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TWO NEW SPECIES AND A NEW GENUS OF MINIATURE CHARACID FISHES (TELEOSTEI: CHARACIFORMES) FROM NORTHERN SOUTH AMERICA

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Abstract.—The first known miniature characid fishes apparently aligned with the Characinae and Cynopotaminae are described as new from the Río Negro and Río Orinoco drainages of Venezuela and tributaries of the Río Amazonas in Colombia. Although the suggested relationships of the new genus (*Priocharax*) and species (*P. ariel* and *P. pygmaeus*) to those subfamilies appear reasonable, their exact phylogenetic relationships within the Characinae and Cynopotaminae remain obscure. The new species are distinguished from others in these subfamilies primarily by a higher number of jaw teeth, a lower number of pelvic- and anal-fin rays, retention of larval pectoral fins in adults, and a minute adult body size of a maximum of about 17 mm in standard length.

The early explorer-naturalists who sampled the South American freshwater fish fauna focused nearly exclusively on species of moderate to large body size, evidently under the mistaken belief that all smaller fishes were juveniles, or if distinct the species were unimportant. Agassiz, during the Thayer Expedition to Brazil in 1865, was the first collector who fully endeavored to collect even the smallest fishes, recognizing that such specimens often represented interesting species of small adult size. During the twelve decades that have passed since that trip numerous species of relatively small adult body sizes have been described from the freshwaters of South America. Recent collecting efforts in Venezuela have yielded miniature species of the family Lebiasinidae (Fernandez and Weitzman 1987) and the subfamily Characidiinae of the Characidae (Weitzman 1986). Those collections also revealed the existence of a miniature species evidently aligned phyletically with the characid subfamilies Characiinae and Cynopotaminae. A second, very similar species, originally collected in the Colombian Amazon, was subsequently found in the collection of the Naturhistoriska Riksmuseet, Stockholm. These two species, assigned herein to a new genus, are described as new and the possible phylogenetic relationships of these taxa are discussed.

Methods and Materials

The counts and measurements are those described by Fink and Weitzman (1974:1–2). All measurements other than standard length (SL) are expressed as a percentage of SL except subunits of the head which are expressed as a percentage of head length or as otherwise noted.

Specimens examined for this study are deposited in the American Museum of Natural History, New York (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); British Museum (Natural History), London (BMNH); California Academy of Sciences, San Francisco (CAS); Field Museum of Natural History, Chicago (FMNH); Museo de Biología, Universidad Central de Venezuela, Caracas (MBUCV); Museu de Ciências, Pontificia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCP);

Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Muséum d'Histoire Naturelle, Génève (MHNG); Muséum National d'Histoire Naturelle, Paris (MNHN); Museu de Zoologia da Universidade de São Paulo (MZUSP); Naturhistoriska Riksmuseet, Stockholm (NRM); Naturhistorisches Museum Wien, Vienna (NMW); University of Michigan, Museum of Zoology, Ann Arbor (UMMZ); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); and Institute of Taxonomic Zoology (Zoölogisch Museum), Amsterdam (ZMA).

Priocharax, new genus

Diagnosis.—New World characid fish group distinguished from all other characids by retaining larval rayless pectoral fin in adults. Distinguished from all other New World characids except some members of Characinae and Cynopotaminae by having lower jaw (dentary bone) with approximately 30 to 50 conical teeth in somewhat irregular single row, and upper jaw (premaxilla and maxilla) with approximately 45 to 90 conical teeth in somewhat irregular single row. Adult body size ranges from about 11 to 17 mm standard length; such diminutive adult body size otherwise unknown in Characinae and Cynopotaminae.

Within the tribe Characini of the Characinae (sensu Géry 1977:302–306) and the Cynopotaminae (Menezes 1976) 16 to 22 branched anal-fin rays of *Priocharax* further distinguish its species from *Acanthocharax* Eigenmann, *Acestrocephalus* Eigenmann, *Asiphonichthys* Cope, *Charax* Scopoli, *Cynopotamus* Valenciennes, *Eucynopotamus* Fowler, *Galeocharax* Fowler, *Gilbertolus* Eigenmann, *Gnathocharax* Fowler, *Heterocharax* Eigenmann, *Hoplocharax* Géry, *Lonchogenys* Myers, *Moralesia* Fowler, *Roestes* Günther, and *Roeboides* Günther all with 26 or more branched anal-fin rays. *Priocharax* posesses i,5 pelvic-fin rays, discriminating it from all other members of Characinae and Cynopotaminae, all with i,7 pelvic-fin rays.

Type species.—*Priocharax ariel,* new species.

Etymology.—*Prio* from the Greek for saw, and *charax* from the Greek characo meaning pointed stake, here used in reference to the characid genus *Charax,* hence a characid fish. *Priocharax* means a saw-bearing characid fish in reference to its numerous small jaw teeth.

