.6	7.8^{2}	38.5^{2}	34.3 }	72.6^{2} }	112.9*
Demarara	1–6	34.0 }	29.3	8.0^{3}	39.0^{2}	36.3 }	75.0^{3} }	

Table 10.—Comparison of means for meristic characters for 8 populations of *Potamorrhaphis guianensis* from the Amazon. (* indicates mean is significantly different from adjacent mean by SNK, alpha = 0.05. Means with the same superscript do not differ from each other but do differ from means with different superscripts).

		Fin rays			Vertebrae			Scales
Population	n	Dorsal	Anal	Pectoral	Precaudal	Caudal	Total	Predorsal
Solimões	19–57	31.4^{1}	27.4*	7.1^{2}	38.4^{1}	32.8*	71.2 }*	113.9
Tocantins	2	32.5^{2}	28.0	7.0^{2}	38.5^{2}	33.5*	72.0	—
Lower	41–96	32.5^{2}	27.9 }*	7.3^{2}	38.4^{1}	33.9	}*	113.5
Middle	2–9	32.7^{3}	28.4	7.0^{2}	38.3^{1}	34.5	72.5	—
Xingu	9–10	32.5^{3}	29.0	6.9^{1}	38.8^{2}	34.2 }*	72.9*	—
Araguia	2	32.5^{2}	29.0 }*	7.0^{2}	39.0^{2}	35.0	74.0	—
Pará	26–38	33.1^{3}	29.0	7.5^{3}	39.4^{2}	34.8	74.3 }*	112.6
Negro	12–18	34.9^{3}	30.2	7.1^{2}	40.1^{3}	36.4	76.4	112.9

and anal-fin rays and precaudal vertebrae). All three populations were significantly different in numbers of caudal vertebrae and pectoral-fin rays.

Two sets of ANCOVA comparisons were also made for morphometric data in *P. guianensis*. First, comparisons were made of two populations in the Guianas and four populations in the Amazon drainage. Second, comparisons were made among the three major populations: Orinoco, Guianas, and Amazon.

No statistically significant differences were found between the Guianas populations. Significant differences were found in 10 of 12 morphometric characters (all but snout length and postorbital distance) among the four Amazon populations (Table 12). Slopes differed for head length, orbit, interorbital width, head depth, and head width. Slopes did not differ but intercepts did for P_1–P_2 and P_2–C distances, preopercle length, and pectoral and pelvic fin lengths. However, the Newman-Keuls Multiple Range Test was able to select which population was significantly different for only three characters: P_1–P_2 and P_2–C distances and interorbital width (Table 13). The Rio Negro population was significantly different from the other three populations in all three characters.

Statistically significant differences in slopes or intercepts were found for eight of the 12 morphometric characters among the three major populations of *P. guianensis*: Orinoco, Guianas, and Amazon (Table 14). Slopes differed for interorbital width, head width, and pelvic fin length. Intercepts differed for P_1–P_2 and P_2–C distances, preopercle length, orbit diameter and head depth. The Newman-Keuls Multiple Range Test was able to determine which population or populations differed significantly in all characters except preopercle length, orbit diameter,

Table 11.—Comparison of means for meristic characters for 3 populations of *Potamorrhaphis guianensis* (* indicates mean is significantly different from adjacent mean by SNK, alpha = 0.05).

		Fin Rays			Vertebrae			Scales
Population	n	Dorsal	Anal	Pectoral	Precaudal	Caudal	Total	Predorsal
Orinoco	36–48	31.6*	27.6*	7.0*	39.3*	32.9*	72.2 }*	105.7 }*
Guianas	63–119	32.6 }*	28.2 }*	7.6*	38.7 }*	33.6*	72.2	106.0
Amazon	115–229	32.5	28.2	7.2*	38.9	34.3*	73.1*	113.4*

Table 12.—Analysis of covariance of regressions of morphometric data on body length in 4 populations of *Potamorrhaphis guianensis* from the Amazon drainage: Solimões (S), Negro (N), Lower Amazon (L), and Pará (P). (* = significant at 0.05).

Character	Pop.	Y =	CD	N		F	P	Q
Head length	S	0.655X − 9.004	.918	39	Regression	2.786	.045	
	N	0.506X + 9.696	.895	11	Slopes	3.913	.011	2.375
	L	0.508X + 7.895	.838	39				
	P	0.535X + 7.140	.915	13				
Snout length	S	0.453X − 3.881	.917	39	Regression	2.233	.089	
	N	0.351X + 8.986	.816	11				
	L	0.397X + 1.915	.808	39				
	P	0.399X + 4.262	.898	13				
P_1–P_2	S	0.513X − 1.700	.977	56	Regression	4.236	.007	
	N	0.512X − 3.820	.989	13	Slopes	0.104	.958	
	L	0.511X − 2.156	.977	51	Intercepts	8.349	<.001	5.236*
	P	0.501X − 0.803	.989	16				
P_2–C	S	0.470X + 1.156	.974	56	Regression	5.382	.002	
	N	0.484X + 2.046	.995	13	Slopes	0.071	.975	
	L	0.472X + 1.861	.976	51	Intercepts	10.675	<.001	7.232*
	P	0.471X + 1.971	.985	16				
Postorbit	S	0.111X + 0.534	.923	56	Regression	2.314	.078	
	N	0.111X + 0.040	.930	13				
	L	0.111X + 0.643	.907	74				
	P	0.101X + 1.722	.847	20				
Preopercle	S	0.062X − 0.185	.923	56	Regression	3.076	.029	
	N	0.059X − 0.094	.941	13	Slopes	1.117	.344	
	L	0.059X + 0.397	.872	68	Intercepts	4.925	.003	−0.900
	P	0.069X − 0.859	.880	20				
Orbit	S	0.042X + 0.776	.913	56	Regression	2.872	.038	
	N	0.034X + 1.523	.908	13	Slopes	3.070	.030	3.347
	L	0.035X + 1.472	.844	75				
	P	0.032X + 1.750	.775	20				
Interorbit	S	0.063X − 0.934	.948	56	Regression	4.684	.003	
	N	0.043X + 0.935	.865	13	Slopes	3.221	.024	4.171*
	L	0.064X − 1.011	.917	75				
	P	0.061X − 0.851	.903	20				
Head D	S	0.076X − 1.053	.950	51	Regression	11.016	<.001	
	N	0.061X + 0.106	.929	13	Slopes	3.188	.026	3.053
	L	0.069X − 0.557	.913	62				
	P	0.064X − 0.104	.962	20				
Head W	S	0.075X − 1.543	.912	51	Regression	6.691	.0003	
	N	0.053X + 0.387	.953	13	Slopes	4.529	.005	3.383
	L	0.063X − 0.344	.916	62				
	P	0.067X − 1.082	.915	20				
P_1 L	S	0.126X − 0.420	.916	45	Regression	4.772	.003	
	N	0.130X − 0.887	.920	13	Slopes	1.790	.152	
	L	0.137X − 1.791	.874	56	Intercepts	7.436	.0001	−5.498
	P	0.107X + 1.101	.745	20				
P_2 L	S	0.086X − 1.406	.914	52	Regression	5.568	.001	
	N	0.093X − 1.766	.892	13	Slopes	2.404	.070	
	L	0.092X − 1.728	.878	67	Intercepts	8.316	<.001	−1.461
	P	0.070X + 0.576	.766	20				

Table 13.—Newman-Keuls Multiple Range Tests of significantly different slopes or intercepts for regressions of morphometric data on body length in 4 populations of *Potamorrhaphis guianensis* from the Amazon drainage. Regressions and analysis of covariance from Table 12. (* = significant at 0.05).

