

# Comparative morphology and classification of South American cynopoeciline killifishes (Cyprinodontiformes: Aplocheilidae), with notes on family-group names used for aplocheiloids

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Accepted 15.vii.2016.

Published online at [www.senckenberg.de/vertebrate-zoology](http://www.senckenberg.de/vertebrate-zoology) on 28.ix.2016.

## Abstract

A comparative morphological study involving all cynopoeciline killifishes indicates that *Leptolebias marmoratus* is more closely related to species of the genera *Campellolebias* and *Cynopoecilus* than to other species of *Leptolebias*, and that *Mucurilebias leitaoi* is the sister group of a clade comprising all other cynopoecilines. *Leptopanchax*, new genus, is described to place species that share urogenital papilla in males separated from the anal-fin origin by broad interspace, basal portion of the urogenital papilla in males not forming a pronounced wide structure, absence of thickened tissue on the basal portion of the anal fin in males, caudal fin oval and symmetrical in males, anterior proximal radials of the anal fin not placed in close proximity in males, presence of a broad iridescent golden stripe on the distal zone of the dorsal fin in males, and caudal fin with vermiculate dark red marks in males. *Poecilopanchax*, new subgenus of *Cynopoecilus*, is diagnosed by having the basihyal narrow, about rectangular, the interarcual element of the dorsal branchial arch ossified, the uncinat process of the third epibranchial distinctively widened, a long filamentous ray on the tip of the anal fin in males, caudal fin lanceolate in males, dark bars on the flank in females, branchiostegal region with intense red pigmentation in males, a brownish red stripe on the basal portion of the dorsal fin in males, and dark red marks extending to the antero-distal margin of the dorsal fin in males. This study follows an old classificatory scheme in which all aplocheiloids are placed in a single family, the Aplocheilidae.

## Key words

Atlantic Forest, Biodiversity, New genus, Systematics, Taxonomy.

## Introduction

The tribe Cynopoecilini comprises seasonal killifishes that inhabit temporary pools in tropical and subtropical areas of eastern and southern Brazil, mostly concentrated in the Atlantic Forest biodiversity hotspot, with one species reaching the adjacent plains of eastern Uruguay (COSTA, 2002a, 2008, 2009). Some cynopoecilines are unique among aplocheiloid killifishes by having specialised morphological structures for internal fertilization (COSTA, 1995, 1998a; COSTA *et al.*, 2016a) and most species are threatened with extinction (*e.g.*, COSTA, 2012).

The Cynopoecilini presently includes 21 valid species in five genera: *Campellolebias* VAZ-FERREIRA & SIERRA, 1974, *Cynopoecilus* REGAN, 1912, *Leptolebias* MYERS, 1952, *Mucurilebias* COSTA, 2014, and *Notholebias* COSTA, 2008 (COSTA, 2008, 2014; COSTA *et al.*, 2016b).

The taxonomic history of cynopoecilines begun with the description of *Cynolebias melanotaenia* REGAN, 1912 (REGAN, 1912a) from southern Brazil, which was immediately placed in a new genus, *Cynopoecilus*, by REGAN (1912b) after reading BERG'S (1897) paper reporting

sexual dimorphism in *Cynolebias* STEINDACHNER, 1876. *Cynopoecilus* was then distinguished from the closely related genus *Cynolebias* by, in the latter genus, males having more rays in the dorsal and anal fins than females and a very distinctive colour pattern. In the following three decades, other cynopoecilines then described from south-eastern Brazil were placed in *Cynopoecilus* (LADIGES, 1934a, b; FARIA & MULLER, 1937; RIBEIRO, 1939).

The first of a series of classification changes was made by MYERS (1942), who transferred all cynopoecilines to *Cynolebias*. Subsequently, MYERS (1952) kept *C. melanotaenia* in *Cynopoecilus* as a monotypic subgenus of *Cynolebias*, and described another subgenus, *Leptolebias*, for the remaining cynopoecilines. However, *Cynolebias* sense MYERS (1942, 1952) was not diagnostically, making difficult to recognise generic limits among South American killifishes, as discussed by WEITZMAN & WOURMS (1967).

VAZ-FERREIRA & SIERRA (1974) described *Campellolebias brucei* VAZ-FERREIRA & SIERRA, 1974 as a new genus and species from southern Brazil, but PARENTI (1981) placed *Campellolebias* and kept *Cynopoecilus* in the synonymy of *Cynolebias*. However, *Cynolebias* sense PARENTI (1981) was polyphyletic, including in its synonymy the genus *Terranatos* TAPHORN & THOMERSON, 1978, later placed in a distinct subfamily (e.g., COSTA, 1998; MURPHY *et al.*, 1999). COSTA (1990a, b) first recognised monophyly of the group comprising *Campellolebias*, *Cynopoecilus*, and *Leptolebias*, which were then considered as valid genera. Eighteen years later, COSTA (2008) found evidence indicating that *Leptolebias* sense COSTA (1990b) was paraphyletic. Consequently, part of the species previously placed in *Leptolebias* were transferred to the genus *Notholebias*. Similarly, another phylogenetic analysis based on 73 morphological characters taken from previous studies but including a rare and possibly extinct species from north-eastern Brazil as terminal taxon, *L. leitaoi* (CRUZ & PEIXOTO, 1991), indicated that this species is the sister group of a more inclusive cynopoecilinae clade, making necessary to place it in a new genus, *Mucurilebias* (COSTA, 2014). However, a recent larger set of morphological data, with a total of 115 characters, indicates that *Leptolebias marmoratus* (LADIGES, 1934), the type species of the genus, is more closely related to species of the genera *Campellolebias* and *Cynopoecilus* than to other species of *Leptolebias*, and that *Mucurilebias leitaoi* is the sister group of a clade comprising all other cynopoecilines (COSTA, 2016). This set of unpublished morphological characters highly supports the new classification here provided for the Cynopoecilini.

## Material and methods

List of examined material is given in Appendix 1. Comparative morphological characters included morphology of bones, urogenital papilla, fins, jaws, frontal squama-

tion, latero-sensory system, contact organs, muscles of the anal-fin support, egg and colour patterns. Osteological characters were examined in specimens cleared and stained according to TAYLOR & VAN DYKE (1985). Terminology for osteological structures followed COSTA (2006a), for muscles, WINTERBOTTOM (1974), for frontal squamation, HOEDEMAN (1958), for cephalic neuromast series, COSTA (2001), and for egg chorion morphology, COSTA & LEAL (2009). Data on colour patterns were obtained from direct examination of live individuals during collections, and photographs of both sides of live individuals, at least two males and one female per collection, taken in aquarium between five and 24 hours after collection. The list of morphological characters appears in Appendix 2, which follows SERENO (2007) for character statement formulation. Distribution of character states among terminal taxa appear in Appendix 3. Diagnoses primarily include lists of apomorphic characters states; in diagnoses and discussion, the abbreviation ch. followed by numbers means character states that are numbered according to Appendix 2.

## Tribe Cynopoecilini COSTA, 1990

**Diagnosis.** Vomerine teeth absent [ch. 3.1], ventral process of angulo-articular rudimentary, poorly or not visible in lateral view [ch. 9.2] (reversed to short process, well-visible in lateral view in *Campellolebias* and *Cynopoecilus*), distinctive postero-ventral process on autopalatine [ch. 13.1], posterior process of quadrate wide [ch. 15.1], symplectic long and narrow [ch. 17.1], E-scales not overlapped [ch. 76.1], supraorbital squamation rudimentary or absent [ch. 77.1].

**Included genera.** *Campellolebias* VAZ-FERREIRA & SIERRA, 1974, *Cynopoecilus* REGAN, 1912, *Leptolebias* MYERS, 1952, *Leptopanchax*, new genus, *Mucurilebias* COSTA, 2014, and *Notholebias* COSTA, 2008

## Key to identification of genera and subgenera of the Cynopoecilini

- 1a. Eye large, occupying most portion of head side, dorsal and ventral margins of orbit close to dorsal and ventral surfaces of head in lateral view; caudal fin in larger males sub-lanceolate, terminating in short filamentous ray on its posterior tip; caudal fin in males dark red with light blue spots; distal margin of dorsal fin in males with narrow bluish or yellowish white stripe; distal margin of anal fin in males with distinctive narrow red stripe; basal portion of unpaired fins without red spots and red bars ..... Genus *Mucurilebias*
- 1b. Eye moderate, dorsal and ventral margins of orbit separated by dorsal and ventral head surfaces by