Key to the Species of *Priocharax*

1. Caudal peduncle depth about 32 to 46 percent of caudal peduncle length; dentary teeth about 38 to 55; lower limb gill-rakers 11 to 13 .... *Priocharax ariel,* new species
– Caudal peduncle depth about 52 to 65 percent of caudal peduncle length; dentary teeth about 28 to 36; lower limb gill-rakers 8 to 10 ....*Priocharax pygmaeus,* new species

Priocharax ariel, new species
Figs. 1–5, Table 1

Holotype.—MBUCV V-15340, male, SL 14.5 mm, Venezuela, Territorio Federal Amazonas, Departamento Río Negro, Caño Manu, tributary of Río Casiquiare approximately 250 m upstream from Solano, 02°00′N, 66°57′W; R. P. Vari, C. J. Ferraris, Jr., O. Castillo, and J. M. Fernandez, 7 Dec 1984.

Paratypes.—Following 16 lots collected with holotype and deposited in cited institutions; all museums received 25 specimens unless otherwise noted; extremes of SL are given only for USNM specimens, lengths of other series fall within that range: USNM 272619, SL 8.8–17.1 mm, 1229 specimens, 41 cleared and counterstained for cartilage and bone; AMNH 57007; ANSP 158006; BMNH 1986.2.4:1-25; CAS 57944; FMNH 96689; MBUCV V-15341, 100 specimens; MCP 9953; MCZ 63031; MHNG 2239.48; MNHN 1986-303; MZUSP 3647, 50 spec-

Table 1.—Morphometrics of *Priocharax ariel* and *P. pygmaeus*. Males of *P. ariel* all with anal-fin hooks. Specimens of *P. ariel* and *P. pygmaeus* of undetermined sex lack anal-fin hooks. Standard length is expressed in mm. First group of measurements are presented as percentages of standard length; second group as percentages of head length.

	Priocharax ariel males				*Priocharax ariel* sex undetermined			*Priocharax pygmaeus* sex undetermined			
	Holotype	n	Range	$\bar{x}$	n	Range	$\bar{x}$	Holotype	n	Range	$\bar{x}$
Standard length	14.5	27	11.8–15.1	14.0	27	11.8–17.1	14.2	16.4	7	10.8–16.4	12.0
Depth at dorsal-fin origin	24.8	27	21.8–24.8	23.4	27	22.0–25.4	23.9	24.4	7	23.2–24.6	23.9
Snout to dorsal-fin origin	55.9	27	53.2–55.9	54.6	27	52.5–55.8	54.3	54.9	7	50.9–56.3	53.7
Snout to pelvic-fin origin	42.4	27	39.5–42.5	40.9	27	39.1–42.4	40.7	42.1	7	42.1–44.6	43.6
Snout to anal-fin origin	53.8	27	53.0–56.6	54.7	27	52.8–56.1	54.3	55.5	7	53.6–56.6	55.6
Peduncle depth	7.6	26	7.2–8.3	7.8	27	7.2–9.0	8.2	7.9	7	7.9–8.4	8.2
Peduncle length	21.4	27	19.2–23.2	20.8	27	18.1–23.7	22.2	12.2	7	12.2–15.8	14.8
Pelvic-fin length	11.0	27	10.2–13.0	11.3	27	9.8–13.7	11.1	11.6	7	9.1–11.6	10.4
Dorsal-fin height	23.4	25	22.0–26.4	23.7	26	21.1–25.2	23.7	24.4	7	24.1–25.7	24.9
Anal-fin anterior lobe length	20.7	27	19.7–22.5	21.2	25	20.0–22.9	21.7	26.2	7	21.1–26.2	23.6
Bony head length	23.4	27	23.0–26.4	24.4	27	22.8–25.3	24.1	25.6	7	25.6–27.9	27.2
Horizontal eye diameter	31.8	27	27.7–33.8	31.5	27	29.7–34.4	32.3	30.0	7	30.0–35.2	33.1
Snout length	23.5	27	20.0–24.7	22.6	27	19.7–24.4	22.6	21.4	7	19.4–24.7	22.1
Interorbital width	35.3	22	32.1–37.2	34.2	26	32.7–38.9	35.3	33.3	7	32.3–36.4	35.1
Upper jaw length	55.9	27	49.9–60.0	55.8	27	50.0–60.0	56.1	48.3	7	43.3–50.9	47.2
Caudal peduncle depth as percent of caudal peduncle length	35.5	26	33.3–42.4	36.8	27	32.1–46.0	39.2	65.0	7	52.6–65.0	56.1

imens; NRM A86/1984495.3603, 50 specimens; NMW 81788; UMMZ 213500, 35 specimens, 10 cleared and counterstained for cartilage and bone; and ZMA 119.456. All following paratypes collected in Venezuela, Territorio Federal Amazonas, R. P. Vari and party unless otherwise noted: USNM 272613, SL 13.9 mm, 1, Departamento Río Negro, lagoon northeast of airport at San Carlos de Río Negro, 01°55′N, 67°02′W, 4 Dec 1984. USNM 272614, SL 14.0 mm, 1, Departamento Río Negro, Caño Chola, where crossed by road from San Carlos de Río Negro to Solano, 01°58′N, 67°00′W, 5 Dec 1984. USNM 272615, SL 11.4–13.6 mm, 10, Departamento Río Negro, small caño off Caño Urami, just upriver of Santa Lucia, 01°17′N, 66°51′W, 6 Dec 1984. AMNH 57008, SL 13.1 mm, 1, Departamento Río Negro, Río Negro at Santa Lucia, 01°17′N, 66°52′W, 4 Feb 1984, C. J. Ferraris and party. USNM 272618, SL 13.7–14.9 mm, 3, Departamento Río Negro, Caño Loro, where crossed by road from San Carlos de Río Negro to Solano, 01°59′N, 66°58′W, 7 Dec 1984. USNM 272616, SL 11.9 mm, 1, Departamento Ature, small caño crossed by road from Puerto Ayacucho to Samariapo, 2 km south of Mirabel, 05°25′N, 67°46′W, 12 Dec 1984. USNM 272617, SL 12.2–12.9 mm, 2, Departamento Ature, Río Platanillal, where crossed by road from Puerto Ayacucho to Samariapo, 05°37′N, 67°35′W, 2 Dec 1984.

