

**REVISION OF THE NEOTROPICAL ANNUAL FISH GENUS
CAMPELLOLEBIAS (CYPRINODONTIFORMES: RIVULIDAE),
WITH NOTES ON PHYLOGENY AND BIOGEOGRAPHY
OF THE CYNPOECILINA**

by

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ABSTRACT. - Monophyly of *Campellolebias* Vaz-Ferreira & Sierra is supported by eight synapomorphies associated with the copulatory organ of males and a derived colour pattern. Three species, *C. brucei* Vaz-Ferreira & Sierra, *C. chrysolineatus* Costa, Lacerda & Brasil, and *C. dorsimaculatus* Costa, Lacerda & Brasil, all endemic to southern Brazil, are recognized and diagnosed by their unique colour patterns. Monophyly of Cynopocilina is reinforced by the presence of 5-7 neuromasts on caudal fin, and sister-group relationship between *Campellolebias* and *Cynopocilus* Regan, by the common possession of a putative ejaculatory muscular pump. Distribution patterns obtained from Cynopocilina clades are compared with those available from other freshwater fishes, constituting a historical biogeographic hypothesis for eastern South America.

RÉSUMÉ. - La monophylie du genre *Campellolebias* Vaz-Ferreira & Sierra est soutenue par un patron de coloration dérivé et huit synapomorphies associées à l'organe copulateur mâle. Trois espèces sont reconnues, *C. brucei* Vaz-Ferreira & Sierra, *C. chrysolineatus* Costa, Lacerda & Brasil, et *C. dorsimaculatus* Costa, Lacerda & Brasil, toutes endémiques du Brésil méridional. Elles se distinguent par leurs patrons de coloration. La monophylie de la sous-famille des Cynopocilina est corroborée par la présence de 5 à 7 neuromastes à la base de la nageoire caudale, les relations de groupes-frères entre *Campellolebias* et *Cynopocilus*, par la présence commune d'une pompe éjaculatoire musculaire présumée. Les aires de répartition géographique des clades des Cynopocilina sont comparées avec celles d'autres poissons d'eau douce pour établir une hypothèse sur l'histoire biogéographique de l'Amérique du Sud orientale.

Key-words. - Cyprinodontiformes, Rivulidae, Annual fishes, Phylogenetic analysis, Cladistics, Eastern South-America, Biogeography.

The genus *Campellolebias* Vaz-Ferreira & Sierra comprises three allopatric species endemic to the coastal plain of southern Brazil, occurring in temporary pools located in the Atlantic forest (Costa *et al.*, 1989). The most noteworthy distinctive generic feature is the possession of a copulatory organ in males, derived from the anterior portion of anal fin (Vaz-Ferreira and Sierra, 1974). However, despite this curious structure, unique among aplocheiloids, little is known about the biology, behaviour and ecology of this genus.

Due to scarcity of characters and available material of species of the genus *Cynolebias* Steindachner and closely related genera, Parenti (1981) decided to place *Cam-*

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pellolebias within the synonymy of *Cynolebias*. Costa (1990a), studying phylogenetic relationships of *Campellolebias*, aligned it with the genera *Cynopoecilus* Regan and *Leptolebias* Myers in the subtribe Cynopoecilina. The purpose of the present study is, in part, to redefine and redescribe *Campellolebias* and its species, providing previously undescribed morphological characters, that are interpreted as evidences of generic monophyly and relationships. Most of these are associated with the copulatory organ.

Campellolebias and its closest relatives, the annual fish genera *Cynopoecilus* and *Leptolebias*, inhabit the coastal plains of eastern Brazil and Uruguay, the three genera having disjunct distribution patterns (Costa, 1990b; Costa, in press a). In the present study, these patterns are compared with those available from other freshwater fish groups showing some congruence, with the goal of obtaining a consistent biogeographic hypothesis for the region.

MATERIAL AND METHODS

Measurements and counts follow Costa (1988). Measurements are presented as percentages of standard length (SL), except for subunits of the head, which are presented as percentages of head length. Osteological studies were made on cleared and stained specimens (c&s) prepared according to Dingerkus and Uhler (1977) and Taylor and Van Dyke (1985). The compound caudal centrum was counted as a single element in vertebrae numbers, which were taken only from cleared and stained material. Supraorbital neuromasts counts were made in a longitudinal row from neuromast closest to anterior naris to neuromast nearest to orbit, not including the transverse neuromasts over rostral region nor any posterior extension series. Abbreviations for institutions are: MNRJ, Museu Nacional do Rio de Janeiro, Rio de Janeiro; MZUSP, Museu de Zoologia, Universidade de São Paulo, São Paulo; UFRJ, Universidade Federal do Rio de Janeiro, Rio de Janeiro; and, ZVC.P, Departamento de Zoología de la Facultad de Humanidades y Ciencias, Montevideo. Comparative material of other aplocheiloids examined in the present study are listed in Costa (in press b).

Bibliographic citations in species synonymy include only papers containing new data on the species or newly proposed classification. Osteological descriptions focus on traits of some importance for phylogenetic analyses of rivulid fishes (Parenti, 1981; Costa, 1990a).

Terminology

Nomenclature for frontal squamation follows Hoedeman (1956), and that concerning cephalic neuromasts follows Gosline's (1949) nomenclature for head sensory canals. Osteological nomenclature is that of Weitzman (1962), with modifications proposed by Vari (1989). Nomenclature for musculature is according to Winterbottom (1974). Concepts of cyprinodontiform suborders and families are according to Parenti (1981).

The copulatory organ of males of *Campellolebias* is herein named the "pseudogonopodium", instead of "gonopodium" as denominated by other authors (Vaz-Ferreira and Sierra, 1974; Parenti, 1981; Costa *et al.*, 1989). The term gonopodium has been widely employed to designate the copulatory organ of the Poeciliidae (e.g., Hubbs, 1924; Rosen and Bailey, 1963), a structure viewed as a set of important systematic characters since Regan (1913). The copulatory organ of *Campellolebias* has been considered a "true gonopodium" (Parenti, 1981), probably due to its similar function compared to the

poeciliid gonopodium. The poeciliid gonopodium, however, is morphologically very distinct from the copulatory organ of *Campellolebias*; it consists of a rod-shaped structure, formed mainly by the enlarged and thickened anal fin rays 3-5, which usually bear a series of segment modifications, such as hooks, denticulations, and ankylosed elements (for a detailed morphological analysis, see Rosen and Gordon [1953]). Besides this, in the insemination mechanism of poeciliids, the gonopodium serves as a transitory chamber for the sperm passage between the urogenital opening of male, located at the base of gonopodium, and the genitalium of female (Rosen and Gordon, 1953). In contrast, males of *Campellolebias* have the urogenital opening located at the subdistal part of pseudogonopodium (see description below). Therefore, sperm transfer occurs directly from that point to female urogenital opening. However, the main argument to erect a new distinctive term is the non-homologous condition of both copulatory organs. Employment of identical terms for two structures has been supported in cases of "at least a weak homology hypothesis" (Coddington, 1990; = primary homology of de Pinna, 1991). The gonopodium is an apomorphic feature defining the subfamily Poeciliinae (Cyprinodontoidae, Poeciliidae), therefore having its origin at the base of that group, which is distantly related to rivulids (Parenti, 1981). Therefore, copulatory organs of poeciliids and *Campellolebias* are clearly non-homologous, and for this reason, the term pseudogonopodium is created to the uniquely derived copulatory organ of *Campellolebias*.

GENUS *CAMPELLOLEBIAS* VAZ-FERREIRA & SIERRA

Campellolebias Vaz-Ferreira & Sierra, 1974: 1 (type species: *Campellolebias brucei* Vaz-Ferreira & Sierra, 1974, by original designation).

Diagnosis

Campellolebias is distinguished from all other members of the Rivulidae by the following synapomorphies: 1) anterior portion of anal fin of males modified into a pseudogonopodium, consisting of a tubular, laterally compressed copulatory organ, including the first two fin rays, and separated from the posterior portion of anal fin by a rupture of the anal fin membrane extending to near fin base; 2) urogenital duct of males elongate, its opening at the subdistal portion of pseudogonopodium; 3) urogenital duct of males attached to pseudogonopodium; 4) first proximal radial of anal fin of males curved posteriorly; 5) first and second distal radials of anal fin of males ossified and enlarged; 6) first two anal fin rays of males thickened; 7) first anal fin ray of males attached to first two proximal radials; 8) upper portion of *inclinatores anales* 1-3 laterally expanded; 9) three dark stripes on ventral part of head, the median one extending from lower jaw to anus, and the lateral stripes, from lower jaw to a point in a vertical through the upper section of preopercular neuromast series.

