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Taxonomy and biological aspects of the Central American cichlid fishes Cichlasoma sieboldii and C. tuba

by

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ABSTRACT: The complex taxonomic history of *Cichlasoma sieboldii* is reviewed. *Cichlasoma punctatum* and its synonym *Theraps terrabae* are included for the first time in the synoymy of *C. sieboldii.* A report of *C. guttulatum* from Panamá is attributable to a misidentification of *C. tuba,* which had not been previously reported from that country.

The morphologic and meristic variation, coloration, ecology and geographic distribution of *C. sieboldii* and C. *tuba* are discussed.. Morphologic and distributional evidence suggest that these two species are Pacific and Atlantic slope derivatives of a common Pliocene ancestor.

There is a marked resemblance between the cichlid fauna of the Atlantic slope of lower Central America and the southeastern region of Costa Rica. The historical reasons for this similarity have been discussed (4). The present study reviews the taxonomic history and discusses the biology of a Pacific slope species, *Cichlasoma sieboldii,* and its Atlantic versant counterpart, *Cichlasoma tuba* (Fig. 1).

MATERIAL AND METHODS

Body measurements are expressed in standard length (SL) in millimeters (mm). Body proportions of *C. sieboldii* as parts per mil appear in Table 1. 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. For comparative purposes a lateral-series scale count as defined by MILLER (14) is included in the descriptions: "The lateral-series scale count begins with the first scale in the upper lateral line, goes to

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the last one in that line, then continues with the scale on the lower lateral line that is next behind the transverse row that extends downward and forward from the last pored scale of the upper lateral line. The last scale recorded is at the end of the lower lateral line, where it meets the base of the caudal fin...".

Collections are listed by country and drainage basins in the following manner: catalog number, general locality with the elevation in meters (m), and the number of specimens in parentheses. Abbreviations are spelled out when used for the first time.

The specimens utilized for the study are deposited at the California Academy of Sciences (CAS and IU), Field Museum of Natural History (CNHM), Natural History Museum of Los Angeles County (LACM), the Museo de Zoología, Universidad de Costa Rica (UCR), and the United States National Museum (USNM), and are listed below.

Cichlasoma sieboldii

COSTA RICA (Pacific versant).

RIO GRANDE DE TARCOLES DRAINAGE: UCR 98-2: Río Turrubares, 30 m (1).

COASTAL STREAM, QUEPOS REGION: UCR 311-3: Quebrada Bonita, 10 m (37).

RIO TERRABA DRAINAGE: CNHM 6478 (holotype of *C. punctatum*) and 6479 (9 paratypes of *C. punctatum*), Buenos Aires de Térraba, 390 m (10); UCR 40-4: Río Pedregoso, 700 m (7) UCR 393-10: Río Pedregoso, 660 m (7); LACM 2940: Río Peje, 560 m (3); LACM (2949): Same locality as LACM 2940 (1); LACM 2852: Same locality as LACM 2940 (9); UCR 41-3: Same locality as LACM 2940 (1); LACM 2915: Río General, 500 m (18); LACM 4741: Río Convento, 540 m (1); LACM 4758: Stream 45.4 km SE of San Isidro de El General, 300 m (1).

RIO SIERPE DRAINAGE: UCR 112-17: Tributary of Río Sierpe, 20 m (7).

RIO ESQUINAS DRAINAGE: UCR 111-17: Quebrada 36, 80 m (74); UCR 757-7: Quebrada Angelina, 60 m (59).

RIO COTO DRAINAGE: UCR 102-2: Tributary of Río Claro, 20 m (6); LACM 4860: Quebrada Kilómetro 19, 20 m (5); LACM 4817: Quebrada San Antonio, 20 m (2); LACM 4795 and 4796: Stream 12.6 km E of Golfito, 15 m (7); LACM 4772 and 4774: Río Caracol, 20 m (157); UCR 756-13: Same locality as LACM 4772 (40); LACM 4738: Río Nuevo, 20 m (7); UCR 101-20: Same locality as LACM 4738 (3); UCR 104-17: Tributary of Río Corredores, 40 m (1); UCR 103-8: Quebrada La Palma, 90 m (11).

PANAMA (Pacific versant)

RIO CONCEPCION DRAINAGE: UCR 450-4: Chiriquí Province, stream 30 km E of Paso Canoas, 160 m (12).

RIO SAN PABLO DRAINAGE: UCR 452-1: Veraguas Province, Río Santa Clara, 130 m (100).

Cichlasoma tuba

NICARAGUA (Atlantic versant)

RIO ESCONDIDO DRAINAGE: UCR 268-9: Chontales Department, Río la Concha, 150 m (5).

COSTA RICA (Atlantic versant)

LAKE NICARAGUA DRAINAGE: UCR 122-18: Río Sapoá, 40 m (2); UCR 123-9: Río Cabalceta, 60 m (80); UCR 124-15: Río Las Vueltas, 60 m (5); UCR 247-1: Río Zapote, 50 m (2).

RIO SAN JUAN DRAINAGE: UCR 835-6 and UCR 836-7: Tributaries of Río Arenal, 530-535 m (9); UCR 263-4: Quebrada Máquina, 90 m (77); LACM 9115-1, 9122-2, 9137-3, 9142-3, 9150-11 and 9196 7: Río Puerto Viejo, 35-55 m (7); UCR 769-10: Quebrada Sábalo, 40 m (11); LACM 9177-1: Quebrada Salto, 40 m (1); LACM 9146-1: Río Sarapiquí, 35 m (1).

RIO PARISMINA DRAINAGE: UCR 10-2: Río El Destierro, 100 m (1).

RIO MADRE DE DIOS DRAINAGE: LACM 9109-2: Río Madre de Dios, 50 m (1); UCR 444-9: Quebrada Salsipuedes, 20 m (49).

PANAMA (Atlantic versant).

RIO GUARUMO DRAINAGE: IU 17544: Río Guabito (1); IU 17547: Río Guarumo (2); USNM uncataloged: Río Guarumo (11).

RIO CRICAMOLA DRAINAGE: IU 17546, 17543 and 11550: Río Cricamola (6); IU 17545: Contonigabi Creek (3).

CICHLASOMA SIEBOLDII KNER AND STEINDACHNER

(Figs. 2 and 3)

Heros sieboldii Kner and Steindachner, *in* Kner, 1863, *Sitzungsber. Bayer Akad. Wiss. München,* 2: 223 (type: Pacific slope of Panamá); Kner and Steindachner, 1865, *Abh. Akad. Wiss. München,* 10: 13 [descrip., fig.; Panamá and "Neu-Granada" (=Panamá)]; Günther, 1869, *Trans. Zool. Soc. Lond.,* 6: 466 (probably = *H. godmani*); Pellegrin, 1904, *Mem. Soc. Zool. France,* 16: 208 (synonym of *C. godmani*).