Diagnosis.—Two species of *Priocharax* diagnosable on basis of complete separation in one morphometric and two meristic characters. In both sexes of *Priocharax ariel* caudal peduncle depth about 32 to 46 percent of caudal depth, contrasted to about 52 to 65 percent in *P. pygmaeus*. *Priocharax ariel* with greater number of lower limb gill rakers on anterior gill-arch, 11 to 13, than *P. pygmaeus*, 8 to 10. Large individuals of

Fig. 1. A, *Priocharax ariel,* new species, holotype, MBUCV V-15340, male SL 14.5; Venezuela, Departamento Río Negro, Caño Manu; B, *Priocharax ariel,* new species, paratype, USNM 272619, female, SL 15.3 mm; same locality as holotype.

both species with greater number of dentary teeth, but counts do not overlap between species. Specimens of *P. ariel* with 38 to 55 dentary teeth ($\bar{x}$ = 44, n = 41), those of *P. pygmaeus* with 28 to 36 teeth ($\bar{x}$ = 32.5, n = 10). Other meristic characters probably will show significant differences, but specimens of *P. pygmaeus* too poorly preserved to allow definitive analysis without clearing and staining many specimens. Some overlap occurs in all following characters, but covariance analysis of larger numbers of *P. pygmaeus* probably would show distinct differences between these species. Branched anal-fin rays 16 to 21 in *P. ariel* ($\bar{x}$ = 18.5, n = 96) and 20 to 22 in *P. pygmaeus* ($\bar{x}$ = 21.0, n = 16); upper limb rakers 3 to 5 in *P. ariel* ($\bar{x}$ = 3.9, n = 41) and 2 or 3 in *P. pygmaeus* ($\bar{x}$ = 2.2, n = 10); premaxillary teeth 22 to 34 in *P. ariel* ($\bar{x}$ = 27.7, n = 41) and 19 to 24 in *P. pygmaeus* ($\bar{x}$ = 21.7, n = 10); maxillary teeth 38 to 58 in *P. ariel* ($\bar{x}$ = 47.7, n = 41) and 27 to 41 in *P. pygmaeus* ($\bar{x}$ = 31.4, n = 10).

Description.—Table 1 presents morphometrics of holotype and measured paratypes. See Fig. 1A, B for body form. Body slender, sides compressed. Greatest body depth at dorsal-fin origin. Dorsal-fin origin somewhat closer to caudal-fin base (at posterior of hypural fan and anterior of caudal-fin rays) than to tip of snout. Dorsal-fin origin approximately intersected by vertical line through anal-fin origin. Pelvic-fin ori-

Fig. 2. Anterolateral view of jaws of *Priocharax ariel*, new species, paratype, UMMZ 213500, male, SL 16.7 mm, same locality as holotype.

gin nearly midway between anal-fin origin and vertical line through most posterior point of opercle. Snout bluntly rounded. Dorsal profile of head and body gently convex from snout tip to dorsal-fin origin. Dorsal profile of body along dorsal-fin base nearly straight, gently sloping posteroventrally. Dorsal body and caudal peduncle profile very slightly concave from dorsal-fin insertion to base of procurrent rays. Caudal peduncle slender, elongate, with sides compressed. Ventral body profile gently convex from symphysis of lower jaw to ventral to pectoral-fin origin. Belly profile from that point to vent and anal-fin origin may be slightly convex, more often straight, or sometimes slightly concave. Body profile along anal-fin base and caudal peduncle to anterior ventral procurrent rays gently concave. Base of anal fin posterodorsally oriented.

Head length approximately one-quarter of standard length. Snout rounded in profile. Jaws about equal, mouth terminal or lower jaw slightly included. Mouth elongate, somewhat posteroventrally inclined. Maxilla elongate; upper jaw long, posterior border reaching to or posterior to vertical line through posterior border of pupil of eye, length half to nearly two-thirds of head length. Eye about one-third of head length. Fleshy interorbital width often over one-third of bony head length, gently convex transversely.

Maxilla with 38 to 58 teeth ($\bar{x}$ = 47.4, n = 41; teeth of holotype not counted); teeth conical, small and slender, in single series along ventral border of bone. Number of teeth increasing with body length. Accessory cusps absent. Premaxilla with 22 to 34 teeth ($\bar{x}$ = 27.7, n = 41) in a single series. Premaxilla teeth similar in form to those of maxilla. Dentary with 38 to 55 teeth ($\bar{x}$ = 44.6, n = 41). Dentary teeth in a single row posteriorly; larger specimens with irregular row of closely placed teeth anteriorly, but two distinct anterior rows never present. Anterior dentary teeth larger than those posterior. All jaw teeth lingually curved to a moderate extent (see Fig. 2).