- broad space in lateral view; caudal fin not terminating in short filamentous ray on its posterior tip; caudal fin never dark red with light blue spots; distal margin of dorsal fin without narrow bluish or yellowish white stripe; distal margin of anal fin without distinctive red stripe; basal portion of unpaired fins in males with red spots and red bars ..... 2
- 2a. Jaws with hypertrophied teeth on middle portion in males; caudal fin with dark reddish brown bars in males; pectoral fin in males with hypertrophied contact organs on its inner surface ..... Genus *Notholebias*
- 2b. Jaws without hypertrophied teeth; caudal fin without dark reddish brown bars; pectoral fin without hypertrophied contact organs ..... 3
- 3a. Caudal fin oval in males, slightly longer than deep; dorsal fin in males with broad iridescent golden stripe on distal zone; caudal fin in males with vermiculate dark red marks; urogenital papilla in males not in close proximity to anal-fin origin; basal portion of urogenital papilla not forming pronounced wide structure in males ..... *Leptopanchax*, new genus
- 3b. Caudal fin never oval in males; dorsal fin without broad iridescent golden stripe on distal zone; caudal fin without vermiculate dark red marks; urogenital papilla in males in close proximity to anal-fin origin; basal portion of urogenital papilla forming pronounced wide structure in males ..... 4
- 4a. Caudal fin asymmetrical in males, dorsal margin slightly rounded and ventral margin straight; flank in males with canary yellow stripes; iris blue in males; caudal fin in males with broad white stripe ventrally bordered by narrow black stripe on its ventral margin ..... Genus *Leptolebias*
- 4b. Caudal fin symmetrical; flank without canary yellow stripes; iris yellow or green; caudal fin without white stripe ..... 5
- 5a. Anterior portion of anal fin in males with inseminating tube formed by first two rays; genital opening in males near tip of first anal-fin ray; anal fin about triangular in males, anterior and distal margins nearly continuous; caudal fin sub-truncate in males; venter in males with longitudinal dark brown stripe on its middle zone; lateral midline of body without broad dark stripe; whole flank in males with iridescent colour marks; caudal peduncle in females with small black spots on its posterior-most portion; head in males with latero-ventral stripe; dorsal and anal fins in males with distinctive concentration of melanophores on their sub-distal region; iris green in males, yellow in females ..... Genus *Campellolebias*
- 5b. Anterior portion of anal fin in males with inseminating fan formed by seven to ten small unbranched rays; genital opening in males situated in broad transverse aperture close to anal-fin base; anal fin about trapezoidal in males, anterior and distal margins not continuous; caudal fin never sub-truncate in males; venter without brown stripe on its middle zone; lateral midline of body in males with broad dark reddish chocolate brown to black stripe; flank in males with iridescent colour marks restricted to lateral midline of body; caudal peduncle without small black spots; head without latero-ventral stripe; dorsal and anal fins without distinctive concentration of melanophores on their sub-distal region; iris yellow in both sexes ..... Genus *Cynopoecilus* (go to 6 for included subgenera)
- 6a. Anal fin in males with long filamentous ray on its tip; anterior portion of anal fin in males without rays curved posteriorly separated from posterior portion of fin by fin membrane gap; caudal fin in males lanceolate; flank in females with dark bars; dorsal fin in males with brownish red stripe on its basal portion; 29–31 scales in longitudinal series; dorsal-fin origin in males at vertical through pelvic-fin base; dorsum without brown spots ..... *Poecilopanchax*, new subgenus
- 6b. Anal fin without filamentous ray on its tip; anterior portion of anal fin in males with three to five branched rays curved posteriorly, separated from posterior portion of fin by fin membrane gap to form inseminating flap; caudal fin rounded; 25–28 scales in longitudinal series; dorsal-fin origin in males at vertical through genital bulb; dorsum in males with brown spots over its anterior portion ..... Subgenus *Cynopoecilus*

### Genus *Mucurilebias* COSTA, 2014

*Mucurilebias* COSTA, 2014: 26 (type species: *Cynolebias leitaoi* CRUZ & PEIXOTO, 1991, by original designation).

**Diagnosis.** Distal portion of epural much wider than distal portion of parhypural [ch. 39.1], pelvic fin short in males, barely reaching urogenital region [ch. 71.1] (independently acquired in *Cynopoecilus* and *Leptolebias*), intense red pigmentation on branchiostegal region in males [ch. 102.1] (independently acquired in *Poecilopanchax*), narrow bluish white stripe on distal margin of dorsal fin in males [ch. 107.1], and distinctive narrow red stripe on distal margin of anal fin in males [ch. 113.1].

**Included species, distribution and habitat.** A single species *M. leitaoi* (CRUZ & PEIXOTO, 1991), known only from a temporary pool within dense 'Tabuleiro' forest in the Rio Mucuri floodplains, north-eastern Brazil (CRUZ & PEIXOTO, 1991; COSTA, 2014).

Unnamed clade comprising the genera *Notholebias*, *Leptopanchax*, *Leptolebias*, *Campellolebias*, and *Cynopoecilus*

**Diagnosis.** Autopalatine curved in lateral view [ch. 12.1] (reversed in *Cynopoecilus*), basihyal length larger than space occupied by three basibranchials [ch. 21.1], absence of lateral flap on anterior portion of fifth ceratobranchial [ch. 34.1], supraorbital series of neuromasts interrupted close to posterior nostril [ch. 79.1] (reversed in *Campellolebias* and *Cynopoecilus*), chorion surface reticulate [ch. 84.1], mushroom-like chorion projections [ch. 85.1] (reversed in *Campellolebias*), and dorsal and anal fins in males with dark red spots or bars on basal portion [ch. 105.1].

Genus *Notholebias* COSTA, 2008

*Notholebias* COSTA, 2008: 156 (type species: *Cynolebias minimus* Myers, 1942, by original designation).

**Diagnosis.** Large teeth concentrated on the medial region of the outer tooth row of premaxilla and dentary [ch. 4.1], postero-ventral process of autopalatine longer than antero-ventral process [ch. 14.1], basihyal narrow, about rectangular [ch. 20.1] (independently acquired in *Poecilopanchax*), ceratobranchial tooth plate extending to anterior extremity of bone [ch. 33.1].

**Included species, distribution and habitat.** Four species, *N. cruzi* (COSTA, 1988), *N. fractifasciatus* (COSTA, 1988), *N. minimus* (MYERS, 1942), and *N. vermiculatus* COSTA & AMORIM, 2013, found in temporary pools within open vegetation formations, including coastal 'Restinga', between Rio São João and Rio Guandu bays, south-eastern Brazil (COSTA, 1988; COSTA & AMORIM, 2013).

Unnamed clade comprising the genera *Leptopanchax*, *Leptolebias*, *Campellolebias*, and *Cynopoecilus*

**Diagnosis.** Absence of dermosphenotic [ch. 1.1] (also in *Mucurilebias*), contact organs on pectoral fin rudimentary or absent [ch. 83.0].

*Leptopanchax*, new genus

**Type species.** *Cynolebias citrinipinnis* COSTA, LACERDA & TANIZAKI, 1988.

**Diagnosis.** Caudal fin oval in males, slightly longer than deep [ch. 73.0], broad iridescent golden stripe on distal zone of dorsal fin in males [ch. 108.1], caudal fin with

vermiculate dark red marks in males [ch. 114.2]. Also distinguished from *Leptolebias* by having caudal fin symmetrical (*vs.* asymmetrical in males), anterior proximal radials of anal fin not placed in close proximity in males (*vs.* placed in close proximity), urogenital papilla not in close proximity to anal-fin origin in males (*vs.* in close proximity), basal portion of urogenital papilla not forming pronounced wide structure in males (*vs.* forming distinctively wide structure), absence of thickened tissue on basal portion of anal fin in males (*vs.* presence), absence of canary yellow stripes on flank in males (*vs.* presence), absence of broad white stripe ventrally bordered by narrow black stripe on ventral margin of caudal fin in males (presence), absence of dark reddish chocolate brown stripe between pectoral-fin base and posterior portion of anal-fin base in males (*vs.* presence), absence of small round dark reddish brown spots on dorsal fin in males (*vs.* presence). In addition, in species of *Leptopanchax*, eggs are deposited at the bottom surface, whereas in *Leptolebias*, male and female immerse within the bottom substrate during spawning.

**Included species, distribution and habitat.** Five species: *L. aureoguttatus* (CRUZ, 1974), *L. citrinipinnis* (COSTA, LACERDA & TANIZAKI, 1988), *L. itanhaensis* (COSTA, 2008), *L. opalescens* (MYERS, 1942), and *L. splendens* (MYERS, 1942), between the Laguna de Maricá system in south-eastern Brazil and river basins draining into the Baía de Paranaguá, southern Brazil. Two species, *L. citrinipinnis* and *L. opalescens* are found in temporary pools within open vegetation formations, including coastal 'Restinga', whereas the remaining species of *Leptopanchax* are found in seasonal shallow channels within dense rain forest (COSTA & LACERDA, 1988; COSTA *et al.*, 1988; COSTA, 2008).

**Etymology.** From the Greek *leptos*, meaning thin or elongate, and *panchax*, a name of uncertain origin, possibly referring to an Indian popular name for aplocheiloid killifishes, often used to compose generic names of the killifish order Cyprinodontiformes. Gender masculine.

Unnamed clade comprising the genera *Leptolebias*, *Campellolebias*, and *Cynopoecilus*

**Diagnosis.** Anterior proximal radials of anal fin in close proximity in males [ch. 43.1], urogenital papilla in close proximity to anal-fin origin in males [ch. 63.1], basal portion of urogenital papilla forming pronounced wide structure in males [ch. 64.1], thickened tissue possibly glandular on basal portion of anal fin in males [ch. 68.1, reversed in *Campellolebias*], dark reddish chocolate brown to black stripe between pectoral-fin base and posterior portion of anal-fin base in males [ch. 90.1], small round dark reddish brown spots on dorsal fin in males [ch. 112.0].