Astronotus sieboldii, Eigenmann, 1893, *Proc. U. S. Nat. Mus.,* 16: 59 (listed).

Cichlasoma sieboldii, Jordan and Evermann, 1898, *Bull. U. S. Nat. Mus.,* 47: 1516 (copy of orig. descrip.); Regan, 1905, *Ann. Mag. Nat. Hist., ser.* 7, 16: 235 (apparent copy of orig. descrip.); Regan, 1906, *Biologia Centrali - Americana, Pisces,* 8: 21 and 186 (listed); Eigenmann, 1910, *Rept. Princeton Univ. Exped. Patagonia,* 1896-1899, 3: 474 (listed); Meek and Hildebrand, 1916, *Fieldiana Zool. Ser.,* 10: 345 (copy of Regan's descrip.); Hildebrand, 1938, *Fieldiana Zool. Ser.,* 22: 335 (descrip.; Río Coto, Costa Rica); Loftin, 1965, Ph.D. diss., Florida State Univ., p. 145 (Chiriquí and Veraguas Prov., Panamá); Miller, 1966, *Copeia,* 1966: 791 (listed; Pacific slope Costa Rica and Panamá); Bussing, 1967, *Rev. Biol. Trop.,* 14: 237 (listed).

Paraneetroplus sieboldii, Regan, 1908, *Ann. Mag. Nat. Hist., ser.* 8, 2: 464 (Río Grande de Térraba, Costa Rica); Behre, 1928, *Ann. Carnegie Mus.,* 18: 323 (Río Chiriquí del Tiré, Panamá), Hubbs, 1953, *Copeia,* 1953: 147 (clarification of type locality); Gosse, 1966, *Bull. Inst. Roy. Sci. Nat. Belgique,* 42 (28): 19 (descrip.; Río Esquinas, Costa Rica).

Neetroplus sieboldii, Jordan, Evermann and Clark, 1930, Appendix 10, *Rept. U. S. Comm. Fish.* for 1928, p. 423 (listed).

Herichthys underwoodi Regan, 1906, op. cit., p. 30 and 186 (type: Costa Rica; fig.; synonym of *C. sieboldii*); Jordan, Evermann and Clark, op. cit.: p. 423 (erroneously listed as synonym of *Tomocichla underwoodi).*

Cichlasoma underwoodi, Meek 1914, *Fieldiana Zool. Ser.,* 10: 127 (Río Grande de Tárcoles, Costa Rica); Alfaro, 1937, *Investigaciones científicas.* San José, p. 229 (Esparta, Costa Rica).

Cichlasoma punctatum Meek, 1909, *Fieldiana Zool. Ser.,* 7: 210 (type: Buenos Aires, Costa Rica); Eigenmann, 1910, op. cit., p. 477 (listed); Meek, 1914, op. cit., p. 127 (listed); Grey, 1947, *Fieldiana Zool. Ser.,* 32: 134 (catalog number of holotype).

Theraps punctatum, Jordan, Evermann and Clark, 1930, op. cit., p. 417 (listed).

Cichlasoma frontale Meek, 1909, op. cit., p. 210 (type: Turrubares, Costa Rica); Eigenmann, 1910, op. cit., p. 477 (listed); Meek, 1914, op. cit., p. 127 (synonym of *C. underwoodi).*

Theraps frontalis, Jordan, Evermann and Clark, op. cit., p. 417 (listed).

Theraps terrabae Jordan and Evermann, 1927, *Proc. Calif. Acad. Sci., ser.* 4, 16: 507 (new name for *C. punctatum*); Jordan, Evermann and Clark, op. cit., p. 417 (synonym of *Theraps punctatum).*

Cichlasoma terrabae, Miller, 1966, op. cit., p. 793 (listed); Bussing, 1967, op. cit., p. 237 (listed).

TAXONOMIC HISTORY: After KNER and STEINDACHNER (8) published the original description of *Heros sieboldii* from Panamanian specimens, subsequent authors have listed the species in several other genera. Other authors have based descriptions of new taxa on Costa Rican specimens of the same species.

REGAN described *Herichthys underwoodi* from a single specimen from "Costa Rica", but in the supplement of the same volume he correctly synonymized it with *C. sieboldii* (15). MEEK (10) described *C. punctatum* from Buenos Aires, Costa Rica and *C. frontale* from Turrabales (*sic*), Costa Rica. Later, MEEK (11) correctly synonymized *frontale* with *underwoodi* but unlike Regan, he still considered the latter form distinct from *sieboldii;* he continued to list *C. punctatum* as a valid species.

JORDAN and EVERMANN (6) noted that *punctatum* was preoccupied in the genus *Cichlasoma* and proposed the new name *terrabae* for this form which inhabits the Río Térraba and other drainages. This change was unneccesary because they referred the species to the genus *Theraps.* Later, JORDAN, EVERMANN and CLARK (7) remedied the error by listing *Theraps terrabae* as a synonym of *Theraps punctatum.*

Theraps and other nominal genera are currently considered infrageneric categories pending the revision of the genus *Cichlasoma,* and MILLER (12) and BUSSING (3) have listed *C. terrabae* as a nominal species. Recent examination of the type specimens of *C. punctatum* (=*C. terrabae*) has revealed that the form must now be placed in the synonymy of *C. sieboldii.*

INTRASPECIFIC VARIATION: The meristic counts and body proportions of the small type specimens of *C. punctatum* are compared with small examples

of *C. sieboldii* from the Río Esquinas drainage in southern Costa Rica and from Veraguas Province, Panamá in Table 1. The range of morphometric variation of ten large specimens from the Esquinas and Coto drainages and Veraguas Province, Panamá are included to suggest where allometric structural changes occur with growth. No striking proportional differences between these samples were found.

TABLE 1

Meristics and proportions in thousandths of standard length of Cichlasoma sieboldii. *The ten type specimens of* Cichlasoma punctatum *are compared with twenty examples of* C. sieboldii *from the Esquinas and San Pablo drainages and ten large specimens from several drainage basins.*