Infraorbital series incomplete, with antorbital bone only element ossified, apparent only in cleared and stained specimens over 13.5 mm SL. Fronto-parietal fontanel large, extending from ethmoid to supraoccipital, completely separating parietals; frontals only in contact at strong epiphyseal bar. Frontal about of same width along entire length; similar in form to that of small juvenile characids. Supraoccipital spine poorly developed (Fig. 3).

Dorsal-fin rays ii,9 in holotype; other examined specimens with 2 unbranched rays followed by 8 to 10 mostly divided rays ($\bar{x}$ = 8.9, n = 96); usually with posterior ray or more rarely posterior two rays not divided to their base. Dorsal-fin height moderate, 20 to 25% of SL. Pectoral fin larval in form (Fig. 4). Radials of two incompletely separated hyaline cartilaginous flat plates articulating anteriorly with vertically elongate cartilaginous coracoscapular plate and posteriorly with striated actinotrich tissue around which rays form in developing larvae of other characids. In specimens about 14 to 15 mm SL coracoscapular plate par-

Fig. 3. Lateral view of posterior portion of neurocranium and Weberian apparatus of *Priocharax ariel,* new species, paratype, UMMZ 213500, male, SL 16.7 mm, same locality as holotype.

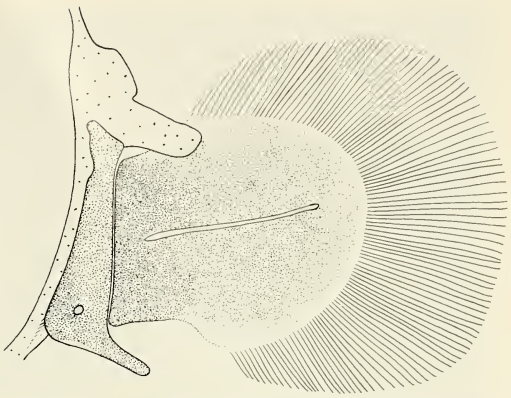

Fig. 4. Lateral view of pectoral girdle of *Priocharax ariel,* new species, paratype, UMMZ 213500, male, SL 16.7 mm, same locality as holotype. Densely stippled structures are cartilage.

tially ossified dorsally. Cleithrum ossified, slender, attached dorsally to slender supracleithrum by relatively loose ligamentous tissue. No notch or spine on cleithrum. Coracoid and other pectoral girdle elements often not ossified, but slight ossification present along ventral border in example drawn. Posttemporal weakly ossified, not shown in Fig. 4. Pelvic-fin rays i,5 in all counted specimens, n = 97. Posterior tip of pelvic fin extending about to region of vent. No hooks present on pelvic, dorsal or pectoral-fin rays. Anal fin iii,20 in holotype; other examined specimens with three unbranched rays followed by 16 to 21 branched rays ($\bar{x}$ = 18.5, n = 96), posterior ray divided to its base. Anal-fin hooks present in 35 specimens from Caño Manu, all other specimens (1319) from that locality without hooks. Hooks occur on posterior margin of three anterior undivided rays and anterior 4 or 5 divided rays (Fig. 5). Usually 6 to 8 hooks per ray, with one short hook per ray segment. Anal-fin margin concave, with anterior elongate lobe and posterior section of short rays. Fin shape similar in specimens with and without hooks. Caudal fin forked, of moderate length; principal rays 10/9 in 91 specimens. Adipose fin absent.

Squamation almost completely absent in most specimens, apparently lost in handling during capture; following counts thus tentative. Scales in lateral series on body about 31 or 32; with no indication of perforated lateral line scales, but scales typically lacking on anterior of body just posterior to cleithrum and supracleithrum. Scale rows between dorsal-fin origin and pelvic-fin origin apparently 7. About 12 or 13 scale rows around narrowest portion of caudal peduncle. Predorsal scales perhaps 11 or 12; scales often present immediately anterior to dorsal fin but always absent or lost just posterior to supraoccipital spine.

Vertebrae 32 to 34 ($\bar{x}$ = 33.1, n = 41).

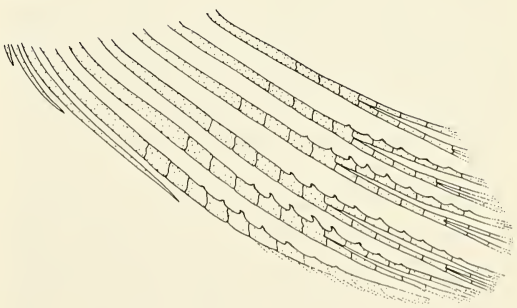

Fig. 5. Lateral view of anterior nine anal-fin rays of *Priocharax ariel,* new species, paratype, UMMZ 213500, male, SL 16.7 mm, same locality as holotype.

Upper limb gill-rakers 3 to 5 ($\bar{x}$ = 3.9, n = 41) and lower limb gill-rakers 11 to 13 ($\bar{x}$ = 12.5, n = 41). Branchiostegal rays 4 (n = 31), 3 rays on anterior and 1 ray on posterior ceratohyal.

