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Relações filogenéticas e revisão taxonômica das espécies do
gênero *Copella* Myers, 1956 (Characiformes: Lebiasinidae)

São José do Rio Preto
2014

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Tese apresentada como parte dos requisitos para obtenção do título de Doutor em Biologia Animal, junto ao Programa de Pós-Graduação em Biologia Animal, Área de Concentração - Sistemática e Evolução, do Instituto de Biociências, Letras e Ciências Exatas da Universidade Estadual Paulista “Júlio de Mesquita Filho”, Campus de São José do Rio Preto.

Orientador: Prof. Dr. Naércio Aquino Menezes

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RESUMO

Uma hipótese de relações filogenéticas do gênero *Copella* é proposta com base na análise de parcimônia de 120 caracteres morfológicos de todas as espécies do gênero reconhecidas como válidas na revisão taxonômica, e de 17 táxons do grupo externo, a maioria membros da família Lebiasinidae. O gênero é corroborado como monofilético com base em 38 sinapomorfias, das quais 13 são exclusivas, 19 homoplásticas, e seis dependentes de otimização. *Copella arnoldi* é o taxon basal, espécie irmã do clado composto por todas as demais espécies do gênero. O clado que inclui *Copella nattereri* e *C. stigmatsemion* é grupo irmão do clado (*C. eigenmanni* (*Copella compta* and *C. vilmae*)). *Copella* é grupo irmão de *Pyrrhulina*, e ambos são membros da subfamília Pyrrhulininae, caracterizados por apresentarem várias perdas ósseas e reduções relacionadas à complexidade da escultura dos seus esqueletos, principalmente em *Copella* e *Pyrrhulina*, quando comparados às espécies de Lebiasininae. Com base na análise filogenética e na observação da série ontogenética de vários representantes de Lebiasinidae, supõe-se que muitos traços morfológicos existentes em Pyrrhulininae tenham evoluído por meio do truncamento no desenvolvimento de caracteres. A análise do material tipo de todas as espécies nominais e de uma grande quantidade de exemplares de *Copella* de diversas drenagens da América do Sul, indicou que seis de dez espécies nominais devem ser reconhecidas como válidas: *Copella arnoldi*, *C. compta*, *C. eigenmanni*, *C. nattereri*, *C. stigmatsemion*, e *C. vilmae*. *Copella arnoldi* é sinônimo sênior de *C. carsevevnnensis*, *C. eigenmanni arnoldi* é sinônimo sênior de *C. metae*, *C. nattereri* é sinônimo sênior de *C. callolepis* e *C. meinken*i, e *C. stigmatsemion*, nova combinação, é sinônimo senior de *C. nigrofasciata*. Espécies de *Copella* ocorrem nas bacias dos rios Amazonas e Orinoco, e drenagens costeiras da Guiana, Guiana Francesa, Suriname e Venezuela.

Palavras-chave: Taxonomia. Filogenia. Peixes Neotropicais. Desenvolvimento truncado. Heterocronia. Lebiasinidae.

ABSTRACT

A hypothesis of the phylogenetic relationships of the genus Copella is proposed on the basis of the parsimony analysis of 120 morphological characters found in all the species of the genus recognized as valid in the taxonomic review, and 17 outgroup taxa, most of them members of the family Lebiasinidae. The genus is corroborated as monophyletic based on 38 synapomorphies, of which 13 are exclusive, 19 homoplastic, and six dependent of optimization. Copella arnoldi is the basal taxa, sister of a clade including the remaining species of the genus. The clade represented by Copella nattereri and C. stigmasemion is sister group of the clade (C. eigenmanni (Copella compta and C. vilmae)). Copella is sister of Pyrrhulina, and both are members of the subfamily Pyrrhulininae characterized by having several bony losses and reductions related to the complexity of the sculpturing of their skeleton, especially in Copella and Pyrrhulina, when compared to species of Lebiasininae. Based on the results of the phylogenetic analysis and on the observation of the ontogenetic series of several representatives of Lebiasinidae, it is supposed that many morphological traits present in the Pyrrhulininae have evolved through developmental truncation of characters. Based on the analysis of the type material of all nominal species and of a large number of specimens of Copella from several drainages in South America, six out of ten nominal species are recognized as valid: Copella arnoldi, C. compta, C. eigenmanni, C. nattereri, C. stigmasemion, and C. vilmae. Copella arnoldi is considered senior synonym of C. carsevennensis, C. eigenmanni is a senior synonym of C. metae, C. nattereri is a senior synonym of C. callolepis and C. meinkenii, and C. stigmasemion, new combination, is a senior synonym of C. nigrofasciata. The species Copella occur in the rio Amazonas and Orinoco basins, and coastal drainages of Guyana, French Guiana, Surinam, and Venezuela.

Keywords: Taxonomy. Phylogeny. Neotropical fishes. Developmental truncation. Heterochrony. Lebiasinidae.

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INTRODUCTION

Fishes of the Neotropical family Lebiasinidae occur in Central America (Costa Rica and Panama), and in all South American countries, except Chile (Weitzman & Weitzman, 2003). The family includes about 70 valid species (Eschmeyer & Fricke, 2013) distributed in two subfamilies, Lebiasininae and Pyrrhulinae, and seven genera: *Copeina* Fowler, *Copella* Myers, *Derhamia* Géry & Zarske, *Lebiasina* Valenciennes, *in* Cuvier & Valenciennes, *Nannostomus* Günther, *Piabucina* Valenciennes, and *Pyrrhulina* Valenciennes (Weitzman & Weitzman, 2003). Members of the family are recognizable by having a rather elongate, cylindrical body, large scales, laterosensory canal of head and body reduced, anal fin short-based, no frontal or parietal fontanel (Weitzman & Weitzman, 2003), and absence of the metapterygoid-quadrate fenestra (Weitzman, 1964).

A historical review of the relationships of members of the Lebiasinidae with other Characiformes is complex and was summarized by Weitzman (1964). Eigenmann (1910) was the first to propose groups of species now belonging to the Lebiasinidae, as Nannostomatinae, Pyrrhulinae, Piabucinae, and Lebiasininae, subfamilies of the Characidae. Lebiasinidae was included among the families recognized by Greenwood, *et al.* (1966) within the Characoidei (= Characiformes), further formally considered as a family by Weitzman & Cobb (1975). The most recent morphological based phylogenetic studies including members of the family recovered Lebiasinidae as monophyletic (Lucena, 1993; Vari, 1995; Buckup, 1998; Netto-Ferreira, 2006, 2010), but not those of Oyakawa (1998) and Moreira (2007), in which Lebiasinidae includes also the Erythrinidae. Molecular based phylogenies also indicated Lebiasinidae either as a monophyletic group (Calcagnotto *et al.*, 2005; Oliveira *et al.*, 2011), or two of three weakly supported hypotheses considering Lebiasinidae non-monophyletic (Ortí &

Meyer, 1997). Such studies (except for the tree in Ortí & Meyer, 1997) indicated members of the Lebiasinidae more closely related to members of the Erythrinioidea (*sensu* Buckup, 1998), a group including Erythrinidae, Ctenoluciidae, Hepsetidae e Lebiasinidae.

Since Weitzman (1964), *Copeina*, *Copella*, *Pyrrhulina*, and *Nannostomus* are treated as belonging to the same group (his tribe Pyrrhulinini). The genera *Copeina*, *Copella*, and *Pyrrhulina* have been long considered as closely related (*e.g.* Eigenmann, 1910; Regan, 1912). Some *Copella* species have been even considered to belong either in *Pyrrhulina* or *Copeina*. On the other hand, the position of *Nannostomus* is more complex (see Weitzman, 1964 for a historical review of the classification of the genus). After the results expressed in Greenwood, *et al.* (1966), Weitzman & Cobb (1975) elevated Lebiasininae to the family level, suprageneric categories were modified, but the basic classification of Weitzman (1964) as indicated below is still in use:

Family Lebiasinidae

Subfamily Lebiasininae

Lebiasina

Piabucina

Subfamily Pyrrhulininae

Tribe Nannostomini

Nannostomus

Tribe Pyrrhulinini

Copeina

Copella

Pyrrhulina

Derhamia, a new genus described by Géry & Zarske (2002) was included in the Lebiasininae, but the phylogenetic analysis of Netto-Ferreira (2006, 2010) suggested the genus is basal taxa within Pyrrhulininae.

The genus *Copella* was created by Myers (1956) based on the presence of a maxilla triply curved (“S” shaped), more pronounced on males. In the same paper, he transferred *Copeina compta* Myers, *Pyrrhulina nattereri* Steindachner, and *Copeina callolepis* Regan, to *Copella* and designated *Copella compta* as the type species. Although Myers (1956) stated that no other species of the “*Pyrrhulina-Copeina*” group could be identified as *Copella*, Géry (1977) found that all the species previously recognized as *Copeina* (*C. arnoldi* Regan, *C. carseveennensis* Regan, *C. eigenmanni* Regan, *C. metae* Eigenmann and *C. nigrofasciata* Meinken) should be transferred to *Copella*, except *Copeina guttata* (Steindachner) and *Copeina osgoodi* Eigenmann. Later on, Géry (1963) and Zarske & Géry (2006) described *Copella vilmae* and *C. meinkeni*, respectively.

The taxonomic problems related to the species of *Copella* range from unclear diagnoses (see Géry, 1977), type material not represented by the same species (Weitzman & Weitzman, 2003), and literature misidentifications (e.g. Zarske & Géry, 2006). Currently, the genus includes ten nominal species: *Copella arnoldi*, *C. carseveennensis*, *C. callolepis*, *C. compta*, *C. eigenmanni*, *C. metae*, *C. nattereri*, *C. nigrofasciata*, *C. vilmae*, and *C. meinkeni*, all, except *C. metae* valid.

Examination of a large amount of material of *Copella* from the Amazon and Orinoco basins and coastal drainages of Brazil, Guyana, French Guiana, Suriname, and Venezuela, and of type material of all nominal species made possible a comprehensive taxonomic revision of the species of *Copella*. A dichotomous identification key and distribution maps are also presented. The phylogenetic relationships of species were studied and a hypothesis of their evolutionary history is included based on morphological characters.

MATERIAL AND METHODS

PHYLOGENETIC ANALYSIS

Phylogenetic methods. The methodology employed for proposing hypotheses of relationships was cladistic, or phylogenetic, as first proposed by Hennig (1950, 1966) and subsequently developed by series of other authors.

Data matrix was built in MESQUITE (Maddison & Maddison, 2011). Tree manipulations, diagnoses and character optimization were executed in WINCLADA (Nixon, 1999-2002). Missing entries (?) represent lack of appropriate material or impossibility of coding the state for that taxon. Inapplicable character states are represented by “-“. Multistate characters were analyzed unordered except when a morphocline could be unambiguously determined. Character state polarity was determined by outgroup comparison.

Parsimony analysis was performed using TNT (Goloboff *et al.*, 2008), through implicit enumeration. Consistency Index (CI) and Retention Index (RI) were obtained from the set of most-parsimonious trees. Accelerated transformations (ACCTRAN) or delayed transformations (DELTRAN) algorithms were used to resolve ambiguous character reconstruction. Each ambiguous character was evaluated independently, following the arguments of Agnarsson & Miller (2008). For Bremer support, Tree Bisection Reconnection (TBR) was applied having as a starting point the two most-parsimonious trees (280 steps), retaining suboptimal trees with a maximum of 50 additional steps (330). Bremer was calculated with the 99688 trees found, with maximum memory limit of 99.999.

Selection of taxa. Twenty three taxa were included as terminals in the analysis. Ingroup is composed of all *Copella* species considered valid in the taxonomic analysis: *Copella arnoldi*, *C.*

compta, *C. eigenmanni*, *C. nattereri*, *C. stigmasemion*, and *C. vilmae*. As presented in the Introduction, *Copella* is a member of the Lebiasinidae. Thus, outgroup is composed of representatives of all genera of Lebiasinidae, in order to sample the morphological variation of the family: *Copeina*, *Derhamia*, *Lebiasina*, *Nannostomus*, and *Piabucina*, and *Pyrrhulina*. Rooting was fixed in *Hoplerythrinus unitaeniatus*, a representative of Erythrinidae, member of Erythrinioidea, accepted as close taxon of Lebiasinidae (Lucena, 1993, Buckup, 1998; Oyakawa, 1998; Netto-Ferreira, 2006, 2010; Moreira, 2007).

At least one male and one female of each terminal taxon were cleared and stained, except for *Copella vilmae* (one male), *Derhamia hoffmannorum* (three immatures), and *Lebiasina* cf. *yuruaniensis* (one male) due to the lack of enough specimens available for the procedure. When possible, several specimens of each species, of distinct ontogenetic stages were analyzed. Ontogenetic series of *Copella eigenmanni*, *Lebiasina* cf. *bimaculata*, *Nannostomus beckfordi*, and *Pyrrhulina spilota* were useful to discuss several aspects of character evolution within the Lebiasinidae. Bony presence in the developmental series was assigned to the earliest sign of ossification based on uptake of alizarin red staining of mineralized bone matrix, following to Bird & Mabee (2003). Notochord length (NL) was taken in specimens with no hypural ossified, and standard length (SL) on those whose mineralization can be seen in any of the hypurals.

With the inclusion of *Derhamia hoffmannorum* in Pyrrhulininae, Netto-Ferreira (2006, 2010) proposed new ranks for the subfamily, the tribe Derhamiini and the tribe Pyrrhulinini encompassing the subtribes Nannostomina and Pyrrhulinina. As this is a result of an unpublished thesis, such classification will not be adopted herein. Thus we follow Weitzman & Cobb (1975) classification, with the inclusion of *Derhamia* in the Pyrrhulininae.

Character considerations. The anatomic study was based on alcohol preserved specimens for

external morphology and cleared and stained (c&s) specimens for osteology, prepared according to Taylor & van Dyke (1985). Previous utilized characters are followed by literature citation and the number of characters analyzed, except for Weitzman (1964), whose character propositions are prior to the application of rigorous methods of phylogenetic reconstruction (Vari, 1995), though were widely utilized and not cited accordingly. Some characters were modified (Mod.) from the literature in order to better represent the condition of the examined taxa. Characters previously proposed but not used in the present study are listed in the “Unutilized characters” section.

Osteological terminology basically follows Weitzman (1962) with the following modifications suggested by subsequent authors (*e.g.* Vari, 1979, 1995; Fink & Fink, 1981, 1996; Zanata & Vari, 2005): mesethmoid instead of ethmoid, vomer instead of prevomer, epioccipital instead of epiotic, endopterygoid instead of mesopterygoid, intercalar instead of opisthotic, anterior ceratohyal instead of ceratohyal, posterior ceratohyal instead of epihyal. Basipterygium is used instead of pelvic bone. Inner arm of the os suspensorium is used instead of os suspensorium, and outer arm of the os suspensorium instead of rib of fourth vertebra, following Britz & Conway (2009) and Britz *et al.* (2009). Abdominal vertebrae are vertebrae associated with ribs or hemal arches without hemal spines. Caudal vertebrae are vertebrae associated with hemal spines. Exceptions to terminological suggestions are explained in the appropriated section.

In the figures, numbers show character state proposed.

TAXONOMIC REVIEW

The taxonomic review follows the species concept discussed by Nelson & Platnick (1981) that consider the smallest detected sample of organisms that have a unique set of characters.

Aquarium magazines were not included in the synonym list, except articles with important taxonomic significance (*e.g.* description of *Pyrrhulina nigrofasciata*). Counts and measurements basically follow Fink & Weitzman (1974), with the addition of depth at dorsal-fin origin, pectoral to pelvic-fin origin, pelvic to anal-fin origin, and anal-fin base length, measured point to point, and the first longitudinal scale row, the first scale row lateral to the predorsal scale series, fourth longitudinal scale row, the mid-dorsal scale series, longitudinal scale rows between dorsal-fin origin and pelvic-fin origin, and longitudinal scale rows between dorsal-fin origin and anal-fin origin. Principal caudal-fin rays include all the branched rays plus one unbranched ray in each lobe, following Hubbs & Lagler (1947) and Lundberg & Baskin (1979). Teeth and unbranched anal-fin ray counts were taken from c&s material. Maxillary teeth count of *C. vilmae* were made on alcohol material by transparency, due to the lack of enough material to c&s. Teeth were only counted in adult specimens, as juveniles have lesser teeth counts. Meristics of the holotype of *Copella stigmaseion* were not taken due to the poor condition of the material.

In the species descriptions, counts are followed by their frequencies in parentheses. Asterisks indicate the counts of the holotype, lectotype or syntypes. Measurements are given as percents of standard length (SL), except for subunits of the head given as percents of head length. Counts of vertebrae were made in c&s specimens and through x-rays. Vertebrae of the Weberian apparatus were counted as four elements and the fused PU1+U1 of the caudal

region as a single element. Color in alcohol does not follow the nomenclature proposed by Weitzman (1966) for *Nannostomus* to avoid problems of homology (the longitudinal mid-lateral stripe on body, defined as “primary stripe”, does not seem to correspond to the same melanophore pattern within *Copella*). Color in life section was based on observation of fresh collected material for *C. arnoldi*, *C. eigenmanni* and *C. nattereri* and on photographs of living specimens for the remaining species.

The anal-fin inclinator muscle of the last pterygiophore is thicker and inserted more distally in the last anal-fin ray of males than of females of several lebiasinids, especially *Copella*. This was confirmed by the examination of the gonads of one male and one female of *Copella arnoldi* (MZUSP 105776), *C. eigenmanni* (MZUSP 81443), *C. nattereri* (MZUSP 87426), and *C. stigmaseion* (MZUSP 101933). *Copella compta* and *C. vilmae* were not dissected due to the lack of enough material for such procedure. The anal-fin inclinator muscle is considerably thick in even early developmental stages of males, before other external secondary sexual features appear, such as dimorphic coloration or elongate fins. Therefore, this structure was used to sex *Copella*. Due to the impossibility to unambiguously set female and immature males (fem/imm) apart, they were treated together. Fin length of males and females or immatures was displayed separately in the tables. Linear regression was applied in fin length of each species in order to detect sexual dimorphism, if any.

Catalog numbers are followed by the number of specimens in alcohol, the number of c&s specimens and the number of specimens prepared for musculature analysis (mus) [according to Datovo & Bockmann (2010)], if any, and their SL range. Municipality originally referred as Tapurucuara was treated as Santa Isabel do Rio Negro, which is the formal name of the city. In the geographic distribution map, localities with no specific data were plotted on the respective city.

Institutional abbreviations are AMNH, American Museum of Natural History, New York, USA; ANSP, Academy of Natural Science of Philadelphia, USA; BMNH, Natural History Museum, London, UK; DZSJRP, Departamento de Zoologia e Botânica da Universidade Estadual Paulista, São José do Rio Preto, Brazil; CAS, California Academy of Science, San Francisco, USA; CM, Carnegie Museum, now at FMNH; CZUT-IC, Colección Zoológica de la Universidad del Tolima, Ictiología, Ibagué, Colombia; FMNH, Field Museum of Natural History, Chicago, USA; IavH, Colección de peces dulceacuícolas del Instituto Alexander Von Humboldt, Villa de Leyva, Colombia; ICNMHN, Unidad de Ictiología del Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá, Colombia; IU, Indiana University (now distributed among several North American museums); INPA, Instituto Nacional de Pesquisa da Amazônia, Manaus, Brazil. MBUCV, Museo de Biología, Universidad Central de Venezuela, Caracas, Venezuela; MCNG, Museo de Ciencias Naturales, Guanare, Venezuela; MCZ, Museum of Comparative Zoology, Cambridge, USA; MHNG, Museum d'Histoire naturelle, Geneve, Switzerland; MNHN, Museum National d'Histoire Naturelle, Paris, France; MHNLS, Museo de Historia Natural La Salle, Caracas, Venezuela; MLS, Museo de La Salle, Universidad de La Salle, Bogotá, Colombia; MPEG, Museu Paraense Emílio Goeldi, Belém, Brazil; MSNG, Museo Civico di Storia Naturale di Genova 'Giacomo Doria', Genova, Italy. MTD F, Museum für Tierkunde, Senckenberg Naturhistorische Sammlungen Dresden, Dresden, Germany; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; NMW, Naturhistorisches Museum, Vienna, Austria; NRM, Naturhistoriska riksmuseet, Stockholm, Sweden; SIU, Southern Illinois University at Carbondale, Carbondale, USA; SMF, Senckenberg-Museum, Frankfurt am Main, Germany; SU, Stanford University, now in CAS; UNIR Fundação Universidade Federal de Rondônia, Porto Velho, Brazil; USNM, National

Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; ZMA, Zoologisches Museum, Universiteit van Amsterdam, Amsterdam, The Netherlands; ZMB, Zoologisches Museum, Humboldt-Universität, Berlin, Germany; ZMH, Zoologisches Museum und Zoologisches Institut, Universität Hamburg, Hamburg, Germany, ZMUC, Zoological Museum, University of Copenhagen, Copenhagen, Denmark.

RESULTS AND DISCUSSION

CHARACTER DESCRIPTION

External morphology

1. Longitudinal dark stripe on head: (0) absent, (1) present. (CI = 100, RI = 100).

Members of the Lebiasinidae have a complex color pattern. It is composed of spots, bands and stripes, whose combination may change (see color in alcohol description of *Copella eigenmanni*). Characters of coloration proposed herein for *Copella* are further illustrated in the “Taxonomic Review” section. For example, *Nannostomus* species are known to have “night pigment”, coloration usually present at night, whereas some species of *Copella* and *Pyrrhulina* have a sexually dimorphic color pattern.

Weitzman (1966) proposed a specific nomenclature for melanophore patterns of *Nannostomus*. According to him, the primary stripe corresponds to the main mid-lateral stripe usually extending from the snout to the caudal fin. Within *Copella*, “primary stripe” on body does not seem to always correspond to the same melanophore pattern (see discussion for “Extension of primary stripe” under “Unutilized character” section) and thus this nomenclature is not followed herein. Therefore, the longitudinal dark stripe that extends from tip of lower jaw to posterior end of opercle seems to be homologous in Lebiasinidae, and is present in most genera (state 1, Fig. 1), except *Lebiasina* and *Piabucina*, which lack such pigmentation (state 0).

A distinct condition is found in *Hoplerithrynus unitaeniatus*, which have two oblique dark stripes posterior to eye. Thus this species was coded as state 0.

2. Series of red spots on body in life: (0) absent, (1) present. (CI = 25, RI = 25).

Some species of the Lebiasinidae present series of red spots on the scales of the body when live (*Copeina*, *Copella nattereri*, *C. stigmatemion*, *Lebiasina bimaculata*, and *Pyrrhulina* cf. *stoli*). These red spots become white or clear areas when the fish is preserved. This is not the same pigmentation that may be present in some adult males of *Copella arnoldi*, in which the spots are white in life and in preserved specimens.

Copella compta, *Lebiasina* cf. *yuruaniensis*, *Piabucina unitaeniata*, *Pyrrhulina* cf. *brevis*, and *P. marilynae* were coded as missing entries as the color in life of these species could not be safely verified.

3. Round dark spot on the dorsal fin of adults: (0) absent, (1) present (CI = 100, RI = 100).

[Bührnheim, 2006: 159; Netto-Ferreira, 2006: 303; 2010: 196; Mirande, 2010: 343]

Most Characiformes have hyaline fins, but a dorsal spot is present for example in the Curimatidae, Characidae and Lebiasinidae. Within the Lebiasinidae, a round dark blotch on middle portions of the dorsal fin represents a unique synapomorphy for the tribe Pyrrhulinini (state 1, Fig. 1). In the species of the remaining genera adult specimens lack any dark round spot (state 0). However, a small blotch on the anterior portions of dorsal fin of is visible in juveniles of *Nannostomus* and *Lebiasina* (e.g. *N. beckfordi*, *N. harrisoni*, *N. marginatus*, *L. bimaculata*, *L. minuta*) (see Weitzman & Cobb, 1975: fig 8 and 23). A similar blotch can also be seen in adults of *Nannostomus trifasciatus* (Weitzman & Cobb, 1975: fig. 27). The presence

of such a dark spot in adults of *Copeina*, *Copella*, and *Pyrrhulina* is probably retention of a juvenile character in specimens of these three genera.

Adults of *Nannostomus marginatus* have the anteriormost two dorsal-fin rays dark, a condition apparently not homologous to the presence of a round blotch on the anterior portions of the dorsal fin present in juveniles (Weitzman & Cobb, 1975: fig. 23) and in *Copeina*, *Copella*, and *Pyrrhulina*. Thus *Nannostomus marginatus* was coded as state 0.

In *Pyrrhulina* cf. *brevis* the character was coded as missing entry due to the lack of alcohol preserved specimens.

4. Dark pigmentation on the anal-fin distal edge of mature males: (0) absent, (1) present. (CI = 50, RI = 87).

Mature males of *Copella*, *Pyrrhulina* and some *Nannostomus* species have the edge of the anal fin dark (Fig. 1). This character can also be seen in females and juveniles of *Copella* and *Pyrrhulina*, but this pigmentation is less conspicuous when present. As this feature is highly polymorphic in females and juveniles, it was only coded in mature males.

In *Pyrrhulina* cf. *brevis* the character was coded as missing entry due to the lack of alcohol preserved specimens.



Figure 1. *Copella arnoldi*, live specimens, MZUSP 105770, (A) male, 39.9 mm SL, (B) female, 27.9 mm SL, Vigia, Pará, Brazil.

5. Dark pigmentation on the dorsal and ventral procurrent caudal-fin rays: (0) absent, (1) present. (CI = 100, RI = 100).

[Netto-Ferreira, 2006: 305; 2010: 198]

Dark dorsal and ventral procurrent caudal-fin rays are only found in the species of the genus *Copella*, a character shared by all species, except *C. arnoldi* and some populations of *C. nattereri* from rio Negro basin. Specimens of *Copella compta* analyzed presented only the ventral procurrent rays dark, a condition probably due to the preservation of the material. Dorsal and ventral procurrent rays dark is present in males and females, though less conspicuous in the later. It was only observed in adults, once juveniles frequently have dorsal and ventral procurrent caudal-fin rays hyaline in all the species.

The absence of pigmentation on the procurent caudal-fin rays was used by Zarske & Géry (2006) as one of the features to diagnose a new species, *Copella meinkeni*. However, according to the present study, *Copella meinkeni* is a junior synonym of *C. nattereri* and this character is interpreted as polymorphic (see Remarks of *Copella nattereri* under the taxonomy review section).

In *Pyrrhulina* cf. *brevis* this character was coded as missing entry due to the lack of alcohol preserved specimens.

6. Faint dark pigmentation at base of the upper caudal-fin lobe on females and juveniles: (0) absent, (1) present. (CI = 100, RI = 100).

Females and juveniles of *Copella compta* and *C. vilmae* have a faint concentration of chromatophores on the base of the upper caudal-fin lobe. This pigmentation can be used as a diagnostic feature to identify females and juveniles of both species, since they are allopatric. No other species analyzed present such pigmentation.

In *Pyrrhulina* cf. *brevis* the character was coded as missing entry due to the lack of alcohol preserved specimens.

7. Dark round spot on middle caudal-fin rays: (0) absent, (1) present. (CI = 100, RI = 100).

[Buckup, 1993: 63; Netto-Ferreira, 2006: 304; Mod.: Netto-Ferreira, 2010: 197]

Lebiasina bimaculata, *Lebiasina* cf. *yuruaniensis*, and *Piabucina unitaeniata* have a conspicuous black round spot on the base of the middle caudal-fin rays. Such character is synapomorphic for this group of species.

In *Copella eigenmanni* and *Pyrrhulina marilynae* the middle caudal-fin rays are dark, but due to the continuation of the mid-lateral dark stripe. In *Copella eigenmanni*, the middle caudal-fin rays are completely dark, from the base to their tips. In *Pyrrhulina marilynae*, the caudal mark is inconspicuous and fades posteriorly (Netto-Ferreira & Marinho, 2013: fig. 1). As the caudal mark in both species seems to be a distinct condition found in *Lebiasina*, they were coded as state 0.

In *Pyrrhulina* cf. *brevis* the character was coded as missing entry due to the lack of alcohol preserved specimens.

8. Sexually dimorphic coloration on flank: (0) absent, (1) present. (CI = 25, RI = 25).

[Mod.: Zanata & Vari, 2005: 192, 195]

Some species of Lebiasinidae present dimorphic coloration on the body. Males develop an ornamented coloration whereas the females retain the juvenile color pattern (Fig. 1). This was observed in *Copella arnoldi*, *C. compta*, *C. vilmae*, *Nannostomus anduzei* and *Pyrrhulina stoli*.

Zanata & Vari (2005: 192, 195) discussed the sexually dimorphic color pattern modifications but as pointed out below (see “Extension of primary stripe” under “Unutilized characters” section), lebiasinid species have a complex color pattern that makes difficult tracing homology without further studies on pigmentation.

This character only considered in preserved material due to the lack of color in life information for several species.

In *Pyrrhulina* cf. *brevis* this character was coded as missing entry due to the lack of alcohol preserved specimens.

9. Mouth position: (0) terminal, (1) superior. (CI = 50, RI = 75).

[Buckup, 1993: 37; Oyakawa, 1998: 72; Netto-Ferreira, 2006: 73; 2010: 42.]

Within the Lebiasinidae, the species considered to have terminal mouth are found only in the genus *Nannostomus*. The remaining members of the family present superior mouth (Figs. 1-3). Netto-Ferreira (2006, 2010) considered *Lebiasina* species as having a “subsuperior” mouth, but coded them as having mouth terminal, since the mouth aperture cannot be observed in dorsal view. However, in all the *Lebiasina* species analyzed herein the mouth is slightly upturned, and it can be seen in dorsal view. Thus *Lebiasina* was considered as having mouth superior (state 1).

10. Relative position of anterior and posterior nares: (0) juxtaposed, close to each other, (1) distant from each other. (CI = 33, RI = 80).

[Buckup, 1993: 39; Oyakawa, 1998: 5; Netto-Ferreira, 2006: 271; 2010: 167]

Most characiforms have the anterior and posterior nares close to each other. Miranda (2010) proposed separated nares as synapomorphy of *Coptobrycon* Géry and *Grundulus*

Valenciennes. Géry (1977) used this character in the key to distinguish *Copella* (nostrils separated from each other, Fig. 2) from *Copeina* and *Pyrrhulina* (nostrils close to each other, Fig. 3). This is an external easy feature to help distinguishing *Copella* from members of the family, except from *Nannostomus*.

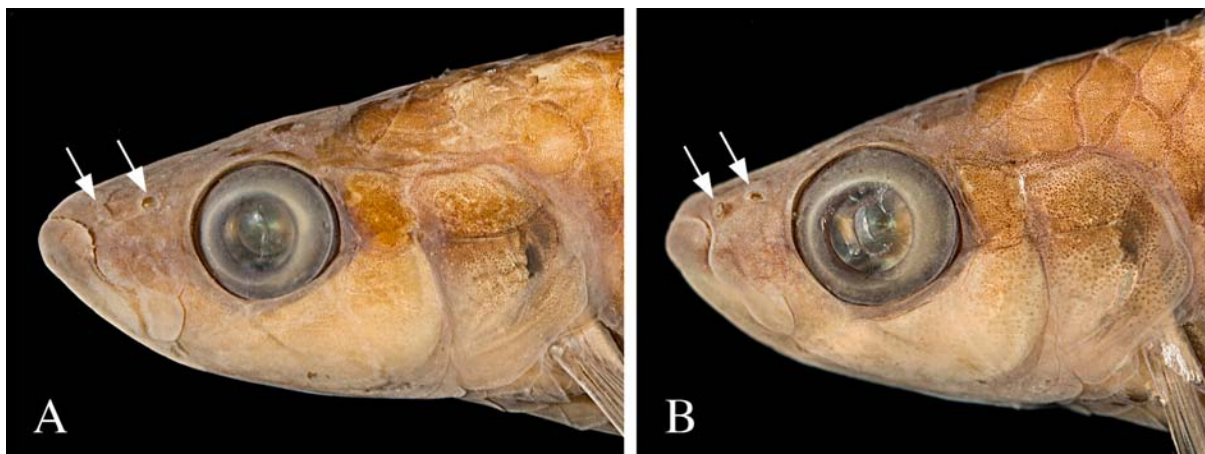


Figure 2. Lateral view of head of *Copella compta*, MZUSP 9162 (A) male, 68.9 mm SL, (B) female, 40.3 mm SL. Arrows show anterior and posterior nares. Also note differences in the curvature of the anterior border of maxilla between male and female.



Figure 3. Lateral view of head of *Pyrrhulina filamentosa*, MHNLS 14271, male, 63.0 mm SL. Arrows show anterior and posterior nares.

11. Extension of first longitudinal scale row on body: (0) from head to end of caudal peduncle, (1) from head to dorsal-fin end, (2) from head to dorsal-fin origin, (3) not reaching dorsal-fin origin. (Unordered). (CI = 60, RI = 85).

[Netto-Ferreira, 2010: 179]

Within the Lebiasinidae the first longitudinal scales row on body extending from head to end of caudal peduncle is an exclusive synapomorphy for *Nannostomus* (shared only with *Hoplerythrinus*) (state 0). In *Copeina*, *Derhamia*, *Lebiasina*, and *Piabucina* it extends from head to dorsal-fin end (state 1). First longitudinal scales row on body not reaching dorsal-fin origin (state 3) is a synapomorphy for the *Copella* and *Pyrrehulina*, further reverted to state 2 (extending from head to dorsal-fin origin) in *Pyrrehulina marilynae* and clade 43.

In *Pyrrehulina* cf. *brevis* the character was coded as missing entry due to the lack of alcohol preserved specimens.

12. Adipose fin: (0) absent, (1) present. (CI = 50/33, RI = 50/0).

[Weitzman, 1964; Backup, 1993: 45; Vari, 1995: 81; Netto-Ferreira, 2006: 240; 2010: 148; Moreira, 2007: 339; Mirande, 2010: 356]

The adipose fin is present in most Characiformes. Among the taxa examined, the only species having adipose fin are *Derhamia hoffmannorum*, *Lebiasina* cf. *yuruaniensis*, and *Piabucina unitaeniata*. The adipose fin is present in the available specimens of *Nannostomus eques* but it

was coded as polymorphic taking into consideration Weitzman's (1966) broader survey of *Nannostomus* species.

13. Comparative length of mature males and females: (0) males and females of the same size or almost, (1) males distinctly longer than females. (Unordered). (CI = 100, RI = 100).

Males and females of all genera, except *Copella*, are basically of the same size. Sexual dimorphism in length is a unique synapomorphy for *Copella*, in which males are distinctly longer than females (Fig. 1). Observations of *Copella arnoldi* kept in aquarium revealed that the males frequently use to laterally pair themselves for display, widely opening all the fins and mouth, and slightly shaking their body. Only larger males used to compete.

Zarske & Géry (2002) commented for *Derhamia*: “probably not reaching more than 65 mm SL in males and 70 mm SL in females in aquarium”. It was not possible to confirm this due to the lack of enough mature material but, if this is correct, *Derhamia hoffmannorum* is the only species analyzed where males are smaller than females. As the difference between both sexes is apparently small, *Derhamia* was coded as state 0.

Data for *Pyrrhulina spilota* was taken from the original description. In *Lebiasina* cf. *yuruaniensis* and *Pyrrhulina* cf. *brevis* the character was coded as missing entries due to the lack of enough alcohol preserved specimens.

14. Elongate fins in mature males: (0) absence, (1) presence. (Unordered). (CI = 50, RI = 89).

[Netto-Ferreira 2006: 282; 2010: 173; Mod.: Mirande, 2010: 268]

Among members of Lebiasinidae, only males of *Copella* and *Pyrrhulina*, except *P. australis* and *P. marilynae* (Netto-Ferreira & Marinho, 2010: fig. 1) have fins longer than females (Fig. 1). Géry (1977) used the presence of “filamentous fins” to distinguish *Copella* from *Copeina*. Long fins on males are possibly used as display when competing for resource (see discussion of character 13).

15. Comparative length of caudal-fin lobes: (0) upper lobe as longer as lower lobe or almost, (1) upper lobe distinctly longer than lower lobe. (CI = 100, RI = 100).

Upper caudal fin lobe longer than the lower one is a unique synapomorphy of the tribe Pyrrhulinini. This is not a sexual dimorphic character and can be observed in both males and females, although more evident in mature males (Fig. 1; Netto-Ferreira & Marinho, 2013: figs. 1 and 2). Both males and females of *Derhamia*, *Nannostomus*, *Lebiasina* and *Piabucina* analyzed do not have the upper caudal-fin lobe elongated (Weitzman & Cobb, 1975: figs. 2-30); the lobes are of the same size or almost. Some species of *Nannostomus* (e.g. *N. eques*) have the lower caudal-fin lobe wider than the upper lobe, but not longer.

Neurocranium

16. Mesethmoid : (0) “T” shaped, (1) rectangular, (2) rounded. (Unordered). (CI = 100, RI = 100).

[Weitzman, 1964; Oyakawa, 1998: 19; Netto-Ferreira, 2006: 30; 2010: 17]

In general, three distinct forms of the mesethmoid are visible in the Lebiasinidae in dorsal view: T-shaped (Netto-Ferreira, 2012: fig. 3b), synapomorphy for the clade represented by *Lebiasina* and *Piabucina*; elongate, approximately rectangular (Weitzman, 1964: fig. 2), unique for *Nannostomus*; and approximately hexagonal or rounded in *Copeina*, *Copella*, *Derhamia* and *Pyrrhulina* (Figs. 4A and 5), also shared by *Hoplerythrinus*.

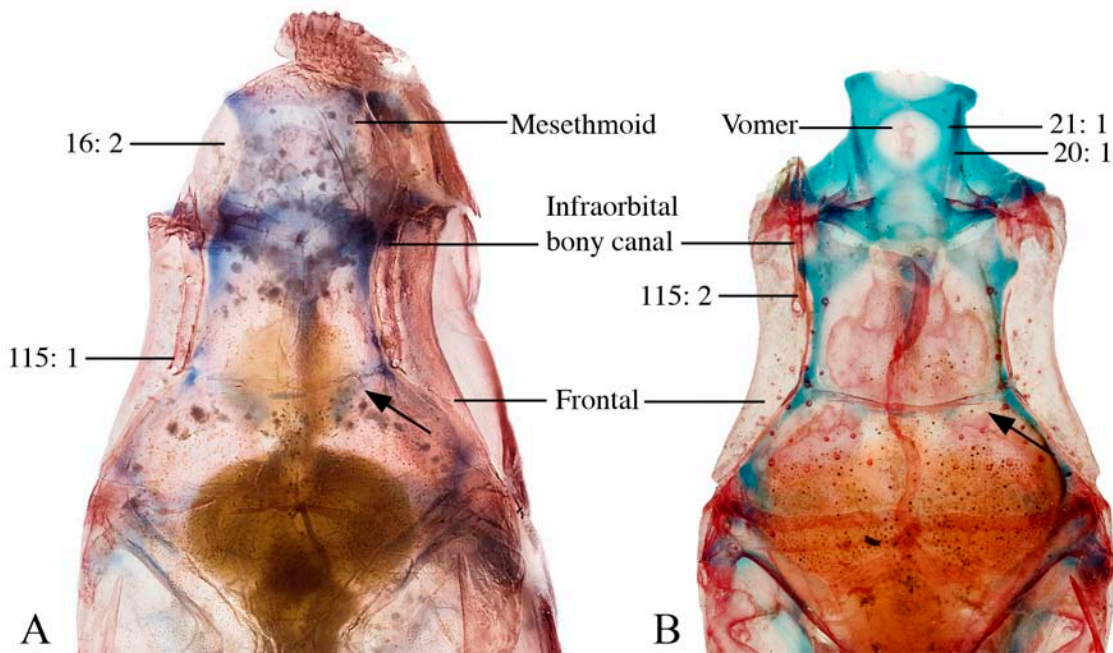


Figure 4. Dorsal view of head of (A) *Copella vilmae*, AMNH 218053, male, 42.4 mm SL, and (B) *Copella nattereri*, MZUSP 87426, male, 38.7 mm SL. Arrows indicate the epiphyseal bar. Mesethmoid was removed in (B).

17. Distance between mesethmoid and vomer: (0) in contact or almost, (1) distant from each other by a large patch of cartilage. (CI = 33, RI = 78).

[Buckup, 1993: 2]

The vomer of *Derhamia*, *Copeina*, *Lebiasina*, *N. eques*, *Piabucina*, and *Pyrrhulina*, except *P. filamentosa*, is comparatively better developed and thicker, especially in *Derhamia*, *Lebiasina*, *Piabucina*, and *N. eques* (state 0, Fig. 6A). In these species, the distance between vomer and mesethmoid is shorter, the bones being in contact or almost. In contrast, the small size of the vomer in *Copella*, *Nannostomus anduzei*, *N. beckfordi* and *N. marginatus* preclude a close contact of this bone with the mesethmoid anteriorly. In these species, the vomer remains distant from the mesethmoid due to the presence of a large patch of cartilage (state 1, Fig. 6B). Although in *Pyrrhulina filamentosa* the vomer is more developed when compared to that of the above-mentioned species, its anterior portion is also far from the mesethmoid, and thus in this species was also coded as representing the state 1.

Characters 17, 18, 19 and 21 describe the variation of the vomer in size and shape within the Lebiasinidae.

18. Longitudinal crest on dorsal surface of vomer: (0) well developed, (1) reduced. (CI = 100, RI = 100).

[Mod.: Lucena, 1993: 4; Oyakawa, 1998: 14; Netto-Ferreira, 2006: 35; 2010: 19]

Dorsal to the vomer, characiforms have a variable developed crest longitudinally disposed. This character was first proposed as “crest reduced or absent” or “present, well developed” (Lucena, 1993; Oyakawa, 1998; Netto-Ferreira, 2006, 2010), but only the development of such crest was considered herein. Based on the material examined, *Derhamia*, *Lebiasina*, *N. eques*, and *Pyrrhulina* have a well-developed and largely ossified crest. In contrast,

the *Copella* species have a reduced crest. In species lacking the dorsal longitudinal crest of vomer the character was coded as inapplicable.

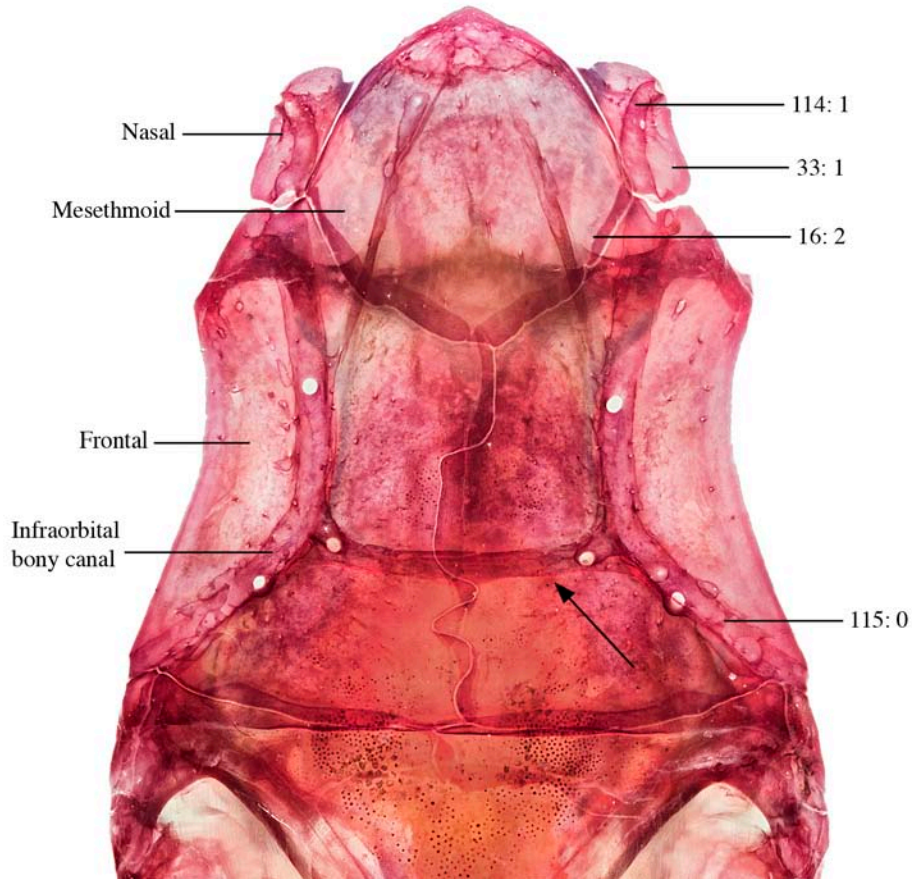


Figure 5. Dorsal view of head of *Pyrrhulina filamentosa*, MHNLS 14271, male, 55.1 mm SL. Arrow indicate the epiphyseal bar.

19. Posterior shaft of vomer: (0) present, (1) absent. (CI = 100, RI = 100).

[Weitzman, 1964; Netto-Ferreira, 2010: 21]

The vomer of characiforms typically has a thin and blade-like posterior portion, and a more or less rectangular thickened anterior portion (Toledo-Piza, 2007). In the examined taxa a

posterior shaft of vomer is present in species of *Derhamia*, *Lebiasina*, and *Piabucina*. (state 0). A similar condition is found in *Brycon* (Weitzman, 1962: fig. 4).

Weitzman (1964) proposed absence of a posterior shaft on vomer, never reaching the parasphenoid, as a synapomorphy of *Nannostomus*, and a better-developed vomer, extending posteriorly onto the parasphenoid, as synapomorphic for *Copeina*, *Copella*, and *Pyrrhulina*. However, the posterior shaft of the vomer is also absent in the latter genera (state 1, Fig. 6). The contact between vomer and parasphenoid observed by Weitzman in the Pyrrhulinini is not due to a better-development of the vomer, but to the presence of a long paired projection of the parasphenoid extending anteriorly in these taxa and in *Nannostomus anduzei* (character 20).

In the species of *Copeina*, *Copella*, *Nannostomus*, and *Pyrrhulina*, the degree of development of the vomer is variable, discussed in the next paragraph. However, it was impossible to find discrete characters regarding its development. Instead, comparative observations relative to other bones were found to be useful (characters 17 and 21).

In *Nannostomus eques* the vomer is rectangular-shaped, well ossified. In the remaining species of *Nannostomus* and in the Pyrrhulinini the vomer is nearly round and much less ossified. In *Copella* and *Nannostomus*, except *N. eques*, the vomer is especially short, represented by a thin layer of bone immerse in the ethmoid plate cartilage (Figs. 4B and 6). Given the phylogenetic hypothesis proposed, the simplification of the vomer structure is clear, with *Copella* and some *Nannostomus* species presenting the less ossified and less ornamented vomer within the family.

The development of the vomer in *Lebiasina* cf. *bimaculata*, a large representative of the Lebiasinidae, starts as a thin ossification on the ventral surface of the ethmoid plate cartilage at approximately 10 mm SL. At 17.0 mm SL, the vomer has a lateral extended head and a pointed posterior portion. The posterior projection of the vomer develops later in *Lebiasina* cf. *bimaculata*. The vomer in the species of *Copeina*, *Copella*, *Nannostomus*, and *Pyrrhulina*

resembles the vomer present in early stages of the species of *Lebiasina*. Its evolutionary change in morphology is interpreted as a possible result of truncation in the development of the vomer representing the plesiomorphic condition.

20. Anterior paired projection of the parasphenoid: (0) absent, (1) present. (CI = 50, RI = 88).

[Netto-Ferreira, 2006: 38; Mirande, 2010: 40. Mod.: Netto-Ferreira, 2010: 22]

Weitzman (1964: 138, 150) proposed as characteristic for Pyrrhulinina (= Pyrrhulinini) the contact between the vomer and the parasphenoid, due to the presence of a better-developed vomer in that group. However, it was observed that such contact is due to the presence of two long paired projections of the parasphenoid, anteriorly directed, extending laterally to the round and poorly developed vomer in these species. Such projections were found in Pyrrhulinini and *Nannostomus anduzei* (Figs. 4B and 6, see also character 19). In contrast, the anterior portion of the parasphenoid is truncated in the species of *Derhamia*, *Lebiasina*, *Piabucina*, and *Nannostomus* (except *N. anduzei*).

Netto-Ferreira (2006, 2010) considered *Nannostomus* as presenting the anterior projection of the parasphenoid but this condition was not observed herein.

21. Contact between the lateral margin of the vomer and the medial margin of the anterior projection of the parasphenoid: (0) present, (1) absent. (CI = 50, RI = 83).

In the Pyrrhulinini and *Nannostomus anduzei*, the parasphenoid presents an anterior paired projection that runs laterally to the vomer (character 20). In the species of *Pyrrhulina* and

Copeina there is a better-developed vomer when compared to the condition found in *Copella* and *Nannostomus anduzei* (and also *Nannostomus beckfordi* and *N. marginatus*, in which there no anterior paired projection of the parasphenoid) (see character 19). In the species of *Pyrrhulina* and *Copeina*, the lateral limit of the vomer contacts the medial surface of the anterior projection of parasphenoid (Fig. 6A). As in *Copella* and *Nannostomus anduzei* the vomer is very small, its lateral limit does not reach the medial portion of the anterior projection of the parasphenoid (Figs. 4B and 6B).

This character was coded as inapplicable for *Derhamia*, *Lebiasina*, and *Nannostomus* species, except *N. anduzei*, as they lack the anterior paired projection of the vomer.

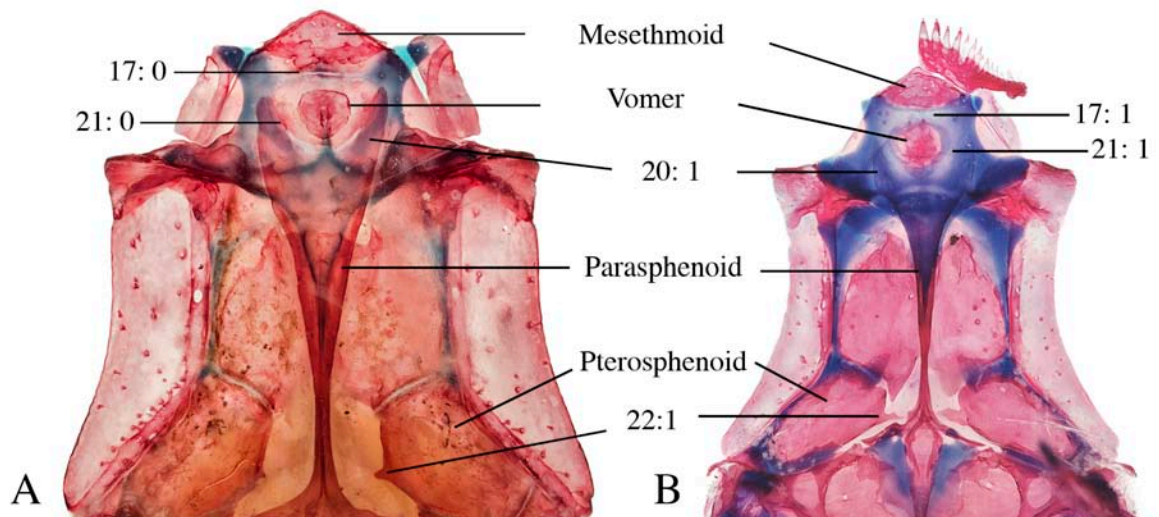


Figure 6. Ventral view of head of (A) *Pyrrhulina australis*, MZUSP 35929, male, 35.9 mm SL, and (B) *Copella arnoldi*, MPEG 8305, male, 29.7 mm SL.

22. Medial projection on the posterior portion of the pterosphenoid: (0) absent, (1) present. (CI = 2225, RI = 62).

[Mod.: Netto-Ferreira, 2010: 30]

The posterior portion of the pterosphenoid within the Lebiasinidae can be smooth (state 0) as in *Copeina*, *Derhamia*, *Lebiasina*, *Pyrrhulina brevis*, *P. semifasciata*, *P. stoli*, *Nannostomus beckfordi* and *N. equesv*, as well as in *Hoplerythrinus*, or with a medial small projection, directed to its counterpart (state 1, Fig. 6), as in the species of *Copella*, *P. australis*, *Pyrrhulina filamentosa* and *Nannostomus anduzei*. The medial projection of *Copella arnoldi* is distinctly longer, almost reaching its counterpart. Such long projection was interpreted by Netto-Ferreira (2010) as a synapomorphy for his clade 98, composed by species considered herein as junior synonyms of *C. arnoldi*. As such condition is only found in *C. arnoldi* and would represent an autapomorphy for this species, the projection length was not coded as a separate character.

Nannostomus marginatus is polymorphic for this character.

23. Position of the sphenotic spine: (0) horizontally oriented, (1) vertically oriented. (CI = 100, RI = 100).

[Lucena, 1993: 117; Vari, 1995: 23; Oyakawa: 1998: 11; Netto-Ferreira, 2006: 60. Mod.: Toledo-Piza, 2007: 19; Netto-Ferreira, 2010: 32]

Vari (1995) noted a reduction of the dorsal portion of the sphenotic spine and its horizontal orientation in species of the Lebiasininae, Erythrinidae and Ctenolucidae. A vertical orientation of the sphenotic spine is synapomorphic for the Pyrrhulininae. In Lebiasininae, the spine is continuous dorsally with the ventrolateral margin of the frontal, both forming the posterior margin of the orbit (Weitzman, 1962: fig. 3).

24. Contact between the frontal and the pterotic: (0) present, (1) absent. (CI = 50, RI = 83).

[Weitzman, 1964; Lucena, 1993: 15; Buckup, 1998: 12; Zanata & Vari, 2005: 38; Netto-Ferreira, 2006: 64; 2010: 34]

The contact between the upper portion of the pterotic and the posterolateral portion of the frontal is present in species of *Copeina*, *Derhamia*, *Lebiasina*, and *Piabucina* (state 0). In species of *Copella*, *Nannostomus*, and *Pyrrhulina*, the pterotic is excluded from the contact with the frontal by the sphenotic (state 1). Such condition was considered diagnostic for *Copeina*, *Copella*, *Nannostomus*, and *Pyrrhulina* by Weitzman (1964: 150, character 11). However, the species of *Copeina* present the state 0, corroborating the observations of Netto-Ferreira (2006, 2010).

The condition described as state 1 was also found in the Characidiinae (Buckup, 1998) and *Lepidarchus adonis* (Zanata & Vari, 2005), both miniature taxa (Netto-Ferreira, 2010).

25. Laterodorsal spine-like process on the pterotic: (0) absent, (1) present. (CI = 50, RI = 87).

[Netto-Ferreira, 2006: 61; 2010: 33].

The laterodorsal portion of the pterotic has a small spine in species of the Pyrrhulinini and *Nannostomus anduzei* (Fig. 7), where the tendon from the anteroventral portion of the posttemporal attaches. Netto-Ferreira (2010) interpreted the presence of such spine as probably related to the absence of the lateral arm of the epioccipital in these taxa, since the tendon from

the anteroventral portion of the posttemporal attaches on the lateral arm of the epioccipital in the remaining Lebiasinidae. The lack of the lateral arm of the epioccipital has been considered a reductive character (see character 27). As both characters seem to be correlated, the presence of such process in the pterotic may also be a result of developmental truncation.

26. Ventral spine-like process on pterotic, medially to the pterotic spine: (0) absent, (1) present. (CI = 25, RI = 70).

The pterotic spine in the Lebiasinidae is a relatively small process ventrolaterally positioned. Besides the pterotic spine, the species of Pyrrhulinini and *Nannostomus anduzei* have a small laterodorsal spine-like process (character 25). Furthermore, in species of *Copella*, *Copeina*, *Derhamia*, and *Pyrrhulina brevis*, *P. filamentosa*, and *P. stoli* there is a ventral spine-like process, medially to the pterotic spine (Fig. 7). In species of *Copeina* and *P. filamentosa*, the pterotic spine and such medial process may be fused distally.

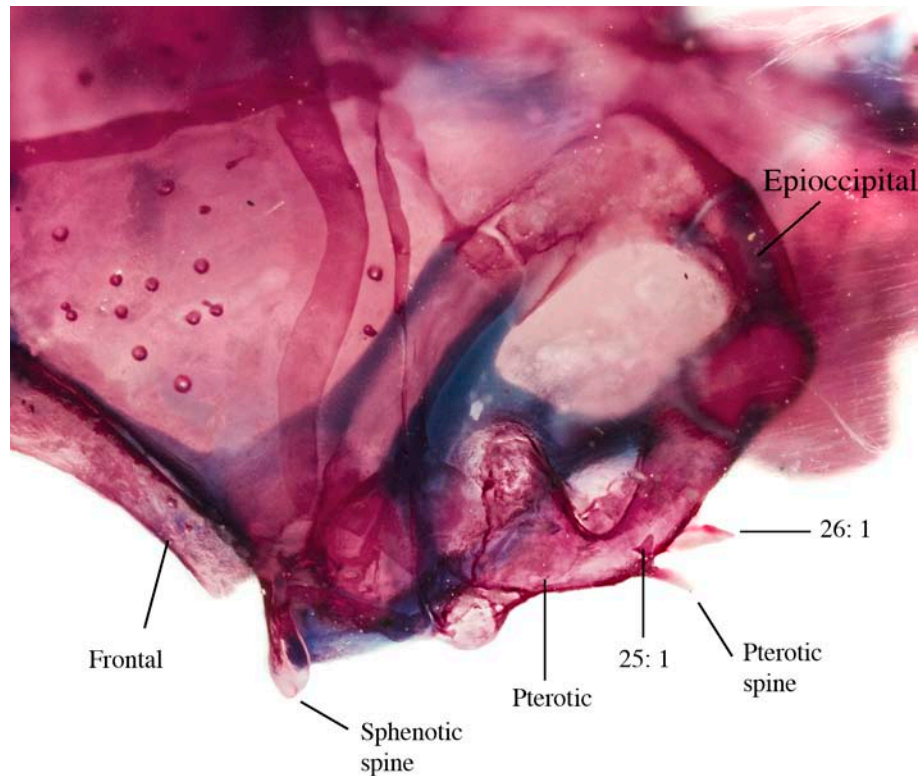


Figure 7. Dorsolateral view of the posterior portion of neurocranium of *Copella arnoldi*, MPEG 8305, male, 29.7 mm SL. Pterotic bone highlighted.

27. Lateral arm of the epioccipital: (0) present, (1) absent. (CI = 50, RI = 87).

[Weitzman, 1964; Oyakawa, 1998: 25; Netto-Ferreira, 2006: 66, 2010: 36; Mirande, 2010: 4]

The epioccipital in Characiformes commonly has a longitudinal lateral arm crossing the posttemporal fossa. Weitzman (1964) commented that the posttemporal fossa of *Copeina*, *Copella*, and *Pyrrhulina* is extremely large. This is due to the absence of the lateral arm of the epioccipital in species of these genera, and also in *Nannostomus anduzei* (Fig. 7 and 8). In the

remaining species analyzed the lateral arm of epioccipital, has a variable width (character 28), crossing the posttemporal fossa.

Weitzman & Fink (1983) observed the absence of the lateral arm of the epioccipital in Crenuchidae (*Klausewitzia aphanes* Weitzman & Kanazawa) and Characidae (*Tyttocharax madeirae* Fowler). Other characids lacking this structure are *Hasemania nana* (Lütken) (Mirande, 2010) and *Cyanogaster noctivaga* Mattox, Britz, Toledo-Piza, Marinho. These are small body sized species.

The development of the epioccipital of *Lebiasina* cf. *bimaculata* shows that the lateral arm ossifies latter than the main portion of the bone (it can be seen at 12.6 mm SL). The condition found in the Pyrrhulinini, *Nannostomus anduzei*, and the above mentioned species is similar to the one found in earlier stages of *Lebiasina* in which the bone is vertically positioned, without a lateral arm. Its evolutionary change in morphology is interpreted as a possible result of truncation in the development of the epioccipital of the ancestor taxa.

28. Relative width of the lateral arm of the epioccipital: (0) wide, approximately as wide as the epioccipital diameter, (1) thin, less wide than the epioccipital radius. (CI = 100, RI = 100).

In the taxa presenting the lateral arm of the epioccipital, a thin and wide lateral arm is present. This character compares the lateral arm width and the epioccipital main body width. Species of *Derhamia*, *Lebiasina*, and *Piabucina* have a distinctly wider lateral arm of epioccipital, when compared to the condition found in *Nannostomus*, except *N. anduzei*, in which it is lacking.

According to the phylogenetic hypothesis given, the reduction of the lateral arm of the epioccipital within the Lebiasinidae is gradual, culminating into its homoplastic absence, once in the tribe Pyrrhulini and another in *N. anduzei* (see character 27).

29. Lateral exoccipital foramen: (0) small, (1) wide. (CI = 100, RI = 100).

[Mod.: Lucena, 1993: 22; Zanata & Vari, 2005: 45; Netto-Ferreira 2006: 68; 2010: 38]

Within the Lebiasinidae, only the species of *Copella* have a wide lateral exoccipital foramen, occupying a large portion of the posterior surface of the exoccipital (Fig. 8A). It is a unique synapomorphy for the genus. In the remaining species of the Lebiasinidae, there is only a small opening (Fig. 8B). *Copeina guttata* is the only species in which the exoccipital foramen is lacking, thus this character was coded as inapplicable for this species. Netto-Ferreira (2010) considered the presence of wide lateral exoccipital foramen in *Copella* as a “paedomorphic” condition. Small representatives of *Lebiasina* cf. *bimaculata* have a small lateral exoccipital foramen, as in the adult. Thus the wide lateral exoccipital foramen of *Copella* is not the condition found in early stages of a *Lebiasina*, a large close related species. Therefore, further evidence is necessary to consider the wide exoccipital foramen of *Copella* as a result of developmental truncation.

Cyanogaster noctivaga, a miniature characid, also presents a very wide lateral occipital foramen. In contrast, Zanata & Vari (2005) observed the absence of the exoccipital foramen in a small-sized species of *Lepidarchus* and its presence in the remaining Alestidae.

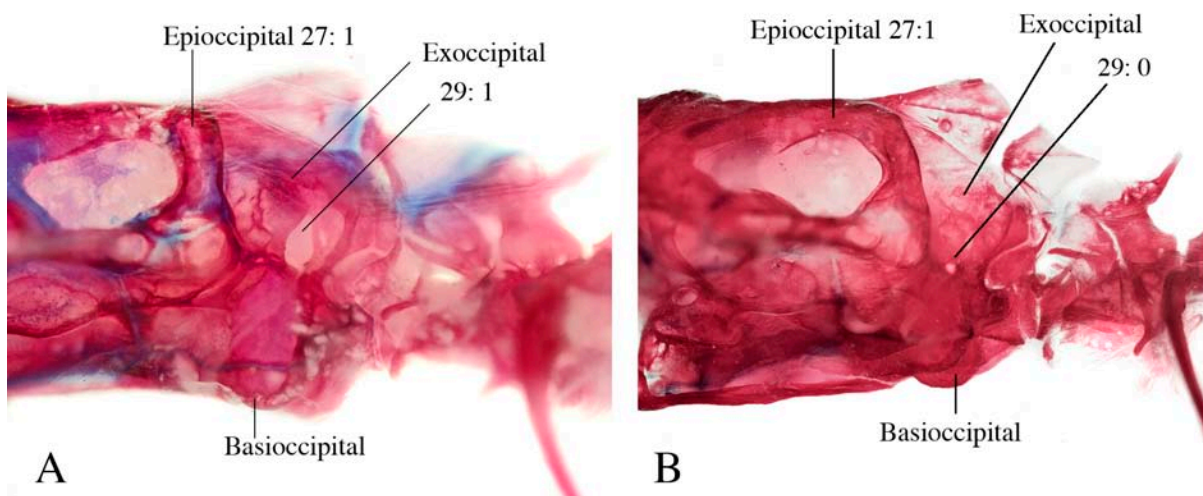


Figure 8. Lateral view of posterior portion of neurocranium of *Copella arnoldi*, MPEG 8305, male, 29.7 mm SL, and (B) *Pyrrhulina marilynae*, MZUSP 61130, male, 30.7 mm SL.

30. Size of ventral longitudinal lamellae of basioccipital: (0) small, (1) large. (CI = 33, RI = 78).

The basioccipital of the Lebiasinidae have two variably developed projections directed lateroposteriorly on its ventral surface. In *Copella* species, *Copeina guttata*, *Pyrrhulina filamentosa*, *P. marilynae* and *P. stoli*, the basioccipital projection is relatively wide, large. In the remaining species of the family, these lamellae are small.

31. Intercalar bone: (0) present, (1) absent. (CI = 100, RI = 100).

[Zanata & Vari, 2005: 42]

The intercalar is a small laminar bone located on the posterior portion of the ventral surface of the neurocranium, in the contact region of the basioccipital, pterotic and prootic. It

serves as the area of attachment for a ligament extending to the dorsal portions of the pectoral girdle (Zanata & Vari, 2005). Zanata & Vari (2005) pointed out that the absence of the intercalar in some small representatives of the Alestidae might be related to reduction of body size. Among the examined taxa of the Lebiasinidae, only *Lebiasina*, *Piabucina*, and *Derhamia* have the intercalar, whereas species of *Copeina*, *Copella*, *Nannostomus*, and *Pyrrhulina* lack it. The absence of intercalar, as other bone losses, is herein considered a result of developmental truncation.

Orbital series and nasal bone

32. Nasal bone: (0) present, (1) absent. (CI = 25, RI = 50).

[Zanata & Vari, 2005: 17]

The nasal bone in the Lebiasinidae is a laminar dermal bone lateral to the mesethmoid, frequently bearing the anterior portion of the supraorbital canal. This and the next character refer only to the nasal bone, not the ossification around the supraorbital canal on the nasal bone (coded in character 114). Several authors have analyzed these structures together (*e.g.* Weitzman, 1964; Lucena, 1993: 31; Oyakawa, 1998: 3, 4; Vari, 1995: 17; Toledo-Piza, 2007: 10; Netto-Ferreira, 2006: 21, 22; 2010: 12; Moreira, 2007: 175; Mirande, 2010: 33, 34), but ossifications of the cephalic sensory canal and ossifications of the dermal bone are independent (Webb, 1989).

Species of *Hoplerithrynus*, *Lebiasina* (except *L. bimaculata*), *Piabucina*, *Pyrrhulina* and *Copella* (except *C. stigmatemion*) have a nasal bone, whereas *L. bimaculata*, *Copella stigmatemion*,

species of *Derhamia*, and of *Nannostomus* lack this bone. The nasal bone is represented by a laminar bone without any bony canal (as in *Copella*, it can be seen in Fig. 6B) or by laminar processes lateral to the laterosensory bony tube (as in *Lebiasina* and *Pyrrhulina*, Fig. 5 and 6A). *Lebiasina bimaculata* and *Nannostomus* (except *Nannostomus anduzei*) only present a bony tube, and no lateral blade. Such condition is herein considered as nasal bone absent, and the ossification of a bony wall around the laterosensory canal, present. *Copella stigmatemion* and *Nannostomus anduzei* lack any bony formation in the area where the nasal is present in the remaining taxa. Thus the nasal bone as well as the ossification around the supraorbital laterosensory canal is absent in these species.

33. Development of nasal: (0) small, (1) well developed. (CI = 50, RI = 83).

Among the taxa with the nasal bone, *Hoplerithrynus unitaeniatus*, species of *Copeina*, *Copella arnoldi* and of *Pyrrhulina* have a well-developed nasal blade (Figs 5 and 6), whereas in species of *Lebiasina*, *Piabucina* and remaining *Copella* species, the nasal is thin and small. In species of *Derhamia*, *Copella stigmatemion*, *Lebiasina* cf. *bimaculata*, and species of *Nannostomus* the character was coded as missing entries due to the lack of ossification of the nasal bone (see discussion under character 32).

34. Anterior extension of the nasal: (0) not reaching the lateral arm of the premaxilla (1) reaching the lateral arm of the premaxilla. (CI = 50, RI = 80).

[Mod.: Netto-Ferreira, 2010: 13]

The lateral process of the mesethmoid is very small in lebiasinids, thus the position of the nasal is discussed with respect of the lateral arm of the premaxilla, as in Netto-Ferreira (2010), in contrast with (Zanata & Vari, 2005: 18; Netto-Ferreira, 2006). Netto-Ferreira (2010) proposes two conditions for state 1: nasal reaching or slightly overlapping the lateral arm of the premaxilla or nasal greatly overlapping the lateral arm of the premaxilla, but it was difficult to recognize distinct conditions.

Among congeners, *Copella arnoldi* has the largest nasal. In this species, the anterior portion of the nasal bone reaches the lateral arm of the premaxilla or the base of the ascending process of the premaxilla (it can be seen in Fig. 6B). The same condition is found in species of *Copeina*, *Pyrrhulina*, *Lebiasina minuta*, and in *Hoplerythrinus unitaeniatus* (state 1). In the remaining species of *Copella*, the nasal is smaller, not extending anteriorly to the tip of the ascending process of the premaxilla (state 0), condition shared with *Piabucina unitaeniata* and *Lebiasina* cf. *yuruaniensis*.

In species of *Derhamia*, *Copella stigmasemion*, *Lebiasina* cf. *bimaculata*, and species of *Nannostomus* the character was coded as missing entries due to the lack of ossification of the nasal bone.

35. Posterior extension of nasal: (0) in contact with the frontal, (1) not in contact with the frontal. (CI = 100, RI = 100).

[Netto-Ferreira, 2006: 25; 2010: 14]

The posterior portion of the nasal is in contact with frontal in species of *Copeina*, *Lebiasina* (except *L. bimaculata*), *Piabucina*, and *Pyrrhulina* (state 0) (Fig. 5). In contrast, it is

not in contact with the frontal in all the species of *Copella* (state 1). This condition is possibly related to the reduction of the nasal in these taxa (Netto-Ferreira, 2010). Netto-Ferreira (2006) found this character to be a synapomorphy of a clade including *Copella eigenmanni*, *Copella nattereri*, and *C. stigmatemion*, but the same result was not reached herein.

In species of *Derhamia*, *Copella stigmatemion*, *Lebiasina* cf. *bimaculata*, and species of *Nannostomus* this character was coded as missing entries due to the lack of ossification of nasal bone.

36. Shape of antorbital: (0) deeper than longer, (1) as long as deep, (2) longer than deeper. (Unordered). (CI = 25, RI = 45).

[Netto-Ferreira, 2006: 2; 2010: 1; Moreira, 2007: 123. Mod.: Bührnheim, 2006: 2006: 13]

Different forms of antorbital can be found within the Lebiasinidae. Among the *Copella* species, the antorbital can be longer than deeper in *C. arnoldi*, *C. nattereri*, *C. stigmatemion*, and *C. vilmae* and as long as deep, roughly round, in *C. compta* and *C. eigenmanni*.

In *Nannostomus marginatus* the character is polymorphic, represented by states 1 and 2. In *Hoplerythrinus unitaeniatus* it was coded as inapplicable due to the lack of the antorbital (Vari, 1995: 1).

37. Shape of first infraorbital: (0) deeper than longer, (1) as long as deep, (2) longer than deeper. (Unordered). (CI = 60, RI = 50).

There are distinct shapes of the first infraorbital within the Lebiasinidae. It can be as long as deep, approximately rounded, in *C. arnoldi*, *C. nattereri*, *Nannostomus stigmasemion*, and *N. anduzei* and deeper than longer in *Copella compta* and *C. eigenmanni*, and the species of *Copeina*, *Derhamia*, *Lebiasina*, *Piabucina* and *Pyrrhulina*. First infraorbital longer than deeper is autapomorphic for *Nannostomus eques*.

38. Shape of second infraorbital: (0) somewhat rectangular, (1) somewhat triangular. (CI = 20, RI = 56).

Most species examined have a somewhat rectangular second infraorbital, with four corners. However, in *Copella compta*, *C. nattereri*, *C. stigmasemion*, *Pyrrhulina semifasciata* and all the *Nannostomus* species this bone is roughly triangular.

39. Position of third infraorbital: (0) posteroventral to eye, (1) ventral to eye. (CI = 100, RI = 100).

[Oyakawa, 1998: 32; Netto-Ferreira, 2006: 8; 2010: 5]

In the Lebiasininae and *Hoplerythrinus unitaeniatus*, the third infraorbital is located posteroventrally to the orbit whereas in the Pyrrhulininae it is ventrally located. In *Nannostomus* and *Derhamia*, the third infraorbital is especially elongate, limiting the most ventral portion of the orbit.

40. Shape of fourth infraorbital: (0) external margin six times or more deeper than the orbital margin of bone, (1) external margin three times or less deeper than orbital margin. (CI = 100, RI = 100).

[Mod.: Zanata & Vari, 2005: 13; Toledo-Piza, 2007: 33; Netto-Ferreira, 2006: 10]

The shape of the fourth infraorbital varies among Characiformes (Zanata & Vari, 2005: 13; Netto-Ferreira, 2006: 10). The Lebiasininae have the external margin of fourth infraorbital greatly expanded, six times or more deeper than its orbital margin. In the Pyrrhulininae, the external margin is three times or less deeper than its orbital margin. This character was coded as inapplicable for *Nannostomus anduzei* due to the lack of fourth infraorbital in this species.

41. Medial process in the orbital margin of the fifth infraorbital: (0) absent, (1) present. (CI = 50, RI = 83).

[Netto-Ferreira, 2006: 12; 2010: 8]

The orbital margin of fifth infraorbital in characiforms is typically smooth. In the Pyrrhulinini and *Nannostomus* members (except *N. eques*) there is a medial process on the orbital margin of the fifth infraorbital anterior to the sphenotic spine whereas in the remaining Lebiasinidae this process is lacking. Netto-Ferreira (2006, 2010) observed a medial process on the sixth infraorbital of *Derhamia* and the *Nannostomus* species, and suggested this is evidence of the fusion between the fifth and sixth infraorbitals in Pyrrhulinini. Ontogenetically, there is no evidence of such fusion. The absence of sixth infraorbital in these species is herein interpreted as

a loss, a common event related to miniaturization. Such loss occurred independently in the smallest species of the family, *Nannostomus anduzei*, which also has lost the fourth and fifth infraorbitals.

This character was coded as inapplicable for *Nannostomus anduzei* due to the lack of fifth infraorbital.

42. Sixth infraorbital: (0) present, (1) absent. (CI = 50, RI = 87).

[Zanata & Vari, 2005: 15; Netto-Ferreira, 2006: 14; 2010: 9; Mattox & Toledo-Piza, 2012: 61. Mod.: Moreira, 2007: 162]

Lucena (1993) coded *Pyrrhulina* as having five infraorbitals, but did not specify which of is absent. The sixth infraorbital is absent in all the species of the Pyrrhulinini, and in *Nannostomus anduzei*. The remaining species of *Nannostomus*, *Derhamia*, *Lebiasina*, and *Piabucina* have the sixth infraorbital. The loss of infraorbitals occur in various Characiformes, and is usually related to small body size (Zanata & Vari, 2005: 12, 15). Additional comments at “Miniaturization and developmental truncation in Lebiasinidae” section.

Jaws and dentition

43. Multicuspid teeth in jaws: (0) present, (1) absent. (CI = 50, RI = 87).

[Weitzman, 1964. Mod.: Buckup, 1993: 38; Lucena, 1993: 46, 53; Buckup, 1998: 72; Netto-Ferreira, 2006: 74; 2010: 43; Mirande, 2010: 118]

Within the Lebiasinidae there are two types of teeth: multicuspid, present in the species of *Derhamia*, *Lebiasina*, *Piabucina* and *Nannostomus*, state 0, Fig. 9A, and conical, present in the Pyrrhulinini (state 1, Fig. 9B and 10) and in the inner dentary tooth row of the species of *Derhamia*, *Lebiasina*, *Piabucina*, and *Nannostomus*, also present in *Hoplerythrinus unitaeniatus*. It has been used to diagnose supraspecific groups within the family (Weitzman, 1964; Géry, 1977).

The condition of multicuspid teeth is only present in adults of *Derhamia*, *Lebiasina*, *Piabucina*, and *Nannostomus*. Observations of ontogenetic series of *Lebiasina* cf. *bimaculata* and *Nannostomus beckfordi* revealed that both species have conical teeth in all these bones in early stages of development (Fig. 11). In *Lebiasina* cf. *bimaculata*, multicuspid teeth can be seen in the premaxilla and dentary at 15.0 mm SL, and in the maxilla at 26.0 mm SL. The evolution of this character in the Pyrrhulinini seems to be related to developmental truncation.

