

PONTIFÍCIA UNIVERSIDADE CATÓLICA DO RIO GRANDE DO SUL
PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

**REVISÃO TAXONÔMICA E FILOGENIA
DA TRIBO COMPSURINI
(CHARACIFORMES: CHARACIDAE:
CHEIRODONTINAE)**

FERNANDO CAMARGO JEREP

PORTO ALEGRE, 2011

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**TESE DE DOUTORADO
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Dedicatória

Dedico este trabalho a todos piabólogos e às piabas
piabas difíceis de serem triadas
piabas difíceis de serem contadas
piabas difíceis de serem identificadas

piabas mal-vistas a primeira vista, e escondidas no passado
interespecificamente aglomeradas em lotes empoeirados
abarrotaadas como sardinhas, em álcool negligenciado
sofrendo de descamação precoce e perda de raio
por errôneo manuseio e formol mal graduado

piaba minúscula, pequena, média e grande,
coletadas em rio, riacho, arroio, lagoa e ponte
piabas que migram da nascente ao estuário
piabas que acabam em lojas de aquário
com colorido prateado, dourado, vermelho, ou azulado
que sustenta garça, ciclídeo, bagre, traíra e botuado

piaba com pseudotímpano e sem mancha umeral
com pedúnculo arqueado ou sem linha lateral
piaba sem dente na maxila e com escamas na caudal
duas fileiras no dentário e i+9 na dorsal

piaba que não inova, piaba que não varia,
piaba desprovida de autapomorfia,
piabas que politomizam hipóteses e monotonizam resultados
homoplasicamente agrupadas em clados mal suportados

piaba de isca, piaba que belisca
piaba que mama mas não fisga.

"You can't cross the sea merely by standing and staring at the water."
Rabindranath Tagore

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A todos os meus Mestres.

Resumo. Compsurini é uma tribo de Cheirodontinae conhecida por abrigar as espécies inseminadoras da subfamília, também caracterizadas por incomuns modificações morfológicas relacionadas ao dimorfismo sexual dos machos. A tribo foi definida por Malabarba, Weitzman & Burns, e se revelou monofilética dentro da filogenia de Cheirodontinae (Malabarba, 1998); porém, a relação entre seus integrantes se mostrou instável quando Malabarba (1998) adicionou novos terminais à análise, cujo a busca de caracteres havia sido focada nos Cheirodontini. Com a descrição de novas espécies após a análise de Malabarba (1998) e a descoberta de oito possíveis novas espécies para a tribo Compsurini, uma análise filogenética dos integrantes de Compsurini foi desenvolvida com o objetivo de testar a monofilia da tribo e elucidar as relações entre seus integrantes. Uma hipótese das relações filogenéticas das espécies de Compsurini foi elaborada através da análise de parcimônia com peso implícito baseada em 278 caracteres abrangendo morfologia externa, osteologia, miologia e ultraestrutura de espermatozoides. Nesta análise, tanto Cheirodontinae quanto Compsurini formaram grupos monofiléticos. As novas sinapomorfias que sustentam Compsurini são: 1) distância entre as extremidades distais dos processos laterais do mesetmóide igual ou menor que sua base; 2) ganchos da nadadeira anal anteriormente direcionados, curvados sobre a superfície lateral dos raios; 3) raios da nadadeira anal com ganchos concentrados na sua metade ou terço distal; 4) nadadeira anal mais pigmentada na sua margem distal nos machos maduros; 5) peça intermediária dos espermatozoides não truncada posteriormente, com canal citoplasmático mais longo que o metade do comprimento do núcleo; e 6) espermatozoides com um grande número de vesículas globulares. Dentro de Compsurini, duas espécies novas da bacia amazônica sem dimorfismo sexual na nadadeira caudal formam o grupo irmão de todos os outros integrantes da tribo. Os gêneros *Kolpotocheirodon*, *Saccoderma*, e *Compsura*, este último com duas espécies novas, se mostraram monofiléticos nesta análise. As espécies da América Central, “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura* e “*Odontostilbe*” *mitoptera*, formaram um clado monofilético, grupo irmão do gênero trans-andino *Saccoderma*, cujas sinapomorfias são referentes ao dimorfismo sexual e ultraestrutura de espermatozoides, suportando a criação de um novo gênero para abrigar estas três espécies até então mantidas em gêneros provisórios. Na revisão taxonômica realizada em paralelo à análise filogenética, o gênero *Compsura* é redescrito juntamente com a descrição de duas espécies novas das bacias do rio Guaporé e Araguaia. O gênero *Macropsobrycon* é redefinido e aqui considerado monotípico com *M. uruguayanae* como espécie tipo. *Saccoderma* também é redescrito e restringido a duas espécies válidas, *S. hastata* e *S. melanostigma*, sendo as espécies *S. falcata* e *S. robusta* consideradas sinônimos de *S. hastata*. Três gêneros e seis novas espécies da tribo são descritas para o alto curso de tributários amazônicos, juntamente com a elaboração de uma chave taxonômica para todas as espécies de Compsurini. Por fim, “*Macropsobrycon*” *xinguensis* é apontada como grupo irmão de *Leptobrycon jatuaranae* ao se reanalisar uma matriz de caracteres morfológicos para Characidae presente na literatura com o acréscimo destas espécies, e assim, é alocada em *Leptobrycon*.

Abstract. Compsurini is a tribe of Cheirodontinae known for hosting inseminating species, and also characterized by unusual morphological modifications related to the male sexual dimorphism. The tribe defined by Malabarba, Weitzman & Burns, was found to be monophyletic in the phylogeny of the Cheirodontinae (Malabarba, 1998), however the relationships among its members was unstable when new terminals were added to the analysis by Malabarba, whose search for characters was focused to the Cheirodontini. With the description of new species after Malabarba's analysis and the discovery of eight possible new species to the tribe Compsurini, a phylogenetic analysis of Compsurini was developed with the aim of testing the monophyly of the tribe and elucidating the relationships among its members. A hypothesis of phylogenetic relationships of Compsurini was built through parsimony analysis under implied weights based on 278 characters including external morphology, osteology, miology and ultrastructure of spermatozoa. In this analysis, both Cheirodontinae and Compsurini were found to be monophyletic. The new synapomorphies supporting Compsurini are: 1) distance between mesethmoid lateral processes distal tips, equal or shorter than mesethmoid posterior region; 2) anal-fin hooks anteriorly directed, curved over lateral surface of the anal-fin ray; 3) anal-fin rays bearing hooks concentrated along distal half or distal third of their length; 4) anal fin more strongly pigmented along distal portion of branched anal-fin rays on mature males; 5) spermatozoa midpiece not truncated posteriorly, and cytoplasmic canal longer than the half length of nucleus; and 6) spermatozoa with numerous globular vesicles. In Compsurini, two new species from the Amazon basin without caudal-fin sexual dimorphism were found to be sister group of the remaining integrants of the tribe. The genera *Kolpotocheirodon*, *Saccoderma*, and *Compsura*, the latter with two new species, were found to be monophyletic in this analysis. The Central America species "*Compsura*" *gorgonae*, "*Odontostilbe*" *dialeptura*, and "*Odontostilbe*" *mitoptera*, formed a monophyletic clade, sister group of the trans-Andean genus *Saccoderma*, which synapomorphies are related to sexual dimorphism and spermatozoa ultrastructure, supporting the creation of a new genus to accommodate these three species hitherto kept in temporary genera. In the taxonomic revision carried out in parallel to the phylogenetic analysis, the genus *Compsura* was redescribed along with the description of two new species from rio Guaporé and rio Araguaia basins. The genus *Macropsobrycon* is redefined and here considered monotypic with *M. uruguayanae* as type-species. *Saccoderma* is also redescribed and restricted to two valid species, *S. hastata* and *S. melanostigma*, and the species *S. falcata* and *S. robusta*, considered synonyms of *S. hastata*. Three genera and six new species of the tribe are described for the high portion of Amazonian tributaries, along with the proposal of a taxonomic key comprising all compsurin species. Finally, on the reanalysis of the morphology-based matrix of characters present in the literature for Characidae, "*Macropsobrycon*" *xinguensis* was found to be sister group of *Leptobrycon jatuaranae* (with the addition of those species), and thus, "*M.* *xinguensis* is located to *Leptobrycon*.

Apresentação. A presente tese reúne resultados obtidos da revisão taxonômica e filogenia dos integrantes da tribo Compsurini (Characidae: Cheirodontinae). A tese está dividida em seis capítulos, onde o primeiro aborda a filogenia dos integrantes da tribo, e os demais abordam aspectos taxonômicos relacionados à descrição e redescrição de gêneros e espécies, direta ou indiretamente relacionados à tribo. Os capítulos estão apresentados sob forma de artigo, formatados de acordo com as normas da revista *Neotropical Ichthyology*, para a qual serão submetidos. O Capítulo I corresponde à análise filogenética dos integrantes de Compsurini, incluindo oito espécies novas para a tribo e a maioria das espécies conhecidas de Cheirodontinae, bem como representantes das principais linhagens monofiléticas reconhecidas em Characidae. A tribo é reconhecida como monofilética, tal como as linhagens e gêneros previamente designados em análises filogenéticas posteriores relacionadas à Cheirodontinae. No Capítulo II, o gênero *Compsura* é revisado com a redescrição da espécie tipo, *Compsura heterura*, que apresenta ampla distribuição na bacia do rio São Francisco e rios costeiros do nordeste brasileiro, e descrição de duas novas espécies das bacias do rio Guaporé e rio Araguaia. O Capítulo III aborda a redefinição do gênero monotípico *Macropsobrycon*, com descrição do dimorfismo sexual encontrado na nadadeira caudal dos machos maduros e redescrição de *M. uruguayanae*, espécie que habita as drenagens do rio Uruguai, sistema da laguna dos Patos e o baixo rio La Plata. O Capítulo IV diz respeito às espécies trans-Andinas da tribo Compsurini: *Saccoderma* é revisado e duas espécies são consideradas válidas para o gênero, *S. hastata* e *S. melanostigma*. As espécies *Saccoderma falcata* e *S. robusta* são consideradas sinônimas de *S. hastata*. Ainda neste capítulo, um novo gênero é proposto para abrigar as espécies de Compsurini da América Central, “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura* e “*Odontostilbe*” *mitoptera*, até então mantidos em gêneros provisórios. Três gêneros e seis novas espécies de Compsurini são descritas no Capítulo V; estas espécies habitam o alto curso de tributários da bacia amazônica, tais como os rios Purus, Madre de Díos, Ucayali e Napo. Neste capítulo também é apresentada uma chave artificial de identificação para todos os integrantes de Compsurini. Por fim, no Capítulo VI, o caracídeo “*Macropsobrycon*” *xinguensis* é proposto como membro de *Leptobrycon*. A proposta é baseada nos resultados obtidos a partir da análise filogenética por parcimônia e pesagem implícita com a inclusão destes táxons numa matriz de 365 caracteres morfológicos e 160 táxons de Characidae, retirada da literatura.

CAPÍTULO I

**Systematics of Compsurini Malabarba, Weitzman & Burns (Characiformes:
Characidae: Cheirodontinae)**

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Abstract

Compsurini is a tribe of Cheirodontinae known for hosting inseminating species, and also characterized by the unusual morphological modifications related to the male sexual dimorphism. The tribe, defined by Malabarba, Weitzman & Burns, was found to be monophyletic in the Cheirodontinae phylogeny (Malabarba, 1998); however the relationships among its members were not completely resolved due to the character search focused on the Cheirodontini. With the description of new species after Malabarba's analysis and the discovery of eight possible new species for the tribe, a phylogenetic analysis of Compsurini was developed with the objectives of testing the monophyly of the tribe and elucidating the relationships among its members. A hypothesis of phylogenetic relationships of 18 species of Compsurini was built based on 278 characters including external morphology, osteology, miology and ultrastructure of spermatozoa. To this end, we used the parsimony method implemented in the software TNT using the method of "implied weights", and with the aid of the "parsimony ratchet" algorithm set to 100 iterations and 100 replications. As outgroup, 60 species of Cheirodontinae and 23 other characids were used, with *Brycon pesu* in the root. The trees obtained with implied weights with the "k"-values 5.3390, 5.8297, 6.3818 and 7.0075, were more stable than the remaining ones, totalizing twelve trees with 1269 steps (CI = 0.25; RI = 0.69) summarized in a strict consensus tree with 1270 steps (CI = 0.25; RI = 0.69). Both Cheirodontinae and Compsurini were found to be monophyletic. The synapomorphies supporting Compsurini are: 1) distance between mesethmoid lateral processes distal tips, equal or shorter than mesethmoid

posterior region; 2) anal-fin hooks anteriorly directed, curved over the lateral surface of the anal-fin ray; 3) anal-fin rays bearing hooks concentrated along distal half or distal third of the rays; 4) anal fin more strongly pigmented along distal portion of branched anal-fin rays on mature males; 5) spermatozoa midpiece not truncated posteriorly, and cytoplasmic canal longer than half length of nucleus; and 6) spermatozoa with numerous small globular vesicles. In Compsurini, two new species from the Amazon basin without caudal-fin sexual dimorphism were found to be sister group of the remaining members of the tribe. The genera *Kolpotocheiroidon*, *Saccoderma*, and *Compsura*, and the latter two new species, were found to be monophyletic in this analysis. The Central America species “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura*, and “*Odontostilbe*” *mitoptera* formed a monophyletic clade, sister group of the trans-Andean genus *Saccoderma*, which supports the creation of a new genus to accommodate these three species hitherto kept in temporary genera.

Resumo

Compsurini é uma tribo de Cheirodontinae conhecida por abrigar as espécies inseminadoras da subfamília, também caracterizadas por modificações morfológicas incomuns relacionadas ao dimorfismo sexual dos machos. A tribo, definida por Malabarba, Weitzman & Burns, mostrou-se monofilética dentro da filogenia de Cheirodontinae (Malabarba, 1998); porém, a relação entre seus integrantes não foi completamente resolvida em consequência da busca de caracteres focada nos Cheirodontini. Com a descrição de novas espécies após a análise de Malabarba (1998) e a descoberta de oito possíveis novas espécies para a tribo, uma análise filogenética dos integrantes de Compsurini foi desenvolvida com o objetivo de testar a monofilia da tribo e elucidar as relações entre seus integrantes. Uma hipótese das relações filogenéticas de 18 espécies de Compsurini foi elaborada com base em 278 caracteres abrangendo morfologia externa, osteologia, miologia e ultraestrutura de espermatozoides. Para tal, foi utilizado o método de parsimônia pelo programa TNT com utilização do método de pesagem por peso implícito, e com auxílio do algoritmo “parsimony ratchet” configurado para 100 replicações e 100 iterações. Como grupo externo, foram utilizadas 60 espécies de Cheirodontinae e 23 de outros caracádeos, com enraizamento em *Brycon pesu*. As árvores obtidas por peso implícito com os valores de “k” 5,3390, 5,8297, 6,3818 e 7,0075 foram as mais estáveis, totalizando doze árvores com 1269 passos (IC = 0,25; IR = 0,69), e cujo consenso estrito apresentou

1270 passos (IC = 0,25; IR = 0,69). Tanto Cheirodontinae quanto Compsurini formaram grupos monofiléticos. As sinapomorfias que sustentam Compsurini são: 1) distância entre as extremidades distais dos processos laterais do mesetmóide igual ou menor que sua base; 2) ganchos da nadadeira anal anteriormente direcionados e curvados sobre a superfície lateral dos raios; 3) raios da nadadeira anal com ganchos concentrados na sua metade ou terço distal; 4) nadadeira anal mais pigmentada na sua margem distal nos machos maduros; 5) peça intermediária dos espermatozóides não truncada posteriormente, com canal citoplasmático mais longo que a metade do comprimento do núcleo; e 6) espermatozóides com um grande número de pequenas vesículas globulares. Dentro de Compsurini, duas espécies novas da bacia amazônica sem dimorfismo sexual na nadadeira caudal são grupo irmão de todos os outros integrantes da tribo. Os gêneros *Kolpotocheirodon*, *Saccoderma* e *Compsura*, este último com duas novas espécies, se mostraram monofiléticos nesta análise. As espécies da América Central, “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura* e “*Odontostilbe*” *mitoptera*, formaram um clado monofilético, grupo irmão do gênero trans-andino *Saccoderma*, suportando a criação de um novo gênero para abrigar estas três espécies até então mantidas em gêneros provisórios.

Key words: Neotropical, Characiforms, Fish, Cladistics.

Introduction

The Compsurini Malabarba, Weitzman & Burns, 1998 is one of the two tribes of the Cheirodontinae, a subfamily of Characidae that includes 17 genera and 56 species of small freshwater fishes, with adults reaching 20 to 40 mm of standard length (Malabarba, 2003; Malabarba *et al.*, 2004; Bührnheim & Malabarba, 2006; Bührnheim & Malabarba, 2007; Bührnheim *et al.*, 2008). The Compsurini fishes have a large distribution range inside the Neotropical ecozone. The northern limit of their distribution is in the southern streams of Costa Rica, where “*Odontostilbe*” *dialeptura* is reported from río Coto at Puntarenas province. The southern limit of the Compsurini geographical range is in the South of Brazil and Uruguay, where *Macropsobrycon uruguayanae* Eigenmann is reported to small tributaries of the rio Uruguai and Laguna dos Patos systems.

The tribe was proposed by Malabarba (1998) in the first cladistic analysis regarding the Cheirodontinae fishes, and it comprised the genera *Acinocheirodon*

Malabarba & Weitzman (new genus and species B in Malabarba, 1998), *Compsura* Eigenmann, *Kolpotocheiroidon* Malabarba & Weitzman (new genus and species A in Malabarba, 1998), *Macropsobrycon*, *Saccoderma* Schultz, and the species from Central America “*Odontostilbe*” *dialeptura*, “*Odontostilbe*” *mitoptera* (Fink & Weitzman), and “*Compsura*” *gorgonae* (Evermann & Goldsborough), provisorily assigned to their respective genera. Concurrently, the tribe Cheirodontini and the *incertae sedis* cheirodontine genera *Aphyocheiroidon* Eigenmann, *Cheirodontops* Schultz, *Holoshesthes* Eigenmann, *Odontostilbe* Cope, *Prodontocharax* Eigenmann & Pearson, and *Pseudocheiroidon* Meek & Hildebrand were delimited and diagnosed for the subfamily (Fig. 1). Malabarba (1998) presented a complete review about the taxonomic history of the Cheirodontinae, and based on the results of the phylogenetic study, the subfamily was found to be monophyletic in a more strict sense than those of Eigenmann (1915) and Géry (1977), containing only 15 genera. After Malabarba (1998), most of the remaining genera previously assigned to Cheirodontinae by former authors were considered *incertae sedis* in Characidae, until the cladistic analysis of Mirande (2010), that distributed them among the subfamilies Tetragonopterinae, Gymnocharacinae, Aphyocharacinae, and Aphyoditeinae. Four synapomorphies supported the restricted Cheirodontinae of Malabarba (1998): the presence of pseudotympanum between the first and second pleural ribs, represented by a muscle hiatus limited dorsally by the *lateralis superficialis* muscle, posteriorly by a naked anterior face of the second pleural rib, posteroventrally by the *obliquus inferioris* muscle, and anteroventrally by the *obliquus superioris* muscle (Ch. 1); presence of pedunculated, largely expanded and distally compressed teeth (Ch. 56); premaxillary teeth arranged in a single regular row with teeth perfectly aligned and similar in shape and cusp number (Ch. 55); and absence of humeral spot (Ch. 64).

The cladistic approach of Malabarba (1998) regarding the Cheirodontinae was centered in the species of the Cheirodontini, consequently most of the taxa and characters used in his work were related to that tribe. In that analysis, the monophyly of both the Cheirodontini and the Compsurini was supported essentially by characters related to the secondary sexual modifications exclusive to each tribe. The tribe Compsurini included all inseminating cheirodontines, which are characterized by the presence of spermatozoa in the ovaries of the mature females (Burns *et al.*, 1997), and by modifications and specializations of scales, rays and/or soft tissues on the caudal fin. Malabarba (1998) quoted the presence of insemination (Ch. 70: 1); incomplete

lateral line (Ch. 60: 1); presence of anteriorly directed hooks on the dorsal surface of some caudal-fin rays (Ch. 39: 1), being distributed along distal lengths on rays 11 to 14 (Ch. 41: 1); and anal fin more strongly pigmented along the distal portion of branched anal-fin rays (Ch. 68: 1), as synapomorphies of the compsurini members.

The cladistic approach of Malabarba (1998) over the compsurini fishes was restricted to 19 characters directly related to the type species of the genera *Acinocheirodon*, *Compsura*, *Kolpotocheirodon*, *Macropsobrycon*, and *Saccoderma*. This author also proposed an alternative cladogram of relationship among the genera of Compsurini, with the inclusion of the three compsurini species from Panama, presently assigned to *Compsura* and *Odontostilbe* ("*O*". *dialeptura*, "*O*". *mitoptera*, and "*C*". *gorgonae*) (Fig. 2). This inclusion changed the previous relationships presented by the compsurini genera in the general cladogram of the subfamily (Fig. 1), resulting in a polytomy embracing most of the members of the tribe. Due to such instability and the need for more investigation over the generic assignment for these species, their relationships were not discussed in that work.

A second hypothesis of relationship of the compsurini members was proposed by Bührnheim (2006) in the phylogenetic study of the species of *Odontostilbe* and *incertae sedis* genera of Cheirodontinae. In that study, Bührnheim included the same compsurini genera of Malabarba (1998), as well as the same characters for the tribe, and found a different hypothesis of relationship for them, with *Compsura* and *Saccoderma* as sister group of (*Kolpotocheirodon* (*Acinocheirodon* + *Macropsobrycon*)) (Fig. 3). In that analysis, the monophyly of Compsurini was only recovered in the parsimony analysis under implied weighting, and was supported by the presence of an almost straight profile in the anal fin of mature males (Ch. 112: 2); the more numerous hooks in both anterior and posterior regions of the anal fin of males than in the middle (Ch. 146: 1); the distribution of anal-fin hooks along distal half or third of the anal-fin rays (Ch.147: 1); caudal-fin hooks dorsal, straight and angled toward caudal-fin base (Ch. 150: 1); distal portions of the principal caudal-fin rays 11 to 14 bearing hooks (Ch. 152: 1); anal-fin pigmented along distal margin in mature males (Ch. 162: 1); presence of insemination (Ch. 168: 1); and sperm nuclei shape elongate (Ch. 169: 1) (Bührnheim, 2006).

A third hypothesis of relationship for the seven compsurini species was proposed by Oliveira (2007), based on ten morphological characters based on spermatozoa ultrastructure. The phylogenetic analysis for eleven species of

Cheirodontinae, resulted in a monophyletic Compsurini with a single synapomorphy related to the presence of the midpiece of the spermatozoa not truncated posteriorly, bearing a long cytoplasmatic canal. Further relationships hypothesized by Oliveira (2007) where: (*Kolpotocheirodon* (*Compsura*, *Macropsobrycon* (*Acinocheirodon*, *Saccoderma* (“*O.*” *dialeptura* + “*O.*” *mitoptera*)))) (Fig. 4).

The compsurin members. *Compsura* was described by Eigenmann (1915), who diagnosed the genus and its type-species, *Compsura heterura*, by the presence of large scales in the caudal fin of males. The genus kept monotypic until Meek & Hildebrand (1916), who assigned *Cheirodon gorgonae* Evermann & Goldsborough, 1909 to the genus, due to the presence of large scales forming “pouches” in the first half of the lower caudal-fin lobe. The naturality of *Compsura* was later questioned by López (1972) and Fink & Weitzman (1974), considering the wide geographical separation between them, as well as the labile characters used at that moment to diagnose small characid genera, leaving Fink & Weitzman to consider both species as members of *Cheirodon*. However, the genus was considered valid in later works (Géry, 1977; Malabarba, 1998; Malabarba & Weitzman, 1999; 2000; Malabarba, 2003; Malabarba *et al.*, 2004; Mirande, 2009, 2010; Javonillo *et al.*, 2010). The genus was diagnosed by Malabarba (1998) based on his phylogenetic analysis as presenting anal-fin hooks more numerous on anterior and posterior regions, and lacking caudal-fin hooks, keeping *Compsura gorgonae* in the genus until further investigation.

Eigenmann (1915) also described *Macropsobrycon*, containing a single species, *M. uruguayanae*, and diagnosed the genus by the presence of one row of feeble conical premaxillary teeth, wide and long toothless maxilla, and the presence of a pseudotympanum. The genus was generally considered closely related to the Aphyoditeinae (Géry, 1960; 1965; 1972). Posteriorly, Géry (1973) described *Macropsobrycon xinguensis* in a revisionary study of the “Aphyoditeina”, referring the new species to the genus due to similarities in the jaws and teeth morphology. However, these similarities were found to be homoplastic by Malabarba (1998), who cladistically showed that these species were artificially grouped. *Macropsobrycon xinguensis* was considered then a species *incertae sedis* in Characidae for not presenting any of the synapomorphies found for the Cheirodontinae (Malabarba, 1998; Reis *et al.*, 2003); a hypothesis posteriorly supported by molecular data (Javonillo *et al.*, 2010). Thus, the monotypic *Macropsobrycon* was re-diagnosed by Malabarba (1998) by the presence of

a large space bearing hypertrophied tissue between the twelfth and thirteenth caudal-fin rays; presence of small and flexible spines along the proximal portion of the lower lobe principal caudal-fin rays; teeth elongated and conical; and the dorsal-fin strongly black-pigmented along the mid-length of the second unbranched and first five branched rays.

The genus *Saccoderma* was erected by Schultz (1944) based on the singular modified caudal-fin scales of *Saccoderma melanostigma*, his new species. Schultz also included in the genus the species *Odontostilbe hastata* Eigenmann (1913), by having the same “dermal sac” on the caudal fin, from which his new species was diagnosed by the color pattern of the dorsal and anal fins. Posteriorly, Dahl (1955) described two Colombian species, *Saccoderma falcata* and *S. robusta*, whose types did not received any catalog number in the original description or subsequent works (Dahl, 1958, 1971; Dahl & Medem, 1964; Dahl *et al.*, 1964), remaining unknown. Based on the analysis of *Saccoderma hastata*, Malabarba (1998) diagnosed the genus by nine autapomorphies: caudal-fin scales reduced in size in the middle caudal-fin rays; hooks on anal-fin rays i,4 only; hypural 1 fused to parhypural; elongate caudal-fin scales; caudal-fin hooks on the rays 13,14-17,18; dentary teeth with seven cusps, five central large forming a sharp cutting edge; three large anterior dentary teeth; complete lateral line; and absence of a black spot in the dorsal fin.

Cheirodon dialepturus and *C. mitopterus* were described by Fink & Weitzman (1974), in a review of the cheirodontine fishes from Central America. These species, however, were transferred provisorially to the genus *Odontostilbe* (Burns *et al.*, 1997; Malabarba, 1998, 2003) until a better understanding of their relationships was available.

The most recently described genera of Compsurini are *Acinocheirodon* and *Kolpotocheirodon*. These genera were initially diagnosed by Malabarba (1998) as new genus and species B and A, and posteriorly formally described in Malabarba & Weitzman (1999) and Malabarba & Weitzman (2000), respectively. *Acinocheirodon*, a monotypic genus with *A. melanogramma* as its type species, was diagnosed by the presence of hooks posterodorsally directed in the anal-fin rays (a reversal from anteriorly directed in the remaining Compsurini); 13th and 14th caudal-fin rays curved dorsally; 13th to 15th caudal-fin rays more spaced than other rays; the most posterior ventral procurrent caudal-fin rays forming a keel; distal margin of the anal-fin not pigmented; the dentary teeth bearing large cusps, forming a sharp cutting edge; lateral line completely pored (a reversal from incomplete lateral line in Compsurini); and the presence of hypertrophied skin flaps in the caudal fin (Malabarba, 1998). Two species

are known for *Kolpotocheirodon*: *K. theloura* Malabarba & Weitzman, the type species, and *K. figueiredoi* Malabarba, Lima & Weitzman. The genus was first diagnosed by the presence of papillae in the skin flaps from the dorsal and caudal fins; hooks restricted to the anal-fin rays i,5; and 12th and 13th caudal-fin rays dorsally concave. In sequence, along with the description of *K. figueiredoi*, Malabarba *et al.* (2004) added to the diagnosis of the genus the presence of a conspicuous dark spot in the anterior portion of the anal fin; pigmentation in the region of the pelvic bone; and the presence of “pineapple-like” organs in the lower lobe of the caudal-fin, a secondary sexually dimorphic structure present in adult males of both species of the genus.

Although only twelve species of Compsurini have been described, a preliminary review of the cheirodontine species revealed the existence of eight new species from the Amazon basin, with peculiar morphological features that indicate a close relationship to the Compsurini. Considering the uncertainty regarding the relationships of the compsurin, and the lack of a deep morphological investigation of the structures related to their secondary sexual dimorphism, this systematic study aims to test, through the parsimony analysis based on morphological characters, the monophyly of Compsurini and the relationship of its representatives. Considering that this study completes the systematic revision of all cheirodontines, the monophyly of all the cheirodontine tribes, as well as the subfamily itself, are tested as a secondary purpose of the present work.

Material and Methods

The specimens herein analysed are deposited in their respective fish collections, as detailed in the List of Examined Material (Appendix I). Samples of the terminal taxa included in this analysis were used for elaboration and codification of the characters, with exception to *Megacheirodon unicus*† (Travassos & Santos), a fossil representative from which the character states were obtained from literature (Malabarba, 1998; Weitzman & Malabarba, 1999; Bührnheim *et al.*, 2008). Specimens fixed in formalyn and preserved in ethanol 70%, dissected under microscope, were used for external morphology and miology. Osteological observations were based on cleared and stained material for cartilage and bones (c&s), prepared according to the method detailed by Taylor & van Dyke (1985). A mean of three specimens per species were cleared and stained, whenever possible, with the objective to evaluate possible intraspecific morphological variation (polymorphism), sexual dimorphism, anomalies, and/or ontogenetic variations. For the study of spermatozoa shape and ultrastructure,

micrographs from gonads obtained from light microscopy, scanning electron microscopy (SEM) and transmission electron microscopy (TEM) were used. For TEM analysis, tissues were dehydrated in acetone, fixed in osmium tetroxide, stained with 0.5% uranyl acetate, and embedded in resin of araldite. Sections were obtained with a ultramicrotome, stained with a saturated solution of uranyl acetate in 50% ethanol and 0.2% lead citrate solution in 1 N NaOH. The sections were viewed in a transmission electron microscope. For SEM analysis, specimens were also dehydrated in an ethanol series and acetone, dried in critical point, coated with carbon and gold, and viewed with scanning electron microscope.

Terminology. The nomenclature of suprageneric groups within Characidae corresponds to Mirande (2010) classification. Myological nomenclature follows Winterbottom (1974) and osteological nomenclature Weitzman (1962), with the modifications adopted by Zanata & Vari (2005) and previously proposed by Nelson (1969), Patterson (1975), and Fink & Fink (1981, 1996).

Institutional abbreviations. Material from the following institutions were analyzed: ANSP - Academy of Natural Sciences of Philadelphia, Philadelphia, USA; CAS - California Academy of Sciences, San Francisco, USA; DZSJRP - Departamento de Zoologia e Botânica, Universidade Estadual Paulista, São José do Rio Preto, Brazil; FMNH - Field Museum of Natural History, Chicago, USA; ICNMHN - Universidad Nacional de Colombia, Museu de Historia Natural, Bogotá, Colombia; INHS - Illinois Natural History Survey, Illinois, USA; INPA - Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; KU - University of Kansas, Kansas, USA; MCP - Museu de Ciências e Tecnologia da PUCRS, Porto Alegre, Brazil; MCZ - Museum of Comparative Zoology, Cambridge, USA; MNRJ - Museu Nacional, Rio de Janeiro, Brazil; MZUSP - Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; NRM - Swedish Museum of Natural History, Stockholm, Sweden; ROM - Royal Ontario Museum, Toronto, Canada; UFRGS - Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; UFRJ - Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; UMMZ - University of Michigan Museum of Zoology, Ann Arbor, USA; UNT - Universidade Nacional do Tocantins, Porto Nacional, Brazil; USNM - National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

Cladistic methodology. In order to investigate the monophyly of Compsurini, and generate hypotheses of phylogenetic relationships among its representatives and character state transformations, the methods of equal weighted parsimony analysis and weighted parsimony analysis were employed using the software TNT version 1.1 (Goloboff, Farris & Nixon, 2008), based on the Hennig's (1966) and subsequent authors' concepts of parsimony. Weighting methods have also been used in analyses, usually with problematic groups where equal weighted parsimony analysis results in hypotheses with low resolution, generally caused by the presence of highly homoplastic characters (Goloboff, 1993; Mirande 2009, 2010). However, the idea behind the weighting methods is to strengthen the evolutionary information from characters with higher congruence with other characters, and with the phylogenetic hypothesis itself. Consequently, characters with low congruence with the phylogenetic hypothesis have their weight decreased, inversely proportional to their number of homoplastic steps (Goloboff, 1993; Mirande 2009, 2010).

The weighted analysis under implied weights (IW) method herein performed followed Goloboff (1993) and Mirande (2009). The IW is a character weighting method, where characters are downweighted as a function of the number of homoplastic steps they have, surveyed during the tree search. One of the possible advantages of this method is that it distinguishes the extra steps of a very homoplastic character from the extra steps of a less homoplastic character through weighting, while in a simple parsimony analysis all characters receive equal weights, regardless of how well or how poorly they fit at a given tree. The characters are downweighted based on a constant "k", which had been chosen arbitrarily up to Mirande (2009), who proposed a methodology for "k"-values search, which is herein adopted. In this method, the "k"-values used in the IW are previously calculated in the derived formula of character fit [$F = k / (S + k)$] in the function of "k" [$k = (FS) / (1 - F)$], from the distribution of the fit/distortion (F) values in regular intervals associated to the "average" number of homoplastic steps (S). The "average" number of homoplastic steps [(number of steps - minimum number of steps) / minimum number of steps], is calculated from the total number of steps, and the minimum number of steps, obtained from the most-parsimonious trees under equal weights. The "k"-values herein used were those that assign to an "average" character the fit values of 50, 52, 54, 56, 58, 60, 62, 64, 66, 68, 70, 72, 74, 76, 78, 80, 82, 84, 86, 88, and 90% of the fit of a perfectly hierarchic character. IW analysis for each "k"-value were performed, and the strict consensus tree

for each one of them saved. The reliability of these 21 consensus trees was assessed through their stability inferred by SPR distances (Goloboff, 2008), known as the number of branch moves necessary to change one tree into another, calculated in the software TNT. Finally, the most stable tree will be the less parameter-dependent, which needs a lower number of changes to turn into any other tree, once it shares a higher number of nodes with the remaining trees. In the case of more than one tree presenting the same SPR distance value, the strict consensus of them will be done.

The methods of new technology described in Nixon (1999) and Goloboff (1999) available in the TNT were applied in both weighted and unweighted analyses. The parsimony ratchet, set to 100 iterations and 100 replications, ran combined with the methods of tree-fusing, sectorial search, and tree-drifting, using the default parameters presented by the software. All characters were treated as unordered and given the same *a priori* weight. The distribution of ambiguous character states was examined according to the ACCTRAN optimization, maximizing reversals to parallelisms, as discussed by de Pinna (1991). The character polarity was only determined after the simultaneous analysis of global parsimony including all ingroup and outgroup taxa, and rooting in the outgroup, following Nixon & Carpenter (1993). *Brycon pesu* Müller & Troschel was the outgroup taxon in which the most parsimonious trees found were rooted. This species was selected based on several previous phylogenetic analyses concerning the Characiformes and the Characidae, in which the genus *Brycon* was found to be a representative of lineages considered basal within Characidae (Benine, 2004; Calcagnoto *et al.*, 2005; Moreira, 2007; Javonillo *et al.*, 2010; Mirande, 2010).

The Bremer (1994) methodology is herein used to calculate the branch support for the most parsimonious trees, and was calculated in the TNT software. The analysis was configured to retain trees suboptimal by 12 steps, generated by TBR (tree bisection and reconnection) from the trees obtained from equal weighted parsimony. For the “implied weighted” analysis, the bremer support values were calculated with 48,000 suboptimal trees obtained by TBR, with suboptimal values varying from 0.01 to 0.60. The support values were plotted in the strict consensus trees from each methodology. This method gives a value that represent the number of extra steps needed to lose a specific branch in the consensus of all most parsimonious trees.

The matrix of data (Table 1) was generated and edited in the software Mesquite version 2.6 (Maddison & Maddison, 2010). Polymorphic conditions were filled out with a “&” between the character state codes (e.g. 0&1), inapplicable character states were

represented by “-”, and missing entries by “?” when the character state could not be observed due to structural damage of the material, lack of appropriate analysis, or missing data from the literature. That is the case for most of the characters concerning the spermatozoa ultrastructure and related to the fossil species *Megacheiroduon unicus*†. In the Table 1, missing data is represented by a “?”, inapplicable data by a “-”, and polymorphisms by a “w” [0&1], “y” [0&2], or “z” [1&2].

The synapomorphies and apomorphies quoted for clades and terminal taxa in the paper are those commonly present in all the most stable trees from the implied weighting analysis, summarizing the phylogenetic hypotheses presented by these trees.

Ingroup and outgroup. A total of 101 characid species were included in the parsimony analysis as terminal taxa. All known representatives of the Compsurini, in a total of ten described and eight non-described species, were chosen as the ingroup in this analysis, due to the preponderance of character (synapomorphies) search for these species relative to the other taxa (Nixon & Carpenter, 1993). Type and non-type material are unknown for the putative compsurin species *Saccoderma falcata* Dahl (1955) and *S. robusta* Dahl (1955), and thus they are not present in this analysis. The outgroup encompasses most of the remaining cheirodontines and several representatives from most of the Characidae subfamilies.

In this study the monophyly of the Cheirodontinae and its tribes Cheirodontini, defined by Malabarba (1998), and Odontostilbini, defined by Bührnheim (2006), were also tested. For this purpose, almost all known cheirodontine species were included in the analysis, characterizing it as the most encompassing analysis of the subfamily, with 34 species from Cheirodontini (11 undescribed), and 26 species from Odontostilbini (eight undescribed). Only the cheirodontines *Odontostilbe gracilis* (Géry), *O. littoris* (Géry), *Prodontocharax howesi* (Fowler), and *Spintherobolus leptoura* Weitzman & Malabarba were not assessed in the analysis due to the difficulty in acquiring the material.

Although the exploration of hypotheses of relationship among the subfamilies of Characidae was not the scope of this study, representatives of most of the characid subfamilies were included, in order to assess character state transformations and putative sister clades of Cheirodontinae. Twenty three non-cheirodontine characid species were used as outgroup, from the following subfamilies and clades (*sensu* Mirande, 2010): Bryconinae (*Brycon pesu*), *Bryconops* clade [*Bryconops*

caudomaculatus (Günther)], Characinae [*Charax stenopterus* (Cope) and *Cynopotamus kincaidi* (Schultz)], Rhoadsiinae (*Rhoadsia altipinna* Fowler), Tetragonopterinae [(*Paracheirodon axelrodi* (Schultz) and *Probolodus heterostomus* Eigenmann), *Hyphessobrycon luetkenii* clade (*Hyphessobrycon bifasciatus* Ellis), *Astyanax* clade [*Astyanax* aff. *fasciatus* (Cuvier) and *A. laticeps* (Cope)], Gymnocharacinae [*Coptobrycon bilineatus* (Ellis)], Aphyocharacinae [*Aphyocharax nattereri* (Steindachner) and *Prionobrama paraguayensis* (Cope)], Aphyoditeinae (*Aphyocharacidium bolivianum* Géry, *Aphyodite grammica* Eigenmann, *Leptobrycon jatuaranae* Eigenmann, “*Macropsobrycon*” *xinguensis* Géry, *Microschemobrycon elongatus* Géry, and *Parecbasis cyclolepis* Eigenmann), Stevardiinae [*Bryconamericus iheringii* (Boulenger), *Cyanocharax alburnus* (Hensel), and *Hemibrycon polyodon* (Günther)]. *Cheirodon stenodon* Eigenmann, is a species *incertae sedis* in Characidae according to Malabarba (1998, 2003), and was also analysed here in a tentative to elucidate its relationship among the characids. The relationships concerning the non-cheirodontine characids are not deeply discussed herein, due to the insufficient outgroup taxa sampling, as well as superficial investigation for particular synapomorphies concerning these groups.

Results and Discussion

Character structure and description. The definition of character and its structural composition followed Sereno (2007). Character is simply defined as a heritable organismal feature, which functions are expressed as independent variables, and its character states as “the mutually exclusive conditions of a character” (Sereno, 2007). In that way, the character statement is composed by the character, whose components are the locator (morphological structure), the variable (aspect that varies), and the variable qualifier (variable modifier); and the statement or character states (Sereno, 2007). Herein, the consistency index (ci) and the retention index (ri) for each character are presented in lower case before the character statement; and references of authors that previously used the character are listed before the statement, even when there are modification in the coding and interpretation of the character states.

The characters are arranged in the text approaching the anatomical structures from anterior to posterior direction, starting with osteological structures from the head to body and fins, scales, muscles, color pattern, soft tissues, and spermatozoa related

characters. Some characters statements are followed by a brief discussion about the distribution, polarity, significance within Cheirodontinae based on the most parsimonious hypothesis of relationships, and when applicable, its presence in others characid groups and previous studies regarding representatives of the family.

The distribution of the character states listed below for the examined taxa is summarized in the Table 1. For the fossil cheirodontine *Megacheiroduon unicus*†, 40 from the 278 characters are coded, they are: 1, 59, 77, 146, 152-164, 169-175, 190, 194-206, 210, and 211. The remaining characters are coded as missing “?” for this species.

CIRCUMORBITAL BONES

Character 1 - (ci = 0.50; ri = 0.80). Infraorbitals, number (Ch. 12 Malabarba, 1994; Ch. 9 Malabarba, 1998; Ch. 18 Weitzman & Malabarba, 1999; Ch. 16 modified from Bührnheim, 2006; Ch. 18 modified from Bührnheim *et al.*, 2008): 0 = six infraorbitals (1 to 6). 1 = less than six infraorbitals.

The presence of six infraorbitals is the general state present in most of the cheirodontines and outgroup taxa (Fig. 5). However, some species present reduction or fusion of some of these bones. That is the case of *Amazonspinther dalmata* and the *Spintherobolus* species, in which the first infraorbital is absent or fused with the second infraorbital, the presence of the fourth is variable, and the fifth and sixth infraorbitals are absent. *Coptobrycon bilineatus* also presents reduction in the number of infraorbitals, with the fifth and sixth infraorbitals also being absent. Mirande (2010) also quoted to *Coptobrycon bilineatus* the absence of the first infraorbital bone, what is likely a polymorphic condition to this species.

Character 2 - (ci = 0.16; ri = 0.50). Antorbital, shape on lateral view (Ch. 13 modified from Bührnheim, 2006): 0 = elongate and narrow. 1 = short and wide.

Most cheirodontine present an elongated and narrow antorbital, extending from the lateral ethmoid, surrounding laterally the nasal organ, and reaching the dorsal border of the maxilla (Fig. 5b). The presence of a short and wide antorbital is only found in the cheirodontines *Amazonspinther dalmata* and in the *Spintherobolus* species, but is also observed in some of the outgroup species (Fig. 5a).

Character 3 - (ci = 0.16; ri = 0.66). Antorbital, anteroventral portion, shape on lateral view: 0 = square shaped, not expanded. 1 = expanded, discoid-shaped, sometimes extending anteriorly.

The presence of the anteroventral portion of antorbital expanded in a round shape is found in most Cheirodontinae (Fig. 5b), except in *Amazonspinter* and in the *Spinterobolus* clade. The shape of this round expansion may vary intraspecifically, and sometimes, although still expanded, it elongatus anteriorly.

Character 4 - (ci = 0.33; ri = 0.50). Antorbital, profile on dorsal view: 0 = straight. 1 = medially concave.

Character 5 - (ci = 0.33; ri = 0.92). First infraorbital, shape (Ch. 14 modified from Bührnheim, 2006): 0 = rectangular, anteroventral region not expanded ventrally, forming a right angle. 1 = subrectangular, with anteroventral region extended anteriorly, forming a acute angle.

The subrectangular first infraorbital is the common state found in the cheirodontines, being absent only in *Axelrodia lindeae* and in the trans-andean species of *Cheirodon*. Notwithstanding, the subrectangular first infraorbital is also present in some outgroup taxa closely related to Cheirodontinae, as *Aphyodite grammica*, *Cheirodon stenodon*, *Leptobrycon jatuaranae*, “*Macropsobrycon*” *xinguensis*, *Paracheirodon axelrodi*, and *Parecbasis cyclolepis*. This character is coded as inapplicable for *Amazonspinter dalmata* and *Spinterobolus* species, that lack the first infraorbital.

Character 6 - (ci = 0.07; ri = 0.43). First infraorbital, laterosensory canal, length (Ch. 10 modified from Malabarba 1994; Ch. 10 modified from Malabarba 1998; Ch. 15 modified from Bührnheim, 2006): 0 = along almost entire length of longest axis of first infraorbital or reaching half its length (Fig. 5a). 1 = nearly absent at posterior portion of first infraorbital, never reaching half its length.

All the taxa herein examined have the laterosensory canal of the first infraorbital. However its length varies, and in some species the canal is restrict to the posterior

portion of the first infraorbital (Fig. 5b). This character is coded as inapplicable to the terminals that do not have the first infraorbital: *Amazonspinther* and *Spintherobolus*.

Character 7 - (ci = 0.40; ri = 0.40). Second infraorbital, posterodorsal corner, position related to the vertical line through the anguloarticular-quadrata articulation: 0 = posterior. 1 = on the same vertical line. 2 = anterior.

This character is found to be variable only among the outgroup taxa. All cheirodontine share the state 0, while a few outgroup species present the posterodorsal corner of the second infraorbital in the same line of the anguloarticular-quadrata articulation (state 1). The presence of the posterodorsal corner of the second infraorbital anterior to the line of the anguloarticular-quadrata articulation is only observed in *Rhoadsia altipinna* (state 2).

Character 8 - (ci = 0.11; ri = 0.48). Third infraorbital, dimension relative to the laterosensory canals of preopercle (Ch. 19 modified from Bührnheim, 2006; Ch. 64, 65 modified from Mirande, 2010): 0 = posteroventral margin of third infraorbital contacting or falling short the longitudinal and the ascending portions of the laterosensory canal of preopercle. 1 = ventrally contacting the laterosensory canal of preopercle, but leaving a posterior naked area between the border of the third infraorbital and the ascending portion of the laterosensory canal of preopercle, as wide as or wider than the canal. 2 = not contacting the longitudinal neither the ascending portions of the laterosensory canal of preopercle, leaving a naked area between the third infraorbital and the laterosensory canal of preopercle.

The size of the third infraorbital varied among the examined species. Generally, it covers all the cheek region, but in some species it is reduced, lacking a nude area ventrally and/or posteriorly. In order to measure the size variation of the third infraorbital among the examined species, the longitudinal and the ascending portions of the preopercle are herein used as landmarks.

Character 9 - (ci = 0.15; ri = 0.50). Fourth infraorbital, shape (Ch. 2 modified from Benine, 2004; Ch. 20 modified from Bührnheim, 2006; Ch. 67 modified from Mirande,

2010): 0 = squarish, similar in width and height (Fig. 5a). 1 = somewhat deeper, rectangular or irregularly shaped, height longer than width (Fig. 5b). 2 = reduced.

The size and shape of the fourth infraorbital is very variable among the species of the in- and outgroup. The fourth infraorbital is coded as reduced (state 2), only in *Amazonspinther* and in the *Spintherobolus* species.

Character 10 - (ci = 0.11; ri = 0.65). Fifth infraorbital, shape (Ch. 4 Benine, 2004; Ch. 21 modified from Bührnheim, 2006): 0 = broad, with expanded lateral laminae from the laterosensory canal (Fig. 5a). 1 = narrow, lateral laminae absent and reduced to the laterosensory canal, sometimes small and irregularly expanded, but not wider than the canal width (Fig. 5b).

A broad fifth infraorbital is not common among the cheirodontines, being found in a very reduced number of species. However it is more frequently among the outgroup species. This character is coded as inapplicable to species that do not have the sixth infraorbital: *Amazonspinther*, *Spintherobolus*, and *Coptobrycon*.

Character 11 - (ci = 0.07; ri = 0.63). Sixth infraorbital, anterior lamella (Ch. 11 modified from Malabarba, 1994; Ch. 22 modified from Bührnheim, 2006): 0 = present. 1 = absent.

In some of the examined species the sixth infraorbital is well-developed and present an anterior bony expansion, following posterodorsally the border of the orbit over the frontal bone (Fig. 5a-b). This character is coded as inapplicable to *Amazonspinther*, *Spintherobolus*, and *Coptobrycon*, that do not have the sixth infraorbital.

Character 12 - (ci = 0.07; ri = 0.14). Sixth infraorbital, anterior lamella, size (Ch. 11 modified from Malabarba, 1994; Ch. 22 modified from Bührnheim, 2006): 0 = anterior lamella small, reduced, once in the width of the laterosensory tube, in a somewhat small lingual-shaped. 1 = anterior lamella lingual-shaped, expanded and contacting the frontal supra-orbital canal until its pore.

The size of the anterior bony expansion of the sixth infraorbital varies among the species that possess it. In most of the species herein examined this expansion is well-developed, reaching the pore of the supra-orbital laterosensory canal of the frontal. This character is coded as inapplicable to species that do not have the sixth infraorbital, or have the sixth infraorbital but lacks an anterior lamellae.

Character 13 - (ci = 0.50; ri = 0.80). Sixth infraorbital, laterosensory canal (Ch. 23 modified from Bührnheim, 2006; Ch. 76 modified from Mirande, 2010): 0 = unbranched, restricted to the posterior portion of the sixth infraorbital (Fig. 5b). 1 = branched, anterior branch extended along the expanded lingual-shaped anterior lamella (Fig. 5a).

Among the examined specimens, the branching of the laterosensory canal of the sixth infraorbital is only found in species whose sixth infraorbital possesses an anterior lingual-shaped lamella, and was only coded to them.

NEUROCRANIUM

Mesethmoid

Character 14 - (ci = 0.20; ri = 0.78). Mesethmoid, dorsal surface, overall shape: 0 = triangular, with lateral margins converging anteriorly. 1 = rectangular, with lateral margins relatively parallel to each other.

In the majority of the Cheirodontinae and in some representatives from the outgroup, as *Aphyocharacidium bolivianum*, *Aphyodite grammica*, *Cheirodon stenodon*, *Microchemobrycon elongatus*, *Paracheirodon axelrodi*, and *Parecbasis cyclolepis*, the portion of the mesethmoid bone anterior to the frontals is rectangular-shaped from dorsal view (state 1; Fig. 6b). The lateral borders of the mesethmoid at this portion are relatively parallel to each other, while in most outgroup species they are anteriorly convergent, resulting in a triangular shape. In the former case, the lateral borders of the mesethmoid follow partially the direction of its ventral diverging lamellae. The rectangular shape of the mesethmoid seems to be an exclusive consequence of the lateral expansion of its dorsal surface, and not of all the mesethmoid bone, once its

ventral diverging lamellae also converge anteriorly as in the triangular-mesethmoid condition.

Character 15 - (ci = 0.20; ri = 0.69). Mesethmoid, anteromedial process, size (Ch. 20 modified from Zanata & Vari, 2005; Ch. 1, Ch. 4 and Ch. 5 modified from Bührnheim, 2006; Ch. 27 modified from Mirande, 2010): 0 = large, extending between premaxillae and reaching anteriorly the tooth bearing border of the premaxillae. 1 = medium size, partially extending between premaxillae, not reaching anteriorly the tooth bearing border of the premaxillae. 2 = short, not extending anteriorly between the premaxillae.

The length of the anteromedial process of the mesethmoid, in general, does not reach the line of the premaxillary teeth base in Cheirodontinae (state 1), and separates completely the premaxillae in most of the outgroup representatives (state 0) (Fig. 7a). However, in the *Heterocheirodon* and *Macropsobrycon uruguayanae* this process of the mesethmoid is poorly developed, not extending between the premaxillae (state 2) (Fig. 7b).

Character 16 - (ci = 0.66; ri = 0.93). Mesethmoid, anteromedial process, shape in lateral view (Ch. 20 modified from Zanata & Vari, 2005; Ch. 2 and Ch. 3 modified from Bührnheim, 2006): 0 = conical. 1 = depressed, flat. 2 = ventrally globular.

The anteromedial process is conical in most examined species of the outgroup, and flat-shaped from lateral view in most small characiids, and basically all cheirodontines (state 1). In *Amazonspinther dalmata* and *Spintherobolus* species, the anteromedial process is globular, and mostly encapsulated by the premaxillae (Fig. 8).

Character 17 - (ci = 0.20; ri = 0.82). Mesethmoid, anteromedial process, shape on dorsal view (Ch. 20 modified from Zanata & Vari, 2005; Ch. 2 modified from Bührnheim, 2006): 0 = pointed, with rather straight margins converging in an acute anterior spine. 1 = forming a short projection, wide at its base and narrow at its tip, with slightly sinusoidal lateral borders, similar to brackets contour.

A wide and short anteromedial process of the mesethmoid is the general pattern found in the Cheirodontinae (Fig. 6b); nevertheless *Amazonspinther dalmata*, the

Spintherobolus species, and *Pseudocheirodon* species share a pointed anteromedial process in dorsal view, which is found in most of the outgroup species (state 0) (Fig. 6a).

Character 18 - (ci = 0.11; ri = 0.33). Mesethmoid, base of anteromedial process, width (Ch. 28 modified from Mirande, 2010): 0 = narrower than mesethmoid body width at the line just posterior to the lateral process. 1 = as wide as, or wider than mesethmoid body width at the line just posterior to the lateral process (Fig. 9).

Character 19 - (ci = 0.25; ri = 0.66). Mesethmoid, lateral process (Ch. 6 modified from Bührnheim, 2006; Ch. 29 modified from Mirande, 2010): 0 = evident. 1 = covered by the dorsal lamina of mesethmoid.

The lateral processes of the mesethmoid comprise bilateral projections on the anterior portion of the mesethmoid (Fig. 6a). They originate from the lateral surface of the mesethmoid, and ventrally, they are continuous to the salient transversal ridge in the ventral surface of the mesethmoid that contacts the anterior, or anterodorsal, portion of the vomer. The distal tip of the lateral process of the mesethmoid supports the anterior portion of the maxilla through ligamentous tissue, and its dorsal surface supports ventrally the ascending process of the premaxilla, which runs over it.

In most characiforms, the lateral process is clearly delimited and well defined. However, in some Characidae herein examined and most Cheirodontinae, the dorsal surface of the mesethmoid is expanded laterally, and in general, just a small projection from the lateral process of the mesethmoid remains as evident from dorsal view (Fig. 6b). Although the reduced lateral process still supports the anterior portion of the maxilla through ligamentous tissue, in most of these species it does not ventrally support the ascending process of the premaxilla; instead, the premaxilla in these species is supported posteroventrally by the ventral transversal ridge, and posteromedially by the anteromedial process of the mesethmoid.

Among the Cheirodontinae the lateral process is totally absent in *Heterocheirodon* spp., *Spintherobolus ankoseion*, *S. broccae*, *Prodontocharax* spp., and *Pseudocheirodon* spp. Among the outgroup species, the absence of the lateral process of the mesethmoid is found in the aphyocharacines *Aphyocharax nattereri* and

Prionobrama paraguayensis, where the well-developed ascending process of the premaxilla runs posteriorly over the anterior portion of the mesethmoid body.

Character 20 - (ci = 0.10; ri = 0.40). Mesethmoid, lateral process, size (Ch. 23 modified from Zanata & Vari, 2005; Ch. 6 modified from Bührnheim, 2006): 0 = distance between their distal tips wider than mesethmoid base at its contacting line with the frontals. 1 = distance between their distal tips equal or shorter than the mesethmoid base at its contacting line with the frontals.

This character is coded as inapplicable to species without the lateral processes of the mesethmoid.

Character 21 - (ci = 0.14; ri = 0.50). Mesethmoid, posterodorsal margin (Ch. 21 modified from Mirande, 2010): 0 = forming the anterior border of the cranial fontanel (Fig. 7a). 1 = not forming the anterior border of the cranial fontanel (Fig. 7b).

This character represents the same anatomical condition as the character 21 of Mirande (2010), which is stated as “contact between frontals anteriorly to frontal fontanel”. In *Brycon pesu*, there is no cranial fontanel once the frontals contact each other medially. For this species, this character is coded as inapplicable.

Character 22 - (ci = 0.50; ri = 0.90). Mesethmoid, ventral longitudinal diverging lamellae (Ch. 22 modified from Zanata & Vari, 2005; Ch. 30 modified from Mirande, 2010). 0 = present, two well-developed lamellae (Fig. 6a). 1 = reduced at the posterior portion of the bone (Fig. 10).

The ventral longitudinal diverging lamellae of the mesethmoid vary in depth and length among the cheirodontine species. In all examined species, the lamellae usually start at the anterior ventral transversal ridge of the mesethmoid, and diverge posteriorly up to the frontals orbital lamellae. In the cheirodontines, the origin of the ventral lamellae varies among the species, and even intraspecifically. It was observed in *Odontostilbe fugitiva* that the convergence point of the ventral lamellae can be at the ventral transversal ridge of the mesethmoid or way posteriorly, at the mid-length of the mesethmoid. They also may not converge at all, starting disconnected at any point along

the longitudinal length of the mesethmoid. However, the presence of the ventral diverging lamellae is easily recognizable on all cheirodontine species, but completely absent in *Axelrodia lindeae*, *Amazonspither dalmata* and the *Spintherobolus* species, as well as in the *Cheirodon* species, which only present a median single lamella extending from the anterior ventral transversal ridge of the mesethmoid up to the frontals. This character is coded as polymorphic for *O. fugitiva*.

Nasal Bone

Character 23 - (ci = 0.11; ri = 0.37). Nasal bone, shape (Ch. 176 modified from Moreira, 2007): 0 = straight (Fig. 7b). 1 = slightly concave (Fig. 7a). 2 = "U"-shaped.

This character is coded as inapplicable only to *Coptobrycon bilineatus*, which does not have a nasal bone.

Character 24 - (ci = 0.28; ri = 0.16). Nasal bone, posterior tip (Ch. 177 modified from Moreira, 2007): 0 = contacting the frontal bone. 1 = one pore distant from frontal bone (Fig. 7a). 2 = more than one pore distant from frontal bone (Fig. 7b).

This character is coded as inapplicable to *Coptobrycon bilineatus*, which does not have a nasal bone.

Character 25 - (ci = 0.22; ri = 0.61). Nasal bone, length (Ch. 18 modified from Zanata & Vari, 2005; Ch. 178 modified from Moreira, 2007): 0 = extending from the frontal anterior margin and overlapping anteriorly the mesethmoid lateral wing. 1 = extending from the frontal anterior margin falling short to the mesethmoid lateral wing (Fig. 7a). 2 = shorter than half the distance between the frontal anterior margin and the mesethmoid lateral wing (Fig. 7b).

This character is coded as inapplicable to *Coptobrycon bilineatus*, which does not have a nasal bone.

Lateral ethmoid

Character 26 - (ci = 1.00; ri = 1.00). Lateral ethmoid, contact with mesethmoid: 0 = present. 1 = absent.

In the examined cheirodontine species, the lateral ethmoid contacts anteromedially the ventral lamella of the mesethmoid. This articulation is absent in the trans-andean *Cheirodon* species: *Cheirodon australe*, *C. galusdai*, *C. kiliani*, and *C. pisciculus*.

Character 27 - (ci = 0.50; ri = 0.00). Lateral ethmoid, portion contacting mesethmoid: 0 = ossified. 1 = cartilaginous.

Axelrodia lindeae and *Amazonspinther dalmata* are the only examined species in which the portion of the lateral ethmoid contacting the mesethmoid is mostly cartilaginous. In the remaining species, those bones are completely ossified. This character is coded as inapplicable for *Cheirodon australe*, *C. galusdai*, *C. kiliani*, and *C. pisciculus*, whose lateral ethmoid does not contact the mesethmoid.

Character 28 - (ci = 1.00; ri = 1.00). Lateral ethmoid, anterodorsal mesethmoid fossa: 0 = present. 1 = absent.

The anterodorsal mesethmoid fossa is a shallow depression extending dorsoventrally in the anteromedial region of the lateral ethmoid, where the ventral diverging lamella of the mesethmoid articulates (Fig. 11a-b). It is absent in *Axelrodia lindeae*, *Amazonspinther dalmata*, and in the *Spintherobolus* species (Fig. 11c). It is coded as inapplicable for *Cheirodon australe*, *C. galusdai*, *C. kiliani*, and *C. pisciculus*, whose lateral ethmoid are not in contact with the mesethmoid.

Character 29 - (ci = 1.00; ri = 1.00). Lateral ethmoid, olfactory nerve foramen, position: 0 = dorsally to the anteromedial process. 1 = medially to the anteromedial process, at the same horizontal line.

All examined species present the foramen of the olfactory nerve dorsally placed in relation to the anteromedial process of the lateral ethmoid, except the species of *Amazonspinther* and *Spintherobolus*, whose foramen is placed medially to the anteromedial process, at the same high in the lateral ethmoid anterior face (Fig. 11c).

Character 30 - (ci = 0.04; ri = 0.46). Lateral ethmoid, anteromedial process (Ch. 14 modified from Mirande, 2010): 0 = robust (Fig. 11a). 1 = thin and sometimes not completely ossified (Fig. 11b).

The lateral ethmoid lacks the anteromedial process in *Charax stenopterus*, and for this species, it is coded as inapplicable.

Character 31 - (ci = 0.50; ri = 0.00). Lateral ethmoid, contact of dorsolateral margin with antorbital. 0 = present. 1 = absent.

The presence of the lateral ethmoid articulating with the antorbital is only found in *Brycon pesu* and *Charax stenopterus*. Although the antorbital may overlap laterally the lateral ethmoid in some of the examined species, these bones are not in contact.

Character 32 - (ci = 0.66; ri = 0.66). Lateral ethmoid, dorsal border: 0 = ossified, contacting the frontal along all its length. 1 = ossified articulation with the frontal through a small ascending expansion dorsolaterally, and medially by chondral articulation. 2 = contacting the frontal only through chondral articulation.

The dorsal border of the lateral ethmoid contacts ventrally the lateral portion of the frontal along all its length in most of the examined species. Although the articulation between these bones is synchondral, the cartilage between them is not well developed once the lateral ethmoid and the frontal are mostly ossified (state 0). In *Amazonspinther dalmata*, *Spintherobolus ankoseion* and *S. broccae*, this kind of articulation is restricted to a dorsolateral ascending expansion of the lateral ethmoid at the most lateral portion of its dorsal border, while the medial portion contacts the frontal by a well developed cartilaginous tissue (state 1). In the *Prodontocharax* species, the contact between the lateral ethmoid and the frontal is exclusively by a well developed cartilaginous tissue (state 2).

Character 33 - (ci = 0.33; ri = 0.50). Lateral ethmoid, laminar lateroventral expansion: 0 = present. 1 = absent.

The lateral ethmoid delimits the orbital cavity anteriorly, and anteroventrally by its lateroventral expansion (Fig. 11a-b). The lateroventral expansion of the lateral ethmoid is present in most of the examined specimens, but it is absent in *Amazonspinther dalmata*, *Spintherobolus ankoseion*, *S. broccae*, and in the *Prodontocharax* species (Fig. 11c).

Character 34 - (ci = 0.33; ri = 0.00). Vomer, posterolateral process: 0 = absent. 1 = present, contacting the anteromedial process of the lateral ethmoid.

The presence of posterolateral process in the vomer, posteriorly contacting the anteromedial process of the lateral ethmoid is only found in *Amazonspinther dalmata*, *Spintherobolus ankoseion*, and *Aphyocharax nattereri*.

Character 35 - (ci = 0.33; ri = 0.60). Rhinosphenoid (Ch. 31 Zanata & Vari, 2005; Ch. 8 Bührnheim, 2006): 0 = present (Fig. 12). 1 = absent.

The rhinosphenoid is absent in *Amazonspinther* and *Spintherobolus*, *Aphyocharax nattereri*, and *Cynopotamus kincaidi* (Fig. 8).

Character 36 - (ci = 0.33; ri = 0.60). Orbitosphenoid, contact with parasphenoid (Ch. 9 modified from Bührnheim, 2006; Ch. 37 modified from Mirande, 2010): 0 = absent. 1 = present.

The orbitosphenoid contacts the parasphenoid only in *Amazonspinther dalmata*, *Spintherobolus* spp., *Aphyocharax nattereri*, and *Cynopotamus kincaidi* (Fig. 8).

Character 37 - (ci = 0.16; ri = 0.16). Orbitosphenoid, dorsal fenestra with frontal: 0 = absent. 1 = present.

The orbitosphenoid is a median bone, V-shaped in cross section, placed between the orbits. The dorsal expansions of the orbitosphenoid contact the frontals ventrally, medially to the ventral orbital lamellae of the frontals. The presence of a fenestra between the dorsal border of the orbitosphenoid and the frontal is observed in some of the examined species. This character is coded as polymorphic to *Saccoderma hastata*.

Character 38 - (ci = 0.10; ri = 0.50). Orbitosphenoid, posteroventral process (Ch. 10 modified from Bührnheim, 2006): 0 = absent. 1 = present.

The posteroventral process of the orbitosphenoid is present in most of the cheirodontines (Fig. 12), except in *Cheirodon galusdai*, *C. parahybae*, *Odontostilbe* n. sp. b and *Odontostilbe splendida*.

Character 39 - (ci = 0.25; ri = 0.00). Orbitosphenoid, posteroventral process, length (Ch. 10 modified from Bührnheim, 2006): 0 = short (Fig. 12). 1 = long, almost reaching the line of articulation between orbitosphenoid and pterosphenoid.

The posteroventral process of the orbitosphenoid falls short in the line of articulation between orbitosphenoid and pterosphenoid in the cheirodontines *Spintherobolus ankoseion*, *S. papilliferus*, *Odontostilbe* n. sp. e, and *O. euspilurus*. It is coded as inapplicable to species whose orbitosphenoid does not have the posteroventral process.

Character 40 - (ci = 0.25; ri = 0.00). Pterosphenoid, fenestra: 0 = absent. 1 = present.

A fenestra between the pterosphenoid and the orbitosphenoid is only present in *Axelrodia lindeae*, *Aphyocharacidium bolivianum*, *Aphyocharax nattereri*, and *Cynopotamus kincaidi*.

Latosensory canals

Character 41 - (ci = 0.33; ri = 0.60). Laterosensory canals in the parietal and pterotic (Ch. 159 modified from Zanata & Vari, 2005; Ch. 12 modified from Bührnheim, 2006; Ch. 87 modified from Mirande, 2010): 0 = present. 1 = absent.

The reduction of the laterosensory canals in the head, and the absence of the parietal and pterotic branches are found in *Amazonspinther*, *Spintherobolus* spp., *Coptobrycon bilineatus*, and *Paracheirodon axelrodi*.

Character 42 - (ci = 0.05; ri = 0.37). Supraorbital laterosensory canal, continuity with pterotic laterosensory canal (Ch. 159 modified from Zanata & Vari, 2005; Ch. 12 modified from Bührnheim, 2006): 0 = present (Fig. 12). 1 = absent (Fig. 13).

Character 43 - (ci = 0.50; ri = 0.66). Supraorbital laterosensory canal, length: 0 = extending from the anterior margin of the frontal and surpassing the line of the epiphyseal bar posteriorly. 1 = limited to the anterior portion of the frontal, not reaching the line of epiphyseal bar.

The supraorbital laterosensory canal limited to the anterior portion of the frontal, not reaching the line of epiphyseal bar is shared by the *Spintherobolus* species and also present in *Coptobrycon bilineatus*.

Character 44 - (ci = 0.08; ri = 0.75). Parietal laterosensory canal, connections (Ch. 156, 157, 158 modified from Zanata & Vari, 2005; Ch. 11 modified from Bührnheim, 2006): 0 = continuous to the supratemporal laterosensory canal posteriorly, and anteriorly to the parietal branch of the supraorbital laterosensory canal of the frontal (Fig. 12). 1 = not continuous to the supratemporal laterosensory canal posteriorly, divided by a gap, but anteriorly continuous to the parietal branch of the supraorbital laterosensory canal of the frontal.

This character is coded as inapplicable to species without the parietal branch of the supraorbital laterosensory canal, like *Amazonspinther dalmata*, *Coptobrycon bilineatus*, *Leptobrycon jatuaranae*, and *Spintherobolus*.

Character 45 - (ci = 1.00; ri = 1.00). Supratemporal laterosensory canal, length: 0 = long, reaching the border of the frontoparietal fontanel. 1 = short, ending at half length away from the frontoparietal fontanel border.

Among the examined species, only the *Kolpotocheiroidon* species share a short supratemporal laterosensory canal. This character is coded as inapplicable to species without the supratemporal laterosensory canal, like *Amazonspinther dalmata*, *Coptobrycon bilineatus*, *Paracheiroidon axelrodi*, and *Spintherobolus*.

Epioccipital

Character 46 - (ci = 0.50; ri = 0.50). Epioccipital bridge (Ch. 6 modified from Weitzman & Fink, 1983; Ch. 7 modified from Bührnheim, 2006): 0 = present. 1 = absent.

Among the examined species, the epioccipital bridge is only absent in *Amazonspinther dalmata*, *Spintherobolus ankoseion* and *S. broccae*.

Posttemporal

Character 47 - (ci = 0.50; ri = 0.75). Posttemporal laterosensory canal: 0 = present. 1 = absent.

The laterosensory canal of the posttemporal is absent in *Amazonspinther dalmata*, the species of *Spintherobolus*, and *Paracheiroduon axelrodi*.

Frontal

Character 48 - (ci = 0.12; ri = 0.72). Frontal, anterior fontanel, size (Ch. 23 modified from Mirande, 2010): 0 = longer than half length between epiphyseal bar and mesethmoid articulation. 1 = shorter than half length between epiphyseal bar and mesethmoid articulation.

In *Brycon pesu*, there are no cranial fontanels once the frontals contact each other medially. To this species, this character was coded as inapplicable.

Extrascapular

Character 49 - (ci = 1.00; ri = 1.00). Extrascapular (Ch. 127 Zanata & Vari, 2005; 99 modified from Bührnheim, 2006): 0 = present. 1 = absent.

The extrascapular is absent in *Axelrodia lindeae*, *Amazonspinther dalmata*, and in the species of *Spintherobolus*.

JAWS

Character 50 - (ci = 0.50; ri = 0.50). Mouth, position (Ch. 75 modified from Bührnheim, 2006): 0 = terminal, mouth opening close to horizontal through the middle of the eye. 1 = superior, located above the horizontal through the middle of the eye. 2 = subterminal, below the horizontal through the lower edge of the eye.

The position of the mouth in the cheirodontines is mostly terminal, or variably placed slightly below the line through the middle of the eye. These two characteristics, as well as all intermediary stages between them, are herein considered as terminal mouth (state 0). The only cheirodontines stated as presenting a superior mouth is *Macropsobrycon uruguayanae* (state 1), but it is also observed in *Cynopotamus kincaidi*, *Leptobrycon jatuaranae*, and “*Macropsobrycon*” *xinguensis*. On the other hand, the presence of a subterminal mouth only stated to the species of *Prodontocharax*.

Premaxilla

Character 51 - (ci = 0.20; ri = 0.50). Premaxilla, ascending process (Ch. 33 modified from Bührnheim, 2006): 0 = present. 1 = absent.

In Cheirodontinae the ascending process of the premaxilla is not as well developed as in the outgroup taxa herein examined (Fig. 14a-c). In general, the cheirodontines premaxilla resembles a half-circle in shape, where the ascending process is characterized as a small pointed projection from the dorsal border of the bone (Fig. 14b), very distinct from the “L”-shaped maxilla present in most of the characids (Fig. 14a). However some cheirodontines’ premaxilla lacks completely the ascending process, which is the case in *Compsurini Cuzco* n. sp., *Compsurini Tingo* n. sp., *Compsurini Yurimaguas* n. sp., *Prodontocharax alleni*, *P. melanotus*, *Pseudocheirodon arnoldi*, *P. terrabae*, *Serrapinnus* n. sp. e, and *Serrapinnus* n. sp. d.

Character 52 - (ci = 0.15; ri = 0.70). Premaxilla, ascending process, shape (Ch. 54 Zanata & Vari, 2005; Ch. 32 modified from Bührnheim, 2006): 0 = distinctly projected, pointed (Fig. 14a). 1 = small projection on the mid-dorsal border of the premaxilla (Fig. 14b). 2 = square-shaped.

A square-shaped ascending process of the premaxilla is an autapomorphy of *Macropsobrycon uruguayanae* (Fig. 14c). This character is coded as inapplicable to

species without the ascending process of the premaxilla: Compsurini Cuzco n. sp., Compsurini Tingo n. sp., Compsurini Yurimaguas n. sp., *Prodontocharax alleni*, *P. melanotus*, *Pseudocheirodon arnoldi*, *P. terrabae*, *Serrapinnus* n. sp. e, and *Serrapinnus* n. sp. d.

Character 53 - (ci = 0.09; ri = 0.72). Premaxilla, ascending process, length (Ch. 104 modified from Mirande, 2010): 0 = running over the lateral process of the mesethmoid. 1 = falling short the lateral tip of the mesethmoid lateral process.

This character is coded as inapplicable to species without the ascending process of the premaxilla: Compsurini Cuzco n. sp., Compsurini Tingo n. sp., Compsurini Yurimaguas n. sp., *Prodontocharax alleni*, *P. melanotus*, *Pseudocheirodon arnoldi*, *P. terrabae*, *Serrapinnus* n. sp. e, and *Serrapinnus* n. sp. d.

Character 54 - (ci = 0.28; ri = 0.80). Premaxilla, medial lamellae (Ch. 34 modified from Bührnheim, 2006): 0 = reduced, forming a shallow oval articular fossa along dorsomedial surface of the premaxilla. 1 = developed, forming a V-shaped bifurcation, the posteromedial lamina oblique to anteromedial lamina. 2 = developed, the posteromedial lamina at the coronal plane and perpendicular to the anteromedial lamina.

The premaxilla, in the examined species, presents a medial fossa that articulates with the anteromedial process of the mesethmoid. In the cheirodontines and some of the outgroup species, two well-developed lamellae extend from the anterior and posterior limits of the fossa (or from the dorsal and ventral limits, if the premaxilla is placed in the longitudinal plane) embracing the mesethmoid anteromedial process (Fig. 15). These lamellae diverge anteromedially and posteromedially in an acute angle in most of the cheirodontines (state 1); however, in the species of *Pseudocheirodon* they diverge in a perpendicular angle (state 2).

Maxilla

Character 55 - (ci = 0.08; ri = 0.69). Maxilla, length (Ch. 8 modified from Malabarba, 1998; Ch. 72 modified from Zanata & Vari, 2005; Ch. 53 modified from Bührnheim, 2006; Ch. 99 and 100 modified from Mirande, 2010): 0 = extending posteriorly the

vertical line through the ventral limit of the lateral ethmoid. 1 = not extending posterior to vertical line through the ventral limit of the lateral ethmoid.

Character 56 - (ci = 0.07; ri = 0.58). Maxilla, longitudinal groove, just below the dorsolateral border (Ch. 46 modified from Bührnheim, 2006): 0 = absent. 1 = present.

Character 57 - (ci = 1.00; ri = 1.00). Maxilla, ventral border, protruding spine-like projection preceding anteriormost teeth (Ch. 47 modified from Bührnheim, 2006): 0 = absent. 1 = present.

The presence of a pointed projection anterior to the first maxillary tooth is observed only in the species of *Pseudocheirodon* (Fig. 16a).

Character 58 - (ci = 0.66; ri = 0.87). Maxilla, main axis, shape (Ch. 5 and 8 modified from Malabarba 1994; Ch. 7 modified from Malabarba, 1998; Ch. 49 modified from Bührnheim, 2006): 0 = maxilla nearly straight, with tooth-bearing portion angled ventrally relative to the premaxillary tooth-bearing portion (Fig. 16b,c). 1 = maxilla ventrally arched, with tooth-bearing portion continuous to the premaxillary tooth-bearing portion line, but posterior toothless portion ventrally arched (Fig. 16a). 2 = maxilla arched dorsally.

The main axis of the maxilla is straight in lateral view in most of the examined species from the ingroup and outgroup. However, in the cheirodontines *Odontostilbe eupilurus*, and in the species from the genera *Prodontocharax* and *Pseudocheirodon*, the bearing portion of the maxilla is continuous to the line of the premaxillary tooth-bearing portion, but posteriorly, the main axis of the maxilla arches ventrally. In the opposite way, in the cheirodontine *Macropsobrycon uruguayanae*, and in the outgroup species *Aphyodite grammica*, *Leptobrycon jatuaranae*, "*Macropsobrycon*" *xinguensis*, and *Parecbasis cyclolepis*, the main axis of the maxilla is dorsally arched.

Character 59 - (ci = 0.07; ri = 0.65). Maxilla, dorsal profile (Ch. 42 modified from Bührnheim *et al.*, 2008): 0 = straight. 1 = slightly concave.

The dorsal profile of the maxilla varies from straight to slightly concave, independently of the main axis shape of the bone.

Character 60 - (ci = 0.25; ri = 0.85). Maxilla, ventral profile: 0 = margin of the tooth bearing portion continuous to the toothless margin (Fig. 16b). 1 = margin of the tooth bearing portion concave, not continuous to the toothless margin (Fig. 16a,c).

This character is coded as inapplicable to species without teeth in the maxilla: *Leptobrycon jatuaranae*, *Macropsobrycon uruguayanae*, “*Macropsobrycon*” *xinguensis*, and *Parecbasis cyclolepis*.

Character 61 - (ci = 0.16; ri = 0.37). Maxilla, relative depth (Ch. 51 modified from Bührnheim, 2006; Ch. 97 modified from Mirande, 2010): 0 = with similar height along its axis (Fig. 16b). 1 = posterior toothless portion deeper, extended ventrally, surpassing the line of the distal tip of the maxillary teeth (Fig. 16a,c).

All cheirodontines and some taxa from the outgroup have a deeper maxilla posteriorly, surpassing ventrally the line of the teeth distal tips (state 1). The only cheirodontine whose maxilla has a similar height along all its length is *Axelrodia lindeae*. This character is coded as inapplicable to species without teeth in the maxilla: *Leptobrycon jatuaranae*, *Macropsobrycon uruguayanae*, “*Macropsobrycon*” *xinguensis*, and *Parecbasis cyclolepis*.

Character 62 - (ci = 0.12; ri = 0.60). Maxilla, ventral profile, toothless portion, relative length (Ch. 50 modified from Bührnheim, 2006): 0 = shorter than tooth bearing portion (Fig. 16a-b). 1 = with approximately the same length of the tooth bearing portion (Fig. 16c). 2 = twice the length of the tooth bearing portion. 3 = extended, more than two times longer than the tooth bearing portion of the maxilla.

This character is coded as inapplicable to species without teeth in the maxilla: *Leptobrycon jatuaranae*, *Macropsobrycon uruguayanae*, “*Macropsobrycon*” *xinguensis*, and *Parecbasis cyclolepis*.

Character 63 - (ci = 0.50; ri = 0.50). Maxilla, posterior region, shape (Ch. 52 modified from Bührnheim, 2006): 0 = forming a flat and plane vertical blade. 1 = lower portion of the posterior region not flat, angled medially.

In *Odontostilbe euspilurus*, *Pseudocheirodon arnoldi* and *P. terrabae*, the lamellar portion of the maxilla is angled medially along its lower portion, resting in a concavity in the dorsolateral region of the lower jaw when the mouth is closed (state 1).

Character 64 - (ci = 0.33; ri = 0.50). Maxilla, posterior extremity, distal profile (Ch. 6 modified from Malabarba 1994; Ch. 6 modified from Malabarba, 1998; Ch. 48 modified from Bührnheim, 2006): 0 = ending in a round profile (Fig. 16b,c). 1 = ending in a sharp angle, due to the ventral margin dorsoposterior convergence toward the dorsal margin of the maxilla (Fig. 16a).

The posterior border of the maxilla narrowing posteriorly and ending in a sharp angle is found in "*Macropsobrycon*" *xinguensis*, *Odontostilbe euspilurus*, *O. pao*, and in the *Pseudocheirodon* species. In this case (state 1), the ventral profile of the lamellar portion of the maxilla converges dorsoposteriorly toward its dorsal profile.

Dentary

Character 65 - (ci = 1.00; ri = 1.00). Dentary, anteroventral foramen (Ch. 5, modified from Malabarba, 1998; Ch. 69 modified from Bührnheim, 2006): 0 = small. 1 = large.