Weberian apparatus (Fig. 3) well developed, all components except claustrum well ossified. Os suspensorium exceptionally large and projecting forward to anterior end of third centrum. Neural spine of fourth vertebra moderately developed. Neural prezygopophyses of fifth centrum undeveloped. Lack of buttressing flanges on base of fifth pleural rib, short neural spine of fourth vertebra and little developed posterior crest of enlarged supraneural all characteristic of juvenile Weberian apparatus in characids.

Color in life.—Translucent without any bright colors; some guanine pigmentation overlying gasbladder; dark chromatophore pattern distributed as discussed below for color in alcohol.

Color in alcohol.—Body-color of holotype pale brown to white (Fig. 1). Dark chromatophores limited, distributed as shown in Figs. 1A, B. Proportionally large chromatophores on head covering brain tissue. Few scattered dark chromatophores on opercle and along base of dorsal, anal and pelvic fins. Dorsal and lateral region of caudal peduncle with few scattered dark chromatophores, and base of caudal fin with dark spot usually consisting of about 10 to 20 contracted chromatophores. Sometimes one or two chromatophores at region of triangular muscular hiatus in body wall posterior to dorsal end of free opercular border. Dorsal, anal and caudal fins with scattered small elongate dark chromatophores along borders of fin rays. A few dark chromatophores present in region of vent.

Sexual dimorphism.—Males with anal-fin hooks described above for anal fin. Anal-fin hooks absent in females and juveniles. Examined specimens apparently not fully sexually mature. Females apparently with developing eggs but no mature eggs found. Males, even those with anal-fin hooks, with only developing testes. Using anal-fin hooks as a criterion, large population sample from type locality with only 35 identifiable males among 1740 specimens; remainder immature or females. Members of this population perhaps approaching sexual maturity at time of capture and many males not matured sufficiently to develop anal-fin hooks.

Etymology.—*Ariel* from the Greek for an airy spirit, in reference to the tiny and translucent nature of this fish in its natural habitat.

Habitat.—The species is an inhabitant of black acidic waters of the upper Río Negro and Río Orinoco drainage systems. The majority of specimens were captured in still waters of shaded rain forest streams. Individuals from the extensive series captured at the type locality were most common in emergent vegetation, along the shore line and around terrestrial plants that were hanging into the water.

Priocharax pygmaeus, new species
Fig. 6, Table 1

Holotype.—NRM THO/1976303.1445, 6, SL 16.4 mm, Colombia, Departamento Amazonas, in Quebrada Pajarito, tributary of Quebrada Bacada, tributary of Quebrada Matamata, a tributary of Río Amazonas, northwest of Leticia, about 04°41′S, 69°57′W; T. Hongslo, 21 Jul 1976.

Paratypes.—Collected with holotype, 87 specimens: NRM THO/1976303.1446, SL 8.0–11.4 mm, 41 specimens, 4 cleared and counterstained for cartilage and bone; USNM 278479, SL 8.1–12.2 mm, 36 specimens, 6 cleared and counterstained for cartilage and bone; MBUCV V-15340, SL 10.0–10.9 mm, 5 specimens; MZUSP 36498, 10.2–10.7 mm, 5 specimens.

Diagnosis.—See diagnosis of *P. ariel.*

Description.—Table 1 presents morphometrics of holotype and measured paratypes. See Fig. 6A, B for body form. Body slender, sides compressed. Greatest body depth at dorsal-fin origin. Dorsal-fin origin