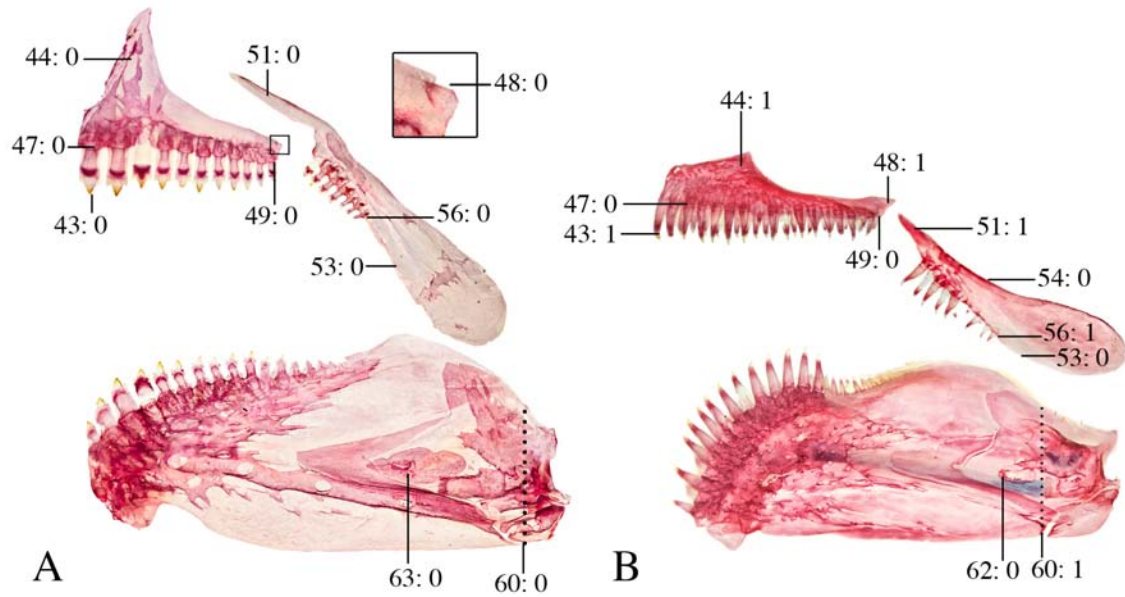


Figure 9. Jaws of (A) *Piabucina unitaeniata*, MZUSP 73090, male, 75.6 mm SL, with the detail of the lateral tip of premaxilla and (B) *Pyrrhulina australis*, MZUSP 35929, male, 36.2 mm SL. Lateral view of right side, inverted.

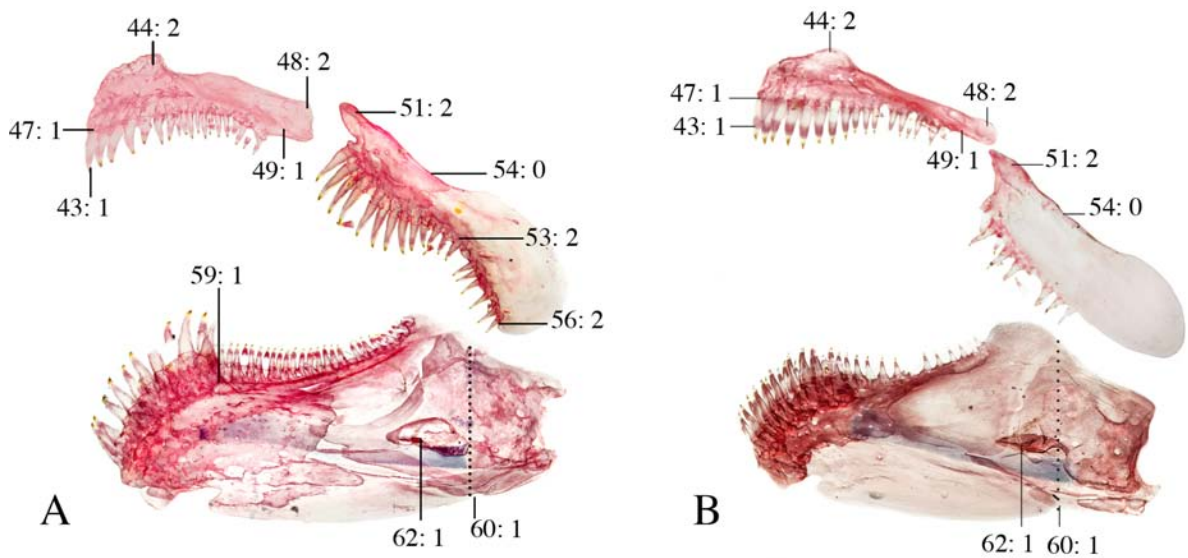


Figure 10. Jaws of *Copella eigenmanni* (A) MZUSP 81143, male, 44.3 mm SL, lateral view of left side, and (B) MZUSP 81143, female, 29.2 mm SL, lateral view of right side, inverted.

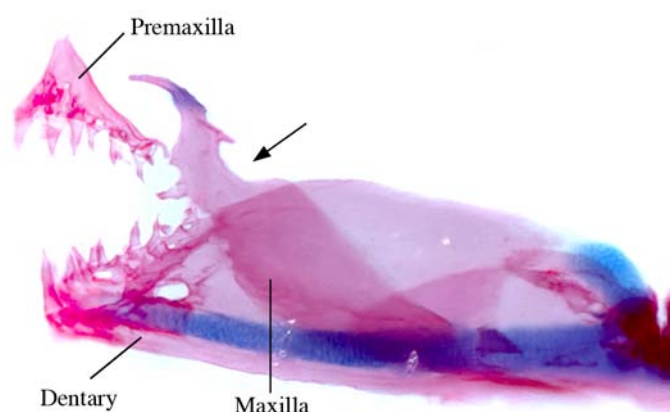


Figure 11. Jaws of a juvenile of *Lebiasina* cf. *bimaculata*, BMNH not cataloged, 10.9 mm SL. Arrow indicates notch at posterior border of maxilla.

44. Development of ascending process of the premaxilla: (0) distinctly long, (1) short, (2) vestigial, represented by a small crest. (Ordered). (CI = 67, RI = 87).

[Mod.: Lucena, 2003: 35; Moreira, 2007: 1; Netto-Ferreira, 2006: 78; 2010: 44]

The ascending process of the premaxilla is long in the species of *Derhamia*, *Lebiasina*, *Piabucina*, and also in *Hoplerythrinus unitaeniatus* (state 0, Fig. 9A), short in *Copella vilmae*, *C. compta*, the species of *Copeina*, *Nannostomus*, and *Pyrhulina* (state 1, Fig. 9B), and vestigial in the remaining species of *Copella* (state 2, Fig. 10). According to the phylogenetic hypothesis of relationship proposed, the ascending process of the premaxilla is longer in the plesiomorphic condition, and short in many small-bodied representatives of other genera.

In the ontogeny of *Lebiasina* cf. *bimaculata*, the premaxilla is one of the first bones to appear. It can be first seen at 3.6 mm NL. At 8.1 mm SL, the mesial portion of the premaxilla, anterior to the ethmoid plate cartilage, is thicker than the lateral portion, forming the ascending

process. It gradually gets thicker and longer during the development. According to the phylogenetic hypothesis of relationship proposed and observations of the premaxilla development within the Lebiasinidae, the short ascending process observed in the species of *Copeina*, *Copella*, *Nannostomus*, and *Pyrrhulina*, especially in *Copella*, is probably a result of truncation in the development of the plesiomorphic taxa. Vestigial ascending process (state 2) is a synapomorphy for *Copella*, further reverted to a short ascending process in *Copella vilmae* and *C. compta* (state 1).

45. Position of the ascending process of the premaxilla related to the mesethmoid: (0) extending over the mesethmoid, (1) extending under the mesethmoid. (CI = 100, RI = 100). (CI = 100, RI = 100).

[Weitzman, 1964. Mod.: Netto-Ferreira, 2006: 82; 2010: 47]

In most characiforms, the ascending process of the premaxilla extends over the lateral wings of the mesethmoid (Weitzman, 1962: fig. 2). In members of *Nannostomus*, the ascending process of the premaxilla extends under it. As a consequence, the dorsal portion of the premaxilla has a depression to receive the mesethmoid (character 46). The premaxilla of *Nannostomus* is not firmly attached, and is somewhat movable (Weitzman, 1964).

46. Groove anterior to the ascending process of the premaxilla: (0) absent, (1) present. (CI = 100, RI = 100).

In the species of *Nannostomus*, the ascending process of the premaxilla is articulated to the ventral portion of the mesethmoid. Anterior to the ascending process, there is a groove where the lateral wing of the mesethmoid is placed (Fernandez & Weitzman, 1987: fig. 3).

47. Ventral profile of premaxilla: (0) straight, (1) gently arched. (CI = 100, RI = 100).

The ventral profile of the premaxilla of most of the Lebiasinidae, in the area of teeth insertion, is straight (state 0, Fig. 9), as in most Characiformes. In *Copella*, the ventral profile of the premaxilla is gently arched. As a consequence, its lateralmost portion is not parallel to the main axis of body, but almost perpendicular (state 1, Fig. 10). Such condition is unique for the genus.

48. Shape of the posterolateral portion of the premaxilla: (0) with a notch, (1) acute, (2) rounded. (CI = 100, RI = 100).

[Mod.: Zanata & Vari, 2005: 52]

Zanata & Vari (2005: fig. 13) observed in all the species of the Alestidae, except the species of *Arnoldichthys*, *Chalceus*, and *Lepidarchus*, the presence of a pedicle-like process extending beyond the posterior limit of the premaxillary dentition and over the lateral surface of the anterior portion of the maxilla, terminating posterolaterally in a pointed or rounded tip. It resembles the premaxilla of the species of *Copella*, though the posterolateral portion of the premaxilla in *Copella* is rounded, never pointed (state 2, Fig. 10). Such condition is unique for the genus. An acute distal portion of the premaxilla is found in *Pyrhulina* (state 1, fig. 9B), but

in contrast, the premaxilla bears teeth in its posterior limit. The absence of teeth in this area of the premaxilla was treated herein as a separate character (character 49).

The condition described by Zanata & Vari (2005) for *Arnoldichthys*, *Chalceus*, and *Lepidarchus* is found in most characids and other Characiformes, in all of which the posterolateral portion of the premaxilla terminates in a distinct notch to accommodate the anterior portion of the maxilla (fig. 14). This is similar to the condition present in the species of *Hoplerthrinus*, *Derhamia*, *Lebiasina*, *Nannostomus*, and *Piabucina* (state 0, Fig. 9A).

49. Teeth on the posterolateral portion of the premaxilla: (0) present, (1) absent. (CI = 100, RI = 100).

The posterolateral portion of the premaxilla in the species of *Copella* is edentulous (state 1, Fig 10), similar to the condition observed in most species of Alestidae by Zanata & Vari (2005: 52). In the remaining members of Lebiasinidae, and also in most Characiformes, the posterolateral limit of the premaxilla is approximating immediately posterior to the point of implantation of the lateralmost premaxillary tooth (state 0, Fig. 9).

Zanata & Vari (2005) assigned the lack the posterior pedicle of the premaxilla (presence of teeth in the lateral portion of the premaxilla) and the presence of a notch at the posterior limit of the bone in *Lepidarchus* as possibly related to miniaturization. The same correlation was not found in the present study.

50. Number of premaxillary teeth rows: (0) one, (1) two. (CI = 100, RI = 100).

[Weitzman, 1964; Oyakawa, 1998: 60; Lucena, 2003: 38; Zanata & Vari: 2005: 57; Netto-Ferreira, 2006: 83]

Within the Lebiasinidae, only adult species of *Pyrrhulina* have two teeth rows on the premaxilla, a synapomorphy used to diagnose the genus (Weitzman, 1964; Géry, 1977). Observation in the ontogenetic series of *Pyrrhulina spilota* shows that in early developmental stages, there is only one tooth series. Later on, the external series starts to develop.

51. Development of the ascending process of the maxilla: (0) distinctly long, (1) short, (2) vestigial. (Ordered). (CI = 67, RI = 89).

[Mod: Lucena, 2003: 34; Netto-Ferreira, 2006: 91; 2010: 51]

The ascending process of the maxilla in the species of *Derhamia*, *Lebiasina*, and *Piabucina* is very long, almost reaching the base of the ascending process of the premaxilla anteriorly (state 0, Fig. 9A). In the species of *Copeina*, *Copella compta*, *Nannostomus*, and *Pyrrhulina*, the ascending process of the maxilla is short, extending anteriorly to the lateral tip of the premaxilla (state 1, Fig. 9B and 12). In the remaining species of *Copella*, the process is very small, vestigial, represented by a triangular process (state 2, Fig. 10).

52. Alignment of the ascending process of the maxilla: (0) medially curved, with distinct angle, (1) relatively straight, aligned approximately parallel to axis of posterior portion of the maxilla. (CI = 100, RI = 100).

When viewed dorsally, the ascending process of the maxilla forms a distinct angle relative to the axis of the main body of the bone in the species of *Copeina*, *Derhamia*, *Nannostomus*, *Lebiasina*, and *Piabucina*, where it is medially directed. In contrast, the species of *Copella* and *Pyrrhulina* have an approximately straight maxilla in dorsal view; the ascending process is aligned with the main axis of the maxilla.

53. Shape of anterior border of the main portion of the maxilla of mature males: (0) approximately straight, (1) convex, (2) “S” shaped. (Unordered). (CI = 67, RI = 87).

The shape of the maxilla of males was proposed by Myers (1927) to distinguish species previously allocated in *Copeina* and *Pyrrhulina*. Myers (1956) erected *Copella* based on this character, which is still useful to diagnose the genus among other members of the family (Géry, 1977). While in the females the anterior border of the maxilla is approximately straight or smoothly convex (Fig. 10B), in males it has a triple curve, convex near the anterior and posterior tips and concave at the middle (state 2, Fig. 10A). Those curves get accentuated as the juvenile male grows. In males of the species of *Lebiasina*, *Copeina*, and in *Pyrrhulina australis* and *Pyrrhulina* cf. *stoli*, the anterior border of the maxilla is straight (state 0, Fig. 9B) while in the remaining species of *Pyrrhulina* it is convex (state 1). The maxilla in the species of *Nannostomus* has a peculiar shape that is mostly due to a conspicuous notch on its posterior border (discussed under character 54). When compared to other lebiasinids, the main portion of the maxilla in species of *Nannostomus* may have an anterior border straight or convex. In *Derhamia* the character was coded as missing entry due to the lack of mature specimens.

54. Shape of the posterior border of the maxilla: (0) straight or slightly concave, (1) with a conspicuous notch. (CI = 100, RI = 100).

The posterior border of the maxilla can be straight, concave, or convex, and is smooth in most Characiformes (Mirande, 2010: figs. 50-56, 68-70; Zanata & Vari, 2005: 16-18). In the Lebiasinidae, except *Nannostomus*, it is straight or slightly concave (Figs. 9 and 10). By contrast, the posterior border of the maxilla in *Nannostomus* has a conspicuous notch (Fig. 12). Curiously, the maxilla of juveniles of *Lebiasina* cf. *bimaculata* closely resembles that of the species of *Nannostomus*, also presenting such a notch at its posterior border (Fig. 11). This, however, was not observed in any developmental stage of species of *Copella* and *Pyrrhulina*. The general shape of the maxilla in the species of *Nannostomus* may probably be result of developmental truncation.

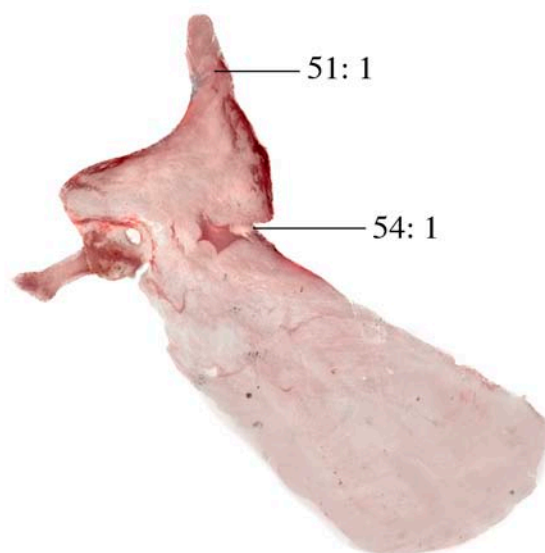


Figure 12. Maxilla of *Nannostomus eques* MZUSP 6423, female, 32.8 mm SL. Lateral view.

55. Extension of posterior tip of the maxilla: (0) reaching the limit between the first and second infraorbitals, (1) reaching approximately the middle of the second infraorbital, (2) reaching approximately the middle of the first infraorbital. (Unordered). (CI = 67, RI = 89).

[Weitzman, 1964. Mod.: Lucena, 1993: 42; Oyakawa, 1998: 57; Netto-Ferreira, 2006: 86, 87; 2010: 50]

Within the Lebiasinidae, there is variation in the length of the maxilla. The smallest maxillae appear in species of *Nannostomus* and *Copella* whereas in species of *Lebiasina* the maxilla is the longest found in the family. In species of *Derhamia*, *Lebiasina* (except *L. bimaculata*), *Piabucina*, *Pyrrhulina*, and *Hoplerythrinus*, the posterior tip of the maxilla extends to the limit between the second and third infraorbitals (state 0). In species of *Copella* and in *L. bimaculata*, it extends to the middle of the second infraorbital (state 1) and in species of *Nannostomus* it reaches approximately the middle of the first infraorbital (state 2).

56. Distribution of the maxillary teeth in males: (0) along one-third or less of the anterior portion of the maxilla, (1) along one-half length of the anterior portion of the maxilla, (2) along the entire length of anterior portion of the maxilla. (Unordered). (CI = 67, RI = 92).

[Mod.: Netto-Ferreira, 2006: 93; 2010: 52]

The distribution of teeth in the maxilla varies within the Lebiasinidae. As it is sexually dimorphic in species of Pyrrhulinini (see character 58), only mature males were considered. Among the *Copella* species, teeth are distributed along the entire length of the posterior portion

of the maxilla (state 2, Fig. 10A). In species of *Pyrrhulina* and *Copeina*, they are distributed along one-half length of the posterior portion of the maxilla (state 1, Fig. 9B) and in species of *Nannostomus*, *Lebiasina*, and *Piabucina*, they are restricted to one-third or less of the posterior portion of the maxilla (state 0, Fig. 9A). In *Derhamia* the character was coded as missing entry due to the lack of mature specimens.

57. Position of the anterior portion of the maxilla in relation to the lateralmost portion of the premaxilla: (0) maxilla not overlapping the premaxilla, (1) maxilla slightly overlapping the premaxilla laterally, (2) maxilla largely overlapping the premaxilla laterally. (Unordered). (CI = 100, RI = 100).

As discussed, the species of *Hoplerythrinus*, *Derhamia*, *Lebiasina*, *Piabucina*, and *Nannostomus* have a notch at posterolateral portion of premaxilla to accommodate the maxilla (character 48). Therefore, the maxilla is located posterior to the premaxilla in these taxa, and does not overlap the premaxilla. Although lacking such notch, the same condition is observed in the species of *Copeina*, in *Pyrrhulina* cf. *brevis*, *P. filamentosa*, *P. semifasciata*, and *Pyrrhulina* cf. *stoli* (state 0). In *Pyrrhulina australis* and *P. marilynae*, the maxilla slightly overlaps the premaxilla (state 1), and in *Copella*, it overlaps a relative large portion of the premaxilla (state 2).

58. Sexual dimorphism related to the number of maxillary teeth: (0) absent, (1) present. (CI = 100, RI = 100).

Netto-Ferreira & Marinho (2013) observed a number of maxillary teeth higher in males of *Pyrrhulina australis*, *P. marilynae*, and *P. vittata* than in the females. Further analysis revealed that the sexually dimorphic number of maxillary teeth is present in all the species of Pyrrhulinini. The males have more teeth than the females (compare maxilla of Fig. 10A with 10B). Difference in the number of maxillary teeth between males and females of species of *Copeina* is not as evident as in the species of *Copella* and *Pyrrhulina*. In *Derhamia hoffmannorum* the character was coded as missing entry due to the lack of mature specimens.

59. Anterolateral projection of the dentary: (0) absent, (1) present. (CI = 50, RI = 83).

[Weitzman, 1964; Netto-Ferreira, 2006: 99; 2010: 55]

Weitzman (1964) stated that the dentary of males in species of *Copella* is modified, and this is correlated with modifications in the dentition and shape of the lower jaw. In species of *Copella*, and also of *Copeina*, the anterolateral portion of the dentary is distinctly projected outward, more pronounced in males (state 1, Fig. 10). In the posterior portion there is a groove where the maxilla accommodates when the mouth is closed. In species of *Derhamia*, *Lebiasina*, *Nannostomus*, and *Pyrrhulina*, the anterolateral portion of the dentary bearing the outer dentary tooth row is continuous with the posterolateral portion of the dentary. Such condition can be seen in the Figs. 9A.

60. Relative position of the ventroposterior tip of the dentary: (0) at vertical through the articulation between the anguloarticular and the quadrate or falling short, (1) at vertical through the middle portions of the anguloarticular. (CI = 33, RI = 71).

The dentary in species of *Copella* is anteroposteriorly short when compared to other lebiasinids. In *Copella*, and also in *Lebiasina* cf. *yuruaniensis* and *Pyrrhulina australis*, the ventroposterior tip of the dentary is not located far posteriorly, instead, it reaches the vertical through the middle portions of the anguloarticular (state 1, Figs. 9B and 10). In contrast, in the remaining lebiasinids and in *Hoplerithrynus unitaeniatus*, the dentary is elongate, its ventroposterior tip is located at the vertical through the articulation between the anguloarticular and the quadrate or falling short to it (Fig. 9A).

61. Extension of the outer dentary tooth row: (0) located only laterally, (1), continuous along the inner tooth row extension, (2) located only anteriorly, not extending laterally. (CI = 100, RI = 100).

[Mod.: Oyakawa, 1998: 61]

The outer dentary tooth row in the species of *Derhamia*, *Lebiasina*, *Nannostomus*, and *Piabucina* is long, almost as long as the inner tooth row (state 1, Fig. 13B). Oyakawa (1998) observed the same condition in the Pyrrhulinini, but not confirmed herein. Our observations indicate instead, that the outer dentary tooth row in members of this tribe is short, located only anteriorly (state 2, Fig. 13A).

In *Hoplerithrynus unitaeniatus*, the outer dentary tooth row is located laterally, distinct from the conditions found in Lebiasinidae.

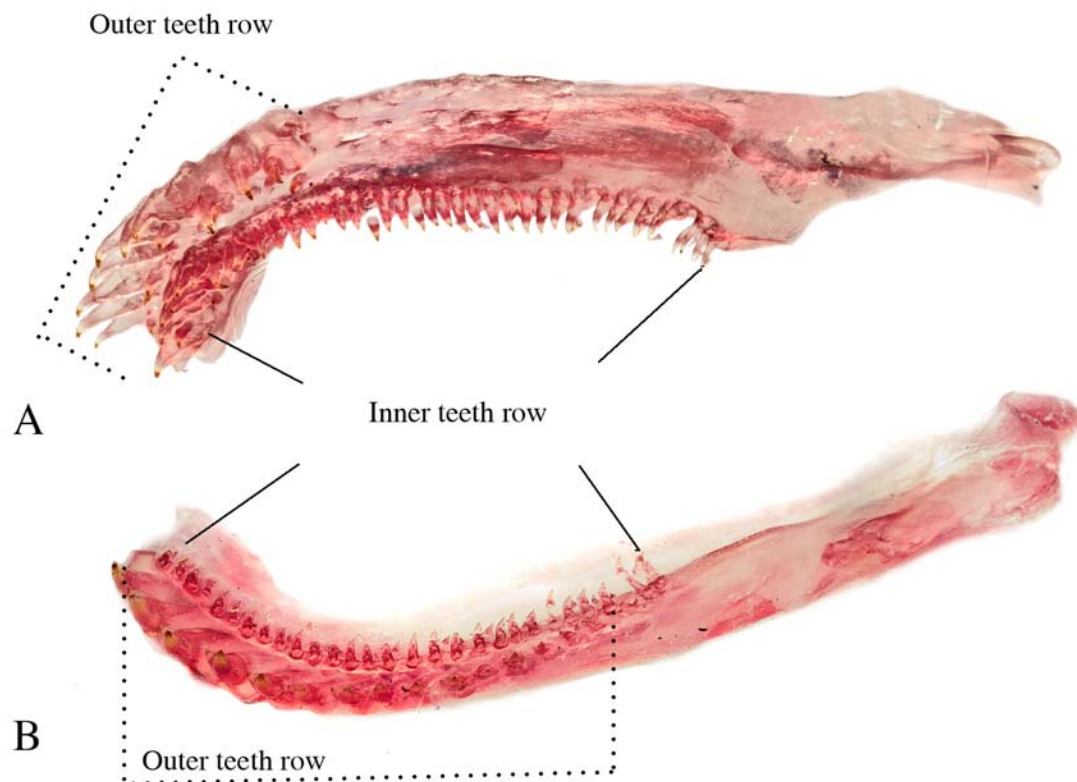


Figure 13. Dorsal view of the dentary of (A) *Copella eigenmanni*, MZUSP 81143, male, 44.3 mm SL, right side, and of (B) *Piabucina unitaeniata*, MZUSP 73090, male, 75.6 mm SL, left side.

62. Coronomeckelian length: (0) small, approximately ten times in the length of Meckel's cartilage, (1) relatively large, approximately five times or less in the length of Meckel's cartilage. (CI = 33, RI = 71).

[Netto-Ferreira, 2006: 110; 2010: 61]

The coronomeckelian is distinct small in the species of *Hoplerythrinus*, *Derhamia*, and *Pyrrhulina* (state 0, Fig. 9B), and relatively large in the remaining species analyzed (state 1, Fig. 9A and 10).

Suspensorium and opercular series

63. Palatine shape: (0) approximately as wide as long, (1) elongate. (CI = 100, RI = 100).

The palatine of most lebiasinids is elongate, approximately hourglass-shaped, but in the species of *Derhamia*, *Lebiasina*, and *Piabucina* this bone is roughly square.

In *Copella nattereri* and *C. stigmatemion* the palatine is cartilaginous and both species retain large portions of cartilage in their skeleton when adults, probably as a result of developmental truncation.

64. Comparative length of ectopterygoid: (0) twice longer than palatine or more, (1) slightly longer than palatine, (2) smaller than palatine. (Unordered). (CI = 50, RI = 80).

[Mod.: Zanata & Vari, 2005: 98; Moreira, 2007: 51; Netto-Ferreira, 2006: 115; 2010: 63]

The ectopterygoid length varies within the Lebiasinidae, but it was not possible to unambiguously define the character states related to this bone based solely on its length. Thus its length was evaluated through comparison with the palatine length.

The ectopterygoid of the species of *Derhamia*, *Lebiasina*, and *Piabucina* is long, twice longer than the palatine (state 0). In species of *Copeina*, *Pyrrhulina*, and in *Copella compta* and

C. eigenmanni, the ectopterygoid is only slightly longer than the palatine (state 1). In *Copella nattereri*, *C. stigmatsemion*, *C. vilmae*, and *Nannostomus* species, the ectopterygoid is reduced, smaller than the palatine, especially in *Nannostomus* (Weitzman, 1964).

This character was coded as inapplicable for *Nannostomus anduzei* as no ectopterygoid was found in this species.

65. Contact between ectopterygoid and quadrate: (0) present, (1) absent. (CI = 50, RI = 80).

[Vari, 2001: 21; Mirande, 2010: 162; Netto-Ferreira, 2006: 123; 2010: 68]

The absence of contact between the ectopterygoid and the quadrate was observed in all the species of *Copella* (in *Copella compta* and *C. eigenmanni* the character was found to be polymorphic) in which the bones are separated by a large portion of the palatoquadrate cartilage, not ossified in these species. The lack of contact between these bones was proposed as synapomorphy for a clade including *Copella eigenmanni*, *C. nattereri*, and *C. stigmatsemion* by Netto-Ferreira (2006, 2010) a result not corroborated in this work.

The ectopterygoid and the quadrate of *Nannostomus beckfordi* and *N. marginatus* are also not contacting each other, but the poor staining of the cartilage in the specimens examined preclude any conclusion concerning the ossification of the palatoquadrate cartilage. In the remaining species of the family, the bones are in contact.

This character was coded as inapplicable for *Nannostomus anduzei* as no ectopterygoid was found in this species.

66. Ectopterygoid teeth: (0) present, (1) absent. (CI = 100, RI = 100).

[Weitzman, 1964; Lucena: 1993: 56; Oyakawa, 1998: 36; Moreira, 2007: 55; Toledo-Piza, 2007: 51; Netto-Ferreira, 2006: 117; 2010: 64]

Within the Lebiasinidae, only the species of *Lebiasina* and *Piabucina* have ectopterygoid teeth. It is also the condition found in *Hoplerythrinus*. In contrast, the remaining members of the family lack this bone. The appearance of ectopterygoid teeth during the development of *Lebiasina* cf. *bimaculata* is relatively late. The ectopterygoid starts to ossify at 8.5 mm SL, and three conical teeth can be first seen on this bone at 11.4 mm SL. At 26.0 mm SL, all the bones of *Lebiasina* cf. *bimaculata* are ossified.

As the presence of a large ectopterygoid bearing teeth is plesiomorphic for the family, tooth losses and ectopterygoid size reduction may be related to developmental truncation present in the evolutionary history of the family.

67. Metapterygoid shape: (0) approximately as long as deep, (1) elongate. (CI = 100, RI = 100).

[Lucena, 1993: 57; Netto-Ferreira, 2006: 127, 2010: 70]

In all lebiasinids and *Hoplerythrinus*, the metapterygoid is elongate. However, in *Lebiasina* and *Piabucina*, this bone is roughly square shaped, as long as deep.

68. Contact between metapterygoid and quadrate: (0) bones in contact through a small projection of the metapterygoid, (1) bones almost in contact, separated by a small patch of

cartilage, (2) far from each other by the presence of a large patch of cartilage. (Unordered). (CI = 100, RI = 100).

The absence of a metapterygoid-quadrate fenestra in the Lebiasinidae is a synapomorphy for the family (Vari, 1995; Weitzman & Weitzman, 2003; Netto-Ferreira, 2006, 2010). Such condition makes the configuration of the contact between metapterygoid and quadrate distinct from that present in other Characiformes. As mentioned before, a large portion of the palatoquadrate cartilage is not ossified in *Copella* (character 65). Consequently, the metapterygoid is distant from the quadrate due to the presence of a large patch of cartilage (state 2). In the species of *Derhamia*, *Pyrrhulina*, and *Nannostomus*, the bones are in contact or almost, only separated by a small patch of cartilage. By contrast, in the species of *Lebiasina* and *Piabucina* there is a singular articulation between the metapterygoid and the quadrate, through a small projection of the metapterygoid (state 0).

In *Hoplerythrinus unitaeniatus* a metapterygoid-quadrate fenestra is present and the character was coded as inapplicable.

69. Foramen in the posterior portion of the metapterygoid: (0) encircled by the metapterygoid, (1) in form of an incomplete arch, bordered posteriorly by cartilage or by the hyomandibular. (CI = 33/50, RI = 60/80).

[Vari & Harold, 2001: 23; Netto-Ferreira, 2006: 128; 2010: 71; Moreira, 2007: 65. Mod.: Mirande, 2010: 168]

The metapterygoid of the Lebiasinidae (except *Nannostomus anduzei*) and most

Characiformes has a foramen on its posterior region. In some studies it was reported a supposed passage of the ramus mandibularis trigeminus nerve through this foramen (Moreira, 2007: 65; Mirande, 2010: 168). However, according to Datovo & Castro (2012), this foramen serves as passage of the afferent pseudobranchial artery in most characiforms, except the Erythrinidae (*Hoplias malabaricus* was the only erythrinid analyzed), in which the afferent pseudobranchial artery passes through the pseudobranchial fissure (a fissure in the *adductor arcus palatini* muscle). As there is no further information on the homology of the metapterygoid foramen of *Hoplerythrinus unitaeniatus*, in which there is a closed foramen at the posterior portion of that bone, it was coded as state 0.

The metapterygoid foramen is completely encircled by the metapterygoid also in *Copella compta*, *C. eigenmanni*, *C. vilmae*, *Derhamia hoffmannorum*, *Lebiasina* cf. *yuruaniensis*, *Piabucina unitaeniata*, and the species of *Pyrrhulina* (state 0). In contrast, in *Copella arnoldi*, *Lebiasina bimaculata*, *Lebiasina* cf. *yuruaniensis*, and the species of *Nannostomus* the metapterygoid foramen is not fully surrounded by metapterygoid. It is in form of an incomplete arch, posteriorly limited by the hyomandibula, or by cartilage (state 1). This character is polymorphic in *Copeina guttata*, *Copella arnoldi*, *C. nattereri*, and *C. stigmatemion*.

70. Position of a canal used as passage for the afferent pseudobranchial artery on the posterior portion of the metapterygoid: (0) perpendicular, (1) oblique. (CI = 100, RI = 100).

[Netto-Ferreira, 2006: 129; 2010: 72]

Netto-Ferreira (2006: 129; 2010: 72) coded the passage of the afferent pseudobranchial artery (= vase for Netto-Ferreira, 2010) through a foramen (state 0) or through a short canal in

the metapterygoid (state 1). These states proposed seems, actually, to correspond to the position in which the afferent pseudobranchial artery passes through the metapterygoid, leaving a canal that is perpendicular or oblique to the bone (corresponding respectively to states 0 and 1 of Netto-Ferreira, 2006, 2010).

Netto-Ferreira (2006: 129) coded *Derhamia* as having the artery passing through a short canal (= oblique, state 1) in the metapterygoid. However, the condition observed herein and by Netto-Ferreira (2010: 72) for *Derhamia* is the one coded as state 0 (= perpendicular). Other taxa in which the artery is perpendicular through the metapterygoid are *Hoplerythrinus*, *Lebiasina minuta* and *Piabucina unitaeniata*. In contrast, the artery is oblique through the metapterygoid in the Pyrrhulinini.

Netto-Ferreira (2010) coded state 0 for *Copella arnoldi* and *C. nattereri*, probably due to the unclosed metapterygoid foramen present in these species. Examination of larger samples revealed that this character is polymorphic in *Copella arnoldi*, *C. nattereri*, *C. stigmasemion*, and *Copeina guttata* (character 69), the metapterygoid foramen can also be fully encircled by that bone in some specimens. Thus, it could be confirmed that the pseudobranchial artery passes obliquely in the metapterygoid, as in the species of *Pyrrhulina* and other species of *Copella*.

As the metapterygoid foramen is not completely encircled by bone in *Lebiasina bimaculata*, *Lebiasina* cf. *yuruaniensis*, and the species of *Nannostomus*. Thus it was not possible to code this character and for this reason they were coded as missing entries.

71. Lamellar process at the posterodorsal portion of the hyomandibular: (0) present, (1) absent. (CI = 50, RI = 83).

[Mod.: Netto-Ferreira, 2006: 136; 2010: 77]

The hyomandibular of Lebiasinidae may present a lamellar process at its posterior portion, dorsal to the articulation with the opercle. It seems not to be the same projection described by Mattox & Toledo-Piza (2012: 90, figs. 24a and 25b). Netto-Ferreira (2006) proposed two conditions for this character: long and short. Later on, however, Netto-Ferreira (2010) defined four conditions: long, short, contiguous and restricted to the area of articulation with the opercle and absent. Since it was not possible to define discrete characters using this codification, only presence or absence of the lamellar process were considered.

The findings of Netto-Ferreira (2010) concerning the presence of the lamellar process in all the species of *Copella*, but *Copella arnoldi*, are corroborated. Regarding the outgroup, only the species of *Pyrrhulina* lacks the process.

Hyoid arch

72. Shape of posterior ceratohyal: (0) round, (1) long. (CI = 100, RI = 100).

The posterior ceratohyal of *Copella compta*, *C. eigenmanni*, and *C. vilmae* is slightly elongate longitudinally (Fig. 14A). It is a synapomorphy for the clade composed of these species. In contrast, in most lebiasinid taxa and in *Hoplerythrinus unitaeniatus*, the posterior ceratohyal is approximately round, as deep as long (Fig. 14B).

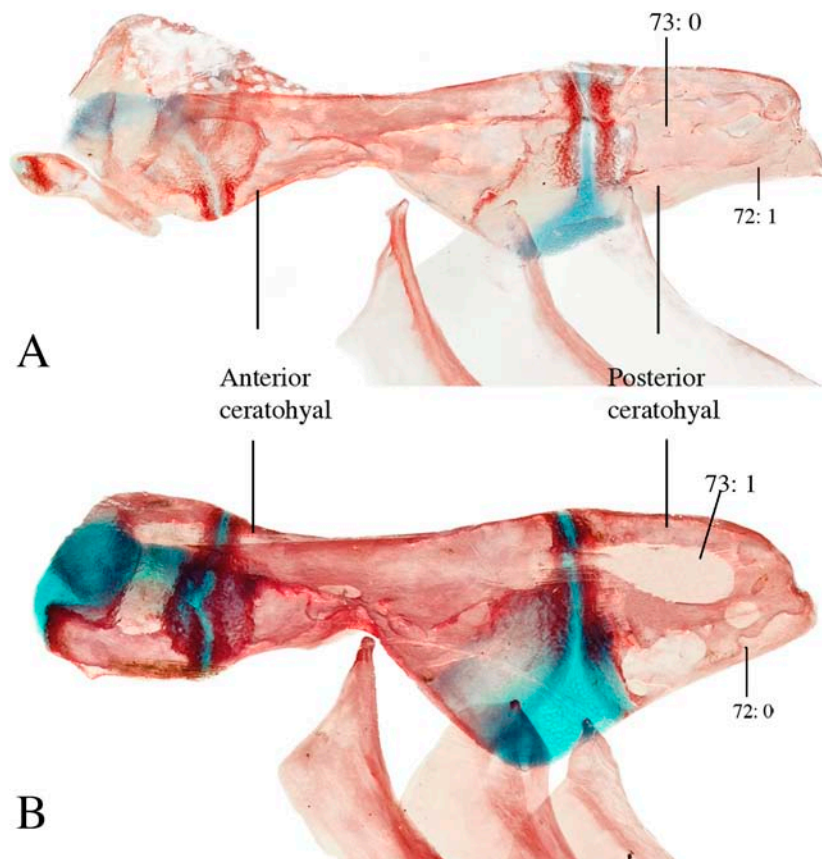


Figure 14. Hyoid arch of (A) *Copella eigenmanni*, MZUSP 81143, male, 44.3 mm SL, ventral hypohyal broken, (B) *Copella nattereri*, MZUSP 87426, male, 38.7 mm SL. Lateral view of left side.

73. Canal on the anterior and posterior ceratohyal: (0) closed, (1) opened. (CI = 33, RI = 33).

The anterior and posterior ceratohyal bear a canal that serves as passage for the hyomandibular branch of the 7th cranial nerve (Mattox & Toledo-Piza, 2007). It enters the lateral portion of the posterior ceratohyal through a foramen. The nerve extends through the canal within the anterior ceratohyal. Mattox & Toledo-Piza (2007) observed whether the nerve is protected by the canal or exposed along the dorsal margin of the anterior ceratohyal. *Lebiasina* and *Piabucina* clearly present state 0. The remaining genera seem to share the same condition,

but it was impossible to code this character.

The present osteological survey indicated that in *Copella nattereri*, *C. stigmatemion*, *Copeina guttata*, and *Nannostomus anduzei*, the canal located on the anterior and the posterior ceratohyals is open, or only partially closed (with a small lamella on its borders) (state 1, Fig. 14B). Such condition is also present in the miniature characid species *Cyanogaster noctivaga* (Mattox *et al.*, 2013: fig. 6). The canal on posterior ceratohyal is completely closed in the remaining lebiasinid species (state 0, Fig. 14A), as in *Phenacogaster*, *Acanthocharax*, *Galeocharax*, and *Lonchogenys* [Mattox & Toledo-Piza (2007: figs 26 a-d, respectively)], and in *Agoniates*, *Salminus*, and *Axelrodia* [Mirande (2010: figs. 80-82, respectively)].

Canal open on anterior and posterior ceratohyals is a condition found in juveniles of *Lebiasina bimaculata*, gradually closing during ontogeny. The presence of an open canal on those bones of *Copella nattereri*, *C. stigmatemion*, *Copeina guttata* and *Nannostomus anduzei* is possibly a result of developmental truncation.

74. Number of branchiostegal rays: (0) five, (1) four, (2) three. (CI = 100, RI = 100).

[Weitzman, 1964; Vari, 1995: 61; Buckup, 1998: 30; Oyakawa, 1998: 48; Zanata & Vari, 2005: 112; Moreira, 2007: 191; Toledo-Piza, 2007: 57; Mirande, 2010: 212, 213. Mod.: Mattox & Toledo-Piza, 2012: 99]

In most characiforms there are four branchiostegal rays. All the taxa of the Erythrinidae have five (Weitzman, 1964), a condition considered synapomorphic for the family by Vari (1995). Mattox & Toledo-Piza (2012) found variation not only in the number of branchiostegal rays, but also in its association with the anterior and posterior ceratohyals. They

pointed out that in the cynodontines and *Acestrorhynchus* there are two branchiostegal rays associated with posterior ceratohyals, in contrast to the condition found in most characiforms, including the Erythrinidae and the Lebiasinidae, in which only one ray is associated with the posterior ceratohyal.

Within the Lebiasinidae, the species of *Derhamia*, *Lebiasina*, and *Piabucina* have four branchiostegal rays, three on the anterior plus one on the posterior ceratohyal, in contrast to the presence of three branchiostegal rays in the species of *Copeina*, *Copella*, *Nannostomus*, and *Pyrhulina*, two on anterior plus one on the posterior ceratohyal (state 1, Fig. 14). The branchiostegal ray absent in the Pyrrhulinini and *Nannostomus* is possibly one of those associated with the anterior ceratohyal in the Lebiasininae and *Derhamia*.

Developmental series of *Nannostomus beckfordi*, *Pyrhulina spilota*, and *Lebiasina* cf. *bimaculata* revealed that the ossification sequence of the branchiostegal rays occurs from the posterior to the anterior ray. It is possible that the reduced number of branchiostegal rays in the Pyrrhulinini and *Nannostomus* results from truncation during the sequential development of the branchiostegal. Thus, the branchiostegal ray lacking in these species corresponds to the anteriormost present in the species of *Derhamia*, *Lebiasina*, and *Piabucina*. The same might have occurred in the species of these genera (that have four rays) regarding the plesiomorphic condition found in the Erythrinidae (five rays).

Branchial arches

75. Tooth plate on ventral portion of second pharyngobranchial: (0) absent, (1) present. (CI = 14, RI = 25).

[Lucena, 1993: 72; Netto-Ferreira, 2006: 155; 2010: 91; Mattox & Toledo-Piza: 105]

This character varies widely within genera of the Lebiasinidae. Netto-Ferreira (2006, 2010) did not find a tooth plate on the ventral portion of the second pharyngobranchial in the *Copella* and *Pyrrhulina* species, but some species of *Pyrrhulina* do present it. In the species of *Copeina*, *Lebiasina bimaculata*, *Lebiasina* cf. *yuruaniensis*, *Nannostomus* (except *N. anduzei*), *Pyrrhulina australis*, *P. filamentosa*, and *P. marilynae* the tooth plate of second pharyngobranchial two is present, whereas in all the species of *Copella*, *Derhamia*, *Lebiasina minuta*, *Nannostomus anduzei*, *Piabucina unitaeniata*, *Pyrrhulina* cf. *brevis*, *P. semifasciata*, *Pyrrhulina* cf. *stoli*, it is lacking.

The absence of teeth on the second pharyngobranchial may possibly be related to progenetic processes within the family.

76. Lateral lamella of urohyal: (0) present, (1) absent. (CI = 33, RI = 60).

[Mod.: Moreira, 2007: 197; Toledo-Piza, 2007: 59; Zanata & Vari, 2005: 113; Netto-Ferreira, 2006: 152; 2010: 90]

The presence of a lateral lamella on the urohyal is a common feature in characiforms. In *Acestrorhynchus* and *Hepsetus* the lamella is lacking, and this represent one of the synapomorphies for *Acestrorhynchus* (Toledo-Piza, 2007). Within the Lebiasinidae, only in the species of *Copella*, except *C. compta*, and *Nannostomus beckfordi* the lateral lamella of urohyal is lacking. In the remaining species examined it is present in variable sizes (character 77).

The lateral lamella of the urohyal is the last structure to appear during the development of this bone in *Lebiasina* cf. *bimaculata*. In the species of *Lebiasina*, the lateral lamella is well developed and large. The presence of a reduced lamella in the species of *Copeina*, *Copella compta*, and *Pyrrhulina marilynae* and its absence in the remaining species of *Copella* and in *Nannostomus beckfordi* is probably a result of developmental truncation of this bone.

77. Transversal lamella of urohyal: (0) well developed, (1) reduced. (CI = 33, RI = 0).

Among Lebiasinidae presenting the lateral lamella of urohyal, a well-developed lamella is found in most lebiasinids presenting this structure, except *Copeina*, *Copella compta*, and *Pyrrhulina marilynae*. This character is polymorphic for *Pyrrhulina* cf. *brevis*. It was coded as inapplicable for species lacking the lamella.

Weberian apparatus

78. Orientation of the os suspensorium outer arm: (0) ventrally directed, (1) anteriorly directed. (CI = 100, RI = 100).

[Netto-Ferreira, 2010: 126]

The anteriorly directed os suspensorium outer arm is a unique synapomorphy for the species of *Copella* and *Pyrrhulina*. In the remaining lebiasinids and in the species of *Hoplerythrinus unitaeniatus*, it is ventrally directed.

Vertebrae and ribs (not including Weberian apparatus)

79. Comparative length of parapophysis of fifth vertebra: (0) as long as posterior parapophyses, (1) distinctly longer than posterior parapophyses. (CI = 100, RI = 100).

Among the taxa analyzed, only the species of *Lebiasina*, *Piabucina*, and *Hoplerythrinus* have the parapophysis of the fifth vertebra as long as the remaining parapophyses. In the remaining taxa, it is distinctly longer than the posterior ones.

Supraneurals

80. Supraneural anterior to neural spine of fifth vertebra: (0) absent, (1) present. (CI = 33, RI = 67).

[Netto-Ferreira, 2006: 220; 2010: 136]

Supraneurals are slender rod-like bones in the Lebiasinidae, lying between the cranium and the dorsal fin. The presence of supraneurals anterior to neural spine of fourth vertebra was documented by several authors (*e.g.* Buckup, 1998: 131; Mirande, 2010: 450; Mattox & Toledo-Piza, 2012: 116), but it is not present in any lebiasinid analyzed. Supraneural anterior to neural spine of fifth vertebra varies within the family, and is present in the species of *Derhamia*, *Lebiasina*, *Nannostomus* (except *N. anduzei*), and *Piabucina*, and absent in the species of *Copeina*, *Copella*, *N. anduzei*, *Pyrrhulina*, and also in *Hoplerythrinus unitaeniatus*.

Damaged clear and stained material prevented codification of the character in *Lebiasina*

cf. *yuruaniensis*.

Pectoral girdle

81. Extrascapular: (0) present, (1) absent. (CI = 50, RI = 87).

[Weitzman, 1964; Lucena, 1993: 93; Buckup, 1998: 52; Zanata & Vari, 2005: 127; Netto-Ferreira, 2006: 163; 2010: 93; Moreira, 2007: 233]

Weitzman (1964) listed absence of the extrascapular as one of diagnostic features of the group including *Copella*, *Copeina*, *Nannostomus*, and *Pyrrhulina*. Netto-Ferreira (2006, 2010) states that the extrascapular is present in the species of *Copeina*. In the present study, the extrascapular was found to be present in the analyzed species of *Derhamia*, *Lebiasina*, *Nannostomus*, and *Piabucina*, and absent in *Copella*, *Nannostomus anduzei*, and *Pyrrhulina*. It is, however, polymorphic for *Copeina*.

82. Second postcleithrum: (0) present, (1) absent. (CI = 50, RI = 83).

[Lucena, 1993: 89; Vari, 1995: 65; Buckup, 1998: 58; Zanata & Vari, 2005: 133; Netto-Ferreira, 2006: 168; 2010: 96; Moreira, 2007: 225; Mirande, 2010: 248).

Within the lebiasinid taxa analyzed, the second postcleithrum is absent in *Pyrrhulina marilynae* and *Copella* (state 1, Fig. 15B). Netto-Ferreira (2010) and Netto-Ferreira & Marinho (2013) propose a putative monophyletic group within *Pyrrhulina*, comprising

Pyrrhulina australis, *P. vittata* and *P. marilynae*, based on the reduction in size (in *P. australis*), or absence (in *P. vittata* and *Pyrrhulina marilynae*) of this bone. The second postcleithrum is present in most Characiformes (state 0, Fig. 15A). The authors mentioned above listed the taxa lacking it.

83. Third postcleithrum: (0) present, (1) absent. (CI = 100, RI = 100).

[Vari, 1995: 64; Lucena, 1993: 90; Buckup, 1998: 59; Zanata & Vari, 2005: 134; Netto-Ferreira, 2006: 169; 2010: 97; Moreira, 2007: 225; Mirande, 2010: 249)

The third postcleithrum is present in most Characiformes. Its absence in several taxa was remarked by the authors listed above. Within the Lebiasinidae, third postcleithrum is only absent in the species of *Pyrrhulina*. This character was recovered as a unique synapomorphy of this genus.

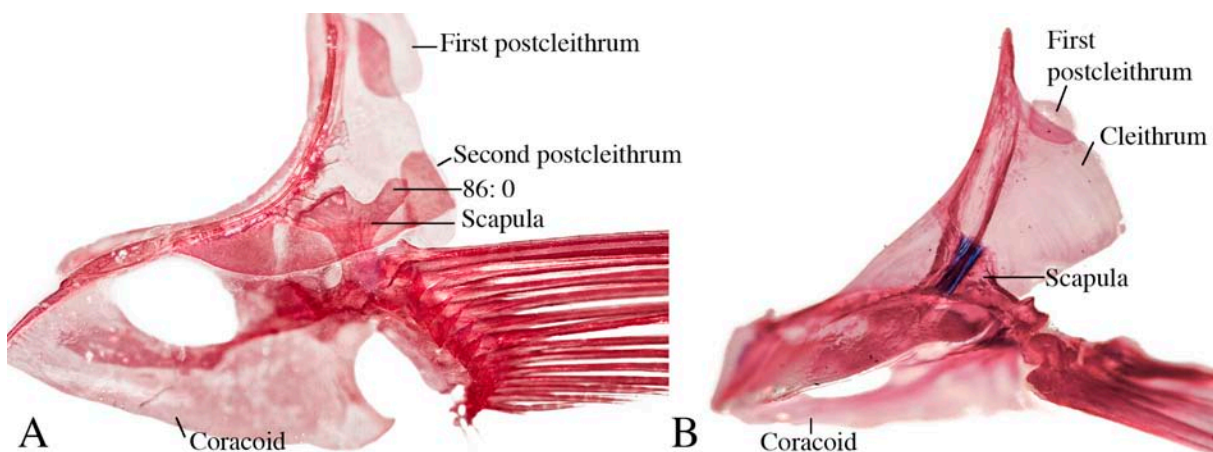


Figure 15. Lateral view of pectoral girdle of (A) *Copeina guttata*, MZUSP 27088, male, 65.3 mm SL, right side, inverted, and (B) *Copella arnoldi*, MPEG 8305, male, 29.7 mm SL, left side.

84. Surface of contact between medial lamella of cleithrum and coracoid: (0) irregular to zigzag shaped, (1) smooth. (CI = 50, RI = 50).

In the Characiformes, the cleithrum frequently has a medial lamella contacting the coracoid medially (Weitzman, 1962: fig. 19), posterior to the interosseous space, which is the fenestra limited dorsally by the cleithrum and ventrally by the coracoid (Starks, 1930: 90). In *Copella arnoldi*, *C. nattereri*, and *C. stigmatemion*, the surface of this bony contact is smooth (state 1, Fig. 16A), whereas in the remaining lebiasinids it is irregular or zigzag shape. This character is polymorphic for *C. compta* and *C. eigenmanni*.

Nannostomus anduzei and *N. beckfordi* have a very small or lacks the interosseous space, condition also observed by Weitzman (1964) in *N. harrisoni*. Thus the contact between the cleithrum and the coracoid is extensive (Weitzman, 1964: fig. 10). *Nannostomus anduzei*, however, the medial lamella of the cleithrum is missing, thus the coracoid is directly in contact with cleithrum. As such conformation results in a different condition, this character was coded as inapplicable for *N. anduzei*.

85. Bony ridge on the lateral portion of coracoid: (0) present, (1) absent. (CI = 50, RI = 83).

[Mirande, 2010: 239]

A bony ridge on the lateral portion of the coracoid, extending from mesocoracoid base to the ventral margin of the interosseous space (Mirande, 2010: fig. 97), is present in all the Lebiasinidae, except *Copella*.

In *Nannostomus anduzei* and *N. beckfordi*, the interosseous space is reduced or lacking

but the bony ridge is present in *N. beckfordi* (state 1), and absent in *N. anduzei* (state 0). *Hoplerythrinus unitaeniatus*, the interosseous space is absent or very reduced. A pronounced bony ridge, however, can be seen in a comparable position to that found in the lebiasinid taxa. Thus, it was coded as state 1.

86. Posterodorsal projection of the lateral portion of scapula, in contact with cleithrum: (0) present, (1) absent. (CI = 100, RI = 100).

The scapula is mediolaterally positioned on the pectoral girdle. In the Lebiasinidae, its lateral portion is in contact with the medial portion of cleithrum. In most species analyzed, this lateral portion of scapula has a posterodorsal projection towards the second postcleithrum (Fig. 15A). This projection is absent only in *Copella* (Fig. 15B).

87. Pointed projection on ventral half of proximal radial 2 of pectoral fin: (0) present, (1) absent. (CI = 17, RI = 37).

The proximal portion of the proximal radials of the pectoral fin in the Lebiasinidae is concave, with two halves to receive the posterior portion of the scapula. In some species, there is a pointed projection on the ventral half of proximal radials 2 and 3 (character 89). This projection is present on the ventral half of proximal radial 2 in *Lebiasina minuta*, *Nannostomus eques*, *N. marginatus*, and all the *Copella* species (except *C. vilmae*) (state 1, Fig. 16A). It is also present in *Hoplerythrinus unitaeniatus*, but absent in the species of *Copeina*, *Copella vilmae*, *Derhamia*, *Lebiasina bimaculata*, *Lebiasina* cf. *yuruaniensis*, *Nannostomus anduzei*, *N. beckfordi*, *Piabucina unitaeniata*, and species of *Pyrrhulina* (state 0, Fig. 16B).

88. Orientation of pointed projection on ventral half of proximal radial 2 of pectoral fin: (0) lateral, (1) medial, (2) anteriorly oriented, parallel to scapula. (Unordered). (CI = 100, RI = 100).

In the species of *Copella* (except *C. vilmae*), the ventral projection on the proximal portion of proximal radial 2 of the pectoral fin is distinctly elongate, and anteriorly oriented, located ventral to scapula. In *Lebiasina minuta*, *Nannostomus eques*, and *N. marginatus*, this projection is medially oriented toward the proximal radial 4, almost parallel to the scapula. The condition in *Hoplerythrinus unitaeniatus* is considered autapomorphic in the present analysis. Its projection is laterally oriented, toward the proximal radial 1.

89. Pointed projection on ventral half of proximal radial 3 of pectoral fin: (0) absent, (1) present. (CI = 50, RI = 75).

Most lebiasinids lack the projection on the ventral half of proximal radial 3 (Fig. 16B). In all the species of *Copella* (except *C. vilmae*) this projection is present (Fig. 16A). This condition is similar to that present on proximal radial 2 described in character 87.

90. Relative width of proximal radial 4: (0) as wide as proximal radials 2 and 3, (1) medially expanded, wider than proximal radials 2 and 3. (CI = 100, RI = 100).

[Netto-Ferreira, 2006: 177; 2010: 102]

The proximal radial four in Pyrrhulinini is laterally expanded, wider than the proximal radials two and three (Fig. 16). In contrast, it is relatively thin in the remaining Lebiasinidae, approximately as wide as proximal radials two and three.

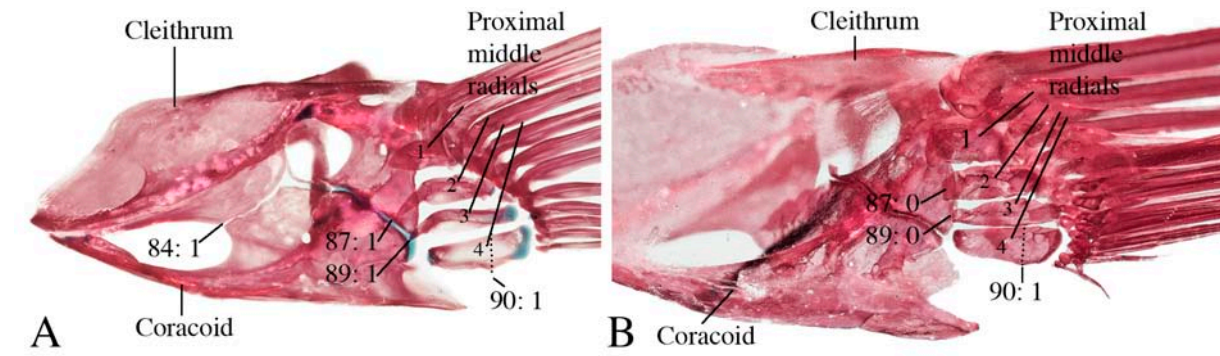


Fig. 16. Ventral view of pectoral girdle of (A) *Copella arnoldi*, MPEG 8305, male, 29.7 mm SL, left side, and (B) *Copeina guttata*, MZUSP 27088, male, 65.3 mm SL, right side, inverted.

Pelvic girdle

91. Relative position of anterior tip of basipterygium: (0) at vertical between ribs of 10th and 11th vertebrae, (1) at vertical between ribs of 9th and 10th vertebrae, (2) at vertical between ribs of 8th and 9th vertebrae, (3) at vertical between ribs of 7th and 8th vertebrae, (4) at vertical between ribs of 6th and 7th vertebrae. (Unordered). (CI = 60, RI = 78).

The relative position of the anterior tip of the basipterygium is more anterior in the Pyrrhulinini and the species of *Nannostomus*, than in the species of *Derhamia*, *Lebiasina*, and *Piabucina*. It is positioned at the vertical between ribs of the 10th and 11th vertebrae only in *Lebiasina minuta*, as an autapomorphy for this species. It is positioned at the vertical between ribs of 9th and 10th vertebrae in the species of *Hoplerthrinus*, *Derhamia*, *Lebiasina*, and

Piabucina, at the vertical between ribs of 8th and 9th vertebrae in *Nannostomus anduzei*, *N. beckfordi*, *Pyrrhulina filamentosa*, and *Copella compta*, *C. eigenmanni*, and *C. vilmae*, and at the vertical between ribs of 7th and 8th vertebrae in *Copella arnoldi*, *C. nattereri* and *C. stigmatsemion*, *Nannostomus eques* and *N. marginatus*, and the species of *Pyrrhulina* (except *P. filamentosa*). In *Copeina guttata* this character is polymorphic, presenting the condition described in states 2 and 3.

92. Secondary crest of basipterygium: (0) absent, (1) present. (CI = 20, RI = 56).

[Mirande, 2010: 264]

The principal crest of the basipterygium is bordered medially by a variously developed lamella. In the species of *Hoplerythrinus*, *Copella*, *Nannostomus*, and *Pyrrhulina australis* and *Pyrrhulina* cf. *brevis* there is a secondary crest medially, diverging anteriorly from the primary crest (Mirande, 2010: fig. 104).

93. Ischiac process: (0) without process, ischiac process medially directed toward its counterpart (1) with a relatively small process posteriorly directed, (2) with a small curved process laterally directed, (3) with a long curved process laterally directed. (Unordered). (CI = 50, RI = 70).

The four-character states proposed describe distinct shapes of the pelvic-fin ischiac process in the Lebiasinidae. The ischiac process of *Lebiasina minuta* is only represented by a rectangular bone projected from the basipterygium toward its counterpart (state 0). In the species of *Copeina*, *Derhamia*, the remaining species of *Lebiasina*, *Nannostomus* (except *N.*

eques), *Piabucina*, *Pyrrhulina* cf. *stoli*, and *P. marilynae*, there is a posteriorly directed process (state 1), comparable to that described in Weitzman (1962: fig. 21). In *Nannostomus eques* and *Pyrrhulina* (except *Pyrrhulina* cf. *stoli*, and *P. marilynae*) there is a short process medially directed with a posterior process at its tip, and a small laterally directed projection distally (state 2). The *Copella* species and *Hoplerythrinus unitaeniatus* present a similar condition described in state 2, but with a distinct long laterally directed projection (state 3).

Dorsal fin

94. Dorsal-fin position in relation to the vertebrae: (0) base of last dorsal-fin ray at vertical through abdominal vertebrae, (1) base of last dorsal-fin ray at vertical through caudal vertebrae. (CI = 33, RI = 75).

The codification of the relative position of the dorsal fin is documented through two characters (see also next character). The base of the last dorsal-fin ray in the species of *Hoplerythrinus*, *Copeina*, *Lebiasina*, *Nannostomus*, and *Piabucina* is located at the vertical through the abdominal vertebrae. In the species of *Derhamia*, *Copella*, and *Pyrrhulina*, the dorsal fin seems to be displaced backwards. In these taxa, the dorsal fin is located at the vertical through the caudal vertebrae.

95. Dorsal fin position in relation to anal fin: (0) base of last dorsal-fin ray anterior to the vertical through anal-fin origin, (1) base of last-dorsal fin ray at vertical through anal-fin origin or posterior. (CI = 50, RI = 83).

[Mod.: Buckup, 1993: 34; Netto-Ferreira, 2006: 239; 2010: 147]

The base of the last dorsal-fin ray in most species analyzed is located anterior to the vertical crossing the anal-fin origin, except in the species of *Derhamia* and *Copella*, in which it is located at the vertical through anal-fin origin or posterior to it. The most posterior condition of the dorsal fin is found in *Copella compta* (Weitzman & Weitzman, 2003), where the base of the last dorsal-fin ray is located at the vertical through the middle of the anal fin.

96. Dorsal-fin proximal-middle radial: (0) present in the anteriormost two to four pterygiophores, (1) present in all pterygiophores. (CI = 100, RI = 100).

[Mod.: Fink & Fink 1981: 106; Netto-Ferreira, 2006: 234; 2010: 144]

The structure of the dorsal fin is similar to that of the anal fin. The dorsal fin development in the species of the lebiasinid genera is also similar to that of the anal fin, described in more detail under character 101. Basically, it was observed that during the ontogeny of species of *Copella* and *Pyrrhulina*, each dorsal fin proximal-middle radial cartilage ossifies as a single unit, the proximal-middle radial. This structure is present in all the pterygiophores of the adults of species of *Copeina*, *Copella* and *Pyrrhulina*. In contrast, during the development of *Lebiasina* cf. *bimaculata*, the anteriormost pterygiophores ossify as a single unit, but the posterior ones ossify separately as proximal and middle radials. The same pattern is found in the adults of species of *Derhamia*, *Lebiasina*, *Piabucina*, *Nannostomus* and *Hoplerythrinus*. Mature males and females of *Nannostomus beckfordi* and *N. eques* may present the proximal and middle dorsal-fin radials in close contact, but the limits between them are

visible.

Netto-Ferreira (2006: 234; 2010: 144) coded absence of the dorsal-fin middle radial in the Pyrrhulininae. However, the shape and position of the proximal-middle radial in the Pyrrhulininae correspond to the shape and position of the proximal and middle radials in related taxa. Analysis of the ontogenetic sequence of ossification of the dorsal-fin proximal-middle radial cartilage in the Lebiasinidae does not confirm either the fusion of the proximal and the distal radial or loss of the middle radial, but the proximal-middle radial cartilage ossify as a single bone, starting at its middle portion, and ending at its distal portion.

97. Dorsal-fin bony stay: (0) separated from last dorsal-fin pterygiophore, (1) not separated from last dorsal-fin pterygiophore. (CI = 33, RI = 50).

[Netto-Ferreira, 2006: 237; 2010: 145]

The dorsal-fin bony stay is a small bone located posterodorsally to the last dorsal-fin pterygiophore, approximately at the vertical through the base of the last dorsal-fin ray. In species of *Derhamia*, *Lebiasina*, *Nannostomus eques*, and *Piabucina*, the dorsal-fin stay is a separated bone. In species of *Copeina*, *Copella*, *Pyrrhulina*, *Nannostomus* (except *N. beckfordi*), and *Hoplerythrinus*, there is a cartilage posterior to the distal tip of the last the dorsal-fin pterygiophore. This cartilage is variously ossified, but never separated from the pterygiophore. Netto-Ferreira (2006: 2010) states that the condition found in species of *Copeina*, *Copella*, *Pyrrhulina*, and some species of *Nannostomus* is the fusion of the bony stay with the last dorsal-fin pterygiophore. However, in small specimens of species of these genera the bones are not separated early in the development. Instead, small specimens of *Lebiasina bimaculata*, which

have a distinct bony stay in their adult phase, have a large cartilage posterior to the distal tip of the last dorsal-fin pterygiophore, condition comparable to that found in species of the Pyrrhulinini and some species of *Nannostomus*. It seems that fusion was not the process that occurred in the evolution of this character but possibly was the result of truncation in the development of the bony stay of the plesiomorphic condition.

Anal fin

98. Ventral projection of the lateral lamellae of proximal radials in adult males: (0) absent, (1) present. (CI = 100, RI = 100).

[Netto-Ferreira, 2006: 44; 2010: 152]

Weitzman (1966) already noted that the structure present in the male's anal fin of several species of the Lebiasinidae is modified for aiding fertilization by guiding sperm toward the female's vent. Most males in the family have an anal-fin ray longer and anteroposteriorly expanded. Other modifications are herein described as characters used in the phylogenetic analysis.

As pointed out by Zanata & Vari (2005: 144), the structure of the proximal radial varies broadly within the Characiformes. In the Lebiasinidae, the proximal radials often have anterior plate-like extensions on their posterior and lateral margins, except for some species of *Nannostomus* that lack the anterior and posterior lamella. In the species of the Pyrrhulinini the lateral lamellae present in the second to seventh proximal radials of mature males have a pointed ventral projection that extend lateral to the dorsal portion of each ray (state 1, Fig. 17A and 18)

These projections are absent in females (Fig. 17B). Netto-Ferreira (2006, 2010) used this character but did not mention it is sexually dimorphic, and only present in the males. Such projection was not observed in other taxa analyzed.

In *Derhamia*, *Hoplerythrinus unitaeniatus*, and *Lebiasina* cf. *yuruaniensis* the character was coded as missing entry due to the lack of adult male specimens.

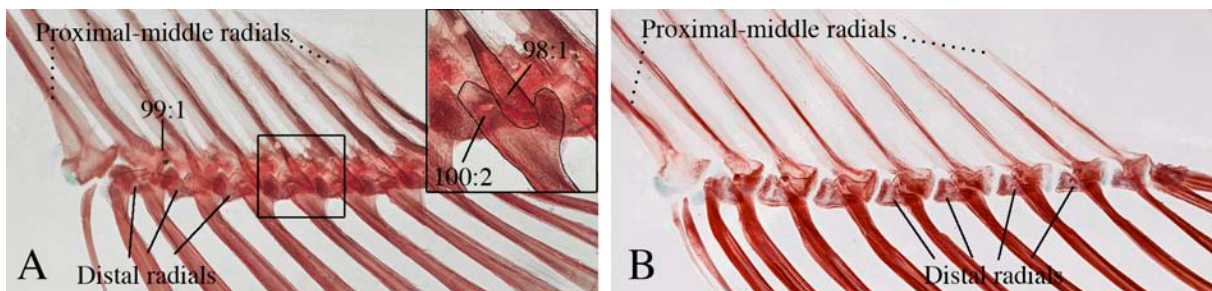


Figure 17. Anal fin of *Copella eigenmanni* (A) MZUSP 81143, male, 44.3 mm SL, and (B) MZUSP 81143, female, 29.2 mm SL, lateral view, left side.

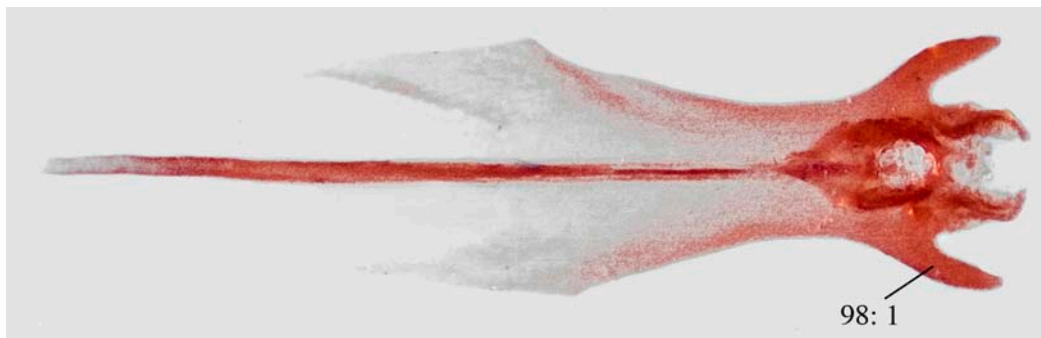


Figure 18. Anal-fin proximal-middle radial of *Copella nattereri*, MZUSP 29343, male, 32.3 mm SL. Frontal view, horizontally positioned.

99. Contact of basal portions of proximal-middle radials of anal-fin of mature males: (0) not in contact, (1) strongly connected. (CI = 100, RI = 100).

[Mod.: Netto-Ferreira, 2006: 243; 2010: 151]

The basal portions of the anal-fin proximal-middle radials of mature males of species of *Copeina*, *Copella*, *Nannostomus*, and *Pyrrhulina* are strongly connected to each other. In the species of *Copeina*, *Copella*, and *Pyrrhulina* the proximal-middle radial is present on all pterygiophores, thus their entire basal portions on the anal fin in these species are strongly connected (state 1, Fig. 17A), in contrast to the species of *Nannostomus*, in which the proximal-middle radial is present only on the four or five anteriormost pterygiophores (see discussion under character 101). Despite the proximal-middle radial presence on the anteriormost two pterygiophores of *Lebiasina bimaculata*, *Lebiasina minuta*, and *Lebiasina cf. yuruaniensis*, they are not in contact to each other in the males (state 0). Netto-Ferreira (2006, 2010) proposed distinct conditions of the character for the species of *Copella*, and *Pyrrhulina* vs. species of *Copeina*, *Nannostomus* (proximal radials “anquilosed” vs. in contact by a sinchondral joint), but this was not observed herein.

In the species of *Derhamia*, *Hoplerythrinus unitaeniatus*, and *Lebiasina cf. yuruaniensis* the character was coded as missing entry due to the lack of adult male specimens.

100. Shape of proximal tips of branched anal-fin rays in mature males: (0) ornamented, (1) spatulate to pointed, (2) expanded. (CI = 100, RI = 100).

[Mod.: Zanata & Vari, 2005: 188-190; Netto-Ferreira, 2006: 248; 2010: 156]

Males of the species of the lebiasinid taxa present a set of anal-fin modifications, probably related to courtship behavior (Weitzman, 1974). In *Lebiasina bimaculata* and *Piabucina*

unitaeniata, the tip of the branched rays has lateral, medial and posterior projections, quite ornamented (state 0), not comparable to those in members of the remaining taxa examined. In species of *Nannostomus*, the tips of the branched rays are highly modified, greatly projected in form of spatula or spiniform process anteriorly oriented (state 1). There are interspecific variations of this character within the species of *Nannostomus* that are not detailed in the present study. In species of *Copeina*, *Copella* and *Pyrrhulina*, the proximal tip of the branched anal-fin rays are expanded, and in some species there is an anteroposterior bifurcation that receive the ventrolateral projection of the proximal radial, which is present in these taxa (Fig. 17A).

101. Anal fin proximal-middle radial: (0) present in four or five anteriormost pterygiophores, (1) only present in two anteriormost pterygiophores, (2) present in all pterygiophores. (CI = 67, RI = 87).

[Mod.: Fink & Fink, 1981: 106; Mirande, 2010: 294; Zanata & Vari, 2005: 191; Netto-Ferreira, 2006: 245; 2010: 153].

The anal fin rays are supported by pterygiophores. Each pterygiophore is generally composed by three components: proximal, middle, and distal radials. Based on observations of the ontogenetic developmental series of species of *Lebiasina* and *Nannostomus*, the proximal and middle radials start as ossifications of an elongate proximal-middle radial cartilage, whereas the distal radial ossifies as a separated small round distal-radial cartilage (Fig. 19). In species of both genera, the proximal-middle radial cartilage starts ossifying at its middle portion, leaving a cartilaginous distal end. Later in the development, the anteriormost pterygiophores ossify

completely as a single unit, the proximal-middle radial. The posteriormost pterygiophores have a distinct second center of ossification distally, corresponding to the middle radial. The distal-radial cartilage also starts to ossify to form the distal radial, present in all pterygiophores. Adults of species of *Derhamia*, *Lebiasina* and *Piabucina* have two anteriormost pterygiophores composed by a proximal-middle radial and a distal radial (state 1), whereas the species of *Nannostomus* have the four to five anteriormost pterygiophores composed by a proximal-middle radial and a distal radial (state 0), and the remaining pterygiophores are composed of distinct proximal, middle and distal radials in all aforementioned genera. *Hoplerythrinus unitaeniatus* share the same condition present in the species of *Nannostomus*, contrary to results obtained by Zanata & Vari (2005), who stated that “the posteroventral process [of the proximal-middle radial of *Hoplias* and *Hoplerythrinus*] on all but the anteriormost proximal radials is cartilaginous in very small individuals of these genera and apparently ossifies as a single unit with the main body of the radial”. The posteriormost pterygiophores in *Hoplerythrinus* are represented by three distinct components, the proximal, middle and distal radials.

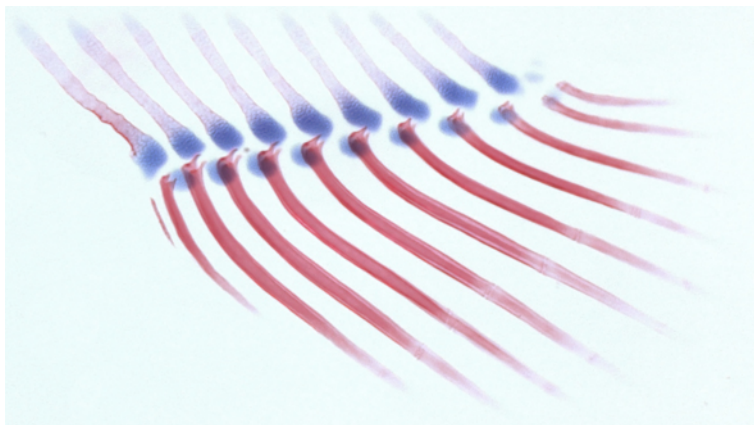


Figure 19. Anal fin of a juvenile of *Lebiasina* cf. *bimaculata*, BMNH not catalogued, 10.9 mm SL. Proximal-middle radial cartilages starting to ossify as proximal radials; middle radials yet not ossified. Distal radial cartilages also not ossified.

By contrast, the proximal-middle radial cartilage in the species of *Pyrrhulina* and *Copella* ossifies as a single unit in all the pterygiophores. Adults of species of both genera and also of *Copeina* have the proximal-middle radials present in all pterygiophores (state 2, Fig. 17). This is the same condition found in species of *Hoplias*. The presence of only two ossified elements on each the anal-fin pterygiophore of these species raises the question of whether the middle anal-fin radial is lost, or there is fusion of the proximal and middle radial or whether the proximal-middle radials cartilage do not ossify in two distinct bones during the ontogeny. Netto-Ferreira (2006: 245; 2010: 153) coded absence of the anal-fin middle radial in the Pyrrhulininae. According to Zanata & Vari, (2005), the proximal-middle radial cartilages in *Hoplias* and *Hoplerythrinus* has a posteroventral process, corresponding to the proximal and middle radials in other lebiasinid taxa. It ossifies as a single unit, failing to reveal any ontogenetic fusion as observed in the Alestidae. This is the same condition found on the anterior pterygiophores of *Derhamia*, *Lebiasina*, *Nannostomus*, *Piabucina*, and *Hoplerythrinus* and in all the pterygiophores of the Pyrrhulinini, and *Hoplias*. Analysis of the ontogenetic sequence of ossification of the proximal-middle radial cartilage in the Lebiasinidae indeed does not reveal either fusion or loss of the middle radial, but the its ossification as a single bone, that starts at its middle portions, ending at its distal portion. Zanata & Vari (2005) states that a similar condition is also found in the Ctenoluciidae.

Weitzman (1962: 40) described the presence of only proximal and distal radials from the first through the fifth pterygiophores on the anal fin of *Brycon meeki*, and of proximal, medial and distal radials on the remaining. Zanata & Vari (2005) and Mirande (2010) confirm the presence of the same pattern in most characids. Mirande (2010: 294) coded the fusion of the proximal and middle radials in the anterior or in all the pterygiophores. However, further phylogenetic and ontogenetic studies of members of the Characidae are necessary to confirm

whether the condition found in characids is homologous to those present in *Derhamia*, *Lebiasina*, *Nannostomus*, and *Piabucina*.

102. Anal-fin bony stay: (0) present, (1) absent. (CI = 50, RI = 87).

[Netto-Ferreira, 2006: 246; 2010: 154]

The anal-fin bony stay is a small bone located posterior to the anal-fin middle radial, approximately at the vertical through the base of the last anal-fin ray. In species of *Copella*, *Pyrrhulina*, and *Copeina*, the anal-fin bony stay is absent.

103. Insertion of the anal-fin inclinator muscle of the last pterygiophore of males: (0) inserted at the median portion of last ray, (1) inserted at base of last ray. (CI = 100, RI = 100).

[Oyakawa, 1998: 106; Netto-Ferreira, 2006: 251; 2010: 159]

The insertion of the very expanded anal-fin inclinator muscle is located at the median portion the last anal-fin ray in males of all the Lebiasinidae (except *Nannostomus*) (state 1, Fig. 20A) and in *Hoplerithrynus* (state 0). In females, the insertion of this muscle is located more proximally than in males, and the muscle is not expanded (Fig. 20B). In species of *Nannostomus*, its insertion is located at the base of the fin, (state 1), as in most Characiformes.

In *Derhamia hoffmannorum* the character was coded as missing entry due to the lack of adult specimens.