P_1–P_2 distance	Intercepts	Q for ranks	
1. Negro	−3.82033	1–4	5.2360*
2. Lower	−2.15627	1–3	6.6185*
3. Solimões	−1.69968	1–2	5.1841*
4. Pará	−0.80284	2–4	0.0900
P_2–C distance	Intercepts	Q for ranks	
1. Solimões	1.15566	1–4	7.2318*
2. Lower	1.86083	1–3	2.7316
3. Pará	1.97143	3–4	4.7068*
4. Negro	2.04583		
Interorbit	Slopes	Q for ranks	
1. Negro	0.04279	1–4	4.1708*
2. Pará	0.06098	1–3	4.7754*
3. Solimões	0.06316	1–2	3.2573*
4. Lower	0.06404	2–4	0.8550

and head depth (Table 15). The Guianas population differed from those in the Amazon and Orinoco in both P_1–P_2 and P_2–C distances. The Orinoco population differed from those in the Guianas and Amazon in pelvic-fin length. All three populations were significantly different from each other in interorbital width and head width.

Material examined.—ORINOCO RIVER: 50 specimens (62.7–126 mm BL) from 19 collections. CAS SU 52683 (7, 99.0–112), 52684 (1, 101), 52686 (8, 88.4–113), 58815 (1, 96.4); CAS 28322 (3, 62.7–110), 28323 (1, 92.3); USNM 209303 (3, 87.8–111), Venezuela, Caño Queribana into Orinoco at Caicara; May 1925; C. Ternetz. ANSP 116533 (1, 119), Colombia, Río Meta, Caño Emma at Finca El Viente S of Matuzal; 4°08′N, 72°39′W; 18 Mar 1973; J. E. Böhlke, W. Saul, W. Smith-Vaniz. USNM 219836 (12, 88.6–114), Venezuela, Delta Amacuro at about km 65; J. N. Baskin *et al.* 80–78. UCV uncat. (1, 87.3), Río Orinoco, 8°36′24″N, 61°00′W; J. N. Baskin 74–79. ANSP uncat. (1, 108) Río Arature, 8°32′N, 61°00′W; 24 Feb 1978; J. N. Baskin 85–78. LACM uncat. (1, 123) same locality; J. N. Baskin 88–78. FMNH uncat. (1, 89.7) Río Orinoco, 8°32′N, 61°02′W, km 74; 25 Feb 1978; J. N. Baskin 80–78. USNM 234948 (2, 92.0–126) Río Orinoco, 8°29′N, 61°18′W, km 82; 22 Feb 1978; J. N. Baskin 64–78. USNM 234947 (1, 125) Río Orinoco, 8°36′N, 61°48′W, km 117; 20 Feb 1978; J. G. Lundberg 47–78. USNM 234946 (2, 79.4–106) Río Arature, 8°32′N, 60°52′06″W; 1979; E. C. Marsh 25–79. CAS uncat. (1, 96.3), USNM 234944 (1, 86.8), and USNM 234945 (2, 78.7–86.3) Río Orocopiche, 8°03′N, 63°40′W; 1979; J. N. Baskin 1, 2, and 5-79. GUIANAS: 144 specimens (40.4–144 mm BL) from 61 collections. KATUMA RIVER, GUYANA. CAS SU 51288 (2, 117–123), headwaters Katuma R.; 25 Apr 1958; A. Fletcher. ESSEQUIBO RIVER, GUYANA: 54 (40.4–130) from 21 collections. CAS IUM 12580 (1, 84.0) lower Potaro R., Tumatumari; Eigenmann 1908 Exped. CAS IUM 12581 (1, 106) Essequibo R., Gluck I.; Eigenmann 1908 Exped. CAS IUM 12582 (1, 89.5) lower Potaro R., Potaro Landing; Eigenmann 1908 Exped. CAS IUM

Table 14.—Analysis of covariance of regressions of morphometric data on body length in the 3 major populations of *Potamorrhaphis guianensis*: Orinoco (O), Guianas (G), and Amazon (A). (* = signficant at 0.05).

Character	Pop.	Y =	CD	N	F		P	Q
Head length	O	0.561X + 0.911	.951	18	Regression	0.610	.545	
	G	0.541X + 4.301	.890	26				
	A	0.584X − 0.499	.899	109				
Snout length	O	0.421X − 1.019	.917	18	Regression	0.534	.588	
	G	0.400X + 2.342	.822	26				
	A	0.424X − 0.516	.887	109				
P_1–P_2	O	0.518X − 2.394	.971	30	Regression	4.509	.012	
	G	0.514X − 3.197	.985	58	Slopes	0.014	.986	
	A	0.515X − 2.512	.981	150	Intercepts	9.003	.0002	6.483*
P_2–C	O	0.476X + 1.217	.959	30	Regression	5.644	.004	
	G	0.461X + 3.903	.982	58	Slopes	0.257	.774	
	A	0.467X + 2.251	.977	150	Intercepts	11.006	<.001	5.912*
Postorbit	O	0.102X + 1.121	.864	30	Regression	1.988	.139	
	G	0.105X + 0.997	.941	59				
	A	0.110X + 0.670	.924	177				
Preopercle	O	0.052X + 0.968	.794	30	Regression	4.221	.016	
	G	0.063X + 0.020	.926	59	Slopes	1.604	.203	
	A	0.062X + 0.011	.911	171	Intercepts	6.752	.001	−0.386
Orbit	O	0.033X + 1.430	.698	30	Regression	3.550	.030	
	G	0.039X + 1.020	.819	59	Slopes	0.714	.419	
	A	0.038X + 1.169	.885	178	Intercepts	6.351	.002	−3.888
Interorbit	O	0.045X + 0.635	.804	30	Regression	13.829	<.001	
	G	0.056X − 0.440	.907	59	Slopes	8.675	.0002	4.865*
	A	0.063X − 0.947	.935	178				
Head D	O	0.060X + 0.237	.856	30	Regression	3.281	.039	
	G	0.068X − 0.327	.963	57	Slopes	1.954	.144	
	A	0.071X − 0.701	.928	160	Intercepts	4.535	.012	−2.902
Head W	O	0.041X + 1.314	.833	30	Regression	16.332	<.001	
	G	0.059X − 0.029	.909	57	Slopes	11.306	<.001	5.855*
	A	0.067X − 0.870	.917	160				
P_1 L	O	0.083X + 3.373	.568	23	Regression	2.268	.106	
	G	0.121X − 0.221	.876	54				
	A	0.127X − 0.737	.883	146				
P_2 L	O	0.051X + 1.978	.566	29	Regression	9.463	.001	
	G	0.080X − 0.978	.885	58	Slopes	6.813	.001	4.857*
	A	0.086X − 1.218	.889	165				