The dentary, in most of the species herein examined, has a small foramen ventrally to the anteriormost pore of the laterosensory canal (Fig. 17b). In *Amazonspinther dalmata* and in the *Spintherobolus* species, this foramen is enlarged, and in some specimens its perimeter is not completely ossified in the ventral portion (Fig. 17a).

Character 66 - (ci = 0.50; ri = 0.85). Dentary, symphyseal joint, interdigitations (Ch. 4 modified from Malabarba, 1998; Ch. 82 modified from Zanata & Vari, 2005; Ch. 68 modified from Bührnheim, 2006; Ch. 111 modified from Mirande, 2010): 0 = present. 1 = absent.

The dentaries are medially articulated through interdigitations in most of the examined species, except *Amazonspinther dalmata* and the species of *Spintherobolus*, whose dentaries lack interdigitations and are articulated only by connective tissue.

Character 67 - (ci = 0.09; ri = 0.52). Dentary, lateral view, tooth bearing portion, relative length (Ch. 62 modified from Bührnheim, 2006): 0 = more than half length of the dorsal border of the dentary bone. 1 = less than half length of the dorsal border of the dentary bone.

Character 68 - (ci = 0.05; ri = 0.40). Dentary, tooth size along tooth bearing portion (Ch. 56 modified from Bührnheim, 2006): 0 = anterior and posterior regions distinct by difference in teeth size (Fig. 17b). 1 = anterior and posterior regions not differentiated by teeth size.

It is possible to recognize two main regions in the dorsal profile of the cheirodontines dentary: the tooth bearing portion, and the edentulous portion. Among the species herein examined, two different regions could be differentiated in the toothed portion of the dentary: an anterior region, usually with a straight profile and medially directed, ending in the symphysis with the contralateral dentary; and the posterior toothed region, which is generally in an ascending portion of the dorsal profile of the dentary. The toothed anterior region generally bears the largest teeth, frequently with similar size and shape; and the posterior region is characterized by the presence of smaller teeth, commonly decreasing posteriorly in size and cusp number (state 0). However, in some of the examined species, the dentary teeth present the same size and shape in the anterior and posterior regions, and are coded as presenting the state 1.

Character 69 - (ci = 0.10; ri = 0.57). Dentary, dorsal view, anterior tooth bearing portion, relative length: 0 = shorter than posterior portion. 1 = longer than posterior portion.

Character 70 - (ci = 0.33; ri = 0.33). Dentary, dorsolateral border, concave (Ch. 66 modified from Bührnheim, 2006): 0 = absent. 1 = present, a concavity in the dorsolateral surface of the dentary, at vertical after the posteriormost teeth of the dentary.

This concavity in the dorsolateral surface of the dentary is observed in *Odontostilbe nareuda*, *O. pao*, and in *Pseudocheiroduon*. In the species of *Pseudocheiroduon*, this concavity is where the medially angled lamellar portion of the maxilla rests. However, the presence of this concavity was not considered dependent of the presence of a maxilla with the lamellar portion medially angled, due to the presence of the concavity in *Odontostilbe nareuda* and *O. pao*, whose lamellar portion of the maxilla is not medially angled.

Anguloarticular

Character 71 - (ci = 0.11; ri = 0.61). Anguloarticular, anterodorsal process, lateral ridge, development (Ch. 57 modified from Bührnheim, 2006; Ch. 107 modified from Mirande, 2010): 0 = inconspicuous (Fig. 17a). 1 = short, not reaching the anterior end of the anguloarticular anterodorsal process. 2 = long, along all the anguloarticular anterodorsal process length (Fig. 17b).

The anguloarticular articulates posteriorly with the quadrate, and anteriorly it supports the dentary bone through an horizontal process which runs medially to the dentary along its longitudinal axis, and an anterodorsal process, which runs laterally to the dentary. The examined species present a ridge that originates from nearby the articulation point with the quadrate, and extends along the axis of the anterodorsal process of the anguloarticular. This ridge may vary in size and degree of development. This character is coded as inapplicable to *Compsurini Leticia n. sp.* and to the *Heterocheiroduon* species, once the anterodorsal process of the anguloarticular is absent.

Character 72 - (ci = 0.50; ri = 0.50). Anguloarticular, anterodorsal process (Ch. 60 modified from Bührnheim, 2006): 0 = present. 1 = absent.

Among the examined specimens this ridge is only absent in *Compsurini Leticia n. sp.* and to the *Heterocheiroduon* species.

Character 73 - (ci = 0.06; ri = 0.51). Anguloarticular, horizontal process, length (Ch. 61 modified from Bührnheim, 2006): 0 = short, not reaching the line through the

toothed portion of the dentary. 1 = elongate, reaching the line through the toothed portion of the dentary (Fig. 17b).

DENTITION

Premaxillary teeth

Character 74 - (ci = 0.20; ri = 0.85). Premaxillary teeth, shape (Ch. 56 modified from Malabarba, 1998; Ch. 3 modified from Weitzman & Malabarba, 1999; Ch. 70 modified from Bührnheim, 2006; Ch. 3 modified from Bührnheim *et al.*, 2008; Ch. 119 modified from Mirande, 2010): 0 = not pedunculated, tooth base enlarged. 1 = pedunculated, largely expanded, and compressed distally (Figs. 14b, 15).

The presence of pedunculated teeth is a very remarkable feature of the cheirodontines, found to be a synapomorphy of the group by Malabarba (1998) and Bührnheim (2006). Herein, the presence of pedunculated teeth is explored in three different characters, regarding its presence in the premaxilla, maxilla and in the dentary independently, due to the fact that some species may not present pedunculated teeth on all those bones. This character is coded as polymorphic to *Rhoadsia altipinna*, that presents pedunculated and not-pedunculated teeth in the same row.

Character 75 - (ci = 0.20; ri = 0.60). Premaxillary medial tooth, relative size to lateral teeth (Ch. 36 modified from Bührnheim, 2006): 0 = same size. 1 = markedly larger.

Among the cheirodontines the presence of premaxillary medial tooth larger than the lateral ones is evidenced only in *Aphyocheirodon hemigrammus*, *Cheirodontops geayi*, *Holoshesthes pequirá*, and in three non-described species of *Holoshesthes*.

Character 76 - (ci = 0.50; ri = 0.50). Premaxillary teeth, size of 1-3 most lateral teeth in the single row (Ch. 37 modified from Bührnheim, 2006): 0 = lateral teeth with similar size or gradually smaller than the preceding teeth. 1 = 1-3 most lateral teeth larger than the preceding teeth.

This character is coded as inapplicable to species with two or more rows of teeth in the premaxilla: *Astyanax aff. fasciatus*, *A. laticeps*, *Bryconamericus iheringii*, *Brycon pesu*,

Bryconops caudomaculatus, *Cyanocharax alburnus*, *Hemibrycon polyodon*,
Hyphessobrycon bifasciatus, *Probolodus heterostomus*, and *Rhoadsia altipinna*.

Character 77 - (ci = 0.66; ri = 0.90). Premaxilla, tooth rows, number (Ch. 55 Malabarba, 1998; Ch. 4 modified from Weitzman & Malabarba, 1999; Ch. 57 modified from Zanata & Vari, 2005; Ch. 35 modified from Bührnheim, 2006; Ch. 4 modified from Bührnheim *et al.*, 2008; Ch. 122 and 123 modified from Mirande, 2010): 0 = three. 1 = two. 2 = one (Figs. 14, 15).

Coded as polymorphic in *Paracheiroidon axelrodi* [1&2], which occasionally present a single tooth anteriorly placed to the single tooth row.

Character 78 - (ci = 0.50; ri = 0.50). Premaxilla, single tooth row, alignment (Ch. 55 Malabarba, 1998; Ch. 57 modified from Zanata & Vari, 2005; Ch. 35 modified from Bührnheim, 2006): 0 = teeth not perfectly aligned (Fig. 14a). 1 = teeth aligned and similar in shape, size and cusp number (Fig. 14b-c, 15).

This character is coded as inapplicable to species with two or more rows of teeth in the premaxilla: *Astyanax* aff. *fasciatus*, *A. laticeps*, *Bryconamericus iheringii*, *Brycon pesu*, *Bryconops caudomaculatus*, *Cyanocharax alburnus*, *Hemibrycon polyodon*, *Hyphessobrycon bifasciatus*, *Probolodus heterostomus*, and *Rhoadsia altipinna*.

Character 79 - (ci = 0.25; ri = 0.76). Premaxillary teeth, base: 0 = spaced. 1 = juxtaposed.

Character 80 - (ci = 0.12; ri = 0.12). Premaxillary teeth, spacement (Ch. 65 modified from Malabarba 1994; Ch. 42 modified from Bührnheim, 2006): 0 = smaller than tooth base width. 1 = equal or bigger than tooth base width.

This character is coded as inapplicable to species whose teeth are juxtaposed.

Character 81 - (ci = 0.07; ri = 0.64). Premaxillary teeth, cusp contact: 0 = absent. 1 = present.

In most cheirodontines and few outgroup species, the most lateral one or two cusps of the premaxillary teeth contact, or overlap, the lateral cusps of the consecutive tooth.

Character 82 - (ci = 0.33; ri = 0.50). Premaxillary teeth, number, in the inner row (Ch. 41 modified from Bührnheim, 2006; Ch. 129 and 130 modified from Mirande, 2010): 0 = at least 5. 1 = at most 4.

This character is coded as inapplicable to species with a single tooth row.

Character 83 - (ci = 0.16; ri = 0.58). Premaxillary teeth, number, in the single row (Ch. 62 modified from Malabarba 1994; Ch. 41 modified from Bührnheim, 2006; Ch. 130 modified from Mirande, 2010): 0 = at most 7. 1 = at least 7.

This character is coded as inapplicable to species with two or more tooth rows.

Character 84 - (ci = 0.50; ri = 0.87). Premaxillary teeth, inner tooth row, polymorphism on cusp number: 0 = present. 1 = absent.

All the premaxillary teeth in the examined cheirodontines present similar size and cusp number, differently from some of the outgroup species whose teeth decrease in size and cusp number laterally.

Character 85 - (ci = 0.20; ri = 0.55). Premaxillary tooth, cusp, number (Ch. 56 modified from Malabarba, 1998; Ch. 3 modified from Weitzman & Malabarba, 1999; Ch. 70 modified from Bührnheim, 2006; Ch. 3 modified from Bührnheim *et al.*, 2008): 0 = multicuspid. 1 = conical.

This character is coded as polymorphic to "*Macropsobrycon xinguensis*", which present mostly conical, but sometimes one or two symphyseal tricuspid teeth in the premaxilla.

Character 86 - (ci = 0.50; ri = 0.50). Premaxillary teeth, cusp, shape: 0 = pointed. 1 = rounded.

The premaxillary teeth usually bear cusps with pointed shape; however, the in *Pseudocheirodon* species and *Rhoadsia altipinna* the cusps of the premaxillary teeth are rounded.

Character 87 - (ci = 0.25; ri = 0.57). Premaxillary teeth, cusp, relative size (Ch. 39 modified from Bührnheim, 2006): 0 = central cusp larger and lateral ones decreasing in size laterally. 1 = all cusps similar in form and size.

This character is coded as inapplicable to species with conical teeth.

Character 88 - (ci = 1.00; ri = 1.00). Premaxillary posteriormost tooth, in the single tooth row, position of the main cusp (Ch. 38 modified from Bührnheim, 2006): 0 = cusp almost perpendicular to the ventral border of premaxilla. 1 = cusps slightly oblique to the ventral border of the premaxilla, curved posteriorly.

In *Aphyocheirodon hemigrammus*, *Cheirodontopsis geayi*, and three new species of *Holoshesthes*, the posteriormost tooth of the premaxilla has its cusps curved posteriorly in relation to the tooth axis. This character is coded as inapplicable to species with two or more tooth rows.

Maxillary teeth

Character 89 - (ci = 0.20; ri = 0.20). Maxillary teeth (Ch. 134 modified from Mirande, 2010): 0 = present. 1 = absent.

Most examined species have teeth in the maxilla (state 0), except the cheirodontine *Macropsobrycon uruguayanae* and the outgroup species *Bryconops caudomaculatus*, *Coptobrycon bilineatus*, *Leptobrycon jatuaranae*, "*Macropsobrycon*" *xinguensis*, and *Parecbasis cyclolepis*.

Character 90 - (ci = 0.50; ri = 0.95). Maxillary teeth, shape (Ch. 56 modified from Malabarba, 1998; Ch. 3 modified from Weitzman & Malabarba, 1999; Ch. 70 modified from Bührnheim, 2006): 0 = tooth base enlarged, with conical cusps. 1 = pedunculated teeth, largely expanded, compressed distally (Fig. 16a,c).

This character is coded as inapplicable to species with toothless maxilla, and coded as polymorphic to *Rhoadsia altipinna* for having conical and pedunculated teeth in the maxilla.

Character 91 - (ci = 0.50; ri = 0.87). Maxillary teeth, cusp, number (Ch. 56 modified from Malabarba, 1998; Ch. 3 modified from Weitzman & Malabarba, 1999; Ch. 70 modified from Bührnheim, 2006; Ch. 138 and 139 modified from Mirande, 2010): 0 = multicuspid. 1 = conical teeth.

This character is coded as inapplicable to species with toothless maxilla, and coded as polymorphic to *Rhoadsia altipinna* for having conical and pedunculated maxillary teeth.

Dentary teeth

Character 92 - (ci = 0.25; ri = 0.86). Dentary teeth, shape (Ch. 56 modified from Malabarba, 1998; Ch. 3 modified from Weitzman & Malabarba, 1999; Ch. 70 modified from Bührnheim, 2006): 0 = tooth larger in the base, with conical cusps. 1 = pedunculated, largely expanded and compressed distally (Fig. 17b).

The dentary teeth of most of the examined cheirodontines are pedunculated, with the exception of *Axelrodia lindeae* and *Macropsobrycon uruguayanae*, which have conical teeth. This condition, however, is only shared by *Coptobrycon bilineatus* and *Rhoadsia altipinna* among the outgroup species.

Character 93 - (ci = 0.16; ri = 0.64). Dentary teeth, size, in the anterior toothed portion (Ch. 148 modified from Mirande, 2010): 0 = laterally decreasing in size. 1 = with same size.

Although the teeth size decrease in the anterior toothed portion seems to be correlated to the decrease in size of the posterior toothed portion, it is herein coded separately once these characters are not dependent in some species.

Character 94 - (ci = 0.25; ri = 0.00). Dentary, teeth, in the posterior toothed portion, size (Ch. 148 modified from Mirande, 2010): 0 = posteriorly decreasing in size (Fig. 17b). 1 = with same size.

Character 95 - (ci = 0.33; ri = 0.00). Dentary teeth, row, number (Ch. 143 modified from Mirande, 2010): 0 = two. 1 = one (Fig. 17).

The presence of two tooth rows in the dentary is only observed in *Aphyocharacidium bolivianum*, *Brycon pesu*, and *Parecbasis cyclolepis*.

Character 96 - (ci = 0.12; ri = 0.65). Dentary, anteriormost teeth, angle of insertion (Ch. 59 modified from Bührnheim, 2006; Ch. 141 modified from Mirande, 2010): 0 = longer axis of the anteriormost teeth perpendicular to the longer axis of the dentary. 1 = longer axis of the anteriormost teeth oblique to the longer axis of the dentary, anteriorly. 2 = longer axis of the anteriormost teeth nearly at the same axis of the dentary, forwardly projected.

Character 97 - (ci = 0.50; ri = 0.88). Dentary teeth, aligned (Ch. 61 modified from Malabarba 1994): 0 = absent. 1 = present.

Character 98 - (ci = 0.20; ri = 0.80). Dentary, teeth, base (Ch. 61 modified from Malabarba 1994): 0 = spaced. 1 = juxtaposed.

Cynopotamus kincaidi has both spaced and juxtaposed teeth in the dentary, and for this species, this character is coded as polymorphic.

Character 99 - (ci = 0.25; ri = 0.00). Dentary teeth, spacement (Ch. 147 modified from Mirande, 2010): 0 = smaller than tooth base width. 1 = equal or bigger than tooth base width.

This character is coded as polymorphic to *Cynopotamus kincaidi* and inapplicable to species with juxtaposed teeth.

Character 100 - (ci = 0.16; ri = 0.28). Dentary teeth, in the anteromedial toothed portion, number (Ch. 63 modified from Malabarba 1994; Ch. 59 Malabarba, 1998; Ch. 73 modified from Bührnheim, 2006): 0 = at most 6. 1 = at least 6.

Character 101 - (ci = 0.14; ri = 0.14). Dentary teeth, cusps, number (Ch. 56 modified from Malabarba, 1998; Ch. 3 modified from Weitzman & Malabarba, 1999; Ch. 70 modified from Bührnheim, 2006): 0 = multicuspid. 1 = conical teeth.

Character 102 - (ci = 0.50; ri = 0.75). Dentary teeth, cusps, shape: 0 = pointed. 1 = rounded. 2 = nearly squared.

It is possible to distinguish three different dentary tooth cusp shape among the examined species. Most of them present pointed cusps, while rounded cusp is only found in the *Pseudocheirodon* species. The presence of squared-shaped cusps in the dentary teeth is restricted to *Acinocheirodon melanogramma*, *Aphyocheirodon hemigrammus*, *Cheirodontops geayi*, *Holoshesthes pequirá*, three new species of *Holoshesthes*, and *Rhoadsia altipinna*.

Character 103 - (ci = 0.50; ri = 0.72). Dentary teeth, cusps, relative size (Ch. 67 modified from Malabarba 1994; Ch. 58 modified from Malabarba, 1998; Ch. 72 modified from Bührnheim, 2006): 0 = cusps decreasing in size from the medial to the lateral ones. 1 = 3 medial cusps larger nearly equal in size. 2 = 5 medial cusps larger, nearly equal in size. 3 = 7 central cusps larger, nearly equal in size.

This character is coded as inapplicable to *Macropsobrycon uruguayanae*, which have conical teeth in the dentary.

Character 104 - (ci = 0.50; ri = 0.70). Dentary teeth, cusps, arrangement (Ch. 67 modified from Malabarba 1994; Ch. 58 modified from Malabarba, 1998; Ch. 71 modified from Bührnheim, 2006): 0 = not forming a continuous cutting edge. 1 = 3 central cusps aligned in row with other teeth cusps forming a continuous cutting edge. 2 = 5 medial cusps aligned in row with other teeth cusps, forming a continuous cutting edge. 3 = 6-7 medial cusps aligned in row with other teeth cusps, forming a continuous cutting edge.

The cusps of the dentary teeth in the examined species are generally arranged in a half-circle at the distal portion of the tooth, with cusps decreasing in size laterally. However, in some of the examined species, the central cusps of the dentary teeth are slightly

enlarged, with similar size, and aligned to each other. The aligned cusps of each tooth are also aligned with the cusps of the other consecutive teeth, forming a sharp cutting edge. The number of central cusps involved in this arrangement may vary from three to seven.

Character 105 - (ci = 0.14; ri = 0.54). Dentary teeth, cusps, maximum number (Ch. 74 modified from Bührnheim, 2006): 0 = five. 1 = one. 2 = three to four. 3 = seven. 4 = up to nine.

Character 106 - (ci = 0.14; ri = 0.78). Dentary teeth, cusps, contact (Ch. 61 modified from Malabarba 1994): 0 = absent. 1 = present.

SUSPENSORIUM

Character 107 - (ci = 0.50; ri = 0.61). Ectopterygoid, posterior portion, contact with quadrate (Ch. 162 modified from Mirande, 2010): 0 = present. 1 = absent.

The ectopterygoid presents different degrees of posterior extension. In some of the examined species, the posterior end of this bone contacts the anterodorsal portion of the quadrate, extending ventrally along its anterior border (Fig. 18). Notwithstanding, in other species the ectopterygoid does not reach the quadrate posteriorly (Fig. 19).

Character 108 - (autapomorphy). Ectopterygoid, teeth (Ch. 28 modified from Bührnheim, 2006; Ch. 159 modified from Mirande, 2010): 0 = absent. 1 = present.

The presence of teeth in the ectopterygoid is found in *Aphyocheiroduon hemigrammus* only.

Character 109 - (ci = 0.25; ri = 0.25). Mesopterygoid, teeth (Ch. 29 modified from Bührnheim, 2006; Ch. 165 modified from Mirande, 2010): 0 = absent. 1 = present.

Among the examined species, the presence of a small cluster of small teeth in the ventral surface of the mesopterygoid is observed in *Acinocheiroduon melanogramma*,

Holohesthes pequirá, *Odontostilbe* n. sp. b, *Odontostilbe* n. sp. e, and *Odontostilbe* n. sp. p.

Character 110 - (ci = 0.06; ri = 0.31). Quadrate, anteroventral portion, foramen (Ch. 149 modified from Miranda, 2010): 0 = absent (Fig. 19). 1 = present.

In some of the examined species, the articulation condyle of the quadrate with the anguloarticular has a foramen, generally only observed in medial and/or dorsal view (Fig. 18).

Character 111 - (ci = 1.00; ri = 1.00). Metapterygoid, fenestra/foramen (Ch. 31 modified from Bührnheim, 2006; Ch. 168 modified from Miranda, 2010): 0 = present. 1 = absent.

In most of the examined species the metapterygoid presents a foramen on its posterior region for the passage of the *ramus mandibularis* of the trigeminus cranial nerve (V) (Fig. 18). This passage, in some species, is not completely surrounded by the metapterygoid, characterizing a fenestra between the metapterygoid and the hyomandibular. However, in *Amazonspinther* and in the *Spintherobolus* species, the metapterygoid has no foramen or fenestra in that region (state 1) (Fig. 19).

Character 112 - (ci = 0.05; ri = 0.42). Hyomandibular, posterordorsal projection: 0 = absent (Fig. 19). 1 = present.

The hyomandibular of some of the examined species presents a small process at its posterodorsal border, sometimes reaching the anterodorsal border of the opercle (state 1) (Fig. 18).

OPERCULAR APPARATUS

Character 113 - (ci = 1.00; ri = 1.00). Preopercle, laterosensory system canal (Ch. 107, modified Zanata & Vari, 2005; Ch. 27 modified from Bührnheim, 2006): 0 = present. 1 = absent.

The preopercle bears a canal of the laterosensory system canal that continues anteriorly through its horizontal arm to the anguloarticular and dentary, and dorsally through its vertical arm to the canals at the roof of the neurocranium (Fig. 18). All examined species present the laterosensory canal of the preopercle with the exception of the genera *Amazonspinther* and *Spintherobolus* (Fig. 19).

Character 114 - (ci = 0.05; ri = 0.42). Preopercle, lateral system canal, ascending portion, length (Ch. 107, modified Zanata & Vari, 2005; Ch. 27 modified from Bührnheim, 2006): 0 = long, reaching the anterodorsal corner of opercle (Fig. 18). 1 = short, reaching the posterior articular surface of the hyomandybular condyle.

This character is coded as inapplicable to the species without the lateral system canal of the preopercle, *Amazonspinther* and *Spintherobolus*.

Character 115 - (ci = 0.33; ri = 0.00). Opercle, posterior border, profile (Ch. 48 modified from Benine, 2004; Ch. 24 modified from Bührnheim, 2006): 0 = convex (Fig. 20). 1 = posterodorsal border nearly straight to concave and posteroventral border convex to pointed (Figs. 18-19).

Two different profiles of the posterior border of the opercle are observed among the examined species. *Brycon pesu*, *Cynopotamus kincaidi*, and *Rhoadsia altipinna*, have a opercle with the posterior border convex, resembling a half-circle (state 0), while the remaining species present an opercle straight to concave along the dorsal portion of its posterior border, and convex along the ventral portion (state 1).

Character 116 - (ci = 0.50; ri = 0.88). Opercle, dorsal border, profile (Ch. 47, modified from Benine, 2004; Ch. 25 modified from Bührnheim, 2006): 0 = convex (Fig. 20). 1 = nearly straight (Fig. 18). 2 = deeply concave (Fig. 19).

The dorsal border of the opercle is convex in most of the outgroup species, and nearly straight in most of the analysed species. However, in *Axelrodia lindeae*, *Amazonspinther dalmata*, *Spintherobolus ankoseion*, and *S. broccae*, the dorsal border of the opercle is deeply concave.

Character 117 - (ci = 0.33; ri = 0.60). Subopercle, anterodorsal portion, profile (Ch. 26 modified from Bührnheim, 2006): 0 = protruded, forming a pointed projection. 1 = convex and not protruded.

The anterodorsal border of the subopercle in most of the examined species is dorsally protruded and pointed. The only taxa whose subopercle lacks this projection are *Amazonspinther dalmata*, *Coptobrycon bilineatus*, and the species of *Spintherobolus*.

HYOID ARCH AND BRANCHIOSTEGAL RAYS

Character 118 - (ci = 0.16; ri = 0.54). Anterior ceratohyal, lower border, profile (Ch. 79 modified from Bührnheim, 2006; Ch. 179 modified from Mirande, 2010): 0 = smooth, with one or two slight marked concavities. 1 = with two conspicuous concavities for branchiostegals attachment.

The anterior ceratohyal in most of the examined species presents two ventral notches for the articulation of the branchiostegal rays (state 1). However, the ventral margin of the anterior ceratohyal in some species is smooth, without conspicuous notches, as observed in *Axelrodia lindeae*, *Amazonspinther dalmata*, all the species of *Spintherobolus*, and in the outgroup taxa: *Brycon pesu*, *Bryconops caudomaculatus*, *Charax stenopterus*, *Cyanocharax alburnus*, *Cynopotamus kincaidi*, *Probolodus heterostomus*, and *Rhoadsia altipinna*.

Character 119 - (ci = 0.16; ri = 0.79). Posteriormost branchiostegal ray, ventral border in males, profile (Ch. 77 modified from Bührnheim, 2006): 0 = without concavity. 1 = concave on its anterior portion.

The posteriormost branchiostegal ray in the mature males of some examined species has a concavity at the ventral border on its proximal portion. Particularly, in the species of *Kolpotocheiroduon* and some other compsurin species, this concavity is remarkably deep (Fig. 21). The concavity of the left and right posteriormost branchiostegal rays form a shallow passage connecting the branchial cavity to the exterior on each side of the isthmus, which can be observed in the ventral region of the head on alcohol preserved mature males. On species where it was possible to examine male specimens from

several maturing stages, it was noticed that the more sexually dimorphic the males are, the larger and more developed the concavity is. There is a possibility that the presence of these concavities is correlated to the presence of gill glands on mature males. Although in some species it was observed the presence of the concavity in mature males not bearing a gill gland, it is possible that these structures present different development rates. This character is coded as missing (?) to species without a mature male representative.

Character 120 - (ci = 0.05; ri = 0.52). Branchiostegals rays, posterior border, shape (Ch. 78 modified from Bührnheim, 2006): 0 = smooth, or with few irregular indentations. 1 = at least the two posteriormost branchiostegals rays crenulated at their posterior border.

UROHYAL

Character 121 - (ci = 0.06; ri = 0.54). Urohyal, posteroventral border, notch: 0 = absent. 1 = present.

The urohyal is a tendon bone that articulates anteriorly with the junction between the ventral and dorsal hypohyals, and posteriorly to the *sternohyoideus* muscle. This bone has the shape of an inverted “Y” in cross section, where a median lamella extends posteriorly from its anterior portion, and two lamellae extend laterally from the ventral region of the median lamella. In most species, the posteroventral border of the median lamella is smooth (state 0), but in some other species the posteroventral border has a notch (state 1) (Fig. 22).

BRANCHIAL APPARATUS

Character 122 - (ci = 1.00; ri = 1.00). Basihyal, ventrolateral border, processes (Ch. 80 modified from Bührnheim, 2006): 0 = absent. 1 = present.

The ventrolateral border of the basihyal is smooth in most of the examined species, with the exception of the genus *Spintherobolus*, whose species present a small process along this border.

Character 123 - (autapomorphy). Basihyal, anterior portion, shape: 0 = convex. 1 = concave.

The anterior portion of the basihyal is convex to almost straight in most of the examined species; however in *Compsurini Cuzco n. sp.*, the anterior border of the basihyal is concave.

Character 124 - (autapomorphy). Basibranchial 1, length (Ch. 81 modified from Bührnheim, 2006): 0 = short, falling short at mid-length of hypobranchials 1. 1 = elongate, extending between the hypobranchials 1 along all their length.

The presence of an elongated basibranchial 1 extending posteriorly between the hypobranchials 1 is only found in *Spintherobolus papilliferus*.

Character 125 - (ci = 0.25; ri = 0.40). Basibranchial 4, constitution (Ch. 82 modified from Bührnheim, 2006): 0 = totally cartilaginous. 1 = with a bony plate over it.

Most of the examined species present a bony plate ossified over the basibranchial 4. However, this plate is missing in some species, like *Axelrodia lindeae*, *Brycon pesu*, *Bryconops caudomaculatus*, *Charax stenopterus*, *Cynopotamus kincaidi*, and *Paracheirodon axelrodi*.

Character 126 - (ci = 0.50; ri = 0.80). Suspensory pharyngeal 2, teeth (Ch. 83 modified from Bührnheim, 2006): 0 = present. 1 = absent.

Most of the examined species present teeth in the suspensory pharyngeal 2; however the suspensorium pharyngeal 2 has no teeth in *Axelrodia lindeae*, *Amazonspinther dalmata*, *Microschemobrycon elongatus*, and in the species of *Spintherobolus*.

Character 127 - (ci = 1.00; ri = 1.00). Suspensory pharyngeal 3, teeth (Ch. 84 modified from Bührnheim, 2006; Ch. 206 modified from Mirande, 2010): 0 = present. 1 = absent.

The suspensory pharyngeal 3 of most of the examined species bears teeth, excepting *Amazonspinther dalmata*, and in the species of *Spintherobolus*.

Gill rakers

Character 128 - (ci = 1.00; ri = 1.00). Gill rakers, first gill arch, lower branch (Ch. 92 modified from Bührnheim, 2006): 0 = present. 1 = absent.

The presence of gill rakers in the first gill arch is the common condition in most of the examined species. This characteristic is only absent in the genera *Amazonspinther* and *Spintherobolus*.

Character 129 - (ci = 0.16; ri = 0.61). Gill raker rows, ceratobranchial 1, number (Ch. 85 modified from Bührnheim, 2006; Ch. 192 modified from Mirande, 2010): 0 = one. 1 = two.

This character is coded as inapplicable to *Amazonspinther* and *Spintherobolus*, which do not have gill rakers in the first gill arch.

Character 130 - (ci = 0.07; ri = 0.47). Gill raker rows, ceratobranchial 2, number (Ch. 85 modified from Bührnheim, 2006; Ch. 193 modified from Mirande, 2010): 0 = one. 1 = two.

This character is coded as inapplicable to *Amazonspinther*, which does not have gill rakers in the second gill arch.

Character 131 - (ci = 1.00; ri = 1.00). Gill rakers, second gill arch, shape (Ch. 91 modified from Bührnheim, 2006; Ch. 197 modified from Mirande, 2010): 0 = elongate and lanceolate. 1 = short and conical.

The presence of short and conical gill rakers in the second gill arch is only found in the species of *Spintherobolus*. This character is coded as inapplicable to *Amazonspinther*, which does not have gill rakers in the second gill arch.

Character 132 - (ci = 0.28; ri = 0.37). Gill rakers, first gill arch, relative size (Ch. 87 modified from Bührnheim, 2006): 0 = gill rakers from upper branch with less than half length than gill rakers from lower branch. 1 = gill rakers from both branches with similar size. 2 = gill rakers from the upper branch with more than half length than gill rakers from the lower branch.

This character is coded as inapplicable to *Amazonspinther* and *Spintherobolus*, which do not have gill rakers in the first gill arch.

Character 133 - (ci = 0.20; ri = 0.33). Gill rakers, first gill arch, upper branch, relative length to the epibranchial width (Ch. 88 modified from Bührnheim, 2006): 0 = equal or smaller. 1 = longer. 2 = twice longer.

This character is coded as inapplicable to *Amazonspinther* and *Spintherobolus*, which do not have gill rakers in the first gill arch.

Character 134 - (autapomorphy). Gill rakers, first gill arch, denticles (Ch. 93 modified from Bührnheim, 2006): 0 = present. 1 = absent.

This character is coded as inapplicable to *Amazonspinther* and *Spintherobolus*, once they do not have gill rakers in the first gill arch.

SUPRANEURALS

Character 135 - (autapomorphy). Supraneurals, fusion (Ch. 13-14, Malabarba, 1994; Ch. 166 modified from Bührnheim, 2006): 0 = absent. 1 = 2nd to 4th supraneurals fused.

In characids, the supraneurals are a series of vertically elongated bones, positioned intramuscularly in the sagittal plane of the predorsal region of the fish body, between the posterior tip of the supraoccipital process and the first dorsal-fin pterygiophore. The number of these elements, as well as the presence of expanded bony lamellae associated to them, may vary among the characids. Among the examined species, these characteristics also varied, but it was also observed a lot of variation intraspecifically so

that they were not assessed herein. However, the fusion of some of these bones is observed in *Odontostilbe paraguayensis* (state 1) (Fig. 23).

DORSAL FIN

Character 136 - (ci = 0.33; ri = 0.60). Branched dorsal-fin rays, number (Ch. 270 modified from Mirande, 2010): 0 = nine. 1 = eight.

The number of branched dorsal-fin rays is not so variable among the characids, and most of the species generally present nine branched rays. Nevertheless, Malabarba & Weitzman (2003) quoted the presence of eighth branched dorsal-fin rays as one of the possible synapomorphies of their clade A group of characids. Among the examined species, the presence of eight branched dorsal-fin rays is observed in the Stevardiinae *Bryconamericus iheringii*, *Cyanocharax alburnus*, *Hemibrycon polyodon*, in the Aphyocharacinae *Aphyocharax nattereri*, *Prionobrama paraguayensis*, and in the Rhoadsiinae *Rhoadsia altipinna*.

Character 137 - (ci = 0.12; ri = 0.61). Second dorsal-fin ray, elongation on males (Ch. 11 modified from Malabarba, 1998; Ch. 102 modified from Bührnheim, 2006): 0 = absent. 1 = present.

This character is coded as missing to *Odontostilbe nareuda*, *Odontostilbe* n. sp. p, and *Prodontocharax alleni*, for not presenting fully mature male representatives.

Dorsal-fin hooks

Character 138 - (ci = 1.00; ri = 1.00). Dorsal fin, hooks on males (Ch. 42 modified from Malabarba 1994; Ch. 138 modified from Bührnheim, 2006): 0 = absent. 1 = present.

The presence of hooks on the dorsal-fin rays is not very common among the characids; however, occasionally, it may be found in fully mature males, associated to the presence of hooks on all the other fins. Herein the presence of hooks on the dorsal-fin rays is only found in *Aphyocharacidium hemigrammus* and *Holoshestes* n. sp. b.

PECTORAL GIRDLE

Character 139 - (ci = 0.66; ri = 0.75). Posttemporal bone, position, relative to the posttemporal fossa (Ch. 94 modified from Bührnheim, 2006; Ch. 252-253 modified from Mirande, 2010): 0 = over posttemporal fossa and partially over the epioccipital. 1 = posterior to the posttemporal fossa and over epioccipital. 2 = posterior to the posttemporal fossa, and over only the dorsal portion of the epioccipital.

On most of the examined species, the posttemporal lies over the posttemporal fossa and partially over the epioccipital (state 0) (Fig. 24a). In the species of the genus *Spintherobolus*, the posttemporal bone is placed posteriorly to the posttemporal fossa, but still over the epioccipital (state 1) (Fig. 24b), differently from *Charax stenopterus*, *Cynopotamus kincaidi*, and *Paracheirodon axelrodi*, where the posttemporal only covers the dorsal portion of the epioccipital (state 2) (Fig. 24c).

Character 140 - (ci = 1.00; ri = 1.00). Supracleithrum, laterosensory canal (Ch. 161 Zanata & Vari, 2005; Ch. 95 modified from Bührnheim, 2006): 0 = present. 1 = absent.

In most of the examined species, the supracleithrum bears the laterosensory canal, connecting the posttemporal canal to the lateral line canal. However, this condition is absent in the species of *Spintherobolus*.

Character 141 - (ci = 0.50; ri = 0.00). Postcleithrum 1 (Ch. 96 modified from Bührnheim, 2006; Ch. 247 modified from Mirande, 2010): 0 = present. 1 = absent.

The absence of the postcleithrum 1 is exclusive to *Amazonspinther dalmata* and *Spintherobolus papilliferus*.

Character 142 - (ci = 0.11; ri = 0.69). Postcleithrum 1, shape (Ch. 96 modified from Bührnheim, 2006): 0 = round, expanded posteriorly (Fig. 25a). 1 = slender, not expanded posteriorly (Fig. 25b).

Character 143 - (ci = 0.50; ri = 0.75). Postcleithrum 3 (Ch. 134 modified from Zanata & Vari, 2005; Ch. 97 modified from Bührnheim, 2006; Ch. 249 modified from Mirande, 2010): 0 = present. 1 = absent.

The postcleithrum 3 is present in most of the examined species, but absent in *Amazonspinther*, *Spintherobolus*, and *Prionobrama paraguayensis*.

Character 144 - (ci = 0.25; ri = 0.57). Postcleithrum 3, shape (Ch. 135 Zanata & Vari, 2005; Ch. 98 modified from Bührnheim, 2006; Ch. 250 of Mirande, 2010): 0 = without lamella. 1 = with posterior lamella.

This character is coded as inapplicable to *Amazonspinther*, *Spintherobolus*, and *Prionobrama paraguayensis*, which do not have the postcleithrum 3.

Character 145 - (ci = 0.33; ri = 0.60). Cleithrum-coracoid, interosseous space, size: 0 = longitudinal diameter larger than the just posterior length of the cleithrum-coracoid articulation. 1 = longitudinal diameter smaller than the just posterior length of the cleithrum-coracoid articulation. 2 = reduced to a pore.

This character is coded as inapplicable to *Amazonspinther* and *Spintherobolus*, which do not have the interosseous space.

Character 146 - (ci = 1.00; ri = 1.00). Coracoid, overall shape (Ch. 13 Malabarba, 1998; Ch. 26 Weitzman & Malabarba, 1999; Ch. 101 modified from Bührnheim, 2006; Ch. 26 modified from Bührnheim *et al.*, 2008): 0 = elongate. 1 = reduced, nearly discoid.

The presence of a reduced coracoid is found only in *Amazonspinther dalmata* and in the species of *Spintherobolus* (Fig. 26b).

Character 147 - (ci = 0.14; ri = 0.50). Coracoid, posteroventral border, shape (Ch. 100 modified from Bührnheim, 2006): 0 = large and pointed. 1 = posterior and ventral borders nearly forming an angle of 90° or slight extended, forming a small point or a truncate corner (Fig. 26a).

Character 148 - (ci = 0.33; ri = 0.00). Pectoral fin, unbranched ray, elongation on males. 0 = absent. 1 = present.

The mature males of a few species herein examined presented the unbranched pectoral-fin ray elongated, which is the case of *Holoshesthes* n. sp. p, “*Odontostilbe*” *mitoptera*, and *Odontostilbe pao*.

PELVIC FIN

Character 149 - (ci = 0.10; ri = 0.67). Pelvic bone, more developed on mature males: 0 = absent. 1 = present.

The mature males of some examined species, characterized by the presence of hooks on fins and/or elongation of rays, also presented the pelvic bones more robust and enlarged than on females. This character is coded as missing to species without cleared and stained representatives from both sex for comparison.

Character 150 - (ci = 0.12; ri = 0.63). Pelvic fin, unbranched ray, elongation on males (Ch. 20 modified from Malabarba 1994; Ch. 15 modified from Malabarba, 1998; Ch. 103 modified from Bührnheim, 2006; Ch. 257 modified from Mirande, 2010): 0 = absent. 1 = present.

This character is coded as missing to *Odontostilbe nareuda*, *Odontostilbe* n. sp. p, and *Prodontocharax alleni*, for not presenting fully mature male representatives.

Pelvic-fin hooks

Character 151 - (ci = 1.00; ri = 1.00). Pelvic fin, hooks on females (Ch. 57 modified from Malabarba 1994; Ch. 16 of Malabarba, 1998; Ch. 139 modified from Bührnheim, 2006): 0 = absent. 1 = present.

The presence of hooks is usually restrict to the mature males of the characids. However, the presence of pelvic-fin hooks is commonly found in mature females of the species of *Cheirodon*.

ANAL FIN

Character 152 - (ci = 0.20; ri = 0.20). Anal fin, anterior rays, length (Ch. 26 modified from Malabarba 1994): 0 = distal tip of anterior rays not surpassing distal tips of last anal-fin rays. 1 = distal tip of anterior rays surpassing the end of the last anal-fin rays.

The anal-fin base of *Amazonspinther dalmata*, *Cheirodon pisciculus*, *C. kiliani*, *Coptobrycon bilineatus*, *Leptobrycon jatuaranae*, and *Spintherobolus papilliferus*, is the shortest among the examined species. In these species, the distal tip of anterior rays surpasses the end of the last anal-fin rays (state 1), while in the remaining examined species the distal tip of the anterior rays does not reach the distal tips of posteriormost anal-fin rays.

Character 153 - (ci = 0.33; ri = 0.00). Anal fin, last unbranched ray, filament-like on mature males: 0 = absent. 1 = present.

The last unbranched ray elongated into a filament is only present in *Holoshesthes* n. sp. p, *Prionobrama paraguayensis*, and *Rhoadsia altipinna*.

Character 154 - (ci = 0.20; ri = 0.63). Anal fin, rays, longer on mature males than on females (Ch. 25 modified from Malabarba 1994; Ch. 20 modified from Malabarba, 1998; Ch. 112 modified from Bührnheim, 2006): 0 = only hook bearing rays slightly longer on males than on females. 1 = all fin rays longer on males than on females.

This character is coded as missing to *Amazonspinther*.

Character 155 - (ci = 0.50; ri = 0.00). Anal fin, anterior rays, elongation on mature males (Ch. 25 modified from Malabarba 1994; Ch. 20 modified from Malabarba, 1998; Ch. 112 modified from Bührnheim, 2006): 0 = all hook bearing rays. 1 = only the last unbranched and first branched rays longer on males than the same rays on females.

In *Nanocheirodon insignis* and *Rhoadsia altipinna*, only the last unbranched and first branched anal-fin rays are longer on males than on females, while in the remaining

examined species, all hook bearing rays are at least slightly longer. This character is coded as missing to *Amazonspinther* and *Prodontocharax alleni*.

Character 156 - (ci = 0.25; ri = 0.57). Anal fin, posterior branched rays, size on mature males. 0 = with same size or smaller than median branched rays. 1 = elongated, longer than median branched rays.

In most of the examined species the anal-fin rays decrease in length posteriorly; thus the last anal-fin rays have the same length or are smaller than the median anal-fin rays. In some of the examined species, the last branched anal-fin rays are elongated, much longer than the median anal-fin rays (Fig. 27). This character is coded as missing to *Amazonspinther*.

Character 157 - (ci = 0.50; ri = 0.95). Anal fin, ray segments, fusion on mature males (Ch. 23 modified from Malabarba 1994; Ch. 18 Malabarba, 1998; Ch. 11 Weitzman & Malabarba, 1999; Ch. 110 modified from Bührnheim, 2006; Ch. 11 modified from Bührnheim *et al.*, 2008): 0 = absent. 1 = present, fused according to males sexual development.

In a small group of cheirodontines the anterior anal-fin rays bearing hooks are hypertrophied on mature males. In some cases, the segments of the anal-fin rays fuse to each other, starting on the proximal region of the rays and progressing distally accordant to the maturation of the specimen (Fig. 28). This character is coded as missing to *Amazonspinther*.

Character 158 - (ci = 0.50; ri = 0.95). Anal fin, ray segments, hypertrophied on mature males (Ch. 22 modified from Malabarba 1994; Ch. 17 Malabarba, 1998; Ch. 10 Weitzman & Malabarba, 1999; Ch. 109 modified from Bührnheim, 2006; Ch. 10 modified from Bührnheim *et al.*, 2008): 0 = absent. 1 = present (Figs. 28, 29, 30).

The mature males of some of the examined species have the anterior anal-fin rays bearing hooks hypertrophied. This character is coded as missing to *Amazonspinther*.

Character 159 - (ci = 0.50; ri = 0.95). Anal fin, hypertrophied ray segments, shape (Ch. 22 modified from Malabarba, 1994; Ch. 17 Malabarba, 1998; Ch. 10 Weitzman & Malabarba, 1999; Ch. 109 modified from Bührnheim, 2006; Ch. 10 modified from Bührnheim *et al.*, 2008): 0 = nearly cylindrical, rod-shaped. 1 = slab-shaped, expanded in the sagittal plane (Figs. 28, 30).

This character is coded as missing to *Amazonspinther*.

Character 160 - (ci = 0.33; ri = 0.00). Anal fin, slab-shaped ray segments, dimension (Ch. 22 modified from Malabarba 1994; Ch. 17 Malabarba, 1998; Ch. 10 Weitzman & Malabarba, 1999; Ch. 109 modified from Bührnheim, 2006): 0 = as wide as deep. 1 = much wider than deep (Fig. 28).

This character is coded as missing to *Amazonspinther* and as inapplicable to species without slab-shaped anal-fin rays.

Character 161 - (ci = 0.50; ri = 0.75). Anal fin, slab-shaped rays, number (Ch. 22 modified from Malabarba 1994; Ch. 17 modified from Malabarba, 1998; Ch. 10 modified from Weitzman & Malabarba, 1999; Ch. 109 modified from Bührnheim, 2006): 0 = 4-5 branched rays. 1 = more than 6.

This character is coded as missing to *Amazonspinther* and as inapplicable to species without slab-shaped anal-fin rays.

Character 162 - (ci = 1.00; ri = 1.00). Anal fin, rays, chevron-shaped segments on mature males (Ch. 32 modified from Weitzman & Malabarba, 1999; Ch. 32 modified from Bührnheim *et al.*, 2008): 0 = absent. 1 = present, proximal portion and posterior branch of 2nd to 5th anal-fin branched rays thickened and with an asymmetrical chevron-shaped segments in lateral view (Fig. 30).

Among the examined species the presence of thickened branched anal-fin rays with an asymmetrical chevron-shaped segments is shared only by *Spintherobolus ankoseion* and *S. broccae*. This character is coded as missing to *Amazonspinther*.

Character 163 - (ci = 0.50; ri = 0.95). Anal fin, anterior rays, base of most proximal lepidotrichia, anterior expansion on mature males (Ch. 24 Malabarba 1994; Ch. 19 modified from Malabarba, 1998; Ch. 12 Weitzman & Malabarba, 1999; Ch. 111 modified from Bührnheim, 2006; Ch. 12 modified from Bührnheim *et al.*, 2008): 0 = absent. 1 = present (Figs. 28, 29, 30).

The anterior anal-fin rays of mature males in some of the examined species have a bony expansion anteriorly directed on their proximal portion. This expansion is the attachment site of the ligament that connects the anterior surface of each anal-fin ray with the posterior surface of the next anterior ray. Although the ligament is present in all the characids herein examined, the expansion of its attachment site is restrict to some species. This character is coded as missing to *Amazonspinther*.

Character 164 - (ci = 0.50; ri = 0.87). Anal fin, anterior rays, base of most proximal lepidotrichia, anterior expansion, size on mature males (Ch. 24 Malabarba 1994; Ch. 19 modified from Malabarba, 1998; Ch. 12 Weitzman & Malabarba, 1999; Ch. 111 modified from Bührnheim, 2006): 0 = not reaching the posterior border of the anterior ray lepidotrichia (Fig. 29). 1 = extending between the lepidotrichia base of the anterior ray (Figs. 28, 30).

This character is coded as missing to *Amazonspinther* and inapplicable to species without the anterior expansion in the base of most proximal anal-fin rays lepidotrichia.

Character 165 - (ci = 1.00; ri = 1.00). Anal fin, rays, ligament between most proximal lepidotrichia, size on mature males (Ch. 86 modified from Malabarba 1994; Ch. 21 Malabarba, 1998; Ch. 113 modified from Bührnheim, 2006): 0 = small. 1 = large, as wide as ray width; connecting the midlength of the posterior face of the anterior lepidotrichia to the proximal anterior portion of the just posterior lepidotrichia.

Although the enlargement of the ligament seems to be correlated with the bony expansion of the ligament attachment site on the anterior surface of the anal-fin rays, these features are treated in different characters because in *Spintherobolus papilliferus* the ligament is enlarged, but the rays lack the anterior bony expansion. This character is coded as missing to *Amazonspinther*.

Character 166 - (autapomorphy). Anal fin, proximal radials, expansion in the coronal plane on mature males (Ch. 107 modified from Bührnheim, 2006): 0 = absent. 1 = present, with laminar expansion more evident in mid portion of the proximal radials.

The most proximal anal-fin radials on the examined species can present anterior and posterior bony lamellae, generally in the ventral portion of the main body of the proximal radial. However, *Axelrodia lindeae* also has small flat lateral expansions in the sagittal plane of the 2nd to 6th or 7th anal-fin proximal radials, evidenced only on mature males.

Character 167 - (autapomorphy). Anal fin, rays, anteriormost proximal radial (Ch. 108 modified from Bührnheim, 2006; Ch. 44 modified from Bührnheim *et al.*, 2008): 0 = with a short anterior lamina, not entering abdominal cavity. 1 = with an anterior lamina slightly entering the abdominal cavity, between distal portions of the 12th-14th pleural ribs.

Amazonspinther dalmata is the only examined species whose anterior lamina of the first anal-fin proximal radial penetrates the abdominal cavity. On the remaining examined species this lamina marginates posteriorly the abdominal cavity, but does not reach the line of the ribs.

Character 168 - ($ci = 0.33$; $ri = 0.95$). Anal fin, interradial membrane, hypertrophied whitish tissue, on mature males (Ch. 42 modified from Malabarba 1994; Ch. 138 modified from Bührnheim, 2006): 0 = slightly developed, not entirely covering the hooks. 1 = deeply developed, entirely covering the hooks.

The presence of hypertrophied whitish tissue associated to anal-fin hooks is often seen among the characids (Weitzman *et al.*, 2005; Lima & Sousa, 2009). It is observed in several degrees of development among the examined species, and among the cheirodontine species with available male specimens in several maturing stages, it was noticed that the development of the whitish tissue occurs in accordance with the anal-fin hooks formation. In some examined species the whitish tissue surrounding the anal-fin hooks is much more developed, and covers entirely the hooks (state 1). This character is

coded as missing and inapplicable to species without mature male representative and species without anal-fin hooks, respectively.

Anal-fin hooks

Character 169 - (ci = 0.33; ri = 0.33). Anal fin, hooks, on mature males (Ch. 42 modified from Malabarba 1994; Ch. 138 modified from Bührnheim, 2006): 0 = present. 1 = absent.

This character is coded as missing to species without mature male representative.

Character 170 - (ci = 0.33; ri = 0.66). Anal fin, hooks, distribution (Ch. 49 and 51 modified from Malabarba 1994; Ch. 28 and 30 modified from Malabarba, 1998; Ch. 143, 144 and 148 modified from Bührnheim, 2006): 0 = hooks larger and more numerous on the anterior portion and progressively reducing to the posterior anal-fin rays. 1 = more numerous in both anterior and posterior portions of the anal fin, reduced in the middle portion of the anal fin. 2 = restricted to the i+4 to 5 anal-fin rays.

The distribution of the hooks among the anal-fin rays varies in the examined species. In most of the examined species the hooks are larger and more numerous in the anterior anal-fin rays, and progressively reduce in number and size posteriorly (state 0). Some compsurin species have larger and more numerous hooks in the anterior and posterior anal-fin rays, while they are reduced and less numerous in the intermediary rays (state 1). A third pattern of hooks distribution is also found in some other compsurin species, which present hooks restricted to the last unbranched and first five branched anal-fin rays (state 2). Differently from the condition presented in the state 0, herein the number and size of the hooks is homogeneous among the anal-fin rays bearing hooks. This character is coded as missing and inapplicable to species without mature male representative and species without anal-fin hooks, respectively.

Character 171 - (autapomorphy). Anal fin, first branched ray, hooks on males (Ch. 46 modified from Malabarba 1994; Ch. 23 Malabarba, 1998; Ch. 141 modified from Bührnheim, 2006): 0 = present. 1 = absent.

Among the species bearing anal-fin hooks, the absence of hooks in the first branched anal-fin ray is only present in *Nanocheiroidon insignis*. This character is coded as missing and inapplicable to species without mature male representative and species without anal-fin hooks, respectively.

Character 172 - (ci = 0.16; ri = 0.37). Anal fin, last unbranched ray, hooks (46 modified from Malabarba 1994; Ch. 23 Malabarba, 1998; Ch. 141 modified from Bührnheim, 2006): 0 = present. 1 = absent or reduced in number (1-3 hooks).

This character is coded as missing and inapplicable to species without mature male representative and species without anal-fin hooks, respectively.

Character 173 - (ci = 0.50; ri = 0.86). Anal fin, hooks, shape (Ch. 146 and 149 modified from Bührnheim, 2006): 0 = posterodorsally directed. 1 = dorsally directed. 2 = anteriorly directed, curved over the lateral surface of the anal-fin ray.

Three different shapes of the bony hooks from the anal-fin rays is present among the examined species. The anal-fin hooks curved and posterodorsally directed, is the most broadly distributed state found in the examined species (state 0) (Figs. 28, 29, 32). Among the Compsurini species two other bony hook shapes are present, hooks dorsally directed, almost parallel to the main body of the ray (state 1), and hooks anteriorly directed, bent laterally over the lateral surface of the rays (state 2) (Fig. 31). This character is coded as missing and inapplicable to species without mature male representative and species without anal-fin hooks, respectively.

Character 174 - (ci = 0.08; ri = 0.70). Anal fin, rays, hooks distribution along rays' length. (Ch. 47 and 48 modified from Malabarba, 1994; Ch. 27 Malabarba, 1998; Ch. 147 modified from Bührnheim, 2006): 0 = concentrated along the middle-length of the rays, with reduced number on the most proximal and most distal portions. 1 = concentrated along distal half or third portions of the rays.

This character is coded as missing and inapplicable to species without mature male representative and species without anal-fin hooks, respectively.

Character 175 - (ci = 0.50; ri = 0.90). Anal fin, most anterior branched ray, number of hooks per segment (Ch. 45 modified from Malabarba 1994; Ch. 22 modified from Malabarba, 1998; Ch. 140 modified from Bührnheim, 2006; Ch. 13 modified from Bührnheim *et al.*, 2008): 0 = 1-2 hooks (rarely 3). 1 = 2-3 hooks (usually 3). 2 = 3-5 hooks (usually 5).

The number of bony hooks per anal-fin ray segment varies from one to five among the examined species. In order to standardize the comparison of the number of hooks per anal-fin ray segment among the examined species, only the hooks of the first branched anal-fin rays were counted and used for comparison; except in *Nanocheirodon insignis*, which does not have hooks on the first branched anal-fin ray, in this case the second branched ray was used instead of the first. This character is coded as missing and inapplicable to species without mature male representative and species without anal-fin hooks, respectively.

Character 176 - (ci = 1.00; ri = 1.00). Anal fin, hooks, bilaterally symmetrical (Ch. 52 modified from Malabarba 1994; Ch. 25 Malabarba, 1998; Ch. 145 modified from Bührnheim, 2006): 0 = present, paired and bilaterally symmetrical (Figs. 31, 32). 1 = absent, bilaterally asymmetrical, with irregular arrangements, unpaired, and differing in number and position between contralateral segments of the lepidotrichia (Figs. 28, 29).

The anal-fin bony hooks are paired and bilaterally symmetrical with the contralateral lepidotrichia in most of the examined species. However the mature males of some representatives of Cheirodontini have asymmetrical bony hooks on the anal-fin rays. This character is coded as missing and inapplicable to species without mature male representative and species without anal-fin hooks, respectively.

ADIPOSE FIN

Character 177 - (ci = 0.50; ri = 0.66). Adipose fin (Ch. 28 modified from Malabarba 1994; Ch. 12 Malabarba, 1998; Ch. 17 Weitzman & Malabarba, 1999; Ch. 105 modified from Bührnheim, 2006; Ch. 17 modified from Bührnheim *et al.*, 2008; Ch. 356 modified from Mirande, 2010): 0 = present. 1 = absent.

Most of the examined species has an adipose fin. The absence of the adipose fin is only observed in the species of *Spintherobolus* and in *Coptobrycon bilineatus*.

CAUDAL VERTEBRAE AND CAUDAL FIN

Character 178 - (ci = 0.20; ri = 0.88). Caudal vertebrae, hemal spines, contact with procurrent caudal-fin rays (Ch. 17 and 18 modified from Malabarba 1994; Ch. 32 Malabarba, 1998; Ch. 9 Weitzman & Malabarba, 1999; Ch. 116 modified from Bührnheim, 2006; Ch. 9 modified from Bührnheim *et al.*, 2008): 0 = hemal spines of preural vertebrae 2, 3 and sometimes 4, articulating with the procurrent caudal-fin rays. 1 = hemal spines of preural vertebrae 2 to 5 contacting the procurrent caudal-fin rays.

Although the presence of the hemal spines from the preural centrum 5 (PU5 or fourth vertebra anterior to the compound centrum PU1+U1) contacting the ventral procurrent caudal-fin rays seems to be correlated to the presence of a higher number of ventral procurrent caudal-fin rays (Ch. 190), some species present this condition even with a lower number of ventral procurrent caudal-fin rays.

Character 179 - (ci = 1.00; ri = 1.00). Caudal vertebrae, hemal spines, shape, on mature males (Ch. 33 Malabarba, 1998; Ch. 117 modified from Bührnheim, 2006): 0 = distal portion of the preural vertebrae 4 to 5 hemal spines narrowing distally. 1 = distal portion of the preural vertebrae 4 to 5 hemal spines slab-shaped on mature males.

This character is coded as missing in *Amazonspinther* and *Spintherobolus papilliferus*.

CAUDAL-FIN PRINCIPAL RAYS

Character 180 - (ci = 1.00; ri = 1.00). Caudal fin, sexual dimorphism: 0 = absent. 1 = present.

The presence of a caudal fin sexually dimorphic is not very common among the characids; however, it is present and well known in some monophyletic groups. The sexual dimorphism in the caudal fin is very remarkable in some Stevardiinae species, formerly known as the Glandulocaudinae (*sensu* Weitzman & Menezes, 1998), whose

mature males can present modification in the shape and development of the caudal-fin rays, in the size, number and shape of the caudal scales, and hypertrophy of soft tissue with putative function of secreting pheromone (Weitzman & Fink, 1985; Weitzman & Menezes, 1998). Regardless some Stevardiinae, the only characid species with mature males bearing sexually dimorphic caudal fin are found in the Compsurini. Although in some cases the compsurin species may show sexual dimorphism related to different structures of the caudal fin, *e.g.* hooks, scales, and/or hypertrophy of soft tissue, the homology of the sexual dimorphism in the tribe is herein tested when treated in a single character concerning all sexually dimorphic features.

Character 181 - (ci = 1.00; ri = 1.00). Caudal fin, principal rays 14 and 15, spaced on mature males (Ch. 30 modified from Malabarba 1994; Ch. 35 modified from Malabarba, 1998; Ch. 119 modified from Bührnheim, 2006): 0 = absent, not different between males and females. 1 = present, spacement between 14 and 15 caudal-fin rays larger on males than on females.

On most of the examined species, the principal caudal-fin rays from the upper and lower lobes are equally spaced. However, the mature males of *Acinocheiroduon* and *Macropsobrycon* have larger spacement between the caudal-fin rays 14 and 15 than the remaining examined species.

Character 182 - (ci = 1.00; ri = 1.00). Caudal fin, principal rays 12 and 13, ventrally curved on mature males (Ch. 35 modified from Malabarba, 1998; Ch. 119 modified from Bührnheim, 2006): 0 = absent. 1 = present.

Among the examined species, the presence of the 12th and 13th caudal-fin rays ventrally curved is only observed in the species of *Saccoderma*.

Character 183 - (ci = 0.50; ri = 0.00). Caudal fin, rays, thickening on mature males (Ch. 29 modified from Malabarba 1994; Ch. 34 Malabarba, 1998; Ch. 118 modified from Bührnheim, 2006): 0 = absent. 1 = present, on hook bearing rays (Fig. 33).

The principal caudal-fin rays bearing hooks in the compsurin fishes are in general slightly thicker and more spaced than the remaining rays of the caudal fin and the

correspondent rays on the females caudal fin. However, in *Acinocheirodon melanogramma* and *Compsurini Purus* n. sp., the caudal rays bearing larger hooks are remarkably expanded on the sagittal plane.

Caudal-fin hooks

Character 184 - (ci = 0.20; ri = 0.55). Caudal fin, lower lobe, hooks (Ch. 41 modified from Malabarba, 1998; Ch. 152 modified from Bührnheim, 2006; Ch. 312 modified from Mirande, 2010): 0 = absent. 1 = present (Figs. 33, 34).

The presence of bony hooks on the caudal-fin rays is only found among the *compsurini* species.

Character 185 - (ci = 1.00; ri = 1.00). Caudal fin, upper lobe, hooks: 0 = absent. 1 = present.

Most of the examined species bearing bony hooks on the caudal fin has them restrictly distributed on the lower lobe caudal-fin rays. The only species bearing hooks on the rays from the upper caudal-fin lobe are *Compsurini Leticia* n. sp. and *Compsurini Yurimaguas* n. sp.

Character 186 - (ci = 1.00; ri = 1.00). Caudal fin, middle rays, large hooks, posteriorly placed: 0 = absent. 1 = present (Figs. 33, 34).

The caudal-fin bony hooks on most of the examined species are relatively small and distributed along most of the caudal rays length. Nevertheless, in *Acinocheirodon melanogramma*, *Macropsobrycon uruguayanae*, and *Compsurini Purus* n. sp., the caudal-fin rays bear large hooks restricted to their most distal portion (state 1). This character is coded as inapplicable to species without hooks on the caudal-fin rays.

Character 187 - (ci = 0.50; ri = 0.00). Caudal fin, hooks, shape (Ch. 56 modified from Malabarba 1994; Ch. 39, Malabarba, 1998; Ch. 150 modified from Bührnheim, 2006): 0 = curved. 1 = straight.

Among the species bearing bony hooks in the caudal fin, two different bony hook shapes can be distinguished, the anteriorly curved and the straight bony hooks. The straight bony hooks are only found in the compsurin species *Acinocheiroduon melanogramma* and Compsurini Purus n. sp.. This character is coded as inapplicable to species without hooks on the caudal-fin rays.

Character 188 - (ci = 1.00; ri = 1.00). Caudal fin, hooks, emerging direction: 0 = dorsally. 1 = laterally.

The bony hooks on the caudal-fin rays of most of the examined species are placed over the dorsal surface of the caudal-fin rays, with their main axis emerging dorsolaterally to the ray. However, although the caudal bony hooks of Compsurini Leticia n. sp., Compsurini Napo n. sp., and Compsurini Yurimaguas n. sp. are also placed over the dorsal surface of the caudal rays, they emerge laterally. This character is coded as inapplicable to species without hooks on the caudal-fin rays.

Character 189 - (autapomorphy). Caudal fin, spinelets, on mature males (Ch. 40 Malabarba, 1998; Ch. 151 modified from Bührnheim, 2006): 0 = absent. 1 = present.

Among the examined species, the presence of small and flexible spines along the proximal portion of the lower lobe caudal-fin rays, is only found in *Macropsobrycon uruguayanae* (Fig. 34). These small and flexible spines were called “spinelets” by Malabarba (1998), who quoted these structures as autapomorphic for *Macropsobrycon*. This character is coded as inapplicable to species without hooks on the caudal-fin rays.

PROCURRENT CAUDAL-FIN RAYS

Character 190 - (ci = 0.50; ri = 0.93). Procurrent caudal-fin rays, ventral elements, number on males (Ch. 42 Malabarba, 1998; Ch. 5 modified by Weitzman & Malabarba, 1999; Ch. 124 modified from Bührnheim, 2006; Ch. 5 modified from Bührnheim *et al.*, 2008; Ch. 302 modified from Mirande, 2010): 0 = 5 to 11 ventral elements. 1 = 11 to 16 ventral elements (Fig. 36a, c-f). 2 = 16 to 30 ventral elements (Figs. 35, 36b).

The number of ventral procurrent caudal-fin rays varies among the examined species in a range from five up to thirty elements. Malabarba (1998: 205-207) considered the higher number of ventral procurrent rays (11 to 28 elements) a synapomorphy of Cheirodontini, and found two derived states related to the number of ventral procurrent rays inside the tribe; with *Heterocheirodon*, *Serrapinnus*, *Spintherobolus*, and New Genus and Species C presenting 11 to 16 elements, and *Cheirodon* and *Nanocheirodon* presenting 16 to 28 elements. Although bearing 16 to 19 ventral procurrent rays, the New Genus and Species C was assigned for the state 1 in the analyses of Malabarba (1998) and Bührnheim (2006). The authors took this decision based on the morphology of the ventral elements, which is distinct of the ventral elements of *Cheirodon* and *Nanocheirodon*, and more similar to the elements of *Heterocheirodon*, *Serrapinnus* and *Spintherobolus*. Herein, New Genus and Species C and B are assigned to the state 2 according to the number of ventral procurrent elements, and the shape and morphology of these elements treated in other characters.

Character 191 - (ci = 0.50; ri = 0.88). Procurrent caudal-fin rays, ventral elements number, related to dorsal elements (Ch. 42 Malabarba, 1998; Ch. 5 modified by Weitzman & Malabarba, 1999; Ch. 124 modified from Bührnheim, 2006): 0 = as many as dorsal elements. 1 = more ventral than dorsal elements, ranges never overlapping.

Most of the examined species present a similar number of ventral and dorsal procurrent caudal-fin rays. Notwithstanding, this condition is not found in the species of the genus *Cheirodon*, *Nanocheirodon*, and New Genus and Species C and B, which are coded as presenting the state 1.

Character 192 - (autapomorphy). Procurrent caudal-fin rays, ventral elements, sexual dimorphism in number of elements (Ch. 32 modified from Malabarba 1994; Ch. 43 Malabarba, 1998; Ch. 125 modified from Bührnheim, 2006): 0 = absent. 1 = larger number of ventral elements on males.

Nanocheirodon insignis is the only examined species whose males present a higher number of ventral procurrent caudal-fin rays than the females.

Character 193 - (ci = 0.50; ri = 0.93). Procurrent caudal-fin rays, anteriormost ventral elements, shape on females (Ch. 33 modified from Malabarba 1994; Ch. 44 Malabarba, 1998; Ch. 7 Weitzman & Malabarba, 1999; Ch. 126 modified from Bührnheim, 2006; Ch. 305 modified from Mirande, 2010): 0 = "V"-shaped in frontal view, lepidotrichias fused distally. 1 = needle-shaped, lepidotrichia fused along their length, usually remaining a small opening near their distal tips. 2 = laminar-shaped.

The females of most of the examined species have the ventral procurrent rays in the shape of a "V" in frontal view, due to the fusion of the contralateral elements only distally. Nevertheless, female representatives of the tribe Cheirodontini present modified conditions, where the contralateral elements of the ventral procurrent rays can be fused along most of their length (state 1) or along their entire length (state 2), being the latter a condition only found in the species of *Heterocheirodon*.

Character 194 - (ci = 0.33; ri = 0.80). Procurrent caudal-fin rays, ventral elements, distal tip direction on females (Ch. 38 modified from Malabarba 1994; Ch. 7 modified from Weitzman & Malabarba, 1999; Ch. 7 modified from Bührnheim *et al.* 2008): 0 = posteriorly directed, following the main axis of the ray. 1 = anteroventrally bent.

In the species of *Cheirodon*, *Nanocheirodon*, New Genus and Species C and B, and in the fossil representative *Megacheirodon unicus*, the distal tip of the female ventral procurrent rays is anteriorly curved, contrasting with the remaining examined species where the distal tip follows the main axis of the procurrent rays.

Character 195 - (ci = 1.00; ri = 1.00). Procurrent caudal-fin rays, ventral elements, shape on males (Ch. 45 modified from Malabarba, 1998; Ch. 6 Weitzman & Malabarba, 1999; Ch. 127 modified from Bührnheim, 2006; Ch. 6 modified from Bührnheim *et al.* 2008): 0 = "V"-shaped in frontal view, lepidotrichias fused distally. 1 = laminar, lepidotrichia fused along their entire length and becoming progressively laminar with maturation (Figs. 35, 36).

All mature males of the Cheirodontini present the ventral procurrent elements in a laminar shape. This character is coded as missing to *Amazonspinther*, once no mature male was identified.

Character 196 - (ci = 0.66; ri = 0.95). Procurrent caudal-fin rays, anteriormost ventral elements, main axis direction on mature males (Ch. 40 modified from Malabarba 1994; Ch. 49 Malabarba, 1998; Ch. 131 modified from Bührnheim, 2006): 0 = posteroventrally directed (Figs. 35, 36a). 1 = ventrally directed (Figs. 36b-e). 2 = radially arranged, forming a ventral semi-circle (Fig. 36f).

In most of the examined species, the ventral procurrent caudal-fin rays main axis is posteroventrally directed on mature males (state 0). However, some species may also present the main axis of the ventral procurrent rays ventrally directed, in a perpendicular angle to the body longitudinal axis (state 1), or even with the elements radially arranged in a semi-circle (state 2).

Character 197 - (ci = 0.50; ri = 0.88). Procurrent caudal-fin rays, ventral elements, distal tip direction, on mature males (Ch. 48 Malabarba, 1998; Ch. 130 modified from Bührnheim, 2006): 0 = following the ray main axis. 1 = anteriorly angled (Fig. 35).

Character 198 - (ci = 0.50; ri = 0.93). Procurrent caudal-fin rays, anteriormost ventral elements, distal tip shape (Ch. 39 modified from Malabarba 1994; Ch. 53 Malabarba, 1998; Ch. 14 Weitzman & Malabarba, 1999; Ch. 135 modified from Bührnheim, 2006; Ch. 14 modified from Bührnheim *et al.*, 2008): 0 = cylindrical and pointed. 1 = spatulated and rounded (Fig. 36a-d). 2 = spatulated and pointed (Figs. 35, 36e-f).

Character 199 - (ci = 1.00; ri = 1.00). Procurrent caudal-fin rays, anterior ventral elements, hypertrophied on mature males: 0 = absent. 1 = present (Figs. 35, 36).

The mature males of all Cheirodontini have the anterior ventral procurrent rays hypertrophied, enlarged in relation to the same procurrent rays in females and juveniles. This character is coded as missing to *Amazonspinther*.

Character 200 - (ci = 0.33; ri = 0.83). Procurrent caudal-fin rays, anterior ventral elements, lateral laminar expansion, on mature males (Ch. 50 Malabarba, 1998; Ch. 132 modified from Bührnheim, 2006): 0 = absent. 1 = present, between the skin and muscles (Figs. 35, 36c).

The anterior ventral elements in the mature males of some examined species have a wide lateral laminar expansion in the line between the caudal-peduncle muscles and the skin. The laminar expansion of each ventral element contacts the lateral laminae of the consecutive elements, forming a lateral internal ridge on each side of the caudal peduncle. The hypertrophied ventral procurrent rays in the mature males of some other examined species of Cheirodontini, may sometimes present a small lateral projection, but they are not laminar nor constitute a continuous lateral ridge, and are not coded here. This character is coded as missing to *Amazonspinther*.

Character 201 - (ci = 0.25; ri = 0.62). Procurrent caudal-fin rays, anterior ventral elements, fused on mature males (Ch. 52 Malabarba, 1998; Ch. 22 Weitzman & Malabarba, 1999; Ch. 134 modified from Bührnheim, 2006; Ch. 22 modified from Bührnheim *et al.*, 2008): 0 = absent. 1 = present, rays not articulating to the parhypural fused to each other (Fig. 36b-c).

The mature males of most of the examined species have the ventral procurrent rays free, not fused to each other. However, in some of the examined species whose mature males present the ventral procurrent rays hypertrophied, these elements are fused to each other along most of their length, excepting their distal tip. This character is coded as missing to *Amazonspinther* and *Serrapinnus* n. sp. upm.

Character 202 - (ci = 0.50; ri = 0.96). Procurrent caudal-fin rays, anterior ventral elements, distal portion, on mature males (Ch. 47 Malabarba, 1998; Ch. 8 Weitzman & Malabarba, 1999; Ch. 129 modified from Bührnheim, 2006; Ch. 8 modified from Bührnheim *et al.* 2008; Ch. 303 modified from Mirande, 2010): 0 = internal, not visible on the ventral surface of caudal peduncle. 1 = projecting externally through muscles and skin, forming a ventral keel (Figs. 35, 36).

Malabarba (1998) and Bührnheim (2006) found the presence of a ventral keel in the caudal peduncle formed by the hypertrophied ventral procurrent caudal-fin rays as a synapomorphy for Cheirodontini, and absent to the species of *Heterocheirodon*. This character is coded as missing to *Amazonspinther*.

Character 203 - (ci = 1.00; ri = 1.00). Procurrent caudal-fin rays, anterior hypertrophied elements, exposed ventral keel profile (Ch. 36 modified from Malabarba 1994; Ch. 47 Malabarba, 1998; Ch. 8 Weitzman & Malabarba, 1999; Ch. 129 modified from Bührnheim, 2006): 0 = straight. 1 = round (Fig. 36e-f).

The ventral profile of the keel formed by the hypertrophied ventral procurrent rays varies among the species that possess it. On most of the species this keel presents a straight and ascending anteriorly profile; however in some species, the hypertrophied ventral elements form a keel with a round profile. This character is coded as missing to *Amazonspinther* and inapplicable to *Heterocheiroduon* and species without hypertrophied anterior procurrent caudal-fin rays.

Character 204 - (ci = 0.33; ri = 0.84). Procurrent caudal-fin rays, anterior ventral hypertrophied elements, size (Ch. 47 Malabarba, 1998; Ch. 8 Weitzman & Malabarba, 1999; Ch. 129 modified from Bührnheim, 2006): 0 = all elements with similar size. 1 = elements conspicuously decreasing in size anteriorly (Figs. 35, 36c).

This character is coded as missing to *Amazonspinther* and inapplicable to species without hypertrophied anterior procurrent caudal-fin rays.

Character 205 - (ci = 1.00; ri = 1.00). Procurrent caudal-fin rays, anterior ventral elements, reduction of their proximal portion, on mature males (Ch. 51 Malabarba, 1998, Ch. 23 Weitzman & Malabarba, 1999; Ch. 133 modified from Bührnheim, 2006; Ch. 23 modified from Bührnheim *et al.*, 2008): 0 = absent. 1 = present (Fig. 36c).

In some of the examined species, the proximal portion of the anterior ventral procurrent caudal-fin rays is reduced, not rising above area of fusion between them; while the posterior dorsal portions of these rays are fused into a flat compressed plate that inserts between the hemal spine of the antepenultimate vertebra and the hemal spines of the adjacent anterior vertebrae. This character is coded as missing to *Amazonspinther*.

Character 206 - (ci = 1.00; ri = 1.00). Procurrent caudal-fin rays, anterior ventral elements, depth of insertion on mature males (Ch. 51 Malabarba, 1998, Ch. 23 Weitzman & Malabarba, 1999; Ch. 133 modified from Bührnheim, 2006; Ch. 23

modified from Bührnheim *et al.*, 2008): 0 = proximal portion not reaching proximal half of the last vertebrae hemal spines. 1 = proximal portion almost reaching hemal arch of the last vertebrae (Fig. 36e-f).

This character is coded as missing to *Amazonspinther*.

Character 207 - (ci = 0.14; ri = 0.60). Procurrent caudal-fin rays, three posterior ventral elements, hypertrophied on mature males (Ch. 41 modified from Malabarba 1994; Ch. 54 Malabarba, 1998; Ch. 136 modified from Bührnheim, 2006): 0 = absent. 1 = present.

Some examined species presented the distal tips of the posterior two to four ventral procurrent rays expanded in the sagittal plane, forming a small keel in the anterior portion of the caudal-fin ventral profile. This character is coded as missing to *Amazonspinther*.

Character 208 - (autapomorphy). Procurrent caudal-fin rays, three posterior ventral elements, abrupt keel on mature males: 0 = absent. 1 = present.

In *Acinocheiroidon melanogramma*, the three posterior ventral elements are strongly hypertrophied forming an abrupt keel (see fig. 3 from Malabarba & Weitzman, 1999).

SCALES

Character 209 - (ci = 1.00; ri = 1.00). Scales, predorsal region, size (Ch. 71 and Ch. 72 modified from Malabarba 1994; Ch. 325 modified from Mirande, 2010): 0 = scales with the same size as the body scales. 1 = scales reduced in size, living the predorsal region partially naked.

Among the examined species, the presence of scales reduced in size on the predorsal region of the body is only found in *Cheiroidon kiliani* and *C. pisciculus*. On the remaining species the scales from the predorsal region are similar in size to the remaining body scales, and no naked area is evident.

LATEROSENSORY SYSTEM ON BODY

Character 210 - (ci = 0.07; ri = 0.68). Scales, on lateral line, pores (Ch. 70 modified from Malabarba 1994; Ch. 60 Malabarba, 1998; Ch. 153 modified from Bührnheim, 2006; Ch. 91 modified from Mirande, 2010): 0 = completely pored. 1 = incompletely pored.

This character is coded as missing to *Odontostilbe* n. sp. h. and as polymorphic to *Serrapinnus* n. sp. me, which can have both complete or incomplete lateral line.

Character 211 - (ci = 0.33; ri = 0.60). Scales, on incomplete lateral line, number (Ch. 70 modified from Malabarba 1994; Ch. 25 modified from Weitzman & Malabarba, 1999; Ch. 60 Malabarba, 1998; Ch. 153 modified from Bührnheim, 2006; Ch. 25 modified from Bührnheim *et al.*, 2008): 0 = more than six scales. 1 = less than six scales.

The number of pored scales along the lateral line varies a lot among the examined species, even intraspecifically. However, in *Amazonspinther* and in the *Spintherobolus* species, the number of pored scales is never higher than six. The same condition is found in the outgroup species *Charax stenopterus* and *Coptobrycon bilineatus*. This character is coded as inapplicable to species with complete lateral line.

Character 212 - (ci = 0.22; ri = 0.78). Laterosensory canal, extension, between caudal-fin rays (Ch. 125 modified from Zanata, 2000; Ch. 163 modified from Zanata & Vari, 2005; Ch. 114 modified from Bührnheim, 2006; Ch. 92 and 93 modified from Mirande, 2010): 0 = not extended, falling short the caudal-fin base. 1 = extending nearly half-length of the middle caudal-fin rays. 2 = extending beyond the half-length of the middle caudal-fin rays.

Caudal scales

Character 213 - (ci = 0.33; ri = 0.33). Scales, caudal-fin lobes, coverage (Ch. 328 modified from Mirande, 2010): 0 = covering less than one third of the lobes length. 1 = covering more than one third of the lobes length.

On all cheirodontines and most of the examined species, the caudal-fin lobes are restricted covered by scales on their base. In some of the outgroup species, the caudal-fin lobes have more than one third of their length covered by scales, generally by scales that decrease in size posteriorly. It is importante to mention that this condition is present on both males and females, and does not characterize a sexually dimorphic feature. That is the case found in *Aphyodite grammica*, *Hemibrycon polyodon*, *Macropsobrycon xinguensis*, and *Parecbasis cyclolepis*.

Character 214 - (ci = 0.33; ri = 0.77). Scales, caudal fin, lower lobe, modified in shape (Ch. 73 modified from Malabarba 1994; Ch. 61 modified from Malabarba, 1998; Ch. 154 modified from Bührnheim, 2006): 0 = absent (Fig. 37a). 1 = present (Fig. 37b-d).

The presence of scales modified in shape and/or size in relation to the body scales, is a character only observed in some Compsurini among the examines species. This character is coded as missing to Compsurini Yurimaguas n. sp. because the caudal fin is damage on all the examined specimens, and most of them lacks the body scales.

Character 215 - (ci = 0.50; ri = 0.87). Scales, caudal fin, upper lobe, modified in shape (Ch. 73 modified from Malabarba 1994; Ch. 61 modified from Malabarba, 1998; Ch. 154 modified from Bührnheim, 2006): 0 = absent. 1 = present.

On the examined species bearing modified scales on the caudal fin, the presence of modified scales in the upper lobe generally coexists with the presence of modified scales in the lower lobe. The only species where it does not happen is Compsurini Purus n. sp., and for that reason those characters are treated separately. This character is coded as missing to Compsurini Yurimaguas n. sp.