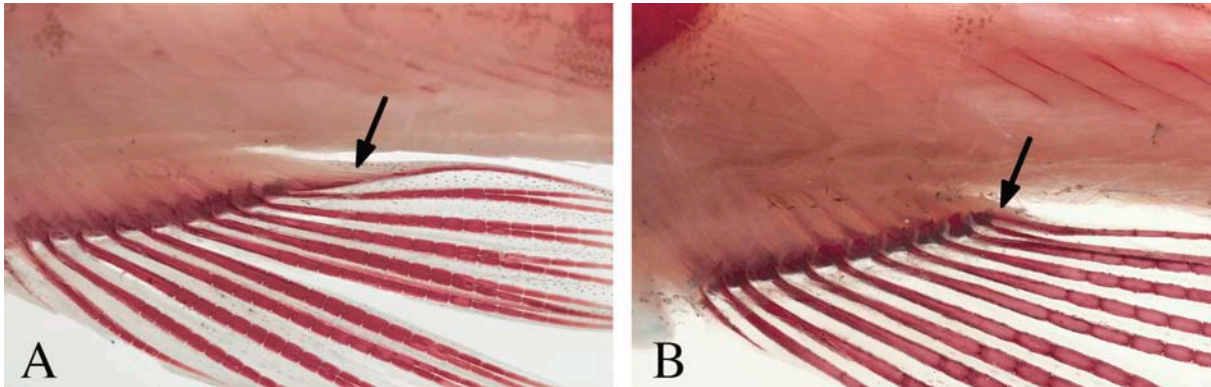


Figure 20. Anal fin of *Copella arnoldi*, MZUSP 105770. Arrows show the anal-fin inclinator muscle of (A) a male, 33.7 mm SL, and (B) a female, 21.7 mm SL.

Caudal fin

104. Number of epurals: (0) two, (1) one. (CI = 33, RI = 67).

[Lucena, 1993: 106, 107; Buckup, 1998: 68, 69; Oyakawa, 1998: 88; Zanata & Vari, 2005: 148; Netto-Ferreira, 2006: 256; 2010: 161; Moreira, 2007: 298; Mirande, 2010: 296, 297]

In Characiformes, the number of epurals ranges from one to three. Within the Lebiasinidae, *Lebiasina bimaculata*, *L. minuta*, the species of *Nannostomus*, and *Piabucina unitaeniata* have two epurals, whereas the species of *Copeina*, *Copella*, *Derhamia*, *Lebiasina* cf. *yuruaniensis*, and *Pyrrhulina* have only one epural, as well as *Hoplerythrinus unitaeniatus*.

This character, as well as other bony losses, is considered a result of developmental truncation of members of Pyrrhulininae.

105. Fusion of hypurals 5 and 6 in the adult: (0) absent, (1) present. (CI = 100, RI = 100).

According to (Netto-Ferreira, 2006: 261; 2010: 163), the reduced number of hypurals in species of *Copeina*, *Copella*, and *Pyrrhulina* is due to the loss of hypural 6. However, observations of juveniles of *Copella arnoldi*, *C. compta*, *C. nattereri*, *C. eigenmanni*, *C. stigmasemion*, *Copeina guttata*, *Pyrrhulina australis*, and *P. spilota* indicated fusion of hypurals 5 and 6 during the ontogeny (Fig. 21). In these species, the adult has the distal portion of hypurals 5+6 expanded and projected ventrally (Fig. 21 C), interpreted by Netto-Ferreira (2006: 261; 2010: 162) as possibly related to the loss of hypural 6. The condition of expanded uppermost hypural is also found in the other species of the Pyrrhulinini, in which no juveniles were available, and is herein interpreted as a result of the fusion of hypurals 5 and 6. *Nannostomus anduzei* has only five hypurals but the distal portion of the uppermost one is not as expanded as those described for the abovementioned species, neither projected ventrally. Due to the lack of further evidence supporting fusion, this character is coded as inapplicable for *N. anduzei*.

In the description of *Derhamia hoffmannorum*, Géry & Zarske (2002) described three upper hypurals for the species. However, in the present analysis, it was observed the presence of four, if “upper hypurals” are interpreted as hypurals present in the upper caudal-fin lobe.

In three adults and one juvenile of *Copella compta* examined, the juvenile specimen was found to have six hypurals, as expected. Two adults have the hypural 5 and 6 fused, with the distal portion expanded and projected ventrally; a thin line partially dividing the two hypurals is visible anteriorly in one specimen and posteriorly in the other one. The largest specimen has six hypurals, and the hypural 5 has its distal portion expanded and projected ventrally. As both character states occur, the condition was considered polymorphic in *Copella compta*.

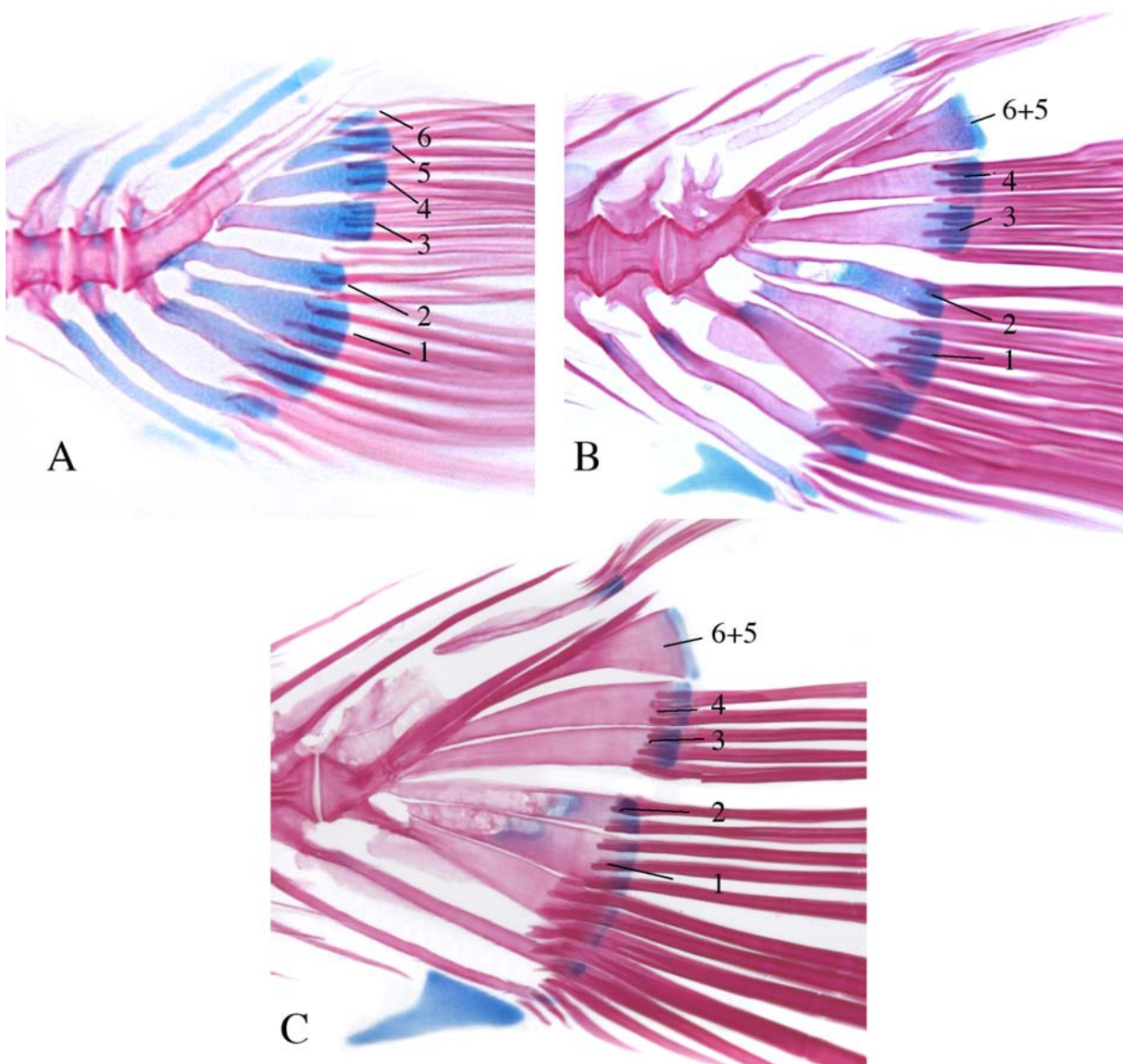


Fig. 21. Caudal fin of *Copella eigenmanni* MZUSP 92573 showing the fusion of hypurals 5 and 6 during the ontogeny (A) 5.3 mm SL, (B) 7.9 mm SL and (C) 22.0 mm SL. Uppermost caudal-fin rays removed in (B) and (C).

106. Total number of caudal-fin rays associated with hypurals of upper lobe: (0) ten, (1) nine. (CI = 50, RI = 50).

[Netto-Ferreira, 2006: 264; 2010: 165]

Among the Lebiasinidae examined, only *Pyrrhulina australis* and *P. marilynae* have nine rays associated with the hypurals of upper caudal-fin lobe. In the species of the remaining taxa, there are ten rays. Netto-Ferreira (2010) and Netto-Ferreira & Marinho (2013) suggested *Pyrrhulina marilynae* to be closely related to the small sized *P. australis*, *P. vittata*, and *P. zigzag*. Among them, *Pyrrhulina australis* and *P. marilynae* share the reduced number caudal-fin rays of the upper lobe.

Weitzman (1962) reported 10 principal rays in the upper caudal-fin lobe in all characids he examined. However, he did not mention whether he considered all branched plus one unbranched ray as principal rays, or rays associated with hypurals (as in Weitzman (1966: 3). In Weitzman (1962: fig. 15), there are 10 rays and all are associated with hypurals.

107. Number of unbranched caudal-fin rays associated with hypurals of the upper lobe: (0) one, (1) two. (CI = 50, RI = 86).

Within the Lebiasinidae, all the species of *Copella*, *Pyrrhulina australis*, and *P. stoli* have two unbranched rays associated with hypurals of the upper lobe. This character is considered polymorphic in *Pyrrhulina marilynae*.

Laterosensory canal system

108. Degree of ossification around infraorbital canal on antorbital: (0) partially enveloping the anterior portion of the infraorbital canal, (1) not ossified. (CI = 17, RI = 17).

[Weitzman, 1964; Netto-Ferreira, 2006: 186; 2010: 107; Moreira, 2007: 125; Mirande, 2010: 72]

The development of a bony canal wall around the infraorbital canal varies within the Lebiasinidae. The developmental series of *Lebiasina* cf. *bimaculata* failed to reveal how the ossification around the infraorbital develops due to lack of enough specimens to complete all the steps of its formation. However, it was observed that the bony canal on the third infraorbital was the first to start ossifying (at 15.1 mm SL) and the first to close (at 26.2 mm SL).

Reduction or total loss of parts of the laterosensory canal system has been associated with miniaturization (*e.g.* Backup, 1993; Weitzman & Vari, 1998; Zanata & Vari, 2005; Bührnheim *et al.*, 2008; Santana & Crampton, 2011). The correlation between progenesis and reduction of body size is further discussed below. According to the phylogenetic analysis given, the presence of reduction or loss of ossification of bony canals of sensory system is likely to be associated with developmental truncation, but is not always related to extremely small size.

The ossification around the sensory canal on the antorbital in the Lebiasinidae is not well developed. When present, it partially envelops the anterior portion of the infraorbital canal (Weitzman, 1964). Within the genus *Copella*, ossifications around the infraorbital canal on antorbital is absent in *C. arnoldi*, *C. nattereri* and *C. stigmatemion*, whereas it may be present or absent in *C. compta* and *C. eigenmanni*. In the outgroup it is present in *Copeina*, *Lebiasina*, *Piabucina*, *Pyrrhulina filamentosa*, *P. marilynae*, and *Pyrrhulina* cf. *stoli*, and absent in *Derhamia*, *P. australis*, *Pyrrhulina* cf. *brevis*, and in *Nannostomus anduzei*, *N. beckfordi* and *N. eques*.

This character is polymorphic for *Copella compta*, *C. eigenmanni* and *Nannostomus marginatus* and was coded as inapplicable for *Hoplerethrinus unitaeniatus* as it lacks the antorbital (Vari, 1995).

109. Degree of ossification of bony canal around infraorbital canal on first infraorbital: (0) bony canal closed, (1) bony canal not closed, (2) not ossified. (Ordered). (CI = 40, RI = 79).

[Weitzman, 1964. Mod.: Lucena, 1993: 30; Netto-Ferreira, 2006: 187; 2010: 108; Mirande, 2010: 73]

Weitzman (1964) states that in Pyrrhulina (= Pyrrhulinini) the bony canals are closed on the first and second infraorbitals. However, this condition was only observed in species of *Copeina* and *Pyrrhulina* within the group (except *P. marilynae*, which may have the bony canal on first infraorbital closed or not ossified, and not closed or not ossified on second infraorbital). In all the *Copella* species, the bony canal on the first infraorbital is not ossified, and is ossified but not as closed tube on the second infraorbital. The lateral line bony canal on the first and second infraorbitals is not ossified in *Nannostomus anduzei*.

In *Lebiasina*, *Nannostomus eques*, *N. marginatus*, and *Piabucina*, the lateral line bony canal is present and closed on first and second infraorbitals (except for the second infraorbital of *Nannostomus marginatus*, in which the bony canal is not ossified). In *Derhamia* and *Nannostomus beckfordi*, the bony canal on both infraorbitals is represented by a crest or is not completely closed.

Pyrrhulina marilynae presents character state 0 and 2 for this character, which represent extreme morphological conditions of an ordered character. Interpretation provided by TNT indicates that the intermediate state is also present in *P. marilynae*, although it was not observed.

110. Degree of ossification of bony canal around infraorbital canal on second infraorbital: (0) bony canal closed, (1) bony canal not closed, (2) not ossified. (Ordered). (CI = 40, RI = 70).

[Weitzman, 1964. Mod.: Netto-Ferreira, 2006: 188; 2010: 109]

See discussion of previous character.

111. Degree of ossification of bony canal around infraorbital canal on third, fourth and fifth infraorbitals: (0) bony canal closed, (1) bony canal not closed. (CI = 33, RI = 67).

[Mod.: Zanata & Vari, 2005: 14; Netto-Ferreira, 2006: 189, 190, 191; 2010: 110, 111, 112]

In the species of *Lebiasina*, *Nannostomus marginatus*, *N. eques*, and *Piabucina*, the lateral-line canal of the third, fourth and fifth infraorbitals are well ossified as a closed tube, whereas in the species of *Copeina*, *Copella*, *Derhamia*, *Pyrrhulina*, and *Nannostomus beckfordi*, the bony lateral line canal on these three bones are represented only by a crest on the orbital margin of the infraorbitals, a non-closed tube (Fig. 22).

This character was coded as inapplicable for *Nannostomus anduzei* due to the lack of the lateral-line canal on the third infraorbital and the lack of fourth and fifth infraorbitals bones.

112. Degree of ossification of bony canal around infraorbital canal on sixth infraorbital: (0) bony canal closed, (1) bony canal not closed. (CI = 100, RI = 100).

[Weitzman, 1964. Mod.: Netto-Ferreira, 2006: 192; 2010: 113]

In *Lebiasina* and *Piabucina*, the bony canal around the sensory canal on sixth infraorbital is closed. In *Nannostomus* species (except *N. anduzei*) and *Derhamia*, it is represented by a crest or by a non-closed tube.

This character was coded as inapplicable for *Copeina*, *Copella*, *Pyrrhulina* and *Nannostomus anduzei* due to the lack of the sixth infraorbital bone.

113. Striae on the surface of infraorbital series: (0) absent, (1) present. (CI = 50, RI = 75).

[Mod.: Mattox & Toledo-Piza, 2007: 50]

Superficial neuromasts are common on the head of members of the Lebiasinidae. Mattox & Toledo-Piza (2007: 50) stated that structures such as pores and striae on head and infraorbital bones are associated with superficial neuromasts. Within the Lebiasinidae, most taxa present small pores, but not striae, spread on infraorbitals. Presence of striae was only observed in the species of *Pyrrhulina* (except *P. australis* and *P. marilynae*) (Fig. 22).

Small pores on the infraorbital are common but it was difficult to code due to the high variability in number and polymorphisms. Whether pores and striae are associated characters in Lebiasinidae, as it apparently are in *Acestrocephalus*, *Charax*, *Phenacogaster*, and *Roeboidea*, should be further investigated.

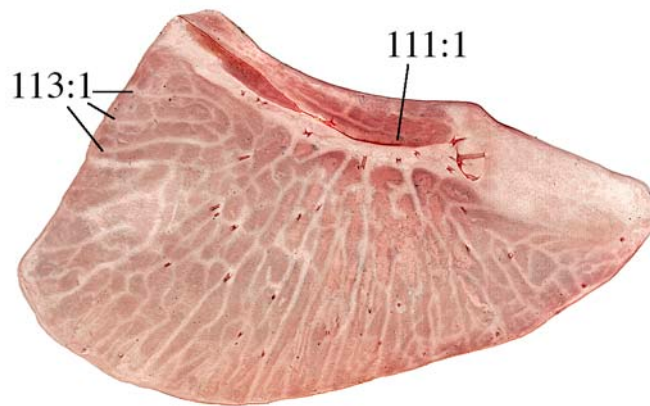


Figure 22. Third infraorbital of *Pyrrhulina semifasciata*, MZUSP 23230, male, 48.3 mm SL, lateral view of right side.

114. Ossification around supraorbital canal on nasal: (0) present, (1) absent. (CI = 50, RI = 83).

In most Lebiasinidae a closed bony tube around the supraorbital canal on nasal is present (Fig. 5 and 6A), except in *Copella* species and *Nannostomus anduzei*. Further comments on the nasal bone and the supraorbital canal on nasal are under character 32.

115. Degree of ossification of bony canal walls of supraorbital canal on frontal: (0) extending to posterolateral portion of frontal, (1) extending to epiphyseal bar, (2) not reaching epiphyseal bar. (Ordered). (CI = 33, RI = 60).

[Mod.: Netto-Ferreira, 2010: 115]

The bony canal around the supraorbital canal is variously developed in the Lebiasinidae. This variation seems to reflect distinct levels of reduction in the morphology of this structure, probably related to developmental truncation of the laterosensory canal, especially in

Nannostomus anduzei and species of *Copella*. The most ossified bony canal around the supraorbital sensory canal is present in the species of *Copeina*, *Derhamia*, *Lebiasina*, *Nannostomus* (except *N. anduzei*), *Piabucina*, and *Pyrrhulina*, and also in *Hoplerythrinus*. In these taxa, the canal extends from the anterior limit of the frontal to its posterolateral portion (state 0, Fig. 5). In contrast, it extends to the epiphyseal bar in *Copella compta*, *C. vilmae*, and *Nannostomus anduzei* (state 1, Fig. 4A), and does not reach the epiphyseal bar in *C. eigenmanni*, *Copella nattereri*, and *C. stigmatemion* (state 2, Fig. 4B, the bony canal is completely absent in one of the sides of this specimen of *Copella nattereri*). This character is polymorphic for *Copella arnoldi*, which may present states 1 and 2.

Early stages of development of the supraorbital bony canal in *Lebiasina* cf. *bimaculata* resembles the conditions described in states 1 and 2, and the adult specimen presents state 0. Ossifications of the supraorbital bony canal can be first seen at 16.7 mm SL on the frontal, above the orbit. Although the canal is not closed at this stage, it resembles the condition described as state 2. At 16.9 mm SL, the supraorbital bony canal is almost closed, and the epiphyseal branch of the supraorbital canal can be first seen. It resembles the condition described as state 1, though lebiasinids coded as state 1 does not present ossification around the epiphyseal branch of the supraorbital canal. At this stage, the supraorbital bony canal on the nasal is almost closed. From this point forward, the structure of the supraorbital mostly resembles the one described in state 0. At 19.2 mm SL, the parietal branch of the supraorbital bony canal can be seen and at 26.2 mm SL, the supratemporal bony canal is already present.

In *Nannostomus marginatus*, the supraorbital canal extends beyond the epiphyseal bar and falls short of the posterolateral limit of the frontal. This condition is comparable to that described in state 0.

116. Degree of ossification around supratemporal canal: (0) extending along posterodorsal margin of parietals, (1) reduced to a small lateral section, (2) not ossified. (Ordered). (CI = 67, RI = 91).

[Weitzman, 1964; Netto-Ferreira, 2010: 119. Mod.: Lucena, 1993; Vari, 1995: 29; Oyakawa, 1998: 26; Zanata & Vari, 2005: 158; Netto-Ferreira, 2006: 198]

The supratemporal canal is present in the species of *Copeina*, *Derhamia*, *Lebiasina*, and *Piabucina*, and absent in *Nannostomus*, *Copella*, and *Pyrrhulina*. In *Derhamia*, *Lebiasina*, and *Piabucina*, the supratemporal canal runs along the posterodorsal margin of the parietals while in *Copeina*, the canal is reduced to a small lateral section near the extrascapular. This condition is also present in *Boulengerella maculata* and *B. lateristriga* (Vari, 1995).

117. Ossification around pterotic canal: (0) present, (1) absent. (CI = 50, RI = 83).

[Weitzman, 1964; Buckup, 1998: 14; Zanata & Vari, 2005: 159; Mod.: Netto-Ferreira, 2006: 195; 2010: 117].

The pterotic canal is present in *Hoplerythrinus*, *Copeina*, *Derhamia*, *Lebiasina*, and *Piabucina*, and absent in *Copella*, *Nannostomus*, and *Pyrrhulina*. The lack of the laterosensory bony canal on pterotic was used by Weitzman (1964) to diagnose a group including *Copeina*, *Copella*, *Nannostomus*, and *Pyrrhulina*. However, corroborating Netto-Ferreira's (2006, 2010) observations, in *Copeina* the canal on the pterotic is present.

118. Ossification around laterosensory canal on posttemporal: (0) present, (1) absent. (CI = 100, RI = 100).

[Netto-Ferreira, 2010: 122. Mod.: Oyakawa, 1998: 79; Netto-Ferreira, 2006: 201; Moreira, 2007: 231]

The laterosensory bony canal on posttemporal is present in *Hoplerythrinus*, *Derhamia*, *Lebiasina*, and *Piabucina* and absent in the remaining taxa.

119. Degree of ossification of bony canal around laterosensory canal on supracleithrum: (0) well developed, (1) poorly developed, (2) not ossified. (CI = 67, RI = 92).

[Buckup, 1998: 54; Zanata & Vari, 2005: 161; Netto-Ferreira, 2006: 202; 2010: 123. Mod.: Lucena, 1998: 54; Oyakawa, 1998: 80]

The laterosensory bony canal on the supracleithrum is represented by a well ossified bony tube in *Hoplerythrinus*, *Derhamia*, *Lebiasina*, and *Piabucina*. In *Copeina* and *Pyrrhulina*, it is poorly developed, represented by a small bony crest at the dorsal portion of the supracleithrum. It is not ossified in *Nannostomus* and *Copella*.

120. First scales of the lateral line series: (0) bearing a canal with a lateral opening (1) bearing a canal without a lateral opening (2) without canal or pore. (Unordered). (CI = 100, RI = 100).

The laterosensory canal system on the body is reduced in the Lebiasinidae (Vari, 1995). When present, perforated lateral line scales are restricted to the anterior portion of body (Weitzman, 1964; Weitzman & Weitzman, 2003). Among the species without pored scales, those belonging to *Copeina*, *Copella* and *Pyrrhulina* are unique in having a small canal without a lateral opening on the first lateral line scale (Fig. 23).

Although Fernandez & Weitzman (1987) describe *Nannostomus anduzei* as having “lateral line scales 0-1, usually 0”, it was coded as having state 2 based on the specimens herein analyzed and due to the uncertainty of whether the “lateral scale 1” referred by Fernandez & Weitzman (1987) is a pored scale, bearing a canal with or without a lateral opening.

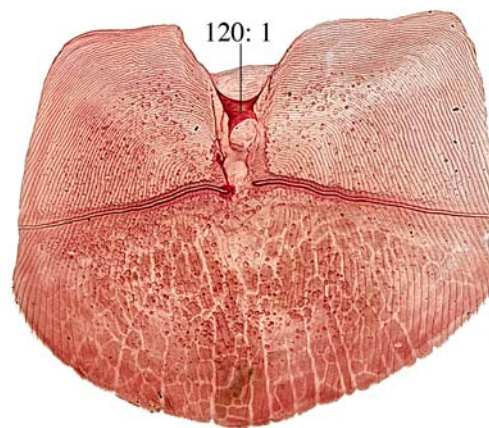


Figure 23. First scale of the lateral line of *Copeina guttata*, MZUSP 27088, male, 65.3 mm SL, Bony canal without a lateral opening in the scale. Medial view.

Characters not used

The following characters previously considered synapomorphic for *Copella* and supraspecific groups, are not included in the present study. A more detailed analysis prevented using them as originally defined.

-Extension of primary stripe. Weitzman (1966) defined and named pigmentation patterns produced by melanophores in *Nannostomus*. The “primary stripe” was considered the main midside stripe usually extending from the snout to the caudal fin. Netto-Ferreira, (2010: 186) coded the posterior extension of such stripe within the Lebiasinidae, but although the primary stripe may be considered homologous within *Nannostomus* it does not seem to represent an homologous feature for all the species of *Copella*, at least regarding the chromatophore distribution on the body. This is why the names suggested by Weitzman (1966) to characterize pigmentation patterns were not used in the descriptions of *Copella* species. For example males and females of *Copella stigmatemion* have a conspicuous black stripe extending from the opercle to the caudal peduncle, with well-delimited borders. This stripe is similar to that present in the *Nannostomus* species, *Pyrrhulina marilynae*, and *Lebiasina* cf. *yuruaensis*. On the other hand, males of *Copella arnoldi* frequently possess a blurred stripe of variable extension on midbody, without well-delimited borders. Males of *Pyrrhulina spilota* also have a similar pigmentation, but represented by a large blotch. This sexually dimorphic longitudinal pigmentation present in *Copella arnoldi* and *Pyrrhulina spilota* does not seem to correspond to the same longitudinal stripe described for *C. stigmatemion*. Moreover, *Copella eigenmanni* and *C. nattereri* have an inconspicuous longitudinal stripe that may fade completely (see Color in alcohol section of both species, and discussion about *Copella nattereri*). *Pyrrhulina filamentosa*, *Copella compta*, and

females of *C. vilmae* have a similar pigmentation, but the lack of enough material prevented further investigation of the coloration pattern. Males of *Copella vilmae* have a series of brown scales interposed with clear ones. This condition was not observed in any other species. Other kinds of pigmentation such as the faint dark color at the base of the scales, present in all the *Copella* species, seems to be widespread in the Lebiasinidae, but with variable intensity, for example, forming conspicuous blotches at scales of body of *Copella eigenmanni*.

The lebiasinid species have a complex pattern of pigmentation that deserves further attention, but to avoid problems of homology and character definitions, characters of coloration with doubtful homology were not considered.

-Wedge-shape joint between vomer and parasphenoid used by Oyakawa (1998: 18) and Netto-Ferreira (2006: 37) This character is a result of the presence or absence of the posterior shaft of the vomer (already described under character 19).

-Anterior border of scales straight. Lucena (1993: ch. 121) proposed conspicuous undulations on the anterior border of the scales of the Lebiasinidae. Netto-Ferreira (2006: ch. 285; 2010: ch. 176) coded *Copella* as having the anterior border of the scales either straight or without conspicuous undulations. All the lebiasinids examined herein have the anterior border of the scales with undulations, including *Copella*.

-Shape of posterior margin of opercle. All the *Copella* species have a roughly trapezoidal opercle. The posterior opercle margin of the species of this genus is convex. Therefore, the distinct conditions recognized by Netto-Ferreira (2010: 80) (convex, concave, and straight), were not observed.

-Nasal nerve foramen delimited only by ethmoidal cartilage. This character was proposed by Netto-Ferreira (2006: 45) as a synapomorphy of *Copella*. Although it might be informative it could not be observed the poorly stained specimens available.

-Presence of lamellar projection on posteroventral portion of orbitosphenoid. This character was proposed by Netto-Ferreira (2010: 29) for some species of *Copella* but morphological variation is gradual, precluding the recognition of discrete character states.

-Presence of groove in the medial portion of the ascending process of premaxilla. Proposed by Netto-Ferreira (2006: 81) as synapomorphic for *Copella* and *Nannostomus* but coded by the same author (Netto-Ferreira 2010: 46) only for *Nannostomus*. The presence of a groove on the premaxilla is related the way this bone is articulated with the mesethmoid. In *Nannostomus*, the premaxilla extends under the mesethmoid, and there is no groove on the ascending process to articulate the premaxilla with the mesethmoid. The presence of a groove on the ascending process of the premaxilla in *Copella* was confirmed here for some species, but it is highly polymorphic, and thus this character was not included.

-Presence of groove on the ventral border of the anterior ceratohyal. Proposed by Netto-Ferreira (2010: 86) for *Copella carsevevnnensis* (= *C. arnoldi*). Increasing samples of *Copella* does not allow the recognition of discrete character states.

-Basihyal length. Oyakawa (1998: 50) and Netto-Ferreira (2006: 140; 2010: 81) observed differences in the basihyal length within the Lebiasinidae and *Copella* species, but again, discrete character states were not observed in the large samples examined.

-Presence of spiniform process in the lateral margin of fifth ceratobranchial. Netto-Ferreira (2010: 92) coded *Copella* cf. *compta* (= *C. eigenmanni*) as lacking the process, in contrast of the presence of such process in the remaining congeners. . According to the present analysis, this process may be represented by a small spine or crest. Thus the proposition of distinct character state was not recognized.

-Form of two anteriormost branchiostegal rays associated with anterior ceratohyal. Netto-Ferreira (2010: 88) added an intermediary state to the character described by Mattox (2010: 101; 2012: 100) and Mirande (2010: 214), to characterize species having a shorter expansion of the anterior margin of anteriormost branchiostegal rays. According to Netto-Ferreira (2010), the presence of a short expansion is present in *Pyrhulina* and *Nannostomus* (except *Nannostomus harisoni*), and absence of such projection characterizes *Copella* (except *Copella* gr. *eigenmanni*). In the present survey, Lebiasininae and *Derhamia* have a notable expansion of the anterior margin of anteriormost branchiostegal rays. However, in *Nannostomus* and *Pyrhulina*, there is a variable length of the anterior portion of the branchiostegal rays, which does not allow a clear distinction of the character states. Sometimes, two conditions were observed in the same individual. Most species of *Copella* lacks such expansion but intermediate states were also detected.

-Presence or absence of supraneural anterior to neural spine of sixth vertebra. Netto-Ferreira (2006: 221; 2010: 137). Not included due to the high incidence of polymorphism.

-Presence and extension or absence of sensory canal on maxilla absent. Absence of a sensory canal on the maxilla was proposed for *Copella nattereri* (Netto-Ferreira, 2006: 182) but this condition was neither corroborated by Netto-Ferreira (2010) nor in the present study.

-Absence of laminar process on anterior margin of tripus. The absence of such process was proposed to characterize *Copella arnoldi* (Netto-Ferreira, 2010: 127) but it is not corroborated in the present study.

-Number of abdominal vertebra (= precaudal vertebra). According to Netto-Ferreira (2006: 222; 2010: 138), *Copella nattereri* has fewer abdominal vertebrae than congeners, but in large samples of this species, discrete character states could not be determined.

-Number of abdominal vertebra (precaudal vertebra) related to number of caudal vertebra. A relative larger number of caudal vertebra was used to characterize *Copella compta* (= *C. eigenmanni*) and *C. carsevennensis* (= *C. arnoldi*) by Netto-Ferreira (2010: 139), but not by Netto-Ferreira (2006: 223). In large samples of both species, no discrete character states were observed.

-Absence of prezygapophysis of fifth vertebra. Proposed by Netto-Ferreira (2006: 216) for *Copella nattereri*. It was neither corroborated by Netto-Ferreira (2010) nor in the present study.

-Scapular foramen delimitation. Within *Copella*, the presence of a scapular foramen with a cartilaginous portion between scapula and cleithrum was proposed for *Copella eigenmanni* (Netto-Ferreira, 2006: 172). However there is variable degree of ossification within several species of *Copella* (e.g. *C. nattereri*, *C. arnoldi*), ranging from having the anterior limit of the scapula foramen cartilaginous or completely bordered by scapula. This variation makes the character difficult to code in *Copella*.

-Number of dorsal procurrent caudal-fin rays. Netto-Ferreira (2010: 164) coded *Copella compta* (= *C. eigenmanni*) as having more dorsal procurrent caudal-fin rays than congeners, contrary to the results of Netto-Ferreira (2006: 263). Additional samples make difficult the recognition of discrete character states.

PHYLOGENETIC ANALYSIS

The analysis of the phylogenetic relationships among *Copella* species, based on 120 morphological characters and 23 terminal taxa, resulted in two equally-most parsimonious cladograms with 280 steps, and CI of 53 and RI of 83 (Fig. 24). The matrix of characters is presented in Appendix 1. Differences on topology between the two most parsimonious trees lie in interspecific relationships between *Lebiasina* and *Piabucina* representatives (Fig. 24). Interspecific relationships of the outgroup will not be discussed in the present study but a complete set of character transformations of each tree is given in the Appendix 2. Phylogenetic diagnosis for *Copella* and intrageneric groups, and for each genus of Lebiasinidae is given below. Numbers in Fig. 24 indicate clades discussed in the following sections. Character numbers correspond to those in “Character Description” above.

According to the present hypothesis, reductions and absences are the derived conditions of several proposed characters. Therefore, in many cases, DELTRAN optimization is better to explain parallel losses and bony simplifications in the Pyrrhulininae. As explained in Material and Methods, optimization was chosen according to each character history.

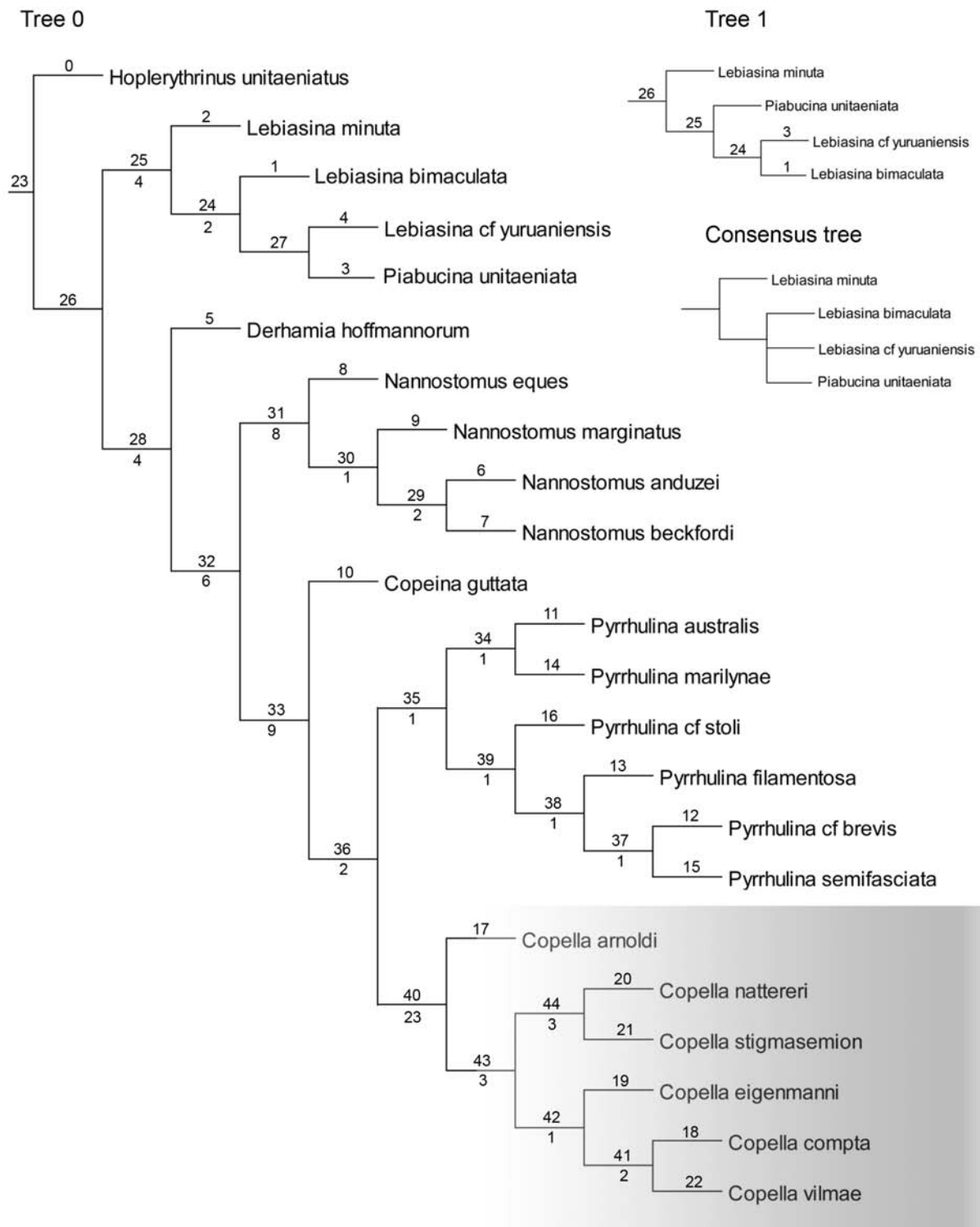


Figure 24. Two equally-most parsimonious trees (280 steps, IC = 53 and RI = 83) and the strict consensus tree. Only differences on topology between the two most parsimonious trees are explicated, remaining branches are of same topology. Shaded area showing ingroup represented

by *Copella* species. Number of clades shown above branches, values of Bremer support shown below branches.

SYNAPOMORPHY SCHEME

OUTGROUP

MONOPHYLY OF CLADE 25 (LEBIASININAE: *LEBIASINA*, *PIABUCINA*)

Exclusive characters

- Mesethmoid “T” shaped (16: 2>0).
- External margin of fourth infraorbital six times or more deeper than the orbital margin (40: 1>0).
- Metapterygoid approximately as long as deep (67: 1>0).

Non-exclusive characters

- Nasal small (33: 1>0).
- Presence of two epurals (104: 1>0).

The two most parsimonious hypotheses resulted in *Piabucina* contained in a clade represented by the species of *Lebiasina*, with Bremer support value of 4. *Lebiasina* is distinguished from *Piabucina* by lacking an adipose fin and the cellular structure of the swim bladder wall (*vs.* presence of adipose fin and non-cellular structure of the swim bladder wall in *Piabucina*). The significance of the characters used to diagnose both genera led several authors

to question the validity of *Piabucina* (Santana *et al.*, 2013). Netto-Ferreira's (2010) analysis considering the interrelationships of the Lebiasininae species resulted in *Lebiasina* and *Piabucina* being both polyphyletic. He suggested *Piabucina* as junior synonymous of *Lebiasina*, but such proposal was not published yet.

MONOPHYLY OF CLADE 28 (PYRRHULININAE: *COPEINA*, *COPELLA*, *DERHAMIA*, *NANNOSTOMUS*, *PYRRHULINA*)

Exclusive characters

- Presence of a longitudinal dark stripe on head (1: 0>1).
- Sphenotic spine vertically oriented (23: 0>1).
- Third infraorbital ventral to eye (39: 0>1).
- Ectopterygoid teeth absent (66: 0>1).
- Metapterygoid and quadrate almost in contact, separated by a small patch of cartilage (68: 0>1).
- Parapophysis of fifth vertebra distinctly longer than posterior parapophyses (79: 0>1).
- Bony canal around infraorbital canal on six infraorbital not closed (112: 0>1).

Ambiguous character

- Presence of ventral spine-like process on pterotic, medially to the pterotic spine (26: 0>1, ACCTTRAN).

The subfamily Pyrrhulininae includes small to medium sized species. There is a clear a reduction of body size within the Lebiasinidae, when specimens of Pyrrhulininae are compared

with representatives of the Lebiasininae (16 mm SL in *Nannostomus anduzei* vs. growing to about 200 mm SL, respectively) and outgroups of the family (Weitzman & Vari, 1988). Several morphological modifications related to bone simplification and bone losses indicate that the evolution within the Pyrrhulininae is largely related to processes of developmental truncations.

Tree out of six of the unique synapomorphies for the Pyrrhulininae are related to reductions: the absence of ectopterygoid teeth (66: 1), metapterygoid and quadrate almost in contact, separated by a small patch of cartilage (68: 0>1), bony wall around infraorbital canal on sixth infraorbital bone not closed (112: 1). Within the Pyrrhulininae, the tribe Pyrrhulinini and *Nannostomus anduzei* lack the sixth infraorbital, one more developmentally truncated condition. This clade has a relatively high Bremer support value (4).

AUTAPOMORPHY OF *DERHAMIA HOFFMANORUM*

Non-exclusive characters

- Adipose fin present (12: 0>1).
- Tooth plate on ventral portion of second pharyngobranchial absent (75: 1>0). This character is recovered as an unambiguous synapomorphy for this clade in only one of the two most parsimonious trees.
- Base of last dorsal-fin ray at vertical through caudal vertebrae (94: 0>1).
- Base of last dorsal-fin ray at vertical through or posterior to anal-fin origin (95: 0>1).
- Dorsal-fin bony stay as a separated bone (97: 1>0).
- Bony canal around infraorbital canal on first infraorbital not closed (109: 0>1).
- Bony canal around infraorbital canal on second infraorbital not closed (110: 0>1).

Ambiguous characters

- Nasal absent (32: 0>1, DELTRAN).
 - Coronomeckelian small, approximately ten times in length of Meckel's cartilage (62: 1>0, ACCTTRAN).
 - Tooth plate on ventral portion of second pharyngobranchial present (75: 0>1, ACCTTRAN).
- This character is recovered as synapomorphy dependent of optimization for this clade in only one of the two most parsimonious tree.
- Ossification of bony canal around infraorbital canal on antorbital absent (108: 0>1, DELTRAN).
 - Bony canal around infraorbital canal on third, fourth and fifth infraorbitals not closed (111: 0>1, DELTRAN).

MONOPHYLY OF CLADE 32 (*COPEINA*, *COPELLA*, *NANNOSTOMUS*, *PYRRHULINA*)

Exclusive characters

- Posterior shaft of vomer absent (19: 0>1).
- Intercalar absent (31: 0>1).
- Palatine elongate (63: 0>1).
- Three branchiostegal rays (74: 1>2).
- Anterior tip of basipterygium at vertical between ribs of 7th and 8th vertebra (91: 1>3).
- Ossification around supratemporal canal reduced to a lateral section (116: 0>1).
- Ossification around laterosensory canal on posttemporal absent (118: 0>1).
- Ossification around laterosensory canal on supracleithrum poorly developed (119: 0>1).

Non-exclusive characters

- Ascending process of premaxilla short (44: 0>1).
- Ascending process of maxilla short (51: 0>1).

Ambiguous characters

- Lateral arm of epioccipital thin, less wide than the epioccipital radius (28: 0>1, ACCTTRAN).
- Medial process on the orbital margin of fifth infraorbital present (41: 0>1, ACCTTRAN).
- Ectopterygoid slightly longer than palatine (64: 0>1, ACCTTRAN).
- Canal used as passage for the afferent pseudobranchial artery on the posterior portion of metapterygoid oblique (70: 0>1, ACCTTRAN).
- Basal portion of anal-fin proximal radials strongly connected in mature males (99: 0>1, DELTRAN).
- Anal fin proximal-middle radial present in four or five anteriormost pterygiophores (101: 1>0, ACCTTRAN).

This clade is relatively well supported (Bremer support value = 6). Several synapomorphies supporting this clade is of reductive nature. Among them, unique transformations are posterior shaft of vomer absent (19: 1), intercalar absent (31: 1), presence of three branchiostegal rays (74: 2), ossification around supratemporal canal reduced to a lateral section (116: 0>1), ossification around laterosensory canal on posttemporal absent (118: 1), ossification around laterosensory canal on supracleithrum poorly developed (119: 1). The short ascending process of premaxilla and maxilla is a homoplastic synapomorphy of reductive nature (44: 1, 51: 1), vestigial in *Copella* (44: 2, 51: 2). Of the synapomorphies of reductive characters

dependent of optimization are: proximal portion of lateral arm of epioccipital thin (28: 1), lost in the Pyrrhulinini, and ossification around supratemporal canal reduced to a lateral section (116: 1), independently lost in *Nannostomus* and the clade represented by *Copella* and *Pyrrhulina*.

MONOPHYLY OF CLADE 31 (*NANNOSTOMUS*)

Exclusive characters

- Mesethmoid rectangular (16: 2:1).
- Ascending process of the premaxilla extending under the mesethmoid (45: 0>1).
- Groove anterior to the ascending process of premaxilla present (46: 0>1)
- Posterior border of maxilla with a conspicuous notch (54: 0>1).
- Posterior tip of maxilla reaching approximately the middle of the first infraorbital (55: 0>2).
- Anal-fin inclinator muscle of the last pterygiophore inserted at base of last ray in males (103: 0>1).

Non-exclusive characters

- Mouth terminal (9: 1>0).
- Anterior and posterior nares distant from each other (10: 0>1).
- First longitudinal scales row of body from head to end of caudal peduncle (11: 1>0).
- Second infraorbital roughly triangular (38: 0>1).
- Foramen on posterior portion of metapterygoid in form of incomplete arch, bordered posteriorly by cartilage or by the hyomandibular (69: 0>1).
- Secondary crest on basipterygium present (92: 0>1).

-
- Presence of two epurals (104: 1>0).
 - Ossification around supratemporal canal absent (116: 1>2).
 - Bony canal around laterosensory canal on supracleithrum absent (119: 1>2).

Ambiguous characters

- Contact between frontal and pterotic absent (24: 0>1, DELTRAN).
- Ventral spine-like process on pterotic, medially to the pterotic spine, absent (26: 1>0, ACCTTRAN).
- Nasal absent (32: 0>1, DELTRAN).
- Antorbital as long as deep (36: 0>1, ACCTTRAN).
- Ectopterygoid smaller than palatine (64: 1>2, ACCTTRAN).
- Pointed projection at ventral half of proximal radial two of pectoral fin present (87: 1>0, ACCTTRAN).
- Proximal tip of branched anal-fin rays spatulate to pointed in mature males (100: 0>1, DELTRAN).
- Ossification of bony canal around infraorbital canal on antorbital absent (108: 0>1, DELTRAN).
- Ossification around pterotic canal absent (117: 0>1, DELTRAN).

The *Nannostomus* is the best-known genus of the family. The species are known as pencilfishes, very popular among aquarists due to their peaceful behavior and colorful bodies. The taxonomy of *Nannostomus* was revised by Weitzman (1966) and Weitzman & Cobb (1975). This clade containing the species of *Nannostomus* is highly supported (Bremer support value = 8). The exclusive synapomorphies supporting it are most related to modifications of the

jaw bones, namely the ascending process of the premaxilla extending under the mesethmoid (45: 1), groove anterior to the ascending process of premaxilla present (46: 1), posterior border of maxilla with a conspicuous notch (54: 1), and posterior tip of maxilla reaching approximately the middle of the first infraorbital (55: 2). Such modifications result in the typical configuration of the terminal mouth of *Nannostomus* (Weitzman, 1964: figs. 1 and 7), which enables the species to pick up small prey on various types of substrata, including plants, rocks and fallen tree branches (Weitzman, 1964).

MONOPHYLY OF CLADE 33 (PYRRHULININI: *COPEINA*, *COPELLA*, *PYRRHULINA*)

Exclusive characters

- Round dark spot on the dorsal fin of adults present: (3: 0>1)
- Upper caudal-fin lobe distinctly longer than the lower (15: 0>1).
- Ventral longitudinal lamellae of basioccipital large (30: 0>1).
- Posterolateral portion of premaxilla acute: (48: 0>1).
- Maxillary teeth of males along one-half length of anterior portion of the maxilla (56: 0>1).
- Number of maxillary teeth sexually dimorphic (58: 0>1).
- Outer dentary tooth row located only anteriorly, not extending further laterally (61: 1>2).
- Proximal radial four medially expanded, wider than proximal radials two and three (90: 0>1).
- Dorsal-fin proximal-middle radial present in all pterygiophores (96: 0>1).
- Ventral projection on the lateral lamellae of proximal anal-fin radials present in adult males (98: 0>1).
- Anal fin proximal-middle radial: (0) present in all pterygiophores (101: 0>2).
- Hypural 5 and 6 fused in the adult (105: 0>1).

-First scales on the lateral line series bearing a canal without a lateral opening (120: 0>1).

Non-exclusive characters

-Anterior paired projection of the parasphenoid present (20: 0>1).

-Laterodorsal spine-like process present on pterotic (25: 0>1).

-Lateral arm of epioccipital present (27: 0>1).

-Sixth infraorbital absent (42: 0>1).

-Multicuspid teeth absent in jaws (43: 1>0).

-Supraneural anterior to neural spine of fifth vertebra absent (80: 1>0).

-Extrascapular absent (81: 0>1).

-Anal-fin bony stay absent (102: 0>1).

Ambiguous characters

-Anterolateral projection on dentary present (59: 0>1, ACCTTRAN).

-Pointed projection at ventral half portion of proximal radial 2 of pectoral fin anteriorly oriented, parallel to scapula (88: 1>2, ACCTTRAN).

-Proximal tip of branched anal-fin rays expanded in mature males (100: 0>2, DELTRAN).

-Bony canal around infraorbital canal on third, fourth and fifth infraorbital not closed (111: 0>1, DELTRAN).

The genera *Copella*, *Copeina* and *Pyrrhulina* are the members of the tribe Pyrrhulinini (clade 33) (Fig. 24), with a high Bremer support value (9). It includes small species that inhabit the surface of the water in small streams and ponds, and have upturned mouths that facilitates eating allochthonous food and small insects (Géry, 1977). They are known to exhibit parental

care. Some species present exuberant coloration (*e.g. Copeina guttata, Copella vilmae, Pyrrhulina spilota*) or are quite plain (*e.g. Pyrrhulina australis*). All species present a round dark spot on the dorsal fin that is retained by adults (3: 1), and upper caudal-fin lobe distinctly longer than the lower lobe (15: 0>1), especially males of *Copella*. Several synapomorphies of this clade are related to reductive characters (3: 1, 25: 1, 27: 1, 42: 1, 43: 0, 81: 1, 102: 1, 111: 1, 120: 1).

AUTAPOMORPHIES OF *COPEINA GUTTATA*

Non-exclusive characters

- A series of red spots present on body in life (2: 0>1).
- Canal on posterior ceratohyal open (73: 0>1).
- Striae present on the surface of infraorbital bones (113: 0>1).

Ambiguous characters

- Transversal lamella of urohyal reduced (77: 0>1, DELTRAN).

The genus *Copeina* includes three nominal species, two of them currently valid. A taxonomic revision of the genus is needed. *Copeina guttata* is possibly the only valid species. It spawns in a hole in the sand, and the eggs are guarded by the male (Géry, 1977), resembling the reproductive behavior of *Hoplias malabaricus* (Prado *et al.*, 2006).

MONOPHYLY OF CLADE 36 (*COPELLA, PYRRHULINA*)

Exclusive characters

-
- First longitudinal scales row on body not reaching dorsal-fin origin (11: 1>3).
 - Ascending process of the maxilla aligned, approximately parallel to axis of posterior portion of maxilla (52: 0>1).
 - Os suspensorium outer arm anteriorly directed (78: 0>1).
 - Two unbranched caudal-fin rays associated with hypurals of the upper lobe (107: 0>1).
 - Ossification around supratemporal canal absent (116: 1>2).

Non-exclusive characters

- Dark pigmentation on anal-fin distal edge present in mature males (4: 0>1).
- Tooth plate on ventral portion of second pharyngobranchial present (75: 1>0). This character is recovered as unambiguous synapomorphy for this clade in only one of the two most parsimonious tree.
- Base of last dorsal-fin ray at vertical through or posterior to anal-fin origin (94: 0>1).

Ambiguous characters

- Mature males with elongate fins (14: 0>1, ACCTTRAN).
- Contact between frontal and pterotic absent (24: 0>1, DELTRAN).
- Ossification around pterotic laterosensory canal absent (117: 0>1, DELTRAN).

Copella is a sister group of *Pyrrhulina* based on five exclusive, tree homoplastic (one of them is recovered as synapomorphy in only one tree) and tree characters dependent of optimization, with Bremer support value of 2. Such close relation was also found by Oyakawa (1998) and Netto-Ferreira (2006, 2010), though in the former, *Copella*, *Pyrrhulina* and *Nannostomus* are grouped in a polytomy. Both genera are very similar externally but can be

easily set apart by the shape of the jaw bones and the nares distant in *Copella* (*vs.* juxtaposed in *Pyrrhulina*).

MONOPHYLY OF *PYRRHULINA* (CLADE 35)

Exclusive characters

- Two premaxillary teeth row (50: 0>1).
- Third postcleithrum absent (83: 0>1).

Non-exclusive characters

- Coronomeckelian small, approximately ten times in the length of Meckel's cartilage (62: 1>0).

Ambiguous characters

- Anterolateral projection of the dentary absent (59: 1>0, ACCTTRAN).
- Lamellar process on posterodorsal portion of hyomandibular absent (71: 0>1, DELTRAN).

Opposed to *Copella*, the clade represented by the species of *Pyrrhulina* has a low Bremer support value (1), and is characterized by two unique features, the presence of two premaxillary teeth row (50: 1) and third postcleithrum absent (83: 1), and the homoplastic characters of ambiguous interpretation listed above. *Pyrrhulina* is represented by 20 nominal species all with taxonomic problems (Géry, 1977; Weitzman & Weitzman, 2003). Some species of *Pyrrhulina* spawn on broad submerged leaves (Géry, 1977).

INGROUP

MONOPHYLY OF *COPELLA* (CLADE 40)

Exclusive characters

- Males distinctly larger than females (13: 0>1).
- A reduced longitudinal crest on the dorsal surface of vomer (18: 0>1).
- A wide lateral exoccipital foramen present (29: 0>1).
- Ascending process of premaxilla vestigial, represented only by a small crest (44: 1>2).
- Ventral profile of premaxilla gently arched (47: 0>1).
- Posterolateral portion of premaxilla rounded (48: 1>2).
- Teeth on the posterolateral portion of premaxilla absent (49: 0>1).
- Ascending process of maxilla vestigial (51: 1>2).
- Anterior border of main portion of the maxilla "S" shaped in mature males (53: 0>2).
- Maxilla greatly overlapping the premaxilla laterally (57: 0>2).
- Metapterygoid and quadrate largely separated from each other by a large patch of cartilage (68: 1>2).
- Posterodorsal projection on lateral portion of scapula in contact with cleithrum absent (86: 0>1).
- Pointed projection on ventral half of proximal radial three of pectoral fin absent (89: 0>1).

Non-exclusive characters

- Anterior and posterior nares distant from each other (10: 0>1).
- Mesethmoid and vomer far from each other by a large patch of cartilage (17: 0>1).
- Medial projection on posterior portion of pterospheonoid present (22: 0>1).

-
- No contact between nasal and frontal posteriorly (35: 0>1).
 - Antorbital longer than deeper (36: 0>2).
 - Posterior tip of maxilla reaching approximately the middle of second infraorbital (55: 0>1).
 - Maxillary teeth distributed along the entire length of anterior portion of the maxilla in males (56: 1>2).
 - Ventroposterior tip of dentary at vertical through middle portion of anguloarticular (60: 0>1).
 - No contact between ectopterygoid and quadrate (65: 0>1).
 - Lateral lamella of urohyal absent (76: 0>1).
 - Second postcleithrum absent (82: 0>1).
 - Bony ridge on lateral portion of coracoid absent (85: 0>1).
 - Secondary crest on basipterygium present (92: 0>1).
 - Ischiac process with long curved process laterally directed (93: 1>3).
 - Base of last dorsal fin ray at vertical through or posterior to anal-fin origin (95: 0>1).
 - Ossification of bony canal around infraorbital canal on antorbital absent (108: 0>1).
 - Bony canal around infraorbital canal on first infraorbital absent (109: 0>2).
 - Bony canal walls of infraorbital canal on second infraorbital not closed (110: 0>1).
 - Ossification around supraorbital canal on nasal absent (114: 1>0).

Ambiguous characters

- Lateral margin of vomer and medial margin of the anterior projection of the parasphenoid not in contact (21: 0>1, DELTRAN).
- First infraorbital as long as deep (37: 0>1, ACCTRAN).
- Contact between medial lamella of cleithrum and coracoid smooth (84: 0>1, ACCTRAN).

-
- A pointed projection on ventral half of proximal radial 2 of pectoral fin (87: 1>0, ACCTRAN).
 - Pointed projection on ventral half of proximal radial 2 of pectoral fin medially oriented (88: 1>2, ACCTRAN).
 - Bony canal around supraorbital canal on frontal extending to epiphyseal bar (115: 0>1, DELTRAN).

Representatives of the genus *Copella* were first included in a phylogenetic context by Oyakawa (1998) (Fig. 25) and later by Netto-Ferreira (2006, 2010) (Figs. 26 and 27, respectively). *Copella*, as previously recognized by Myers (1956) and Géry (1977), was considered as a monophyletic assemblage by the aforementioned authors. In the present analysis the monophyletic nature of *Copella* is also corroborated, with a high Bremer support value (23), based on 38 synapomorphies, of which 13 are unique for the genus, 19 homoplastic, and 6 characters of ambiguous transformations. Of the 38 synapomorphies, 13 were previously proposed by Oyakawa (1998) and Netto-Ferreira (2006, 2010), and 25 are herein proposed or considered synapomorphic for the first time for the genus. A large amount of synapomorphies for *Copella* is considered of reductive nature (characters 17: 1, 18: 1, 21: 1, 44: 2, 51: 2, 68: 2, 76: 1, 82: 1, 108: 1, 109: 2, 110: 1, 114: 0, 115: 1), mainly related to reduction or loss of ossification around sensory canals, several simplifications and some bony losses. According to the morphological comparative study and the given hypothesis of relationships, such characters have probably evolved from developmental truncation, further discussed below. Several synapomorphies of *Copella* are related to jaw modifications (characters 44: 2, 47: 1, 48: 2, 49: 1, 51: 2, 53: 2, 55: 1, 56: 2, 57: 2, 60: 1) resulting in the typical configuration of the mouth in *Copella*, used to diagnose the genus (Géry, 1977: 146). The maxilla strongly curved (53: 2) and

the presence of maxillary teeth distributed along the entire length of posterior border of maxilla in males (56: 2), and males distinctly larger than females (13: 1) are sexual dimorphic features unique for the genus. Other modifications are related to the pectoral fin (82: 1, 84: 1, 85: 1, 86: 1, 87: 0, 88: 2 89: 1) and pelvic girdle (92: 1, 93: 3).

The small sample of *Copella* species used by Oyakawa (1998) (two species analyzed) precluded the proposal of any hypothesis of relationships within it, but the analysis of the Lebiasinidae and Lebiasininae performed by Netto-Ferreira (2006, 2010, respectively), enabled the proposition of a hypothesis of relationships for the genus (Figs. 26 and 27). Both resulted in *Copella arnoldi* (his *C. arnoldi*, *C. eigenmanni* and *C. carsevevnnensis*) and *C. nattereri* as successive sister taxa of the clade composed by *Copella stigmasemion* (his *C. nigrofasciata*) and *C. eigenmanni* (his *C. compta* and *C. metae*). Differences between both hypotheses lie in the inclusion of terminal species by Netto-Ferreira (2010) that are herein considered junior synonymous. In the present study, *Copella compta* and *C. vilmae* were included for the first time in a cladistic context, new characters for *Copella* were proposed, and all the characters used for the definition of the genus by the aforementioned author were revised and included (except those listed and justified under “Characters not used” section). The basal position of *Copella arnoldi* within the genus is the only result congruent with that of Netto-Ferreira (2006, 2010) (Figs. 26 and 27).

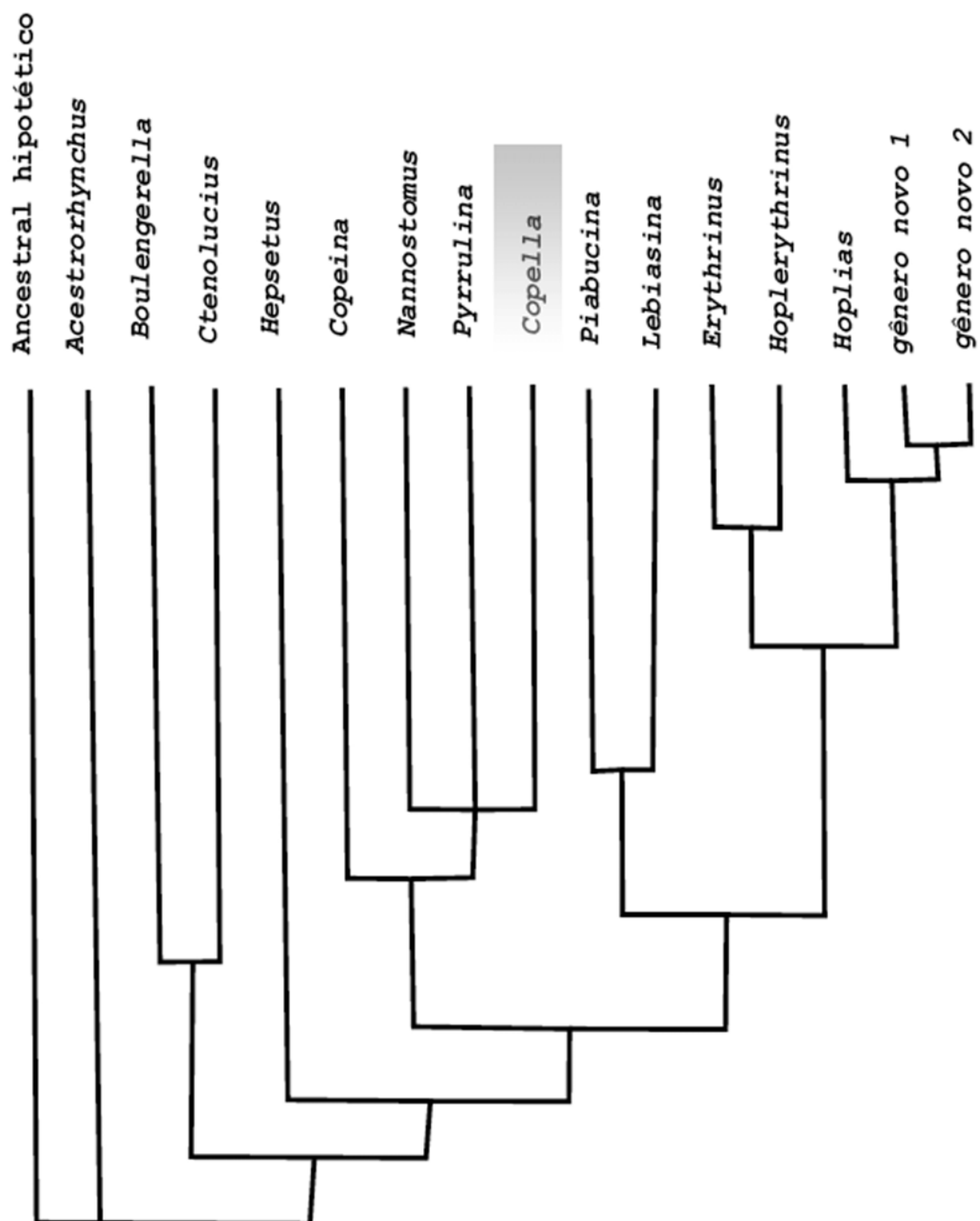


Figure 25. Hypothesis of relationships of the Erythrinae according to Oyakawa (1998). The genus *Copella* is represented by two species, *Copella arnoldi* and *C. nattereri*.

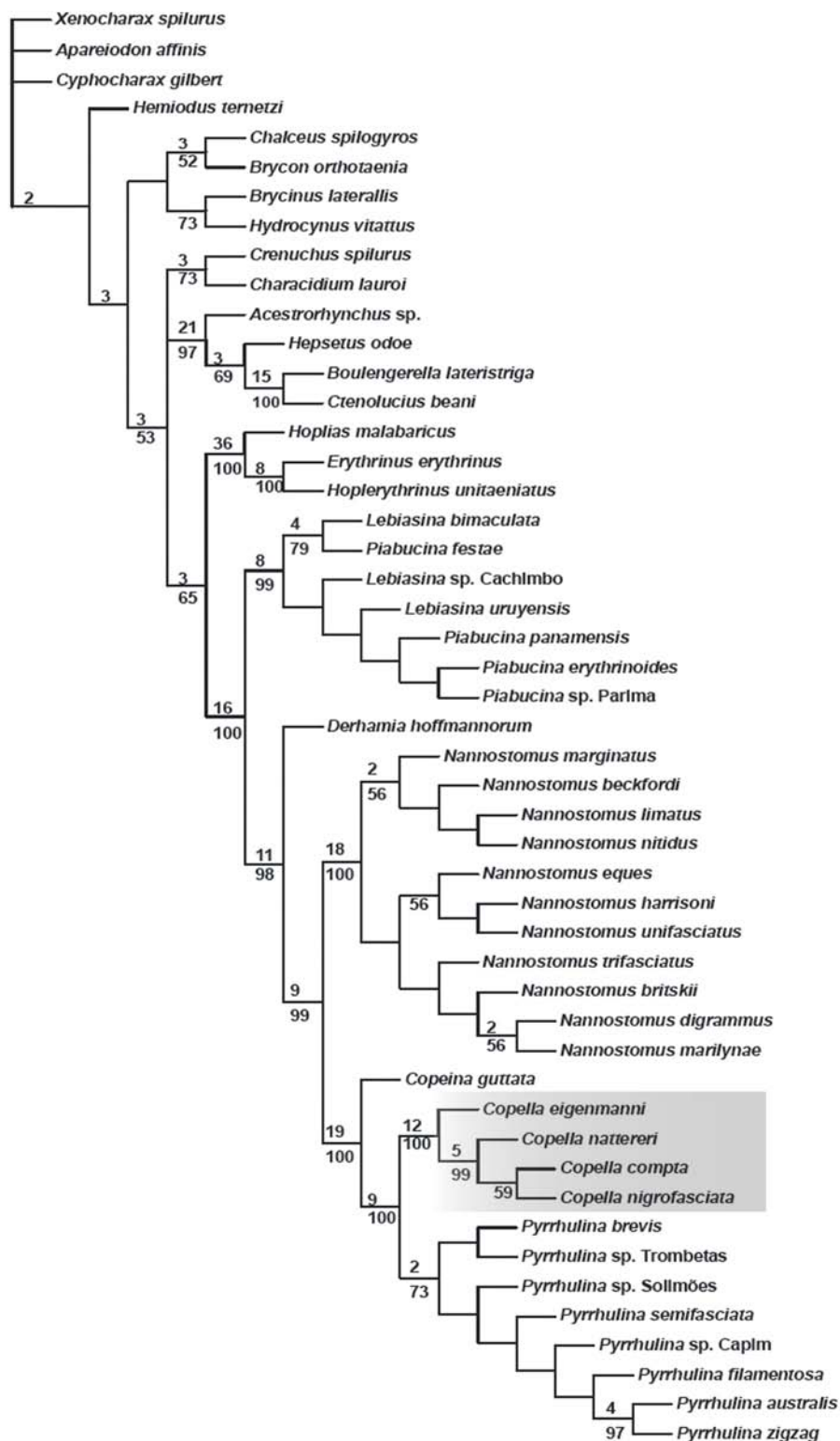


Figure 26. Hypothesis of relationships of the Lebiasinidae, according to Netto-Ferreira (2006).
Representatives of *Copella* are highlighted.

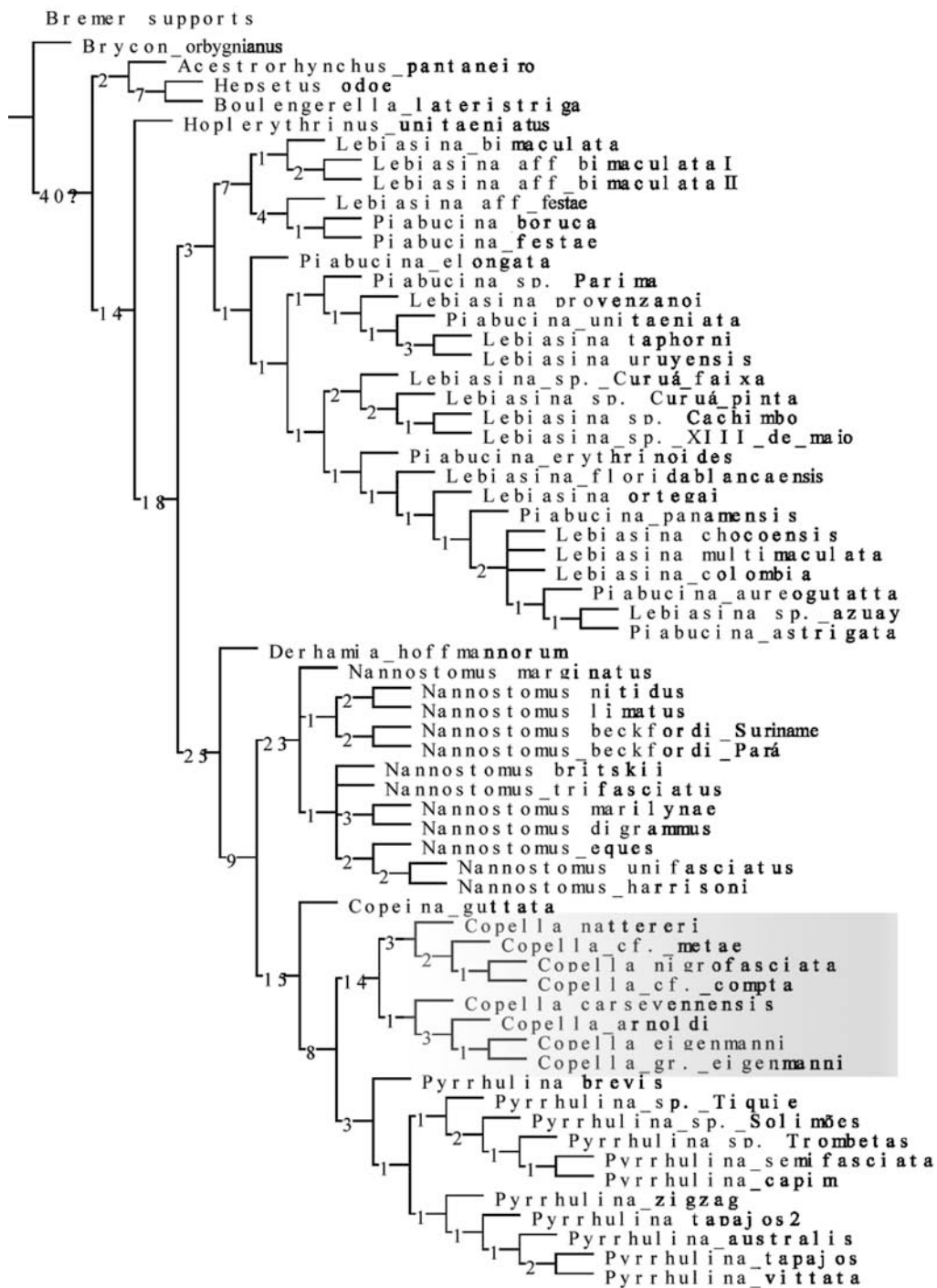


Figure 27. Hypothesis of relationships of the Lebiasininae, according to Netto-Ferreira (2010).

Representatives of *Copella* are highlighted.

AUTAPOMORPHIES OF *COPELLA ARNOLDI*

Non-exclusive characters

- Sexually dimorphic coloration on flank present (8: 0>1).

Ambiguous characters

- Lamellar process at posterodorsal portion of hyomandibular absent (71: 0>1, DELTRAN).

MONOPHYLY OF CLADE 43 (*COPELLA COMPTA*, *C. EIGENMANNI*, *C. NATTERERI*, *C. STIGMASEMION*, *C. VILMAE*).

Exclusive characters

- Dark pigmentation on the dorsal and ventral procurrent caudal-fin rays present (5: 0>1).

Non-exclusive characters

- First longitudinal scales row on body extending from head to dorsal-fin origin (11: 3>2).
- Nasal small (33: 1>0).
- Nasal not reaching the lateral arm of the premaxilla anteriorly (34: 1>0).
- Bony canal around laterosensory canal on supracleithrum poorly developed (119: 1>2).

Ambiguous characters

- Second infraorbital roughly triangular (38: 0>1, ACCTTRAN).

Clade 43 is relatively well supported (Bremer value = 3). Its monophyly is based on the unique presence of dark pigmentation on the dorsal and ventral procurent caudal-fin rays (5: 1) [also as synapomorphy for a clade represented by similar species (*C. eigenmanni*, *C. nattereri*, *C. stigmatemion*) in Netto-Ferreira (2006, 2010)] and on the first longitudinal scale row on body shorter (11: 2), nasal small (33: 0, 34: 0), reduction of ossification around the sensory canal on supracleithrum (119: 2) and second infraorbital triangular (38: 1). Other characters considered by Netto-Ferreira (2006, 2010) as synapomorphic for this similar clade were not included or are distinctly coded herein, and not considered as synapomorphies (see discussion under characters 35, 65, and “basihyal length” and “extension of primary stripe” under “Unutilized characters”).

MONOPHYLY OF CLADE 42 (*COPELLA COMPTA*, *C. EIGENMANNI*, *C. VILMAE*).

Exclusive characters

-Anterior ceratohyal long (72: 0>1).

Non-exclusive characters

-Anterior tip of basipterygium at vertical between ribs of 8th and 9th vertebra (91: 3>2).

Ambiguous characters

-Antorbital as long as deep (36: 2>1, ACCTRAN).

-First infraorbital deeper than longer (37: 1>0, ACCTRAN).

-Contact between medial lamella of cleithrum and coracoid irregular to zigzag shaped (84: 1>0, ACCTRAN).

This clade has a low Bremer value (= 1), and is supported by a unique feature, the presence of a long ceratohyal (72: 1). Other synapomorphies are related to the shape of the bones of the infraorbital series (36: 1, 37: 0), relative position of basipterygium (91: 2) and shape of the contact area between the cleithrum and the coracoid (84:0). In this clade the largest species of the genus are included (SL 55.5 mm in *C. vilmae* to 68.9 in *C. compta* vs. 37.0 mm in *C. stigmatemion* to 45.0 mm in *C. nattereri*).

AUTAPOMORPHIES OF *COPELLA EIGENMANNI*

Ambiguous characters

- Second infraorbital roughly triangular (38: 1>0, ACCTRAN).
- Bony canal around supraorbital canal on frontal not reaching epiphyseal bar (115: 1>2, DELTRAN).

CLADE 41 (*COPELLA COMPTA*, *C. VILMAE*).

Exclusive characters

- Dark pigmentation at base of the upper caudal-fin lobe in females and juveniles present (6: 0>1).

Non-exclusive characters

- Sexually dimorphic coloration on flank present (8: 0>1).
- Ascending process of premaxilla short (44: 2>1).

The type species of the genus, *Copella compta*, is sister taxon of *C. vilmae* (clade 41), with Bremer support value of 2. The monophyly of this clade is based on the unique presence of a faint dark pigmentation at the base of upper caudal-fin lobe in females and juveniles (6: 1). Dimorphic coloration on body (8: 1) and presence of a short (not vestigial as in congeners) ascending process of premaxilla are homoplastic (44: 1).

AUTAPOMORPHIES OF *COPELLA COMPTA*

Non-exclusive characters

- Ascending process of maxilla short (51: 2>1).
- Lateral lamella of urohyal present (76: 1>0).

Ambiguous characters

- Transversal lamella of urohyal reduced (77: 0>1, DELTRAN).

AUTAPOMORPHIES OF *COPELLA VILMAE*

Non-exclusive characters

- Ectopterygoid smaller than palatine (64: 1>2)
- Pointed projection on ventral half of proximal radial 2 of pectoral fin absent (87: 0>1).
- Pointed projection on ventral half of proximal radial 3 of pectoral fin absent (89: 1>0).

Ambiguous characters

- Antorbital longer than deeper (36: 1>2, ACCTRAN).

CLADE 44 (*COPELLA NATTERERI*, *C. STIGMASEMION*).

Non-exclusive characters

- Series of red spots on body present in live specimens (2: 0>1).
- Ectopterygoid smaller than palatine (64: 1>2).
- Canal on posterior ceratohyal open (73: 0>1).

Ambiguous characters

- Bony canal around supraorbital canal on frontal not reaching epiphyseal bar (115: 1>2, DELTRAN).

Clade 42 is sister of clade 44, represented by *Copella nattereri* and *C. stigmatsemion*, with Bremer support value of 3. *Copella nattereri* and *C. stigmatsemion* are sister taxa based on the homoplastic presence of series of red spots on body (2: 1), ectopterygoid smaller than palatine (64: 2), and modifications related to the small body size: canal on posterior ceratohyal open (73: 1) and bony canal around supraorbital canal on frontal not reaching the epiphyseal bar (115: 2). Curiously, both *Copella nattereri* and *C. stigmatsemion* are species in which the skeleton is mostly cartilaginous among the examined taxa, even in fully-grown adult specimens.

AUTAPOMORPHY OF *COPELLA NATTERERI*

None

AUTAPOMORPHY OF *COPELLA STIGMASEMION*

Ambiguous characters

-Nasal absent (32: 0>1).