Drainage	Térraba *	Esquinas	San Pablo	Several
Dorsal spines	17	16-17	16-17	17
Dorsal rays	11-12	12-13	12	11-13
Anal spines	4-5	4-5	5	4-5
Anal rays	8-10	8-10	8-9	8-10
Pectoral rays	15-16	15-16	16	16
Caudal rays	16	16	16	16
Total gill rakers	7-10	8-10	8-10	9-10
Pores upper lat. line	19-22	20-23	19-22	20-22
Pores lower lat. line	10-12	9-12	9-12	10-12
Longitudinal scales	30-31	30-31	30-31	30-31
Scales above lat. line	5	4-5	4-5	4-5
Scales below lat. line	—	10-11	11-12	10-12
Standard length (mm)	64.0-80.0	64.0-79.3	65.7-82.3	105.7-143.0
Head length	311-339	323-340	323-350	306-331
Orbit diameter	74-87	82-94	84-96	65-79
Snout length	127-151	137-149	138-150	148-163
Upper jaw length	71-105	90-97	92-103	90-101
Bony interorbital	94-111	86-106	97-108	104-138
Suborbital distance	72-88	80-85	76-86	82-96
Greatest depth	367-429	383-415	426-456	373-456
Peduncle depth	139-155	139-149	144-150	130-147
Peduncle length	178-201	152-172	155-176	159-177
Predorsal distance	365-414	387-403	385-414	372-401
Preanal distance	649-715	644-696	665-690	642-696
Prepectoral distance	305-324	298-322	301-326	293-313
Prepelvic distance	358 390	347-373	301-384	330-370
Length pectoral fin	218-278	237-254	230-250	221-257
Length pelvic fin	201-267	232-254	247-273	217-318
Length dorsal fin base	524-605	570-597	585-612	576-616
Length anal fin base	190-234	204-241	215-234	200-253
Length mid-caudal rays	226-234	261-280	278-300	254-325
Length 6th dorsal spine	99-118	103-128	118-131	85-122
Length last dorsal spine	99-140	123-142	140-153	111-157

* Type specimens of *Cichlasoma punctatum*.

An analysis of meristic variation of samples collected throughout the geographic range of the species reveals only slight mean differences between neighboring populations (Table 2). Other meristic counts (frequency in parentheses) for *C. sieboldii* are: pectoral rays including all rudiments 15 (3), 16 (85), 17 (2); total number of gill rakers on first arch 7 (1), 8 (5), 9 (33), 10 (47), 11 (2); lateral-series scale count 30 (4), 31 (27), 32 (64), 33 (6); transverse scales above lateral line 4 ½ (20), 5 ½ (25); transverse scales below lateral line 10 (5), 11 (5), 12 (1); scales around caudal peduncle 18 (9), 19 (4), 20 (1).

The number of mandibular pores of the lateral-line system has been shown to be of taxonomic significance within the genus *Cichlasoma;* members of the *Thorichthys* species group generally have five mandibular pores, whereas most other species have four such pores (13). Young specimens (30 mm) of *C. sieboldii* have four mandibular pores, but with increasing age the two posterior-most pores of the series are increased to several minute openings which join the mandibular canal. Even in small specimens the preopercular canal presents this system of groups of minute pores. In large specimens the ramification of the pores of the preoperculo-mandibular and other canals is so extensive that the minute openings form a continuous network of pores in this region. Other members of the *Theraps* species group (*C. godmani, C. guttulatum, C. masculicauda, C. nicaraguense* and *C. tuba*) reveal the same ontogenetic tendency of an increase in numbers of sensory pores. *Neetroplus nematopus,* perhaps derived from *Theraps*-like ancestors, also shows this specialization.

DENTITION: The teeth on a pair of cleaned and dried jaws and pharyngeal bones of a 139.2 mm specimen of *C. sieboldii* are as follows. Each premaxilla bears an outer row of 12 enlarged conical teeth which gradually decrease in size laterally; the brown tips are triangular with slightly rounded apices in front view; in cross-section these teeth are triangular with a very flat anterior surface and the posterior surface, which bears a small secondary cusp on the six largest medial teeth, is directed posteriorly. Three or four irregular rows of minute teeth lie just behind the outer row; their blunt-pointed tips are expanded and appear triangular in cross-section. Each dentary bears an outer row of six large teeth medially, and from 11 to 13 smaller teeth laterally; the transition from the large medial to smaller lateral teeth is slightly more abrupt than in the premaxillae. In other respects the dentary teeth resemble the premaxillary teeth.

The pharyngeal apparatus bears curved sharp-pointed teeth; all are greatly laterally compressed and subdistally expanded, the larger median ones often bearing a tiny secondary cusp on the inside of the curved surface.

COLORATION IN LIFE: Both sexes are quite similar, although the species presents considerable intraspecific variation. The nuptial coloration is distinctive, but similar in both sexes.

TABLE 2

Geographic variation of selected meristic counts of Cichlasoma sieboldii. *All localities are in Costa Rica except Río San Pablo, Veraguas Province, Panamá.*

	Dorsal spines				Dorsal rays				Anal spines			Anal rays			
Drainage	16	17	18	$\bar{x}$	11	12	13	$\bar{x}$	4	5	$\bar{x}$	8	9	10	$\bar{x}$
Tárcoles		1		17.0		1		12.0	1		5.0		1		9.0
Térraba	2	21	1	17.0	11	13		11.5	7	17	4.7	15	7	2	8.5
Esquinas	3	27		16.9		25	5	12.2	2	28	4.9	3	25	2	9.0
Coto	3	27		16.9		23	7	12.2	4	26	4.9	6	22	2	8.9
San Pablo	4	24	2	16.9	6	23	1	11.8	2	28	4.9	18	12		8.4
TOTAL	12	100	3	16.9	17	85	13	12.0	15	100	4.9	42	67	6	8.7

	Pores upper lat. line						Pores lower lat. line						Long. scales				
Drainage	19	20	21	22	23	$\bar{x}$	8	9	10	11	12	$\bar{x}$	29	30	31	32	$\bar{x}$
Tárcoles				1		22.0				1		11 0			1		31.0
Térraba	1	7	10	4		20.8			3	8	6	11.2	3	13	6		30.1
Esquinas		4	14	9	3	21.4		2	9	16	3	10.7		7	23		30 8
Coto		6	18	5	1	21.0			7	18	5	10.9	1	15	12	2	30.5
San Pablo	1	5	11	11	2	21.3	1	4	5	14	6	10.7	4	16	10		30.2
TOTAL	2	22	53	30	6	21.1	1	6	24	57	20	10.8	8	51	51		30.4

C. sieboldii is dark gray-green above and pale gray or white on the lower sides and ventrum; the transition from the dark dorsal to pale ventral coloration is usually very abrupt. Specimens from some populations (Fig. 3B) have small dark puncticulations over the dorsal half of the body. The head is uniformly gray-green. Six vertical black bars or blotches occur on many specimens (Fig. 2A), although these are diffuse or totally obscured in reproductively active individuals. An additional short bar, which is inclined forward over the head, is seen on some individuals. Mature specimens have a pair of nearly horizontal dark lines connecting the anterior borders of the eyes; the interspace is a somewhat paler gray than the surrounding ground color and thus these markings are quite conspicuous when the fish is viewed from above.

A large male *C. sieboldii* from Panamá (UCR 450-4) and Costa Rican specimens (sex undetermined at the time) had the lateral scales of the body edged in purple or rose-color. The base of the pectoral fin was rose-colored with a bluish spot above and below this region.