Character 216 - (ci = 1.00; ri = 1.00). Caudal fin, middle rays, scales, reduced in size on mature males (Ch. 74 modified from Malabarba 1994; Ch. 62 Malabarba, 1998; Ch. 155 modified from Bührnheim, 2006): 0 = absent. 1 = present, scales reduced in size over the base of the middle caudal-fin rays (Fig. 37b).

“Odontostilbe” dialeptura and *“Odontostilbe” mitoptera* are the only examined species that present modified scales reduced in size over the middle caudal-fin rays. On the

middle caudal-fin rays of those species, the modified scales are reduced, and longitudinally elongated, generally associated to hypertrophied whitish tissue. On the remaining examined species the scales over the base of the middle caudal-fin rays are not reduced. This character is coded as missing to *Compsurini Yurimaguas n. sp.* and as inapplicable to species without modified caudal-fin scales.

Character 217 - (ci = 1.00; ri = 1.00). Caudal fin, elongated modified scales (Ch. 75 modified from Malabarba 1994; Ch. 63 Malabarba, 1998; Ch. 156 modified from Bührnheim, 2006): 0 = absent. 1 = present, one or two elongate scales on the distal portion of the middle caudal-fin rays (Fig. 37d).

The species of *Saccoderma* present an uncommon modified caudal-fin scale attached over the middle caudal-fin rays. This scale, placed at the dorsoposterior region of the caudal organ in *Saccoderma*, is longitudinally elongated, medially concave, and has all its margins free and laterally bent, being attached to the middle caudal-fin rays only by its central portion by tissue. This character is coded as missing to *Compsurini Yurimaguas n. sp.* and as inapplicable to species without any modified caudal-fin scales.

Character 218 - (ci = 1.00; ri = 1.00). Caudal fin, modified scales, with free borders (Ch. 73 modified from Malabarba 1994; Ch. 61 modified from Malabarba, 1998; Ch. 154 modified from Bührnheim, 2006): 0 = absent. 1 = present; scales with free borders, attached over the caudal fin by its central portion instead of the anterior portion, presenting a concave aspect, bowl-like shape (Fig. 37b-d).

The modified caudal-fin scales with free borders attached over the fin only by its central portion instead of the anterior margin is present in the species of *Saccoderma* and on the *compsurini* species from the Panama. These scales have a concave aspect, presenting a shallow bowl-like shape. This character is coded as missing to *Compsurini Yurimaguas n. sp.* and as inapplicable to species without modified caudal-fin scales.

Character 219 - (autapomorphy). Caudal fin, modified scales, forming pockets (Ch. 73 modified from Malabarba 1994; Ch. 61 modified from Malabarba, 1998; Ch. 154 modified from Bührnheim, 2006): 0 = absent. 1 = present (Fig. 37c).

“*Compsura*” *gorgonae* is the only examined species whose the modified caudal-fin scales form pocket-like structures. Over the lower caudal-fin lobe of this species, the last modified scales from the lateral line and from the two series of scales below it, present the posterior border convex, laterally raised, resulting in a structure formed by two to three consecutive pockets associated to hypertrophied whitish tissue. This character is coded as missing to Compsurini Yurimaguas n. sp. and as inapplicable to species without modified caudal-fin scales.

Character 220 - (ci = 0.50; ri = 0.66). Caudal fin, modified scales, forming a pouch (Ch. 73 modified from Malabarba 1994; Ch. 61 modified from Malabarba, 1998; Ch. 154 modified from Bührnheim, 2006): 0 = absent. 1 = present (Fig. 37d).

In some of the compsurin species, the caudal-fin modified scales form a pouch-like structure with a single posteroventral opening. This pouch structure differs from the pocket scales of “*Compsura*” *gorgonae* by the presence of an internal chamber between the modified scales (representing the roof of the chamber) and the caudal fin (representing the floor of the chamber). The chamber ends anteriorly in the base of the lower lobe caudal-fin rays, and posteriorly in a wall of hypertrophied whitish tissue connecting the modified scales to the caudal fin. This character is coded as missing to Compsurini Yurimaguas n. sp.

Character 221 - (ci = 1.00; ri = 1.00). Caudal fin, last lateral line scale, involved in the pouch scale: 0 = absent. 1 = present (Fig. 38).

Among the species that have a pouch scale in the caudal fin, only in *Compsura* and in Compsurini Purus n. sp. the last modified scales of the lateral line is involved in the structure of the pouch. This character is coded as missing to Compsurini Yurimaguas n. sp. and as inapplicable to species without a pouch-scale in the caudal fin.

Character 222 - (ci = 1.00; ri = 1.00). Caudal fin, last modified pouch-scale from the first longitudinal line below lateral line, dorsoposterior margin extended posteriorly: 0 = absent. 1 = present (Fig. 38a).

This character is coded as missing to Compsurini Yurimaguas n. sp. and as inapplicable to species without a pouch-scale in the caudal fin.

Character 223 - (autapomorphy). Caudal fin, last modified pouch-scale from the longitudinal line below lateral line, posterodorsal border, continuous to skin flap: 0 = absent. 1 = present.

In the species of *Compsura* and *Saccoderma*, the posterodorsal border of the last modified scale from the first longitudinal line below lateral line is attached and continuous to the skin flap of the interradiial membrane. This character is coded as missing to Compsurini Yurimaguas n. sp. and as inapplicable to species without a pouch-scale in the caudal fin.

Character 224 - (autapomorphy). Caudal fin, pouch-scale, opening: 0 = formed by the last modified scale from the lateral line and first longitudinal line below the lateral line. 1 = formed by the last modified scale from the first and second longitudinal line below the lateral line (Figs. 37d, 38a).

This character is coded as missing to Compsurini Yurimaguas n. sp. and as inapplicable to species without a pouch-scale in the caudal fin.

Character 225 - (ci = 1.00; ri = 1.00). Caudal fin, pouch structure, opening position: 0 = from 14th to 19th principal caudal-fin rays. 1 = from 13th to 19th principal caudal-fin rays. 2 = from 13th to 18th principal caudal-fin rays.

On the species of *Saccoderma* the opening of the pouch scale is located over the 14th to 19th principal caudal-fin rays (state 0); while on the species of *Compsura* and in the Compsurini Purus n. sp., the opening of the pouch extends from the 13th caudal-fin ray to the 19th (state 1) and 18th (state 2) respectively. This character is coded as missing to Compsurini Yurimaguas n. sp. and as inapplicable to species without a pouch-scale in the caudal fin.

SKIN FLAPS on FINS

Character 226 - (ci = 0.50; ri = 0.85). Skin flaps, caudal fin, lower lobe, length: 0 = restrict to the first third of the rays length. 1 = running for more than half length of the rays.

Most of the examined species present skin flaps along the caudal-fin rays. In general, these flaps extend along the first third of the caudal-fin rays, narrowing posteriorly, along the dorsal margin of the principal caudal-fin rays in the lower lobe, and along the ventral margin of the principal caudal-fin rays in the dorsal lobe. In some of the compsurin species, these flaps extend along most of the caudal-fin rays length. This character is coded as missing to *Compsurini Yurimaguas n. sp.* and *Compsurini Leticia n. sp.*, due to bad preservation condition of the available specimens.

Character 227 - (ci = 1.00; ri = 1.00). Skin flaps, dorsal fin, papillae on males (Ch. 87 modified from Malabarba 1994; Ch. 36 Malabarba, 1998; Ch. 120 modified from Bührnheim, 2006): 0 = absent. 1 = present, marginating skin flaps.

The mature males of the *Kolpotocheiroduon* species have papillae along the margin of the skin flaps in the dorsal fin, a character only found in these species. The margin of the dorsal-fin skin flaps in the remaining examined species is smooth.

Character 228 - (autapomorphy). Skin flaps, caudal fin, papillae (Ch. 87 modified from Malabarba 1994; Ch. 36 Malabarba, 1998; Ch. 120 modified from Bührnheim, 2006): 0 = absent. 1 = present, marginating skin flaps.

The presence of papillae and tabs in the skin flaps of the caudal fin is only observed in *Kolpotocheiroduon theloura*, on the remaining species the skin flaps are smooth, even in *Kolpotocheiroduon figueiredoi*, which also present “pineapple” organs over them.

Character 229 - (ci = 1.00; ri = 1.00). Skin flaps, caudal fin, “pineapple” organs, on mature males (Ch. 121 modified from Bührnheim, 2006): 0 = absent. 1 = present.

The “pineapple” organs were described as a synapomorphy for the *Kolpotocheiroduon* species along with the description of *K. figueiredoi* by Malabarba *et al.* (2004).

Character 230 - (ci = 0.50; ri = 0.88). Skin flaps, caudal fin, lower lobe, distribution (Ch. 37 Malabarba, 1998; Ch. 122 modified from Bührnheim, 2006): 0 = absent over the 18th to 19th principal caudal-fin rays. 1 = present over the 18th to 19th principal caudal-fin rays.

Most of the examined species do not present skin flaps over the 18th and 19th principal caudal-fin rays, except some of the Compsurini species. This character is coded as missing to Compsurini Yurimaguas n. sp. and Compsurini Leticia n. sp. due to the absence of specimens with the caudal fin in a good condition.

Character 231 - (ci = 0.33; ri = 0.50). Skin flaps, caudal fin, lower lobe, hypertrophied and whitish (Ch. 89 modified from Malabarba 1994; Ch. 38 Malabarba, 1998; Ch. 123 modified from Bührnheim, 2006): 0 = absent. 1 = present.

Some of the skin flaps in the caudal fin of some compsurin species are enlarged and whitish, due to their hypertrophy. This condition is generally associated to the presence of hooks in the caudal-fin rays, but not all species bearing hooks on the caudal-fin rays present such skin flaps.

MUSCLES

Character 232 - (ci = 0.25; ri = 0.82). Pseudotympanum, between the first and second pleural ribs (Ch. 1 modified from Malabarba 1994; Ch. 1 Malabarba, 1998; Ch. 2 Weitzman & Malabarba, 1999; Ch. 163 modified from Bührnheim, 2006; Ch. 339 modified from Mirande, 2010): 0 = absent. 1 = present.

Herein, pseudotympanum is considered a muscular gap on the lateral side of the body over the anterior swim bladder, with the putative function to facilitate the sound transmission from the exterior to the anterior swim bladder, and then to the inner ear through the Weberian apparatus. The presence of pseudotympanum between the first and second pleural ribs is present in most of the Cheirodontinae and some of the outgroup species. Bührnheim (2006) and Mirande (2010) assigned the presence of pseudotympanum between the first and second pleural rib to *Axeroldia lindeae*, however a complete dissection of alcohol preserved specimens revealed that the large

Cheirodontinae-like pseudotympanum present in this species is actually anterior to the first pleural rib. Instead of a pseudotympanum between the first and second ribs, *Axelrodia lindeae* has a reduction of the muscular layers in that place. This character was miscoded in those previous analyses, as well as the designation that the species lacks a pseudotympanum anterior to the first pleural rib.

Character 233 - (ci = 1.00; ri = 1.00). Pseudotympanum, between the first and second pleural ribs, delimitation (Ch. 1 Malabarba, 1998; Ch. 2 Weitzman & Malabarba, 1999; Ch. 163 modified from Bührnheim, 2006; Ch. 339 modified from Mirande, 2010): 0 = a narrow hiatus on muscles covering the anterior swim bladder, limited dorsally by the *lateralis superficialis* muscle, posteriorly and anterodorsally by the *obliquus superioris* muscles. 1 = a large, nearly triangular hiatus on muscles covering the anterior swim bladder, limited dorsally by the *lateralis superficialis* muscle, posteriorly by a naked anterior surface of the second pleural rib, posteroventrally by the *obliquus inferioris* and anteroventrally by the *obliquus superioris* muscle. 2 = a large, nearly triangular hiatus on muscles covering the anterior swim bladder, limited dorsally by the *lateralis superficialis* muscle, posterodorsally by the *obliquus superioris* muscle, posteriorly by the naked anterior surface of the second pleural rib, posteroventrally by the *obliquus inferioris* muscle, ventrally by the *obliquus superioris* muscle, and anteriorly by the naked posterior surface of the first pleural rib.

All the Cheirodontinae present a pseudotympanum as described in the state 1. The only outgroup species that present this same condition is *Cheirodon stenodon*. The Aphyoditeinae species *Aphyocharacidium bolivianum* and *Microschemobrycon elongatus* present a pseudotympanum as described in the state 2. The presence of narrow muscular hiatus (state 0) is present in the outgroup species *Charax stenopterus*, *Cynopotamus kincaidi*, and *Paracheirodon axelrodi*. This character is coded as inapplicable to species without a pseudotympanum between the first and second pleural ribs.

Character 234 - (ci = 1.00; ri = 1.00). Muscular reduction, anterior to first pleural rib: 0 = absent. 1 = present, *obliquus superiores* muscle absent and respective area covered only by the *obliquus inferiores*.

Excluding the species bearing a pseudotympanum in the region anterior to the first pleural rib, most of the Cheirodontinae species have a muscular reduction in this region. The only outgroup species that presents this condition is *Cheirodon stenodon*. This character is coded as inapplicable to species with a pseudotympanum anterior to the first pleural rib.

Character 235 - (ci = 0.50; ri = 0.83). Pseudotympanum, anterior to first pleural rib (Ch. 2 modified from Malabarba, 1998; Ch. 21 modified from Weitzman & Malabarba, 1999; Ch. 164 modified from Bührnheim, 2006): 0 = absent. 1 = present.

A small pseudotympanum anterior to the first pleural rib is present in the miniaturized cheirodontines *Amazonspinther dalmata*, *Axelrodia lindeae*, and the *Spintherobolus* species; also in *Charax stenopterus* and *Paracheirodon axelrodi*.

Character 236 - (ci = 0.50; ri = 0.00). Pseudotympanum, anterior to first pleural rib, delimitation (Ch. 2 modified from Malabarba 1994; Ch. 2 modified from Malabarba, 1998; Ch. 21 modified from Weitzman & Malabarba, 1999; Ch. 164 modified from Bührnheim, 2006): 0 = presence of a small pseudotympanum anterior to the first pleural rib, partially filled by muscular tissue, and limited to the anterodorsal portion ahead of the first pleural rib, about less than 1/3 or less of the size of the posterior pseudotympanum. 1 = present, limited dorsally by the *lateralis superficialis* muscle, posteriorly by a naked anterior surface of the first pleural rib, and anteroventrally by the *obliquus superioris* muscle, slightly smaller or half of size of the posterior pseudotympanum

This character is coded as inapplicable to species without a pseudotympanum anterior to the first pleural rib.

Character 237 - (ci = 0.50; ri = 0.95). Caudal peduncle, ventrally arched, on mature males (Ch. 3 Malabarba, 1998; Ch. 165 modified from Bührnheim, 2006): 0 = absent, aligned with the main body axis. 1 = present, deeply arched ventrally, sometimes the last vertebrae reaches 45° relative to the first caudal vertebrae (Fig. 39).

Malabarba (1998) found the presence of a caudal peduncle deeply arched on mature males as a synapomorphy for the genus *Serrapinnus*. Herein, a similar curvature of the caudal peduncle was also observed in some species of *Spintherobolus* and in both species of the New Genus, although in a slightly way. The arching of the caudal peduncle in some of the examined species is probably due to the action of the *hipaxialis* muscle in the caudal peduncle, which is proportionally slightly more developed than on the mature males of the remaining examined species. Malabarba (1998) mentioned that the *infracarinalis posterior* muscle is also developed in the *Serrapinnus*, and probably participates in the curvature of the peduncle once it unites the last anal-fin pterigiophores to the ventral procurrent caudal-fin rays. Herein it was observed that, although more developed, the *infracarinalis posterior* muscle does not attach posteriorly to the ventral procurrent caudal-fin rays, but runs laterally to them and attaches to the lower principal caudal-fin rays.

Character 238 - (ci = 0.25; ri = 0.92). Abdomen, ventral region, concavity, on mature males: 0 = absent. 1 = present, between pelvic-fin insertion and anal-fin origin (Fig. 27).

The ventral region between the pelvic-fin insertion and the origin of the anal fin is deeply concave in the mature males of some cheirodontines, mainly from the tribes Compsurini and Cheirodontini. Although not observed in the outgroup species herein examined, this ventral concavity is commonly observed in the mature males of other sexually dimorphic characids, like the *Scopaeocharax atopodus* (Böhlke) (see males specimen, fig. 7 from Weitzman & Fink, 1985), and some *Mimagoniates* species (see fig. 79 from Menezes & Weitzman, 2009).

Character 239 - (ci = 0.33; ri = 0.77). Abdomen, ventral region, concavity, on mature males, size: 0 = slightly concave (Fig. 39). 1 = deeply concave (Fig. 27).

Among the examined species, some compsurin species present a much deeper ventral concavity than the remaining species. This character is coded as inapplicable to species without a ventral abdominal concavity.

Character 240 - (ci = 0.33; ri = 0.66). Caudal peduncle, dorsal and ventral margins, profile on mature males (Ch. 4 modified from Malabarba 1994): 0 = straight or slightly

concave, with ventral scales contacting *hipaxialis* muscles. 1 = convex, with ventral scales and skin non-attached on *hipaxialis* muscles, resulting in an internal chamber between them and a slightly camber on caudal-peduncle ventral surface.

The mature males of most of the examined species have the dorsal and ventral margins of the caudal peduncle straight or slightly concave, with the skin and scales on these regions close contacting the muscles of the caudal peduncle. However, some compsurin species present the dorsal and ventral margins of the caudal peduncle convex, due to unattachment of the skin from the caudal peduncle muscles and formation of a cavity between them. The function of this morphological modification needs deeper investigation, but seems to be related to the courtship or sexual behavior of those species, once it is only present on mature males.

Character 241 - (ci = 1.00; ri = 1.00). Caudal fin, lower lobe, muscle *interradialis*, extending between rays: 0 = present. 1 = absent.

The muscle *interradialis* is a series of muscles interconnecting the principal caudal-fin rays (Winterbottom, 1974), but also each ray to the mid-line of the body axis. Each bundle of muscle can connect adjacent rays but often extends over more than one ray. In most of the examined species, the muscle *interradialis* in the lower lobe extends posteriorly between the caudal-fin rays in a relatively equal extension (see fig. 49 from Weitzman & Fink, 1985). However, in the mature males of the *Saccoderma*, the *interradialis* muscles interconnecting the lower lobe principal caudal-fin rays are absent.

Character 242 - (ci = 0.33; ri = 0.50). Caudal fin, lower lobe, muscle *interradialis*, between rays: 0 = equally extending posteriorly between all rays. 1 = more extended posteriorly between the lower lobe caudal-fin rays.

In the species of *Compsura*, "*Compsura*" *gorgonae*, and *Compsurini* *Purus* n. sp., the muscles *interradialis* interconnecting the lower lobe principal caudal-fin rays are more extended posteriorly than on the remaining examined species. This character is coded as inapplicable to *Saccoderma*, on which the muscle *interradialis* does not extend between the lower lobe caudal-fin rays.

Character 243 - (ci = 0.50; ri = 0.00). Caudal fin, lower lobe, muscle *interradialis*, between rays, development: 0 = equally thicker between all rays. 1 = thicker between the caudal-fin rays 11 to 15.

In *Acinocheirodon melanogramma* and “*Compsura*” *gorgonae*, the muscles *interradialis* interconnecting the principal caudal-fin rays 11 to 15 are thicker and deeper than on the remaining examined species. This character is coded as inapplicable to *Saccoderma*, on which the muscle *interradialis* does not extend between the lower lobe caudal-fin rays.

Character 244 - (ci = 0.33; ri = 0.66). Caudal fin, base of caudal-fin rays, muscle *interradialis*, development: 0 = equally developed and distributed radially in the upper and lower lobes. 1 = thicker and more concentrated in the ventral direction in the lower lobe.

Most of the examined species present the bundles of the muscle *interradialis* that connect the principal caudal-fin rays to the midline of the caudal peduncle with the same size and degree of development on the upper and on the lower lobes of the caudal fin. However, the bundles from the lower caudal-fin lobe are more developed than in the upper lobe in “*Compsura*” *gorgonae*, *Compsurini Purus* n. sp., and representatives of *Compsura* and *Saccoderma*.

COLOR PATTERN

Character 245 - (autapomorphy). Mentonian region, small black blotch. 0 = absent. 1 = present.

Among the examined species, the presence of a dark spot in the metonian region, due to the high concentration of melanophores, is only found in *Macropsobrycon uruguayanae*.

Character 246 - (ci = 1.00; ri = 1.00). Region under the eyes, black pigmented area. 0 = absent. 1 = present.

The region ventrally to the lower edge of the eye in *Spintherobolus ankoseion* and *S. broccae* is pigmented in black. Among the examined species this condition is only found on those species.

Character 247 - (ci = 0.20; ri = 0.75). Humeral spot (Ch. 64 Malabarba, 1998; Ch. 157 modified from Bührnheim, 2006; Ch. 341 modified from Mirande, 2010): 0 = present. 1 = absent.

The absence of the humeral spot was found to be a synapomorphy of the Cheirodontinae on previous analysis (Malabarba, 1998; Bührnheim, 2006). Herein, the absence of the humeral spot is considered the condition where no conspicuous mark or even slightly higher concentration of melanophores is present in the humeral region. The humeral spot is coded as absent on all cheirodontines and also in some species of the outgroup.

Character 248 - (ci = 1.00; ri = 1.00). Ventral region, over pelvic-fin bone, pigmented. 0 = absent. 1 = present.

Most examined species present the ventral region of the body unpigmented, free from melanophores. However the species of the *Kolpotocheirodon* have the ventral region over the pelvic-fin bone pigmented, in the shape of a faint dark triangle.

Dorsal fin

Character 249 - (ci = 0.33; ri = 0.60). Dorsal fin, color pattern, conspicuous small spot (Ch. 65 Malabarba, 1998; Ch. 159 modified from Bührnheim, 2006): 0 = absent. 1 = present, on the anterior portion of the fin.

A conspicuous small spot in the anterior portion of the dorsal fin is present in the three species of the *Compsura*, *Acinocheirodon melanogramma*, *Kolpotocheirodon figueiredoi*, and *Macropsobrycon uruguayanae*. Although the position of this spot may vary among these species, *e.g.* from between the first two unbranched dorsal-fin rays to between the last unbranched and first branched dorsal-fin rays, herein we considered the presence of this spot in the dorsal-fin homologous.

Character 250 - (ci = 0.12; ri = 0.53). Dorsal fin, scattered melanophores, distribution (Ch. 81 modified from Malabarba 1994; Ch. 158 and Ch. 160 modified from Bührnheim, 2006): 0 = homogeneously scattered. 1 = concentrated on the distal portion of the fin.

Character 251 - (ci = 0.50; ri = 0.25). Dorsal fin, color pattern, blotch (Ch. 79 and Ch. 83 modified from Malabarba 1994; Ch. 67 modified from Malabarba, 1998; Ch. 161 modified from Bührnheim, 2006; Ch. 343 modified from Mirande, 2010): 0 = absent. 1 = on the proximal portion of the fin. 2 = on the distal portion of the fin. 3 = on the mid-length of the fin.

In most of the examined species, the dorsal fin is hyaline with some scattered melanophores on the interradial membrane and/or along the margins of the dorsal-fin rays. However some of the examined species have a dark blotch in the dorsal fin, whose position may vary in the fin, being found on the base of the fin in *Amazonspinther dalmata*, *Serrapinnus notomelas*, and *Serrapinnus* n. sp. d; on the distal portion in *Holoshesthes pequirá*, *Odontostilbe* n. sp. b, and *Serrapinnus* n. sp. upm; and in *Prodontocharax melanotus* it is present in the mid-length of the fin.

Logitudinal stripe

Character 252 - (autapomorphy). Lateral band (Ch. 78 modified from Malabarba 1994): 0 = not extending over pseudotympanum. 1 = lateral band extend over pseudotympanum reaching the opercle.

The only examined species whose lateral line extends anteriorly over the humeral area up to the opercle is *Serrapinnus* n. sp. me. The remaining examined species present the longitudinal stripe fainting anteriorly, disappearing or becoming extremely narrow anterior to the vertical line through the dorsal-fin origin.

Anal-fin

Character 253 - (ci = 0.50; ri = 0.92). Anal fin, color pattern (Ch. 84 modified from Malabarba 1994; Ch. 68 Malabarba, 1998; Ch. 162 modified from Bührnheim, 2006): 0

= homogeneously pigmented. 1 = more strongly pigmented along distal portion of branched anal-fin rays on mature males.

The more strongly pigmentation of the distal portion of the anal-fin rays on mature males was found to be a synapomorphy of the Compsurini by Malabarba (1998) and Bührnheim (2006). On Compsurini Cuzco n. sp. and Compsurini Leticia n. sp. this condition is not possible to be certified due to the old state of preservation of their specimens and consequent color vanishing. For these species this character is coded as missing.

Character 254 - (ci = 0.50; ri = 0.50). Anal fin, color pattern, proximal portion of anteriormost rays, conspicuous spot. 0 = absent. 1 = present.

The presence of a conspicuous small spot in the anterior portion of the anal fin is present in the species of *Kolpotocheirodon*, and *Macropsobrycon uruguayanae*. Although the position of this spot varies along the vertical axis of the anal fin among these species, herein we considered the presence of this spot in the anterior portion of the anal fin homologous.

Character 255 - (ci = 1.00; ri = 1.00). Anal fin, posterior branched rays, dark stripe (Ch. 77 modified from Malabarba 1994; Ch. 35 of Weitzman & Malabarba, 1999): 0 = absent. 1 = present, a longitudinal stripe occurs on the caudal region, dorsal to the anterior lobe of the anal fin, extending over the posteriormost branched rays.

Among the examined species, the presence of a longitudinal dark stripe extending posteriorly from the caudal region above the anterior portion of the anal fin through the last branched anal-fin rays, is found only in *Spintherobolus ankoseion* and *S. broccae*.

Caudal- spot

Character 256 - (ci = 0.14; ri = 0.50). Caudal peduncle spot: 0 = present. 1 = absent.

Character 257 - (ci = 0.40; ri = 0.85). Caudal peduncle spot, shape: 0 = round. 1 = narrowing posteriorly over middle caudal-fin rays base. 2 = fainting posteriorly

This character is coded as inapplicable to species without caudal spot.

Character 258 - (ci = 0.33; ri = 0.00). Caudal spot, posterior extension over middle caudal-fin rays: 0 = present. 1 = absent.

This character is coded as inapplicable to species without caudal spot.

Character 259 - (ci = 0.40; ri = 0.76). Caudal spot, posterior extension: 0 = reaching distal end of middle caudal-fin rays. 1 = reaching midlength of middle caudal-fin rays. 2 = over the base of the middle rays.

This character is coded as inapplicable to species without caudal spot, or whose caudal spot does not extend posteriorly.

NEUROMASTS

Character 260 - (ci = 1.00; ri = 1.00). Neuromasts, seried and exposed on head and body (Ch. 69 modified from Malabarba, 1998; Ch. 16 modified from Weitzman & Malabarba; Ch. 167 modified from Bührnheim, 2006; Ch. 15 modified from Bührnheim *et al.*, 2008): 0 = absent. 1 = present.

The presence of exposed neuromasts forming lines in the head is only found in *Amazonspinther dalmata* and in the species of *Spintherobolus*. This condition was detailly describe by Weitzman & Malabarba (1999) for the species of *Spintherobolus*, and posteriorly found in *Amazonspinther dalmata* by Bührnheim *et al.* (2008).

UROGENITAL PAPILLA

Character 261 - (ci = 0.50; ri = 0.75). Urogenital papilla, hypertrophied, on mature males: 0 = absent. 1 = present (Fig. 40b).

On mature males of some compsurin species the urogenital papilla is hypertrophied, and more expanded ventrally than in the other examined species. In lateral view, the

hypertrophied urogenital papilla resembles a ladle, with its concave side facing anteriorly.

Character 262 - (autapomorphy). Urogenital opening, on adult females, shape: 0 = round. 1 = slit-shaped (Fig. 41a).

In *Acinocheiroidon melanogramma* the females urogenital papillae is slit-shaped, and deeper located in the body than on the remaining examined species.

Character 263 - (ci = 0.25; ri = 0.40). Urogenital papilla, hypertrophied on adult females: 0 = absent. 1 = present (Fig. 41a).

The hypertrophy of the female urogenital papilla was not deeply investigated in the characids, and among the examined species is restrict to some species of Compsurini. The correlation of the hypertrophy of the urogenital papilla with the presence of insemination needs deeper investigation.

Character 264 - (ci = 0.50; ri = 0.50). Urogenital papilla, hypertrophied in two longitudinal skin flaps on adult females: 0 = absent. 1 = present (Fig. 41a).

Adult females of some compsurin species have the urogenital papilla hypertrophied in two longitudinal and thick skin flaps. A similar condition was found by Parenti (2008) on females of some species of *Oryzias* (Beloniformes, Adrianichthyidae), and classified this condition as “bilobed” urogenital papilla.

Character 265 - (ci = 1.00; ri = 1.00). Knob-like hypertrophied tissue, anterior to anal opening on mature males: 0 = absent. 1 = present (Fig. 40b).

The mature males of the species of *Compsura* have a knob of whitish-tissue just anterior to the anal opening. This knob is formed by the hypertrophy of the tissue anterior to the anal opening. Once it is present only on sexually dimorphic males, it's function may be related to the sexual behavior of those species, however its hystological constitution and putative functions need deeper investigation.

INSEMINATION AND SPERMATOOZOA

Character 266 - (ci = 1.00; ri = 1.00). Insemination (Ch. 70 Malabarba, 1998; Ch. 168 modified from Bührnheim, 2006; Ch. 358 modified from Mirande, 2010): 0 = absent. 1 = present.

The insemination was recognized by Meisner (2005) as the process where spermatozoa are introduced into the reproductive tract of the female, but not resulting in internal fertilization. The process of insemination has been documented on several characids, and certainly appeared independently several times in the evolutionary history of the group (Burns *et al.*, 1997; Burns *et al.*, 1998; Pecio *et al.*, 2005; Weitzman *et al.*, 2005; Burns & Weitzman, 2005). This character was not investigated and coded as missing to *Kolpotocheirodon figueiredoi*, *Compsura Araguaia* n. sp., *Compsura Guaporé* n. sp., *Compsurini Leticia* n. sp., *Compsurini Tingo* n. sp., *Compsurini Yurimaguas* n. sp., *Leptobrycon jatuaranae*, *Parecbasis cyclolepis*, and *Rhoadsia altipinna*.

Character 267 - (ci = 0.50; ri = 0.88). Sperm nuclei, shape (Ch. 71 modified Malabarba, 1998; Ch. 169 modified from Bührnheim, 2006; Ch. 359 modified from Mirande, 2010): 0 = spherical, aquasperm (Fig. 42a). 1 = elongated, introsperm (Fig. 42b,c).

The spermatozoa have been classified in two basic categories according to the shape of their heads: “aquasperm”, when the nucleus is spherical to ovoid, and generally associated to external fertilizing species; and “introsperm”, a kind of spermatozoa commonly found on inseminating or internal fertilizing species, and characterized by the elongation of the nuclei and midpiece regions (Jamieson, 1991). Among the examined species the presence of introsperm is only found in some compsurin representatives. This character was not investigated and coded as missing to *Kolpotocheirodon figueiredoi*, *Compsura Araguaia* n. sp., *Compsura Guaporé* n. sp., *Compsurini Leticia* n. sp., *Compsurini Tingo* n. sp., *Compsurini Yurimaguas* n. sp., *Leptobrycon jatuaranae*, *Parecbasis cyclolepis*, and *Rhoadsia altipinna*.

Character 268 - (ci = 1.00; ri = 1.00). Introsperm nucleus, shape (Ch. 1 and Ch. 2 modified from Oliveira, 2007): 0 = bullet-shaped (Fig. 42b). 1 = sausage-shaped (Fig. 42c).

The introsperm degree of elongation may vary from moderately to extremely elongated, as observed in the characids *Glandulocauda melanogenys*, *Mimagoniates* spp., and *Pseudocorynopoma* spp. (Burns *et al.*, 1995). Among the examined species two distinct shapes is observed, an slightly elongated form classified as bullet-shaped (state 0), and a sausage-shaped form, more elongated (state 1). This character is only coded to species which spermatozoa is introsperm.

Character 269 - (autapomorphy). Accessory microtubules (Oliveira, 2007; Oliveira “paper”): 0 = absent. 1 = present.

Oliveira (2007) found the presence of accessory microtubules only in *Macropsobrycon uruguayanae*. This character is also coded to *Acinocheiroduon melanogramma*, *Compsura heterura*, *Kolpotocheiroduon theloura*, *Compsurini Purus* n. sp., *Compsurini Napo* n. sp., *Saccoderma melanostigma*, *S. hastata*, “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura*, “*O.*” *mitoptera*, *Cheiroduon interruptus*, *Serrapinnus calliurus*, *Serrapinnus heterodon*, and *Holoshesthes pequiria*.

Character 270 - (autapomorphy). Striated rootlet (Oliveira, 2007): 0 = absent. 1 = present.

Among the examined species, a striated rootlet is present only in *Macropsobrycon uruguayanae* (Oliveira, 2007). Although not included in this analysis, this character was also observed in the characid *Brittanichthys axelrodi* according to Javonillo *et al.* (2007). This character is only coded to *Acinocheiroduon melanogramma*, *Compsura heterura*, *Macropsobrycon uruguayanae*, *Kolpotocheiroduon theloura*, *Compsurini Purus* n. sp., *Compsurini Napo* n. sp., *Saccoderma melanostigma*, *S. hastata*, “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura*, “*O.*” *mitoptera*, *Cheiroduon interruptus*, *Serrapinnus calliurus*, *S. heterodon*, and *Holoshesthes pequiria*.

Character 271 - (ci = 0.50; ri = 0.80). Nuclear rotation (Ch. 3 modified from Oliveira, 2007): 0 = present, with flagellum posterior to the nucleus. 1 = absent, with flagellum attached laterally to the nucleus.

The nuclear rotation is a process that occurs during the cell differentiation along the spermiogenesis, where the nucleus rotates over the centriolar complex, so that the head, midpiece and flagellum end aligned (Mattei, 1970; Pecio *et al.*, 2007). The absence of nuclear rotation has been observed in several characid inseminating species bearing introsperm [*Mimagoniates barberi* and *M. microlepis* in Pecio & Rafinski (1994, 1999) and Burns *et al.* (1998); *Diapoma speculiferum*, *Pseudocorynopoma doriae*, *Scopaeocharax rhinodus*, *Tyttocharax tambopatensis* and *T. cochui*, in Burns *et al.* (1998) and Pecio *et al.* (2005); *Bryconadenos tanaothoros* in Weitzman *et al.* (2005); and *Brittanichthys axelrodi* in Javonillo *et al.* (2007); and *Corynopoma riisei* in Pecio *et al.* (2007)], however it is not always correlated to this condition, being found also on species with aquasperm (Mattei, 1970). This character is only coded to *Acinocheiroidon melanogramma*, *Compsura heterura*, *Macropsobrycon uruguayanae*, *Kolpotocheiroidon theloura*, *Compsurini Purus* n. sp., *Compsurini Napo* n. sp., *Saccoderma melanostigma*, *S. hastata*, “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura*, “*O.*” *mitoptera*, *Cheiroidon interruptus*, *Serrapinnus calliurus*, *S. heterodon*, and *Holoshesthes pequirá*.

Character 272 - (ci = 1.00; ri = 1.00). Cytoplasmic canal, midpiece, shape and length (Ch. 4 modified from Oliveira, 2007): 0 = midpiece roundish nearly truncated posteriorly and cytoplasmic canal length approximately half nucleus length. 1 = midpiece not truncated posteriorly; cytoplasmic canal length longer than half nucleus length.

Among the examined species the compsurin species have the cytoplasmic canal of the spermatozoa longer than the nucleus length. This character is only coded to *Acinocheiroidon melanogramma*, *Compsura heterura*, *Macropsobrycon uruguayanae*, *Kolpotocheiroidon theloura*, *Compsurini Purus* n. sp., *Compsurini Napo* n. sp., *Saccoderma melanostigma*, *S. hastata*, “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura*, “*O.*” *mitoptera*, *Cheiroidon interruptus*, *Serrapinnus calliurus*, *S. heterodon*, and *Holoshesthes pequirá*.

Character 273 - (ci = 0.50; ri = 0.66). Centriolar complex, position in relation to the nuclear fossa (Ch. 5 modified from Oliveira, 2007): 0 = both centrioles outside the nuclear fossa. 1 – anterior tip of the proximal centriole located inside the nuclear fossa and the distal centriole outside. 2 = both centrioles partially inside the nuclear fossa.

This character is only coded to *Acinocheiroduon melanogramma*, *Compsura heterura*, *Macropsobrycon uruguayanae*, *Kolpotocheiroduon theloura*, Compsurini Purus n. sp., Compsurini Napo n. sp., *Saccoderma melanostigma*, *S. hastata*, “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura*, “*O.*” *mitoptera*, *Cheirodon interruptus*, *Serrapinnus calliurus*, *S. heterodon*, and *Holoshesthes pequiria*.

Character 274 - (ci = 0.50; ri = 0.80). Centrioles, position to each other (Ch. 6 modified from Oliveira, 2007): 0 = parallel. 1 = perpendicular.

The presence of the centrioles positioned perpendicularly to each other is present in *Acinocheiroduon* and in the trans-andean compsurin species. This character is also coded to *Compsura heterura*, *Macropsobrycon uruguayanae*, *Kolpotocheiroduon theloura*, Compsurini Purus n. sp., Compsurini Napo n. sp., *Cheirodon interruptus*, *Serrapinnus calliurus*, *S. heterodon*, and *Holoshesthes pequiria*.

Character 275 - (ci = 0.50; ri = 0.80). Mitochondria, position (Ch. 7 modified from Oliveira, 2007): 0 = in the midpiece, posterior to the nucleus and around the origin of the flagellum. 1 = near the tip of nucleus (without nuclear rotation) and distant from the origin of the flagellum.

Acinocheiroduon shares with the trans-andean compsurin species, the mitochondria located in the distal portion of the nucleus. This character is also coded to *Compsura heterura*, *Macropsobrycon uruguayanae*, *Kolpotocheiroduon theloura*, Compsurini Purus n. sp., Compsurini Napo n. sp., *Cheirodon interruptus*, *Serrapinnus calliurus*, *S. heterodon*, and *Holoshesthes pequiria*.

Character 276 - (ci = 1.00; ri = 1.00). Nucleus, anterior border, shape (Ch. 8 modified from Oliveira, 2007): 0 = semicircular or emarginated. 1 = asymmetric, clearly oblique to the longest axis of the nucleus.

The presence of an oblique anterior border of the spermatozoa nucleus is present in the trans-andean compsirin species "*Compsura*" *gorgonae*, "*Odontostilbe*" *dialeptura*, and "*O.*" *mitoptera*. This character is also coded to *Acinocheiroduon melanogramma*, *Compsura heterura*, *Macropsobrycon uruguayanae*, *Kolpotocheiroduon theloura*, *Compsurini Purus* n. sp., *Compsurini Napo* n. sp., *Saccoderma melanostigma*, *S. hastata*, *Cheiroduon interruptus*, *Serrapinnus calliurus*, *S. heterodon*, and *Holoshesthes pequiria*.

Character 277 - (ci = 1.00; ri = 1.00). Vesicles, shape (Ch. 9 modified from Oliveira, 2007): 0 = elongated vesicles. 1 = large number of small and globular vesicles.

The presence of a large number of small and globular vesicles is found in the representatives from Cheiroduonini and Odontostilbini. This character is also coded to *Acinocheiroduon melanogramma*, *Compsura heterura*, *Macropsobrycon uruguayanae*, *Kolpotocheiroduon theloura*, *Compsurini Purus* n. sp., *Compsurini Napo* n. sp., *Saccoderma melanostigma*, *S. hastata*, "*Compsura*" *gorgonae*, "*Odontostilbe*" *dialeptura*, and "*O.*" *mitoptera*.

Character 278 - (ci = 1.00; ri = 1.00). Vesicles, position (Ch. 10 modified from Oliveira, 2007): 0 = located only after the mitochondria, in the basal region of the midpiece. 1 = located after the mitochondria, in the basal region of the midpiece and along the cytoplasmic collar in one side of the nucleus.

The presence of vesicles in the basal region of the midpiece and along the cytoplasmic collar of the spermatozoa is only present in the compsirin species from Panama. This character is only coded to *Acinocheiroduon melanogramma*, *Compsura heterura*, *Macropsobrycon uruguayanae*, *Kolpotocheiroduon theloura*, *Compsurini Purus* n. sp., *Compsurini Napo* n. sp., *Saccoderma melanostigma*, *S. hastata*, "*Compsura*" *gorgonae*, "*Odontostilbe*" *dialeptura*, "*O.*" *mitoptera*, *Cheiroduon interruptus*, *Serrapinnus calliurus*, *S. heterodon*, and *Holoshesthes pequiria*.

Phylogenetic diagnoses for clades and terminal taxa. The parsimony analysis under equal weights of 101 species codified for 278 morphological characters, being 20

autapomorphics, resulted in 43 equally parsimonious trees with 1253 steps long, with consistency index (CI) of 0.25 and retention index (RI) of 0.70. Those hypotheses are summarized in a strict consensus tree with 1293 steps (CI = 0.25; RI = 0.69) (Fig. 43). The IW trees obtained from “k”-values 5.3390, 5.8297, 6.3818, and 7.0075 were found to be more stable than the trees resulted from the other “k”-values. The data concerning all the IW trees obtained from different “k”-values, and the SPR values among them, are shown in the Tables 2 and 3, respectively. The IW analysis with the four “k”-values between 5.3390 and 7.0075 resulted in a total of twelve trees with 1269 steps (CI = 0.25; RI = 0.69), and the strict consensus from those IW trees has 1270 steps (CI = 0.25; RI = 0.69) (Fig. 44). Both parsimony analyses, with implied weights and equal weights, recovered the monophyly of the subfamily, its tribes and some of their internal nodes; however the IW analysis showed a better resolution of the genera and species relationships inside the tribes, and it is the phylogenetic hypothesis in which the discussion is focused and all the synapomorphies and characters indices (ci and ri) taken from. The synapomorphies and autapomorphies also found for the same clades on the equal weighting parsimony analysis are marked with an asterik (*). The ci, ri and number of steps for each character are given in the Appendix II, and their transitions and total number of steps for each character in the Appendix III. The number of the clades was given by the TNT software, and the synapomorphies for each clade are summarized in the Appendix IV. The Bremer support values are presented in the base of the clades in the Fig. 45 for the equal weighted parsimony analysis, and in the Fig. 46 for the IW analysis based on the trees obtained under the “k”-value 6.3818.

The following list of synapomorphies, reversals, and independent acquisitions will be restricted to the Cheirodontinae tribes and internal major clades, and will only reach a more inclusive level for the Compsurini, focus of the present work.

Monophyly of Cheirodontinae Eigenmann, 1915

(Clade 106)

Aphiocharacinae Eigenmann, 1909, 1910 [in part; diagnosis, list of genera and species].

Aphyocharacinae Eigenmann, 1912 [in part; emended].

Cheirodontinae Eigenmann, 1915 [in part; diagnosis, list of genera and species]. -

Malabarba, 1998 [cladistic diagnosis; list and diagnosis of genera]. - Mirande, 2009

[cladistic diagnosis; list of genera]. - Mirande, 2010 [cladistic diagnosis].

- 1*. Anteroventral portion of the antorbital expanded in discoid shape, sometimes extending anteriorly [Ch. 3: 0 > 1]. Reversed in Clade 158.
- 2*. Medial lamellae of premaxilla developed, forming a V-shaped bifurcation with posteromedial lamina oblique to anteromedial lamina [Ch. 54: 0 > 1]. Reversed in *Macropsobrycon uruguayanae* and Clade 158.
- 3*. Margin of the tooth bearing portion of the maxilla concave, not continuous to the toothless margin [Ch. 60: 0 > 1]. Reversed in Compsurini *Leticia n. sp.*, *Cheirodon kiliani*, and *Axelrodia lindeae*.
- 4*. Toothless portion of the maxilla with approximately the same length of the tooth bearing portion [Ch. 62: 3 > 1]. Reversed to state 3 in *Axelrodia lindeae*, *Odontostilbe n. sp. p.*, Compsurini *Leticia n. sp.*, *Saccoderma* (Clade 127), Clade 138, Clade 143, and Clade 162; independent acquired in *Pseudocheirodon arnoldi*, Clade 118 and Clade 140; transformed to state 0 in Clade 176; transformed to state 2 in *Serrapinnus heterodon*, *S. kriegi* Clade 102, Clade 120, Clade 137, Clade 155, Clade 156, and Clade 165.
- 5*. Premaxillary teeth pedunculated, largely expanded, and compressed distally [Ch. 74: 0 > 1]. Reversed in *Macropsobrycon uruguayanae*, Compsurini *Leticia n. sp.* and Clade 156.
- 6*. Premaxillary teeth contacting each other by their cusps [Ch. 81: 0 > 1]. Reversed in *Prodontocharax*, *Macropsobrycon uruguayanae*, Compsurini *Leticia n. sp.*, *Cheirodon parahybae*, *Serrapinnus microdon*, Clade 163 (independent acquired in *Aphyocheirodon hemigrammus*), Clade 138, and Clade 156.
- 7*. Maxillary teeth pedunculated, largely expanded, and compressed distally [Ch. 90: 0 > 1]. Reversed in Clade 156.
- 8*. Teeth from the dentary pedunculated, largely expanded, and compressed distally [Ch. 92: 0 > 1]. Reversed in *Macropsobrycon uruguayanae* and *Axelrodia lindeae*.
- 9*. Mature males with ventral border of posteriormost branchiostegal ray concave on its anterior portion [Ch. 119: 0 > 1]. Reversed in *Nanocheirodon insignis*, *Serrapinnus kriegi*, and Clade 140; independent acquired in *Serrapinnus* (Clade 144).

Synapomorphy ambiguously optimized for this clade:

- 10*. Presence of the sixth infraorbital anterior lamella [Ch. 11: 1 > 0].

The Cheirodontinae is herein supported as monophyletic by nine synapomorphies, being the presence of the anterior lamella in the sixth infraorbital ambiguously optimized by ACCTRAN for this clade. In the analysis of Malabarba (1998), the Cheirodontinae was found to be monophyletic based on four synapomorphies: presence of a pseudotympanum between the first and second pleural ribs (Ch. 232); lack of humeral spot (Ch. 247); pedunculated teeth (Chs. 74, 90, and 92); and a single regular tooth row with teeth perfectly aligned and similar in shape and cusp number (Chs. 77 and 78). The same synapomorphies were found by Weitzman & Malabarba (1999) and Bührnheim *et al.* (2008) for Cheirodontinae. From these characters, only the presence of pedunculated teeth was found to be a synapomorphy for the Cheirodontinae in this work. Herein, the presence of a pseudotympanum between the first and second pleural ribs is a synapomorphy for *Cheirodon stenodon* + Cheirodontinae (Fig. 44, Clade 107); and the lack of humeral spot is a synapomorphy for the Clade 109. The “single regular tooth row with teeth perfectly aligned and similar in shape and cusp number”, treated as a single character by Malabarba (1998), was herein split in two independent characters, one concerning the presence of one tooth row in the premaxilla (Ch. 77), and other the alignment of the single row of premaxillary teeth (Ch. 78). The presence of one tooth row in the premaxilla was found to be a synapomorphy for the Clade 111, and the single row of premaxillary teeth perfectly aligned was coded in the root of the cladogram due to the inapplicability of this character to the outgroup species bearing more than one tooth row, with transformation to not aligned tooth row in the Clade 192 (*Charax stenopterus* + *Cynopotamus kincaidi*) and in *Paracheirodon axelrodi*. In this analysis, the pedunculated shape of the cheirodontines teeth were explored on three different characters, corresponding the their presence in the premaxilla, dentary, and maxilla. The presence of pedunculated teeth was experimentally split in three disconnected characters due to the non-correspondence of their presence on those three bones in some of the examined species. The *Amazonspinther*, *Spintherobolus*, and *Compsurini* Leticia n. sp. were coded as missing pedunculated teeth in the premaxilla, but present them on the dentary. However, the coexistence of pedunculated teeth in the premaxilla, dentary and maxilla as synapomorphies for Cheirodontinae evidenced that for this group, the presence of pedunculated teeth on these bones is homologous. The only synapomorphies herein presented and also found by Bührnheim (2006) for the Cheirodoninae are the medial

lamellae of premaxilla developed (Ch. 54), and the toothless portion of the maxilla with approximately the same length of the tooth bearing portion (Ch. 62).

Monophyly of *Odontostilbini* Bührnheim, 2006

(Clade 172)

1*. Posteroventral border of the urohyal with a notch [Ch. 121: 0 > 1]. Reversed in *Odontostilbe pao*, *Odontostilbe fugitiva*, *Holoshesthes pequiria*, *Holoshesthes* n. sp. k, and Clade 179; independently acquired in *Cheirodon australe*, *Serrapinnus micropterus*, *S. microdon*, and *S. notomelas*.

2*. Elongation of the second unbranched dorsal-fin ray on males [Ch. 137: 0 > 1]. Reversed in *Odontostilbe* n. sp. h, *Odontostilbe* n. sp. e, Clade 161, and Clade 176; independently acquired in “*Odontostilbe*” *mitoptera*, and Clade 155.

3*. Pelvic-fin unbranched ray elongated on males [Ch. 150: 0 > 1]. Reversed in *Odontostilbe parecis*, *Odontostilbe* n. sp. e, *Pseudocheirodon* (Clade 182) and Clade 161; independently acquired in “*Odontostilbe*” *mitoptera*.

Synapomorphies ambiguously optimized for this clade:

4*. Postcleithrum 1 round and expanded posteriorly [Ch. 142: 1 > 0]. Reversal.

5*. Abdomen without ventral concavity on mature males [Ch. 238: 1 > 0]. Reversal.

6*. Both centrioles partially inside the nuclear fossa [Ch. 273: 0 > 2].

The tribe *Odontostilbini* was proposed by Bührnheim (2006), encompassing the species belonging to the previously known *incertae sedis* genera of *Cheirodontinae* (Malabarba, 1998). In the systematic work of the *Odontostilbe*, Bührnheim (2006) found thirteen derived characters supporting her new tribe. From these, only the elongation of the unbranched pelvic-fin ray on males was also found here as a synapomorphy of the *Odontostilbini*. Herein, the elongation of the second unbranched dorsal-fin ray, and the presence of a notch in the posteroventral border of the urohyal were also found to be synapomorphies of the tribe.

Monophyly of *Odontostilbe pao*, *Odontostilbe euspilurus*, *Pseudocheirodon*, and *Prodontocharax*

(Clade 177)

1. Posterior extremity of the maxilla ending in a sharp angle, due to the ventral margin dorsoposterior convergence toward the dorsal margin of the maxilla [Ch. 64: 0 > 1].

Synapomorphy ambiguously optimized for this clade:

2. Anteroventral portion of the quadrate without a foramen [Ch. 110: 1 > 0].

Monophyly of *Odontostilbe euspilurus*, *Pseudocheirodon*, and *Prodontocharax*

(Clade 176)

1*. Fifth infraorbital broad, with expanded lateral laminae from the laterosensory canal [Ch. 10: 1 > 0].

2*. Maxilla ventrally arched, with tooth-bearing portion continuous to the premaxillary tooth-bearing portion line, but posterior toothless portion ventrally arched [Ch. 58: 0 > 1].

3*. Maxilla toothless portion shorter than tooth bearing portion [Ch. 62: 1 > 0].

4*. Second unbranched dorsal-fin ray not elongated on males [Ch. 137: 1 > 0].

Synapomorphy ambiguously optimized for this clade:

5*. Posterior region of the maxilla with lower portion angled medially [Ch. 63: 0 > 1].

Monophyly of *Pseudocheirodon* and *Prodontocharax*

(Clade 181)

1*. Lateral process of the mesethmoid absent [Ch. 19: 0 > 1].

2*. Anteromedial process of the lateral ethmoid robust [Ch. 30: 1 > 0].

3*. Absence of the premaxilla ascending process [Ch. 51: 0 > 1].

4*. Absence of developed bony folds in the dentary symphyseal joint [Ch. 66: 0 > 1].

5*. Anguloarticular lower branch elongate, reaching or falling short to the line through the toothed portion of the dentary [Ch. 73: 0 > 1].

6*. Longer axis of the anteriormost dentary teeth nearly at the same axis of the dentary, forwardly projected [Ch. 96: 1 > 2].

Synapomorphies ambiguously optimized for this clade:

7*. Anterior and posterior tooth bearing regions of the dentary distinct by difference in teeth size [Ch. 68: 1 > 0].

8*. Dentary teeth bearing three to four cusps [Ch. 105: 3 > 2].

9. Quadrate with an anteroventral foramen [Ch. 110: 0 > 1].

10*. At least the two posteriormost branchiostegals rays crenulated [Ch. 120: 0 > 1].

Monophyly of *Pseudocheirodon*

(Clade 182)

1*. Anteromedial process of the mesethmoid pointed in dorsal view [Ch. 17: 1 > 0].

Reversal.

2*. Premaxillary medial lamellae developed, the posteromedial lamina at the coronal plane and perpendicular to the anteromedial lamina [Ch. 54: 1 > 2]. Uniquely derived.

3*. Maxilla ventral border with a protruding spine-like projection preceding anteriormost teeth present [Ch. 57: 0 > 1]. Uniquely derived.

4*. Dorsolateral border of the dentary forming a concavity, at vertical after the posteriormost teeth of the dentary [Ch. 70: 0 > 1]. Independently acquired in *Odontostilbe nareuda*, and *O. pao*.

5*. Premaxillary tooth cusps rounded [Ch. 86: 0 > 1]. Uniquely derived.

6*. All premaxillary tooth cusps similar in form and size [Ch. 87: 0 > 1]. Independently acquired in Clade 120.

7*. Dentary tooth cusps rounded [Ch. 102: 0 > 1]. Uniquely derived.

8*. Dentary teeth with the seven central cusps larger, nearly equal in size [Ch. 103: 0 > 3]. Uniquely derived.

9*. Dentary tooth cusps arranged in 6-7 medial cusps aligned in row with other teeth cusps, forming a continuous cutting edge [Ch. 104: 0 > 3]. Uniquely derived.

10*. Unbranched pelvic-fin ray not elongated on males [Ch. 150: 1 > 0]. Reversal.

11*. Anal-fin hooks concentrated along distal half or third portion of the rays [Ch. 174: 0 > 1]. Independently acquired in “New Genus” n. sp. b, *Megacheirodon unicus*, *Serrapinnus* (Clade 144), Clades 104 and 128.

12*. Caudal spot reaching midlength of middle caudal-fin rays [Ch. 259: 2 > 1]. Uniquely derived.

Synapomorphy ambiguously optimized for this clade:

13*. Dentary teeth bearing up to nine cusps [Ch. 105: 2 > 4]. Independently acquired in “New Genus” (Clade 139).

In the systematics of the Cheirodontinae performed by Malabarba (1998), three synapomorphies were found to *Pseudocheirodon*: the symphyseal dentary joint

articulated by strong ligamentous tissue (Ch. 66); posterior tip of the premaxilla narrow (Ch. 51); and maxilla with tooth-bearing portion continuous to the premaxillary teeth and toothless portion angled ventrally (Ch. 58). Herein the characters 66 and 51 were found to be synapomorphies of *Pseudocheirodon* + *Prodontocharax*, and the character 58 a synapomorphy of the *Odontostilbe euspilurus* + (*Prodontocharax* + *Pseudocheirodon*). Bührnheim (2006) found sixteen synapomorphies to *Pseudocheirodon*, most of them also found here.

Monophyly of *Prodontocharax*

(Clade 180)

- 1*. Dorsal margin of the lateral ethmoid articulating to the frontal medially, and laterally through chondral articulation [Ch. 32: 0 > 2]. Uniquely derived.
- 2*. Lamina lateroventral expansion of the lateral ethmoid absent [Ch. 33: 0 > 1]. Independently acquired in Clade 158.
- 3*. Mouth below the horizontal through the lower edge of the eye [Ch. 50: 0 > 2]. Uniquely derived.
4. Posterior extremity of the maxilla ending in a round profile [Ch. 64: 1 > 0].
- 5*. Premaxillary teeth do not contacting each other by their cusps [Ch. 81: 1 > 0]. Reversal.
- 6*. Anteromedial toothed portion of the dentary with at least six teeth [Ch. 100: 0 > 1]. Independently acquired in *Axelrodia lindeae*.
- 7*. Dentary teeth do not contacting each other by their cusps [Ch. 106: 1 > 0]. Reversal.
8. Ectopterygoid not contacting the quadrate [Ch. 107: 0 > 1]. Independently acquired in *Odontostilbe pao*, Clade 104, Clade 145, and Clade 168.
- 9*. Absence of hyomandibular posterodorsal projection [Ch. 112: 1 > 0]. Reversal.
- 10*. Gill rakers from the first gill arch with similar size in the upper and lower branches [Ch. 132: 2 > 1]. Uniquely derived.

Synapomorphy ambiguously optimized for this clade:

- 11*. Posterior region of the maxilla vertically flat and plane [Ch. 63: 1 > 0]. Reversal.

Malabarba (1998) defined *Prodontocharax* with four synapomorphies based on the analysis of its type species, *Prodontocharax melanotus*: the curved maxilla with tooth bearing portion aligned with the premaxillary teeth; a short maxilla, not reaching

the contact between the first and second infraorbitals; elongated and conical to tricuspid teeth in the jaws; and a black spot in the midlength of the dorsal-fin rays. The first synapomorphy found by Malabarba (1998) was found to be a synapomorphy of *Pseudocheirodon* + *Prodontocharax* here. The length of the maxilla was analysed in a different parameter in this study (Ch. 55, in relation to the lateral ethmoid), and its short length in *Prodontocharax* was not found to be a synapomorphy for the genus; nor the conical to tricuspid teeth in the jaws. The black spot in the dorsal-fin is herein considered a autapomorphy of *Prodontocharax melanotus*, instead of a synapomorphy of the genus.

Monophyly of *Odontostilbe ecuadorensis* and *Holoshesthes*

(Clade 166)

1. Dorsal profile of the maxilla slightly concave [Ch. 59: 0 > 1].
2. Tooth bearing portion of the dentary more than half length of the dorsal border of the dentary bone [Ch. 67: 1 > 0].
3. Anterior tooth bearing portion of the dentary shorter than posterior portion [Ch. 69: 1 > 0].

Monophyly of *Holoshesthes*, *Aphyocheirodon*, and *Cheirodontops*

(Clade 165)

1. Ascending process of the premaxilla distinctly projected, pointed [Ch. 52: 1 > 0].
Reversal.
2. Ascending process of the premaxilla running over the lateral process of the mesethmoid [Ch. 53: 1 > 0]. Reversal.
3. Maxilla extending posteriorly the vertical line through the ventral limit of the lateral ethmoid [Ch. 55: 1 > 0]. Reversal.
4. Presence of a longitudinal groove, just below the dorsolateral border of the maxilla [Ch. 56: 0 > 1]. Independently acquired in *Compsurini* Leticia n. sp., *Odontostilbe parecis*, *Odontostilbe* n. sp. p, Clade 102, Clade 128, and Clade 143.
5. Toothless portion of the maxilla with twice the length of the tooth bearing portion [Ch. 62: 1 > 2]. Independently acquired in *Acinocheirodon*, *Heterocheirodon* (Clade

142), *Serrapinnus kriegi*, *S. heterodon*, Clade 120, Clade 137, Clade 156, and Clade 155.

6*. Medial tooth of the premaxilla markedly larger than lateral teeth [Ch. 75: 0 > 1].

Uniquely derived in Cheirodontinae.

7*. Longer axis of the anteriormost dentary teeth perpendicular to the longer axis of the dentary [Ch. 96: 1 > 0]. Reversal.

8*. Dentary teeth cusps nearly squared [Ch. 102: 0 > 2]. Independently acquired in *Acinocheirodon*.

9*. Dentary teeth with 3 medial cusps larger and nearly equal in size [Ch. 103: 0 > 1]. Independently acquired in *Acinocheirodon*, and Clade 154.

10*. Dentary teeth with 3 central cusps aligned in row with other teeth cusps forming a continuous cutting edge [Ch. 104: 0 > 1]. Independently acquired in *Acinocheirodon*, and *Serrapinnus heterodon*.

11. Dentary teeth with five cusps [Ch. 105: 3 > 0]. Reversal.

12. Dorsal-fin scattered melanophores concentrated on the distal portion of the fin [Ch. 250: 0 > 1]. Independently acquired in *Macropsobrycon*, *Compsura* (Clade 118), *Saccoderma melanostigma*, “*Odontostilbe*” *mitoptera*, Clade 143 and 173.

Holoshesthes was considered synonym of *Odontostilbe* by Malabarba (1998) based on the analysis of the type species only (*Holoshesthes pequiri*), but as a valid genus by Bührnheim (2006) with three new species, with *Chirodon pequiri* Steindachner as its type species, and the genera *Aphyocheirodon* and *Cheirodontops* as junior synonyms. Although the names *Aphyocheirodon* and *Cheirodontops* are still used here, the validation of the *Holoshesthes* is supported by twelve synapomorphies.

Monophyly of Cheirodontini and Compsurini

(Clade 105)

1*. Ascending process of the premaxilla falling short the lateral tip of the mesethmoid lateral process [Ch. 53: 0 > 1]. Reversed in *Macropsobrycon*, *Serrapinnus heterodon*, and Clade 128; independently acquired in Clade 170.

2*. Anal-fin hypertrophied whitish tissue on mature males deeply developed, covering entirely the hooks [Ch. 168: 0 > 1]. Reversed in *Axelrodia lindeae* and *Heterocheirodon* (Clade 142).

The relationships among the Cheirodontinae tribes were never evidenced in previous phylogenetic analysis of the subfamily. The tribes used to form a polytomy in the base of Cheirodontinae. Although only supported by two synapomorphies in this analysis, Compsurini was found to be sister group of Cheirodontini, by sharing the ascending process of the premaxilla falling short the lateral tip of the mesethmoid lateral process (Ch. 53); and for presenting the whitish tissue surrounding the anal-fin hooks deeply developed, covering enterily the anal-fin bony hooks (Ch. 168). Among the examined species, a high degree of development of the presumable glandular whitish tissue on the anal fin was only found on the mature male representatives of these two tribes. Although also bearing anal-fin hooks associated to a certain amount of whitish tissue, no mature male from the Odontostilbini or from the outgroup species presented so hypertrophied tissue in the anal-fin interrarial membrane. The presence of highly developed tissue in the anal fin of mature males is known for the some Stevardiinae, forming sometimes well-developed secretory glands, as found in the species of *Bryconadenos* Weitzman, Menezes, Evers & Burns, 2005 (Weitzman *et al.*, 2005). However the stevardiines are not closely related to the cheirodontines, and both subfamilies mutually do not share most of the synapomorphies by which they are defined.

Monophyly of Cheirodontini Eigenmann, 1915

(Clade 137)

1*. Ascending portion of the preopercle lateral system canal short, reaching the posterior articular surface of the hyomandybular condyle [Ch. 114: 0 > 1]. Reversed in *Serrapinnus* (Clade 144), but independent acquired in *Serrapinnus kriegi*, *S. microdon*, *Serrapinnus* n. sp. ac, and *Aphyocheirodon hemigrammus*, Compsurini Purus n. sp., *Kolpotocheirodon* (Clade 123), *Macropsobrycon*, *Odontostilbe* n. sp. b, and *Saccoderma hastata*.

2*. The two posteriormost branchiostegals rays crenulated at its posterior border [Ch. 120: 0 > 1]. Reversed in *Amazonspinther*, “New Genus” n. sp. c, Clade 150, and Clade 154; independent acquired in *Odontostilbe splendida*, *Odontostilbe* n. sp. h, *Odontostilbe* n. sp. p, and Clade 181.

- 3*. Hemal spines of preural vertebrae 2 to 5 contacting the procurent caudal-fin rays [Ch. 178: 0 > 1]. Reversed in *Amazonspinther*; independently acquired in Compsurini Leticia n. sp.
- 4*. Females anteriormost ventral procurent caudal-fin rays needle-shaped, lepidotrichia fused along their length, usually remaining a small opening near their distal tips [Ch. 193: 0 > 1]. Reversed in Clade 156; transformed to state 2 in *Heterocheiroduon* (Clade 142); independently acquired in *Spintherobolus* (Clade 160).
- 5*. Ventral procurent caudal-fin rays on males laminar, lepidotrichia fused along their entire length and becoming progressively laminar with maturation [Ch. 195: 0 > 1]. Uniquely derived.
- 6*. Anteriormost ventral procurent caudal-fin rays hypertrophied on mature males [Ch. 199: 0 > 1]. Uniquely derived.
- Synapomorphies ambiguously optimized for this clade:
- 7*. Third infraorbital ventrally contacting the laterosensory canal of preopercle, but leaving a posterior naked area between border of the third infraorbital and ascending portion of the laterosensory canal of preopercle, as wide as or wider than the canal [Ch. 8: 0 > 1]. Reversed in Clade 140; transformed to state 2 in *Cheiroduon* (Clade 135), and Clade 156; independently acquired in *Cheiroduon parahybae*, *Macropsobrycon*, *Pseudocheiroduon terrabae*, and Clade 178.
- 8*. Sixth infraorbital without anterior lamella [Ch. 11: 0 > 1]. Reversed in “New Genus” n. sp. c and in *Serrapinnus* (Clade 144); independently acquired in *Serrapinnus* n. sp. ups and Clade 121.
- 9*. Toothless portion of the maxilla with twice the length of the tooth bearing portion [Ch. 62: 1 > 2]. Reversed in Clade 140; transformed to state 3 in *Axelrodia lindeae*, Clade 138 and Clade 143; independently acquired in *Serrapinnus heterodon*, *S. kriegi*, Clade 155, and Clade 156.
- 10*. Eleven to sixteen ventral procurent caudal-fin rays on males [Ch. 190: 0 > 1]. Reversed in *Amazonspinther*; transformed to state 2 in Clade 136 and Clade 139.
- 11*. Distal tip of the anteriormost ventral procurent caudal-fin rays on males square-shaped [Ch. 198: 0 > 1]. Transformed to state 2 in “New Genus” n. sp. c, Clade 136, and Clade 152.
- 12*. Distal portion of the anteriormost ventral procurent caudal-fin rays on males projecting externally through muscles and skin, forming a ventral keel [Ch. 202: 0 > 1]. Reversed in *Heterocheiroduon* (Clade 142).

The Cheirodontini was diagnosed by Malabarba (1998) by a series of modifications of the ventral procurrent caudal-fin rays not found in any other characid. Based on the number, shape and hypertrophy of the ventral procurrent caudal rays, Malabarba (1998) diagnosed the genus *Cheirodon*, *Spintherobolus*, and the only known Cheirodontinae fossil representative *Megacheirodon*, and proposed four new genera to the tribe: *Heterocheirodon*, *Nanocheirodon*, *Serrapinnus*, and a new genus not yet described (herein referred as “New Genus”). Cheirodontini is herein diagnosed based on twelve synapomorphies, from these, five were previously found by Malabarba (1998): presence of a high number of ventral procurrent caudal-fin rays, ranging from 11 to 28 (Ch. 190); lepidotrichia of each ventral procurrent caudal-fin ray of males fused along their entire length, becoming progressively laminar with maturation (Ch. 195); females presenting the anterior ventral procurrent rays needle-shaped (Ch. 193); ventral procurrent caudal-fin rays on males projecting through the muscles and skin (Ch. 202); and hemal spines of the last four vertebrae anterior to the compound centrum elongated and supporting the ventral procurrent rays (Ch. 178). Malabarba (1998) also found the presence of interrupted lateral line as diagnostic to the tribe, which was not found to be a synapomorphy here neither in Bührnheim (2006), and was not assessed in Weitzman & Malabarba (1999) and Bührnheim *et al.* (2008). In this study, Cheirodontini hosted the same genera of Malabarba (1998) and Weitzman & Malabarba (1999), with the addition of *Axelrodia lindeae* and *Amazonspinther* (Bührnheim, 2006, and Bührnheim *et al.*, 2008, respectively).

Monophyly of *Nanocheirodon* + *Cheirodon*

(Clade 136)

1*. Anterior and posterior regions of the tooth bearing region of the dentary not distinct by teeth size [Ch. 68: 0 > 1].

2*. More ventral procurrent caudal-fin rays than dorsal, ranges never overlapping [Ch. 191: 0 > 1].

3*. Distal tip of the ventral procurrent caudal-fin rays of females anteroventrally bent [Ch. 194: 0 > 1].

4*. Distal tip of the ventral procurrent caudal-fin rays on mature males anteriorly angled [Ch. 197: 0 > 1].

5*. Antermost ventral procurrent caudal-fin rays with a lateral laminar expansion on mature males, between the skin and muscles [Ch. 200: 0 > 1].

Synapomorphies ambiguously optimized for this clade:

6*. Logitudinal diameter of the cleithrum-coracoid, interosseous space smaller than the just posterior cleithrum-coracoid articulation length [Ch. 145: 0 > 1].

7*. Sixteen to thirty ventral procurrent caudal-fin rays [Ch. 190: 1 > 2].

8*. Distal tip of the antermost ventral procurrent caudal-fin rays pointed on males [Ch. 198: 1 > 2].

9*. Antermost hypertrophied procurrent caudal-fin rays elements decreasing in size anteriorly [Ch. 204: 0 > 1].

Monophyly of *Nanocheirodon*

1*. Ventral border of the posteriormost branchiostegal ray on mature males without concavity [Ch. 119: 1 > 0]. Independently acquired in Clade 140.

2*. Only the last unbranched and first branched anal-fin rays longer on males than same rays on females [Ch. 155: 0 > 1]. Uniquely derived in Cheirodontinae.

3*. Absence of hooks on the first branched anal-fin ray on males [Ch. 171: 0 > 1]. Uniquely derived.

4*. Last unbranched anal-fin ray without hooks or in a reduced number (1-3 hooks) [Ch. 172: 0 > 1]. Independently acquired in *Odontostilbe* n. sp. p, *Serrapinnus micropterus*, Clade 151 and 157.

5*. Larger number of ventral procurrent caudal-fin rays on males [Ch. 192: 0 > 1]. Uniquely derived.

Malabarba (1998) described *Nanocheirodon* based on the distinct characters presented by its type species, *Cheirodon insignis* Steindachner, 1880. The genus was diagnosed by the last unbranched and first branched anal-fin rays longer on males than these same rays on females (Ch. 155); larger number of ventral procurrent caudal-fin rays on males (Ch. 192); and the absence of hooks on the first branched anal-fin ray on males (Ch. 171). Herein two more synapomorphies were found to the genus: the ventral border of the posteriormost branchiostegal ray on mature males without concavity (Ch. 119); and the absence of hooks in the last unbranched anal-fin ray too (Ch. 172). Although not evidenced here, Bührnheim (2006) also found the following characters as

synapomorphies for *Nanocheiroduon*: the absence of overlapping teeth in the single tooth row of the premaxilla; a flange on the anterodorsal portion of the maxilla; the lateral ridge of the upper portion of the anguloarticular thick, and with a slightly convex surface well-marked in dorsal view; and the lower border of the dentary straight.

Monophyly of *Cheiroduon*

(Clade 135)

1*. Ventral longitudinal diverging lamellae of the mesethmoid, reduced at the posterior portion of the bone [Ch. 22: 0 > 1]. Independent acquired in Clade 156.

2*. Lateral ridge of the anguloarticular upper portion, short, not reaching the anterior end of the anguloarticular upper portion [Ch. 71: 1 > 2]. Independently acquired in *Aphyocheiroduon hemigrammus*, *Cheiroduontops geayi*, *Compsurini Cuzco* n. sp., *Compsurini Purus* n. sp., *Kolpotocheiroduon* (Clade 123), *Prodontocharax melanotus*, and *Saccoderma melanostigma*.

3*. Two gill raker rows in the ceratobranchial 1 [Ch. 129: 0 > 1]. Independently acquired in *Heterocheiroduon* (Clade 142), *Prodontocharax melanotus*, and Clade 178.

4*. Two gill raker rows in the ceratobranchial 2 [Ch. 130: 0 > 1]. Independently acquired in *Heterocheiroduon* (Clade 142), *Macropsobrycon*, *Prodontocharax melanotus*, and Clade 157 and 178.

5*. Presence of pelvic-fin hooks on females [Ch. 151: 0 > 1]. Uniquely derived.

Synapomorphy ambiguously optimized for this clade:

6*. Third infraorbital not contacting the longitudinal nor the ascending portions of the laterosensory canal of preopercle, leaving a naked area between the third infraorbital and the laterosensory canal of preopercle [Ch. 8: 1 > 2]. Reversed in *Cheiroduon parahybae*; independently acquired in *Aphyocheiroduon hemigrammus*, and Clade 156.

The only synapomorphy found by Malabarba (1998) diagnosing *Cheiroduon* was the presence of pelvic-fin hooks on females (Ch. 151), which was also found as uniquely derived for the genus here.

Monophyly of trans-andean *Cheiroduon* species

(Clade 132)

1*. First infraorbital rectangular [Ch. 5: 1 > 0].

2*. Lateral ethmoid not contacting dorsally the mesethmoid [Ch. 26: 0 > 1].

**Monophyly of *Heterocheiroduon*, “New Genus”, *Axelrodia*, *Megacheiroduon*†,
Amazonspinther, *Spintherobolus*, and *Serrapinnus*
(Clade 141)**

1. Ascending process of the premaxilla as a small projection on the mid-dorsal border of the the bone [Ch. 52: 0 > 1].

2*. Longer axis of the anteriormost teeth nearly at the same axis of the dentary, forwardly projected [Ch. 96: 1 > 2].

3*. At most seven cusps in the dentary teeth [Ch. 105: 0 > 3].

4*. Anal-fin ray segments hypertrophied on mature males [Ch. 158: 0 > 1].

5*. Anterior anal-fin rays with anterior expansion on the base of the most proximal lepidotrichia on mature males [Ch. 163: 0 > 1].

6*. Ligament between most proximal lepidotrichia of the anal-fin anterior rays large, as wide as the ray width [Ch. 165: 0 > 1].

7*. Anal fin hooks bilaterally asymmetrical [Ch. 176: 0 > 1].

Synapomorphies ambiguously optimized for this clade:

8*. Anteromedial process of the lateral ethmoid robust [Ch. 30: 1 > 0].

9*. Distal tips of the three posteriormost hypertrophied procurrent caudal-fin rays expanded, forming a small keel in the ventral profile of the caudal fin on mature males [Ch. 207: 0 > 1].

**Monophyly of *Heterocheiroduon*
(Clade 142)**

1*. Anteromedial process of mesethmoid short, not extending anteriorly between the premaxillae [Ch. 15: 1 > 2]. Independently acquired in *Macropsobrycon*.

2*. Absence of mesethmoid lateral process [Ch. 19: 0 > 1]. Independently acquired in Clades 159 and 181.

3*. Dorsal profile of the maxilla slightly concave [Ch. 59: 0 > 1]. Independently acquired in *Macropsobrycon*, *Compsurini* Leticia n. sp., *Odontostilbe splendida*,

Odontostilbe n. sp. h, *Odontostilbe* n. sp. p, *Saccoderma* (Clade 127), *Serrapinnus microdon*, Clades 160 and 166.

4*. Absence of the anguloarticular anterodorsal process [Ch. 72: 0 > 1]. Independently acquired in *Compsurini* *Leticia* n. sp.

5*. Two gill raker rows in the ceratobranchial 1 [Ch. 129: 0 > 1]. Independently acquired in *Cheirodon* (Clade 135), *Prodontocharax melanotus*, and Clade 178.

6*. Two gill raker rows in the ceratobranchial 2 [Ch. 130: 0 > 1]. Independently acquired in *Cheirodon* (Clade 135), *Macropsobrycon*, *Prodontocharax melanotus*, and Clades 158 and 178.

7*. Absence of more developed pelvic bone on mature males [Ch. 149: 1 > 0]. Reversal.

8*. Hypertrophied whitish tissue on the anal fin of mature males slightly developed, not covering entirely the hooks [Ch. 168: 1 > 0]. Independently acquired in *Axelrodia lindeae*.

9*. Antermost ventral procurrent caudal-fin rays of females laminar-shaped [Ch. 193: 1 > 2]. Uniquely derived.

10*. Lateral line completely pored [Ch. 210: 1 > 0]. Independent acquired in *Acinocheirodon*, “New Genus” n. sp. c, “*Odontostilbe*” *mitoptera*, *Saccoderma* (Clade 127), *Serrapinnus heterodon*, *Serrapinnus* n. sp. t, and Clade 171.

Synapomorphy ambiguously optimized for this clade:

11*. Distal portion of the antermost ventral procurrent caudal-fin rays internal, not visible on the ventral surface of caudal peduncle on mature males [Ch. 202: 1 > 0].

Uniquely reversed.

Malabarba (1998) found two synapomorphies for *Heterocheirodon* which also supported the genus in this analysis: the laminar-shaped antermost ventral procurrent caudal-fin rays of females (Ch. 193: 2), and the antermost ventral procurrent caudal-fin rays not visible on the ventral surface of caudal peduncle on mature males (Ch. 202: 0).

Monophyly of “New Genus”, *Axelrodia*, *Megacheirodon*†, *Amazonspinther*, *Spintherobolus*, and *Serrapinnus*

(Clade 140)

- 1*. Anal-fin ray segments fused according to the mature males sexual development [Ch. 157: 0 > 1].
- 2*. Hypertrophied anal-fin ray segments slab-shaped on mature males, expanded in the sagittal plane [Ch. 159: 0 > 1].
- 3*. Two to three hooks (usually 3) in the most anterior anal-fin ray [Ch. 175: 0 > 1].
- 4*. Main axis of the anteriormost ventral procurrent caudal-fin rays ventrally directed on mature males [Ch. 196: 0 > 1].
- 5*. Caudal peduncle ventrally arched on mature males, sometimes the last vertebrae reaches 45° relative to the first caudal vertebrae [Ch. 237: 0 > 1].

Synapomorphies ambiguously optimized for this clade:

- 6*. Laterosensory canal of the first infraorbital along almost the entire length of the longest axis of the first infraorbital or reaching its half length [Ch. 6: 1 > 0].
- 7*. Posteroventral margin of third infraorbital contacting or falling short the longitudinal and the ascending portions of the laterosensory canal of preopercle [Ch. 8: 1 > 0].
- 8. Toothless portion of the maxilla with approximately the same length of the tooth bearing portion [Ch. 62: 2 > 1].
- 9*. Posteriormost branchiostegal ray without ventral concavity on mature males [Ch. 119: 1 > 0].
- 10*. Postcleithrum 1 round and expanded posteriorly [Ch. 142: 1 > 0].

Monophyly of “New Genus”

(Clade 139)

- 1*. Up to nine cusps in the dentary teeth [Ch. 105: 3 > 4]. Independently acquired in *Pseudocheirodon* (Clade 182).
- 2*. More ventral than dorsal procurrent caudal-fin rays elements, ranges never overlapping [Ch. 191: 0 > 1]. Independently acquired in Clade 136.
- 3*. Distal tip of the ventral procurrent caudal-fin rays anteroventrally bent on females [Ch. 194: 0 > 1]. Independently acquired in *Megacheirodon* and Clade 136.
- 4*. Distal tip of the ventral procurrent caudal-fin rays anteriorly angled on mature males [Ch. 197: 0 > 1]. Independently acquired in Clade 136.

5*. The anteriormost ventral procurrent caudal-fin rays not articulating to the parhypural fused on mature males [Ch. 201: 0 > 1]. Independently acquired in *Serrapinnus piaba*, Clade 155 and 157.

Synapomorphies ambiguously optimized for this clade:

6*. Anteromedial process of the lateral ethmoid thin and sometimes not completely ossified [Ch. 30: 0 > 1]. Independently acquired in *Axelrodia lindeae*, *Serrapinnus calliurus*, *Serrapinnus* n. sp. d, *Serrapinnus* n. sp. m, *Serrapinnus* n. sp. t, and Clade 159.

7*. Sixteen to thirty ventral procurrent caudal-fin rays on males [Ch. 190: 1 > 2]. Independently acquired in Clade 136.

8*. Anterimost hypertrophied procurrent caudal-fin rays decreasing in size anteriorly [Ch. 204: 0 > 1]. Independently acquired in Clade 136 and 157.

The “New Genus” was proposed by Malabarba (1998) with a single species, referred by him as New Genus and Species C. In that work, the “New Genus” was diagnosed with three synapomorphies: the anterior branched anal-fin rays 1 through 5 slab-shaped on mature males; lateral line complete; and the main axis of the ventral procurrent caudal-fin rays not supported by the parhypural is perpendicular to the body, and the most anterior ones anteriorly directed; however none of these characters were found here as synapomorphies. In this work a new species of Cheirodontinae is included in the “New Genus”, which is supported by eight synapomorphies.