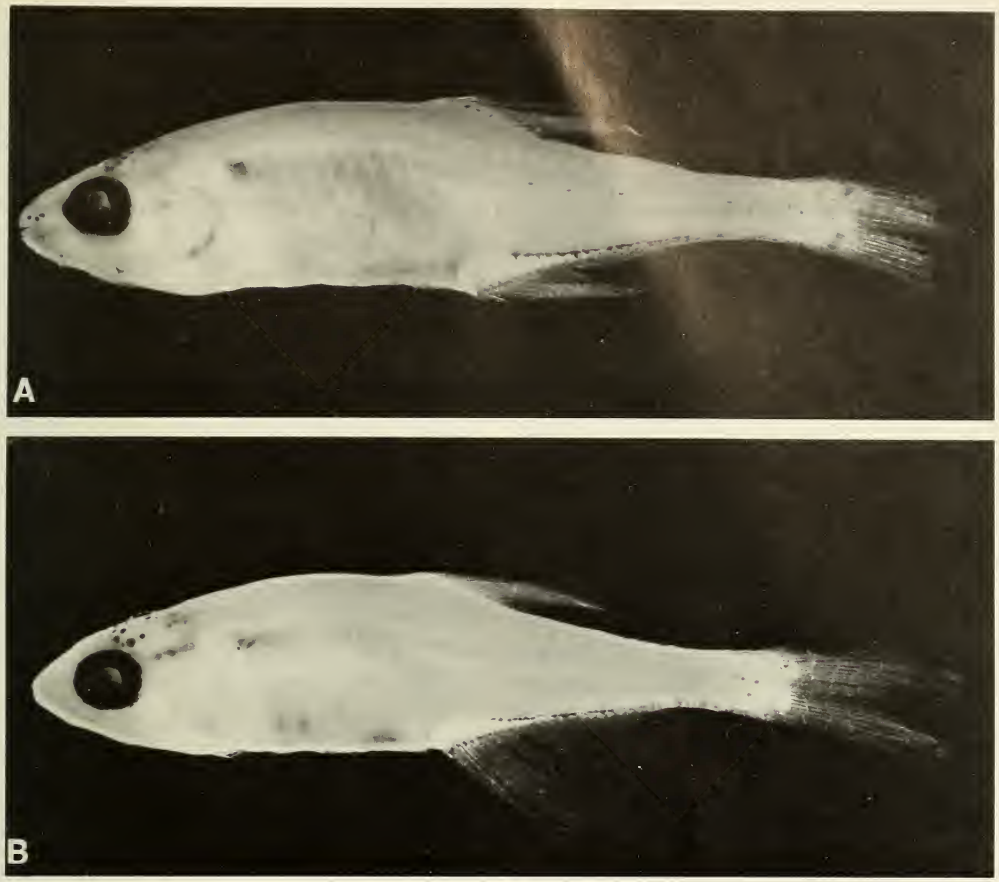

Fig. 6. A, *Priocharax pygmaeus,* new species, holotype, NRM THO/1976303.1445, SL 16.4 mm, Quebrada Pajarito, Río Amazonas system, northeast of Leticia, Colombia; B, *Priocharax pygmaeus,* new species, paratype, USNM 278479, SL 10.8 mm, same locality as holotype.

somewhat closer to caudal-fin base (hypural joint) than to tip of snout. Dorsal-fin origin approximately intersected by vertical line through anal-fin origin, or slightly in advance of that line. Pelvic-fin origin nearly midway between anal-fin origin and vertical through most posterior point of opercle. Snout bluntly rounded. Dorsal profile of head and body gently convex from snout tip to dorsal-fin origin. Dorsal profile of body along dorsal-fin base nearly straight, gently sloping posteroventrally. Dorsal body and caudal peduncle profile very slightly concave from dorsal-fin insertion to base of procurrent rays. Caudal peduncle slender, elongate, with sides compressed. Ventral body profile gently convex from symphysis of lower jaw to ventral to pectoral-fin origin. Belly profile from that point to vent and anal-fin origin may be slightly convex, more often straight, or sometimes slightly concave. Body profile along anal-fin base and caudal peduncle to anterior ventral procurrent rays gently concave. Base of anal fin posterodorsally oriented.

Head length moderate, approximately one-quarter of standard length. Snout rounded in profile, of moderate length. Jaws about equal, mouth terminal or lower jaw slightly included. Mouth elongate, somewhat posteroventrally inclined. Maxilla elongate; upper jaw long, posterior border

reaching approximately to or posterior to vertical line through center of pupil of eye, length half or somewhat less than half of head length. Eye large, about one-third of head length. Fleshy interorbital width wide, often somewhat over one-third of bony head length, gently convex transversely.

Maxilla with 27 to 41 teeth ($\bar{x}$ = 31.6, n = 10; holotype with 41); teeth conical, small and slender, in single series along ventral border of bone. Larger specimens with greater number of teeth. Accessory cusps absent. Premaxilla with 19 to 24 teeth ($\bar{x}$ = 22.7, n = 10, holotype with 24) in a single series. Premaxilla teeth similar in form to those of maxilla. Dentary with 28 to 36 teeth ($\bar{x}$ = 32.5, n = 10, holotype with 36). Dentary teeth in single row posteriorly; larger specimens with irregular row of closely placed teeth anteriorly, but two distinct anterior rows never present. Anterior dentary teeth larger than posterior. All jaw teeth lingually curved to a moderate extent.

Infraorbital series incomplete, with antorbital bone only element ossified, apparent only in cleared and stained specimen of 12.2 mm SL. Fronto-parietal fontanel large, extending from ethmoid to supraoccipital, completely separating parietals; frontals only in contact at strong epiphyseal bar. Frontal about of same width along entire length; similar in form to that of small juvenile characids. Supraoccipital spine poorly developed.

Dorsal-fin rays ii,9 in 15 counted specimens including holotype. Usually with posterior ray or more rarely posterior two rays not divided to their base. Dorsal-fin height moderate, about 25% of SL. Pectoral fin larval in form. Radials as described above for *P. ariel*. Cleithrum ossified, slender, attached dorsally to slender supracleithrum by relatively loose ligamentous tissue. Coracoid and other pectoral girdle elements apparently not ossified or chondrified. Posttemporal weakly ossified. Pelvic-fin rays i,5 in all counted specimens, n = 15. Fin of moderate length, posterior tip extending about to region of vent. No hooks present on pelvic, dorsal or pectoral-fin rays. Anal fin v,21 in holotype; all examined specimens with four or five unbranched rays ($\bar{x}$ = 4.1, n = 15) followed by 20 to 22 branched rays ($\bar{x}$ = 21.7, n = 15), posterior ray divided to its base. Anal-fin hooks not present in any specimens. Anal-fin margin concave, with anterior elongate lobe and posterior section of short rays. Caudal fin forked, of moderate length; principal rays 10/9 in 91 specimens. Adipose fin absent.

Squamation completely absent in all specimens. Although some scale pockets visible, their distribution not consistent enough for counts.