## Genus *Leptolebias* MYERS, 1952

*Leptolebias* MYERS, 1952: 140 (type species: *Cynopoecilus marmoratus* LADIGES, 1934, by original designation; first proposed as a subgenus of *Cynolebias* STEINDACHNER, 1876).

**Diagnosis.** Caudal fin asymmetrical in males, dorsal margin slightly rounded and ventral margin straight [ch. 73.4], presence of canary yellow stripes on flank in males [ch. 88.1], iris blue in males [ch. 104.1] (independently acquired in *L. splendens*), broad white stripe ventrally bordered by narrow black stripe on ventral margin of caudal fin in males [ch. 115.1].

**Included species, distribution and habitat.** A single species, *L. marmoratus* (LADIGES, 1934), found in temporary channels within dense rain forest, in the floodplains of rivers draining into the Baía de Guanabara, south-eastern Brazil (COSTA, 2002b).

### Unnamed clade comprising the genera *Campellolebias* and *Cynopoecilus*

**Diagnosis.** Posterior process of vomer distinctively longer than main portion of bone [ch. 2.1], ventral process of angulo-articular short, well-visible in lateral view [ch. 9.1], dorsal-fin origin anterior to anal-fin origin [ch. 41.1], anterior proximal radials of anal fin rod-shaped in males [ch. 42.1], anterior *inclinatores* and *depressores anales* hypertrophied in males [ch. 49.1], presence of muscular ejaculatory pump on basal portion of urogenital region in males [ch. 50.1], pelvic bones medially separated [ch. 59.1], pelvic fin sub-triangular in males [ch. 72.1], supraorbital series continuous in its anterior portion [ch. 79.0], dark pigmentation present on flank in females, forming distinctive dark marks [ch. 91.1], dark reddish brown pigmentation extending between orbit and posterior limit of head in males [ch. 100.1].

## Genus *Campellolebias* VAZ-FERREIRA & SIERRA, 1974

*Campellolebias* VAZ-FERREIRA & SIERRA, 1974: 14 (type species: *Campellolebias brucei* VAZ-FERREIRA & SIERRA, 1974; type by original designation and monotypy).

**Diagnosis.** Fifth ceratobranchial slender, boomerang-shaped [ch. 32.1], postero-basal portion of last neural spine with small process bearing ligament attached to anterior tip of epural [ch. 36.1], anterior two rays of anal fin in males long, thickened, separated from the posterior part of the fin by a deep gap in the fin membrane just posterior to second ray to form an inseminating tube [ch. 46.1], genital duct extending along anterior margin of anal fin, its opening near the tip of first anal-fin ray

[ch. 60.1], urogenital papilla firmly attached to anal fin in males [ch. 62.1], anal fin about triangular in males, anterior and distal margins nearly continuous [ch. 69.1], caudal fin subtruncate in males [ch. 73.2], mushroom-like chorion projections absent [ch. 85.1], longitudinal dark brown stripe on middle zone of venter in males [ch. 94.1], small black spots on posterior-most portion of caudal peduncle in females [ch. 95.1], latero-ventral stripe on head in males [ch. 96.1], distinctive concentration of melanophores on sub-distal region of dorsal and anal fins in males [ch. 110.1].

**Included species, distribution and habitat.** Four species, *C. brucei* VAZ-FERREIRA & SIERRA, 1974, *C. chrysolineatus* COSTA, LACERDA & BRASIL, 1989, *C. dorsimaculatus* COSTA, LACERDA & BRASIL, 1989, and *C. intermedius* COSTA & DE LUCA, 2006, found in temporary swamps and pools, sometimes in open vegetation areas, often at the border of dense rain forests, between the Rio Ribeira de Iguape basin, south-eastern Brazil and Rio Tubarão basin, southern Brazil (COSTA *et al.*, 1989; COSTA, 2006b).

## Genus *Cynopoecilus* REGAN, 1912

*Cynopoecilus* REGAN, 1912b: 642 (type species: *Cynolebias melanotaenia* REGAN, 1912, type by original designation and monotypy).

**Diagnosis.** Constriction on median portion of autopalatine [ch. 11.1], autopalatine nearly straight in lateral view [ch. 12.0] (a reversal), teeth on second pharyngobranchial [ch. 25.0] (a reversal), minute accessory caudal fin cartilages [ch. 40.1], series of seven to ten small unbranched rays connected to first two developed anal-fin proximal radials to form an inseminating fan [ch. 45.1], genital opening situated in broad transverse aperture in males [ch. 61.1], iridescent colour marks restricted to lateral midline of body [ch. 86.1], broad dark reddish chocolate brown to black stripe on lateral midline of body [ch. 89.1], iris yellow in both sexes [ch. 104.0] (a reversal).

### *Poecilopanchax*, new subgenus

**Type species.** *Cynopoecilus notabilis* FERRER, WINGERT & MALABARBA, 2014.

**Diagnosis.** Basihyal narrow, about rectangular [ch. 20.1] (independently acquired in *Notholebias*), interarcual element of dorsal branchial arch ossified [ch. 24.1], uncinuate process of third epibranchial distinctively widened [ch. 27.1], long filamentous ray on tip of anal fin in males [ch. 70.1], caudal fin lanceolate in males [ch. 73.3], dark bars on flank in females [ch. 92.1], branchiostegal region with intense red pigmentation in males [ch. 102.1] (independently acquired in *Mucurilebias*), brownish red stripe on basal portion of dorsal fin in males [ch. 109.1], dark

red marks extending to antero-distal margin of dorsal fin in males [ch. 111.0] (a reversal). Also distinguished from the subgenus *Cynopoecilus* by the presence of more scales in the longitudinal series (29–31 vs. 25–28), dorsal-fin origin at vertical through pelvic-fin origin in males (vs. through genital bulb), cartilaginous proximal region of anterior proximal radials of anal fin not distinctively lengthened in males (vs. long), absence of membrane gap forming inseminating flap (vs. presence), supraorbital scales absent or rudimentary (vs. well-developed), and absence of brown spots over anterior portion of dorsum in males (vs. presence).

**Included species, distribution and habitat.** Only the type species, *C. notabilis* FERRER, WINGERT & MALABARBA, 2014, found in temporary channels within dense semi-deciduous seasonal forest, in Laguna dos Patos drainage, southern Brazil (FERRER *et al.*, 2014; personal observation).

**Etymology.** From the Greek *poecilus*, meaning multi-coloured, and *panchax*, a name of uncertain origin, possibly referring to an Indian popular name for aplocheiloid killifishes, often used to compose generic names of the killifish order Cyprinodontiformes. Gender masculine.

**Remarks.** The recently described taxon *Cynopoecilus notabilis*, although sharing all the nine diagnostic synapomorphies with species of *Cynopoecilus* (see above), exhibits a series of distinctive morphological features, including some apomorphic conditions unique among cynopoecilines (e.g., interacual element of dorsal branchial arches ossified, dorsal fin with numerous rays and anteriorly placed on body, long filamentous ray on tip of anal fin in males). This striking morphological gap between *C. notabilis* and the clade comprising all species of *Cynopoecilus*, justifies recognition of the new subgenus *Poecilopanchax*.

### Subgenus *Cynopoecilus* REGAN, 1912

*Cynopoecilus* REGAN, 1912b: 642 (type species: *Cynolebias melanoaenia* REGAN, 1912, type by original designation and monotypy).

**Diagnosis.** Cartilaginous proximal region of first three or four proximal radials of anal fin long in males [ch. 44.1], three to five branched rays connected to proximal radials 3–6 curved posteriorly, separated from posterior portion of fin by fin membrane gap to form inseminating flap [ch. 48.1], supraorbital scales well-developed [ch. 77.0], and brown spots over anterior portion of dorsum in males [ch. 93.1].

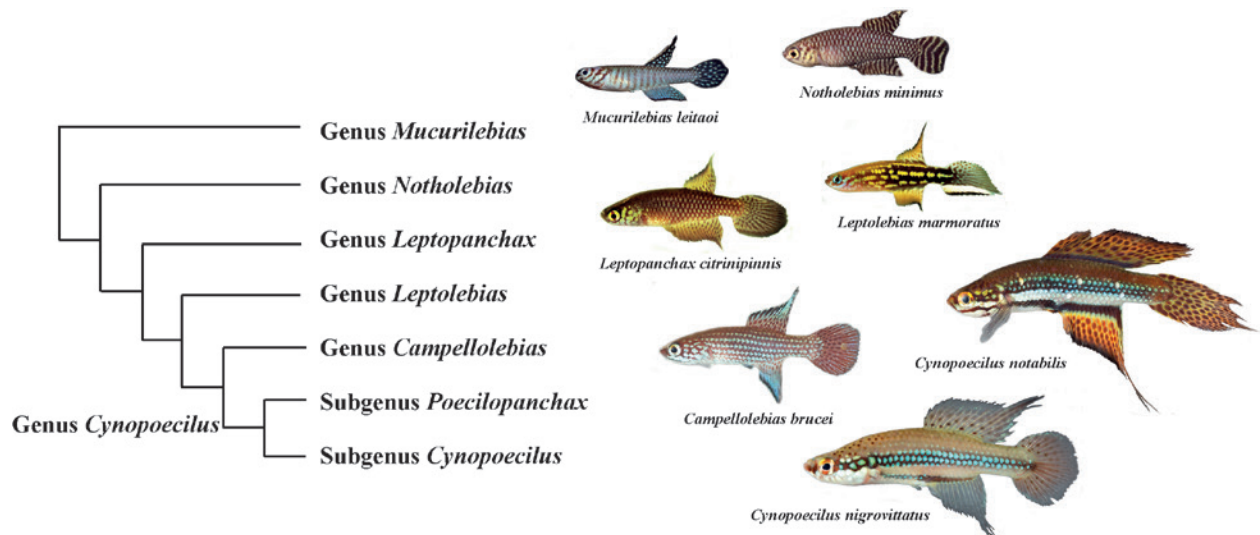
**Included species, distribution and habitat.** Five species, *C. feltrini* COSTA, AMORIM & MATTOS, 2016, *C. fulgens* COSTA, 2002, *C. intimus* COSTA, 2002, *C. melanoaenia* (REGAN, 1912), and *C. nigrovittatus* COSTA, 2002,

