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Pterobrycon myrnae, a **remarkable new glandulocaudine characid fish from Costa Rica**

by

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ABSTRACT: A new species of characid fish, in which the males have greatly enlarged scales on the middle of the flanks, is described from southern Costa Rica. During courtship the expanded tips of these "paddle scales" serve as a stimulus to the female which later takes a spermatophore into her mouth. The peculiar sexual dimorphism of *P. myrnae* is described and coloration of live specimens, courtship behavior and ecology are discussed.

The genus *Pterobrycon* is redescribed and the new form is compared to its only congener, *P. landoni* Eigenmann of the Río Atrato, Colombia. *Microbrycon minutus* Eigenmann and Wilson is placed in the synonymy of *P. landoni.* Each species of *Pterobrycon* occupies a region of tropical wet lowland forest which is presently isolated from other such areas by a dry forest biotope. During the humid climate of the Pleistocene glacial periods, wet forest broadly connected the Central American and Colombian lowlands. The dry climatic periods of the interglacials and post-Pleistocene have isolated Central American from Colombian humid forest refuges and resulted in the sub-division of *Pterobrycon, Rhoadsia, Nannorhamdia, Gymnotus* and perhaps other fish genera.

Pterobrycon is a member of the Glandulocaudinae, the characid subfamily with the most marked sexual dimorphism. Mature males have peculiarly modified scales and glands at the base of the caudal fin, rows of hooklets on the anal-fin rays and sometimes also on the pelvic and/or caudal fin rays, and frequently enlargement of the median fins accompanied by filamentous extension of the fin rays. In addition, males of *Pterobrycon* and of several other forms display a bilaterally paired "moveable spot" near the middle

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of the body. In *Gephyrocharax melanocheir* and *Pseudocorynopoma doriae* the intensively pigmented spots are formed on the distally expanded portion of one or two pectoral fin rays; in *Hysteronotus megalostomus* on the middle rays of the pelvic fins; and in *Corynopoma* on the expanded tip of the "gill paddles", which are elongate posteriorly-directed extensions of the opercle (5). In *Pterobrycon* the spots occur on the expanded ends of one or two "paddle scales", greatly enlarged scales on the middle of the flank. It has been suggested that the moveable spots in all of these forms act as a stimulus in a mating ritual which leads to oral fertilization by the female after she takes a sperm packet and then her eggs into her mouth (5).

The type species of *Pterobrycon* is *P. landoni* Eigenmann (8), described as a new genus and species from a single male specimen taken in the Atrato basin of Colombia. *Microbrycon minutus* Eigenmann (9), also described as a new genus and species from the Atrato basin, is apparently based on two specimens of the same species which lack the dimorphic male characters (2, 10). No further specimens of *Pterobrycon* had been reported until the new species described in this paper was discovered in Costa Rica.

MATERIAL AND METHODS

All body measurements refer to standard length (SL) in millimeters (mm). All proportional measurements in the text are expressed as times in SL or times in head length. Body proportions as thousandths of SL appear in Table 1. Anterior unbranched fin rays are indicated by small Roman numerals. The last two dorsal and anal rays are counted as one only when their bases are in contact; when the base of the last ray is not touching the penultimate ray, each ray is counted separately.

Type and comparative specimens are deposited at the Academy of Natural Sciences of Philadelphia (ANSP), California Academy of Sciences (CAS), Field Museum of Natural History (CNHM), Centre National de la Recherche Scientifique, France (CNRS), Natural History Museum of Los Angeles County (LACM), Museum of Comparative Zoology at Harvard University (MCZ), Museo de Zoología, Universidad de Costa Rica (UCR), and United States National Museum (USNM).

Pterobrycon Eigenmann

TYPE SPECIES: *Pterobrycon landoni* Eigenmann 1913, *Indiana Univ. Studies*, 18: 3.

DIAGNOSIS: Small, slender glandulocaudine characids, body silvery with a dark blotch at base of caudal fin. A small black or copper-orange spot above last rays of anal fin in males. Humeral marking and pseudotympanum absent. Dorsal fin ii, 7-9; anal fin v-vii, 15-25; pectoral fin i, 9-10; pelvic fin i, 7; caudal

TABLE 1

Meristics and proportions in thousandths of standard length of holotype and twenty paratypes of Pterobrycon myrnae, *of the holotype* of P. landoni *and the paratype of* Microbrycon minutus

	Pterobrycon myrnae n. sp.			*P. landoni*	*M. minutus*
	Paratypes*		Holotype	Holotype**	Paratypes***
Dorsal rays	ii, 7-9		ii, 8	ii, 8	10
Anal rays	v-vii, 23-25		vi, 24	vi, 15	18
Pectoral rays	i, 9-10		i, 9	i, 10	—
Pelvic rays	i, 7		i, 7	i, 7	—
Caudal rays	10/9		10/9	10/9	—
Total gill rakers	13-18		16	15	—
Lateral line scales	38-40		39	—	ca. 32
Scales above lat. line	6-7		7	—	—
Predorsal scales	19-22		21	—	—
Maxillary teeth	0-3		3/3	1/2	1
Large dentary teeth	4		4/4	4/-	4
Outer premax. teeth	4-5		4/4	3/2	4
Inner Premax. teeth	4-5		4/4	4/4	5
	males	females			
Standard length (mm)	24.1-37.2	31.0-39.1	33.2	18.1	17.4
Head length	249-274	242-261	259	276	241
Eye diameter	90-105	82-100	93	111	98
Snout length	69-76	70-79	75	61	46
Upper jaw length	110-117	67-110	105	116	—
Maxillary length	73-78	67-78	75	—	92
Bony interorbital	83-100	82-95	93	99	103
Greatest depth	221-310	291-324	265	182	218
Peduncle depth	96-115	104-116	96	105	92
Peduncle length	124-151	118-145	151	227	207
Predorsal distance	605-652	625-653	623	601	586
Preanal distance	593-638	600-645	605	601	626
Prepectoral distance	269-286	258-284	271	293	264
Prepelvic distance	428-469	427-468	428	442	—
Height dorsal fin	183-226	179-226	226	243	—
Height anal fin	180-213	173-215	196	265	—
Length pectoral fin	256-296	258-289	283	320	—
Length pelvic fin	142-220	140-155	196	320	—

* 10 males and 10 females from UCR 112-14, 114-4, 173-2, 304-5, 306-10, 309-7, 343-1, 495-2, USNM 210988 and 211460.

** Data taken by S. H. Weitzman.

*** Proportions of paratype by W. A. B., meristics from EIGENMANN (9).

fin 10/9; adipose fin present. Caudal spur present or absent. Lateral line incomplete (pores restricted to the first few scales in lateral series) or complete. Premaxillary with two series and dentary with a single series of multicuspid teeth. Maxillary with 0-3, usually multicuspid teeth. Vertebrae (precaudal and caudal including hypural complex) 16 + 21-24; total vertebrae 37-40.

One or two greatly prolonged paddle scales that extend to above the vent arise in humeral region of mature males; tips of paddle scales expanded and pigmented. Other male secondary sexual characters are: a caudal pouch on lower half of caudal fin supported by one large and several smaller modified scales; last ray of anal fin much longer than rays immediately preceding it; middle pelvic rays produced.

Pterobrycon myrnae, n. sp.

(Figs. 1, 2)

Pterobrycon sp., Bussing and Roberts, 1971, *Copeia*, 1971: 179 (reproduction).