Monophyly of *Axelrodia*, *Megacheiroduon*[†], *Amazonspinther*, *Spintherobolus*, and *Serrapinnus*
(Clade 145)

1*. Distal portion of the preural vertebrae 4 to 5 hemal spines slab shaped on mature males [Ch. 179: 0 > 1].

Synapomorphies ambiguously optimized for this clade:

2. Sixth infraorbital anterior lamella lingual-shaped, expanded, and contacting the frontal supra-orbital canal until its pore [Ch. 12: 0 > 1].

3. Anterior and posterior regions of the tooth bearing portion of the dentary not distinct by teeth size [Ch. 68: 0 > 1].

4. Posterior portion of the ectopterygoid not contacting the quadrate [Ch. 107: 0 > 1].

- 5*. More than six slab-shaped anal-fin rays [Ch. 161: 0 > 1].
6. Three posteriormost ventral procurrent caudal-fin rays not hypertrophied on mature males [Ch. 207: 1 > 0].

Monophyly of *Axelrodia*, *Megacheirodon*[†], *Amazonspinther*, and *Spintherobolus*
(Clade 156)

- 1*. First infraorbital rectangular [Ch. 5: 1 > 0].
- 2*. Third infraorbital not contacting the longitudinal nor the ascending portions of the laterosensory canal of preopercle, leaving a naked area between the third infraorbital and the laterosensory canal of preopercle [Ch. 8: 0 > 2].
- 3*. Ventral longitudinal diverging lamellae of the mesethmoid reduced at the posterior portion of the bone [Ch. 22: 0 > 1].
- 4*. Absence of the lateral ethmoid anterodorsal articulation fossae with mesethmoid [Ch. 28: 0 > 1].
- 5*. Extrascapular absent [Ch. 49: 0 > 1].
- 6*. Lateral ridge of the anguloarticular upper portion inconspicuous [Ch. 71: 1 > 0].
- 7*. Premaxillary teeth not pedunculated [Ch. 74: 1 > 0].
- 8*. Premaxillary teeth base juxtaposed [Ch. 79: 0 > 1].
- 9*. Premaxillary teeth contacting each other by their cusps [Ch. 81: 1 > 0].
- 10*. Conical teeth in the premaxilla [Ch. 85: 0 > 1].
- 11*. Maxillary teeth not pedunculated [Ch. 90: 1 > 0].
- 12*. Conical teeth in the maxilla [Ch. 91: 0 > 1].
- 13*. Dentary teeth base juxtaposed [Ch. 98: 0 > 1].
- 14*. Dentary teeth without cusps contact [Ch. 106: 1 > 0].
15. Absence of the quadrate anteroventral foramen [Ch. 110: 1 > 0].
- 16*. Dorsal border of the opercle deeply concave [Ch. 116: 1 > 2].
- 17*. Lower border of the anterior ceratohyal smooth, with one or two slight marked concavities [Ch. 118: 1 > 0].
- 18*. Absence of teeth in the suspensory pharyngeal 2 [Ch. 126: 0 > 1].
- 19*. Presence of a pseudotympanum anterior to first pleural rib [Ch. 235: 0 > 1].
- 20*. Absence of ventral concavity in the abdomen of mature males [Ch. 238: 1 > 0].

Synapomorphies ambiguously optimized for this clade:

- 21*. Base of anteromedial process of the mesethmoid as wide as, or wider than mesethmoid body width at the line just posterior to the lateral process [Ch. 18: 0 > 1].
- 22*. Distance between the distal tips of the lateral process of the mesethmoid equal or shorter than mesethmoid base at its contacting line with the frontals [Ch. 20: 0 > 1].
- 23*. Portion of the lateral ethmoid contacting the mesethmoid cartilaginous [Ch. 27: 0 > 1].
- 24*. Dentary teeth bearing one cusp [Ch. 105: 3 > 1].
- 25*. Gill rakers from the first gill arch without denticles [Ch. 134: 0 > 1].
- 26*. Cleithrum-coracoid interosseous space reduced to a pore [Ch. 145: 0 > 2].
- 27*. Antermost ventral procurrent caudal-fin rays "V"-shaped in frontal view, with lepidotrichias fused distally on females [Ch. 193: 1 > 0].
- 28*. Caudal spot without a posterior extension over middle caudal-fin rays [Ch. 258: 0 > 1].
- 26*. Caudal spot reaching end of middle caudal-fin rays [Ch. 259: 2 > 0].

Monophyly of *Megacheiroduon*[†], *Amazonspinther*, and *Spintherobolus*

(Clade 158)

- 1*. First infraorbital absent or fused with the second infraorbital [Ch. 1: 0 > 1].
- 2. Anterior expansion of the most proximal lepidotrichia extending between the lepidotrichia base of the anterior anal-fin ray on mature males [Ch. 164: 0 > 1].
- 3*. Presence of lateral laminar expansions in the antermost ventral procurrent caudal-fin rays on mature males [Ch. 200: 0 > 1].
- 4*. Antermost ventral procurrent caudal-fin rays fused on mature males [Ch. 201: 0 > 1].
- 5*. Proximal portion of the antermost ventral procurrent caudal-fin rays reduced [Ch. 205: 0 > 1].

Synapomorphies ambiguously optimized for this clade:

- 6*. Antorbital short and wide on lateral view [Ch. 2: 0 > 1].
- 7*. Anteroventral portion of the antorbital square shaped, not expanded [Ch. 3: 1 > 0].
- 8*. Fourth infraorbital reduced [Ch. 9: 1 > 2].
- 9*. Anteromedial process of the mesethmoid ventrally globular [Ch. 16: 1 > 2].
- 10*. Anteromedial process of the mesethmoid pointed on dorsal view [Ch. 17: 1 > 0].

- 11*. Nasal bone shorter than half the distance between the frontal anterior margin and the mesethmoid lateral wing [Ch. 25: 1 > 2].
- 12*. Olfactory nerve foramen of the lateral ethmoid medially to the anteromedial process, at the same horizontal line. [Ch. 29: 0 > 1].
- 13*. Dorsal border of the lateral ethmoid ossified articulation with the frontal through a small ascending expansion dorsolaterally, and medially by chondral articulation [Ch. 32: 0 > 1].
- 14*. Laminar lateroventral expansion of the lateral ethmoid absent [Ch. 33: 0 > 1].
- 15*. Rhinosphenoid absent [Ch. 35: 0 > 1].
- 16*. Orbitosphenoid contacting the parasphenoid [Ch. 36: 0 > 1].
- 17*. Absence of laterosensory canals in the parietal and pterotic [Ch. 41: 0 > 1].
18. Supraorbital laterosensory canal not continuous to the pterotic laterosensory canal [Ch. 42: 0 > 1].
- 19*. Absence of the epioccipital bridge [Ch. 46: 0 > 1].
- 20*. Absence of the posttemporal laterosensory canal [Ch. 47: 0 > 1].
- 21*. Medial lamella of the premaxilla reduced, forming a shallow oval articular fossa along dorsomedial surface of the premaxilla [Ch. 54: 1 > 0].
- 22*. Large dentary anteroventral foramen [Ch. 65: 0 > 1].
- 23*. Dentary symphyseal joint without interdigitations [Ch. 66: 0 > 1].
24. Dentary tooth bearing portion with anterior and posterior regions distinct by difference in teeth size [Ch. 68: 1 > 0].
- 25*. Dentary teeth bearing three to four cusps [Ch. 105: 1 > 2].
- 26*. Metapterygoid without fenestra or foramen [Ch. 111: 0 > 1].
- 27*. Hyomandibular without posterodorsal projection [Ch. 112: 1 > 0].
- 28*. Preopercle without laterosensory canals [Ch. 113: 0 > 1].
- 29*. Anterodorsal portion of the subopercle convex and not protruded. [Ch. 117: 0 > 1].
- 30*. Suspensory pharyngeal 3 without teeth [Ch. 127: 0 > 1].
- 31*. Lower branch of the first gill arch without gill rakers [Ch. 128: 0 > 1].
- 32*. Ceratobranchial 2 bearing two gill raker rows [Ch. 130: 0 > 1].
- 33*. Gill rakers on the second gill arch short and conical [Ch. 131: 0 > 1].
- 34*. Postcleithrum 1 absent [Ch. 141: 0 > 1].
- 35*. Postcleithrum 3 absent [Ch. 143: 0 > 1].
- 36*. Posteroventral border of the coracoids large and pointed [Ch. 147: 1 > 0].
- 37*. Four to five slab-shaped anal-fin rays [Ch. 161: 1 > 0].

38*. Antermost hypertrophied procurrent caudal-fin rays decreasing in size anteriorly [Ch. 204: 0 > 1].

39*. Neuromasts, serial and exposed on head and body [Ch. 260: 0 > 1].

Monophyly of *Megacheirodon*†

1*. Anal-fin bony hooks concentrated along distal half or third portion of the rays [Ch. 174: 0 > 1].

2*. Distal tip of the ventral procurrent caudal-fin rays anteroventrally bent on females. [Ch. 194: 0 > 1].

Monophyly of *Amazonspinther* and *Spintherobolus*

(Clade 157)

1*. Maxilla dorsal profile slightly concave [Ch. 59: 0 > 1].

2*. Coracoid, reduced, nearly discoid [Ch. 146: 0 > 1].

3*. Less than six pored scales in the lateral line [Ch. 211: 0 > 1].

Synapomorphies ambiguously optimized for this clade:

4*. Distal tip of the anterior anal-fin rays surpassing the end of the last anal-fin rays [Ch. 152: 0 > 1].

5*. Hooks on the last unbranched anal-fin ray absent or reduced in number (1-3 hooks) [Ch. 172: 0 > 1].

Monophyly of *Amazonspinther*

1*. Nasal bone straight [Ch. 23: 1 > 0]. Reversal.

2*. Vomer bearing posterolateral process contacting the anteromedial process of the lateral ethmoid [Ch. 34: 0 > 1]. Independently acquired in *Spintherobolus ankoseion*.

3*. Posterior border of the branchiostegals rays smooth, or with few irregular indentations [Ch. 120: 1 > 0]. Reversal.

4*. Antermost proximal radial of the anal-fin rays with an anterior lamina slightly entering the abdominal cavity, between distal portions of the 12th-14th pleural ribs [Ch. 167: 0 > 1]. Uniquely derived.

- 5*. Hemal spines of preural vertebrae 2, 3 and sometimes 4, not articulating with the procurent caudal-fin rays [Ch. 178: 1 > 0]. Reversal.
- 6*. Ventral procurent caudal-fin rays with 5 to 11 elements on males [Ch. 190: 1 > 0]. Reversal.
- 7*. Main axis of the anterior ventral procurent caudal-fin rays posteroventrally directed on mature males [Ch. 196: 1 > 0]. Reversal.
- 8*. Dorsal fin with dark blotch on the proximal portion [Ch. 251: 0 > 1]. Independently acquired in Clade 153.

Amazonspinther dalmata was diagnosed by Bührnheim *et al.* (2008) by the autapomorphic presence of three conspicuous black blotches on the base of the dorsal, anal, and caudal fins (character not included in this analysis). Furthermore, the species also present two uniquely derived characters, the anteriormost proximal radial of the anal-fin rays with an anterior lamina slightly entering the abdominal cavity, and a elongate caudal peduncle with 27.3 to 30.2% of SL (character not included in this analysis). Bührnheim *et al.* (2008) also proposed two reversals as apomorphies to *Amazonspinther*, the low number of ventral procurent caudal-fin rays (Ch. 190) and the hemal spines of preural vertebrae 2, 3 and sometimes 4, not articulating with the procurent caudal-fin rays (Ch. 178), both corroborated by the present analysis.

Monophyly of *Spintherobolus*

(Clade 160)

- 1*. Supraorbital laterosensory canal limited to the anterior portion of the frontal, not reaching the line of epiphyseal bar [Ch. 43: 0 > 1]. Uniquely derived among the Cheirodontinae; independently acquired in *Coptobrycon bilineatus*.
- 2*. Processes in the ventrolateral border of the basihyal [Ch. 122: 0 > 1]. Uniquely derived.
- 3*. Posttemporal bone posterior to the posttemporal fossa, and over the epioccipital [Ch. 139: 0 > 1]. Uniquely derived.
- 4*. Absence of the supraclathrum laterosensory canal [Ch. 140: 0 > 1]. Uniquely derived.
- 5*. Absence of adipose fin [Ch. 177: 0 > 1]. Uniquely derived among the Cheirodontinae; independently acquired in *Coptobrycon bilineatus*.

Synapomorphies ambiguously optimized for this clade:

- 6*. Base of anteromedial process of the mesethmoid narrower than mesethmoid body width at the line just posterior to the lateral process [Ch. 18: 1 > 0]. Reversal.
- 7*. Lateral ethmoid ossified in the portion contacting mesethmoid [Ch. 27: 1 > 0]. Reversal.
- 8*. Posteroventral process of the orbitosphenoid falling short the line of articulation between orbitosphenoid and pterospheneid [Ch. 39: 0 > 1]. Reversed in *Spintherobolus broccae*; independently acquired in *Odontostilbe euspilurus* and *Odontostilbe* n. sp. e.
- 9*. Ascending process of the premaxilla as a small projection on the mid-dorsal border of the premaxilla [Ch. 52: 0 > 1]. Independently acquired in *Cheirodon parahybae*, Clade 122, Clade 141 and Clade 170.
- 10*. Antermost ventral procurrent caudal-fin rays needle-shaped on females, lepidotrichia fused along their length, usually remaining a small opening near their distal tips [Ch. 193: 0 > 1]. Independently acquired in Clade 137.
- 11*. Caudal peduncle spot fainting posteriorly [Ch. 257: 0 > 2]. Uniquely derived, missing for *Spintherobolus papilliferus*.
- 12*. Caudal spot with posterior extension over middle caudal-fin rays [Ch. 258: 1 > 0]. Reversal.

With the discovery of *Amazonspinther* several synapomorphies previously quoted by Malabarba (1998) and Weitzman & Malabarba (1999) for *Spintherobolus* started to support the *Amazonspinther* + *Spintherobolus*. However Bührnheim *et al.*, 2008 listed two characters still synapomorphic for *Spintherobolus*: the lack of adipose fin (Ch. 177) and the relatively small eye (character not included in this analysis). Herein a total of 12 synapomorphies were found for *Spintherobolus*, most of them new for the genus.

Monophyly of *Serrapinnus*

(Clade 144)

- 1*. Presence of an anterior lamella in the sixth infraorbital [Ch. 11: 1 > 0]. Reversal.
2. Sixth infraorbital anterior lamella lingual-shaped, expanded, and contacting the frontal supra-orbital canal until its pore [Ch. 44: 1 > 0]. Reversal, with transformation to state 1 in Clade 147 and 151.

- 3*. Longer axis of the anteriormost teeth oblique to the longer axis of the dentary, anteriorly [Ch. 96: 2 > 1]. Reversal; transformation to state 0 in *Serrapinnus heterodon*.
4. Ascending portion of preopercle lateral canal long, reaching the anterodorsal corner of opercle [Ch. 114: 1 > 0]. Reversal; transformation to state 1 in *Serrapinnus kriegi*, *S. microdon*, and *Serrapinnus* n. sp. ac.
- 5*. Anal-fin hooks concentrated along distal half or third portion of the rays [Ch. 174: 0 > 1]. Reversed in Clade 151 and 153; independently acquired in “New Genus” n. sp. b, *Megacheirodon*, *Pseudocheirodon* (Clade 182), Clade 104, and Clade 128.

Synapomorphy ambiguously optimized for this clade:

6. Posteriormost branchiostegal ray concave on its anterior portion on mature males [Ch. 119: 0 > 1]. Reversed in *Serrapinnus kriegi*.

The genus *Serrapinnus* was described by Malabarba (1998) to include several species previously in *Cheirodon*, *Odontostilbe*, and *Holoshesthes*. These species were grouped by Malabarba (1998) for sharing the caudal peduncle of mature males ventrally arched (Ch. 237), and the main axis of the ventral procurrent caudal-fin rays not supported by the parhypural, perpendicular to the body axis (Ch. 196). However, the presence of the caudal peduncle ventrally arched was also observed on mature males of the “New Genus”, and some of the *Spintherobolus* species, and in this analysis turned out to be a synapomorphy of the Clade 140. The character 196 also resulted as a synapomorphy of the Clade 140, once it was observed in *Axelrodia lindeae*, *Megacheirodon*, “New Genus”, *Spintherobolus*, and *Serrapinnus*.

Monophyly of Compsurini Malabarba, Weitzman & Burns in Malabarba, 1998

(Clade 104)

- 1*. Distance between mesethmoid lateral processes distal tips, equal or shorter than mesethmoid base [Ch. 20: 0 > 1]. Reversed in *Acinocheirodon* and Clade 120; independently acquired in *Aphyocheirodon hemigrammus*, *Serrapinnus* n. sp. a, and Clade 156.
- 2*. Anal-fin hooks anteriorly directed, curved over lateral surface of the anal-fin ray [Ch. 173: 0 > 2]. Uniquely derived; reversed to state 0 in *Acinocheirodon*, and to state 1 in Compsurini Cuzco n. sp. and Compsurini Leticia n. sp.

3*. Anal-fin rays bearing hooks concentrated along distal half or third portion of the rays [Ch. 174: 0 > 1]. Reversed in Clade 120 and independently acquired in Clade 128; independently acquired in *Megacheirodon*, “New Genus” n. sp. b, *Pseudocheirodon* (Clade 182), and Clade 144.

4*. Anal fin more strongly pigmented along distal portion of branched anal-fin rays on mature males [Ch. 253: 0 > 1]. Uniquely derived; reversed in *Acinocheirodon*.

5*. Spermatozoa midpiece not truncated posteriorly, and cytoplasmic canal length is longer than half nucleus length [Ch. 272: 0 > 1]. Uniquely derived.

6*. Spermatozoa with high number of small globular vesicles [Ch. 277: 1 > 0].

Reversal.

Synapomorphies ambiguously optimized for this clade:

7. Ectopterygoid posterior portion not contacting the quadrate [Ch. 107: 0 > 1].

Reversed in Compsurini Cuzco n. sp., *Kolpotocheirodon* (Clade 123), *Macropsobrycon*, and “*Odontostilbe*” *dialeptura*; independently acquired in *Odontostilbe pao*, *Prodontocharax* (Clade 180), Clade 145, and Clade 168.

8. Anterior tip of the proximal centriole located inside the nuclear fossa and the distal centriole outside [Ch. 273: 0 > 1]. Uniquely derived; reversed in *Kolpotocheirodon theloura* and Central America compsurins (Clade 130).

The tribe Compsurini was erected by Malabarba, Weitzman & Burns in Malabarba, 1998, based on six synapomorphies: presence of insemination (Ch. 266); anal-fin hooks positioned along the posterolateral border of the ray, with distal tip anteriorly directed and curved over the lateral surface of the ray (Ch. 176); hooks on the caudal-fin rays (Ch. 184); hooks along the distal length of the 11th to 14th caudal-fin rays (Ch. 186); lateral line interrupted (Ch. 210); and the anal fin more strongly pigmented along the distal portion of the branched rays (Ch. 253). Subsequently in the systematics of the *Odontostilbe*, Bührnheim (2006) found the following additional synapomorphies for the Compsurini: distal margin of the males anal fin almost straight to slight concave (Chs. 154 and 156); hooks on the anal-fin ray of males more numerous in both anterior and posterior portions of the fin (Ch. 170); anal-fin hooks more numerous and distributed along distal half or third portion of anal-fin rays (Ch. 174); and sperm nuclei elongate (Ch. 267). However, only three of those synapomorphies supported the monophyly of the compsurins in this analysis, the shape and direction of the anal-fin bony hooks, the anal-fin hooks distributed along the distal half or third portion of anal-

fin rays, and the sexually dimorphic color pattern that the compsurini mature males present in the anal fin. The remaining characters found by Malabarba (1998) and Bührnheim (2006) as synapomorphies of the tribe, are now supporting and defining the relationships of some internal nodes within the Compsurini.

Oliveira (2007) found a monophyletic Compsurini based on a single character related to the presence of the midpiece of the spermatozoa not truncated posteriorly, bearing a long cytoplasmic canal (Ch. 272). In addition to this character, two more characters obtained from the ultrastructure of spermatozoa supported herein the monophyly of the Compsurini, the reversal of spermatozoa with a large number of small and globular vesicles, and the anterior tip of the proximal centriole located inside the nuclear fossa and the distal centriole outside.

Monophyly of Compsurini Cuzco n. sp. and Compsurini Tingo n. sp.

(Clade 126)

1. Premaxilla without the ascending process [Ch. 51: 0 > 1]. Independently acquired in Compsurini Yurimaguas n. sp., *Serrapinnus* n. sp. d, *Serrapinnus* n. sp. e, and Clade 181.

Synapomorphy ambiguously optimized for this clade:

2. Laterosensory canal along almost the entire length of the longest axis of the first infraorbital or reaching its half length [Ch. 6: 1 > 0]. Reversal.

Autapomorphies of Compsurini Cuzco n. sp.

1*. Anterior lamella of the sixth infraorbital lingual-shaped, expanded, and contacting the frontal supra-orbital canal until its pore [Ch. 12: 0 > 1]. *Acinocheiroidon*, *Compsura* Guaporé n. sp., Clade 145, and Clade 171.

2*. Orbitosphenoid with a dorsal fenestra with frontal [Ch. 37: 0 > 1]. Independently acquired in *Axelrodia lindeae*, *Serrapinnus micropterus*, Compsurini Leticia n. sp., and Clade 102.

3*. Lateral ridge of the anguloarticular short, not reaching the anterior end of the anguloarticular anterodorsal process [Ch. 71: 2 > 1]. Reversed to state 1 in *Aphyocheiroidon hemigrammus*, *Cheiroidon* (Clade 135), *Cheiroidontops geayi*,

Compsurini Purus n. sp., *Kolpotocheiroidon* (Clade 123), *Prodontocharax melanotus*, and *Saccoderma melanostigma*.

4*. Anterior portion of the basihyal concave [Ch. 123: 0 > 1]. Uniquely derived.

5. Anal-fin hooks dorsally directed [Ch. 173: 2 > 1]. Independently acquired in Compsurini Leticia n. sp.

6*. Laterosensory canal extending nearly half-length of the middle caudal-fin rays [Ch. 212: 0 > 1]. Independently acquired in Clade 171.

Autapomorphy ambiguously optimized for this species:

7. Ectopterygoid posterior portion contacting the quadrate [Ch. 107: 1 > 0]. Reversal.

Autapomorphies of Compsurini Tingo n. sp.

1*. Fourth infraorbital squarish, similar in width and height [Ch. 9: 1 > 0]. Reversal.

2*. Fifth infraorbital broad, with expanded lateral laminae from the laterosensory canal [Ch. 10: 1 > 0]. Reversal.

3*. Longer axis of the anteriormost teeth nearly at the same axis of the dentary, forwardly projected [Ch. 96: 1 > 2]. Compsurini Yurimaguas n. sp., *Odontostilbe* n. sp. m, *O. pulchra*, Clade 141, and Clade 181.

4. Dentary teeth bearing at most seven cusps [Ch. 105: 0 > 3]. Independently acquired in Clade 122, Clade 141 and Clade 171.

5*. Postcleithrum 1 round and expanded posteriorly [Ch. 142: 1 > 0]. Reversal.

6*. All anal-fin rays longer on males than on females [Ch. 154: 0 > 1]. Independently acquired in *Acinocheiroidon*, Compsurini Yurimaguas n. sp., and Clade 119.

7. Anal-fin hooks more numerous in both anterior and posterior portions of anal fin, and reduced in the middle portion of anal fin [Ch. 170: 0 > 1].

8. Urogenital papilla hypertrophied on adult females [Ch. 263: 0 > 1]. Independently acquired in Clade 122.

Monophyly of *Acinocheiroidon*, *Macropsobrycon*, Compsurini Purus n. sp., Compsurini Napo n. sp., Compsurini Leticia n. sp., Compsurini Yurimaguas n. sp., *Kolpotocheiroidon*, *Compsura*, “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura*, “*Odontostilbe*” *mitoptera*, and *Saccoderma*
(Clade 103)

1. Presence of sexual dimorphism in the caudal fin [Ch. 180: 0 > 1]. Uniquely derived.
2. Presence of hooks in the lower lobe of the caudal fin [Ch. 184: 0 > 1]. Uniquely derived; reversed in Clade 120; independently acquired in *Kolpotocheiroduon theloura*, “*Odontostilbe*” *mitoptera*, and *Saccoderma* (Clade 127).
3. Sperm nuclei elongated, intrasperm [Ch. 267: 0 > 1]. Uniquely derived; reversed in *Kolpotocheiroduon theloura*.

Monophyly of *Acinocheiroduon* and *Macropsobrycon*

(Clade 102)

1. Fourth infraorbital squarish, similar in width and height [Ch. 9: 1 > 0]. Reversal.
2. Orbitosphenoid bearing a dorsal fenestra with the frontal [Ch. 37: 0 > 1]. Independently acquired in *Axelrodia lindeae*, *Compsurini* Cuzco n. sp., *Compsurini* Leticia n. sp., and *Serrapinnus micropterus*.
3. Maxilla with a longitudinal groove just below the dorsolateral border [Ch. 56: 0 > 1]. Independently acquired in *Compsurini* Leticia n. sp., *Odontostilbe parecis*, *Odontostilbe* n. sp. p, Clade 128, Clade 143 and Clade 165.
4. Spacement between 14 and 15 caudal-fin rays bigger on males than on females [Ch. 181: 0 > 1]. Uniquely derived.
5. Skin flaps on the lower lobe of the caudal fin, hypertrophied and associated to whitish tissue [Ch. 231: 0 > 1]. Independently acquired in “*Odontostilbe*” *dialeptura* and (Clade 123).
6. Conspicuous small spot on the anterior portion of the dorsal fin [Ch. 249: 0 > 1]. Independently acquired in *Compsura* (Clade 124) and *Kolpotocheiroduon figuiredoi*.

Synapomorphies ambiguously optimized for this clade:

7. Toothless portion of the maxilla with twice the length of the tooth bearing portion [Ch. 62: 1 > 2]. Reversed to toothless maxilla in *Macropsobrycon*; independently acquired in *Serrapinnus heterodon* and Clades 120, 137, 155, 156, and 165.
8. Dentary teeth with 3 medial cusps larger nearly equal in size [Ch. 103: 0 > 1]. Reversed to conical teeth in *Macropsobrycon*; independently acquired in Clades 154 and 165.
9. Gill rakers on the upper branch of the first gill arch equal or smaller than the epibranchial width [Ch. 133: 1 > 0]. Reversal, transformed to state 2 in *Macropsobrycon*.

Autapomorphies of *Acinocheiroduon*

- 1*. Fifth infraorbital broad, with expanded lateral laminae from the laterosensory canal [Ch. 10: 1 > 0]. Reversal.
2. Sixth infraorbital with a lingual-shaped anterior lamella, expanded, and contacting the frontal supra-orbital canal until its pore [Ch. 12: 0 > 1]. Independently acquired in *Compsura* Guaporé n. sp., *Compsurini* Cuzco n. sp., Clade 145, and Clade 171.
3. Distance between distal tips of the mesethmoid lateral processes wider than mesethmoid base at its contacting line with the frontals [Ch. 20: 1 > 0]. Reversal.
4. Maxilla extending posteriorly the vertical line through the ventral limit of the lateral ethmoid [Ch. 55: 1 > 0]. Reversal.
5. Lower branch of the anguloarticular elongate, reaching or falling short to the line through the toothed portion of the dentary [Ch. 73: 0 > 1]. Independently acquired in *Saccoderma* (Clade 127), *Serrapinnus heterodon*, Clade 168 and Clade 181.
6. Longer axis of the anteriormost dentary teeth perpendicular to the longer axis of the dentary [Ch. 96: 1 > 0]. Reversal.
- 7*. Dusp of the dentary teeth cusps nearly squared [Ch. 102: 0 > 2]. Independently acquired in Clade 165.
- 8*. Dentary teeth with central cusps aligned in row with other teeth cusps forming a continuous cutting edge [Ch. 104: 0 > 1]. Independently acquired in *Serrapinnus heterodon* and Clade 165.
- 9*. Mesopterygoid bearing teeth [Ch. 109: 0 > 1]. Independently acquired in *Holoshesthes pequiria*, *Odontostilbe* n. sp. b, and Clade 173.
- 10*. Postcleithrum 1 round and expanded posteriorly [Ch. 142: 1 > 0]. Reversal.
- 11*. Pelvic bone more developed on mature males [Ch. 149: 1 > 0]. Reversal.
12. All anal-fin rays longer on males than on females [Ch. 154: 0 > 1]. Independently acquired in *Compsurini* Tingo n. sp., *Compsurini* Yurimaguas n. sp., and Clade 119.
13. Posterior branched anal-fin rays elongated, longer than median branched rays. [Ch. 156: 0 > 1]. Independently acquired in Clade 119.
- 14*. Anal-fin hooks posterodorsally directed [Ch. 173: 2 > 0]. Reversal.
- 15*. Hook bearing caudal-fin rays thickened on mature males [Ch. 183: 0 > 1]. Independently acquired in *Compsurini* Purus n. sp.

16*. Three posteriormost ventral procurent caudal-fin rays hypertrophied on mature males, with distal tips expanded, forming a small keel in the ventral profile of the caudal fin [Ch. 207: 0 > 1]. Independently acquired in *Compsurini Purus* n. sp., “*Odontostilbe*” *mitoptera*, *Serrapinnus* n. sp. upm, Clade 141, and Clade 150.

17*. Three posteriormost ventral procurent caudal-fin rays forming abrupt keel on mature males [Ch. 208: 0 > 1]. Uniquely derived.

18. Lateral line completely pored [Ch. 210: 1 > 0]. Reversal.

19*. Muscle *interrradialis* in the lower lobe of the caudal fin thicker between the caudal-fin rays 11 to 15 [Ch. 243: 0 > 1]. Uniquely derived.

20*. Anal fin without conspicuous color pattern on mature males [Ch. 253: 1 > 0]. Reversal.

21. Caudal-peduncle spot narrowing posteriorly over middle caudal-fin rays base [Ch. 257: 0 > 1]. Independently acquired in *Cheirodon kiliani*, and Clade 119.

22*. Urogenital opening slit-shaped on adult females [Ch. 262: 0 > 1]. Uniquely derived.

23. Nuclear rotation absent, with flagellum attached laterally to the nucleus [Ch. 271: 0 > 1]. Independently acquired in Clade 128.

24. Centrioles positioned perpendicular to each other [Ch. 274: 0 > 1]. Independently acquired in Clade 128.

25. Mitochondria positioned near the tip of nucleus (without nuclear rotation) and distant from the origin of the flagellum [Ch. 275: 0 > 1]. Independently acquired in Clade 128.

Autapomorphy ambiguously optimized for this species:

26. Lateral ethmoid contacting the mesethmoid [Ch. 6: 1 > 0]. Reversal.

Autapomorphies of *Macropsobrycon*

1*. Third infraorbital ventrally contacting the laterosensory canal of preopercle, but leaving a posterior naked area between border of the third infraorbital and ascending portion of the laterosensory canal of preopercle, as wide as or wider than the canal [Ch. 8: 0 > 1]. Independently acquired in *Pseudocheirodon terrabae*, Clade 137 and Clade 178.

2*. Anteromedial process of the mesethmoid short, not extending anteriorly between the premaxillae [Ch. 15: 1 > 2]. Independently acquired in *Heterocheirodon* (Clade 142).

- 3*. Nasal bone straight [Ch. 23: 1 > 0]. Reversal.
- 4*. Posterior tip of the nasal bone more than one pore distant from frontal bone [Ch. 24: 1 > 2]. Independently acquired in *Cheirodon kiliani* and *Heterocheirodon yatai*.
- 5*. Nasal bone shorter than half the distance between the frontal anterior margin and the mesethmoid lateral wing [Ch. 25: 1 > 2]. Independently acquired in *Cheirodon kiliani*, *Compsurini Napo n. sp.*, *Kolpotocheirodon* (Clade 123), and Clade 157.
- 6*. Anteromedial process of the lateral ethmoid robust [Ch. 30: 1 > 0]. Reversal.
7. Supraorbital laterosensory canal not continuous to pterotic laterosensory canal [Ch. 42: 0 > 1]. Independently acquired in *Aphyocheirodon hemigrammus*, *Compsurini Leticia n. sp.*, *Compsurini Purus n. sp.*, *Heterocheirodon yatai*, *Kolpotocheirodon* (Clade 123), *Serrapinnus n. sp. ac*, Clade 130, Clade 146 and Clade 158.
- 8*. Anterior fontanel of the frontal bigger than half length between epiphyseal bar and mesethmoid articulation [Ch. 48: 1 > 0]. Reversal.
- 9*. Mouth superior, located above the horizontal through the middle of the eye [Ch. 50: 0 > 1]. Uniquely derived among the Cheirodontinae.
- 10*. Ascending process of the premaxilla square-shaped [Ch. 52: 0 > 2]. Uniquely derived.
- 11*. Ascending process of the premaxilla running over the lateral process of the mesethmoid [Ch. 53: 1 > 0]. Reversal.
- 12*. Medial lamella of the premaxilla reduced, forming a shallow oval articular fossa along dorsomedial surface of the premaxilla [Ch. 54: 1 > 0]. Reversal.
- 13*. Main axis of the maxilla arched dorsally [Ch. 58: 0 > 2]. Uniquely derived among the Cheirodontinae.
14. Dorsal profile of the maxilla slightly concave [Ch. 59: 0 > 1]. Independently acquired in *Compsurini Leticia n. sp.*, *Heterocheirodon* (Clade 142), *Odontostilbe n. sp. h*, *Odontostilbe n. sp. p*, *O. splendida*, *Saccoderma* (Clade 127), *Serrapinnus microdon*, Clade 157, and Clade 166.
15. Premaxillary teeth not pedunculated, with tooth base enlarged [Ch. 74: 1 > 0]. Reversal.
- 16*. Space between premaxillary teeth equal or bigger than tooth base width [Ch. 80: 0 > 1]. Independently acquired in *Cheirodon parahybae*, *Prodontocharax alleni*, *Serrapinnus microdon*, Clade 138.
17. Cusps of the premaxillary teeth not contacting each other [Ch. 81: 1 > 0]. Reversal.
- 18*. Premaxillary teeth conical [Ch. 85: 0 > 1]. Independently acquired in Clade 156.

- 19*. Maxilla toothless [Ch. 89: 0 > 1]. Uniquely derived among the Cheirodontinae.
- 20*. Dentary teeth larger in the base, with conical cusps [Ch. 92: 1 > 0]. Reversal.
- 21*. Space between dentary teeth equal or bigger than tooth base width [Ch. 99: 0 > 1]. Uniquely derived among the Cheirodontinae.
- 22*. Dentary teeth conical [Ch. 101: 0 > 1]. Independently acquired in *Axelrodia lindeae*.
23. Dentary teeth bearing one cusp [Ch. 105: 0 > 1]. Independently acquired in *Axelrodia lindeae* and *Spintherobolus papilliferus*.
- 24*. Cusps of dentary teeth not contacting each other [Ch. 106: 1 > 0]. Reversal.
- 25*. Hyomandibular without the posterordorsal projection [Ch. 112: 1 > 0]. Reversal.
- 26*. Preopercle ascending laterosensory canal short, reaching the posterior articular surface of the hyomandibular condyle [Ch. 114: 0 > 1]. Independently acquired in *Aphyocheirodon hemigrammus*, *Compsurini Purus n. sp.*, *Kolpotocheirodon* (Clade 123), *Odontostilbe n. sp. b.*, *Saccoderma hastata*, *Serrapinnus kriegi*, *Serrapinnus microdon*, *Serrapinnus n. sp. ac*, Clade 137.
- 27*. Two rows of gill rakers in the ceratobranchial 2 [Ch. 130: 0 > 1]. Independently acquired in *Cheirodon* (Clade 135), *Heterocheirodon* (Clade 142), *Prodontocharax melanotus*, Clade 157 and Clade 178.
- 28*. Postcleithrum 3 without lamella [Ch. 144: 1 > 0]. Reversal.
- 29*. Caudal fin with spinelets on mature males [Ch. 189: 0 > 1]. Uniquely derived.
- 30*. Lower lobe of the caudal fin bearing a scale modified in shape [Ch. 214: 0 > 1]. Independently acquired in *Compsurini Purus n. sp.* and Clade 119.
- 31*. Upper lobe of the caudal fin bearing a scale modified in shape [Ch. 215: 0 > 1]. Independently acquired in Clade 119.
- 32*. Mentonian region with a small black blotch [Ch. 245: 0 > 1]. Uniquely derived.
- 33*. Dorsal fin with scattered melanophores concentrated on the distal portion of the fin [Ch. 250: 0 > 1]. Independently acquired in *Compsura* (Clade 118), "*Odontostilbe*" *mitoptera*, *Saccoderma melanostigma*, Clade 143, Clade 165 and Clade 173.
- 34*. Anal fin with a conspicuous spot in the proximal portion of anteriormost rays [Ch. 254: 0 > 1]. Independently acquired in *Kolpotocheirodon* (Clade 123).
35. Spermatozoa bearing accessory microtubules [Ch. 269: 0 > 1]. Uniquely derived.
36. Spermatozoa bearing striated rootlet [Ch. 270: 0 > 1]. Uniquely derived.

Autapomorphies ambiguously optimized for this species:

37. Posterior portion of the ectopterygoid contacting the quadrate [Ch. 107: 1 > 0].

Reversal.

38. Gill rakers on the upper branch of the first gill arch twice longer than the epibranchial width [Ch. 133: 0 > 2]. Uniquely derived among the Cheirodontinae.

Monophyly of Compsurini Purus n. sp., Compsurini Napo n. sp., Compsurini Leticia n. sp., Compsurini Yurimaguas n. sp., *Kolpotocheirodon*, *Compsura*, “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura*, “*Odontostilbe*” *mitoptera*, and *Saccoderma*

(Clade 122)

1. Ascending process of the premaxilla as a small projection on the mid-dorsal border of the premaxilla [Ch. 52: 0 > 1]. Reversed in Clade 128; independently acquired in *Cheirodon parahybae*, Clade 141, Clade 160 and Clade 170.

2. Dentary teeth bearing at most seven cusps [Ch. 105: 0 > 3]. Reversed to state 0 in Compsurini Leticia n. sp.; independently acquired in *Cheirodon interruptus*, Compsurini Tingo n. sp., Clade 141 and Clade 171.

3. Anal-fin hooks restricted to the i+5 anal-fin rays [Ch. 170: 0 > 2]. Reversed to state 0 in Clade 125 and to state 1 in Clade 119.

4. Abdominal region of the mature males deeply concave ventrally [Ch. 239: 0 > 1]. Reversed to state 0 in Compsurini Napo n. sp. and in *Compsura* (Clade 118).

5. Urogenital papilla hypertrophied on adult females [Ch. 263: 0 > 1]. Reversed to state 0 in Compsurini Leticia n. sp., and Clade 119; independently acquired in Compsurini Tingo n. sp.

Synapomorphy ambiguously optimized for this clade:

6. Caudal fin modified scales forming a pouch [Ch. 220: 0 > 1]. Reversed in the Central America compsurins (Clade 130).

Autapomorphies of Compsurini Purus n. sp.

1*. Supraorbital laterosensory canal not continuous to the pterotic laterosensory canal [Ch. 42: 0 > 1]. Independently acquired in *Aphyocheirodon hemigrammus*, Compsurini Leticia n. sp., *Heterocheirodon yatai*, *Kolpotocheirodon* (Clade 123), *Macropsobrycon*, *Serrapinnus* n. sp. ac, Clade 130, Clade 146 and Clade 158.

- 2*. Anterior-medial tooth bearing portion of dentary shorter than posterior portion [Ch. 69: 1 > 0]. Reversal.
- 3*. Lateral ridge of the anterodorsal process of the anguloarticular short, not reaching the anterior end of the anguloarticular anterodorsal process [Ch. 71: 2 > 1]. Independently acquired in *Aphyocheiroduon hemigrammus*, *Cheirodontops geayi*, *Cheirodon* (Clade 135), *Compsurini Cuzco* n. sp., *Kolpotocheiroduon* (Clade 123), *Prodontocharax melanotus*, and *Saccoderma melanostigma*.
- 4*. Ascending laterosensory canal of the preopercle short, reaching the posterior articular surface of the hyomandibular condyle [Ch. 114: 0 > 1]. Independently acquired in *Aphyocheiroduon hemigrammus*, *Kolpotocheiroduon* (Clade 123), *Macropsobrycon*, *Odontostilbe* n. sp. b, *Saccoderma hastata*, *Serrapinnus kriegi*, *S. microdon*, *Serrapinnus* n. sp. ac, and Clade 137.
- 5*. Caudal-fin rays bearing hooks thickened on mature males [Ch. 183: 0 > 1]. Independently acquired in *Acinocheiroduon*.
- 6*. Three posteriormost ventral procurrent caudal-fin rays hypertrophied on mature males, with distal tips expanded, forming a small keel in the ventral profile of the caudal fin [Ch. 207: 0 > 1]. Independently acquired in *Acinocheiroduon*, “*Odontostilbe*” *dialeptura*, *Serrapinnus* n. sp. upm, Clade 141 and Clade 150.
- 7*. Presence of scale modified in shape in the lower lobe of the caudal-fin [Ch. 214: 0 > 1]. Independently acquired in *Macropsobrycon* and Clade 119.
- 8*. Muscle *interradialis* in the caudal-fin lower lobe more extended posteriorly between rays [Ch. 242: 0 > 1]. Independently acquired in Clade 119.
- 9*. Muscle *interradialis* in the caudal fin thicker and more concentrated in the ventral direction in the lower lobe [Ch. 244: 0 > 1]. Independently acquired in Clade 119.
- 10*. Urogenital papilla hypertrophied in two longitudinal skin flaps on adult females [Ch. 264: 0 > 1]. Independently acquired in *Kolpotocheiroduon* (Clade 123).

Autapomorphies ambiguously optimized for this species:

11. Caudal-fin hooks straight. [Ch. 187: 0 > 1]. Independently acquired in *Acinocheiroduon*.
12. Opening of the caudal-fin pouch scale over the 13th to 18th principal caudal-fin rays [Ch. 225: 0 > 2]. Uniquely derived.

Monophyly of Compsurini Napo n. sp., Compsurini Leticia n. sp., Compsurini Yurimaguas n. sp., *Kolpotocheiroduon*, *Compsura*, “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura*, “*Odontostilbe*” *mitoptera*, and *Saccoderma*
(Clade 121)

1. Sixth infraorbital without anterior lamella [Ch. 11: 0 > 1]. Reversed in Compsurini Yurimaguas n. sp., and Clade 117; independently acquired in Clade 137.
2. Middle caudal-fin rays with large posteriorly placed hooks [Ch. 186: 1 > 0].
Reversal.
3. Skin flaps on the lower lobe of the caudal fin running for more than half length of the ray [Ch. 226: 0 > 1]. Reversed in Central America compsurins (Clade 130).
4. Lower lobe of the caudal fin bearing skin flaps over the 18th to 19th principal caudal-fin rays [Ch. 230: 0 > 1]. Reversed in “*Odontostilbe*” *dialeptura*.

Synapomorphies ambiguously optimized for this clade:

5. Posterodorsal border of the last modified pouch-scale from the longitudinal line below the lateral line continuous to skin flap [Ch. 223: 0 > 1]. Uniquely derived.
6. Pouch-scale opening formed by the last modified scale from the first and second longitudinal line below the lateral line [Ch. 224: 0 > 1]. Uniquely derived.

Monophyly of Compsurini Napo n. sp., Compsurini Leticia n. sp., and Compsurini Yurimaguas n. sp.
(Clade 124)

1. Caudal-fin hooks emerging laterally from the dorsolateral surface of the caudal-fin rays [Ch. 188: 0 > 1]. Uniquely derived.

Autapomorphies of Compsurini Napo n. sp.

- 1*. Nasal bone straight [Ch. 23: 1 > 0]. Reversal.
- 2*. Nasal bone shorter than half the distance between the frontal anterior margin and the mesethmoid lateral wing [Ch. 25: 1 > 2]. Independently acquired in *Kolpotocheiroduon* (Clade 123), *Macropsobrycon* and Clade 157.
- 3*. Anteromedial process of the lateral ethmoid robust [Ch. 30: 1 > 0]. Reversal.
4. Abdomen slightly concave ventrally [Ch. 239: 1 > 0]. Reversal.

Monophyly of Compsurini Leticia n. sp. and Compsurini Yurimaguas n. sp.

(Clade 125)

1. Hooks on the upper lobe of the caudal fin [Ch. 185: 0 > 1]. Uniquely derived.
2. Caudal-peduncle dorsal and ventral margins convex on mature males, with scales and skin non-attached on hipaxialis muscles, resulting in an internal chamber between them and a slightly camber on caudal-peduncle ventral surface [Ch. 240: 0 > 1].

Independently acquired in *Kolpotocheirodon* (123) and Clade 130.

Synapomorphy ambiguously optimized for this clade:

3. Anal-fin hooks bigger and more numerous on the anterior portion and progressively reduced to the posterior anal-fin rays [Ch. 170: 2 > 0]. Reversal; transformed to state 1 in Compsurini Yurimaguas n. sp.

Autapomorphies of Compsurini Leticia n. sp.

1. Orbitosphenoid with dorsal fenestra with frontal [Ch. 37: 0 > 1]. Independently acquired in *Axelrodia lindeae*, Compsurini Cuzco n. sp., *Serrapinnus micropterus* and Clade 102.
2. Supraorbital laterosensory canal not continuous with the pterotic laterosensory canal [Ch. 42: 0 > 1]. Independently acquired in *Aphyocheirodon hemigrammus*, Compsurini Purus n. sp., *Heterocheirodon yatai*, *Kolpotocheirodon* (Clade 123), *Macropsobrycon*, *Serrapinnus kriegi*, *Serrapinnus* n. sp. ac, *Serrapinnus* n. sp. ups, Clade 130, Clade 133, and Clade 158.
3. Maxilla with a longitudinal groove just below the dorsolateral border [Ch. 56: 0 > 1]. Independently acquired in *Odontostilbe parecis*, *Odontostilbe* n. sp. p, Clade 102, Clade 128, Clade 143 and Clade 165.
4. Dorsal profile of the maxilla slightly concave [Ch. 59: 0 > 1]. Independently acquired in *Heterocheirodon* (Clade 142), *Macropsobrycon*, *Odontostilbe splendida*, *Odontostilbe* n. sp. h, *Odontostilbe* n. sp. p, *Saccoderma* (Clade 127), *Serrapinnus microdon*, Clade 160 and Clade 166,
5. Margin of the tooth bearing portion of the maxilla continuous to the toothless margin [Ch. 60: 1 > 0]. Reversal.

6. Toothless portion of the maxilla extended, more than two times longer than the tooth bearing portion of the maxilla [Ch. 62: 1 > 3]. Independently acquired in *Axelrodia lindeae*, *Odontostilbe* n. sp. p, *Saccoderma* (Clade 127), Clade 138, Clade 143 and Clade 162.

7*. Absence of anguloarticular anterodorsal projection [Ch. 72: 0 > 1]. Independently acquired in *Heterocheiroidon* (Clade 142).

8. Premaxillary teeth not pedunculated, with tooth base enlarged [Ch. 74: 1 > 0].

Reversal.

9. Cusps of the premaxillary teeth not contacting each other [Ch. 81: 1 > 0]. Reversal.

10. Dentary teeth bearing five cusps [Ch. 105: 3 > 0]. Reversal.

11*. Absence of pelvic bone more developed on mature males [Ch. 149: 1 > 0].

Reversal.

12*. Anal-fin hooks dorsally directed [Ch. 173: 2 > 1]. Independently acquired in *Compsurini Cuzco* n. sp.

13*. Hemal spines of preural vertebrae 2 to 5 contacting the procurrent caudal-fin rays [Ch. 178: 0 > 1]. Independently acquired in Clade 137.

14. Urogenital papilla not hypertrophied on adult females [Ch. 263: 1 > 0]. Reversal.

Autapomorphies of *Compsurini Yurimaguas* n. sp.

1. Sixth infraorbital bearing an anterior lamella [Ch. 11: 1 > 0]. Reversal.

2*. Premaxilla without ascending process [Ch. 51: 0 > 1]. Independently acquired in *Serrapinnus* n. sp. d, *Serrapinnus* n. sp. e and Clade 126.

3*. Longer axis of the anteriormost dentary teeth nearly at the same axis of the dentary, forwardly projected [Ch. 96: 1 > 2]. Independently acquired in *Compsurini Tingo* n. sp., *Odontostilbe pulchra*, *Odontostilbe* n. sp. m, Clade 141 and Clade 181.

4*. All anal-fin rays longer on males than on females [Ch. 154: 0 > 1]. Independently acquired in *Acinocheiroidon*, *Compsurini Tingo* n. sp. and Clade 119.

Autapomorphy ambiguously optimized for this species:

5. Anal-fin hooks more numerous in both anterior and posterior portions of anal fin, reduced in the middle portion of anal fin [Ch. 170: 0 > 1]. Independently acquired in *Compsurini Tingo* n. sp., and Clade 119.

**Monophyly of *Kolpotocheirodon*, *Compsura*, “*Compsura*” *gorgonae*, “*Odontostilbe*”
dialeptura, “*Odontostilbe*” *mitoptera*, and *Saccoderma***

(Clade 120)

1. Distance between distal tips of the mesethmoid lateral processes wider than mesethmoid base at its contacting line with the frontals [Ch. 20: 1 > 0]. Reversal.

Synapomorphies ambiguously optimized for this clade:

2. Laterosensory canal along almost the entire length of the longest axis of the first infraorbital or reaching its half length [Ch. 6: 1 > 0]. Reversal.

3. Base of anteromedial process of the mesethmoid as wide as, or wider than mesethmoid body width at the line just posterior to the lateral process [Ch. 18: 0 > 1]. Reversed in Clade 128; independently acquired in *Odontostilbe* n. sp. h and Clade 156.

4. Toothless portion of the maxilla with twice the length of the tooth bearing portion [Ch. 62: 1 > 2]. Reversed to state 1 in *Compsura* (Clade 118); transformed to state 3 in *Saccoderma* (Clade 127); independently acquired in *Acinocheirodon*, *Serrapinnus heterodon*, *S. kriegi*, Clade 137, Clade 155, Clade 156, and Clade 165.

5. Premaxillary teeth with all cusps similar in form and size. [Ch. 87: 0 > 1]. Reversed in Clade 128; independently acquired in *Pseudocheirodon* (Clade 182).

6. Anal fin with hooks concentrated along middle-length of the rays, with reduced number on the most proximal and most distal portions [Ch. 174: 1 > 0]. Reversal.

7. Lower lobe of the caudal fin without hooks [Ch. 184: 1 > 0]. Reversal.

8. Scales reduced in size over the middle caudal-fin rays base. [Ch. 261: 0 > 1].

Uniquely derived; reversed in Clade 128.

Monophyly of *Kolpotocheirodon*

(Clade 123)

1*. Fourth infraorbital squarish, similar in width and height [Ch. 9: 1 > 0]. Reversal.

2*. Fifth infraorbital broad, with expanded lateral laminae from the laterosensory canal [Ch. 10: 1 > 0]. Reversal.

3*. Nasal bone shorter than half the distance between the frontal anterior margin and the mesethmoid lateral wing [Ch. 25: 1 > 2]. Independently acquired in *Cheirodon kiliani*, *Compsurini* Napo n. sp., *Macropsobrycon* and Clade 158.

- 4*. Supraorbital laterosensory canal not continuous with pterotic laterosensory canal [Ch. 42: 0 > 1]. Independently acquired in *Aphyocheirodon hemigrammus*, Compsurini *Leticia* n. sp., Compsurini *Purus* n. sp., *Heterocheirodon yatai*, *Macropsobrycon*, *Serrapinnus* n. sp. ac, Clade 130, Clade 134, Clade 146 and Clade 158.
- 5*. Supratemporal laterosensory canal short, ending at half length away the frontoparietal fontanel [Ch. 45: 0 > 1]. Uniquely derived.
- 6*. Lateral ridge of the anguloarticular anterodorsal process short, not reaching the anterior end of the anguloarticular anterodorsal process [Ch. 71: 2 > 1]. Independently acquired in *Aphyocheirodon hemigrammus*, *Cheirodontops geayi*, *Cheirodon* (Clade 135), Compsurini *Cuzco* n. sp., Compsurini *Purus* n. sp., *Prodontocharax melanotus*, and *Saccoderma melanostigma*.
- 7*. Ectopterygoid posterior portion contacting the quadrate [Ch. 107: 1 > 0]. Reversal.
- 8*. Ascending portion of the ascending laterosensory canal of the preopercle short, reaching the posterior articular surface of the hyomandibular condyle [Ch. 114: 0 > 1]. Independently acquired in *Aphyocheirodon hemigrammus*, Compsurini *Purus* n. sp., *Macropsobrycon*, *Saccoderma hastata*, *Serrapinnus kriegi*, *S. microdon*, *Serrapinnus* n. sp. ac, and Clade 137.
- 9*. Papillae marginating the dorsal-fin skin flaps on males [Ch. 227: 0 > 1]. Uniquely derived.
- 10*. “Pineapple” organs on the caudal-fin skin flaps on mature males [Ch. 229: 0 > 1]. Uniquely derived.
- 11*. Skin flaps on the lower lobe of the caudal fin hypertrophied and associated to whitish tissue [Ch. 231: 0 > 1]. Independently acquired in “*Odontostilbe dialeptura*” and Clade 102.
- 12*. Caudal-peduncle dorsal and ventral margins convex on mature males, with scales and skin non-attached on hipaxialis muscles, resulting in an internal chamber between them and a slightly camber on caudal-peduncle ventral surface [Ch. 240: 0 > 1]. Independently acquired in Clades 125 and 130.
- 13*. Ventral region over pelvic-fin bone pigmented [Ch. 248: 0 > 1]. Uniquely derived.
- 14*. Anal fin with a conspicuous spot in the proximal portion of anteriormost rays [Ch. 254: 0 > 1]. Independently acquired in *Macropsobrycon*.
- 15*. Urogenital papilla hypertrophied in two longitudinal skin flaps on adult females [Ch. 264: 0 > 1]. Independently acquired in Compsurini *Purus* n. sp.

Synapomorphies ambiguously optimized for this clade:

16*. Sperm nuclei spherical, aquasperm [Ch. 267: 1 > 0]. Reversal.

17*. Spermatozoa with both centrioles are outside the nuclear fossa [Ch. 273: 1 > 0].
Reversal.

Autapomorphy of *Kolpotocheirodon theloura*

1*. Presence of papillae marginating the caudal-fin skin flaps [Ch. 228: 0 > 1]. Uniquely derived.

Autapomorphies ambiguously optimized for this species:

2. Laterosensory canal nearly absent at the posterior portion of the first infraorbital, never reaching its half length. [Ch. 6: 0 > 1]. Independently acquired in *Aphyocheirodon hemigrammus*, *Odontostilbe* n. sp. h, *Serrapinnus* n. sp. a, and Clade 108.
3. Lower lobe of the caudal fin bearing hooks [Ch. 184: 0 > 1]. Independently acquired in “*Odontostilbe*” *dialeptura*, *Saccoderma* (Clade 127), and Clade 103.

Autapomorphies of *Kolpotocheirodon figueiredoi*

- 1*. Absence of the quadrate anteroventral foramen [Ch. 110: 1 > 0]. Reversal.
- 2*. Absence of hyomandibular posterordorsal projection [Ch. 112: 1 > 0]. Reversal.
- 3*. Dorsal fin with a conspicuous small spot on the anterior portion of the fin [Ch. 249: 0 > 1]. Independently acquired in *Compsura* (Clade 118) and Clade 102.

Monophyly of *Compsura*, “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura*, “*Odontostilbe*” *mitoptera*, and *Saccoderma* (Clade 119)

1. All anal-fin rays longer on males than on females [Ch. 154: 0 > 1]. Independently acquired in *Acinocheirodon*, *Compsurini* *Tingo* n. sp., and *Compsurini* *Yurimaguas* n. sp.
2. Lower lobe of the caudal fin bearing a scale modified in shape [Ch. 214: 0 > 1]. Independently acquired in *Compsurini* *Purus* n. sp. and *Macropsobrycon*.
3. Upper lobe of the caudal fin bearing a scale modified in shape [Ch. 215: 0 > 1]. Independently acquired in *Macropsobrycon*.

4. Muscle *interradialis* in the base of the caudal-fin rays thicker and more concentrated in the ventral direction in the lower lobe [Ch. 244: 0 > 1]. Reversed in Clade 129; independently acquired in *Compsurini Purus n. sp.*
5. Caudal peduncle spot narrowing posteriorly over middle caudal-fin rays base [Ch. 257: 0 > 1]. Independently acquired in *Acinocheirodon* and *Cheirodon kiliani*.
6. Urogenital papilla hypertrophied on adult females [Ch. 263: 1 > 0]. Reversal.

Synapomorphies ambiguously optimized for this clade:

7. Anal-fin posterior branched rays elongated on mature males, longer than median branched rays [Ch. 156: 0 > 1]. Reversed in *Saccoderma* (Clade 127); independently acquired *Acinocheirodon*.
8. Anal-fin hooks more numerous in both anterior and posterior portions of anal fin, reduced in the middle portion of anal fin [Ch. 170: 2 > 1]. Reversed to state 2 in *Saccoderma* (Clade 127); independently acquired in *Compsurini Tingo n. sp.* and *Compsurini Yurimaguas n. sp.*
9. Muscle *interradialis* more extended posteriorly between the lower lobe caudal-fin rays than the upper lobe rays [Ch. 242: 0 > 1]. Reversed in Clade 129; independently acquired in *Compsurini Purus n. sp.*

Monophyly of *Compsura*

(Clade 118)

- 1*. Anteromedial process of the lateral ethmoid robust [Ch. 30: 1 > 0]. Reversal.
- 2*. Postcleithrum 1 round and expanded posteriorly [Ch. 142: 1 > 0]. Reversal.
- 3*. Last modified pouch-scale from the first longitudinal line below lateral line, with dorsoposterior margin extended posteriorly [Ch. 222: 0 > 1]. Uniquely derived.
- 4*. Abdomen slightly concave ventrally on mature males [Ch. 239: 1 > 0]. Reversal.
- 5*. Conspicuous small spot on the anterior portion of the dorsal fin [Ch. 249: 0 > 1]. Independently acquired in *Kolpotocheirodon figueiredoi* and Clade 102.
- 6*. Scattered melanophores concentrated on the distal portion of the dorsal fin [Ch. 250: 0 > 1]. Independently acquired in *Macropsobrycon*, "*Odontostilbe*" *mitoptera*, *Saccoderma melanostigma*, Clade 143, Clade 165 and Clade 173.
- 7*. Knob-like hypertrophied tissue anterior to the anal opening on mature males [Ch. 265: 0 > 1]. Uniquely derived.

Synapomorphies ambiguously optimized for this clade:

- 8*. Anteromedial process of the lateral ethmoid robust [Ch. 30: 1 > 0]. Reversal.
9. Toothless portion of the maxilla with approximately the same length of the tooth bearing portion [Ch. 62: 2 > 1]. Independently acquired in *Pseudocheirodon arnoldi*, Clade 137, and Clade 140.
- 10*. Hyomandibular without posterordorsal projection [Ch. 112: 1 > 0]. Reversal.
- 11*. Opening of the caudal-fin pouch scaleover the 13th to 19th principal caudal-fin rays [Ch. 225: 0 > 1]. Uniquely derived.

No autapomorphy found for *Compsura Araguaia* n. sp.

Monophyly of *Compsura heterura* and *Compsura Guaporé* n. sp.

(Clade 117)

1. Sixth infraorbital without anterior lamella [Ch. 11: 1 > 0]. Reversal.

Autapomorphy of *Compsura heterura*

- 1*. Pelvic bone equally developed on mature males and females [Ch. 149: 1 > 0].
Reversal.

Autapomorphy ambiguously optimized for this species:

2. Hyomandibular with a posterordorsal projection [Ch. 112: 0 > 1]. Independently acquired in Clade 115.

Autapomorphy of *Compsura Guaporé* n. sp.

1. Sixth infraorbital with anterior lamella lingual-shaped, expanded, and contacting the frontal supra-orbital canal until its pore [Ch. 12: 0 > 1]. Independently acquired in *Acinocheirodon*, *Compsurini Cuzco* n. sp., Clade 145 and Clade 171.

Monophyly of *Saccoderma*, and “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura*,

“*Odontostilbe*” *mitoptera*

(Clade 128)

1. Ascending process of the premaxilla distinctly projected, pointed [Ch. 52: 1 > 0].
Reversal.
2. Ascending process of the premaxilla falling short the lateral tip of the mesethmoid lateral process [Ch. 53: 1 > 0]. Reversal.
3. Scales with free borders, attached over the caudal fin by its central portion instead of the anterior portion, presenting a concave aspect, bowl-like shape [Ch. 218: 0 > 1].
Uniquely derived.
4. Absence of nuclear rotation, with flagellum attached laterally to the nucleus [Ch. 271: 0 > 1]. Independently acquired in *Acinocheirodon*.
5. Centrioles perpendicular to each other [Ch. 274: 0 > 1]. Independently acquired in *Acinocheirodon*.
6. Mitochondria positioned near the tip of nucleus (without nuclear rotation) and distant from the origin of the flagellum. [Ch. 275: 0 > 1]. Independently acquired in *Acinocheirodon*.

Synapomorphies ambiguously optimized for this clade:

7. Base of anteromedial process of the mesethmoid narrower than mesethmoid body width at the line just posterior to the lateral process [Ch. 18: 1 > 0]. Reversal.
8. Maxilla extending posteriorly the vertical line through the ventral limit of the lateral ethmoid [Ch. 55: 1 > 0]. Reversal.
9. Maxilla with a longitudinal groove just below the dorsolateral border [Ch. 56: 0 > 1].
Reversed in "*Compsura*" *gorgonae*; independently acquired in *Compsurini* Leticia n. sp., *Odontostilbe parecis*, *Odontostilbe* n. sp. p, Clade 102, Clade 143 and Clade 165.
10. Premaxillary teeth with central cusp larger and lateral ones decreasing in size laterally [Ch. 87: 1 > 0]. Reversal.
11. Anal-fin hooks concentrated along distal half or third portion of the rays [Ch. 174: 0 > 1]. Independently acquired in *Megacheirodon*, "New Genus" n. sp. b, *Pseudocheirodon* (Clade 182), *Serrapinnus* (Clade 144), and Clade 104.
12. Urogenital papilla not hypertrophied on mature males [Ch. 261: 1 > 0]. Reversal.

Monophyly of *Saccoderma*

(Clade 127)

- 1*. Anteromedial process of the mesethmoid well-developed, extending between premaxillae and reaching anteriorly the tooth bearing border of the premaxillae [Ch. 15: 1 > 0]. Reversal.
- 2*. Maxilla dorsal profile slightly concave [Ch. 59: 0 > 1]. Independently acquired in *Macropsobrycon*, *Heterocheiroidon* (Clade 142), *Odontostilbe splendida*, *Odontostilbe* n. sp. h, *Odontostilbe* n. sp. p, *Serrapinnus microdon*, Clade 157 and Clade 166.
3. Lower branch of the anguloarticular elongate, reaching or falling short to the line through the toothed portion of the dentary [Ch. 73: 0 > 1]. Independently acquired in *Acinocheiroidon*, *Serrapinnus heterodon*, Clade 168 and Clade 181.
- 4*. First to third most lateral premaxillary teeth larger than the preceding ones [Ch. 76: 0 > 1]. Independently acquired in *Cheirodontopsis geayi*.
5. Longer axis of the anteriormost dentary teeth perpendicular to the longer axis of the dentary [Ch. 96: 1 > 0]. Reversal.
- 6*. Dentary teeth with 5 medial cusps larger, nearly equal in size [Ch. 103: 0 > 2]. Uniquely derived among the Cheirodontinae.
- 7*. Dentary teeth with 5 medial cusps aligned in row with other teeth cusps, forming a continuous cutting edge [Ch. 104: 0 > 2]. Uniquely derived among the Cheirodontinae.
- 8*. Caudal-fin rays 12 and 13 ventrally curved on mature males [Ch. 182: 0 > 1]. Uniquely derived.
9. Lateral line scales completely pored [Ch. 210: 1 > 0]. Reversal.
- 10*. Laterosensory canal extending beyond the half-length of the middle caudal-fin rays [Ch. 212: 0 > 2]. Uniquely derived.
- 11*. One or two elongate modified scales on the distal portion of the middle caudal-fin rays [Ch. 217: 0 > 1]. Uniquely derived.
- 12*. Muscle *interradialis* extending posteriorly between the caudal-fin rays [Ch. 241: 0 > 1]. Uniquely derived.
- 13*. Intrasperm nucleus elongated [Ch. 268: 0 > 1]. Uniquely derived.
- Synapomorphies ambiguously optimized for this clade:
- 14*. Toothless portion of the maxilla extended, more than two times longer than the tooth bearing portion of the maxilla [Ch. 62: 2 > 3]. Independently acquired in *Axelrodia lindeae*, *Compsurini Leticia* n. sp., *Odontostilbe* n. sp. p, Clade 138, Clade 143, and Clade 162.
- 15*. Posterior branched anal-fin rays with same size or smaller than median branched rays on mature males [Ch. 156: 1 > 0]. Reversal.

16*. Anal-fin hooks restricted to the i+5 anal-fin rays [Ch. 170: 1 > 2]. Independently acquired in Clade 122.

17. Caudal-fin rays on the lower lobe with hooks [Ch. 184: 0 > 1]. Independently acquired in *Kolpotocheiroidon theloura*, “*Odontostilbe*” *dialeptura* and Clade 103.

Autapomorphy of *Saccoderma hastata*

1*. Ascending portion of the preopercle lateral system canal short, reaching the posterior articular surface of the hyomandybular condyle [Ch. 114: 0 > 1].

Independently acquired in *Aphyocheiroidon hemigrammus*, *Compsurini Purus* n. sp., *Kolpotocheiroidon* (Clade 123), *Macropsobrycon*, *Odontostilbe* n. sp. b, *Serrapinnus kriegi*, *S. microdon*, *Serrapinnus* n. sp. ac and Clade 137.

Autapomorphies of *Saccoderma melanostigma*

1*. Lateral ridge of the anguloarticular upper portion short, not reaching its anterior end [Ch. 71: 2 > 1]. Independently acquired in *Aphyocheiroidon hemigrammus*,

Cheirodontops geayi, *Cheirodon* (Clade 135), *Compsurini Cuzco* n. sp., *Compsurini Purus* n. sp., *Kolpotocheiroidon* (Clade 123), *Prodontocharax melanotus*.

2*. Dorsal-fin scattered melanophores concentrated on the distal portion of the fin [Ch. 250: 0 > 1]. Independently acquired in *Compsura* (Clade 118), *Macropsobrycon*, “*Odontostilbe*” *mitoptera*, Clade 143, Clade 165 and Clade 173.

Monophyly of Central America compsurins: “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura* and “*Odontostilbe*” *mitoptera*

(Clade 130)

1*. Caudal fin modified scales not forming a pouch [Ch. 220: 1 > 0]. Reversal.

2. Skin flaps restrict to the first third of the caudal-fin ray length [Ch. 226: 1 > 0]. Reversal.

3*. Caudal peduncle dorsal and ventral margins convex, with scales and skin non-attached on *hipaxialis* muscles, resulting in an internal chamber between them [Ch. 240: 0 > 1]. Independently acquired in *Compsura* (Clade 118) and *Kolpotocheiroidon* (Clade 123).

- 4*. Centriolar complex outside the nuclear fossa [Ch. 273: 1 > 0]. Reversal.
- 5*. Nucleus anterior border asymmetric, clearly oblique to the longest axis of the nucleus [Ch. 276: 0 > 1]. Uniquely derived.
- 6*. Vesicles located after the mitochondria, in the basal region of the midpiece and along the cytoplasmic collar in one side of the nucleus [Ch. 278: 0 > 1]. Uniquely derived.

Synapomorphy ambiguously optimized for this clade:

- 7*. Supraorbital laterosensory canal not continuous to the pterotic laterosensory canal [Ch. 42: 0 > 1]. Reversed in "*Odontostilbe*" *mitoptera*; independently acquired in *Aphyocheiroidon hemigrammus*, *Compsurini Leticia* n. sp., *Compsurini Purus* n. sp., *Heterocheiroidon yatai*, *Kolpotocheiroidon* (Clade 123), *Macropsobrycon*, *Serrapinnus* n. sp. ac, Clade 134 and 158.

Autapomorphies of "*Compsura*" *gorgonae*

- 1*. Nasal bone straight [Ch. 23: 1 > 0]. Reversal.
- 2*. Absence of the quadrate anteroventral foramen [Ch. 110: 1 > 0]. Reversal.
- 3*. Modified caudal-fin scales forming pockets [Ch. 219: 0 > 1]. Uniquely derived.
- 4*. Muscle *interradialis* thicker between the caudal-fin rays 11 to 15 [Ch. 243: 0 > 1]. Independently acquired in *Acinocheiroidon*.

Autapomorphies ambiguously optimized for this species:

- 5*. Maxilla not extending posteriorly the vertical line through the ventral limit of the lateral ethmoid [Ch. 55: 0 > 1]. Independently acquired in Clade 107.
- 6*. Maxilla without a longitudinal groove [Ch. 56: 1 > 0]. Reversal.

Monophyly of "*Odontostilbe*" *dialeptura* and "*Odontostilbe*" *mitoptera*

(Clade 129)

1. Caudal-fin scales reduced in size over the middle caudal-fin rays base [Ch. 216: 0 > 1]. Uniquely derived.
2. Muscle *interradialis* equally developed and distributed radially in the upper and lower caudal-fin lobes [Ch. 244: 1 > 0]. Reversal.

Synapomorphy ambiguously optimized for this clade:

3. Muscle *interradialis* on the lower lobe equally extending posteriorly between all caudal-fin rays [Ch. 242: 1 > 0]. Reversal.

Autapomorphies of “*Odontostilbe*” *dialeptura*

1*. Ectopterygoid not contacting the quadrate [Ch. 107: 1 > 0]. Reversal.

2*. Three posteriormost ventral procurrent caudal-fin rays hypertrophied on mature males, distal tips expanded, forming a small keel in the ventral profile of the caudal fin [Ch. 207: 0 > 1]. Independently acquired in *Acinocheiroduon*, *Compsurini Purus* n. sp. *Serrapinnus* n. sp. upm, Clade 141 and 150.

3*. Absence of skin flaps over the 18th to 19th principal caudal-fin rays [Ch. 230: 1 > 0]. Reversal.

4*. Presence of hypertrophied skin flaps associated to whitish tissue in the caudal fin [Ch. 231: 0 > 1]. Independently acquired in *Kolpotocheiroduon* (Clade 123) and Clade 102.

Autapomorphy ambiguously optimized for this species:

5. Caudal fin bearing hooks on the lower lobe [Ch. 184: 0 > 1]. Independently acquired in *Kolpotocheiroduon theloura*, *Saccoderma* (Clade 127) and Clade 103.

Autapomorphies of “*Odontostilbe*” *mitoptera*

1*. Elongation of the second dorsal-fin ray on males [Ch. 137: 0 > 1]. Independently acquired in Clade 155 and Clade 172.

2*. Elongation of the unbranched pectoral-fin ray on males [Ch. 148: 0 > 1]. Independently acquired in *Holoshesthes* n. sp. p and *Odontostilbe pao*.

3*. Elongation of the unbranched pelvic-fin ray on males [Ch. 150: 0 > 1]. Independently acquired in Clade 172.

4. Lateral line completely pored [Ch. 210: 1 > 0]. Reversal.

5*. Dorsal-fin melanophores concentrated on the distal portion of the fin [Ch. 250: 0 > 1]. Independently acquired in *Compsura* (Clade 118), *Macropsobrycon*, *Saccoderma melanostigma*, Clade 143, Clade 165 and Clade 173.

Autapomorphy ambiguously optimized for this species:

6. Supraorbital laterosensory canal continuous to the pterotic laterosensory canal [Ch. 42: 1 > 0]. Reversal.

Relationships and considerations about *Paracheiroduon axelrodi* and *Cheirodon stenodon* with the Cheirodontinae

Monophyly of *Paracheiroduon axelrodi*, *Cheirodon stenodon* and Cheirodontinae
(Clade 108)

1. Supraorbital laterosensory canal not continuous to the pterotic laterosensory canal [Ch. 42: 0 > 1]. Reversed in Cheirodontinae (Clade 106); independently acquired in *Aphyocharax nattereri*, *Aphyocheiroduon hemigrammus*, *Aphyodite grammica*, *Charax stenopterus*, *Compsurini Leticia* n. sp., *Compsurini Purus* n. sp., *Coptobrycon bilineatus*, *Heterocheiroduon yatai*, *Kolpotocheiroduon* (Clade 123), *Macropsobrycon*, *Serrapinnus* n. sp. ac, Clades 130, 134, 146 and 158.
- 2*. Parietal laterosensory canal not continuous to the supratemporal laterosensory canal posteriorly, divided by a gap, but anteriorly continuous to the parietal branch of the supraorbital laterosensory canal of frontal [Ch. 44: 0 > 1]. Reversed in “New Genus” n. sp. c, *Serrapinnus* (Clade 144), Clade 171; independently acquired in *Hypheosobrycon bifasciatus*, Clades 147, 151, 161, 185 and 190.
- 3*. Dorsal profile of the maxilla straight [Ch. 59: 1 > 0]. Reversal.
4. Dentary anterior tooth bearing portion of the dentary longer than posterior portion on dorsal view [Ch. 69: 0 > 1]. Reversed in *Axelrodia lindeae*, *Compsurini Purus* n. sp., *Serrapinnus heterodon*, and Clade 166; independently acquired in *Aphyocharacidium bolivianum*, *Parecbasis cyclolepis*, and Clades 189, 190, 193.
5. Premaxillary teeth base spaced [Ch. 79: 1 > 0]. Reversal.
- 6*. At most seven teeth in the single row of the premaxilla [Ch. 83: 1 > 0]. Reversal.
- 7*. Maximum of five cusps in the dentary teeth [Ch. 105: 12 > 0]. Reversal.
- 8*. Dentary teeth contacting each other by their cusps [Ch. 106: 0 > 1]. Reversed in *Macropsobrycon*, *Pseudocheiroduon* (Clade 182), Clade 131 and 156; independently acquired in *Parecbasis cyclolepis* and Clade 193.

Synapomorphies ambiguously optimized for this clade:

- 9*. First infraorbital laterosensory canal nearly absent at the posterior portion of the first infraorbital, never reaching its half length [Ch. 6: 0 > 1]. Reversed in *Acinocheiroduon*, *Cheirodon stenodon*, Clades 120, 126, 140 and 171; independently acquired in *Aphyocheiroduon hemigrammus*, *Aphyodite grammica*, *Charax stenopterus*,

Hyphessobrycon bifasciatus, *Kolpotocheiroduon theloura*, *Odontostilbe* n. sp. h, and *Serrapinnus* n. sp. a.

10. Pelvic bone more developed on mature males [Ch. 149: 0 > 1]. Reversed in *Acinocheiroduon*, *Compsura heterura*, *Compsurini Leticia* n. sp., *Heterocheiroduon* (Clade 142), “New Genus” n. s. c, and Clade 169; independently acquired in *Aphyocharacidium bolivianum*, *Aphyocharax nattereti* and *Odontostilbe euspilurus*.

11*. Anal fin concentrated along middle-length of the rays, with reduced number on the most proximal and most distal portions [Ch. 174: 1 > 0]. Reversal.

12*. Muscular reduction anterior to first pleural rib, with *obliquus superiores* muscle absent and respective area covered only by the *obliquus inferiores* [Ch. 234: 0 > 1].

Uniquely derived.

Monophyly of *Cheiroduon stenodon* and *Cheiroduontinae*

(Clade 107)

1. Anteromedial process of the mesethmoid with medium size, partially extending between premaxillae, not reaching anteriorly the tooth bearing border of the premaxillae [Ch. 15: 0 > 1]. Reversed in *Cheiroduontops geayi*, *Holoshesthes* n. sp. k, *Odontostilbe* n. sp. e, *Saccoderma* (Clade 127), *Serrapinnus heterodon*; transformed in state 2 in *Heterocheiroduon* (Clade 142) and *Macropsobrycon*; independently acquired in *Microchemobrycon elongatus* and Clades 186.

2. Maxilla not extending posteriorly the vertical line through the ventral limit of the lateral ethmoid [Ch. 55: 0 > 1]. Reversed in *Acinocheiroduon*, *Axelrodia lindeae*, *Odontostilbe microcephala*, *Odontostilbe* n. sp. p, *O. parecis*, Clade 128, Clade 143 and Clade 165; independently acquired in *Microchemobrycon elongatus* and Clade 186.

3*. Dentary teeth base spaced [Ch. 98: 1 > 0]. Reversal.

4*. Pseudotympanum between the first and second pleural ribs as a large, nearly triangular hiatus on muscles covering the anterior swim bladder, limited dorsally by the *lateralis superficialis* muscle, posteriorly by a naked anterior surface of the second pleural rib, posteroventrally by the *obliquus inferioris* and anteroventrally by the *obliquus superioris* muscle [Ch. 233: 0 > 1]. Uniquely derived.

5*. No pseudotympanum anterior to first pleural rib [Ch. 235: 1 > 0]. Reversal.

6*. Presence of caudal peduncle spot [Ch. 256: 1 > 0]. Reversal.

Synapomorphies ambiguously optimized for this clade:

- 7*. Maxilla without longitudinal groove [Ch. 56: 1 > 0]. Reversal.
- 8*. Lateral ridge of the anguloarticular long, along all the anterodorsal process length [Ch. 71: 1 > 2]. Reversed in *Aphyocheirodon hemigrammus*, *Cheirodontopsis geayi*, *Cheirodon* (Clade 135), *Compsurini Cuzco* n. sp., *Compsurini Purus* n. sp., *Kolpotocheirodon* (Clade 123), *Prodontocharax melanotus*, and *Saccoderma melanostigma*; independently acquired in *Parecbasis cyclolepis*.
- 9*. Postcleithrum 1 slender, not expanded posteriorly [Ch. 142: 0 > 1]. Reversed in *Acinocheirodon*, *Compsura* (Clade 118), *Compsurini Tingo* n. sp., Clade 140 and Clade 172; independently acquired in *Coptobrycon bilineatus* and *Prionobrama paraguayensis*.
- 10*. Abdomen ventral concavity between pelvic-fin insertion and anal-fin origin on mature males [Ch. 238: 0 > 1]. Reversed in Clades 134, 156 and 172.

Weitzman & Fink (1983) were the first to study the genus *Paracheirodon* Géry in the field of the systematics, defining the genus based on eight synapomorphies related to the color pattern, and arrangement of the bones of the skull and pectoral girdle. In that work, Weitzman & Fink designated three species to the genus, the type-species *Paracheirodon innesi* (Myers), *P. axelrodi* (Schultz), and *P. simulans* (Géry), and inferred possible relationships among them. However the relationships of *Paracheirodon* with the remaining characids was not approached and the genus was considered *incertae sedis* in Characidae (Malabarba, 1998; Lima *et al.*, 2003). Although previously considered closely related to the cheirodontines, due to the small size and the single tooth row in the premaxilla, molecular and morphology based phylogenetic analyses of the characids have recently shown that *Paracheirodon* is closely related to other characids bearing two tooth rows in the premaxilla than to the Cheirodoninae (Javonillo *et al.*, 2010; Mirande, 2010). The close relationship of *Paracheirodon axelrodi* with the Cheirodontinae found in this analysis, is probably due to the small number of outgroup taxa and superficial search for characters and homologies focused on them. Furthermore, some synapomorphies herein supporting *Paracheirodon axelrodi* as sister group of (*Cheirodon stenodon* + Cheirodontinae) are related to reductions or loss of bones in the skull, muscles, and the laterosensory canals in the head, which are generally associated to the processes of miniaturization and reduction of body size, being found independently in non-related small characiids (Weitzman & Vari, 1988).

The Cheirodontinae as defined by Malabarba (1998) and as diagnosed here, is supported by the presence of aligned and pedunculated teeth in the premaxilla, a character not found in the *Paracheirodon* species neither in *Cheirodon stenodon*. Malabarba (1998: 204-205) discussed the premaxillary tooth morphology and arrangement of those species in a comparison with the cheirodontines condition, remarking their non-aligned tooth condition, as well as the presence of two tooth rows in *Paracheirodon simulans*. Although Malabarba (1998: 205, fig. 9) illustration shows the dentition of *Cheirodon stenodon* as presenting the third medial tooth of the premaxilla displaced outward, it was also observed here specimens of *C. stenodon* bearing two small teeth forming an external row in the premaxilla. For this reason this species is coded as presenting two tooth rows, and it is not considered to be a member of *Cheirodon* nor a Cheirodontinae. We remark that its relationship with the remaining characids needs deeper investigation.