12584 (2, 99.1–128) Lama Stop-off; Eigenmann 1908 Exped. CAS IUM 12585 (2, 79–98) Rupununi Pan, opposite Massara Landing; Eigenmann 1908 Exped. CAS IUM 12586 (2, 92.4–97.8) Essequibo R. at Rockstone; Eigenmann 1908 Exped. CAS SU 21881 (1, 126) Lama Stop-off; Eigenmann 1908 Exped. USNM 66279 (1, 81.9) Rupununi Pan, opposite Massara Landing; Eigenmann 1908 Exped. ANSP 39799–800 (2, 76.0–104) Rupununi R.; J. Ogilvie. CAS IUM 12579 (3, 66.9–107) Konawaruk Pool; Eigenmann 1908 Exped. MCZ 30193 (1, 101) Essequibo R. at Rockstone; Eigenmann 1908 Exped. ZMH 17821 (5, 64.8–120) Essequibo R. at

Table 15.—Newman-Keuls Multiple Range Tests of significantly different slopes or intercepts for regressions of morphometric data on body length in 3 populations of *Potamorrhaphis guianensis*. Regressions and analysis of covariance from Table 14. (* = significant at 0.05).

P_1–P_2 distance	Intercepts	Q for ranks	
1. Guianas	−3.19720	1–3	6.4825*
2. Amazon	−2.51170	1–2	4.8271*
3. Orinoco	−2.39392	2–3	1.9974
P_2–C distance	**Intercepts**	**Q for ranks**	
1. Orinoco	1.21725	1–3	5.9121*
2. Amazon	2.25079	1–2	0.4837
3. Guianas	3.90308	2–3	6.1374*
Interorbit	**Slopes**	**Q for ranks**	
1. Orinoco	0.04490	1–3	4.8653*
2. Guianas	0.05559	1–2	2.9825*
3. Amazon	0.06284	2–3	3.6200*
Head width	**Slopes**	**Q for ranks**	
1. Orinoco	0.04135	1–3	5.8550*
2. Guianas	0.05900	1–2	4.9729*
3. Amazon	0.06714	2–3	3.3266*
Pelvic fin length	**Slopes**	**Q for ranks**	
1. Orinoco	0.05103	1–3	4.8574*
2. Guianas	0.08017	1–2	4.6335*
3. Amazon	0.08606	2–3	1.5534

Rockstone; 9 Nov 1938; W. Griem. NHMV uncat. (1, 68.2) Rupununi Pan opposite Massara Landing; Eigenmann 1908 Exped. NHMV uncat. (1, 40.4) Rupununi R.; Haseman. NHMV uncat. (1, 94.3) Rupununi R.; 23 Feb 1913; Haseman. NHMV uncat. (6, 73.8–120) Rupununi R. BMNH 1972.7.27.1014–20 (6, 86.7–116) Rupununi R. at Karanambo; 2 Aug 1958; R. H. Lowe-McConnell. BMNH 1972.7.27.1010–1013 (4, 56.8–72.3) Rupununi R., Pirara Stop-off; 1957; R. H. Lowe-McConnell. MCZ 48560 (1, 124) Rupununi R., Agua Branc, tributary of Manari R.; 8 May 1971; C. Hopkins. MCZ 48559 (2, 94.3–97.4) Rupununi R., Agua Branc, tributary of Manari R.; 20 Apr 1971; C. Hopkins. AMNH 15192 (10, 60.8–130) Essequibo R. at Rockstone; Mar 1938; Pinkus. DEMARARA RIVER, GUYANA: 6 (68.6–133) from 3 collections. CAS IUM 12583 (2, 88.5–111) Wismar; Eigenmann 1908 Exped. BMNH 1926.5.27.9–10 (2, 116–133) Demarara R.; Imp. Bur. Ent. BMNH 1936.4.4.38–39 (2, 68.6–97.7) Wismar. NICKERIE RIVER, SURINAM: 19 (80.2–136) from 5 collections. ZMA 105.814 (4, 80.2–118) 12 km WSW Standansie Falls; 4 Apr 1967; H. Nijssen—120. RMNH uncat. (N-1) (1, 122) L tributary below Blanche Marie Falls; 16 Feb 1971; M. Boeseman. RMNH (N-2) (2, 98.8–121) above Camp Standansie; 30 Jan 1971; M. Boeseman. RMNH uncat. (N-3) (4, 86.0–136) Tjawassi Cr.; 7 Feb 1971; M. Boeseman. RMNH uncat. (N-4) (8, 98.7–127) R tributary of Fallawatra, 35 mi from outlet; 2 Feb 1971; M. Boeseman. SARAMACCA RIVER, SURINAM: 4 (117–140) from 2 collections. ZMA 105.604 (2, 125–140) Toebaka Cr.; 2 Mar 1967; H. Nijssen—110. ZMA 105.627 (2, 117–130) Kleine Saramacca R.; 27 Feb 1967; H. Nijssen—