Description

Campellolebias comprises three similar, allopatric species, *C. brucei* Vaz-Ferreira & Sierra, *C. chrysolineatus* Costa, Lacerda & Brasil, and *C. dorsimaculatus* Costa, Lacerda & Brasil, distinguishable among themselves mainly by colour patterns (see the identification key below). The following description is applicable to all three species of *Campellolebias*.

General body morphology. - Dorsal profile of body nearly straight from snout to nape, gently convex from this point to posterior dorsal fin base, and approximately straight on caudal peduncle; ventral profile of body convex from tip of lower jaw to a vertical through center of eye, nearly straight from this point to posterior border of head, convex from a vertical through pectoral fin base to posterior anal fin base, and approximately straight at caudal peduncle. Larger examined specimen (UFRJ 284), 38.6 mm SL, an old male, has a prominent protuberance on top of head, above eye, similar to predorsal ridge as described by Parenti (1981).

Fins and ray counts. - Dorsal and anal fins pointed posteriorly in males, tips of both fins reaching at least middle of caudal fin; dorsal and anal fins rounded in females. Dorsal fin origin in front of vertical through anal fin origin, which is in a vertical through base of 2nd to 4th dorsal fin ray. Caudal fin subtruncate in males, rounded in females. Posterior margin of pectoral fin rounded, reaching vertical through anus in males, and through pelvic fin base in females. Pelvic fin bases separated by interspace. Tip of pelvic fin reaching between base of 1st to 3rd anal fin ray in males, and reaching a vertical through urogenital papilla in females. Dorsal fin rays 14-17 (iv-viii, 6-10, i-iii); anal fin rays 14-16 (ii, 9-11, ii-iii in females, ii+o-ii, 5-11, ii-vi in males); caudal fin rays 24-27 (vi-vii, 11-15, 6-8); pectoral fin rays 13-14 (i-iii, 6-10, iii-v); pelvic fin rays 5-6 (i-ii, 3, i).

Pseudogonopodium (Fig. 1A-B). - Anterior portion of anal fin of males modified into a tubular, laterally compressed copulatory organ (pseudogonopodium), which includes the first two fin rays and is separated from posterior portion of anal fin by a rupture of anal fin membrane extending to near fin base. Pseudogonopodium overlaps posterior portion of anal fin in an angle between 20-40° with the main axis of the body. Tip of pseudogonopodium reaching base of 6th to 8th anal fin ray. Urogenital papilla elongate, included within anterior border of pseudogonopodium, its opening located at subdistal portion of pseudogonopodium. Elongate urogenital duct originating in a sac-like structure, in front of first radial proximal bone. A thick membrane involving entire pseudogonopodium. Pseudogonopodium is mobile, actuating as a copulatory organ (G. Campello Brasil, pers. com.), probably only its tip being inserted in female during copulation.

Scales and latero-sensory system. - Scales cycloid, basal radii 21-24. Frontal squamation E-patterned, E-scales separated by interspace. No scale between supraorbital series of neuromasts and orbital margin. No canal or groove on supraorbital or preopercular regions. Supraorbital series of neuromasts 9-11, anterior and posterior portion continuous, posterior neuromasts arranged in a slightly curved line. No distinctively larger neuromast over dermosphenotical region. Five to seven neuromasts on median portion of caudal fin base just posterior to caudal fin squamation, occurring individually between rays. Longitudinal series of scales 25-28; transverse series of scales 7-8; predorsal scales 12-16; scale rows around caudal peduncle 12.

Jaws (Fig. 2A-B). - Ascending process of premaxilla trapezoidal, its distal edge truncate and wider than base of process. Longitudinal length of ascending process about half of longest length of premaxilla. Alveolar arm of premaxilla anteriorly expanded. Rostral cartilage longer than wide, about as long as ascending process. Ventral process of angulo-articular short, about equal in length to retro-articular.

Jaw suspensorium (Fig. 2C). - Mesopterygoid reduced, about half of autopalatine. Anterior and ventral edges of quadrate forming an angle of about 120°. Symplectic elongate, its length about 1.5 times the length of hyomandibula. Upper tip of preopercle pointed.

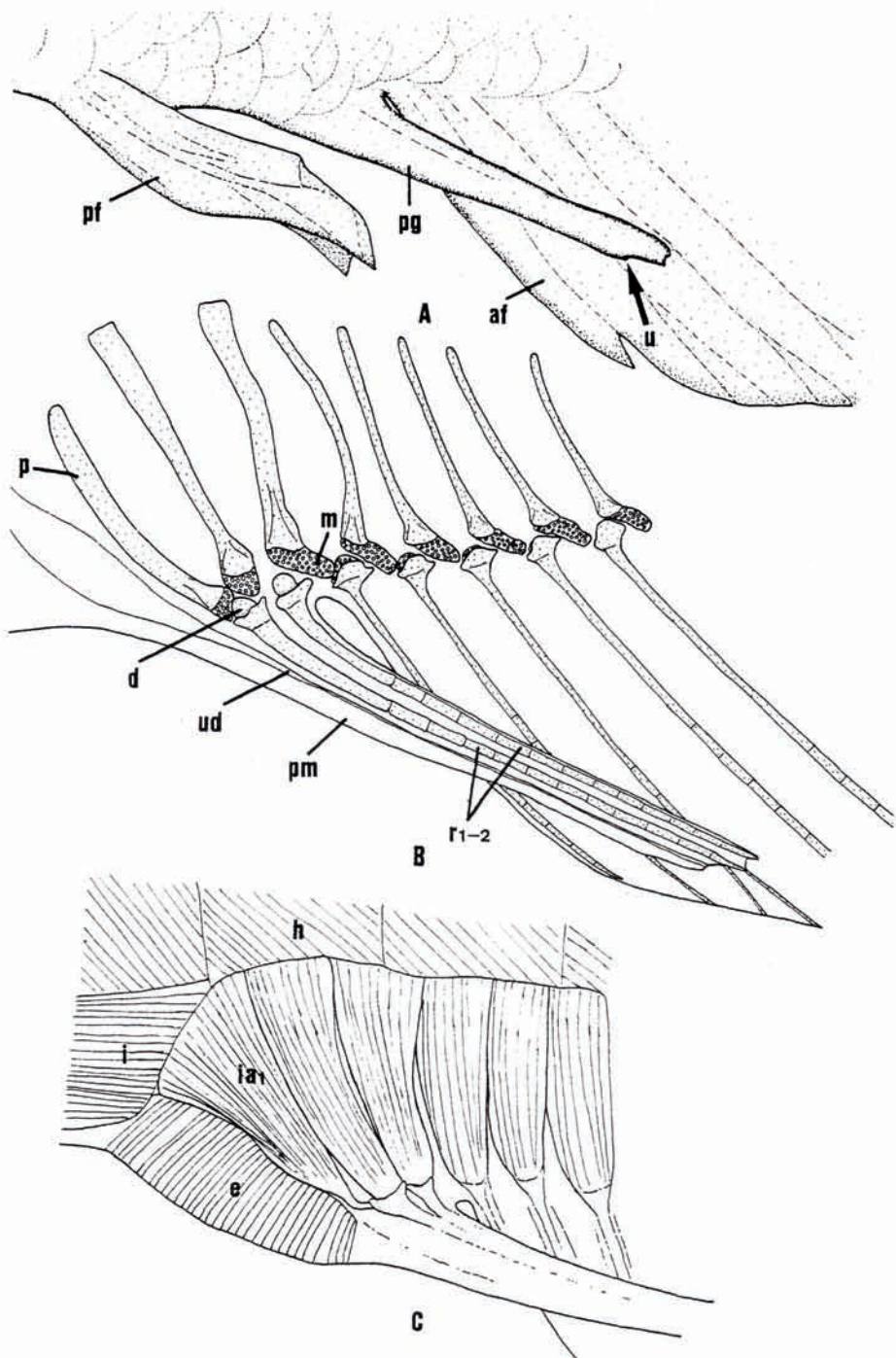
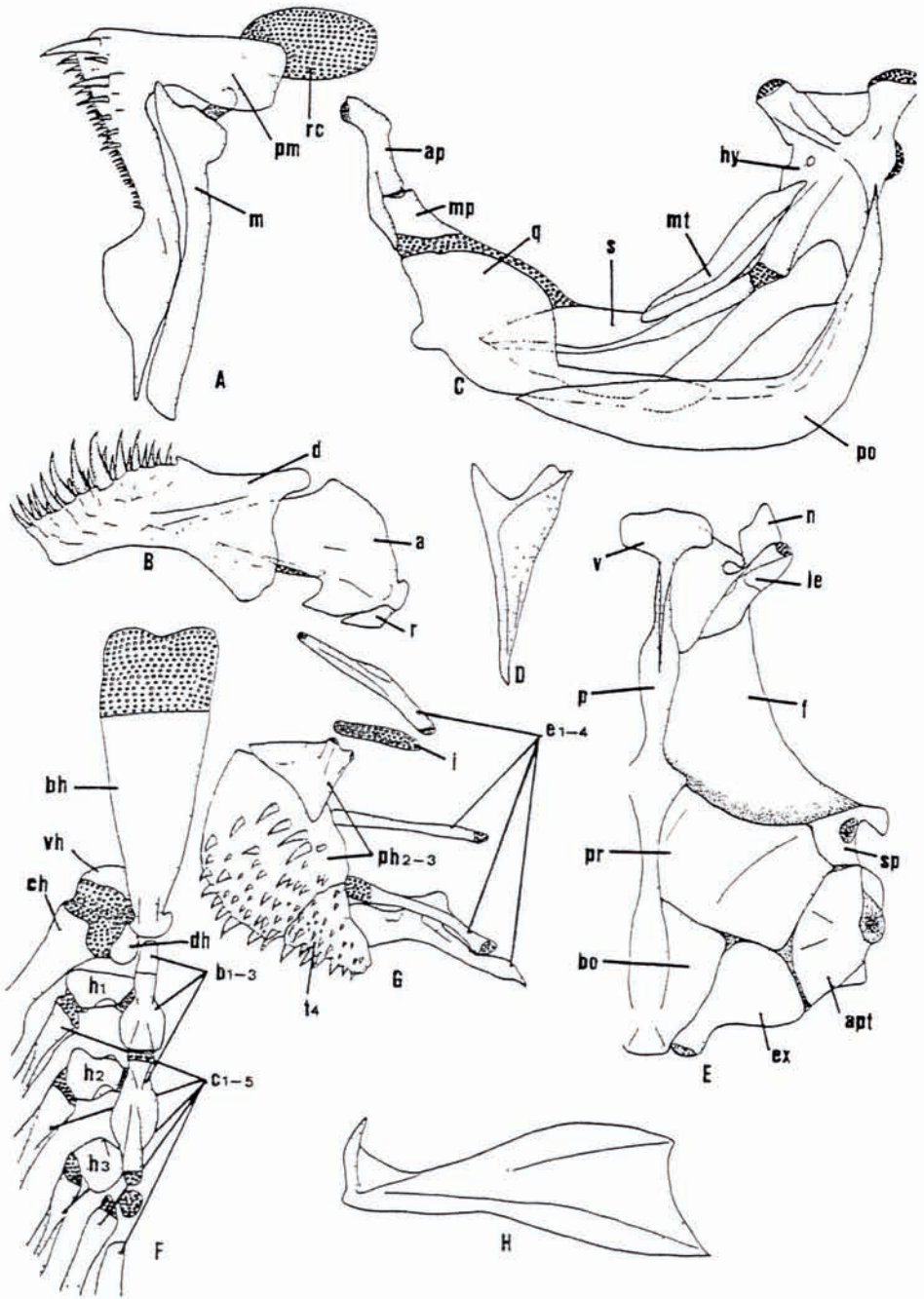