HOLOTYPE: LACM 33857-1, a mature male, 33.2 mm, Costa Rica, Puntarenas Province, Osa Peninsula in Quebrada Aguabuena (elevation 30 m), Río Rincón drainage 2 km W of Rincón, original collection number UCR 495-2, 4-10 May 1971, collected by R. McDiarmid.

PARATYPES: All collections were made in Puntarenas Province, Pacific coast of Costa Rica (Fig. 3). Collection numbers marked with an asterisk (*) contain mature male specimens. A "quebrada" is a small river or stream. Abbreviations are spelled out when used for the first time. The elevation of each locality is given in meters (m). Distances are expressed as kilometers (km) by road or air kilometers (airkm). Collections are listed by drainages; following the collection date is the number of specimens in parentheses, and their size range in millimeters (mm).

RIO RINCON DRAINAGE: *UCR 495-2: Same data as holotype (12) 31.5-39.1 mm. UCR 173-2: Quebrada Aguabuena (30 m) 1 km upstream from Tropical Science Center near Rincón, 28 February 1967 (10) 28.4-36.5 mm. LACM 33860-1: Same data as UCR 173-2 (7) 28.1-36.0 mm. USNM 211458: Same data as UCR 173-2 (7) 28.7-35.0 mm. *UCR 250-2: Quebrada Banegas (10 m) 0.8 km upstream from Pacific road 3 airkm SW of Rincón, 1 March 1968 (28) 21.9-39.3 mm. *LACM 33861-1: Same data as UCR 250-2 (40) 24.2-34.7 mm. *USNM 211459: Same data as UCR 250 2 (40) 23.4-38.6 mm. *USNM 211460: Banegas swamp (10 m) near Quebrada Banegas at Pacific road ca. 3 airkm SW of Rincón, 14 August 1973 (3) 24.8-27.0 mm. *UCR 69-1: Flooded gravel pit (20 m) in Río Riyito near Charcos 2 airkm S of Rincón airfield, 10 August 1966 (4) 29.4-33.3 mm. *UCR 343-1: Same locality as UCR 69-1, 5 August 1969 (12) 21.6-38.0 mm. *UCR 164-1: Same locality as UCR 69-1, 7 August 1967 (5) 24.1-33.9 mm. *MCZ 49191: Same data as UCR 164-1 (7) 26.0-29.0 mm. *USNM 211461: Same data as UCR 164-1 (5) 26.6-28.0 mm.

INDEPENDENT DRAINAGES, PARRITA-QUEPOS AREA: UCR 304-5: Tributary (15 m) of Río Jicote 0.5 km S of Loma on Puriscal-Parrita road, 16 January 1969 (29) 20.6-32.4 mm. UCR 306-10: Tributary (20 m) of Quebrada Visita ca. 4 km E of Esterillos on Loma-Esterillos road, 16 January 1969 (7) 31.4-38.7 mm. UCR 309-7: Drainage canal (20 m) tributary of Río Palo Seco 4 km E of Parrita on Parrita-Quepos road, 17 January

1969 (3) 30.0-35.1 mm. UCR 311-8: Quebrada Bonita (10 m) S of Damas 9 km NW of Quepos, 18 January 1969 (2) 34.2-35.2 mm.

RIO SIERPE DRAINAGE: UCR 112-14: Tributary (20 m) of Río Sierpe at Interamerican Highway (IH) 1 km SE of Venecia and 200 m SE of Río Salamá Nuevo, 5 January 1967 (34) 21.6-38.1 mm. LACM 33858-8: Same data as UCR 112-14 (20) 22.1-34.1 mm. CNRS (J. Gery) 0598: Same data as UCR 112-14 (6) 29-35.5 mm. *USNM 210988: Same locality as UCR 112-14, 1 March 1973 (3) 28.9-35.5 mm. UCR 114-4: Tributary (20 m) of Río Sierpe 2 km SE of Palmar Sur at IH, 6 January 1967 (10) 26.0-33.5 mm. USNM 211462: Same data as UCR 114-4 (10) 26.6 35.5 mm. LACM 33859-1: Same data as UCR 114-4 (10) 26.0-33.5 mm. LACM 4850: Same locality as UCR 114-4, 4 January 1964 (7) ? mm.

RIO TERRABA DRAINAGE: LACM 4840: Branch of Río Térraba (20 m) 4 km NW of Palmar Norte on road to Puerto Cortés, 4 January 1964 (1) ? mm.

RIO ESQUINAS DRAINAGE: UCR 111-4: Quebrada 36 (80 m) 12 km W of Pueblo Río Claro at IH, 5 January 1967 (3) 32.5-36.0 mm.

COMPARATIVE MATERIAL: *Pterobrycon landoni* Eigenmann, holotype CM 5051 (now CNHM 56250): Colombia, Chocó Department, tributary of Río Atrato near Boca de Raspadura, 12 March 1912 (1 mature male) 18.1 mm. *Microbrycon minutus* Eigenmann and Wilson, paratype IUM 13109 (now at CAS): Colombia, Chocó Dept. Río Truandó a tributary of Río Atrato, 1913 (1 female) 17.4 mm. *Gephyrocharax intermedius* Meek and Hildebrand, paratype (?) IU 13994 (now at CAS): Panamá, Panamá Province, Río Chame (1 male) 32.4 mm. ANSP 99885: Panamá, Chiriquí Prov., Río Estí, ca. 2 km N of Gualaca, 16 December 1961 (27) 36.2-45.0 mm. Additional UCR material utilized includes 24 specimens of *Gephyrocharax intermedius* and 49 specimens of *Gephyrocharax atracaudata* from Panamá.

DIAGNOSIS: The species differs from its only known congener, *Pterobrycon landoni* in several meristic and proportional characteristics. Several of the differences are only evident in mature males. Characters for *P. myrnae* are presented first, followed by those for *P. landoni*: complete vs. incomplete lateral line; anal-fin rays 23-25 vs. 15; caudal peduncle 6.6-9.1 vs. 4.4 times in SL; two spatulate, wide-stalked paddle scales in males, vs. a single (?) thin-stalked paddle scale with bilobed tip, on each side of body (compare Figs. 4B and 4C); enlarged U-shaped caudal scale on males forming a pouch on each side of peduncle, and enclosing ventral procurrent rays, vs. each caudal pouch bordered above by an enlarged scale which does not enclose the procurrent rays (compare Figs. 5 and 6); length of last anal-fin ray of males 7.7 vs. 5.5 times in SL; length of dorsal fin 4.4-5.6 vs. 4.1 times in SL; length of pectoral fin 3.4-4.1 vs. 3.1 times in SL; length of pelvic fin of males (length of lateral unbranched ray) 4.5-7.0 vs. 2.6 times in SL; hooklets on all branched rays of pelvic fin vs. hooklets on only one branched ray; hooklets on first 11-13 branched anal-fin rays, vs. hooklets on first 7 branched rays.

COMPARISON WITH *Gephyrocharax intermedius*: Female and immature specimens of *P. myrnae* superficially resemble *G. intermedius* of western Panamá. The figure of *G. intermedius* in GREY (11) is a good likeness except that the very small adipose fin was inadvertently omitted from the drawing

(R. K. Johnson pers. comm.). In life, both forms are silvery with a black caudal spot, but only *G. intermedius* has notable round unpigmented areas on the upper and lower base of the caudal fin. In specimens preserved in alcohol, the unpigmented caudal areas are visible and a dark humeral bar which is nearly obscured by a layer of guanine in live material, appears in *G. intermedius. P. myrnae* has unpigmented caudal areas, but no humeral markings.