Both spinous and soft dorsal fins of mature specimens are narrowly margined with red or orange. On most individuals red or maroon spots occur on the soft dorsal and anal fins and on the caudal fin. Most collections from the Esquinas and Coco drainages contain fishes with little or no spotting on the median fins (Figs. 3A and 3C). The spinous dorsal fin of some females is black (Fig. 3C). The pectoral and pelvic fins are gray.

On breeding individuals of both sexes the ventral half of head, including the lower lip and isthmus, become jet black. The upper two-thirds of the body often become very dark, and these dark regions contrast strikingly with the white breast and ventrum of the fish (Figs. 2B, 3A and 3B).

SEXUAL DIMORPHISM: Except for the black spinous dorsal fins of some females, other color differences between sexes were not noted. Elongate pelvic filaments were noted in large specimens of both sexes. Large specimens lack the produced dorsal and anal filaments common in other species of *Cichlasoma*. Very large specimens (probably larger than 250 mm) were seen in the field, but not captured, thus it is not certain which sex tends to be the larger of a breeding pair. Specimens as small as 70 mm were collected in breeding condition. The male urogenital papilla is conical with a pointed tip and terminal opening. The female papilla is dorso-ventrally flattened and has a rounded termination with a wide opening on its ventral surface.

ECOLOGY: This species is found in a variety of water conditions from moderately swift current to stagnant pools. Both sexes care for the young. A cursory examination of the stomach contents of four large specimens of *C. sieboldii* showed only plant matter consisting of finely triturated white pulp, grasses and filamentous algae. One specimen contained only shredded plant matter consisting mainly of grasses (Gramineae, subfamily Panicoideae) and lesser quantities of other plant tissue (Commelinidae and unidentified dicoty-

ledons). A small individual (78 mm) had eaten seeds, algae and aquatic insects.

DISTRIBUTION: ALFARO (1) recorded *C. underwoodi* (=*sieboldii*) from streams at Esparta, Costa Rica and this constitutes the northernmost record for the species. The southern record for *C. sieboldii* is the Río Santa María watershed in Veraguas Province, Panamá where LOFTIN (9) took the species between 50 and 305 m elevation. HUBBS (5) pointed out that the type locality of "Neu-Granada" for *C. sieboldii* refers to Panamá rather than Colombia as reported by Meek and Hildebrand and other authors. The species is restricted to the Pacific versant (Fig. 1).

CICHLASOMA TUBA MEEK

Tomocichla underwoodi Regan, 1908 *Ann. Mag. Nat. Hist., ser. 8,* 2: 463 (type: Río Iroquois, Costa Rica); Jordan, Evermann and Clark, 1930, Appendix 10, *Rept. U. S. Comm. Fish.* 1928, p. 423 (listed).

Cichlasoma tuba Meek, 1912, *Fieldiana Zool. Ser.,* 10: 73 (type: Victoria, Costa Rica); Meek, 1914, *Fieldiana Zool. Ser.,* 10: 124 (synonym of *Tomocichla underwoodi*); Grey, 1947, *Fieldiana Zool. Ser.,* 32: 134 (type apparently lost); Miller, 1966, *Copeia,* 1966: 793 (Atlantic slope of Costa Rica); Bussing, 1967, *Rev. Biol. Trop.,* 14: 237 (listed); Villa, 1971, *Sinopsis Peces de Nic.,* p. 102 (Río Mico, Nicaragua).

Cichlasoma guttulatum, Behre (not Günther), 1928, *Ann. Carnegie Mus.,* 18: 321 (misidentification; tributaries of Laguna de Chiriquí, Panamá); Hildebrand, 1938, *Fieldiana Zool. Ser.,* 22: 334 (listed on basis of Behre); Loftin, 1965, Ph.D. diss., Florida State Univ., p. 145 (listed).

TAXONOMIC HISTORY: Under the present taxonomic arrangement whereby most of the Central American cichlids are included in the genus *Cichlasoma, Tomocichla* becomes a synonym of *Cichlasoma,* and the species *underwoodi* is unavailable because another species, *Herichthys underwoodi,* is a junior synonym of *Cichlasoma sieboldii.* The next available name, *C. tuba,* therefore applies to this species.

I examined twelve specimens identified as *Cichlasoma guttulatum* by Behre, from all the localities she listed for that species (2). I identify the specimens as *C. tuba,* although BEHRE (2) stated that Regan agreed with her referral of the species to *C. guttulatum.* The specimens, formerly part of the Indiana University collection, are presently deposited at the California Academy of Sciences.

LOFTIN (9) collected, but did not report on eleven specimens of *C. tuba* from the Río Guarumo, Panamá (field numbers HL-195 and HL-196, deposited at the USNM).

VARIATION: Few meristic differences exist between the Nicaraguan and Costa Rican populations of *C. tuba,* except that the Nicaraguan samples have five anal spines whereas most Costa Rica specimens have four anal fin spines

TABLE 3

Geographic variation of selected meristic counts of Cichlasoma tuba. *The Río Escondido is in southern Nicaragua. Collection sites in tributaries of the Río San Juan and the Río Madre de Dios are in Costa Rica*

Drainage	Dorsal spines			Dorsal rays					Anal spines			Anal rays			
	15	16	$\bar{x}$	13	14	15	16	$\bar{x}$	4	5	$\bar{x}$	9	10	11	$\bar{x}$
Escondido	1	4	15.8		4	1		14.2		5	5.0	1	4		9.8
San Juan	5	25	15.8	1	14	12	3	14.6	30		4.0		17	13	10.4
Madre de Dios	3	27	15 9		13	17		14.6	28	2	4.1		24	6	10.2
TOTAL	9	56	15.9	1	31	30	3	14.5				1	45	19	10.3

Drainage	Pores upper lat. line						Pores lower lat. line					Long scales				
	20	21	22	23	24	$\bar{x}$	10	11	12	13	$\bar{x}$	30	31	32	33	$\bar{x}$
Escondido		1	2	1	1	22.4		3	2		11.4		2	3		31.6
San Juan	2	11	13	4		21.6	2	18	9	1	11 3	2	7	21		31.6
Madre de Dios		4	16	10		22.2	1	20	7	2	11.3		4	23	3	32.0
TOTAL	2	16	31	15	1	22.0	3	41	18	3	11.3	2	13	47	3	31.8

(Table 3). The lateral-series scale counts are (frequency in parentheses) 32 (9), 33 (47), 34 (9). Four mandibular sensory pores are present; as in *C. sieboldii,* the two posterior pores are modified with age into numerous minute openings.

Individual fish of both sexes may have enlarged fleshy lip folds (Figs. 4C and 5C). All degrees of development from normal to fleshy lips are generally seen at any locality. The degree of fleshiness is not correlated to sex or age.