Fig. 1. - Pseudogonopodium and associated structures of *Campellolebias*. **A:** *C. brucei*, 21.4 mm SL, UFRJ 293, external morphology, left lateral view; **B:** *C. dorsimaculatus*, 25.9 mm SL, UFRJ 2192, bony support, left lateral view (dots indicate bone, and circles cartilage); **C:** *C. chrysolineatus*, 38.6 mm SL, UFRJ 284, musculature, left lateral view. Abbreviations: af, anal fin; d, distal radial; e, muscular ejaculatory pump; h, *hypaxialis*; i, *infracarnalis medius*; ial, *inclinator analis* 1; m, medial radial; p, proximal radial; pf, pelvic fin; pg, pseudogonopodium; pm, pseudogonopodial membrane; r1-2, anal fin rays 1-2; u, urogenital opening; ud, urogenital duct.



Circumorbital bones and neurocranium (Fig. 2D-E). - Lacrimal triangular and moderately twisted, its torsion about 160° around its longitudinal axis. Dermosphenotic absent. Posterior process of vomer elongate, its tip slightly surpassing mid-length of anterior portion of parasphenoid. Median part of anterior portion of parasphenoid distinctively widened. Vomerian teeth absent. Two short epioccipital processes, not reaching vertical crossing posterior margin of exoccipital.

Hyoid and gill arches (Fig. 2F-H). - Basihyal almost triangular, its lateral margins forming angle of about 25° ; longitudinal length of cartilaginous portion about 25% of longitudinal length of entire basihyal. Dorsal hypohyal small, its longest extent about half that of ventral hypohyal. Urohyal deep, greatest depth about 35% of length. Interhyals absent. First epibranchial elongate, about as long as 2nd. Interarcual cartilage elongate, about 55% of length of 1st epibranchial. No ventral process on 4th ceratobranchial. Teeth on 4th ceratobranchial absent. Pharyngobranchial teeth absent. Gill rakers on first branchial arch 2+7.

Pectoral girdle (Fig. 3). - Ventral process of posttemporal absent. Supracleithrum elongate, about as long as posttemporal. Pectoral radials 4, small, thin and rounded.

Bony support of pseudogonopodium (Fig. 1B). - Two unbranched rays, wider than rays of the posterior portion of the anal fin. Proximal radials rod-like, first two attached to first ray, first one slightly curved posteriorly. Medial radials cartilaginous, fused to proximal radials. Distal radials of pseudogonopodial rays ossified and elongate.

Vertebrae. - A single hypural plate. Lateral processes parallel to neural spine of first vertebra absent. Neural prezygapophyses of caudal vertebrae absent. Total number of vertebrae 26-27 in *C. brucei* (precaudal 11-12, caudal 15-16), and 28-29 in *C. chrysolineatus* and *C. dorsimaculatus* (precaudal 12-13, caudal 16).

Superficial muscles associated to pseudogonopodium (Fig. 1C). - Upper portion of *inclinatores anales* 1-3 laterally expanded, forming a fan-shaped muscular structure. *Inclinator analis* 2, directly attached to basal part of pseudogonopodial ray 1, *inclinator analis* 1 connected by a tendon to the same ray. Muscular fibres transversely arranged around base of genital papilla.

Fertilization, egg morphology and development

Internal fertilization occurs after a typical courtship behaviour, in which male simultaneously erects tips of dorsal and anal fins in an angle of about 90° with the main axis of body, and folds anterior and posterior edges of those fin (Costa *et al.*, 1989). Hexagonal reticulations over egg membrane, tufts of short, curved hooks emerging from hexagon tips. Egg diameter about 1.3 mm. Development typically annual, occurring diapause stages (G. Campello Brasil, pers. com.).

Fig. 2. - Head bones of *Campellolebias dorsimaculatus*. **A**: dorsal view of left upper jaw; **B**: lateroventral view of left lower jaw; **C**: lateral view of left jaw suspensorium; **D**: anterolateral view of left lacrimal; **E**: ventral view of median and left portion of neurocranium; **F**: dorsal view of median and left portion of ventral hyoid and gill arches (ceratobranchial 5 teeth not represented); **G**: ventral view of left dorsal gill arch; **H**: left lateral view of urohyal. Abbreviations: a, angulo-articular; ap, autopalatine; apt, autopterotic; b1-3, basibranchials 1-3; bh, basihyal; bo, basioccipital; c1-5, ceratobranchials 1-5; ch, ceratohyals; d, dentary; dh, dorsal hypohyal; e1-4, epibranchials 1-4; ex, exoccipital; f, frontal; h1-3, hypobranchials 1-3; hy, hyomandibula; i, interarcual cartilage; le, lateral ethmoid; m, maxilla; mp, mesopterygoid, mt, metapterygoid; n, nasal; p, parasphenoid; ph2-3, pharyngobranchials 2-3; pm, premaxilla; po, preopercle; pr, prootic; q, quadrate; r, retro-articular; rc, rostral cartilage; s, symplectic; sp, sphenotic; t4, tooth plate pharyngobranchial 4; v, vomer; vh, ventral hypohyal. Dots indicate bone, and circles cartilage.