Vertebrae 32 or 33 ($\bar{x}$ = 32.9, n = 9, holotype with 33). Upper limb gill-rakers 2 or 3 ($\bar{x}$ = 2.2 n = 10, holotype with 3) and lower limb gill-rakers 9 in all specimens. Branchiostegal rays 4 (n = 15), 3 rays on anterior and 1 ray on posterior ceratohyal.

Weberian apparatus well developed, similar to that of *P. ariel*.

Color in life.—Report as "transparent, faint pink" by T. Hongslo.

Color in alcohol.—Holotype pigmentation very similar to that of *P. ariel* (Fig. 6). Fewer dark chromatophores present in specimens of *P. pygmaeus*; however, those specimens may have faded more in preservative since they were collected eight years earlier.

Etymology.—*Pygmaeus* from the Greek for dwarf, in reference to the tiny size of this fish.

Habitat.—The species was collected from a shaded or partially shaded rainforest stream about two meters wide in water to about one meter deep. The bottom was "clay" with much leaf litter and no submerged plants. The water temperature was 25.2°C, the pH about 5.5 and the water was somewhat turbid. Water type was not noted.

Relationships

Priocharax is an example of the problems inherent in studies of the phylogenetic relationships of miniature, paedomorphic

species. The species of *Priocharax* have or appear to have plesiomorphic character states relative to the conditions described below in various characines and cynopotamines. Plesiomorphic features can be distinguished from paedomorphic characters only when phylogenetic hypotheses and developmental information for characters in ingroup and outgroup taxa are available. Unfortunately the state of our understanding of relationships among likely close relatives of *Priocharax* is unsatisfactory (see discussion below). As a consequence of that situation it is beyond the scope of this study to advance a detailed corroborated hypothesis of phylogenetic relationships based on shared derived characters. This lack of a corroborated hypothesis of phylogenetic relationships also means that we cannot presently discriminate the pattern of plesiomorphy versus paedomorphosis in *Priocharax* and its putative relatives. Polarity statements and hypotheses of the paedomorphic nature of some features are instead advanced within the context of broader outgroup comparisons. Fink (1982), Weitzman and Fink (1983:345–346, 390), and Weitzman and Fink (1985:9–10) discussed the issues raised by paedomorphic, possibly progenetic, characters, especially where outgroup information may be inadequate.

The phylogenetic relationships of *Priocharax* within the Characidae are difficult to resolve satisfactorily. The apparent derived and non-paedomorphic characters of numerous conic teeth and elongate maxillae in the genus suggest that its relationships lie in the putative subfamily Characinae of Géry (1977:302), in particular with the genera *Acanthocharax, Acestrocephalus, Charax, Cynopotamus, Galeocharax, Gnathocharax, Heterocharax, Lonchogenys,* and *Roeboides.* A hypothesis of a phyletic association of *Priocharax* to and within the Characinae is complicated by the lack of any proposed derived characters that support the concept of the monophyly of the subfamily. Géry (1977:295) attempted to delimit the Characinae in his admittedly artificial key to the subfamilies of his Characidae. Although his key has some limited use in a typological sense, no evidence was presented that his Characinae was monophyletic.

According to Géry the subfamily consisted of three tribes: the Characini, the Bramocharacini, and the Acestrorhynchini. Weitzman and Fink (1983:342, 344), based on Rosen (1972:12), questioned the recognition of a separate tribe for *Bramocharax* Gill and Bransford, and the assignment of that genus to the Characinae. They agreed with Rosen (1972) that *Bramocharax* is most likely a derivative of *Astyanax* Baird and Girard, a member of the large characid subfamily Tetragonopterinae. Menezes and Géry (1983:587, 588) recognized the Acestrorhynchini as a subfamily rather than as a tribe and noted that at present "there is not enough information available to study the relationships of *Oligosarcus* Günther and *Acestrorhynchus* Eigenmann [the genera of the Acestrorhynchinae] with [other] characiform genera." Furthermore those authors also noted that the "Acestrorhynchinae may not be a monophyletic group." The remaining tribe, the Characini, is also of questionable monophyly. Menezes (1976) considered the genera *Cynopotamus, Galeocharax* and *Acestrocephalus* to be a separate monophyletic subfamily, the Cynopotaminae, but now Menezes (pers. commun.) informs us that this separation may no longer be tenable in light of a more detailed phylogenetic analysis.

On the basis of preliminary observations, Menezes (in Sazima 1983:88) suggested that some of the remaining Characinae and Characini of Géry are polyphyletic, with *Exodon* Müller and Troschel being more closely related to members of the Tetragonopterinae than to the remaining genera of the Characini. Sazima (1983:88) noted that his behavioral evidence appeared to confirm Menezes' concepts. Vari (1986:332, 333) discussed the tentative relationships of his new genus and species, *Serrabrycon magoi* Vari. He noted that although he placed

Table 2.—Number of teeth on jaw bones and number of branched anal-fin rays in *Priocharax ariel, P. pygmaeus,* and genera of the Characinae discussed in text. Dentary tooth information for *Lonchogenys* and dentary and premaxillary tooth counts for *Acanthocharax* presented as range of outer tooth row counts followed by range of inner tooth row counts. Tooth data for *Lonchogenys* based on two cleared and stained specimens, 40.1–45.2 mm SL (USNM 270232) and anal-fin ray counts on 12 specimens (USNM 270230, 270231, 270232). Tooth data and anal-fin ray counts for *Heterocharax* based on 7 cleared and stained specimens, 21.7–34.0 mm SL (USNM 278994) and for *Acanthocharax* on 1 paratype (USNM 66109).