P. myrnae has less anal-fin rays, v-vii, 23-25 vs. iv-v, 26-30; a slimmer body, males 3.2-4.5 vs. 3.1-3.4 times in SL and females 3.1-3.4 vs. 2.9-3.2 times in SL; and a slimmer caudal peduncle, males 8.7-10.4 vs. 6.9-8.0 times in SL and females 8.6-10.0 vs. 7.9-9.1 times in SL. The large caudal scale of *P. myrnae* is sharply flared outwards from the body and not covered by smaller scales; the caudal spur is not greatly expanded dorso-ventrally, and is fully enclosed in the ventral extension of the caudal scale (Fig. 5). The caudal scale of *G. intermedius* is slightly flared outward, and overlaid with small scales; the caudal spur is expanded dorso-ventrally and not wholly enclosed by the caudal scale.

DESCRIPTION: Body elongate, laterally compressed. Body depth at dorsal fin origin less in mature males than in mature females; depth in SL 3.2-4.5 times in males and 3.1-3.4 times in females. Predorsal profile slightly convex; profile abruptly angular, especially in females at dorsal-fin origin. Postdorsal profile straight or slightly convex. Ventral profile rounded anteriorly, straight along anal-fin base. Depth greatest near pelvic-fin origin, or for some females, at anal-fin origin. Caudal peduncle depth 8.6-10.4 times in SL; caudal peduncle length from end of anal-fin base to middle of caudal base, greater in males; caudal peduncle length in SL 6.6-8.3 times in males and 6.9-9.1 times in females.

Head length 3.7-4.1 times in SL. Eyes large, horizontal orbit diameter 2.5-3.1 times in head length. Least width of bony interorbital 2.7-3.0 times in head length. Snout length less than orbit diameter, 3.2-3.8 times in head length. Nasal cavities very large. A pair of grooves of unknown function on interorbital space in both sexes (Fig. 4D). Such grooves are also present on *Gephyrocharax intermedius* and *G. atricaudata.*

Maxillary long, forming a slight angle with premaxillary when mouth closed and an angle of 70-90 degrees to longitudinal axis of fish. Length of upper jaw, from snout tip to postero-ventral end of maxillary, variable in both sexes, 2.2-3.6 times in head length. Maxillary length from angle with premaxillary to postero-ventral end, 3.2-3.7 times in head length. Maxillary teeth uniserial, usually 1 or 2 tricuspid teeth on each bone. Variation (frequency in parentheses) includes: two specimens without teeth on one side, with 1 (15), 2 (18) and 3 (5); when present, third maxillary tooth smaller and conical. Premaxillary teeth in two series: outer row tricuspids 4 (27), 5 (13); inner row quincuspids 4 (38), 5 (2). Lower jaw extending anterior to tip of snout; gape directed antero-dorsally. Three large quincuspid anterior teeth on each dentary. Large teeth followed by two tricuspid teeth, one-half and one-quarter size respectively, of anterior large teeth; the largest of these two smaller teeth occasionally quincuspid, the smaller sometimes conical. Finally, a series of 3-7 minute conical teeth laterally, 3 (1), 4 (3), 5 (12), 6 (20), 7 (3). No teeth on vomer, palatines or pterygoids.

Cranial fontanel absent on a mature female and nearly closed on a mature male cleared and alizarin-stained specimens. Gill rakers of upper limb short, counting rudiments 3 (12), 4 (12), 5 (7), 6 (8), 7 (1). Gill rakers of lower limb (including angle) longer, width at base about twice the length, 10 (2), 11 (21), 12 (17). Total gill rakers 13 (1), 14 (9), 15 (10), 16 (6), 17 (8), 18 (6).

Lateral line strongly decurved anterior to pelvic fins, then continuing to caudal-fin base along midline. Lateral line complete, total pores 38 (15), 39 (3), 40 (2); last 3 pored scales over base of caudal fin. Last scale reduced to tube lying along first median ray of ventral caudal series (Fig. 5). Transverse scale rows between base of dorsal fin and lateral line 6 (9) or 7 (11). Predorsal scale count 19 (6), 20 (6), 21 (6), 22 (2). Axillary scales dorsal to pelvic-fin base, but not pectoral fins. A single row of scales forming a sheath at base of anal fin. Terminal scales at base of caudal fin enlarged, extending slightly onto caudal-fin base, especially over caudal musculature.

Dorsal fin far back on body, usually with ii, 8 rays, range ii, 7 (1), ii, 8 (18), ii, 9 (1) rays; origin always somewhat posterior to anterior anal-fin base. Predorsal distance 1.5-1.7 times in SL. Height of dorsal fin, as determined by length of longest fin ray (first branched ray), 4.4-5.6 times in SL.

Anal fin usually with 6 undivided rays anteriorly, range v (1), vi (18), vii (1); branched rays 23 (5), 24 (9), 25 (6). Preanal distance 1.6-1.7 times in SL. Height of anal fin (length of first branched ray) 4.7-5.8 times in SL. Branched rays toward middle of fin and terminal ray prolonged in mature males, thus forming posterior notch (Figs. 1 and 4A). Ventral margin of anal fin slightly concave in females and juveniles. Mature males with minute antrorse hooks on first 11-14 branched, and sometimes, last posterior unbranched anal-fin rays. Hooklets arise in two rows on posterior surface of rays, but curve laterally and anteriorly; one hook per ray segment.

Pectoral fins low on body, i, 9 (7) or i, 10 (13) rays. Median-most ray unbranched, but counted as a branched ray. Distance from tip of snout to anteriormost portion of pectoral-fin base (prepectoral distance) 3.5-3.9 times in SL. Tip of fins reaching beyond pelvic fin insertion to midpoint between pelvic fin insertion and anus. Length of pectoral fin (length of anterior unbranched ray) 3.4-4.1 times in SL.

Pelvic fin rays i, 7 in 20 specimens. Three median-most rays unbranched but counted as branched. Distance from tip of snout to insertion of pelvic fin (prepelvic distance) 2.1-2.3 times in SL. Tips of pelvic fins reaching anal-fin origin of mature males only. Length of pelvic fin (length of lateral unbranched ray) sexually dimorphic, 4.5-7.0 times in SL in males, and 6.5-7.2

times in SL of females. Three pelvic-fin elements greatly prolonged in mature males; these consist of two filaments of last branched ray and succeeding unbranched ray. Two rows of antrorse hooklets on all but first unbranched pelvic ray of mature males. Hooklets on ventral surface of rays and directed anteriorly; 1-3 hooklets per ray segment.

Caudal fin with 10/9 principal caudal rays (17 branched rays) in 20 specimens. Ventral procurrent caudal-fin rays separate in males, forming a caudal spur enclosed in modified caudal scales.

Total vertebrae 37 (1) or 38 (3). Precaudal vertebrae (without haemal spine) 16 (4), caudal vertebrae including hypural complex 21 (1) or 22 (3).

SEXUAL DIMORPHISM: Maturing males of *Pterobrycon myrnae* undergo a series of radical modifications in scalation, fin structure and coloration. The first sign of secondary sexual characters in males is the initiation of paddle scale and caudal scale modifications (Figs. 4B and 5). The paddle scales of ten males examined correspond to the seventh and eighth scales in a longitudinal series commencing behind the dorsal margin of the eye. The regular pattern of scale rows is disrupted near the insertion of the paddle scales, but they arise approximately equidistant between the mid-dorsal series and the lateral line series (third scale row from each). When the paddle scales have reached one-half their full length, a caudal pouch is evident and the caudal spur is beginning to separate from the fin proper; middle pelvic-fin rays have extended to nearly twice their original length and hooks are developing on pelvic and anal-fin rays. A gravid female from UCR 495-2 has slightly elongated scales on her flanks which correspond to the paddle scales of mature males.