Habitat

Species of the genus *Campellolebias* have been found in shallow (10-60 cm deep) temporary pools, close or within forests, water dark brown coloured and acid (pH 4.5-5.0) (Costa *et al.*, 1989).

Intragenetic relationships

The scarcity of distinctive characters for *Campellolebias* species does not permit the elaboration of a phylogenetic hypothesis for them. *Campellolebias chrysolineatus* and *C. dorsimaculatus* share a higher total number of vertebrae (28-29 vs. 26-27 in *C. brucei*), but this condition seems to be plesiomorphic since it occurs in most outgroups (e.g. 28-31 in *Cynopocilus melanotaenia* Regan). The presence of six longitudinal rows of brilliant spots, uniquely shared by *C. brucei* and *C. chrysolineatus*, does not occur in closely related genera, probably consisting a synapomorphy for both species.

Key to the species of *Campellolebias*

- 1a.** - Ground colour of body sides pale purplish, with golden spots in males; caudal peduncle depth 12.6-13.9% SL in males, 11.3-13.6% SL in females; 28-29 vertebrae. ... **2**
- 1b.** - Ground colour of body red crimson, with metallic green spots in males; caudal peduncle depth 14.4-16.0% SL in males, 14.1-15.4% SL in females; 26-27 vertebrae.
.....*C. brucei*
- 2a.** - Six longitudinal rows of golden spots on body sides of males, six pale gray longitudinal stripes in females; no black blotch on unpaired fin bases; caudal fin of males brownish red with golden dots.....*C. chrysolineatus*
- 2b.** - Nine to ten reddish brown bars alternate with golden small spots on body sides of males, irregular gray blotches or dark gray bars on body sides of females; males with one, and females with one to three black blotches on posterobasal region of dorsal fin; a black blotch on posterobasal portion of anal fin, and another one on basal portion of caudal fin of females; caudal fin of males pale green, with dark reddish brown spots.....
.....*C. dorsimaculatus*

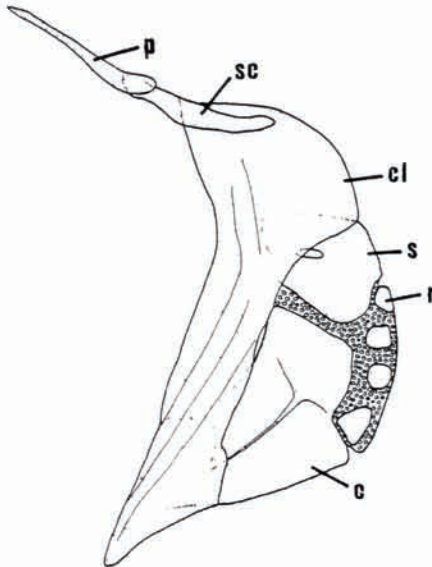


Fig. 3. - Lateral view of left pectoral girdle of *Campellolebias dorsimaculatus* (male, 25.9 mm SL, UFRJ 2192) (postcleithrum 3 not represented). Abbreviations: c, coracoid; cl, cleithrum; p, posttemporal; r, pectoral radials; s, scapula; sc, supracleithrum. Dots indicate bone, and circles cartilage.

CAMPELLOLEBIAS BRUCEI VAZ-FERREIRA & SIERRA

(Fig. 4)

Campellolebias brucei Vaz-Ferreira & Sierra, 1974: 1 (original description, temporary swamp between Criciuma and Tubarão, Estado de Santa Catarina, Brazil). Milgram, 1975:80 (reproductive behaviour). Costa *et al.*, 1989: 71 (colour illustrations).

Cynolebias brucei. Parenti, 1981: 430 (assignment to *Cynolebias*).

Cynolebias (Campellolebias) brucei. Parenti, 1981: 430 (mention of *Campellolebias* as a subgenus of *Cynolebias*).

Material examined

Paratypes. - ZVC, P 2127, male, 28.5 mm SL. - ZVC, P 2126, female, 20.3 mm SL, Brazil: Estado de Santa Catarina, temporary swamp between Criciuma and Tubarão, G.C. Brasil, 28 Nov. 1972.

Other material. - UFRJ 293, 3 males, 21.5-27.6 mm SL, and 3 females, 17.8-20.5 mm SL. - UFRJ 1854, 2 males, 24.8-26.1 mm SL, and 2 females, 19.4-20.0 mm SL (all c&s), Brasil: Estado de Santa Catarina, Tubarão, G.C. Brasil and M.T.C. Lacerda, Aug. 1988.

Diagnosis

Distinguished from all other species of the genus by having 26-27 vertebrae (vs. 28-29), caudal peduncle depth 14.4-16.0% SL in males, 14.1-15.4% SL in females (vs. 12.6-13.9% SL in males, 11.3-13.6% SL in females), and ground colour of body red crimson, with metallic green spots in males (vs. ground colour pale purplish, with golden spots).

Table I. - Morphometric data of *Campellolebias brucei*. Morphometric data 1-7 are expressed as percentage of standard length (SL), and 8-10 as percentage of head length. p: paratype.

	Males					Females				
	ZVC,P	UFRJ	UFRJ	UFRJ	UFRJ	UFRJ	ZVC,P	UFRJ	UFRJ	UFRJ
	2127	293	1854	293	293	293	2126	1854	293	293
	p	-	-	-	-	-	p	-	-	-
SL (mm)	28.5	27.6	24.8	21.5	21.4	20.5	20.3	19.4	19.3	17.8
1. Body depth	29.0	28.6	29.9	28.6	28.9	28.8	26.7	27.6	28.1	27.4
2. Depth of caudal peduncle	15.8	14.4	16.0	15.2	15.0	15.4	14.3	14.7	14.7	14.1
3. Predorsal length	59.2	53.5	56.9	55.9	56.7	58.0	61.7	58.7	57.4	58.5
4. Prepelvic length	57.1	52.8	53.8	56.1	54.2	55.6	57.3	56.8	56.6	57.0
5. Length of dorsal fin base	26.4	29.9	27.8	28.0	28.6	25.9	24.0	26.4	28.6	27.0
6. Length of anal fin base	23.7	22.9	23.4	23.5	25.2	17.1	18.8	18.1	20.4	20.1
7. Head length	31.3	30.3	31.0	32.6	32.1	31.7	27.7	31.6	30.8	31.2
8. Head depth	70.3	68.3	73.9	70.7	68.1	71.6	73.0	72.0	69.3	73.2
9. Head width	65.2	72.8	70.0	69.2	69.3	72.1	75.0	70.7	74.7	74.5
10. Eye diameter	35.2	36.7	37.7	39.3	41.3	38.2	40.1	40.7	40.3	39.6

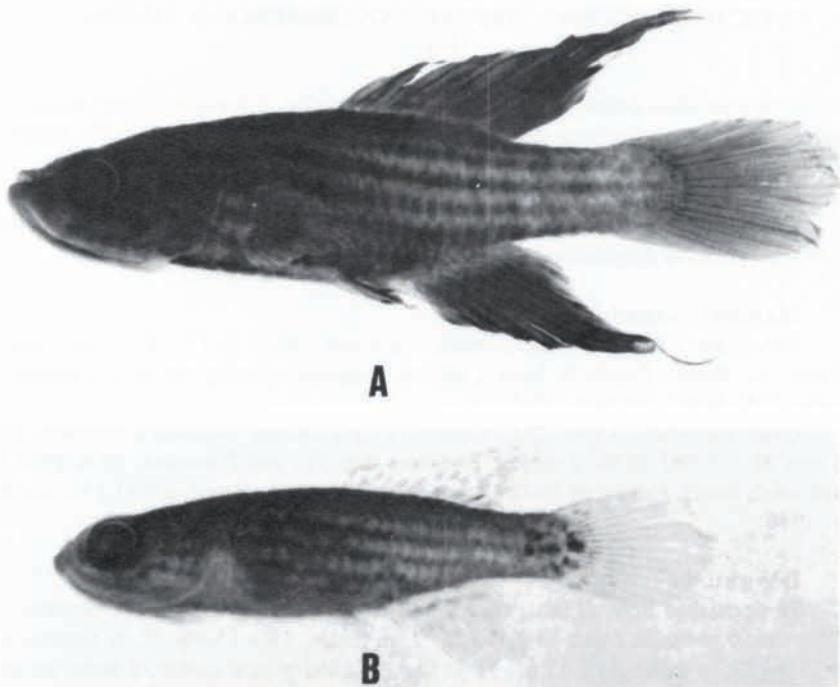


Fig. 4. - *Campellolebias brucei*. A, male, UFRJ 293, 27.6 mm SL; B, female, UFRJ 293, 20.5 mm SL; both from Tubarão, Santa Catarina, Brazil.