106. SURINAME RIVER, SURINAM: 52 (89.0–144) from 25 collections. ZMA 106.206 (1, 119) Marowijne Cr., 63 km S Afobaka; 22 Oct 1966; H. Nijssen—79. ZMA 105.706 (1, 112) Suriname R., 1 km S Botopasi; 22 Mar 1967; H. Nijssen—117. ZMA 105.785 (1, 93.5) Awala Cr., 1.5 km S Botopasi; 18 Mar 1967; H. Nijssen—111. ZMA 105.703 (2, 101–112) Jenjee Cr., 7.5 km N Botopasi; 21 Mar 1967; H. Nijssen—114. ZMA 105.204 (5, 108–130) Sara Cr., Brokopondo, 27 km S of village dam; 14 Oct 1966; H. Nijssen—76. ZMA 105.503 (11, 110–140) Marchall Cr.; 8 Dec 1966; H. Nijssen—87. RMNH uncat. S-1 (1, 109) Kwambado Kr., R. tributary of Sara Kr.; 22 Dec 1963; M. Boeseman. RMNH uncat. S-2 (2, 93.8–99.3) Langatabbetje, upper Sara Kr.; 12–14 Dec 1965; G. F. Mees. RMNH uncat. S-3 (1, 89.0) Langatabbetje, upper Sara Kr.; 11 Dec 1965; G. F. Mees. RMNH uncat. S-4 (2, 112–120) Compagnie Kr.; 19 Dec 1965; G. F. Mees. RMNH uncat. S-5 (3, 123–138) Jabokai Kr.; 18 Feb 1964. RMNH uncat. S-6 (1, 92.6) Compagnie Kr.; 13 Apr 1965; G. F. Mees. RMNH uncat. S-7 (1, 125) Gran Kr., 12 km from outlet; 21 July 1964; M. Boeseman. RMNH uncat. S-8 (1, 122) R. tributary middle Gran Kr.; 30 July 1964; M. Boeseman. RMNH uncat. S-9 (3, 108–129) Amaniparicreek, R. tributary of Sara Kr.; 24 Feb 1964; M. Boeseman. RMNH uncat. B-1 (2, 119–137) Brokopondo, Taproepa Kr.; 20 Jan 1964. RMNH uncat. B-2 (2, 127–128) Brokopondo; 17 Dec 1963; M. Boeseman. RMNH uncat. B-3 (1, 113) Brokopondo, Suriname R.; 12 May 1964; M. Boeseman. RMNH uncat. B-4 (1, 136) Brokopondo, Suriname R.; 2 May 1964; M. Boeseman. RMNH 2549 (1, 126) Brokopondo, Marchall Kr.; 28 Dec 1965; G. F. Mees. RMNH uncat. B-6 (3, 120–144) Brokopondo, between Brokopondo and Afobaka; 13 Dec 1963; M. Boeseman. RMNH uncat. B-7 (3, 90.4–144) Brokopondo, Taproepa Kr.; 22 Dec 1963; M. Boeseman. RMNH uncat. B-8 (1, 96.3) Brokopondo; 10 Jan 1964; M. Boeseman. RMNH uncat. B-9 (1, 110) Brokopondo, Suriname R.; 13 Feb 1964; M. Boeseman. RMNH uncat. B-10 (1, 118) Brokopondo, Suriname R.; 5 Jan 1964; M. Boeseman. MARONI (=MAROWIJNE) RIVER, SURINAM—FRENCH GUIANA: 7 (54.8–132) from 3 collections. ZMA 106.207 (2, 128–132) Kamaloea Cr., 9 km SE outlet Gran Cr.; 24 Apr 1967; H. Nijssen—131. ZMA 108.334 (4, 54.8–82.1) Albina; 7 Aug 1960; H. Pijpers. USNM 211329 (1, 94.6) Grand Santi; 6 Sept 1971; E. Remale. MANA RIVER, FRENCH GUIANA: MNHN 833 (1, 123) La Mana; holotype of *Belone scolopacina*. AMAZON RIVER: 264 specimens (33.7–180) from 83 collections. RIO SOLIMÕES: 58 (33.7–180) from 22 collections. CAS SU 50636 (3, 117–126) Colombia, Caquetá Prov., R. Orteguaza between Tres Esquinas and Solano; 12 Feb 1958. USNM 234943 (1, 119) Ecuador, Pastaza Prov., R. Bufeo, tributary of lower Borbonoza R.; Feb 1963; Olalla. USNM 163891 (2, 107–130) Ecuador, Pastaza Prov., Chichirota on lower Borbonoza R.; R. Olalla. CAS IUM 15811 (1, 133) Peru, Loreto, Morona R.; Oct 1920; W. R. Allen. CAS IUM 15815 (1, 96.8) Peru, Loreto, Pacaya R.; Aug 1920; W. R. Allen. ANSP 73163 (2, 89.9–121) Peru, Loreto, Ucayali R. at Contamana; 1937; W. C. Morrow. ANSP uncat. (5, 75.2–114) Peru, Loreto, R. Nanay near Iquitos; 19 Oct 1955; Hohn. UMIM 1110 (1, 97.2) Peru, Loreto, near Iquitos; 12 Sept 1954; L. R. Rivas. NHMV uncat. (2, 123–133) Peru, Loreto, Iquitos; Steindachner. NHMV uncat. (4, 101–114) Peru, Loreto, Iquitos; Steindachner. CAS SU 17272 (2, 102–136), 36849 (2, 107–114), 36850 (1, 120), 36851 (1, 90.8), 36852 (5, 88.0–120), 36853 (1, 91.0), 58700 (1, 33.7), Peru, Loreto, vicinity of Pebas in Rio Ampiyaca, Tuye Cano, etc.; 1936–41; W. G. Scherer. ZMH

17711 (9, 109–143) Peru, Loreto, between Iquitos and Leticia, 1937; H. Pietsch. ZMH 17673 (1, 110) Peru, Loreto between Iquitos and Leticia; 1936; H. Pietsch. UAIC 4165 (2, 96.2–103) Colombia, Amazonas, tributary to Loreto Yacu R.; 17 June 1971. MCZ 2760 (3, 68.7–106) Brazil, Tabatinga (=Sapurara); Thayer Exped. MCZ 8799 (8, 85.0–147) Brazil, R. Hyavary (=Javarí) near Tabatinga; Thayer Exped. MIDDLE AMAZON, BRAZIL: 10 (103–180) from 5 collections. MCZ 2758 (3, 103–180) Brazil, Jutaí; Thayer Exped. SMF 6714 (2, 104–125) Brazil, R. Solimões, Iguarapé Preto; 14 Mar 1961; H. Schultz. USNM 222298 (3, 132–172) Brazil, R. Tefé, Juruparu, half way up river; Aug 1979; M. Goulding. MCZ 8800 (1, 118) Codajás; Thayer Exped. MCZ 52601 (1, 118) Brazil, Amazonas, Rio Solimões, Ilha de Morta opposite Paraná de Janauacá; 3°25′S, 60°21′W; 20 Nov 1976; W. L. Fink 76-1. RIO NEGRO, BRAZIL: 42 (65.2–134) from 6 collections. MCZ 52600 (14, 75.3–134) Brazil, tributary of Rio Cuieiras 3 km from Rio Negro; 2°50′S, 60°35′W; 27 Nov 1976; W. L. Fink 76-5. NHMV uncat. (1, 121) Brazil, R. Branco at Boa Vista; 1912; Haseman. NHMV uncat. (1, 105) Brazil, R. Cavamé, tributary of R. Branco at Boa Vista. IRSNB uncat. (1, 110) Brazil, Arquipélago das Anavilhanas, sta. 179; 18 Nov 1967. IRSNB uncat. (1, 105) Brazil, Arquipélago das Anavilhanas, sta. 180; 19 Nov 1967. USNM 228955 (24, 65.2–115) Guyana, Pirara R. area; 31 Jan 1953. LOWER AMAZON, BRAZIL: 105 (56.0–165) from 39 collections. MCZ 2754 (5, 110–259) Manacapuru; Thayer Exped. ZMH 16032 (1, 134) Manacapuru; 1924; W. Ehrhardt. ZMH 17483 (1, 118) Manaus. BMNH 1893.4.24.40 (1, 124) Manaus; J. C. Antony. FMNH 94710 (2, 101–135) Manaus; C3156; 29 Nov 1909. BMNH uncat. (1, 125) Lago Doro near Manaus; Nov 1972. CAS SU 52682 (5, 85.1–134) Manaus, Igarapé de Mai Grais; 25 Dec 1924; C. Ternetz. USNM 179527, 179528, 179529 (14, 67.3–132) Rio Urubu 25 mi from Itacoatiara; H. Axelrod. CAS SU 52685 (2, 122–124) Igarapé da Mae Joana; C. Ternetz. CAS uncat. (1, 99.2) Igarapé da Mae Joana; 25 Dec 1924; C. Ternetz. 3 CAS uncat. (5, 93.8–137) Lago Grande into Amazon; Oct–Nov 1924; C. Ternetz. IRSNB uncat. (1, 112) Igarapé Matapi, Lago Matapi, Trombetas R., sta. 136; 2 Dec 1964. MCZ 8770 (1, 136) Villa Bella above Óbidos, L. Agassiz; Thayer Exped. MCZ 8798 (2, 92.5–92.8) Villa Bella above Óbidos, L. Agassiz; Thayer Exped. MCZ 1036 (1, 122) Óbidos; Jeffreys. MCZ 8801 (1, 109) Óbidos, Thayer Exped. MCZ 2757 (7, 56.0–122) Óbidos, Thayer Exped. IRSNB uncat. (3, 134–165) Bras du R. Cururu, mission franciscaire du Cururu, Haut Tapajox, sta. 129; 21 Nov 1964. CAS SU 1926 (2, 131) Itaituba; Agassiz. CAS IUM 6959 (3, 94.0–106) Itaituba Bay; C. F. Hartt. MZUSP 8512 (5, 74.0–93.0) Santarém, tributary of R. Mapiri; 25 Dec 1963. CAS SU 64332 (1, 103) and 3 CAS uncat. (7, 108–137), Santarém market; Sept–Oct 1924; C. Ternetz. NHMV uncat. (4, 95.5–123) Santarém; Haseman. MCZ 1028 (1, 110) Santarém; J. C. Fletcher. MCZ 8787 (1, 129) Santarém; Thayer Exped. MCZ 8806 (1, 118) Santarém; 1873; C. Linden. FMNH 94711 (1, 88.0) Santarém; C3284; 15 Dec 1909. MCZ 4682 (2, 133) Pôrto do Moz; Thayer Exped. MCZ 8788 (18, 114–157) Gurupá; Agassiz. NHMV 3 uncat. lots (5, 140–163) Gurupá; Steindachner. S. AMAZON TRIBUTARIES, BRAZIL: 14 (65.9–119) from 3 collections. USNM 201436 (10, 72.4–118) upper Rio Xingu, Mato Grosso; H. Schultz. USNM 191595 (2, 112–119) R. Araguaia near Aruana; 1960; H. Axelrod. CAS IUM uncat. (2, 65.9–86.1) Tocantins R.; 26 Apr 1924; C. Ternetz. PARÁ REGION, BRAZIL: 38 (82.9–160) from 10 collections. BMNH 1849.11.9.59–61 (3, 131–154) Capim R.; syntypes *Belone* *taeniata.* MCZ 46067 (3, 147–152) R. Apeú, Boa Vista, Castanhal, Pará; July 1965; N. Menezes. MCZ 46065 (8, 116–157) Igarapé Icatu, Belém; July 1965; N. Menezes. MCZ 46066 (1, 107) R. Arari, Ilha da Marajó; July 1965; N. Menezes. MCZ 46075 (2, 82.9–124) Igarapé Paracuri, Icoaraci; July 1965; N. Menezes. NHMV uncat. (1, 116) Pará; Mus. Goldi; Steindachner. NHMV uncat. (1, 146) Lema bei Pará; 1913; Haseman. NHMV uncat. (3, 105–151) Sema, Pará; 6 Aug 1913; Haseman. MZUSP uncat. (13, 113–160) Pará, Belém, Utinga. MZUSP uncat. (3, 151–159) Igarapé Apeú, Boa Vista; July 1965; N. Menezes.