As the paddle scales approach full length, the distal portion is still unpigmented and the caudal scalation is incompletely developed. Three long pelvic-fin filaments composed of the two branches of the fifth and of the unbranched sixth rays reach posteriorly as far as the posterior half of the anal fin. Hooklets have developed on all pelvic-fin rays but never occur on the lengthened filamentous portion. Anterior anal-fin rays lengthen as hooklets develop on them; the terminal ray also lengthens, but the penultimate few rays which never bear hooklets do not lengthen, which results in a deep notch at the end of the anal fin (Figs. 1 and 4A).

In fully developed males the outer paddle scale is usually slightly longer than the inner one and both bear irregular black subdistal blotches. The paddle scales reach to a point below the dorsal-fin origin or nearly to a point below the middle of the dorsal-fin base (compare Figs. 4A and 4D); paddle scale length of mature examples is variable and goes 2.8-3.5 times in SL. By lifting a paddle scale, a thin sheet of elastic muscular tissue is seen along the under side of the enlarged scale. This muscular tissue is fixed to the body wall slightly posterior to where the paddle scale itself inserts, and may keep it adnate against the body and may also assist in raising the scale during courtship activities. Unlike other more deciduous body scales, the base of each paddle scale is firmly bound to the body wall. On dissection, branches of the body musculature can be seen inserted on the paddle scale base.

The terminal scale on the lower half of the caudal peduncle is modified and raised to form a pouch on the caudal peduncle base. The pouch is lined by epidermis, but contains no grossly visible glandular tissue. The enlarged scale is U-shaped (Fig. 5) with many grooves on the outwardly flared border and is bound ventrally to its mate by epidermis. Several lower procurrent caudal rays are separate from the main fin and form a spur as in *Gephyrocharax* and other glandulocaudine genera. This spur is enclosed in and bound by epidermis to the bottom of the caudal pouch. The last scale of the lateral line series is reduced to an osseous cylinder which lies over a small, but distinct, white gland (?) on the base of the mid-caudal rays. As scale and fin modifications reach maximum development, copper-colored spots begin to appear on several parts of the body (Fig. 4A); these often darken to a red-orange or bronze-orange color.

Between the base of the pelvic fins and the origin of the anal fin, the belly of mature males is produced in a partially hollow, fleshy keel, which in well-developed males, protrudes through a pair of basal scale rows which meet at the midline only anteriorly. Posteriorly the keel is deepest and in well-preserved material is dorso-ventrally flattened to form a wide fleshy surface above a basal scale sheath. A small pointed urogenital papilla lies at the posterior termination of the keel; the anus lies just anteriorly, well inside the interior of the hollow keel. The soft-tipped female papilla is concealed between parallel scale rows which meet at the midventral line.

COLORATION IN LIFE: Female, silvery on sides, head and belly; back non-reflective gray; a dark caudal blotch and no other markings. Mature male, ground color similar to that of female, but with iridescent copper to red-orange spots on several parts of body (Fig. 4A): at base of pectoral fins; associated with melanophores on base of first dorsal-fin rays; on adipose fin; just posterior to insertion of paddle scales; dorsal to and slightly posterior to pelvic-fin bases; superimposed on melanophores of anal spot; dorsal to center of anal-fin base; dorsal to posterior termination of anal-fin base; and along distal margin of paddle scales. Young developed males have black-tipped paddle scales which later (in August in aquarium specimens) lose part of the melanin and take on a bright canary-yellow to red-orange color along the entire distal border.

COLORATION IN ALCOHOL: Ground color pale yellow in both sexes. Diffuse plumbous band, about pupil's diameter in width, arising posterior to eye and extending to caudal-fin base; color most intense posteriorly. Lateral band superimposed on a very thin dark line. A roughly diamond-shaped dark blotch on base of caudal peduncle; dorsal portion extending onto prominent musculature on dorsal half of caudal-fin base. No humeral spot or other markings on females and juveniles. Mature males with black blotch above anus; this spot often covered by, and less intense than, distal blotch of paddle scales. A slight darkening is present around insertion of paddle scales and their tips have a large subterminal black blotch. Base of first three or four dorsal rays black. A black blotch in center of adipose fin. Other fin rays clear.

ETYMOLOGY: The species is named for my wife Myrna, who has made innumerable sacrifices to facilitate my studies of Central American fishes. I propose the common name "paddle scale characin" for this species.

ECOLOGY: The species was found only in small, shallow streams overhung by trees or abundantly lined by shrubs and grasses. The streams were clear or moderately clear in the dry period. Fishes formed loose aggregates of several to a few dozen individuals swimming slightly below the surface. Food consists largely of aquatic and terrestrial insects. The species is attracted to any disturbance on the surface.

Juveniles, unripe females and immature males showing incipient development of paddle scales were collected in January. Collections made in February reveal unripe females and numerous immature males with paddle scales about one-half their length at maturity. In March mature individuals of both sexes were common. Twenty-four specimens were collected on 2 February 1971 (same locality as UCR 112-14) and no paddle scale or other modifications were noted on the specimens. These succumbed to an infection and were replaced by approximately 80 specimens taken at the same site on 21 March 1971. Many of the latter males had well developed paddle scales, but others were not completely developed. Collections made in May contain numerous ripe males and females, but also some immature males with incompletely developed secondary sexual characters; these latter fishes are large and deep-bodied and are only distinguishable externally from females by the early development of paddle scales. Small (24.8 mm) ripe females and males (24.1 mm) were collected with large ripe individuals of both sexes in August. Collections are not available from Setpember through December, although development during this period was followed in aquarium specimens.

Precipitation in southern Costa Rica where *P. myrnae* is found, varies from 3000 to 6000 mm per year. The dry season occurs from January through March when rainfall is markedly reduced. Reproduction occurs largely during the rainy season between March to at least August. Young hatched early in the year presumably are the first to mature the succeding year; they develop secondary sexual characteristics in six weeks, and begin spawning at the close of the dry season or as the rains commence in April. Juveniles collected in January probably represent young from late spawnings of the previous year (August or later) which do not mature until the next May or June.

Since no specimens with well-developed paddle scales were taken in January and February collections, it appears that in nature males either survive for only a single season, lose their secondary sexual modifications yearly, or less likely, migrate to a region or habitat not yet sampled by collectors.

Specimens kept in aquaria have lived more than three years. After about an age of one year, many seemingly healthy individuals of both sexes lose their equilibrium and soon die. This could indicate that *P. myrnae* is an annual species in nature. Males which survive into the second and third years do not exhibit prime coloration, but occasionally engage in courtship behavior. Some old males retain the paddle scales intact, but they are usually not noticeable because the distal pigmentation is lost. Other males become quite thin and at death reveal small, but well-formed paddle scales which suggests that they were partially reabsorbed. Since females vigorously bite the expanded tip of the paddle scales during courtship, this probably accounts for ragged and missing scales of some preserved specimens taken from aquaria and nature.

BEHAVIOR IN AQUARIA: Courtship and possible sperm transfer was observed on 21 August 1971. The sexes had been maintained separately since March 1971. The previously black-tipped paddle scales of males had become bright yellow and black and were held slightly above the bronze-orange spot which lies dorsally to the vent.

At 4 PM two pairs were placed in a 120 gallon, well-planted tank. The fish had been maintained at 27 C, but the temperature of the large tank was 24 C. About 40 *Pseudocheirodon affinis* and several *Phallichthys amates* were the only other fishes in the tank. Upon introduction, the males of *P. myrnae* immediately began driving each other away and pursuing the females. Occasionally a male would snap at another male and then swim away head down, vibrating the entire body strongly for several seconds, with the other male following.