DENTITION: The dentition of an adult *C. tuba* 160 mm long is as follows. Each premaxilla bears an outer row of 14 enlarged conical teeth which gradually decrease in size laterally; the tips are brown and broadly rounded; the median teeth are greatly compressed antero-posteriorly, but are rounded in cross-section near their bases where a small secondary cusp is seen on the posterior surface of the larger teeth. Four rows of minute teeth lie just behind the outer row; these pointed teeth are also strongly compressed in cross-section. Each dentary bears 16 to 18 teeth in the outer row, the five or six medial teeth are considerably larger than the lateral teeth; in shape and cross-section these are similar to the premaxillary teeth.

Each upper pharyngeal bone bears sharp-pointed teeth, the median ones robust and triangular in cross-section, the lateral ones are compressed. The median teeth of the lower pharyngeal plate are robust and tubercular, but with minute pointed tips and round in cross-section; the lateral teeth have pointed tips and are compressed in cross-section. Some of the large medial pharyngeal teeth have a small secondary cusp near the base.

COLORATION IN LIFE: Both sexes of *C. tuba* are usually very dark gray or nearly black above; an olive-green tone is often evident. The dark dorsal coloration extends ventrally to the lower edge of the pectoral fins anteriorly and to the lower fourth of the caudal peduncle behind. The ventrum is pale gray or dark above and dusky olive below. The eye is bright red. Two horizontal dark lines enclosing a pale gray area lie on the snout and connect the anterior borders of the eyes (Figs. 4A and 5A). Considerable purple coloration occurs on the middle sides in a band about four or five scale-rows wide from behind the head to near the base of the caudal fin. Each scale in this region is purple at the base and green or gold on the edges. On some fish lavender blotches occur on the cheek and lower operculum. As many as nine black vertical bars are visible on the body of some specimens (Fig. 5C), but usually only a few bars are apparent posteriorly.

The soft dorsal and anal fins and caudal fin are dusky and spotted with irregular black markings. The tip of the membrane uniting the dorsal spines is rose-colored, giving an inconspicuous colored margin to this fin. The dorsal margin of the caudal fin is black; this dark pigmentation is restricted to the margin distally, but covers the entire upper lobe at its base (Figs. 4A and 5 C). The pectoral fins are clear; the pelvic fins are dusky gray. Young individuals

less than 50 mm long have unpigmented caudal and soft dorsal and anal fins which probably serve to break up the visual outline of the fish.

A large breeding male *C. tuba* (275 mm) from the Río San Juan drainage had a bright rosy stripe from the opercle to the base of the caudal fin. The dorsum was golden-olive; the belly a lighter shade of the same color. The black upper margin of the caudal fin was very conspicuous. The head was violet with three dark lines connecting the eyes across the snout. The urogenital papilla was conical with a terminal opening. Females of this species, as in *C. sieboldii*, have a broad-tipped urogenital papilla with a ventral opening.

ECOLOGY: An analysis of 33 adults (146-280 mm) of *C. tuba* from the San Juan drainage reveals that they are predominantly herbivorous (92% of volume of food ingested). The following is a breakdown of stomach contents in percentages of total volume: terrestrial leaves 40%, bryophytes or algae 34%, fruit 18%, aquatic insects and the river shrimp *Macrobrachium* 6%, and sand or detritus 2%. Large specimens often were seen with a large tree leaf projecting from the mouth or nibbling at floating "chilamate" figs. Four young specimens (21-37 mm) contained only aquatic insects.

The species is common in lowland rivers or large streams which have moderate to considerable current. The young are usually found in the swiftest water on the bottom or behind rocks. The eggs are laid on flat rocks or fallen logs in areas of moderate current velocity. The newly hatched fry are guarded by both parents in quiet water over a shallow sandy bottom.

DISTRIBUTION: *C. tuba* is known only on the Atlantic versant from the Río Escondido drainage, Nicaragua (17) to the Río Cricamola, Panamá (2; Fig. 1).

REMARKS

REGAN originally placed *C. sieboldii* in the *Theraps* section of *Cichlasoma*, but subsequently on the basis of its compressed teeth, he referred it to *Paraneetroplus* (15). He considered *Tomocichla underwoodi* (=*C. tuba*) distinctive enough to merit generic rank because of the posterior placement of the pelvic fins (16). In a recent listing of Central American fishes, MILLER (12) referred *C. sieboldii* to the section *Theraps*, but was uncertain of the placement of *C. tuba*. I propose that *C. sieboldii* and *C. tuba* are closely allied members of the section *Theraps*.

Cichlasoma sieboldii and *C. tuba* share in common with other members of the *Theraps* group, the general physiognomy, small mouth, convex snout, short dorsal fin spines, rounded soft dorsal and anal fins, short pectoral fins, etc. The two species also share other characterics: low anal fin spine counts (4 or 5); compressed jaw teeth; subterminal mouth; dark pigmentation dorsally, abruptly white below; purple coloration on the lateral scales; and dark stripes across the snout.

On the basis of this combination of superficial characteristics and the parallel geographic distribution of Atlantic and Pacific slope geminate pairs, I have suggested that *C. sieboldii* and *C. tuba* are derived from a common ancestral population which inhabited an insular landmass during the Pliocene (4). As this island became part of the emerging Isthmian Link in the Late Pliocene, Pacific and Atlantic versant populations were permanently isolated and have diverged into two distinctive forms.

Cichlasoma tuba, which is sympatric with at least a dozen other cichlids, has specialized more than *C. sieboldii.* The strongly compressed teeth of *tuba* and the development in some individuals of fleshy lip folds presumably are feeding adaptations. The emarginate caudal fin may be of importance in swimming in its swift water habitat.

Cichlasoma sieboldii is sympatric with five other cichlid species and with its generalized rounded caudal fin, is not restricted to a narrow range of habitats. The slightly compressed triangular jaw teeth do not depart greatly from the generalized conical tooth form of most species of *Cichlasoma.*

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RESUMEN

Con base en una revisión bibliográfica, se examina la compleja historia taxonómica de la mojarra *Cichlasoma sieboldii.* Se considera por primera vez a *C. punctatum* y *Theraps terrabae* como sinónimos de *C. sieboldii.* El informe sobre *C. guttulatum* de Panamá se debió a la mala identificación de *C. tuba,* especie sobre la que se informa por primera vez de Panamá.

Se incluye una discusión de la variación morfológica y merística, coloración de individuos vivos, ecología, y distribución geográfica de *C. sieboldii* y *C. tuba.* Las evidencias morfológicas y zoogeográficas sugieren que estas dos especies representan poblaciones de las vertientes Pacífica y Atlántica, respectivamente, de un antepasado del Plioceno.