MINIATURIZATION AND DEVELOPMENTAL TRUNCATION IN LEBIASINIDAE

Although the main objective of the present contribution is to resolve the intrarelationships of *Copella*, insights derived from the present study will be briefly presented. During the osteological survey, several apparently reductive characters were found in members of Pyrrhulinae, smaller representatives of Lebiasinidae. To better understand the processes that has lead to the evolution of such characters, a comparative study was made between the osteological development of *Lebiasina* cf. *bimaculata*, a relatively large-sized representative of the Lebiasinidae, and the osteological development of smaller representatives, *Nannostomus beckfordi* and *Pyrrhulina spilota*, with further comparisons to adults of other small-sized species, such as *Copella nattereri* and *N. anduzei*. This work is in preparation and its result is beyond the scope of the thesis and will not be discussed herein. During such study, aspects of the evolution of reductive characters were clarified and some are discussed under “Character description” section. Based in the ontogenetic series of larger representatives of the family, and also in the literature information, of the 120 characters proposed, around 35 seem to have been affected by developmental truncation at the character level (3: 1, 17: 1, 18: 1, 19: 1, 21: 1, 25: 1, 27: 1, 28: 1, 31: 1, 42: 1, 43: 1, 44: 1 and 2, 51: 1 and 2, 54: 1, 66: 1, 68: 2, 76: 1, 77: 1, 81: 1, 82: 1, 83: 1, 97: 1, 102: 1, 104: 1, 108: 1, 109: 1 and 2, 110: 1 and 2, 111: 1, 112: 1, 114: 1, 115: 1 and 2, 116: 1 and 2, 117: 1, 118: 1, 119: 1 and 2, 120: 1 and 2).

The definition of heterochrony has a complex history of meaning but since DeBeer (1930), the term has been widely used as the developmental displacement of a feature relative to the time that this same feature appeared in the development of an ancestral form (Gould 1977). Heterochrony can produce paedomorphosis, which is the displacement of ancestral features to later stages of the ontogeny of descendents (Gould, 1977). There are two types of

paedomorphosis: neoteny and progenesis. Neoteny is when somatic development is delayed relative to gonad development, the neotenic descendant are scale up replicas of the juvenile stages of their ancestors, whereas in progenesis, the sexual maturation is speeded up in relation to somatic development (Alberch *et al.*, 1979). Progenesis can happen at the level of the organism, resulting in the extreme and rare cases of the developmentally truncated taxa, which are organisms that resemble early developmental stages of their larger relatives in most of their characters. This is the case of *Paedocypris progenetica* Kottelat, Britz, Tan & Witte. It can also happen at the level of character complexes, or at the level of characters, resulting in organisms that are almost identical copies of their relatives, but with developmental truncations in specific character complexes or characters. This character-level truncation seems to have happened in some members of Lebiasinidae, especially the small to medium-sized Pyrrhulininae.

Representatives of the family Lebiasinidae range in size from very small species, as the 16.0 mm SL *Nannostomus anduzei*, to medium-sized species, like *Piabucina* that grow to about 200 mm SL in (Weitzman & Vari, 1998; Weitzman & Weitzman, 2003). Considering the present hypothesis of relationships, the evolutionary reduction of length is evident within the family, especially if compared to the outgroup Erythrinoidea (*sensu* Buckup, 1998).

Weitzman & Vari (1988), and subsequently Costa & Le Bail (1999) provided a list of South American miniature fishes, including species that mature sexually at under 20 mm SL or are not known to exceed 25 to 26 mm. Among the miniature fishes listed by Weitzman & Vari (1988) are three small-sized Lebiasinidae, *Nannostomus anduzei*, *N. marginatus*, and *N. minimus* Eigenmann. Although the term “miniature” only implies very small body size, in freshwater fishes it is commonly associated with the presence of apparently truncated morphological characters (often referred as “reductive characters”), such as reduction of ossification around the laterosensory canal system of head and body, reductions in the number

of fin rays and body scales, and reduction of the complexity of sculpturing on the surface of bones (Weitzman & Vari, 1998). The correlation between miniature and the presence of reductive characters may be due to the fact that extremely small organisms often present truncation of their development at least in a few characters or character complexes, probably due to heterochronic processes evolved on their evolution. However, worth to highlight is that large size species may also present features related to developmental truncation [*e.g.* reduction in the ossification of the lateral line system in the head of the Alestidae *Phenacogrammus auranticus* (Pellegrin) (Zanata & Vari, 2005), or in the body in *Boulengerella lateristriga* Spix & Agassiz and *B. maculata* Valenciennes (Vari, 1995)], and miniaturization may happen without significative reductions in morphology [*e.g.* the minute but not truncated *Acanthemblemaria paula* Johnson & Brothers]. See also discussion of Weitzman & Fink (1985: 64).

Character transitions indicative of developmental truncation plotted in the presented tree topology (Fig. 28) indicate that reductive characters are especially concentrated within Pyrrhulinae. The evolution of reductive traits observed in members of subfamily seem to have occurred gradually, resulting in terminal taxa of distinct “levels” of reductive features in their skeleton. Developmental truncation of the whole organism, as in *Paedocypris*, was not observed in any taxa analyzed. Instead, several representatives of the subfamily Pyrrhulinae better correspond to the proportional dwarves of Gould (1971) and Britz & Conway (2009): they resemble miniature adults of larger species (*e.g.* *Lebiasina*), but still have considerable number of reductive features in their skeleton. Truncated characters are especially concentrated in *Nannostomus anduzei*, the clade 33 (*Copeina*, *Copella*, and *Pyrrhulina*), and clade 40 (*Copella*).

analyzed, *Nannostomus marginatus*, and *N. eques* each have a maximum length of 35.0 mm SL, and *N. beckfordi* grows to 65.0 mm SL (Weitzman & Weitzman, 2003). Pyrrhulinini species are usually larger than 40.0 mm SL (maximum length of 30 mm SL in *P. marilynae*), and even reach 85.0 mm SL in *P. filamentosa* (Weitzman & Weitzman, 2003)]. The consequences of size decrease for adult morphology may be highly variable depending on the kind of ontogenetic scaling and developmental processes involved (Hanken & Wake, 1993).

The phenomenon of heterochronic changes may have played a more important role in the evolution of teleost fishes than we recognize (Johnson & Brothers, 1993). Considering the outstanding number of small South American freshwater fishes (Weitzman & Vari, 1988), little is known about the processes involved in the evolution of small fishes. The morphological differences among miniaturized taxa deserve a closer look. The insights herein presented, though preliminary, represent an attempt to contribute to further the knowledge of the effects of heterochrony in the evolution of small body size in Characiformes.

MATERIAL EXAMINED

Ingroup

Copella arnoldi. MPEG 8305 (197, 15.0-32.5 mm SL, 2 c&s, 29.7-30.5 mm SL), rio Caripiaçu at road Vila dos Cabanos, near Caripi beach, Barcarena, Pará, 20 Sep 2001, W. Wosiacki & W. Bezerra. MPEG 10398 (28, 14.2-33.4 mm SL, 2 c&s, 27.4-31.5 mm SL), igarapé Curuazinho, rio Pará, Melgaço, Pará, 1°44'12.9"S 51°25'54"W, 17 Nov 2003, L. Montag. MZUSP 105770 (130, 16.6-40.1 mm SL, 6 c&s, 12.8-31.4 mm SL, 2 mus, 21.7 and 33.7 mm SL), stream and lagoon, headquarters of Lagoa Azul farm, Vigia, Pará, 0°56'8"S 48°4'38"W, 27 Mar 2010, M. Marinho *et al.*

Copella compta. INPA 9162 (37, 16.9-68.9 mm SL, 4 c&s, 17.0-50.8 mm SL), stream at camp, rocks, Morro dos Seis Lagos, 23 Mar 1990, J. Zuanon, *et al.*

Copella eigenmanni. ANSP 128751 (21, 20.0-33.0 mm SL, 1 c&s, 28.4 mm SL), small stream at Hacienda Humacita, flowing generally South, presumably the general Lake Mozambique complex, 250 ft of stream collected, mostly above the bridge, Meta, 3°58'N 73°4'W, 21 Feb 1972, J. Böhlke & N. Foster. ANSP 159176 (34, 16.5-33.5 mm SL, 1 c&s 26.3 mm SL), caño crossing road to Las Trincheras, 2.7 km South of intersection Ciudad Bolivar-Caicara road, Bolivar, 4°39'N 72°39'W, 20 Nov 1985, W. Saul *et al.* MZUSP 64616 (7, 21.7-31.4 mm SL, 3 c&s, 35.0-36.4 mm SL), stream affluent of rio Tiquié, Fronteira community, Brazil-Colombia limit, rio Negro drainage, Amazonas, 31 Oct 2002, F. Lima. MZUSP 81443 (69, 12.7-55.6 mm SL, 3 c&s, 26.0-44.3 mm SL), igarapé do Buriti, Caruru community, rio Tiquié, rio Negro drainage, Amazonas, 0°16'29"N 69°54'54"W, 20-25 Oct and 8 Nov 2002, F. Lima. MZUSP 85149 (107, 12.8-48.3 mm SL, 8 c&s, 12.6-22.0 mm SL), igarapé do Buriti, Caruru community, rio Tiquié, rio Negro drainage, Amazonas, 0°16'N 69°54'W, 29 Jun to 1 Jul 2004, F. Lima. MZUSP 92573 (62, 8.1-16.8 mm SL, 35 c&s, 6.6-22.5 mm SL), igapó lake of igarapé Castanha affluent rio Tiquié, downstream Santa Rosa community, rio Negro drainage, Amazonas, 0°5'41"N 69°39'W, 3 Aug 2006, F. Lima *et al.*

Copella nattereri. MZUSP 29343 (79, 20.5-33.6 mm SL, 4 c&s, 23.9-32.3 mm SL), lake in island, rio Negro, Barcelos, Amazonas, 0°58'S 62°57'W, 29 Feb 1980, M. Golding. MZUSP 15550 (17, 14.5-32.3 mm SL, 2

c&s, 28.5-33.2 mm SL), lago Jacaré, headwaters of serrinha, Reserva Biológica de Trombetas, Trombetas, Pará, 1°20'S 56°51'W, 25 Jul 1979, R. Castro. MZUSP 87426 (24, 11.4-42.2 mm SL, 2 c&s, 26.5 and 38.7 mm SL), stream affluent of Rio Preto da Eva, Rio Preto da Eva, Amazonas, 2°44'35"S 59°40'7.8"W, 6 Jul 2003, Exc. MZUSP/USP.

Copella stigmatemion. MZUSP 23232 (387, 13.3-23.4 mm SL, 10 c&s, 11.8-20.4 mm SL), lago Miuá, upstream Codajás, rio Solimões, Careiro, Amazonas, 3°51'S 60°4'W, 25 Aug 1968, Expedição Permanente da Amazônia. MZUSP 23510 (83 of 111, 22.9-32.0 mm SL, 4 c&s, 23.0-31.7 mm SL), igarapé number three, rio Solimões, Fonte Boa, Amazonas, 2°31'S 66°6'W, 25 Oct 1968, Expedição Permanente da Amazônia. MZUSP 85603 (20, 17.5-34.0 mm SL, 2 c&s, 23.0-28.8 mm SL), stream about 0.3 km North of Km 3.9 of Jenaro Herrera-Colonia Angamos road, 4°53.91'S 73°38.366'W, 16 Jan 2004, H. Ortega, R. Reis & F. Lima. MZUSP 101933 (24, 13.2-34.9 mm SL, 2 c&s, 27.4 and 32.0 mm SL), igarapé Ting Ling, right margin of rio Jari, downstream Chachoeira Santo Antônio, Laranjal do Jari, Amapá, 00°49'54"S 52°40'25"W, 16 Oct 2007, M. Carvalho *et al.*

Copella vilmae. AMNH 218053 (4, 36.5-46.6 mm SL, 1 c&s, 42.4 mm SL), rio Amazonas at Letícia, Amazonas, 15-30 Ago 1965.

Outgroup

Copeina guttata. MZUSP 27088 (215, 34.5-65.5 mm SL, 2 c&s, 31.2 and 65.3 mm SL), Lago Buiúçu, Ati-Paraná, Northwest Fonte Boa, Brazil, 11 and 12 Oct, 1968, Expedição Permanente da Amazônia. MZUSP 47702 (2 c&s, 65.2-58.8 mm SL), Arroio de Ivita-Pucallpa, Caserio Neshuya, Prov. Cel. Portillo, Ucayali, Peru, 8 Mar 1979, H. Ortega.

Derhamia hoffmanorum. MTD F 26491 (holotype, male, 60.9 mm SL), sand bank at the confluent of the rio Kamarang and rio Mazaruni, Northwest Guyana north of Roraima, Oct 2001, P. & M. Hoffmann. ROM 83862 (7, 22.6-50.1 mm SL, 3 c&s, 21.9-36.2 mm SL), Memboru creek at an artificial sandy beach, rio Membaru, Guyana, Apr 2008, Lopez-Fernandez *et al.*

Hoplerythrinus unitaeniatus. MZUSP 47695 (1 c&s, 97.7 mm SL), Santo Inácio, first bridge on Cáceres-Porto Limão road, Cáceres, Mato Grosso, 26 Mar 1977, CEPIPAM. MZUSP 96825 (4, 33.0-223.0 mm SL), tributary of Rio Braço Norte, affluent of rio Peixoto de Azevedo, Tapajós basin, 19 Oct 2007, Birindelli *et al.*

Lebiasina bimaculata MZUSP 80085 (54, 28.2-88.3 mm SL, 3 c&s, 20.7-61.8 mm SL), rio Jequetepeque (ponto 2), Chilete, Cajamarca, Peru, 7°13'35"S 78°50'0"W, 26-XI-2002, C. Oliveira *et al.*

Lebiasina minuta MZUSP 101423, 94, 14.8-68.4 mm SL, 2 c&s 55.7-58.0 mm SL, rio Xingu drainage, rio Treze de Maio, rio Iriri basin, near BR-163, 8°47'3"S 54°58'29"W, Altamira, Pará, Brazil, 22 Jan 2009, A. L. Netto-Ferreira, *et al.*

Lebiasina cf. yuruanensis. MZUSP 73092, 1 c&s, 60.1 mm SL. Quebrada Cantarrana, about 30 km North of Icabarú, Gran Sabana, Bolivar. L. Marrero.

Nannostomus anduzei MZUSP 40330 (651, 1.6-14.6 mm SL, 5 c&s, 11.9-14.5 mm SL), igarapé do Irene, lago de caatinga, rio Negro basin, Brazil, Feb 1987, M. Golding.

Nannostomus beckfordi MZUSP 22910 (10, 24.6-27.4 mm SL, 3 c&s, 25.8-27.0 mm SL), igarapé Apeú, Boa Vista, Pará, Brazil, 3-4 Feb 1964, Vanzolini.

Nannostomus eques MZUSP 6423 (51, 14.8-28.0 mm SL, 2 c&s, 29.2-32.8 mm SL), Igarapé Chefe, headwater of Lago Beruri, Amazonas, Brazil, 9 Nov 1967, Expedição Permanente da Amazônia. MZUSP 63513 (19, 22.5-34.9 mm SL), São João, Tapurucuara, Brazil, 27 Oct 1972, Expedição Permanente da Amazônia.

Nannostomus marginatus MZUSP 23512 (25, 15.6-23.4 mm SL, 3 c&s, 22.4-24.6 mm SL), igarapé número 3, Fonte Boa, Amazonas, Brazil, 25 Oct 1968, Expedição Permanente da Amazônia. MZUSP 101928 (69, 18.2-24.2 mm SL), igarapé Ting Ling, right margin of rio Jari, downstream Santo Antônio fall, 0°49'54"S 52°40'25"W, Laranjal do Jari, Amapá, Brazil, 16 Oct 2007, Carvalho *et al.*

Piabucina unitaeniata MZUSP 73090 (8, 51.4-104.2 mm SL, 1 c&s, 75.6 mm SL), rio Tarota, Aporawao, Gran Sabana, Bolivar, Venezuela, 1 Feb 1984, M. Antônio.

Pyrrhulina australis MZUSP 35929 (106, 14.2-38.5 mm SL, 4 c&s, 14.5-36.2 mm SL), lagoons at Santo Antônio do Paraíso farm, Itiquira, Mato Grosso do Sul, Brazil, 1979, J. Medeiros & J. Oliveira.

Pyrrhulina cf. brevis. MZUSP 24328 (2 c&s, 41.0-48.1 mm SL), igarapé Centrinho, rio Tapajós, Barreirinha, Pará, Brazil, 24 Nov 1970, Expedição Permanente da Amazônia.

Pyrrhulina filamentosa MHNLS 14271 (2, 45.0 and 63.0 mm SL, 2 c&s, 55.0 and 55.1 mm SL), caño Ibaruma, serrania de Imataca, delta rio Orinoco, Venezuela, Y. Ponte.

Pyrrhulina marilynae MZUSP 61130 (23, 16.9-26.3 mm SL, 2 c&s, 24.7 and 30.7 mm SL), Nova Mutum, headspring flowing into Rio Criqueirín, tributary of Rio dos Patos, 19 Feb 2000, graduate students of MZUSP.

Pyrhulina semifasciata. MZUSP 23230 (4, 27.1-43.6 mm SL, 3 c&s, 42.7-48.3 mm SL), Lago Miuíá,
upstream Codajás, Amazonas, Brazil, 3°50'S 62°5'W, 25 Sep 1968, Expedição Permanente da Amazônia.

TAXONOMIC REVIEW

Based on the analysis of the type material of all nominal species and of a large amount of specimens of *Copella* from several localities in South America drainages, six of the ten nominal species of the genus are recognized as valid: *Copella arnoldi*, *C. compta*, *C. eigenmanni*, *C. nattereri*, *C. stigmasemion*, and *C. vilmae*. *Copella arnoldi* is senior synonym of *C. carsevegnensis*, *C. eigenmanni* is senior synonym of *C. metae*, *C. nattereri* is senior synonym of *C. callolepis* and *C. meinkenii*, and *C. stigmasemion*, new combination, is senior synonym of *C. nigrofasciata*. A probably new species of *Copella* from the upper rio Negro basin is presented, though not described due to the lack of enough material for a proper description.

COPELLA, MYERS, 1956

Copella Myers, 1956: 12 [*C. compta* type species by original designation; transferred *Copeina callolepis* and *Pyrrhulina nattereri* to *Copella*].—Weitzman, 1964: 150 [osteological notes; included in subtribe Pyrrhulinina].—Weitzman & Cobb, 1975: 2 [in the tribe Pyrrhulinini].—Vari, 1995: 5 [phylogenetic analysis of the Ctenoluciidae].—Weitzman & Weitzman, 2003: 241 [literature compilation].—Oyakawa, 1998: 1 [phylogenetic analysis of the Erythrinioidea].—Netto-Ferreira, 2006: 2 [phylogenetic analysis of the Lebiasinidae].—Oyakawa & Netto-Ferreira, 2007: 64 [literature compilation].—Netto-Ferreira, 2010: 1 [phylogenetic analysis of the Lebiasininae].

Type species: *Copeina compta* Myers, 1927. Type by original designation.

Gender: Feminine.

Included species: *Copella arnoldi*, *C. compta*, *C. eigenmanni*, *C. nattereri*, *C. stigmasemion*, and *C. vilmae*.

Diagnosis. *Copella* can be easily distinguished from other genera of the Lebiasinidae by having the anterior portion of the maxilla triple curved in males (*vs.* approximately straight or convex), and by males being distinctly longer than females (*vs.* males and females of about the same size). Additionally, *Copella* is distinguished from other genera of the family, except *Nannostomus*, by having anterior and posterior nares distant from each other (*vs.* juxtaposed, close to each other). It is distinguished from *Nannostomus* by having a black spot on the dorsal fin (*vs.* dorsal fin hyaline), elongate fins, especially on males (*vs.* fins not elongate), and

upturned mouth (*vs.* terminal). Other osteological characters diagnostic for *Copella* are listed under “Monophyly of *Copella*” in the “Phylogenetic Analysis” section.

Remarks. *Copella* has similar pattern of external sexually dimorphic features of the other lebiasinids, concerning modifications on the anal fin. The rays are anteroposteriorly thickened and longer in males than in females (Vari, 1995), bearing thickened membranes and well-developed erector and depressor muscles (Netto-Ferreira, 2012). Breeding tubercles were only found in *Copella compta*. Additionally, males are distinctly longer than females, with elongate fins and modified maxillae. In males, the anterior border of the maxilla is triple curved, and bears more teeth than in the females. Some species have a sexually dimorphic coloration. Other sexual dimorphic features are described under the “Character description” section.

Distribution. Species of *Copella* occurs in the rio Amazonas basin in Brazil, Colombia, Guyana, Peru, and Venezuela, Orinoco basin in Colombia and Venezuela, and coastal drainages of Guyana, French Guiana, Surinam, and Venezuela.

Key to the species of Copella

1a. Procurrent caudal-fin rays hyaline; area extending from posteroventral portion of dentary to ventral portion of eye darkly pigmented; white brilliant spots usually present on scales of body, in live or preserved male specimens.....*Copella arnoldi*
(lower rio Amazon basin, coastal drainages of Guyana, French Guiana, Surinam, and mouth of rio Orinoco).

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- 1b. Procurrent caudal-fin rays black (except in some populations of *C. nattereri* from the rio Negro); no dark pigmentation on the area extending from posteroventral portion of dentary to ventral portion of eye; white spots on body scales may be present in preserved species, but they are red in life.....2
- 2a. Middle caudal-fin rays dark.....*Copella eigenmanni*
(rio Orinoco basin, upper rio Negro and upper rio Putumayo, rio Amazonas basin).
- 2b. Middle caudal-fin rays hyaline.....3
- 3a. 15-19 predorsal scales; first longitudinal scale row with 14-18 scales; fourth longitudinal scale row with 24-28 scales; clear spots (red in life) absent on posterior portion of body scales..... 4
- 3b. 12-14 predorsal scales; first longitudinal scale row with 11-14 scales; fourth longitudinal scale row with 20-24 scales; clear spots (red in life) present on posterior portion of body scales.....5
- 4a. Males with rows of conspicuous dark scales irregularly disposed on body, gradually lighter posteriorly; females and juveniles with brownish inconspicuous wide stripe on flank.....*Copella vilmae*
(upper rio Amazonas, surroundings of Letícia, Colombia).
- 4b. Males lacking dark scales irregularly disposed on body, bearing a faint longitudinal dark stripe on flank; females with a plain coloration, without longitudinal dark stripe on body.....*Copella compta*
(upper rio Negro upstream São Gabriel da Cachoeira, Brazil and Venezuela).
- 5a. Clear spots (red in life) on posterior portion of body scales, limited dorsally, posteriorly and ventrally by dark pigmentation, frequently horseshoe-like shaped; longitudinal dark stripe, when present, formed by subjacent pigmentation.....*Copella nattereri*
-

(rio Amazonas from Letícia, Colombia, to mouth of rio Tapajós, rio Negro basin and upper and middle rio Orinoco basin).

5b. Clear spots (red in life) frequently restricted to the fourth longitudinal scale row of body, not limited by dark pigmentation; longitudinal black stripe conspicuous, formed by superficial pigmentation, located below the row of clear spots.....*Copella stigmatemion*

(rio Amazonas, rio Madeira, and coastal drainages of Pará State at Brazil).

COPELLA ARNOLDI (REGAN, 1912)

Figures 29-36; Tables 1 and 2

Pyrrhulina filamentosa.—Eigenmann & Eigenmann, 1889: 110 [possibly not *Pyrrhulina filamentosa*].—Eigenmann, 1912: 104 [in part, from rio Demerara at Kumaka, rios Lama and Aruka, Guyana].—Magalhães, 1931: 179, fig. 95 [misidentification; brief description; breeding behavior].

Copeina arnoldi Regan, 1912: 393 [type locality: Amazon (= lower Amazon basin)].—Myers, 1927: 111 [comparison with *Copeina* (= *Copella*) *compta*].—Fowler, 1948: 344 [listed; *Copeina callolepis*, *C. eigenmanni* and *C. carsevennensis* placed as synonym].—Boeseman, 1952: 184 [Maroni basin, Surinam; listed].—Meinken, 1952: 116 [comparison with *Pyrrhulina nigrofasciata* (= *Copella stigmasemion*)].—Boeseman, 1953: 13 [rio Surinam basin; listed].—Boeseman, 1954: 18 [rio Paramaribo basin, Surinam; listed].—Boeseman, 1956: 186 [literature compilation].—Myers, 1956: 13 [comparison with *Holotaxis melanostomus* (= *Pyrrhulina melanostoma*)].—Krekorian & Dunham, 1972 a, b [breeding behavior].—Krekorian & Dunham, 1973 [breeding behavior].—Krekorian, 1976 [breeding behavior].

Copeina eigenmanni Regan, 1912: 393 [in part, from Pará (Brazil), rios Aruka and Lama (Guyana)].—Fowler, 1948: 344 [literature compilation; in part, from Pará and Guyana placed as synonym of *Copeina* (= *Copella*) *arnoldi*].

Copeina carsevennensis Regan, 1912: 394 [type locality: Carsevenne, French Guiana (= rio Calçoene, Amapá, Brazil)].—Myers, 1927: 111 [comparison with *Copeina* (= *Copella*) *compta*].—Fowler, 1948: 344 [literature compilation; placed as synonym of *Copeina* (= *Copella*) *arnoldi*].

Copella arnoldi.—Géry, 1977: 143 [new combination; brief description; figure as “*Copella* of the *arnoldi*-group”].—Planquette *et al.*, 1996: 178 [rio Maroni, French Guiana; brief description; unnumbered fourth figure pg. 179].—Weitzman & Weitzman, 2003: 241 [literature compilation, introduced at Trinidad & Tobago].—Keith *et al.*, 2006: 30 [Litany drainage, French Guiana; cited].—Zarske & Géry, 2006: 44 [identification key].—Oyakawa & Netto-Ferreira, 2007: 64 [literature compilation].—Montag *et al.*, 2009: 245 [Ilha do Marajó; listed].—Netto-Ferreira, 2010: 331 [phylogenetic analysis of Lebiasininae].—Zarske, 2011: 14 figs. 12-16, 18-19, 34-35 [rio Xingu; redescription; photo of the syntype from BMNH 1909.4.2.23-26; taxonomic notes].—Mol *et al.*, 2012 [rios Corantijn, Saramacca, Commewijne, Marowijne; listed].

Copella eigenmanni.—Géry, 1977: 147 [new combination; specimen of Atlantic coast; possibly synonym of *C. metae*].—Vari, 1995: 5 [material used in phylogenetic analysis].—Weitzman & Weitzman, 2003: 242 [mouth of rio Orinoco; literature compilation; comments on type locality].—Zarske & Géry, 2006: 44 [identification key].—Netto-Ferreira, 2006: 20 [phylogenetic analysis of Lebiasinidae].—Oyakawa & Netto-Ferreira, 2007: 64 [literature compilation; incomplete information about type locality].—Mol *et al.*, 2012 [considers synonym of *Copella arnoldi*].—Netto-Ferreira, 2010: 331 [phylogenetic analysis of Lebiasininae].

Copella carsevennensis.—Géry, 1965a: 120 [Mooi Wana and foot of Albina-hills, Suriname; listed].—Géry, 1977: 146 [new combination; literature compilation; unnumbered figure pg. 146, left].—Planquette *et al.*, 1996: 178 [rio Maroni, rio Mana, rio Sinnamary, rio Kourou, rio Comté, rio Kaw, rio Arouague and rio Oiapoque, French Guiana; brief description; unnumbered first fig. pg. 179].—Keith *et al.*, 2006: 30 [Litany drainage, French Guiana; cited].—Mérigoux *et al.*, 1998: 30 [rios Malmanouri and Karouabo, French Guiana; listed].—

Weitzman & Weitzman, 2003: 241 [literature compilation].—Zarske & Géry, 2006: 44 [identification key].—Oyakawa & Netto-Ferreira, 2007: 64 [literature compilation; comments on type locality].—Netto-Ferreira, 2010: 331 [phylogenetic analysis of Lebiasininae].—Zarske, 2011: 32, figs. 25-30 [redescription; picture of 3 syntypes from BMNH 1911.10.31.140; syntypes of *Copeina eigenmanni* from Guyana possibly conspecific with *Copella carsevennensis*; taxonomic notes].—Mol *et al.*, 2012 [considers synonym of *Copella arnoldi*].

Copella spec. aff. *arnoldi*.—Zarske & Géry, 2006: 44 [identification key].

Copella sp..—Montag *et al.*, 2008: 18 [FLONA de Caxiuanã in igarapé; listed].

Copella nattereri.—Montag *et al.*, 2009: 245 [misidentification; listed].

Copella metae.—Lasso & Sánchez-Duarte, 2011: 64 [misidentification; listed].



Figure 29. Syntypes of *Copeina arnoldi*, BMNH 1909.4.2.25-26, (A) male, 34.4 mm SL, (B) female, 25.4 mm SL, Amazon, Brazil.



Figure 30. Syntypes of *Copeina carsevennensis*, BMNH 1899.7.26.1-5, immatures, (A) 24.3 mm SL (B) 22.9 mm SL and (C) 18.5 mm SL, Carsevenne, French Guiana (= rio Calçoene, Amapá, Brazil).

Diagnosis. *Copella arnoldi* can be distinguished from all congeners, except some specimens of *C. nattereri*, by having the ventral procurrent caudal-fin rays hyaline (*vs.* black). It can be distinguished from *C. nattereri* by the absence of a black mark on each body scale (*vs.* presence). Additionally, it is distinguished from all congeners by having a pigmented area extending anterodorsally from ventral tip of the dentary to ventral portion of the eye (*vs.* absent). Some males of *Copella arnoldi* are unique among congeners in having white brilliant spots at scales of the third, fourth, fifth and sixth longitudinal scale rows.



Figure 31. *Copella arnoldi*, (A) MPEG 23064, male, 33.2 mm SL, Marapanim, Pará, Brazil; MZUSP 105770, (B) male, 38.2 mm SL, flipped horizontally, (C) male, 33.6 mm SL, (D) male, 33.7 mm SL, male, (E) male, 33.5 mm SL, (F) female, 30.9 mm SL, Vigia, Pará, Brazil.



Figure 32. *Copella arnoldi*, live specimen not preserved, male, Vitória do Xingú, Pará, Brazil.

Photo: Hans-Georg Evers.



Figure 33. *Copella arnoldi* live specimen not preserved, males above and below, female in the middle, Vitória do Xingú, Pará, Brazil. Photo: Hans-Georg Evers.

Description. Morphometrics in Tables 1 and 2. Largest examined male 42.3 mm SL, female 32.5 mm SL. Greatest body depth located slightly anterior to vertical through pelvic-fin origin. Body cylindrical, slightly compressed laterally. Dorsal profile of body straight or slightly convex from tip of snout to end of supraoccipital, straight or slightly convex from that point to dorsal-fin origin, posteroventrally inclined along dorsal-fin base and straight along caudal peduncle. Ventral profile of body convex from anterior tip of dentary to the vertical through anterior margin of orbit, straight from that point to the vertical through pectoral-fin origin, slightly convex from that point to pelvic-fin origin, straight from pelvic-fin origin to anal-fin origin, posterodorsally inclined along anal-fin base and straight along caudal peduncle.

Mouth upturned. Premaxillary teeth in one row, with 15 (2), 18 (2), or 19 (1) teeth, decreasing in size laterally. Number of maxillary teeth sexually dimorphic, 9 (1), 10 (1), or 12 (1) in males, 3 (1) or 5 (1) in females, decreasing in size posteriorly, especially in males. Dentary teeth in two rows, outer with 8 (2), 10 (1), 11(1), or 12 (1) teeth, increasing in size laterally, inner with 24 (2), 25 (1), 28 (1), or 30 (1) teeth, decreasing in size laterally.

Dorsal fin with ii, 8 (109)* rays, second and third branched rays longer. Pectoral fin with i, 8 (10)*, 9 (65), 10 (24), or 11 (2) rays, first three branched rays longer. Pelvic fin with i, 6 (1), 7 (99)*, or 8 (2) rays, third branched ray longest. Anal fin with iii (6), 8 (2) or 9 (99)*, rays, fourth and fifth branched rays longer. Caudal fin with i, 7 (4), 8 (88)*, or 9 (2) rays in upper lobe, first and second branched rays longer, and 5 (1), 6 (3), or 7 (58)*, i rays in lower lobe, first and second branched rays longer. Upper caudal-fin lobe longer than lower.

Predorsal scales 13 (23)*, 14 (54)*, or 15 (20), in one series. First longitudinal scale row with 12 (8), 13 (30)*, 14 (52)*, or 15 (7) scales. Fourth longitudinal scale row with 23 (42)*, 24 (38), 25 (14), or 26 (2) scales. Longitudinal scale rows between dorsal-fin origin and pelvic-fin origin 5 (21)* or 6 (75). Longitudinal scale row between dorsal-fin origin and anal-fin origin 5

(106)*. Circumpeduncular scale rows 10 (106)*. Total number of vertebrae 34 (1), 35 (19), 36 (17), or 37 (5)*.

Table 1. Morphometrics of *Copella arnoldi*. Syntypes of *Copeina arnoldi* BMNH 109.4.2.25-26 (2), syntypes of *Copeina carsevennensis* BMNH 1899.7.26.1-5 (2), paralectotypes of *Copella eigenmanni* BMNH 1911.10.31.140 (2) and non-type material DZSJRP 11120 (2), DZSJRP 11231 (8), MHNLS 12458 (3), MHNG 2200.34 (4), MHNG 2200.36 (6), MHNG 2647.005 (6), MNHN 1898.0053 (3), MPEG 8223 (2), MPEG 8305 (6), MPEG 10398 (5), MPEG 10716 (4), MZUSP 23064 (20), MZUSP 105770 (14), ZMA 101.937 (5), ZMA 104.197 (2), ZMA 104.288 (4), ZMA 105.694 (4), ZMA 106.105 (4), and ZMA 106.137 (2), n = number of specimens, SD = Standard deviation. Range does not include primary types.

	<i>Copeina arnoldi</i>		<i>Copeina carsevennensis</i>		n	Range			Mean	SD
	Syntypes		Syntypes							
Standard length (mm)	25.4	34.4	22.9	24.3	106	19.5	-	41.8	30.8	
Percents of standard length										
Body depth	20.1	19.5	19.8	19.6	106	16.8	-	23.2	19.8	1.1
Dorsal- to caudal-fin origin	37.9	34.2	40.5	37.7	106	33.7	-	43.6	37.6	1.3
Snout to dorsal-fin origin	62.4	64.5	59.9	64.0	106	60.4	-	66.0	63.2	1.3
Snout to pectoral-fin origin	22.4	22.0	22.7	22.0	106	19.9	-	25.8	22.3	1.1
Snout to pelvic-fin origin	51.5	50.3	46.2	45.4	106	43.5	-	52.5	48.4	1.6
Snout to anal-fin origin	74.2	73.2	68.7	69.3	106	67.6	-	75.1	71.2	1.6
Pectoral- to pelvic-fin origin	29.9	30.3	25.3	23.8	106	22.7	-	30.4	27.3	1.6
Pelvic- to anal-fin origin	23.4	23.7	23.4	21.6	106	20.8	-	29.5	23.9	1.4
Pectoral-fin length males	-	22.2	-	-	74	18.9	-	32.3	24.1	3.1
Pectoral-fin length fem/imm	22.3	-	19.9	20.5	32	19.6	-	23.3	21.4	0.9
Pelvic-fin length males	-	26.7	-	-	74	17.8	-	32.3	24.1	3.1
Pelvic-fin length fem/imm	20.5	-	19.0	18.3	32	17.8	-	21.7	19.9	0.9
Dorsal-fin length males	-	30.8	-	-	72	26.5	-	58	38.1	6.6
Dorsal-fin length fem/imm	25.5	-	-	24.6	30	25.6	-	33.4	28.7	1.7
Anal-fin length males	-	22.7	-	-	73	18.7	-	31.6	24.1	3.1
Anal-fin length fem/imm	19.4	-	18.1	19	31	18.5	-	21.5	19.8	0.8
Anal-fin base length	9.2	9.2	8.0	9.4	106	7.7	-	12.6	9.9	1.0
Caudal peduncle depth	9.1	9.3	8.4	9.0	106	7.6	-	10.2	9.1	0.6
Caudal peduncle length	20	17.5	21.5	21.5	106	16.3	-	22.7	19.7	1.3
Head length	22.1	21.8	23.5	23.0	105	20.3	-	25.9	22.9	1.1
Percents of head length										
Eye diameter	38.8	31.8	39.2	39.1	104	29.0	-	40.3	35.4	2.5
Snout length	25.5	27.3	24.2	27.4	105	22.8	-	34.8	27.6	2.1
Interorbital distance	38.8	37.7	36.4	36.2	105	33.1	-	42.3	37.7	1.9
Upper jaw length	28.4	27.2	29.9	30.6	105	20.7	-	35.2	30.1	2.3

Table 2. Meristics of syntypes of *Copeina arnoldi* BMNH 109.4.2.25-26 (2) and syntypes of *Copeina carsevennensis* BMNH 1899.7.26.1-5 (2).

	<i>Copeina arnoldi</i>		<i>Copeina carsevennensis</i>	
	Syntypes		Syntypes	
Predorsal scales	13	14	15	15
First longitudinal scale row	13	14	15	13
Fourth longitudinal scale row	-	23	25	25
Longitudinal scale rows dorsal to pelvic	5	5	6	5
Longitudinal scale rows dorsal to anal	5	5	5	5
Circumpeduncular scale rows	10	10	10	10
Pectoral-fin rays	i8	i8	i8	i9
Pelvic-fin rays	i6	i7	i7	i7
Dorsal-fin rays	ii8	ii8	ii8	ii8
Branched anal-fin rays	9	-	9	9
Caudal-fin rays	i8,7i	-	-	-

Color in alcohol. Overall ground coloration of body beige. Dark stripe extending from anterior tip of dentary to posterior tip of opercle (Figs 29-33). Dark pigmentation extending anterodorsally from the posteroventral portion of dentary to ventral portion of eye (Fig. 34). Thin predorsal dark stripe, frequently wider over second and third scales. Faint dark pigmentation located at base and at posterior border of scales of body (Fig. 31). Ventral region clear. Small dark blotch behind opercle on males and females. Males with a blur dark stripe of variable extension and intensity, extending from opercle to, at most, vertical through anal-fin base end (Figs. 31A-D, 32 and 33). Dorsal fin with black round spot above smaller white one. Remaining fins hyaline. Pelvic and anal fin usually with dark edge, more intense in males. Some specimens from Surinam and mouth of rio Orinoco with distal portion of first pelvic-fin ray conspicuous black. Some males presenting white brilliant spots at scales of third, fourth, fifth and sixth longitudinal scale rows, mainly restricted to median portion of body (Figs. 31A-C, 32

and 33). Males bearing very long dorsal fin with more elongated black spot on dorsal fin, extending to its tip.

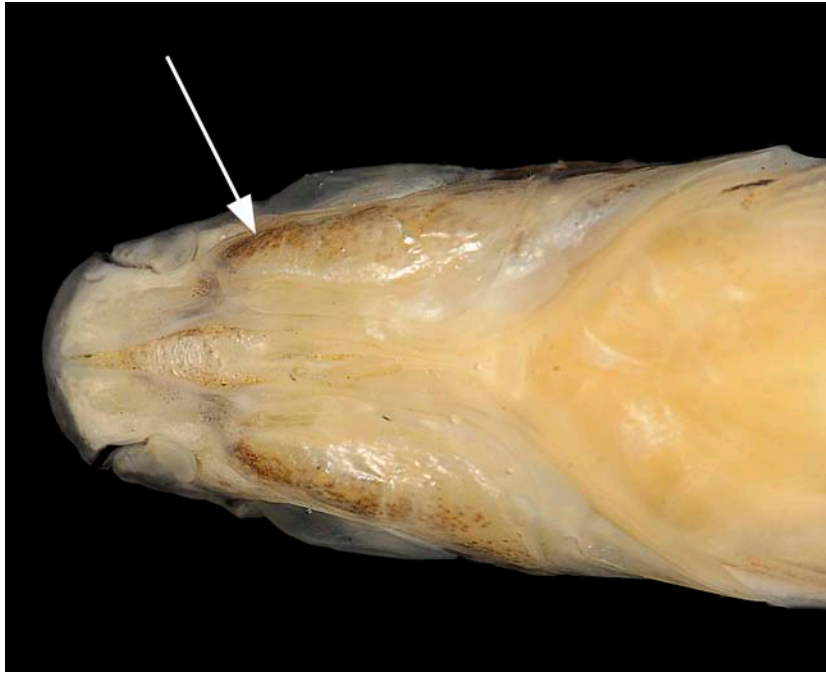


Figure 34. Ventral view of head of *Copella arnoldi*, MZUSP 105770, 35.3 mm SL showing characteristic pigmentation below eye.

Color in life. Dark stripe extending from anterior tip of dentary to posterior tip of opercle. Upper and lower jaw yellowish to reddish. Overall body coloration light brown or beige, ventral portion clear. Fins yellow to orange. Dorsal fin with black spot dorsal to small, white round spot. Some males with white brilliant spots on scales of third, fourth, fifth and sixth longitudinal scale rows, mainly restricted to median portion of body. Some males with dark stripe extending from opercle to, at most, vertical through anal-fin base end, of variable intensity. Males with base of dorsalmost rays of upper caudal-fin lobe, and tip of basalmost rays of lower caudal-fin intense red (Figs. 32 and 33).

Sexual dimorphism. Males longer than females. Males with more maxillary teeth than females (see description above). Pectoral, pelvic, dorsal, anal fins distinctly longer in males than in females. There is a variation in relative fin lengths among males, some with equivalent standard lengths presenting distinct fin lengths (Fig. 35 gráfico), but among the males from the same collection event, longer males tend to have longer fins and are more intensively colored than other males. This may be related to the hierarchical position within the shoal. Tip of pectoral fin may extend beyond pelvic-fin origin in males, but never to this point in females. Tip of adpressed pelvic fin reaching up to two-thirds the length of the caudal peduncle in males, but only to level of anus in females. Tip of adpressed dorsal fin reaching up to one-half the length of the median caudal-fin rays in males, and approximately to one-half the length of the caudal peduncle in females. Tip of adpressed anal-fin reaching to the level of first ventral procurrent rays in males, and to two-thirds of the length of the caudal peduncle in females. Upper caudal-fin lobe longer than lower, especially in males. Color pattern differences described in “Color in alcohol” section.

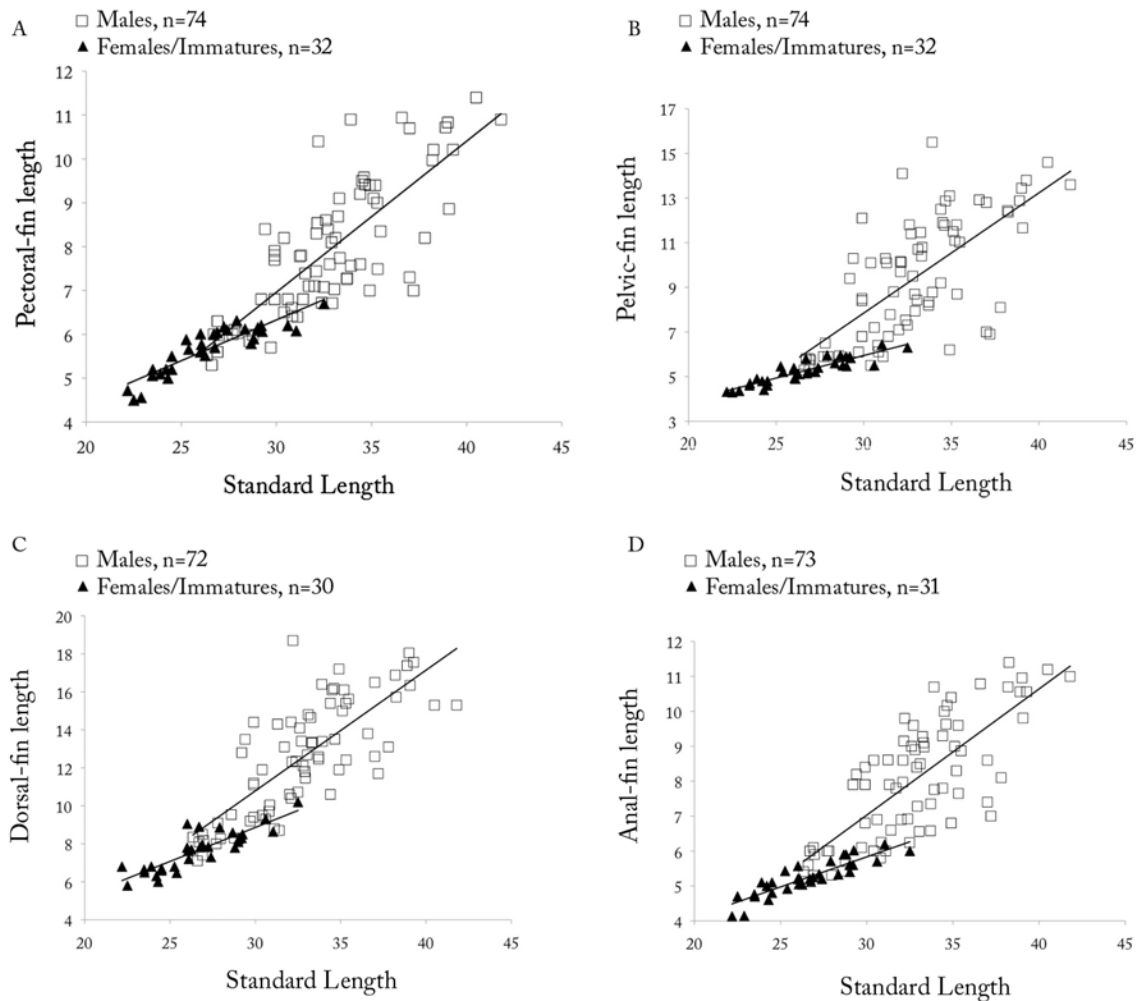


Figure 35. *Copella arnoldi*, pectoral-, pelvic-, dorsal- and anal-fin lengths as function of SL by sex.

Distribution. Lower rio Amazon basin, coastal drainages of Pará and Amapá, Brazil, Guyana, French Guiana, Surinam, mouth of rio Orinoco and coastal drainages of Sucre and Monagas, Venezuela (Fig. 36).

Behavioral notes. *Copella arnoldi* is widely known among aquarists by its unique breeding behavior and parental care (see Krekorian & Dunham, 1972a; Krekorian & Dunham, 1972b; Krekorian & Duham, 1973; Krekorian, 1976). The male and the female line up side by side at

the surface of the water and jump together out of the water, to breed. After fertilization the eggs are laid at the underside of an emergent leaf and the male then splashes them with its tail for about three days until they hatch, hence the popular name “Splash tetra”.

Eight individuals of *Copella arnoldi*, five males and three females, captured with MZUSP 105770, not preserved, were kept in aquarium and observed. Territoriality was observed in two males, frequently chasing other males and displaying parallel to each other, opening their fins and mouths widely. These two males were slightly larger than the other males and had extremely long fins. They were more colorful, having more brilliant white spots, and a darker black stripe on body, compared to the other males. The remaining males were smaller, without exuberant coloration, some of them with colors similar to those of the females. Only one of the largest males had access to the mature female, whose abdomen was orange, full of ovocytes. These observations bring the question of whether the differences in coloration among males of *Copella arnoldi* in the same shoal are somehow related to the hierarchical position in the group. However, this deserves further studies.

Just before lining up to jump out of the water toward the upper glass of the aquarium, the female follows the male, touching her abdomen at the anterodorsal portion of the male several times, swimming agitatedly. This seems to be the same behavior described by Zarske (2011; fig. 30), but interpreted as an attempt of the female to push the male down to the bottom. He proposed such breeding behavior as one of the differences between *Copella arnoldi* and *C. carsevennensis*. However, as he pointed out, the couple never spawned to confirm his hypothesis.

Remarks. Regan (1912) described *Copella arnoldi* (rio Amazonas) and *C. carsevennensis* (Carsevenne, French Guiana = rio Calçoene, coastal drainage of Amapá, Brazil) based on the

position of the dorsal fin that would distinguish *C. arnoldi* by having “the dorsal-fin origin nearer to base of caudal than to head” (*vs.* “origin of dorsal fin equidistant from head and base of caudal, or a little nearer head”). Géry (1977) diagnoses both species also by the number of longitudinal scales (23-24 *vs.* 26) and Planquette *et al.* (1996) by the presence of a black stripe in a low position on body reaching the level of the anal fin in *C. arnoldi* contrasting with an uniform coloration, except by the presence of a small stripe that do not surpass the level of the pectoral fin, in *C. carsevennensis*. Zarske (2011) also distinguished *Copella arnoldi* from *C. carsevennensis* (Zarske, 2011: tab. 8) by occasionally having a black stripe on the anterior half of body (*vs.* absence), presence of series of white brilliant spots at the posterior half of the body (*vs.* absence), and having the distal edge of dorsal, pelvic and anal fins black (*vs.* fins never with a conspicuous black border). Zarske (2011) observed that males of *C. arnoldi* have two color patterns that could be related to sexual activity (Zarske, 2011: figs. 15-16, and 18-19). Interestingly, the “sexual inactive” males (Zarske, 2011: figs. 15 and 19) have the same color pattern of the supposed males of *C. carsevennensis* (Zarske, 2011: figs. 28-30). Furthermore, some diagnostic features of *C. arnoldi* (white spots on the posterior half of the body and distal edge of fins black) can be seen in the figure of the supposed *C. carsevennensis* (see Zarske, 2011: fig. 30].

In the present analysis, data taken from type and non-type material from several localities in Brazil, French Guiana, Surinam, Guyana and Venezuela (Fig. 36) did not reveal any morphological feature that could effectively separate the two species. Morphometric and meristic data (including those related to dorsal fin position and longitudinal scale counts) largely overlap among the populations examined. Likewise, no color differences were observed that could justify the maintenance of two names. Indeed, there is color pattern variation in males (see Color in alcohol). However, males with exuberant coloration, presenting a longitudinal

dark stripe, with white brilliant spots were syntopically collected with males that present similar coloration of the females, without dark stripe or white spots on the body. Furthermore, males with intermediate coloration are always present (Fig. 31B-D). If color variation among males is related to the hierarchical position, sexual activity, or environmental influences, this should be further investigated by studies using different approaches. The features presented in the literature to distinguish the aforementioned *Copella arnoldi* from *C. carsevegnensis* are herein interpreted as variation within a single species. Thus, *Copella carsevegnensis* is considered a junior synonym of *C. arnoldi*, as previously proposed by Fowler (1948).

Zarske (2011) states that the type locality of *Copella arnoldi* is Ilha do Arapiranga, near Belém, Pará, which according to him is a collecting site area explored by German aquarists in the past. However, this is highly speculative. Based on the distribution of *C. arnoldi* given as the “Amazon”, the only possible inference is that the types might have come from anywhere in the lower Amazon basin. Thus, in the map of distribution (Fig. 36), the type locality of *Copella arnoldi* is plotted at Belém arbitrarily.

Eigenmann (1912) listed several localities for *Pyrrhulina filamentosa* from Guyana collected in 1908. Within this material, only the paralectotypes of *Copeina eigenmanni* from rios Aruka and Lama, and one specimen from rio Demerara, Kumaka (CAS 227312), actually belonging to *Copella arnoldi*, were examined.

Schultz (1944) cited *Copeina* (= *Copella*) *arnoldi* from Caripito, Venezuela, where *Copella eigenmanni* may also occur. Although Schultz’s citation is probably right, it could not be confirmed whether he is referring to *Copella arnoldi* or *C. eigenmanni*.

Kenny (1995) and Weitzman & Weitzman (2003) listed *Copella arnoldi* for Trinidad and Tobago but this could not be confirmed in the present study.

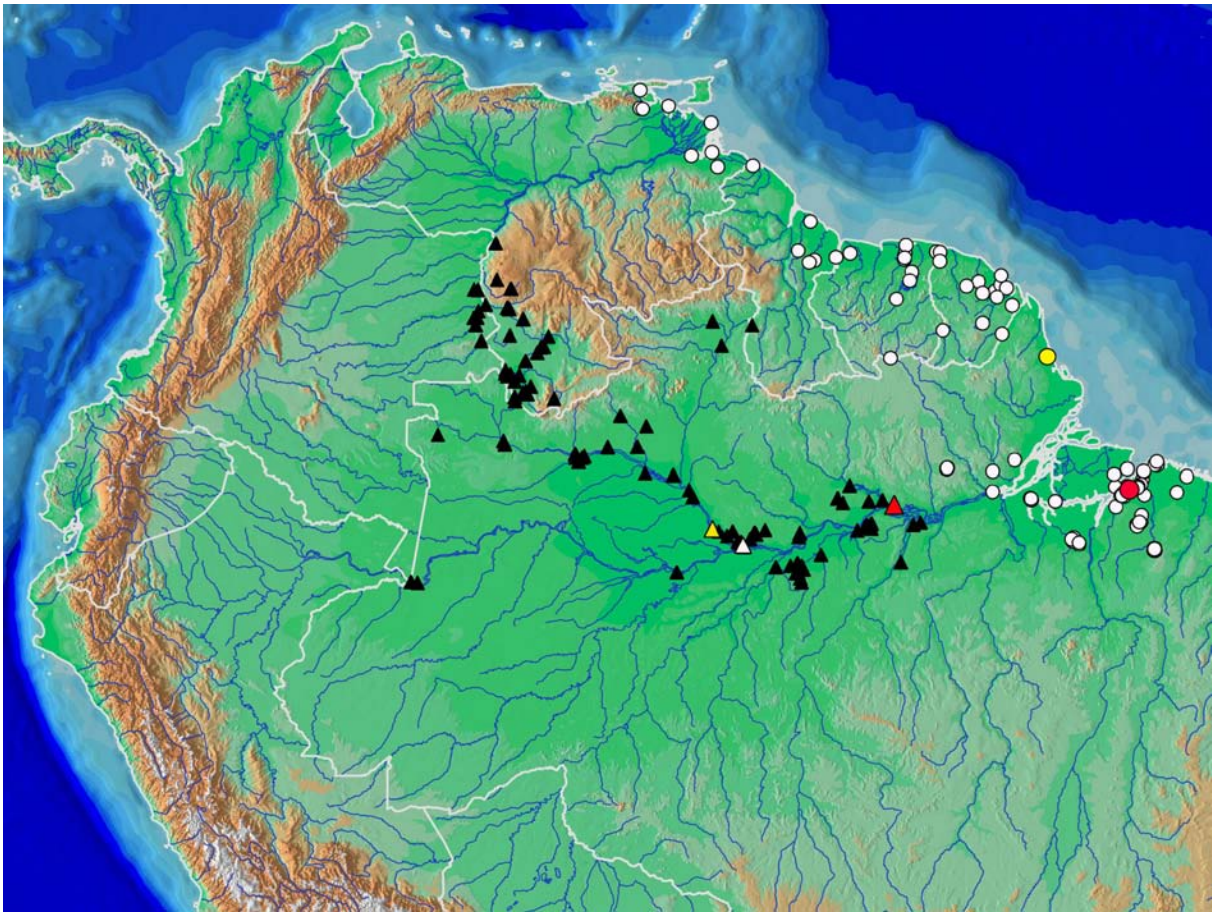


Figure 36. Distribution of *Copella arnoldi* represented by circles (type locality of *C. arnoldi* in red, plotted arbitrarily in the lower Amazon basin; of *Copeina carseveennensis* in yellow) and *C. nattereri* represented by triangles (type locality of *C. nattereri* in red, of *C. meinkenii* in yellow, and of *Copeina callolepis* in white, plotted arbitrarily in the Amazon basin). Some symbols may represent more than one locality or lot of specimens.

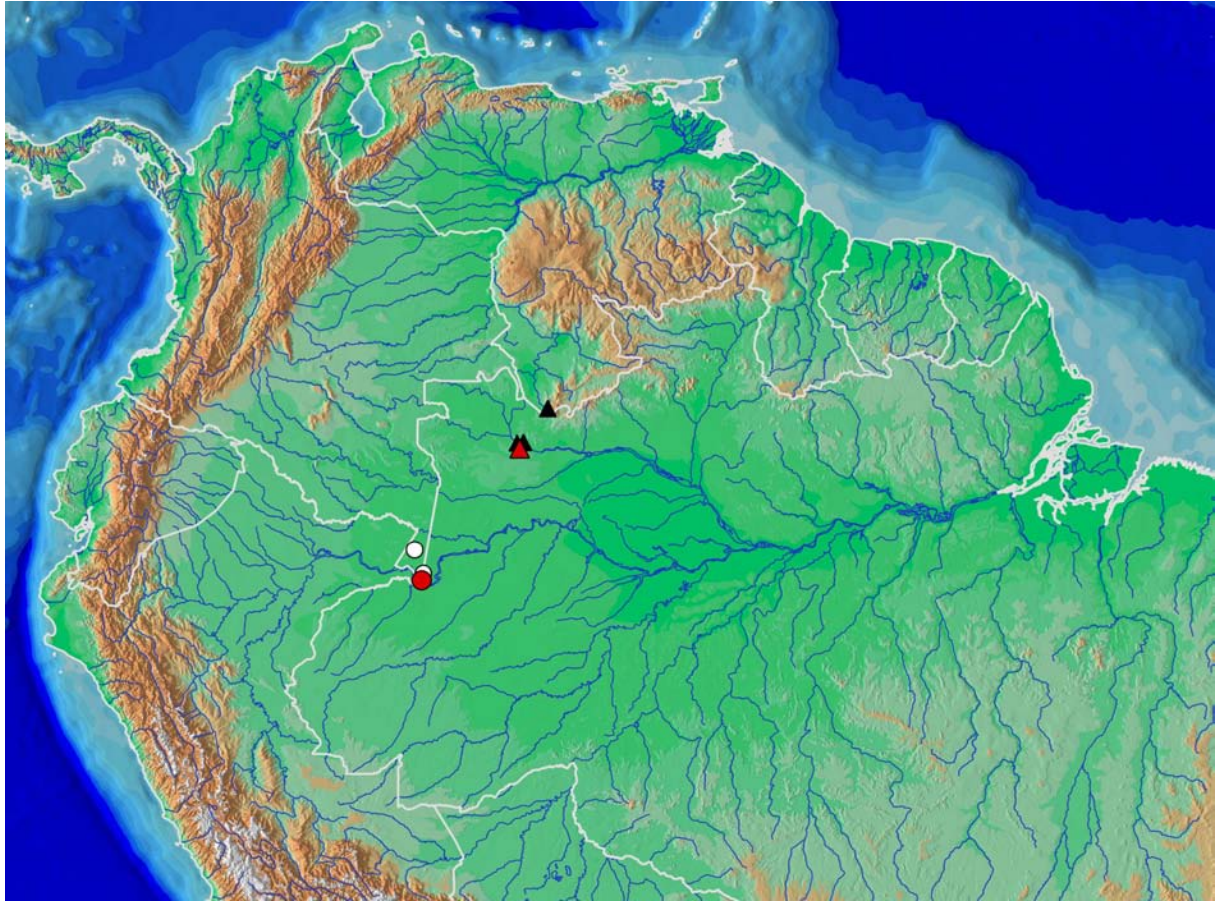


Figure 37. Distribution of *Copella compta* represented by triangles (type locality in red) and *C. vilmae* represented by circles (type locality in red). Some symbols may represent more than one locality or lot of specimens.

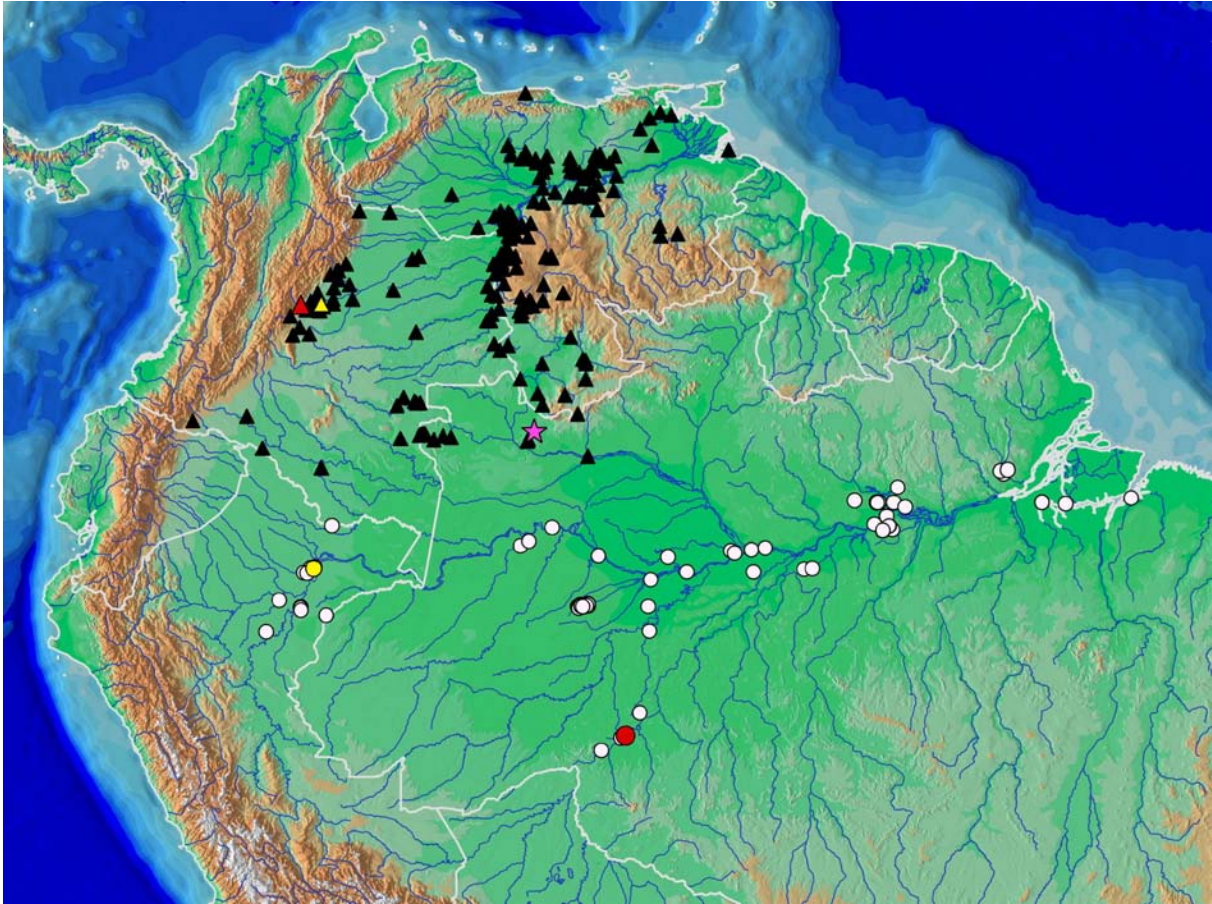


Figure 38. Distribution of *Copella eigenmanni* represented by triangles (type locality of *C. eigenmanni* in red, plotted at Villavicencio, see text, of *Copeina metae* plotted in yellow), *C. stigmatsemion* represented by circles (type locality of *C. stigmatsemion* in red), of *Pyrrhulina nigrofasciata* in yellow, plotted arbitrarily in the upper Amazon basin at Peru), and *Copella* sp. represented by a star. Some symbols may represent more than one locality or lot of specimens.

MATERIAL EXAMINED

Type material

BMNH 1909.4.2.25-26 (2 syntypes of *Copeina arnoldi*, 25.4 and 34.4 mm SL), Amazon (=lower rio Amazonas basin), Arnoldi. BMNH 1899.7.26.1-5 [ex MNHN] (5 syntypes of *Copeina carsevennensis*, 17.0-24.3 mm SL), Carsevenne (=rio Calçoene, Amapá, Brazil, approximately 2°30'N 50°57'W). BMNH 1911.10.31.140 (7 paralectotypes of *Copeina eigenmanni*, 14.8-20.9 mm SL), rio Aruka, Guyana [=approximately 8°12'N 59°44'W], 1908, C. Eigenmann. BMNH 1894.5.18.40-41 (2 paralectotypes of *Copeina eigenmanni*, Pará [=Brazil]. BMNH 1911.10.31.146 (1 paralectotype of *Copeina eigenmanni*, 21.6 mm SL), rio Lama, Guyana [=approximately 6°32'N 58°1'W], 1908, C. Eigenmann.

Non-type material

Rio Amazonas basin, Brazil. DZSJRP 11106 (7, 15.5-27.6 mm SL), stream without name, at main road of Jutaituba farm, rio Pacajá, rio Pará, Portel, Pará, 2°59'34"S 50°11'18"W, 23 Apr 2008, J. Serra *et al.* DZSJRP 11120 (4, 16.1- 33.1 mm SL), igarapé Santo Antônio at Jutaituba farm, rio Jacundá, Baião, Pará, 3°2'10"S 50°0'W, 24 Apr 2008, J. Serra *et al.* DZSJRP 11231 (22, 21.2-35.5 mm SL), stream without name, rio Pacajá, rio Pará, Baião, Pará, 3°4'57"S 49°59'59"W, 21 Apr 2008, J. Serra *et al.* DZSJRP 11237 (2, 24.9 and 25.0 mm SL), stream without name at Jutaituba farm, rio Pacajá, rio Pará, Baião, Pará, 2°53'32"S 50°9'37"W, 26 Apr 2008, J. Serra *et al.* DZSJRP 11239 (2, 16.5 and 22.7 mm SL), igarapé Moconho at Jutaituba farm, rio Pacajá, rio Pará, Baião, Pará, 2°55'57"S 50°13'3"W, 26 Apr 2008, J. Serra *et al.* INPA 39737, igarapé da Carol, Lago Ajuruxi, RESEX Cajari, Mazagão Ajuruxi, Amapá, 0°34'27.5"S 51°54'57.7"W, N. Junior. MCZ 46128 (1, 28.7 mm SL), stream at km 18, Castanhal-Belém road, Amazonas, Santa Isabel, Pará, Jul 1965, N. Menezes. MNHN 1898.0053 (6, 22.3-31.0 mm SL), Carsevenne (= rio Calçoene, Amapá), Geay. MPEG 2940 (41, 15.1-22.4 mm SL), mouth of rio Goiapi, Cachoeira do Arari, Ilha do Marajó, Cachoeira do Arari, Pará, 8 Sep 1990, M. Assunção. MPEG 2941 (22, 14.7-27.4 mm SL), mouth of rio Goiapi, Cachoeira do Arari, Ilha do Marajó, Cachoeira do Arari, Pará, 08 Sep 1990, M. Assunção. MPEG 4778 (1, 21.9 mm SL), mouth of rio Goiapi, Cachoeira do Arari, Ilha do Marajó, Cachoeira do Arari, Pará, 1 Nov 1991, M. Assunção. MPEG 4988 (4, 17.2-20.4 mm SL), rio Guamá, Mocambo reservoir, Belém, Pará, 16 Sep 1997, N. Bittencourt. MPEG 5710 (8, 14.9-20.9 mm SL), rio Guamá, Mocambo reservoir, Belém, Pará, 19 Mar 1999, F. Pimentel. MPEG 6559 (36, 14.0-31.7 mm SL), igarapé Curuá, Caxiuanã (ECFPn), Melgaço, Pará, 1°42.6'S 51°26.9'W, 6 Oct 2000, L. Montag. MPEG 6563 (3, 17.7-23.8 mm SL), igarapé Curuá, Caxiuanã (ECFPn), Amazonas, Melgaço, Pará, 1°42.6'S 51°26.9'W, 6 Oct 2000, L. Montag. MPEG 6946 (4, 23.5-29.0 mm SL), tributary of rio Cachoeirinha, headquarter, Paragominas, Pará, 3°12'7"S 47°45'6"W, 14 Apr 2003, A. Bezerra & V. Sena. MPEG 6950 (1, 33.9 mm SL), tributary of rio Cachoeirinha, headquarter, Capim, Paragominas, Pará, 3°12'7"S

47°45'6"W, 17 Apr 2003, V. Sena. MPEG 7138 (1, 23.1 mm SL), rio Arienga, São Sebastião, Barcarena, Pará, 1°38'S 48°43'W, 26 Mar 2003, A. Sousa & V. Sena. MPEG 7142 (3, 11.0-16.4 mm SL), stream under transmission line of PA 481, Barcarena, Pará, 1°38'S 48°45'W, 27 Mar 2002, A. Sousa & V. Sena. MPEG 7162 (1, 22.8 mm SL), Vila Arienga, Barcarena, Pará, 26 Mar 2002. MPEG 7172 (1, 22.7 mm SL), igarapé Tauá, near PA 483, Barcarena, Pará, 1°34'S 48°42'W, 25 Mar 2002, V. Sena. MPEG 7181 (9, 14.5-22.0 mm SL), steam at PA 483, near Castanhalzinho, Barcarena, Pará, 1°38'S 48°39'W, 27 Mar 2002, A. Bezerra & V. Sena. MPEG 7182 (1, 38.9 mm SL), igapó Torre, Estação Científica Ferreira Penna, Pará, Melgaço, Pará, 1 Jun 2002, L. Montag. MPEG 7182 (6, 13.3-35.7 mm SL), igarapé Caripiaçu, at road of beach Caripi at Vila dos Cabanos, 1.5 km of beach, Barcarena, Pará, 1°29'S 48°42'W, 22 Mar 2002, V. Sena. MPEG 7183 (1, 23.8 mm SL), igarapé Tauá, tributary of rio Barcarena, under transmission line at PA 481, Barcarena, Pará, 1°39'05"S 48°39'13"W, 23 Mar 2002, A. Bezerra & V. Sena. MPEG 7334 (8, 16.6-27.7 mm SL), igarapé Paraquequara, headquarter of Mineração farm, Paragominas, Pará, 3°16'40"S 47°43'53"W, 14 Dec 2002, A. Bezerra & V. Sena. MPEG 7403 (1, 20.6 mm SL), igarapé Paraquequara, near Monte Santo farm, Paragominas, Pará, 3°16'18"S 47°46'5"W, 13 Dec 2002, A. Sousa & V. Sena. MPEG 7446 (1, 17.4 mm SL), stream tributary of rio Paraquequara, headquarter of Monte Santo farm, near Trinchreira II, Paragominas, Pará, 3°15'18"S 47°45'13"W, 14 Dec 2002, A. Sousa & V. Sena. MPEG 7484 (7, 15.2-26.8 mm SL), igarapé Paraquequara, headquarters of Monte Santo farm, Paragominas, Pará, 3°13'30"S 47°45'09"W, 15 Dec 2002, A. Sousa & V. Sena. MPEG 7490 (1, 23.1 mm SL), Pesqueiro São Raimundo, quadra 32, Almeirim, Pará, 26 Jul 1999, J. Junior. MPEG 7495 (1, 30.4 mm SL), igarapé Paraquequara, headquarters of Mineração farm, Paragominas, Pará, 3°16'40"S 47°43'53"W, 14 Dec 2002, V. Sena. MPEG 8217 (4, 14.9-25.3 mm SL), stream headwater of rio Galego, Mário Célio farm, rio Caete, Bragança, Pará, 29 Apr 2005, R. Silva. MPEG 8223 (2, 32.7 and 34.5 mm SL), stream headwater of rio Galego, Mário Célio farm, rio Caete, Bragança, Pará, 14 Apr 2005, R. Silva. MPEG 8305 (197, 15.0-32.5 mm SL, 2 c&s, 29.7-30.5 mm SL), rio Caripiaçu at road Vila dos Cabanos, near Caripi beach, Barcarena, Pará, 20 Sep 2001, W. Wosiacki & W. Bezerra. MPEG 8366 (7, 15.3-28.3 mm SL), headwater rio Galego, Bairro do Samaumapara, Bragança, Pará, 20 May 2005, R. Silva. MPEG 9413 (9, 11.8-23.5 mm SL), igarapé Anuerazinho, Tomé-Açu, Pará, 2°32'39.2"S 48°16'10.5"W, 1 Jul 2005, A. Sousa. MPEG 9416 (9, 20.4-32.0 mm SL), rio Paranã, Castanhal farm, Ponta de Pedras, Pará, 1°22'9.3"S 48°55'24.7"W, 18 Dec 2003, A. Sousa. MPEG 9418 (3, 12.8-18.4 mm SL), igarapé Arrainha, Tomé-Açu, Pará, 2°25'11.1"S 48°12'13.1"W, 1 Jul 2005, A. Sousa. MPEG 9419 (1, 23.4 mm SL), igarapé Marupaíba, Tomé-Açu, Pará, 2°13'14"S 48°8'14.3"W, 1 Jul 2005, A. Sousa. MPEG 9421 (17, 17.9-32.1 mm SL), rio Puraquequara, Caxiuanã (ECFPn), Melgaço, Pará, 1 Nov 1999, R. Barthem. MPEG 9422 (125, 11.6-28.5 mm SL), rio Caxiuanã, FLONA de Caxiuanã, Melgaço, Pará, 1 Dec 2004, L. Montag. MPEG 9425 (2, 25.8 and 26.5 mm SL), stream headwater of rio Galego, Bragança, Pará, 15 Apr 2005, R. Silva. MPEG 9428 (86, 13.5-24.9 mm SL), rio Caxiuanã, FLONA de Caxiuanã, Amazonas, Melgaço, Pará, 1°45.7'29"S 51°23.9'19"W, 29 Nov 2004, L. Montag. MPEG 9554 (2, 15.4 and 21.4 mm SL), igarapé Anuera-Grande, Tomé-Açu, Pará, 2°30'2.9"S 48°16'52.6" W, 30 Jun 2005, A. Sousa. MPEG 10231 (2, 17.9 and 22.5 mm SL), stream of Balneário Taiassuí, Benevides, Pará, 5 Jun 2006, L. Montag. MPEG 10385 (1, 14.5 mm SL), igarapé

Curuazinho, Melgaço, Pará, 1°43.9'18.1"S 51°26'W, 14 Nov 2003, L. Montag. MPEG 10387 (18, 13.7-30.7 mm SL), igarapé Curuá, rio Pará, Melgaço, Pará, 1°42'51"S 51°27'36"W, 13 Nov 2003, L. Montag. MPEG 10398 (28, 14.2-33.4 mm SL, 2 c&s, 27.4-31.5 mm SL), igarapé Curuazinho, rio Pará, Melgaço, Pará, 1°44'12.9"S 51°25'54"W, 17 Nov 2003, L. Montag. MPEG 10402 (1, 17.1 mm SL), igarapé Moju, Melgaço, Pará, 23 Nov 2003, L. Montag. MPEG 10411 (3, 16.6-21.7 mm SL), stream, Melgaço, Pará, 22 Nov 2003, L. Montag. MPEG 10419 (1, 17.4 mm SL), stream, Melgaço, Pará, 1 Dec 2004, L. Montag. MPEG 10715 (423, 15.6-29.9 mm SL), igarapé FLONA de Caxiuanã, rio Pará, Melgaço, Pará, 19 Nov 2004, L. Montag. MPEG 10716 (238, 12.9-29.8 mm SL), igarapé FLONA de Caxiuanã, rio Pará, Melgaço, Pará, 1°45.6'S 51°25.46'W, 30 Nov 2004, L. Montag. MPEG 11261 (22, 13.9-29.5 mm SL), rio Puraquequara, FLONA de Caxiuanã, Melgaço, Pará, 1°43,9'38"S 51°28,2'9"W, 14 Nov 2003, L. Montag. MPEG 11271 (1, 38.7 mm SL), igapó Torre, Estação Científica Ferreira Penna, rio Pará, Melgaço, Pará, 1 Jun 2002, L. Montag. MPEG 11469 (37, 14.0-30.1 mm SL), igarapé Grande, rio Pará, Melgaço, Pará, 8 Jun 2008, L. Montag. MPEG 11491 (12, 13.2-22.4 mm SL), igarapé Curuá, Melgaço, Pará, 1 Jun 2002, L. Montag. MPEG 12124 (27, 10.1-26.5 mm SL), stream of balneário Taiassuí, Benevides, Pará, 19 Apr 2003, W. Wosiacki. MPEG 12478 (9, 14.4-21.6 mm SL), stream of balneário Taiassuí, Benevides, Pará, 1°23'43.7"S 48°14'57.3"W, 13 Nov 2006, A. Hercos. MPEG 12577 (12, 10.1-22.9 mm SL), igarapé do Gelo, Benevides, Pará, 1°21'41"S 48°14'41"W, 6 May 2006, M. Medonça. MPEG 15557 (1, 25.1 mm SL), rio Ipitinga, Almeirim, Pará, 0°51'13.8"S 53°57'5.8"W, 23 Oct 2008, T. Freitas. MPEG 15586 (11, 14.6-28.0 mm SL), rio Ipitinga, Almeirim, Pará, 0°49'59.2"S 53°56'7.7"W, 23 Oct 2008, T. Freitas. MPEG 15619 (10, 17.8-22.1 mm SL), rio Ipitinga, Almeirim, Pará, 0°49'2"S 53°56'27"W, 25 Oct 2008, T. Freitas. MPEG 15640 (7, 16.0-26.2 mm SL), rio Ipitinga, Almeirim, Pará, 0°49'51.9"S 53°57'19.6"W, 26 Oct 2008, T. Freitas. MPEG 15651 (1, 18.3 mm SL), rio Ipitinga, Almeirim, Pará, 0°49'43.8"S 53°56'53.4"W, 26 Oct 2008, T. Freitas. MPEG 15652 (4, 17.8-24.7 mm SL), rio Ipitinga, Almeirim, Pará, 0°49'43.8"S 53°56'53.4"W, 26 Oct 2008, T. Freitas. MPEG 15673 (7, 17.4-25.1 mm SL), rio Ipitinga, Almeirim, Pará, 0°48'33.7"S 53°55'51.7"W, 27 Oct 2008, T. Freitas. MPEG 15778 (1, 21.7 mm SL), rio Ipitinga, Almeirim, Pará, 0°49'24.2"S 53°55'43.4"W, 30 Oct 2008, T. Freitas. MPEG 17822 (10, 14.1-20.2 mm SL), igarapé Taiassuí, Benevides, Pará, 1°23'46"S 48°14'59.4"W, 1 Sep 2009, W. Wosiacki. MPEG 18254 (2, 21.4 and 23.3 mm SL), igarapé Ponte Quebrada, rio Guamá, Ourém, Pará, 1°32'17.5"S 47°05'2.9"W, 15 Nov 2009, B. Pamplona. MZUSP 23064 (129, 15.3-38.8 mm SL), alegre, 15 km NE of Marapanim, black water stream, Marapanim, Pará, 0°43'S 47°40'W, 12 Sep 1965, Expedição do Departamento de Zoologia. MZUSP 101948 (7, 19.7-24.6 mm SL), rio Caracuru and stream without name, affluent of rio Caruru, near Vila Santa Maria, rio Jari, Monte Dourado, Pará, 0°54'55"S 52°34'39"W, 10 Oct 2007, M. Carvalho *et al.* MZUSP 105746 (18, 10.0-22.2 mm SL), igarapé Mocajuteua, affluent of rio Moju, rio Tocantins, Igarapé Miri, Pará, 1°57'51"S 48°54'18"W, 9 Apr 2010, M. Marinho & D. Bastos. MZUSP 105756 (22, 15.5-31.9 mm SL), igarapé Lagoa Azul, affluent of rio Tauá, Santo Antônio do Tauá, Pará, 1°9'6"S 48°6'35"W, 2 Apr 2010, M. Marinho & D. Bastos. MZUSP 105763 (2, 21.9 and 24.4 mm SL), clear water igarapé at Bacuriteua, affluent of rio Marapanim, Pará, 0°37'36"S 47°40'45"W, 3 Apr 2010, M. Marinho & D. Bastos. MZUSP 105770 (130, 16.6-40.1 mm SL, 6 c&s, 12.8-31.4 mm SL, 2 mus, 21.7-

33.7 mm SL), stream and lagoon, headquarters of Lagoa Azul farm, Vigia, Pará, 0°56'8"S 48°4'38"W, 27 Mar 2010, M. Marinho *et al.* MZUSP 105776 (14, 19.9-34.9 mm SL), rio igarapé-Açú, affluent of rio Guamá, Bujaru, Pará, 1°37'12"S 48°3'10"W, 4 Apr 2010, M. Marinho & D. Bastos. MZUSP 105780 (4, 27.5-29.8 mm SL), stream in reservoir at road near Caripi, rio Tocantins, Barcarena, Pará, 1°29'58"S 48°42'08"W, 9 Apr 2010, M. Marinho & D. Bastos. MZUSP 105799 (7, 12.7-29.8 mm SL), stream affluent of rio Marapanim, Marapanim, Pará, 0°42'46"S 47°43'13"W, 4 Apr 2010, M. Marinho & D. Bastos. MZUSP 105810 (1, 25.4 mm SL), igarapé do Tubo, affluent of rio Mojuim, Vigia, Pará, 1°4'49"S 48°1'55"W, 2 Apr 2010, M. Marinho & D. Bastos. MZUSP 106100 (6, 11.4-37.6 mm SL), stream of balneário Olho no Olho, Ilha do Marajó, Salvaterra, Pará, 0°50'51"S 48°34'1"W, 10 Apr 2010, M. Marinho & D. Bastos. MZUSP 106153 (8, 23.2-31.3 mm SL), stream at PA 318, affluent of rio Marapanim, Marapanim, Pará, 0°42'30"S 47°43'42"W, 3 Apr 2010, M. Marinho & D. Bastos. USNM 88272 (4, 20.2-34.6 mm SL), Maranhão, 1926, G. Ormaechea. USNM 203574 (3, 20.6-26.0 mm SL), small stream in Santa Isabel do Pará, near Belém, Pará, 18 Jul 1935, H. Cerron. ZMB non-catalogued (5, 31.9-39.4 mm SL), Ilha do Arapiranga, Pará, Broderson, 1928.