found in temporary pools in open vegetation areas, sometimes at semi-deciduous forest border. The study of material recently collected in the broad area between the type locality of *C. fulgens* and *C. multipapillatus* COSTA, 2002 (see list of localities in Appendix 1), indicated that the latter species is a synonym of the former. Species of the subgenus *Cynopoecilus* occurs between the Rio Tubarão basin in southern Brazil and the Laguna dos Patos-Lagoa Mirim system in southern Brazil and adjacent areas of Uruguay (COSTA, 2002a; COSTA *et al.*, 2016b).

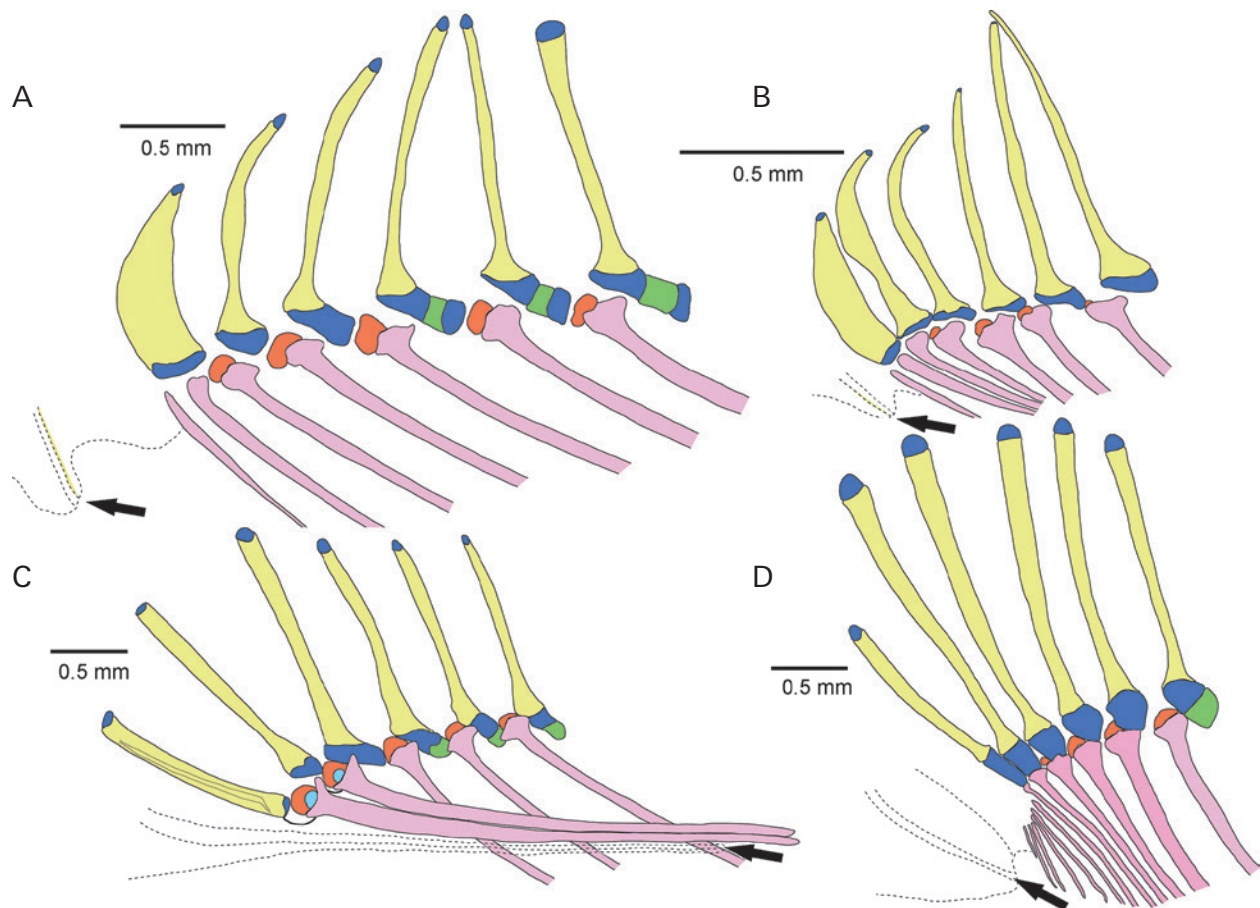
## Discussion

**Classification of the Cynopoecilini.** The comparative morphological analysis indicated relationships among the main lineages of the Cynopoecilini that highly support clades not delineated in other analyses and provided new diagnostic characters for clades already delineated in previous studies. This phylogenetic tree is based on a recent phylogenetic study (COSTA, 2016) combining the morphological characters herein listed and molecular data taken from COSTA *et al.* (2016a).

Monophyly of *Leptolebias* as diagnosed by COSTA (2008) is not corroborated. A clade including only *L. marmoratus* and all species of *Campellolebias* and *Cynopoecilus* is supported by six synapomorphies, among which four are related to the genital region and adjacent part of the anal fin in males: anterior proximal radials of the anal fin in close proximity [ch. 43.1], urogenital papilla in close proximity to the anal-fin origin [ch. 63.1], basal portion of the urogenital papilla forming a pronounced wide structure [ch. 64.1], and presence of a distinctively thickened tissue on the basal portion of the anal fin [ch. 68.1] (Figs. 2B–D). All these character states differ from the plesiomorphic condition shared by all other cynolebiasines, including species of *Leptopanchax* (Fig. 2A). Interestingly, all those derived character states are present in *L. marmoratus*, a species having external fertilization as its only reproductive strategy, but lacking the specialized morphological features of the anal fin structure found in species of *Campellolebias* and *Cynopoecilus*, which adopted an internally fertilizing mode of reproduction (COSTA *et al.*, 2016a). In *L. marmoratus*, the anterior rays and proximal radials are placed in close proximity as in other species of the clade (Fig. 2A), but they are not elongated to support a specialized musculature as in species of *Campellolebias* and *Cynopoecilus* (Figs. 2C–D); and the urogenital papilla of *L. marmoratus* is robust and placed close to the anal fin as in other species of the clade (Fig. 2B), but lacking the internal muscular ejaculatory pump present in those species. The remaining two synapomorphies of the clade comprising *Leptolebias*, *Campellolebias* and *Cynopoecilus* refer to derived colour patterns in males: a dark reddish chocolate brown to black stripe between pectoral-fin base and posterior portion of the anal-fin base [ch. 90.1]



**Fig. 1.** Phylogenetic relationships among cynopoeciline genera and subgenera supported by the comparative analysis of 115 morphological characters.

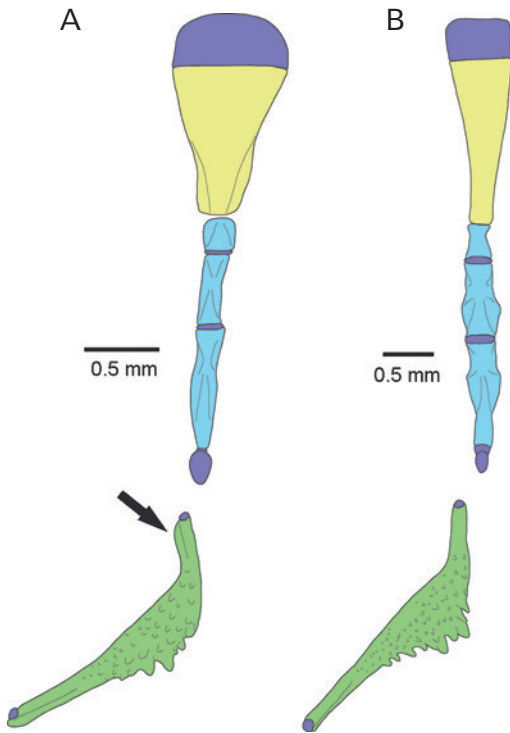


**Fig. 2.** Morphology of the anal-fin osseous support in cynopoeciline males. Anterior part of the anal-fin support, left lateral view, in: (A) *Leptopanchax citrinipinnis*; (B) *Leptolebias marmoratus*; (C) *Campellolebias dorsimaculatus* (D) *Cynopoecilus melanotaenia*. Yellow: proximal radials; red: distal radials; green: medial radials; light purple: fin rays; dark blue: cartilages. Dotted line indicates urogenital papilla and duct, arrow, urogenital opening.

and small round dark reddish brown spots on the dorsal fin [ch. 112.0] (Fig. 1).