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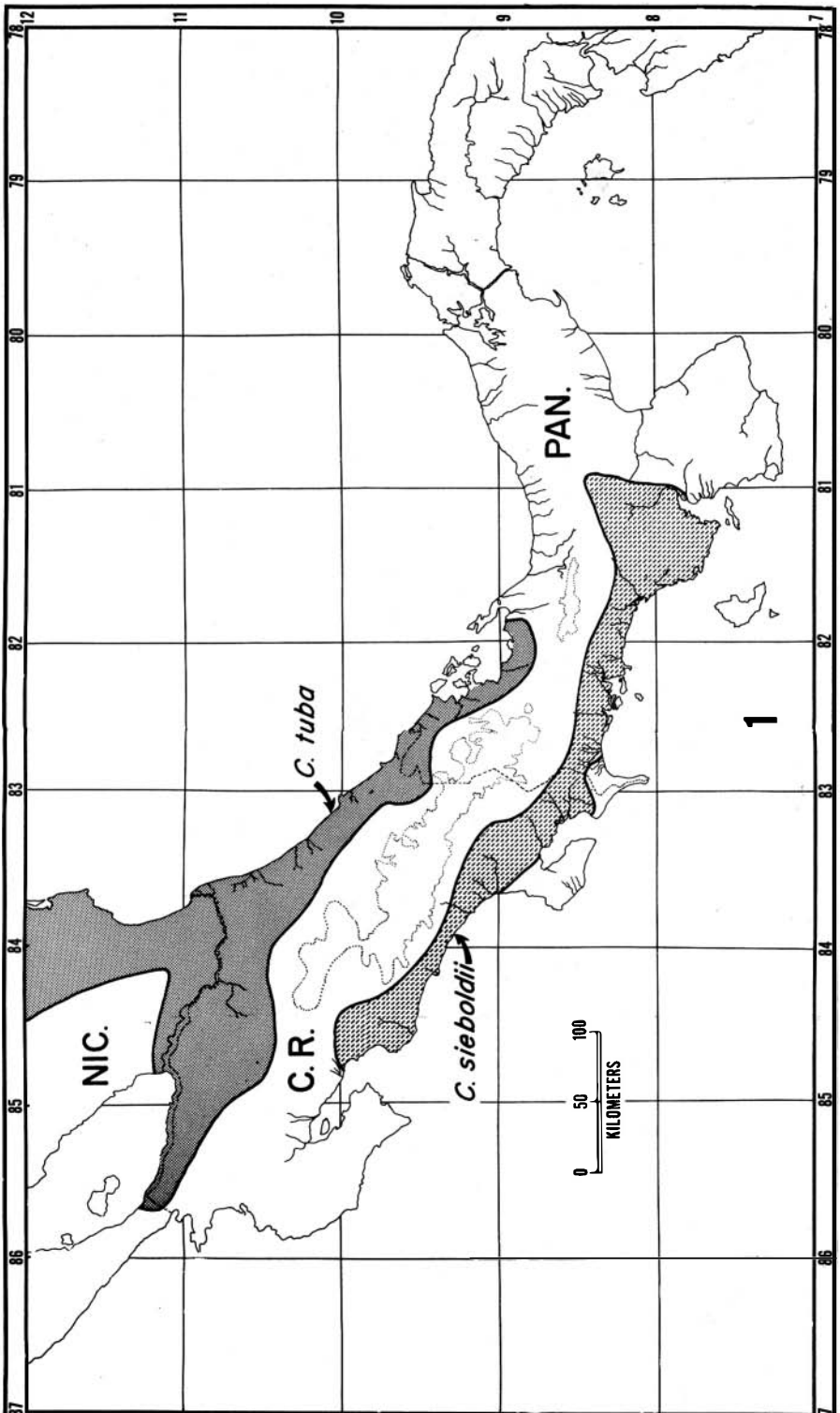
Fig. 1. Approximate distribution of *Cichlasoma tuba* on the Atlantic versant, and *Cichlasoma sieboldii* on the Pacific versant of Central America. *C. tuba* reaches the Río Escondido drainage of Nicaragua just slightly above the upper margin of the map. Although *C. tuba* has been collected in the Río Sapoá and other tributaries of Lake Nicaragua, it is apparently ecologically unsuited to the lacustrine environment of the lake itself.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C. tuba
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Fig. 2. *Cichlasoma sieboldii,* males. A, UCR 311-3,82.6 mm, from Quebrada Bonita near Quepos, Costa Rica; B, UCR 452-1, 80.5 mm, from the Río Concepción drainage, Panamá; C, UCR 98-2, 64.0 mm, from Río Turrubares, Costa Rica.