When a male encountered a female alone, he would sharply erect both paddle scales laterally and upward at an angle about 45° with the body axis. If the female showed interest the paddle scales on the side of the body closest to the female were projected laterally at right angles to the body surface while being vibrated strongly. The female responded to this display by snapping repeatedly at the paddle scales. Then the female bit violently and in rapid succession (6-8 times) at the distal paddle tip as the male turned slowly in a circle with the paddles of one side projecting toward the female. The other pair of paddles was held against the body. It is remarkable that the paddle scales were not damaged by the violent twisting and biting of the female. As the female bit at the paddle scales and the male moved in a circle, an oblong yellowish object about 1 mm in diameter, presumably a sperm packet, suddenly appeared, and the female twice grasped it in her mouth and released it. Finally a *Pseudocheirodon* grasped the small object as it sank and apparently ate it.

Further displays occurred, but were often interrupted before the biting behavior of the female, in which case the male then darted away to pursue another female. About 20 minutes after the first spermatophore (?) was seen, another larger (2 mm) bilobed yellow object appeared while the pair was courting. The female grasped it in her mouth and it was not seen again. Further courtship activity took place, but with no biting or release of spermatophores. The males, but not females, became dark steel-gray during ocurtship behavior. At no time during courtship were the anal and pelvic fins of the male seen to grasp the female. Perhaps such an action was so rapid that it was unobserved or conversely, these hooklet-covered fins are not utilized in copulation. Unfortunately no evidence of a spawning was subsequently seen.

As far as they go, these observations reaffirm the hypothesis of BUSSING and ROBERTS (5) except that the spermatophore is yellowish not black. This is not strange considering that the expanded tip of the paddle scales, which presumably acts as an attention-getting device, is colored yellow as well as black. The courtship parallels that described for *Corynopoma riisei* by CORWIN (6).

GEOGRAPHIC DISTRIBUTION: *P. myrnae* is known only from southern Costa Rica on the Pacific versant (Fig. 3). Specimens were collected in or near the following principal drainage basins: Río Pirrís (Parrita), Río Grande de Térraba, Río Esquinas and Río Rincón. The species is apparently confined to the northern portion of the Isthmian Fish Province as delimited by BUSSING (4). This represents the northern known terminus of the Glandulocaudinae. The Glandulocaudinae are represented by three species of *Gephyrocharax* in Panamá and by numerous and diverse genera in South America.

Pterobrycon landoni Eigenmann

Pterobrycon landoni Eigenmann, 1913, *Indiana Univ. Studies,* 18: 3-4.
Microbrycon minutus Eigenmann and Wilson, 1914, *In* Eigenmann, 1914, *Indiana Univ. Studies*, 19: 3.

Dr. Stanley H. Weitzman kindly furnished the following information for the holotype and only known male specimen of *P. landoni*: The specimen is somewhat dehydrated, and most of the scales are missing. The scales that remain indicate an incomplete lateral line at least as long as that shown by EIGENMANN and MYERS (10). The distal end of the paddle scale is soft and apparently not ossified; its distal portion is more bilobed (Fig. 4C) than shown in EIGENMANN and MYERS (10). Its length from the dorsal base of the paddle scale to the distal extreme goes 3.4 times in SL. EIGENMANN (8) stated that the paddle scale was ". . . the third from the median dorsal series and about the seventh from the head. . .", thus it arises at the same site as the anteriormost paddle scale of *P. myrnae*. On the basis of scale pockets, predorsal scales were estimated at 17 or 18.

Although many scales near the base of the caudal fin are missing, the two major modified scales are present. Figure 6 is a reconstruction of caudal scalation using damaged scales from both sides of the holotype; the scale margins of the large pouch scale and the one above it are ridged as in the large caudal scale of *P. myrnae.*

Dentition similar to that of *P. myrnae.* Maxillary teeth tricuspid, 2 on right side, 1 on left side. Premaxillary teeth in two series: outer row tricuspids, 2 on right side, 3 on left side; inner row quincuspids, 4 on each side. Dentary teeth in one series: right dentary damaged; left dentary with one large anterior quadricuspid tooth followed by two equally large quincuspid teeth, two tricuspid teeth one-half and one-quarter size of anterior large teeth respectively, and seven minute conical teeth laterally. No teeth on vomer, palatines or pterygoids.

Gill rakers on one side: upper limb 6, lower limb (including angle) 9. Precaudal vertebrae 16, caudal vertebrae including hypural complex 24. Fin hooklets present only on most median branched ray of pelvic fins and on seven anterior branched anal-fin rays. Adipose fin (missing in EIGENMANN and MYERS' plate, 10) present. Color pattern and other aspects as in original description. Meristic and proportional data are presented in Table 1.

EIGENMANN and MYERS (10) indicated that *Microbrycon minutus* may represent the female of *P. landoni.* BÖHLKE (2) in a key to genera of glandulocaudine characids, considered the two species the same, but presented no additional evidence. Meristics and body proportions of the holotype of *P. landoni* and a paratype of *M. minutus,* of approximately the same size, are similar (Table 1). Both nominal species have a similar morphotype, including the rather strongly convex forehead which, with the large eye, give a neotenic appearance to the fish. Both forms have not been reported since they were described from separate tributaries of the Río Atrato (Fig. 3). With the discovery of *P. myrnae,* all differences between the nominal species *landoni* and *minutus* (and the genera) can now be confidently attributed to sexual dimorphism.

REMARKS

The disjunct distribution of the two closely related, yet distinctive, species of *Pterobrycon* requires an explanation. A similar distribution is shown by the pimelodid catfish *Nannorhamdia lineata,* known only from southern Costa Rica, which has its nearest congener in the Río Atrato, Colmobia and perhaps closest relative, *N. spurrellii,* in the Río San Juan, Colombia (3). The small characid *Rhoadsia eigenmanni* of the Atlantic slope of Costa Rica is also widely separated from its only two congeners in western Ecuador (10). The genus *Gymnotus* is represented by one or two species in Central America, and another form in northern Colombia, but in Panamá is known only from the extreme western portion. Other species such as *Imparales panamensis* (3) have discontinuous distributions in this general region, but this probably reflects insufficient collecting.

If one plots the species of each genus of Central American fish on maps, it is apparent that much of the species diversity of many freshwater fishes is due to speciation *in situ,* and not only to recent invasion of South American forms. Another glandulocaudine genus, *Gephyrocharax,* is an example which is represented in the above region and northern Colombia by eight species. In the majority of cases species distributions are non-overlapping, and each major river system has its own distinctive species. Some freshwater fishes with such complementary distributions in Panamá probably evolved in isolation on Middle Tertiary isthmian landmasses, but on the basis of a Pliocene arrival of most of the ostariophysans (4), other types of barriers must be proposed.

Concurrent with the reestablishment of the Isthmian Link in the Pliocene, general cooling and climatic effects to the north, led to the development of xeric conditions on most of the Pacific coast of Central America (1, 7). The alternate humid climate of the glacial periods and the dry climate of the Pleistocene and post-Pleistocene interglacials also had a profound effect on the tropical lowland biota (12). During the interglacials humid forests in northern South America and Central America were considerably reduced, but presumably a number of forest refuges persisted throughout the Pleistocene (12). HAFFER (12) believed that the endemic bird forms found in the Caribbean Costa Rican, Chiriquí (Pacific slope of southern Costa Rica and western Panamá) and Chocó (western Colombia) refuges, originated *in situ.* The distributions of *P. myrnae* and *P. landoni* correspond to the Chiriquí and Chocó refuges respectively.