Potamorrhaphis eigenmanni A. de Miranda Ribeiro
Fig. 4d

Belone taeniata (not of Günther, 1866) Perugia, 1891:654 (Villa Maria, Mato Grosso).—Boulenger, 1896:37 (Descalvados, Mato Grosso).

Belone (*Potamorrhaphis*) *taeniata* (not of Günther, 1866) Perugia, 1897:26 (Río Madidi, tributary of Río Madeira).

Potamorrhaphis guianensis (not of Schomburgk, 1843) Eigenmann, McAtee, and Ward, 1907:143 (Río Paraguay at Tuyuyu).—Pearson, 1924:52 (Lake Rogoagua and near Reyes, Río Beni basin, Bolivia), 58 (500–1500 ft. altitude).—Pearson, 1937:112 (present in both the Beni-Mamoré and Paraguay basins).—Fowler, 1940b:102 (listed from the Madeira-Mamoré and Paraguay water sheds after Perugia 1897, and Pearson 1924).—Pozzi, 1945:264, 276 (Río Paraguay).—Luengo, 1972:22 (Mato Grosso).

Potamorrhaphis eigenmanni A. de Miranda Ribeiro, 1915:I-13 (original description; Pôrto Esperidião, Rio Jaurú, Mato Grosso).—P. de Miranda Ribeiro, 1953: 395 and 1961:7 (reference to original description and types).—MacDonagh, 1938:188–190 (comparison of types of *B. taeniata* and specimens from Manaus and the Demarara River with 7 specimens from the Paraguay River by Dr. Trewavas, BMNH; *B. taeniata* D 32–34, A 28–31 vs. *P. eigenmanni* D 28–31, A 24–27). Pozzi, 1945:264, 276 (Río Paraná and R. Paraguay).—Collette, 1974a: 34 (listed as nominal species).—Castello *et al.,* 1978:134 (description; middle Paraná River, Argentina; fig. 8).

Potamorrhaphis taeniata (not of Günther, 1866) Pozzi, 1945:264, 276 (in part, Río Paraguay).

Diagnosis.—Most similar to *P. guianensis* from which it differs most markedly in lower numbers of dorsal- and anal-fin rays, vertebrae, and predorsal scales (Tables 1–7).

Types.—*Potamorrhaphis eigenmanni* A. de Miranda Ribeiro, 1915. Lectotype: MNRJ 1343A (95.0 mm); Brazil, Mato Grosso, Rio Jaurú at Pôrto Esperidião; A. de Miranda Ribeiro; selected by P. Miranda Ribeiro (1953:395). D 29; A 26; P_1 8 (?); P_1–P_2 distance 47.5 mm; P_2–C distance 45.3 mm. Paralectotype: MNRJ 1343 (95.0 mm).

Geographic variation.—There are two major populations of *P. eigenmanni,* located in the Paraguay-Paraná drainage basin and in the upper Río Madeira, a tributary of the Amazon. Material is available from three tributaries of the Madeira, the Mamoré, Guaporé, and Beni rivers (Fig. 5). One specimen of *P. eigenmanni* comes from further downstream in the Madeira, below the junction