Coastal drainages, Guyana. CAS 227312 (1, 31.8 mm SL), rio Demerara in Kumaka, 24 Sep 1908, C. Eigenmann. FMNH 85373 (20, 22.8-30.6 mm SL), igarapé Dakara, upstream Luis Chung's Compound, rio Demerara, 6 Aug 1975, Thomerson, Hicks & Taphorn. MHNH 2002-3517 (1, 42.6 mm SL), "collection de Guyana". MHNH 2002-3558 (4, 37.7-42.1 mm SL), "collection de Guyana". USNM 345977 (1, 34.9 mm SL), rio Berbiche drainage, near Dubulai Ranch, KT-2, 30 Jun 1996, T. Bergquist. USNM 345978 (7, 13.1 mm SL), Kaikotin creek, rio Berbiche drainage near Dubulai Ranch, 21 Jun 1996, T. Bergquist.

Coastal drainages, French Guiana. MCZ 54406 (5, 14.3-24.7 mm SL), Kaw, 12 Jul 1979, R. Mittermier *et al.* MHNG 2200.013 (10 of 15, 15.1-27.9 mm SL), Cabassan, Cayenne. MHNG 2200.036 (6, 23.9-42.3 mm SL), Crique "Magan", Moy. Comté, rio Comté, 30 Aug 1978, P. Lamarque. MHNG 2200.037 (2, 30 and 37.6 mm SL), stream affluent of rio Approuague, 1925, C. Ternetz. MHNG 2615.099 (3, 13.1-17.6 mm SL), rio Sinnamary, crique Alaparoubo, 31 Aug 1995, D. Ponton & S. Mérioux. MHNG 2616.002 (3, 27.3-44.5 mm SL), rio Synnamary, right affluent upstream Saut Dalles, Ponton & Mérioux, 27 Oct 1995. MHNG 2647.005 (16, 30.7-39.8 mm SL), Crique Grillon, affluent of rio Orapu, rio Mahury drainage, Roura, 4°16'48.1"N 52°27'4.4"W, 07 Nov 2003, C. Weber *et al.* MNHN 2681.094 (1, 37.3 mm SL), stream at forest, opposite to Roche-Mon-Père, about 1 hour downstream Camopi by boat and 15 min downstream crique Sikini, rio Oiapok, St Georges-Oyapok, 3°16'56.3"N 52°12'36.6"W, 6 Nov 2006, Fisch-Muller *et al.* MHNG 2724.014 (1, 43.6 mm SL), stream at left bank of before crique Balanfois, rio Arrataye, rio Approuague basin, 21-22 Nov 2010, Montoya-Burgos *et al.* MNHN 2001.0267 (7, 17.0-71.9 mm SL), rio Synnamary, Cayenne, Ponton & Merigoux, 1996. MNHN 2001.0268 (3, 27.0-34.2 mm SL), Synnamary, Cayenne, Ponton & Merigoux, 1995. MNHN 2001.1534 (8, 20.1-36.5 mm SL), rio Oiapoque, Cayenne, Dec 1986, Planquette *et al.* MNHN 2001.1879 (7, 24.8-40.1 mm SL), Crique Japigny, rio Approuague, Cayenne, 17 Nov 1988, Boujard *et al.* MNHN 2002-0863 (1, 37.5 mm SL), crique Litany, "nivraie de Boum-boum au niveau de son abates", Antécume Pata, St. Laurent du Maroni, 20 Dec 2001, Fermon *et al.* MHNH 2003.0093 (8, 18.4-28.4 mm SL), Crique downstream Antécume Pata, rio Litany, rio Maroni drainage, Commergnat *et al.*, 25 Oct 2002.

MHNH 2003.2520 (11, 22.3-40.5 mm SL), rio Approuague, Decouverte, Cayenne, 10 Nov 2003, Weber. MNHN 2004.0355 (1, 34.4 mm SL), rio Serpent, rio Maroni drainage, Nov 2003, Ecobios. MNHN 2004.3030 (5, 18.6-24.5 mm SL), rio Leblond, rio Sinnamary drainage, Trinite, 14 Nov 2001. MNHN 2004.3110 (11, 18.7-32.3 mm SL), rio Leblond, rio Synnamari drainage, Trinite, 13 Nov 2001, Brenm. MNHN 2004.3146 (14, 14.7-29.6 mm SL), stream, rio Ouanary, rio Oiapoque basin, Cayenne, 4°5'49"N 51°57'54"W, 21 Oct 2004, Vigouroux, Roland & Nandrin. MNHN 2011.0305 (2, 32.8 and 37.0 mm SL), Aya, rio Sinnamary drainage, Trinité massif, 4°36'36"N 53°21'32"W, Aug 2009, Melki. ZMA 106.137 (2, 34.6 and 37.1 mm SL), side of Marowijne, 10 Apr 1969, H. Nijssen.

Coastal drainages, Surinam. ANSP 189192 (1, 31.6 mm SL), Coropinae Creek, rio Suriname drainage, Republiek, 5°29'57"S 55°12'52"W, 28 Apr 2007, M. Sabaj & P. Willink. MHNG 1554.021 (7, not measured), small stream at forest, Brownsberg National Park, Oct 1976, P. De Rham. MHNG 2200.034 (10 of 15, 12.7-40.4 mm SL), Mooi Wana, crique near bridge at road Albina-Moengo, Maroni, Mar 1962, H. Pijpers. USNM 226869 (8, 17.6-21.8 mm SL), Lana Creek, near 4 Km upstream from intersection West of rio Corantijn, Nickerie, 5°28'N 57°15'W, 7 Sep 1980, R. Vari *et al.* USNM 226873 (1, 27.6 mm SL), creek without name, Corantijn, Nickerie, 5°32'N 57°10'W, 15 May 1980, H. Madarie. USNM 226878 (1, 21.2-31.8 mm SL), Koekwie Kreek, Corantijn, Nickerie, 5°31'N 57°10'W, 15 May 1980, H. Madarie. USNM 311229 (4, 20.5-34.0 mm SL), edge of bay in blackwater creek at savanna, ¾ miles West of Islands Bosbeheer, headquarter at Zanderij, 43 Km South of Paramaribo, Pará, 14 Apr 1969, D. Dunham. USNM 311233 (4, 21.8-27.9 mm SL), black water creek, Islands Bosbeheeri, headquater at Zanderij, 43 km, sul de Paramaribo, 10 Apr 1969, D. Dunham. USNM 332108 (1, 30,7 mm SL), Berlyn, Pará creek, Pará, 14 Sep 1969, H. Pypers. USNM 409768 (4, 27.1-34.1 mm SL), forest stream right tributary of upper rio Paloemeu, upstream of 50 m high waterfall, 2°27'22"N 55°37'35"W, 16 Mar 2012, J. Mol & W. You. ZMA 101.937 (28, 13.5-35.3 mm SL), Onverwacht, Paran-Zandery road, Oct 1956, J. Yanderkamp. ZMA 101.943 (13, 12.5-36.7 mm SL), Zandery, Bosbivak, 22 Apr 1956, J. Komp. ZMA 104.197 (15, 18.8-36.0 mm SL), small creek at woodzuter camp, foot of Albina Hill, Mar 1962, H. Pijpers. ZMA 104.288 (34, 15.1-35.6 mm SL), Mooi Wana, crique near bridge of Albina-Moengo road, Maroni, Mar 1962, H. Pijpers. ZMA 105.511 (10, 13.4-35.5 mm SL), "Nordelijke tak v/d Tapoeripa-kreek, ca 3 km ten N van Brokopondo", 13 Nov 1966, H. Nijssen. ZMA 105.694 (16, 21.3-36.4 mm SL), "Jenjeekreek a/d rechteroever u/d rio Suriname, 7.5 km ten North van Botopasi", 21 Mar 1967, H. Nijssen. ZMA 105.829 (1, 25.7 mm SL), "Jenjeekreek n/d rechteroever v/d rio Nickerie, 12 km (geografisch) te W2W v/d stondansi \$ val distr Nickerie", 5 Apr 1967, H. Nijssen. ZMA 106.105 (46, 16.3-39.7 mm SL), "Marowijne (=Gran) creek gestuwd, geografisch ca 53.5 km ten 2. van Afobaka's stuwdam, ca 80 cm. Diep, visqif. Brokopondo, rotend blad", 25 May 1966, H. Nijssen. ZMA 106.107 (13 of 20, 27.1-39.5 mm SL), "Marowijne (=Gran) kreek ca. 58 km ten 2 van Afobaka's stuwdam (distr. Brokopondo)", 9 Jun 1966, H. Nijssen. ZMA 106.113 (6, 26.5-39.5 mm SL), "Marowijne (=Gran) kreek ca. 60 km (geografisch) ten 2 van Afobaka's stuwdam (gestuwd)", Brokopondo, 8 Jun 1966, H. Nijssen.

Rio Orinoco basin. Venezuela. MBUCV 12451 (1, 21.6 mm SL), caño Ajies, affluent of rio Turuepano, at comunidade de Ajies, Sucre, 8 Dec 1980, J. Baskin & O. Castillo. MHNLS 14272 (96, 16.6-25.0 mm SL),

caño Ibaruma, caño Guaramo, near headwaters, Serrania de Imataca, Antonio Dias, Delta Amacuro, 8°10'N 60°47'W, 22 Feb 1995, V. Ponte. MHNLS 14278 (46, 12.1-25.1 mm SL), caño Dorina, affluent of rio Araguaio, Laguna Morichal Ataibo, comunidade Dorina, Antonio Dias, Delta Amacuro, 8°10'N 60°47'W, 22 Aug 1991, V. Ponte, W. Wilbert & Aquilino. MHNLS 14279 (32, 16.9-24.7 mm SL), caño Capure, caño Jotajana, Pedernales, Delta Amacuro, 9°59'N 62°15'W, Apr 1997, V. Ponte. MHNLS 14285 (49, 16.4-25.5 mm SL), caño Ibaruma, caño Guaramo near cabeceira, mouth of rio Orinoco, Serrania de Imataca, Antonio Dias, Delta Amacuro, 8°10'N 60°47'W, 2 Mar 1995, V. Ponte. MHNLS 14286 (3, 14.5-17.4 mm SL), caño Pagayo, mouth of rio Grande, near Isla Pagayo, Antonio Dias, Delta Amacuro, 8°36'N 60°57'W, 8 Mar 1995, V. Ponte. MHNLS ex 9558 (23, 18.0-28.7 mm SL), caño Guiniquina, Tucupita, Delta Amacuro, 9°29'N 60°59'W, 28 Apr 1992, V. Ponte. MHNLS ex 14284 (10, 16.8-24.8 mm SL), caños El Toro and Acoima, near base camp, first raudal, Serrania de Imataca, Antonio Dias, Delta Amacuro, 8°30'N 61°34'W, 22 Nov 1993, V. Ponte & O. Lasso. SMF 21381 (2, 36.4-37.1 mm SL), "Zuchttier", South America, Tropicarium ded, 1961.

Coastal drainages, Venezuela. MBUCV 12440 (69, 14.0-22.3 mm SL), small caño at caño Ajies, approximately 3 km South of comunidade de Ajies, Sucre, 8 Dec 1980, J. Baskin & O. Castillo. MHNLS 12458 (12, 18.3-30.4 mm SL), quebrada la Guacharaca, affluent of rio Cachipo, Punceres, Monagas, 9°55'11"N 63°6'20"W, 7 May 1997, L. Lasso, V. Ponte & D. Figueira. MHNLS ex 12459 (2, 21.5 and 28.2 mm SL), rio Cachipo, setor Sabana II, Alcantarilla N 3, Punceres, Monagas, 9°55'11"N 63°6'20"W, 7 May 1997, L. Lasso, V. Ponte & D. Figueira. MHNLS 12460 (1, 21.3 mm SL), rio Guarapiche, affluent of rio San Juan, South of Santo Antonio de Maturin, Maturin, Monagas, 9°53'53"N 63°1'10"W, 8 May 1997, L. Lasso, V. Ponte & D. Figueira. MHNLS 12461 (16 of 17, 16.2-21.6 mm SL), floodplain at road Zamora camp, near Cachipo, Maturin, Monagas, 9°56'1"N 63°1'42"W, May 1997, L. Lasso, V. Ponte & D. Figueira. MHNLS 12463 (2, 21.0 and 22.6 mm SL), rio Cachipo, Reserva Floresal Guarapiche, Maturin, Monagas, 9°57'8"N 63°0'59"W, 8 May 1997, L. Lasso, V. Ponte & D. Figueira.

COPELLA COMPTA (MYERS, 1927)

Figures 37, 39-41; Tables 3 and 4

Copeina compta Myers, 1927: 111 [Type locality: Brazil, creek above São Gabriel rapids, rio Negro].—Fowler, 1948: 344 [literature compilation].—Böhlke, 1953: 23 [type catalog].—Zarske (2011): 14 [cited].

Copella compta.—Myers, 1956: 12 [new combination].—Géry, 1963: 25 [comparison with *C. vilmae*].—Géry, 1977: 147 [comparison with *Copella vilmae*, unnumbered figure of pg. 147].—Weitzman & Weitzman, 2003: 242 [literature compilation].—Oyakawa & Netto-Ferreira, 2007: 64 [literature compilation].—Wallace, 2002: 134, fig. 97 [listed].



Figure 39. Holotype of *Copeina compta*, male, CAS 60496, 52.0 mm SL, rio Negro at São Gabriel da Cachoeira, Amazonas, Brazil.

Diagnosis. *Copella compta* can be distinguished from all congeners, except *C. vilmae*, by having 16-18 scales in the first longitudinal scale row (*vs.* 13-15), and further by having 26-27 scales in the fourth longitudinal scale row (*vs.* 23-25). Males of *C. compta* can be distinguished from the males of *C. vilmae* by the absence of rows of conspicuous dark scales irregularly arranged on body (*vs.* presence); females of *C. compta* can be distinguished from the females of *C. vilmae* by the absence of a dark longitudinal band on body (*vs.* presence). *Copella compta* is the largest

species of the genus, the males reaching 68.9 mm SL and the females 48.1 mm SL (*vs.* less than 55.5 mm SL and 44.2 mm SL, respectively, in the congeners).



Figure 40. *Copella compta*, MZUSP 9162 (A) male, 68.9 mm SL, (B) female, 40.3 mm SL, São Gabriel da Cachoeira, Amazonas, Brazil.

Description. Morphometrics in Tables 3 and 4. Largest examined male 68.9 mm SL, female 48.0 mm SL. *Copella compta* is the largest species of the genus. Greatest body depth located at vertical through pelvic-fin origin. Body cylindrical, slightly compressed laterally. Dorsal profile of body straight or slightly convex from tip of snout to end of supraoccipital, straight or slightly convex from that point to dorsal-fin origin, posteroventrally inclined along dorsal-fin base and straight along caudal peduncle. Ventral profile of body convex from anterior tip of dentary to the vertical through anterior margin of orbit, straight from that point to the vertical through pectoral-fin origin, straight to slightly convex from that point to pelvic-fin origin, straight from pelvic-fin origin to anal-fin origin, posterodorsally inclined along anal-fin base and straight along caudal peduncle.

Mouth upturned. Premaxillary teeth in one row, with 20 (2), 21 (1) teeth, decreasing in size laterally. Number of maxillary teeth sexually dimorphic, 14 (1) in males, and 5 (1) or 8 (1) in females, decreasing in size posteriorly, especially in males. Dentary teeth in two rows, outer with 10 (1), 11 (1), 12 (1), increasing in size laterally, inner with 36 (2), 37 (1) teeth, decreasing in size laterally.

Dorsal fin with ii, 8 (49)* rays, second and third branched rays longer. Pectoral fin with i, 8 (2), 9 (20)*, or 10 (24) rays, first three branched rays longer. Pelvic fin with i, 7 (49)*, rays, third branched ray longest. Anal fin with iii (4), 8 (1), or 9 (49)* rays, fourth and fifth branched rays longer. Caudal fin with i, 7 (1) or 8 (47) rays in upper lobe, first and second branched rays longer, and 6 (1) or 7 (47)*, i rays in lower lobe, second and third branched rays longer. Upper caudal-fin lobe longer than lower one.

Predorsal scales 17 (16), 18 (32)*, or 19 (1), in one series. First longitudinal scale row with 16 (3), 17 (32)*, or 18 (12) scales. Fourth longitudinal scale row with 26 (16), 27 (33)* or 28 (1) scales. Longitudinal scale rows between dorsal-fin origin and pelvic-fin origin 6 (50)*. Longitudinal scale rows between dorsal-fin origin and anal-fin origin 5 (50)*. Circumpeduncular scale rows 10 (50)*. Total number of vertebrae 36 (2)* and 37 (11).

Table 3. Morphometrics of *Copella compta*. Holotype of *Copeina compta* CAS 60496, paratypes of *Copeina compta* CAS 60497 (7), MCZ 31568 (3) MHNG 2200.018 (1), SU 18070 (5) and non-type material AMNH 231274 (9), INPA 9162 (23), and MZUSP 27457 (2), n = number of specimens, SD = Standard deviation. Range does not include the holotype.

	<i>Copeina compta</i> Holotype	n	Range			Mean	SD
Standard length (mm)	50.6	50	23.6	-	68.9	39.6	10.7
Percents of standard length							
Body depth	16.9	50	13.8	-	19.3	16.5	1.2
Dorsal- to caudal-fin origin	31.9	50	30.5	-	35.5	32.7	1.3
Snout to dorsal-fin origin	68.4	50	64.4	-	69.9	67.8	1.2
Snout to pectoral-fin origin	21.7	50	19.3	-	24.4	22.3	1.2
Snout to pelvic-fin origin	47.2	50	45.7	-	50.9	48.4	1.1
Snout to anal-fin origin	71.2	50	67.3	-	73.1	70.7	1.1
Pectoral- to pelvic-fin origin	25	50	24.5	-	28.8	27.0	1.1
Pelvic- to anal-fin origin	24.1	50	20.5	-	25.3	23.0	1.1
Pectoral-fin length males	22.7	21	16.1	-	23.9	20.6	2.0
Pectoral-fin length fem/imm	-	27	18.4	-	23	19.7	0.9
Pelvic-fin length males	33.8	23	14.0	-	33.8	23.9	5.5
Pelvic-fin length fem/imm	-	28	16.6	-	26.3	20.7	2.1
Dorsal-fin length males	35.7	22	18.4	-	40.9	29.9	5.7
Dorsal-fin length fem/imm	-	27	23.1	-	33.9	27.3	2.8
Anal-fin length males	21.6	23	15.2	-	21.6	17.9	1.4
Anal-fin length fem/imm	-	28	16.3	-	19.1	17.5	0.7
Anal-fin base length	9.2	50	6.8	-	10.0	8.3	0.6
Caudal peduncle depth	9.2	50	7.4	-	9.7	8.8	0.5
Caudal peduncle length	19.7	50	18.4	-	24.0	20.9	1.3
Head length	22.5	50	19.9	-	24.9	23.2	1.1
Percents of head length							
Eye diameter	30.0	49	27.3	-	40.3	33.5	3.1
Snout length	27.1	50	25	-	33.6	28.5	2.0
Interorbital distance	34.9	49	28.6	-	37.8	34.1	1.8
Upper jaw length	-	50	26.8	-	39.1	33.7	2.0

Table 4. Meristics of the holotype of *Copeina compta* CAS 60496.

	<i>Copeina compta</i>
	Holotype
Scales lateral series	27
Longitudinal series dorsal-pelvic	6
Longitudinal series dorsal-anal	5
First longitudinal scale row	17
Predorsal scales	18
Circumpeduncular scales	10
Caudal-fin rays	-
Dorsal-fin rays	ii8
Branched anal-fin rays	iii9
Pectoral-fin rays	i9
Pelvic-fin rays	i7

Color in alcohol. Overall ground coloration of body beige to brown. Dark stripe extending from anterior tip of dentary to posterior tip of opercle. Dorsal portion of body dark. Thin dark stripe at predorsal region. Dorsolateral scales on body with dark posterior border, forming a reticulate pattern. Males with dark longitudinal band on fourth and fifth longitudinal scale rows, extending from opercle to end of caudal peduncle or only conspicuous behind opercle, fading posteriorly, with anterior portion of scales of posterior portion of body dark. Females without dark band on body, the anterior portion of scales of third to sixth longitudinal series faint dark. Ventral region of body clear. Dorsal procurrent caudal-fin rays hyaline in males and females (probably as result of poor preserved material), ventral procurrent caudal-fin rays dark in males and females. Females and juveniles with inconspicuous dark spot at base of upper caudal-fin lobe. Dorsal fin with black round spot. Pectoral, pelvic, anal and caudal fins hyaline; distal profile of pelvic and anal fins and tip of largest dorsal-fin rays frequently dark (Figs. 39 and 40).

Color in life. Not known.

Sexual dimorphism. Males longer than females. Males with more maxillary teeth than females (see description above). Pectoral, pelvic, dorsal and anal fins only slightly longer in males than in females (Fig. 41). Tip of pectoral fin reaching to the vertical through 12th scale of first longitudinal row in males, and through ninth scale in females. Tip of adpressed pelvic fin reaching to vertical through bases between first and four branched anal-fin rays in males, and to anal-fin origin in females. Tip of adpressed dorsal fin reaching up to caudal-fin base in males, and approximately to two-third length of caudal peduncle in females. Upper caudal-fin lobe longer than lower, especially in males. Color pattern differences described in “Color in alcohol” section.

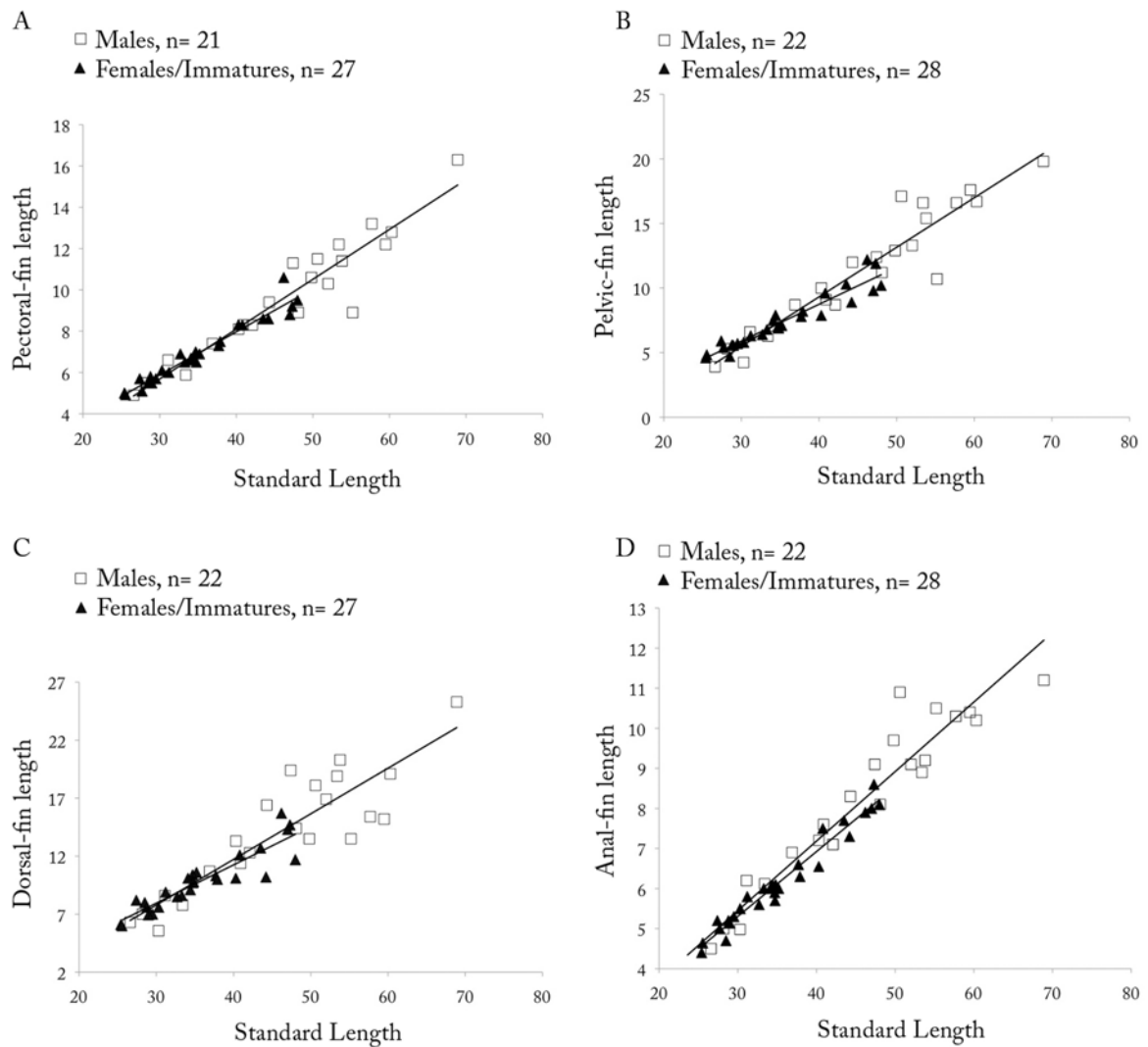


Figure 41. *Copella compta*, pectoral-, pelvic-, dorsal- and anal-fin length as function of SL by sex.

Distribution. Upper rio Negro upstream São Gabriel da Cachoeira, Brazil and Venezuela (Fig. 37).

Remarks. Myers originally described *Copeina compta* based on the holotype (“type”) IU 17693 (now CAS 60497) (Fig. 39) and two lots of paratypes IU 17694 (now CAS 60497) and MCZ 31568, with no specification of the number of specimens in each lot. The lot SU 18070 has the

same data as those cited by Myers and the corresponding specimens are considered paratypes, probably splitted from the original lots after the description. SU 18070 had originally 11 specimens (Böhlke, 1953) but now there are nine specimens in alcohol (five were analyzed), one c&s, and one considered missing. During this study, it was found that the missing paratype is MHNG 2200.038.

Zarske & Géry (2006) cited one specimen of *Copella compta* from near Barcelos (fig. 24) and one living specimen without locality (fig. 25). Although the meristic data given match with those of *C. compta*, this locality was not recovered in this study. The identification could not be confirmed.

Citations of *Copella compta* by Bogotá-Gregory & Maldonado-Ocampo (2006) and Maldonado-Ocampo *et al.* (2008) for rio Amazonas at Colombia could not be confirmed.

MATERIAL EXAMINED

Type material

CAS 60496 [ex IU 17693] (holotype of *Copeina compta*, 50.6 mm SL), CAS 60497 [ex IU 17694] (17 paratypes of *Copeina compta*, 18.3-37.6 mm SL), MCZ 31568 (3 paratypes of *Copeina compta*, 23.6-39.1 mm SL), MHNG 2200.38 (1 paratype of *Copeina compta*, 33.3 mm SL), SU 18070 (9 paratypes of *Copeina compta*, 21.4-55.7 mm SL, 1 c&s), creek above São Gabriel Rapids, rio Negro, Amazonas Brazil, C. Ternetz, 28-30 Jan 1925.

Non-type material

Rio Amazonas basin, Brazil. INPA 9162 (37, 16.9-68.9 mm SL, 4 c&s, 17.0-50.8 mm SL), stream at camp, rocks, Morro dos Seis Lagos, 23 Mar 1990, J. Zuanon, *et al.* LBP 7076 (34, 14.9-41.4 mm SL), affluent of igarapé Miua, rio Negro, São Gabriel da Cachoeira, Amazonas, 0°6.2'S 66°53.7'W, Oliveira *et al.*, 14 Aug 2008. MZUSP 27457 (2, 28.4 and 29.4 mm SL), Morro dos Seis Lagos, São Gabriel da Cachoeira-Cucui, rio Negro, São Gabriel da Cachoeira, Amazonas, 0°7'S 67°5'W, 16 Nov 1982, L. Portugal. *Venezuela.* AMNH 231274 (20, 16.9-59.5 mm SL), tributary of rio Mawarinuma, at Serra da Neblina base camp, Amazonas, 0°55'N 66°10'W, 7-11 Feb 1984, C. Ferraris, W. Buck & R. Royero-I. AMNH 231273 (11, 12.0-28.0 mm SL), tributary of rio Mawarinuma, at Serra da Neblina base camp, Amazonas, 0°55'N 66°10'W, 5 Feb 1984, C. Ferraris, W. Buck & H. Olivaria. AMNH 231275 (9, 13.0-46.0 mm SL), tributary of rio Mawarinuma, at Serra da Neblina base camp, Amazonas, 0°55'N 66°10'W, 10 Feb 1984, C. Ferraris & R. Royero-I.

COPELLA EIGENMANNI (REGAN, 1912)

Figures 38, 42-47; Tables 5 and 6

Copeina eigenmanni Regan, 1912: 393 [in part, from Bogotá; type locality: Bogotá (Colombia)].—Eigenmann, 1922: 233 [specimens from Bogotá placed as synonym of *Copeina* (= *Copella*) *metae*].

Copeina metae Eigenmann, 1914: 229 [type locality: Barrigona, rio Meta, Colombia].—

Eigenmann, 1922: 233: pl. XX, fig. 3 [*Copeina* (= *Copella*) *eigenmanni* from Bogotá placed as synonym].—Myers, 1927: 111 [comparison with *C. compta*].—Fowler, 1945: 2 [rio Meta at Villavicencio; listed].—Böhlke, 1953: 23 [type catalog].

Copella metae.—Géry, 1977: 143 [new combination].—Taphorn, 1992: 465, figs. 295 and 296 [rio Aguaro; brief description].—Weitzman & Weitzman, 2003: 242 [literature compilation; comments on misidentifications regarding *C. nigrofasciata* (= *Copella stigmaseion*)].—Zarske & Géry, 1997: 13, fig. 5 [photo of one paratype SU 24656, wrong labeled as “Syntypus. CAS 124 656”; comparison with *Pyrrhulina zigzag*].—Netto-Ferreira, 2006: 20 [phylogenetic analysis of Lebiasinidae].—Zarske & Géry, 2006: 44 [identification key].—Galvis *et al.*, 2007a: 166, fig. 194 a e b [streams near Villavicencio and Puerto Gaitán; brief description].—Maldonado *et al.*, 2006: 122 [rio Tomo, Colombia; listed].—Maldonado *et al.*, 2008: 183 [literature compilation].—Urbano-Bonilla *et al.*, 2009: 158 [Casanare basin, Colombia; listed].—Netto-Ferreira, 2010: 331 [phylogenetic analysis of Lebiasininae].

Copella compta.—Netto-Ferreira, 2006: 20 [phylogenetic analysis of Lebiasinidae].—Galvis *et al.*, 2007b: 180, fig. 214 [rio Vaupés and caño Mitúceño surrounding Mitú; misidentification; brief description].

Copella cf. compta.—Galvis *et al.*, 2007a: 165, fig. 193 [near Puerto Inírida; brief description].—
Netto-Ferreira, 2010: 331 [phylogenetic analysis of Lebiasininae].—

Copella eigenmanni.—Zarske, 2011: 29, figs. 21-24 [lectotype designation from Bogotá; redescription; taxonomic notes].



Figure 42. Lectotype of *Copeina eigenmanni*, BMNH 1869.7.25.6 male, 37.7 mm SL, Bogotá (= probably rio Meta), Colombia.



Figure 43. Holotype of *Copeina metae*, CAS 60494, male, 28.8 mm SL, Barrigona [= Puerto Barrigón], rio Meta, Colombia.

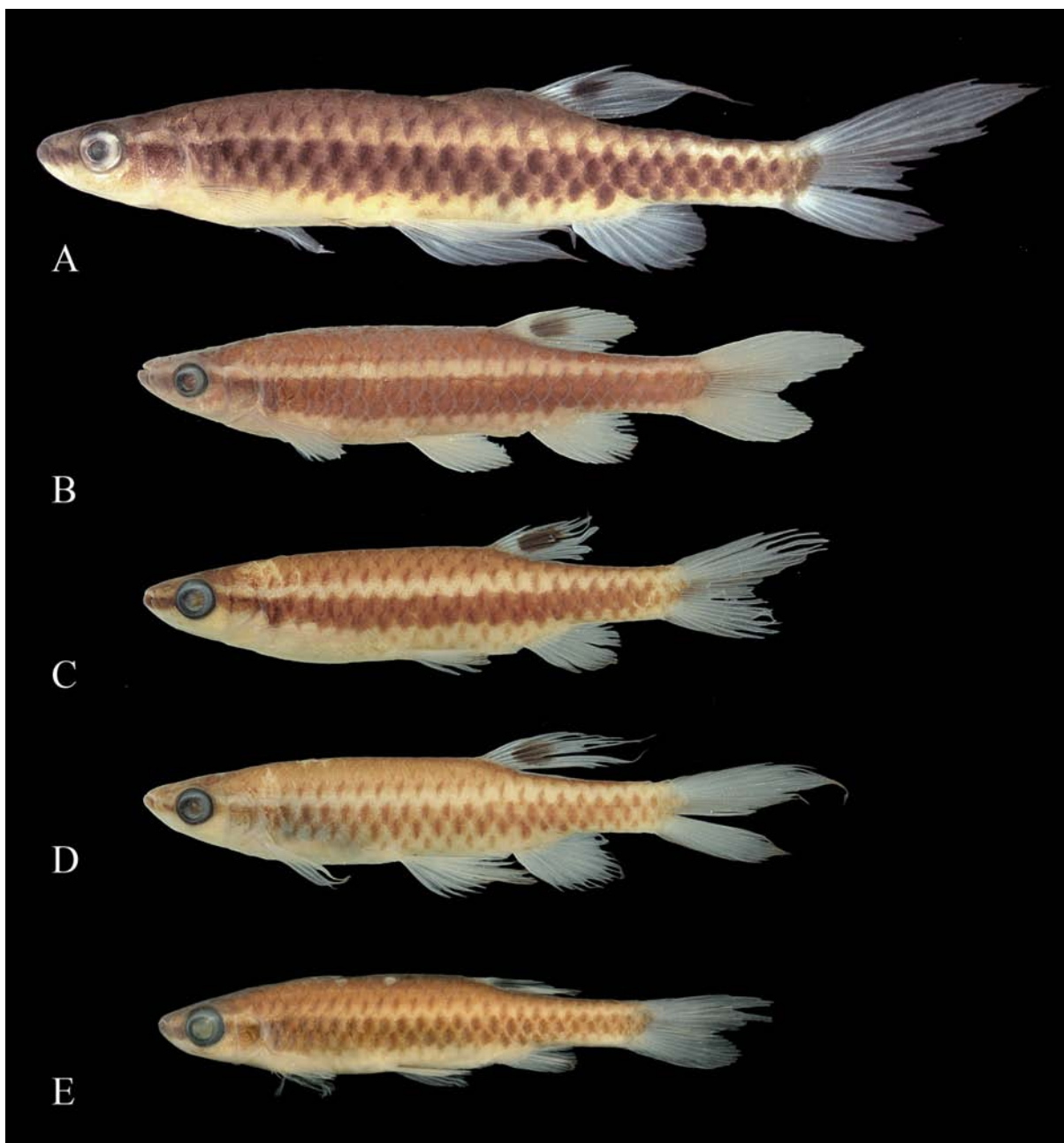


Figure 44. *Copella eigenmanni*: (A) male, MZUSP 81443, 50.5 mm SL, rio Tiquié, Amazonas, Brazil, (B) male, ICNMHN 1386, 37.5 mm SL, Maya, rio Meta, Colombia, (C) male ICNMHN 942, 32.3 mm SL, (D) male, ICNMHN 942, 36.3 mm SL, Cumaral, rio Meta, Colombia, (E), female, MZUSP 81143, 34.3 mm SL, rio Tiquié, Amazonas, Brazil.



Figure 45. *Copella eigenmanni*, live specimen, MZUSP 81443, male, approximately 50 mm SL, rio Tiquié, Amazonas, Brazil. Photo: A. Cabalzar & F. Lima.



Figure 46. *Copella eigenmanni*, live specimen, MZUSP 81443, juvenile, rio Tiquié, Amazonas, Brazil. Photo: Photo: A. Cabalzar. & F. Lima.

Diagnosis. *Copella eigenmanni* can be distinguished from all congeners by having the middle caudal-fin rays dark (*vs.* hyaline or with a small dark patch at base of middle caudal-fin rays on *Copella stigmatemion*). Additionally, it can be distinguished from *C. arnoldi* by having the procurrent caudal-fin rays black (*vs.* hyaline), from *C. compta* by having 14-15 scales on the first longitudinal scale row (*vs.* 16-17), from *C. nattereri* by the absence of a black spot on the

posterior portion of each body scale (*vs.* presence), from *C. stigmatsemion* by the absence of a series of conspicuous clear spot on each scale of the fourth longitudinal scale row (*vs.* presence), from males of *C. vilmae* by the absence of discontinuous longitudinal series of dark scales on body (*vs.* continuous), and from females of *C. vilmae* by the absence of a small dark spot at the base of the upper caudal-fin lobe (*vs.* presence).

Description. Morphometrics in Tables 5 and 6. Largest examined male 56.4 mm SL, female 44.2 mm SL. Greatest body depth located slightly anterior to vertical through pelvic-fin origin. Body cylindrical, slightly compressed laterally. Dorsal profile of body straight to slightly convex from tip of snout to the end of supraoccipital, straight to slightly convex from that point to dorsal-fin origin, posteroventrally inclined along dorsal-fin base, and straight along caudal peduncle. Ventral profile of body convex from the anterior tip of dentary to the vertical through anterior margin of orbit, straight from that point to the vertical through pectoral-fin origin, slightly convex from that point to pelvic-fin origin, straight from pelvic-fin origin to anal-fin origin, posterodorsally inclined along anal-fin base and straight along caudal peduncle.

Mouth upturned. Premaxillary teeth in one row, with 14 (1), 15 (1), 17 (2), 19 (1), 20 (2), 21 (1) teeth, decreasing in size laterally. Maxillary teeth sexually dimorphic, 13 (3), 14 (1), 20 (1) teeth in males, 7 (2), 9 (1) teeth in females, decreasing in size laterally, especially in males. Dentary teeth in two rows, outer with 9 (2), 10 (2), 11 (1) teeth, 12 (2), 13 (1) increasing in size laterally, inner with 24 (1), 25 (1), 26 (1), 27 (1), 28 (1), 30 (1), 33 (1), 42 (1) teeth, decreasing in size laterally.

Dorsal fin with ii, 7 (1) or 8 (89)*, rays, second and third branched rays longer. Pectoral fin with i, 8 (6), 9 (57)*, 10 (25), or 11 (1) rays, second and third branched rays longer, not reaching pelvic-fin origin. Pelvic fin with i, 7 (89)* or 8 (2) rays, third or fourth branched rays

longer. Anal fin with iii (3), 9* (91) rays, third and fourth branched rays longer. Caudal fin with i, 7 (15), 8 (70), or 9 (1) rays in upper lobe, first three branched rays longer, and 6 (4), 7 (81), or 8 (1), i, rays in lower lobe, second and third branched rays longer. Upper caudal-fin lobe longer than lower.

Predorsal scales 14 (19), 15 (68)*, or 16 (4), in one series. First longitudinal scale row with 14 (40) or 15 (49)* scales. Fourth longitudinal scale row with 22 (2), 23 (18), 24 (45), or 25 (25)* scales. Longitudinal scale rows between dorsal-fin origin and pelvic-fin origin 5 (28) or 6 (66)*. Longitudinal scale rows between dorsal-fin origin and anal-fin origin 5 (91)*. Circumpeduncular scale rows 10 (91)*. Total number of vertebrae 33 (2), 34 (9), or 35 (1).

Table 5. Morphometrics of *Copella eigenmanni*. Lectotype of *Copeina eigenmanni* BMNH 1869.7.25.6, holotype of *Copeina metae* CAS 60494, paratypes of *C. metae* CAS 60495 (10) and non-type material FMNH 55166 (2), FMNH 103819 (10), FMNH 159182 (8), ICN 1385 (4), ICN 12192 (2), MBUCV 11336 (10), MHNG 2200.028 (7), MZUSP 81443 (10), MZUSP 85149 (10), USNM 269898 (2), USNM 269899 (7), USNM 272409 (4), and USNM 272412 (2), n = number of specimens, SD = Standard deviation. Range does not include primary types.

	<i>Copeina eigenmanni</i>	<i>Copeina metae</i>	n	Range			Mean	SD
	Lectotype	Holotype						
Standard length (mm)	37.7	28.8	88	22.0	-	56.2	33.1	6.7
Percents of standard length								
Body depth	18.5	20.1	88	14.3	-	21.7	18.6	1.2
Dorsal- to caudal-fin origin	34.8	35.4	88	32.9	-	39.1	36.2	1.2
Snout to dorsal-fin origin	65.7	64.6	88	61.1	-	67.3	64.6	1.5
Snout to pectoral-fin origin	23.0	23.3	88	19.7	-	26	22.8	1.1
Snout to pelvic-fin origin	46.6	46.9	87	45.7	-	52.6	48.5	1.3
Snout to anal-fin origin	73.2	70.8	88	68.1	-	74.5	71.2	1.4
Pectoral- to pelvic-fin origin	27.4	25.3	87	16.2	-	32.3	26.4	1.7
Pelvic- to anal-fin origin	27.1	23.3	87	17.6	-	26.1	23.3	1.4
Pectoral-fin length males	15.4	-	47	16.3	-	25.2	19.6	2.0
Pectoral-fin length fem/imm	-	17.0	37	16.8	-	21.5	19.1	1.1
Pelvic-fin length males	19.4	-	46	18.1	-	34.1	23.4	4.3
Pelvic-fin length fem/imm	-	18.1	40	16.3	-	19.9	18.4	0.8
Dorsal-fin length males	22.2	-	48	21.6	-	41.1	29.4	4.8
Dorsal-fin length fem/imm	-	23.6	39	20.9	-	26.9	24	1.5
Anal-fin length males	18.4	-	48	18.1	-	23.4	20.5	1.5
Anal-fin length fem/imm	-	18.1	39	16.1	-	21.3	18.5	1.2
Anal-fin base length	10.8	8.3	88	6.2	-	11.0	9.0	0.8
Caudal peduncle depth	9.6	10.4	88	8.2	-	11.7	9.6	0.6
Caudal peduncle length	23.6	20.8	88	17	-	22.8	19.7	1.4
Head length	22.0	24.3	88	18.4	-	26.7	23.4	1.2
Percents of head length								
Eye diameter	29.3	34.3	88	25.6	-	39	32.2	3.2
Snout length	32.2	28.6	88	24.6	-	45.6	31.6	5.3
Interorbital distance	35.5	-	88	28.8	-	50.6	36.1	3.5
Upper jaw length	31.9	25.7	88	25.1	-	37.9	31.9	2.6

Table 6. Meristics of lectotype of *Copeina eigenmanni* BMNH 1869.7.25.6 and holotype of *Copeina metae* CAS 60494.

	<i>Copeina eigenmanni</i>	<i>Copeina metae</i>
	Lectotype	Holotype
Predorsal scales	15	15
First longitudinal scale row	15	-
Fourth longitudinal scale row	25	23
Longitudinal scale rows dorsal to pelvic	6	6
Longitudinal scale rows dorsal to anal	5	5
Circumpeduncular scale rows	10	-
Pectoral-fin rays	i9	-
Pelvic-fin rays	i7	i7
Dorsal-fin rays	ii8	ii8
Branched anal-fin rays	9	9
Caudal-fin rays	-	i8,7i

Color in alcohol. Overall ground coloration of body beige to brown. Dark stripe extending from anterior tip of dentary to posterior tip of opercle. Dorsal portion of body dark. Thin dark stripe at predorsal region. Anterior portion of the scales of the third to the sixth longitudinal scale rows dark, with apparently subjacent dark coloration on the posterior portion of the scales on the fourth and the fifth longitudinal scale rows of variable intensity, frequently forming a conspicuous longitudinal dark band (Fig. 44). Some specimens with a longitudinal conspicuous clear stripe at the third longitudinal scale row, contrasting with a conspicuous dark band on the fourth and the fifth longitudinal scale rows extending from the opercle to the caudal peduncle, (fig. 44B); some specimens with a clear stripe on the third longitudinal scale row and dark spots on the anterior portion of scales of the third to sixth longitudinal scale rows (Figs. 44D and E); and some individuals with an intermediate color pattern, having a clear stripe on the third longitudinal scale row, dark spots on the anterior portion of the third to the sixth longitudinal scale rows, and a subjacent dark band not conspicuous on the fourth and fifth longitudinal scale rows (Fig. 44A and C). Ventral region of body clear. Dorsal and ventral procurent caudal fin rays black. Dorsal fin with a black round spot; some males with tip of dorsal fin dark. Pectoral,

pelvic, anal and caudal fins hyaline; distal profile of pelvic and anal fins usually dark. Middle caudal fin rays dark, this coloration fading away toward tips of rays.

Color in life. Dorsal portion of body grayish. Upper portion of eye orange. Body with a variable color pattern (see Color in Alcohol). Specimens with longitudinal black band on the fourth to the fifth longitudinal scale rows have a conspicuous metallic gray to purple band above it, on the third row, and a metallic green coloration on the portion located mid-dorsally on the caudal peduncle (Fig. 45); specimens without a longitudinal black band with a lighter metallic grey to purple band on the third row, and a reddish pigmentation on the fourth and the fifth longitudinal scale rows on the caudal peduncle (Fig. 46). Fins yellow to orange. A pink spot at the dorsal-fin base and upper and lower portions of caudal fin lobes.

Sexual dimorphism. Males longer than females. Males with more maxillary teeth than females (see description above). Pectoral, pelvic, dorsal and anal fins only slightly longer in males than in females. Fin lengths varying among males, some with the same standard length having different fin lengths (Fig. 47). Tip of adpressed pelvic fin reaching up to base of last branched anal-fin ray in males, and up to anus in females. Tip of adpressed dorsal fin reaching up to caudal-fin base in males, and approximately up to one-half the length of the caudal peduncle in females. Upper caudal-fin lobe longer than lower one, especially in males. No sexual dimorphism in color pattern was observed in *Copella eigenmanni*.

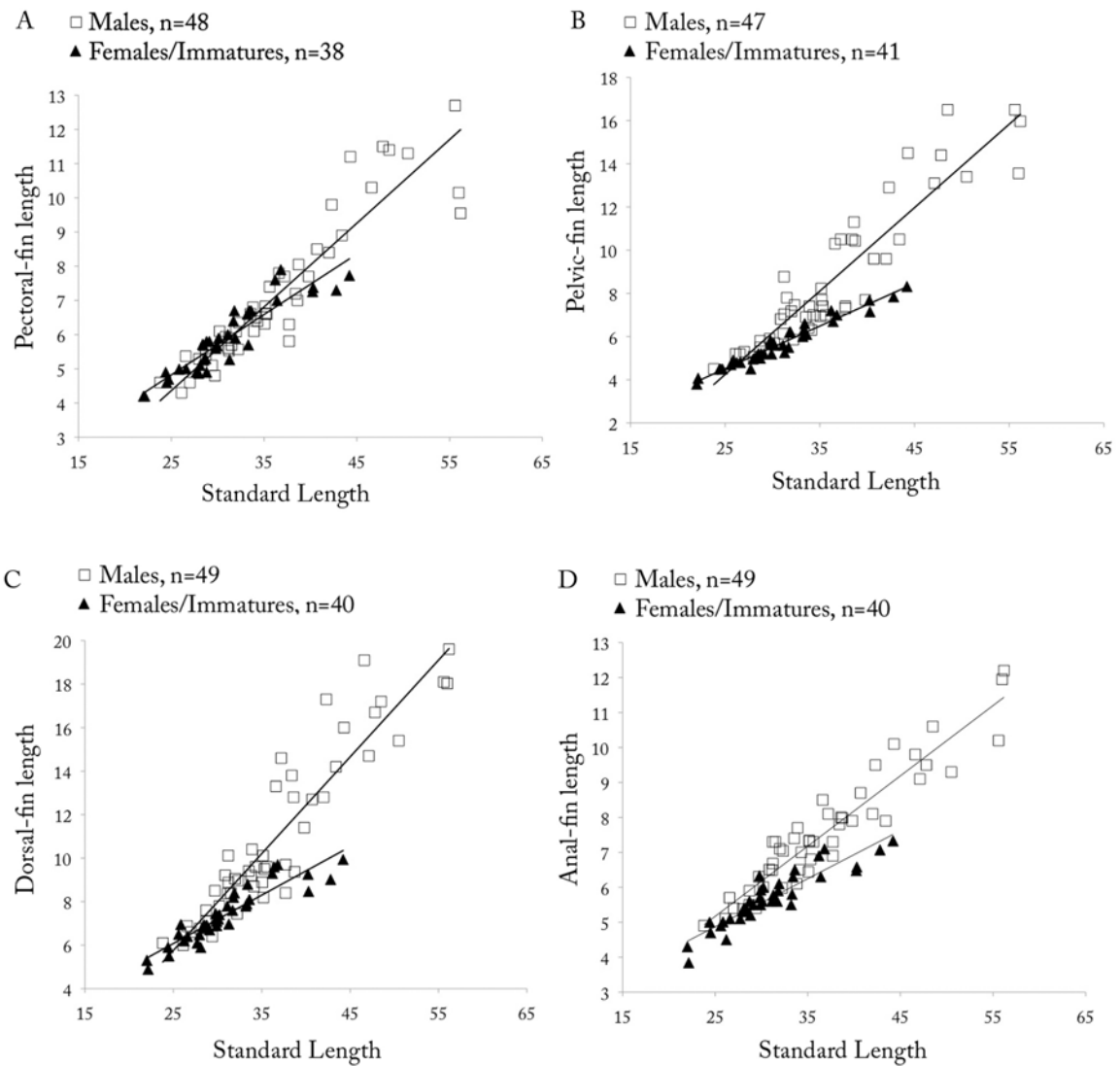


Figure 47. *Copella eigenmanni*, pectoral-, pelvic-, dorsal- and anal-fin length as function of SL by sex.

Distribution. Rio Orinoco basin, Colombia and Venezuela; upper rio Negro, Brazil and Venezuela and upper rio Putumayo drainage, Colombia, rio Amazonas basin (Fig. 38).

Remarks. The original description of *Copella eigenmanni* is based on specimens designated as syntypes from several localities: Pará, Brazil, Guyana, and Bogotá, Colombia [probably

collected near Villavicencio on the rio Meta, according to Weitzman & Weitzman (2003)]. Regan (1912) mentioned color differences among specimens from Brazil, Guyana, and Colombia: “In the smaller examples there is sometimes an indistinct dusky band on the anterior part of the body and an indication of a pale stripe above the dark one on the head. In the larger ones, from Bogotá, a silvery stripe from eye to caudal fin separates a broad dark band below from the dark colour of the back”. However keep them all under the same name. Eigenmann (1914) described *Copeina metae* from the rio Meta and remarked: “Regan records presumably this species from Bogotá. His specimens were probably collected in the Meta, and some at least of those reported from Bogotá represent the present species”. Our findings agree with Eigenmann’s conclusion that *Copeina metae* is conspecific with the type specimens of *C. eigenmanni* from Bogotá.

Zarske (2011) designated as lectotype for *Copella eigenmanni* specimen from Bogotá (Fig. 42), and by doing so synonymyzes *Copella metae* with *C. eigenmanni* and kept the old catalog number (BMNH 1869.7.25.6-7) for the lectotype, but apparently did not pay attention to the fact that the original lot was represented by two specimens which should be considered respectively lectotype and paralectotype. This situation is now resolved with designation of BMNH 1869.7.25.6 for the lectotype and BMNH 1869.7.25.7, for the paralectotype. Zarske (2011; pags. 24 and 34) tentatively identified paralectotypes from Brazil and Guyana as *C. arnoldi* and *C. carsevennensis*, respectively. These are herein recognized as belonging to *C. arnoldi*.

Eigenmann (1914) described *Copeina metae* based in the holotype (IU 13521 a) (Fig. 43) and 34 paratypes (IU 13521). Presently, the holotype is under catalog number CAS 60494 and only 26 paratypes are under CAS 60495 and two under SU 246526. The lots CAS 69238 (6 specimens) and FMNH 55166 (4 specimens) have the same data of the type material,

however, according to D. Catania and M. Rogers, there is no further information that could indicate they are type material. Therefore, eight paratypes of *Copeina metae* remain missing.

Ortega and Vari (1986) cited *Copella metae* for Peru but the presence of this species in Peru could be not confirmed. Only *C. stigmatemion* is recorded for that country.

MATERIAL EXAMINED

Type material

BMNH 1869.7.25.6 [ex 1869.7.25.6-7] (Lectotype of *Copeina eigenmanni*, 37.7 mm SL), Bogotá, Colombia, Cutter. BMNH 1869.7.25.7 (1 paralectotype of *Copeina eigenmanni*, 29.2 mm SL), Bogotá, Colombia, Cutter. CAS 60494 [ex IU 13251a] (holotype of *Copeina metae*, 28.8 mm SL), CAS 60495 [ex IU 13251] (26 paratypes of *Copeina metae*, 11.7-30.5 mm SL), SU 24656 (2 paratypes of *Copeina metae*, 24.5-28.8 mm SL), Barrigona [=Puerto Barrigón], rio Meta, Colombia, M. Gonzáles, 1914.

Non-type material

Rio Orinoco basin, Colombia. ANSP 84390 (1, 20.0 mm SL), Villavicencio, Meta, Oct 1940, C. Miles. ANSP 121628 (1, 30.4 mm SL), Lomalinda, near rio Ariari, Southeast of Villavicencio, Meta, 21 Aug 1969, E. Huggins. ANSP 128621 (5, 22.2-38.4 mm SL), stream into Lake Mozambique (Mozambique ranch), North of ranch house, rio Meta drainage, Meta, 3°58'N 73°4'W, 25 May 1969, J. Böhlke & N. Foster. ANSP 128751 (21, 20.0-33.0 mm SL, 1 c&s, 28.4 mm SL), small stream at Hacienda Humacita, flowing generally South, presumably the general Lake Mozambique complex, 250 ft of stream collected, mostly above the bridge, Meta, 3°58'N 73°4'W, 21 Feb 1972, J. Böhlke & N. Foster. ANSP 128752 (10, 19.4-29.9 mm SL), laguna North of Lake Mozambique, Hacienda Mozambique, rio Meta drainage, Meta, 3°58'N 73°4'W, 23 Mar 1971, J. Böhlke *et al.* ANSP 128753 (50, 16.4-29.5 mm SL), Rancho El Viento, small embayment in long chain of continuous lagunas draining into rio Meta, 4°39'N 72°39'W, 30 May 1969, J. Böhlke *et al.* ANSP 128754 (1, 22.9 mm SL), small stream flowing generally South, entering general Lake Mozambique complex, Hacienda Humacita, rio Meta drainage, Meta, 3°58'N 73°4'W, 23 Mar 1971, J. Böhlke *et al.* ANSP 128755 (5, 21.1-25.2 mm SL), caño Angosturas at Hacienda Humacita and just below, rio Meta drainage, Meta, 3°58'N 73°4'W, 28 Mar 1971, J. Böhlke *et al.* ANSP 128756 (50, 15.3-24.1 mm SL), small stream flowing generally South, presumably general Lake Mozambique complex, Hacienda Humacita, Meta, 3°58'N 73°4'W, 24 Feb 1972, J. Böhlke *et al.* ANSP 128757 (26, 18.2-28.0 mm SL), caño Rico em La Defensa, Northwest of Laguna Mozambique, becomes Cano Buenaventura before entering rio Negro, Meta, 3°59'N 73°8'W, 6 Mar 1971, S. Roback. ANSP 128758 (50, 15.1-24.5 mm SL), laguna West of North shore of Lake Mozambique (second one to the Northwest) at Hacienda Mozambique, with outlet to the rio Metica, rio Meta drainage, Meta, 3°58'N 73°4'W, 6 Mar 1971, S. Roback. ANSP 128759 (87 de 111, 22.6-32.2 mm SL), small stream flowing generally South at Hacienda Humacita, entering general Lake Mozambique complex at, rio Meta drainage, Meta, 3°58'N 73°4'W, 6 Mar 1971, S. Roback. ANSP 128760 (4, 15.6-22.3 mm SL), caño El Viento, Finca El Viento South of Matazul, Meta, 4°8'N 72°39'W, 6 Mar 1971, S. Roback. ANSP 128761 (12, 13.4-23.9 mm SL), caño Emma, Finca El Viento, approximately 33.5 km Northwest of Puerto López, Meta, 4°8'N 72°39'W, 6 Mar

1971, S. Roback. ANSP 130085 (3, 15.5-20.9 mm SL), pond at Hacienda El Viento, 32 km Northeast of Puerto-López, Meta, 15 Feb 1973, J. Richardson Jr. ANSP 130088 (1, 15.7 mm SL), Mozambique Ranch pond, Meta, 6 Dec 1969, S. Roback. ANSP 130089 (7, 10.9-2.9 mm SL), pond at Rancho El Viento, Meta, 10 Dec 1969. ANSP 131689 (1, 17.7 mm SL), pool about 10 km East of Villavicencio, Meta, 6 Mar 1971, S. Roback. Foster. ANSP 131690 (7, 10.6-19.9 mm SL), Pond 1 in Palm Forest, East of Hacienda Mozambique, Meta, 7 Mar 1971, S. Roback. ANSP 131691 (1, 19.8 mm SL), Pond 1, 16 km Southwest of Puerto Lopes, third dam from La Balsa road, Meta, 2 Mar 1971, S. Roback. ANSP 131692 (1, 13.6 mm SL), Pond 2 in Palm Forest East of Hacienda Mozambique, 16 km Southwest of Puerto Lopez, Meta, 7 Mar 1971, S. Roback. ANSP 131693 (1, 15.7 mm SL), Pond 3, 16 km Southwest of Puerto López, first dam from La Balsa road, Meta, 1 Mar 1971, S. Roback. ANSP 133999 (1, 22.5 mm SL), Quebrada Venturosa, between La Balsa and Puerto López, rio Meta drainage, Meta, 4°5'N 72°58'W, 21 Mar 1975, J. Böhlke, W. Saul & L. Fuiman. ANSP 134454 (1, 21.7 mm SL), tributary of caño La Raya (first caño North of La Siberia), rio Meta drainage, Meta, 4°5'N 73°5'W, 10 Mar 1975, J. Böhlke, W. Saul & L. Fuiman. ANSP 141556 (15, 13.1-23.6 mm SL), hallow seepage in low area West of tip of lake, before creek on East side Hacienda Mozambique, Meta, 3°58'N 73°4'W, 29 Feb 1972, D. & N. ANSP 178757 (214, 10.6-27.7 mm SL), hallow seepage in low area West of tip of lake, before creek on East side Hacienda Mozambique, Meta, 3°58'N 73°4'W, 27 Mar 1971, J. Böhlke *et al.* ANSP 191042 (22, 21.6-36.9 mm SL), seepage run-off into Lake Mozambique (North side), Mozambique ranch, Meta, 3°58'N 73°4'W, 25 May 1969, J. Böhlke & N. Foster. ANSP 191044 (2, 25.0 and 34.0 mm SL), seepage run-off into Lake Mozambique (North side), Mozambique ranch, Meta, 3°58'N 73°4'W, 25 May 1969, J. Böhlke & N. Foster. CZUT-IC 4084 (1, 20.0 mm SL), Canõ Guamirza, Guainia, 2°58'13"N 67°50'13"W, 15 Dec 2009-29 May 2010, F. Villa & A. Ortega. CZUT-IC 4089 (2, 19.5 and 23.7 mm SL), rio Guainia, San Jose-Playa community, Guainia, 4°41'44"N 68°2'7"W, 10 Dec 2009-29 May 2010, F. Villa & A. Ortega. CZUT-IC 4613 (4, 16.3-17.3 mm SL), caño Cubideño, Cubideño bridge, rio Meta drainage, Casanare, 24 Sep 2010, A. Ortega & A Urbano. CZUT-IC 4664 (4, 20.1-26.7 mm SL), Reserva Palmarito, rio Cravo Sur, rio Meta, Casanare, 25 Sep 2010, A. Ortega & A Urbano. CZUT-IC 5088 (1, 24.0 mm SL), Canõ Guamirza, Guainia, 2°58'13"N 67°50'13"W, 15 Dec 2009-29 May 2010, F. Villa & A. Ortega. FMNH 112220 (20 de 73, 21.5-25.6 mm SL), tributary of rio Manacacias, 1 km West of Puerto Guaitán, Meta, 3 Apr 1974, Thomerson *et al.* IAvH 876 (33, 16.0-24.7 mm SL), Puerto Gaitán, Meta, 3°13'49"N 73°52'39"W, 22 Feb 1984, M. Blanco *et al.* IAvH 885 (63, 11.8-25.1 mm SL), caño Muco at San Francisco farm, Puerto Gaitán-Gaviotas road, rio Vichada drainage, Meta, 3°13'49"N 73°52'39"W, 9 Dec 1983, M. Blanco *et al.* IAvH 1144 (250, 14.7-32.3 mm SL), caño Muco at Hacienda San Francisco, 22 km of Puerto Gaitán-Gaviotas road (deviation Km 17), Meta, 3°13'49"N 73°52'39"W, 22 Mar 1984, M. Blanco *et al.* IAvH 1205 (5, 14.4-21.0 mm SL), caño Muco at San Francisco farm, Puerto Gaitán-Gaviotas road, Meta, 3°13'49"N 73°52'39"W, 23 Feb 1984, M. Blanco *et al.* IAvH 1420 (11, 15.6-24.5 mm SL), Centro Gaviotas, caño Elvimida, Cumaribo, Vichada, 4°35'N 70°52'W, 23 Feb 1984, M. Blanco *et al.* IAvH 1575 (1, 22.4 mm SL), caño San Francisco, rio Muco drainage, Puerto Gaitán, Meta, 3°28'N 73°40'W, 23 Feb 1984, M. Blanco *et al.* IAvH 1590 (64, 12.0-32.4 mm SL), caño San Francisco, rio Muco drainage, Puerto Gaitán, Meta, 3°28'N 73°40'W, 23 Feb 1984,

M. Blanco *et al.* IAvH 1591 (35, 11.7-21.0 mm SL), caño San Francisco, río Muco drainage, Puerto Gaitán, Meta, 3°28'N 73°40'W, 23 Feb 1984, M. Blanco *et al.* IAvH 2284 (1, 23.0 mm SL), caño NN, affluent of caño Bocón, río Inírida drainage, Puerto Inírida, Guainía, 3°39'N 68°1'W, 11 Mar 2007, H. Thorbjörn. IAvH 2431 (1, 14.6 mm SL), caño Muco at Hacienda San Francisco, 22 km of Puerto Gaitán-Gaviotas road (deviation Km 17), río Vichada drainage, Meta, 3°13'49"N 73°52'39"W, 22 Mar 1984, Blanco *et al.* IAvH 2492 (20, 15.5-23.7 mm SL), Morichal near río Yucao, río Meta drainage, Puerto López, Meta, 4°5'N 72°58'W, 27 Nov 1978, Scully & Garzón. IAvH 3404 (20, 16.4-27.0 mm SL), caño Moriche, río Meta drainage, Casanare, 11 Aug 1994, F. Rodríguez. IAvH 4179 (5, 14.8-18.2 mm SL), Madre Vieja, río Tomo basin, río Meta drainage, Cumaribo, Vichada, 5°21'55"N 67°51'33.3"W, 17 Feb 2004, Maldonado *et al.* IAvH 7906 (2, 26.0 and 28.1 mm SL), Quebrada La Palomera, affluent of río Cravo Sur, río Meta drainage, Yopal, Casanare, 5°22'9.5"N 72°16'17.3"W, 10 Apr 2006, Bogotá *et al.* IAvH 7907 (2, 27.8 and 28.5 mm SL), stream affluent of río Caja vereda Jaguito, río Meta drainage, Tauramena, Casanare, 5°3'6.1"N 72°45'22.6"W, 11 Apr 2006, Bogotá *et al.* IAvH 9938 (17, 13.8-26.4 mm SL), caño Fruta, 1 hour upstream Sarrapia, río Meta drainage, Cumaribo, Vichada, 4°26'28.8"N 67°55'W, 11 Mar 2007, Bogotá & F. Villa. IAvH 10774 (1, 18.0 mm SL), stream of río Tomo drainage, Cumaribo, Vichada, 5°21'32"N 67°51'46.2"W, 30 Jan 2004, Maldonado *et al.* IAvH 11223 (13, 19.7-50.4 mm SL), caño La Insula, Alto Neblinas way, Finca Unillanos, río Meta drainage, Puerto Gaitán, Meta, 4°18'59.8"N 72°39'57.6"W, 11 Mar 2007, Aya & Rincón. IAvH 11269 (4, 19.4-22.7 mm SL), laguna El Tinije, Aguazul, Casanare. IAvH ex 3405 (24, 12.4-25.0 mm SL), caño Agua Limón, Orinoco, Arauquita, Arauca, 6°55'N 70°58'W, 2 Nov 2003, G. Castaño. ICNMNH 942 (40, 20.6-36.4 mm SL), El Presentado, quebrada Tascona, affluent of río Guacavia, río Metica, río Meta drainage, Cumaral, Meta, 30 Jan 1985, C. Román-Valencia. ICNMNH 1037 (28, 18.3-33.5 mm SL), caño Limón, caño Verde, río Arauca drainage, 7 Mar 1977, P. Cala & P. Velásquez. ICNMNH 1382 (32, 16.9-24.3 mm SL), río Tomo at Estación Tuparro, Vichada, 21 Feb 1972, P. Cala. ICNMNH 1383 (62, 12.7-27.8 mm SL), caño Baronas, Guaviare, Puerto Lleras, Meta, 2 Dec 1976, P. Cala. ICNMNH 1385 (4, 39.6-56.4 mm SL), quebrada Yaguaso, río Meta drainage, Aguazul, Casanare, 8 Sep 1981, P. Cala. ICNMNH 1386 (17, 13.4-37.8 mm SL), caño Macapay, río Meta drainage, Maya, Cundinamarca, 18 Jun 1976, P. Cala. ICNMNH 1389 (5, 16.3-42.9 mm SL), caño Carraño, río Muco, río Vichada drainage, Puerto Gaitán, Meta, 17 Jun 1974, P. Cala. ICNMNH 1395 (5, 31.2-50.1 mm SL), río Muco, río Vichada drainage, 14 Jul 1974, P. Cala. ICNMNH 1406 (3, 19.6-28.4 mm SL), caño Urimica, río Tomo drainage, Gaviotas, Vichada, 15 Jul 1974, P. Cala. ICNMNH 1409 (22, 14.3-18.9 mm SL), río Inírida, Puerto Inírida, Guainía, 8 Jan 1972, P. Cala. ICNMNH 1410 (58, 10.8-25.4 mm SL), caño Cajuy, Hda. Tanané, río Meta drainage, Meta, 18 Jan 1967, C. Velásquez. ICNMNH 1428 (1, 16.5-26.9 mm SL), caño Zuria, río Meta drainage, Villavicencio, Meta, 12 Nov 1987, P. Cala & P. Benavides. ICNMNH 1432 (9, 20.4-26.1 mm SL), caño Caimán affluent of río Muco, río Vichada drainage, Vichada, 14 Jul 1974, P. Cala. ICNMNH 1433 (1, 23.5 mm SL), río Arauca, Saravena, Arauca, 5 Mar 1977, P. Cala. ICNMNH 1435 (51, 13.0-46.2 mm SL), caño Limón, caño Poporio, río Ariari drainage, Guaviare, Meta, 29 Nov 1976, P. Cala. ICNMNH 1939 (1, 38.6 mm SL), río Yucao, río Meta drainage, Puerto Gaitán, Meta, 1 Nov 1992, W. Castro & R. Sánchez. ICNMNH 10485 (1, 32.1 mm SL), confluence

of caño Chaparral and caño Grande, rio Tomo drainage, Vichada, 1 Jul 2004, S. Gavassa. ICNMMNH 11177 (10, 11.4-24.6 mm SL), caño Pica Pico, La Hermosa, Finca Nicaragua, rio Meta drainage, Paz de Ariporo Casanare, 1 Oct 2004, M. Gutiérrez. ICNMMNH 11219 (5, 12.2-14.8 mm SL), caño Moreno La Hermosa, Finca Nicaragua, rio Meta drainage, Paz de Ariporo, Casanare 5°38'15.4"N 70°12'41"W, 9 Nov 2004, M. Gutiérrez. ICNMMNH 11251 (3, 17.6-19.6 mm SL), estero 1, La Hermosa, Finca Nicaragua, rio Meta drainage, Paz de Ariporo, Casanare, 5°37'31.61"N 70°15'16.8"W, 29 Oct 2004, M. Gutiérrez. ICNMMNH 11268 (1, 22.8 mm SL), estero 2, La Hermosa, Finca Nicaragua, rio Meta drainage, Paz de Ariporo, Casanare, 31 Oct 2004, M. Gutiérrez. ICNMMNH 11276 (10, 8.7-23.1 mm SL), estero 3, La Hermosa, Finca Nicaragua, rio Meta drainage, Paz de Ariporo, Casanare, 5°36'51.8"N 70°14'36.1"W, 8 Nov 2004, M. Gutiérrez. ICNMMNH 11335 (18, 12.9-19.4 mm SL), laguna Rebalse, La Hermosa, Finca Nicaragua, rio Meta drainage, Paz de Ariporo, Casanare 5°36'11.1"N 70°16'45.1"W, 1 Nov 2004, M. Gutiérrez. ICNMMNH 12189 (1, 22.6 mm SL), caño Porfía, affluent of rio Yucao, rio Meta drainage, Puerto Gaitán, Meta, 1 Nov 2004, Proyecto Ornamentales Orinoco. ICNMMNH 12190 (1, 17.8 mm SL), caño La Berraquera, affluent of rio Yucao, rio Meta drainage, Puerto Gaitán, Meta, 1 Nov 2004, Proyecto Ornamentales Orinoco. ICNMMNH 12192 (3, 25.5-39.4 mm SL), Centro de Acopio, rio Guainía, Puerto Inírida, 1 Feb 2005, Proyecto Ornamentales Orinoco. ICNMMNH 12879 (10, 13.0-20.6 mm SL), caño Porfía, affluent of rio Yucao, rio Meta, Puerto Gaitán, Meta, 1 Nov 2004, Proyecto Ornamentales Orinoco. ICNMMNH 12881 (2, 24.2 and 26.9 mm SL), Fazenda la Neblina, caño la Neblina affluent of rio Manacacías, rio Meta, Puerto Gaitán, Meta, 1 Nov 2004, Proyecto Ornamentales Orinoco. ICNMMNH 12979 (6, 18.5-33.3 mm SL), caño la Pecuca affluent of rio Guacaula, rio Meta, Cumaral, Meta, 1 Oct 1990, G. Galvis. ICNMMNH 12980 (5, 23.0-34.0 mm SL), caño Caibe, rio Meta drainage, Cumaral, Meta, 1 Apr 1995, G. Galvis. ICNMMNH 13069 (1, 24.7 mm SL), caño Seco, affluent of rio Acacias, rio Meta, La Esmeralda, Meta, 1 Apr 1995, J. Mojica & Estudiantes Sistemática Animal. ICNMMNH 15841 (1, 24.8 mm SL), mouth of rio Orottoy, affluent of rio Acacias, rio Meta drainage, Acacias, Meta, 1 Feb 2005, H. Mojica & H. Casas. MLS 937 (10, 25.3-29.8 mm SL), secondary branch of rio Cusiana, Yopal, Casanare, 4°54'8,5"N 72°30'8,8"W, Buitrago, Uriel. FMNH 55166 (4, 11.7-30.5 mm SL), rio Meta at Barrigona, Orinoco, M. Gonzales. MLS 939 (7, 17.0-30.2 mm SL), quebrada El Zorno, Yopal, Casanare, 5°10'12,6"N 72°29'59,8"W Buitrago, Uriel. MHNG 2200.29 (7, 21.2-26.6 mm SL), upper rio Meta, about 30 miles Southeast of Villavicencio, Orinoco, Dec 1963, R. Socolof. MHNLS 23579 (6, 17.2-20.9 mm SL), marginal branch of Macasabe lagoon, right bank of rio Guaviare, Vichada, 3°57'20.3"N 67°56'32.2"W, 5 Aug 2008, C. Lasso *et al.* MHNLS 23580 (2, 17.6 and 18.8 mm SL), marginal branch of Macasabe lagoon, right bank of rio Guaviare, Vichada, 3°57'20.3"N 67°56'32.2"W, 5 Aug 2008, C. Lasso *et al.* MHNLS 23755 (5, 26.9-38.7 mm SL), quebrada affluent of caño Tonina, tributary of left bank of caño Bocon, Los Pozos de Floro, Vichada, 3°39'38,3"N 68°3'53,7"W, 1 Aug 2008, C. Lasso *et al.* SIU 311376 (2, 24.0 and 31.6 mm SL), tributary of rio Manacacías, 1 km West of Puerto Gaitán, Meta, 3 Apr 1974, Thomerson *et al.* SU 50584 (1, 33.6 mm SL), floodplain stream at left bank of rio Oteguaza, 2.3 miles upstream Três Esquinas, 0°48'N 75°15'W, 8 Feb 1958, White *et al.* USNM 311008 (88, 13.7-32.6 mm SL), rio Uaupés, Mitu, 18 Aug 1989, H. Axelrod. USNM 323152 (6, 16.6-19.4 mm SL), caño Muco about 15 km toward Puerto Coreno from

Puerto Gaitán, Orinoco, Vichada, 15 Jul 1992, Thomerson *et al.* MLS 313 (2, 29.0 and 36.0 mm SL), caño Carnicerías, Cumaral, Meta, 4°11'59"N 73°12'59.2"W. MLS 923 (17, 20.6-30.0 mm SL), quebrada El Moricho, Northeast of rio Charte, Yopal, Casanare, 4°44'41.2"N 72°10'34.9"W, Buitrago, Uriel.