General Conclusion

After Malabarba (1998), the monophyly of the Cheirodontinae have been recovered on several works based on morphological and molecular data (Calcagnotto *et al.*, 2005; Bührnheim, 2006; Mirande, 2009; 2010; Javonillo *et al.*, 2010). Regardless congruent in the monophyly of the Cheirodontinae, the different hypotheses of relationships of the subfamily with the remaining characids are not accordant, with the position of the cheirodontines' sister group varying among the Characinae, Aphyocharacinae, and Aphyoditeinae. Herein, a deep effort was employed on the character search for the establishment of the cheirodontines internal relationships, and taking any inference on the outgroup taxa relationships would be inconclusive.

The Cheirodontinae, as diagnosed here, presents three distinct lineages which have been classified in the tribes Cheirodontini, Compsurini, and Odontostilbini (Malabarba, 1998; Bührnheim, 2006). The monophyly of the Cheirodontini and Compsurini are mainly supported by characters related to the conspicuous sexual dimorphism evidenced on the mature male of their species. The odontostilbins however, do not present conspicuous sexual dimorphism, despite the elongation of the dorsal and pelvic fins first ray in the mature males of some species, which supported their monophyly. An evidence about the relationships of those tribes was firstly here recovered here, with the compsurins more closely related to the cheirodontins than to the odontostilbins based on two non-ambiguous synapomorphies found on both implied

weighted and equal weighted analyses: the highly hypertrophied whitish tissue in the interradiial membrane of the anal-fin rays, and the ascending process of the premaxilla falling short the distal tip of the mesethmoid lateral process.

The cheirodontins present remarkable modifications of the anal-fin rays and ventral procurent caudal-fin rays, directly associated to the sexual dimorphism displayed on the mature males. These modifications are generally related to the hypertrophy and/or increase in number of those elements. Three equally parsimonious hypotheses of the cheirodontin genera relationships were presented by Malabarba (1998: 205). The incongruence among them concerned the sister group of the subclade C (*Serrapinnus* (*Spintherobolus* + *Megacheirodon*)), which resolution could be equally the *Heterocheirodon*, the “New genus & species C”, or a tritomy between these terminals. In the implied weighted hypothesis of Bührnheim (2006), the cheirodontin genera presented the same topology found here, with *Nanocheirodon* and *Cheirodon* forming a lineage sister group of (*Heterocheirodon* (“New Genus” (*Serrapinnus* (*Axelrodia* (*Megacheirodon* (*Amazonspinther* (*Spintherobolus*))))))).

Among the Cheirodontinae, the relationships of the odontostilbins genera are certainly the most challenging to be established. As quoted by Bührnheim (2006), the members of this tribe lack all the informative primary and secondary sexual dimorphic characters so useful to recover the generic level relationships on the other cheirodontine tribes. Nevertheless, some internal monophyletic lineages showed to be resilient on the implied weighted and equal weighted analyses of Bührnheim (2006), like the clades represented by the genera *Holoshesthes*, *Pseudocheirodon*, and *Prodontocharax*. Herein, the same clades were recovered, but with *Pseudocheirodon* as sister group of *Prodontocharax*, and both as sister group of *Odontostilbe euspilurus*. These clades of Odontostilbini are supported by modifications associated to the feeding mechanism of their components, however most of the representatives of the tribe still lack informative characters to establish their relationships, like the species of the paraphyletic *Odontostilbe*.

The genera and species of Compsurini are characterized by the conspicuous sexually dimorphic modifications present on the mature males, as well as by the presence of the inseminating process, generally associated to the diversification on the shape of the spermatozoa and position of the intracellular organelles. Despite of the fact that most of the characters related to the spermatozoa ultrastructure are still missing for several taxa (*Kolpotocheiron figueiredoi*, *Compsura Araguaia* n. sp., *Compsura*

Guaporé n. sp., Compsurini Leticia n. sp., Compsurini Tingo n. sp., and Compsurini Yurimaguas n. sp.), both the primary sexual dimorphism and the secondary sexual dimorphism on the anal and caudal fins, related to modifications of the shape, number and distribution of hooks and scales, greatly corroborated to the establishment of the hypothesis of relationships as herein presented.

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Literature Cited

- Benine, R. C. 2004. Análise filogenética do gênero *Moenkhausia* Eigenmann, 1903 (Characiformes: Characidae) com uma revisão dos táxons do alto rio Paraná. Unpublished MSc. Thesis, Universidade Estadual Paulista, Botucatu, 317p.
- Bremer, K. 1994. Branch support and tree stability. *Cladistics*, 10: 295–304.
- Bührnheim C. M. 2006. Sistemática de *Odontostilbe* Cope, 1870 com a Proposição de uma Nova Tribo Odontostilbini e Redefinição dos Gêneros *Incertae Sedis* de Cheirodontinae (Ostariophysi: Characiformes: Characidae). Unpublished Ph. D. Dissertation, Pontifícia Universidade Católica de Rio Grande do Sul, Porto Alegre, 315p.
- Bührnheim, C. M. & L. R. Malabarba. 2006. Redescription of the type species of *Odontostilbe* Cope, 1870 (Teleostei: Characidae: Cheirodontinae), and description of three new species from the Amazon basin. *Neotropical Ichthyology*, 4(2): 167-196.
- Bührnheim, C. M. & L. R. Malabarba. 2007. Redescription of *Odontostilbe pulchra* (Gill, 1858) (Teleostei: Characidae: Cheirodontinae), and description of two new species from the río Orinoco basin. *Neotropical Ichthyology*, 5(1): 1-20.

- Bührnheim, C. M., T. P. Carvalho, L. R. Malabarba & S. H. Weitzman. 2008. A new genus and species of characid fish from the Amazon basin - the recognition of a relictual lineage of characid fishes (Ostariophysi: Cheirodontinae: Cheirodontini). *Neotropical Ichthyology*, 6(4): 663-678.
- Burns, J. R. & S. H. Weitzman. 2005. Insemination in ostariophysan fishes, pp. 107-134. In: Uribe, M. C. & H. J. Grier, editors. *Viviparous Fishes*. Homestead, Florida, USA. New Life Publications.
- Burns, J. R., S. H. Weitzman & L. R. Malabarba. 1997. Insemination in eight species of cheirodontine fishes (Teleostei: Characidae: Cheirodontinae). *Copeia*, 1997: 433-438.
- Burns, J. R., S. H. Weitzman, H. J. Grier & N. A. Menezes. 1995. Internal fertilization, testis and sperm morphology in glandulocaudine fishes (Teleostei: Characidae: Glandulocaudinae). *Journal of Morphology*, 224: 131-145.
- Burns, J. R., S. H. Weitzman, K. R. Lange & L. R. Malabarba. 1998. Sperm ultrastructure in characid fishes (Teleostei: Ostariophysi). Pp 235-244. In: Malabarba L. R., R. E. Reis, R. P. Vari, Z. M. S. Lucena, C. A. S. Lucena (Eds.). *Phylogeny and classification of neotropical fishes*. Porto Alegre, Edipucrs, 603p..
- Calcagnotto, D., S. A. Schaefer & R. DeSalle. 2005. Relationships among characiform fishes inferred from analysis of nuclear and mitochondrial gene sequences. *Molecular Phylogenetics and Evolution*, 36(1): 135-153.
- Dahl, G. 1955. An ichthyological reconnaissance of the Sinu River. *Revista Linneana*, 1 (1): 11-19.
- Dahl, G. 1958. Los peces del río Sinú – Informe preliminar. Publicación de la secretaría de agricultura y Ganadería de Córdoba. Montería. 9-47p.
- Dahl, G. 1971. Los peces del norte de Colombia. Instituto de Desarrollo de los Recursos Naturales Renovables (INDERENA), Bogota. 391p.
- Dahl, G. & F. Medem. 1964. Informe sobre la fauna acuática del Río Sinu. I Parte. Los Peces y la Pesca del Río Sinu. Corporación Autónoma Regional de los Valles del Magdalena y del Sinu -CVM-. Departamento de Investigaciones Ictiológicas y Faunísticas. 109p.
- Dahl, G., F. Medem & A. Ramos Henao. 1964. El “Bocachico” contribución al estudio de su biología y de su ambiente. Departamento de Pesca de la Corporación Autónoma Regional de los Valles del Magdalena y del Sinú, 144p.
- Eigenmann, C. H. 1915. The Cheirodontinae, a subfamily of minute characid fishes of South America. *Memoirs of the Carnegie Museum*, 7(1): 1-99, pls. 1-17.

- Fink, S. V. & W. L. Fink. 1981. Interrelationships of the ostariophysan fishes (Teleostei). *Zoological Journal of the Linnean Society*, 72(4): 297-353.
- Fink, S. V. & W. L. Fink. 1996. Interrelationships of the ostariophysan fishes (Teleostei). Pp: 209-249. In: *Interrelationships of Fishes*. Stiassny, M. L. J., L. R. Parenti & G. D. Johnson (Eds.). San Diego, Academic Press, 496p.
- Fink, W. L. & S. H. Weitzman. 1974. The so-called Cheirodontin fishes of Central America with descriptions of two new species (Pisces: Characidae). *Smithsonian Contributions to Zoology*, 172: 1-46.
- Géry, J. 1960. Contributions to the study of characoid fishes. II. The generic position of *Hyphessobrycon innesi* and *Cheirodon axelrodi*, with a review of the morphological affinities of some Cheirodontinae (Pisces, Cypriniformes). *Bulletin of Aquatic Biology*, 2(12): 1-18.
- Géry, J. 1965. A new genus from Brazil - *Brittanichthys*. *Tropical Fish Hobbyist*, 13(6): 13-23, 61-69.
- Géry, J. 1972. Corrected and supplemented descriptions of certain Characoid fishes described by Henry W. Fowler, with revisions of several of their genera. *Studies on the Neotropical Fauna*, 7: 1-35.
- Géry, J. 1973. New and little-known Aphyoditeina (Pisces, Characoidei) from the Amazon basin. *Studies on the Neotropical Fauna*, 8: 81-137.
- Géry, J. 1977. *Characoids of the world*. T.F.H. Publications, Neptune City, 672p.
- Goloboff, P. A. 1993. Estimating character weights during tree search. *Cladistics*, 9(1): 83-91.
- Goloboff, P. A. 1999. Analyzing large data sets in reasonable times: solutions for composite optima. *Cladistics*, 15: 415-428.
- Goloboff, P. A. 2008. Calculating SPR distances between trees. *Cladistics*, 24: 591-597.
- Goloboff, P. A., J. S. Farris & K. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*, 24: 774-786.
- Hennig, W. 1966. *Phylogenetic Systematics*. University of Illinois, Urbana, Illinois.
- Jamieson, B. G. M. 1991. *Fish evolution and systematics: evidence from spermatozoa*. Cambridge University Press, Cambridge.
- Javonillo, R., J. R. Burns & S. H. Weitzman. 2007. Reproductive morphology of *Bryttanichthys axelrodi* (Teleostei: Characidae), a miniature inseminating fish from South America. *Journal of Morphology*, 268: 23-32.

- Javonillo, R., L. R. Malabarba, S. H. Weitzman & J. R. Burns. 2010. Relationships among major lineages of characid fishes (Teleostei: Ostariophysi: Characiformes), based on molecular sequence data. *Molecular Phylogenetics and Evolution*, 54: 498-511.
- Lima, F. C. T. & L. M. Sousa. 2009. A new species of *Hemigrammus* from the upper rio Negro basin, Brazil, with comments on the presence and arrangement of anal-fin hooks in *Hemigrammus* and related genera (Ostariophysi: Characiformes: Characidae). *Aqua, International Journal of Ichthyology*, 15(3):153-168.
- Lima, F. C. T., L. R. Malabarba, P. A. Buckup, J. F. P. Silva, R. P. Vari, A. Harold, R. Benine, O. T. Oyakawa, C. S. Pavanelli, N. A. Menezes, C. A. S. Lucena, R. E. Reis, F. Langeani, L. Casatti, V. A. Bertaco, C. R. Moreira & P. H. F. Lucinda. 2003. Genera *Incertae Sedis* in Characidae. Pp. 106-169. In: Reis, R. E., S. O. Kullander & C. J. Ferraris Jr. (Eds.). *Check List of the Freshwater fishes of South and Central America*. Porto Alegre, Edipucrs, 729p.
- López, M. I. 1972. Contribución al estudio de los peces Cheirodontinae (Familia Characidae) de Cost Rica y Panama: generos *Compsura* y *Pseudocheirodon*. *Revista de Biología Tropical*, 20(1): 93-129.
- Maddison, W. P. & D. R. Maddison. 2008. Mesquite: A Modular System for Evolutionary Analysis. Version 2.6, <http://mesquiteproject.org>.
- Malabarba, L. R. 1994. Sistemática de Cheirodontinae Ostariophysi: Characiformes: Characidae). Unpublished Doctoral Dissertation. USP, São Paulo, 287p.
- Malabarba, L. R. 1998. Monophyly of the Cheirodontinae, characters and major clades (Ostariophysi: Characidae). Pp. 193-233. In: Malabarba, L. R., R. E. Reis, R. P. Vari, Z. M. S. Lucena & C. A. S. Lucena (Eds.). *Phylogeny and Classification of Neotropical Fishes*. Porto Alegre, Edipucrs, 603p.
- Malabarba, L. R. 2003. Cheirodontinae. Pp. 215–221. In: Reis, R. E., S. O. Kullander & C. J. Jr Ferraris (Eds.). *Check List of the Freshwater Fishes of South and Central America*. Porto Alegre, Edipucrs, 729p.
- Malabarba, L. R., F. C. T. Lima & S. H. Weitzman. 2004. A new species of *Kolpotocheirodon* (Teleostei: Characidae: Cheirodontinae: Compsurini) from Bahia, northeastern Brazil, with a new diagnosis of the genus. *Proceedings of the Biological Society of Washington*, 117(3): 317–329.
- Malabarba, L. R. & S. H. Weitzman. 1999. A new genus and species of South American fishes (Teleostei: Characidae: Cheirodontinae) with a derived caudal fin, including

- comments about inseminating cheirodontines. *Proceedings of the Biological Society of Washington*, 112(2): 410–432.
- Malabarba, L. R. & S. H. Weitzman. 2000. A new genus and species of inseminating (Teleostei: Characidae: Cheirodontinae: Compsurini) from South America with uniquely derived caudal-fin dermal papillae. *Proceedings of the Biological Society of Washington*, 113(1): 269–283.
- Mattei, X. 1970. Spermio genèse comparée des poissons. Pp. 57-69. In: *Comparative Spermatology* (B. Baccetti ed.). New York, Academic Press, 575p.
- Meek, S. E. & S. F. Hildebrand. 1916. The fishes of the freshwaters of Panama. *Field Museum of Natural History, Zoological Series*, 10(15): 217-374.
- Meisner, A. D. 2005. Male modifications associated with insemination in teleosts. Pp. 165-190. In: Grier H.J. & M.C. Uribe (Eds). *Viviparous Fishes*. New Life Publications, Homestead Florida.
- Menezes, N. A. & S. H. Weitzman. 2009. Systematics of the Neotropical fish subfamily Glandulocaudinae (Teleostei: Characiformes: Characidae). *Neotropical Ichthyology*, 7(3): 295-370.
- Mirande, J. M. 2009. Weighted parsimony phylogeny of the family Characidae (Teleostei: Characiformes). *Cladistics*, 25: 574–613.
- Mirande, J. M. 2010. Phylogeny of the family Characidae (Teleostei: Characiformes): from characters to taxonomy. *Neotropical Ichthyology*, 8(3): 385-568.
- Moreira, C. R. 2007. Relações filogenéticas na ordem Characiformes (Teleostei: Ostariophysi). Unpublished Ph. D. Dissertation, Universidade de São Paulo, São Paulo, 468p.
- Nelson, G. 1969. Gill arches and the phylogeny of fishes with notes on the classification of the vertebrates. *Bulletin of the American Museum of Natural History*, 141(4): 475-522.
- Nixon, K. C. 1999. The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics*, 15: 407-414.
- Nixon K. C. & J. M. Carpenter. 1993. On outgroups. *Cladistics*, 9: 413-426.
- Oliveira, C. L. C., J. R. Burns, L. R. Malabarba & S. H. Weitzman. 2008. Sperm Ultrastructure in the Inseminating *Macropsobrycon uruguayanae* (Teleostei: Characidae: Cheirodontinae). *Journal of Morphology*, 269: 691–697.

- Parenti, L. R. 2008. A phylogenetic analysis and taxonomic revision of ricefishes, *Oryzias* and relatives (Beloniformes, Adrianichthyidae). *Zoological Journal of the Linnean Society*, 154: 494-610.
- Patterson, C. 1975. The braincase of pholidophorid and leptolepid fishes with a review of the Actinopterygian braincase. *Philosophical Transactions of the Royal Society B*, 269: 275-529.
- Pecio, A., J. R. Burns & S. H. Weitzman. 2005. Sperm and spermatozeugma ultrastructure in the inseminating species *Tytocharax cochui*, *T. tambopatensis* and *Scopaeocharax rhinodus* (Pisces:Teleostei: Characidae: Glandulocaudinae: Xenurobryconini). *Journal of Morphology*, 263: 216-226.
- Pecio, A., J. R. Burns & S. H. Weitzman. 2007. Comparison of spermiogenesis in the externally fertilizing *Hemigrammus erythrozonus* and the inseminating *Corynopoma riisei* (Teleostei: Characiformes: Characidae). *Neotropical Ichthyology*, 5(4): 457-470.
- Pecio, A. & J. Rafinski. 1994. Structure of the testis, spermatozoa and spermatozeugmata of *Mimagoniates barberi* Regan, 1907 (Teleostei: Characidae), an internally fertilizing, oviparous fish. *Acta Zoologica*, 75: 179-185.
- Pecio, A. & J. Rafinski. 1999. Spermiogenesis in *Mimagoniates barberi* (Teleostei: Ostariophysi: Characidae), an oviparous, internally fertilizing fish. *Acta Zoologica*, 80: 35-45.
- de Pinna, M. C. C. 1991. Concepts and tests of homology in the cladistic paradigm. *Cladistics*, 7: 367-394.
- Reis, R. E., S. O. Kullander & C. J. Ferraris (Eds.). 2003. *Check List of the Freshwater Fishes of South and Central America*. Porto Alegre, Edipucrs, 729 p.
- Schultz, L. P. 1944. The fishes of the family Characinidae from Venezuela, with descriptions of seventeen new forms. *Proceedings of the United States National Museum*, 95(3181): 235-267.
- Sereno, P. C. 2007. Logical basis for morphological characters in phylogenetics. *Cladistics*, 23: 565-587.
- Taylor, W. R. & G. C. van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybiurn*, 9(2): 107-119.
- Weitzman, S. H. 1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. *Stanford Ichthyological Bulletin*, 8(1): 3-77.

- Weitzman, S. H. & L. R. Malabarba. 1999. Systematics of *Spintherobolus* (Teleostei: Characidae: Cheirodontinae) from eastern Brazil. *Ichthyological Exploration of Freshwaters*, 10(1): 1-43.
- Weitzman, S. H. & W. L. Fink. 1983. Relationships of the neon tetras, a group of South American fresh water fishes (Teleostei, Characidae), with comments on the phylogeny of New World Characiforms. *Bulletin of the Museum of Comparative Zoology*, 150(6): 339-395.
- Weitzman, S. H. & S. V. Fink. 1985. Xenobryconin phylogeny and putative pheromone pumps in glandulocaudine fishes (Teleostei: Characidae). *Smithsonian Contributions to Zoology*, 421: 1-121.
- Weitzman, S. H. & N. A. Menezes. 1998. Relationships of the tribes and genera of the Glandulocaudinae (Ostariophysi: Characiformes: Characidae) with a description of a new genus, *Chrysobrycon*. Pp. 171-192. In: L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. S. Lucena & C. A. S. Lucena (Eds.), *Phylogeny and Classification Neotropical Fishes*, Porto Alegre, Edipucrs, 603p.
- Weitzman, S. H. & R. P. Vari. 1988. Miniaturization in South American freshwater fishes; an overview and discussion. *Proceedings of the Biological Society of Washington*, 101(2): 444-465.
- Weitzman, S. H., N. A. Menezes, H-G. Evers & J. R. Burns. 2005. Putative relationships among inseminating and externally fertilizing characids, with a description of a new genus and species of brazilian inseminating fish bearing an anal-fin gland in males (Characiformes: Characidae). *Neotropical Ichthyology*, 3(3): 329-360.
- Winterbottom, R. 1974. A descriptive synonymy of the striated muscles of the Teleostei. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 125(12): 225-317.
- Zanata, A. M. & R. P. Vari. 2005. The family Alestidae (Ostariophysi, Characiformes): a phylogenetic analysis of a trans-Atlantic clade. *Zoological Journal of the Linnean Society*, 145(1): 1-144.

TABLES

Table 1. Continued.

Taxa	Characters																															
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0		
Compsurini	0	0	1	1	0	0	1	1	2	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	
<i>Actinocheiroidon melanogramma</i>	0	1	1	1	0	0	0	1	1	1	0	0	0	1	1	0	0	2	1	0	0	2	1	0	0	1	0	0	1	0	0	
<i>Compsura heterura</i>	0	2	0	1	1	0	2	1	-	2	0	0	0	1	0	1	0	2	1	0	1	0	0	1	0	0	1	0	0	1	0	
<i>Macropsobrycon uruguayanae</i>	0	1	1	1	0	0	1	1	-	2	0	0	0	1	0	1	0	2	1	0	1	0	0	1	0	0	1	0	0	1	0	
<i>Kolpotocheiroidon thelouira</i>	0	1	1	1	0	0	0	1	1	2	0	0	0	1	0	1	0	0	2	1	0	1	0	0	1	0	0	1	0	0	0	
<i>Kolpotocheiroidon figueiredoi</i>	0	1	1	1	0	0	0	1	1	2	0	0	0	1	0	1	0	0	2	1	0	0	1	0	0	1	0	0	1	0	0	
<i>Compsurini Purus</i> n.sp.	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	1	0	0	2	1	0	0	1	0	0	1	0	0	1	0	0
<i>Compsura</i> Araguaia n.sp.	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	2	1	0	0	2	1	0	0	1	0	0	1	0	0	0
<i>Compsura</i> Guaporé n.sp.	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	2	1	0	0	2	1	0	0	1	0	0	1	0	0	0
<i>Compsurini Napo</i> n.sp.	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	2	1	0	0	2	1	0	0	1	0	0	1	0	0	0
<i>Compsurini Yurimaguas</i> n.sp.	1	-	-	1	1	0	0	0	1	1	0	0	0	1	0	0	1	0	0	2	1	0	0	1	0	0	0	0	1	0	0	0
<i>Compsurini Tingo</i> n.sp.	1	-	-	1	1	0	0	0	1	1	0	0	0	1	0	0	1	0	0	2	1	0	0	1	0	0	0	0	1	0	0	0
<i>Compsurini Leticia</i> n.sp.	0	1	1	1	1	0	0	1	1	3	0	0	0	1	0	0	0	1	0	0	2	1	0	0	0	1	0	0	0	0	0	0
<i>Compsurini Cuzco</i> n.sp.	1	-	0	1	1	0	0	1	1	1	0	0	0	1	0	0	0	1	0	1	0	0	2	1	0	0	1	0	0	0	0	0
<i>Saccoderma melanostigma</i>	0	0	1	0	1	0	0	1	1	3	0	0	0	1	0	1	0	1	0	1	0	1	2	1	0	0	1	0	0	0	0	0
<i>Saccoderma hastata</i>	0	0	0	1	0	1	0	0	1	1	3	0	0	0	1	0	1	0	1	0	1	2	1	0	0	1	0	0	0	0	0	0
" <i>Odontostilbe</i> " <i>ditaleptura</i>	0	0	0	1	0	0	0	1	1	2	0	0	0	1	0	1	0	0	2	1	0	0	1	0	0	1	0	0	0	0	0	0
" <i>Odontostilbe</i> " <i>mitoptera</i>	0	0	0	1	0	0	0	1	1	2	0	0	0	1	0	1	0	0	2	1	0	0	1	0	0	1	0	0	0	0	0	0
" <i>Compsura</i> " <i>gorgonae</i>	0	0	0	1	1	0	0	0	1	1	2	0	0	0	1	0	1	0	0	2	1	0	0	1	0	0	0	0	0	0	0	0
Cheirodontini	0	0	1	1	0	0	0	1	1	2	0	0	0	1	1	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	0	0
<i>Cheirodon australe</i>	0	0	1	1	0	0	0	1	1	2	0	0	0	1	0	1	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	0
<i>Cheirodon galusdai</i>	0	0	1	1	0	0	0	1	1	2	0	0	0	1	0	1	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	0
<i>Cheirodon ibicuiensis</i>	0	0	1	1	0	0	0	1	1	2	0	0	0	1	0	1	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	0
<i>Cheirodon interruptus</i>	0	0	1	1	0	0	0	1	1	2	0	0	0	1	0	1	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	0
<i>Cheirodon paratybae</i>	0	1	1	1	0	0	0	1	1	2	0	0	0	1	0	1	0	0	2	1	0	1	0	0	0	0	1	0	0	0	0	0
<i>Cheirodon kiliani</i>	0	0	1	1	0	0	0	0	1	3	0	0	0	1	0	1	0	0	2	1	0	1	0	0	0	0	1	0	0	0	0	0
<i>Cheirodon pisciculus</i>	0	0	1	1	0	0	0	1	1	3	0	0	0	1	0	1	0	0	2	1	0	1	0	0	0	0	1	0	0	0	0	0
<i>Nanocheiroidon insignis</i>	0	0	1	1	0	0	0	1	1	2	0	0	0	1	0	1	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	0
"New Genus" n. sp. c	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	1	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	0
"New Genus" n. sp. b	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	1	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	0
<i>Heterocheiroidon jacutensis</i>	0	1	1	1	0	0	1	1	1	2	0	0	0	1	0	1	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	0
<i>Heterocheiroidon yatani</i>	0	1	1	1	0	0	1	1	1	2	0	0	0	1	0	1	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	0
<i>Serrapinnus</i> n. sp. upm	0	0	1	1	0	1	0	0	1	1	3	0	0	0	1	0	1	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0
<i>Serrapinnus</i> n. sp. ups	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	1	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	0
<i>Serrapinnus</i> n. sp. a	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	1	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	0
<i>Serrapinnus</i> n. sp. ac	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	1	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	0
<i>Serrapinnus callurus</i>	0	1	1	1	0	0	0	1	1	1	0	0	0	1	0	1	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	0
<i>Serrapinnus</i> n. sp. d	1	-	-	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	0
<i>Serrapinnus</i> n. sp. e	1	-	-	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0	0

Table 1. Continued.

Taxa	Characters																																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31			
<i>Serrapinnus heterodon</i>	0	0	0	1	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Serrapinnus kriegi</i>	0	1	1	1	0	0	0	1	1	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus n. sp. me</i>	0	1	1	1	0	0	0	1	1	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus microdon</i>	0	0	1	1	0	0	1	1	1	3	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus micropterus</i>	0	1	1	1	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus n. sp. mi</i>	0	1	1	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus notomelas</i>	0	1	1	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus piaba</i>	0	1	1	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus n. sp. t</i>	0	1	1	1	0	0	0	1	1	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Axelrodia lindaeae</i>	0	0	1	1	0	0	0	0	0	3	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Amazonaspinther dalnata</i>	0	0	1	0	1	0	0	1	1	2	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Spintherobolus ankoseiton</i>	0	1	1	0	1	0	0	1	1	2	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Spintherobolus broccae</i>	0	1	1	0	1	0	0	1	1	2	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Spintherobolus papilliferus</i>	0	1	1	0	1	0	0	1	1	2	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Megacheiroidon unicus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Odontostilbini	0	0	0	1	0	0	1	1	1	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aphyochiroidon hemigrammus</i>	0	0	1	0	1	0	0	1	1	1	0	1	1	0	2	1	0	0	1	-	1	1	0	0	0	1	0	1	0	1	0	1	0	0
<i>Cheirodontops geayi</i>	0	0	1	0	1	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0
<i>Holosheshtes n. sp. b</i>	0	0	1	0	1	0	1	1	1	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0
<i>Holosheshtes n. sp. k</i>	0	0	1	0	1	0	1	1	1	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0
<i>Holosheshtes n. sp. p</i>	0	0	1	0	1	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0
<i>Holosheshtes pequirá</i>	0	0	1	0	1	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0
<i>Odontostilbe dierythrura</i>	0	1	1	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe ecuadorensis</i>	0	1	1	1	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe n. sp. e</i>	0	0	1	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe eupilaris</i>	0	1	1	1	0	0	1	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe fugitiva</i>	0	1	1	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe n. sp. h</i>	0	0	1	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe microcephala</i>	0	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe nareuda</i>	0	0	1	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe pao</i>	0	1	1	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe paraguayensis</i>	0	1	1	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe n. sp. p</i>	0	0	1	0	1	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe n. sp. b</i>	0	0	1	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe parecis</i>	0	1	1	0	1	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe pulchra</i>	0	1	1	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe splendida</i>	0	1	1	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 1. Continued.

Taxa	Characters																			
	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
<i>Prodontocharax alleni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Prodontocharax melanosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pseudocheirodon arnoldi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pseudocheirodon terrabae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Outgroup																				
<i>Aphyocharacidium bolivianum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aphyocharax nattereri</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aphyodite grammica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Asryanax</i> aff. <i>fasciatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Asryanax laiteps</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bryconamericus iheringii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Brycon pesu</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bryconops caudomaculatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Charax stenopterus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cheirodon stenodon</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coptobrycon bilineatus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cyanocharax alburnus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cynopotamus kincaidii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hemibrycon polyodon</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hypessobrycon bifasciatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Leptobrycon jatauaranae</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
" <i>Macropsobrycon</i> " <i>xinguensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Microschemobrycon elongatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Paracheirodon axelrodi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pareuchasis cyclolepis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Priotonbrama paraguayensis</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Probolodus heterostomus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rhoadsia altipinna</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 1. Continued.

Taxa	Characters																												
	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Compsurini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Actinocheirodon melanoqramma</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Compsura heterura</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Macropsobrycon uruguayanae</i>	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Kolpotocheirodon thelouira</i>	0	0	1	0	0	0	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Kolpotocheirodon figueiredoi</i>	0	0	1	0	0	0	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Compsurini Purus</i> n.sp.	0	0	1	0	0	0	2	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Compsura Araguaia</i> n.sp.	0	0	1	0	0	0	1	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Compsura Guaporé</i> n.sp.	0	0	1	0	0	0	1	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Compsurini Napo</i> n.sp.	0	0	1	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Compsurini Yurimaguas</i> n.sp.	0	0	1	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Compsurini Tingo</i> n.sp.	0	0	1	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Compsurini Leticia</i> n.sp.	0	0	?	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Compsurini Cuzco</i> n.sp.	0	0	?	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Saccoderma melano stigma</i>	0	0	1	0	0	0	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Saccoderma hastata</i>	0	0	1	0	0	0	1	0	2	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
" <i>Odontostilbe</i> " <i>ditaleptura</i>	0	0	1	0	0	0	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
" <i>Odontostilbe</i> " <i>mitoptera</i>	0	0	1	0	0	0	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
" <i>Compsura</i> " <i>gorgonae</i>	0	0	1	0	0	0	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cheirodontini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cheirodon australe</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cheirodon galusdai</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cheirodon ibicuihensis</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cheirodon interruptus</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cheirodon paratybae</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cheirodon kiliani</i>	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cheirodon pisciculus</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nanocheirodon insignis</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
"New Genus" n. sp. c	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
"New Genus" n. sp. b	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heterocheirodon jacutensis</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heterocheirodon yatai</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus</i> n. sp. upm	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus</i> n. sp. ups	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus</i> n. sp. a	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus</i> n. sp. ac	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus callurus</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus</i> n. sp. d	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus</i> n. sp. e	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 1. Continued.

Taxa	Characters																													
	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
<i>Serrapinnus heterodon</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus krtégi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus</i> n. sp. me	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus microdon</i>	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus micropterus</i>	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus</i> n. sp. mi	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus notomelas</i>	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus piaba</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Serrapinnus</i> n. sp. t	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Axelrodia lindaeae</i>	0	0	0	0	0	0	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Amazonaspither dalnata</i>	1	0	0	0	0	0	1	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Spintherobolus ankoseiton</i>	0	0	0	1	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Spintherobolus broccae</i>	0	0	0	1	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Spintherobolus papilliferus</i>	0	0	0	0	1	-	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Megacheiroidon unicus</i>	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Odontostilbini	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aphyocheiroidon hemigrammus</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Chairodontops geayi</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Holoshesthes</i> n. sp. b	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Holoshesthes</i> n. sp. k	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Holoshesthes</i> n. sp. p	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Holoshesthes pequirá</i>	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe dierythura</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe ecuadorensis</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe</i> n. sp. e	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe euspilurus</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe fugitiva</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe</i> n. sp. h	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe microcephala</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe nareuda</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe pao</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe paraguayensis</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe</i> n. sp. p	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe</i> n. sp. b	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe parecis</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe pulchra</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odontostilbe splendida</i>	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 1. Continued.

Taxa	Characters																													
	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
<i>Prodontocharax alleni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Prodontocharax melanois</i>	3	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pseudocheirodon arnoldi</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pseudocheirodon terrabae</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Outgroup																														
<i>Aphyocharacidium bolivianum</i>	0	0	0	0	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aphyocharax nattereri</i>	0	0	0	0	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aphyodite grammica</i>	0	0	0	0	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Asryanax</i> aff. <i>fasciatus</i>	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Asryanax laiteps</i>	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bryconamericus iheringii</i>	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Brycon pesu</i>	0	0	0	0	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bryconops caudomaculatus</i>	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Charax stenopterus</i>	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cheirodon stenodon</i>	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coptobrycon bilineatus</i>	0	0	0	0	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cyanocharax alburnus</i>	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cynopotamus kincaidi</i>	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hemibrycon polyodon</i>	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hyphessobrycon bifasciatus</i>	0	0	0	0	1	-	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Leptobrycon jatauaranae</i>	0	0	0	0	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
" <i>Macropsobrycon</i> " <i>xinguensis</i>	0	0	0	0	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Microschemobrycon elongatus</i>	0	0	0	0	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Paracheirodon axelrodi</i>	0	0	0	0	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Parecbasis cyclolepis</i>	0	0	0	0	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Priotonbrama paraguayensis</i>	0	0	0	0	1	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Probolodus heterostomus</i>	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rhoadsia altipinna</i>	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 2. Results of the IW under different parameters. Trees used for the final phylogenetic hypothesis are in bold.

"k"-values	Number of trees	Steps	Best score	Tree-Fit	Average-character fit (F)	Average homoplastic steps (S)
3.0031	2	1301	99.92	158.07	0.50	3.0031949
3.2534	3	1301	96.63	161.37	0.52	3.0031949
3.5254	3	1301	93.33	164.67	0.54	3.0031949
3.8222	9	1291	90.02	167.98	0.56	3.0031949
4.1472	9	1280	86.68	171.32	0.58	3.0031949
4.5047	8	1280	83.32	174.68	0.60	3.0031949
4.8999	9	1277	79.93	178.06	0.62	3.0031949
5.3390	3	1269	76.52	181.48	0.64	3.0031949
5.8297	3	1269	73.07	184.92	0.66	3.0031949
6.3817	3	1269	69.59	188.41	0.68	3.0031949
7.0074	3	1269	66.07	191.93	0.70	3.0031949
7.7225	3	1270	62.50	195.50	0.72	3.0031949
8.5475	3	1267	58.87	199.13	0.74	3.0031949
9.51011	3	1267	55.18	202.82	0.76	3.0031949
10.6476	3	1267	51.41	206.58	0.78	3.0031949
12.0127	3	1266	47.56	210.43	0.80	3.0031949
13.6812	3	1263	43.61	214.39	0.82	3.0031949
15.7667	3	1263	39.54	218.45	0.84	3.0031949
18.4482	3	1260	35.34	222.65	0.86	3.0031949
22.0234	3	1260	30.99	227.00	0.88	3.0031949
27.0287	3	1260	26.47	231.53	0.90	3.0031949

Table 3. SPR values between the IW consensus trees resulted from 21 different “k”-values. The SPR values from the most stable trees whose strict consensus represents the final phylogenetic hypothesis are in bold.

		“k”-values																				
		3.0032	3.2535	3.5255	3.8222	4.1473	4.5048	4.8999	5.3390	5.8297	6.3818	7.0075	7.7225	8.5476	9.5101	10.6477	12.0128	13.6812	15.7668	18.4482	22.0234	27.0288
Trees	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	32
0	-	7	7	10	16	16	17	22	22	22	22	21	22	22	22	22	23	28	28	32	32	32
1	7	-	0	3	9	9	10	15	15	15	15	17	18	18	18	18	16	21	21	24	24	24
2	7	0	-	3	9	9	10	15	15	15	15	17	18	18	18	18	16	21	21	24	24	24
3	10	3	3	-	6	6	7	12	12	12	12	14	17	17	17	14	19	19	19	22	22	22
4	16	9	9	6	-	0	1	6	6	6	6	8	11	11	11	9	13	13	13	18	18	18
5	16	9	9	6	0	-	1	6	6	6	6	8	11	11	11	9	13	13	13	18	18	18
6	17	10	10	7	1	1	-	5	5	5	5	7	9	9	9	7	12	12	12	17	17	17
7	22	15	15	12	6	6	5	-	0	0	0	2	3	3	3	1	6	6	6	11	11	11
8	22	15	15	12	6	6	5	0	-	0	0	2	3	3	3	1	6	6	6	11	11	11
9	22	15	15	12	6	6	5	0	0	-	0	2	3	3	3	1	6	6	6	11	11	11
10	22	15	15	12	6	6	5	0	0	0	-	2	3	3	3	1	6	6	6	11	11	11
11	21	17	17	14	8	8	7	2	2	2	2	-	1	1	1	3	8	8	8	13	13	13
12	22	18	18	17	11	11	9	3	3	3	3	1	-	0	0	2	7	7	7	12	12	12
13	22	18	18	17	11	11	9	3	3	3	3	1	0	-	0	2	7	7	7	12	12	12
14	22	18	18	17	11	11	9	3	3	3	3	1	0	0	-	2	7	7	7	12	12	12
15	23	16	16	14	9	9	7	1	1	1	1	3	2	2	2	-	5	5	5	10	10	10
16	28	21	21	19	13	13	12	6	6	6	6	8	7	7	7	5	-	0	0	5	5	5
17	28	21	21	19	13	13	12	6	6	6	6	8	7	7	7	5	0	-	0	5	5	5
18	32	24	24	22	18	18	17	11	11	11	11	13	12	12	12	10	5	5	5	-	0	0
19	32	24	24	22	18	18	17	11	11	11	11	13	12	12	12	10	5	5	5	0	0	0
20	32	24	24	22	18	18	17	11	11	11	11	13	12	12	12	10	5	5	5	0	0	0
Total	423	299	299	266	195	195	182	138	138	138	138	161	171	171	171	147	200	200	200	268	268	268

FIGURES

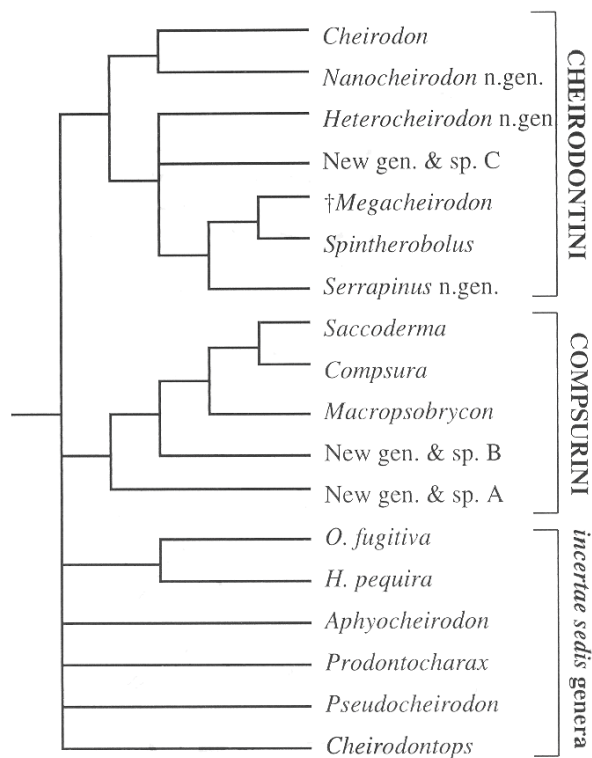


Fig. 1. Hypothesis of relationships of the Cheirodontiinae by Malabarba (1998).

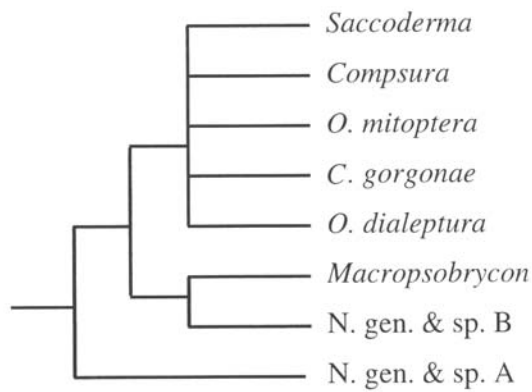


Fig. 2. Hypothesis of relationships of the Compsurini with addition of the Central America species, by Malabarba (1998).

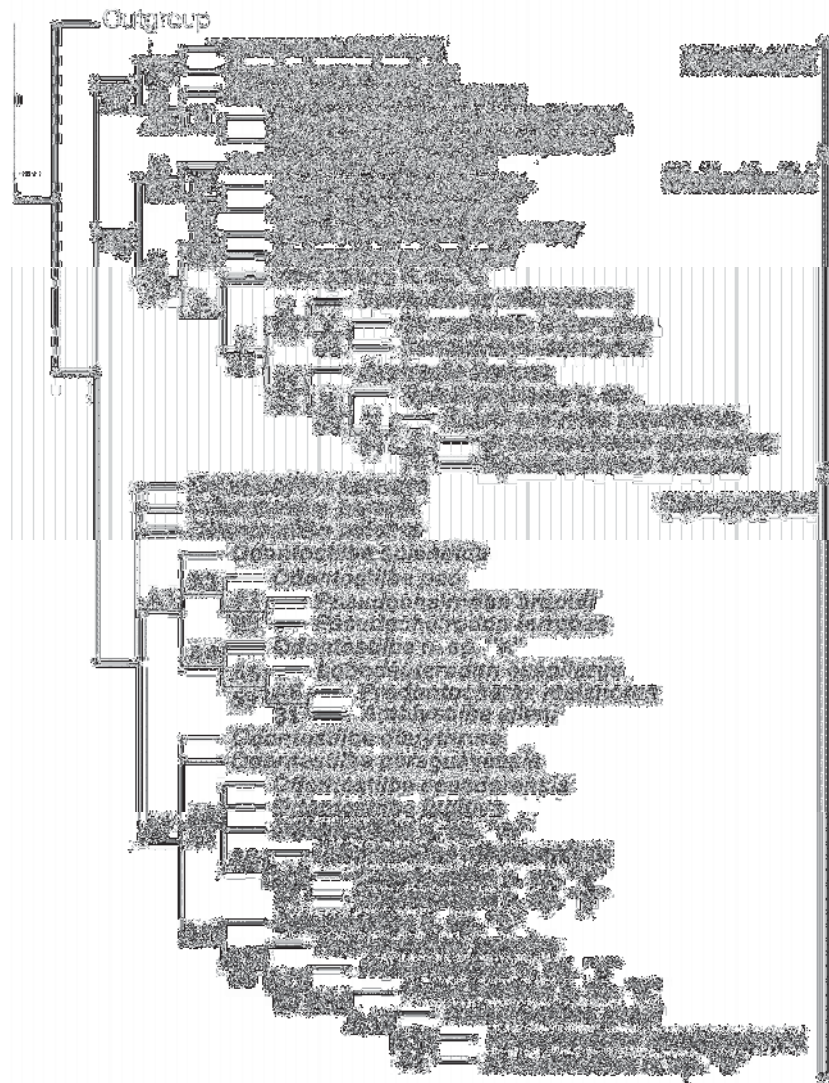


Fig. 3. Implied weighted cladogram of the Bührnheim (2006) hypothesis of relationships of the Cheirodontinae.

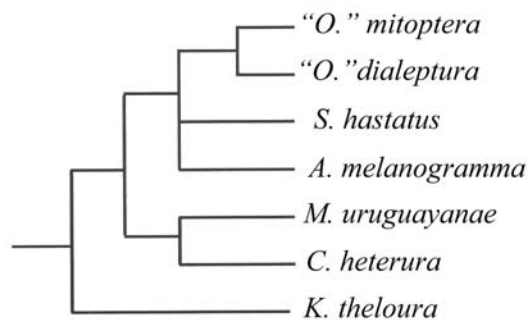


Fig. 4. Hypothesis of relationships of the Compsurini by Oliveira (2007), based on spermatozoa ultrastructure.

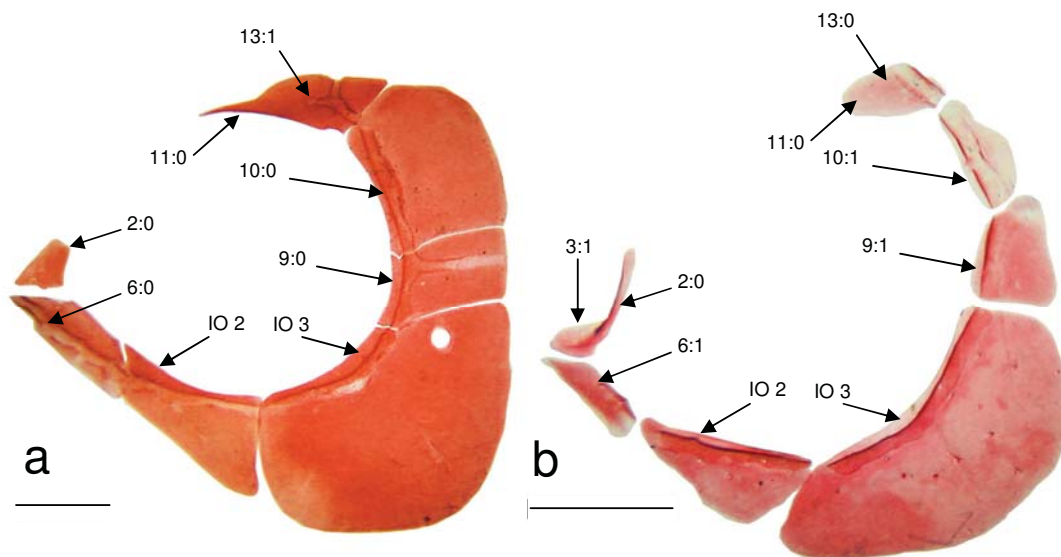


Fig. 5. Infraorbital series of (a) *Brycon pesu* MCP 17092, 57.3 mm SL (scale bar = 2 mm) and (b) “New Genus” n. sp. c MZUSP 40535, 26.9 mm SL. (scale bar = 1 mm). Lateral view, anterior to left. IO = infraorbital.

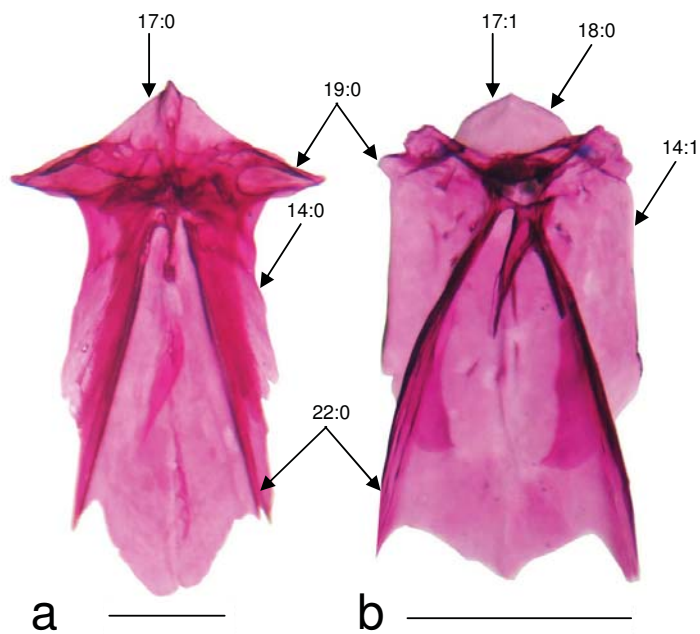


Fig. 6. Mesethmoid bone of (a) *Rhoadsia altipinna* FMNH 79077, ca. 60.0 mm SL (scale bar = 2 mm) and (b) *Odontostilbe fugitiva* INPA 18465, ca. 30.0 mm SL (scale bar = 1 mm). Ventral view, anterior to up.

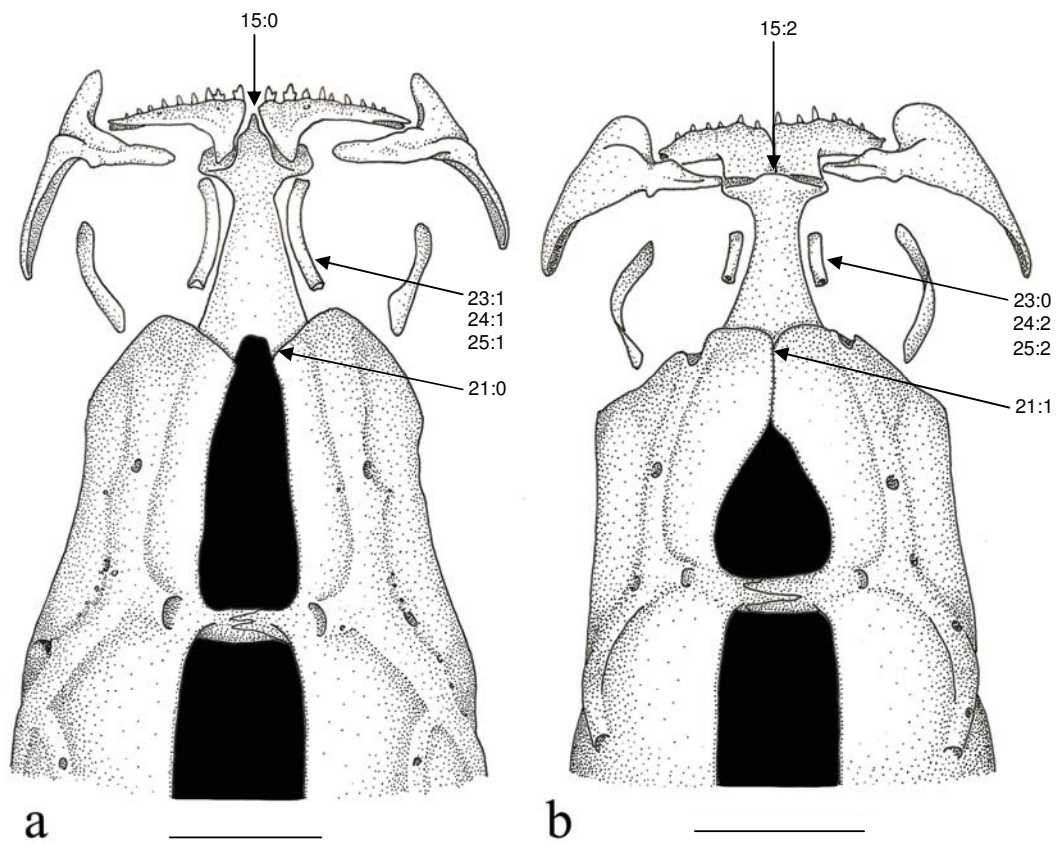


Fig. 7. Skull (a) “*Macropsobrycon*” *xinguensis* MCP 34546, 29.4 mm SL; and (b) *Macropsobrycon uruguayanae* MCP 11939, 32.6 mm SL, (scale bars = 1 mm). Dorsal view, anterior to up.

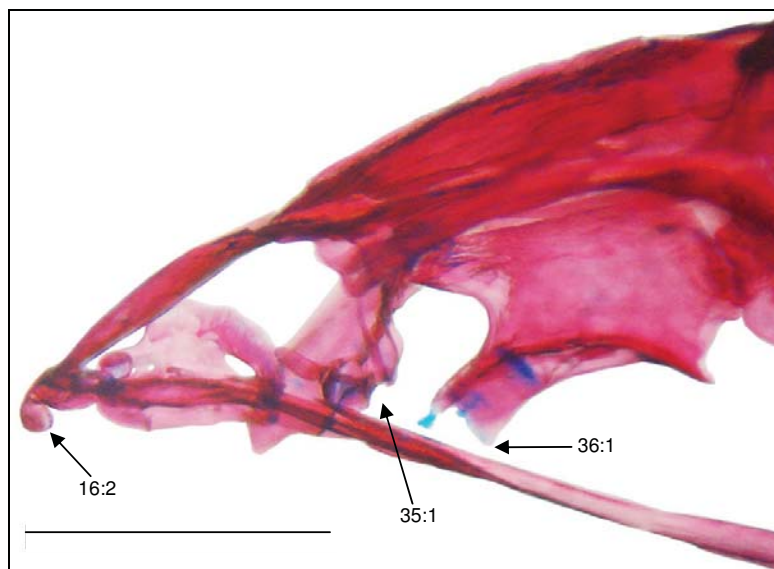


Fig. 8. Skull of *Spintherobolus broccea* MCP 19196, 17.4 mm SL (scale bar = 1 mm). Lateral view, anterior to left.

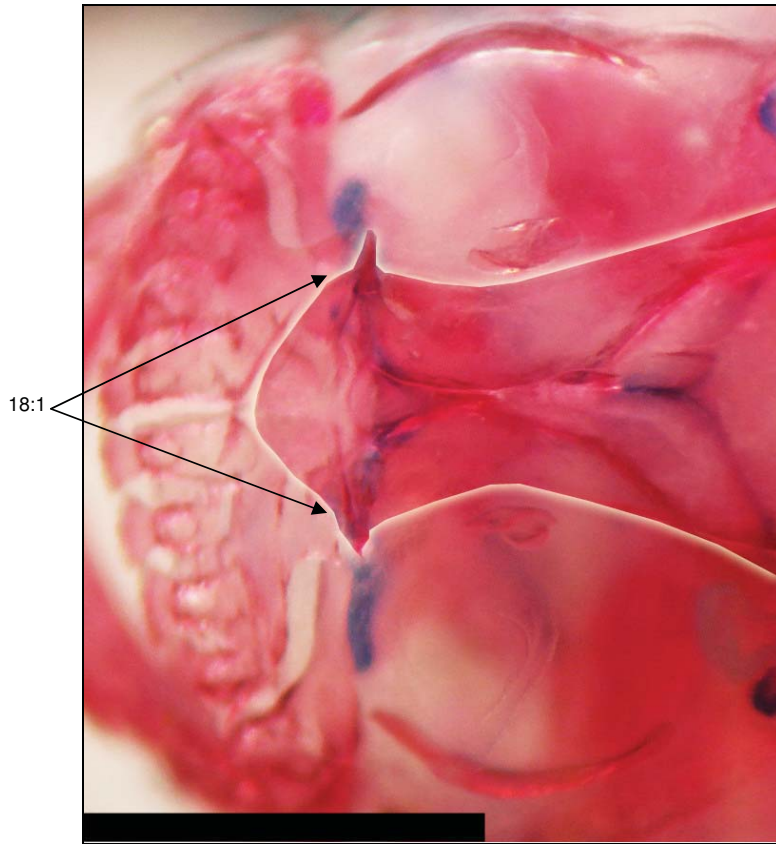


Fig. 9. Snout region of *Kolpotocheirodon figueiredoi* MZUSP 55219, 27.7 mm SL (scale bar = 1 mm). Dorsal view, anterior to left.



Fig. 10. Mesethmoid bone of *Cheirodon galusdai* MCP 14717, SL unknown (scale bar = 1 mm). Ventral view, anterior to left.

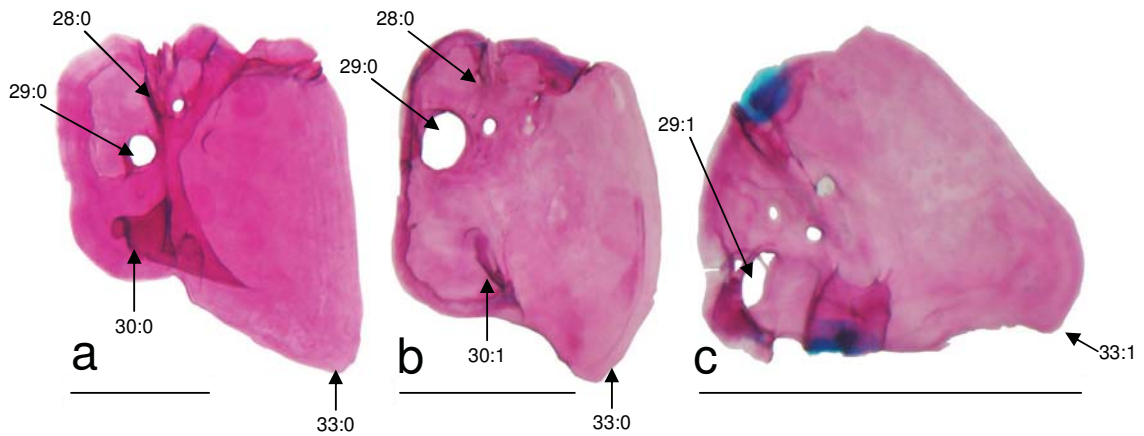


Fig. 11. Left lateral ethmoid bone of (a) *Rhoadsia altipinna* FMNH 79077, ca. 60.0 mm SL (scale bar = 2 mm), (b) *Odontostilbe fugitiva* INPA 18465, ca. 30.0 mm SL (scale bar = 1 mm), and (c) *Spintherobolus broccae* MCP 19196, 17.4 mm SL (scale bar = 1 mm). Frontal view, anterior to left.

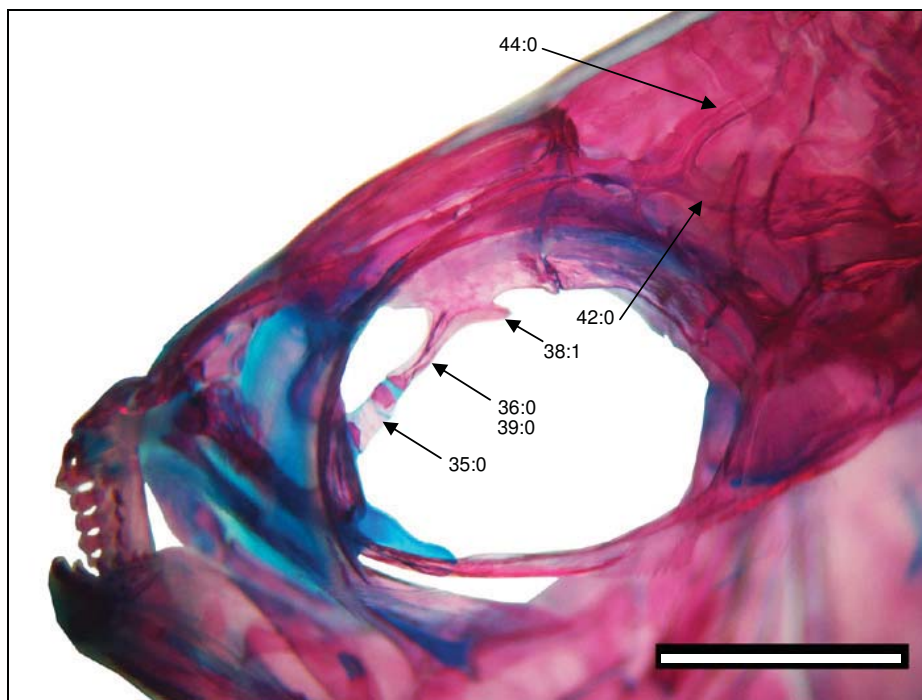


Fig. 12. Cranium of *Heterocheiroidon jacuhiensis* MCP 21672, 41.3 mm SL (scale bar = 2 mm). Lateral view, anterior to left.

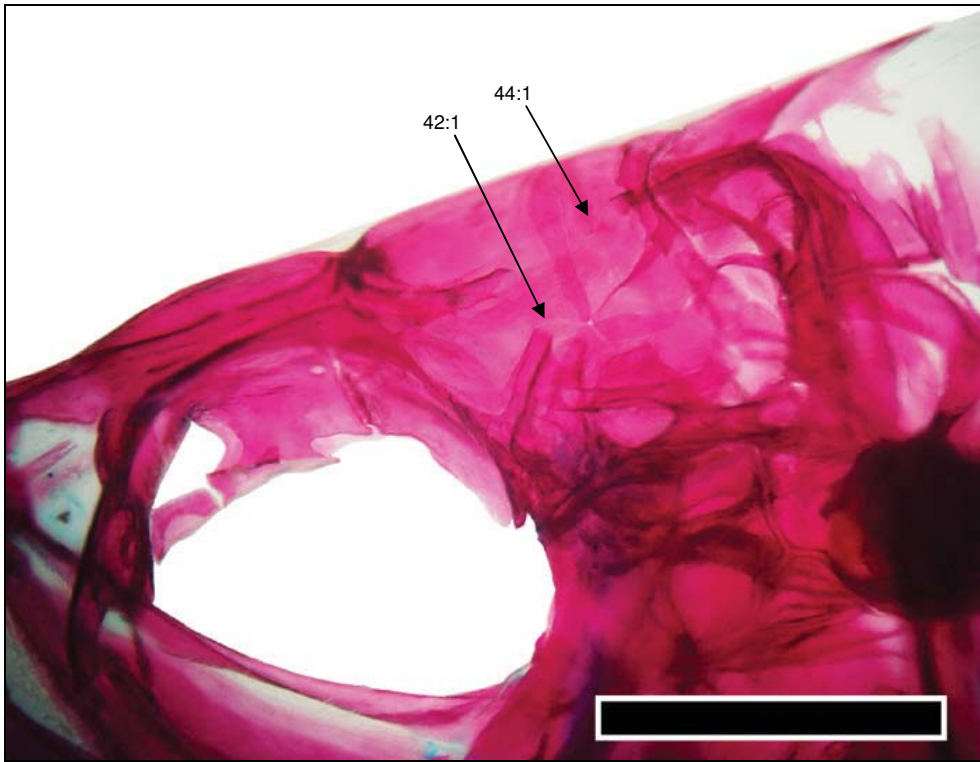


Fig. 13. Cranium of *Macropsobrycon uruguayanae* MCP 11939, 31.8 mm SL (scale bar = 2 mm). Lateral view, anterior to left.

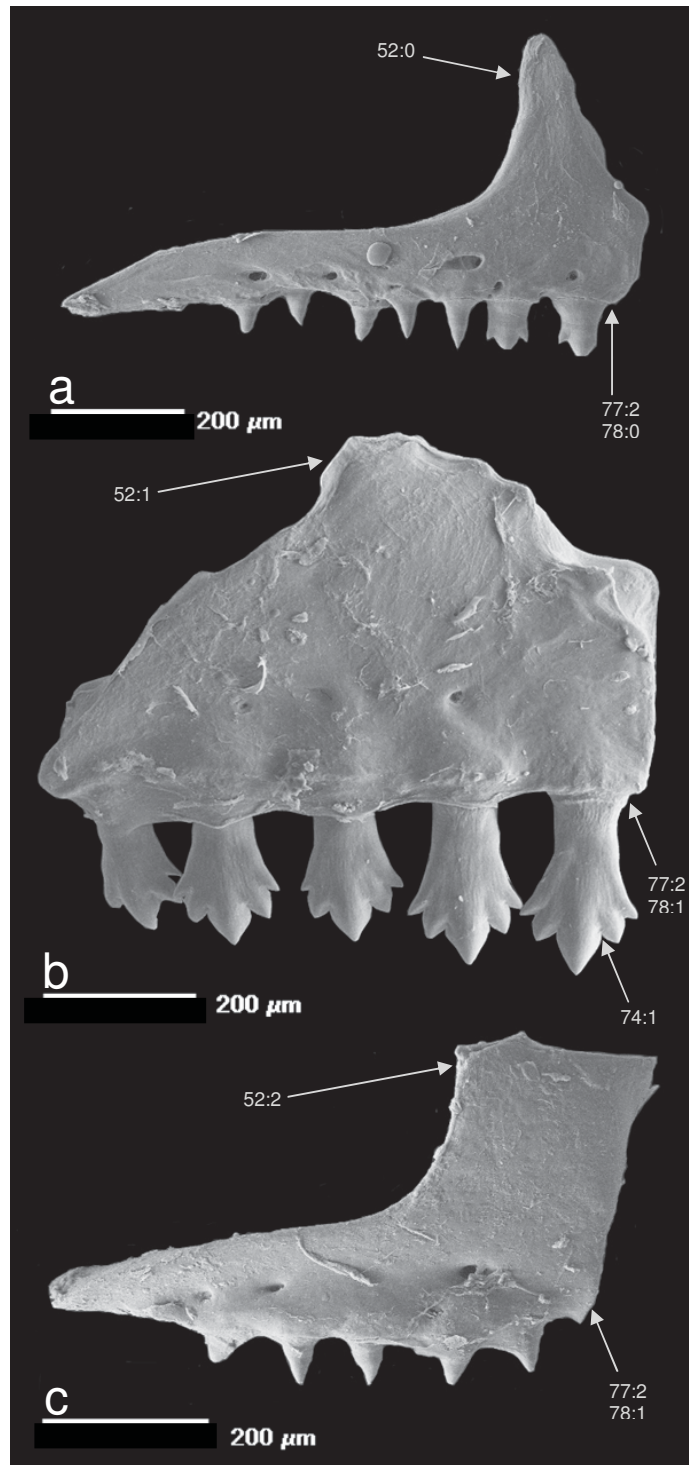


Fig. 14. Scanning electronic micrographs of the premaxillae of (a) “*Macropsobrycon*” *xinguensis* MCP 34546, 28.9 mm SL, (b) *Serrapinnus* n. sp. ac UFRGS 9216, 29.1 mm SL, and (c) *Macropsobrycon uruguayanae* MCP 20900, 27.9 mm SL. Right side, frontal view, anterior to right.

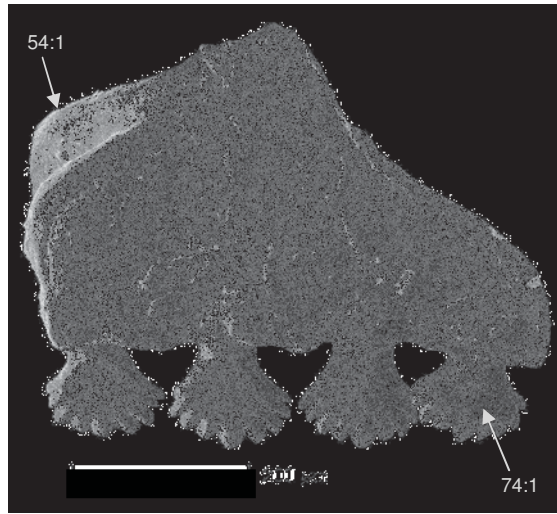


Fig. 15. Scanning electronic micrograph of the premaxilla of “New Genus” n. sp. b UFRJ 1260, 25.1 mm SL. Left side, frontal view.

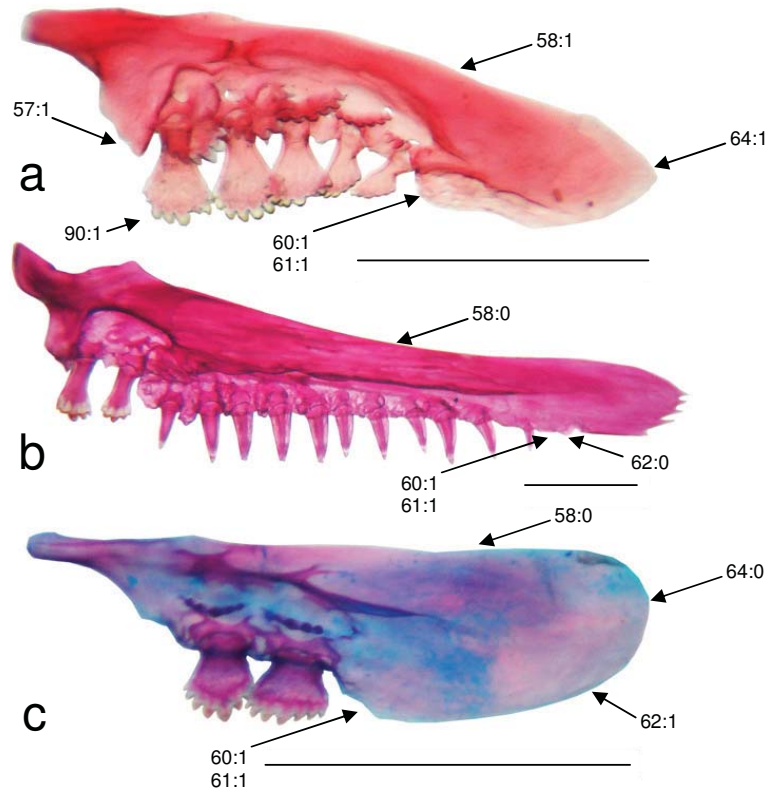


Fig. 16. Right maxillae of (a) *Pseudocheirodon terrabae* UMMZ 194214, 40.0 mm SL (scale bar = 1 mm), (b) *Rhoadsia altipinna* FMNH 79077, ca. 60.0 mm SL (scale bar = 2 mm), and (c) *Compsura heterura* MCP 17093, 28.0 mm SL (scale bar = 1 mm). Medial view (a,b), lateral view (c), anterior to left.

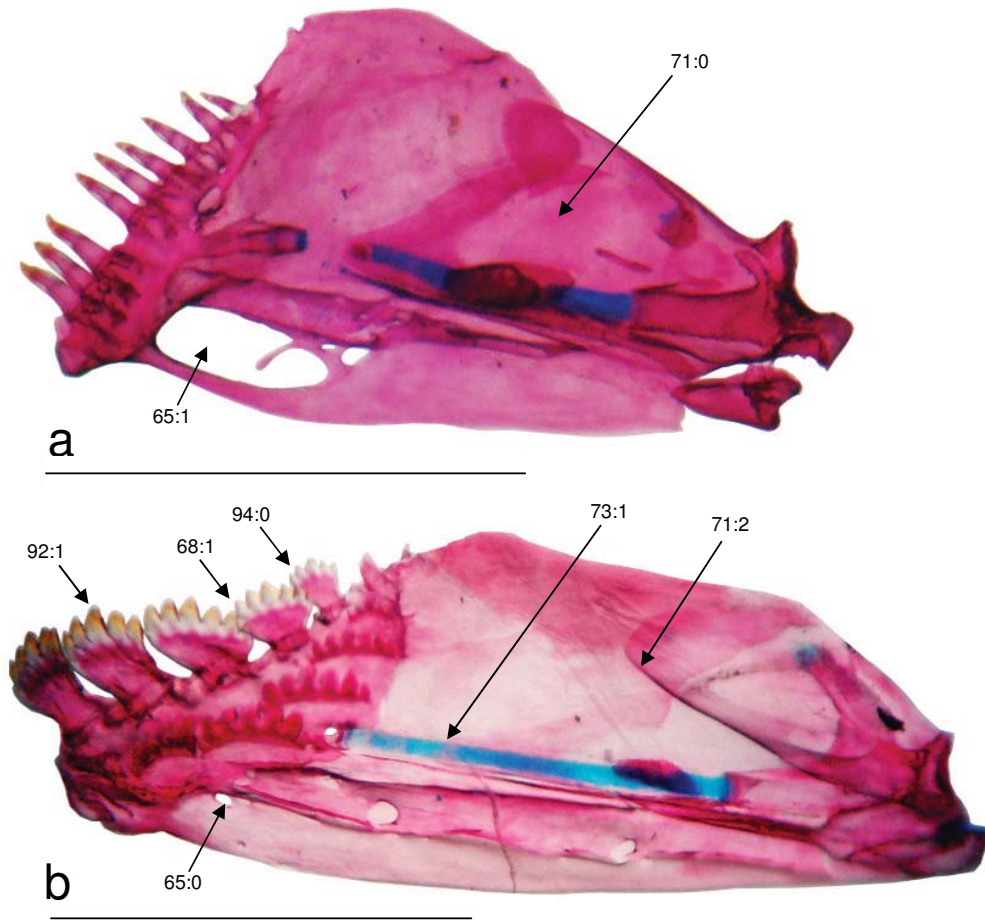


Fig. 17. Left dentary of (a) *Spintherobolus broccae* MCP 19196, 17.4 mm SL, and (b) *Saccoderma hastata* ICN 1464, 25.6 mm SL. Lateral view, anterior to left. Scale bars = 1 mm.

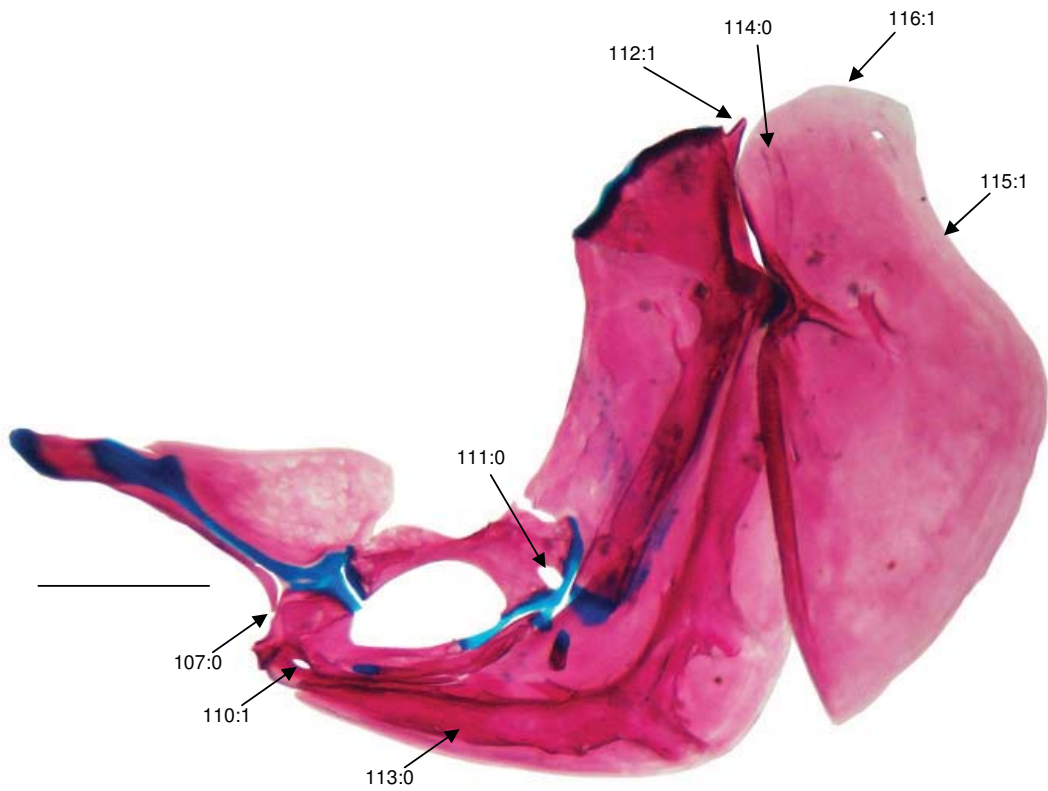


Fig. 18. Suspensorium of “New Genus” n. sp. c, MZUSP, 40535 26.9 mm SL (scale bar = 1 mm). Lateral view, anterior to left.

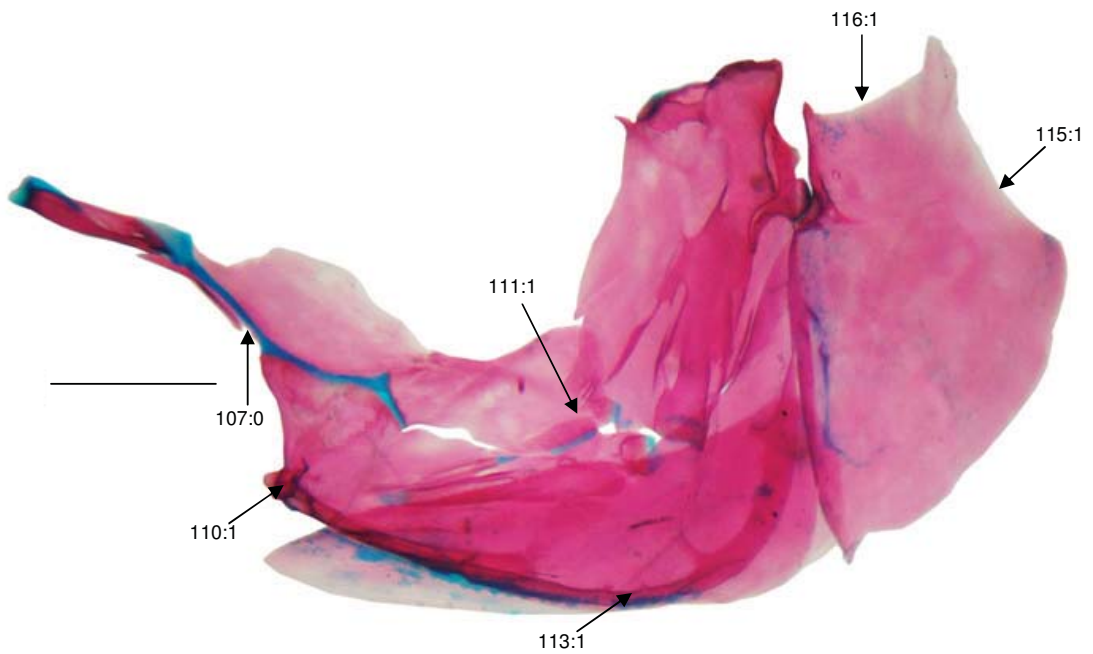


Fig. 19. Suspensorium of *Spitherobolus ankoseion* MCP, 12561 24.7 mm SL (scale bar = 1 mm). Lateral view, anterior to left.

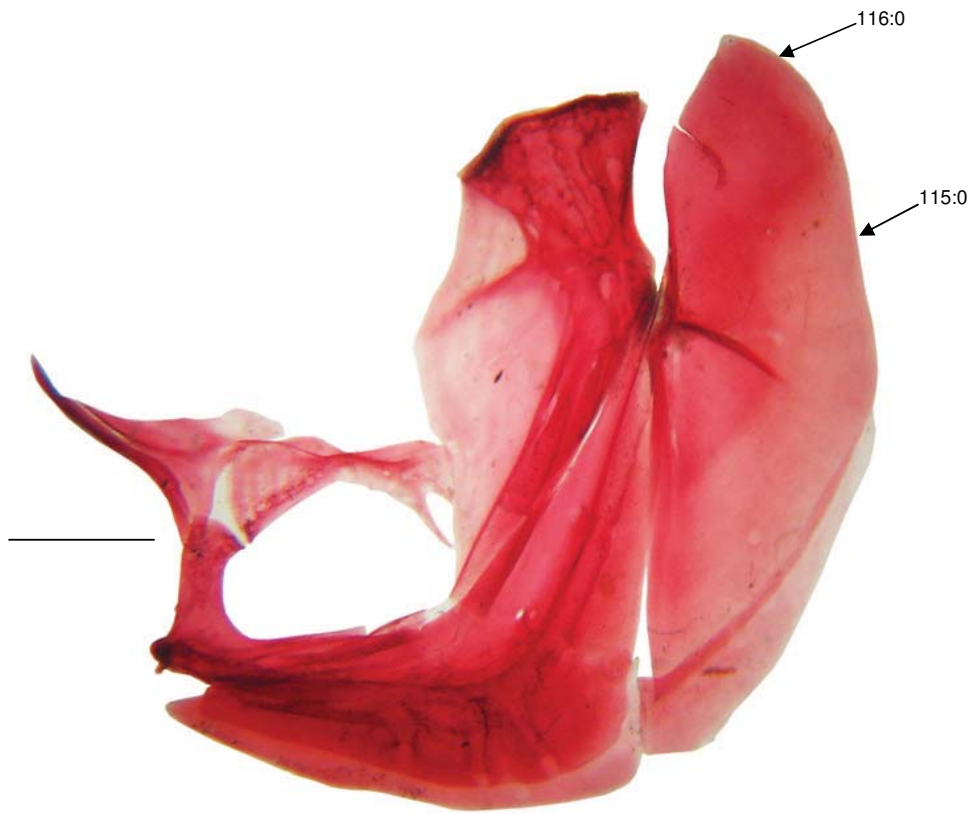


Fig. 20. Suspensorium of *Brycon pesu* MCP 17092, 57.3 mm SL (scale bar = 2 mm). Lateral view, anterior to left.