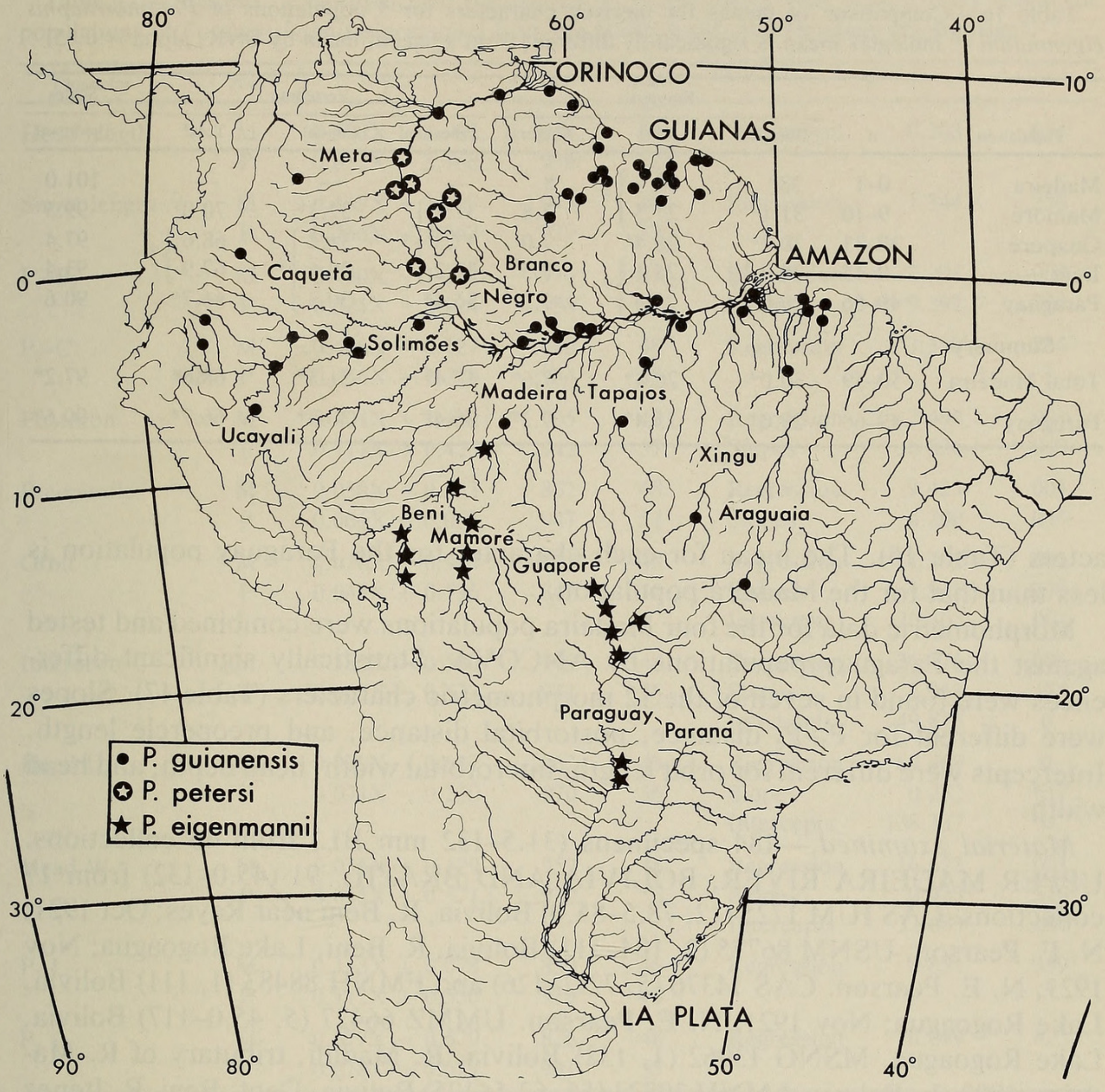

Fig. 5. Distribution of the 3 species of *Potamorrhaphis* based on specimens examined.

with these three tributaries. ANOVA comparisons of seven meristic characters were made among the five populations of *P. eigenmanni* (Table 16). The four Madeira populations were then combined and this combined population was tested against the Paraguay population (last 2 lines in Table 16).

In comparing the five populations, statistically significant differences between means were found for five of seven characters, all tested except numbers of pectoral-fin rays and predorsal scales (Table 16). There is a general pattern of decreasing counts from the Madeira (one specimen) to the Mamoré, Guaporé, Beni and finally the Paraguay. In some cases, population means do not differ from each other: Madeira and Mamoré (anal-fin rays); Mamoré, Guaporé, and Beni, (precaudal vertebrae); Guaporé and Beni (total vertebrae); Guaporé, Beni, and Paraguay (caudal vertebrae); Beni and Paraguay (dorsal- and anal-fin rays). Combining all the Madeira populations and testing their mean against that of the Paraguay population showed statistically significant differences in all seven char-

Table 16.—Comparison of means for meristic characters for 5 populations of *Potamorrhaphis eigenmanni* (* indicates mean is significantly different from adjacent mean by SNK, alpha = 0.05).

		Fin rays			Vertebrae			Scales
Population	n	Dorsal	Anal	Pectoral	Precaudal	Caudal	Total	Predorsal
Madeira	0–1	33*	28 }*	8	—	—	—	101.0
Mamoré	9–10	31.1*	27.5 }	7.8	37.7 }	32.3*	70.0*	99.5
Guaporé	30–33	30.2*	26.4*	7.0	37.3 }*	31.2 }	68.6 }*	97.4
Beni	9–15	28.7 }*	25.1 }*	7.5	37.2 }	30.6 }*	67.9 }	93.4
Paraguay	49–66	29.0 }	25.4 }	7.2	36.4*	30.3 }	66.7*	90.6
Summary								
Total Madeira	50–59	30.0*	26.3*	7.6*	37.4*	31.3*	68.6*	97.2*
Paraguay	49–66	29.0*	25.4*	7.2*	36.4*	30.3*	66.7*	90.6*

acters (Table 16). The mean for each character for the Paraguay population is less than that for the Madeira population.

Morphometric data for the four Madeira populations were combined and tested against the Paraguay populations by ANCOVA. Statistically significant differences were found in seven of the 12 morphometric characters (Table 17). Slopes were different for P_1–P_2 distance, postorbital distance, and preopercle length. Intercepts were different for orbit length, interorbital width, head depth, and head width.

Material examined.—184 specimens (31.5–132 mm BL) from 46 collections. UPPER MADEIRA RIVER, BOLIVIA AND BRAZIL: 91 (45.0–132) from 17 collections. CAS IUM 17254 (2, 78.5–85.0) Bolivia, R. Beni near Reyes; Oct 1921; N. E. Pearson. USNM 86775 (2, 104–111) Bolivia, R. Beni, Lake Rogoagua; Nov 1921; N. E. Pearson. CAS 14376 (5, 72.2–126) and FMNH 88483 (1, 111) Bolivia, Lake Rogoagua; Nov 1921; N. E. Pearson. UMMZ 66427 (5, 45.0–117) Bolivia, Lake Rogoagua. MSNG 13962 (1, 132) Bolivia, R. Madidi, tributary of R. Madeira; 1893; L. Balzan. AMNH 39823 (55, 62.5–125) Bolivia, Dept. Beni, R. Itenez (Guaporé), 10 km SE Costa Marques, Brazil; 10 Sept 1964; R. M. Bailey and R. Ramos. SMF 11866 (1, 89.1) Bolivia, Mamoré; C. A. Hahn. NHMV 11125 (2, 80.0–82.5) and NHMV 1126 (2, 88.4–90.4) Bolivia, R. Guaporé; C. Natterer. FMNH 94702 (2, 89.7–94.2) Bolivia, San Joaquin on R. Machupo; C2935; 4 Sept 1909. FMNH 94703 (1, 97.4) Bolivia, Maciel, R. Guaporé; C2830; 23 July 1909. FMNH 94705 (1, 70.0) Bolivia, Maciel, R. Guaporé; C2845; 28 July 1909. FMNH 94704 (1, 109) Bolivia, Maciel, R. Guaporé; C2881; 3 Aug 1909. FMNH 94707 (1, 51.5) Brazil, Bastos, R. Alegre into R. Guaporé; 8 mi S Villa de Mato Grosso; C2795; 26 June 1909. IRSNB 19588 (6, 86.2–127) Brazil, Rondônia, Guajará-Mirim, Sta. 184; 26 Nov 1967. IRSNB 19589 (3, 108–112) Brazil, Rondônia, Guajará-Mirim, Sta. 185; 26 Nov 1967. IRSNB uncat. (1, 136) Brazil, Rondônia, Pôrto Velho, Igarapé dos Milagres; Sta. 181; 24 Nov. 1967. PARAGUAY RIVER: 91 (31.5–123) from 27 collections. MNRJ 1343 (2, 95.0) Brazil, Mato Gross, R. Jaurú, Pôrto Esperidião; A. de Miranda Ribeiro, lectotype and paralectotype of *Potamorrhaphis eigenmanni*. MNRJ 1344 (1, 106) Brazil, Mato Grosso, Lagoa de Cáceres, Corumbá; 1913; F. L. Hoehne. FMNH 94708 (1, 97.8) Campos Alegre, R. Jaurú, C2759. FMNH 94709 (2, 95.5–97.8) São Luiz de Cáceres; C2758; 27