The clade comprising the genera *Notholebias*, *Leptopanchax*, *Leptolebias*, *Campellolebias*, and *Cynopo-*

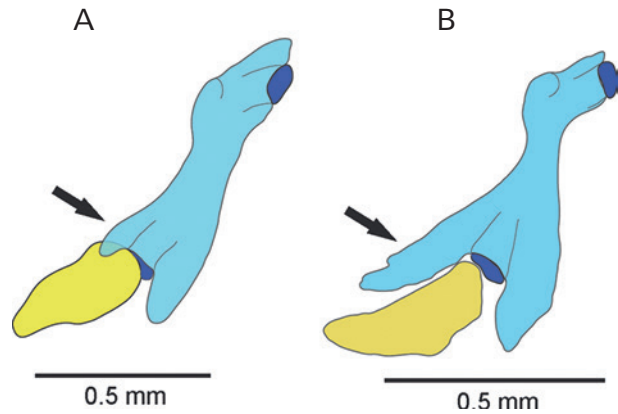
*ecilus*, the sister group of *Mucurilebias*, is supported by seven synapomorphies, among which three are first described (synapomorphies 21.1, 34.1, 12.1). Synapomorphies ch. 21.1, basihyal length approximately equal or



**Fig. 3.** Morphology of ventral branchial and hyoid bones in cynopoecilines. Middle portion of branchial and hyoid elements, dorsal view, of: (A) *Mucurilebias leिताoi*; (B) *Cynopoecilus notabilis*. Yellow: basihyal; light blue: basibranchials; green: fifth ceratobranchial; dark purple: cartilages. Arrow indicates the lateral flap on the anterior portion of the fifth ceratobranchial.

longer than space occupied by three basibranchials (Fig. 3B; vs. shorter) and ch. 34.1, absence of lateral flap on anterior portion of fifth ceratobranchial (Fig. 3B) are unique among members of the subfamily Cynolebiinae, in which the primitive condition, like in *Mucurilebias*, is always present (Fig. 3A). Synapomorphy ch. 12.1, autopalatine curved in lateral view (Fig. 4B) (vs. approximately straight; Fig. 4A), implicates in assuming a reversal for *Cynopoecilus*, in which the autopalatine is approximately straight as in *Mucurilebias* and other Cynolebiinae.

The forest-dweller taxon *C. notabilis*, besides highly differing from all other species of *Cynopoecilus* by several morphological features, exhibits nine autapomorphies, which justify its inclusion in the new subgenus *Poecilopanchax*. More remarkable is the ossification of the interarcual element of the dorsal branchial arch, resulting in an interarcual bone [ch. 24.1; Fig. 5B). The presence of this bone, not reported in the recent description of the species (FERRER *et al.*, 2014), is unique among members of the order Cyprinodontiformes, in which that element is always cartilaginous (Fig. 5A) or absent. Two autapomorphies of *Poecilopanchax* are also unique among members of the subfamily Cynolebiasinae: uncinat process of the third epibranchial distinctively widened [ch. 27.1] (Fig 6B) and presence of a brownish red stripe on the basal portion of the dorsal fin in males [ch. 109.1] (Fig. 1); and three are unique among cynopoecilines: a long filamentous ray on the tip of the anal fin in males [ch. 70.1], caudal fin



**Fig. 4.** Morphology of anterior jaw suspensorium bones in cynopoecilines. Upper portion of the anterior jaw suspensorium, medial view, of: (A) *Mucurilebias leिताoi*; (B) *Notholebias minimus*. Yellow: entopterygoid; light blue: autopalatine; dark blue: cartilages. Arrow indicates the postero-ventral process of the autopalatine.

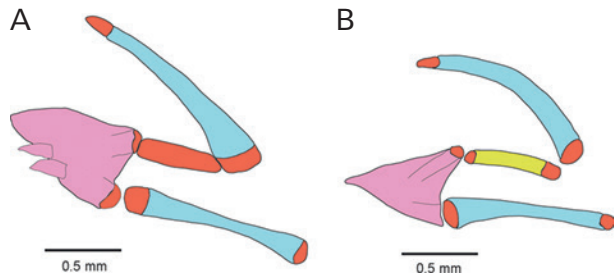
lanceolate in males [ch. 73.3), and dark bars on the flank in females [ch. 92.1] (Fig. 1). In other cynopoecilines, the uncinat process of the third epibranchial is narrow (Fig 6A), there is neither a red stripe on the basal portion of the dorsal fin nor a long filamentous ray on the tip of the anal fin, and the caudal fin is never lanceolate, although a small projection on the posterior part of the fin is present in *Mucurilebias*. The remaining three autapomorphies of *Poecilopanchax* are not unique among cynopoecilines: basihyal narrow, about rectangular [ch. 20.1] (Fig 2B; independently acquired in *Notholebias*), branchiostegal region with intense red pigmentation in males [ch. 102.1] (independently acquired in *Mucurilebias*), and dark red marks extending to antero-distal margin of dorsal fin in males [ch. 111.0] (a reversal).

The Cynopoecilini is further supported by a distinctive postero-ventral process on the autopalatine [ch. 13.1] (Figs. 4A–B), which is conspicuous in *Notholebias*, *Leptopanchax*, and *Leptolebias* (Fig. 4B), but minute in species of *Mucurilebias*, *Campellolebias*, and *Cynopoecilus*. This process does not occur in any other aplocheilid killifish (Fig. 4A).

**Family-group names used for aplocheiloid killifishes.**

Aplocheiloid killifishes have been classified in three families: Aplocheilidae BLEEKER, 1859, Nothobranchiidae GARMAN, 1895, and Rivulidae MYERS, 1925 (PARENTI, 1981; COSTA, 2004). The first step for this classification was given by PARENTI (1981) in recognising the suborder Aplocheiloidei containing two families, the Aplocheilidae, comprising Old World genera, and the Rivulidae, comprising New World genera. After molecular (MURPHY & COLLIER, 1997) and morphological evidence indicating Aplocheilidae sensu PARENTI (1981) to be paraphyletic, COSTA (2004) proposed a new classification also including Nothobranchiidae for continental Africa genera, and restricting Aplocheilidae to the genera endemic to Asia, Madagascar, and Seychelles. More recently, VAN DER LAAN *et al.* (2014) showed that the stem Rivul- used for





**Fig. 5.** Morphology of anterior dorsal branchial bones in cynopocilines. Anterior portion of the dorsal branchial skeleton, ventral view, of: (A) *Cynopocilus nigrovittatus*; (B) *Cynopocilus notabilis*. Light blue: epibranchials; purple: second pharyngobranchial; yellow: interarcual ossification; red: cartilages.

the family-group name Rivulidae was preoccupied by Rivulini GROTE (1895) for Lepidoptera.

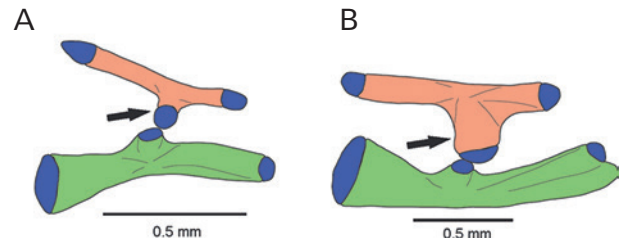
Instead of using a new name at the family rank to New World aplocheiloids, I herein follow NELSON (1994) in considering all aplocheiloids in a single family, the Aplocheilidae, which in this broad sense is well-supported by both morphology (PARENTI, 1981; COSTA, 1998b, 2013) and DNA sequences (MURPHY & COLLIER, 1997; POHL *et al.*, 2015). Aplocheilidae is a well-established family-group name (VAN DER LAAN *et al.*, 2014), making its use as a single aplocheiloid family more stable along time, besides avoiding the impact of a new name at the family rank for a popular aquarium fish group. Following this proposal, Aplocheilidae includes three subfamilies: Aplocheilinae BLEEKER, 1859, equivalent to Aplocheilidae sensu COSTA (2004), Cynolebiinae HOEDEMAN, 1961, equivalent to Rivulidae sensu PARENTI (1981), and Nothobranchiinae GARMAN, 1895, equivalent to Nothobranchiidae sensu COSTA (2004).

## Acknowledgements

I am grateful to C. P. BOVE and B. B. COSTA for help in numerous successful and unsuccessful trips to collect cynopociline killifishes. Thanks are also due to P. F. AMORIM, G. ARANHA, M. A. BARBOSA, J. IGNACIO, A. KATZ, J. L. MATTOS, F. PEREIRA, J. RAPOSO, O. SIMÕES and G. SILVA for help in field studies and laboratory assistance; to M. CHEFFE, C. FELTRIN, and T. LITZ for sending me material for study; to M. BRITTO, D. CATANIA, C. A. LUCENA, J. MACLAINE, and O. OYAKAWA, for curatorial support and hospitality during visits to their institutions; and to A. ZARSKÉ by editorial support. A previous version of this paper benefited from the criticisms and suggestions provided by two anonymous reviewers. This study was supported by CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico - Ministério de Ciência e Tecnologia).