Description

Morphometric characters are presented in table I. General morphology, meristic data, latero-sensory system, bones, and musculature of pseudogonopodium as described for the genus.

Colouration in alcohol

Males. - Dark chromatophores concentrated in six stripes along median portion of longitudinal scale rows, stripes wider than their interspaces. Dark chromatophores irregular and densely distributed on sides and top of head. Dark chromatophores concentrated in three stripes on ventral part of head, the median stripe on midventral line extending from lower jaw to anus, wider between isthmus and anus; two ventrolateral stripes through ventral section of preopercular neuromast series, from lower jaw to a point in a vertical through dorsal section of preopercular neuromast series; areas adjacent to stripes scarcely pigmented. Dorsal, caudal and pelvic fins, and anal fin posterior to pseudogonopodium, dense and homogeneously pigmented, caudal fin lighter. Pseudogonopodium scarcely pigmented, a few dark chromatophores on its distal portion. Pectoral fin hyaline, minute chromatophores along fin ray margins.

Females. - Dark chromatophores concentrated in six well defined longitudinal stripes on median portion of longitudinal scale rows, interconnected on anteromedian part of body; small, rounded patches of melanophores on caudal peduncle. Dark chromatophores concentrated on distal border of opercular scales, top of head and jaws. Three

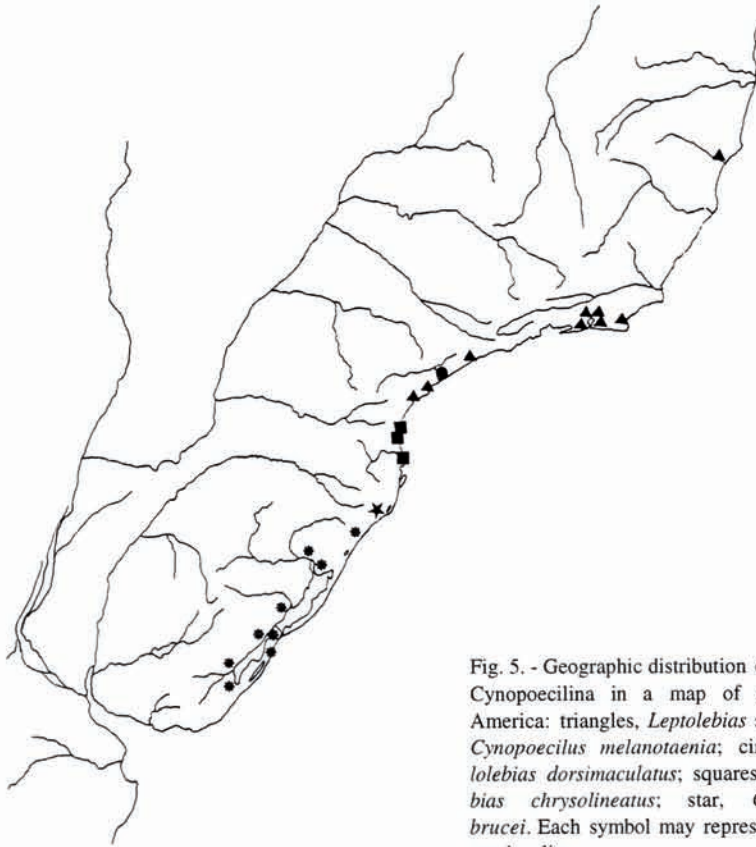


Fig. 5. - Geographic distribution of the subtribe Cynopoecilina in a map of eastern South America: triangles, *Leptolebias* spp.; asterisks, *Cynopoecilus melanotaenia*; circle, *Campellobias dorsimaculatus*; squares, *Campellobias chrysolineatus*; star, *Campellobias brucei*. Each symbol may represent more than one locality.

faint longitudinal stripes on ventral part of head, the median stripe from lower jaw to posterior part of isthmus, two ventrolateral stripes from lower jaw to angle between dorsal and ventral sections of preopercular neuromast series. Small rounded spots spread over unpaired fins, sometimes darker on posterobasal portion of dorsal fin. Pelvic fin dark pigmented. Pectoral fin hyaline.

Colouration in life

Males. - Sides of body red crimson, with six rows of metallic green spots along median part of longitudinal series of scales. Opercular region metallic green, distal border of scales and postorbital region red crimson. Ventral part of head and anteroventral region of body white, with three dark reddish brown longitudinal stripes. Jaws reddish dark brown. Iris green, a dark reddish gray bar crossing eye. Dorsal fin brownish red, a green line on fin borders, and anterior edge dark gray. Caudal fin pale red, green dots scattered over fin, and a green line on upper and lower margins of some specimens. Pseudogonopodium purplish gray. Anal fin brownish red, its basal portion purplish gray, anterior margin black, and a green line contouring all borders. Pelvic fin brownish red, golden line on borders. Pectoral fin hyaline.

Females. - Sides of body pale brown, with six dark gray longitudinal stripes, which are interconnected in anteromedian portion of body; small black spots on caudal peduncle. Opercular region golden. Ventral part of head and anteroventral portion of body white. Jaws dark reddish brown. Iris golden, a dark gray bar crossing eye. Dorsal, caudal and anal fins hyaline, with dark gray spots scattered over fins, and darker on posterobasal portion of dorsal fin of some specimens. Pelvic fin gray. Pectoral fin hyaline.

Distribution

Campellolebias brucei has been found in temporary pools between Tubarão and Criciúma, Estado de Santa Catarina, southern Brazil (Fig. 5).

CAMPELLOLEBIAS CHRYSOLINEATUS COSTA, LACERDA & BRASIL

(Fig. 6)

Campellolebias chrysolineatus Costa, Lacerda & Brasil, 1989: 69 (original description, pool on edge of forest, Araquari, Estado de Santa Catarina, Brazil; colour illustrations).

Material examined

Holotype. - MZUSP 38817, male, 29.5 mm SL, Brazil: Estado de Santa Catarina, pool on edge of forest near Araquari, M.T.C. Lacerda, G.C. Brasil, J.C. Ghisolfi and V. Franciozi, 21 Nov. 1987.

Paratypes. - MZUSP 38818, 1 male, 17.9 mm SL, and 1 female, 24.5 mm SL. - MZUSP, 38819, male, 23.6 mm SL; MNRJ 11494, 2 males, 22.2 and 32.1 mm SL; ZVC.P uncat., 2 males, 15.7 and 16.6 mm SL, all collected with the holotype. - MZUSP 38344, 3 males, 20.3-34.7 mm SL, and 8 females, 22.0-32.3 mm SL. - MZUSP 38428, 1 male, about 25.0 mm SL, and 1 female, about 25.0 mm SL (all c&s), same locality as holotype; C. Tatsuta, V. Teixeira, C. Gastaldi and V. Franciozi, Apr. 1986.

Other material. - UFRJ 284, 1 male, 38.6 mm SL, and 1 female, 27.2 mm SL, Brazil: Estado de Santa Catarina, Itapema; G.C. Brasil, 19 Aug. 1988.

Diagnosis

Distinguished from all its congeners by having 28-29 vertebrae (vs. 26-27 in *C. brucei*), caudal peduncle depth 12.6-13.9% SL in males, 12.0-13.6% SL in females (vs. 14.4-16.0% SL in males, 14.1-15.4% SL in females of *C. brucei*), ground colour of body pale purplish, with six longitudinal rows of golden spots in males (vs. ground colour red crimson, with metallic green spots in males of *C. brucei*, and ground colour purplish brown with nine to ten reddish brown bars alternate with golden small spots in males of *C. dorsimaculatus*), and six pale gray longitudinal stripes on body sides of females (vs. irregular gray blotches or dark gray bars in females of *C. dorsimaculatus*).