Table 17.—Analysis of covariance of regressions of morphometric data against body length for populations of *Potamorrhaphis eigenmanni* from the Madeira (M) and Paraguay (P) drainages.

Character	Pop.	Y =	CD	N	F		P
Head length	M	0.598X − 1.904	.954	40	Regression	0.203	.654
	P	0.617X − 3.768	.959	32			
Snout length	M	0.449X − 3.309	.945	40	Regression	1.344	.250
	P	0.456X − 4.667	.929	32			
P_1–P_2	M	0.480X − 1.212	.976	48	Regression	7.291	.008
	P	0.521X − 2.024	.988	55	Slopes	9.297	.003
P_2–C	M	0.486X − 0.127	.980	48	Regression	3.510	.064
	P	0.456X + 2.273	.984	55			
Postorbit	M	0.101X + 1.452	.905	48	Regression	12.496	.001
	P	0.117X + 0.425	.942	57	Slopes	6.836	.010
Preopercle	M	0.058X + 0.533	.862	48	Regression	9.423	.003
	P	0.066X + 0.057	.947	57	Slopes	4.200	.043
Orbit	M	0.036X + 0.944	.915	48	Regression	11.302	.001
	P	0.041X + 0.796	.847	56	Slopes	1.911	.170
					Intercepts	20.305	.001
Interorbit	M	0.582X − 0.540	.949	48	Regression	26.476	.001
	P	0.063X − 0.572	.931	56	Slopes	2.053	.155
					Intercepts	49.875	0
Head D	M	0.070X − 0.627	.962	48	Regression	69.469	0
	P	0.071X − 0.220	.970	56	Slopes	0.252	.617
					Intercepts	138.337	0
Head W	M	0.056X + 0.129	.952	48	Regression	16.623	.001
	P	0.055X + 0.571	.932	56	Slopes	0.425	.516
					Intercepts	32.683	.001
P_1 L	M	0.115X + 0.078	.839	46	Regression	0.851	.359
	P	0.112X + 0.550	.919	48			
P_2 L	M	0.077X − 0.579	.876	48	Regression	0.049	.825
	P	0.078X − 0.679	.901	55			

May 1909. FMNH 94706 (14, 36.0–107) Paraguay, Puerto Suarez; C2690; 6 May 1909. MNM 641 (23, 57.0–89.4) Brazil, Mato Grosso, Laguna Gaibu near Amolar; 25 Oct 1955. MSNG 39849 (1, 78.8) Brazil, Mato Grosso, Villa Maria; L. Balzan. FMNH 70389 (1, 64.5) Brazil, Mato Grosso, Descalvados; July 1926; Schmidt and Sanborn. FMNH 70390 (4, 76.7–104) Brazil, Mato Grosso, Descalvados; July 1926; Schmidt and Sanborn. FMNH 70391 (6, 66.5–105) Brazil, Mato Grosso, Conceicão; 24 July 1926; Schmidt and Sanborn. FMNH 70392 (1, 89.1) Brazil, Mato Grosso, Conceicão; 10 Aug 1926; K. P. Schmidt. CAS 10267 (1, 90.2) Brazil, Mato Grosso. MACN uncat. (2, 86.0–88.0) Brazil, Mato Grosso; Burmeister Exped. BMNH 1895.5.17.259–60 (2, 72.3–81.3) Brazil, Mato Grosso; C. Ternetz. BMNH 1900.4.14.87–90 (4, 68.6–92.8) Carandasinho; A. Boretti. MSNG 14021 (2, 64.0–98.4) Paraguay, Puerto 14 Mayo; 1900; F. Silvestri. NHMV uncat. (2, 102–123) Buchten Paraguay; Natterer. NHMV uncat. (2, 96.0–105) Buchten Paraguay; Natterer. NHMV 11127 (2, 82.7–89.8) Paraguay; Natterer. NHMV 11128 (4, 68.8–83.3) Paraguay; Natterer. BMNH 1910.5.26.51 (1, 126) Paraguay; Tudor.

Table 18.—Analysis of covariance of regressions of morphometric data on body length for the 3 species of *Potamorrhaphis*: *P. petersi* (P), *P. guianensis* (G), and *P. eigenmanni* (E). (* = significant at 0.05).

Character	Pop.	Y =	CD	N	F		P	Q
Head length	P	0.545X − 2.962	.971	10	Regression	12.985	<.001	
	G	0.580X − 0.168	.910	153	Slopes	1.010	.366	
	E	0.607X − 2.757	.957	72	Intercepts	24.741	0	8.832*
Snout length	P	0.410X − 3.924	.962	10	Regression	9.878	<.001	
	G	0.423X − 0.443	.890	153	Slopes	1.184	.308	
	E	0.454X − 4.166	.937	72	Intercepts	18.382	0	1.970
P_1–P_2	P	0.479X − 3.520	.990	16	Regression	63.152	0	
	G	0.516X − 2.822	.982	238	Slopes	4.150	.016	3.227*
	E	0.499X − 0.371	.981	103				
P_2–C	P	0.516X + 1.783	.991	16	Regression	70.964	0	
	G	0.463X + 2.919	.977	238	Slopes	5.868	.003	4.489*
	E	0.471X + 1.107	.982	103				
Postorbit	P	0.097X + 0.417	.940	16	Regression	33.426	0	
	G	0.110X + 0.568	.931	266	Slopes	1.786	.169	
	E	0.107X + 1.112	.913	105	Intercepts	64.460	0	14.047*
Preopercle	P	0.057X − 0.304	.952	16	Regression	32.673	0	
	G	0.060X + 0.167	.910	260	Slopes	0.437	.646	
	E	0.061X + 0.403	.900	105	Intercepts	64.758	0	15.555*
Orbit	P	0.035X + 0.799	.914	16	Regression	21.877	0	
	G	0.038X + 1.060	.873	267	Slopes	0.548	.578	
	E	0.037X + 0.995	.843	104	Intercepts	43.081	0	11.407*
Interorbit	P	0.055X − 1.353	.948	16	Regression	54.788	0	
	G	0.063X − 1.025	.925	267	Slopes	3.322	.037	2.500
	E	0.058X − 0.330	.905	104				
Head D	P	0.065X − 1.161	.928	16	Regression	39.884	0	
	G	0.070X − 0.610	.935	247	Slopes	1.398	.248	
	E	0.067X − 0.071	.920	104	Intercepts	77.768	0	15.524*
Head W	P	0.071X − 1.908	.907	16	Regression	12.956	<.001	
	G	0.066X − 0.792	.908	247	Slopes	12.862	<.001	6.453*
	E	0.053X + 0.555	.922	104				
P_1 L	P	0.111X − 0.460	.933	14	Regression	13.834	<.001	
	G	0.126X − 0.734	.886	223	Slopes	3.382	.035	1.743
	E	0.112X + 0.451	.883	94				
P_2 L	P	0.086X − 2.237	.967	16	Regression	8.906	.0002	
	G	0.087X − 1.441	.886	252	Slopes	2.990	.052	
	E	0.077X − 0.626	.897	103	Intercepts	14.583	<.001	5.516*