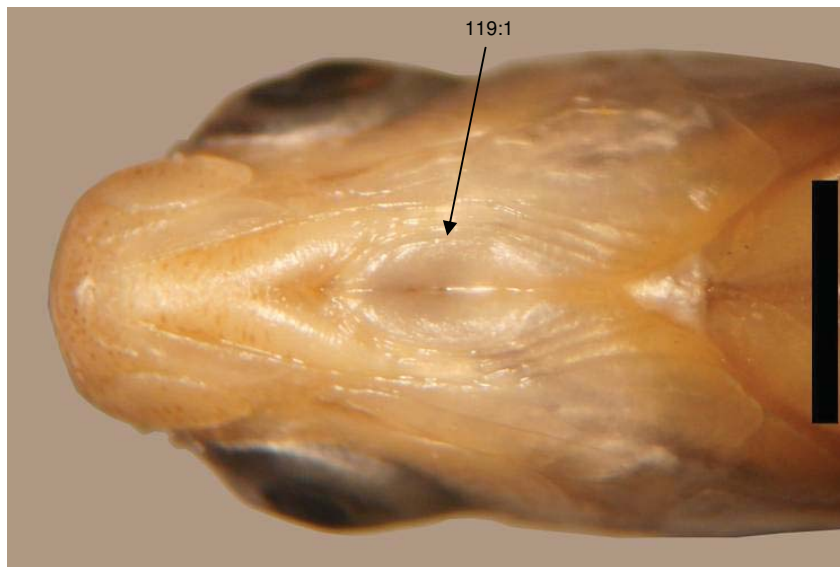


Fig. 21. Branchial isthmus of *Kolpotocheiroduon theloura* MNRJ 18081, 27.5 mm SL plate (scale bar = 2 mm). Ventral view, anterior to left.



Fig. 22. Urohyal of *Cheirodon galusdai* MCP 14717, SL unknown (scale bar = 1 mm). Lateral view, anterior to left.

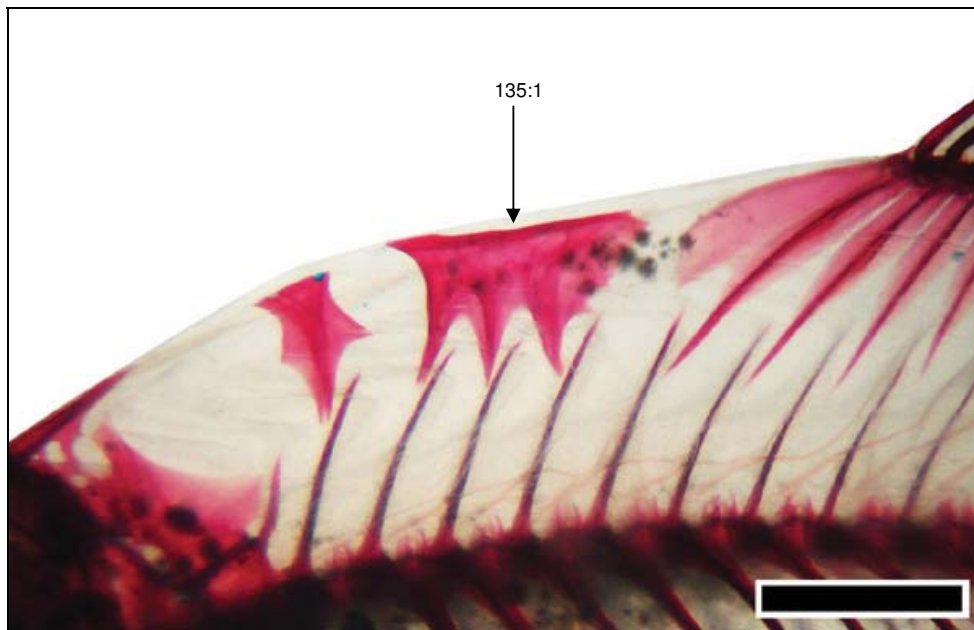


Fig. 23. Supraneurals of *Odontostilbe paraguayensis* MCP 35618, 22.0 mm SL (scale bar = 2 mm). Lateral view, anterior to left.

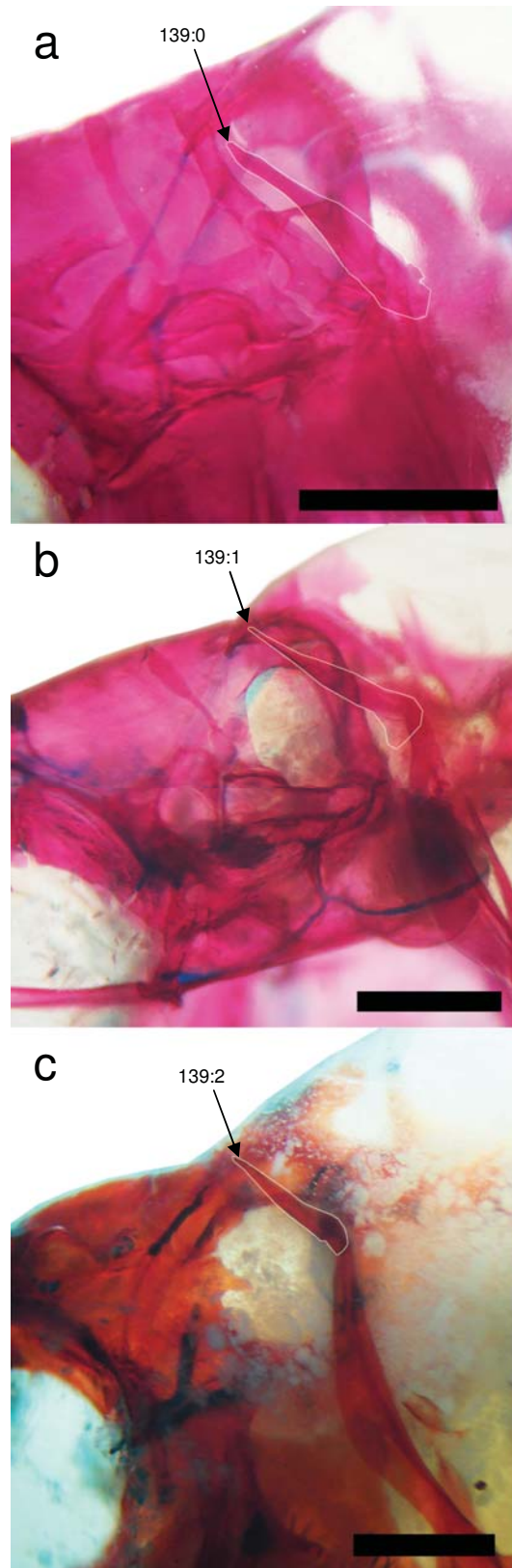


Fig. 24. Posterior region of the cranium of (a) *Serrapinnus* n. sp. ac UFRGS 9216, 27.6 mm SL, (b) *Spintherobolus ankoseion* MCP 12561, 24.7 mm SL, and (c) *Paracheiroidon axelrodi* MCP11994, 28.9 mm SL. Lateral view, anterior to left. Scale bars = 1 mm.

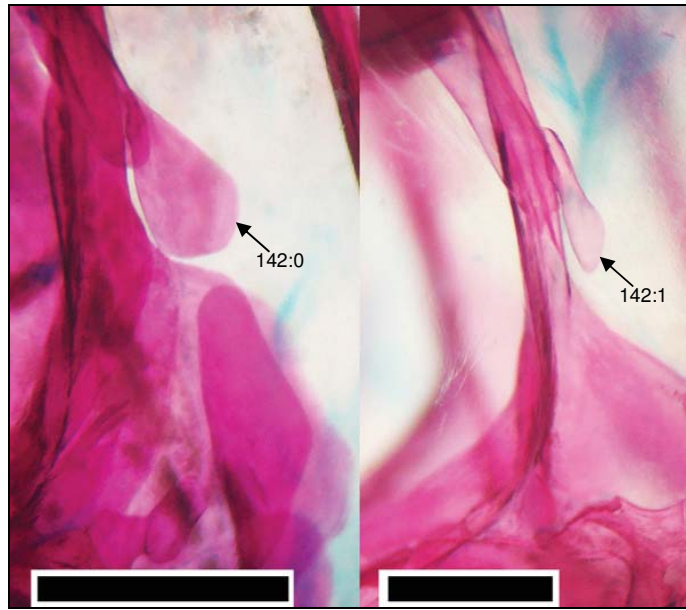


Fig. 25. Postcleithrum 1 of (a) *Serrapinnus* n. sp. ac UFRGS 9216, 27.6 mm SL, and (b) *Heterocheiroduon jacuhiensis* MCP 21672, 41.3 mm SL. Lateral view, anterior to left. Scale bars = 1 mm.

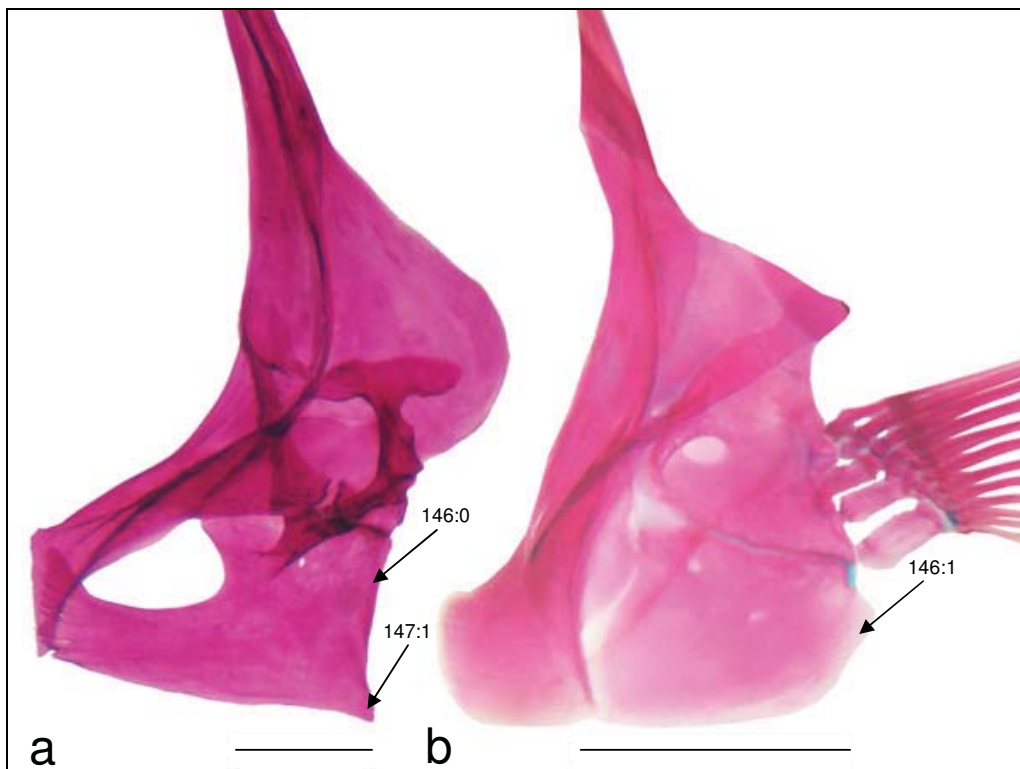


Fig. 26. Pectoral girdle of (a) *Odontostilbe fugitiva* INPA 18465, ca. 30.0 mm SL, and (b) *Spintherobolus ankoseion* MCP 12561, 24.7 mm SL. Lateral view, anterior to left. Scale bars = 1 mm.



Fig. 27. “*Odontostilbe*” *dialeptura* USNM 208524, holotype, 28.0 mm SL.

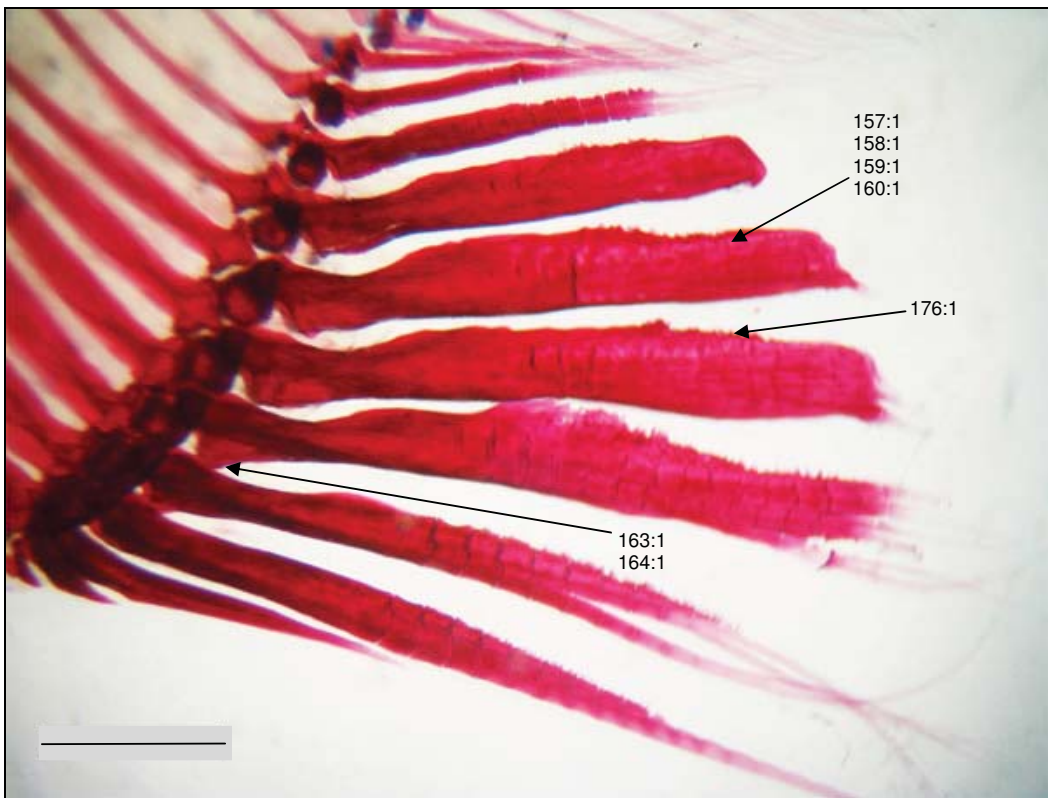


Fig. 28. Anterior hypertrophied anal-fin rays of *Serrapinnus calliurus* MCP 12537, 36.4 mm SL (scale bar = 1 mm). Lateral view, anterior to left.

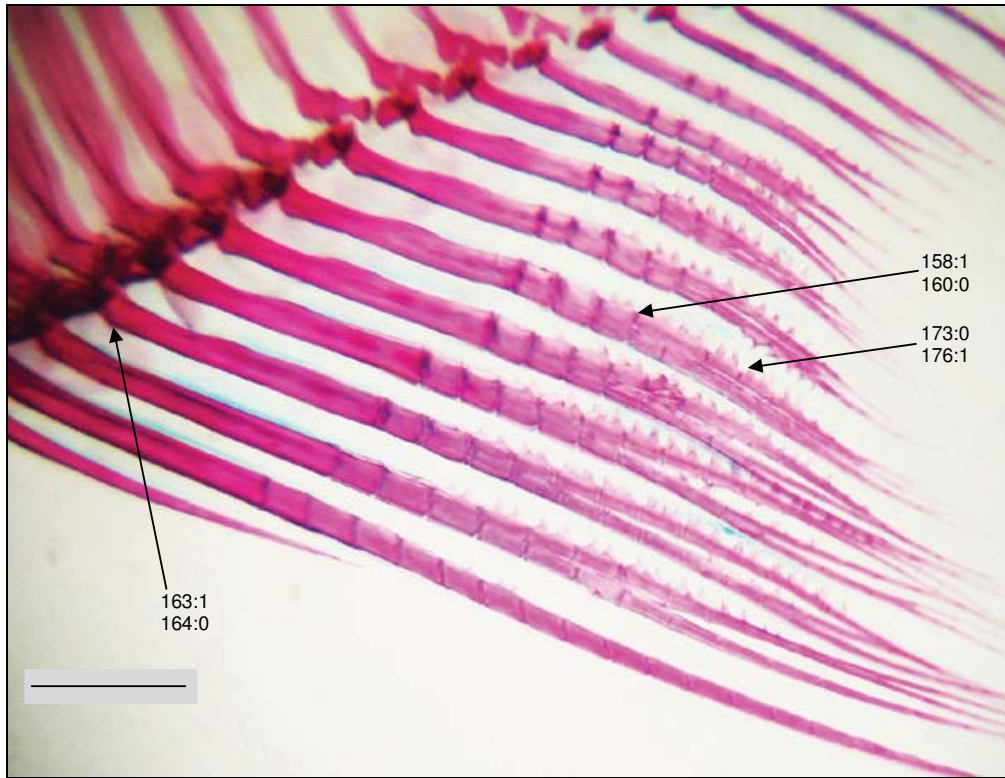


Fig. 29. Anterior hypertrophied anal-fin rays of *Heterocheiroduon jacuhiensis* MCP 21672, 41.3 mm SL (scale bar = 1 mm). Lateral view, anterior to left.

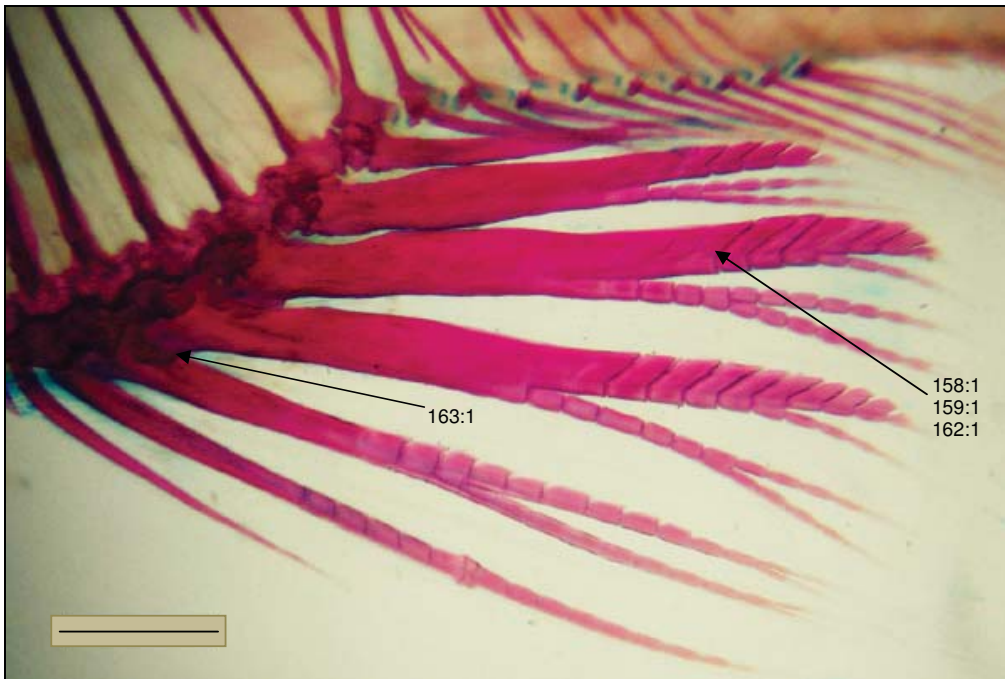


Fig. 30. Anterior hypertrophied anal-fin rays of *Spintherobolus ankoseion* MCP 12561, 24.7 mm SL (scale bar = 1 mm). Lateral view, anterior to left.

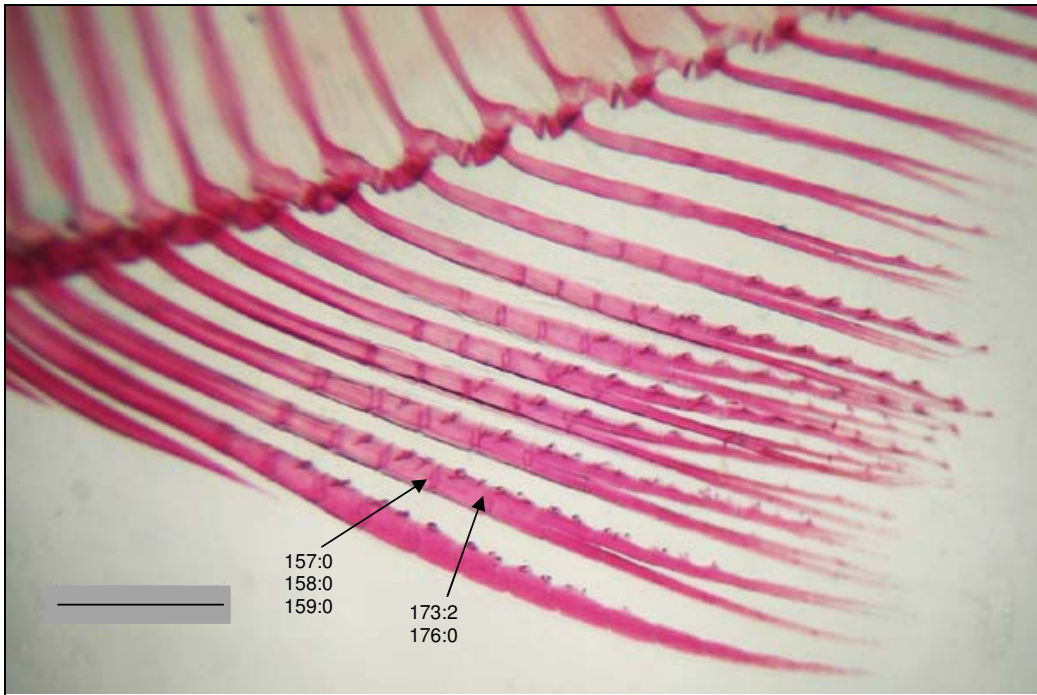


Fig. 31. Anterior anal-fin rays of *Macropsobrycon uruguayanae* MCP 20900, 34.3 mm SL (scale bar = 1 mm). Lateral view, anterior to left.

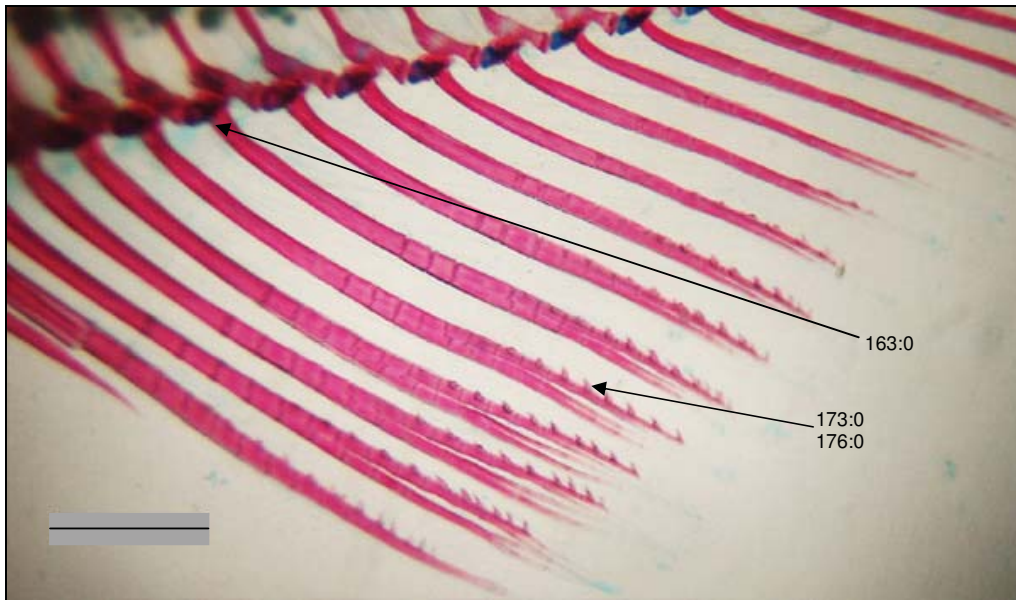


Fig. 32. Anterior anal-fin rays of *Acinocheiroidon melanogramma* MCP 19238, 31.9 mm SL (scale bar = 1 mm). Lateral view, anterior to left.

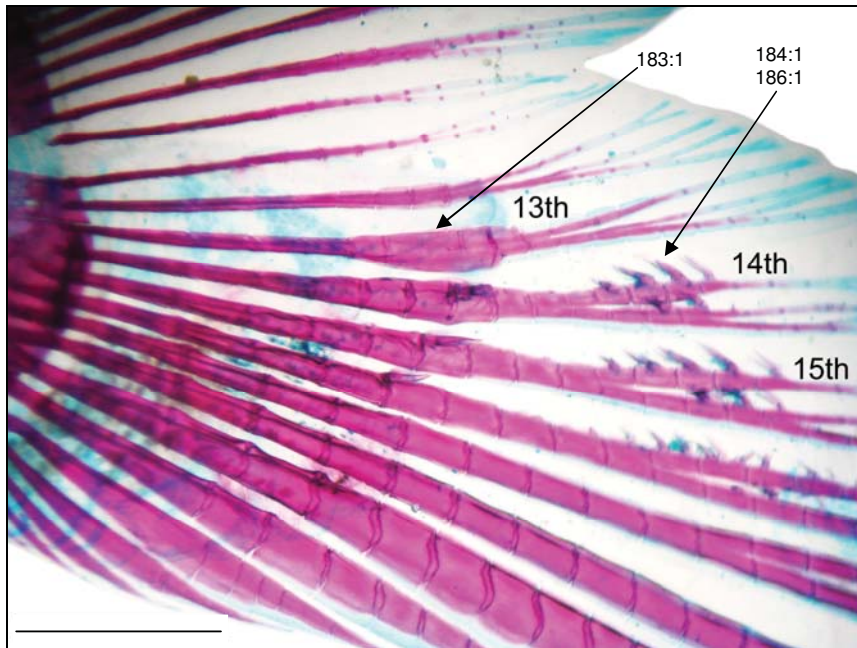


Fig. 33. Lower lobe of the caudal fin of *Compsurini Purus n. sp.*, mature male, MCP 41716, 23.6 mm SL (scale bar = 1 mm). Lateral view, anterior to left.

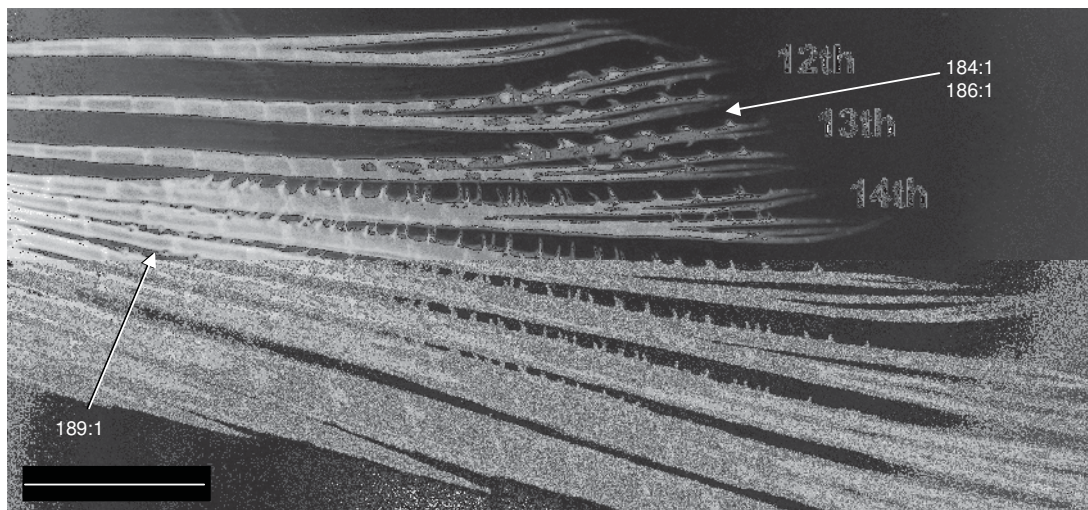


Fig. 34. Lower lobe of the caudal fin of *Macropsobrycon uruguayanae*, mature male, MCP 20900, 34.2 mm SL (scale bar = 1 mm). Lateral view, anterior to left.

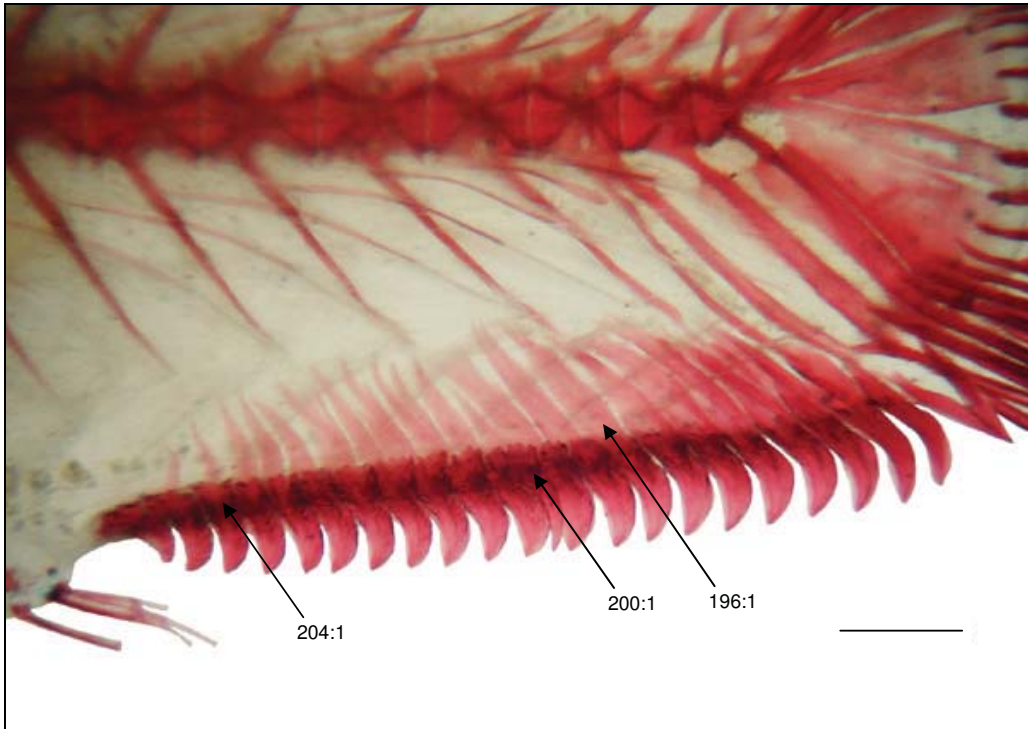


Fig. 35. Ventral procurent caudal-fin rays *Cheirodon australe* UMMZ 215046, male 39.7 mm SL (scale bar = 1 mm). Lateral view, anterior to left.

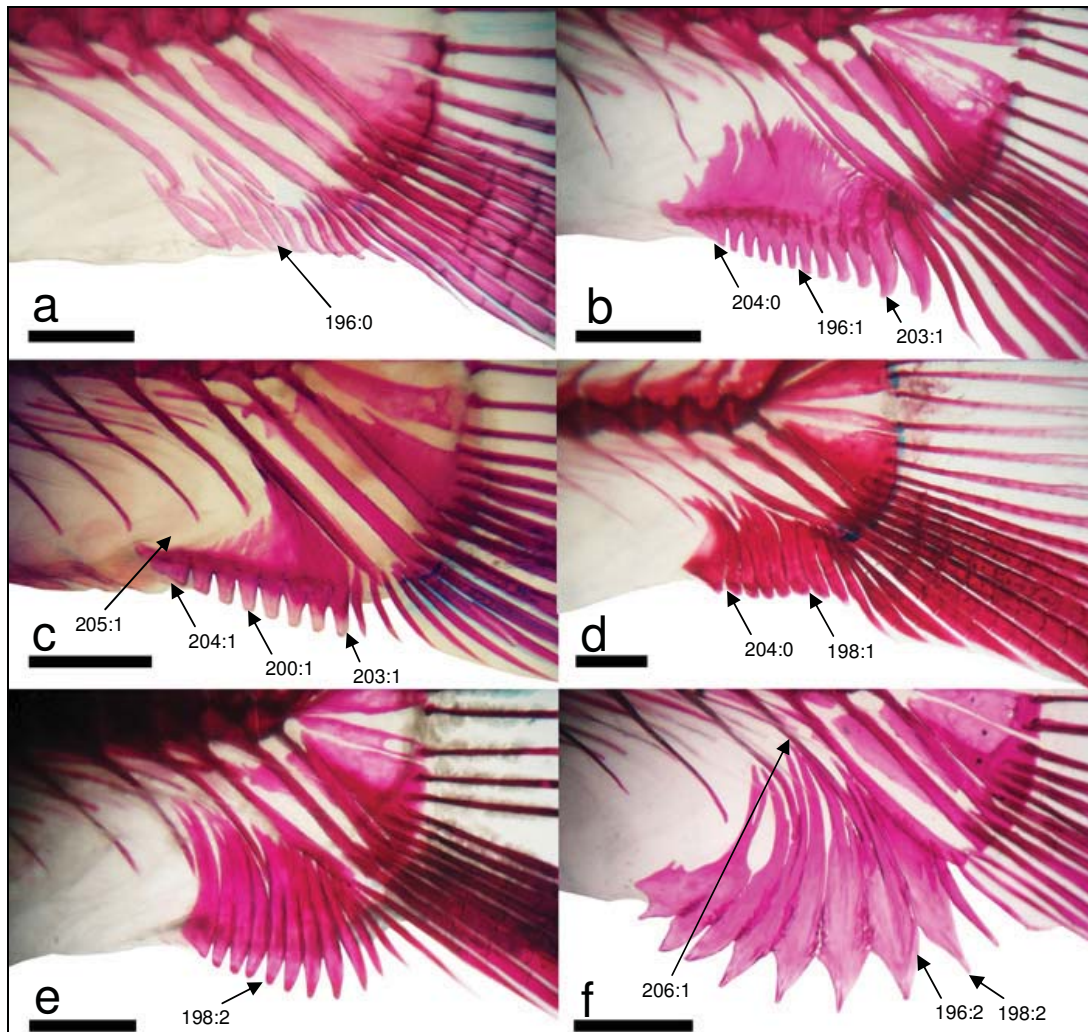


Fig. 36. Mature male ventral procurent caudal-fin rays of (a) *Heterocheiroidon jacuhiensis* MCP 21672, 41.3 mm SL; (b) “New Genus” n. sp. b UFRJ 1260, 25.6 mm SL; (c) *Spintherobolus ankoseion* MCP 12561 24.7 mm SL; (d) *Serrapinnus calliurus* MCP 12537, 36.4 mm SL; (e) *Serrapinnus* n. sp. t MCP 40417, 30.8 mm SL; and (f) *Serrapinnus* n. sp ac UFRGS 12023, 26.5 mm SL. Lateral view, anterior to left. Scale bars = 1 mm.

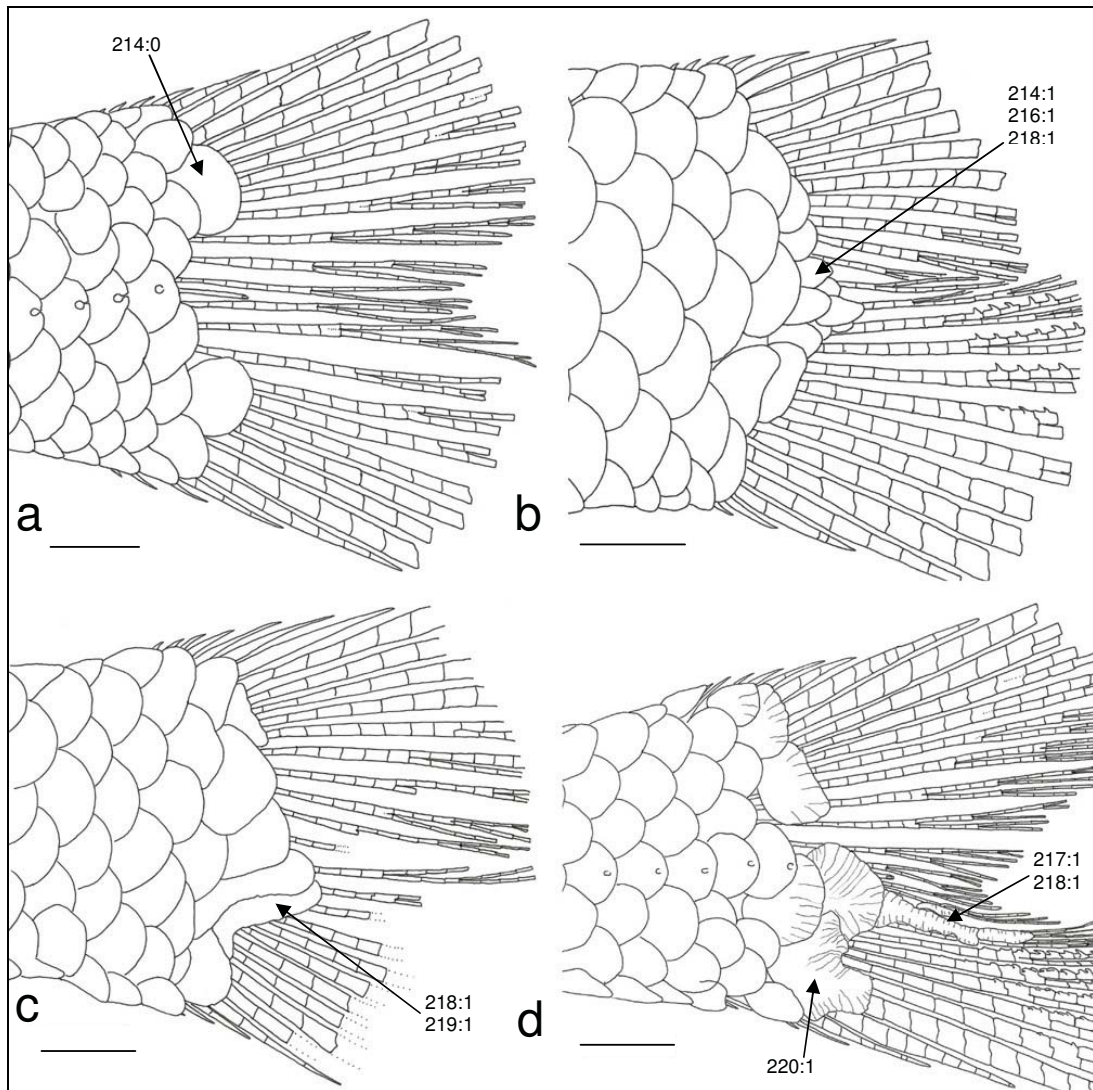


Fig. 37. Mature male caudal peduncle and caudal-fin base of **(a)** *Odontostilbe fugitiva* USNM 362043, 29.1 mm SL; **(b)** *'Odontostilbe' dialeptura*, USNM 209509, 31.9 mm SL; **(c)** *'Compsura' gorgonae* caudal fin, USNM 208543, 25.9 mm SL; and **(d)** *Saccoderma melanostigma* USNM 121522, 28.1 mm SL. Lateral view, anterior to left. Scale bars = 1 mm.

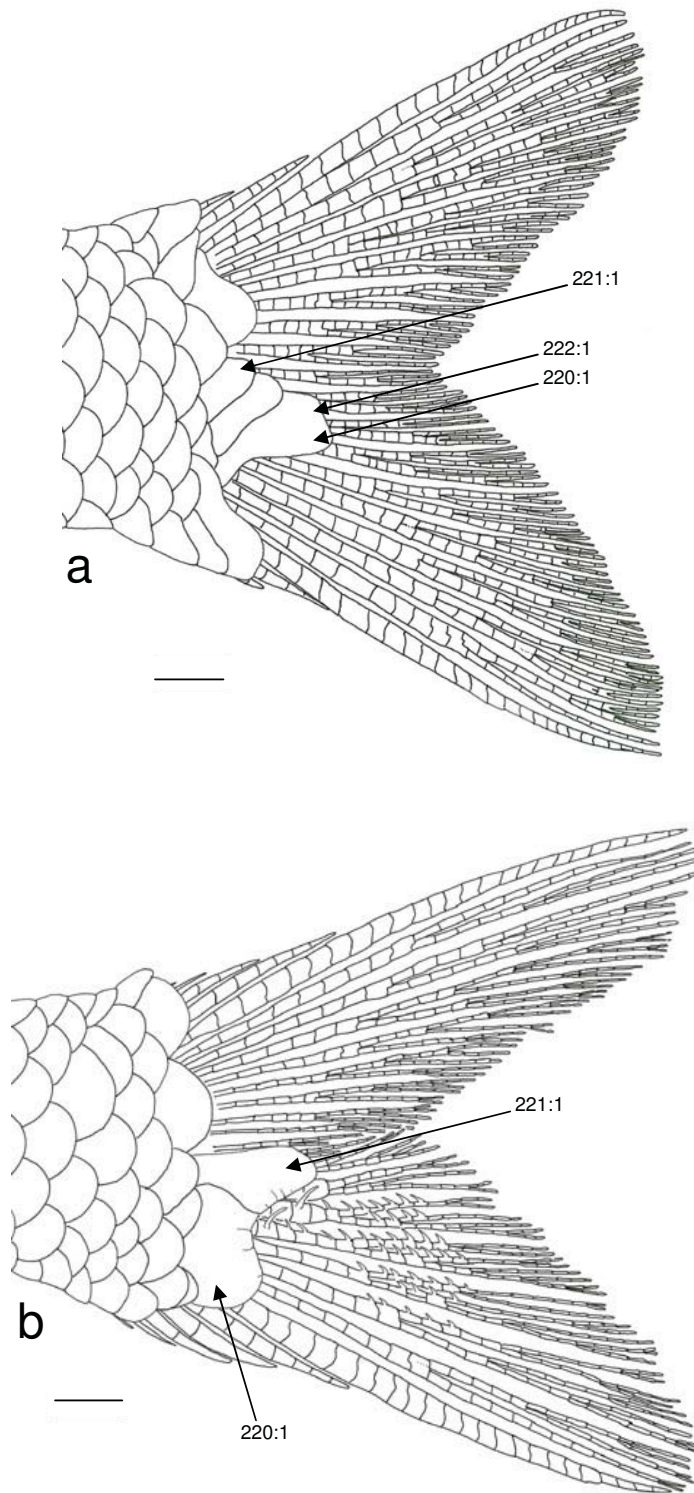


Fig. 38. Mature male caudal peduncle and caudal-fin base of **(a)** *Compsura heterura* MCP 30939, 27.7 mm SL; and **(b)** *Compsurini Purus* n. sp. MCP 41716, 25.9 mm SL. Lateral view, anterior to left. Scale bars = 1 mm.

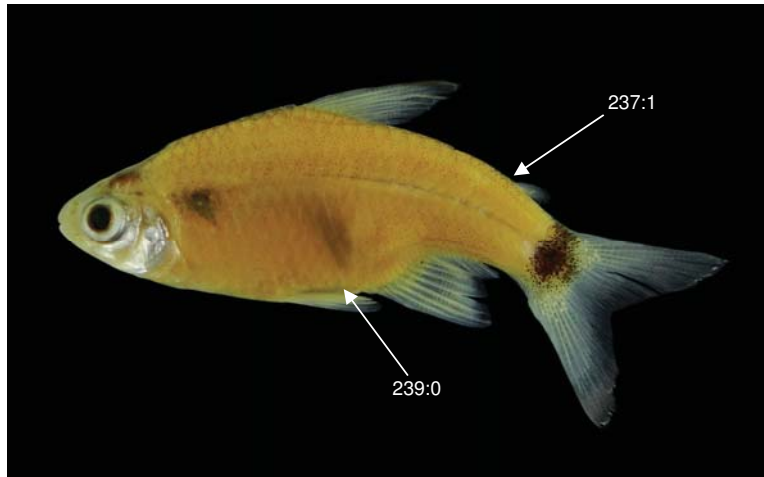


Fig. 39. Mature male of *Serrapinnus calliurus* MCP 16404, 27.7 mm SL, with caudal peduncle ventrally arched.

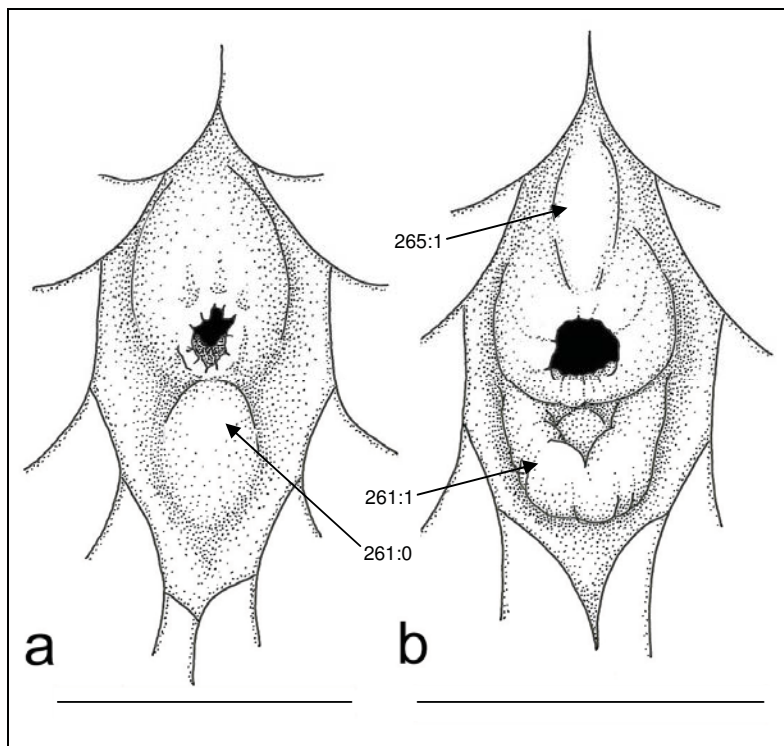


Fig. 40. Urogenital papillae of mature males of (a) *Serrapinnus calliurus* MCP 19414, 31.4mm SL; and (b) *Compsura heterura* MCP 31368, 25.6 mm SL. Ventral view, anterior to up. Scale bars = 1 mm.

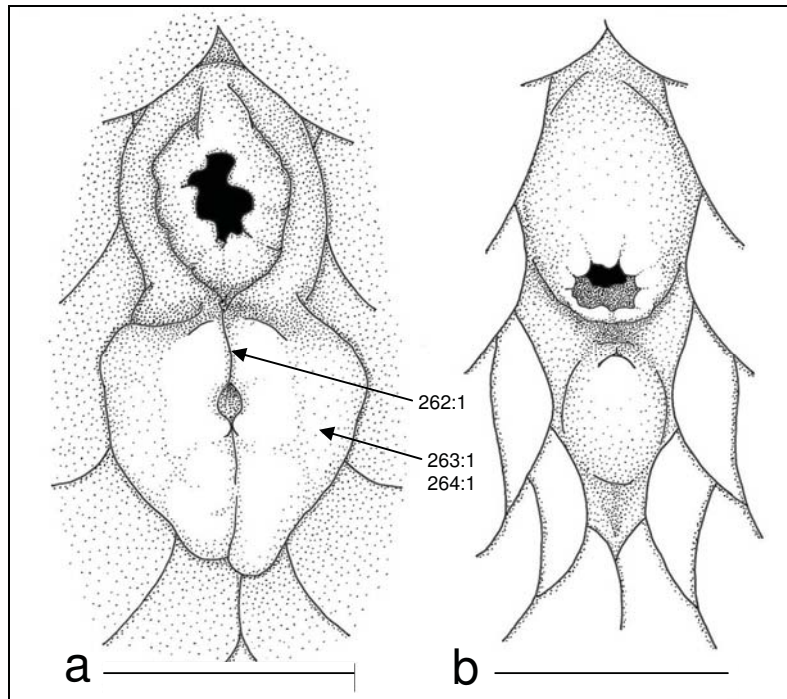


Fig. 41. Urogenital papillae area of female specimens of (a) *Compsurini Purus* n. sp., MCP 41716, 29.0 mm SL; and (b) *Serrapinnus calliurus*, MCP 19414, 35.2 mm SL. Ventral view, anterior to up. Scale bars = 1 mm.

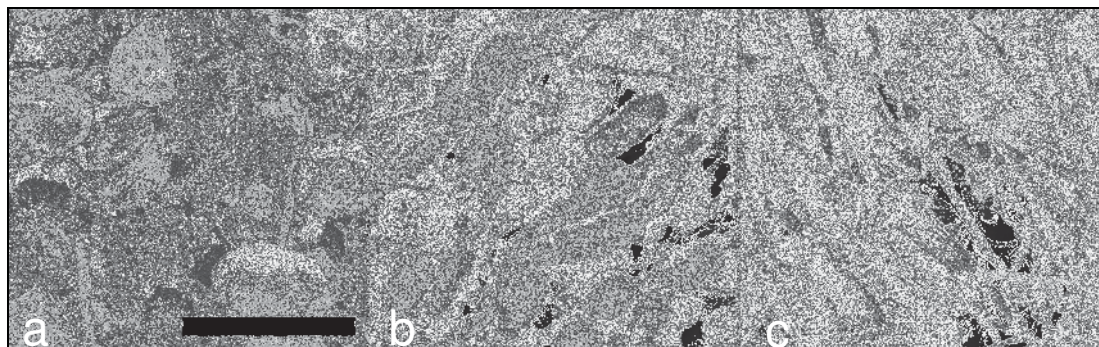


Fig. 42. Scanning micrographs of the spermatozoa of (a) *Serrapinnus* n. sp. mi MCP 37779, 30.1 mm SL; (b) “*Compsura*” *gorgonae* UMMZ 180769, 27.3 mm SL; and (c) *Saccoderma hastata* CAS 70909, 22.9 mm SL. Scale bar = 5 micrometers.



Fig. 43. Strict consensus tree from equal weighted parsimony analysis with 1293 steps (CI = 0.25; RI = 0.69), obtained from 43 equally parsimonious trees with 1253 steps (CI = 0.25; RI = 0.70), representing the hypothesis of relationship for the Compsurini and outgroup taxa.

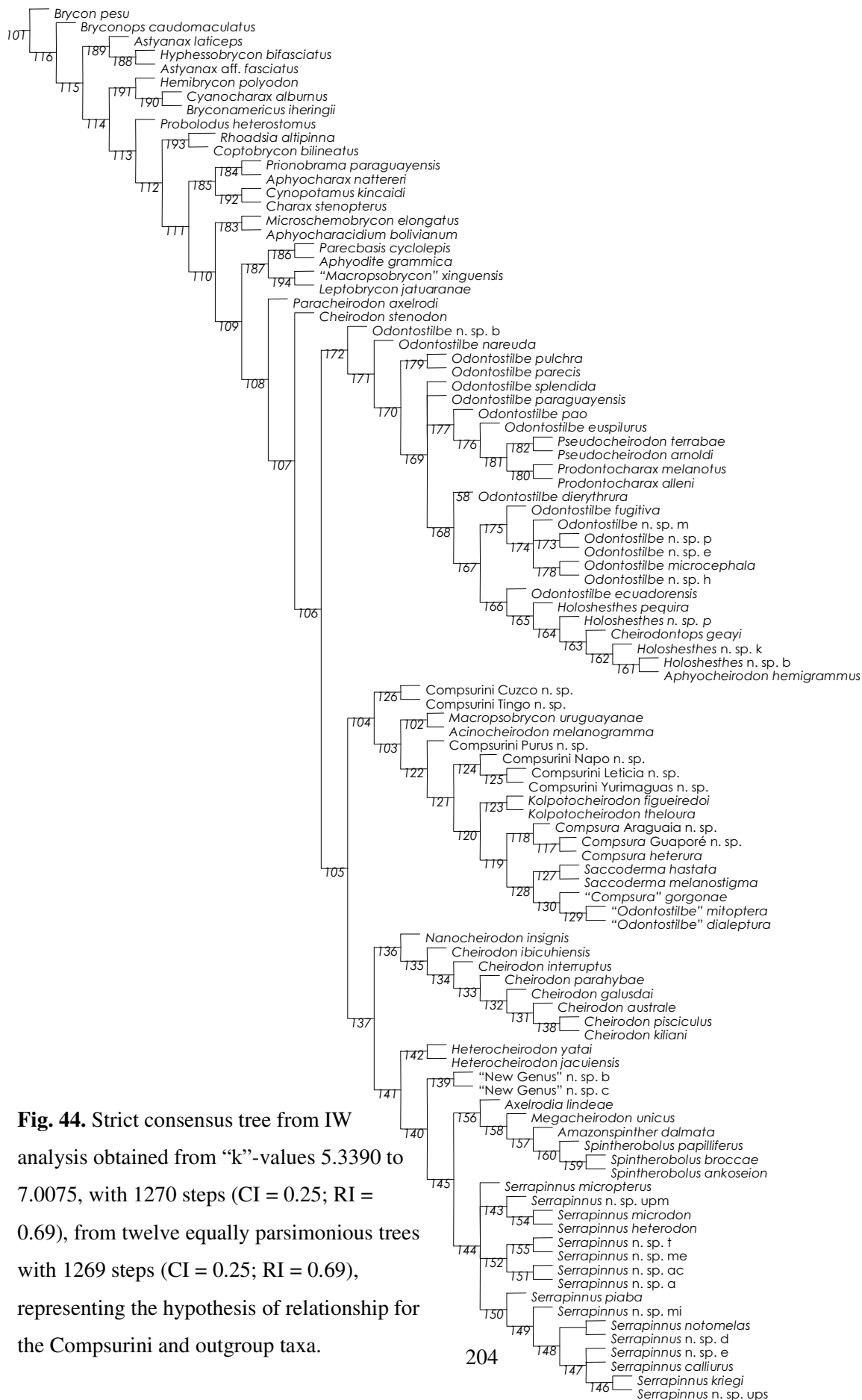


Fig. 44. Strict consensus tree from IW analysis obtained from “k”-values 5.3390 to 7.0075, with 1270 steps (CI = 0.25; RI = 0.69), from twelve equally parsimonious trees with 1269 steps (CI = 0.25; RI = 0.69), representing the hypothesis of relationship for the Compsurini and outgroup taxa.

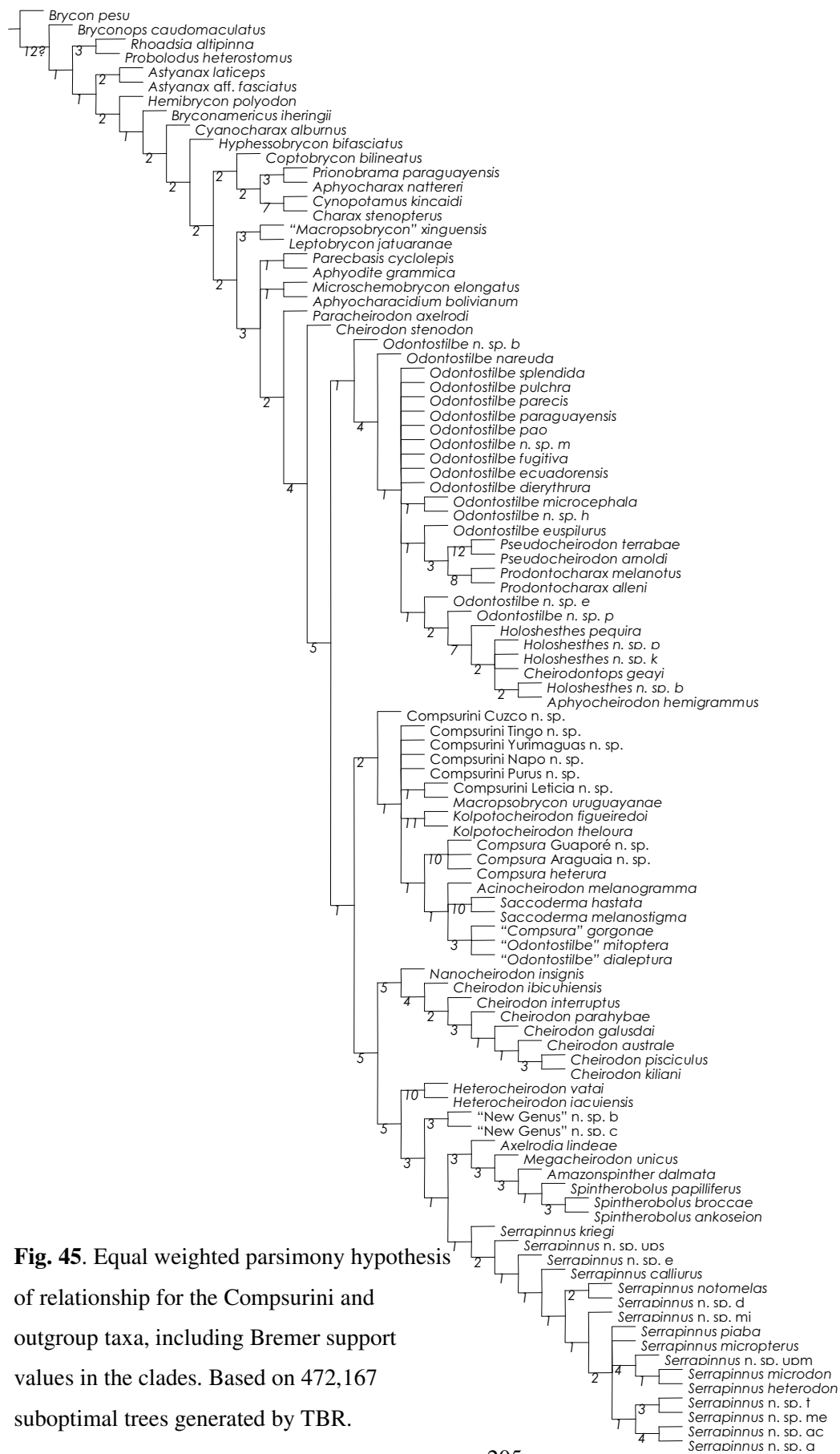


Fig. 45. Equal weighted parsimony hypothesis of relationship for the Compsurini and outgroup taxa, including Bremer support values in the clades. Based on 472,167 suboptimal trees generated by TBR.



Fig. 46. Hypothesis of relationship for the Compsurini and outgroup taxa obtained from implied weighted analysis under “k” = 6.3818, including absolute Bremer support values in the clades. Based on 48,000 suboptimal trees generated by TBR.

APPENDIXES

Appendix I. List of examined material.

Characidae: *Aphyocharacidium bolivianum*. MCP 37960, 3 c&s of 12 alc., Brazil, Acre, Sena Madureira, rio Purus basin. MCP 39636, 11, Brazil, Amazonas, Humaitá, rio Açuá. *Aphyocharax nattereri*. MCP 34718, 2 c&s (1 male, 1 female) of 13, Brazil, Pará, Almeirim, rio Amazonas basin, Comunidade de São Raimundo, Pesqueiro. *Aphyodite grammica*. MCP 14927, Brazil, Amazonas, rio Negro, ilha Buiú-Au. MCP 16893, 2 c&s, Brazil, Amazonas, rio Negro, confluence with rio Urubaxi. *Astyanax* aff. *fasciatus*. MCP 18685, 7, Brazil, Rio Grande do Sul, Jacuí, rio Jacuí basin. MCP 33402, 3 c&s, Brazil, Rio Grande do Sul, Guafba, lago Guaíba. *Astyanax laticeps*. MCP 25690, 1 c&s of 3, Brazil, Rio Grande do Sul, Maquiné, rio Tramandaí basin, arroio Água Parada. *Bryconamericus iheringii*. MCP 19672, 1 c&s of 60, Brazil, Rio Grande do Sul, Getúlio Vargas, rio Uruguay basin, rio Abaúna. *Brycon pesu*. MCP 17092, 2 c&s, Brazil, Pará, São Luiz, rio Tapajós. *Bryconops caudomaculatus*. MCP 22960, 3 c&s of 34, Brazil, Pará, Puraquequara, rio Amazonas basin, igarapé Puraquequara. *Charax stenopterus*. MCP 11298, 2 c&s of 3, no procedence. *Cheirodon stenodon*. MZUSP 37175, 4 c&s of 19. MZUSP 35346, 6, Brazil, São Paulo, Conchas/Bofete, ribeirão Água Fria. *Coptobrycon bilineatus*. MCP 39051, 2 c&s (1 male, 1 female) of 8, Brazil, São Paulo, southeast rio Itatinga, under bridge, 2 Km from visitor center, Parque das Neblinas. *Cyanocharax alburnus*. MCP 34720, 39 c&s, Brazil, Rio Grande do Sul, Porto Alegre, lago Guaíba. *Cynopotamus kincaidi*. MCP 15701, 2, Brazil, Mato Grosso, Cáceres, rio Paraguai. MCP 17121, 1 c&s, Brazil, Mato Grosso, rio Paraguay basin, mouth of the rio Aricá in the rio Cuiabá. *Hemibrycon polyodon*. KU 20004, 42 of 84 (2 c&s), 15.5-72.3 mm SL, N shore río Pastaza below río Negro (town), Tungurahua, 26 Jul 1968, G. R. Smith & J. D. Lynch. *Hyphessobrycon bifasciatus*. MCP 9976, 1 c&s, Brazil, Rio Grande do Sul, Restinga Seca, rio Jacuí. MCP 28998, 4 c&s of 20, Brazil, Minas Gerais, Muriaé, rio Paraíba do Sul basin, rio da Gloria, affluent of rio Muriaé. *Leptobrycon jatuaranae*. MCP 14936, 3 c&s of 20, Brazil, Amazonas, rio Negro, confluence with rio Urubaxi. “*Macropsobrycon*” *xinguensis*. MCP 32144, 1 c&s of 5, Brazil, Mato Grosso, Nova Canaã do Norte, rio Kaiapá. MCP 34546 3 c&s of 12, Brazil, Mato Grosso, Nova Canaã do Norte, rio Kaiapá. *Microschemobrycon elongatus*. MCP 23351, 2 c&s of 50, Brazil, Pará, Tomé Açu, igarapé Urucure, affluent of rio Acará. *Paracheirodon axelrodi*. MCP 11994, 2 c&s, aquarium material. *Parecbasis cyclolepis*. MZUSP 26146, 3 c&s of 7, Peru, Ucayali, Cel. Portillo, Bagazan, rio Ucayali. *Prionobrama paraguayensis*. MCP 14923, 3 c&s of 15, Brazil, Mato Grosso, Barão do Melgaço, Boca do Croara. *Probolodus heterostomus*. MCP 13813, 3 c&s of 5, Brazil, Minas Gerais, Ipatinga, rio Doce basin, rio Taquaruçú. *Rhoadsia altipinna*. FMNH 79077, 1 c&s of 49, Ecuador, río Pelenque.

Cheirodontinae. Compsurini: *Acinocheirodon melanogramma*. MCP 19238, 1 male c&s, Brazil, Minas Gerais, east of rio Jequitinhonha. MCP 40701, 1 c&s, Brazil, Minas Gerais, Itira, rio Jequitinhonha. MZUSP 5132, 1 male c&s, Brazil, Itaobin, rio Jequitinhonha. *Compsura heterura*. MCP 17093, 3 c&s of 185, Brazil, Minas Gerais, rio São Francisco basin, rio Verde Pequeno. “*Compsura*” *gorgonae*. MCP 16132, 2 c&s of 36, Panama, Darien, río Chucunaque basin, rio Meteti. *Compsurini* Araguaia n. sp.. MCP 40302, 2 c&s of 7, Brazil, Mato Grosso, Porto Alegre do Norte, rio Araguaia basin, rio Xavantino. *Compsurini* Guaporé n. sp. MZUSP 37663, 3 c&s of 123, Brazil, Mato Grosso, Vila Bela da Santíssima Trindade, rio Guaporé. UFRGS 12014, 12, Brazil, Mato Grosso, Vila Bela da Santíssima Trindade, affluent of rio Guaporé. *Compsurini* Purus n. sp. MCP 41716, 2 c&s of 42, Brazil, Acre, Sena Madureira,

affluent of rio São Pedro. *Compsurini Napo* n. sp. ANSP 149671, 3 c&s of 54, Peru, Huanucu, Vicinity Tingo Maria, main stream of rio Tullamayo. *Compsurini Yurimaguas* n. sp. CAS 71733, 3 c&s of 21, Peru, Departamento de Lore, Rio Amazon. *Compsurini Leticia* n. sp. ROM -ICH 56384, 3 c&s of 22, Colombia, Leticia, Amazonas river. *Compsurini Tingo* n. sp. MCP 14957, 3 c&s of 15, Peru, Tingo Maria. *Compsurini Cuzco* n. sp. USNM 295636, 3 c&s of 15, Peru, Dept. Madre de Dios, Prov. Manu, affleunt of upper rio Madre de Dios. *Kolpotocheirodon figueiredoi*. MZUSP 55219, 3 c&s of 26, Brazil, Bahia, Iraquara, rio Pratinha. *Kolpotocheirodon theloura*. MCP 11161, paratype, 1 c&s, Brazil, Goiás, rio Paranaíba basin, Ribeirão da Gama, above mouth of rio Taquara. MNRJ 18081, 2 c&s of 133, Brazil, Minas Gerais, Palmital, rio São Francisco basin, lagoa Perta-Pé. *Macropsobrycon uruguayanae*. MCP 11937, 4 c&s of 208, Brazil, Rio Grande do Sul, Dom Pedrito, rio Santa Maria. MCP 20900, 9 c&s of 87, Brazil, Rio Grande do Sul, São Gabriel, stream on rio Jacuí basin. *Odontostilbe dialeptura*. MCP 11992, 5 c&s, Panamá, Herrera province. USNM 208511, 2c&s of 12, Panamá, Panama Province, rio Corona. *Odontostilbe mitoptera*. MCP 14713, 2 c&s of 5, Costa Rica, rio Claro-Golfito. USNM 208514, 2 c&s of 11, Panamá, Cocle, rio Tambo. *Saccoderma hastata*. ICNMHN 6478, 1 c&s of 23, Colombia, Boyacá, Departamento Boyacá, rio Magdalena. CAS 70909, 2 c&s of 48, Colombia, Chocó, rio Truanto, rio Atrato basin. *Saccoderma melanostigma*. FMNH 85280, 3 c&s of 22, Venezuela, Zulia, El Paso, rio Guasare. **Cheirodontini:** *Amazonspinther dalmata*.. MCP 37571, paratype, 1 c&s, Brazil, Amazonas, Humaitá-Canutama, rio Madeira basin. MCP 37572, paratype 1 c&s of 2, Brazil, Amazonas, Canutama, stream of rio Açuá, rio Purus basin. *Axelrodia lindeae*. MCP 37338, 13, Brazil, Amazonas, Humaitá, rio Madeira basin, rio Traíra. MCP 37314, 4 c&s (1 male, 3 females) of 166, Brazil, Acre, rio Purus basin, igarapé Marizinho, BR 364, rio Antimari drainage. *Cheirodon australe*. UMMZ 215046, 3 c&s of 17, Chile, Valdivia, rio Calle-Calle, rio Valdivia drainage. *Cheirodon galusdai*. UMMZ 212703, 3 c&s of 23, Chile, rio Itata. *Cheirodon ibicuiensis*. MCP 11910, 2 c&s, Brazil, Rio Grande do Sul, São Rafael, rio Uruguay basin, rio Ibicuí. MCP 39676, 2 c&s, Brazil, Rio Grande do Sul, rio Jacuí. *Cheirodon interruptus*. MCP 6971, 4 c&s, Brazil, Rio Grande do Sul, Dom Pedrito, rio Santa Maria. UMMZ 212702, 4 c&s of 22, Chile, rio Quilimari. *Cheirodon kiliani*. UMMZ 219454, 2 c&s of 7, Chile, Valdivia, rio Calle-Calle. *Cheirodon parahybae*. MNRJ 18009, 2 c&s of 94, Brazil, Rio de Janeiro, Campos dos Goytacazes, Lagoa Brejo Grande. *Cheirodon pisciculus*. MCP 11987, 2 c&s, Chile, Santiago, Curacavi. New genus n. sp. b. UFRJ 1260, 4 c&s of 62, Brazil, Mato Grosso, Cocalinho, rio das Mortes. New genus n. sp. c. MZUSP 40535, 7 c&s, Brazil, Goiás, Iaciara, ribeirão Macambira. *Heterocheirodon jacuiensis*. MCP 21672, 2 c&s of 190, Brazil, Rio Grande do Sul, Nossa Senhora da Glória, rio Jacuí basin, marginal pool of the rio das Antas. *Heterocheirodon yatai*. MCP 11287, 4 c&s of 15, Brazil, Rio Grande do Sul, Dom Pedrito, rio Uruguay basin, rio Santa Maria. MCP 15475, 1 c&s, Brazil, Rio Grande do Sul, Dom Pedrito, rio Uruguay basin, rio Santa Maria. *Nanocheirodon insignis*. USNM 121511, 6 c&s of 352, Venezuela, rio Maracaibo basin, rio Machango. USNM 121518, 4 c&s of 134, Venezuela, rio Maracaibo basin, rio Negro. *Serrapinnus* n. sp. upm. DZSJRP 5582, 2 c&s of 50, Brazil, Goiás, Indiara, headwater of córrego Galheiro, rio Paranaíba basin. *Serrapinnus* n. sp. ups. MCP 14872, 2 c&s of 546, Brazil, São Paulo, Rancharia, rio Paraná basin. *Serrapinnus* n. sp. a. MZUSP 40359, 2 c&s of 12, Brazil, Tocantins, Arraias, rio Paranã. UFRGS 12023, 2 c&s of 55, Brazil, Goiás, Montes Claros de Goiás, affluent of rio Claro. *Serrapinnus* n. sp. ac. UFRGS 9216, 5 c&s of 13, Brazil, Rio

Grande do Norte, rio Ceará-Mirim. *Serrapinnus calliurus*. MCP 12537, 4 c&s of 21, Brazil, Rio Grande do Sul, São Nicolau, arroio Canoin. *Serrapinnus* n. sp. d. MCP 39012, 2 c&s of 68, Brazil, Rondônia, Ouro Preto do Oeste, affluent of rio Machado. *Serrapinnus* n. sp. e. MCP 37311, 3 c&s of 25, Brazil, Amazonas, Manaus, rio Amazonas. *Serrapinnus heterodon*. MCP 26896, 4 c&s of 16, Brazil, Bahia, east rio Utinga, affluent rio Paraguaçu. *Serrapinnus kriegi*. MCP 12043, 5 c&s, Paraguay, Cerrito, Estância Montreal Potrero. *Serrapinnus* n. sp. m. UNT 7227, 4 c&s of 54, Brazil, Tocantins, rio Paranã basin. *Serrapinnus microdon*. MCP 15077, 5 c&s of 30, Brazil, Mato Grosso, Cuiaba, rio Paraguay basin. *Serrapinnus micropterus*. MCP 37316, 3 c&s of 10, Brazil, Amazonas, Manaus, rio Amazonas basin, lago Camaleão, island Marchantaria. *Serrapinnus* n. sp. mi. Madeira. MCP 37779, 2 c&s of 154, Brazil, Mato Grosso, Pontes e Lacerda, affluent of rio Galera, rio Guapore basin. *Serrapinnus notomelas*. MCP 14873, 2 c&s of 126, Brazil, São Paulo, Sagres, rio do Peixe basin. *Serrapinnus piaba*. MCP 14007, 4 c&s of 25, Brazil, Minas Gerais, Moema, rio São Francisco. *Serrapinnus* n. sp. t. MZUSP 40362, 4 c&s of 31, Brazil, Goiás, Galheiros, riacho Seco. MCP 40417, 3 c&s of 61, Brazil, Mato Grosso, Porto Alegre do Norte, affluent of rio Araguaia basin. *Spintherobolus ankoseion*. MCP 12561, 2 c&s, Brazil, Paraná, Paranaguá. *Spintherobolus broccae*, MCP 19196, 1 c&s 5, Brazil, Rio de Janeiro, Cachoeira de Macacu, rio Macacu. *Spintherobolus papilliferus*, MZUSP 49408, 1 c&s of 4, Brazil, São Paulo, Paranapiacaba, rio Tietê basin. MZUSP 51022, 1 c&s of 16, Brazil, São Paulo, Paranapiacaba and Campo Grande, rio Tietê basin. **Odontostilbini:** *Cheirodontops geayi*. CAS 64344, 1 c&s of 66, Venezuela, Portuguesa, río Maria basin. USNM 349409, 2 c&s of 12, Venezuela, Portuguesa, Quebrada Seca, río Portuguesa basin, río Las Marias. *Aphyocheirodon hemigrammus*. MNRJ 19470, 1 c&s of 9, Brazil, São Paulo, Botucatu, rio Tietê basin. NRM 17307, 1 c&s of 15, rio Paraná basin, rio Tietê. *Holoshesthes* n. sp. “b”. ANSP 156876, paratypes, 2 c&s of 46, Venezuela, Moradas, lagoon Flores. *Holoshesthes* n. sp. “k”. KU 13508, paratypes, 1 c&s of 40, Ecuador, Sucumbíos, rio Napo basin, rio Aguarico at Santa Cecilia. KU 13509, paratypes, 1 c&s of 61, Ecuador, Napo, río Aguarico at Santa Cecilia. *Holoshesthes* n. sp. “p”. FMNH 113499, 1 c&s of 30, Peru, Loreto, laguna Rimachi, río Pastaza, río Marañon basin. MZUSP 30364, 1 c&s of 106, Brazil, Acre, Tarauacá, upper rio Juruá basin, rio Tarauacá. *Odontostilbe euspilurus*. ANSP 143702, 2 c&s of 8, Peru, Cuzco/Madre de Dios, mouth of río Carbon. MCP 38420, 2 c&s, Ecuador, Napo, río Napo basin, distributary of río Payamino. *Odontostilbe dierythura*. MCP 38624, 2 c&s of 7, Bolívia, Cochabamba, río Madeira, río Ichilo basin, río Samusabety. *Odontostilbe ecuadorensis*. KU 13524, paratypes, 1 c&s of 32, Ecuador, Napo, isolated pool of río Aguarico at Santa Cecilia. *Odontostilbe fugitiva*. ANSP 178908, 2 c&s of 12, Peru, Loreto, Maynas, lower río Itaya. INPA 18506, 3 c&s of 50, Brazil, Amazonas, Paraná do Xiborena. INPA 18465, 4 c&s of 73, Brazil, Amazonas, Ilha da Marchantaria. *Odontostilbe microcephala*. USNM 319279, 4 c&s of 200, Bolivia, Dept. Santa Cruz, río Parapetí. USNM 321173, 3 c&s of 49, Bolivia, Dept. Chuquisaca, río Camatindi. *Odontostilbe nareuda*. FMNH 106433, paratypes, 1 c&s of 30, Bolivia, Pando, rio Madeira basin, creek at right margin of río Nareuda. *Odontostilbe pao*. MCP 40976, paratypes, 1 c&s of 2, Venezuela, Cojedes, río Pao at el Caserio, El Pueblito. *Odontostilbe paraguayensis*. MCP 35618, 2 c&s, Brazil, Mato Grosso, Jauquara, rio Paraguay basin, rio Jauquara, affluent rio dos Pássaros. *Odontostilbe parecis*. MCP 37319, paratypes, 2 c&s of 80, Brazil, Mato Grosso, Pontes e Lacerda, rio Madeira basin, creek affluent of rio Galera. *Holoshesthes pequirá*. MCP 33240, 1 c&s of 61, Brazil, Mato Grosso, Jauquara, rio Paraguay basin, rio

Jauquara, affluent rio dos Pássaros. *Odontostilbe pulchra*. INHS 40101, 2 c&s of 20, Trinidad, Cumuto River, 5 km S Brazil on the road to Talparo. *Odontostilbe splendida*. MCP 38862, paratypes, 1 male c&s of 27, Colômbia, Meta, rio Meta basin, rio Negrito, system of the rio Orinoco. *Odontostilbe* n. sp. "b". MCP 12110, paratypes, 6 c&s, Brazil, São Paulo, rio Tietê basin, marginal pools of the rio Corumbataí. *Odontostilbe* n. sp. "e". MCP 26004, 1 c&s of 4, Brazil, São Paulo, rio Paranapanema, reservoir Jurumirim. *Odontostilbe* n. sp. "h". MCP 13307, 1 c&s of 25, Brazil, Santa Catarina, Volta Grande, rio Uruguay basin, rio do Peixe at Volta Grande. MCP 13312, 4 c&s, Brazil, Rio Grande do Sul, Marcelino Ramos, rio Uruguay basin, rio Ligeiro. *Odontostilbe* n. sp. "m". ROM 63983, paratypes, 1 male c&s of 34, Peru, Madre de Dios, rios Amazonas. ROM 63986, paratypes, 2 c&s, Peru, PNM - Pakitza, Manu river, beach near mouth of Pachija. MCP 14948, paratypes, 2 female c&s of 10, Peru, Cuzco, Asuncion. *Odontostilbe* n. sp. "p". MCP 20337, 2 c&s of 48, Brazil, Goiás, upper rio Paraná, rio Corumbá, affluent of rio Paranaíba. *Prodontocharax alleni*. USNM 280541, 3 c&s of 11, Peru, Ucayali, rio Ucayali. *Prodontocharax melanotus*. ANSP 143528, 2 c&s of 78, Peru, Madre de Dios, at Shintuya, upper Madre de Dios. *Pseudocheiroidon arnoldi*. MCP 16134, 2 c&s, Panamá, Pacific drainage, rio Bayano basin. *Pseudocheiroidon terrabae*. UMMZ 194214, 4 c&s of 33, Costa Rica, Puntarenas, Pacific drainage.

Comparative material. *Acinocheiroidon melanogramma*: ANSP 176238, paratypes, 7, 21.9-26.2 mm SL, Brazil, Minas Gerais, rio Jequitá drainage. *Aphyodite grammica*: FMNH, holotype, 24.3 mm SL, Guiana, Konawaruk. MZUSP 29874, 20, 21.9-26.9 mm SL, Brazil, rio Negro. *Brittanichthys axelrodi*: MCP 14931, 17, 16.3-22.2 mm SL, 3 c&s, Brazil, Boa Vista, rio Negro. *Cheiroidon australe*: USNM 084317, paratypes, 12, 28.4-49.8 mm SL, Chile, Los lagos Region at Puerto Varas. *Cheiroidon dialepturus*: USNM 208524, holotype, 26.8 mm SL, Panama, Veraguas, rio San Pedro Basin. *Cheiroidon galusdai*: USNM 084319, paratypes, 10, 30.6-52.3 mm SL, Chile, Rio Locomilla at San Xavier. *Cheiroidon gorgonae*: USNM 64094, holotype, 22.1 mm SL, Panama, Canal Zone, small seepage pool below spillway of the reservoir dam at Gorgona. *Cheiroidon kiliani*: USNM 227310, paratype, 1, 25.2 mm SL. Valdivia-Chile, rio Cau-Cau. *Cheiroidon microdon*: FMNH 57867, holotype, 32.2 mm SL, Brazil, Caceres, rio Ibicuhy. *Cheiroidon micropterus*: CAS 59780, holotype, 23.9 mm SL, Brazil, Para, rio Amazonas drainage at Santarém. *Cheiroidon mitopterus*: USNM 208539, holotype, 34.6 mm SL, Panama, Cocle, rio Tucue, tributary of rio Cocle del Norte. *Cheiroidon notomelas*: FMNH 57829, holotype, 28.2 mm SL, Brazil, Miguel Calmone. *Cheiroidontops geayi*: USNM 121507, holotype, 35.5 mm SL, Venezuela, Estado de Aragua, rio Guarico. *Compsura heterura*: FMNH 57825, holotype, 28.7 mm SL, Brazil, rio Itapicuru, Queimadas. *Holesthes heterodon*: CAS 117522, paratypes, 4, 32.2-36.5 mm SL, Brazil, Minas Gerais, rio Grande, Jaguará. *Kolpotocheiroidon figueiredoi*: MCP 22345, paratypes, 25.1-30.5 mm SL, rio Pratinha, Iraquara. *Kolpotocheiroidon theloura*: MCP 11161, paratype, 25.9 mm SL, ribeirão do Gama, just above, the mouth of ribeirão Taquara. *Leptobrycon jatuaranae*: MCP 14936, 17, 20.8-25.1 mm SL, 3 c&s, Brazil, Amazonas, rio Negro. *Microschemobrycon guaporensis*: FMNH 57926, holotype, 29.1 mm SL, Brazil, Maciel, rio Guaporé. *Odontostilbe hastatus*: FMNH 56383, holotype, 30.2 mm SL, Colombia, Soplaviento. *Oligobrycon microstomus*: holotype, 31.0 mm SL, Brazil, Jacarehy on Rio Parahyba. *Oxybrycon* sp.: MCP 33105, 8, 13.7-14.9 mm SL, 2 c&s, Venezuela, Titi lagoon, upper Orinoco basin. *Parecbasis cyclolepis*: FMNH 56677, holotype, 56.3 mm SL, Brazil, rio Madeira. MZUSP 26146, 7,

40.3-53.5 mm SL, Peru, Ucayali, río Ucayali. *Pristella aubynei*: FMNH 52698, 34.9 mm SL, British Guiana. *Prodonotocharax alleni*: CAS 117472, holotype, 32.8 mm SL, Peru, Ucayali, rio Amazonas basin. *Prodonotocharax melanotus*: CAS 59793, holotype, 44.9 mm SL, Bolivia, la Paz, rio Amazonas drainage at Tumupasa. *Pseudocheirodon affinis*: CAS 117516, paratype, 32.1-35.4 mm SL, Panama, río Gatun, at Gatun. *Saccoderma melanostigma*: USNM 121519, holotype, 26.7 mm SL, Venezuela, río San Juan, South of Mene Grande. *Spintherobolus broccae*: FMNH 58864, paratype, 18.7 mm SL, Brazil, Rio de Janeiro. *Spintherobolus papilliferus*: FMNH 104802, holotype, 32.9 mm SL, Brazil, São Paulo, Alto da Serra. *Thrissobrycon pectinifer*: SU 16944, holotype, 26.8 mm SL, Brazil, Cucuhy, rio Negro. MCP 14932, 12, 26.4-30.2 mm SL, 3 c&s, Brazil, rio Arirara.