Rio Orinoco basin, Venezuela. AMNH 230891 (4, 24.0-31.6 mm SL), rio cora-cora, fourty minutes upstream Yutaje camp, rio Ventuari, Amazonas, 5°36'39"N 66°7'57"W, 27 Apr 1999, S. Schaefer, F. Provenzano & R. Rojas. AMNH 233001 (4, 17.6-22.8 mm SL), rio Cuao, Raudal Cielo, West side of Isla del Cielo, fifteen minutes by foot from SAS01-04 base camp, Amazonas, 7 Mar 2001, S. Schaefer, F. Provenzano & J. Baskin. ANSP 130036 (80, 14.1-19.6 mm SL), tributary of rio Guariquito, 24 km Southeast of Calabozo on Estrada to Cazorla, Guarico, 8°38'N 67°20'W, 27 Nov 1966, N. Foster. ANSP 135721 (14, 16.2-29.0 mm SL), rio Tauca on Maripa-Ciudad Bolivar road, Bolivar, 7°28'N 64°52'W, 5 Feb 1977, J. Böhlke & W. Saul. ANSP 135737 (46, 19.2-33.1 mm SL), Morichal Zamorai (stream) between rios Tauca and Tiquire at Maripa-Ciudad Bolivar road, Bolivar, 3 Feb 1977, J. Böhlke, W. Saul, Ferrer-Veliz. ANSP 146228 (31, 19.0-30.0 mm SL), Morichal Zamorai (stream) between rios Tauca and Tiquire at Maripa-Ciudad Bolivar road, Bolivar, 7°28'N 64°54'W, 3 Feb 1972, J. Böhlke *et al.* ANSP 149409 (3, 23.4-29.1 mm SL), Puerto Ayacucho, Amazonas, 13 Mar 1950, J. Rivero. ANSP 159160 (1, 20.1 mm SL), shore and backwater of rio Sipapo at Raudal del Caldero, about 3 km above confluence with rio Orinoco, Amazonas, 5°4'N 67°46'W, 14 Nov 1985, B. Chernoff *et al.* ANSP 159162 (36, 16.0-25.8 mm SL), Morichal 26.9 km of Puerto Ayacucho, along Puerto Ayacucho-Caicara road, Orinoco, 15 Nov 1985, B. Chernoff *et al.* ANSP 159170 (8, 18.1-32.1 mm SL), Morichal Poso Vagabundo, Caicara-Ciudad Bolívar road, 3 km east of Maripa, Bolivar, 7°25'N 69°9'30"W, 19 Nov 1985, A. Machado. ANSP 159176 (34, 16.5-33.5 mm SL, 1 c&s 26.3 mm SL), caño crossing road to Las Trincheras, 2.7 km South of intersection Ciudad Bolivar-Caicara road, Bolivar, 4°39'N 72°39'W, 20 Nov 1985, W. Saul *et al.* ANSP 159182 (51, 15.2-35.3 mm SL), stream 21 km Southeast of El Burro at Caiacara-Puerto Ayacucho road, Amazonas, 26 Nov 1985, W. Saul *et al.* ANSP 159184 (100, 14.0-27.4 mm SL), caño and swamp 19 km Southwest of El Burro on Caiacara-Puerto Ayacucho road, Amazonas, Nov 1985, W. Saul *et al.* ANSP 159186 (1, 34.5 mm SL), caño 15.1 km East of ferry crossing on Caicara-Puerto Ayacucho highway, Bolivar, 28 Nov 1985, B. Chernoff *et al.* ANSP 159188 (12, 16.1-31.9 mm SL), swamp 22.1 km East of rio Parguaza, ferry crossing on Caicara-Puerto Ayacucho highway, Amazonas, 28 Nov 1985, B. Chernoff *et al.* ANSP 159192 (1, 19.9 mm SL), caño crossing dirt road near entrance to Hacienda Fundo Malama (Sr. Biales), about 15 km North Sipao, Bolivar, 7°35'N 65°22'W, 19 Nov 1985, W. Saul & R. Royero. ANSP 159193 (12, 18.5-22.4 mm SL), caño at concrete bridge near Hacienda Fundo Malama (Sr. Biales), about 11 km North of Sipao, Puerto Ayacucho, Amazonas, 6°8'N 67°22'W, 19 Nov 1985, W. Saul & R. Rovero. ANSP 165661 (5, 18.4-22.0 mm SL), caño Horeda, at border of Bolivar-Amazonas Terr., about 68 km Northeast of Puerto Ayacucho, on Puerto Ayacucho-Puerto Paez highway, Bolivar, 7°33'N 65°23'W, 10 Nov 1989, S. Schaefer *et al.* ANSP 165688 (5, 16.8-22.8 mm SL), caño Potrerito, affluent of rio Cinaruco, 24 km South of rio Cinaruco on San Fernando de Apure-Puerto Paez highway, Apure, 6°25'N 67°32'W, 11 Nov 1989, S. Schaefer *et al.* CAS 69237 (21, 22.6-40.3 mm SL), caño tributary of rio Guarico at Calabozo, Guarico, 11 Feb 1938, F. Bond. CAS 69312 (6, 23.4-31.0 mm SL), rio Guaire at Caracas, Federal District, 22 Aug 1949, F. Bond. FMNH 85597 (4, 27.0-39.7 mm SL), pequeno

park 800 m of Porto Ayacucho-San Mariapo road, Amazonas, 13 Jan 1975, J. Thomerson *et al.* FMNH 103819 (20 of 170, 19.9-31.0 mm SL), caño Provincial, about 10 km North of Puerto Ayacucho, Amazonas, 21 Jan 1991, B. Chernoff *et al.* MBUCV 328 (5, 28.3-35.3 mm SL), headwaters of Morichal de Yagrumito, South of Palenque, rio Orituco, rio Apure drainage, Guárico, 7 May 1960, F. Webezahn & G. Bergold. MBUCV 5208 (12, 20.4-26.8 mm SL), caño El Limón, Temblador-San Felix road (at Barrancas de Fajardo), Monagas, 3 May 1968, R. Ampueda & L. Duque. MBUCV 7270 (12, 19.9-27.1 mm SL), caño located at 20 km of San Fernando de Atabapo-Santa Barbara road, Amazonas, 13 Apr 1972, A. Cortéz. MBUCV 12536 (8, not measured), caño Carinagua, next pisciculture of M.A.C., rio Cataniapo, Amazonas, 5°38'11"N 67°35'33"W, 28 Feb 1981, G. Pereira. MBUCV 12563 (3, 23.3-33.3 mm SL), small stream crossing Puerto Ayacucho-Caicara road at 97 km of Puerto Ayacucho, Amazonas, 1 Mar 1981, G. Pereira. MBUCV 12585 (1, 19.4 mm SL), small stream crossing Puerto Ayacucho-Caicara Road, about 172 km of Puerto Ayacucho, Bolívar, 2 Mar 1981, G. Pereira. MBUCV 12736 (1, 37.8 mm SL), caño Las Pavas, affluent of rio Cataniapo, about 3 km of Puerto Ayacucho-Gavilan road, Amazonas, 5°34'42"N 67°32'16"W, 29 Jul 1981, R. Royero *et al.* MBUCV 12805 (9, 26.1-45.0 mm SL), caño Las Pavas, affluent of rio Cataniapo, about 3 km of Puerto Ayacucho-Gavilan road, Amazonas, 5°34'42"N 67°32'16"W, 29 Jul 1981, R. Royero *et al.* MBUCV 14069 (4, 19.9-28.8 mm SL), small stream affluent of rio Cataniapo, 12.5 km of Puerto Ayacucho-Gavilán road, Amazonas, 5°34'N 67°30'36"W, 6 May 1982, R. Royero *et al.* MBUCV 14337 (1, 32.9 mm SL), caño upstream Sarama Sota, upper rio Cataniapo, Amazonas, 5°38'N 67°7'40"W, 20 Aug 1984, R. Royero *et al.* MBUCV 14434 (35, 18.3-28.6 mm SL), caño Ucuoto, about 5 km of mouth, rio Cataniapo, Amazonas, 25 Dec 1983, R. Royero & L. López. MBUCV 14464 (2, 17.7 and 19.7 mm SL), mouth of caño Colorado, rio Cataniapo, Amazonas, 5°34'32"N 67°13'46"W, 23 Dec 1983, R. Royero & L. López. MBUCV 17478 (3, 29.9-39.6 mm SL), Pozo de Lucas, about 7 km South of San Fernando de Atabapo, Amazonas, 8 Apr 1982, R. Royero & G. Pereira. MBUCV 17725 (6, 15.7-42.1 mm SL), floodplain at 22.1 km east of ferry cross at Caicara-Puerto Ayacucho road, rio Parguaza, Bolívar, 28 Nov 1985, A. Machado & D. Ibarra. MBUCV 17741 (2, 21.0 and 21.3 mm SL), caño Rodeo, 100 km east of gas station of Maripa at Ciudad Bolívar-Caicara road, rio Caura, Bolívar, 21 Nov 1985, J. Lundberg, B. Saúl & R. Royero. MBUCV 17916 (5, 21.3-35.1 mm SL), caño crossing road to Las Trincheras, 2.7 km South Ciudad Bolívar-Caicara road, rio Caura, Bolívar, 7°22'N 64°56'W, 20 Nov 1985, J. Lundberg, B. Saúl & R. Royero. MBUCV 18249 (19, 13.0-22.8 mm SL), stream and floodplain at 19 km Southeast El Burro, Caicara-Puerto Ayacucho road, Amazonas, 26 Nov 1985, A. Machado *et al.* MBUCV 19717 (9, 19.9-41.2 mm SL), caño North of base camp, rio Mavaca, Amazonas, 20 Mar 1989, C. Ferraris *et al.* MBUCV 24402 (1, 25.3 mm SL), small stream at right bank (upstream) about 600 m upstream caño Gavilán mouth, rio Cataniapo, Amazonas, 5°32'13"N 67°23'18"W, 20 Dec 1984, R. Royero. MBUCV 24723 (1, 28.2 mm SL), caño La Piedrita at bridge, Temblador-Barrancas road, Monagas, 14 Feb 1978, Aguana & Padilla. MBUCV 27485 (34, 15.8-26.4 mm SL), rio Moquete, Morichal near Paso Bajito, rio Caris, Anzoátegui, 3 Oct 1984, A. Machado *et al.* MBUCV 27621 (1, 24.7 mm SL), caño Mapirito, rio Guanipa, Monagas, 19 Jan 1994, G. Pereira. MBUCV 28126 (3, 25.5-31.5 mm SL), rio Moquete, Morichal near Paso Bajito, rio Caris, Anzoátegui, 3 Dec 1984, A. Machado *et al.* MBUCV 28167 (6, 18.1-26.7 mm SL), Morichal, affluent of rio

Moquete, near Paso Bajito, El Corozo road, Anzoátegui, 14 Feb 1984, A. Machado *et al.* MBUCV 28269 (3, 22.0-27.8 mm SL), rio Moquete, Morichal, near Paso Bajito, Anzoátegui, 2 Feb 1984, A. Machado *et al.* MBUCV 28341 (18 de 19, 20,1-25,9 mm SL), rio Moquete, Morichal, near Paso Bajito, Anzoátegui, 2 Feb 1984, A. Machado *et al.* MBUCV 28350 (44, 16.6-29.5 mm SL), Morichal affluent of rio Moquete, near Paso Bajito, rio Caris, Anzoátegui, 2 Feb 1984, A. Machado *et al.* MBUCV 28358 (54, 13.6-34.2 mm SL), Morichal, affluent of rio Moquete, about 10 km West of Paso Bajito, El Corozo road, rio Moquete, rio Caris, Anzoátegui, 2 Feb 1984, A. Machado *et al.* MBUCV 28428 (40, 14.2-21.3 mm SL), rio Caris, paso Los Cocos at tributary stream, Anzoátegui, 1 Feb 1984, A. Machado *et al.* MBUCV 28451 (10, 17.1-26.1 mm SL), fundo La Esperanza, rio Caris, Anzoátegui, 3 Oct 1984, A. Machado *et al.* MBUCV 28466 (21, 14.2-26.1 mm SL), paso Coera, rio Caris, Anzoátegui, 1 Feb 1984, A. Machado *et al.* MBUCV 28596 (1, 24.4 mm SL), paso Los Cocos, rio Caris, about 40 km South of El Tigre, Anzoátegui, 1 Feb 1984, A. Machado *et al.* MBUCV 28663 (27, 15.7-35.6 mm SL), rio Atapirire, bridge between Campo Aricuna and El Tigre road, Anzoátegui, 4 Oct 1984, A. Machado. MBUCV 29201 (5, 29.2-32.0 mm SL), rio Corocoro, 40 min upstream from Yutaje, Amazonas, 27 Apr 1999, S. Schaefer *et al.* MBUCV 29318 (3, 26.3-30.9 mm SL), rio Cuao, pools upstream raudal del Danto, rio Sipapo drainage, Amazonas, 5°12'39"N 67°33'35"W, 30 Apr 1999, S. Schaefer *et al.* MBUCV 29661 (2, 27.8 and 34.5 mm SL), caño Yurage, affluent of rio Cataniapo, between Merey community and Paso Las Pavas, Amazonas, 5°32'19"N 67°24'36"W, 15 Aug 2000, F. Provenzano *et al.* MBUCV 29696 (4, 10.8-30.1 mm SL), caño Peramán, affluent of rio Cataniapo at San Pedro community, Amazonas, 14 Oct 2000, J. Fernández & L. Marcano. MBUCV 29742 (1, 38.9 mm SL), caño Danto, affluent of rio Cataniapo, Amazonas, 16 Oct 2000, J. Fernández & L. Marcano. MBUCV 29759 (4, 11.2-23.3 mm SL), caño Las Pavas, affluent of rio Cataniapo, Amazonas, 16 Oct 2000, J. Fernández & L. Marcano. MBUCV 29767 (1, 37.2 mm SL), cañito upstream caño Gávilan, affluent of rio Cataniapo, Amazonas, 17 Oct 2000, J. Fernández & L. Marcano. MBUCV 30752 (15, 11.2-15.5 mm SL), caño Gallineta, affluent of rio Cataniapo, Amazonas, 30 Jan 2001, J. Fernández *et al.* MBUCV 30776 (4, 19.0-31.3 mm SL), caño Danto, affluent of rio Cataniapo, Amazonas, 31 Jan 2001, J. Fernández *et al.* MBUCV 31346 (24, 18.9-26.6 mm SL), rio Aro, Morichal at Road East of Esmeralda, Bolívar, 7°34'7"N 64°15'45"W, 25 Mar 2002, F. Provenzano & A. Rojas. MBUCV 31767 (8, 26.4-31.8 mm SL), caño Danto, affluent of rio Cataniapo, Amazonas, 23 Jan 2002, J. Fernández *et al.* MBUCV 33134 (58, 16.7-34.9 mm SL), Morichal Castillito, affluent of rio San Jose, Anzoátegui, 8°39'20.4"N 64°40'2.79"W, 28 May 2006, A. Marcano *et al.* MBUCV 33159 (22, 13.7-35.7 mm SL), Morichal Rabanal, Anzoátegui, 8°36'29.38"N 64°39'11.51W, 28 May 2006, A. Marcano *et al.* MBUCV 33335 (8, 19.4-35.0 mm SL), Morichal Cabeza de Coporo South of Santa Clara through Puerto Ayacucho, Anzoátegui, 8°27'12.54"N 64°38'35.80"W 30 May 2006, A. Marcano *et al.* MBUCV 33345 (16, 21.9-34.8 mm SL), quebrada San Antonio, rio Pao drainage, Anzoátegui, 30 May 2006, A. Marcano *et al.* MBUCV 33582 (19, 21.8-32.5 mm SL), Morichal Castillito, affluent of rio San Jose, rio Pao, Anzoátegui, 8°39'20.4"N 64°40'2.79"W, 2 Sep 2006, A. Marcano *et al.* MBUCV 33587 (40, 18.8-37.3 mm SL), Morichal Rabanal, rio Pao, Anzoátegui, 8°36'29.38"N 64°39'11.51W, 2 Sep 2006, A. Marcano *et al.* MBUCV 33591 (89, 11.6-35.5 mm SL), Morichal Cabeza de Coporo, Anzoátegui, 8°27'12.54"N 64°38'35.80"W, 3 Sep 2006, A. Marcano *et al.*

MBUCV 33617 (3, 23.1-34.4 mm SL), quebrada San Antonio, South of Santa Clara, Anzoátegui, 8°27'12.54"N 64°38'35.80"W, 3 Sep 2006, A. Marcano *et al.* MBUCV 34191 (12, 15.0-29.4 mm SL), Morichal Veladero, under bridge at Zuata-Sitio Turístico Bayona road, near deviation to Fundo Trujillo, Anzoátegui, 7°59'45.79"N 65°8'21.37"W, 19 May 2007, A. Herrera *et al.* MBUCV 34249 (17, not measured), Morichal Veladero, behind camping of Sitio Turístico Bayona, Anzoátegui, 7°56'1.72"N 65°9'59.63"W, 20 May 2007, A. Herrera *et al.* MBUCV 34347 (65, 13.7-31.2 mm SL), Morichal Quebrada El Cebruno, rio San Bartolo, Anzoátegui, 7°56'38"N 64°59'38.63"W, 20 May 2007, A. Herrera *et al.* MBUCV 34359 (not measured), Morichal Cachicamo, after Hato Cachicamo, rio Maripe, Anzoátegui, 8°1'21.5"N 64°59'10.3"W, 20 May 2007, A. Herrera *et al.* MBUCV 34414 (1, 26.4 mm SL), Morichal Pesquero, at Finca El Saco, Anzoátegui, 8° 7'20.2"N 65°17'9.9", 22 May 2007, A. Herrera *et al.* MBUCV 34576 (15, not measured), Morichal Agua Blanca, Anzoátegui, 8°7'0.7"N 65°23'36.10"W, 23 May 2007, A. Herrera *et al.* MBUCV 34648 (9, 18.9-24.9 mm SL), Morichal del Diablo, isolated lagoon at floodplain, Guárico, 8°20'7.9"N 65°34'29.0"W, 24 May 2007, A. Herrera *et al.* MBUCV 34654 (927, not measured), Morichal Guacharaca, isolated lagoon, morichal branch, Guárico, 8°8'56.34"N 65°32'44.08"W, 25 May 2007, A. Herrera *et al.* MBUCV 34756 (3, 15.3-22.9 mm SL), Morichal El Playazo, rio Zuata, Guárico, 8°32'39.20"N 65°34'5.43"W, 26 May 2007, A. Herrera *et al.* MBUCV 34838 (1, 14.0 mm SL), rio El Muerto and tributary at road to Santa María de Ipire, rio Zuata, Guárico, 0°51'59.6"N 65°20'10.3"W, 12 Aug 2007, F. Provenzano *et al.* MBUCV 34865 (5, not measured), Morichal rio Mapire, at canal with isolated pool, Anzoátegui, 8°15'20.63"N 64°56'43.03"W, 13 Aug 2007, F. Provenzano *et al.* MBUCV 34884 (303, not measured), Morichal El Merey, rio Mapire, Anzoátegui, 8°15'45.65"N 64°55'17.29"W, 13 Aug 2007, F. Provenzano *et al.* MBUCV 34888 (49, 15.5-34.4 mm SL), Morichal Casupo, balneário El Encanto, rio Mapire, Anzoátegui, 8°10'7.82"N 64°49'41.08"W, 13 Aug 2007, F. Provenzano *et al.* MBUCV 34998 (216, 13.4-37.4 mm SL), Morichal El Zamuro, rio Ature, Anzoátegui, 8°38'23.89"N 64°48'26.52"W, 7 Oct 2007, A. Herrera *et al.* MBUCV 35049 (8, 13.7-21.9 mm SL), Lavadero de Granza, affluent of rio San Pedro, perto de Mapire, Anzoátegui, 7°44'17.11"N 64°43'39.60"W, 8 Oct 2007, A. Herrera *et al.* MBUCV 35413 (50, 19.4-35.0 mm SL), Morichal Palenque, headwaters of rio Aguaro, North of Santa Rita, rio Guariquito, Guárico, 8°23'34.58"N 66°19'13.01"W, 24 Sep 2008, A. Marcano *et al.* MBUCV 35427 (14, 15.3-22.2 mm SL), Morichal Mariota, affluent of rio Aguaro, North of Santa Rita, rio Guariquito, Guárico, 8°17'0.63"N 66°19'38.94"W, 24 Sep 2008, A. Marcano *et al.* MBUCV 35444 (17, 14.5-30.8 mm SL), Morichal El Perro, affluent of rio Manapire, North of Santa Rita, rio Guariquito, Guárico, 8°16'53.49"N 66°17'36.60"W, 24 Sep 2008, A. Marcano *et al.* MBUCV 35467 (27, 16.7-31.1 mm SL), Morichal Chucuto, affluent of rio Manapire, North of Santa Rita, rio Guariquito, Guárico, 8°36'16.16"N 66°15'16.45"W, 24 Sep 2008, A. Marcano *et al.* MBUCV 35541 (1, 23.1 mm SL), Morichal El Perro, affluent of rio Manapire, North of Santa Rita, rio Guariquito, Guárico, 8°16'52.96"N 66°17'35.49"W, 25 Sep 2008, A. Marcano *et al.* MCNG 1757 (1, 24.6 mm SL), caño Macaurel at Hato Santiago, Apure, Guarico, 8°31'20"N 67°2'W, 28 Oct 1980, DTC80-118. MCNG 2245 (6, 15.1-18.5 mm SL), Hato El Encanto, rio Riecito, Apure, 30 Nov 1980, SR80-8. MCNG 2653 (2, 26.1 and 25.4 mm SL), caño Yatuje at the end of road, Amazonas, 5°32'50"N 66°6'57"W, 15 Mar 1981, SR81-20. MCNG 2653

(2, 26.1 and 25.4 mm SL), caño Yatuje at the end of road, Amazonas, 5°32'50"N 66°6'57"W, 15 Mar 1981, SR81-20. MCNG 3015 (1, 18.8 mm SL), río Manapiare, near Yutaje, Amazonas, 5°35'N 66°17'50"W, 16 Mar 1981, SR81-23. MCNG 3321 (1, 21.9 mm SL), Hato San Jose del Aguaro near stream opposite to house, río Aguaro, Guarico, 7°57'30"N 66°29'W, 29 Sep 1981, SR81-62. MCNG 6820 (1, 16.3 mm SL), caño La Pica, near río Cinaruco, Apure, 6°48'N 67°49'20"W, 16 Jan 1982, DCT82-25. MCNG 11390 (6, 18.7-23.2 mm SL), affluent of río Agua Blanca, Parque Aguaro-Guaritico about 39 km Southeast of Palenque, río Apure, Guárico, 8°43'30"N 66°53'50"W, 13 Apr 1984, DCT84-49. MCNG 11770 (6, 14.5-21.2 mm SL), caño affluent of río Aguaro, Hato Los Pavones at 12 km West of Santa Rita, río Apure, Guarico, 8°7'50"N 66°22'30"W, 22 Sep 1981, DCT81-125. MCNG 13216 (35, 17.9-36.4 mm SL), small stream east of San José, caño Agua Blanca, río Apure, Guarico, 8°34'N 66°49'20"W, 14 Apr 1984, DCT84-51. MCNG 6685 (13.0, mm SL), caño Caripito at El Palomo at 150 km Southwest of Caicara del Bolivar, 6°33'N 67°0'30"W, 30 Mar 1982, DCT82-37. MCNG 14806 (7, 15.4-18.9 mm SL), río San José, East of Road out of Palenque, 39 km Southeast of Palenque, río Guariquito, Guárico, 8°40'N 66°54'W, 22 Jan 1986, DCT86-13. MCNG 14831 (1, 16.6 mm SL), Morichal near 17 km South of DCT 86-13, 6 km east way of grazón, río San José, río Guariquito drainage, Guárico, 8°34'40"N 66°52'25"W, 22 Jan 1986, DCT86-14. MCNG 14884 (1, 19.9 mm SL), río San José, West side of Aguaro-Guariquito, 57 km South of Palenque, río Guariquito, Guárico, 8°29'N 66°53'10"W, 22 Jan 1986, DCT86-15. MCNG 15187 (1, 22.1 mm SL), caño 29 km east of río Cuchivero, road 19 at bridge (21 km east of Santa Rosalia), río Suapire, Bolivar, 7°21'N 65°53'W, 25 Jan 1986, DCT86-25. MCNG 15223 (1, 17.2 mm SL), río Urbani, affluent of río Caura, 16 km South of road 19, on the way of las Tricheras, río Caura, Bolivar, 7°19'N 64°58'W, 25 Jan 1986, DCT86-27. MCNG 15235 (1, not measured), caño El Rodeo, affluent of río Pao, road 19, near El Vaquiro, Bolivar, 7°20'N 64°35'W, 25 Jan 1986, DCT86-28. MCNG 16288 (10, 21.5-35.8 mm SL), Morichal Tauca, Road to Caicara, about 20 km of Sipao, affluent of río Tucuragua, Bolivar, 7°23'N 65°35'W, 20 May 1985, WC85-3. MCNG 16406 (2, 25.9 and 28.3 mm SL), Caicara del Orinoco-El Tigre road, about 1 km, left and right side of the road, Anzoátegui, 7°31'N 66°1'W, 24 Aug 1986, EC86-4. MCNG 16170 (1, 29.9-30.8 mm SL), río Morichal Largo, at bridge near El Salto village, Monagas, 8°56'N 63°7'W, 17 Aug 1984, LN84-17. MCNG 17149 (9, 18.2-24.1 mm SL), caño Macanilla, upstream R. Chaviripa through Puerto Ayacucho, Bolivar, 7°12'N 66°22'W, 19 Dec 1986, EC86-6. MCNG 17442 (1, 17.1 mm SL), balneario Pozo Azul, at road El Burro-Puerto Ayacucho, Amazonas, 5°50'N 67°29'W, 20 Dec 1986, EC86-7. MCNG 17455 (108, 18.5-34.5 mm SL), Morichal at Puerto Ayacucho-Sabaneta road, Amazonas, 5°25'N 67°45'W, 23 Dec 1986, EC86-9. MCNG 17464 (4, 16.4-19.4 mm SL), river between Puerto Ayacucho and Galipero, Amazonas, 5°37'N 67°36'W, 25 Dec 1986, EC86-12. MCNG 17699 (3, 27.3-27.9 mm SL), caño about 31 km South of way to Puerto Ayacucho, Bolivar, 6°13'N 67°10'30"W, 18 Apr 1984, DCT84-63. MCNG 17736 (1, 26.1 mm SL), caño Chivaripa between Puerto Paez and Caicara, 79 km Southeast Road to Puerto Ayacucho, Bolivar, 6°28'30"N 67°2'30"W, 18 Apr 1984, DCT84-65. MCNG 17743 (13, 18.9-30.2 mm SL), caño Agua Mena about 20 km Southeast Road to Puerto Ayacucho, Bolivar, 6°14'30"N 67°16'W, 18 Apr 1984, DCT84-62. MCNG 20099 (2, 18.3 and 24.4 mm SL), caño La Pica 5 km East of new embankment, Capanaparo, Apure, 6°55'N 67°25'W, 1 May 2011, ABD89-21. MCNG

20263 (12, 13.7-18.9 mm SL), Laguna Brava at savanna, Finca Catalino, Capanaparo, Apure, 6°57'N 67°39'W, 28 Apr 1989, DCT89-127. MCNG 21144 (8, 17.9-27.9 mm SL), caño Urbana at bridge, 29 km North of Jabillal, rio Caura, Bolivar, 7°0'N 64°45'W, 4 Mar 2011, DCT89-59. MCNG 21643 (2, not measured), rio Guayapo at 149 km of confluence with rio Sipapo, Amazonas, 4°23'N 67°2'W, 20 May 1980, LN89-47. MCNG 21662 (3, 28.4-35.3 mm SL), cañito at 150 m Northwest of camping CVG-TECMIN at 149 km of confluence with rios Guayapo and Sipapo, Amazonas, 4°23'N 67°2'W, 22 May 1989, LN89-49. MCNG 22967 (1, 26.2 mm SL), caño Blanco affluent of rio Asisa, near Asisa community (Frente 02-Pica 2 of TECMIN), rio Ventuari, Amazonas, 4°30'N 65°46'30"W, 7 Oct 2011, LN89-121. MCNG 23361 (9, 15.5-33.6 mm SL), caño Bocachica North of airport of Maroa, via Yavita, rio Casiquiare, Amazonas, 2°47'N 67°40'W, 9 Aug 2011, DCT89-133. MCNG 23632 (22, 18.2-30.5 mm SL), caño Pozo Azul at balneario Pozo Azul, Puerto Ayacucho, Amazonas, 5°50'N 67°29'W, 13 May 1989, LN89-36. MCNG 23706 (3, 21.6-36.3 mm SL), Arekuna, Campam, EDELCA at Morichal, rio Caroni, Bolivar, 6°30'N 62°53'W, 3 Jul 1990, DCT90-5. MCNG 23897 (2, 15.5 and 16.2 mm SL), small pools at wood at 500m of rio Ventuari, Amazonas, 4°16'N 66°23'W, 28 Sep 1989, LN89-106. MCNG 23901 (13, 12.7-24.8 mm SL), small isolated and interconnected pools at morichal at open savanah (CVG-Tecmin Frente 6 pica 2), West of rio Guapuchí, rio Ventuari, Amazonas, 4°14'N 66°44'W, 23 Sep 1989, LN89-96. MCNG 23908 (10, not measured), rio Morichal Largo, at bridge near El Salto village, Monagas, 8°56'N 63°7'W, 6 Nov 1989, LN84-17. MCNG 25668 (3, 19.9-22.1 mm SL), small stream at left side of rio Mavaca, Amazonas, 1°55'N 65°6'W, 3 Feb 1991, LN91-23. MCNG 26114 (4, not measured), small stream affluent of rio Siapa, 1°26'N 65°43'W, 20 Apr 1991, ABD91-28. MCNG 26419 (3, 13.8-16.3 mm SL), rio Cataniapo, near Las Pavas community, Amazonas, 5°32'25"N 67°29'30"W, 3 Sep 1991, OLM91-3. MCNG 26566 (3, not measured), caño San Miguel, West Galeras de Cinaruco, Apure, 6°34'24"N 67°17'32"W, 20 Jan 1992, LN92-7. MCNG 26596 (7, 11.9-22.7 mm SL), caño Pozo Azul at balneario, Amazonas, 5°45'49"N 67°29'21"W, 21 Jan 1992, LN92-8. MCNG 26606 (2, 18.6 and 23.4 mm SL), caño Agua Linda near Caicara-Puerto Ayacucho road, Bolivar, 5°50'24"N 67°27'10"W, 22 Jan 1992, LN92-9. MCNG 26874 (34, 15.0-38.1 mm SL), caño at jungle of rio Mavaca, Amazonas, 2°28'N 65°6'W, 25 Jan 1991, LN91-12. MCNG 26893 (1, 26.2 mm SL), Laguna West of Cinaruco, rio Apure, Apure, 6°33'6"N 67°30'43"W, 23 Jan 1992, LN92-12. MCNG 26993 (8, 24.2-30.8 mm SL), caño Guayabal, 44 km South of Puerto Ayacucho, road to Samariapo, Amazonas, 5°20'16"N 67°42'29"W, 20 Mar 1991, ABD91-12. MCNG 27006 (19, 15.7-30.7 mm SL), caño at 61 km east of Puerto Ayacucho-Caicara, rio Cataniapo, Amazonas, 5°35'47"N 67°12'38"W, 19 Mar 1991, ABD91-6. MCNG 27051 (9, 18.0-30.3 mm SL), east side of Isla Ratón, floodplain near Sabanita, Amazonas, 5°5'N 67°48'W, 14 Aug 1992, DCT92-8. MCNG 27144 (54, 16.1-29.4 mm SL), caño Morichal, near 1 km North of Esmeralda and rio Mavaca, Amazonas, 3°10'30"N 65°33'W, 22 Jan 1991, LN91-5. MCNG 26975 (1, 27.4 mm SL), caño Kaprina, 21 km West of rio Parguaza, Puerto Ayacucho-Caicara road, rio Cataniapo, Amazonas, 19 Mar 1991, ABD91-5. MCNG 27218 (8, 21.7-30.7 mm SL), isolated lagoon at meander of rio Mavaca, Amazonas, 2°22'30"N 65°5'30"W, 31 Jan 1991, LN91-19. MCNG 28769 (7, 27.5-35.9 mm SL), caño La Rueda, 24 km South of Puerto Ayacucho at road to Samariapo, Amazonas, ABD91-7. MCNG 30392 (14, 16.0-35.4 mm SL), caño

about 20 min walking South of Macuruco, caño El Loro, Amazonas, 21 Aug 1994, ABD94-1. MCNG 30402 (7, 18.2-32.8 mm SL), Tobogan de la Selva about 3 km of La Coromoto community, Puerto Ayacucho-Samariapo road, Amazonas, 5°23'45"N 67°36'30"W, 29 Aug 1994, ABD94-7. MCNG 31506 (6, 14.8-22.2 mm SL), Parque Nacional Aguaro-Guariquito, Morichal Charcote (opened morichal), rio San Bartolo, rio Guariquito, Guarico, 8°24'16"N 66°34'23"W, 5 Jan 1995, DCT95-4. MCNG 31867 (10, 17.7-23.4 mm SL), Parque Nacional Aguaro-Guariquito, Morichal Simon (way to La Esperanza from El Mejo), tributary of rio San Bartolo, Guarico, 8°30'45"N 66°35'49"W, 9 Jan 1995, DCT95-12. MCNG 28781 (21, 23.2-32.9 mm SL), caño 28 km South of Puerto Ayacucho, road to Samariapo, Amazonas, ABD91-8. MCNG 30378 (1, 20.7 mm SL), base of Yapacana hill, near caño Cotua, Amazonas, 22 Aug 1994, ABD94-3. MCNG 33128 (21, 14.1-40.8 mm SL), rio Autana, Raudal Perez, Amazonas, 24 Aug 1996, RNR92-1. MCNG 34545 (3, 25.2-30.0 mm SL), Galeras del Cinaruco, rio Apure, Apure, 6°34'N 67°15'W, 16 Jan 1996, DRO96-1. MCNG 36468 (32, 31.0-45.3 mm SL), quebrada entering morichal El Pozo, through CVG de caucho camping, Amazonas, 13 Jul 1994, DCT94-36. MCNG 36472 (1 of 5, 18.0 mm SL), caño Ucata, near Ucata community, Amazonas, 12 Jul 1994, DCT94-33. MCNG 36479 (7, 17.8-31.9 mm SL), Balneario Pozo Azul, Bolivar, 18 Aug 1992, PP92-1. MCNG 39995 (5, 15.6-21.8 mm SL), Laguna Oheros, rio Cinaruco, rio Apure, 6°32'48"N 67°25'54"W, 16 Feb 1999, DAA99-82. MCNG 40540 (3, not measured), rio Cinaruco, Espinar lagoon, Apure, 6°33'22"N 67°22'33"W, 17 Mar 1999, DAA99-127. MCNG 41789 (1, 23.3 mm SL), rio Matiyure at Mantecal and La Trinidad-Rincón Hondo road, rio Apure, Apure, 7°26'54"N 69°6'47"W, 4 Apr 1999, NL17-99. MCNG 42403 (29, 16.7-27.0 mm SL), small stream at 6 km South of rio Cinaruco, between El Burro and San Fernando de Apure, Apure, 6°31'22"N 67°33'4"W, 21 Jan 1999, LN99-37. MCNG 43444 (8, 25.6-36.3 mm SL), Pozo Azul near rio Cinaruco, Apure, 16 Mar 1999, DAA99-417. MCNG 43929 (3, 25.6-30.6 mm SL), caño Caicara at bridge near modules of UNELLEZ, Apure, 3 Jul 1999, OLM99-20. MCNG 45599 (29, 13.8-30.4 mm SL), rio Orinoco near Campamento Manaka, about 150 m of mouth of caño Carmen, Amazonas, 3°48'37"N 67°1'23"W, 10 Feb 2002, CGM02-04. MCNG 45979 (4, 17.9-23.1 mm SL), Maniapure, Bolivar, 15 Feb 2001, FA2001-01. MCNG 45984 (1, 19.7 mm SL), Maniapure, Bolivar, 15 Feb 2001, FA2001-02. MCNG 47333 (7, 20.1-23.4 mm SL), rio Ventuari at porto f Cucurital camping, Amazonas, 4°7'3"N 66°40'47"W, 26 Jun 2002, CGM02-54. MCNG 47342 (33, 15.8-41.6 mm SL), caño Carinagua near "Alto Carinagua" community, Amazonas, 5°40'42"N 67°32'7"W, 9 Oct 2002, CGM02-59. MCNG 48508 (10, 18.7-30.3 mm SL), caño at Tobogan de la selva, Amazonas, 16 Jun 1999, MFA99-1. MCNG 48711 (10, 13.0-22.3 mm SL), caño La Pica, Apure, 17 Feb 2001, FA2001-7. MCNG 49818 (47, not measured), caño Yakiguapo at rio Ventuari, Amazonas, 4°4'56"N 66°54'18"W, 6 Dec 2002, CGM02-74. MCNG 49905 (2, 23.1 and 23.9 mm SL), caño Moriche, 116 km North of Macuruco, 169 km Northwest of San Fernando de Atabapo, rio Ventuari, Amazonas, 4°45'5"N 66°21'32"W, 7 Apr 2004, VEN04-14. MCNG 50531 (2 of 4, 17.5-18.0 mm SL), Laguna de Macuruco, Amazonas, 7 Dec 2003, OLM03-22. MCNG 50573 (8, 19.2-29.5 mm SL), modules of UNELLEZ at gates, Apure, 30 Jun 2002, MCRA02-630. MCNG 51140 (7, 19.4-35.4 mm SL), at Tobogancito, about 1 km upstream Tobogan de la Selva, Amazonas, 4 Jun 2003, OLM03-2. MCNG 51147 (2, 20.2 and 32.5 mm SL), at Tobogancito, about 1 km of balneário of Tobogan de la Selva, Amazonas, 4 Jun

2003, OLM03-3a. MCNG 52513 (11, 18.4-24.8 mm SL), caño La Guardia at moriches near Isla Moriches, río Capanaparo, Apure, 6°42'59"N 67°30'39"W, 16 Mar 2005, CGM05-39. MCNG 53133 (15, 15.6-18.7 mm SL), caño La Guardia, Apure, 6°50'40"N 67°19'50"W, 26 Feb 2005, CGM05-53. MCNG 53579 (36, 16.1-20.5 mm SL), caño La Guardia near Las Boconas lagoon, río Capanaparo, Apure, 6°42'59"N 67°30'39"W, 10 Mar 2005, cgm05-44. MCNG 53617 (2, 14.6 and 15.9 mm SL), río Pasiba at lagoon Pasibita, Amazonas, 16 Jan 2005, SCW05-24. MCNG 53953 (4, 28.6-49.7 mm SL), stream 30 km South of Puerto Ayacucho, Amazonas, 1 Apr 2004, VEN04-2. MCNG 54038 (49, 17.7-33.9 mm SL), Laguna La Rompía, río Apure, Apure, 8 Jun 1982, OCVI82-5. MCNG 54039 (46, 11.4-37.1 mm SL), caño at 18 km from deviation of El Burro and Puerto Ayacucho, at Caicara road, Bolívar, 31 Mar 1983, OCIII83-9. MCNG 54040 (7, 31.7 mm SL), río Apure 200 m of Ma Nieves bridge, Apure, 8 Jun 1982, OCVI82-4. MCNG 54359 (2, not measured), caño El Carmen, Amazonas, 2003, OR2.3. MHNG 2200.028 (10 of 26, 14.9-45.11 mm SL), stream affluent of río Carrao, 5 km East of Canaima, Bolívar, 10 Feb 1968, E. Hoigné. MHNLS 912 (9, 25.3-34.6 mm SL), río Temi, Guainia, Amazonas, 2°55'8"N 55°8'67"W, 30 Nov 1973, Arleo. MHNLS 2234 (4, 19.0-25.3 mm SL), río Águaro, Guarico, 4 Apr 1974, Hoogesteijn, Reul & Rafael. MHNLS 5338 (7 of 8, 25.9-35.7 mm SL), caño Caripo, Pijiguaos, Bolívar, 4 Feb 1988, C. Lasso, G. Colonnello & C. Gauveca. MHNLS 5339 (1, 24.6 mm SL), small pool at quebrada La Tigra, Pijiguaos, Bolívar, 24 Apr 1988, C. Lasso, G. Colonnello & C. Gauveca. MHNLS 5340 (6, 22.6-44.6 mm SL), small pool at quebrada La Tigra, Pijiguaos, Bolívar, 27 Apr 1988, C. Lasso, G. Colonnello & C. Gauveca. MHNLS 5341 (1, 32.1 mm SL), caño Chorro de Água, las Bateas, Pijiguaos, Bolívar, 27 Apr 1988, C. Lasso, G. Colonnello & C. Gauveca. MHNLS 5342 (9, 21.4-35.6 mm SL), La Solanera, Pijiguaos, Bolívar, 26 Apr 1988, C. Lasso, G. Colonnello & C. Gauveca. MHNLS 5343 (3, 19.5-23.8 mm SL), quebrada Trapichote, crossing through El Jobal, Bolívar, 28 Apr 1988, C. Lasso, G. Colonnello & C. Gauveca. MHNLS 5577 (1, 27.3 mm SL), río Suapure, crossing through El Jobal, Bolívar, 28 Apr 1988, C. Lasso, G. Colonnello & C. Gauveca. MHNLS 5736 (3, 22.7-31.6 mm SL), poço Suapi, mouth at río Suapure, Pijiguaos, Bolívar, 29 Apr 1988, C. Lasso, G. Colonnello & C. Gauveca. MHNLS 9268 (17, 19.8-36.9 mm SL), río Guarapiche, affluent of río San Juan, South of San Antonio de Maturin, Monagas, 2 Apr 1985, H. Roman. MHNLS 9921 (12, 14.7-24.7 mm SL), caño Inajana, upstream through caño Jotajana, Delta Amacuro, 15 Feb 1993, V. Ponte & W. Wilbert. MHNLS 12465 (26, 14.8-27.8 mm SL), río Cachipo, setor Cachipo, Reserva Florestal Guarapiche, Maturin, Monagas, 9°57'8"N 63°0'59"W, 16 May 1997, C. Lasso, V. Ponte & D. Figueira. MHNLS 13427 (27, 18.9-29.3 mm SL), Morichal Pozo Vagabundo, affluent of río Caura, Maripa, Bolívar, 7°23'41"N 65°9'78"W, 15 May 2000, C. Lasso, C. Vispo & K. Nakamura. MHNLS 13428 (2, not measured), Morichal Pozo Vagabundo, affluent of río Caura, Maripa, Bolívar, 7°23'41"N 65°9'78"W, 15 May 2000, C. Lasso, C. Vispo & K. Nakamura. MHNLS 13434 (14, 14.1-28.4 mm SL), Morichal Merecure, affluent of río Caura, Maripa, Bolívar, 7°25'49"N 65°10'15"W, 15 May 2000, C. Lasso, C. Vispo & K. Nakamura. MHNLS 13458 (12, 15.2-26.0 mm SL), Morichal Curimar, estrada Maripa-Sipao, affluent of río Terecay, Bolívar, 7°28'22"N 65°19'07"W, 15 May 2000, C. Lasso, C. Vispo & K. Nakamura. MHNLS 14502 (1, not measured), caño Culebra, affluent of río Cataniapo, Atures, Amazonas, 5°32'50"N 67°26'53"W, 19 Jun 2001, C. Lasso *et al.* MHNLS 14503 (5, 14.4-48.6 mm SL), caño

Las Pavas, affluent of rio Cataniapo, 12.9 km of bridge, Atures, Amazonas, 5°34'26"N 67°30'15"W, 17 Aug 2001, C. Lasso *et al.* MHNLS 14504 (1, not measured), caño Danta, affluent of rio Cataniapo, Danta community, Atures, Amazonas, 5°34'32"N 67°32'28"W, 19 Aug 2001, C. Lasso *et al.* MHNLS 14677 (4, not measured), caño Peraman, affluent of rio Cataniapo, at San Pedro community, Atures, Amazonas, 5°34'32"N 67°32'28"W, 23 Apr 2002, J. Fernandez & L. Marcano. MHNLS 14709 (1, not measured), caño Danto, affluent of rio Cataniapo, Atures, Amazonas, 5°24'32"N 67°32'28"W, 24 Apr 2002, J. Fernandez & L. Marcano. MHNLS 14715 (1, not measured), caño Danto, affluent of rio Cataniapo, Atures, Amazonas, 5°24'32"N 67°32'28"W, 24 Apr 2002, J. Fernandez & L. Marcano. MHNLS 14727 (1, not measured), caño Las Pavas, Atures, Amazonas, 5°34'26"N 67°30'15"W, 24 Apr 2002, J. Fernandez & L. Marcano. MHNLS 14791 (1, 25.6 mm SL), right bank of caño Culebra, affluent of lower rio Cataniapo, Atures, Amazonas, 5°32'50"N 67°26'53"W, 03 May 2001, J. Fernandez. MHNLS 14850 (1, not measured), Las Pavas, affluent of lower rio Cataniapo, Atures, Amazonas, 5°34'0"N 67°30'30"W, 27 Jun 2001, J. Fernandez. MHNLS 14984 (8, 17.2-28.8 mm SL), Morichal North of Cainama population, Parque Nacional Cainama, rio Caroni drainage, Bolívar, 6°12'35.9"N 62°51'8.7"W, 2 Sep 2002, C. Nascimento. MHNLS 15978 (1, 21.2 mm SL), caño Lapa, rio Tuparro, Vichada, 16 Jun 2004, M. Lugo. MHNLS 16384 (15, not measured), caño Culebra, affluent of rio Cataniapo, Puerto Ayacucho, Amazonas, 5°36'6"N 67°36'35"W, 17 Jan 2005, C. Lasso, A. Cervo & J. Fernandez. MHNLS 16487 (5, not measured), caño Culebra, right bank of rio Cataniapo, Puerto Ayacucho, Amazonas, 5°32'50"N 67°26'53"W, 19 Jan 2005, J. Fernandez. MHNLS 16539 (8, 24.3-33.9 mm SL), caño Danta right bank of rio Cataniapo, Ature, Amazonas, 5°34'32"N 67°32'28"W, 20 Jan 2005, J. Fernandez. MHNLS 16748 (1, not measured), caño Sarrapia, affluent of rio Cataniapo, upstream rocks, Puerto Ayacucho, Amazonas, 27 Jan 2005, J. Fernandez. MHNLS 16779 (2, not measured), caño Las Pavas, affluent of right margin of rio Cataniapo, Atures, Amazonas, 5°34'26"N 67°30'15"W, 28 Jan 2005, J. Fernandez. MHNLS 16791 (1, not measured), caño Las Pavas, affluent of right bank of rio Cataniapo, Atures, Amazonas, 5°34'26"N 67°30'15"W, 31 Jan 2005, J. Fernandez. MHNLS 16878 (4, not measured), rio Cataniapo, bridge nacional road, Atures, Amazonas, 5°36'15"N 67°35'1"W, 1 Feb 2005, C. Lasso *et al.* MHNLS 16878 (4, not measured), rio Cataniapo, bridge nacional road, Atures, Amazonas, 5°36'15"N 67°35'1"W, 1 Feb 2005, C. Lasso *et al.* MHNLS 18056 (7, 15.1-23.5 mm SL), caño Guapuchi, affluent of rio Ventuari, Amazonas, 4°11'35.7"N 66°44'56.7"W, 25 Jul 2005, C. Lasso *et al.* MHNLS 18169 (2, 25.3 and 34.6 mm SL), caño El Carmen, Amazonas, 3°57'22.3"N 67°5'25"W, 27 Jul 2005, C. Lasso *et al.* MHNLS 18186 (12, 16.0-35.1 mm SL), morichal caño verde, close to Manaka camping, Amazonas, 27 Jul 2005, C. Lasso *et al.* MHNLS 18233 (5, not measured), caño La Guardia, affluent of rio Cataniapo, Mosquito Torto section (at morichal), Apure, 6°49'30.3"N 67°19'43"W, 12 Aug 2005, C. Montaña. MHNLS 18309 (4, 15.5-16.9 mm SL), caño La Guardia, affluent of rio Cataniapo, morichal 3, Apure, 6°49'22.3"N 67°19'6.6"W, 15 Aug 2005, C. Montaña. MHNLS 19041 (34, 17.3-27.3 mm SL), rio Cuao, Raudal, El Danto community, Amazonas, 5°2'39"N 67°33'36.6"W, 2 May 2006, C. Lasso & J. C. Rodriguez. MHNLS 19128 (6, not measured), Tobogan de La Selva, Puerto Ayacucho-Samariapo road, Puerto Ayacucho, Amazonas, 5°23'14.6"N 67°37'0"W, 15 May 2006, C. Lasso & J. C. Rodriguez. SU 59116 (2, 32.1 and 33.9 mm SL), quebrada San Jaime, tributary of rio Amana,

15 km South of Maturin, Monagas, 19 Mar 1939, F. Bond. SU 59325 (4, 22.3-29.1 mm SL), tributary of rio Guarico, Calabozo, Guarico, 14 May 1939, F. Bond. USNM 272404 (137, 13.3-29.5 mm SL), small stream at Road from Puerto Ayacucho to Samariapo, 2 km of Mirabel, Amazonas, 12 Dec 1984, R. Vari, C. Ferrari & O. Castillo. USNM 272403 (25, 12.2-31.1 mm SL), igarapé Guayabal Puerto Ayacucho-Samariapo road, Amazonas, 12 Dec 1984, R. Vari, C. Ferraris & O. Castillo. USNM 235895 (13, 18.8-31.6 mm SL), small stream and swamp on both sides of Rt 19 about 8 km east of rio Aro, 79 km West of Ciudad Bolivar, Bolivar, 4 Nov 1979.

Rio Amazonas basin, Brazil. LBP 6911 (7, 20.6-32.0 mm SL), igarapé Km 50, BR 307, rio Negro, São Gabriel da Cachoeira, Amazonas, 0°6.803'S 66°48.744'W, Oliveira *et al.*, 9 Aug 2008. LBP 7105 (1, 29.4 mm SL), igarapé Km 35, BR 307, rio Negro, São Gabriel da Cachoeira, Amazonas, 0°3.381'S 66°51.007'W, Oliveira *et al.*, 17 Aug 2008. MZUSP 74064 (24, 15.5-30.1 mm SL), highland stream at São João, near Santa Isabel do Rio Negro, rio Negro drainage, Amazonas, 0°24'S 65°2'W, 23 Oct 1972, Expedição Permanente da Amazônia. MZUSP 74065 (30, 18.9-29.2 mm SL), highland stream at São João, near Santa Isabel do Rio Negro, rio Negro drainage, Amazonas, 0°24'S 65°2'W, 23 Oct 1972, Expedição Permanente da Amazônia. MZUSP 74066 (2, 19.6 and 24.8 mm SL), highland stream at São João, near Santa Isabel do Rio Negro, rio Negro drainage, Amazonas, 0°24'S 65°2'W, 23 Oct 1972, Expedição Permanente da Amazônia. MZUSP 64575 (3, 47.6-56.1 mm SL), igarapé Yoariwasotoamakúya, affluent of rio Tiquié, Cachoeira Comprida community, rio Negro drainage, Amazonas, 0°15'44"N 70°1'5"W, 23 Oct 2000, Índios Tuyuka. MZUSP 64576 (2, 30.0 and 33.7 mm SL), igarapé do Buriti, Caruru community, rio Tiquié, rio Negro drainage, Amazonas, 0°16'27"N 69°54'56"W, 25 Oct 2000, F. Lima *et al.* MZUSP 64616 (7, 21.7-31.4 mm SL, 3 c&s, 35.0-36.4 mm SL), stream affluent of rio Tiquié, Fronteira community, Brazil-Colombia limit, rio Negro drainage, Amazonas, 31 Oct 2002, F. Lima. MZUSP 64687 (9, 11.7-18.9 mm SL), igarapé Umari at São Pedro community, rio Tiquié, rio Negro drainage, Amazonas, 0°15'41"N 69°57'23"W, Oct 2000, F. Lima *et al.* MZUSP 66658 (2, 15.2 and 17.0 mm SL), mouth of stream upstream Cachoeira do Caruru, Caruru community, rio Tiquié, rio Negro drainage, Amazonas, 0°16'27"N 69°54'56"W, 22 Oct 2000, F. Lima. MZUSP 81292 (3, 13.5-14.5 mm SL), rio Tiquié downstream Cachoeira Comprida community and lower portion of igarapé do Urumutum, rio Negro drainage, Amazonas, 0°15'N 70°1'W, 15 Nov 2002, F. Lima *et al.* MZUSP 81339 (6, 14.0-42.8 mm SL), igarapé Umari Norte, from Cachoeira do Caruru to Cachoeira da Abelha, São Pedro community, rio Tiquié, rio Negro drainage, Amazonas, 0°16'N 69°58'16"W, 2002, F. Lima *et al.* MZUSP 81403 (21, 15.1-21.0 mm SL), igarapé Açaí, near São Pedro community, rio Tiquié, rio Negro drainage, Amazonas, 0°16'N 69°58'W, Nov 2002, F. Lima *et al.* MZUSP 81437 (4, 14.5-20.9 mm SL), rapids upstream cachoeira do Caruru, Caruru community, rio Tiquié, rio Negro drainage, Amazonas, 0°16'29"N 69°54'54"W, 19 Jun 2002, F. Lima. MZUSP 81443 (69, 12.7-55.6 mm SL, 3 c&s, 26.0-44.3 mm SL), igarapé do Buriti, Caruru community, rio Tiquié, rio Negro drainage, Amazonas, 0°16'29"N 69°54'54"W, 20-25 Oct and 8 Nov 2002, F. Lima. MZUSP 81452 (10, 9.3-31.9 mm SL), marginal lagoons downstream São Pedro community, rio Tiquié, rio Negro drainage, Amazonas, 0°16'N 69°56'W, 24 Oct 2002, F. Lima *et al.* MZUSP 81478 (5, 17.7-42.4 mm SL), clear water stream opposite to old São Pedro community, rio Tiquié, rio Negro drainage, Amazonas, 23 Oct 2000, F. Lima *et al.*

MZUSP 81494 (14, 11.5-26.5 mm SL), igarapé Mipiriyapotemakāya, affluent of igarapé Açaí, rio Tiquié, rio Negro drainage, Amazonas, 0°15'55"N 69°58'16"W, 29 Oct 2002, F. Lima *et al.* MZUSP 81551 (2, 17.8 and 18.9 mm SL), rio Tiquié, between São Pedro community and Cachoeira da Pedra Curta, rio Negro drainage, Amazonas, 0°16'N 69°58'W, 26 Oct 2002, F. Lima *et al.* MZUSP 84998 (11, 17.3-41.7 mm SL), stream at old São Pedro community, rio Tiquié, rio Negro drainage, Amazonas, 0°16'04,4"N 69°58'21,5"W, 22 Jun 2004, F. Lima. MZUSP 85034 (10, 13.3-41.4 mm SL), black water stream affluent of rio Tiquié, Fronteira community, rio Negro drainage, Amazonas, 0°15'35,2"N 70°2'42,6"W, 24 Jun 2004, F. Lima. MZUSP 85079 (1, 25.3 mm SL), Fronteira community, rio Tiquié, rio Negro drainage, Amazonas, 0°15'35,2"N 70°2'42,6"W, 24 Jun 2004, F. Lima. MZUSP 85149 (107, 12.8-48.3 mm SL, 8 c&s, 12.6-22.0 mm SL), igarapé do Buriti, Caruru community, rio Tiquié, rio Negro drainage, Amazonas, 0°16'N 69°54'W, 29 Jun to 1 Jul 2004, F. Lima. MZUSP 85192 (1, 23.0 mm SL), igarapé at São Tomé community, rio Negro drainage, Amazonas, 1 Jul 2004, F. Lima. MZUSP 92563 (11, 18.2-42.1 mm SL), stream affluent of rio Tiquié, Cunuri community, rio Negro drainage, Amazonas, 0°12'23"N 69°22'28"W, 27 Aug 2006, F. Lima. MZUSP 92573 (62, 8.1-16.8 mm SL, 35 c&s, 6.6-22.5 mm SL), igapó lake of igarapé Castanha affluent rio Tiquié, downstream Santa Rosa community, rio Negro drainage, Amazonas, 0°5'41"N 69°39'W, 3 Aug 2006, F. Lima *et al.* MZUSP 93345 (8, 14.7-41.1 mm SL), stream affluent of rio Tiquié, Serra do Mucura community, rio Negro drainage, Amazonas, 0°10'7"N 69°7'46"W, 10-11 Nov 2006, F. Lima *et al.*

Colombia. CZUT-IC 4542 (1, 13.7 mm SL), rio Cuduyarí, Piramiri, Vaupés, 1°22'0"N 70°33'6"W, 7 Nov 2009, F. Villa & A. Ortega. CZUT-IC 4854 (3, 15.9-25.5 mm SL), rio Guaduyuri, San Javier community, Vaupés, 7 Nov 2009, F. Villa & A. Ortega. CZUT-IC 4932 (4, 17.3-50.3 mm SL), caño el Sol, rio Vaupés, rio Negro drainage, Vaupés, 1°12'N 70°4'W, 10 Nov 2009, F. Villa & A. Ortega. CZUT-IC 7881 (1, 45.4 mm SL), rio Papuri, Piracuara community, rio Negro drainage, Yavarate, Vaupés, 21 Jul 2009, J. Suarez. IAvH 2331 (6, 28.3-32.9 mm SL), Quebrada Isue, rio Igará-Paraná, La Chorrera, Amazonas, 0°44'N 73°1'W, 5 Mar 1993, J. Perdomo. ICNMMNH 14057 (1, 38.8 mm SL), caño Mituceño, affluent of rio Vaupés, Mitú, Amazonas, 1°13'59,3"N 70°12'34,16"W, 1 Aug 2005, Proyecto Ornamentales Amazonas. ICNMMNH 14058 (1, 21.1 mm SL), caño Mituceño, affluent of rio Vaupés, Mitú, Amazonas, 1°13'59.3"N 70°12'34.16"W, 1 Aug 2005, Proyecto Ornamentales Amazonas. ICNMMNH 14059 (2, 15.4 and 16.3 mm SL), caño Mituceño, affluent of rio Vaupés, Mitú, Amazonas, 1°13'59.3"N 70°12'34.16"W, 1 Aug 2005, Proyecto Ornamentales Amazonas. ICNMMNH 14060 (10, 12.0-20.3 mm SL), caño Mituceño, affluent of rio Vaupés, Mitú, Amazonas, 1°13'59,3"N 70°12'34,16"W, 1 Aug 2005, Proyecto Ornamentales Amazonas. ICNMMNH 17170 (3, 18.2-23.3 mm SL), upper rio Apaporis, upstream Jiri-Jirimo, Apaporis, Vaupés, 19 Mar 2009, F. Arbeláez. ICNMMNH 11140 (77, 16.8-32.1 mm SL), rio Putumayo drainage, Orito, Putumayo, 1 Jul 2004, C. A. Cipamocha. MLS 175 (6, 25.8-27.2 mm SL), Puerto Narino, May 1957, H. Niceforo. MZUSP 85022 (1, 30.6 mm SL), Puerto Colombia community (=Pupunha) and downstream, rio Tiquié, Vaupés, 0°13'54.6"N 70°4'47.7"W, 23 Jun 2004, F. Lima. ZMB 31746 (3, 34.8-36.0 mm SL), near locality of metae, H. Franke.

Venezuela. MBUCV 11336 (190, 15.1-36.3 mm SL), cañito at road to Solano, about 6.2 km northeast San Carlos de Rio Negro, rio Negro, 16 Nov 1977, K. Clark. MBUCV 15110 (5, 20.4-34.3 mm SL), caño Chola,

at San Carlos de rio Negro-Solano road, rio Negro, Amazonas, 5 Dec 1984, R. Vari *et al.* MBUCV 15124 (5, 19.3-22.1 mm SL), caño Loro, at San Carlos de rio Negro-Solano road, rio Negro, rio Negro, Amazonas, 7 Dec 1984, A. Machado & D. Ibarra. MCNG 53804 (62, 24.8-42.7 mm SL), rio Baria, 350 meters from camp base, rio Negro, Amazonas, 8 Feb 2005. USNM 272412 (7, 24.0-43.2 mm SL), igarapé Temblador at San Carlos de Rio Negro-Solano road, upstream portion, Amazonas, 5 Dec 1984, R. Vari *et al.* USNM 269899 (27, 19.4-39.8 mm SL), Caño Loro where crossed by road from San Carlos de Rio Negro to Solano, Amazonas, 7 Dec 1984, A. Machado & D. Ibarra. USNM 272409 (6, 19.7-31.1 mm SL), flooded grasslands to side of road from San Carlos de Rio Negro-Solano, about 2 km from San Carlos, Amazonas, 4 Dec 1984, J. Fernandez & O. Castillo. USNM 269898 (9, 16.4-28.3 mm SL), Caño Chola, where crossed by road San Carlos de Rio Negro to Solano, Amazonas, 5 Dec 1984, R. Vari *et al.* USNM 272413 (1, 29.2 mm SL), flooded grasslands to side of road from San Carlos de Rio Negro-Solano, about 2 km from San Carlos, Amazonas, 4 Dec 1984, J. Fernandez & O. Castillo.

COPELLA NATTERERI (STEINDACHNER, 1876)

Figures 36,48-53; Tables 7 and 8

Pyrrhulina nattereri Steindachner, 1876: 8, pl. 2, fig. 5 and 6a [in part, see Remarks; type locality: Óbidos, in a tributary of the rio Amazonas].—Eigenmann & Eigenmann, 1889: 112 [in part, rio Trombetas and several localities at the rio Amazonas from Codajás to Óbidos, see discussion; brief description].—Regan, 1912 [Amazonas, brief description].—Fowler, 1940: 263 [literature compilation].—Meinken, 1952: 116 [comparison with *Pyrrhulina nigrofasciata* (= *Copella stigmasemion*)].

Copeina callolepis Regan, 1912: 393 [type locality: Amazonas].—Myers, 1927: 111 [comparison with *C. compta*].—Fowler, 1948: 344 [literature compilation; placed as synonym of *Copeina arnoldi*].—Weitzman & Weitzman, 2003: 242 [placed as synonym of *Copella nattereri*].—Zarske, 2011: 37-39, fig. 31 [revalidation; taxonomic notes].

Copeina nattereri.—Eigenmann, 1910: 428 [new combination; listed].

Copella nattereri.—Myers, 1956 [new combination, *Copella callolepis* as possible synonym].—Géry, 1963: 28 [comparison with *C. vilmae*; considers *Copella callolepis* conspecific with *C. nattereri*].—Géry, 1977: 147 [brief description; unnumbered figs of pg. 144 (third) and 145].—Weitzman & Weitzman, 2003: 242 [*Copeina callolepis* placed as synonym; literature compilation].—Arbeláez *et al.*, 2004: 103 [rio Amazonas at Letícia; listed].—Bogotá-Gregory & Maldonado-Ocampo, 2006: 47 [literature compilation].—Netto-Ferreira, 2006: 20 [phylogenetic analysis of Lebiasinidae].—Zarske & Géry, 2006: 19, figs. 2-3, 18 (lower specimen) [lectotype designation; photo of lectotype NMW 95055; redescription; taxonomic notes].—Galvis *et al.*, 2007a: 167, fig. 195 [Puerto Inírida; brief description].—Netto-Ferreira, 2010: 331 [phylogenetic analysis of Lebiasininae].

Copella callolepis.—Myers, 1956 [new combination; possible synonym of *C. nattereri*].—Géry, 1963: 28 [considers *Copella callolepis* conspecific with *C. nattereri*].—Zarske & Géry, 2006: 21, figs. 4-6 [lectotype designation; photo lectotype BMNH 1909.4.2.27; placed as synonym of *Copella nattereri*].

Copella cf. *arnoldi*.—Bogotá-Gregory & Maldonado-Ocampo, 2005: 64, Bogotá-Gregory & Maldonado-Ocampo, 2006: 74, Maldonado-Ocampo *et al.*, 2008: 183 [misidentification; listed].

Copella vilmae.—Mojica *et al.*, 2005: 200, Bogotá-Gregory & Maldonado-Ocampo, 2006: 74, Maldonado *et al.*, 2008 [rio Amazonas at Leticia; misidentification; listed].—Gutiérrez-E, 2006: 118, plate 8, fig. a, Galvis *et al.*, 2007b: 180, figs. 215 [misidentification; brief description].

Copella meinkeni Zarske & Géry, 2006: 27, figs. 12-15, 18 (upper specimen) [type locality: rio Negro at Novo Airão; identification key].—Zarske, 2011: 38, fig. 32 [taxonomic comment].

Copella spec. aff. *meinkeni*.—Zarske & Géry, 2006: 31, fig. 1, 16-17, 21, 26 [rio Tapajós, rio Amazonas at Santarém and Rio Preto da Eva, rio Negro, description; identification key].

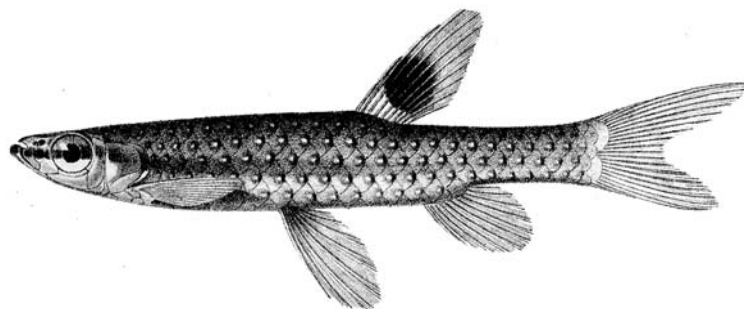


Figure 48. *Copella nattereri*, plate II, fig. 5 of Steindachner (1876).

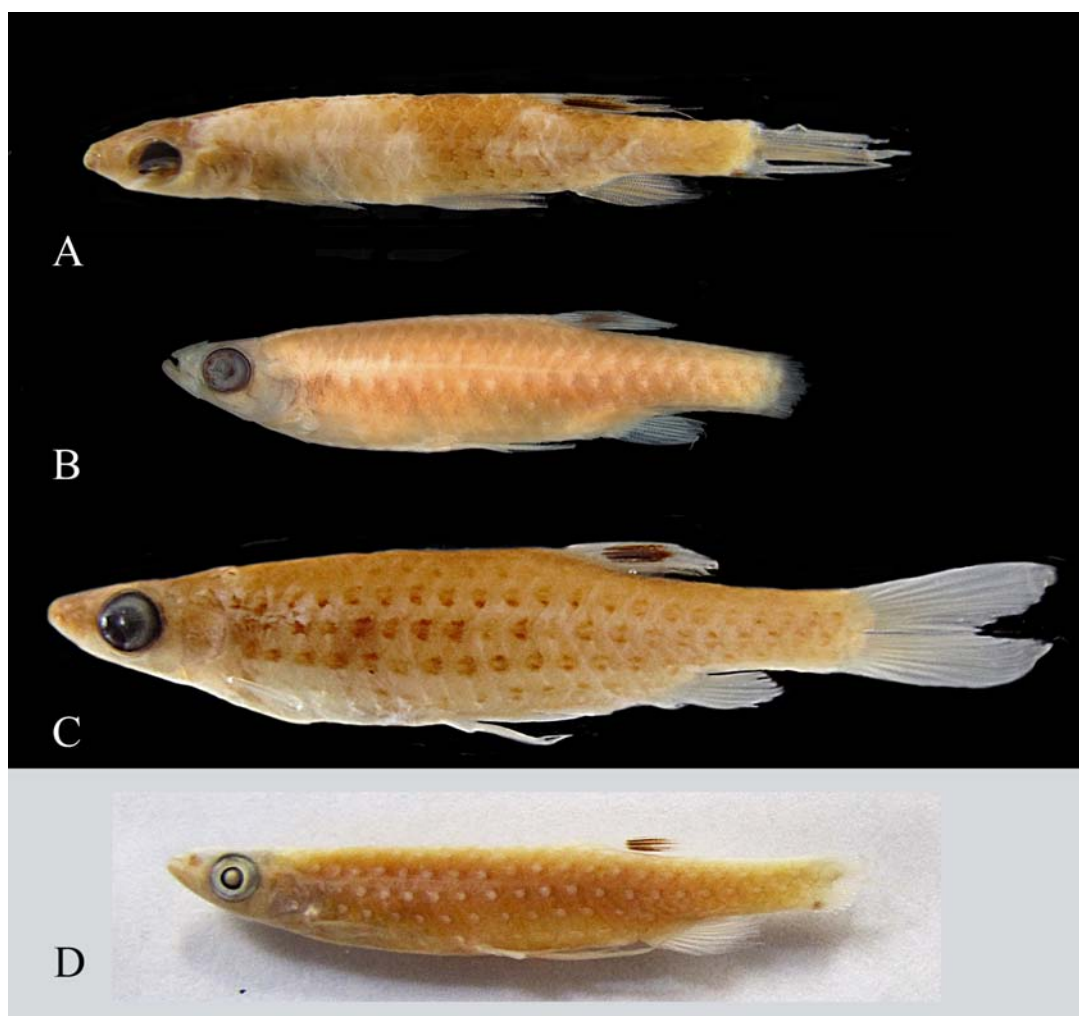


Figure 49. (A) Lectotype of *Pyrrhulina nattereri*, NMW 95055, male, 33.7 mm SL, Óbidos, Pará, Brazil, (B) lectotype of *Copeina callolepis*, BMNH 1909.4.2.27, male, 31.9 mm SL, Óbidos, Pará, Brazil, (C) holotype of *Copella meinkeni*, MTD F 30587, probably female, 40.6 mm SL, clear water stream on Southern Western bank of rio Negro about 5 km downstream Novo Airão, Amazonas, Brazil, (D) paratype of *Copella meinkeni*, NMW 56973 (33.0 mm SL), Codajás and Tabatinga, Brazil.



Figure 50. *Copella nattereri*, MZUSP 87426, (A) male, 39.3 mm SL, (B) female, 27.3 mm SL, (C) female, 25.7 mm SL, Rio Preto da Eva, Amazonas, Brazil, (D) MPEG 15913, female, 27.3 mm SL, rio Madeira, Maués, Amazonas, Brazil.



Figure 51. *Copella nattereri*, freshly-collected specimens, MZUSP 109514 a) male not preserved b) male, 35.8 mm, rio Negro, Santa Isabel do Rio Negro, Amazonas, Brazil.



Figure 52. *Copella nattereri*, live specimen not preserved, male. Photo: O. Lucanus.

Diagnosis. *Copella nattereri* can be distinguished from all congeners by the presence of a dark spot on each scale of the flank (*vs.* absence). It can be further distinguished from all the species, except *Copella stigmatsemion*, by having clear spots (red to purple in life) on the scales of the

flank, (*vs.* absence). It is distinguished from *C. stigmatemion* by the absence of a conspicuous black longitudinal band (*vs.* when present, longitudinal band dusky and not conspicuous).

Description. Morphometrics in Table 7 and 8. Largest examined male 45.0 mm SL, female 40.5 mm SL. Greatest body depth located slightly anterior to vertical through dorsal-fin origin. Body cylindrical, slightly compressed laterally. Dorsal profile of body straight to slightly concave from tip of snout to the end of supraoccipital, straight to slightly convex from that point to dorsal-fin origin, posteroventrally inclined along dorsal-fin base and straight along caudal peduncle. Ventral profile of body convex to posteroventrally inclined from anterior tip of dentary to the vertical through anterior margin of orbit, straight from that point to the vertical through pectoral-fin origin, slightly convex from that point to pelvic-fin origin, straight from pelvic-fin origin to anal-fin origin, posterodorsally inclined along anal-fin base and straight along caudal peduncle.

Mouth upturned. Premaxillary teeth in one row, with 15 (1), 16 (1), 18 (1), 19 (1), 20 (1), 21 (1), 22 (1), 24 (1) teeth, decreasing in size laterally. Number of maxillary teeth sexually dimorphic, 11 (1), 12 (1), 13 (1), 14 (1), 20 (1) in males, 6 (1), 7 (1), 8 (1) in females, decreasing in size posteriorly, especially on males. Dentary teeth in two rows, outer with 8 (1), 10 (3), 11 (3), 12 (1), increasing in size laterally, inner with 24 (3), 27 (1), 30 (1), 31 (2), 34 (1) teeth, decreasing in size laterally.

Dorsal fin with ii, 7 (1) or 8 (74)* rays, second and third branched rays longer. Pectoral fin with i, 8 (3), 9 (22)*, or 10 (26) rays, first three branched rays longer, their tips never reaching pelvic fin. Pelvic fin with i, 7 (73)* or 8 (3) rays, third branched ray longest. Anal fin with iii (5), 9 (74)* or 10 (1) rays, third and fourth branched rays longer. Caudal fin with i, 7 (7), 8 (58), or 9 (1) in upper lobe, first and second branched rays longer, and 6 (2), 7 (67) or 8

(1), i rays in lower lobe, second and third branched rays longer. Upper caudal-fin lobe longer than lower.

Predorsal scales 12 (6), 13 (42), or 14 (23)*. First longitudinal scale row with 11 (2), 12 (7), 13 (37), or 14 (24) scales. Fourth longitudinal scale row with 20 (2), 21 (14), 22 (35), or 23 (16) scales. Longitudinal scale rows between dorsal-fin origin and pelvic-fin origin 5 (29)* or 6 (43). Longitudinal scale rows between dorsal-fin origin and anal-fin origin 5 (71)*. Circumpeduncular scale rows 10 (70)*. Total number of vertebrae 32 (13)*, 33 (20) and 34 (5).

Table 7. Morphometrics of *Copella nattereri*. Lectotype of *Pyrrhulina nattereri* NMW 95055, lectotype of *Copeina callolepis* BMNH 1909.4.2.27, holotype of *Copella meinkeni* MTD F 30587, paralectotypes of *P. nattereri* NMW 57148 (1), NMW 56974 (3), paralectotype of *C. callolepis* BMNH 1909.4.2.28 (1), paratypes of *C. meinkeni* MHNG 2577.32 (1), MTD F 30588-30592 (5), and non-type material ANSP 191389 (3), ICN 16375 (3), ICN 16891 (2), MCZ 6259 (10), MHNG 2577.048 (5), MZUSP 63522 (3), MZUSP 63526 (3), MZUSP 63527 (2), MZUSP 66733 (4), MZUSP 66766 (8) MZUSP 87426 (10), MZUSP 109514 (6), and USNM 311005 (3), n = number of specimens, SD = Standard deviation. Range does not include primary types.

	<i>Pyrrhulina nattereri</i>	<i>Copeina callolepis</i>	<i>Copella meinkeni</i>					
	Lectotype	Lectotype	Holotype	n	Range	Mean	SD	
Standard length (mm)	33.7	31.9	40.6	73	21.6	45.0	30.2	6.2
Percents of standard length								
Body depth	15.6	19.8	20.6	73	14.0	22.9	18.7	1.7
Dorsal- to caudal-fin origin	33.8	38.9	38.1	73	35.1	63.3	38.4	3.3
Snout to dorsal-fin origin	63.7	62.2	62.1	73	36.6	66.3	62.1	3.4
Snout to pectoral-fin origin	24.7	23.2	24.6	73	21.6	26.7	24.1	1.1
Snout to pelvic-fin origin	48.6	47.2	50.6	73	24.4	51.9	48.8	3.3
Snout to anal-fin origin	72.9	70.9	74.8	73	23.0	76.4	71.4	6.0
Pectoral- to pelvic-fin origin	22.9	27.4	25.1	73	21.5	28.5	25.6	1.6
Pelvic- to anal-fin origin	23.1	23.7	25.9	73	21.6	26.7	24.2	1.2
Pectoral-fin length males	17.8	-	-	35	14.6	22.1	18.5	1.8
Pectoral-fin length fem/imm	-	-	17.5	28	15.8	21.8	18.7	1.3
Pelvic-fin length males	24.7	20.5	-	41	15.5	38.6	25.1	6.5
Pelvic-fin length fem/imm	-	-	18.2	29	16.0	20.8	18.0	1.1
Dorsal-fin length males	29.4	22.6	-	40	20.2	53.3	30.8	8.0
Dorsal-fin length fem/imm	-	-	22.4	29	21.4	28.9	24.0	1.6
Anal-fin length males	21.9	16.7	-	44	16.3	25.9	21.6	2.3
Anal-fin length fem/imm	-	-	17.5	29	16.3	22.8	18.9	1.4
Anal-fin base length	9.4	9.2	8.0	73	6.7	10.3	8.8	0.7
Caudal peduncle depth	8.1	10.9	9.9	73	7.1	10.8	9.3	0.7
Caudal peduncle length	20.0	19.2	17.7	73	17.1	21.6	19.5	0.9
Head length	24.0	23.3	25.4	73	21.2	26.0	23.9	1.2
Percents of head length								
Eye diameter	33.5	34.4	36.8	72	30.1	42.6	35.6	2.5
Snout length	31.5	26.7	33.2	72	25.0	33.3	29.7	2.0
Interorbital distance	34.6	37.9	36.4	72	33.7	41.9	38.0	2.0
Upper jaw length	27.5	32.5	29.7	70	21.8	35.2	28.0	2.4

Table 8. Meristic of lectotype of *Pyrrhulina nattereri* NMW 95055, lectotype of *Copeina callolepis* BMNH 1909.4.2.27, and holotype of *Copella meinkeni* MTD F 30587.