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**Fig. 6.** Morphology of posterior dorsal branchial bones in cynopocilines. Posterior portion of the dorsal branchial skeleton, postero-ventral view, of: (A) *Notholebias minimus*; (B) *Cynopocilus notabilis*. Pink: epibranchial 3; green: epibranchial 4; dark blue: cartilages. Arrow indicates the uncinated process of epibranchial 3.

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## Appendix 1

List of material examined. C&S, means specimens cleared and stained for osteological analysis, H, holotype, L, lectotype, N, neotype, P, paratype, S, syntype; Abbreviations for institutions are: BMNH, Natural History Museum, London; CAS (SU), California Academy of Sciences, San Francisco, formerly deposited in the Stanford University; MCP, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica, Porto Alegre; MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro; MZUSP, Museu de Zoologia, Universidade de São Paulo, São Paulo; UFRJ, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro; and, ZVC-P, Facultad de Humanidades y Ciencias, Departamento Zoología de Vertebrados, Montevideo.

**Genus *Campellolebias*:** *C. brucei*: Brazil: Estado de Santa Catarina: — ZVC-P 2126, 1 P; ZVC-P 2127, 1 P; near Criciúma, 28°46'43"S 49°19'36"W. — UFRJ 293, 7; UFRJ 1854, 4 (C&S); UFRJ 4493, 111; UFRJ 4494, 6 (C&S); near Criciúma, 28°45'45"S 49°17'32"W. — UFRJ 8382, 2; UFRJ 8383, 3; UFRJ 8374, 25; Florianópolis, 27°39'56"S 48°33'18"W. *C. chrysolineatus*: Brazil: Estado de Santa Catarina: — MZUSP 38817, H; MZUSP 38818, 2 P; MZUSP 38819, 1 P; MNRJ 11494, 2 P; MZUSP 38344, 11 P; near Araquari, 26°23'00"S 48°40'00"W. — UFRJ 5210, 6; UFRJ 5211, 2 (C&S); between Araquari and Balneário Barra do Sul, 26°24'46"S 48°38'23"W. — UFRJ 6317, 2; UFRJ 6318, 21; UFRJ 6319, 6 (C&S); UFRJ 10763; 2 (C&S); between Araquari and Balneário Barra do Sul, 26°24'33"S 48°38'31"W. *C. dorsimaculatus*: Brazil: Estado de São Paulo: — MZUSP 38813, H; MZUSP 38814, 1 P; MZUSP 38815, 12 P; MZUSP 38816, 1 P; MZUSP 11493, 2 P; MNRJ 11493, 2 P; UFRJ 6309, 2; UFRJ 6310, 3 (C&S); UFRJ 6311, 1; Iguape, 24°40'00"S 47°26'04"W. *C. intermedius*: Brazil: Estado de São Paulo: — UFRJ 6312, H; UFRJ 6313, 1 P; UFRJ 6314, 2 P; UFRJ 6315, 4 P (C&S); UFRJ 6316, 33; near Juquiá, about 24°20'S 47°35'W. **Genus *Cynopoeilus*:** *C. feltrini*: All from Estado de Santa Catarina, Brazil. — UFRJ 10662, H; UFRJ 10597, 22 P; UFRJ 10598, 6 P (C&S); UFRJ 10482, 5 P; UFRJ 10620, 7 P; Laguna, 28°30'26"S 48°48'01"W. — UFRJ 276, 6; UFRJ 1857, 2 (C&S); Araranguá, 28°55'51"S 49°30'53"W. — UFRJ 5234, 4; Sombrio. *C. fulgens*: All from Estado do Rio Grande do Sul, Brazil. — MCP 26929, H; MCP 26930, 5 P; UFRJ 5230, 5 P (C&S); 5 km N of São José do Norte, 31°58'01"S 51°59'48"W. — MCP 26933, H of *C. multipapillatus*; MCP 26934, 10; UFRJ 5232, 40; UFRJ 5233, 8 (C&S); UFRJ 4821, 118; near Lagoa da Fortaleza, 30°09'37"S 50°13'26"W. — UFRJ 10727, 54; UFRJ 10156, 6; near Osório, 29°57'34"S 50°13'53"W. — UFRJ 10174, 62; UFRJ 10157, 5; near Osório, 29°59'20"S 50°11'33"W. — UFRJ 10171, 62; UFRJ 10158, 4; near Cidreira, 30°09'09"S 50°14'25"W. — UFRJ 10704, 33; UFRJ 10159, 5; 35 km from Mostardas, 30°50'59"S 50°41'21"W. — UFRJ 10172, 84; UFRJ 10161, 4; Estreito, 31°49'19"S 51°41'21"W. — UFRJ 10726, 28; UFRJ 10160, 6; Tavares, 31°15'52"S 51°02'40"W. *C. intimus*: all from the upper Rio Jacuí drainage, Estado do Rio Grande do Sul, Brazil. UFRJ 4489, 13 P; UFRJ 4490, 6 P (C&S); Vila Block, 29°56'33"S 53°42'24"W. *C. melanoaenia*: Estado do Rio Grande do Sul, Brazil: BMNH 1909.9.5.15-22, 8 S; Estação Quinta. — UFRJ 4837, 14; UFRJ 5225, 4 (C&S); Estação Quinta, 32°04'33"S 52°15'54"W. — UFRJ 4980, 13; Estação Quinta, 32°04'15"S 52°15'51"W. — UFRJ 5033, 105 ex.; near Cassino, 32°07'40"S 52°11'03"W. — UFRJ 10703, 31; UFRJ 107402, 1 (C&S); UFRJ 10163, 7; between Quinta and Cassino, 32°06'01"S 52°09'55"W. — UFRJ 4008, 26; UFRJ 5228, 5 (C&S); Pontal da Barra, 31°46'54"S 52°13'45"W. — UFRJ 4979, 40; UFRJ 5019, 3 (C&S); near Pelotas, 31°54'26"S 52°18'58"W. — UFRJ 5058, 16; Taim, 32°31'47"S 52°32'31"W. — UFRJ 4947, 50; UFRJ 5223, 8 (C&S); near Taim, 32°44'16"S 52°38'32"W. — UFRJ 10729, 15; UFRJ 10162, 8; road BR-471, 32°44'40"S 52°38'41"W. — UFRJ 4498, 81; UFRJ 5224, 7 (C&S); near Cristal, 31°06'56"S 52°01'41"W. — UFRJ 4487, 32; UFRJ 4491, 4 (C&S); near Camaquã, 30°55'17"S 51°54'01"W. — UFRJ 10728, 3; UFRJ 10164, 5; near Cristal, 31°04'41"S 52°02'18"W. Uruguay: Departamento de Rocha: — UFRJ 10771, 10; Barra de Valizas, 34°19.81'S 53°48.89'W. — UFRJ 10772, 14; Barra de Valizas, 34°19.34'S 53°49.36'W. — UFRJ 10773, 176; Arroyo Valizas, 34°21.55'S 53°50.64'W. — UFRJ 10774, 7; canal Andreoni, 33°55.21'S 53°32.61'W. — UFRJ 10776, 6; near Río Cebollatí, 33°36.82'S 54°18.00'W. — UFRJ 10775, 25; Lascano, 33°27.28'S 54°18.06'W. Departamento de Trinta y Tres: — UFRJ 10769, 12; Paso de Dragón, 32°45.95'S 53°43.16'W. — UFRJ 10770, 37; UFRJ 10778, 2; Paso de Dragón, 32°45.95'S 53°43.19'W. — UFRJ 10777, 40; near Arroyo Yermal, 33°13.30'S 54°23.93'W. *C. nigrovittatus*: All from lower Rio Jacuí drainage, Estado do Rio Grande do Sul, Brazil. MCP 26931, H; MCP 26932, 10 P; UFRJ 4976, 45 P; UFRJ 5012, 6 P (C&S); Montenegro, 29°40'13"S 51°25'32"W. — UFRJ 4977, 23 P; UFRJ 5039, 46 P; Rio Cai floodplains, 29°49'21"S 51°21'09"W. — UFRJ 4820, 30 P; near São Jerônimo, 30°03'27"S 51°46'33"W. — UFRJ 4829, 43 P; UFRJ 5231, 6 P (C&S); between General Câmara and São Jerônimo, 29°56'20"S 51°46'00"W. *C. notabilis*: All from lower Rio Jacuí drainage, Estado do Rio Grande do Sul, Brazil. — UFRJ 10166, 4; UFRJ 10176, 4; UFRJ 10648, 2 (C&S); Banhado dos Pachecos, 30°05'48"S 50°51'06"W. **Genus *Leptolebias*:** *L. marmoratus*: Brazil: Estado do Rio de Janeiro: — MCP 28604, N; UFRJ 5404, 1; UFRJ 5355, 24; UFRJ 5403, 1; UFRJ 5356, 4 (C&S); UFRJ 5220, 6 (C&S); Vila de Cava, 22°39'30"S 43°25'46"W. — MNRJ 4739, 8 S of *C. sicheleri*; CAS (SU) 36523, H of *C. zingiberinus*; CAS (SU) 36523, 10; road to Petrópolis, 22°38'09"S