UMMZ 207843 (1, 102) Paraguay, R. Aquidaban at Paso Horqueta *ca.* 24 km NNW of Loreto; 5–6 Sept. 1979; J. Taylor *et al.* UMMZ 205601 (1, 48.1) Paraguay, overflowing inlet along E shore of R. Paraguay *ca.* 1 km S from Puente Remanso bridge; 21 May 1979; J. Taylor *et al.* UMMZ 207252 (1, 55.8) Paraguay, R. Montelindo *ca.* 155.8 km NW of Benjamin Aceval; 16 Aug 1979; G. R. Smith and J. N. Taylor. UMMZ 205885 (1, 31.5) Paraguay, E shore of R. Paraguay; 11 June 1979; R. M. Bailey *et al.* UMMZ 207901 (4, 54.0–123) Paraguay, R. Aquidaban at Paso Horqueta *ca.* 24 km NNW of Loreto; 6 Sept 1979; J. Taylor *et* *al.* UMMZ 206673 (5, 68.4–102) Paraguay, R. Aquaray Guazei 5.4 km S of junction with road W to San Pedro; 22 July 1979; J. Taylor. PARANÁ RIVER, ARGENTINA: MACN 4291 (1, 77.5) R. Paraná; 12 Nov 1895.

Discussion

As hypothesized previously (Collette 1966), *Potamorrhaphis* probably evolved from inshore marine needlefishes similar to *Strongylura,* having three pairs of upper pharyngeal tooth plates (UP_2, UP_{3+4}, and UP_5), a truncate caudal fin, and unforked pelvic fins smaller than the pectoral fins. *Potamorrhaphis* and *Belonion* share such specialized characters as a rounded caudal fin, few large teeth on the pharyngeal bones, pectoral-fin rays reduced to eight or fewer, nasal barbel elongate, and an association of the expanded first neural spine with the supraoccipital crests and exoccipital flange. *Potamorrhaphis* diverged from *Belonion* by elongating the posterior part of its body and increasing the numbers of caudal vertebrae and dorsal- and anal-fin rays. The evolutionary line leading to *Belonion* continued to specialize by reduction of body size, number of vertebrae, branchiostegal rays, and pectoral-fin rays and by the loss of a pharyngeal tooth plate (UP_5).

The three species of *Potamorrhaphis* form a series with increasing numbers of dorsal- and anal-fin rays, vertebrae (precaudal, caudal, and total), and predorsal scales from *P. eigenmanni* to *P. guianensis* to *P. petersi.* The differences in these characters are greater between *P. petersi* and *P. guianensis* than between the latter and *P. eigenmanni.* In comparison with presumably less specialized needlefishes, such as *Strongylura, P. eigenmanni* appears to be the least specialized of the three species, *P. petersi* the most. Geographically, the three species form a similar series from south to north with *P. eigenmanni* concentrated in the Paraguay-Paraná system, *P. guianensis* distributed throughout the Amazon and the Guianas, and *P. petersi* concentrated in the Upper Río Orinoco. Apparently, *P. eigenmanni* has invaded the Amazon through the Mato Grosso into the Upper Rio Madeira in Bolivia and Brazil. Similarly, *P. petersi* seems to have moved through the Río Casiquiare into the upper Rio Negro in Brazil. I know of no sympatric occurrences of *P. eigenmanni* with *P. guianensis,* although the latter does occur farther downstream in the Rio Madeira (Fig. 5). Similarly, *P. petersi* occurs in the upper Rio Negro and *P. guianensis* farther downstream. Some intergradation may have taken place between *P. eigenmanni* and *P. guianensis* in the Rio Madeira and between *P. petersi* and *P. guianensis* in the Rio Negro as suggested by the frequency distributions of meristic characters (Tables 1–2, 4–7).

This south-to-north pattern, from the Paraná to the Amazon to the Orinoco, is similar to the recent interpretation of the origins of the parasitic helminths of South American freshwater stingrays (Potamotrygonidae) by Brooks, Thorson, and Mayes (1981). Both *Potamorrhaphis* and the Potamotrygonidae are absent from the Rio São Francisco system of eastern Brazil. However, the Potamotrygonidae range west into the Maracaibo and Magdalena drainages from which *Potamorrhaphis* is absent. Brooks *et al.* further hypothesize that the relationships of the Potamotrygonidae are not with Atlantic dasyatids but rather with Pacific *Urolophus.* While I have no morphological information that would support the origin of *Potamorrhaphis* from Atlantic or Pacific *Strongylura*, I should note that a parasitic ergasilid copepod, *Ergasilus orientalis,* was reported from two species of needlefishes, *Potamorrhaphis guianensis* from the Amazon and *Strongylura incisa* from northern Australia (Cressey and Collette 1970) as well as from a goby and an atherinid from Japan. If these copepod populations really are conspecific, this distribution would tend to support the hypothesis of Brooks *et al.* (1981).

Recognition of *P. eigenmanni* as a distinct species confirms the total number of species in the family as 32 and the known neotropical species as nine in four genera: *Potamorrhaphis* (3), *Belonion* (2, see Collette 1966), *Pseudotylosurus* (2, see Collette 1974b), and *Strongylura* (2, *S. hubbsi* in the Usumacinta Province of México and Guatemala, see Collette 1974c, and *S. fluviatilis* west of the Andes in Colombia and Ecuador). I have previously (Collette 1974c:618) called attention to the large number of freshwater needlefishes compared to halfbeaks in the neotropics and the reverse situation in the freshwaters of the Indo-Australian region. The nine neotropical freshwater species of belonids comprise 28.1% of the species in the family; the two Indo-Australian freshwater species 6.3%. The two neotropical freshwater halfbeaks, *Hyporhamphus mexicanus* Alvarez in the Usumacinta Province of Middle America and *H. brederi* (Fernández Yépez) in the Orinoco and Amazon basins, comprise 2.9% of the approximately 70 species in the family; the approximately 14 Indo-Australian freshwater species (in the genera *Dermogenys, Nomorhamphus, Hemirhamphodon, Hyporhamphus,* and *Zenarchopterus*) 20.0%. Historical, evolutionary, or ecological explanation of this complementarity in distribution is needed.

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National Marine Fisheries Service Systematics Laboratory, National Museum of Natural History, Washington, D.C. 20560.