	<i>Pyrrhulina nattereri</i>	<i>Copeina callolepis</i>	<i>Copella meinkeni</i>
	Lectotype	Lectotype	Holotype
Predorsal scales	14	13	13
First longitudinal scale row	-	12	13
Fourth longitudinal scale row	-	21	21
Longitudinal scale rows dorsal to pelvic	5	5	6
Longitudinal scale rows dorsal to anal	5	5	5
Circumpeduncular scale rows	-	10	10
Pectoral-fin rays	i9	i8	i9
Pelvic-fin rays	i6i	i7	i7
Dorsal-fin rays	ii8	ii8	ii8
Branched anal-fin rays	9	9	9
Caudal-fin rays	-	-	i8,7i

Color in alcohol. Overall ground coloration of body beige to brown. Dorsal portion of body dark, ventral clear. Dark stripe extending from anterior tip of dentary to posterior tip of opercle. Thin predorsal dark stripe, sometimes wider and with guanine deposition over second and third scales. A clear spot on posterior portion of scales of second or third to sixth longitudinal scale rows, limited dorsally, posteriorly and ventrally by dark pigmentation, usually horseshoe-like shaped. Scales with posterior border dark in some individuals (Figs. 50A and 51A). Subjacent coloration of flank homogeneous (Fig. 50A, B and D) or with a clear band on third longitudinal scale row, contrasting with dark band of subjacent pigmentation, on fourth to fifth longitudinal scale rows of variable intensity, more conspicuous anteriorly (Fig. 50C). Ventral region of body clear. Black round spot on dorsal fin above a smaller white one. Remaining fins hyaline. Pelvic and anal fin usually with dark edge, usually more intense in males. Dorsal and ventral procurrent caudal-fin rays hyaline or dark (Fig. 51A). Pigmentation of procurrent caudal-fin rays more conspicuous in males than females and usually absent in

juveniles. Adult specimens with hyaline procurrent caudal-fin rays only found in the rio Negro basin (Fig. 51B).

Color in life. Dorsolateral portion of body grayish, ventral portion creamy. Distal portion of scales on second or third to sixth longitudinal scale rows with red to purple spots, limited dorsally, posteriorly and ventrally by dark pigmentation. A dark longitudinal band on fourth and fifth longitudinal scale rows. Fins orange colored to hyaline (Figs. 51 and 52).

Sexual dimorphism. Males longer than females. Males with more maxillary teeth than females (see description above). Pelvic, dorsal and anal fin of males longer than in females (Fig. 53). Length of pectoral fin apparently not dimorphic. Tip of adpressed pelvic fin reaching up to base of last branched anal-fin ray in males, and up to anus in females. Tip of adpressed dorsal fin reaching up one-half the length of middle caudal-fin rays in males, and approximately up to one-half the length of caudal peduncle in females. Tip of adpressed anal-fin reaching up to the level of first ventral procurrent rays in males, and up to two-third length of caudal peduncle in females (Fig. 53). Upper caudal-fin lobe longer than lower, especially in males. No evidence of sexual dimorphism related to color pattern in this species.

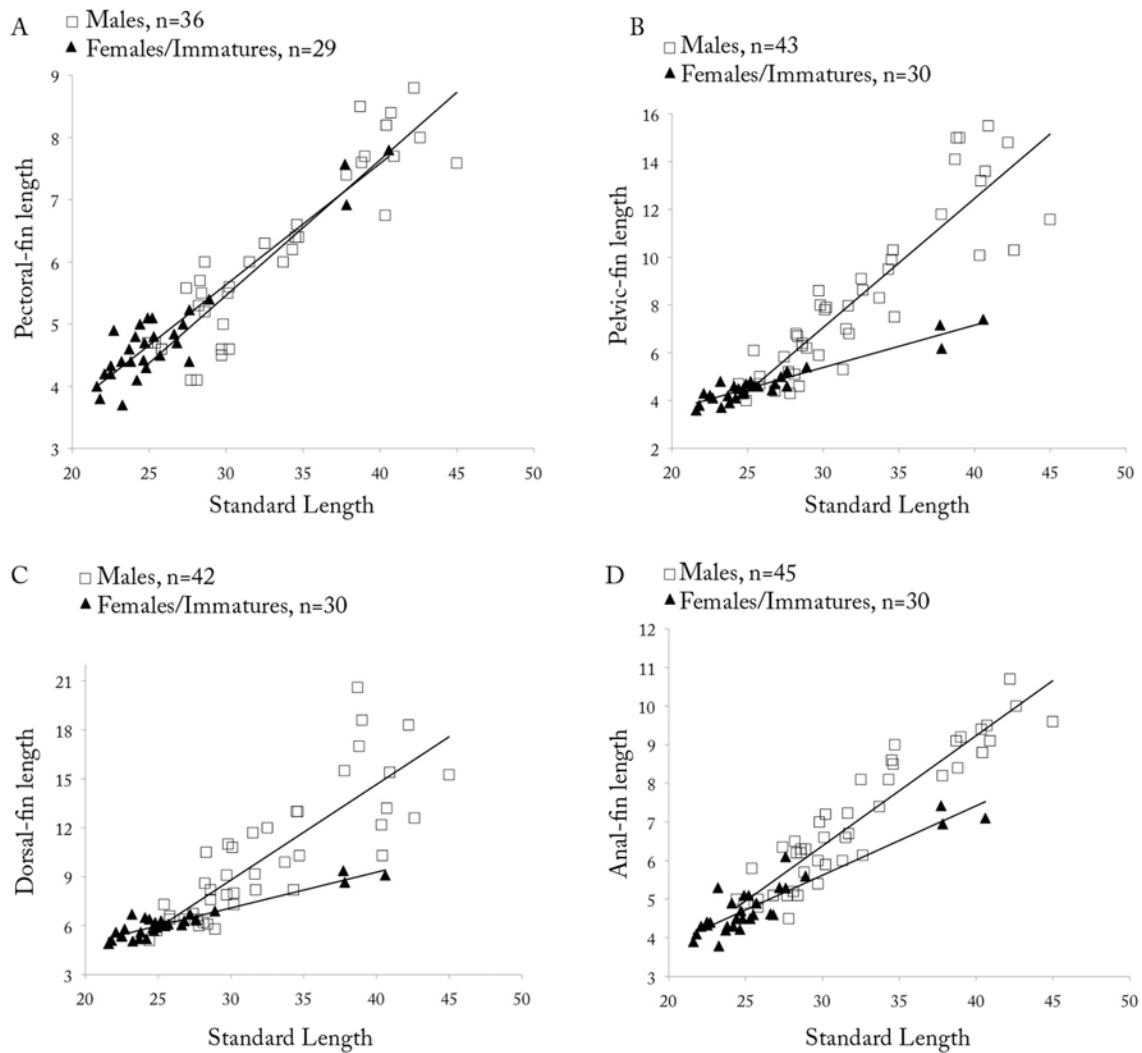


Figure 53. *Copella nattereri*, pectoral-, pelvic-, dorsal- and anal-fin length as function of SL by sex.

Distribution. Rio Amazonas at Letícia, Colombia; rio Amazonas from mouth of rio Negro to mouth of rio Tapajós, Brazil; rio Negro basin, Brazil, Venezuela and Guyana; upper and middle rio Orinoco basin, Venezuela (Fig. 36).

Remarks. The description of *Pyrrhulina nattereri* by Steindachner (1876) is based on specimens designated as syntypes from two localities: “Joh. Natterer collected the here-described species in

many samples at the mouth of the Rio Negro and by Prof. Agassiz [= Thayer Expedition] at Óbidos in an tributary of the Amazon”. Possible types of *Pyrrhulina nattereri* are known to be deposited in the NMW, MSNG, ZMUC and MCZ museums. The specimens deposited at NMW from the Thayer Expedition collected in Óbidos are considered type material (NMW 56974, 57148 and 95055). The lot NMW 56973 from Codajás and Tabatinga, is questionably marked as type material of *Pyrrhulina nattereri*, but the locality does not match with those mentioned in the original description and cannot be considered type material. Later on, this lot was listed by Zarske & Géry (2006) as paratypes of *Copella meinkenii* (= *Copella nattereri*) (Fig. 49D). Samples deposited in the Genova and Copenhagen museums are said to be from the rio Amazonas without further information. The material from Genova (MSNG 9239, 1 specimen), and Copenhagen (ZMUC P241264 and P241265, 2 specimens) were donated by Steindachner in 30 Oct 1880 (G. Doria personal communication) and in 1876 (J. Nielsen personal communication), respectively, and therefore should be considered paralectotypes of *Pyrrhulina nattereri*. On the other hand, there is no information to justify considering the 57 specimens (MCZ 6259) deposited at Harvard, collected during the Thayer Expedition in Óbidos, as types material (more information below). It is not clear whether Steindachner analyzed this material or not during his stay at Harvard from 1870-1871 (before he left to take part in Hassler’s expedition from 1871 to 1872, according to Borodin, 1929). Since this material has not been specifically designated I find no reason to consider it as type material.

Despite Zarske’s effort in searching the material from the mouth of the rio Negro, it was never found and considered probably lost (Zarske & Géry, 2006). The lack of details on the origin of the samples deposited at MSNG and ZMUC raises the possibility that it could have come from that locality, but this is not confirmed.

In the present study, only the types of *Copella nattereri* from the NMW museum could be examined. The lot NMW 56974 has five numbered paralectotypes. Numbers 1, 2 and 5 (28.8, 28.8 and 32.0 mm SL, respectively) represent, indeed, *C. nattereri*. Number 3 probably belongs to *C. stigmatsemion* (28.9 mm SL) and number 4 (24.0 mm SL) is a specimen of *Copella* not precisely identified due to its poor condition. The lot NMW 57148 has four paralectotypes in poor conditions. The smallest (16.4 mm SL) is a *Nannostomus* sp. with a dark band on body and the remaining are *Copella nattereri*.

The topotypes under MCZ 6259 mentioned above as not representing type material were actually part of a mixture including other lots bearing MCZ numbers 6263+6300+6835+6836+6837. Examination of the 78 specimens in this mixture revealed the presence of *Copella nattereri* (57 specimens, 18.3-30.7 mm SL), *C. stigmatsemion* (9, 28.9-32.9 mm SL), *Copella* sp. (10, 17.3-28.1 mm SL) and *Pyrrhulina* sp. (2, 25.9-29.2 mm SL, in poor condition). The 57 specimens of *Copella nattereri* kept MCZ catalog number 6259 and the others received the numbers MCZ 170504, MCZ 170505, and 170506, respectively.

Steindachner (1876) originally describes *Pyrrhulina* (= *Copella*) *nattereri* based in the presence of a bright spot close to the posterior edge of the body scales, bordered with dark brown pigmentation, except for its anterior edge. Steindachner also mentions that a weak dark longitudinal band is not rare between the third and the fourth longitudinal scale rows (Fig. 48). Zarske & Géry (2006) chose a lectotype for *Copella nattereri* and discussed about its identity, stating that it does not correspond to the same species that has been traditionally referred by aquarists as *Copella nattereri* (the “spotted tetra”), but to what has been named *Copella nigrofasciata* (= *Copella stigmatsemion*), species that has a black longitudinal band and one to three conspicuous longitudinal rows of clear spots on body (Fig. 56), and made available a new name for the spotted tetra, *Copella meinkeni* (Fig. 49C). The analysis of the lectotype of

Pyrrhulina nattereri revealed that it clearly has the same color pattern as described by Steindachner (Fig. 49A), not the characteristic coloration of *Copella stigmatemion*. Therefore, *C. meinkenii* is considered junior synonym of *Copella nattereri*, the valid name for the spotted tetra.

Regan (1912) described *Copeina callolepis* (now in *Copella*) (Fig. 49B), species with identical color pattern to that of *Pyrrhulina* (= *Copella*) *nattereri*, not comparing the specimens he had with specimens of the latter species. Weitzman & Weitzman (2003) and Zarske & Géry (2006) considered Regan's species a junior synonym of *Copella nattereri*. Later on, Zarske (2011) revalidated *Copella callolepis* based on the specimens listed in Zarske & Géry (2006) as "*Copella* spec. aff. *meinkenii*", and distinguished *C. callolepis* from his *Copella meinkenii* (= *Copella nattereri*) by having small body length (*vs.* large) and a black mark on the ventral procurrent caudal-fin rays (*vs.* hyaline). Regarding body length, the largest specimen examined with dark ventral procurrent caudal-fin rays (the presumable *C. callolepis*) has 42.2 mm SL *vs.* largest specimen with hyaline procurrent rays 45.0 mm SL (which is one of the paratypes of *C. meinkenii*, a large, fat, probably aquarium specimen). Such difference is not considered significant to diagnose *Copella callolepis* from *C. nattereri*. The presence of a black mark on the ventral procurrent caudal-fin rays is herein considered variable within *Copella nattereri* (see Color in alcohol section). Although both conditions (presence and absence of a dark mark on the procurrent caudal-fin rays) are only found in the adult specimens from the rio Negro basin (Fig. 51B) (adults of the remaining localities where this species is found have procurrent caudal-fin rays dark and, juveniles from all the localities usually lack a dark mark on procurrent caudal-fin rays). Therefore this feature was not found to be unambiguous to recognize a different species. Furthermore, dark procurrent rays can be even observed in some paratypes of *C. meinkenii* (NMW 56973: Fig. 49D). In conclusion, no morphometric, meristic, osteological or

other color features were found to justify considering *Copella callolepis* or *C. meinkenii* valid species. For this reason both species are considered junior synonyms of *C. nattereri*.

Zarske & Géry (2006) listed “15 out of 30” specimens of the lot MHNG 2205.096 as paratypes of *Copella meinkenii*. There are actually a total of 41 specimens in the lot, including the paratypes, which are mixed.

The specific localities cited by Eigenmann & Eigenmann (1889) for *Pyrrhulina* (= *Copella*) *nattereri* are: rio Trombetas, rio Amazonas at Villa Bella (= Parintins), Manaus, Silves, Lago Saracá, Lago Hyanauari (= Janauari), Codajás, and Jatuarana [probably near Parintins (Lima *et al.*, 2003)].

Ulrey (1895) listed *Pyrrhulina* (= *Copella*) *nattereri* for the lower Amazon, Brazil, but I had no opportunity to confirm his identification.

Type material of *Copella nattereri* and synonym species not examined is: MSNG 9239 (1, Paralectotype of *Pyrrhulina nattereri*), rio Amazonas. ZMUC P241264 and P241265 (2, *Pyrrhulina nattereri*), rio Amazonas. MTD F 29454–29456, 3 paralectotype of *C. meinkenii*. MTD F 17133–17136, 4 paralectotype of *C. meinkenii*. Priv. Coll. Géry: 1076: 1–2.2006, 2 Ex paralectotype of *C. meinkenii*, rio Trombetas.

MATERIAL EXAMINED

Type material

Rio Amazonas basin, Brazil. NMW 56974 (5 paralectotypes of *Pyrrhulina nattereri*, 24.0-32.0 mm SL) and NMW 57148 (3 of 4 paralectotypes of *Pyrrhulina nattereri*, 16.4-31.6 mm SL), same data as the lectotype, see Remarks for additional information. NMW 95055 [ex NMW 57148] (lectotype of *Pyrrhulina nattereri*, 33.7 mm SL), Óbidos [=Pará], in a tributary of the rio Amazonas, 1865, Thayer Expedition. BMNH 1909.4.2.27 (lectotype of *Copeina callolepis*) and BMNH 909.4.2.28 (1 paralectotype of *Copeina callolepis*), Amazon, J. Arnoldi. MHNG 2577.032 (1 paratype of *Copella meinkeni*, 24.4 mm SL), rio Araçá, lake near Boa Vista, rio Negro, 0°11'S 63°11'W, 1-16 Jan 1987, A. Hanrieder. MNHG 2577.048 (19 paratypes of *Copella meinkeni*, 21.0-31.7 mm SL), rio Araçá, Negro, Amazonas, 0°1'S 63°11'W, 1-31 Jan 1987. MHNG 2205.096 (in part: 15 paratypes of *Copella meinkeni* of 41 non types, 11.5-20.5 mm SL), rio Tarumã around Manaus, 3°0'34"S 60°4'58"W, 1919 Oct 1965, J. Géry. MTD F 30587 (holotype of *Copella meinkeni*, 40.6 mm SL), clear water stream on Southern Western bank of rio Negro about 5 km downstream Novo Airão, Amazonas, Brazil, 1986, W. Staeck. MTD F 30588-30592 (5 paratypes of *Copella meinkeni*, 37.7-45.0 mm SL), Brazil, Lamarque AM 10 km 21+2, near pisciculture, 30 Oct 1978. NMW 56973 (7 paratypes of *Copella meinkeni*, 27.5-37.0 mm SL), Codajás and Tabatinga, Brazil, 1874 donation, Thayer Expedition.

Non-type material

Rio Amazonas basin, Brazil. MCZ 6259 (57, 18.3-30.7 mm SL), rio Amazonas at Óbidos [approximately 1°52'S 55°30'W], Nov-Dec 1865, Thayer Expedition. MHNG 2200.020 (9, 22.1-41.1 mm SL), stream at Rio Preto da Eva, at Manaus-Itacoatiara road, Amazonas, 21 Nov 1976, H. Axelrodi, M. Brittan & B. Frank. MHNG 2200.021 (2, 33.1 and 40.8 mm SL), Santa Isabel do Rio Negro, upper rio Negro, Amazonas, Oct 1962. MHNG 2205.095 (7 of 14, 17.0-23.4 mm SL), igarapé Aduja, rio Itu, rio Negro, Amazonas, 0°44'N 63°41'W, 10 Nov 1962. MHNG 2205.097 (1, 18.8 mm SL), "rio Negro?", Amazonas, 1 Oct 1965. MHNG 2575.099 (3, 24.4-27.5 mm SL), rio Araçá, rio Negro, Amazonas, 1 Jan 1983-31 Dec 1984. MHNG 2576.050 (5, 12.0-18.8 mm SL), igarapé Mamolé, tributary of rio Cuiuni, rio Negro, Amazonas, 0°45'S 63°9'W, 16-17 Nov 1984. MHNG 2576.069 (10 of 14, 8.1-20.6 mm SL), right bank of lower portion of stream tributary of rio Tapajós, surrounding the city upstream, Santarém, Pará, 27 Sep 1980, S. Kullander. MHNG 2711.041 (12, 27.1-29.2 mm SL), rio Araçá, Negro, Amazonas, 1°S 63°11'W, 1-16 Jan 1987. A. Hanrieder. MPEG 130 (1, 30.4 mm SL), Ilha de Tamaquaré, rio Negro, Santa Isabel do Rio Negro, Amazonas, 7 Feb 1980, M. Golding. MPEG 131 (8, 16.8-27.1 mm SL), rio Negro, Anavilhanas, Novo Airão, Amazonas, 1 Apr 1982, M. Golding. MPEG 132 (1, 24.0 mm SL), Ilha de Buiu-açú, near rio Urubaxi, rio Negro, Santa Isabel do Rio Negro, Amazonas, 6 Feb 1980, M. Golding. MPEG 9290 (1, 30.0 mm SL), headwater of igarapé Juruti Grande,

Amazonas, Juruti, Pará, 2°34'29.7"S 56°24'12.2"W, 5 Aug 2004, W. Wosiacki. MPEG 9291 (2, 27.8 and 39.0 mm SL), headwater of igarapé Juruti Grande, Juruti, Pará, 2°34'36"S 56°24'3"W, 4 Aug 2004, W. Wosiacki. MPEG 9820 (7, 10.8-21.4 mm SL), igarapé Juruti Grande, right tributary, Juruti, Pará, 2°29'39.4"S 56°20'43.8"W, 6 Sep 2002, W. Wosiacki. MPEG 10936 (9, 15.2-25.2 mm SL), igarapé Itapiranga, Juruti, Pará, 2°28.2'13.7"S 56°11'40.4"W, 23 Aug 2006, A. Hercos. MPEG 10938 (2, 20.7 and 35.5 mm SL), igarapé Itapiranga, Juruti, Pará, 2°28.2'13.7"S 56°11'40.5"W, 22 Aug 2006, A. Hercos. MPEG 10943 (1, 16.4 mm SL), igarapé Itapiranga, Juruti, Pará, 2°28.2'13.7"S 56°11'40.4"W, 22 Aug 2006, A. Hercos. MPEG 10960 (9, 13.7-18.7 mm SL), igarapé Itapiranga, Juruti, Pará, 2°28.2'13.7"S 56°11'40.4"W, 22 Aug 2006, A. Hercos. MPEG 12913 (5, 15.5-21.2 mm SL), igarapé Itapiranga, Juruti, Pará, 16 Dec 2006, L. Montag. MPEG 12915 (1, 20.0 mm SL), igarapé Itapiranga, Juruti, Pará, 30 Dec 2006, L. Montag. MPEG 12946 (1, 21.5 mm SL), igarapé Itapiranga, Juruti, Pará, 16 Dec 2006, L. Montag. MPEG 12948 (2, 21.7 and 21.9 mm SL), igarapé Guaraná, Juruti, Pará, 16 Dec 2006, L. Montag. MPEG 13765 (6, 28.5-33.4 mm SL), igarapé Itapiranga, Juruti, Pará, 2°28.2'S 56°11.51'W, 13 May 2007, A. Hercos. MPEG 13788 (2, 18.2 and 27.0 mm SL), igarapé Itapiranga, Juruti, Pará, 2°28.2'S 56°11.513'W, 13 May 2007, A. Hercos. MPEG 14225 (5, 23.4-31.1 mm SL), igarapé Itapiranga, Juruti, Pará, 2°28.2'S 56°11.513'W, 29 Nov 2007, A. Hercos. MPEG 14227 (4, 19.9-27.5 mm SL), igarapé Itapiranga, Juruti, Pará, 2°28.2'S 56°11.513'W, 29 Nov 2007, A. Hercos. MPEG 14233 (2, 17.0 and 19.4 mm SL), igarapé Guaraná, Juruti, 2°29.77'S 56°13.84'W, 28 Nov 2007. MPEG 14347 (6, 20.5-32.8 mm SL), igarapé Mutum, Juruti, Pará, 2°36.8'S 56°11.6'W, 27 Nov 2007, A. Hercos. MPEG 14430 (2, 15.2 and 23.9 mm SL), rio Sacará, Trombetas, Oriximiná, Pará, 1°48'9.3"S 56°16'32.9"W, 20 Oct 2007, W. Wosiacki. MPEG 14596 (2, 21.2 and 22.1 mm SL), rio Sacará, Trombetas, Oriximiná, Pará, 1°48'9.3"S 56°16'32.9"W, 20 Oct 2007, W. Wosiacki. MPEG 15108 (2, 21.0 and 21.4 mm SL), igarapé do Piraquara, Nhamundá, Faro, Pará, 1°50'43.5"S 57°12'53.6"W, 23 Jan 2008, L. Montag. MPEG 15329 (4, 24.1-29.7 mm SL), Trilha T1, Nhamundá, Faro, Pará, 1°42'23.3"S 57°12'10.1"W, 26 Jan 2008, L. Montag. MPEG 15352 (1, 32.9 mm SL), Trilha T1, Nhamundá, Faro, Pará, 1°42'23.3"S 57°12'10.1"W, 26 Jan 2008, L. Montag. MPEG 15429 (5, 18.1-23.8 mm SL), Porto Cikel, Nhamundá, Faro, Pará, 1°42'48.4"S 57°12'48.4"W, 27 Jan 2008, L. Montag. MPEG 15905 (9, 9.9-33.9 mm SL), igarapé Itaubaizinho, affluent of rio Paraconi, FLONA do Pau Rosa, Maués, Amazonas, 3°50'18.3"S 58°13'0"W, 16 Feb 2009, F. Silva. MPEG 15906 (1, 28.8 mm SL), igarapé Itaubaizinho, affluent of rio Paraconi, FLONA do Pau Rosa, Maués, Amazonas, 3°49'50.2"S 58°17'36.5"W, 17 Feb 2009, F. Silva. MPEG 15907 (67, 15.9-34.5 mm SL), igarapé Itaubaizinho, affluent of rio Paraconi, FLONA do Pau Rosa, Maués, Amazonas, 3°46'38.4"S 58°15'12.9"W, 15 Feb 2009, F. Silva. MPEG 15908 (24, 23.8-33.9 mm SL), igarapé Cipoteua, rio Paraconi drainage, FLONA do Pau Rosa, Maués, Amazonas, 3°46'57.1"S 58°19'0.6"W, 14 Feb 2009, F. Silva. MPEG 15909 (9, 22.6-33.9 mm SL), igarapé Itaubaizinho, affluent of rio Paraconi, FLONA do Pau Rosa, Maués, Amazonas, 3°43'36.9"S 58°36.9'58"W, 13 Feb 2009, F. Silva. MPEG 15911 (20, 24.3-31.9 mm SL), igarapé Itaubaizinho, affluent of rio Paraconi, FLONA do Pau Rosa, Maués, Amazonas, 3°56'25.2"S 58°26'43.4"W, 25 Feb 2009, F. Silva. MPEG 15912 (5, 24.4-33.2 mm SL), igarapé Uixi, affluent of rio Paraconi, FLONA do Pau Rosa, Maués, Amazonas, 3°46'38.4"S 58°15'12.9"W, 15 Feb 2009, F. Silva. MPEG 15913 (41, 21.0-

33.4 mm SL), affluent of igarapé Palhai, rio Paraconi drainage, FLONA do Pau Rosa, Maués, Amazonas, 4°13'6.6"S 58°16'54.9"W, 21 Feb 2000, F. Silva. MPEG 15914 (28, 13.7-30.6 mm SL), igarapé Itaubalzinho, affluent of rio Paraconi, FLONA do Pau Rosa, Maués, Amazonas, 3°56'23.2"S 58°22'4.5"W, 23 Feb 2009, F. Silva. MPEG 15915 (9, 21.8-24.7 mm SL), igarapé Itaubalzinho, affluent of rio Paraconi, FLONA do Pau Rosa, Maués, Amazonas, 4°48'56.8"S 58°17'42.5"W, 18 Feb 2009, F. Silva. MPEG 15919 (4, 16.5-30.1 mm SL), drainage of Lago do Elias, Paranã do Uraria, Maués, Amazonas, 3°43'29.8"S 58°16'18.3"W, 12 Feb 2009, F. Silva. MPEG 15974 (5, 10.4-14.5 mm SL), igarapé Azedal, rio Paraconi drainage, FLONA do Pau Rosa, Maués, Amazonas, 3°58'12.2"S 58°24'16.1"W, 24 Feb 2009, F. Silva. MPEG 15975 (1, 14.0 mm SL), igarapé Itaubalzinho, rio Paraconi drainage, FLONA do Pau Rosa, Maués, Amazonas, 3°48'56.8"S 58°17'42.5"W, 18 Feb 2009, F. Silva. MPEG 15976 (1, 22.8 mm SL), igarapé Palhalzinho, rio Paraconi drainage, FLONA do Pau Rosa, Maués, Amazonas, 3°49'50.2"S 58°17'36.5"W, 17 Feb 2009, F. Silva. MPEG 15977 (14, 14.9-27.1 mm SL), igarapé Itaubalzinho, affluent of rio Paraconi, FLONA do Pau Rosa, Maués, Amazonas, 4°6'6.1"S 58°18'58.4"W, 22 Feb 2009, F. Silva. MPEG 15978 (1, 26.0 mm SL), Lago do Elias, Paranã do Urariá, surroundings of FLONA do Pau Rosa, Maués, Amazonas, 3°43'29.8"S 58°16'18.3"W, 12 Feb 2009, F. Silva. MPEG 16019 (7, 8.8-25.0 mm SL), igarapé Itaubalzinho, affluent of rio Paraconi, FLONA do Pau Rosa, Maués, Amazonas, 3°38'12.2"S 58°24'16.1"W, 24 Feb 2009, F. Silva. MPEG 16021 (1, 25.9 mm SL), igarapé Itaubalzinho, affluent of rio Paraconi, FLONA do Pau Rosa, Maués, Amazonas, 3°56'25.2"S 58°26'43.4"W, 25 Feb 2009, F. Silva. MPEG 16039 (32, 10.5-17.7 mm SL), igarapé Itaubalzinho, affluent of rio Paraconi, FLONA do Pau Rosa, Maués, Amazonas, 3°48'56.8"S 58°17'42.5"W, 15 Mar 2009, F. Silva. MPEG ex 15917 (21, 11.7-32.2 mm SL), igarapé Tamoatá, rio Paraconi drainage, FLONA do Pau Rosa, Maués, Amazonas, 3°44'47.1"S 58°18'7.6"W, 14 Feb 2009, F. Silva. MZUSP 5576 (1, 17.5 mm SL), lagoa Parauacuí, Trombetas, Oriximiná, Pará, 1°46'S 55°52'W, 9 Feb 1967, Expedição Permanente da Amazônia. MZUSP 5810 (25, 14.4-21.1 mm SL), lago Saracá, Amazonas, Silves, Amazonas, 2°52'S 58°22'W, 17-18 Mar 1967, Expedição Permanente da Amazônia. MZUSP 6233 (7, 13.4-25.7 mm SL), lake at rio Negro margin upstream Manaus, rio Negro, Amazonas, 3°10'S 60°0'W, 28 Apr 1967, Expedição Permanente da Amazônia. MZUSP 6804 (8, 22.3-34.2 mm SL), igarapé do Rei, island close to the rio Cuieiras mouth, rio Negro, Amazonas, 2°42'S 60°20'W, 26 Jan 1977, Alpha Helix Amazon Expedition. MZUSP 6827 (81, 13.3-26.5 mm SL), igarapé Tarumãzinho and affluent number 1, North of Manaus, rio Negro, Amazonas, 3°2'S 60°9'W, Nov 1967, Expedição Permanente da Amazônia. MZUSP 6930 (32, 13.4-20.7 mm SL), stream of lago Puraquequara, Amazonas, 2°56'S 59°49'W, 23 Nov 1967, Expedição Permanente da Amazônia. MZUSP 7289 (91, 12.1-30.8 mm SL), stream of rio Maraú, Maués, Amazonas, 3°24'S 57°42'W, 3 Dec 1967, Expedição Permanente da Amazônia. MZUSP 7346 (379, 11.7-31.3 mm SL, 1 c&s, 31.6 mm SL), igarapé Limãozinho, Maués, Amazonas, 3°24'S 57°42'W, 4 Dec 1967, Expedição Permanente da Amazônia. MZUSP 7411 (25, 16.9-33.6 mm SL), stream of lago Saracá, Silves, Amazonas, 2°52'S 58°22'W, 6 Dec 1967, Expedição Permanente da Amazônia. MZUSP 7476 (110, 17.5-32.4 mm SL), rio Sanabani, Silves, Amazonas, 2°45'S 58°20'W, 7-8 Dec 1967, Expedição Permanente da Amazônia. MZUSP 7798 (2, 18.5 and 21.5 mm SL), stream of lago José-Açu, Parintins, Amazonas, 2°40'S 56°37'W, 11-12 Dec 1967, Expedição Permanente da Amazônia. MZUSP 8408

(118, 11.8-32.7 mm SL), igarapé Jacundá, Alter do Chão, Tapajós, Santarém, Pará, 2°30'S 54°57'W, 23 Dec 1967, Expedição Permanente da Amazônia. MZUSP 8448 (75, 11.9-23.5 mm SL), igarapé Jacundá, Alter do Chão, Tapajós, Santarém, Pará, 2°30'S 54°57'W, 23 Dec 1967, Expedição Permanente da Amazônia. MZUSP 8488 (110, 14.1-26.9 mm SL), igarapé affluent of left bank of rio Mapiri, Amazonas, Santarém, Pará, 2°26'S 54°44'W, 25 Dec 1967, Expedição Permanente da Amazônia. MZUSP 15550 (17, 14.5-32.3 mm SL, 2 c&s, 28.5-33.2 mm SL), lago Jacaré, headwaters of serrinha, Reserva Biológica de Trombetas, Trombetas, Pará, 1°20'S 56°51'W, 25 Jul 1979, R. Castro. MZUSP 23575 (3, 13.2-14.0 mm SL), lagoon of Mr. Durval Magalhães, Tapequém-Roraima road, 47 km from Boa Vista, rio Branco, Boa Vista, Roraima, 2°50'N 60°40'W, 9 Feb 1969, T. Roberts. MZUSP 23673 (19, 10.1-24.7 mm SL), lago Jacaré, Trombetas, Pará, 1°20'S 56°51'W, 7-11 Oct 1969, Expedição Permanente da Amazônia. MZUSP 24246 (1, 18.0 mm SL), igarapé Jituarana, right bank of rio Tapajós near Boim, Tapajós, Pará, 3°0'S 55°15'W, 27 Oct 1970, Expedição Permanente da Amazônia. MZUSP 24964 (1, 18.3 mm SL), rio Cuieiras and affluents, rio Negro, Amazonas, 2°50'S 60°30'W, Jan 1977, Alpha Helix Amazon Expedition. MZUSP 27454 (1, 22.9 mm SL), Pedra do Gavião, rio Negro, Barcelos, Amazonas, 1°28'S 61°38'W, Nov 1983, L. Portugal. MZUSP 27456 (9, 17.9-23.2 mm SL), Pedra do Gavião, rio Negro, Barcelos, Amazonas, 1°28'S 61°38'W, 13-14 Nov 1982, L. Portugal. MZUSP 29342 (94, 12.6-27.2 mm SL), rio Negro downstream rio Daraá (central lake in island), rio Negro, Amazonas, 0°28'S 64°46'W, 17 Feb 1980, M. Golding. MZUSP 29343 (79, 20.5- 33.6 mm SL, 4 c&s, 23.9-32.3 mm SL), lake in island, rio Negro, Barcelos, Amazonas, 0°58'S 62°57'W, 29 Feb 1980, M. Golding. MZUSP 29344 (265, 20.5-33.6 mm SL), Anavilhanas, rio Negro, Amazonas, 2°42'S 60°45'W, Mar 1982, M. Golding. MZUSP 29345 (2, 18.1 and 24.0 mm SL), central lake of ilha de Buiú-Açu, near rio Urubaxi, rio Negro, Amazonas, 0°31'S 64°50'W, 6 Feb 1980, M. Golding. MZUSP 29346 (6, 14.3-16.4 mm SL), central lake of ilha de Buiú-Açu, near rio Urubaxi, rio Negro, Amazonas, 0°31'S 64°50'W, 6 Feb 1980, M. Golding. MZUSP 31334 (1, 30.7 mm SL), igapó at Anavilhanas, rio Negro, Amazonas, 2°42'S 60°45'W, Apr 1982, M. Golding. MZUSP 55135 (3, 18.7-26.4 mm SL), São João near Santa Isabel do Rio Negro, margins of lake in island, rio Negro, Amazonas, 21 Oct 1972, Expedição Permanente da Amazônia. MZUSP 58331 (5, 17.3-26.1 mm SL), channel between lakes at São João near Santa Isabel do Rio Negro, rio Negro, Amazonas, 0°24'S 65°2'W, 24 Oct 1972, Expedição Permanente da Amazônia. MZUSP 58609 (37, 19.2-28.7 mm SL), lake of rio Aiuanã, rio Negro, Amazonas, 29 Oct 1972, Expedição Permanente da Amazônia. MZUSP 58611 (2, 18.5 and 21.1 mm SL), pool of rock at rio Negro, rio Negro, Barcelos, Amazonas, 0°12'S 64°4'W, 1 Nov 1972, Expedição Permanente da Amazônia. MZUSP 59166 (75, 17.5-31.6 mm SL), lake in lowland at Cantagalo, rio Negro, Amazonas, 28 Jan 1972, Expedição Permanente da Amazônia. MZUSP 59955 (7, 16.0-28.2 mm SL), highland stream at Cantagalo, rio Negro, Amazonas, 24 Jan 1972, Expedição Permanente da Amazônia. MZUSP 61926 (7, 19.2-25.5 mm SL), rio Aiuanã, near Santa Isabel do Rio Negro, rio Negro, Amazonas, 0°24'S 65°2'W, 22 Oct 1972, Expedição Permanente da Amazônia. MZUSP 62156 (3, 17.3-29.0 mm SL), lagoon in island of rio Negro, Paricatuba, rio Negro, Santa Isabel do Rio Negro, Amazonas, 0°31'S 65°1'W, 14 Nov 1972, Expedição Permanente da Amazônia. MZUSP 62167 (8, 12.5-19.3 mm SL), stream of lowland at rio Negro, Santa Isabel do Rio Negro, rio Negro, Amazonas, 0°24'S 65°2'W, 19 Oct 1972,

Expedição Permanente da Amazônia. MZUSP 62202 (8, 12.5-27.3 mm SL), chanel between lakes at São João near Santa Isabel do Rio Negro, rio Negro, Amazonas, 0°24'S 65°2'W, 24 Oct 1972, Expedição Permanente da Amazônia. MZUSP 62225 (3, 17.9-19.6 mm SL), lagoon in island of rio Negro, Paricatuba, Santa Isabel do Rio Negro, Amazonas, 0°31'S 65°1'W, 14 Nov 1972, Expedição Permanente da Amazônia. MZUSP 63517 (12, 12.9-27.8 mm SL), stream of lowland at Santa Isabel do Rio Negro, rio Negro, Amazonas, 0°24'S 65°2'W, 19 Oct 1972, Expedição Permanente da Amazônia. MZUSP 63522 (4, 23.7-26.8 mm SL), rio Aiuanã near Santa Isabel do Rio Negro, lake and stream headwater of lake, rio Negro, 0°24'S 65°2'W, 22 Oct 1972, Expedição Permanente da Amazônia. MZUSP 63523 (6, 19.0-33.0 mm SL), rio Aiuanã, near Santa Isabel do Rio Negro, lake and stream headwater lake, rio Negro, Amazonas, 0°24'S 65°2'W, 22 Oct 1972, Expedição Permanente da Amazônia. MZUSP 63524 (2, 20.9 and 26.8 mm SL), rio Aiuanã, near Santa Isabel do Rio Negro, lake and stream headwater lake, rio Negro, Amazonas, 22 Oct 1972, Expedição Permanente da Amazônia. MZUSP 63525 (1, 16.5 mm SL), stream of lowland at Tapurucuara, Amazonas, 0°24'S 65°2'W, 19 Oct 1972, Expedição Permanente da Amazônia. MZUSP 63527 (2, 24.9 and 34.7 mm SL), São João near Santa Isabel do Rio Negro, rio Negro, Amazonas, 0°24'S 65°2'W, 24 Oct 1972, Expedição Permanente da Amazônia. MZUSP 63528 (1, 22.1 mm SL), São João, Santa Isabel do Rio Negro, rio Negro, Amazonas, 0°24'S 65°2'W, 27 Oct 1972, Expedição Permanente da Amazônia. MZUSP 63529 (2, 18.5 and 23.58 mm SL), São João, near Santa Isabel do Rio Negro, rio Negro, Amazonas, 0°24'S 65°2'W, 24 Oct 1972, Expedição Permanente da Amazônia. MZUSP 63530 (4, 18.1-24.9 mm SL), São João near Santa Isabel do Rio Negro, highland stream at rio Negro, Amazonas, 0°24'S 65°2'W, 23 Oct 1972, Expedição Permanente da Amazônia. MZUSP 66723 (7, 16.9-22.4 mm SL), São João, near Santa Isabel do Rio Negro, margins of lake in island, rio Negro, Amazonas, 21 Oct 1972, Expedição Permanente da Amazônia. MZUSP 66724 (1, 18.1 mm SL), São João, near Santa Isabel do Rio Negro, margins of lake in island, rio Negro, Amazonas, 21 Oct 1972, Expedição Permanente da Amazônia. MZUSP 66729 (21, 17.8-26.3 mm SL), stream of lowland at Santa Isabel do Rio Negro, rio Negro, Amazonas, 0°24'S 65°2'W, 19 Oct 1972, Expedição Permanente da Amazônia. MZUSP 66730 (8, 12.7-19.4 mm SL), stream of lowland at Santa Isabel do Rio Negro, rio Negro, Amazonas, 0°24'S 65°2'W, 19 Oct 1972, Expedição Permanente da Amazônia. MZUSP 66732 (4, 20.6-26.8 mm SL), São João near Santa Isabel do Rio Negro, margins of lake in island rio Negro, Amazonas, 21 Oct 1972, Expedição Permanente da Amazônia. MZUSP 66733 (10, 19,7-31,5 mm SL), São João near Santa Isabel do Rio Negro, margins o lake in island, rio Negro, Amazonas, 21 Oct 1972, Expedição Permanente da Amazônia. MZUSP 66745 (7, 15,3-28,7 mm SL), stream at São João near Santa Isabel do Rio Negro, rio Negro, Amazonas, 0°24'S 65°2'W, 27 Oct 1972, Expedição Permanente da Amazônia. MZUSP 66750 (1, 27.7 mm SL), stream at São João, near Santa Isabel do Rio Negro, rio Negro, Amazonas, 0°24'S 65°2'W, 27 Oct 1972, Expedição Permanente da Amazônia. MZUSP 66766 (20, 14.2-35.1 mm SL), São João near Santa Isabel do Rio Negro, chanel of lake, rio Negro, Amazonas, 0°24'S 65°2'W, 23 Oct 1972, Expedição Permanente da Amazônia. MZUSP 66767 (13, 12.3-20.5 mm SL), São João near Santa Isabel do Rio Negro, chanel of lake, rio Negro, Amazonas, 0°24'S 65°2'W, 23 Oct 1972, Expedição Permanente da Amazônia. MZUSP 74233 (19, 15.0-23.5 mm SL), stream of lowland at Santa Isabel do Rio Negro, rio Negro, Amazonas, 0°24'S 65°2'W, 19 Oct 1972, Expedição Permanente da Amazônia.

MZUSP 74236 (5, 21.8-27.2 mm SL), lake of rio Aiuanã, rio Negro, Amazonas, 0°38'S 64°56'W, 29 Oct 1972, Expedição Permanente da Amazônia. MZUSP 74237 (13, 15.0-28.5 mm SL), lake of rio Aiuanã, rio Negro, Amazonas, 0°38'S 64°56'W, 29 Oct 1972, Expedição Permanente da Amazônia. MZUSP 74238 (21, 18.0-25.6 mm SL), lake of rio Aiuanã, rio Negro, Amazonas, 0°38'S 64°56'W, 29 Oct 1972, Expedição Permanente da Amazônia. MZUSP 74264 (39, 18.3-30.0 mm SL), igarapé Jaradá, affluent of right margin of rio Cuieiras, about 40 km of mouth, rio Negro, Manaus, Amazonas, 31 Jan 1977, Alpha Helix Amazon Expedition. MZUSP 74287 (5, 20.4-27.7 mm SL), igarapé Sirinau, right margin of rio Cuieiras, about 25 km of mouth, rio Negro, Manaus, Amazonas, 2°42'S 60°20'W, 30 Jan 1977, Alpha Helix Amazon Expedition. MZUSP 74519 (7, 20.8-24.1 mm SL), igarapé Arraia, right margin of rio Cuieiras, about 25 km of mouth, rio Negro, Amazonas, 2°42'S 60°20'W, 27 Jan 1977, Alpha Helix Amazon Expedition. MZUSP 74774 (3, 18.3-21.9 mm SL), igarapé Arraia, right margin of rio Cuieiras, about 25 km of mouth, rio Negro, Amazonas, 2°42'S 60°20'W, 27 Jan 1977, Alpha Helix Amazon Expedition. MZUSP 74781 (8, 21.9-32.2 mm SL), igarapé do Rei, island close to rio Cuieiras mouth, rio Negro, Amazonas, 2°42'S 60°20'W, 26 Jan 1977, Alpha Helix Amazon Expedition. MZUSP 85222 (16, 18.8-24.6 mm SL), stream headwater of lake at Cantagalo, rio Negro, Amazonas, 25 Jan 1972, Expedição Permanente da Amazônia. MZUSP 85223 (3, 15.3-17.1 mm SL), stream of lowland at Ilha Grande de Tapurucuara, rio Negro, Amazonas, 12 Nov 1972, Expedição Permanente da Amazônia. MZUSP 85224 (5, 13.5-28.3 mm SL), rocky pool communicating with rio Negro, Tapera, rio Negro, Amazonas, 0°12'S 64°4'W, 1 Nov 1972, Expedição Permanente da Amazônia. MZUSP 87424 (17, 13.0-23.2 mm SL), floodplain at pousada do Paraíso, near igarapé do Tauari, Rio Preto da Eva, Amazonas, 2°47'25.2"S 59°38'10.8"W, 5 Jul 2003, Exc. MZUSP/USP. MZUSP 87425 (1, 14.7 mm SL), igarapé Água Verde, at Road on the left margin of Rio Preto da Eva, downstream city, Rio Preto da Eva, Amazonas, 2°44'22.7"S 59°41'15.5"W, 5 Jul 2003, Exc. MZUSP/USP. MZUSP 87426 (24, 11.4-42.2 mm SL, 2 c&s, 26.5-38.7 mm SL), stream affluent of Rio Preto da Eva, Rio Preto da Eva, Amazonas, 2°44'35"S 59°40'7.8"W, 6 Jul 2003, Exc. MZUSP/USP. MZUSP 87427 (4, 13.5-26.7 mm SL), igarapé Agripino, affluent of Rio Preto da Eva, Rio Preto da Eva, Amazonas, 2°43'59.3"S 59°40'48"W, 6 Jul 2003, Exc. MZUSP/USP. MZUSP 87428 (1, 15.2 mm SL), rio Urubu, at Patauí farm, ramal ZF-9, Km 103-104 of road to Itacoatiara, Rio Preto da Eva, Amazonas, 2°39'37.8"S 59°22'21.7"W, 8 Jul 2004, Exc. MZUSP/USP. MZUSP 92144 (1, 17.4 mm SL), stream affluent of rio Tiquié, Serra do Mucura community, rio Negro, Amazonas, 0°10'7"N 69°7'46"W, 10 Aug 2006, F. Lima *et al.* MZUSP 92838 (5, 14.0-19.3 mm SL), igarapé Juá, 7 km from Santarém by Road to the airport, Amazonas, Santarém, Pará, 2°26'S 54°46'52"W, 13 Nov 2006, L. Sousa & J. Birindelli. MZUSP 92855 (1, 18.4 mm SL), imprecise locality (aquarium store of Samuel at Santarém), 17 Oct 2006, L. Sousa & J. Birindelli. MZUSP 95276 (9, 17.1-28.1 mm SL), stream at left margin of rio Cuieiras, about 20 km of mouth, rio Negro, Manaus, Amazonas, 3°0'S 60°11'W, 27 Jan 1977, Alpha Helix Amazon Expedition. MZUSP 108818 (2, 21.0 and 25.5 mm SL), entrance of igarapé Demuriari, left margin of rio Negro, upstream São Gabriel da Cachoeira, leaves at floodplain area, rio Negro, São Gabriel da Cachoeira, Amazonas, 0°0'51"S 67°10'16"W, 12 Dec 2005, J. Muriel-Cunha, J. Zuanon. MZUSP 108819 (1, 25.8 mm SL), igarapé Barixia, right margin of rio Negro, rio Negro, São Gabriel da Cachoeira, Amazonas, 0°7'24"S 67°7'54"W, 14 Dec

2005, J. Muriel-Cunha, J. Zuanon & E. Trajano. NRM (3, 11.4–25.7 mm SL), stream at savannah at upper rio Araçá, rio Negro, Amazonas, 11 Nov 1984. MZUSP 24255 (52, 14.7–28.1 mm SL), igarapé-Açú, Tapajós, Aveiro, Pará, 30 Oct 1970, Expedição Permanente da Amazônia. MZUSP on loan Marilyn (3, 13.4–15.0 mm SL), Boa Vista, Roraima, 9–10 Feb 1969. MZUSP 112781 (5, 18.0–25.5 mm SL), igarapé Bandeira, affluent of rio Jufari, Caracaí, Roraima, 1°2'56"S 62°8'43"W, 3 Sep 2011, Oyakawa *et al.* MZUSP 112541 (53, 23.5–32.29 mm SL), igarapé do Campo, affluent of rio Jufari, near Caicubi village, Caracaí, Roraima, 1°4'1"S 62°7'40"W, 28 Aug 2011, Oyakawa *et al.* MZUSP 112789 (14, 11.5–24.0 mm SL), igarapé Pretinho, affluent of igarapé Caicubi, Caracaí, Roraima, 0°56'46"S 62°6'26"W, 31 Aug 2011, Oyakawa *et al.* MZUSP 113116 (46, 10.0–32.0 mm SL), igarapé Santa Fé, affluent of rio Jufari, Caracaí, Roraima, 1°0'34"S 62°13'4"W, 1 Sep 2011, Oyakawa *et al.* MZUSP 113139 (40, 9.5–25.0 mm SL), mouth of igarapé Pupunha at igarapé Caicubi, Caracaí, Roraima, 0°59'25"S 62°5'56"W, 5 Sep 2011, Oyakawa *et al.* MZUSP 113194 (11, 14.1–30.4 mm SL), igarapé Tubana, affluent of rio Jurai, rio Negro, 1°5'25"S 62°7'35"W, 5 Sep 2011, Oyakawa *et al.* MZUSP 113276 (2, 31.1–31.8 mm SL), igarapé Pretinho, affluent of igarapé Caicubi, Caracaí, Roraima, 1°1'46"S 62°6'60"W, 26 Aug 2011, Oyakawa *et al.* MZUSP 113354 (24, 9.9–30.2 mm SL), igarapé Pretinho, upstream mouth of igarapé Branquinho, rio Negro, Caracaí, Roraima, 0°55'50"S 62°6'30"W, 9 Sep 2011, Oyakawa, 2012. MZUSP 113382 (3, 19.8–22.3 mm SL), temporary pool connecting with igarapé Pupunha, 1.9 km behind Vila de Caicubi, rio Negro, Roraima, 1°1'32"S 62°5'47"W, 11 Sep 2011, O. Oyakawa *et al.* UFRO-I 8422 (2, 16.6 and 23.3 mm SL), lago Sampaio, rio Madeira mouth, Nova Olinda do Norte, Amazonas, 3°45'50.6"S 59°1.6'45.3"W, 25 Jan 2011, F. Vieira. USNM 300956 (17, 15.9–24.4 mm SL), rio Unini, rio Negro, Amazonas, 19 Nov 1988, H. Axelrod. USNM 317518 (2, 30.2 and 30.6 mm SL), rio Negro, downstream rio Daraá, central lake in island, rio Negro, Amazonas, 11 Feb 1980, M. Golding.

Colombia. ICNMMNH 6214 (4, 17.4–28.9 mm SL), quebrada La Arenosa, Km 9.5 at Leticia-Tarapacá road, 8 Nov 2001, C. Castellanos. ICNMMNH 16375 (3, 22.3–28.4 mm SL), quebrada La Arenosa, Km 10.5 Leticia-Tarapacá road, Finca Agape, Leticia, 1 Oct 2005, Proyecto Ornamentales Amazonas. ICNMMNH 13609 (1, 20.9 mm SL), quebrada La Arenosa, Km 11 Leticia-Tarapacá road, Leticia, Amazonas, 19 Nov 1997, J. Mojica & Estudiantes Biología. ICNMMNH 16891 (10, 15.6–34.4 mm SL), quebrada La Arenosa, Km 10.5 Leticia-Tarapacá road, Leticia, 1 Apr 2007, J. I. Mojica & C. Castellanos. SMF 9925 (4, 27.1–32.1 mm SL), igarapé Preto, upper rio Solimões, Brazil, H. Schultz, 1961. SMF 9927 (2, 28.5–33.7 mm SL), igarapé Preto, upper rio Solimões, Brazil, H. Schultz, 1961. USNM 311005 (6, 19.8–31.9 mm SL), meadow stream near Leticia, 3 Dec 1974, D. Kramer.

Rio Orinoco basin, Colombia. CZUT-IC 4289 (1, 18.8 mm SL), rio Guainia, San Jose-Playa community, Guainia, 10 Dec 2009–29 May 2010, F. Villa & A. Ortega. CZUT-IC 4297 (10, 11.6–23.0 mm SL), caño Piedras, rio Guainia, Guainia, 2°6'17"N 67°6'40"W, 9 Dec 2009–29 May 2010, F. Villa & A. Ortega. CZUT-IC 4316 (1, 15.2 mm SL), caño Guamarza, rio Guainia, Guainia, 2°58'13"N 67°50'13"W, 10 Dec 2009, F. Villa & A. Ortega. IavH 2259 (4, 15.5–20.8 mm SL), laguna El Pavón of caño Bocón, rio Inírida, Puerto Inírida, Guainia, 3°40'N 67°57'W, M. Blanco *et al.* IavH 2289 (1, 25.1 mm SL), caño Bocón, rio Inírida, Puerto Inírida, Guainia, 3°40'N 67°57'W, 1 Jul 1976, H. Thorbjörn. IavH 2828 (2, 16.9 and 17.7 mm SL),

caño Caranacoa, río Inírida, Puerto Inírida, Guainia, 3°51'55"N 67°55'26"W, 29 Mar 1974, M. Blanco. IavH 9937 (2, 15.5 and 15.9 mm SL), mouth of caño Cajaro to Matavén, Cumaribo, Vichada, 4°30'36,2"N 68°3'27.5"W, 14 Mar 2007, Bogotá & F. Villa. ICNMMNH 12191 (32, 12.8-26.0 mm SL), caño Bocón, laguna Tonina, río Inírida, Puerto Inírida, Proyecto Ornamentales Orinoco. MNHLS 23690 (11, 17.0-19.1 mm SL), caño San Joaquin, affluent of left margin of río Inírida, upstream serras Mavicure, opposite to Remanso community, Vichada, 3°26'47"N 68°0'10"W, 20 Feb 2008, C. Lasso *et al.* MNHLS 23760 (11, 12.3-22.1 mm SL), caño Tonina, affluent of left margin of caño Bocon, Vichada, 3°39'38,3"N 68°3'53.7"W, 20 Feb 2008, C. Lasso *et al.* MNHLS 23774 (6, 15.0-21.1 mm SL), laguna La Ceiba, floodplain of left margin of río Inírida, between caño Bocon margin and Caranacoa community, Vichada, 3°41'43.3"N 67°57'14.3"W, 20 Feb 2008, C. Lasso *et al.* MNHLS 23818 (3, 16.6-18.6 mm SL), caño Vitina, affluent of right margin of río Inírida, waters upstream Playa de Caranacoa, Vichada, 3°44'30.8"N 67°57'10.5"W, 20 Feb 2008, C. Lasso *et al.*

Guyana. ANSP 190682 (3, 18.8-22.0 mm SL), Manari River, río Takutu, río Branco, 10.2 km Northeast Lethem, Rupununi, 3°26'35"N 59°44'34"W, 1 Nov 2003, M. Sabaj *et al.* SU 50442 (4, 14.5-20.3 mm SL), río Nappi and others streams of río Tacatu, río Branco, Rupununi, 20 Sep 1957, McConnel & H. Rosemary.

Venezuela. MBUCV 11301 (4, not measured), caño Chola, Road to Solano, 17.7 km from San Carlos do Rio Negro, río Negro, Amazonas, 22 Jan 1978, K. Clark. MBUCV 15105 (1, 22.7 mm SL), backwater on rocks at island in the middle of río Negro, Amazonas, 4 Dec 1984, A. Machado *et al.* MBUCV 15115 (10, 15.9-23.7 mm SL), small stream at caño Urama, ustream Santa Lucia, río Negro, Amazonas, 6 Dec 1984, R. Vari *et al.* MCNG 53773 (1, 25.1 mm SL), río Yatua, 1°28'11"N 66°30'30"W, 5 Feb 2011.

Rio Orinoco, Venezuela. AMNH 230891 (4, 24.0-31.6 mm SL), río cora-cora, forty minutes upstream Yutaje camp, río Ventuari, Amazonas, 5°36'39"N 66°7'57"W, 27 Apr 1999, S. Schaefer, F. Provenzano & R. Rojas. ANSP 161409 (3, 17.0-21.7 mm SL), caño east margin of río Casiquiare about 7 km downstream mouth of río Pamoni, Amazonas, 2°48'N 65°58'W, 20 Mar 1987, B. Chernoff *et al.* ANSP 190678 (71, 11.2-23.7 mm SL), caño Caripo, about 5 min of the confluence of río Casiquiare with Orinoco, left side, about 3 km upstream mouth, Amazonas, 3°6'N 65°50'W, 16 Mar 1987, B. Chernoff, J. Fernandez & O. Castillo. ANSP 190680 (4, 20.9-25.1 mm SL), stream affluent of río Casiquiare about 22 km downstream mouth of río Pamoni, east side, Amazonas, 2°47'N 66°3'W, 20 Mar 1987, B. Chernoff *et al.* ANSP 191389 (1, 28.3 mm SL), caño Parhueña, upstream bridge of Road 12, about 35 km Northeast Puerto Ayacucho, Amazonas, 5°53'30,7"S 67°24'13.5"W, 21 Mar 2010, M. Sabaj Pérez *et al.* MBUCV 7705 (4, 19.1-21.2 mm SL), laguna de Titi, San Fernando de Atabapo, Amazonas, 5 Dec 1973, A. Cortéz. MBUCV 7828 (8, 13.3-19.0 mm SL), caño Guasuriapana, affluent of río Atabapo, Amazonas, 24 Feb 1974, H. Lopez, O. Silva & A. Cortéz. MBUCV 7854 (18, 11.4-18.9 mm SL), caño Cascaradura, near San Fernando de Atabapo, Amazonas, 1 Dec 1973, A. Cortéz & R. Navarro. MBUCV 8144 (1, not measured), caño Cascaradura, affluent of río Orinoco, about 7 km east San Fernando de Atabapo-Santa Barbara del Orinoco road, Amazonas, 13 Apr 1972, A. Cortéz. MBUCV 8644 (9, 14.6-23.4 mm SL), caño Moroto, near San Fernando de Atabapo, Orinoco, Amazonas, 13 Feb 1974, A. Cortéz. MBUCV 9462 (8, 15.2-22.2 mm SL), caño Cascaradura, affluent of río Orinoco, about 7 km east San Fernando

de Atabapo-Santa Barbara del Orinoco road, Amazonas, 16 Feb 1974, Moscó *et al.* MBUCV 14807 (2, 25.2 and 29.0 mm SL), rio Baria, about 3 km downstream Base La Neblina camp, Casiquiare, rio Negro, Amazonas, 25 Feb 1985, R. Royero & L. López. MBUCV 14821 (1, 43.2 mm SL), rio Baria, about 2 km downstream Base La Neblina camp, Casiquiare, rio Negro, Amazonas, 25 Feb 1985, R. Royero & L. López. MBUCV 14914 (1, 29.4 mm SL), rio Baria, aside Base La Neblina camp, Casiquiare, Amazonas, 27 Feb 1985, R. Royero *et al.* MBUCV 15120 (28, 14.0-22.1 mm SL), caño Manu, affluent of rio Casiquiare, about 250 m upstream Solano, Amazonas, 7 Dec 1984, R. Vari *et al.* MBUCV 17533 (7, 30.5 mm SL), caño Cascaradura, about 10 km San Fernando de Atabapo-Santa Barbara del Orinoco road, Orinoco, Amazonas, 19 Feb 1974, A. Cortéz & G. Colomine. MCNG 23578 (5, 15.7-19.6 mm SL), rio Atacavi at La Paloma community, 3°8'N 66°59'W, 7 Nov 2011. MCNG 28451 (1, 32.4 mm SL), Laguna José, about 4 km upstream sitio 93-4, Casiquiare, Amazonas, 1°45'50"N 66°50'20"W, 4 Feb 1993. MCNG 33901 (6, 16.-16.3 mm SL), about q hour before Boa Vista, Venezuela-Boa Vista road, Canaima, rio Branco drainage, 3°33'12"N 60°56'13"W, MCNG 35068 (4, 15.6-20.4 mm SL), caño Cachiapo, Casiquiare, Amazonas, 1°56'35"N 66°42'14"W, 19 Jan 1997. MCNG 35137 (2, 17.9 and 19.6 mm SL), rio Casiquiare, laguna Cadamuhedeyedi (diablo), Casiquiare, Amazonas, 2°22'25"N 66°31'5"W, 28 Jan 1997. MCNG 35287 (1, 11.6 mm SL), Laguna Curamoni, rio Casiquiare, Amazonas, 2°37'5"N 66°9'43"W, 1 Feb 1997. MCNG 35388 (2, 19.0 and 22.7 mm SL), rio Casiquiare, downstream caño Cachiapo, Amazonas, 1°56'35"N 66°42'14"W, 19 Jan 1997, KOW97-5. MCNG 35883 (2, 29.9 and 30.8 mm SL), 1.5 km from Rio Autana camp, near 'Los Raudales de Ceguera' community, rio Sipapo, Amazonas, 4°48'16"N 67°28'56"W, 11 Sep 2011, OLM97-7. MCNG 35954 (1, 17.5 mm SL), surroundings 'Puerto Esperanza', rio Sipapo, Amazonas, 4°42'37"N 67°44'58"W, 7 Sep 1997, OLM97-2. MCNG 37716 (204, 13.6-28.1 mm SL), Siapa, Amazonas, 2°5'47"N 66°11'18"W, 18 Jan 1998, LN98-31. MCNG 37948 (7, not measured), caño Iguarapo, tributary of rio Casiquiare, about 100 m of confluence, before Piedra Culimacare, Amazonas, 1°59'N 66°45'W, 8 Jan 1998, LN98-5. MCNG 38158 (13, 12.6-25.3 mm SL), caño Buridajow near confluence with rio Pasimoni, Amazonas, 21 Jan 1998, LN98-37. MCNG 38346 (228, 15.6-28.3 mm SL), drying pool at floodplain, downstream right margin of rio Siapa, near rio Emoni, Amazonas, 18 Jan 1998, LN98-30. MCNG 41969 (1, 27.7 mm SL), Laguna Arapacoa at Piedra Arapacoa, rio Pasimoni, Amazonas, 1°51'21"N 66°35'11"W, 7 Jan 1999, LN99-8. MCNG 42021 (9, 16.6-21.6 mm SL), caño Cachiapo, about 1 km upstream confluence of rio Casiquiare, Amazonas, 1°56'34"N 66°42'14"W, 6 Jan 1999, LN99-6. MCNG 42034 (6, 18.3-20.9 mm SL), caño Buridajow, about 1 km upstream confluence of rio Casiquiare Pasimoni, Amazonas, 1°48'27"N 66°33'7"W, 8 Jan 1999, LN99-9. MCNG 42052 (4, 15.4-19.0 mm SL), rio Pasimoni at beach Guisuri, Amazonas, 1°39'21"N 66°34'40"W, 8 Jan 1999, LN99-10. MCNG 42088 (4, 14.6-18.6 mm SL), Laguna de Candela, bank of rio Pasimoni, headwater of rio Yatua, Laguna de Candela, Amazonas, 1°31'42"N 66°33'52"W, 9 Jan 1999, LN99-12. MCNG 47657 (1, 18.8 mm SL), about 2 km upstream mouth of do rio Guapuchi toward "Arenas Blancas" community, rio Ventuari, Amazonas, 4°7'49"N 66°45'14"W, 17 Apr 2003, NKL03-05. MCNG 53716 (1, 28.0 mm SL), rio Yatua at flooded wood, about 3.17 km upstream camp base, Amazonas, 31 Jan 2005, OLM05-5. MNHLS 19046 (2, 23.4 and 30.1 mm SL), stream tributary of left margin of rio Autana, between Salto Perez

and Ceguera community, Amazonas, 4°46'50,6"N 67°37'3"W, 2 May 2006, C. Lasso & J. Rodriguez. MNHLS 22810 (127, 10.8-21.3 mm SL), Laguna Macurucu, Amazonas, 3°55'20"N 67°0'10"W, 25 Nov 2003, C. Lasso *et al.* USNM 269900 (254, 12.7-27.5 mm SL), igarapé Manu tributary of Casiquiare canal, about 250 miles upstream Solano, Amazonas, 7 Dec 1984, R. Vari *et al.* USNM 269901 (41, 7.2-28.5 mm SL), small caño of caño Urami, just upstream Santa Lucia, Amazonas, 1°17'N 66°51'W, 6 Dec 1984, R. Vari *et al.* USNM 272396 (65, 12.2-26.5 mm SL), lagoon Northeast of airport of São Carlos do Rio Negro, Amazonas, 4 Dec 1984. USNM 386132 (10, 16.2-23.8 mm SL), caño Cascadura, San Fernando de Atabapo, Amazonas, 10 Dec 1973.

COPELLA STIGMASEMION (FOWLER, 1913), NEW COMBINATION

Figures 38, 54-59; Tables 9 and 10

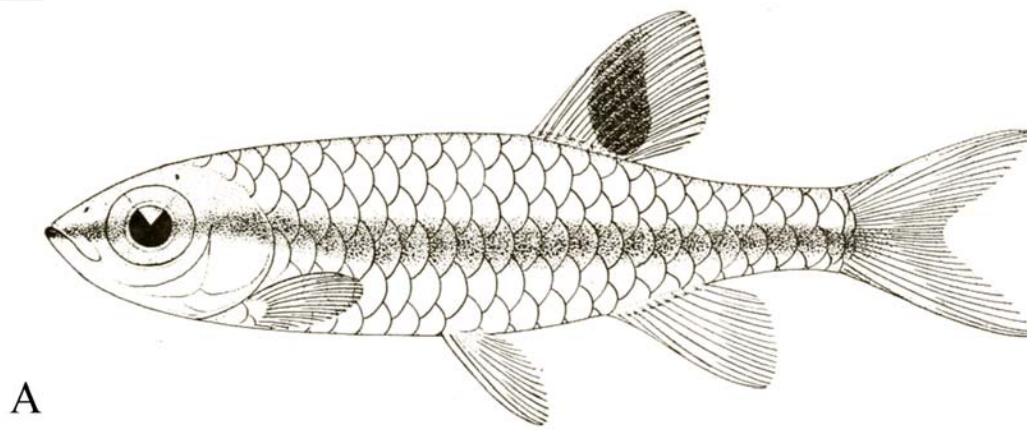
Nannostomus stigmasemion Fowler, 1913: 523-524, fig. 4 [type locality: tributary of the rio Madeira near Porto Velho, Brazil]. Fowler, 1948: 259 [listed].

Pyrrhulina nigrofasciata Meinken, 1952: 115-117, figs. 1-3 [type locality: upper rio Amazonas at Peru].—Géry, 1977: 147 [possible synonym of *Copella metae*].—Wilkens, 1977: 156 [type catalog].

Copella nigrofasciata.—Ortega & Vari, 1986: 10 [rio Amazonas, Peru; listed, probable new combination].—Zarske & Géry, 1997: 14, fig. 4 [photo of possible syntype ZMH 1211; comparison with *Pyrrhulina zigzag*].—Weitzman & Weitzman, 2003: 242 [literature compilation; comparison with *C. metae*].—Netto-Ferreira, 2006: 20 [phylogenetic analysis of Lebiasinidae].—Zarske & Géry, 2006: 26, figs. 11, 22 [identification key].—Oyakawa & Netto-Ferreira, 2007: 64 [literature compilation].—Montag *et al.*, 2008: 18 [FLONA de Caxiuanã in igarapé; listed].—Netto-Ferreira, 2010: 331 [phylogenetic analysis of Lebiasininae].—

Copella eigenmanni.—Géry, 1977: 141 [misidentification of unnumbered figure pg. 141 labeled “possibly *C. eigenmanni*”].

Copella nattereri.—Zarske & Géry, 2006: 24, figs. 7-9 and 20 [misidentification; redescription; taxonomic notes; identification key].



A



B

Figure 54. Holotype of *Nannostomus stigmatsemion*, tributary of the rio Madeira near Porto Velho, Brazil, (A) fig. 4 of Fowler (1913), (B) ANSP 39188, immature, 10.8 mm SL, flipped horizontally (photo by K. Luckenbill & M. Sabaj-Perez).



Fig 55. Largest syntype of *Pyrrhulina nigrofasciata* ZMH 1211, male, 35.8 mm SL, upper rio Amazonas.



Figure 56. *Copella stigmatemion*, (A) MZUSP 101930, female, 29.9 mm SL, rio Jari, Amapá, Brazil; MPEG 16249: (B) male, 32.3 mm SL, (C) female, 26.0 mm SL, rio Solimões, Coari, Amazonas, Brazil.



Figure 57. *Copella stigmatemion*, live male, aquarium specimen not preserved. Photo: Hans-Georg Evers.



Figure 58. *Copella stigmatemion*, live male, aquarium specimen not preserved. Photo by T. Christoffersen.

Diagnosis. *Copella stigmatemion* can be distinguished from all congeners by having a series of conspicuous clear spots on each scale along the fourth longitudinal scale row, not followed by a black spot (*vs.* absence of clear spot in *Copella compta*, *C. eigenmanni* and *C. vilmae*; clear spots not on the fourth longitudinal scale row in some males of *C. arnoldi*; clear spots followed by dark spots on *C. nattereri*). Additionally, *C. stigmatemion* can be distinguished from all congeners, except some specimens of *C. eigenmanni*, by having a black longitudinal band on body from the dentary to the caudal peduncle (*vs.* absence or longitudinal dark band extending up to the anal fin).

Description. Morphometrics in Table 5. Largest examined male 37.6 mm SL, female 30.4 mm SL. Greatest body depth located slightly anterior to vertical through pelvic-fin origin. Body cylindrical, slightly compressed laterally. Dorsal profile of body straight to slightly convex from tip of snout to end of supraoccipital, slightly convex from that point to dorsal-fin origin, posteroventrally inclined along dorsal-fin base and straight along caudal peduncle. Ventral profile of body convex to posteroventrally inclined from anterior tip of the dentary to the

vertical through anterior margin of orbit, straight from that point to the vertical through pectoral-fin origin, slightly convex from that point to the pelvic-fin origin, straight from pelvic-fin origin to anal-fin origin, posterodorsally inclined along anal-fin base and straight along caudal peduncle.

Mouth upturned. Premaxillary teeth in one row, with 14 (3), 15 (1), 16 (3), 17 (1) teeth, decreasing in size laterally. Number of maxillary teeth sexually dimorphic, 11 (2), 15 (1), 16 (1) in males, 5(2), 6 (1), 9 (1) in females, decreasing in size posteriorly, especially on males. Dentary teeth in two rows, outer with 7 (1), 8 (2), 9 (4), 10 (1) increasing in size laterally, inner with 21 (2), 22 (1), 23 (1), 25 (2), 26 (1), 34 (1) teeth, decreasing in size laterally.

Dorsal fin with ii, 8 (62) or 9 (2) rays, second and third branched rays longer. Pectoral fin with i, 8 (8), 9 (44), or 10 (12) rays, second branched ray longest, not reaching pelvic-fin origin on males and females. Pelvic fin with i, 7 (59) or 8 (5) rays, third branched ray longest. Anal fin with iii (11), 8 (2), or 9 (62) rays, third and fourth fifth branched rays longer. Caudal fin with i, 7 (3), 8 (52), or 9 (4) rays in upper lobe, first and second branched rays longer, and 7 (59) or 8 (1), i rays in lower lobe, first and second branched rays longer. Upper caudal-fin lobe longer than lower one. Predorsal scales 12 (4), 13 (35), or 14 (23), in one series. First longitudinal scale row with 12 (4), 13 (39) or 14 (11) scales. Fourth longitudinal scale row with 21 (1), 22 (10), 23 (32), or 24 (19) scales. Longitudinal scale rows between dorsal-fin origin and pelvic-fin origin 5 (24) or 6 (40). Longitudinal scale rows between dorsal-fin origin and anal-fin origin 5 (57) or 6 (8). Circumpeduncular scale rows 10 (65). Total number of vertebrae 32 (11), 33 (30), 34 (16), or 35 (3).

Table 9. Morphometrics of *Copella stigmatemion*. Holotype of *Nannostomus stigmatemion* ANSP 39188, largest syntype of *Pyrrhulina nigrofasciata* ZMH 1211, remaining syntypes of *Pyrrhulina nigrofasciata* ZMH 1212 (3) and non-type material BMNH 1952.7.31.3-5 (3), MPEG 9927 (1), MPEG 13775 (7), MPEG 15917 (6), MPEG 16249 (6), MPEG 17409 (5), MZUSP 23510 (7), MZUSP 85603 (8), MZUSP 85597 (1), MZUSP 101930 (3), MZUSP 101933 (3), MZUSP 103302 (1), UFRO-I 6386 (10), n = number of specimens, SD = Standard deviation. Ranges do not include primary types.

	<i>Nannostomus stigmatemion</i>	<i>Pyrrhulina nigrofasciata</i>						
	Holotype	Largest syntype	n	Range			Mean	SD
Standard length (mm)	10.8	35.8	64	17.3	-	37.6	28.4	5
Percents of standard length								
Body depth	19.4	20.4	64	14.1	-	21	18.3	1.6
Dorsal- to caudal-fin origin	40.7	40.2	64	35.4	-	41.4	38.5	1.3
Snout to dorsal-fin origin	63.9	63.1	64	56.9	-	65.1	61.8	1.5
Snout to pectoral-fin origin	26.9	21.5	64	20.9	-	26.3	23.7	1.6
Snout to pelvic-fin origin	48.1	51.1	64	45.4	-	51.7	48.4	1.5
Snout to anal-fin origin	68.5	73.2	64	67.1	-	73.9	70.2	1.5
Pectoral- to pelvic-fin origin	22.2	29.9	62	21.8	-	29.7	25.3	2.5
Pelvic- to anal-fin origin	19.4	21.5	64	19.7	-	25.9	22.5	0.7
Pectoral-fin length males	-	15.4	34	16.3	-	22.0	18.8	0.9
Pectoral-fin length fem/imm	-	-	31	16.2	-	22.4	18.3	1.2
Pelvic-fin length males	-	18.7	34	15.6	-	33.7	25.1	0.7
Pelvic-fin length fem/imm	-	-	32	15.8	-	20.0	17.6	1.2
Dorsal-fin length males	-	26.8	34	21.3	-	47.7	31.3	2.0
Dorsal-fin length fem/imm	-	-	31	19.6	-	25.7	22.5	1.1
Anal-fin length males	-	19.6	34	16.6	-	27.6	22.4	0.6
Anal-fin length fem/imm	-	-	32	15.9	-	21.3	18.5	1.5
Anal-fin base length	10.2	8.9	64	6.9	-	10.4	8.7	0.8
Caudal peduncle depth	8.3	9.5	64	7.8	-	10.7	9.0	1.0
Caudal peduncle length	18.5	21.8	64	16.7	-	26.2	20.8	2.2
Head length	27.8	22.1	64	21.4	-	26.8	23.8	1.4
Percents of head length								
Eye diameter	36.7	29.1	62	31.6	-	43.0	36.2	2.8
Snout length	30.0	31.6	64	25.4	-	32.8	28.6	1.6
Interorbital distance	36.7	38.0	64	32.9	-	39.7	36.3	1.6
Upper jaw length	26.7	27.8	64	22.7	-	33.9	28.3	1.8

Table 10. Meristics of the largest probable syntype of *Pyrrhulina nigrofasciata* ZMH 1211. Meristic data of *Nannostomus stigmasemion* was not taken due to the poor condition of the material.

	<i>Pyrrhulina nigrofasciata</i>
	Largest syntype
Predorsal scales	12
First longitudinal scale row	12
Fourth longitudinal scale row	24
Longitudinal scale rows dorsal to pelvic	6
Longitudinal scale rows dorsal to anal	5
Circumpeduncular scale rows	10
Pectoral-fin rays	i9
Pelvic-fin rays	i7
Dorsal-fin rays	ii8
Branched anal-fin rays	9
Caudal-fin rays	i8,7i

Color in alcohol. Overall ground coloration of body beige to brown. Dorsal portion of body dark. Thin predorsal dark stripe, frequently wider over second and third scales. Scales on middorsal portion of body with posterior border dark, forming a slight reticulate pattern; some specimens with a small dark spot at posterior border of the scale on that region (Fig. 56). Black stripe extending from the anterior tip of dentary to the end of caudal peduncle, along the fourth and fifth longitudinal scale rows. Clear longitudinal stripe over the third longitudinal scale row. Conspicuous clear spot on each scale of the fourth longitudinal scale row, from behind opercle to the vertical through the end of dorsal-fin base and on each scale of the third longitudinal scale row of the caudal peduncle (Fig. 56A and B). Rarely, specimens with clear spot also on each scale of the third to fifth longitudinal scale rows (Fig. 56 C). Ventral region of body clear. Dorsal fin with black round spot. Remaining fins hyaline. Pelvic and anal fin usually with dark edge, more intense in males. Some males with distal tip of dorsal fin dark. Some specimens with base of middle caudal-fin rays faint dark. Dorsal and ventral procurent caudal-fin rays

dark, forming a black triangle on the base of the lower caudal-fin lobe. Dorsal procurrent caudal-fin rays hyaline and ventral procurrent caudal-fin rays hyaline faint in juveniles.

Color in life. Dorsal portion of body beige to gray. Black stripe extending from the anterior tip of the dentary to the end of the caudal peduncle, along the fourth and fifth longitudinal scale rows (Fig. 57). Black stripe rarely faded (Fig. 58) during courtship or when the specimens are frightened (T. Christoffersen personal observation). Clear longitudinal stripe over the third longitudinal scale row. Red spot on each scale of the fourth longitudinal scale row, from behind opercle to the vertical through the end of dorsal-fin base, and on each scale of the third longitudinal scale row of the caudal peduncle (Fig. 57 and 58). Rarely, specimens with a red spot on each scale of the second to fifth longitudinal scale rows. Ventral portion of body white. Fins yellow to orange. Basal portion of dorsal fin red. Some specimens with base of longest upper and lower caudal-fin rays red.