A vegetation map (12) of the region shows the effect of the high precipitation on the refuges mentioned and reveals that they were effectively isolated from one another by areas of xeric climate during dry interglacial periods. These areas of dry forest are important barriers to terrestrial faunal dispersal (14, 15, 16). I believe there is ample evidence that the effects of low precipitation restrict the distribution of freshwater fishes as well as the terrestrial fauna.

For example, the Pacific slope of northwestern Costa Rica is subject to a protracted dry season from November to April. Its ichthyofauna is essentially a depauperate Atlantic versant fauna which reached the Pacific slope by way of stream capture south of Lake Nicaragua (4). A few species are widespread, but several are restricted only to certain tributaries. These uncommon or rare species are often common on the Atlantic slope. I propose that populations of those fishes best-adapted to a mesic climate are held in check by the drastic reduction in water area during, and especially at the close of the dry season. Dry years would have an especially harsh effect on the fauna.

Fishes inhabiting rivers in a xeric climate have to contend with: 1) high salinity, as fish are forced toward the mouths of some rivers, 2) low current velocity, 3) high temperature, 4) low dissolved oxygen, 5) high population densities and subsequent higher predation, and greater competition for available food sources, and 6) seasonal food sources, i.e., fewer insects during the dry season. There is also a relationship between minimum size of a river and species diversity. Faunal impoverishment is typical of areas where rivers are small and unstable. Much of the Pacific slope of Panamá is subject to a xeric climate similar to that of northwestern Costa Rica.

Freshwater fish evolution in Central America has also been affected by alternate flooding and emergence of the land during Pleistocene glacial times. The Pacific slope area of Panamá was considerably increased during each glacial age (13). The repeated reduction in area of the Pacific slope in interglacial times would have resulted in an alternate expansion and contraction of fish populations. Thus, changes in sea level, continued tectonic activity, and climatic changes with resultant changes in vegetation, created the isolation necessary for repeated speciation and has in some cases eliminated populations, which has resulted in disjunct distributions of closely related forms, such as the two species of *Pterobrycon.* I submit that a combination of the above factors have eliminated the isthmian populations of *Pterobrycon, Nannorhamdia, Rhoadsia, Gymnotus* and perhaps other extinct forms.

ACKNOWLEDGMENTS

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RESUMEN

Se describe un nuevo pez carácido, *Pterobrycon myrnae,* de Costa Rica. Los machos presentan dos pares de escamas alargadas en la parte media de los costados. Durante el cortejo, las extremidades ensanchadas de estas "escamas-paleta" sirven de estímulo a la hembra, la que posteriormente introduce un espermatóforo en su boca. Se describe este curioso dimorfismo sexual, la coloración de ejemplares vivos, el comportamiento de cortejo y la ecología de *P. myrnae.*

Se describe en forma más amplia el género *Pterobrycon,* y se compara la nueva especie con su único congénero, *P. landoni* Eigenmann del Río Atrato, Colombia. Se considera a *Microbrycon minutus* Eigenmann y Wilson como sinónimo de *P. landoni.* Las dos especies de *Pterobrycon* habitan re-

giones de bosque lluvioso tropical que actualmente están aisladas de otras regiones similares por una zona de bosque seco. Durante el clima húmedo de los períodos glaciares del Pleistoceno, un bosque húmedo unió las regiones, ahora separadas, de Centro América y Colombia. El clima seco de los períodos interglaciares y del post-Pleistoceno aisló los refugios de bosque húmedo, lo que provocó la evolución de nuevas especies de los géneros *Pterobrycon, Rhoadsia, Nannorhamdia, Gymnotus* y tal vez otros géneros.

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Fig. 1. *Pterobrycon myrnae,* adult male paratype USNM 210988, 31.0 mm, from tributary of Río Salamá Nuevo, southern Costa Rica. Photograph by S. H. Weitzman and W. L. Fink.

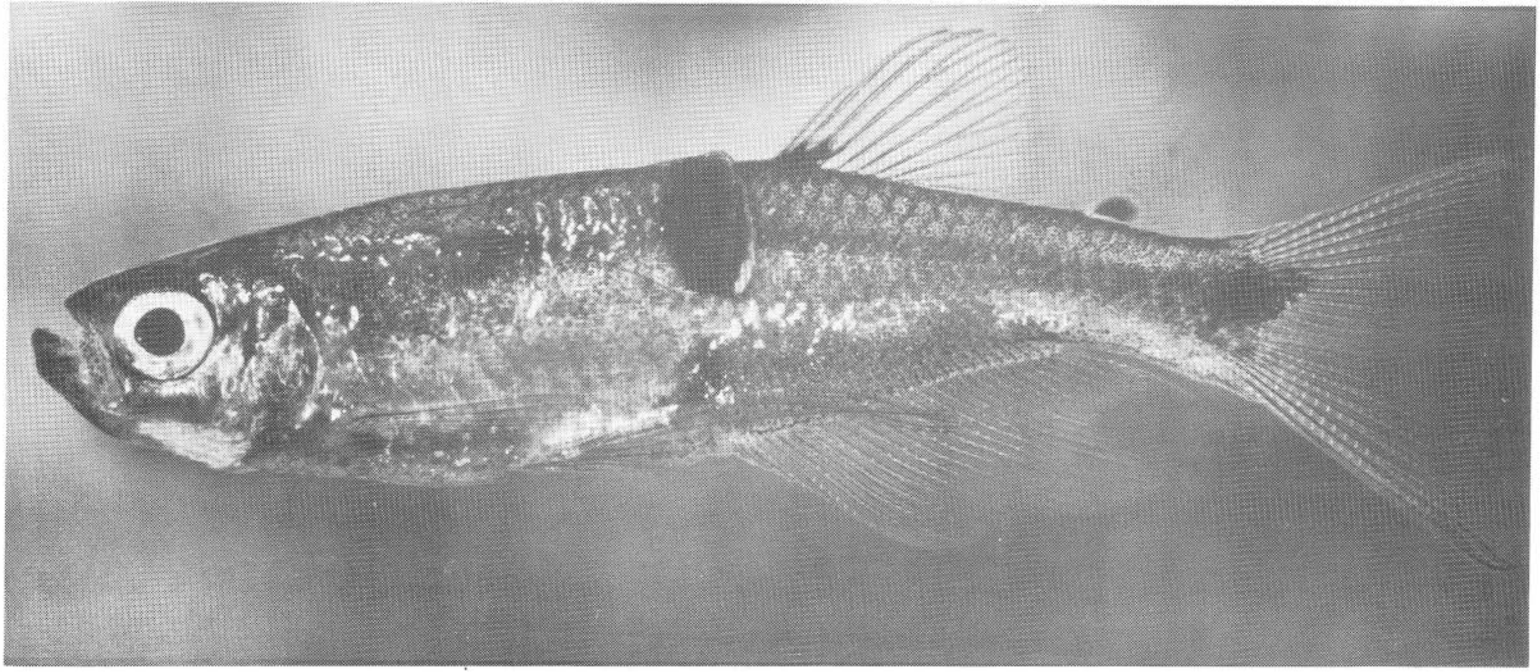

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Fig. 2. *Pterobrycon myrnae*, adult female paratype, USNM 210988, 35.5 mm, same locality as Fig. 1. Photograph by S. H. Weitzman and W. L. Fink.