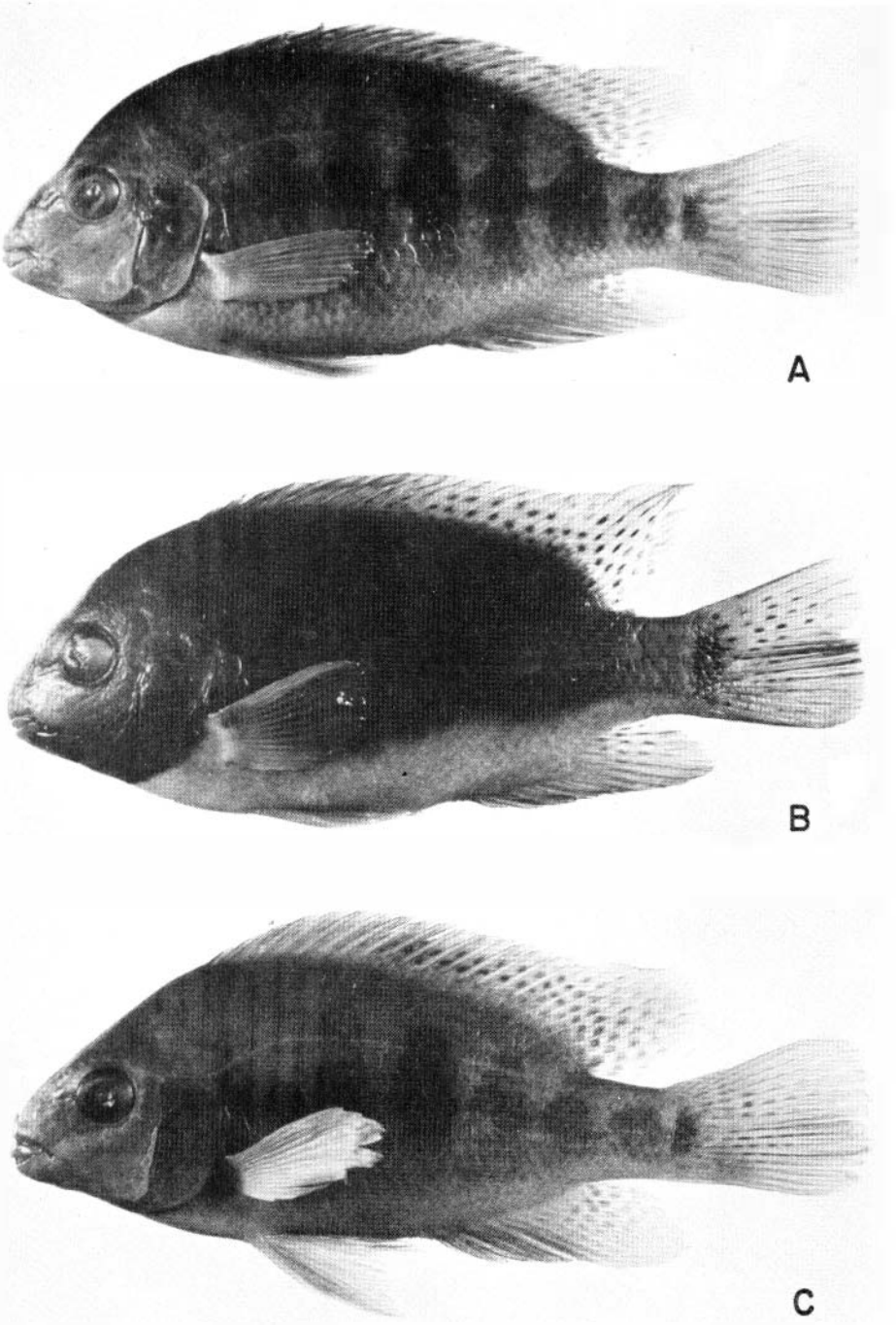

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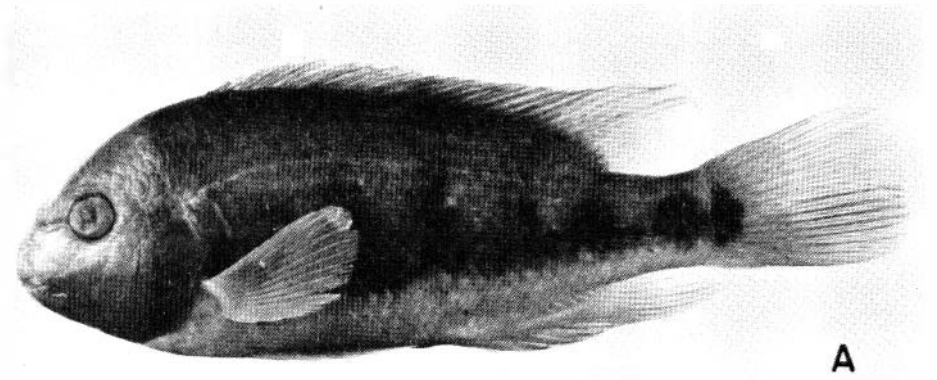
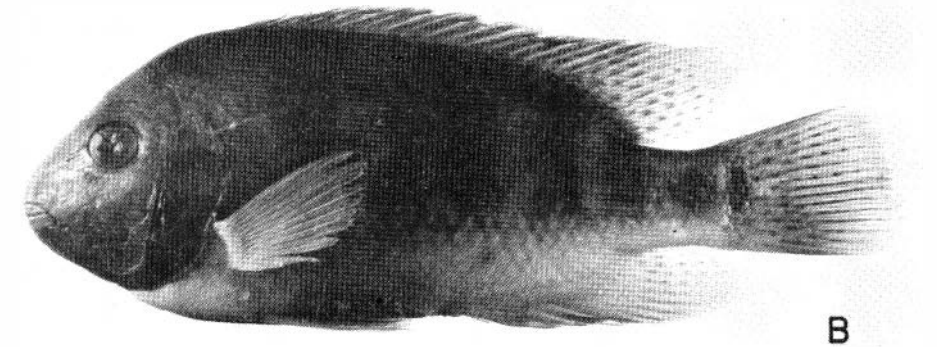
Fig. 3. *Cichlasoma sieboldii,* females. A, UCR 111-17, 108.5 mm; B, UCR 101-20, 106.8 mm; C, UCR 111-17, 74.5 mm. All specimens from the Coto drainage, Costa Rica.





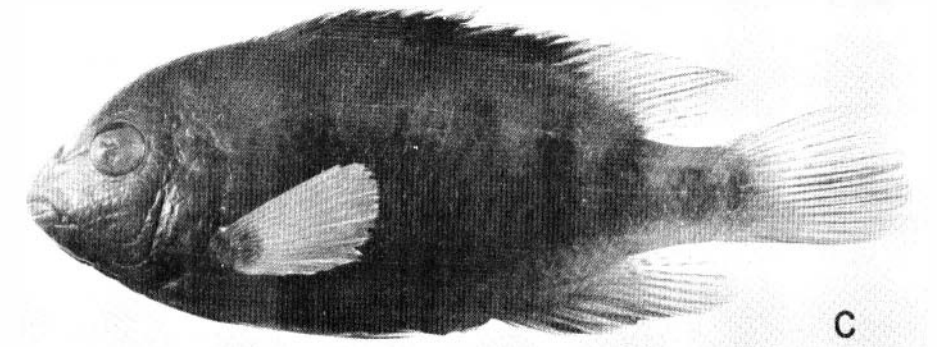


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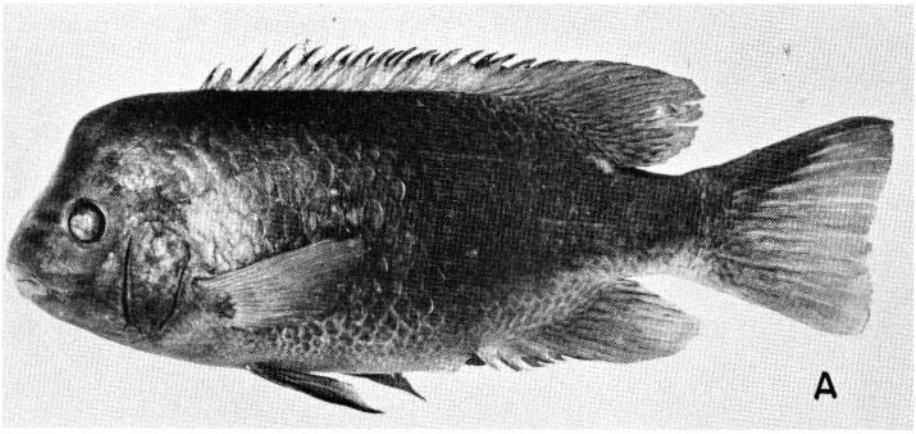
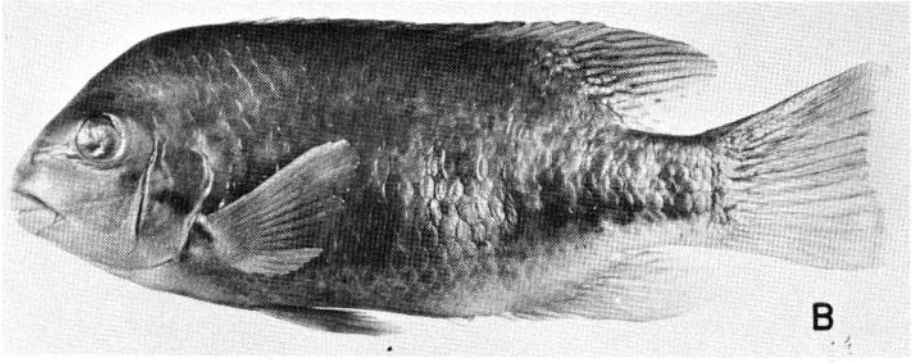
Fig. 4. *Cichlasoma tuba.* A, LCM?, a male 275 mm, from the Río San Juan drainage, Costa Rica; B, UCR 124-15, a female 177.00 mm, from Río Sapoá, a tributary of Lake Nicaragua; C, LACM,? head of a large male, to show fleshy lip development, from the Río San Juan drainage, Costa Rica.