Description

Morphometric characters are presented in table II. General morphology, meristic data, latero-sensory system, bones, and musculature of pseudogonopodium as described for the genus.

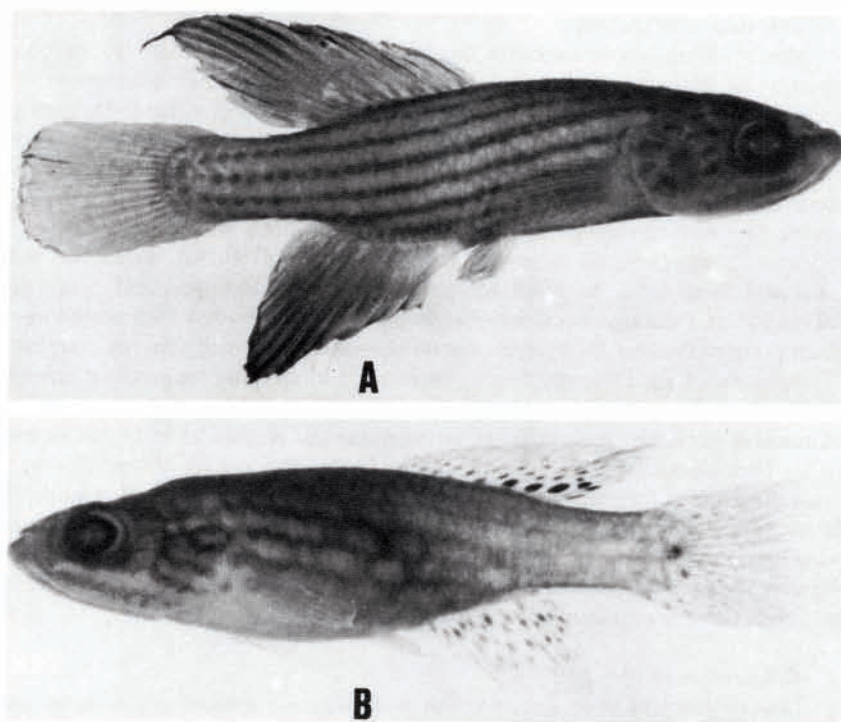


Fig. 6. - *Campellolebias chrysolineatus*. A: holotype, male, MZUSP 38817, 29.5 mm SL, Araquari, Santa Catarina, Brazil; B: female, UFRJ 284, 27.2 mm SL, Itapema, Santa Catarina, Brazil.

Table II. - Morphometric data of *Campellolebias chrysolineatus*. Morphometric data 1-7 are expressed as percentage of standard length (SL), 8-10 as percentage of head length. h: holotype; p: paratype.

	Males				Females			
	MNRJ	MZUSP	UFRJ	MZUSP	MZUSP	UFRJ	MZUSP	MZUSP
	11494	38817	11494	38818	38344	284	38344	38344
	p	h	p	p	p	-	p	p
SL (mm)	32.1	29.5	22.2	28.0	32.3	27.2	23.4	22.6
1. Body depth	27.0	24.6	23.3	24.6	26.3	24.8	24.2	24.6
2. Depth of caudal peduncle	13.7	13.6	12.6	13.9	13.3	12.0	13.6	12.2
3. Predorsal length	56.2	56.2	55.6	58.3	59.2	57.6	55.8	57.2
4. Prepelvic length	54.4	55.5	51.1	51.1	57.8	56.6	57.1	58.8
5. Length of dorsal fin base	29.0	28.2	28.5	24.8	24.5	25.0	25.8	26.6
6. Length of anal fin base	26.1	26.3	25.1	23.4	18.0	18.5	21.2	19.9
7. Head length	30.1	29.9	30.4	31.2	28.3	29.2	29.8	29.7
8. Head depth	66.8	70.9	65.0	71.1	72.4	71.0	64.8	71.8
9. Head width	68.4	66.6	67.7	67.9	73.1	75.8	73.6	76.0
10. Eye diameter	35.9	33.4	35.9	38.1	31.9	38.1	36.2	37.9

Colouration in alcohol

Males. - Dark chromatophores concentrated in six longitudinal stripes on median portion of longitudinal scale rows, stripes narrower than their interspaces. Dark chromatophores irregular and densely distributed on sides and top of head. Dark chromatophores concentrated in three stripes on ventral part of head, the median stripe on mid-ventral line, extending from lower jaw to anus, wider between isthmus and anus; two ventrolateral stripes through ventral section of preopercular neuromast series, from lower jaw to a point in a vertical through dorsal section of preopercular neuromast series, or just posterior to it; areas adjacent to stripes scarcely pigmented. Dorsal, caudal and pelvic fins, and anal fin posterior to pseudogonopodium dense and homogeneously pigmented, caudal fin lighter. Pseudogonopodium scarcely pigmented, a few dark chromatophores on its distal portion. Pectoral fin hyaline, minute chromatophores along fin ray margins.

Females. - Dark chromatophores concentrated in six faint longitudinal stripes on median portion of longitudinal scale rows, interconnected on anteromedian part of body; small, rounded patches of melanophores on anteromedian portion of body and on caudal peduncle. Dark chromatophores concentrated on border of opercular scales, top of head and jaws. Three faint longitudinal stripes on ventral part of head, the median stripe from lower jaw to posterior part of isthmus, two ventrolateral stripes from lower jaw to angle between dorsal and ventral sections of preopercular neuromast series. Small rounded spots spread over unpaired fins, and darker on posterobasal portion of dorsal fin of some specimens. Pelvic fin dark pigmented. Pectoral fin hyaline.

Colouration in life

Males. - Sides of body light purplish pink, with six rows of golden spots along median part of longitudinal series of scales. Opercular region golden, border of scales and postorbital region pale red. Ventral part of head and anteroventral region of body white, with three dark brown longitudinal stripes. Jaws dark brown. Iris greenish golden, a dark purplish gray bar crossing eye. Dorsal fin brownish red, a golden line on fin borders, distal portion of rays golden in some individuals, and anterior edge dark gray. Caudal fin brownish red, golden dots scattered over fin, and with a golden line on upper and lower margins of some specimens. Pseudogonopodium purplish gray. Anal fin brownish red, basal portion purplish gray, anterior margin black, and a golden line contouring all borders. Pelvic fin brownish red, golden line on borders. Pectoral fin hyaline.

Females. - Sides of body pale brown, with six pale gray longitudinal stripes, which are darker and interconnected in anteromedian portion of body; small black spots on anteromedian portion of body and on caudal peduncle. Opercular region golden. Ventral part of head and anteroventral portion of body white. Jaws dark brown. Iris golden, a dark gray bar crossing eye. Dorsal, caudal and anal fins hyaline, with dark gray spots scattered over fins, sometimes darker on posterobasal portion of dorsal fin. Pelvic fin gray. Pectoral fin hyaline.

Distribution

Temporary pools between São Francisco do Sul and Itapema, Estado de Santa Catarina, southern Brazil (Fig. 5).

CAMPELLOLEBIAS DORSIMACULATUS COSTA, LACERDA & BRASIL

(Fig. 7)

Campellolebias dorsimaculatus Costa, Lacerda & Brasil, 1989: 66 (original description, pool on edge of forest, Iguape, Estado de São Paulo, Brazil; colour illustrations).

Material examined

Holotype. - MZUSP 38813, male, 28.3 mm SL, Brazil: Estado de São Paulo, pool on border of forest near Iguape; G.C. Brasil and D. Nielsen, 31 Mar. 1988.

Paratypes. - MZUSP 38814, 1 female, 26.5 mm SL. - MZUSP 38815, 3 males, 17.5-19.1 mm SL, and 3 females, 13.9-14.1 mm SL. - UFRJ 2192, 1 male, 25.9 mm SL, and 1 female, 19.5 mm SL (all c&s), collected with the holotype. - MZUSP 38816, 2 males, 14.1 and 17.1 mm SL, and 7 females, 15.3-18.6 mm SL. - MNRJ 11493, 1 male, 18.8 mm SL, and 1 female, 17.0 mm SL. - ZVC,P uncat., 1 male, 18.8 mm SL, and 1 female, 14.4 mm SL; same locality and collectors as holotype, 19 Jul. 1988.