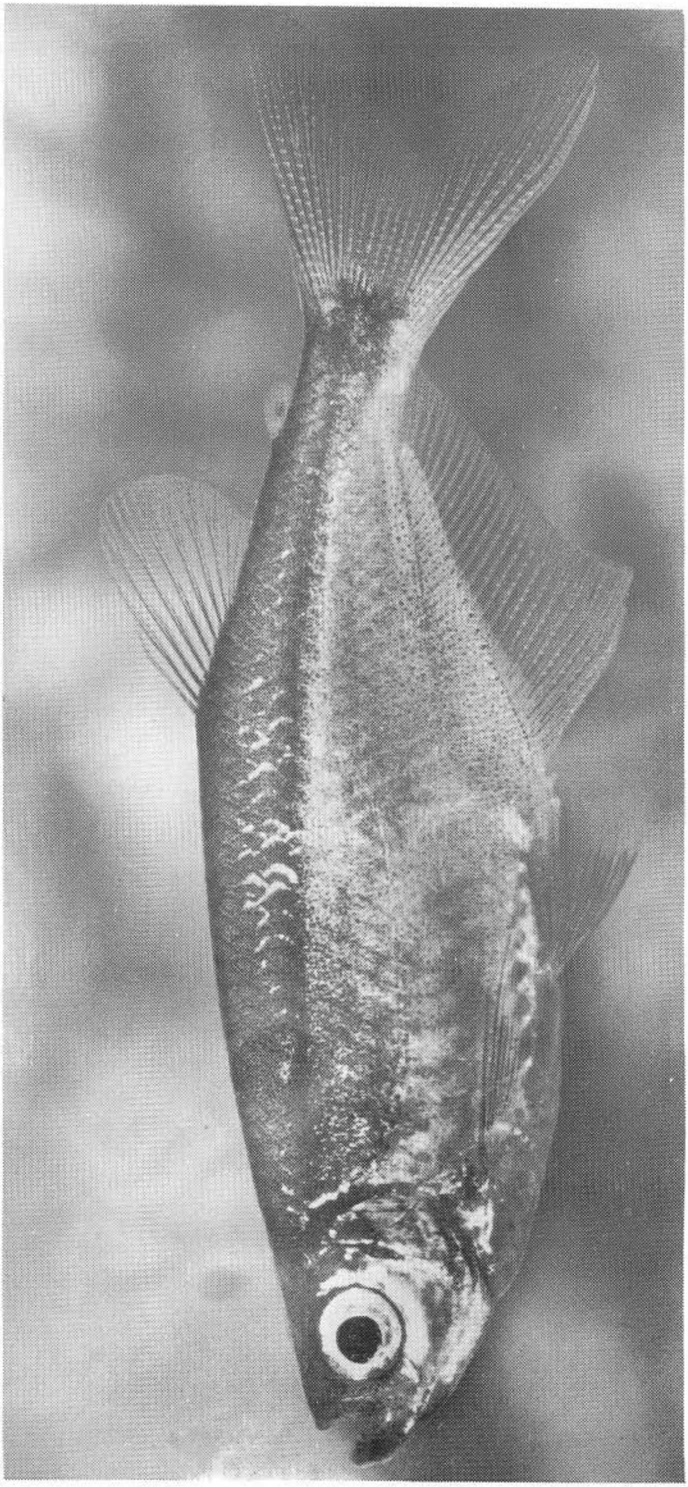

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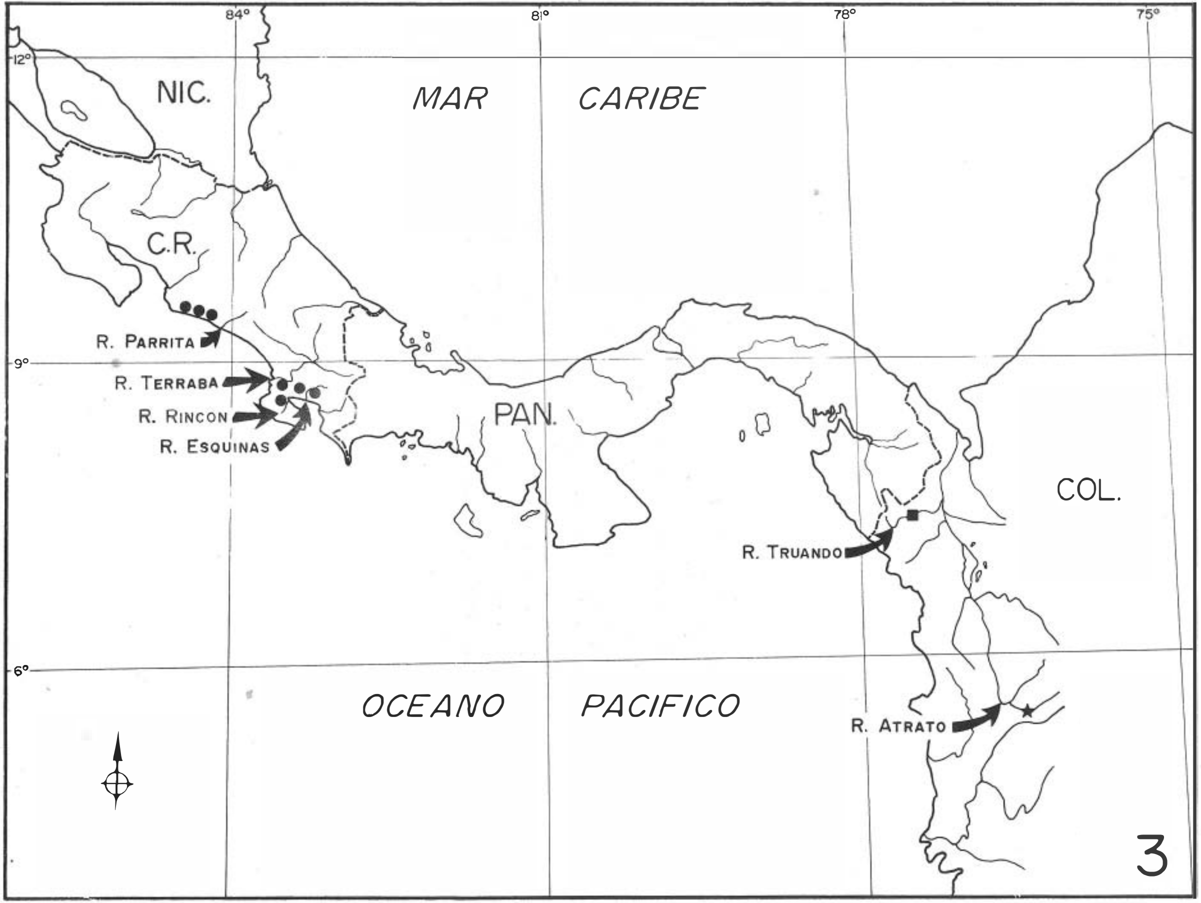
Fig. 3. Locality records of *Pterobrycon*. Each symbol represents one or more collections. Dots indicate *P. myrnae* in Costa Rica; star is type locality of *P. landoni;* square is type locality of *Microbrycon minutus* (=females of *P. landoni*). Latter two collections are in Río Atrato basin, Colombia.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R. ATRATO
OCEANO
PACIFICO

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Fig. 4. A, *Pterobrycon myrnae,* male showing principal melanophore patterns on paddle scales, caudal base, head and dorsal and adipose fins. Areas of copper to orange coloration outlined by dotted lines at: base of paddle scales and pelvic fins; above anus and anal fin; and at dorsal-fin origin. B, Growth stages of paddle scales of *P. myrnae.* C, Sketch of paddle scale of holotype of *P. landoni* by S. H. Weitzman. D, Dorsal view of *P. myrnae* showing grooves on interorbital space and normal position of paddle scales.