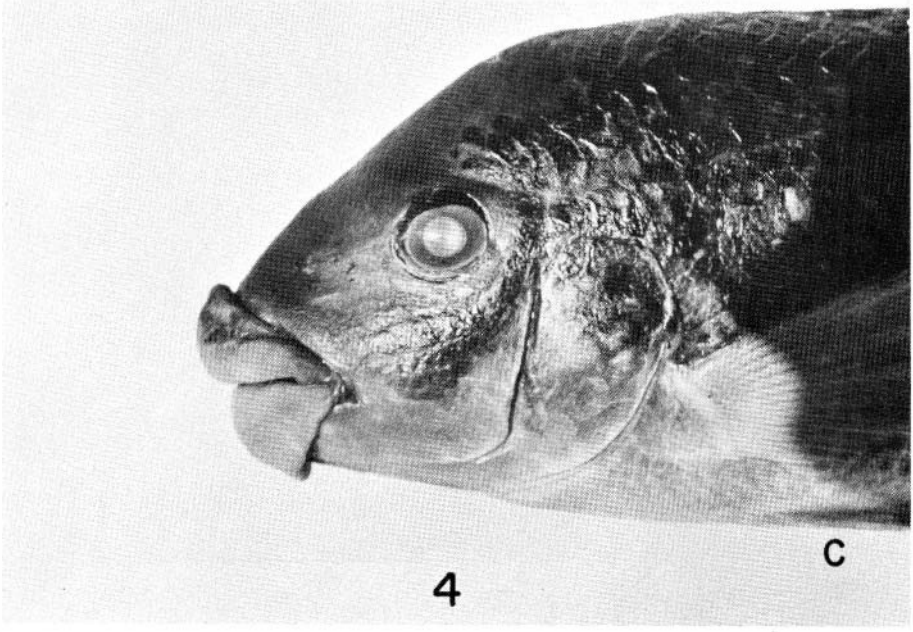


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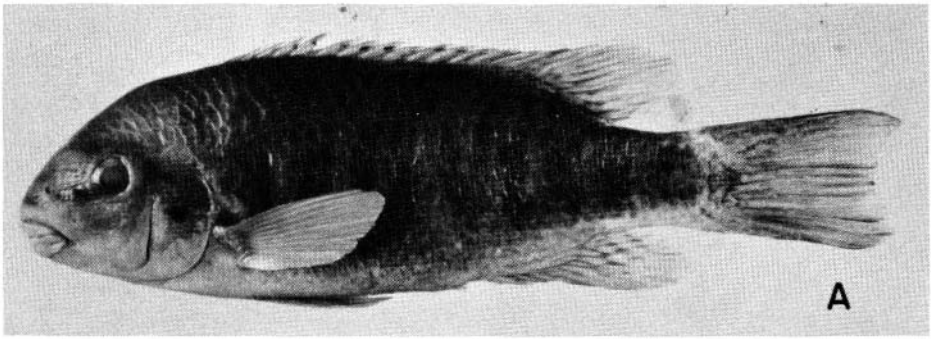
Fig. 5. *Cichlasoma tuba,* females. A, UCR 836-7, 177.5 mm, from the Río Arenal drainage, Costa Rica; B, UCR 268-9, 113.3 mm, from a tributary of Río Mico, Nicaragua; C, UCR 444-9, 88.3 mm, from the Río Madre de Dios drainage, Costa Rica.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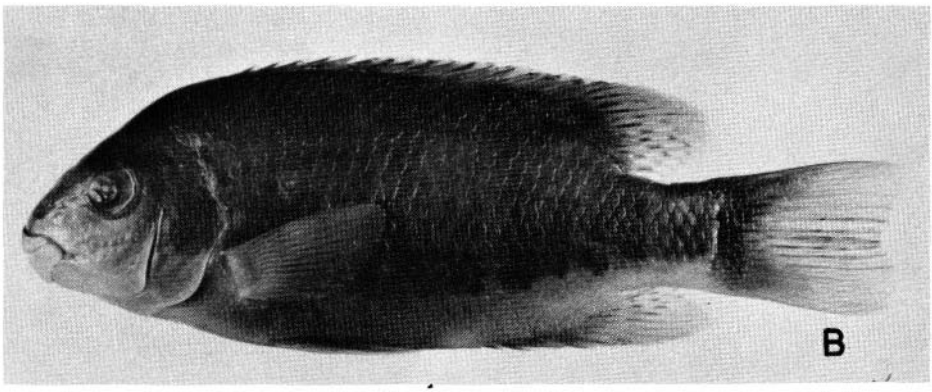
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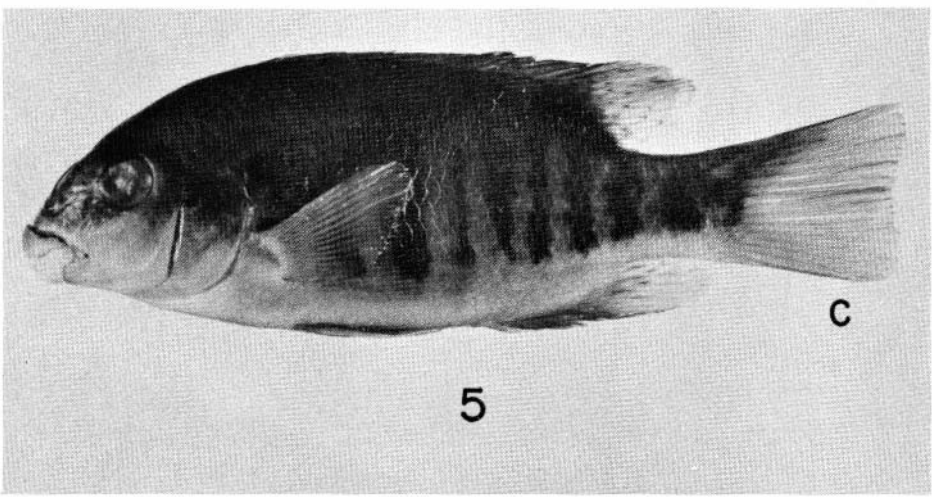
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