43°15'57"W. **Genus *Leptopanchax***: *L. aureoguttatus*: Brazil: Estado do Paraná: – MNRJ 28924, L; MNRJ 19495, 2; UFRJ 199, 7; between Paranaguá and Matinhos, 25°42'16"S 48°34'27"W. – CAS (SU) 50191, 11; road east of Paranaguá. – UFRJ 6331, 11, UFRJ 6332, 5 (C&S); near Praia de Leste, 25°40'42" 48°30'13"W. Estado de São Paulo: UFRJ 5212, 35; UFRJ 5213, 10 (C&S); Iguaçu, 24°43'24"S 47°34'43"W. – MNRJ 19480, 7; MNRJ 19451, 8; MNRJ 19473, 6; MNRJ 19550, 2; Registro, about 24°31'S 47°51'W. *L. citrinipinnis*: Brazil, Rio de Janeiro: – MZUSP 37199, H; MNRJ 11310, 3 P; MZUSP 37198, 6 P; MZUSP 37197, 3 P; UFRJ 175, 1 (c&s); MNRJ 19432, 22; MNRJ 15400, 8; UFRJ 2202, 14; UFRJ 184, 2; UFRJ 2202, 14; UFRJ 3679, 3 C&S; UFRJ 3036, 5; UFRJ 4396, 10; UFRJ 4397, 5; UFRJ 4399, 6; UFRJ 4400, 13; UFRJ 4401, 2; UFRJ 4402, 7; UFRJ 10761, 3 (C&S); UFRJ 4403, 1; UFRJ 4404, 11; UFRJ 4405, 5; UFRJ 5187, 19; UFRJ 6304, 16; UFRJ 6305, 4; UFRJ 8899, 4; UFRJ 8805, 10; UFRJ 8806, 15; Barra de Maricá, 22°57'57"S 42°53'33"W. – MNRJ 17684, 7; Itaipuaçu, 22°58'04"S 42°57'31"W. *L. itanhaensis*: Brazil, Estado de São Paulo: – UFRJ 6453, H; UFRJ 6323, 4 P; UFRJ 6324, 4 P; UFRJ 5219, 8 P (C&S); Itanhaém, 24°13'09"S 46°55'25"W. *L. opalescens*: Brazil: Rio de Janeiro: – CAS (SU) 36522, 6 P; MNRJ 11301, 3; road to Petrópolis, 22°38'24"S 43°16'31"W. – MNRJ 10621, H of *C. nanus*; MNRJ 10622, 1; MZUSP 25229/30, 2; Vila de Cava, 22°39'55"S 43°26'24"W. – UFRJ 9443, 6; UFRJ 9444, 10; Gericinó, 22°51'06"S 43°26'16"W. *L. splendens*: Brazil, Rio

de Janeiro: – CAS (SU) 36528, 3 P; MNRJ 8514, 23; MNRJ 11302, 1; road to Petrópolis, 22°38'09"S 43°15'57"W. – MNRJ 11413, 3; MZUSP 38443, 2 (C&S); Citrolândia, 22°34'43"S 43°01'30"W. **Genus *Mucurilibias***: *M. leिताoi*: Brazil: Estado da Bahia: – UFRJ 171, 1 (C&S); Mucuri, 18°06'05"S 39°39'47"W. **Genus *Notholebias***: *N. cruzi*: Brazil: Estado do Rio de Janeiro: – MZUSP 36297, H; MZUSP 36298, 8 P; MNRJ 11289, 3 P; MNRJ 11290, 6 P; MNRJ 11291, 2 P; Barra de São João, 22°33'50"S 41°58'56"W. – UFRJ 173, 1 (C&S); UFRJ 5287, 3; UFRJ 2073, 6; Barra de São João, 22°34'34"S 41°59'10"W. *N. fractifasciatus*: Brazil: Estado do Rio de Janeiro: – MZUSP 36423, H; MZUSP 36424, 11 P; MNRJ 11292, 20 P; UFRJ 6452, 8 (C&S); Inoã, 22°55'21"S 42°55'42"W. – UFRJ 5358, 51; UFRJ 5357, 10 (C&S); Maricá, 22°54'26"S 42°49'20"W. *N. minimus*: Brazil: Estado do Rio de Janeiro. – UFRJ 4832, 44; UFRJ 6581, 10 (C&S); Bosque da Barra, 22°59'50"S 43°22'17"W. – MZUSP 36296, 11; MZUSP 36301, 3; MNRJ 11287, 4; UFRJ 6576, 10 (C&S); UFRJ 6575, 14; Sero-pédica, 22°43'28"S 43°42'12"W. – UFRJ 8269, 3; UFRJ 8268, 30; Campo Grande, 22°57'00"S 43°36'45"W. *N. vermiculatus*: Brazil: Estado do Rio de Janeiro: – UFRJ 8980, H; UFRJ 8898, 11 paratypes; UFRJ 8899, 3 P; UFRJ 8801, 6 P; near Sampaio Correia, 22°51'53"S 42°33'15"W. – UFRJ 8981, 1 P; UFRJ 8902, 10 P (C&S); UFRJ 8983, 8 P; UFRJ 8984, 60 P; near Sampaio Correia, 22°51'19"S 42°34'10"W. – UFRJ 8804, 6; UFRJ 8902, 4; UFRJ 8903, 23; UFRJ 8908, 4; near Jaconé, 22°56'16"S 42°40'23"W.

## Appendix 2

List of characters and character states, according to the following sequence: osteology and myology (1–59), genital region (60–65), fins (66–73), jaws and branchiostegal region (74–75), frontal squamation (76–77), latero-sensory system (78–81), contact organs (82–83), egg morphology (84–85), and colour patterns (86–115).

- [1] Dermosphenotic: (0) present; (1) absent.
- [2] Vomer, posterior process, relative length to main portion of bone: (0) equal or slightly longer; (1) distinctively longer.
- [3] Vomer, teeth: (0) present; (1) absent.
- [4] Premaxilla and dentary, outer tooth row, larger teeth, arrangement: (0) along whole tooth patch; (1) concentrated on medial region.
- [5] Premaxilla, antero-proximal region, shape, and associated position of mouth cleft: (0) angular, mouth terminal; (1) slightly curved, mouth superior.
- [6] Maxilla, main axis, torsion: (0) not twisted; (1) slightly twisted.
- [7] Maxilla, ventral process, distal expansion: (0) absent; (1) present.
- [8] Dentary, coronoid process, extent relative to dorsal portion of angulo-articular: (0) extending above; (1) not extending above.
- [9] Angulo-articular, ventral process, shape: (0) well-developed, long; (1) short, well-visible in lateral view; (2) rudimentary, poorly or not visible in lateral view.
- [10] Autopalatine, ventral extremity, extent relative to dorsal portion of quadrate: (0) contacting; (1) not contacting.
- [11] Autopalatine, median portion, constriction: (0) absent; (1) present.
- [12] Autopalatine, general shape in lateral view: (0) nearly straight; (1) curved.
- [13] Autopalatine, postero-ventral process: (0) absent; (1) present.
- [14] Autopalatine, postero-ventral process, length relative to antero-ventral process: (0) shorter; (1) longer.
- [15] Quadrate, posterior process, shape: (0) narrow; (1) wide.
- [16] Mesopterygoid, extent relative to quadrate: (0) long, reaching metapterygoid and overlapping quadrate; (1) short, posterior tip in vertical through middle of quadrate, ventral portion slightly overlapping quadrate; (2) very short, posterior tip in vertical through anterior portion of quadrate.
- [17] Symplectic, shape: (0) short and deep; (1) long and narrow.