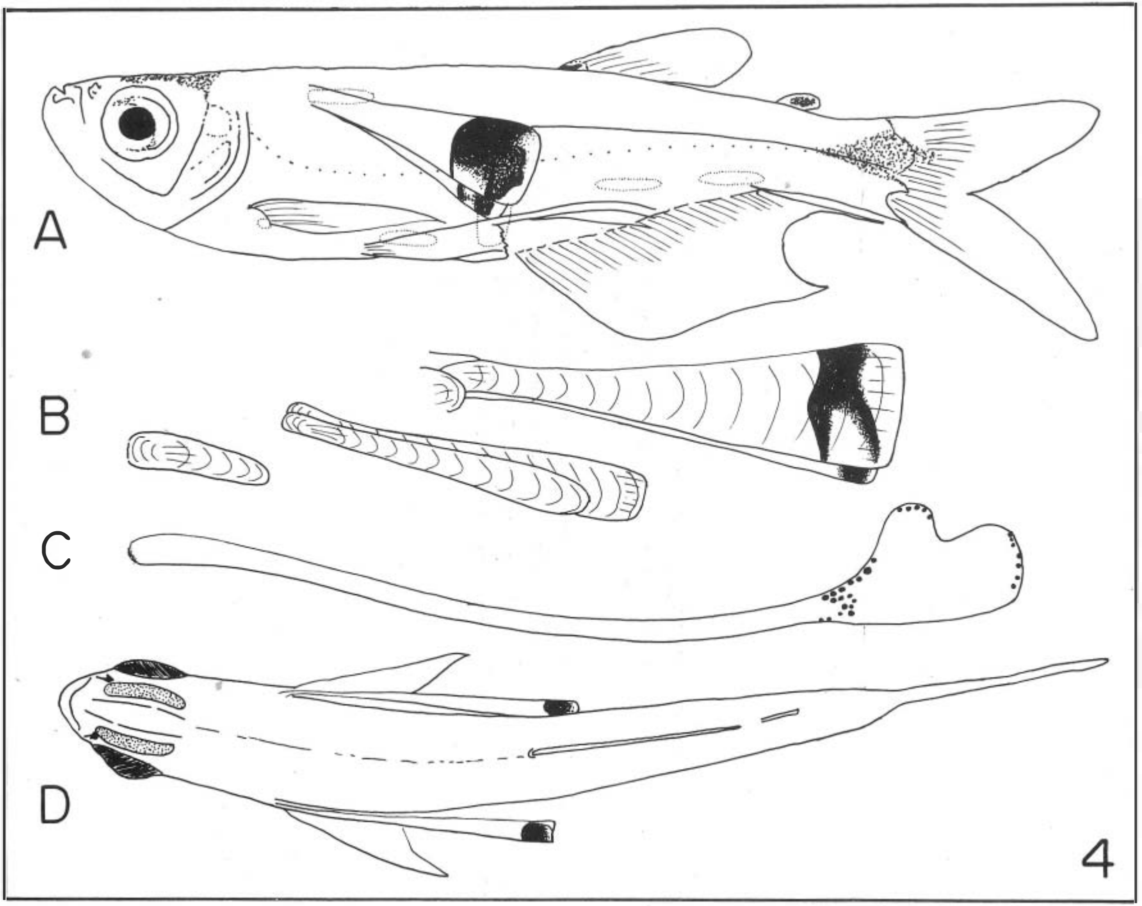
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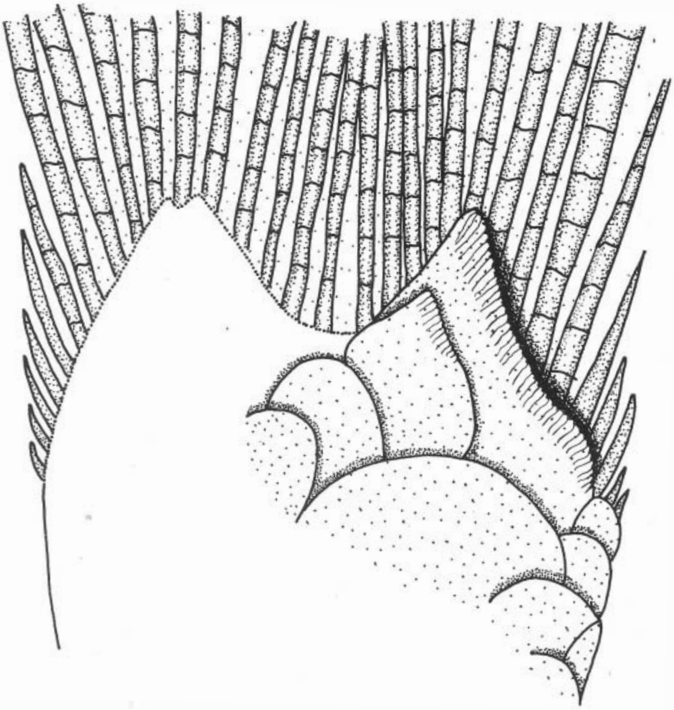
Fig. 5. Detail of scales at base of caudal fin of male *Pterobrycon myrnae,* uncataloged cleared and stained specimen, 28.5 mm, from same locality as Fig. 1.

Fig. 6. Detail of scales at base of caudal fin of male *Pterobrycon landoni,* reconstruction using scales from both sides of holotype, 18.1 mm, Río Atrato basin, Colombia, by S. H. Weitzman.



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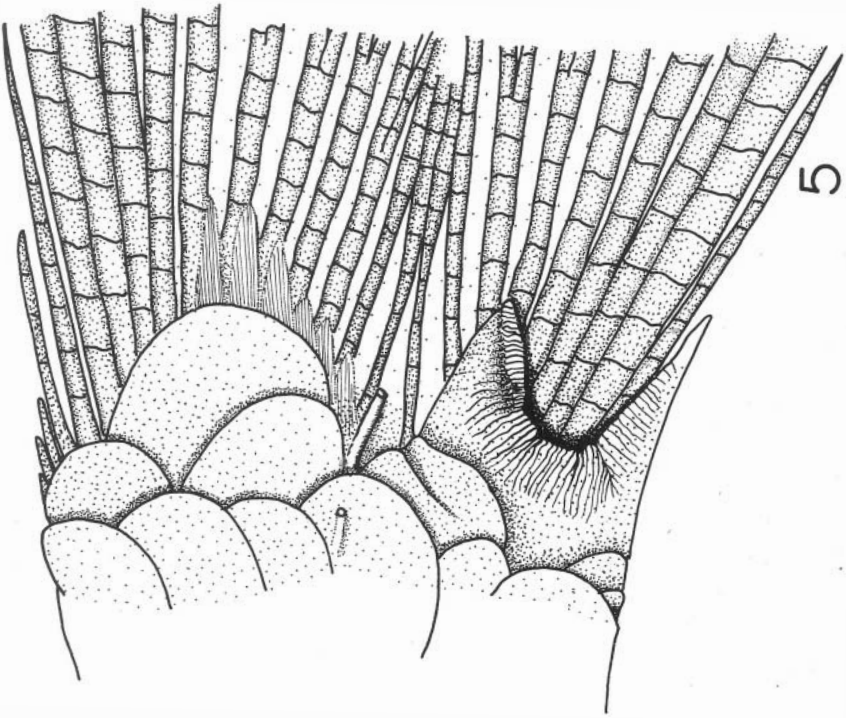

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