Diagnosis

Distinguished from all other members of the genus by having 9 to 10 reddish brown bars alternate with golden small spots on body sides of males, and irregular gray blotches or dark gray bars on body sides of females (vs. 6 longitudinal rows of brilliant spots on body sides of males, and 6 gray longitudinal stripes on body sides of females), males with one, females with one to 3 black blotches on posterobasal region of dorsal fin, and a black blotch on posterobasal portion of anal fin and another one on basal portion of caudal fin of females (vs. no black blotch on unpaired fin bases), and caudal fin of males pale green, with dark reddish brown spots (vs. brownish red with golden dots).

Table III. - Morphometric data of *Campellolebias dorsimaculatus*. Morphometric data 1-7 are expressed as percentage of standard length (SL), and 8-10 as percentage of head length. h: holotype; p: paratype.

	Males				Females			
	MZUSP	UFRJ	MNRJ	MZUSP	MZUSP	UFRJ	MZUSP	MNRJ
	38813	2192	11493	38816	38814	2192	38816	11493
	h	p	p	p	p	p	p	p
SL (mm)	28.3	25.9	18.8	17.0	26.5	19.5	18.7	17.0
1. Body depth	28.1	29.0	24.3	24.8	24.2	22.6	24.0	24.8
2. Depth of caudal peduncle	13.7	12.8	13.4	13.2	11.3	12.3	12.1	13.2
3. Predorsal length	54.0	49.3	53.9	52.9	54.5	57.4	57.7	52.9
4. Prepelvic length	54.0	53.0	51.7	53.5	55.3	58.2	59.6	53.5
5. Length of dorsal fin base	28.1	30.0	27.8	31.3	27.9	27.4	27.2	31.3
6. Length of anal fin base	23.7	24.6	25.1	26.4	19.4	20.0	17.9	26.4
7. Head length	28.3	28.6	30.6	30.7	24.9	29.7	29.5	30.7
8. Head depth	68.0	69.6	67.9	98.5	73.5	67.3	71.7	68.5
9. Head width	69.3	68.9	70.1	69.4	79.6	73.4	69.9	69.4
10. Eye diameter	33.1	32.4	37.2	42.3	36.4	36.2	39.0	42.3

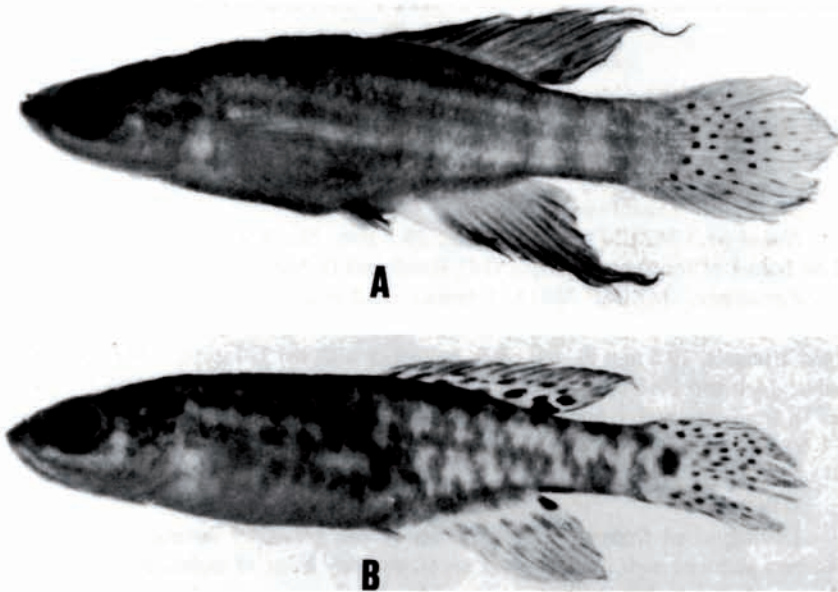


Fig. 7. - *Campellolebias dorsimaculatus*. A: holotype, male, MZUSP 38813, 28.3 mm SL; B: paratype, female, 38814 mm SL; both from near Iguape, São Paulo, Brazil.

Description

Morphometric characters are presented in table III. General morphology, meristic data, latero-sensory system, bones, and musculature of pseudogonopodium as described for the genus.

Colouration in alcohol

Males. - Dark chromatophores scattered over body sides, more concentrated in six longitudinal stripes on median portion of longitudinal scale rows, and still slightly more concentrated on nine or ten transverse bars, darker on caudal peduncle. Dark chromatophores irregular and densely distributed on sides and top of head. Dark chromatophores concentrated in three stripes on ventral part of head, median stripe on midventral line, extending from lower jaw to anus, wider between isthmus and anus; two ventrolateral stripes through ventral section of preopercular neuromast series, from lower jaw to a point in a vertical through dorsal section of preopercular neuromast series; areas adjacent to stripes scarcely pigmented. Dorsal and pelvic fins, and anal fin, posterior to pseudogonopodium, densely pigmented; melanophores concentrated on posterobasal portion of dorsal fin. Caudal fin lighter, with rounded patches of melanophores regularly arranged. Pseudogonopodium scarcely pigmented, a few dark chromatophores on anterior and posterior margins. Pectoral fin hyaline, minute chromatophores along fin ray margins.

Females. - Dark chromatophores irregularly distributed on body sides, forming irregular blotches or, in some specimens, bars on posterior half of body. Dark chromatophores concentrated on border of opercular scales, top of head and jaws. Three faint longitudinal stripes on ventral part of head, the median stripe from lower jaw to posterior part of isthmus, two ventrolateral stripes from lower jaw to angle between dorsal and ventral

sections of preopercular neuromast series. A dark rounded blotch on the center of caudal fin base, one to three black blotches on posterobasal portion of dorsal fin, and one black blotch on posterobasal portion of anal fin. Smaller and lighter rounded spots spread over unpaired fins, except on distal portion of dorsal and anal fins, densely pigmented with small dark chromatophores. Pelvic fin dark pigmented. Pectoral fin hyaline.

Colouration in life

Males. - Sides of body purplish brown, with nine to ten reddish brown bars alternate with golden dots. Opercular region golden, border of scales and postorbital region reddish brown. Ventral part of head and anteroventral region of body white, with three dark brown longitudinal stripes. Jaws dark brown. Iris golden, a dark gray bar crossing eye. Dorsal fin reddish brown, a golden line on fin edges, dark brown spots on basal portion and a black blotch on posterobasal region. Caudal fin pale green, basal portion golden, dark reddish brown spots scattered over fin, a golden line on upper and lower margins. Pseudogonopodium purplish gray. Anal fin reddish brown, basal portion purplish gray, anterior margin black, and a golden line contouring all borders. Pelvic fin reddish brown, golden line on borders. Pectoral fin hyaline.

Females. - Sides of body pale brown, with irregular dark gray blotches, sometimes dark gray bars on posterior half of body. Opercular region golden. Ventral part of head and anteroventral portion of body white. Jaws dark brown. Iris golden, a dark gray bar crossing eye. Dorsal and anal fins hyaline, with dark gray blotches scattered over fins, and black blotches on posterobasal portions, one to three on dorsal and one on anal fin. Caudal fin hyaline, a black blotch on basal portion, small dark gray spots over all the fin. Pelvic fin gray. Pectoral fin hyaline.

Distribution

Known only from its type locality, a temporary pool near Iguape, Estado de São Paulo, Brazil (Fig. 5).

DISCUSSION

Phylogeny of the *Cynopoecilina*

Relationships of *Campellolebias* were first discussed by Costa (1990a), who found some apomorphic features corroborating a monophyly hypothesis of a group comprising *Campellolebias*, *Cynopoecilus*, and *Leptolebias*: 1) E-scales separated by an interspace; 2) hexagonal reticulation over egg chorion; and, 3) mushroom-like protusions over egg chorion. These three characters are supported in the present study. For a discussion of character polarization, see Costa (1990a). An additional apomorphic feature shared by the three genera above was observed in the present study: 4) Five to seven neuromasts on caudal fin base. These neuromasts are present on median portion of caudal fin base just posterior to caudal fin squamation, individually occurring between rays. Other closely related genera present only one or two neuromasts on caudal fin base.