Appendix II. The number of steps, **ci**, and **ri** for the 278 morphological characters used in the implied weighted parsimony analysis (aut = autapomorphic).

Ch. 1	2	0.50	0.80	Ch. 51	5	0.20	0.50	Ch. 101	7	0.14	0.14
Ch. 2	6	0.16	0.50	Ch. 52	13	0.15	0.70	Ch. 102	4	0.50	0.75
Ch. 3	3	0.16	0.66	Ch. 53	11	0.09	0.72	Ch. 103	6	0.50	0.72
Ch. 4	3	0.33	0.50	Ch. 54	7	0.28	0.80	Ch. 104	6	0.50	0.70
Ch. 5	3	0.33	0.92	Ch. 55	12	0.08	0.69	Ch. 105	27	0.14	0.54
Ch. 6	14	0.07	0.43	Ch. 56	13	0.07	0.58	Ch. 106	7	0.14	0.78
Ch. 7	5	0.40	0.40	Ch. 57	1	1.00	1.00	Ch. 107	18	0.50	0.61
Ch. 8	17	0.11	0.48	Ch. 58	3	0.66	0.87	Ch. 108	1	aut	aut
Ch. 9	13	0.15	0.50	Ch. 59	14	0.07	0.65	Ch. 109	4	0.25	0.25
Ch. 10	9	0.11	0.65	Ch. 60	4	0.25	0.85	Ch. 110	16	0.06	0.31
Ch. 11	14	0.07	0.63	Ch. 61	6	0.16	0.37	Ch. 111	1	1.00	1.00
Ch. 12	13	0.07	0.14	Ch. 62	25	0.12	0.60	Ch. 112	17	0.05	0.42
Ch. 13	2	0.50	0.80	Ch. 63	2	0.50	0.50	Ch. 113	1	1.00	1.00
Ch. 14	5	0.20	0.78	Ch. 64	3	0.33	0.50	Ch. 114	17	0.05	0.42
Ch. 15	10	0.20	0.69	Ch. 65	1	1.00	1.00	Ch. 115	3	0.33	0.00
Ch. 16	3	0.66	0.93	Ch. 66	2	0.50	0.85	Ch. 116	4	0.50	0.88
Ch. 17	5	0.20	0.82	Ch. 67	11	0.09	0.52	Ch. 117	3	0.33	0.60
Ch. 18	9	0.11	0.33	Ch. 68	20	0.05	0.40	Ch. 118	6	0.16	0.54
Ch. 19	4	0.25	0.66	Ch. 69	10	0.10	0.57	Ch. 119	6	0.16	0.79
Ch. 20	10	0.10	0.40	Ch. 70	3	0.33	0.33	Ch. 120	20	0.05	0.52
Ch. 21	7	0.14	0.50	Ch. 71	17	0.11	0.61	Ch. 121	15	0.06	0.54
Ch. 22	2	0.50	0.90	Ch. 72	2	0.50	0.50	Ch. 122	1	1.00	1.00
Ch. 23	17	0.11	0.37	Ch. 73	15	0.06	0.51	Ch. 123	1	aut	aut
Ch. 24	7	0.28	0.16	Ch. 74	5	0.20	0.85	Ch. 124	1	aut	aut
Ch. 25	9	0.22	0.61	Ch. 75	5	0.20	0.60	Ch. 125	4	0.25	0.40
Ch. 26	1	1.00	1.00	Ch. 76	2	0.50	0.50	Ch. 126	2	0.50	0.80
Ch. 27	2	0.50	0.00	Ch. 77	3	0.66	0.90	Ch. 127	1	1.00	1.00
Ch. 28	1	1.00	1.00	Ch. 78	2	0.50	0.50	Ch. 128	1	1.00	1.00
Ch. 29	1	1.00	1.00	Ch. 79	4	0.25	0.76	Ch. 129	6	0.16	0.61
Ch. 30	23	0.04	0.46	Ch. 80	8	0.12	0.12	Ch. 130	13	0.07	0.47
Ch. 31	2	0.50	0.00	Ch. 81	13	0.07	0.64	Ch. 131	1	1.00	1.00
Ch. 32	3	0.66	0.66	Ch. 82	3	0.33	0.50	Ch. 132	7	0.28	0.37
Ch. 33	3	0.33	0.50	Ch. 83	6	0.16	0.58	Ch. 133	10	0.20	0.33
Ch. 34	3	0.33	0.00	Ch. 84	2	0.50	0.87	Ch. 134	1	aut	aut
Ch. 35	3	0.33	0.60	Ch. 85	5	0.20	0.55	Ch. 135	1	aut	aut
Ch. 36	3	0.33	0.60	Ch. 86	2	0.50	0.50	Ch. 136	3	0.33	0.60
Ch. 37	6	0.16	0.16	Ch. 87	4	0.25	0.57	Ch. 137	8	0.12	0.61
Ch. 38	10	0.10	0.50	Ch. 88	1	1.00	1.00	Ch. 138	1	1.00	1.00
Ch. 39	4	0.25	0.00	Ch. 89	5	0.20	0.20	Ch. 139	3	0.66	0.75
Ch. 40	4	0.25	0.00	Ch. 90	2	0.50	0.95	Ch. 140	1	1.00	1.00
Ch. 41	3	0.33	0.60	Ch. 91	2	0.50	0.87	Ch. 141	2	0.50	0.00
Ch. 42	18	0.05	0.37	Ch. 92	4	0.25	0.86	Ch. 142	9	0.11	0.69
Ch. 43	2	0.50	0.66	Ch. 93	6	0.16	0.64	Ch. 143	2	0.50	0.75
Ch. 44	12	0.08	0.75	Ch. 94	4	0.25	0.00	Ch. 144	4	0.25	0.57
Ch. 45	1	1.00	1.00	Ch. 95	3	0.33	0.00	Ch. 145	6	0.33	0.60
Ch. 46	2	0.50	0.50	Ch. 96	16	0.12	0.65	Ch. 146	1	1.00	1.00
Ch. 47	2	0.50	0.75	Ch. 97	2	0.50	0.88	Ch. 147	7	0.14	0.50
Ch. 48	8	0.12	0.72	Ch. 98	5	0.20	0.80	Ch. 148	3	0.33	0.00
Ch. 49	1	1.00	1.00	Ch. 99	4	0.25	0.00	Ch. 149	10	0.10	0.67
Ch. 50	4	0.50	0.50	Ch. 100	6	0.16	0.28	Ch. 150	8	0.12	0.63

Ch. 151	1	1.00	1.00	Ch. 194	3	0.33	0.80	Ch. 237	2	0.50	0.95
Ch. 152	5	0.20	0.20	Ch. 195	1	1.00	1.00	Ch. 238	4	0.25	0.92
Ch. 153	3	0.33	0.00	Ch. 196	3	0.66	0.95	Ch. 239	3	0.33	0.77
Ch. 154	5	0.20	0.63	Ch. 197	2	0.50	0.88	Ch. 240	3	0.33	0.66
Ch. 155	2	0.50	0.00	Ch. 198	4	0.50	0.93	Ch. 241	1	1.00	1.00
Ch. 156	4	0.25	0.57	Ch. 199	1	1.00	1.00	Ch. 242	3	0.33	0.50
Ch. 157	2	0.50	0.95	Ch. 200	3	0.33	0.83	Ch. 243	2	0.50	0.00
Ch. 158	2	0.50	0.95	Ch. 201	4	0.25	0.62	Ch. 244	3	0.33	0.66
Ch. 159	2	0.50	0.95	Ch. 202	2	0.50	0.96	Ch. 245	1	aut	aut
Ch. 160	3	0.33	0.00	Ch. 203	1	1.00	1.00	Ch. 246	1	1.00	1.00
Ch. 161	2	0.50	0.75	Ch. 204	3	0.33	0.84	Ch. 247	5	0.20	0.75
Ch. 162	1	1.00	1.00	Ch. 205	1	1.00	1.00	Ch. 248	1	1.00	1.00
Ch. 163	2	0.50	0.95	Ch. 206	1	1.00	1.00	Ch. 249	3	0.33	0.60
Ch. 164	2	0.50	0.87	Ch. 207	7	0.14	0.60	Ch. 250	8	0.12	0.53
Ch. 165	1	1.00	1.00	Ch. 208	1	aut	aut	Ch. 251	6	0.50	0.25
Ch. 166	1	aut	aut	Ch. 209	1	1.00	1.00	Ch. 252	1	aut	aut
Ch. 167	1	aut	aut	Ch. 210	14	0.07	0.68	Ch. 253	2	0.50	0.92
Ch. 168	3	0.33	0.95	Ch. 211	3	0.33	0.60	Ch. 254	2	0.50	0.50
Ch. 169	3	0.33	0.33	Ch. 212	9	0.22	0.78	Ch. 255	1	1.00	1.00
Ch. 170	6	0.33	0.66	Ch. 213	3	0.33	0.33	Ch. 256	7	0.14	0.50
Ch. 171	1	aut	aut	Ch. 214	3	0.33	0.77	Ch. 257	5	0.40	0.85
Ch. 172	6	0.16	0.37	Ch. 215	2	0.50	0.87	Ch. 258	3	0.33	0.00
Ch. 173	4	0.50	0.86	Ch. 216	1	1.00	1.00	Ch. 259	5	0.40	0.76
Ch. 174	12	0.08	0.70	Ch. 217	1	1.00	1.00	Ch. 260	1	1.00	1.00
Ch. 175	4	0.50	0.90	Ch. 218	1	1.00	1.00	Ch. 261	2	0.50	0.75
Ch. 176	1	1.00	1.00	Ch. 219	1	aut	aut	Ch. 262	1	aut	aut
Ch. 177	2	0.50	0.66	Ch. 220	2	0.50	0.66	Ch. 263	4	0.25	0.40
Ch. 178	5	0.20	0.88	Ch. 221	1	1.00	1.00	Ch. 264	2	0.50	0.50
Ch. 179	1	1.00	1.00	Ch. 222	1	1.00	1.00	Ch. 265	1	1.00	1.00
Ch. 180	1	1.00	1.00	Ch. 223	1	aut	aut	Ch. 266	1	1.00	1.00
Ch. 181	1	1.00	1.00	Ch. 224	1	aut	aut	Ch. 267	2	0.50	0.88
Ch. 182	1	1.00	1.00	Ch. 225	2	1.00	1.00	Ch. 268	1	1.00	1.00
Ch. 183	2	0.50	0.00	Ch. 226	2	0.50	0.85	Ch. 269	1	aut	aut
Ch. 184	5	0.20	0.55	Ch. 227	1	1.00	1.00	Ch. 270	1	aut	aut
Ch. 185	1	1.00	1.00	Ch. 228	1	aut	aut	Ch. 271	2	0.50	0.80
Ch. 186	1	1.00	1.00	Ch. 229	1	1.00	1.00	Ch. 272	1	1.00	1.00
Ch. 187	2	0.50	0.00	Ch. 230	2	0.50	0.88	Ch. 273	4	0.50	0.66
Ch. 188	1	1.00	1.00	Ch. 231	3	0.33	0.50	Ch. 274	2	0.50	0.80
Ch. 189	1	aut	aut	Ch. 232	4	0.25	0.82	Ch. 275	2	0.50	0.80
Ch. 190	4	0.50	0.93	Ch. 233	2	1.00	1.00	Ch. 276	1	1.00	1.00
Ch. 191	2	0.50	0.88	Ch. 234	1	1.00	1.00	Ch. 277	1	1.00	1.00
Ch. 192	1	aut	aut	Ch. 235	2	0.50	0.83	Ch. 278	1	1.00	1.00
Ch. 193	4	0.50	0.93	Ch. 236	2	0.50	0.00				

Appendix III. List of transitions and total number of steps for each character. The number of the clades correspond to the IW strict consensus cladogram (Fig. 44).

Character 1 (2 steps)

Root: 0
Coptobrycon bilineatus: 0 > 1
Clade 158: 0 > 1

Character 2 (6 steps)

Root: 1
Clade 115: 1 > 0
Hyphessobrycon bifasciatus: 0 > 1
Clade 184: 0 > 1
Leptobrycon jatuaranae: 0 > 1
Cheironodon stenodon: 0 > 1
Clade 158: 0 > 01
Clade 157: 01 > 1

Character 3 (6 steps)

Root: 01
Clade 116: 01 > 1
Brycon pesu: 01 > 0
Clade 112: 1 > 01
Clade 111: 01 > 0
Rhoadsia altipinna: 01 > 1
Coptobrycon bilineatus: 01 > 0
Clade 186: 0 > 1
Clade 106: 0 > 1
Clade 158: 1 > 01

Clade 157: 01 > 0

Character 4 (3 steps)

Root: 01
Clade 116: 01 > 1
Brycon pesu: 01 > 0
Clade 193: 1 > 0
Clade 194: 1 > 0

Character 5 (3 steps)

Root: 0
Clade 109: 0 > 1
Clade 156: 1 > 0
Clade 132: 1 > 0

Character 6 (14 steps)

Root: 0
Hyphessobrycon bifasciatus: 0 > 1
Charax stenopterus: 0 > 1
Clade 108: 0 > 01
Paracheironodon axelrodi: 01 > 1
Aphyodite grammica: 0 > 1
Cheironodon stenodon: 01 > 0
Clade 171: 01 > 0
Odontostilbe n. sp. b: 01 > 1
Clade 136: 01 > 1
Clade 126: 01 > 0

Clade 140: 01 > 0

Clade 142: 01 > 1
Compsurini n. sp. Purus: 01 > 1
Macropsobrycon uruguayanae: 01 > 1
Acinocheironodon melanogramma: 01 > 0
Clade 124: 01 > 1
Clade 119: 01 > 0
Kolpotocheironodon figueiredoi: 01 > 0
Kolpotocheironodon theloura: 01 > 1
Serrapinnus n. sp. a: 0 > 1
Odontostilbe n. sp. h: 0 > 1
Aphyocheironodon hemigrammus: 0 > 1

Character 7 (5 steps)

Root: 1
Clade 115: 1 > 0
Rhoadsia altipinna: 0 > 2
Clade 192: 0 > 1
Aphyocharacidium bolivianum: 0 > 1
Aphyodite grammica: 0 > 1
Character 8 (17 steps)
Root: 0
Clade 189: 0 > 2
Clade 191: 0 > 01
Hemibrycon polyodon: 01 > 1

Cyanocharax alburnus: 01 > 0
 Bryconamericus iheringii: 01 > 1
 Coptobrycon bilineatus: 0 > 2
 Clade 192: 0 > 2
 Aphyocharacidium bolivianum: 0 > 1
 Clade 194: 0 > 012
 Macropsobrycon xinguensis: 012 > 2
 Leptobrycon jatauaranae: 012 > 1
 Clade 137: 0 > 01
 Clade 136: 01 > 012
 Clade 140: 01 > 0
 Clade 142: 01 > 1
 Nanocheiroidon insignis: 012 > 1
 Clade 135: 012 > 2
 Macropsobrycon uruguayanae: 0 > 1
 Clade 156: 0 > 2
 Cheiroidon parahybae: 2 > 1
 Pseudocheiroidon terrabae: 0 > 1
 Clade 178: 0 > 1
 Aphyocheiroidon hemigrammus: 0 > 2
Character 9 (13 steps)
 Root: 0
 Bryconops caudomaculatus: 0 > 1
 Clade 113: 0 > 1
 Rhoadsia altipinna: 1 > 0
 Clade 183: 1 > 0
 Cynopotamus kincaidi: 1 > 0
 Parecbasis cyclolepis: 1 > 0
 Macropsobrycon xinguensis: 1 > 0
 Clade 102: 1 > 0
 Compsurini n. sp. Tingo: 1 > 0
 Clade 158: 1 > 12
 Clade 123: 1 > 0
 Clade 157: 12 > 2
 Prodontocharax alleni: 1 > 0
 Aphyocheiroidon hemigrammus: 1 > 0
Character 10 (9 steps)
 Root: 0
 Clade 111: 0 > 01
 Clade 184: 01 > 1
 Clade 109: 01 > 1
 Clade 183: 01 > 0
 Cynopotamus kincaidi: 01 > 0
 Charax stenopterus: 01 > 1
 Parecbasis cyclolepis: 1 > 0
 Compsurini n. sp. Tingo: 1 > 0
 Acinocheiroidon melanogramma: 1 > 0
 Clade 176: 1 > 0
 Clade 123: 1 > 0
 Serrapinnus n. sp. upm: 1 > 0
Character 11 (14 steps)
 Root: 01
 Brycon pesu: 01 > 0
 Bryconops caudomaculatus: 01 > 1
 Clade 189: 01 > 0
 Clade 191: 01 > 1
 Clade 112: 01 > 1
 Probolodus heterostomus: 01 > 0
 Cynopotamus kincaidi: 1 > 0
 Aphyocharacidium bolivianum: 1 > 0
 Parecbasis cyclolepis: 1 > 0
 Clade 106: 1 > 01
 Clade 172: 01 > 0
 Clade 137: 01 > 1
 Clade 104: 01 > 0
 Clade 121: 0 > 1
 Clade 144: 1 > 0
 New Genus n. sp. c: 1 > 0
 Compsurini n. sp. Yurimaguas: 1 > 0
 Clade 117: 1 > 0
 Serrapinnus n. sp. ups: 0 > 1
Character 12 (13 steps)
 Root: 01
 Brycon pesu: 01 > 1
 Clade 115: 01 > 0
 Astyanax fasciatus: 0 > 1
 Clade 185: 0 > 01
 Cynopotamus kincaidi: 01 > 1
 Clade 187: 0 > 01
 Parecbasis cyclolepis: 01 > 1
 Clade 171: 0 > 1
 Compsurini n. sp. Cuzco: 0 > 1
 Clade 145: 0 > 01
 Acinocheiroidon melanogramma: 0 > 1
 Clade 144: 01 > 1
 Serrapinnus n. sp. a: 1 > 0
 Odontostilbe n. sp. h: 1 > 0
 Compsura n. sp. Guaporé: 0 > 1
 Clade 146: 1 > 01
 Serrapinnus kriegi: 01 > 0
 Aphyocheiroidon hemigrammus: 1 > 0
Character 13 (2 steps)
 Root: 0
 Clade 185: 0 > 01
 Cynopotamus kincaidi: 01 > 1
 Clade 175: 0 > 1
Character 14 (5 steps)
 Root: 0
 Clade 110: 0 > 1
 Clade 194: 1 > 0
 Axelrodia lindeae: 1 > 0
 Serrapinnus n. sp. a: 1 > 0
 Spintherobolus papilliferus: 1 > 0
Character 15 (10 steps)
 Root: 0
 Microschemobrycon elongatus: 0 > 1
 Clade 186: 0 > 1
 Clade 107: 0 > 1
 Clade 142: 1 > 2
 Macropsobrycon uruguayanae: 1 > 2
 Serrapinnus heterodon: 1 > 0
 Clade 127: 1 > 0
 Odontostilbe n. sp. e: 1 > 0
 Clade 162: 1 > 01
 Holoshesthes n. sp. k: 01 > 0
 Holoshesthes n. sp. b: 01 > 1
 Aphyocheiroidon hemigrammus: 01 > 0
Character 16 (3 steps)
 Root: 0
 Clade 110: 0 > 1
 Charax stenopterus: 0 > 1
 Clade 158: 1 > 12
 Clade 157: 12 > 2
Character 17 (5 steps)
 Root: 0
 Clade 110: 0 > 01
 Clade 108: 01 > 1
 Microschemobrycon elongatus: 01 > 0
 Aphyocharacidium bolivianum: 01 > 1
 Clade 186: 01 > 1
 Clade 194: 01 > 0
 Clade 158: 1 > 01
 Clade 182: 1 > 0
 Clade 157: 01 > 0
Character 18 (9 steps)
 Root: 0
 Clade 193: 0 > 1
 Aphyocharacidium bolivianum: 0 > 1
 Paracheiroidon axelrodi: 0 > 1
 Parecbasis cyclolepis: 0 > 1
 Clade 156: 0 > 01
 Clade 120: 0 > 01
 Axelrodia lindeae: 01 > 1
 Clade 123: 01 > 1
 Clade 128: 01 > 0
 Clade 118: 01 > 1
 Clade 160: 01 > 0
 Amazonspinter dalmata: 01 > 1
 Odontostilbe n. sp. h: 0 > 1
Character 19 (4 steps)
 Root: 0
 Clade 184: 0 > 1
 Clade 142: 0 > 1
 Clade 181: 0 > 1
 Clade 159: 0 > 1
Character 20 (10 steps)
 Root: 0
 Coptobrycon bilineatus: 0 > 1
 Clade 185: 0 > 01
 Clade 192: 01 > 1
 Clade 186: 0 > 1
 Clade 104: 0 > 1
 Acinocheiroidon melanogramma: 1 > 0
 Clade 156: 0 > 01
 Clade 120: 1 > 0
 Axelrodia lindeae: 01 > 1
 Amazonspinter dalmata: 01 > 0
 Serrapinnus n. sp. a: 0 > 1
 Spintherobolus papilliferus: 01 > 1
 Aphyocheiroidon hemigrammus: 0 > 1
Character 21 (7 steps)
 Root: 0
 Clade 112: 0 > 01
 Hyphessobrycon bifasciatus: 0 > 1
 Clade 193: 01 > 1
 Clade 110: 01 > 1
 Clade 192: 01 > 0
 Prionobrama paraguayensis: 01 > 1
 Aphyocharax nattereri: 01 > 0
 Paracheiroidon axelrodi: 1 > 0
 Macropsobrycon xinguensis: 1 > 0
 Axelrodia lindeae: 1 > 0
Character 22 (2 steps)
 Root: 0
 Clade 135: 0 > 1
 Clade 156: 0 > 1
Character 23 (17 steps)
 Root: 1
 Clade 193: 1 > 01
 Rhoadsia altipinna: 01 > 0
 Clade 183: 1 > 2
 Cynopotamus kincaidi: 1 > 0
 Paracheiroidon axelrodi: 1 > 0
 Clade 171: 1 > 0
 Cheiroidon ibicuiensis: 1 > 0
 Macropsobrycon uruguayanae: 1 > 0
 Clade 167: 0 > 1
 Cheiroidon parahybae: 1 > 0
 Compsurini n. sp. Napo: 1 > 0
 Prodontocharax alleni: 0 > 1
 Odontostilbe n. sp. m: 1 > 0
 Amazonspinter dalmata: 1 > 0
 Odontostilbe microcephala: 1 > 0
 Cheiroidon kiliani: 1 > 0
 Compsura gorgonae: 1 > 0
 Aphyocheiroidon hemigrammus: 1 > 0
Character 24 (7 steps)
 Root: 01
 Clade 116: 01 > 1
 Brycon pesu: 01 > 0
 Clade 192: 1 > 2
 Odontostilbe paraguayensis: 1 > 0
 Heterocheiroidon yatai: 1 > 2
 Macropsobrycon uruguayanae: 1 > 2
 Odontostilbe n. sp. m: 1 > 0
 Cheiroidon kiliani: 1 > 2
Character 25 (9 steps)
 Root: 0
 Hyphessobrycon bifasciatus: 0 > 1
 Clade 111: 0 > 1
 Cynopotamus kincaidi: 1 > 0
 Macropsobrycon xinguensis: 1 > 0
 Macropsobrycon uruguayanae: 1 > 2
 Clade 158: 1 > 12
 Clade 123: 1 > 2
 Compsurini n. sp. Napo: 1 > 2
 Clade 157: 12 > 2
 Cheiroidon kiliani: 1 > 2

Character 26 (1 step)
Root: 0
Clade 132: 0 > 1
Character 27 (2 steps)
Root: 0
Clade 156: 0 > 01
Axelrodia lindeae: 01 > 1
Clade 160: 01 > 0
Amazonspinter dalmata: 01 > 1
Character 28 (1 step)
Root: 0
Clade 156: 0 > 1
Character 29 (1 step)
Root: 0
Clade 158: 0 > 01
Clade 157: 01 > 1
Character 30 (23 steps)
Root: 0
Clade 188: 0 > 1
Clade 112: 0 > 01
Cyanocharax alburnus: 0 > 1
Rhoadsia altipinna: 01 > 0
Coptobrycon bilineatus: 01 > 1
Clade 184: 01 > 1
Clade 183: 01 > 1
Cynopotamus kincaidi: 01 > 0
Clade 186: 01 > 0
Clade 194: 01 > 1
Paracheiiron axelrodi: 01 > 0
Clade 107: 01 > 1
Clade 141: 1 > 01
Clade 142: 01 > 0
Clade 139: 01 > 1
Cheiiron ibicuhiensis: 1 > 0
Macropsobrycon uruguayanae: 1 > 0
Clade 144: 01 > 0
Clade 181: 1 > 0
Axelrodia lindeae: 01 > 1
Cheiiron parahybae: 1 > 0
Compsurini n. sp. Napo: 1 > 0
Serrapinnus n. sp. upm: 0 > 1
Clade 118: 1 > 0
Clade 164: 1 > 0
Amazonspinter dalmata: 01 > 0
Serrapinnus n. sp. t: 0 > 1
Spintherobolus papilliferus: 01 > 0
Clade 159: 01 > 1
Serrapinnus n. sp. d: 0 > 1
Serrapinnus calliurus: 0 > 1
Holoshesthes n. sp. b: 0 > 1
Character 31 (2 steps)
Root: 01
Clade 116: 01 > 1
Brycon pesu: 01 > 0
Charax stenopterus: 1 > 0
Character 32 (3 steps)
Root: 0
Clade 158: 0 > 01
Clade 180: 0 > 2
Amazonspinter dalmata: 01 > 1
Spintherobolus papilliferus: 01 > 0
Clade 159: 01 > 1
Character 33 (3 steps)
Root: 0
Clade 158: 0 > 01
Clade 180: 0 > 1
Amazonspinter dalmata: 01 > 1
Spintherobolus papilliferus: 01 > 0
Clade 159: 01 > 1
Character 34 (3 steps)
Root: 0
Aphyocharax nattereri: 0 > 1
Amazonspinter dalmata: 0 > 1
Spintherobolus ankoseion: 0 > 1
Character 35 (3 steps)
Root: 0
Aphyocharax nattereri: 0 > 1
Cynopotamus kincaidi: 0 > 1
Clade 158: 0 > 01
Clade 157: 01 > 1
Character 36 (3 steps)
Root: 0
Aphyocharax nattereri: 0 > 1
Cynopotamus kincaidi: 0 > 1
Clade 158: 0 > 01
Clade 157: 01 > 1
Character 37 (6 steps)
Root: 0
Astyanax laticeps: 0 > 1
Clade 102: 0 > 1
Compsurini n. sp. Cuzco: 0 > 1
Axelrodia lindeae: 0 > 1
Serrapinnus micropterus: 0 > 1
Compsurini n. sp. Leticia: 0 > 1
Saccoderma hastata: 0 > 01
Character 38 (10 steps)
Root: 0
Clade 113: 0 > 01
Probolodus heterostomus: 01 > 1
Astyanax fasciatus: 0 > 1
Rhoadsia altipinna: 01 > 0
Coptobrycon bilineatus: 01 > 1
Clade 185: 01 > 0
Clade 108: 01 > 1
Microschemobrycon elongatus: 01 > 0
Aphyocharacidium bolivianum: 01 > 1
Clade 186: 01 > 0
Clade 194: 01 > 1
Odontostilbe n. sp. b: 1 > 0
Odontostilbe splendida: 1 > 0
Clade 133: 1 > 01
Cheiiron parahybae: 01 > 0
Clade 131: 01 > 1
Cheiiron galusdai: 01 > 0
Character 39 (4 steps)
Root: 0
Odontostilbe euspilurus: 0 > 1
Clade 160: 0 > 01
Odontostilbe n. sp. e: 0 > 1
Spintherobolus papilliferus: 01 > 1
Spintherobolus broccae: 01 > 0
Spintherobolus ankoseion: 01 > 1
Character 40 (4 steps)
Root: 0
Aphyocharax nattereri: 0 > 1
Cynopotamus kincaidi: 0 > 1
Aphyocharacidium bolivianum: 0 > 1
Axelrodia lindeae: 0 > 1
Character 41 (3 steps)
Root: 0
Coptobrycon bilineatus: 0 > 1
Paracheiiron axelrodi: 0 > 1
Clade 158: 0 > 01
Clade 157: 01 > 1
Character 42 (18 steps)
Root: 0
Coptobrycon bilineatus: 0 > 1
Aphyocharax nattereri: 0 > 1
Charax stenopterus: 0 > 1
Clade 108: 0 > 01
Paracheiiron axelrodi: 01 > 1
Aphyodite grammica: 0 > 1
Cheiiron stenodon: 01 > 1
Clade 106: 01 > 0
Heterocheiiron yatai: 0 > 1
Clade 134: 0 > 1
Compsurini n. sp. Purus: 0 > 1
Macropsobrycon uruguayanae: 0 > 1
Clade 158: 0 > 01
Clade 123: 0 > 1
Clade 157: 01 > 1
Compsurini n. sp. Leticia: 0 > 1
Serrapinnus n. sp. ac: 0 > 1
Clade 130: 0 > 01
Compsura gorgonae: 01 > 1
Clade 146: 0 > 1
Odontostilbe mitoptera: 01 > 0
Odontostilbe dialeptura: 01 > 1
Aphyocheiiron hemigrammus: 0 > 1
Character 43 (2 steps)
Root: 0
Coptobrycon bilineatus: 0 > 1
Clade 160: 0 > 1
Character 44 (12 steps)
Root: 0
Clade 190: 0 > 1
Hyphessobrycon bifasciatus: 0 > 1
Clade 185: 0 > 01
Clade 184: 01 > 1
Cynopotamus kincaidi: 01 > 0
Charax stenopterus: 01 > 1
Clade 108: 0 > 1
Clade 171: 1 > 0
Clade 144: 1 > 0
New Genus n. sp. c: 1 > 0
Odontostilbe euspilurus: 0 > 1
Clade 151: 0 > 1
Clade 147: 0 > 1
Clade 161: 0 > 1
Character 45 (1 step)
Root: 0
Clade 123: 0 > 1
Character 46 (2 steps)
Root: 0
Clade 158: 0 > 01
Amazonspinter dalmata: 01 > 1
Spintherobolus papilliferus: 01 > 0
Clade 159: 01 > 1
Character 47 (2 steps)
Root: 0
Paracheiiron axelrodi: 0 > 1
Clade 158: 0 > 01
Clade 157: 01 > 1
Character 48 (8 steps)
Root: 0
Clade 110: 0 > 01
Clade 183: 01 > 1
Clade 186: 01 > 1
Clade 194: 01 > 0
Paracheiiron axelrodi: 01 > 0
Clade 107: 01 > 1
Macropsobrycon uruguayanae: 1 > 0
New Genus n. sp. b: 1 > 0
Clade 133: 1 > 0
Axelrodia lindeae: 1 > 0
Holoshesthes n. sp. b: 1 > 0
Character 49 (1 step)
Root: 0
Clade 156: 0 > 1
Character 50 (4 steps)
Root: 0
Cynopotamus kincaidi: 0 > 1
Clade 194: 0 > 1
Macropsobrycon uruguayanae: 0 > 1
Clade 180: 0 > 2
Character 51 (5 steps)
Root: 0
Clade 126: 0 > 1
Clade 181: 0 > 1
Compsurini n. sp. Yurimaguas: 0 > 1
Serrapinnus n. sp. d: 0 > 1
Serrapinnus n. sp. e: 0 > 1
Character 52 (13 steps)
Root: 0
Rhoadsia altipinna: 0 > 1
Paracheiiron axelrodi: 0 > 1
Clade 170: 0 > 1
Clade 141: 0 > 1

Clade 122: 0 > 1
 Macropsobrycon uruguayanae: 0 > 2
 Clade 156: 1 > 01
 Axelrodia lindeae: 01 > 0
 Clade 143: 1 > 0
 Cheirodon parahybae: 0 > 1
 Clade 174: 1 > 0
 Clade 165: 1 > 0
 Clade 128: 1 > 0
 Clade 160: 01 > 1
 Amazonspinther dalmata: 01 > 0
Character 53 (11 steps)
 Root: 0
 Rhoadsia altipinna: 0 > 1
 Paracheirodon axelrodi: 0 > 1
 Parecbasis cyclolepis: 0 > 1
 Clade 105: 0 > 1
 Clade 170: 0 > 1
 Macropsobrycon uruguayanae: 1 > 0
 Clade 165: 1 > 0
 Clade 128: 1 > 0
 Clade 173: 1 > 0
 Serrapinnus heterodon: 1 > 0
 Odontostilbe microcephala: 1 > 0
Character 54 (7 steps)
 Root: 0
 Rhoadsia altipinna: 0 > 1
 Charax stenopterus: 0 > 1
 Parecbasis cyclolepis: 0 > 1
 Clade 106: 0 > 1
 Macropsobrycon uruguayanae: 1 > 0
 Clade 158: 1 > 01
 Clade 182: 1 > 2
 Clade 157: 01 > 0
Character 55 (12 steps)
 Root: 0
 Microschemobrycon elongatus: 0 > 1
 Clade 186: 0 > 1
 Clade 107: 0 > 1
 Odontostilbe parecis: 1 > 0
 Acinocheirodon melanogramma: 1 > 0
 Axelrodia lindeae: 1 > 0
 Clade 143: 1 > 0
 Clade 165: 1 > 0
 Clade 128: 1 > 01
 Clade 127: 01 > 0
 Odontostilbe n. sp. p: 1 > 0
 Odontostilbe microcephala: 1 > 0
 Compsura gorgonae: 01 > 1
 Clade 129: 01 > 0
Character 56 (13 steps)
 Root: 0
 Clade 115: 0 > 01
 Clade 189: 01 > 1
 Clade 113: 01 > 0
 Clade 191: 01 > 1
 Clade 109: 0 > 01
 Prionobrama paraguayensis: 0 > 1
 Clade 187: 01 > 1
 Paracheirodon axelrodi: 01 > 1
 Clade 107: 01 > 0
 Clade 102: 0 > 1
 Odontostilbe parecis: 0 > 1
 Clade 143: 0 > 1
 Clade 165: 0 > 1
 Clade 128: 0 > 01
 Compsurini n. sp. Leticia: 0 > 1
 Clade 127: 01 > 1
 Odontostilbe n. sp. p: 0 > 1
 Compsura gorgonae: 01 > 0
 Clade 129: 01 > 1
Character 57 (1 step)
 Root: 0
 Clade 182: 0 > 1
Character 58 (3 steps)
 Root: 0
 Clade 187: 0 > 2
 Macropsobrycon uruguayanae: 0 > 2
 Clade 176: 0 > 1
Character 59 (14 steps)
 Root: 1
 Hyphessobrycon bifasciatus: 1 > 0
 Bryconamericus iheringii: 1 > 0
 Clade 108: 1 > 0
 Microschemobrycon elongatus: 1 > 0
 Clade 142: 0 > 1
 Odontostilbe splendida: 0 > 1
 Macropsobrycon uruguayanae: 0 > 1
 Clade 166: 0 > 1
 Clade 157: 0 > 1
 Compsurini n. sp. Leticia: 0 > 1
 Serrapinnus microdon: 0 > 1
 Clade 127: 0 > 1
 Odontostilbe n. sp. p: 0 > 1
 Odontostilbe n. sp. h: 0 > 1
Character 60 (4 steps)
 Root: 0
 Clade 106: 0 > 1
 Axelrodia lindeae: 1 > 0
 Compsurini n. sp. Leticia: 1 > 0
 Cheirodon kiliani: 1 > 0
Character 61 (6 steps)
 Root: 0
 Clade 188: 0 > 1
 Clade 112: 0 > 01
 Clade 190: 0 > 1
 Clade 193: 01 > 1
 Clade 110: 01 > 1
 Clade 184: 01 > 0
 Cynopotamus kincaidi: 01 > 1
 Charax stenopterus: 01 > 0
 Axelrodia lindeae: 1 > 0
Character 62 (25 steps)
 Root: 0
 Clade 189: 0 > 3
 Clade 190: 0 > 023
 Cyanocharax alburnus: 023 > 3
 Bryconamericus iheringii: 023 > 2
 Clade 110: 0 > 3
 Aphyocharacidium bolivianum: 3 > 2
 Clade 106: 3 > 1
 Clade 137: 1 > 12
 Clade 136: 12 > 2
 Clade 142: 12 > 2
 Clade 102: 1 > 12
 Clade 139: 12 > 1
 Acinocheirodon melanogramma: 12 > 2
 Clade 176: 1 > 0
 Clade 156: 12 > 123
 Clade 144: 12 > 1
 Clade 120: 1 > 12
 Axelrodia lindeae: 123 > 3
 Clade 143: 1 > 3
 Clade 123: 12 > 2
 Clade 165: 1 > 2
 Clade 157: 123 > 2
 Clade 155: 1 > 2
 Clade 128: 12 > 123
 Clade 118: 12 > 1
 Compsurini n. sp. Leticia: 1 > 3
 Pseudocheirodon arnoldi: 0 > 1
 Serrapinnus heterodon: 3 > 2
 Clade 138: 2 > 3
 Clade 130: 123 > 2
 Clade 127: 123 > 3
 Odontostilbe n. sp. p: 1 > 3
 Clade 162: 2 > 3
 Serrapinnus kriegi: 1 > 2
Character 63 (2 steps)
 Root: 0
 Clade 176: 0 > 01
 Odontostilbe euspilurus: 01 > 1
 Clade 182: 01 > 1
 Clade 180: 01 > 0
Character 64 (3 steps)
 Root: 0
 Macropsobrycon xinguensis: 0 > 1
 Clade 177: 0 > 1
 Clade 180: 1 > 0
Character 65 (1 step)
 Root: 0
 Clade 158: 0 > 01
 Clade 157: 01 > 1
Character 66 (2 steps)
 Root: 0
 Clade 181: 0 > 1
 Clade 158: 0 > 01
 Clade 157: 01 > 1
Character 67 (11 steps)
 Root: 0
 Bryconops caudomaculatus: 0 > 1
 Hyphessobrycon bifasciatus: 0 > 1
 Coptobrycon bilineatus: 0 > 1
 Clade 110: 0 > 1
 Prionobrama paraguayensis: 0 > 1
 Aphyodite grammica: 1 > 0
 Clade 166: 1 > 0
 Clade 178: 1 > 0
 Serrapinnus heterodon: 1 > 0
 Spintherobolus papilliferus: 1 > 0
 Holoshesthes n. sp. b: 0 > 1
Character 68 (20 steps)
 Root: 0
 Clade 184: 0 > 1
 Aphyodite grammica: 0 > 1
 Leptobrycon jatauaranae: 0 > 1
 Clade 170: 0 > 1
 Clade 136: 0 > 1
 Odontostilbe splendida: 1 > 0
 Clade 145: 0 > 01
 Clade 133: 1 > 0
 Clade 181: 1 > 01
 Axelrodia lindeae: 01 > 1
 Clade 150: 01 > 1
 Serrapinnus micropterus: 01 > 1
 Clade 143: 01 > 0
 Clade 182: 01 > 0
 Clade 157: 01 > 0
 Clade 155: 01 > 1
 Clade 151: 01 > 0
 Prodontocharax melanotus: 01 > 0
 Prodontocharax alleni: 01 > 1
 Clade 164: 1 > 01
 Odontostilbe n. sp. p: 1 > 0
 Odontostilbe microcephala: 1 > 0
 Holoshesthes n. sp. p: 01 > 0
 Cheirodon pisciculus: 0 > 1
 Cheirodontops geayi: 01 > 0
 Clade 146: 1 > 0
 Holoshesthes n. sp. k: 01 > 1
 Holoshesthes n. sp. b: 01 > 0
 Aphyocheirodon hemigrammus: 01 > 1
Character 69 (10 steps)
 Root: 0
 Clade 189: 0 > 1
 Clade 190: 0 > 1
 Clade 193: 0 > 1
 Clade 108: 0 > 1
 Aphyocharacidium bolivianum: 0 > 1
 Parecbasis cyclolepis: 0 > 1
 Compsurini n. sp. Purus: 1 > 0
 Clade 166: 1 > 0
 Axelrodia lindeae: 1 > 0
 Serrapinnus heterodon: 1 > 0
Character 70 (3 steps)
 Root: 0
 Odontostilbe nareuda: 0 > 1
 Odontostilbe pao: 0 > 1

Clade 182: 0 > 1
Character 71 (17 steps)
Root: 1
Bryconops caudomaculatus: 1 > 0
Clade 113: 1 > 0
Clade 110: 0 > 01
Clade 109: 01 > 012
Prionobrama paraguayensis: 0 > 1
Microschemobrycon elongatus: 01 > 1
Aphyocharacidium bolivianum: 01 > 0
Clade 194: 012 > 1
Paracheirodon axelrodi: 012 > 1
Clade 107: 012 > 2
Parecbasis cyclolepis: 012 > 2
Aphyodite grammica: 012 > 0
Clade 135: 2 > 1
Compsurini n. sp. Cuzco: 2 > 1
Compsurini n. sp. Purus: 2 > 1
Clade 156: 2 > 0
Clade 123: 2 > 1
Prodontocharax melanotus: 2 > 1
Saccoderma melanostigma: 2 > 1
Cheirodontops geayi: 2 > 1
Aphyocheirodon hemigrammus: 2 > 1
Character 72 (2 steps)
Root: 0
Clade 142: 0 > 1
Compsurini n. sp. Leticia: 0 > 1
Character 73 (15 steps)
Root: 1
Bryconops caudomaculatus: 1 > 0
Hyphessobrycon bifasciatus: 1 > 0
Cyanocharax alburnus: 1 > 0
Coptobrycon bilineatus: 1 > 0
Clade 110: 1 > 01
Clade 109: 01 > 0
Microschemobrycon elongatus: 01 > 0
Aphyocharacidium bolivianum: 01 > 1
Clade 168: 0 > 1
Acinocheirodon melanogramma: 0 > 1
Clade 181: 0 > 1
Odontostilbe fugitiva: 1 > 0
Serrapinnus heterodon: 0 > 1
Clade 127: 0 > 1
Odontostilbe n. sp. p: 1 > 0
Odontostilbe n. sp. h: 1 > 0
Holoshesthes n. sp. b: 1 > 0
Character 74 (5 steps)
Root: 0
Clade 193: 0 > 01
Coptobrycon bilineatus: 01 > 1
Clade 106: 0 > 1
Macropsobrycon uruguayanae: 1 > 0
Clade 156: 1 > 0
Compsurini n. sp. Leticia: 1 > 0
Character 75 (5 steps)
Root: 0
Clade 192: 0 > 1
Microschemobrycon elongatus: 0 > 1
Aphyodite grammica: 0 > 1
Cheirodon stenodon: 0 > 1
Clade 165: 0 > 1
Character 76 (2 steps)
Root: 0
Clade 127: 0 > 1
Cheirodontops geayi: 0 > 1
Character 77 (3 steps)
Root: 01
Clade 116: 01 > 1
Brycon pesu: 01 > 0
Clade 111: 1 > 2
Paracheirodon axelrodi: 2 > 12
Cheirodon stenodon: 2 > 1
Character 78 (2 steps)
Root: 1
Clade 192: 1 > 0

Paracheirodon axelrodi: 1 > 0
Character 79 (4 steps)
Root: 0
Clade 111: 0 > 1
Clade 108: 1 > 0
Macropsobrycon xinguensis: 1 > 0
Clade 156: 0 > 1
Character 80 (8 steps)
Root: 0
Coptobrycon bilineatus: 0 > 1
Clade 185: 0 > 01
Cynopotamus kincaidi: 01 > 1
Macropsobrycon xinguensis: 0 > 1
Macropsobrycon uruguayanae: 0 > 1
Cheirodon parahybae: 0 > 1
Prodontocharax alleni: 0 > 1
Serrapinnus microdon: 0 > 1
Clade 138: 0 > 1
Character 81 (13 steps)
Root: 0
Clade 113: 0 > 01
Probolodus heterostomus: 01 > 1
Clade 193: 01 > 1
Clade 111: 01 > 0
Aphyocharacidium bolivianum: 0 > 1
Clade 106: 0 > 1
Macropsobrycon uruguayanae: 1 > 0
Clade 156: 1 > 0
Cheirodon parahybae: 1 > 0
Clade 180: 1 > 0
Compsurini n. sp. Leticia: 1 > 0
Serrapinnus microdon: 1 > 0
Clade 138: 1 > 0
Clade 163: 1 > 0
Aphyocheirodon hemigrammus: 0 > 1
Character 82 (3 steps)
Root: 0
Clade 114: 0 > 01
Clade 191: 01 > 1
Probolodus heterostomus: 01 > 1
Clade 111: 01 > 0
Rhoadsia altipinna: 01 > 0
Coptobrycon bilineatus: 01 > 1
Character 83 (6 steps)
Root: 0
Clade 111: 0 > 1
Clade 108: 1 > 0
Axelrodia lindeae: 0 > 1
Prodontocharax alleni: 0 > 1
Spintherobolus papilliferus: 0 > 1
Aphyocheirodon hemigrammus: 0 > 1
Character 84 (2 steps)
Root: 0
Clade 113: 0 > 1
Macropsobrycon xinguensis: 1 > 0
Character 85 (5 steps)
Root: 0
Clade 192: 0 > 1
Microschemobrycon elongatus: 0 > 1
Clade 194: 0 > 01
Leptobrycon jatuaranae: 01 > 1
Macropsobrycon uruguayanae: 0 > 1
Clade 156: 0 > 1
Character 86 (2 steps)
Root: 0
Rhoadsia altipinna: 0 > 1
Clade 182: 0 > 1
Character 87 (4 steps)
Root: 0
Rhoadsia altipinna: 0 > 1
Clade 120: 0 > 01
Clade 123: 01 > 1
Clade 182: 0 > 1
Clade 128: 01 > 0
Clade 118: 01 > 1
Character 88 (1 step)

Root: 0
Clade 164: 0 > 1
Character 89 (5 steps)
Root: 0
Bryconops caudomaculatus: 0 > 1
Coptobrycon bilineatus: 0 > 1
Clade 187: 0 > 01
Clade 194: 01 > 1
Parecbasis cyclolepis: 01 > 1
Aphyodite grammica: 01 > 0
Macropsobrycon uruguayanae: 0 > 1
Character 90 (2 steps)
Root: 0
Rhoadsia altipinna: 0 > 01
Clade 106: 0 > 1
Clade 156: 1 > 0
Character 91 (2 steps)
Root: 0
Rhoadsia altipinna: 0 > 01
Clade 185: 0 > 1
Clade 156: 0 > 1
Character 92 (4 steps)
Root: 0
Clade 193: 0 > 1
Clade 106: 0 > 1
Macropsobrycon uruguayanae: 1 > 0
Axelrodia lindeae: 1 > 0
Character 93 (6 steps)
Root: 0
Clade 112: 0 > 01
Rhoadsia altipinna: 01 > 0
Coptobrycon bilineatus: 01 > 1
Clade 184: 01 > 1
Cynopotamus kincaidi: 01 > 1
Charax stenopterus: 01 > 0
Clade 108: 01 > 1
Microschemobrycon elongatus: 01 > 1
Aphyocharacidium bolivianum: 01 > 0
Clade 194: 01 > 0
Parecbasis cyclolepis: 01 > 1
Aphyodite grammica: 01 > 0
Character 94 (4 steps)
Root: 0
Coptobrycon bilineatus: 0 > 1
Aphyocharax nattereri: 0 > 1
Cynopotamus kincaidi: 0 > 1
Axelrodia lindeae: 0 > 1
Character 95 (3 steps)
Root: 01
Clade 116: 01 > 1
Brycon pesu: 01 > 0
Aphyocharacidium bolivianum: 1 > 0
Parecbasis cyclolepis: 1 > 0
Character 96 (16 steps)
Root: 0
Probolodus heterostomus: 0 > 2
Rhoadsia altipinna: 0 > 2
Clade 110: 0 > 01
Clade 109: 01 > 1
Microschemobrycon elongatus: 01 > 1
Aphyocharacidium bolivianum: 01 > 0
Clade 141: 1 > 2
Compsurini n. sp. Tingo: 1 > 2
Odontostilbe pulchra: 1 > 2
Acinocheirodon melanogramma: 1 > 0
Clade 144: 2 > 1
Clade 181: 1 > 2
Axelrodia lindeae: 2 > 0
Clade 165: 1 > 0
Compsurini n. sp. Yurimaguas: 1 > 2
Odontostilbe n. sp. m: 1 > 2
Serrapinnus heterodon: 1 > 0
Clade 127: 1 > 0
Character 97 (2 steps)
Root: 0
Clade 112: 0 > 1

Axelrodia lindeae: 1 > 0
Character 98 (5 steps)
 Root: 1
 Clade 113: 1 > 01
 Probolodus heterostomus: 01 > 0
 Clade 193: 01 > 0
 Clade 111: 01 > 1
 Cynopotamus kincaidi: 1 > 01
 Clade 194: 1 > 0
 Clade 107: 1 > 0
 Clade 156: 0 > 1
Character 99 (4 steps)
 Root: 01
 Probolodus heterostomus: 01 > 1
 Rhoadsia altipinna: 01 > 0
 Coptobrycon bilineatus: 01 > 1
 Clade 107: 01 > 0
 Macropsobrycon xinguensis: 01 > 1
 Leptobrycon jatuaranae: 01 > 0
 Macropsobrycon uruguayanae: 0 > 1
Character 100 (6 steps)
 Root: 0
 Charax stenopterus: 0 > 1
 Clade 187: 0 > 01
 Aphyocharacidium bolivianum: 0 > 1
 Clade 186: 01 > 1
 Macropsobrycon xinguensis: 01 > 0
 Leptobrycon jatuaranae: 01 > 1
 Axelrodia lindeae: 0 > 1
 Clade 180: 0 > 1
Character 101 (7 steps)
 Root: 0
 Clade 185: 0 > 01
 Clade 192: 01 > 1
 Prionobrama paraguayensis: 01 > 1
 Aphyocharax nattereri: 01 > 0
 Microschemobrycon elongatus: 0 > 1
 Aphyodite grammica: 0 > 1
 Leptobrycon jatuaranae: 0 > 1
 Macropsobrycon uruguayanae: 0 > 1
 Axelrodia lindeae: 0 > 1
Character 102 (4 steps)
 Root: 0
 Rhoadsia altipinna: 0 > 2
 Acinocheiroidon melanogramma: 0 > 2
 Clade 182: 0 > 1
 Clade 165: 0 > 2
Character 103 (6 steps)
 Root: 0
 Rhoadsia altipinna: 0 > 2
 Clade 102: 0 > 01
 Acinocheiroidon melanogramma: 01 > 1
 Clade 182: 0 > 3
 Clade 165: 0 > 1
 Clade 154: 0 > 1
 Clade 127: 0 > 2
Character 104 (6 steps)
 Root: 0
 Rhoadsia altipinna: 0 > 2
 Acinocheiroidon melanogramma: 0 > 1
 Clade 182: 0 > 3
 Clade 165: 0 > 1
 Serrapinnus heterodon: 0 > 1
 Clade 127: 0 > 2
Character 105 (27 steps)
 Root: 0
 Bryconops caudomaculatus: 0 > 3
 Clade 113: 0 > 0123
 Probolodus heterostomus: 0123 > 2
 Clade 193: 0123 > 3
 Clade 111: 0123 > 12
 Clade 192: 12 > 1
 Prionobrama paraguayensis: 12 > 1
 Aphyocharax nattereri: 12 > 2
 Clade 108: 12 > 0
 Microschemobrycon elongatus: 12 > 1
 Aphyocharacidium bolivianum: 12 > 2
 Parecbasis cyclolepis: 12 > 2
 Aphyodite grammica: 12 > 1
 Macropsobrycon xinguensis: 12 > 2
 Leptobrycon jatuaranae: 12 > 1
 Clade 171: 0 > 3
 Clade 141: 0 > 3
 Clade 122: 0 > 3
 Compsurini n. sp. Tingo: 0 > 3
 Clade 139: 3 > 4
 Macropsobrycon uruguayanae: 0 > 1
 Clade 156: 3 > 123
 Cheiroidon interruptus: 0 > 3
 Clade 181: 3 > 234
 Axelrodia lindeae: 123 > 1
 Clade 143: 3 > 0
 Clade 182: 234 > 4
 Clade 180: 234 > 2
 Clade 165: 3 > 0
 Clade 157: 123 > 12
 Clade 151: 3 > 0
 Compsurini n. sp. Leticia: 3 > 0
 Amazonspinner dalmata: 12 > 2
 Odontostilbe n. sp. p: 3 > 0
 Spintherobolus papilliferus: 12 > 1
 Clade 159: 12 > 2
 Cheiroidon kiliani: 0 > 2
Character 106 (7 steps)
 Root: 0
 Clade 193: 0 > 1
 Clade 108: 0 > 1
 Parecbasis cyclolepis: 0 > 1
 Macropsobrycon uruguayanae: 1 > 0
 Clade 156: 1 > 0
 Clade 180: 1 > 0
 Clade 131: 1 > 0
Character 107 (18 steps)
 Root: 0
 Clade 190: 0 > 1
 Coptobrycon bilineatus: 0 > 1
 Aphyocharacidium bolivianum: 0 > 1
 Cheiroidon stenodon: 0 > 1
 Clade 104: 0 > 01
 Clade 122: 01 > 1
 Compsurini n. sp. Cuzco: 01 > 0
 Compsurini n. sp. Tingo: 01 > 1
 Clade 168: 0 > 1
 Clade 145: 0 > 01
 Macropsobrycon uruguayanae: 01 > 0
 Acinocheiroidon melanogramma: 01 > 1
 Odontostilbe pao: 0 > 1
 Clade 144: 01 > 1
 Axelrodia lindeae: 01 > 0
 Clade 123: 1 > 0
 Clade 180: 0 > 1
 Clade 157: 01 > 1
 Clade 149: 1 > 0
 Holoshesthes pequirá: 1 > 0
 Serrapinnus n. sp. a: 1 > 0
 Serrapinnus heterodon: 1 > 0
 Odontostilbe dialeptura: 1 > 0
Character 108 (1 step)
 Root: 0
 Aphyocheiroidon hemigrammus: 0 > 1
Character 109 (4 steps)
 Root: 0
 Odontostilbe n. sp. b: 0 > 1
 Acinocheiroidon melanogramma: 0 > 1
 Clade 173: 0 > 1
 Holoshesthes pequirá: 0 > 1
Character 110 (16 steps)
 Root: 0
 Bryconops caudomaculatus: 0 > 1
 Clade 112: 0 > 1
 Hyphessobrycon bifasciatus: 0 > 1
 Cyanocharax alburnus: 0 > 1
 Clade 183: 1 > 0
 Aphyocharax nattereri: 1 > 0
 Parecbasis cyclolepis: 1 > 0
 Clade 177: 1 > 01
 Odontostilbe pao: 01 > 0
 Clade 156: 1 > 0
 Clade 181: 01 > 1
 Odontostilbe euspilurus: 01 > 0
 Kolpotocheiroidon figueiredoi: 1 > 0
 Odontostilbe n. sp. p: 1 > 0
 Odontostilbe n. sp. h: 1 > 0
 Compsura gorgonae: 1 > 0
 Serrapinnus kriegi: 1 > 0
 Aphyocheiroidon hemigrammus: 1 > 0
Character 111 (1 step)
 Root: 0
 Clade 158: 0 > 01
 Clade 157: 01 > 1
Character 112 (17 steps)
 Root: 0
 Clade 115: 0 > 01
 Clade 113: 01 > 1
 Clade 191: 01 > 0
 Astyanax laticeps: 01 > 1
 Hyphessobrycon bifasciatus: 01 > 0
 Astyanax fasciatus: 01 > 1
 Coptobrycon bilineatus: 1 > 0
 Aphyocharax nattereri: 1 > 0
 Clade 187: 1 > 01
 Clade 194: 01 > 0
 Parecbasis cyclolepis: 01 > 1
 Aphyodite grammica: 01 > 0
 Macropsobrycon uruguayanae: 1 > 0
 Odontostilbe dierythrura: 1 > 0
 New Genus n. sp. b: 1 > 0
 Clade 133: 1 > 0
 Clade 158: 1 > 01
 Clade 180: 1 > 0
 Clade 157: 01 > 0
 Clade 118: 1 > 01
 Kolpotocheiroidon figueiredoi: 1 > 0
 Serrapinnus n. sp. me: 1 > 0
 Compsura n. sp. Araguaia: 01 > 0
 Compsura n. sp. Guaporé: 01 > 0
 Compsura heterura: 01 > 1
Character 113 (1 step)
 Root: 0
 Clade 158: 0 > 01
 Clade 157: 01 > 1
Character 114 (17 steps)
 Root: 0
 Clade 189: 0 > 1
 Probolodus heterostomus: 0 > 1
 Coptobrycon bilineatus: 0 > 1
 Aphyocharax nattereri: 0 > 1
 Parecbasis cyclolepis: 0 > 1
 Odontostilbe n. sp. b: 0 > 1
 Clade 137: 0 > 1
 Compsurini n. sp. Purus: 0 > 1
 Macropsobrycon uruguayanae: 0 > 1
 Clade 144: 1 > 0
 New Genus n. sp. c: 1 > 0
 Clade 123: 0 > 1
 Serrapinnus n. sp. ac: 0 > 1
 Serrapinnus microdon: 0 > 1
 Saccoderma hastata: 0 > 1
 Serrapinnus kriegi: 0 > 1
 Aphyocheiroidon hemigrammus: 0 > 1
Character 115 (3 steps)
 Root: 01
 Clade 116: 01 > 1
 Brycon pesu: 01 > 0
 Rhoadsia altipinna: 1 > 0
 Cynopotamus kincaidi: 1 > 0
Character 116 (4 steps)
 Root: 0

Coptobrycon bilineatus: 0 > 1
 Clade 109: 0 > 1
 Clade 156: 1 > 2
 Spinttherobolus papilliferus: 2 > 1
Character 117 (3 steps)
 Root: 0
 Coptobrycon bilineatus: 0 > 1
 Prionobrama paraguayensis: 0 > 1
 Clade 158: 0 > 01
 Clade 157: 01 > 1
Character 118 (6 steps)
 Root: 0
 Clade 115: 0 > 1
 Probolodus heterostomus: 1 > 0
 Cyanocharax alburnus: 1 > 0
 Rhoadsia altipinna: 1 > 0
 Clade 192: 1 > 0
 Clade 156: 1 > 0
Character 119 (6 steps)
 Root: 0
 Clade 189: 0 > 1
 Clade 106: 0 > 1
 Clade 140: 1 > 01
 Nanocheiroidon insignis: 1 > 0
 Clade 139: 01 > 0
 Clade 156: 01 > 0
 Clade 144: 01 > 1
 Serrapinnus kriegi: 1 > 0
Character 120 (20 steps)
 Root: 0
 Clade 191: 0 > 1
 Hyphessobrycon bifasciatus: 0 > 1
 Coptobrycon bilineatus: 0 > 1
 Clade 185: 0 > 01
 Clade 184: 01 > 1
 Cynopotamus kincaidi: 01 > 0
 Charax stenopterus: 01 > 1
 Clade 194: 0 > 1
 Cheiroidon stenodon: 0 > 1
 Clade 137: 0 > 1
 Odontostilbe splendida: 0 > 1
 New Genus n. sp. c: 1 > 0
 Clade 181: 0 > 01
 Clade 150: 1 > 0
 Clade 182: 01 > 1
 Clade 154: 1 > 0
 Prodontocharax melanotus: 01 > 0
 Prodontocharax alleni: 01 > 1
 Amazonspintther dalmata: 1 > 0
 Odontostilbe n. sp. p: 0 > 1
 Odontostilbe n. sp. h: 0 > 1
 Serrapinnus notomelas: 0 > 1
 Serrapinnus n. sp. e: 0 > 1
 Serrapinnus n. sp. ups: 0 > 1
Character 121 (15 steps)
 Root: 0
 Probolodus heterostomus: 0 > 1
 Cyanocharax alburnus: 0 > 1
 Clade 185: 0 > 1
 Paracheiroidon axelrodi: 0 > 1
 Parecbasis cyclolepis: 0 > 1
 Clade 172: 0 > 1
 Clade 179: 1 > 0
 Odontostilbe pao: 1 > 0
 Serrapinnus micropterus: 0 > 1
 Odontostilbe fugitiva: 1 > 0
 Holoshesthes pequiri: 1 > 0
 Serrapinnus microdon: 0 > 1
 Cheiroidon australe: 0 > 1
 Serrapinnus notomelas: 0 > 1
 Holoshesthes n. sp. k: 1 > 0
Character 122 (1 step)
 Root: 0
 Clade 160: 0 > 1
Character 123 (1 step)
 Root: 0
 Compsurini n. sp. Cuzco: 0 > 1
Character 124 (1 step)
 Root: 0
 Spinttherobolus papilliferus: 0 > 1
Character 125 (4 steps)
 Root: 0
 Clade 115: 0 > 1
 Clade 192: 1 > 0
 Paracheiroidon axelrodi: 1 > 0
 Axelrodia lindeae: 1 > 0
Character 126 (2 steps)
 Root: 0
 Microschemobrycon elongatus: 0 > 1
 Clade 156: 0 > 1
Character 127 (1 step)
 Root: 0
 Clade 158: 0 > 01
 Clade 157: 01 > 1
Character 128 (1 step)
 Root: 0
 Clade 158: 0 > 01
 Clade 157: 01 > 1
Character 129 (6 steps)
 Root: 0
 Cynopotamus kincaidi: 0 > 1
 Parecbasis cyclolepis: 0 > 1
 Clade 142: 0 > 1
 Clade 135: 0 > 1
 Prodontocharax melanotus: 0 > 1
 Clade 178: 0 > 1
Character 130 (13 steps)
 Root: 0
 Bryconamericus iheringii: 0 > 1
 Rhoadsia altipinna: 0 > 1
 Aphyocharax nattereri: 0 > 1
 Cynopotamus kincaidi: 0 > 1
 Aphyocharacidium bolivianum: 0 > 1
 Clade 186: 0 > 1
 Cheiroidon stenodon: 0 > 1
 Clade 142: 0 > 1
 Clade 135: 0 > 1
 Macropsobrycon uruguayanae: 0 > 1
 Clade 158: 0 > 01
 Prodontocharax melanotus: 0 > 1
 Clade 178: 0 > 1
 Clade 160: 01 > 1
Character 131 (1 step)
 Root: 0
 Clade 158: 0 > 01
 Clade 160: 01 > 1
Character 132 (7 steps)
 Root: 0
 Clade 115: 0 > 2
 Hyphessobrycon bifasciatus: 2 > 0
 Clade 185: 2 > 02
 Clade 184: 02 > 0
 Cynopotamus kincaidi: 02 > 0
 Charax stenopterus: 02 > 2
 Microschemobrycon elongatus: 2 > 0
 Aphyodite grammica: 2 > 0
 Clade 180: 2 > 1
Character 133 (10 steps)
 Root: 0
 Clade 113: 0 > 1
 Astyanax fasciatus: 0 > 1
 Cyanocharax alburnus: 0 > 1
 Rhoadsia altipinna: 1 > 0
 Aphyocharax nattereri: 1 > 0
 Cynopotamus kincaidi: 1 > 2
 Microschemobrycon elongatus: 1 > 0
 Clade 194: 1 > 2
 Clade 102: 1 > 012
 Macropsobrycon uruguayanae: 012 > 2
 Acinocheiroidon melanogramma: 012 > 0
Character 134 (1 step)
 Root: 0
 Clade 156: 0 > 01
 Axelrodia lindeae: 01 > 1
Character 135 (1 step)
 Root: 0
 Odontostilbe paraguayensis: 0 > 1
Character 136 (3 steps)
 Root: 0
 Clade 191: 0 > 1
 Rhoadsia altipinna: 0 > 1
 Clade 184: 0 > 1
Character 137 (8 steps)
 Root: 0
 Rhoadsia altipinna: 0 > 1
 Clade 172: 0 > 1
 Clade 176: 1 > 0
 Clade 155: 0 > 1
 Clade 173: 1 > 01
 Odontostilbe n. sp. e: 01 > 0
 Odontostilbe n. sp. h: 1 > 0
 Odontostilbe mitoptera: 0 > 1
 Clade 161: 1 > 0
Character 138 (1 step)
 Root: 0
 Clade 161: 0 > 1
Character 139 (3 steps)
 Root: 0
 Clade 192: 0 > 2
 Paracheiroidon axelrodi: 0 > 2
 Clade 160: 0 > 1
Character 140 (1 step)
 Root: 0
 Clade 160: 0 > 1
Character 141 (2 steps)
 Root: 0
 Clade 158: 0 > 01
 Amazonspintther dalmata: 01 > 1
 Spinttherobolus papilliferus: 01 > 1
 Clade 159: 01 > 0
Character 142 (9 steps)
 Root: 0
 Coptobrycon bilineatus: 0 > 1
 Prionobrama paraguayensis: 0 > 1
 Clade 107: 0 > 01
 Cheiroidon stenodon: 01 > 1
 Clade 172: 01 > 0
 Clade 105: 01 > 1
 Clade 140: 1 > 01
 Compsurini n. sp. Tingo: 1 > 0
 Clade 145: 01 > 0
 Acinocheiroidon melanogramma: 1 > 0
 New Genus n. sp. b: 01 > 0
 New Genus n. sp. c: 01 > 1
 Clade 118: 1 > 0
Character 143 (2 steps)
 Root: 0
 Prionobrama paraguayensis: 0 > 1
 Clade 158: 0 > 01
 Clade 157: 01 > 1
Character 144 (4 steps)
 Root: 0
 Clade 114: 0 > 1
 Rhoadsia altipinna: 1 > 0
 Clade 184: 1 > 01
 Aphyocharax nattereri: 01 > 0
 Macropsobrycon uruguayanae: 1 > 0
Character 145 (6 steps)
 Root: 0
 Clade 183: 0 > 2
 Paracheiroidon axelrodi: 0 > 1
 Odontostilbe n. sp. b: 0 > 1
 Clade 136: 0 > 01
 Nanocheiroidon insignis: 01 > 1
 Clade 134: 01 > 1
 Cheiroidon ibicuhensis: 01 > 0
 Clade 156: 0 > 02
 Axelrodia lindeae: 02 > 2

Character 146 (1 step)
 Root: 0
 Clade 157: 0 > 1
Character 147 (7 steps)
 Root: 0
 Clade 114: 0 > 1
 Hyphessobrycon bifasciatus: 0 > 1
 Clade 193: 1 > 0
 Aphyocharax nattereri: 1 > 0
 Cynopotamus kincaidi: 1 > 0
 Aphyodite grammica: 1 > 0
 Clade 158: 1 > 01
 Clade 157: 01 > 0
Character 148 (3 steps)
 Root: 0
 Odontostilbe pao: 0 > 1
 Holoshesthes n. sp. p: 0 > 1
 Odontostilbe mitoptera: 0 > 1
Character 149 (10 steps)
 Root: 0
 Aphyocharax nattereri: 0 > 1
 Clade 108: 0 > 01
 Aphyocharacidium bolivianum: 0 > 1
 Clade 107: 01 > 1
 Clade 169: 1 > 0
 Clade 142: 1 > 0
 Acinocheiroidon melanogramma: 1 > 0
 New Genus n. sp. c: 1 > 0
 Odontostilbe euspilurus: 0 > 1
 Compsurini n. sp. Leticia: 1 > 0
 Compsura heterura: 1 > 0
Character 150 (8 steps)
 Root: 0
 Rhoadsia altipinna: 0 > 1
 Prionobrama paraguayensis: 0 > 1
 Clade 172: 0 > 1
 Odontostilbe parecis: 1 > 0
 Clade 182: 1 > 0
 Clade 173: 1 > 01
 Odontostilbe n. sp. e: 01 > 0
 Odontostilbe mitoptera: 0 > 1
 Clade 161: 1 > 0
Character 151 (1 step)
 Root: 0
 Clade 135: 0 > 1
Character 152 (5 steps)
 Root: 0
 Coptobrycon bilineatus: 0 > 1
 Leptobrycon jataranae: 0 > 1
 Clade 157: 0 > 01
 Amazonspinther dalmata: 01 > 1
 Clade 138: 0 > 1
 Spintherobolus papilliferus: 01 > 1
 Clade 159: 01 > 0
Character 153 (3 steps)
 Root: 0
 Rhoadsia altipinna: 0 > 1
 Prionobrama paraguayensis: 0 > 1
 Holoshesthes n. sp. p: 0 > 1
Character 154 (5 steps)
 Root: 0
 Prionobrama paraguayensis: 0 > 1
 Compsurini n. sp. Tingo: 0 > 1
 Acinocheiroidon melanogramma: 0 > 1
 Clade 119: 0 > 1
 Compsurini n. sp. Yurimaguas: 0 > 1
Character 155 (2 steps)
 Root: 0
 Rhoadsia altipinna: 0 > 1
 Nanocheiroidon insignis: 0 > 1
Character 156 (4 steps)
 Root: 0
 Cheiroidon stenodon: 0 > 1
 Acinocheiroidon melanogramma: 0 > 1
 Clade 119: 0 > 01
 Clade 118: 01 > 1
 Clade 130: 01 > 1
 Clade 127: 01 > 0
Character 157 (2 steps)
 Root: 0
 Clade 140: 0 > 1
 Spintherobolus papilliferus: 1 > 0
Character 158 (2 steps)
 Root: 0
 Clade 141: 0 > 1
 Spintherobolus papilliferus: 1 > 0
Character 159 (2 steps)
 Root: 0
 Clade 140: 0 > 1
 Spintherobolus papilliferus: 1 > 0
Character 160 (3 steps)
 Root: 1
 New Genus n. sp. c: 1 > 0
 Serrapinnus micropterus: 1 > 0
 Serrapinnus heterodon: 1 > 0
Character 161 (2 steps)
 Root: 01
 Clade 139: 01 > 0
 Clade 144: 01 > 1
 Clade 158: 01 > 0
 Axelrodia lindeae: 01 > 1
Character 162 (1 step)
 Root: 0
 Clade 159: 0 > 1
Character 163 (2 steps)
 Root: 0
 Clade 141: 0 > 1
 Spintherobolus papilliferus: 1 > 0
Character 164 (2 steps)
 Root: 0
 Clade 158: 0 > 1
 Clade 148: 0 > 1
Character 165 (1 step)
 Root: 0
 Clade 141: 0 > 1
Character 166 (1 step)
 Root: 0
 Axelrodia lindeae: 0 > 1
Character 167 (1 step)
 Root: 0
 Amazonspinther dalmata: 0 > 1
Character 168 (3 steps)
 Root: 0
 Clade 105: 0 > 1
 Clade 142: 1 > 0
 Axelrodia lindeae: 1 > 0
Character 169 (3 steps)
 Root: 0
 Clade 193: 0 > 1
 Paracheiroidon axelrodi: 0 > 1
 Spintherobolus papilliferus: 0 > 1
Character 170 (6 steps)
 Root: 0
 Clade 122: 0 > 2
 Compsurini n. sp. Tingo: 0 > 1
 Clade 119: 2 > 12
 Clade 125: 2 > 012
 Clade 118: 12 > 1
 Compsurini n. sp. Leticia: 012 > 0
 Compsurini n. sp. Yurimaguas: 012 > 1
 Clade 130: 12 > 1
 Clade 127: 12 > 2
Character 171 (1 step)
 Root: 0
 Nanocheiroidon insignis: 0 > 1
Character 172 (6 steps)
 Root: 0
 Prionobrama paraguayensis: 0 > 1
 Nanocheiroidon insignis: 0 > 1
 Serrapinnus micropterus: 0 > 1
 Clade 157: 0 > 01
 Clade 151: 0 > 1
 Clade 160: 01 > 1
 Odontostilbe n. sp. p: 0 > 1
Character 173 (4 steps)
 Root: 0
 Clade 104: 0 > 2
 Compsurini n. sp. Cuzco: 2 > 1
 Acinocheiroidon melanogramma: 2 > 0
 Compsurini n. sp. Leticia: 2 > 1
Character 174 (12 steps)
 Root: 0
 Clade 115: 0 > 1
 Clade 185: 1 > 0
 Clade 108: 1 > 01
 Clade 107: 01 > 0
 Clade 104: 0 > 1
 Clade 144: 0 > 1
 New Genus n. sp. b: 0 > 1
 Clade 120: 1 > 01
 Clade 123: 01 > 0
 Clade 182: 0 > 1
 Megacheiroidon unicus: 0 > 1
 Clade 151: 1 > 0
 Clade 128: 01 > 1
 Clade 118: 01 > 0
 Clade 153: 1 > 0
Character 175 (4 steps)
 Root: 0
 Clade 140: 0 > 1
 Cheiroidon ibicuhensis: 0 > 1
 Clade 149: 1 > 2
 Serrapinnus n. sp. ac: 1 > 2
Character 176 (1 step)
 Root: 0
 Clade 141: 0 > 1
Character 177 (2 steps)
 Root: 0
 Coptobrycon bilineatus: 0 > 1
 Clade 160: 0 > 1
Character 178 (5 steps)
 Root: 0
 Cyanocharax alburnus: 0 > 1
 Cheiroidon stenodon: 0 > 1
 Clade 137: 0 > 1
 Compsurini n. sp. Leticia: 0 > 1
 Amazonspinther dalmata: 1 > 0
Character 179 (1 step)
 Root: 0
 Clade 145: 0 > 1
Character 180 (1 step)
 Root: 0
 Clade 103: 0 > 1
Character 181 (1 step)
 Root: 0
 Clade 102: 0 > 1
Character 182 (1 step)
 Root: 0
 Clade 127: 0 > 1
Character 183 (2 steps)
 Root: 0
 Compsurini n. sp. Purus: 0 > 1
 Acinocheiroidon melanogramma: 0 > 1
Character 184 (5 steps)
 Root: 0
 Clade 103: 0 > 1
 Clade 120: 1 > 01
 Clade 118: 01 > 0
 Kolpotocheiroidon figueiredoi: 01 > 0
 Kolpotocheiroidon theloura: 01 > 1
 Clade 127: 01 > 1
 Compsura gorgona: 01 > 0
 Odontostilbe mitoptera: 01 > 0
 Odontostilbe dialeptura: 01 > 1
Character 185 (1 step)
 Root: 0
 Clade 125: 0 > 1
Character 186 (1 step)

Root: 1
 Clade 121: 1 > 0
Character 187 (2 steps)
 Root: 01
 Clade 121: 01 > 0
 Compsurini n. sp. Purus: 01 > 1
 Macropsobrycon uruguayanae: 01 > 0
 Acinocheiroidon melanogramma: 01 > 1
Character 188 (1 step)
 Root: 0
 Clade 124: 0 > 1
Character 189 (1 step)
 Root: 0
 Macropsobrycon uruguayanae: 0 > 1
Character 190 (4 steps)
 Root: 0
 Clade 137: 0 > 012
 Clade 141: 012 > 12
 Clade 136: 012 > 2
 Clade 142: 12 > 1
 Clade 145: 12 > 1
 Clade 139: 12 > 2
 Amazonspinther dalmata: 1 > 0
Character 191 (2 steps)
 Root: 0
 Clade 136: 0 > 1
 Clade 139: 0 > 1
Character 192 (1 step)
 Root: 0
 Nanocheiroidon insignis: 0 > 1
Character 193 (4 steps)
 Root: 0
 Clade 137: 0 > 1
 Clade 142: 1 > 2
 Clade 156: 1 > 01
 Axelrodia lindeae: 01 > 0
 Clade 160: 01 > 1
 Amazonspinther dalmata: 01 > 0
Character 194 (3 steps)
 Root: 0
 Clade 136: 0 > 1
 Clade 139: 0 > 1
 Megacheiroidon unicus: 0 > 1
Character 195 (1 step)
 Root: 0
 Clade 137: 0 > 1
Character 196 (3 steps)
 Root: 0
 Clade 140: 0 > 1
 Clade 151: 1 > 2
 Amazonspinther dalmata: 1 > 0
Character 197 (2 steps)
 Root: 0
 Clade 136: 0 > 1
 Clade 139: 0 > 1
Character 198 (4 steps)
 Root: 0
 Clade 137: 0 > 012
 Clade 141: 012 > 1
 Clade 136: 012 > 2
 New Genus n. sp. c: 1 > 2
 Clade 152: 1 > 2
Character 199 (1 step)
 Root: 0
 Clade 137: 0 > 1
Character 200 (3 steps)
 Root: 0
 Clade 136: 0 > 1
 New Genus n. sp. b: 0 > 1
 Clade 158: 0 > 1
Character 201 (4 steps)
 Root: 0
 Clade 139: 0 > 1
 Clade 158: 0 > 1
 Clade 155: 0 > 1
 Serrapinnus piaba: 0 > 1
Character 202 (2 steps)
 Root: 0
 Clade 137: 0 > 01
 Clade 136: 01 > 1
 Clade 140: 01 > 1
 Clade 142: 01 > 0
Character 203 (1 step)
 Root: 0
 Clade 152: 0 > 1
Character 204 (3 steps)
 Root: 01
 Clade 136: 01 > 1
 Clade 142: 01 > 0
 Clade 139: 01 > 1
 Clade 144: 01 > 0
 Clade 158: 01 > 1
 Axelrodia lindeae: 01 > 0
Character 205 (1 step)
 Root: 0
 Clade 158: 0 > 1
Character 206 (1 step)
 Root: 0
 Clade 152: 0 > 1
Character 207 (7 steps)
 Root: 0
 Clade 141: 0 > 01
 Clade 142: 01 > 1
 Clade 145: 01 > 0
 Clade 139: 01 > 1
 Compsurini n. sp. Purus: 0 > 1
 Acinocheiroidon melanogramma: 0 > 1
 Clade 150: 0 > 1
 Serrapinnus n. sp. upm: 0 > 1
 Odontostilbe dialeptura: 0 > 1
Character 208 (1 step)
 Root: 0
 Acinocheiroidon melanogramma: 0 > 1
Character 209 (1 step)
 Root: 0
 Clade 138: 0 > 1
Character 210 (14 steps)
 Root: 0
 Clade 112: 0 > 1
 Hyphessobrycon bifasciatus: 0 > 1
 Cyanocharax alburnus: 0 > 1
 Cynopotamus kincaidi: 1 > 0
 Aphyocharacidium bolivianum: 1 > 0
 Parecbasis cyclolepis: 1 > 0
 Clade 171: 1 > 0
 Clade 142: 1 > 0
 Acinocheiroidon melanogramma: 1 > 0
 New Genus n. sp. c: 1 > 0
 Clade 155: 1 > 01
 Serrapinnus n. sp. t: 01 > 0
 Serrapinnus heterodon: 1 > 0
 Clade 127: 1 > 0
 Odontostilbe mitoptera: 1 > 0
Character 211 (3 steps)
 Root: 0
 Coptobrycon bilineatus: 0 > 1
 Clade 192: 0 > 01
 Charax stenopterus: 01 > 1
 Clade 157: 0 > 1
Character 212 (9 steps)
 Root: 1
 Bryconops caudomaculatus: 1 > 0
 Clade 113: 1 > 0
 Hyphessobrycon bifasciatus: 1 > 0
 Cynopotamus kincaidi: 0 > 1
 Parecbasis cyclolepis: 0 > 1
 Clade 171: 0 > 1
 Compsurini n. sp. Cuzco: 0 > 1
 Pseudocheiroidon arnoldi: 1 > 0
 Clade 127: 0 > 2
Character 213 (3 steps)
 Root: 0
 Hemibrycon polyodon: 0 > 1
 Clade 187: 0 > 01
 Clade 186: 01 > 1
 Macropsobrycon xinguensis: 01 > 1
 Leptobrycon jatuaranae: 01 > 0
Character 214 (3 steps)
 Root: 0
 Compsurini n. sp. Purus: 0 > 1
 Macropsobrycon uruguayanae: 0 > 1
 Clade 119: 0 > 1
Character 215 (2 steps)
 Root: 0
 Macropsobrycon uruguayanae: 0 > 1
 Clade 119: 0 > 1
Character 216 (1 step)
 Root: 0
 Clade 129: 0 > 1
Character 217 (1 step)
 Root: 0
 Clade 127: 0 > 1
Character 218 (1 step)
 Root: 0
 Clade 128: 0 > 1
Character 219 (1 step)
 Root: 0
 Compsura gorgonae: 0 > 1
Character 220 (2 steps)
 Root: 01
 Clade 122: 01 > 1
 Macropsobrycon uruguayanae: 01 > 0
 Clade 130: 1 > 0
Character 221 (1 step)
 Root: 1
 Clade 128: 1 > 01
 Clade 127: 01 > 0
Character 222 (1 step)
 Root: 0
 Clade 118: 0 > 1
Character 223 (1 step)
 Root: 01
 Compsurini n. sp. Purus: 01 > 0
 Clade 119: 01 > 1
Character 224 (1 step)
 Root: 01
 Compsurini n. sp. Purus: 01 > 0
 Clade 119: 01 > 1
Character 225 (2 steps)
 Root: 012
 Compsurini n. sp. Purus: 012 > 2
 Clade 118: 012 > 1
 Clade 127: 012 > 0
Character 226 (2 steps)
 Root: 0
 Clade 121: 0 > 1
 Clade 130: 1 > 0
Character 227 (1 step)
 Root: 0
 Clade 123: 0 > 1
Character 228 (1 step)
 Root: 0
 Kolpotocheiroidon theloura: 0 > 1
Character 229 (1 step)
 Root: 0
 Clade 123: 0 > 1
Character 230 (2 steps)
 Root: 0
 Clade 121: 0 > 1
 Odontostilbe dialeptura: 1 > 0
Character 231 (3 steps)
 Root: 0
 Clade 102: 0 > 1
 Clade 123: 0 > 1
 Odontostilbe dialeptura: 0 > 1
Character 232 (4 steps)
 Root: 0
 Clade 111: 0 > 01

Clade 184: 01 > 0
 Clade 192: 01 > 1
 Clade 183: 01 > 1
 Clade 187: 01 > 0
 Clade 108: 01 > 1
 Axelrodia lindeae: 1 > 0
Character 233 (2 steps)
 Root: 0
 Clade 183: 0 > 2
 Clade 107: 0 > 1
Character 234 (1 step)
 Root: 0
 Clade 108: 0 > 01
 Clade 107: 01 > 1
Character 235 (2 steps)
 Root: 1
 Clade 107: 1 > 0
 Clade 156: 0 > 1
Character 236 (2 steps)
 Root: 01
 Charax stenopterus: 01 > 0
 Clade 108: 01 > 1
 Spintherobolus papilliferus: 1 > 0
Character 237 (2 steps)
 Root: 0
 Clade 140: 0 > 1
 Spintherobolus papilliferus: 1 > 0
Character 238 (4 steps)
 Root: 0
 Clade 107: 0 > 01
 Cheirodon stenodon: 01 > 1
 Clade 172: 01 > 0
 Clade 105: 01 > 1
 Clade 134: 1 > 0
 Clade 156: 1 > 0
Character 239 (3 steps)
 Root: 0
 Clade 122: 0 > 1
 Compsurini n. sp. Napo: 1 > 0
 Clade 118: 1 > 0
Character 240 (3 steps)
 Root: 0
 Clade 123: 0 > 1
 Clade 125: 0 > 1
 Clade 130: 0 > 1
Character 241 (1 step)
 Root: 0
 Clade 127: 0 > 1
Character 242 (3 steps)
 Root: 0
 Compsurini n. sp. Purus: 0 > 1
 Clade 119: 0 > 01
 Clade 118: 01 > 1
 Compsura gorgonae: 01 > 1
 Clade 129: 01 > 0
Character 243 (2 steps)
 Root: 0
 Acinocheiron melanogramma: 0 > 1
 Compsura gorgonae: 0 > 1
Character 244 (3 steps)
 Root: 0
 Compsurini n. sp. Purus: 0 > 1
 Clade 119: 0 > 1
 Clade 129: 1 > 0
Character 245 (1 step)
 Root: 0
 Macropsobrycon uruguayanae: 0 > 1
Character 246 (1 step)
 Root: 0
 Clade 159: 0 > 1
Character 247 (5 steps)
 Root: 0
 Bryconops caudomaculatus: 0 > 1
 Coptobrycon bilineatus: 0 > 1
 Clade 109: 0 > 01
 Clade 108: 01 > 1

Parecbasis cyclolepis: 01 > 0
 Aphyodite grammica: 01 > 1
 Macropsobrycon xinguensis: 01 > 1
 Leptobrycon jatuaranae: 01 > 0
Character 248 (1 step)
 Root: 0
 Clade 123: 0 > 1
Character 249 (3 steps)
 Root: 0
 Clade 102: 0 > 1
 Clade 118: 0 > 1
 Kolpotocheiron figueiredoi: 0 > 1
Character 250 (8 steps)
 Root: 0
 Macropsobrycon uruguayanae: 0 > 1
 Clade 143: 0 > 1
 Clade 165: 0 > 1
 Clade 118: 0 > 1
 Clade 173: 0 > 1
 Saccoderma melanostigma: 0 > 1
 Odontostilbe mitoptera: 0 > 1
 Aphyocheiron hemigrammus: 1 > 0
Character 251 (6 steps)
 Root: 0
 Odontostilbe n. sp. b: 0 > 2
 Serrapinnus n. sp. upm: 0 > 2
 Prodontocharax melanotus: 0 > 3
 Holoshesthes pequirá: 0 > 2
 Amazonspinner dalmata: 0 > 1
 Clade 153: 0 > 1
Character 252 (1 step)
 Root: 0
 Serrapinnus n. sp. me: 0 > 1
Character 253 (2 steps)
 Root: 0
 Clade 104: 0 > 1
 Acinocheiron melanogramma: 1 > 0
Character 254 (2 steps)
 Root: 0
 Macropsobrycon uruguayanae: 0 > 1
 Clade 123: 0 > 1
Character 255 (1 step)
 Root: 0
 Clade 159: 0 > 1
Character 256 (7 steps)
 Root: 01
 Clade 116: 01 > 0
 Brycon pesu: 01 > 1
 Clade 112: 0 > 01
 Hyphessobrycon bifasciatus: 0 > 1
 Rhoadsia altipinna: 01 > 0
 Coptobrycon bilineatus: 01 > 1
 Clade 110: 01 > 1
 Clade 184: 01 > 1
 Clade 192: 01 > 0
 Clade 107: 1 > 0
 Spintherobolus papilliferus: 0 > 1
Character 257 (5 steps)
 Root: 2
 Clade 110: 2 > 02
 Clade 107: 02 > 0
 Acinocheiron melanogramma: 0 > 1
 Clade 119: 0 > 1
 Clade 160: 0 > 02
 Clade 159: 02 > 2
 Cheiron kiliani: 0 > 1
Character 258 (3 steps)
 Root: 0
 Hyphessobrycon bifasciatus: 0 > 1
 Clade 156: 0 > 01
 Axelrodia lindeae: 01 > 1
 Amazonspinner dalmata: 01 > 1
 Clade 159: 01 > 0
Character 259 (5 steps)
 Root: 0
 Clade 110: 0 > 02

Cynopotamus kincaidi: 0 > 1
 Clade 107: 02 > 2
 Clade 156: 2 > 02
 Clade 182: 2 > 1
 Cheirodon australe: 2 > 0
 Clade 159: 02 > 0
Character 260 (1 step)
 Root: 0
 Clade 158: 0 > 01
 Clade 157: 01 > 1
Character 261 (2 steps)
 Root: 0
 Clade 120: 0 > 01
 Clade 123: 01 > 1
 Clade 128: 01 > 0
 Clade 118: 01 > 1
Character 262 (1 step)
 Root: 0
 Acinocheiron melanogramma: 0 > 1
Character 263 (4 steps)
 Root: 0
 Clade 122: 0 > 1
 Compsurini n. sp. Tingo: 0 > 1
 Clade 119: 1 > 0
 Compsurini n. sp. Leticia: 1 > 0
Character 264 (2 steps)
 Root: 0
 Compsurini n. sp. Purus: 0 > 1
 Clade 123: 0 > 1
Character 265 (1 step)
 Root: 0
 Clade 118: 0 > 1
Character 266 (1 step)
 Root: 0
 Clade 104: 0 > 01
 Clade 103: 01 > 1
Character 267 (2 steps)
 Root: 0
 Clade 103: 0 > 1
 Clade 123: 1 > 01
 Kolpotocheiron theloura: 01 > 0
Character 268 (1 step)
 Root: 0
 Clade 127: 0 > 1
Character 269 (1 step)
 Root: 0
 Macropsobrycon uruguayanae: 0 > 1
Character 270 (1 step)
 Root: 0
 Macropsobrycon uruguayanae: 0 > 1
Character 271 (2 steps)
 Root: 0
 Acinocheiron melanogramma: 0 > 1
 Clade 128: 0 > 1
Character 272 (1 step)
 Root: 0
 Clade 104: 0 > 1
Character 273 (4 steps)
 Root: 012
 Clade 137: 012 > 0
 Clade 104: 012 > 1
 Clade 123: 1 > 01
 Kolpotocheiron theloura: 01 > 0
 Holoshesthes pequirá: 012 > 2
 Clade 130: 1 > 0
Character 274 (2 steps)
 Root: 0
 Acinocheiron melanogramma: 0 > 1
 Clade 128: 0 > 1
Character 275 (2 steps)
 Root: 0
 Acinocheiron melanogramma: 0 > 1
 Clade 128: 0 > 1
Character 276 (1 step)
 Root: 0
 Clade 130: 0 > 1

Character 277 (1 step)
Root: 1

Clade 104: 1 > 0
Character 278 (1 step)

Root: 0
Clade 130: 0 > 1

Appendix IV. List of synapomorphies for each clade, and autapomorphies for each terminal taxa. Clades number correspond to the IW strict consensus cladogram (Fig. 44).