	Priocharax				
	ariel	*pygmaeus*	*Lonchogenys*	*Heterocharax*	*Acanthocharax*
Teeth					
Premaxillary	22–34	19–24	12–16	8–11	6/10
Maxillary	38–58	27–41	42–50	20–24	60
Dentary	38–55	28–36	16–18/11–14	33–38	4/33
Branched anal-fin rays	16–22	20–22	34–38	31–35	28

it in the Tetragonopterinae, its possession of a mosaic of characters left open the possibility that the phylogenetic relationships of *Serrabrycon* Vari could be with the Characinae. *Serrabrycon magoi,* if a characine, is one with a short based anal-fin (15 or 16 rays posterior to the anterior undivided rays) similar to that of *Priocharax* species. The number of teeth on the maxilla, premaxilla and dentaries of *Serrabrycon* are less than those in *Priocharax* and the genera also differ in tooth forms. These differences do not, of course, refute a hypothesis of a close phylogenetic relationship between the taxa. The various uncertainties associated with taxa such as *Exodon* and *Serrabrycon* together with the lack of proposed synapomorphies for possible members of Géry's Characinae complicate a consideration of the relationships of *Priocharax* among *Charax* and putatively associated genera.

The numerous conic jaw teeth and elongate maxilla of *Priocharax* suggest a possible relationship with genera of the Characinae and Cynopotaminae. Among the genera listed at the beginning of this section, *Acanthocharax, Acestrocephalus, Cynopotamus, Galeocharax, Lonchogenys* and *Priocharax,* particularly *P. ariel,* have very high maxillary and total dentary tooth counts (Tables 2, 3). *Heterocharax* and those genera with the exception of *Acestrocephalus* have high total dentary tooth counts (above 28) compared to other Characinae. These high tooth counts might be synapomorphies relating these genera, but we prefer not to advance a hypothesis of relationships based solely on that one system.

One possible synapomorphy common to at least *Priocharax, Roeboides* and *Cynopotamus* is the retention of a larval pectoral fin anatomy at relatively large body sizes. Many characids convert from the larval pectoral fin anatomy to an essentially adult form at about 6 to 9 mm SL (pers. obs.). *Priocharax,* in contrast, retains the larval fin to at least 17 mm SL and at least one undetermined species of *Roeboides* (USNM 279251) retains that fin form up to 26 mm SL. *Cynopotamus atratoensis* (Eigenmann) has a larval pectoral fin in specimens as large as 41 mm SL (CAS-IUM 15033, paratypes). The distribution of this feature in most genera of the Characinae and Cynopotaminae is unknown. Thus it would be inappropriate to use it as a synapomorphy for putative subgroups in those subfamilies until its phyletic distribution has been thoroughly analyzed.

The possession of a larval pectoral fin has also been reported within the Characidae by Durbin (1909:55) for the tetragonopterid *Dermatocheir catablepta* Durbin. That species, since moved to *Hyphessobrycon* by

Table 3.—Number of teeth on jaw bones and number of branched anal-fin rays in *Priocharax ariel, P. pygmaeus,* and genera of the Cynopotaminae discussed in text. Dentary tooth information for genera of the Cynopotaminae presented as range of outer tooth row counts followed by range of inner tooth row counts.

	Priocharax				
	ariel	*pygmaeus*	*Acestrocephalus*	*Cynopotamus*	*Galeocharax*
Teeth					
Premaxilla	22–34	19–24	9–13	8–12	8–12
Maxilla	38–58	27–41	30–44	42–60	36–54
Dentary	38–55	28–36	3/9–13	2–4/22–35	3–4/7–11
Branched anal-fin rays	16–22	20–22	29–36	36–53	36–45

Géry (1977:462), is known only from an 18 mm holotype described as having the "Pectoral short and paddle-shaped with a fringe of soft rays" (Durbin 1909:56). Although sharing an evidently very similar form of pectoral fin with the species of *Priocharax, H. catableptus* differs from *Priocharax* and the species of the Characinae and Cynopotaminae in the form and distribution of the oral teeth. Although Géry's alignment of *H. catableptus* with other *Hyphessobrycon* species appears reasonable, the question of the phylogenetic relationships of the species, and the significance of the retention of the larval form of pectoral fin, requires further study once additional material of the species becomes available.

A variety of apparently derived characters listed in "keys" by Géry (1977:302–330) such as a notch and spine along the ventral margin of the cleithrum, a sharp ventral preopercular angle or spine, enlarged coracoid bones forming a keel along the ventral border of the cleithrum, ctenoid body scales, outwardly projecting mammilliform teeth (discussed by Sazima and Machado 1982), and certain body shape configurations (e.g., a dorsal hump in the body profile anterior to the dorsal-fin origin) occur in various subunits of the Characinae or Cynopotaminae, or both. Although these characters have been used in part to diagnose genera and species groups, the current lack of cladistic phylogenetic analyses of these subfamilies prevents an evaluation of the usefulness of these features in diagnosing monophyletic groups at this time.

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