Costa (1990a) erected a hypothesis of sister-group relationship between *Campellolebias* and *Cynopoecilus*, based on three synapomorphies: 1) pelvic fin bases separated by an interspace; 2) dorsal fin origin in front of anal fin origin; and, 3) proximal radials of anal fin rod-like (see Costa [1990a] for discussion of character polarization). This phylogenetic proposal was reinforced by Costa (in press a), adding another synapomorphy:

4) internal fertilization. An additional character supporting this hypothesis was observed in the present study: 5) muscular fibres transversely arranged in front of anal fin support (Fig. 1C). This muscular structure, absent in other rivulids, is probably related to internal fertilization, occurring both in *Campellolebias* and *Cynopoecilus*. The location of this structure, at the base of urogenital papilla, and the transverse arrangement of fibres around urogenital duct, suggests that it serves as a pumping mechanism during the process of sperm transfer towards the female. This would become possible the emission of a greater amount of sperm in a short time period.

Biogeography of the *Cynopoecilina*

The *Cynopoecilina* occur in coastal plains of eastern South America, from southern Bahia State, Brazil (about 17°S) to southeastern Uruguay (about 34°S) (Fig. 5). Although some recent studies have focused on revisions of taxa endemic to the eastern coastal plains (e.g., Vari, 1992; Rosa and Costa, 1993) or ichthyofauna of included regions (e.g., Costa, 1987; Sabino and Castro, 1990; Malabarba, 1989), little is known about monophyly of groups widespread along the entire area or relationships of their included members. An exception is the genus *Mimagoniates* Regan, for which a hypothesis of phylogenetic relationships (Menezes and Weitzman, 1990) is available. However, the high overlap between distribution patterns of the clades make the group inadequate for biogeographical comparisons. This geographical area, in which are inserted large urban centers like Rio de Janeiro and São Paulo, has been sampled by ichthyologists for the last two centuries. However, still today, field work reveals new fish taxa belonging to groups previously known only from septentrional parts of South America (Costa and Campos-da-Paz, 1992; Costa and Bockmann, 1994). Therefore, due to the scarcity of phylogenetic studies of freshwater fishes from eastern South America, the present biogeographic analysis is based on coincident distribution patterns of putatively monophyletic, endemic genera and species.

The designation of the distribution area of the *Cynopoecilina* as an endemism area is supported by the nearly coincident distribution patterns of some freshwater fish species (each one probably constituting a species complex), including *Hypheobrycon bifasciatus* Ellis (Characidae), *Phalloceros caudimaculatus* (Hensel) (Poeciliidae), and *Geophagus brasiliensis* (Quoy & Gaimard) and *Cichlasoma facetum* (Jenyns) (Cichlidae). The genus *Mimagoniates* also has a similar distribution pattern, but extending to the upper section of rio Paraguay basin (Weitzman *et al.*, 1988). All taxa above present about the same northern distribution limit as *Cynopoecilina* but, in the South, they further occur in at least the lower part of rio Paraná basin. This suggests, by parsimony, that the *Cynopoecilina* inhabit a well defined endemism area (area A + B + C in figure 8), but with a restricted distribution pattern in the South.

An assemblage of three species of the genus *Cyphocharax* Fowler (Curimatidae), *C. voga* (Hensel), *C. santacatarinae* (Fernández-Yépez), and *C. gilbert* (Quoy & Gaimard), has a distribution pattern similar to that of the *Cynopoecilina* (Vari, 1992). However, despite the high phenetical similitude (Vari, 1992) among those *Cyphocharax* species, Vari (1992) did not find any evidence of monophyly for a group including only them. Nevertheless, the distribution patterns of each *Cyphocharax* species, *C. gilbert*, *C. santacatarinae*, and *C. voga*, is similar to those of each *Cynopoecilina* genera, *Leptolebias*, *Campellolebias*, and *Cynopoecilus*, respectively. Additional taxa corroborate the hypothesis that each of the three cited areas (areas A, B, and C in figure 8) constitute endemism areas: the species (probably species complex) *Acentronichthys leptos* Eigenmann

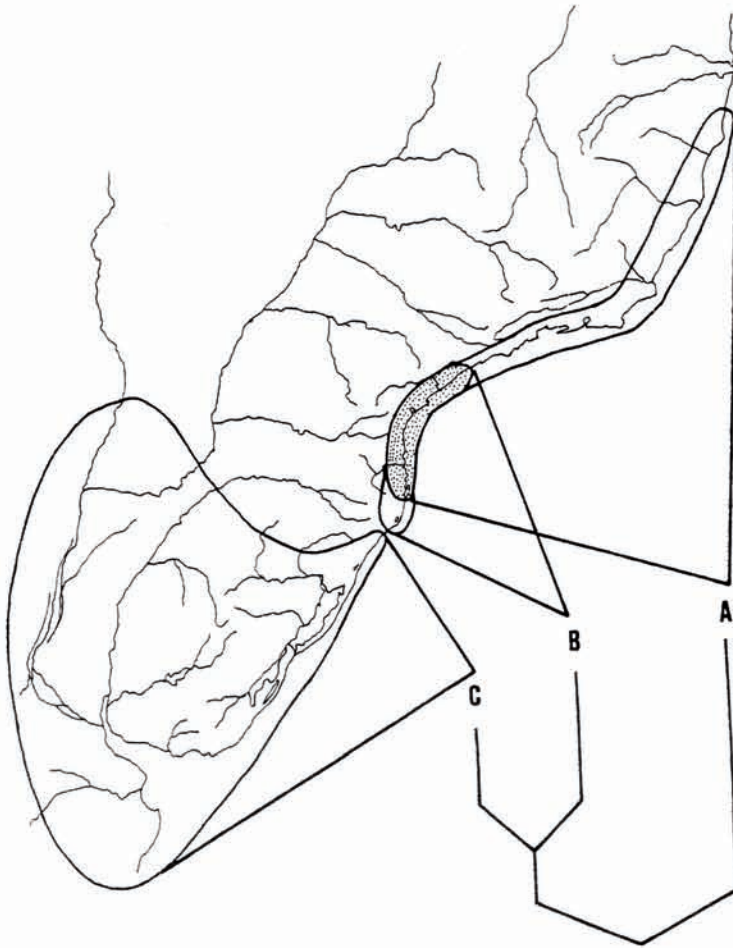


Fig. 8. - Tracks (A,B,C) of *Cynopoecilina* genera and other monophyletic freshwater fish groups.

& Eigenmann (Pimelodidae), *Gymnotus pantherinus* Steindachner (Gymnotidae), and *Hyphessobrycon reticulatus* Ellis and *Hollandichthys multifasciatus* (Eigenmann & Norris) (Characidae), and members of a clade comprising *Rivulus santensis* Kohler and closely related species according to Costa (1991) (Rivulidae) present distribution patterns similar to that of *Leptolebias* (area A in figure 8); *Pseudocorynopoma heterandria* Eigenmann (Characidae) has a distribution pattern similar to that of *Campellolebias* (area B in figure 8); and, *Pseudocorynopoma doriae* Perugia (Characidae), *Cynolebias adolffi* Ahl and closely related species according to Costa (in press b) (Rivulidae), and all included species of the genera *Scleronema* Eigenmann (Trichomycteridae) (de Pinna, pers. com.) and *Gymnogeophagus* Ribeiro (Cichlidae) (Reis and Malabarba, 1988), present distribution patterns similar to that of *Cynopoecilus* (area C in figure 8). Most taxa sharing a similar distribution pattern with *Cynopoecilus* also occur in the lower Paraná basin, again indicating that *Cynopoecilus* has a restricted pattern derived from a general corroborated distribution pattern (area C in figure 8). Similarly, all taxa sharing a congruent pattern with *Leptolebias* occur furthermore to South (about 27.5°S), parsimoniously suggesting that

Leptolebias has a restricted pattern from a larger endemism area (area A in figure 8). A wide superposition area occurs between areas A and B (Fig. 8), indicating the existence of a composite endemism area, derived from the fusion of segments of areas A and B. The hypothesis of the distribution area of the clade *Campellolebias* + *Cynopoecilus* as an endemism area is supported by the distribution pattern of the genus *Pseudocorynopoma* Perugia (Characidae) (Weitzman *et al.*, 1988).

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