- [18] Preopercle, shape: (0) robust, L-shaped, with a well developed anteromedian rim; (1) thin, C-shaped, with a reduced anteromedian rim.
- [19] Pre-opercle, dorsal portion, shape: (0) broad and rounded; (1) narrow and pointed.
- [20] Basihyal, shape: (0) broad, triangular; (1) narrow, about rectangular.
- [21] Basihyal, length relative to length occupied by basibranchials: (0) shorter; (1) longer.
- [22] Urohyal, shape: (0) deep; (1) slender.
- [23] Interhyal, ossification: (0) ossified; (1) cartilaginous.
- [24] Interarcual element, ossification: (0) cartilaginous; (1) ossified.
- [25] Second pharyngobranchial, teeth: (0) present; (1) absent.
- [26] Epibranchials, shape: (0) short; (1) long.
- [27] Third epibranchial, uncinat process, shape: (0) narrow; (1) broad.
- [28] First hypobranchial, proximal edge, shape: (0) plain, terminating in single cartilage connected to second basibranchial; (1) bifid, terminating in cartilage connected to second basibranchial and another smaller cartilage connected to first basibranchial.
- [29] First hypobranchial, distal edge, articular face extent: (0) restricted to cartilaginous head of first ceratobranchial; (1) anteriorly expanded.
- [30] First hypobranchial, antero-lateral tip, anterior projection: (0) absent; (1) present.
- [31] Fourth ceratobranchial, teeth: (0) present; (1) absent.
- [32] Fifth ceratobranchial, shape in dorsal view: (0) moderately robust, approximately triangular; (1) slender, boomerang-shaped.
- [33] Fifth ceratobranchial, anterior portion, tooth plate extent: (0) separated from extremity by space; (1) near anterior condyle.
- [34] Fifth ceratobranchial, anterior portion, lateral flap: (0) present; (1) absent.
- [35] Caudal vertebrae, neural pre-zygapophyses, development: (0) well-developed; (1) rudimentary.
- [36] Caudal vertebrae, last neural spine, postero-basal portion, small process bearing ligament attached to anterior tip of epural: (0) absent; (1) present.
- [37] Caudal skeleton, hypurals, fusion degree: (0) separate; (1) fused.
- [38] Caudal skeleton, epural and parhypural, proximal region: (0) broad and approximately straight; (1) narrow and curved anteriorly.
- [39] Caudal skeleton, epural, distal portion, width relative to width of distal portion of parhypural: (0) approximately equal; (1) much wider.
- [40] Caudal skeleton, minute accessory caudal cartilages: (0) absent; (1) present.
- [41] Dorsal fin, origin relative to anal-fin origin: (0) posterior; (1) anterior.
- [42] Anal fin in males, anterior proximal radials, shape: (0) drop-shaped or sub-triangular; (1) rod-shaped.
- [43] Anal fin in males, anterior proximal radials, proximal region, proximity: (0) separated by interspace; (1) in close proximity.
- [44] Anal fin in males, first three or four proximal radials, cartilaginous proximal region, shape: (0) short; (1) long.
- [45] Anal fin in males, anterior portion, series of seven to ten small unbranched rays connected to first two developed anal-fin proximal radials to form an in-seminating fan: (0) absent; (1) present.
- [46] Anal fin in males, anterior two rays, shape and relative position to posterior portion of anal fin: (0) thin, short, not isolated from the posterior part of the fin; (1) long, thickened, separated from the posterior part of the fin by a deep gap in the fin membrane just posterior to second ray to form an in-seminating tube.
- [47] Anal fin in males, anterior two rays, basal portion, lateral sharp projections: (0) absent; (1) present.
- [48] Anal fin in males, sub-anterior portion, three to five branched rays connected to proximal radials 3-6, shape and relative position to posterior portion of anal fin: (0) straight, not separated from posterior portion of fin; (1) curved posteriorly, separated from posterior portion of fin by fin membrane gap.
- [49] Anal fin muscular support, anterior *inclinator*es and *depressor*es *anales*, development: (0) tiny; (1) hypertrophied.
- [50] Urogenital region in males, ejaculatory pump consisting of bulb-like structure formed by transverse muscular fibres: (0) absent; (1) present.
- [51] Pectoral fin, posttemporal, ventral process: (0) present; (1) absent.
- [52] Pectoral fin, supra-cleithrum, shape: (0) short; (1) long.
- [53] Pectoral fin, cleithrum, posterior flange: (0) present; (1) absent.
- [54] Pectoral fin, radials, shape: (0) well-ossified, cub form; (1) thin, weakly ossified, disc shaped.
- [55] Pectoral fin, radials, relative extent between ventral pectoral-fin radial and coracoid: (0) wide; (1) narrow.
- [56] Pectoral fin, dorsal-most radial, development: (0) well-developed; (1) rudimentary or absent.
- [57] Pectoral fin, first postcleithrum: (0) present; (1) absent.
- [58] Pelvic fin, ischial process: (0) present; (1) absent.
- [59] Pelvic fin bones, relative medial position: (0) in contact; (1) separated.
- [60] Genital duct and opening in males, relative position to anal fin: (0) duct terminating anterior to anal fin, opening close to anal-fin origin; (1) duct extending along anterior margin of anal fin, opening near the tip of first anal-fin ray.
- [61] Genital opening in males, shape: (0) small orifice; (1) broad transverse aperture.
- [62] Urogenital papilla in males, attachment to anal fin: (0) free; (1) attached.

- [63] Urogenital papilla in males, relative position to anal-fin origin: (0) separated by interspace; (1) in close proximity.
- [64] Urogenital papilla in males, basal portion, shape: (0) not distinctive; (1) forming pronounced wide structure.
- [65] Urogenital papilla in females: (0) minute gap; (1) prominent pocket-like structure overlapping anterior anal-fin origin.
- [66] Dorsal and anal fins in males, posterior extremity, shape: (0) rounded; (1) pointed.
- [67] Dorsal fin in males, tip, fin ray extension: (0) absent; (1) present.
- [68] Anal fin, basal portion, thickened tissue (possibly glandular): (0) absent; (1) present.
- [69] Anal fin in males, general shape: (0) about rectangular, anterior and distal margins of fin well-delineated; (1) about triangular, anterior and distal margins nearly continuous.
- [70] Anal fin in males, tip, long filamentous ray: (0) absent; (1) present.
- [71] Pelvic fin in males, posterior extent: (0) anal fin; (1) urogenital papilla.
- [72] Pelvic fin in males, shape: (0) nearly drop-shaped; (1) sub-triangular.
- [73] Caudal fin in males, shape: (0) oval, slightly longer than deep; (1) round, about so long as deep; (2) subtruncate; (3) lanceolate; (4) asymmetrical, dorsal margin slightly rounded, ventral margin straight.
- [74] Opercular and branchiostegal membrane, connection: (0) completely separated; (1) partially separated, gap posteriorly ending near middle of preopercle.
- [75] Jaws, shape and ventral branchiostegal gap shape: (0) long and broad, gaps between opercular and branchiostegal membranes parallel; (1) short and narrow, gaps between opercular and branchiostegal diverging anteriorly.
- [76] E-scales, relative medial position: (0) overlapped; (1) not overlapped.
- [77] Supraorbital squamation, development: (0) well developed; (1) rudimentary or absent.
- [78] Supraorbital series, anterior and posterior sections, arrangement: (0) separate; (1) continuous.
- [79] Supraorbital series, interruption at level of posterior nostril: (0) absent; (1) present.
- [80] Supraorbital series, neuromasts anterior to interrupted zone: (0) 2; (1) 1.
- [81] Caudal fin, base, neuromasts, number: (0) 1–2; (1) 4–7.
- [82] Flank, scale margin: (0) absent; (1) present.
- [83] Pectoral fin, inner surface: (0) absent; (1) present.
- [84] Chorion, surface: (0) plain to verrucate; (1) reticulate.
- [85] Chorion, surface, mushroom-like chorion projections: (0) absent; (1) present.
- [86] Flank in males, iridescent colour, arrangement pattern: (0) over whole flank; (1) restricted to midline of body; (?) taxa without iridescent marks.
- [87] Flank in males, iridescent marks, longitudinal arrangement: (0) continuous rows along flank; (1) fragmented rows along flank; (2) isolated in alternated scales to form vertical zigzag bars.
- [88] Flank in males, iridescent marks, colour: (0) light blue to yellowish green; (1) canary yellow
- [89] Flank in males, lateral midline, broad dark reddish chocolate brown to black stripe: (0) absent; (1) present.
- [90] Flank in males, ventral portion between pectoral-fin base and posterior portion of anal-fin base, dark reddish chocolate brown to black stripe: (0) absent; (1) present.
- [91] Flank in females, dark pigmentation: (0) rudimentary or absent; (1) present, forming distinctive dark marks.
- [92] Flank in females, dark bars: (0) absent; (1) present.
- [93] Dorsum in males, anterior portion, brown spots: (0) absent; (1) present.
- [94] Venter in males, middle zone, longitudinal dark brown stripe: (0) absent; (1) present.
- [95] Caudal peduncle in females, posterior-most portion, middle zone, black spots: (0) absent; (1) present.
- [96] Head in males, latero-ventral portion, stripe: (0) absent; (1) present.
- [97] Head in males, opercular region, three dark red bars (orbital, pre-opercular, opercular): (0) absent; (1) present.
- [98] Head in males, side, ascending oblique red stripe connecting orbital and opercular bars at level of ventral margin of orbit: (0) absent; (1) present.
- [99] Head in males, side, descending oblique dark reddish brown stripe connecting orbital bar and pectoral-fin base: (0) absent; (1) present.
- [100] Head in males, side, dark reddish brown pigmentation extending between orbit and posterior limit of head: (0) absent; (1) present.
- [101] Head in males, side, dark reddish brown pigmentation between lower jaw and orbit: (0) absent; (1) present.
- [102] Head in males, branchiostegal region, intense red pigmentation: (0) absent; (1) present.
- [103] Iris, bar through centre of eye: (0) absent; (1) present.
- [104] Iris in males, colour: (0) yellow to yellowish brown; (1) green; (2) blue.
- [105] Unpaired fins in males, distinctive dark red marks: (0) absent; (1) present.
- [106] Unpaired fins in males, distinctive white dots: (0) absent; (1) present.
- [107] Dorsal fin in males, distal zone, narrow bluish white stripe: (0) absent; (1) present.
- [108] Dorsal fin in males, distal zone, broad iridescent golden stripe: (0) absent; (1) present.
- [109] Dorsal fin in males, basal portion, brownish red stripe: (0) absent; (1) present.



*Cynopoecilus melanotaenia*

11101111111?10121110101001001010011011011111100111111101110101111100111111010?11011100111010001001101010000010000

*Cynopoecilus nigrovittatus*

1110111111010121110111001001010011011011111100111111101110101111100111111010?11011100111010001001101010000010000

*Cynopoecilus fulgens*

1110111111010121110101001001010011011011111100111111101110101111100111111010?11011100111010001001101010000010000