Sexual dimorphism. Males longer than females. Males with more maxillary teeth than females (see description above). Pelvic, dorsal and anal fins longer in males (Fig. 59). Pectoral fin apparently not sexually dimorphic. Tip of adpressed pelvic fin reaching up to base of third branched anal-fin ray in males, and up to anus in females. Tip of adpressed dorsal fin reaching up caudal-fin base in males and approximately up to one-half the length of caudal peduncle in females. Tip of adpressed anal-fin reaching up to the level of first ventral procurrent rays in males, and up to two-third the length of caudal peduncle in females. Upper caudal-fin lobe longer than lower one, more evident in males.

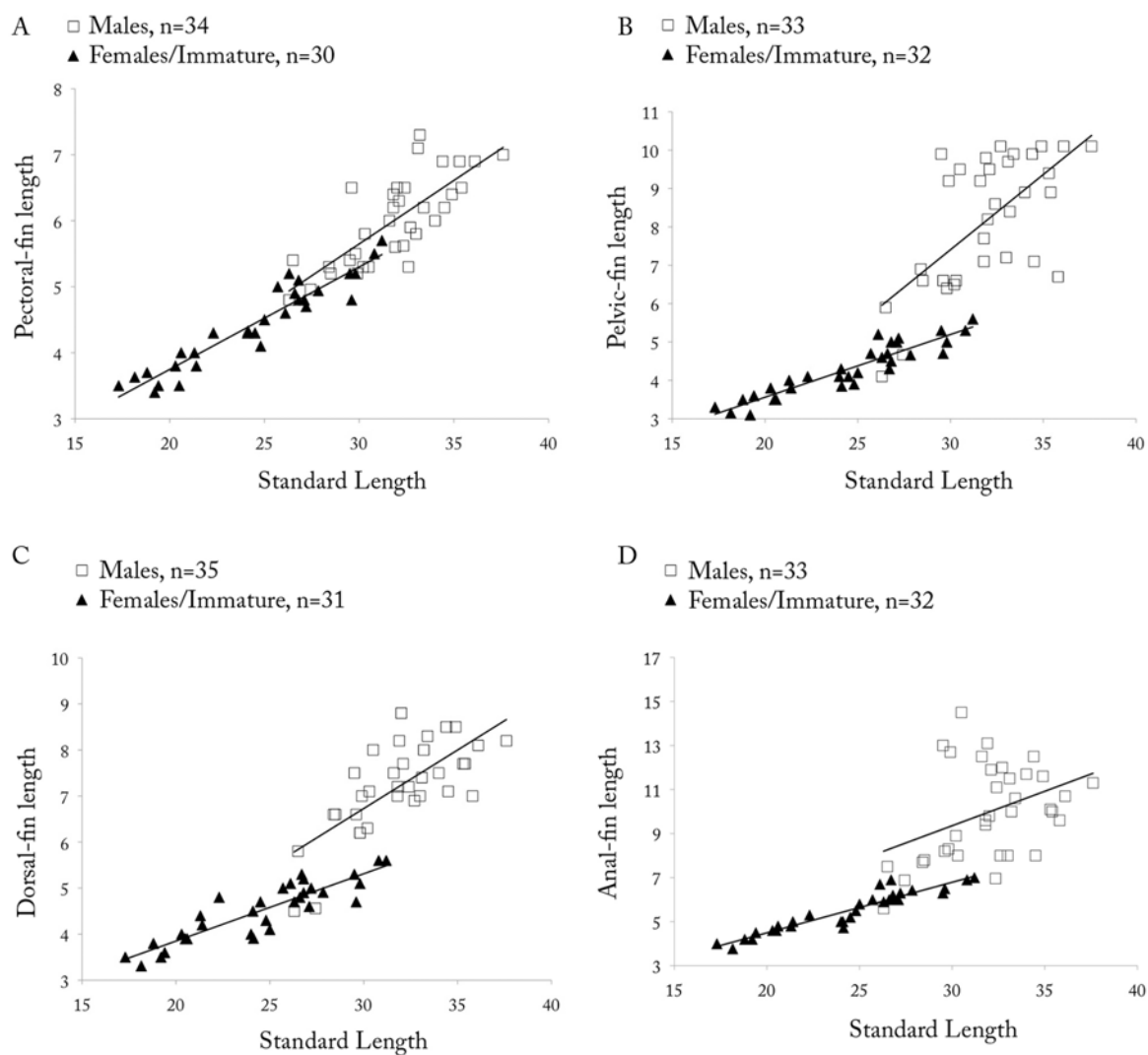


Figure 59. *Copella stigmatsemion*, pectoral-, pelvic-, dorsal- and anal-fin lengths as function of SL by sex.

Distribution. *Copella stigmatsemion* is known in the Amazon basin from the rio Ucayali and Putumayo drainages in Peru, rio Amazonas and rio Madeira in Brazil, and coastal drainages of the Pará State, Brazil (Fig. 38).

Remarks. *Nannostomus* (= *Copella*) *stigmatsemion* was described by Fowler (1913) from the rio Madeira basin near Porto Velho, based on a single juvenile specimen 10.8 mm SL. This

specimen was not cited by Weitzman & Weitzman (2003), but inside the jar with the holotype there is a label written by S. Weitzman: “This specimen described by Fowler as *Nannostomus stigmatsemion* is a juvenile of *Copella nattereri*”. Although poorly preserved, it was possible to notice that the specimen is indeed a *Copella*, not a *Nannostomus* species. However, it lacks the characteristic pigmentation of *Copella nattereri*, represented by the presence of one black spot on each scale; instead it has a black longitudinal band on body (Fig. 54B). This could be confirmed by the drawing of the holotype in the original description (Fig. 54A). Additionally, according to our study, *Copella nattereri* only occurs near the mouth of the rio Madeira, far from the surroundings of Porto Velho. The only species that occurs in the rio Madeira basin near Porto Velho is *Copella nigrofasciata*, the so-called black-banded *Copella*. The analysis of the possible types (see below) of *Pyrrhulina* (= *Copella*) *nigrofasciata* described by Meinken (1952) revealed that they are conspecific with *Copella stigmatsemion*. Following the principle of priority, and that the senior synonym was described before 1899, *Copella stigmatsemion* is considered a senior synonym of *Copella nigrofasciata*.

Meinken (1952) originally described *Pyrrhulina nigrofasciata* based on three aquarium specimens, two males and one female, said to be imported from the Peruvian Amazon, sent by J. Franke. Possible syntypes are deposited as BMNH 1952.7.31.3-5 (1 male, 32.3 mm SL, 1 female 24.1 mm SL, and 1 unsexed 27.4 mm SL) and as ZMH 1211 (1 male 35.8 mm SL) and ZMH 1212 (1 male 32.6 mm SL, 1 female 29.6 mm SL and 1 unsexed 26.3 mm SL), sent by Meinken in 1952 (O. Crimmen and R. Thiel personal communication). All specimens correspond to the same species referred here as *Copella stigmatsemion*. By comparing the measurements given by Meinken (1952) of a fully grown male and a female (37.2 mm SL and 31.0 mm SL respectively) to the measurements taken from the probable syntypes, most of the data match with those of the male ZMH 1211 (35.8 mm SL) (Fig. 55) and the female ZMH

1212 (29.6 mm SL), which are the largest male and the largest female of the possible syntypes. However, the lot ZMH 1212 has a total of three specimens, more than what Meinken had in his hands. It is not possible to know if one specimen was incorporated to ZMH 1212 after Meinken's description, but based on the data available, it is most likely that the original syntypes of *Pyrrhulina nigrofasciata* are correspond to those in the ZMH collection.

One of the specimens of the paralectotypes of *Pyrrhulina nattereri* (NMW 56974), is probably *Copella stigmatemion*, but this could not be confirmed due to the poor conditions of the material.

Copella nigrofasciata (= *C. stigmatemion*) cited by Bogotá-Gregory & Maldonado-Ocampo (2006) and Maldonado *et al.* (2008) are probably misidentifications of *Copella eigenmanni*.

MATERIAL EXAMINED

Type material

ANSP 39188 (holotype of *Nannostomus stigmasemion*, 10.8 mm SL), tributary of the rio Madeira near Porto Velho, Brazil. BMNH 1952.7.31.3-5 (3 possible syntypes of *Pyrrhulina nigrofasciata*, 24.1, 27.4 and 32.3 mm SL), imported from upper rio Amazon, Meinken, 1951. ZMH 1211 (1 possible syntype of *Pyrrhulina nigrofasciata*, 35.8 mm SL, male), imported from rio Amazon, Meinken, 1951. ZMH 1212 (3 possible syntypes of *Pyrrhulina nigrofasciata*, 26.3, 29.6 and 32.6 mm SL) imported from rio Amazon, Meinken, 1951.

Non-type material

Rio Amazonas basin, Brazil. MCZ 6334 (17, 17.1-25.3 mm SL), lago Codajás (lago Badajós), Amazonas [=approximately 3°24'S 62°38'W], 27 Nov-6 Dec 1865, Thayer Expedition. MCZ 6354 (2, 23.3 and 27.6 mm SL), Lago Curupira, Amazonas [=approximately 3°46'S 58°33'W], Nov-Dec 1865, Thayer Expedition. MCZ 170504 (9, 18.3-30.7 mm SL), rio Amazonas at Óbidos [approximately 1°52'S 55°30'W], Nov-Dec 1865, Thayer Expedition. MHNG 2200.022 (14, not measured), rio Purus, Boca de Tapauá, 5°37'27"S 63°11'18"W, 21 Nov 1976, H. Axelrodi, M. Brittan & B. Frank. MHNG 2200.025 (2, not measured), stream 35 km Northwest of Óbidos, 12 Dec 1967, R. Geisler. 2200.026 (1, not measured), Rio Curuçamba, North of Obidos, 9 Dec 1967, R. Geisler. MPEG 129 (1, 17.1 mm SL), rio Tefé drainage, Mucura, Tefé, Amazonas, 5 Aug 1979, M. Golding. MPEG 5795 (3, 24.3-33.2 mm SL), São Raimundo, Almeirim, Pará, 18 Aug 2006, J. Junior. MPEG 9267 (3, 25.0-35.7 mm SL), igarapé Mutum, Juruti, Pará, 2°36'44.8"S 56°11'37.3"W, 2 Aug 2004, W. Wosiacki & A. Bezerra. MPEG 9811 (20, 19.0-38.5 mm SL), headwaters of rio Ribeiro, Juruti, Pará, 2°25'6.8"S 56°26'37.7"W, 18 Sep 2005, W. Wosiacki. MPEG 9817 (59, 19.5-36.3 mm SL), headwaters of rio Ribeiro, Juruti, Pará, 2°25'6.8"S 56°26'37.7"W, 18 Sep 2005, B. Prudente. MPEG 9927 (2, 19.1 and 38.0 mm SL), stream under transmission line at PA 481, Barcarena, Pará, 1°38'S 48°45'W, 4 Sep 2002, A. Sousa & V. Sena. MPEG 10407 (2, 14.7 and 18.3 mm SL), igarapé Santa Rosa, rio Pará, Melgaço, Pará, 22 Nov 2003, L. Montag. MPEG ex 10416 (30, 16.5-27.8 mm SL), stream, FLONA de Caxiuanã, rio Pará, Melgaço, Pará, 1°45.62'S 51°25.46'W, 30 Nov 2004, L. Montag. MPEG 10437 (42, 11.3-16.0 mm SL), stream, FLONA de Caxiuanã, rio Pará, Melgaço, Pará, 4 Nov 2004, L. Montag. MPEG 10477 (5, 11.6-16.9 mm SL), stream, FLONA de Caxiuanã, rio Pará, Melgaço, Pará, 1°45.62'S 51°25.46'W, 30 Nov 2004 L.F.A. MPEG 10487 (2, 14.8 and 16.4 mm SL), stream, FLONA de Caxiuanã, rio Pará, Melgaço, Pará, 29 Nov 2004, L. Montag. MPEG 10493 (27, 10.1-16.0 mm SL), stream, FLONA de Caxiuanã, rio Pará, Melgaço, Pará, 1 Dec 2004, L. Montag. MPEG 10497 (2, 11.4 and 16.9 mm SL), stream, FLONA de Caxiuanã, rio Pará, Melgaço, Pará, 1 Dec 2004, L. Montag. MPEG 10502 (1, 12.7 mm SL), stream, FLONA de Caxiuanã, rio Pará, Melgaço, Pará, 4 Dec 2004, L. Montag. MPEG 10903 (5, 19.0-30.9 mm SL), igarapé Vitória, Juruti, Pará, 2°10'47"S

56°4'38.5"W, 24 Aug 2006, A. Hercos. MPEG 10904 (78, 15.3-32.8 mm SL), igarapé Vitória, Juruti, Pará, 2°10'47"S 56°4'38.5"W, 25 Aug 2006, A. Hercos. MPEG 10908 (2, 19.5 and 26-5 mm SL), igarapé São Francisco, Juruti, Pará, 2°34'50.7"S 55°54'13.8"W, 19 Aug 2006, A. Hercos. MPEG 10914 (1, 19.4 mm SL), igarapé Vitória, Juruti, Pará, 2°10'47"S 56°4'38.5"W, 24 Aug 2006, A. Hercos. MPEG 10919 (60, 14.9-35.1 mm SL), igarapé Vitória, Juruti, Pará, 2°10'47"S 56°4'38.5"W, 24 Aug 2006, A. Hercos. MPEG 10933 (3, 18.2-29.6, igarapé Vitória, Juruti, Pará, 2°10'47"S 56°4'38.5"W, 24 Aug 2006, A. Hercos. MPEG 10934 (1, 31.6 mm SL), igarapé Socó, Juruti, Pará, 2°28'14.2"S 56°00'12.7"W, 18 Aug 2006, A. Hercos. MPEG 10935 (7, 20.8-31.2 mm SL), igarapé Vitória, Juruti, Pará, 2°10'47"S 56°4'38.5"W, 24 Aug 2006, A. Hercos. MPEG 10942 (8, 23.0-35.8 mm SL), igarapé Vitória, Juruti, Pará, 2°10'47"S 56°4'38.5"W, 24 Aug 2006, A. Hercos. MPEG 10949 (1, 16.3 mm SL), igarapé Mutum, Juruti, Pará, 2°36'44.5"S 56°11'35.5"W, 18 Aug 2006, A. Hercos. MPEG 11667 (1, 20.2 mm SL), Lago Cacuri, rio Pará, Melgaço, Pará, 21 Jan 2002, L. Montag. MPEG 12823 (1, 16.8 mm SL), igarapé São Francisco, Juruti, Pará, 15 Dec 2006, L. Montag. MPEG 12824 (7, 16.5-23.2 mm SL), igarapé São Francisco, Juruti, Pará, 13 Dec 2006, L. Montag. MPEG 12825 (1, 16.2 mm SL), igarapé São Francisco, Juruti, Pará, 14 Dec 2006, L. Montag. MPEG 12827 (1, 18.8 mm SL), igarapé São Francisco, Juruti, Pará, 15 Dec 2006, L. Montag. MPEG 12828 (2, 12.3 and 19.6 mm SL), igarapé Socó-Barroso, Juruti, Pará, 12 Dec 2006, L. Montag. MPEG 12829 (2, 13.3 and 14.9 mm SL), igarapé da Ponte, Juruti, Pará, 14 Dec 2006, L. Montag. MPEG 12830 (10, 13.6-27.7 mm SL), igarapé Socó-Barroso, Juruti, Pará, 13 Dec 2006, L. Montag. MPEG 12832 (75, 11.7-25.0 mm SL), igarapé da Ponte, Juruti, Pará, 13 Dec 2006, L. Montag. MPEG 12833 (2, 18.8 and 21.1 mm SL), igarapé Mutum, Juruti, Pará, 11 Dec 2006, L. Montag. MPEG 12834 (7, 15.8-21.6 mm SL), Igarapé Mutum, Juruti, Pará, 12 Dec 2006, L. Montag. MPEG 12835 (2, 15.6 and 18.0 mm SL), igarapé da Ponte, Juruti, Pará, 14 Dec 2006, L. Montag. MPEG 12836 (2, 12.5 and 14.4 mm SL), igarapé Socó-Barroso, Juruti, Pará, 12 Dec 2006, L. Montag. MPEG 12837 (167, 16.8-32.8 mm SL), igarapé da Ponte, Juruti, Pará, 30 Dec 2008, L. Montag. MPEG 12838 (2, 23.0 and 23.7 mm SL), igarapé da Ponte, Juruti, Pará, 14 Dec 2006, L. Montag. MPEG 12839 (4, 12.1-18.1 mm SL), igarapé Mutum, Juruti, Pará, 11 Dec 2006, L. Montag. MPEG 12840 (2, 16.9 and 23.3 mm SL), igarapé da Ponte, Juruti, Pará, 24 Aug 2006, L. Montag. MPEG 12954 (1, 23.2 mm SL), igarapé Mutum, Juruti, Pará, 14 Dec 2006, L. Montag. MPEG 13629 (1, 25.4 mm SL), igarapé Mutum, Juruti, Pará, 2°36'S 56°11.6'W, 12 May 2007, A. Hercos. MPEG 13645 (3, 22.0-23.3 mm SL), igarapé Socó-Barroso, Juruti, Pará, 2°28'12"S 56°00'36"W, 16 May 2007, A. Hercos. MPEG 13663 (66, 23.9-35.8 mm SL), igarapé da Ponte, Juruti, Pará, 2°10.8'S 56°4.7'W, 17 May 2007, A. Hercos. MPEG 13704 (1, 29.3 mm SL), igarapé Mutum, Juruti, Pará, 2°36.76'S 56°11.64'W, 11 May 2007, A. Hercos. MPEG 13708 (6, 17.6-27.1 mm SL), igarapé Socó-Barroso, Juruti, Pará, 2°28'12"S 56°0'36"W, 16 May 2007, A. Hercos. MPEG 13775 (7, 24.4-33.2 mm SL), igarapé da Ponte, Juruti, Pará, 2°10.8'S 56°4.67'W, A. Hercos. MPEG 14282 (3, 14.1-19.9) igarapé Mutum, Juruti, Pará, 2°36.7'S 56°11.6'W, 27 Nov 2007, A. Hercos. MPEG 14318 (1, 30.8 mm SL), rio Araticum, rio Trombetas, Oriximiná, Pará, 1°45'34.7" 56°22'35.5"W, 22 Oct 2007, W. Wosiacki. MPEG 14325 (3, 29.8-36.6 mm SL), rio Patauá, rio Trombetas, Oriximiná, Pará, 1°46'14.5"S 56°21'14.7"W, 7 Jun 2007, W. Wosiacki. MPEG 14332 (1, 27.5 mm SL), rio Araticum, rio Trombetas,

Oriximiná, Pará, 1°45'34.7"S 56°22'35.5"W, 17 Oct 2007, W. Wosiacki. MPEG 14385 (11, 11.7-26.0 mm SL), igarapé Mutum, Juruti, Pará, 2°36.76'S 56°11.614'W, 27 Nov 2007, A. Hercos. MPEG 14399 (7, 24.1-36.2 mm SL), rio Patauá, rio Trombetas, Oriximiná, Pará, 1°46'14.5"S 56°21'12.7"W, 18 Oct 2007, W. Wosiacki. MPEG 14400 (8, 11.6-31.4 mm SL), rio Araticum, rio Trombetas, Oriximiná, Pará, 1°46'32.6"S 56°22'32.1"W, 18 Oct 2007, W. Wosiacki. MPEG 14406 (11, 11.6-26.2 mm SL), rio Patauá, rio Trombetas, Oriximiná, Pará, 1°46'14.5"S 56°21'12.7"W, 18 Oct 2007, W. Wosiacki. MPEG 14407 (1, 34.6 mm SL), rio Trombetas, Porto Trombetas, Oriximiná, Pará, 1°45'32.2"S 56°17'58.4"W, L. Montag. MPEG 14451 (3, 14.8-16.4 mm SL), igarapé da Ponte, Juruti, Pará, 2°10.8'S 56°4.667'W, 30 Nov 2007, A. Hercos. MPEG 14464 (13, 12.0-24.4 mm SL), igarapé Socó-Barroso, Juruti, Pará, 2°28'12"S, 56°4.12'W, 1 Dec 2007, A. Hercos. MPEG 14499 (6, 13.1-29.21 mm SL), igarapé da Ponte, Juruti, Pará, 2°10.9'S 56°4.67'W, 30 Nov 2007, A. Hercos. MPEG 14629 (17, 16.9-27.4 mm SL), igarapé da Ponte, Juruti, Pará, 2°10.8'S 56°4.667'W, 30 Nov 2007, A. Hercos. MPEG 14635 (4, 12.4-18.5 mm SL), igarapé Socó-Barroso, Juruti, Pará, 2°28'12"S 56°4.12'W, 1 Dec 2007, A. Hercos. MPEG 15094 (1, 18.9 mm SL), rio Branco, Juruti, Pará, 2°20'46.3"S 51°1'24.3"W, 18 Feb 2008, W. Wosiacki. MPEG 15117 (3, 25.5-36.5 mm SL), Trilha T1, Nhamundá, Faro, 1°42'23.3"S 57°2'10.1"W, 25 Aug 2006, L. Montag. MPEG 15182 (39, 13.6-36.3 mm SL), igarapé I.M.T., rio Urucu, rio Solimões, Coari, Amazonas, 4°48'27.1"S 65°1'58.4"W, 6 Feb 2008, L. Montag. MPEG 10756 (1, 20.2 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4.87°S 65.25°W, 15 Aug 2006, W. Wosiacki. MPEG 10757 (3, 13.1-20.7 mm SL), igarapé Macaco, rio Urucu, rio Solimões, Coari, Amazonas, 4.86°S 65.8°W, 15 Aug 2006, W. Wosiacki. MPEG 10758 (2, 21.0 and 32.7 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4.87°S 65.25°W, 15 Aug 2006, W. Wosiacki. MPEG 10759 (15, 17.4-24.5 mm SL), igarapé Lontra, rio Urucu, rio Solimões, Coari, Amazonas, 4.88°S 65.15°W, 21 Aug 2006, W. Wosiacki. MPEG 10760 (1, 24.4 mm SL), rio Urucu, rio Solimões, Coari, Amazonas, 4.89°S 65.32°W, 19 Aug 2006, W. Wosiacki. MPEG 10761 (20, 11.0-30.7 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4.86°S 65.27°W, 15 Aug 2006, W. Wosiacki. MPEG 10762 (18, 10.2-30.6 mm SL), rio Urucu drainage, rio Solimões, Coari, Amazonas, 4.84°S 65.26°W, 18 Aug 2006, W. Wosiacki. MPEG 10763 (4, 13.1-19.3 mm SL), igarapé Lontra, rio Urucu, rio Solimões, Coari, Amazonas, 4.87°S 65.2°W, 21 Aug 2006, W. Wosiacki. MPEG 10764 (2, 13.7 and 17.4 mm SL), rio Urucu drainage, rio Solimões, Coari, Amazonas, 4.84°S 65.26°W, 1 Aug 2006, W. Wosiacki. MPEG 10765 (2, 18.0 and 19.1 mm SL), igarapé Lontra, rio Urucu, rio Solimões, Coari, Amazonas, 4.86°S 65.27°W, 21 Aug 2006, W. Wosiacki. MPEG 11200 (1, 25.1 mm SL), rio Urucu drainage, rio Solimões, Coari, Amazonas, 8 Aug 2006, W. Wosiacki. MPEG 11201 (1, 21.6 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4.86°S 65.27°W, 2 Aug 2006, W. Wosiacki. MPEG 11202 (9, 11.5-19.1 mm SL), rio Urucu drainage, rio Solimões, Coari, Amazonas, 4.84°S 65.26°W, 18 Aug 2006, W. Wosiacki. MPEG 12258 (6, 15.1-27.2 mm SL), igarapé Lontra, rio Urucu, rio Solimões, Coari, Amazonas, 4.84°S 65.9°W, 18 Nov 2006, W. Wosiacki. MPEG 13266 (2, 27.4 and 29.0 mm SL), igarapé Lontra, rio Urucu, BOGPM, rio Solimões, Coari, Amazonas, 4°50'37"S 65°1'50.16"W, 6 Apr 2007, W. Wosiacki. MPEG 13266 (2, 27.4 and 29.0 mm SL), igarapé Lontra, rio Urucu, BOGPM, rio Solimões, Coari, Amazonas, 4°50'37"S 65°1'50.16"W, 6 Apr 2007, W. Wosiacki. MPEG 15187 (1, 26.9 mm SL), igarapé

Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°49'43"S 65°1'45.4"W, 8 Feb 2008, L. Montag. MPEG 15203 (10, 13.1-37.0 mm SL), igarapé da Cobra, rio Urucu, rio Solimões, Coari, Amazonas, 4°53'32.7"S 65°11'8.2"W, 6 Feb 2008, L. Montag. MPEG 15227 (2, 7.8 and 11.5 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°49'43"S 65°15'19.6"W, 7 Feb 2008, L. Montag. MPEG 15917 (24, 12.1-31.4 mm SL), igarapé Tamoatá, rio Paraconi drainage, FLONA do Pau Rosa, rio Madeira, Maués, Amazonas, 3°44'47.1"S 58°18'7.6"W, 14 Feb 2009, F. Silva. MPEG 16246 (19, 21.9-34.3 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°53'18.3"S 65°9'25.5"W, 16 Dec 2008, L. Montag. MPEG 16247 (51, 15.4-33.4 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°53'32.7"S 65°11'8.2"W, 28 Jul 2008, W. Wosiacki. MPEG 16248 (45, 11.4-30.5 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°52'19.56"S 65°14'58.56"W, L. Montag. MPEG 16249 (33, 17.7-35.4 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°53'32.7"S 65°11'8.2"W, 28 Jul 2008, W. Wosiacki. MPEG 16250 (2, 25.3 and 35.4 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°51'43.9"S 65°15'54.4"W, 25 Jul 2008, W. Wosiacki. MPEG 16251 (5, 16.1-29.5 mm SL), igarapé Tartaruga, rio Urucu, rio Solimões, Coari, Amazonas, 4°56'13.2"S 65°18'22.5"W, 26 Jul 2008, W. Wosiacki. MPEG 16252 (12, 15.2-30.5 mm SL), rio Urucu, rio Solimões, Coari, Amazonas, 4°48'56"S 65°1'45.4"W, L. Montag. MPEG 16253 (16, 13.1-33.6 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°53'32.7"S 65°11'8.2"W, 28 Jul 2008, W. Wosiacki. MPEG 16254 (12, 16.5-27.2 mm SL), igarapé Tartaruga, rio Urucu, rio Solimões, Coari, Amazonas, 4°56'13.2"S 65°18'22.5"W, 26 Jul 2008, W. Wosiacki. MPEG 16266 (2, 20.5 and 21.2 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°53'4.9"S 65°13'34.5"W, 15 Jun 2009, L. Montag. MPEG 16267 (3, 16.8-21.5 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°51'43.9"S 65°15'54.4"W, W. Wosiacki. MPEG 16268 (13, 13.0-30.1 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°53'18.3"S 65°9'25.5"W, 28 Jul 2008, W. Wosiacki. MPEG 16269 (4, 11.7-17.5 mm SL), igarapé I.M.T., rio Urucu, rio Solimões, Coari, Amazonas, 4°49'28.92"S 65°1'50.16"W, 10 Apr 2007, W. Wosiacki. MPEG 16270 (7, 12.2-20.4 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°51'43.9"S 65°15'54.4"W, 25 Jul 2008, W. Wosiacki. MPEG 16271 (9, 14.0-38.0 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°50'18.96"S 65°1'50.1"W, 4 Apr 2008, W. Wosiacki. MPEG 16272 (74, 13.3-35.4 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°53'4.9"S 63°13'34.5"W, W. Wosiacki. MPEG 16273 (2, 17.8 and 20.3 mm SL), igarapé Tartaruga, rio Urucu, rio Solimões, Coari, Amazonas, 4°53'4.3"S 65°20'6.5"W, 27 Jul 2009, W. Wosiacki. MPEG 16274 (6, 18.5-32.0 mm SL), igarapé I.M.T., rio Solimões, Coari, Amazonas, 4°48'55.9"S 65°1'45.5"W, 29 Jun 2009, W. Wosiacki. MPEG 16275 (1, 16.8 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°52'20.3"S 65°15'0.7"W, 25 Jul 2008, W. Wosiacki. MPEG 16276 (3, 17.9-20.0 mm SL), igarapé Tartaruga, rio Urucu, rio Solimões, Coari, Amazonas, 4°53'4.3"S 65°13'6.5"W 27 Jul 2008 W. Wosiacki. MPEG 16277 (1, 18.1 mm SL), igarapé Marta, rio Urucu, rio Solimões, Coari, Amazonas, 4°51'39.2"S 65°4'40.4"W, 19 Jul 2008, W. Wosiacki. MPEG 16774 (69, 12.7-25.8 mm SL), rio Urucu drainage, rio Solimões, Coari, Amazonas, 4°S 65°W, 6 Aug 2009, B. Prudente. MPEG 16775 (138, 12.9-34.5 mm SL), rio Urucu drainage, rio Solimões, Coari, Amazonas, 4°53'2.6"S 65°13'33.8"W, 3 Aug 2009, B.

Prudente. MPEG 16776 (9, 14.1-21.7 mm SL), igarapé Marta, rio Urucu, rio Solimões, Coari, Amazonas, 4°51'39.3"S 65°4'40.2"W, 3 Aug 2009, B. Prudente. MPEG 16777 (5, 18.7-28.9 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°51'44"S 65°15'53.8"W, 2 Aug 2009, B. Prudente. MPEG 16778 (4, 15.1-19.9 mm SL), igarapé Tartaruga, rio Urucu, rio Solimões, Coari, Amazonas, 4°53'4.3"S 65°20'6.5"W, 6 Aug 2009, B. Prudente. MPEG 16779 (1, 12.6 mm SL), rio Urucu drainage, rio Solimões, Coari, Amazonas, 4°52'4.7"S 65°7'25.3"W, 5 Aug 2009, B. Prudente. MPEG 16780 (2, 12.6 and 17.9 mm SL), rio Urucu drainage, rio Solimões, Coari, Amazonas, 4°52'40.7"S 65°14'13.9"W, 7 Aug 2009, B. Prudente. MPEG 16783 (3, 7.9-27.1 mm SL), igarapé Tamanduá, rio Urucu, rio Solimões, Coari, Amazonas, 4°52'18.7"S 65°14'59.6"W, 3 Aug 2009, B. Prudente. MPEG 17408 (25, 20.5-35.7 mm SL), igarapé I.M.T., rio Urucu, rio Solimões, Coari, Amazonas, 4°48'55.2"S 65°1'46.1"W, 4 Aug 2009, B. Prudente. MPEG 17409 (235, 13.8-35.7 mm SL), rio Urucu drainage, rio Solimões, Coari, Amazonas, 4°52'40.7"S 65°14'13.9"W, 7 Aug 2009, B. Prudente. MZUSP 5915 (7, 14.2-20.3 mm SL), lago Jacaré, right margin of rio Solimões, upstream Manacapuru, Manacapuru, Amazonas, 3°17'S 60°38'W, 29-31 Mar 1967, Expedição Permanente da Amazônia. MZUSP 6052 (3, 18.7-21.5 mm SL), Lago Rei, ilha do Careiro, rio Negro drainage, Careiro da Várzea, Amazonas, 3°8'S 59°43'W, 12 Apr 1967, Expedição Permanente da Amazônia. MZUSP 6636 (55, 13.1-21.1 mm SL), stream of lago Manacapuru, rio Solimões, Manacapuru, Amazonas, 3°13'S 60°45'W, 13 Nov 1967, Expedição Permanente da Amazônia. MZUSP 9669 (24, 16.0-21.1 mm SL), lago Supiá, opposite to Codajás, rio Solimões, Codajás, Amazonas, 3°51'S 62°4'W, 24 Aug 1968, Expedição Permanente da Amazônia. MZUSP 9447 (87 of 111, 18.8-28.5 mm SL), igarapé Cajuassú, rio Cuminá, rio Trombetas, Pará, 1°19'S 55°45'W, 26 Jan 1968, Expedição Permanente da Amazônia. MZUSP 23232 (387, 13.3-23.4 mm SL, 10 c&s, 11.8-20.4 mm SL), lago Miuá, upstream Codajás, rio Solimões, Careiro, Amazonas, 3°51'S 60°4'W, 25 Aug 1968, Expedição Permanente da Amazônia. MZUSP 23253 (5, 12.5-15.7 mm SL), rio Solimões drainage, Coari, Amazonas, 4°5'S 63°9'W, 28 Aug 1968, Expedição Permanente da Amazônia. MZUSP 23419 (29, 17.5-25.0 mm SL), lago Buiucu, Ati-Paraná, Northwest of Fonte Boa, rio Solimões, Fonte Boa, Amazonas, 2°31'S 66°6'W, 11-12 Aug 1968, Expedição Permanente da Amazônia. MZUSP 23489 (6, 24.8-29.6 mm SL), stream near Porto Antunes, rio Jutai drainage, rio Solimões, Amazonas, 3°4'S 67°3'W, 22 Oct 1968, Expedição Permanente da Amazônia. MZUSP 23490 (8, 17.0-21.2 mm SL), stream near Porto Antunes, rio Jutai drainage, rio Solimões, Amazonas, 3°4'S 67°3'W, 22 Oct 1968, Expedição Permanente da Amazônia. MZUSP 23495 (5, 19.3-32.3 mm SL), stream at rio Içapó, rio Jutai mouth, rio Solimões, Amazonas, 2°56'S 66°48'W, 22 Oct 1968, Expedição Permanente da Amazônia. MZUSP 23510 (83 of 111, 22.9-32.0 mm SL, 4 c&s, 23.0-31.7 mm SL), igarapé number three, rio Solimões, Fonte Boa, Amazonas, 2°31'S 66°6'W, 25 Oct 1968, Expedição Permanente da Amazônia. MZUSP 29339 (6, 14.2-28.3 mm SL), Vista Escura, rio Tefé, Amazonas, 3°22'S 64°43'W, 4 Aug 1979, M. Golding. MZUSP 29340 (21, 19.5-23.1 mm SL), Supiã-Pucu, Capim beach, rio Tefé, Tefé, Amazonas, 3°22'S 64°43'W, 21 Jul 1979, M. Golding. MZUSP 31424 (1, 26.7 mm SL), Jurupari, Tefé, Amazonas, 3°22'S 64°43'W, 1 Aug 1979, M. Golding. MZUSP 52646 (3, 16.8-27.0 mm SL), igarapé Saracazinho, rio Trombetas, Porto Trombetas, Pará, 19 Mar 1997, E. Caramaschi & R. Reis. MZUSP 52667 (7, 13.6-34.8 mm SL), igarapé Periquito, upstream road, rio Trombetas, Porto Trombetas, Pará, 17 Mar 1997,

E. Caramaschi & R. Reis. MZUSP 52678 (1, 21.7 mm SL), igarapé Saracá, downstream road, rio Trombetas, Porto Trombetas, Pará, 17 Mar 1997, E. Caramaschi & R. Reis. MZUSP 52691 (3, 12.0–23.0 mm SL), igarapé Saracá, upstream road, rio Trombetas, Porto Trombetas, Pará, 15 Mar 1997, E. Caramaschi & R. Reis. MZUSP 52705 (10, 15.8–22.3 mm SL), igarapé Saracá, upstream road, rio Trombetas, Porto Trombetas, Pará, 18 Mar 1997, E. Caramaschi & R. Reis. MZUSP 52739 (1, 17.0 mm), headwater of igarapé Papagaio, rio Trombetas, Porto Trombetas, Pará, 2 Aug 1997, E. Caramaschi & R. Reis. MZUSP 52747 (13, 17.3–28.0 mm SL), igarapé Saracá, upstream, rio Trombetas, Porto Trombetas, Pará, 30 Aug 1997, E. Caramaschi & R. Reis. MZUSP 52758 (2, 28.6 and 32.5 mm SL), igarapé Papagaio, a jusante, braço esquerdo, rio Trombetas, Porto Trombetas, Pará, 30 Aug 1997, E. Caramaschi & R. Reis. MZUSP 52793 (6, 14.2–22.0 mm SL), igarapé Periquito, upstream, rio Trombetas, Porto Trombetas, Pará, 2 Aug 1997, E. Caramaschi & R. Reis. MZUSP 101930 (4, 12.6–29.5 mm SL), igarapé Arapiranga, affluent of left margin of rio Jari, Porto do Figueira, downstream Cachoeira Santo Antônio, Laranjal do Jari, Amapá, 00°48'4"S 52°27'20"W, 25 Mar 2008, C. Moreira, T. Loboda & M. Soares. MZUSP 101931 (5, 16.3–20.5 mm SL), rio Caracuru and stream without name, affluent of rio Caruru, surroundings Vila Santa Maria, rio Jari drainage, Monte Dourado, Amapá, 00°54'55"S 52°34'39"W, 10 Aug 2007, M. Carvalho *et al.* MZUSP 101932 (1, 33.9 mm SL), igarapé Arapiranga, affluent of left margin of rio Jari, Sombra da Mata, downstream Cachoeira Santo Antônio, Laranjal do Jari, Amapá, 00°47'40"S 52°27'9"W, 25 Mar 2008, C. Moreira, T. Loboda & M. Soares. MZUSP 101933 (24, 13.2–34.9 mm SL, 2 c&s, 27.4 and 32.0 mm SL), igarapé Ting Ling, right margin of rio Jari, downstream Chachoeira Santo Antônio, Laranjal do Jari, Amapá, 00°49'54"S 52°40'25"W, 16 Oct 2007, M. Carvalho *et al.* MZUSP 102039 (2, 18.0 and 19.5 mm SL), igarapé Ting Ling, right margin of rio Jari, downstream Chachoeira Santo Antônio, Laranjal do Jari, Amapá, 00°49'54"S 52°40'25"W, 16 Aug 2007, M. Carvalho *et al.* MZUSP 103302 (12, 19.4–34.9 mm SL), igarapé Arapiranga at Balneário Sombra da Mata, left margin of rio Jari, downstream Cachoeira, Laranjal do Jari, Amapá, 00°47'41"S 52°27'10"W, 16 Feb 2009, J. Birindelli, L. Sousa & M. Soares. MZUSP 103273 (4, 23.5–32.8 mm SL), igarapé Arapiranga, affluent of left margin of rio Jari, Porto do Figueira, downstream Cachoeira Santo Antônio, Laranjal do Jari, Amapá, 00°48'5"S 52°27'20"W, 16 Feb 2009, J. Birindelli, L. Sousa & M. Soares. UFRO-I 2757 (2, 13.6 and 16.0 mm SL), igarapé Jatuarana, near confluence of rio Madeira, Porto Velho, Rondônia, 8°49'49.6"S 64°2'45.7"W. UFRO-I 6386 (22, 13.9–21.9 mm SL), stream at Estação Ecológica do Cuniã Madeira, rio Madeira, Porto Velho, Rondônia, 8°4'43.3"S 63°28'34.4"W. UFRO-I 6387 (2, 13.4 and 15.8 mm SL), igarapé Karipuna, upstream mouth of rio Madeira, Porto Velho, Rondônia, 9°12'19.7"S 64°37'57.3"W. USNM 229404 (3, 15.5–18.4 mm SL), Camaleão, ilha de Marchantaria, Amazonas, 3°11'10.9"S 60°7'51.4"W, 27 Sep 1977, P. Bayley. SMF 21321 (37, 17.0–26.6 mm SL), Manacapuru, Solimões.

Peru. ANSP 165007 (14, 18.0–35.2 mm SL), small stream about 70 km South of Iquitos, near Jenaro Herrera, rio Ucayali, Loreto, 5°0'0"S 73°38'0" W, 23 Aug 1989, P. Fromm *et al.* ANSP 165043 (3, 20.5–25.6 mm SL), stream of rio Yanayacu, West of Miraflores, rio Marañon, rio Ucayali, Loreto, 4°42'0"S 74°17'0"W, 21 Aug 1989, P. Fromm *et al.* ANSP 167195 (11, 16.6–25.8 mm SL), small stream five minutes by foot from right margin of rio Nanay, about 1 km upstream Minchana, Loreto, 3°53'0"S 73°27'0"W, 11 Sep 1989, Dan & P.

Fromm. ANSP 167196 (2, 20.5 and 22.1 mm SL), brook crossing left trail about 10 min from Minchana, rio Nanay, Loreto, 3°53'0"S 73°27'0"W, 11 Sep 1989, Dan & P. Fromm. ANSP 167197 (5, 10.9-21.2 mm SL), creek about 15 min paddle up rio Momon from Amazon camp, rio Ucayali, Loreto, 3°42'0"S 73°13'0"W, 3 Sep 1989, Dan & P. Fromm. ANSP 167198 (5, 22.5-32.4 mm SL), brook crossing left trail about 20 min walk from Minchana, rio Nanay, Loreto, 3°53'0"S 73°27'0"W, 3 Sep 1990, Dan & P. Fromm. ANSP 167199 (23, 12.6-29.6 mm SL), stream upstream Nina Rumi, left margin of rio Nanay, Loreto, 3°44'0"S 73°20'0"W, 9 Sep 1990, Dan & P. Fromm. ANSP 167200 (56, 16.3-28.9 mm SL), stream almost dry, about six Miles up rio from confluence from rio Momon, left bank, Loreto, 3°46'0"S 73°15'0" W, 23 Aug 1989, Dan & P. Fromm. ANSP 167201 (38, 11.4-27.5 mm SL), Laguna Rocafuerte, right margin of rio Nanay, about six miles up from confluence with rio Momon, Loreto, 3°46'0"S 73°15'0" W, 23 Aug 1990, Dan & P. Fromm. ANSP 167222 (1, 21.8 mm SL), stream almost dry at left margin of rio Nanay, about five miles downstream Santa Clara, Loreto, 3°45'0"S 73°17'0" W, 4 Sep 1990, Dan & P. Fromm. ANSP 178193 (4, 14.5-19.1 mm SL), caño Santa Rita, right margin, tributary of rio Nanay, 3.32 miles Northwest of Iquitos, near Pampa Chica community, Maynas, Loreto, 3°45'23"S 73°17'28"W, 2 Aug 2001, M. Sabaj *et al.* ANSP 180757 (12, 20.3-26.5 mm SL), mouth of stream feeding laguna connected to rio Nanay, about two hours upstream from Santa Clara by outboard motor boat, Maynas, Loreto, 3°52'21"S 73°32'43" W, 16 Aug 2003, M. Sabaj *et al.* ANSP 190681 (1, 18.0 mm SL), rio Nanay, large Sandy beach on downstream end of island upstream from Santa Clara, Southwest of Iquitos, Loreto, 3°46'45"S 73°22'6" W, 14 Aug 2003, M. Sabaj, N. Salcedo & B. Sidlauskas. MHNG 2200.024 (1, not measured), swamp at tributary of rio Corrientes. MZUSP 85597 (31, 11.0-33.1 mm SL), stream at Km 3 of Jenaro Herrera-Colonia Angamos road, upstream "aguajal", Requena, Loreto, 4°55.889'S 73°38.756'W, 14 Jan 2004, H. Ortega *et al.* MZUSP 85603 (20, 17.5-34.0 mm SL, 2 c&s, 23.0-28.8 mm SL), stream about 0.3 km North of Km 3.9 of Jenaro Herrera-Colonia Angamos road, 4°53.91'S 73°38.366'W, 16 Jan 2004, H. Ortega, R. Reis & F. Lima. MZUSP 26697 (8, 16.3-31.1 mm SL), Jenaro Herrera, Arboreto, Requena, Loreto, 30 Jun 1979, P. de Rham. MZUSP 26698 (1, 21.9 mm SL), Jenaro Herrera, Loreto, 20 Aug 1979, H. Ortega. NRM 37465 (8, 17.8-24.8 mm SL), unnamed stream, about 200 m to the left of the road from Iquitos, Just before Santa Clara, rio Nanay drainage, Loreto, 7 Sep 1981, S. Kullander & A. Urtega. NRM 18655 (15, 12.4-27.5 mm SL), quebrada Sapuena at Km 10 on road Jenaro Herrera-Colonia Angamos, Loreto, 31 Aug 1983, S. Kullander *et al.* NRM 18662 (64, 14.4-31.3 mm SL), stream in arboretum at Km 3 on road Jenaro Herrera-Colonia Angamos, Loreto, 2 Sep 1983, S. Kullander, A. Urtega & T. Townshend. NRM 17038 (1, 27.1 mm SL), stream in civil village intended for fish pond close to source, rio Yavarí system, Colonia Angamos, Loreto, 1 Aug 1984 S. Kullander *et al.* NRM 49109 (3, 25.3-34.6 mm SL), Quebrada de las Granjas, rio Putumayo, Loreto, 21 Jul 1986, S. Kullander *et al.* NRM 49108 (27, 17.3-35.1 mm SL), fish pond in construction at Southwest village margin, rio Putumayo drainage, Loreto, 21 Jul 1986 S. Kullander *et al.* NRM 48119 (4, 14.1-25.6 mm SL), three small stream at Eastern margin of village, rio Putumayo, Loreto, 21 Jul 1986, S. Kullander *et al.*

COPELLA VILMAE GÉRY, 1963

Figures 37, 60-65; Tables 11 and 12

Copella vilmae Géry, 1963: 25, figs. 1-2 [type locality: Igarapé Preto, affluent of upper rio Amazonas near Belém, about 60 km below Letícia, Amazonas, Peru-Colombia-Brazil border].—Géry, 1965b: 11 [notes on habitat].—Géry, 1977: 147 [comparison with *Copella compta*, unnumbered figures pg. 149].—Vari & Howe, 1991: 15 [listed].—Weitzman & Weitzman, 2003: 242 [literature compilation].—Zarske & Géry, 2006: 41 e 44 [identification key].—Oyakawa & Netto-Ferreira, 2007: 64 [literature compilation].—Zarske, 2011: 32 [taxonomic notes].



Figure 60. Holotype of *Copella vilmae*, SMF 5931, 43.9 mm SL, Igarapé Preto near Belém, 60 km downstream Letícia, Colombia.



Figure 61. *Copella vilmae*: (A) paratype, male, USNM 198135, 46.4 mm SL, (B) USNM paratype, male, 45.4 mm SL, Igarapé Preto near Belém, 60 Km downstream Letícia, Colombia, (C) AMNH 218052, female, 30.5 mm SL, rio Amazonas at Letícia, Colombia. Photos A and B by Sandra Raredon.



Figure 62. *Copella vilmae*, live males, aquarium specimens not preserved. Photo by O. Lucanus.



Figure 63. *Copella vilmae*, live male, aquarium specimen not preserved. Photo by T. Christoffersen.



Figure 64. *Copella vilmae*, live female, aquarium specimen not preserved. Photo by T. Christoffersen.

Diagnosis. *Copella vilmae* are easily distinguished from the remaining congeners by the presence of an interrupted longitudinal series of dark scales on body in males (*vs.* presence of a continuous longitudinal series of dark scales forming a longitudinal band or absence of any

longitudinal color pattern). Females of *C. vilmae* can be diagnosed from the remaining congeners, except females of *C. compta*, by the presence of a small dark spot at the base of the upper caudal-fin lobe (*vs.* absence). Females of *C. vilmae* can be distinguished from females of *C. compta* by the presence of a brownish longitudinal band on body (*vs.* absence).

Description. Morphometrics in Tables 11 and 12. Largest examined male 55.5 mm SL, female 36.4 mm SL. Greatest body depth located at vertical through pelvic-fin origin. Body cylindrical, slightly compressed laterally. Dorsal profile of body straight to slightly convex from tip of snout to end of supraoccipital, slightly convex from that point to dorsal-fin origin, posteroventrally inclined along dorsal-fin base and straight along caudal peduncle. Ventral profile of body convex from the anterior tip of dentary to the vertical through anterior margin of orbit, straight from that point to the vertical through the pectoral-fin origin, straight to slightly convex from that point to pelvic-fin origin, straight from pelvic-fin origin to anal-fin origin, posterodorsally inclined along the anal-fin base and straight along the caudal peduncle.

Mouth upturned. Premaxillary teeth in one row, with 19 (1), 20 (2) teeth, decreasing in size laterally. Number of maxillary teeth sexually dimorphic, 15 (1) in males and 5 (1), 7 (2) in females, decreasing in size posteriorly, especially on males. Dentary teeth in two rows, outer with 12 (1), increasing in size laterally, inner with 29 (1) teeth, decreasing in size laterally.

Dorsal fin with ii, 8 (42)* rays, second and third branched rays longer. Pectoral fin with i, 8 (2), 9 (28)*, or 10 (11) rays, second and third branched rays longer. Pelvic fin with i, 7 (42)* rays, third and fourth branched ray longer. Anal fin with iii (6), 8 (38)*, i rays, third and fourth branched rays longer. Caudal fin with i, 7 (2), 8 (38)* rays in upper lobe, second and third branched rays longer, and 6 (1), 7 (38)*, or 8 (1), i rays in lower lobe, second and third branched rays longer. Upper caudal-fin lobe longer than lower.

Predorsal scales 15 (9)*, 16 (32), or 17 (1), in one series. First longitudinal scale row with 14 (4), 15 (24)* 16 (12), or 17 (1) scales. Fourth longitudinal scale row with 24 (8), 25 (19)*, or 26 (14) scales. Longitudinal scale rows between dorsal-fin origin and pelvic-fin origin 5 (16)* or 6 (25). Longitudinal scale rows between dorsal-fin origin and anal-fin origin 5 (42)*. Circumpeduncular scale rows 10 (42)*. Total number of vertebrae 34 (2) or 35 (3).

Table 11. Morphometrics of *Copella vilmae*. Holotype of *Copella vilmae* SMF 5931, paratypes of *C. vilmae* MHNG 2200.018 (2), SMF 5967-5978 (4), USNM 198135 (4) and non-type material AMNH 218052 (3), AMNH 218053 (5), IavH 8385 (2), IavH 11192 (6), IavH 11193 (13), n = number of specimens, SD = Standard deviation. Ranges do not include the holotype.

	<i>Copella vilmae</i>		n	Range	Mean	SD
	Holotype					
Standard length (mm)	43.9	41	21.8	55.5	35.1	6.4
Percents of standard length						
Body depth	18.6	41	15.3	21.9	18.2	1.5
Dorsal- to caudal-fin origin	35.8	41	32.9	37.6	35.1	1.0
Snout to dorsal-fin origin	65.9	40	62.7	68.7	65.7	1.4
Snout to pectoral-fin origin	22.3	40	21.3	25.9	22.7	0.9
Snout to pelvic-fin origin	49.7	40	42.6	51.3	48.5	1.4
Snout to anal-fin origin	73.1	39	67.2	74.2	71.0	1.4
Pectoral- to pelvic-fin origin	27.9	41	22.7	29.2	26.7	1.5
Pelvic- to anal-fin origin	24.7	40	20.0	27.4	23.2	1.3
Pectoral-fin length males	30.7	17	19.7	28.7	23.6	2.6
Pectoral-fin length fem/imm	-	24	16.8	24.1	21.2	1.8
Pelvic-fin length males	35.0	17	16.3	36.9	26.4	4.9
Pelvic-fin length fem/imm	-	24	17.7	23.5	20.9	1.8
Dorsal-fin length males	49.2	17	25.2	41.6	34.2	5.6
Dorsal-fin length fem/imm	-	24	19.9	34.2	28.9	3.6
Anal-fin length males	23.7	16	16.9	23.4	21.2	1.7
Anal-fin length fem/imm	-	24	14.8	22.9	18.5	1.5
Anal-fin base length	10.3	41	7.1	10.9	8.8	0.9
Caudal peduncle depth	9.3	41	6.9	10.5	8.9	0.7
Caudal peduncle length	19.4	41	17.0	23.6	20.2	1.4
Head length	22.3	40	20.0	24.5	22.7	0.9
Percents of head length						
Eye diameter	33.9	39	29.2	40.3	34.8	2.8
Snout length	28.2	38	25.4	34.8	28.7	1.8
Interorbital distance	35.6	40	32.1	40.2	35.4	1.9
Upper jaw length	35.6	39	28.5	38.2	33.1	2.5

Table 12. Meristics of the holotype of *Copella vilmae*.

	<i>Copella vilmae</i>
	Holotype
Predorsal scales	15
First longitudinal scale row	15
Fourth longitudinal scale row	25
Longitudinal scale rows dorsal to pelvic	5
Longitudinal scale rows dorsal to anal	5
Circumpeduncular scale rows	10
Pectoral-fin rays	i9
Pelvic-fin rays	i7
Dorsal-fin rays	ii8
Branched anal-fin rays	9
Caudal-fin rays	i8,7i

Color in alcohol. Overall ground coloration of body beige. Dark stripe extending from anterior tip of dentary to posterior tip of opercle. Dorsal portion of body dark. Inconspicuous dark pigmentation located at base of scales. Largest males with a series of brown scales interposed with clear ones mainly on the fourth longitudinal scale row, but also on the third and the fifth rows, without a fixed arrangement. Brown scales on the anterior portion of body deep dark, gradually lighter posteriorly (Fig. 60, 61A and B). Females and juveniles with distinct colorations of males, consisting of inconspicuous wide brownish stripe on the flank, on the fourth and fifth longitudinal scale rows, extending from opercle to caudal peduncle, and clear longitudinal stripe above it (Fig. 61 C). Juvenile males with color pattern intermediate between those of adult males and females, with a longitudinal wide stripe on the flank, a clear stripe above it, and a series of dark brown scales on the fourth longitudinal scale row. Dorsal fin with a black round spot. Remaining fins hyaline. Pelvic and anal fins usually with dark edge, more intense in males. Dorsal and ventral procurrent caudal-fin rays dark, darker in males. Females and juveniles with an inconspicuous dark spot at base of upper caudal-fin lobe.

Color in life. Dorsal portion of body olivaceous, ventral portion yellowish anteriorly and deep pink posteriorly. Males with a series of brilliant green scales irregularly arranged, mainly on the fourth longitudinal scale row. Base of dorsal fin, base of the dorsalmost rays of upper caudal-fin lobe, and tip of basalmost rays of lower caudal-fin deep pink in males (Figs. 62 and 63). Females with a metallic-green longitudinal band on body, extending from opercle to the end of caudal peduncle (Fig. 64).

Sexual dimorphism. Males longer than females. Males with more maxillary teeth than females (see description above). Pelvic, dorsal, and anal fins longer in males than in females. Pectoral-fin length apparently not sexually dimorphic. There is variation in relative fin length among males. Males with the same Standard Length may present distinct fin lengths (Fig. 65). Tip of adpressed dorsal fin reaching up to one-half the length of upper caudal-fin lobe rays in males, and approximately to two-third the length of caudal peduncle length in females. Tip of pectoral fin may surpass pelvic-fin origin in males, but never in females. Tip of adpressed pelvic fin reaching up base of last anal-fin rays in males, and up to anus in females. Upper caudal-fin lobe longer than lower one, especially in males. Differences in the color pattern described on “Color in alcohol” section.

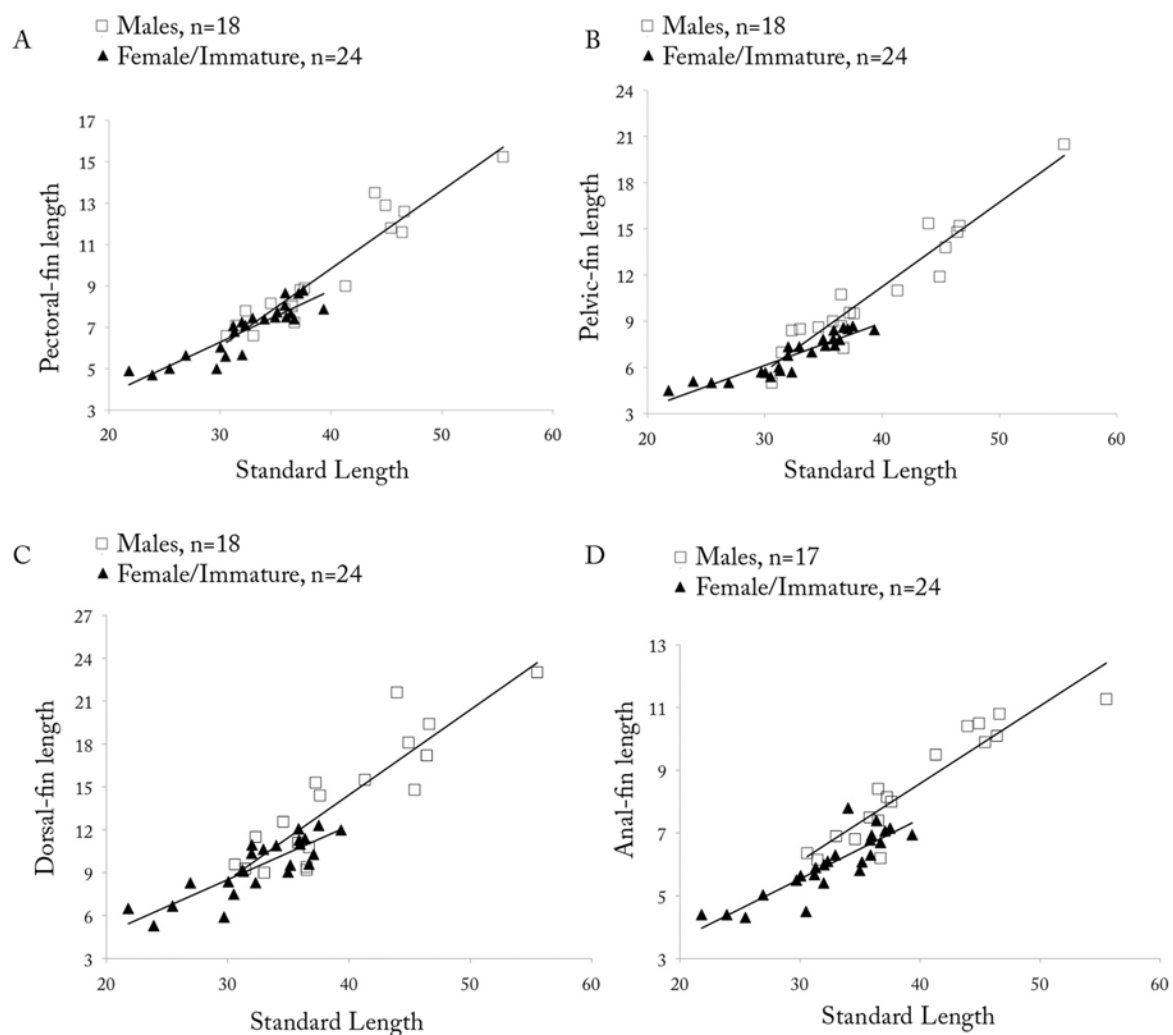


Figure 65. *Copella vilmae*, pectoral-, pelvic-, dorsal- and anal-fin length as function of SL by sex.

Distribution. *Copella vilmae* is known from the upper rio Amazonas, surroundings of Letícia, Colombia (Fig. 37).

Remarks. Géry (1963) described *Copella vilmae* based on the holotype (Fig. 60) and 20 paratypes. Four paratypes were kept in aquarium and then deposited at SU. These four specimens are now under USNM 198135. Among the remaining 16 paratypes, 12 were said to

be deposited at SMF 5967-78 and nothing is said about the other four paratypes. At SMF, I only analyzed 11 paratypes stored in a single jar under SMF 5967-77, separated by small glass tubes. The paratype SMF 5978 was not available and it was not possible to confirm whether it is missing. The remaining four paratypes cited in the description are deposited at MHNG 2200.018.

MATERIAL EXAMINED

Type material

SMF 5931 (holotype of *Copella vilmae*, 43.9 mm SL), MHNG 2200.018 (4, 22.1-45.3 mm SL), SMF 5967-77 (11, 18.6-31.8 mm SL), USNM 198135 [ex SU] (4, 33.0-46.4 mm SL), Igarapé Preto, affluent of upper rio Amazonas, near Belém, 60 Km downstream Letícia, Amazonas, Colombia, Dez 1960, H. Shultz.

Non-type material

Rio Amazonas basin, Colombia. AMNH 218052 (5, 25.9-34.0 mm SL), rio Amazonas at Letícia, Amazonas, 15-30 Ago 1965. AMNH 218053 (4, 36.5-46.6 mm SL, 1 c&s, 42.4 mm SL), rio Amazonas at Letícia, Amazonas, 15-30 Ago 1965. IavH 8385 (2, 29.6 and 31.8 mm SL), affluent of rio Purité, Letícia, Amazonas, 3°41'54"S 70°12'24.2"W, 27 Mar 2006, Arbeláez *et al.* IavH 11192 (11, 18.8-55.5 mm SL), headwaters of caño Salado, 15 minutes North of Estación Biológica El Zafire, Letícia, Amazonas, 4°0'S 69°53'W, 1 Dec 2008, Bogotá & Arcangel. IavH 11193 (10, 21.9-37.1 mm SL), caño Gravilla, Estación Biológica El Zafire, Letícia, Amazonas, 4°0'S 69°53'W, 1 Dec 2008, Bogotá & Arcangel. IavH 11194 (28, 17.2-39.4 mm SL), stream affluent of caño Salado, Estación Biológica El Zafire, Brazil-Colombia border, Letícia, Amazonas, 4°0'S 69°53'W, 1 Dec 2008, Bogotá & Arcangel. IavH ex 9410 (3, 22.9 mm SL), quebrada 2, affluent of rio Purité, three hours from Salados Varios, PNN Amacayacu, Letícia, Amazonas, 3°41'37.5"S 70°12'26.5"W, 24 Mar 2006, Arbeláez *et al.* IavH ex 8380 (2, 17.0 and 24.3 mm SL), affluent of rio Purité, Letícia, Amazonas, 3°41'37.5"S 70°12'26.5"W, 24 Mar 2006, Arbeláez *et al.* IavH ex 8384 (2, 20.4 and 21.6 mm SL), affluent of rio Purité, Letícia, Amazonas, 3°41'54"S 70°12'24.2"W, 26 Mar 2006, Arbeláez *et al.* SMF 5966 (2, 13.3 and 23.5 mm SL), same data as type material.

COPELLA SP. N.

Figure 66; Tables 13 and 14

Remarks. This unique male specimen from the rio Negro near São Gabriel da Cachoeira does not fit in combination of features of any species of *Copella*. It can be distinguished from *Copella arnoldi* by having dark procurent caudal-fin rays (*vs.* hyaline), from *C. eigenmanni* by having the middle caudal-fin rays hyaline (*vs.* dark), from *C. compta* by having 15 predorsal scales (*vs.* 17-18) and 24 scales on the fourth longitudinal scale row (*vs.* 26-27), from *C. nattereri* by the absence of a dark mark on each scale on the body (*vs.* presence), from *C. stigmaseion* in having an inconspicuous dark band on body (*vs.* conspicuous black longitudinal band) with no series of clear spots above it (*vs.* series of clear spots above the black band present), and from *C. vilmae* by the absence of a series of brown scales interposed with clear ones on body of males (*vs.* presence). This probable new species will be described as soon as more material is available.



Figure 66. *Copella* sp. n. USNM 380911, rio Negro near São Gabriel da Cachoeira, Brazil.

Photo by S. Raredon.

Table 13. Morphometrics of *Copella* sp. n. USNM 380911 (1).

	<i>Copella</i> sp. n.
Standard length (mm)	51.3
Percents of standard length	
Depth at dorsal fin origin	10.7
Dorsal-fin origin to caudal-fin base	18.1
Snout to dorsal-fin origin	32.9
Snout to pectoral-fin origin	11.7
Snout to pelvic-fin origin	25.0
Snout to anal-fin origin	36.7
Pectoral to pelvic-fin origin	13.7
Pelvic to anal-fin origin	12.0
Pectoral-fin length	10.4
Pelvic-fin length	13.8
Dorsal fin length	12.7
Anal-fin length	9.7
Anal-fin base length	4.6
Caudal peduncle depth	5.2
Caudal peduncle length	10.5
Head length	12.4
Percents of head length	
Horizontal eye diameter	3.5
Snout length	4.1
Interorbital distance	4.5
Upper-jaw length	3.9

Table 14. Meristics of *Copella* sp. n.

	<i>Copella</i> sp. n.
Predorsal scales	15
First longitudinal scale row	14
Fourth longitudinal scale row	24
Longitudinal scale rows dorsal to pelvic	6
Longitudinal scale rows dorsal to anal	5
Circumpeduncular scale rows	10
Pectoral-fin rays	i9
Pelvic-fin rays	i7
Dorsal-fin rays	ii8
Branched anal-fin rays	9
Caudal-fin rays	i8,7i

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APPENDIX 1

Character matrix of 120 characters for the species of *Copella* and examined outgroup.

Copella arnoldi

1011000111 3011121111 1111111-11 1011121011 1102001210
2120122111 21111112[01]1 100201-110 1101110211 3131111112
2101101121 1-00[12]21111

Copella compta

1?11110111 2011121111 1111111-11 1000110111 1101001210
1120122111 2111[01]11201 0102001110 110[01]110211
2131111112 2101[01]01[01]21 1-00121121

Copella eigenmanni

1011100011 2011121111 1111111-11 1000110011 1102001210
2120122111 2111[01]11201 010201-110 110[01]110211
2131111112 2101101[01]21 1-00221121

Copella nattereri

111[01][01]00011 2011121111 1111111-11 1000121111 1102001210
2120122111 21121112[01]1 001201-110 1101110211 3131111112
2101101121 1-00221121

Copella stigmatemion

1111100011 2011121111 1111111-11 11---21111 1102001210
2120122111 21121112[01]1 001201-110 1101110211 3131111112
2101101121 1-00221121

Copella vilmae

1011110111 2011121111 1111111-11 1000120111 1101001210
2120122111 2112111201 010201-110 1100111-01 2131111112
2101101121 1-00121121

Derhamia hoffmanorum

1000000010 1100020000 -010010000 01---00011 0010000000
00?00?0?00 1000011100 0001000011 0000001-00 1011100???
10?1000111 1101000000

Copeina guttata

1110000010 1000120011 0010111--1 1011000011 1101000100
1000010110 21110111[01]1 0012101010 1000001-01 [23]010011112
2101100000 1-11010111

Hoplerythrinus unitaeniatus

0000000001 0000-20000 -0000000000 00110-3101 0000000000
0000020000 0000001-00 0000100000 0000000000 1131001??
0101010-00 0001000000

Lebiasina bimaculata

0100001010 1000000000 -0000000000 01---00000 0010000000
0000100000 110000001? 0001100001 0000001-00 1010000000
1000000000 0001000000

Lebiasina minuta

0000000010 1000000000 -0000000000 0001000000 0010000000
0000000000 1100000000 0001000001 0000000100 000000100?
10000[01]0000 0001000000

Lebiasina cf. yuruaniensis

0?00001010 11?0000000 -0000000000 0000000000 0010000000
0000000001 110000001? 000110000? 0000001-00 1010000??
1001000000 0001000000

Nannostomus anduzei

1000000101 0000011-11 1111101-00 11---1111- -111110000
1011200000 111--1111? 001201-010 100-101-00 2110001011
0010-00122 --0012112-

Nannostomus beckfordi

1000000001 0000011-10 -011000100 11---11111 1011110000
1001200000 111211111? 0002100011 0000001-00 2110000011
0010000111 1101021120

Nannostomus eques

100?000001 0[01]00010010 -011000100 11---22111 0011110000
1001200000 111201111? 0002100011 0000000100 3120001011
0010000100 010122112-

Nannostomus marginatus

1001000001 0000011-10 -[01]11000100 11---[12]0111
1011110000 1001200000 111211111? 0002100011 0000000100
3110001011 0010000[01]02 0101021120

Piabucina unitaeniata

0?00001010 1100000000 -0000000000 0000000000 0010000000
0000000000 1100000000 0001000001 0000001-00 1010000000
1000000100 0001000000

Pyrrhulina australis

1011000010 3000120011 0111101-00 1011010011 1101000101
1100011101 2011011101 1002100110 1010001-01 3121011112
2101111100 1-01021111

Pyrrhulina cf. brevis

1???????10 ?0?11200110 011111-0010 1100001111 0100010111
1001010020 1101110110 0200[01]110 1010001-01 3121011112
210110?100 1-11021111

Pyrrhulina filamentosa

1011000010 3001121011 0111111-01 1011000011 1101000101
1110010100 2011011101 1002100110 1010001-01 2021011112
2101100000 1-11021111

Pyrrhulina marilynae

1?11000010 2000120011 0011101-01 1011000011 1101000101
1100011100 2011011101 1002001110 1110001-01 3011011112
210111[01]0[02][01] 1-01021111

Pyrrhulina semifasciata

1011000010 3001120011 0011101-00 1011020111 1101000101
1110010100 2011011101 1002000110 1010001-01 3021011112
2101100100 1-11021111

Pyrrhulina cf. stoli

1111000110 3001120011 0011111-01 1011020011 1101000101
1100010100 2011011101 1002000110 1010001-01 3011011112
2101101000 1-11021111

APPENDIX 2

List of synapomorphies of clades and terminal taxa based on the two most-parsimonious cladograms. Ambiguous optimizations are followed by ACCTRAN (A), DELTRAN (D).

<i>Hoplerythrinus unitaeniatus:</i>	1: 0>1
No autapomorphies	23: 0>1
Clade 26:	26: 0>1 (A)
No synapomorphies	32: 0>1 (A)
Clade 25, <i>Lebiasina</i> :	39: 0>1
16: 2>0	66: 0>1
33: 1>0	68: 0>1
40: 1>0	79: 0>1
62: 0>1 (D)	99: 0>1 (A)
67: 1>0	100: 0>1 (A)
101: 0>1 (D)	108: 0>1 (A)
104: 1>0	111: 0>1 (A)
<i>Lebiasina minuta</i> :	112: 0>1
75: 1>0 (only tree 0)	<i>Derhamia hoffmannorum</i> :
91: 1>0	12: 0>1
93: 1>0	25: 0>1 (D)
87: 1>0 (A)	32: 0>1 (D)
Clade 24:	62: 1>0 (A)
2: 0>1 (A)	75: 1>0 (only tree 0)
7: 0>1	87: 0>1 (D)
12: 0>1 (only tree 1, A)	94: 0>1
34: 1>0 (only tree 1)	95: 0>1
69: 0>1 (A)	97: 1>0
87: 0>1 (D)	101: 0>1 (D)
97: 1>0	108: 0>1 (D)
<i>Lebiasina bimaculata</i> :	109: 0>1
2: 0>1 (D)	110: 0>1
12: 1>0 (only tree 1, A)	111: 0>1 (D)
32: 0>1	Clade 32:
55: 0>1	19: 0>1
69: 0>1 (only tree 0, D)	24: 0>1 (A)
Clade 27:	28: 0>1 (A)
12: 0>1 (only tree 0)	31: 0>1
34: 1>0 (D)	41: 0>1 (A)
69: 0>1 (only tree 1)	44: 0>1
75: 0>1 (only tree 1, A, D)	51: 0>1
<i>Lebiasina</i> cf. <i>yuruaniensis</i> :	62: 0>1 (D)
12: 0>1 (only tree 1, D)	63: 0>1
60: 0>1	64: 0>1 (A)
69: 0>1 (only tree 0, D)	70: 0>1 (A)
104: 0>1	74: 1>2
<i>Piabucina unitaeniata</i> :	75: 0>1 (only tree 1, A)
12: 0>1 (only tree 1)	91: 1>3
69: 1>9 (only tree 0, A)	99: 0>1 (D)
75: 1>0 (only tree 0)	101: 1>0 (A)
108: 0>1	116: 0>1
Clade 28, Pyrrhulininae:	117: 0>1 (A)

118: 0>1	21: 0>1 (D)
119: 0>1	22: 0>1
Clade 31, <i>Nannostomus</i> :	25: 0>1
9: 1>0	27: 0>1
10: 0>1	42: 0>1
11: 1>0	53: 0>1
16: 2>1	73: 0>1
24: 0>1 (D)	75: 1>0
26: 1>0 (A)	76: 0>1
28: 0>1 (D)	80: 1>0
32: 0>1 (D)	81: 0>1
36: 0>1 (A)	85: 0>1
38: 0>1	109: 1>2
45: 0>1	110: 1>2
46: 0>1	114: 1>0
54: 0>1	115: 0>1
55: 0>2	<i>Nannostomus beckfordi</i> :
64: 1>2 (A)	97: 1>0
64: 0>2 (D)	111: 0>1 (D)
69: 0>1	Clade 33:
75: 0>1 (only tree 1, D)	3: 0>1
87: 1>0 (A)	15: 0>1
92: 0>1	20: 0>1
100: 0>1 (D)	25: 0>1
103: 0>1	26: 0>1 (D)
104: 1>0	27: 0>1
108: 0>1 (D)	30: 0>1
111: 1>0 (A)	32: 1>0 (A)
116: 1>2	41: 0>1 (D)
117: 0>1 (D)	42: 0>1
119: 1>2	43: 1>0
<i>Nannostomus eques</i> :	48: 0>1
36: 1>2 (A)	56: 0>1
37: 0>2	58: 0>1
41: 1>0 (A)	59: 0>1
93: 1>2	61: 1>2
115: 0>2	64: 0>1 (D)
Clade 30	70: 0>1 (D)
17: 0>1	77: 0>1 (A)
36: 0>1 (D)	80: 1>0
41: 0>1 (D)	81: 0>1
65: 0>1	88: 1>2 (A)
110: 0>1	90: 0>1
<i>Nannostomus marginatus</i> :	96: 0>1
4: 0>1	98: 0>1
110: 1>2	100: 1>2 (A)
Clade 29	100: 0>2 (D)
37: 0>1	101: 0>2
87: 0>1	102: 0>1
91: 3>2	105: 0>1
109: 0>1	108: 1>0 (A)
111: 0>1 (D)	111: 0>1 (D)
<i>Nannostomus anduzei</i> :	120: 0>1
8: 0>1	<i>Copeina guttata</i> :
20: 0>1	2: 0>1

21: 1>0 (A)	36: 0>2
24: 1>0 (A)	Clade 38
59: 0>1 (D)	53: 0>1
73: 0>1	93: 1>2
75: 0>1 (only tree 1, D)	107: 1>0
77: 0>1 (D)	<i>Pyrrhulina semifasciata:</i>
87: 0>1 (D)	26: 1>0
113: 0>1	36: 0>2
117: 1>0 (A)	38: 0>1
Clade 36:	Clade 37:
4: 0>1	30: 1>0
11: 1>3	108: 0>1
14: 0>1 (A)	<i>Pyrrhulina cf. brevis:</i>
24: 0>1 (D)	92: 0>1
52: 0>1	<i>Pyrrhulina filamentosa:</i>
71: 0>1 (A)	17: 0>1
75: 1>0 (only tree 0, tree 1, A, D)	22: 0>1
78: 0>1	75: 0>1
94: 0>1	91: 3>2
107: 0>1	Clade 40, <i>Copella:</i>
116: 1>2	10: 0>1
117: 0>1 (D)	13: 0>1
Clade 35, <i>Pyrrhulina:</i>	14: 0>1 (D)
21: 1>0 (A)	17: 0>1
50: 0>1	18: 0>1
59: 1>0 (A)	21: 0>1 (D)
62: 1>0	22: 0>1
71: 0>1 (D)	29: 0>1
77: 1>0 (A)	35: 0>1
83: 0>1	36: 0>2
87: 0>1 (D)	37: 0>1 (A)
Clade 34:	44: 1>2
14: 1>0 (A)	47: 0>1
26: 1>0	48: 1>2
57: 0>1	49: 0>1
106: 0>1	51: 1>2
<i>Pyrrhulina australis:</i>	53: 0>2
22: 0>1	55: 0>1
30: 1>0	56: 1>2
36: 0>1	57: 0>2
60: 0>1	59: 0>1 (D)
75: 0>1	60: 0>1
92: 0>1	65: 0>1
93: 1>2	68: 1>2
108: 0>1	76: 0>1
<i>Pyrrhulina marilynae:</i>	82: 0>1
11: 3>2	84: 0>1 (A)
77: 0>1	85: 0>1
82: 0>1	86: 0>1
Clade 39:	87: 1>0 (A)
14: 0>1 (D)	88: 1>2 (D)
113: 0>1	89: 0>1
<i>Pyrrhulina cf. stoli:</i>	92: 0>1
2: 0>1	93: 1>3
8: 0>1	95: 0>1

108: 0>1
109: 0>2
110: 0>1
114: 1>0
115: 0>12
Copella arnoldi:
8: 0>1
37: 0>1 (D)
71: 0>1 (D)
84: 0>1 (D)
Clade 43:
4: 0>1
10: 3>2
32: 1>0
33: 1>0
37: 0>1 (A)
70: 0>1 (A)
114: 1>2 (A)
118: 1>2
Clade 44:
2: 0>1
37: 0>1 (D)
38: 0>1 (D)
64: 1>2
73: 0>1
84: 0>1 (D)
115: 1>2 (D)
Copella nattereri:
No autapomorphies

Copella stigmasemion:
32: 0>1
Clade 42:
35: 2>1 (A)
36: 1>0 (A)
71: 0>1
83: 1>0 (A)
90: 3>2
Copella eigenmanni:
36: 2>1 (D)
115: 1>2 (D)
38: 1>0 (A)
Clade 41:
5: 0>1
7: 0>1
37: 0>1 (D)
43: 2>1
114: 2>1 (A)
Copella compta:
51: 2>1
76: 1>0
36: 2>1 (D)
77: 0>1 (D)
Copella vilmae:
36: 1>2 (A)
64: 1>2
87: 0>1
89: 1>0