Acinocheiroidon melanogramma:

Char. 10: 1 > 0
Char. 12: 0 > 1
Char. 20: 1 > 0
Char. 55: 1 > 0
Char. 73: 0 > 1
Char. 96: 1 > 0
Char. 102: 0 > 2
Char. 104: 0 > 1
Char. 109: 0 > 1
Char. 142: 1 > 0
Char. 149: 1 > 0
Char. 154: 0 > 1
Char. 156: 0 > 1
Char. 173: 2 > 0
Char. 183: 0 > 1
Char. 207: 0 > 1
Char. 208: 0 > 1
Char. 210: 1 > 0
Char. 243: 0 > 1
Char. 253: 1 > 0
Char. 257: 0 > 1
Char. 262: 0 > 1
Char. 271: 0 > 1
Char. 274: 0 > 1
Char. 275: 0 > 1

Compsura heterura:

Char. 149: 1 > 0

Macropsobrycon uruguayanae:

Char. 8: 0 > 1
Char. 15: 1 > 2
Char. 23: 1 > 0
Char. 24: 1 > 2
Char. 25: 1 > 2
Char. 30: 1 > 0
Char. 42: 0 > 1
Char. 48: 1 > 0
Char. 50: 0 > 1
Char. 52: 0 > 2
Char. 53: 1 > 0
Char. 54: 1 > 0
Char. 58: 0 > 2
Char. 59: 0 > 1
Char. 74: 1 > 0
Char. 80: 0 > 1
Char. 81: 1 > 0
Char. 85: 0 > 1
Char. 89: 0 > 1
Char. 92: 1 > 0
Char. 99: 0 > 1
Char. 101: 0 > 1
Char. 105: 0 > 1
Char. 106: 1 > 0
Char. 112: 1 > 0
Char. 114: 0 > 1
Char. 130: 0 > 1
Char. 144: 1 > 0
Char. 189: 0 > 1
Char. 214: 0 > 1
Char. 215: 0 > 1
Char. 245: 0 > 1
Char. 250: 0 > 1

Char. 254: 0 > 1
Char. 269: 0 > 1
Char. 270: 0 > 1

Kolpotocheiroidon theloura:

Char. 228: 0 > 1

Kolpotocheiroidon figueiredoi:

Char. 110: 1 > 0
Char. 112: 1 > 0
Char. 249: 0 > 1

Compsurini n. sp. Purus:

Char. 42: 0 > 1
Char. 69: 1 > 0
Char. 71: 2 > 1
Char. 114: 0 > 1
Char. 183: 0 > 1
Char. 207: 0 > 1
Char. 214: 0 > 1
Char. 242: 0 > 1
Char. 244: 0 > 1
Char. 264: 0 > 1

Compsura n. sp. Araguaia:

No autapomorphies

Compsura n. sp. Guaporé:

Char. 12: 0 > 1

Compsurini n. sp. Napo:

Char. 23: 1 > 0
Char. 25: 1 > 2
Char. 30: 1 > 0
Char. 239: 1 > 0

Compsurini n. sp. Yurimaguas:

Char. 11: 1 > 0
Char. 51: 0 > 1
Char. 96: 1 > 2
Char. 154: 0 > 1

Compsurini n. sp. Tingo:

Char. 9: 1 > 0
Char. 10: 1 > 0
Char. 96: 1 > 2
Char. 105: 0 > 3
Char. 142: 1 > 0
Char. 154: 0 > 1
Char. 170: 0 > 1
Char. 263: 0 > 1

Compsurini n. sp. Leticia:

Char. 37: 0 > 1
Char. 42: 0 > 1
Char. 56: 0 > 1
Char. 59: 0 > 1
Char. 60: 1 > 0
Char. 62: 1 > 3
Char. 72: 0 > 1
Char. 74: 1 > 0
Char. 81: 1 > 0
Char. 105: 3 > 0
Char. 149: 1 > 0
Char. 173: 2 > 1
Char. 178: 0 > 1
Char. 263: 1 > 0

Compsurini n. sp. Cuzco:

Char. 12: 0 > 1
Char. 37: 0 > 1
Char. 71: 2 > 1

Char. 123: 0 > 1
Char. 173: 2 > 1
Char. 212: 0 > 1

Saccoderma melanostigma:

Char. 71: 2 > 1

Char. 250: 0 > 1

Saccoderma hastata:

Char. 114: 0 > 1

Odontostilbe dialeptura:

Char. 107: 1 > 0

Char. 207: 0 > 1

Char. 230: 1 > 0

Char. 231: 0 > 1

Odontostilbe mitoptera:

Char. 137: 0 > 1

Char. 148: 0 > 1

Char. 150: 0 > 1

Char. 210: 1 > 0

Char. 250: 0 > 1

Compsura gorgonae:

Char. 23: 1 > 0

Char. 110: 1 > 0

Char. 219: 0 > 1

Char. 243: 0 > 1

Cheiroidon australe:

Char. 121: 0 > 1

Char. 259: 2 > 0

Cheiroidon galusdai:

No autapomorphies

Cheiroidon ibicuihiensis:

Char. 23: 1 > 0

Char. 30: 1 > 0

Char. 175: 0 > 1

Cheiroidon interruptus:

Char. 105: 0 > 3

Cheiroidon parahybae:

Char. 8: 2 > 1

Char. 23: 1 > 0

Char. 30: 1 > 0

Char. 52: 0 > 1

Char. 80: 0 > 1

Char. 81: 1 > 0

Cheiroidon kiliani:

Char. 23: 1 > 0

Char. 24: 1 > 2

Char. 25: 1 > 2

Char. 60: 1 > 0

Char. 105: 0 > 2

Char. 257: 0 > 1

Cheiroidon pisciculus:

Char. 68: 0 > 1

Nanocheiroidon insignis:

Char. 119: 1 > 0

Char. 155: 0 > 1

Char. 171: 0 > 1

Char. 172: 0 > 1

Char. 192: 0 > 1

New Genus n. sp. c:

Char. 11: 1 > 0

Char. 44: 1 > 0

Char. 114: 1 > 0

Char. 120: 1 > 0

Char. 149: 1 > 0
 Char. 160: 1 > 0
 Char. 198: 1 > 2
 Char. 210: 1 > 0
New Genus n. sp. b:
 Char. 48: 1 > 0
 Char. 112: 1 > 0
 Char. 174: 0 > 1
 Char. 200: 0 > 1
Heterocheiroidon jacuiensis:
 No autapomorphies
Heterocheiroidon yatai:
 Char. 24: 1 > 2
 Char. 42: 0 > 1
Serrapinnus n. sp. upm:
 Char. 10: 1 > 0
 Char. 30: 0 > 1
 Char. 207: 0 > 1
 Char. 251: 0 > 2
Serrapinnus n. sp. ups:
 Char. 11: 0 > 1
 Char. 120: 0 > 1
Serrapinnus n. sp. a:
 Char. 6: 0 > 1
 Char. 12: 1 > 0
 Char. 14: 1 > 0
 Char. 20: 0 > 1
 Char. 107: 1 > 0
Serrapinnus n. sp. ac:
 Char. 42: 0 > 1
 Char. 114: 0 > 1
 Char. 175: 1 > 2
Serrapinnus calliurus:
 Char. 30: 0 > 1
Serrapinnus n. sp. d:
 Char. 30: 0 > 1
 Char. 51: 0 > 1
Serrapinnus n. sp. e:
 Char. 51: 0 > 1
 Char. 120: 0 > 1
Serrapinnus heterodon:
 Char. 15: 1 > 0
 Char. 53: 1 > 0
 Char. 62: 3 > 2
 Char. 67: 1 > 0
 Char. 69: 1 > 0
 Char. 73: 0 > 1
 Char. 96: 1 > 0
 Char. 104: 0 > 1
 Char. 107: 1 > 0
 Char. 160: 1 > 0
 Char. 210: 1 > 0
Serrapinnus kriegi:
 Char. 62: 1 > 2
 Char. 110: 1 > 0
 Char. 114: 0 > 1
 Char. 119: 1 > 0
Serrapinnus n. sp. me:
 Char. 112: 1 > 0
 Char. 252: 0 > 1
Serrapinnus microdon:
 Char. 59: 0 > 1
 Char. 80: 0 > 1
 Char. 81: 1 > 0
 Char. 114: 0 > 1
 Char. 121: 0 > 1
Serrapinnus micropterus:
 Char. 37: 0 > 1
 Char. 121: 0 > 1
 Char. 160: 1 > 0
 Char. 172: 0 > 1
Serrapinnus n. sp. mi:
 No autapomorphies
Serrapinnus notomelas:
 Char. 120: 0 > 1
 Char. 121: 0 > 1
Serrapinnus piaba:
 Char. 201: 0 > 1
Serrapinnus n. sp. t:
 Char. 30: 0 > 1
Axelrodia lindeae:
 Char. 14: 1 > 0
 Char. 21: 1 > 0
 Char. 37: 0 > 1
 Char. 40: 0 > 1
 Char. 48: 1 > 0
 Char. 55: 1 > 0
 Char. 60: 1 > 0
 Char. 61: 1 > 0
 Char. 69: 1 > 0
 Char. 83: 0 > 1
 Char. 92: 1 > 0
 Char. 94: 0 > 1
 Char. 96: 2 > 0
 Char. 97: 1 > 0
 Char. 100: 0 > 1
 Char. 101: 0 > 1
 Char. 125: 1 > 0
 Char. 166: 0 > 1
 Char. 168: 1 > 0
 Char. 232: 1 > 0
Amazonspinther dalmata:
 Char. 23: 1 > 0
 Char. 34: 0 > 1
 Char. 120: 1 > 0
 Char. 167: 0 > 1
 Char. 178: 1 > 0
 Char. 190: 1 > 0
 Char. 196: 1 > 0
 Char. 251: 0 > 1
Spintherobolus ankoseion:
 Char. 34: 0 > 1
Spintherobolus broccae:
 No autapomorphies
Spintherobolus papilliferus:
 Char. 14: 1 > 0
 Char. 67: 1 > 0
 Char. 83: 0 > 1
 Char. 116: 2 > 1
 Char. 124: 0 > 1
 Char. 157: 1 > 0
 Char. 158: 1 > 0
 Char. 159: 1 > 0
 Char. 163: 1 > 0
 Char. 169: 0 > 1
 Char. 236: 1 > 0
 Char. 237: 1 > 0
 Char. 256: 0 > 1
Megacheiroidon unicus:
 Char. 174: 0 > 1
 Char. 194: 0 > 1
Aphyocheiroidon hemigrammus:
 Char. 6: 0 > 1
 Char. 8: 0 > 2
 Char. 9: 1 > 0
 Char. 12: 1 > 0
 Char. 20: 0 > 1
 Char. 23: 1 > 0
 Char. 42: 0 > 1
 Char. 71: 2 > 1
 Char. 81: 0 > 1
 Char. 83: 0 > 1
 Char. 108: 0 > 1
 Char. 110: 1 > 0
 Char. 114: 0 > 1
 Char. 250: 1 > 0
Cheirodontops geayi:
 Char. 71: 2 > 1
 Char. 76: 0 > 1
Holoshesthes n. sp. b:
 Char. 30: 0 > 1
 Char. 48: 1 > 0
 Char. 67: 0 > 1
 Char. 73: 1 > 0
Holoshesthes n. sp. k:
 Char. 121: 1 > 0
Holoshesthes n. sp. p:
 Char. 148: 0 > 1
 Char. 153: 0 > 1
Holoshesthes pequirá:
 Char. 107: 1 > 0
 Char. 109: 0 > 1
 Char. 121: 1 > 0
 Char. 251: 0 > 2
Odontostilbe dierythra:
 Char. 112: 1 > 0
Odontostilbe ecuadorensis:
 No autapomorphies
Odontostilbe n. sp. e:
 Char. 15: 1 > 0
 Char. 39: 0 > 1
Odontostilbe euspilurus:
 Char. 39: 0 > 1
 Char. 44: 0 > 1
 Char. 149: 0 > 1
Odontostilbe fugitiva:
 Char. 73: 1 > 0
 Char. 121: 1 > 0
Odontostilbe n. sp. h:
 Char. 6: 0 > 1
 Char. 12: 1 > 0
 Char. 18: 0 > 1
 Char. 59: 0 > 1
 Char. 73: 1 > 0
 Char. 110: 1 > 0
 Char. 120: 0 > 1
 Char. 137: 1 > 0
Odontostilbe microcephala:
 Char. 23: 1 > 0
 Char. 53: 1 > 0
 Char. 55: 1 > 0
 Char. 68: 1 > 0
Odontostilbe n. sp. m:
 Char. 23: 1 > 0
 Char. 24: 1 > 0
 Char. 96: 1 > 2
Odontostilbe nareuda:
 Char. 70: 0 > 1
Odontostilbe pao:
 Char. 70: 0 > 1
 Char. 107: 0 > 1
 Char. 121: 1 > 0
 Char. 148: 0 > 1
Odontostilbe paraguayensis:
 Char. 24: 1 > 0
 Char. 135: 0 > 1
Odontostilbe n. sp. p:
 Char. 55: 1 > 0
 Char. 56: 0 > 1
 Char. 59: 0 > 1
 Char. 62: 1 > 3
 Char. 68: 1 > 0
 Char. 73: 1 > 0
 Char. 105: 3 > 0
 Char. 110: 1 > 0
 Char. 120: 0 > 1
 Char. 172: 0 > 1
Odontostilbe n. sp. b:
 Char. 38: 1 > 0
 Char. 109: 0 > 1
 Char. 114: 0 > 1
 Char. 145: 0 > 1
 Char. 251: 0 > 2
Odontostilbe parecis:
 Char. 55: 1 > 0
 Char. 56: 0 > 1
 Char. 150: 1 > 0
Odontostilbe pulchra:

Char. 96: 1 > 2
Odontostilbe splendida:
Char. 38: 1 > 0
Char. 59: 0 > 1
Char. 68: 1 > 0
Char. 120: 0 > 1
Prodontocharax alleni:
Char. 9: 1 > 0
Char. 23: 0 > 1
Char. 80: 0 > 1
Char. 83: 0 > 1
Prodontocharax melanotus:
Char. 71: 2 > 1
Char. 129: 0 > 1
Char. 130: 0 > 1
Char. 251: 0 > 3
Pseudocheirodon arnoldi:
Char. 62: 0 > 1
Char. 212: 1 > 0
Pseudocheirodon terrabae:
Char. 8: 0 > 1
Aphyocharacidium bolivianum:
Char. 7: 0 > 1
Char. 8: 0 > 1
Char. 11: 1 > 0
Char. 18: 0 > 1
Char. 40: 0 > 1
Char. 62: 3 > 2
Char. 69: 0 > 1
Char. 81: 0 > 1
Char. 95: 1 > 0
Char. 100: 0 > 1
Char. 107: 0 > 1
Char. 130: 0 > 1
Char. 149: 0 > 1
Char. 210: 1 > 0
Aphyocharax nattereri:
Char. 34: 0 > 1
Char. 35: 0 > 1
Char. 36: 0 > 1
Char. 40: 0 > 1
Char. 42: 0 > 1
Char. 94: 0 > 1
Char. 110: 1 > 0
Char. 112: 1 > 0
Char. 114: 0 > 1
Char. 130: 0 > 1
Char. 133: 1 > 0
Char. 147: 1 > 0
Char. 149: 0 > 1
Aphyodite grammica:
Char. 6: 0 > 1
Char. 7: 0 > 1
Char. 42: 0 > 1
Char. 67: 1 > 0
Char. 68: 0 > 1
Char. 75: 0 > 1
Char. 101: 0 > 1
Char. 132: 2 > 0
Char. 147: 1 > 0
Astyanax fasciatus:
Char. 12: 0 > 1
Char. 38: 0 > 1
Char. 133: 0 > 1
Astyanax laticeps:
Char. 37: 0 > 1
Bryconamericus iheringii:
Char. 59: 1 > 0
Char. 130: 0 > 1
Brycon pesu:
No autapomorphies
Bryconops caudomaculatus:
Char. 9: 0 > 1
Char. 67: 0 > 1
Char. 71: 1 > 0
Char. 73: 1 > 0
Char. 89: 0 > 1
Char. 105: 0 > 3
Char. 110: 0 > 1
Char. 212: 1 > 0
Char. 247: 0 > 1
Charax stenopterus:
Char. 6: 0 > 1
Char. 16: 0 > 1
Char. 31: 1 > 0
Char. 42: 0 > 1
Char. 54: 0 > 1
Char. 100: 0 > 1
Cheirodon stenodon:
Char. 2: 0 > 1
Char. 75: 0 > 1
Char. 77: 2 > 1
Char. 107: 0 > 1
Char. 120: 0 > 1
Char. 130: 0 > 1
Char. 156: 0 > 1
Char. 178: 0 > 1
Coptobrycon bilineatus:
Char. 1: 0 > 1
Char. 8: 0 > 2
Char. 20: 0 > 1
Char. 41: 0 > 1
Char. 42: 0 > 1
Char. 43: 0 > 1
Char. 67: 0 > 1
Char. 73: 1 > 0
Char. 80: 0 > 1
Char. 89: 0 > 1
Char. 94: 0 > 1
Char. 107: 0 > 1
Char. 112: 1 > 0
Char. 114: 0 > 1
Char. 116: 0 > 1
Char. 117: 0 > 1
Char. 120: 0 > 1
Char. 142: 0 > 1
Char. 152: 0 > 1
Char. 177: 0 > 1
Char. 211: 0 > 1
Char. 247: 0 > 1
Cyanocharax alburnus:
Char. 30: 0 > 1
Char. 73: 1 > 0
Char. 110: 0 > 1
Char. 118: 1 > 0
Char. 121: 0 > 1
Char. 133: 0 > 1
Char. 178: 0 > 1
Char. 210: 0 > 1
Cynopotamus kincaidi:
Char. 9: 1 > 0
Char. 11: 1 > 0
Char. 23: 1 > 0
Char. 25: 1 > 0
Char. 35: 0 > 1
Char. 36: 0 > 1
Char. 40: 0 > 1
Char. 50: 0 > 1
Char. 94: 0 > 1
Char. 115: 1 > 0
Char. 129: 0 > 1
Char. 130: 0 > 1
Char. 133: 1 > 2
Char. 147: 1 > 0
Char. 210: 1 > 0
Char. 212: 0 > 1
Char. 259: 0 > 1
Hemibrycon polyodon:
Char. 213: 0 > 1
Hyphessobrycon bifasciatus:
Char. 2: 0 > 1
Char. 6: 0 > 1
Char. 21: 0 > 1
Char. 25: 0 > 1
Char. 44: 0 > 1
Char. 59: 1 > 0
Char. 67: 0 > 1
Char. 73: 1 > 0
Char. 110: 0 > 1
Char. 120: 0 > 1
Char. 132: 2 > 0
Char. 147: 0 > 1
Char. 210: 0 > 1
Char. 212: 1 > 0
Char. 256: 0 > 1
Char. 258: 0 > 1
Leptobrycon jatuaranae:
Char. 2: 0 > 1
Char. 68: 0 > 1
Char. 101: 0 > 1
Char. 152: 0 > 1
Macropsobrycon xinguensis:
Char. 9: 1 > 0
Char. 21: 1 > 0
Char. 25: 1 > 0
Char. 64: 0 > 1
Char. 79: 1 > 0
Char. 80: 0 > 1
Char. 84: 1 > 0
Microchemobrycon elongatus:
Char. 15: 0 > 1
Char. 55: 0 > 1
Char. 59: 1 > 0
Char. 75: 0 > 1
Char. 85: 0 > 1
Char. 101: 0 > 1
Char. 126: 0 > 1
Char. 132: 2 > 0
Char. 133: 1 > 0
Paracheirodon axelrodi:
Char. 18: 0 > 1
Char. 21: 1 > 0
Char. 23: 1 > 0
Char. 41: 0 > 1
Char. 47: 0 > 1
Char. 52: 0 > 1
Char. 53: 0 > 1
Char. 78: 1 > 0
Char. 121: 0 > 1
Char. 125: 1 > 0
Char. 139: 0 > 2
Char. 145: 0 > 1
Char. 169: 0 > 1
Parecbasis cyclolepis:
Char. 9: 1 > 0
Char. 10: 1 > 0
Char. 11: 1 > 0
Char. 18: 0 > 1
Char. 53: 0 > 1
Char. 54: 0 > 1
Char. 69: 0 > 1
Char. 95: 1 > 0
Char. 106: 0 > 1
Char. 110: 1 > 0
Char. 114: 0 > 1
Char. 121: 0 > 1
Char. 129: 0 > 1
Char. 210: 1 > 0
Char. 212: 0 > 1
Prionobrama paraguayensis:
Char. 56: 0 > 1
Char. 67: 0 > 1
Char. 71: 0 > 1
Char. 117: 0 > 1
Char. 142: 0 > 1
Char. 143: 0 > 1
Char. 150: 0 > 1
Char. 153: 0 > 1

Char. 154: 0 > 1
Char. 172: 0 > 1

Probolodus heterostomus:

Char. 96: 0 > 2
Char. 114: 0 > 1
Char. 118: 1 > 0
Char. 121: 0 > 1

Rhoadsia altipinna:

Char. 7: 0 > 2
Char. 9: 1 > 0
Char. 52: 0 > 1
Char. 53: 0 > 1
Char. 54: 0 > 1
Char. 86: 0 > 1
Char. 87: 0 > 1
Char. 96: 0 > 2
Char. 102: 0 > 2
Char. 103: 0 > 2
Char. 104: 0 > 2
Char. 115: 1 > 0
Char. 118: 1 > 0
Char. 130: 0 > 1
Char. 133: 1 > 0
Char. 136: 0 > 1
Char. 137: 0 > 1
Char. 144: 1 > 0
Char. 150: 0 > 1
Char. 153: 0 > 1
Char. 155: 0 > 1

Clade 102:

Char. 9: 1 > 0
Char. 37: 0 > 1
Char. 56: 0 > 1
Char. 181: 0 > 1
Char. 231: 0 > 1
Char. 249: 0 > 1

Clade 103:

Char. 180: 0 > 1
Char. 184: 0 > 1
Char. 267: 0 > 1

Clade 104:

Char. 20: 0 > 1
Char. 173: 0 > 2
Char. 174: 0 > 1
Char. 253: 0 > 1
Char. 272: 0 > 1
Char. 277: 1 > 0

Clade 105:

Char. 53: 0 > 1
Char. 168: 0 > 1

Clade 106:

Char. 3: 0 > 1
Char. 54: 0 > 1
Char. 60: 0 > 1
Char. 62: 3 > 1
Char. 74: 0 > 1
Char. 81: 0 > 1
Char. 90: 0 > 1
Char. 92: 0 > 1
Char. 119: 0 > 1

Clade 107:

Char. 15: 0 > 1
Char. 55: 0 > 1
Char. 98: 1 > 0
Char. 233: 0 > 1
Char. 235: 1 > 0
Char. 256: 1 > 0

Clade 108:

Char. 44: 0 > 1
Char. 59: 1 > 0
Char. 69: 0 > 1
Char. 79: 1 > 0
Char. 83: 1 > 0
Char. 105: 12 > 0
Char. 106: 0 > 1

Clade 109:

Char. 5: 0 > 1
Char. 116: 0 > 1

Clade 110:

Char. 14: 0 > 1
Char. 16: 0 > 1
Char. 62: 0 > 3
Char. 67: 0 > 1

Clade 111:

Char. 25: 0 > 1
Char. 77: 1 > 2
Char. 79: 0 > 1
Char. 83: 0 > 1

Clade 112:

Char. 97: 0 > 1
Char. 110: 0 > 1
Char. 210: 0 > 1

Clade 113:

Char. 9: 0 > 1
Char. 71: 1 > 0
Char. 84: 0 > 1
Char. 133: 0 > 1
Char. 212: 1 > 0

Clade 114:

Char. 144: 0 > 1
Char. 147: 0 > 1

Clade 115:

Char. 2: 1 > 0
Char. 7: 1 > 0
Char. 118: 0 > 1
Char. 125: 0 > 1
Char. 132: 0 > 2
Char. 174: 0 > 1

Clade 116:

No synapomorphies

Clade 117:

Char. 11: 1 > 0

Clade 118:

Char. 30: 1 > 0
Char. 142: 1 > 0
Char. 222: 0 > 1
Char. 239: 1 > 0
Char. 249: 0 > 1
Char. 250: 0 > 1
Char. 265: 0 > 1

Clade 119:

Char. 154: 0 > 1
Char. 214: 0 > 1
Char. 215: 0 > 1
Char. 244: 0 > 1
Char. 257: 0 > 1
Char. 263: 1 > 0

Clade 120:

Char. 20: 1 > 0

Clade 121:

Char. 11: 0 > 1
Char. 186: 1 > 0
Char. 226: 0 > 1
Char. 230: 0 > 1

Clade 122:

Char. 52: 0 > 1
Char. 105: 0 > 3
Char. 170: 0 > 2
Char. 239: 0 > 1
Char. 263: 0 > 1

Clade 123:

Char. 9: 1 > 0
Char. 10: 1 > 0
Char. 25: 1 > 2
Char. 42: 0 > 1
Char. 45: 0 > 1
Char. 71: 2 > 1
Char. 107: 1 > 0
Char. 114: 0 > 1
Char. 227: 0 > 1
Char. 229: 0 > 1
Char. 231: 0 > 1

Char. 240: 0 > 1
Char. 248: 0 > 1
Char. 254: 0 > 1
Char. 264: 0 > 1

Clade 124:

Char. 188: 0 > 1

Clade 125:

Char. 185: 0 > 1
Char. 240: 0 > 1

Clade 126:

Char. 51: 0 > 1

Clade 127:

Char. 15: 1 > 0
Char. 59: 0 > 1
Char. 73: 0 > 1
Char. 76: 0 > 1
Char. 96: 1 > 0
Char. 103: 0 > 2
Char. 104: 0 > 2
Char. 182: 0 > 1
Char. 210: 1 > 0
Char. 212: 0 > 2
Char. 217: 0 > 1
Char. 241: 0 > 1
Char. 268: 0 > 1

Clade 128:

Char. 52: 1 > 0
Char. 53: 1 > 0
Char. 218: 0 > 1
Char. 271: 0 > 1
Char. 274: 0 > 1
Char. 275: 0 > 1

Clade 129:

Char. 216: 0 > 1
Char. 244: 1 > 0

Clade 130:

Char. 220: 1 > 0
Char. 226: 1 > 0
Char. 240: 0 > 1
Char. 273: 1 > 0
Char. 276: 0 > 1
Char. 278: 0 > 1

Clade 131:

Char. 106: 1 > 0

Clade 132:

Char. 5: 1 > 0
Char. 26: 0 > 1

Clade 133:

Char. 48: 1 > 0
Char. 68: 1 > 0
Char. 112: 1 > 0

Clade 134:

Char. 42: 0 > 1
Char. 238: 1 > 0

Clade 135:

Char. 22: 0 > 1
Char. 71: 2 > 1
Char. 129: 0 > 1
Char. 130: 0 > 1
Char. 151: 0 > 1

Clade 136:

Char. 68: 0 > 1
Char. 191: 0 > 1
Char. 194: 0 > 1
Char. 197: 0 > 1
Char. 200: 0 > 1

Clade 137:

Char. 114: 0 > 1
Char. 120: 0 > 1
Char. 178: 0 > 1
Char. 193: 0 > 1
Char. 195: 0 > 1
Char. 199: 0 > 1

Clade 138:

Char. 62: 2 > 3
Char. 80: 0 > 1

Char. 81: 1 > 0
Char. 152: 0 > 1
Char. 209: 0 > 1
Clade 139:
Char. 105: 3 > 4
Char. 191: 0 > 1
Char. 194: 0 > 1
Char. 197: 0 > 1
Char. 201: 0 > 1
Clade 140:
Char. 157: 0 > 1
Char. 159: 0 > 1
Char. 175: 0 > 1
Char. 196: 0 > 1
Char. 237: 0 > 1
Clade 141:
Char. 52: 0 > 1
Char. 96: 1 > 2
Char. 105: 0 > 3
Char. 158: 0 > 1
Char. 163: 0 > 1
Char. 165: 0 > 1
Char. 176: 0 > 1
Clade 142:
Char. 15: 1 > 2
Char. 19: 0 > 1
Char. 59: 0 > 1
Char. 72: 0 > 1
Char. 129: 0 > 1
Char. 130: 0 > 1
Char. 149: 1 > 0
Char. 168: 1 > 0
Char. 193: 1 > 2
Char. 210: 1 > 0
Clade 143:
Char. 52: 1 > 0
Char. 55: 1 > 0
Char. 56: 0 > 1
Char. 62: 1 > 3
Char. 105: 3 > 0
Char. 250: 0 > 1
Clade 144:
Char. 11: 1 > 0
Char. 44: 1 > 0
Char. 96: 2 > 1
Char. 114: 1 > 0
Char. 174: 0 > 1
Clade 145:
Char. 179: 0 > 1
Clade 146:
Char. 42: 0 > 1
Char. 68: 1 > 0
Clade 147:
Char. 44: 0 > 1
Clade 148:
Char. 164: 0 > 1
Clade 149:
Char. 107: 1 > 0
Char. 175: 1 > 2
Clade 150:
Char. 120: 1 > 0
Char. 207: 0 > 1
Clade 151:
Char. 44: 0 > 1
Char. 105: 3 > 0
Char. 172: 0 > 1
Char. 174: 1 > 0
Char. 196: 1 > 2
Clade 152:
Char. 198: 1 > 2
Char. 203: 0 > 1
Char. 206: 0 > 1
Clade 153:
Char. 174: 1 > 0
Char. 251: 0 > 1
Clade 154:

Char. 103: 0 > 1
Char. 120: 1 > 0
Clade 155:
Char. 62: 1 > 2
Char. 137: 0 > 1
Char. 201: 0 > 1
Clade 156:
Char. 5: 1 > 0
Char. 8: 0 > 2
Char. 22: 0 > 1
Char. 28: 0 > 1
Char. 49: 0 > 1
Char. 71: 2 > 0
Char. 74: 1 > 0
Char. 79: 0 > 1
Char. 81: 1 > 0
Char. 85: 0 > 1
Char. 90: 1 > 0
Char. 91: 0 > 1
Char. 98: 0 > 1
Char. 106: 1 > 0
Char. 110: 1 > 0
Char. 116: 1 > 2
Char. 118: 1 > 0
Char. 126: 0 > 1
Char. 235: 0 > 1
Char. 238: 1 > 0
Clade 157:
Char. 59: 0 > 1
Char. 146: 0 > 1
Char. 211: 0 > 1
Clade 158:
Char. 1: 0 > 1
Char. 164: 0 > 1
Char. 200: 0 > 1
Char. 201: 0 > 1
Char. 205: 0 > 1
Clade 159:
Char. 19: 0 > 1
Char. 162: 0 > 1
Char. 246: 0 > 1
Char. 255: 0 > 1
Clade 160:
Char. 43: 0 > 1
Char. 122: 0 > 1
Char. 139: 0 > 1
Char. 140: 0 > 1
Char. 177: 0 > 1
Clade 161:
Char. 44: 0 > 1
Char. 137: 1 > 0
Char. 138: 0 > 1
Char. 150: 1 > 0
Clade 162:
Char. 62: 2 > 3
Clade 163:
Char. 81: 1 > 0
Clade 164:
Char. 30: 1 > 0
Char. 88: 0 > 1
Clade 165:
Char. 52: 1 > 0
Char. 53: 1 > 0
Char. 55: 1 > 0
Char. 56: 0 > 1
Char. 62: 1 > 2
Char. 75: 0 > 1
Char. 96: 1 > 0
Char. 102: 0 > 2
Char. 103: 0 > 1
Char. 104: 0 > 1
Char. 105: 3 > 0
Char. 250: 0 > 1
Clade 166:
Char. 59: 0 > 1
Char. 67: 1 > 0

Char. 69: 1 > 0
Clade 167:
Char. 23: 0 > 1
Clade 168:
Char. 73: 0 > 1
Char. 107: 0 > 1
Clade 169:
Char. 149: 1 > 0
Clade 170:
Char. 52: 0 > 1
Char. 53: 0 > 1
Char. 68: 0 > 1
Clade 171:
Char. 12: 0 > 1
Char. 23: 1 > 0
Char. 44: 1 > 0
Char. 105: 0 > 3
Char. 210: 1 > 0
Char. 212: 0 > 1
Clade 172:
Char. 121: 0 > 1
Char. 137: 0 > 1
Char. 150: 0 > 1
Clade 173:
Char. 53: 1 > 0
Char. 109: 0 > 1
Char. 250: 0 > 1
Clade 174:
Char. 52: 1 > 0
Clade 175:
Char. 13: 0 > 1
Clade 176:
Char. 10: 1 > 0
Char. 58: 0 > 1
Char. 62: 1 > 0
Char. 137: 1 > 0
Clade 177:
Char. 64: 0 > 1
Clade 178:
Char. 8: 0 > 1
Char. 67: 1 > 0
Char. 129: 0 > 1
Char. 130: 0 > 1
Clade 179:
Char. 121: 1 > 0
Clade 180:
Char. 32: 0 > 2
Char. 33: 0 > 1
Char. 50: 0 > 2
Char. 64: 1 > 0
Char. 81: 1 > 0
Char. 100: 0 > 1
Char. 106: 1 > 0
Char. 107: 0 > 1
Char. 112: 1 > 0
Char. 132: 2 > 1
Clade 181:
Char. 19: 0 > 1
Char. 30: 1 > 0
Char. 51: 0 > 1
Char. 66: 0 > 1
Char. 73: 0 > 1
Char. 96: 1 > 2
Clade 182:
Char. 17: 1 > 0
Char. 54: 1 > 2
Char. 57: 0 > 1
Char. 70: 0 > 1
Char. 86: 0 > 1
Char. 87: 0 > 1
Char. 102: 0 > 1
Char. 103: 0 > 3
Char. 104: 0 > 3
Char. 150: 1 > 0
Char. 174: 0 > 1
Char. 259: 2 > 1

Clade 183:
Char. 9: 1 > 0
Char. 23: 1 > 2
Char. 110: 1 > 0
Char. 145: 0 > 2
Char. 233: 0 > 2
Clade 184:
Char. 2: 0 > 1
Char. 19: 0 > 1
Char. 68: 0 > 1
Char. 136: 0 > 1
Clade 185:
Char. 91: 0 > 1
Char. 121: 0 > 1
Char. 174: 1 > 0
Clade 186:
Char. 3: 0 > 1
Char. 15: 0 > 1
Char. 20: 0 > 1
Char. 55: 0 > 1
Char. 130: 0 > 1
Clade 187:

Char. 58: 0 > 2
Clade 188:
Char. 30: 0 > 1
Char. 61: 0 > 1
Clade 189:
Char. 8: 0 > 2
Char. 62: 0 > 3
Char. 69: 0 > 1
Char. 114: 0 > 1
Char. 119: 0 > 1
Clade 190:
Char. 44: 0 > 1
Char. 61: 0 > 1
Char. 69: 0 > 1
Char. 107: 0 > 1
Clade 191:
Char. 120: 0 > 1
Char. 136: 0 > 1
Clade 192:
Char. 7: 0 > 1
Char. 8: 0 > 2
Char. 24: 1 > 2

Char. 75: 0 > 1
Char. 78: 1 > 0
Char. 85: 0 > 1
Char. 118: 1 > 0
Char. 125: 1 > 0
Char. 139: 0 > 2
Clade 193:
Char. 4: 1 > 0
Char. 18: 0 > 1
Char. 69: 0 > 1
Char. 92: 0 > 1
Char. 106: 0 > 1
Char. 147: 1 > 0
Char. 169: 0 > 1
Clade 194:
Char. 4: 1 > 0
Char. 14: 1 > 0
Char. 50: 0 > 1
Char. 98: 1 > 0
Char. 120: 0 > 1
Char. 133: 1 > 2

CAPÍTULO II

Revision of the genus *Compsura* Eigenmann, 1915 (Characidae: Cheirodontinae: Compsurini), with description of two new species from the Amazon basin, Brazil

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Abstract

The genus *Compsura* is redefined based on eleven synapomorphies. Three species are recognized, including the type species redescribed herein, and two new species, from the rio Guaporé and rio Araguaia basins. *Compsura heterura* is readily diagnosed from the other species by the presence of a conspicuous dark spot between the distal portion of the first unbranched dorsal-fin ray and second unbranched dorsal-fin rays, and the lanceolate-shaped spot in the caudal peduncle not reaching the dorsal and ventral edge of the caudal peduncle. *Compsura* Guaporé n. sp. is diagnosed from the other species of the genus by the higher number of branched anal-fin rays (19-22, mean = 20.2; n = 50), and *Compsura* Araguaia n. sp. is distinguished by the lower number of branched anal-fin rays (16-19, mean = 18.1; n = 20) and absence of conspicuous spot in the dorsal fin. The taxonomic status of “*Compsura*” *gorgonae* is also discussed, and it is not considered a representative of *Compsura*.

Resumo

O gênero *Compsura* é redefinido com base em onze sinapomorfias. Três espécies são reconhecidas, incluindo a espécie-tipo que é aqui redescrita, e duas espécies novas, das bacias do rio Guaporé e rio Araguaia. *Compsura heterura* é prontamente diagnosticada das outras espécies pela presença de uma mancha escura conspícua entre a porção distal do

primeiro raio não ramificado da nadadeira dorsal e o segundo raio não ramificado, e a mancha em formato de lança no pedúnculo caudal não alcançando os limites dorsal e ventral do pedúnculo. *Compsura* Guaporé n. sp. difere pelo elevado número de raios ramificados na nadadeira anal (19-22, média = 20.2; n = 50), e *Compsura* Araguaia n. sp. é distinguível pelo reduzido número de raios ramificados na nadadeira anal (16-19, média = 18.1; n = 20) e ausência da mancha conspícua na nadadeira dorsal. O status taxonômico de “*Compsura*” *gorgonae* também é discutido, e a espécie não é considerada um representante de *Compsura*.

Key words: Systematics, Taxonomy, Neotropical region, Caudal organ.

Introduction

Compsura Eigenmann is a characid genus recognized as a member of the monophyletic Cheirodontinae (Malabarba, 1998; Malabarba, 2003; Mirande, 2009; Javonillo *et al.*, 2010). It was described by Eigenmann (1915) in a revisionary study of the cheirodontines, from specimens collected by Haseman in rio Itapicuru (Municipality of Queimadas) and rio São Francisco (Municipality of Barreiras) basins. Eigenmann diagnosed the genus and its type species, *Compsura heterura*, from *Cheirodon* Girard, which also have an incompletely pored lateral line, by having a pigmented dorsal-fin - black upper half of the first dorsal membrane together with black tip of the dorsal - and by the presence of large scales in the caudal fin of males, extending along the base of the middle caudal-fin rays. Eigenmann (1915: 5, 10) described the modified caudal scales in *Compsura* and *Odontostilbe hastata* Eigenmann (*Saccoderma hastata*) as minor deviations of the Cheirodontinae generalized type, remarking their resemblance to the Glandulocaudinae (part of Stevardiinae at present). Regardless these similarities, Eigenmann (1915: 13, 16) hypothesized a close relationship of *Compsura* to *Cheirodon* and *Mixobrycon* Eigenmann, since they share an incomplete lateral line and teeth with five or more cusps.

The genus remained monotypic until Meek & Hildebrand (1916) added *Cheirodon gorgonae* Evermann & Goldsborough, a cheirodontine species occurring in Northwestern Colombia (río Atrato basin) through Panamá to South of Costa Rica, due to the presence of

large scales in the lower caudal-fin lobe. Despite the presence of the large caudal-fin scales on males, Meek & Hildebrand (1916: 273) also diagnosed the genus *Compsura* from *Cheirodon* by the non-projecting interhaemal spines (ventral procurvent caudal-fin rays) in the caudal peduncle.

The similarity between *Compsura* and *Cheirodon* was also briefly discussed by Géry (1960: 5) when describing *Cheirodon axelrodi*, distinguishing the genera only by the presence of modified caudal-fin scales in *Compsura*. Géry (1965: 14) also mentioned the sexual dimorphism of *Compsura* in the description and differential diagnosis of his new genus *Brittanichthys*, which although presents sexual dimorphism in the caudal fin, also has conical teeth instead of the “*Cheirodon*-like” teeth of *Compsura*. The genus was posteriorly re-diagnosed by López (1972: 103), in a morphological and geographical review of the Cheirodontinae from Panamá and Costa Rica, raising the question and necessity to assess if *Compsura heterura* and *C. gorgonae* would not be the same species. In an opposite way, Fink & Weitzman (1974: 4) raised uncertainty about the congeneric status of both the species considering the wide geographical separation between them, as well as the labile characters used at that moment to diagnose small characid genera. According to the authors, the characters used to define *Compsura* were more or less random among the characids, and even the modified caudal-fin scales could be an independent appearance, once they were also found in the “glandulocaudins”, and on the new species readily described in that work, *Cheirodon dialepturus* Fink & Weitzman and *Cheirodon mitopterus* Fink & Weitzman. Fink & Weitzman (1974: 4) also compared the modified caudal-fin scales from both species, and concluded that they differed in number and arrangement. Due to the inconsistency in distinguishing *Compsura* from *Cheirodon* by different caudal-fin scales arrangement, and once the species of *Compsura* present different arrangements among themselves, Fink & Weitzman considered their species as members of *Cheirodon*, and both genera as synonyms.

In the compilation of the “characoid” fishes of the world, Géry (1977: 574) considered *Compsura* as a valid genus of his “strict sense Cheirodontinae”, although agreeing with Fink & Weitzman, that *C. gorgonae* is “scarcely separable from *Cheirodon* in the generic level”.

The monophyly of the Cheirodontinae was cladistically evaluated by Malabarba (1998), with the definition of its major lineages. In that analysis, the *Compsura* species were grouped in a monophyletic clade with the genera *Acinocheirodon* Malabarba & Weitzman (as N. gen. & sp. B in Malabarba, 1998), *Kolpotocheirodon* Malabarba & Weitzman (as N. gen. & sp. A in Malabarba, 1998), *Macropsobrycon* Eigenmann, *Saccoderma* Schultz, and the central-american species “*Odontostilbe*” *dialeptura* (Fink & Weitzman) and “*O.*” *mitoptera* (Fink & Weitzman), named tribe Compsurini, comprising the inseminating cheirodontines defined by Burns *et al.* (1997). However, the relationships among the compsurin representatives were not established in that analysis, bringing no further resolution to the relationships between the *Compsura heterura* and *C. gorgonae* (Malabarba, 1998, 2003). Subsequent works describing some compsurin species also quote the caudal-fin modified scales of the *Compsura* species (Malabarba & Weitzman, 1999: 428; Malabarba & Weitzman, 2000: 281) hypothesizing a possible relationship with the genus *Saccoderma*, which also present a pouch-like structure formed by modified caudal-fin scales.

The genus was listed as a Cheirodontinae by Mirande (2009, 2010) in his phylogenetic analysis of the Characidae, although none of its species was included in the analysis; and by Javonillo *et al.* (2010) in the molecular-based phylogeny of the major lineages of the Characidae, but no evidence of its relationship with the remaining Compsurini was evaluated.

As part of a revisionary project of the compsurin species, the examination of museum collections revealed that the geographical range of *Compsura heterura* is much wider than previously thought, as well as the existence of two new species close-related to *C. heterura*. Herein we redefine the genus *Compsura*, based on eleven synapomorphies, redescribe the type species updating its geographic distribution, and assign two new species to the genus. The taxonomic status of “*Compsura*” *gorgonae* is also commented.

Material and Methods

Counts and measurements were taken according to Fink & Weitzman (1974), as possible on the left side of the specimens. Measures were taken point-to-point straight-line with a 0.01

precision caliper. The head length measure is defined as the distance between the tip of the snout and the posterior margin of subopercle (Bührnheim & Malabarba, 2006). Total vertebrae number includes the four vertebrae of the Weberian apparatus, and the terminal “half centrum” (Malabarba & Weitzman, 1999). The gill rakers were counted from the first branchial arch, and the gill raker in the junction of the ceratobranchial and the epibranchial was referred to the epibranchial count. The counts of vertebrae, supraneurals, teeth, and gill rakers were based on cleared and stained (c&s) specimens following Taylor & van Dyke (1985) protocol. The counts referred to the holotype are followed by an asterisk in the description. Drawings of the jaws, anal fin, caudal fin, and scales were prepared in a stereomicroscope with camera lucida.

The following abbreviations are given to identify the longitudinal series of scales in the lateral region of the fish body: LL - lateral line series of scales; LD1 - longitudinal series of scales above LL; LD2 - longitudinal series of scales above LD1; LD3 - longitudinal series of scales above LD2; LV1 - longitudinal series of scales below LL; and LV2 - longitudinal series of scales below LV1.

The sex identification of specimens was based on Gonçalves *et al.* (2005) and Bührnheim & Malabarba (2006), where males and females are recognized by dissection, or by the presence of sexual dimorphism in specimens with similar size in the same sample. Specimens smaller than the smallest specimen showing sexual dimorphism in each lot are termed as unsexed, as well as specimens belonging to lots where sexual dimorphism is absent.

Material from the following institutions were analyzed in this study: ANSP - Academy of Natural Sciences of Philadelphia, Philadelphia, USA; CAS - California Academy of Sciences, San Francisco, USA; FMNH - Field Museum of Natural History, Chicago, USA; MCP - Museu de Ciências e Tecnologia, Porto Alegre, Brazil; MNRJ - Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil; MZUSP - Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; SU - Stanford University, Palo Alto, USA; UFRGS - Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; UFRJ - Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; and USNM - National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

Abbreviations given along with the number of specimens are the following: m - morphometric and meristic.

The synonymic list is based on an extensive search in the literature. Diagnoses given in the text are based on the phylogenetic analysis of the Compsurini by Jerep & Malabarba (in manuscript, Chapter I).

Results

Compsura Eigenmann, 1915

Compsura Eigenmann, 1915: 5 [comparison with *Odontostilbe hastata* and Glandulocaudinae]; 10 [relationship with *Odontostilbe hastata* and Glandulocaudinae]; 13 [relationship with Cheirodontinae, misspelled *Compsoura*], 16 [key to Cheirodontinae genera], 60 [diagnosis; type species by original designation and monotypy: *Compsura heterura* Eigenmann, 1915]. -Meek & Hildebrand, 1916: 273 [description; inclusion of *Cheirodon gorgonae* in *Compsura*]. -Eigenmann, 1917:37 [chronological list of generic names, misspelled *Compsoura*]. -Géry, 1960: 5, 7 [comparison with *Cheirodon*]. -Géry, 1965: 14 [comparison with *Brittanichthys*]. -López, 1972: 93-97 [distribution; historical systematics]; 103 [key to some Cheirodontinae genera; diagnosis]. -Géry, 1977: 550 [valid as *Compsura* in key to Cheirodontinae strict sense]; 574 [comparison to *Cheirodon* and *Saccoderma*]. -Malabarba, 1998: 199, 216 [phylogenetic diagnosis and relationships to cheirodontine genera; included in the new tribe Compsurini]. -Malabarba & Weitzman, 1999: 428 [comparison with *Saccoderma*]. -Malabarba & Weitzman, 2000: 270 [relationship with integrants of Compsurini]; 280 [caudal organ comparison with *Saccoderma*]. -Malabarba, 2003: 216 [listed in Cheirodontinae]. -Malabarba, Lima & Weitzman, 2004: 325 [dorsal-fin spot comparison]. -Mirande, 2009: 8 [listed in Cheirodontinae]. -Javonillo *et al.*, 2010: 505-507 [in the relationship cladogram of Characidae]. *Cheirodon*. -Fink & Weitzman, 1974: 4-5 [*Compsura* as junior synonym of *Cheirodon*].

Diagnosis. *Compsura* is diagnosed from all characid species by the presence of cheirodontine synapomorphies, and from all cheirodontine genera by the following apomorphies (Jerep & Malabarba, in manuscript): anteromedial process of the lateral ethmoid robust [Ch. 30: 0]; postcleithrum 1 round and expanded posteriorly [Ch. 142: 0]; last modified pouch-scale from the first longitudinal line below lateral line, with dorsoposterior margin extended posteriorly [Ch. 222: 1]; abdomen slightly concave ventrally on mature males [Ch. 239: 0]; conspicuous small spot on the anterior portion of the dorsal fin [Ch. 249: 1]; scattered melanophores concentrated on the distal portion of the dorsal fin [Ch. 250: 1]; knob-like hypertrophied tissue anterior to the anal opening on mature males [Ch. 265: 1]; anteromedial process of the lateral ethmoid robust [Ch. 30: 0]; toothless portion of the maxilla with approximately the same length of the tooth bearing portion [Ch. 62: 1]; hyomandibular without posterodorsal projection [Ch. 112: 0]; and opening of the caudal-fin pouch scale over the 13th to 19th principal caudal-fin rays [Ch. 225: 1].

***Compsura heterura* Eigenmann, 1915**

Figs. 1-5

Compsura heterura Eigenmann, 1915: 6 [discussion of mouth size]; 9 [illustration of teeth]; 12 [distribution]; 60 [type species by original designation and monotypy]; 61 [original description; dentition figured; caudal scales figure; head figure; type locality Queimadas, Bahia, Brazil, rio Itapicuru basin, and Barreiras, Minas Gerais, Brazil, rio São Francisco basin; dentition, head and tail illustration]; plate X [type illustration]. - Meek & Hildebrand, 1916: 273 [cited as type species of *Compsura*]. -Henn, 1928: 58 [type material listed from Carnegie Museum]. -Böhlke, 1953: 23 [type material listed from the Natural History Museum of Stanford University]. -López, 1972: 97 [relationship to *Compsura gorgonae*]. -Géry, 1977: 575 [listed as strict sense Cheirodontinae]. -Ibarra & Stewart, 1987: 27 [type material listed from Field Museum of Natural History]. -Rosa & Menezes, 1996: 654 [conservation status: unknown]. -Burns, 1997 [listed as inseminating species]. -Malabarba, 1998 [included in the new tribe Compsurini]. -Malabarba & Weitzman, 1999: 416 [comparison to

Acinocheirodon melanogramma]. -Malabarba & Weitzman, 2000: 280 [comparison to *Kolpotocheirodon theloura*]. -Malabarba, 2003: 217 [listed in Cheirodontinae].

Malabarba *et al.* 2004: 324 [comparison to *Kolpotocheirodon figueiredoi*]. -Malabarba, 2007: 37 [listed in Cheirodontinae]. -Dias & Fialho, 2009 [feeding biology]. -Javonillo *et al.* 2010: [listed in analyzed material]. -Azevedo *et al.* 2010 [comparison with reproductive biology of *Macropsobrycon uruguayanae*]. -Oliveira *et al.* 2010 [reproductive period, fecundity, and histology of gonads].

Cheirodon heterura (Eigenmann, 1915) -Fink & Weitzman, 1974: 4, 5 [transferred to *Cheirodon*]; 18 [fig.11 illustration of caudal scales].

Diagnosis. *Compsura heterura* readily differs from its congeners by two traits from its color pattern, the presence of a conspicuous dark spot between the distal portion of the first unbranched dorsal-fin ray and second unbranched dorsal-fin rays (*vs.* absence of conspicuous dark spot in the dorsal fin); and the lanceolate-shaped spot in the caudal peduncle not reaching the dorsal and ventral edges of the caudal peduncle (*vs.* caudal spot reaching the dorsal and ventral edges of the caudal peduncle). Furthermore, *C. heterura* presents the last three scales from the lateral line series modified in shape and size involved in the caudal organ structure, while on the other species only the last two scales are modified. Moreover, *C. heterura* can be distinguished from *C. Guaporé* n. sp. by the lower number of branched anal-fin rays (15-20, mean = 17.4; n = 207 *vs.* 19-22, mean = 20; n = 50).

Description. Morphometrics given in Table 1. Body slightly elongate and compressed, deepest at dorsal-fin origin. Dorsal profile convex from snout tip to dorsal-fin origin, straight or slightly convex from that point to end of dorsal-fin base, straight or slightly convex from end of dorsal-fin base to adipose-fin origin. Dorsal and ventral caudal-peduncle profile slightly concave. Ventral profile convex from dentary anterior end to pelvic-fin insertion, straight to deeply concave (on mature males) until anal-fin origin, straight to slightly convex on anal-fin base. Snout short, mouth terminal, between horizontal lines projected through pupil ventral border and orbit ventral edge.

Premaxilla with 3(1) to 5(2) teeth bearing 7(2) to 9(1) cusps, aligned and similar in size. Maxilla short, not reaching vertical line through orbit anterior edge, bearing 2*(3) heptacuspoid teeth, rarely third distal conical tooth. Dentary with 5(3) aligned heptacuspoid teeth similar in size, followed by teeth decreasing in size posteriorly, 1(2) pentacuspoid tooth, 1(3) tricuspoid tooth, 1(1) conical tooth (Fig. 2).

Dorsal-fin origin slightly posterior to vertical through pelvic-fin origin, on middle of body. Dorsal-fin rays ii, 7(1), 8(8), 9*(252). Adipose-fin origin at vertical line through third to fourth last anal-fin ray insertion. Anal-fin origin slightly posterior to last dorsal-fin ray insertion; anterior rays longer than posterior ones; distal profile deep concave on females, slightly concave to straight on mature males. Anal-fin rays iii*(256), iv(5), 15*(2), 16(35), 17(121), 18(87), 19(12), 20(4); last unbranched until seventeenth branched anal-fin ray of mature or maturing males bearing small and retrorse hooks, often associated to hypertrophied whitish tissue (Fig. 3). Hooks placed from middle length of anal-fin rays, attached at posterior margin, usually posterior branch of branched portion, bent over lateral surface, and directed anteriorly to anal-fin frontal margin; larger on most anterior and most posterior anal-fin rays. One, rarely two, hooks per anal-fin ray segment. Pectoral-fin rays i, 9*(83), 10(145), 11(30); longest rays surpassing pelvic-fin insertion. Pelvic-fin insertion anterior to vertical line passing through dorsal-fin origin. Pelvic-fin rays i, 7*(256), 8(4); all of them bearing 1-3 unilateral ventromedial antrorse hooks per ray segment on mature males. Caudal fin with 17(1), 18(6), 19*(244), 20(3) principal rays; 10(1), 11(2) dorsal procurrent caudal-fin rays; 9(1), 10(3) ventral procurrent caudal-fin rays.

Lateral line series 30(1), 31(13), 32(60), 33*(107), 34(62), 35(16), 36(2) scales; 6*(8), 7(10), 8(30), 9(49), 10(60), 11(44), 12(28), 13(16), 14(11), 15(2), 16(1) perforated scales. Scale rows between dorsal-fin insertion and lateral line 5*(113), 6(143), 7(1); scale rows between lateral line and pelvic-fin insertion 4*(209), 5(9). Predorsal scales 8(1), 9*(69), 10(147), 11(42), 12(2); postdorsal scales 7(5), 8*(72), 9(154), 10(30); scale rows around caudal peduncle 12(2), 13(11), 14*(145), 16(1). Last scales of longitudinal series over base of caudal-fin modified in shape and size; scales hypertrophied on mature males, forming scale pouch in lower caudal-fin lobe (see caudal organ description, Fig. 4).

Mature males with gill gland on first branchial arch. Gill rakers on first branchial arch, 2(3) on hypobranchial, 7(2), 8(1) on ceratobranchial, 5(1), 6(2) on epibranchial.

Supraneurals 4(3). Precaudal vertebrae 11(1), 12(2). Caudal vertebrae 16(2), 17(1).

Pseudotympanum as large muscular hiatus between first and second pleural ribs, limited dorsally by *lateralis superficialis* muscle, posteriorly by naked anterior face of second pleural rib, posteroventrally by *obliquus inferioris* muscle, anteroventrally by *obliquus superioris* muscle.

Color in alcohol. Overall body color varying from light to medium yellowish in preserved specimens (Fig. 1). Head dark brownish dorsally. Region of infraorbitals 3-5 and opercular apparatus silvery on freshly preserved specimens and yellowish on older ones. Dark melanophores more densely scattered around nares, lips, dorsal surface of head, and more sparsely over body. Humeral spot absent, however humeral region darkened due to presence of pseudotympanum. Melanophores distributed at posterior margin scales in dorsal and dorsolateral regions of body, resulting in slight reticulated pattern. Dark longitudinal line extending laterally on body, starting narrower at vertical through dorsal-fin origin and widening posteriorly till merging with caudal spot; sometimes silvery. Caudal region with few melanophores distributed along myosepta of *epaxialis* and *hypaxialis* muscles. More often caudal spot elliptical, narrowing posteriorly over middle caudal-fin rays, conferring itself a lanceolate shape, not reaching dorsal or ventral margins of caudal peduncle. Variation can be found in this pattern; sometimes caudal spot not merged with dark longitudinal stripe presenting round shape, instead of lanceolate shape. All fins hyaline with scattered melanophores. Dorsal fin with small elongated spot between distal tip of first unbranched ray and midpoint of second unbranched ray, and distal portion with higher concentration of melanophores. Anal fin on mature males with higher concentration of melanophores at distal margin, sometimes forming dark distal stripe.

Color in life. Overall body and head color pattern semitransparent with silvery to whitish shades. Lateral body band silvery. Melanophores distribution pattern as described in color in alcohol. Anal, pelvic and caudal fin of mature males orangish to reddish.

Sexual dimorphism. Mature males can be differentiated from females by the presence of hooks on pelvic and anal fins (Fig. 3). Males also present the anal-fin rays more elongated

than on females, gradually decreasing in size posteriorly, conferring to the fin a slightly concave to straight distal profile. The pelvic fin reaches the anal-fin origin only on mature males. The scales modified in shape over the caudal-fin base of *Compsura heterura* are found in both sexes, but are more developed in size on males than on females (see caudal organ discussion); these scales are associated to hypertrophied tissue structuring a caudal pouch in the lower lobe of the fin (Fig. 4). Mature males tend to present a knob-shaped hypertrophied tissue ventrally to the anal opening, and the urogenital papilla is hypertrophied, resembling a ladle. The color pattern of the fins also differs between males and females, once mature males have a higher amount of melanophores at the distal portion of the anal-fin rays, which results in a tenuous dark band along the distal margin of the fin, as well as a orangish to reddish pelvic, anal and caudal fins. The modification of the branchial filaments of the first branchial arch into a gill gland is also found only in mature males.

Distribution. The known distribution of *Compsura heterura* encompasses coastal rivers from Northeastern to Northern Brazil, from the rio Itapicurú basin in the State of Bahia to the rio Parnaíba basin in the Maranhão and Piauí States. The distribution also includes the entire upper, middle and lower São Francisco system (Fig. 5).

Analyzed material.

Compsura heterura. **Type material. Brazil:** FMNH 57825, holotype (28.7 mm SL), rio Itapicuru, Queimadas, 2 March 1908, J. D. Haseman. FMNH 57826, paratypes, 10, (2 broken, 2 bent, 6 mc, 2 males, 28.5-28.8 mm SL, 4 females, 27.9-28.8 mm SL), rio Itapicuru, Queimadas, 2 March 1908, J. D. Haseman. FMNH 57827, paratype, (22.7 mm SL), Bahia, Barreiras, lagoa of Rio Grande, 3 Jan 1907, J. D. Haseman. FMNH 57828, paratype, (22.8 mm SL), Bahia, Santa Rita, 24 Jan 1907, J. D. Haseman. SU 17513, paratype, (female, 28.5 mm SL), Bahia, Prov. rio Itapecuru, at Queimadas, 2 Mar 1908, John D. Haseman.

Non-type material. Brazil. Rio Itapicurú basin: ANSP 187185, 20 (10 unsexed 18.1-22.0 mm SL, 10 mc 20.6-24.6 mm SL), Bahia, Itapicuru basin (type locality) Senhor do Bomfim, rio das Pedras, rio Itapicuru basin, 10°59'10"S 40°24'17"W, 13 June 2005, A. M.

Zanata *et al.* **Rio Parnaíba basin:** MCP 22947, 89, (19.3-29.9 mm SL, 18 mc 23.3-29.9 mm SL), Piauí, Teresina, riacho Sumaré (=Mutuni) on highway Teresina/Bom Jardim, 26 Jul 1998, R. E. Reis *et al.* MCP 22948, 28, (19.9-29.1 mm SL, 17 mc 25.0-29.1 mm SL), Piauí, Teresina, riacho dos Macacos, on highway Teresina/Bom Jardim, 26 Jul 1998, R. E. Reis, *et al.* MCP 22949, 131, (16.3-28.2 mm SL, 15 mc 22.5-28.2 mm SL), Maranhão, Igarapé do Pinto on highway Pará/Maranhão (BR 316), ca. 58 km ESE of Caxias, 26 Jul 1998, R. E. Reis, *et al.* **Rio Jaguaribe and rio Choró basin:** MCP 32613, 1, (mc 24.6 mm SL), Ceará, river on highway BR 116 ca 32 km South of Icó, affluent of rio Salgado, rio Jaguaribe, 24 Jul 2002, C. A. S. Lucena, *et al.* MNRJ 13430, 93, (16.0-26.7 mm SL, 19 mc 22.8-26.7 mm SL), Ceará, Baturité, riacho Olho d'Água, affluent of rio Potiú, 9 Aug 1945, A. L. Carvalho. **Rio Una basin:** MCP 30939, 24, (15.7-30.1 mm SL), Alagoas, rio Barreiro on highway BR 101 between Pilar and São Miguel dos Campos, affluent of Sumauma, lagoa Mamguaba, 21 Jul 2002, C. A. S. Lucena, *et al.* (note: 3 additional specimens with older aspect, possibly from other lot). MCP 30997, 94, (16.0-30.1 mm SL), Pernambuco, rio Ipojuca on the mouth of rio do Brejo, Vila dos Pilões, 19 Jul 2002, C. A. S. Lucena, *et al.* MCP 31079, 340, (15.6-29.9 mm SL), Pernambuco, rio Amaraji ca. 5 km South of Ribeirão, on highway BR 101, between Ribeirão and Palmares, affluent of rio Sirinhaém, 19 Jul 2002, C. A. S. Lucena, *et al.* MCP 31368, 437, (14.6-30.3 mm SL, 21 mc 26.0-30.3 mm SL), Pernambuco, rio Preto, on highway BR 101 and 5 Km North of Palmares, affluent of rio Una, 19 Jul 2002, C. A. S. Lucena, *et al.* MCP 32605, 1, (25.0 mm SL), Pernambuco, rio da Prata mouth in rio Una, on highway Agrestina/Catende, 28 Jul 2002, C. A. S. Lucena, *et al.* **Rio Vaza Barris basin:** MCP 40033, 9 mc, (23.4-28.5 mm SL), Bahia, Jeremoabo, rio Vaza Barris, Apa Serra Branca, Raso da Catarina, 18 Jan 2006, V. Abilhoa. **Rio Paraíba basin:** MCP 32608, 12, (11.0-25.5 mm SL, 4 mc 19.0-25.4 mm SL), Paraíba, rio Paraíba, on highway Queimadas/ Barra de Sant'anna, 28 Jul 2002, C. A. S. Lucena, *et al.* MCP 38621, 2 mc, (27.3-29.9 mm SL), Paraíba, Cruz do Espírito Santo, rio Paraíba close to Cruz do Espírito Santo, 29 Jan 2005, R. E. Reis, *et al.* **Rio Mamanguape basin:** MCP 31409, 22, (9 mc 20.4-23.5 mm SL), Paraíba, rio Cachoreira in Guarabira, on highway Guarabira/Sapé, affluent of Mamanguape, 27 Jul 2002, C. A. S. Lucena, *et al.* MCP 31410, 2 mc, (23.7-24.8 mm SL), Paraíba, stream in the Cofreiro Fechado farm, on highway Areias/Pilões, affluent of Mamanguape, 27 Jul 2002, C. A. S. Lucena, *et al.* MCP

38596, 12, (9 mc 24.7-25.9 mm SL), Paraíba, stream affluent of rio Mamaguape, between Guarabiri and Pirpirituba, 29 Jan 2005, R. E. Reis, *et al.* **Rio Ceará Mirim basin:** MCP 34071, 5 mc, (26.2-31.0 mm SL), Rio Grande do Norte, rio Ceará Mirim, district of Umari, 24 Jul 2001, L. Malabarba & H. Gurgel. MCP 34077, 18, (25.8-30.0 mm SL), Rio Grande do Norte, rio Ceará Mirim, district of Umari, 24 Jul 2001, L. Malabarba & H. Gurgel. UFRGS 12004, 66, (27.0-30.0 mm SL), Rio Grande do Norte, rio Ceará Mirim, 22 Feb 2002, H. Gurgel. UFRGS 12005, 36, (24.9-31.1 mm SL, 15 mc 24.9-31.0 mm SL), Rio Grande do Norte, rio Ceará Mirim, 12 Mar 2002, H. Gurgel. **Rio Piranha basin:** MCP 31380, 9, (22.3-25.1 mm SL), Paraíba, affluent of rio Piranhas on highway BR 427 between Pombal and Serra Negra, 26 Jul 2002, C. A. S. Lucena, *et al.* MCP 31397, 45, (20.6-28.5 mm SL, 10 mc 25.4-27.9 mm SL), Paraíba, rio Piranhas on highway BR 230 between Pombal and Sousa, ca 5 Km from Pombal, 26 Jul 2002, C. A. S. Lucena, *et al.* MCP 38391, 10, (24.3-27.7 mm SL, 10 mc 25.1-27.8 mm SL), Paraíba, Santa Helena, rio Itoré in Santa Helena, 29 Jan 2005, R. E. Reis, *et al.* MCP 38574, 18, (23.0-29.1 mm SL), Paraíba, Santa Helena, rio Una, close to Pacatuba dam, 29 Jan 2005, R. E. Reis, *et al.* **Rio Apodi basin:** MCP 30961, 51, (19.3-32.1 mm SL, 20 mc 27.7-31.4 mm SL), Rio Grande do Norte, between riacho da Cruz and Olho d'água do Borges, ca. 1 km from riacho da Cruz, affluent of rio Apodi, rio Bonsucesso, 25 Jul 2002, C. A. S. Lucena, *et al.* MCP 30969, 15, (21.0-29.9 mm SL), Rio Grande do Norte, stream affluent of rio Apodi on highway São Miguel/Encanto ca. 22 km from São Miguel, affluent of rio Bonsucesso, 25 Jul 2002, C. A. S. Lucena, *et al.* MCP 31082, 40, (18.6-30.6 mm SL), Rio Grande do Norte, riacho do Olho D'água in Olho d'água do Borges, 25 Jul 2002, C. A. S. Lucena, *et al.* **Upper rio São Francisco basin:** MCP 16504, 1 mc, (23.7 mm SL), Minas Gerais, Moema, rio São Francisco, under the bridge on highway BR 262, 02 Feb 1983, Y. Sato. MCP 17060, 4, (22.3-23.5 mm SL, 3 mc 22.3-23.5 mm SL), Minas Gerais, Felixlândia, stream after dam in J.B. farm, close to highway BR 040, 12 Jul 1993, S. Schaefer, *et al.* MCP 19924, 4, (19.8-24.1 mm SL, 2 mc 23.8-24.1 mm SL), Minas Gerais, Paracatu, córrego Santo Antônio, Jun 1996, P. Pompeu. MZUSP 39177, 9 (19.8-27.4 mm SL, 6 mc 24.7-27.4 mm SL), Minas Gerais, ribeirão do Gado, 26 Nov 1987, Y. Sato. MZUSP 39201, 1 mc (26.2 mm SL), Minas Gerais, córrego Cachoeira Grande, tributary of São Francisco river, 29 Nov 1987, Y. Sato. MZUSP 39433, 1 mc (24.4 mm SL), Minas Gerais, Rio Formoso, 8 Feb 1988, Y.

Sato. MZUSP 39459, 2 mc (25.0-25.7 mm SL), Minas Gerais, Barra do rio Formoso, rio São Francisco, 8-10 Feb 1988, Y. Sato. MZUSP 39539, 2 mc (21.7-26.9 mm SL), Minas Gerais, BR 365, córrego Jenipapo, 12 Feb 1988, Y. Sato. MZUSP 42794, 1 mc (30.2 mm SL), Minas Gerais, Três Marias, rio São Francisco, 16 Feb 1987, H. Britski & I. Dias.

Middle rio São Francisco basin: ANSP 171996, 4 mc, (1 male 25.6 mm SL, 3 females 23.63-24.15 mm SL), Minas Gerais, Francisco Sá, rio Catitu, tributary of rio Verde Grande, 32 km Norte de Montes Claros on highway to Janaúba, 16°31'18"S 43°40'49"W, 20 Jul 1993, S. A. Schaefer *et al.* MCP 16469, 8, (15.4-27.0 mm SL), Minas Gerais, stream in Cana Brava, *ca.* 13 km West of Monte Azul, on highway to Jaíba, 19 Jul 1993, R. E. Reis, *et al.* MCP 16837, 102, (18.4-28.9 mm SL), Minas Gerais, rio Poções in São Sebastião dos Poções, *ca.* 11 km South of Montalvânia, 16 Jul 1993, R. E. Reis, *et al.* MCP 16854, 34, (20.7-26.0 mm SL), Minas Gerais, arroio *ca.* 15 km from Januária to Tejuco, 14 Jul 1993, R. E. Reis, *et al.* MCP 17014, 43, (15.2-26.8 mm SL), Bahia, riacho Santana 31 km South of Bom Jesus da Lapa, on highway to Malhada, 18 Jul 1993, R. E. Reis, *et al.* MCP 17058, 19, (19.7-28.7 mm SL), Bahia, rio Tatu in Barra do Cocos, 7 km from Cocos, 16 Jul 1993, S. Schaefer, *et al.* MCP 17059, 21, (22.0-29.1 mm SL), Bahia, rio Cocos (= rio Gameleira), Cocos town, 16 Jul 1993, S. Schaefer, *et al.* MCP 17093, 185, (17.5-28.1 mm SL; 3 c&s 25.4-28.0 mm SL), Minas Gerais, rio Verde Pequeno, on highway from Urandi to Espinosa, 19 Jul 1993, R. E. Reis, *et al.* MCP 19928, 1 (23.4 mm SL) Minas Gerais, Ponte da Taquara, rio Paraopeba, 1994, C. Alves. MCP 25179, 1, (21.1 mm SL) Minas Gerais, rio Japuré in Bom Retiro, on highway between Manga and Montalvânia, 15 Jul 1993, R. E. Reis, *et al.* MCP 25180, 2, (19.7-23.1 mm SL) Minas Gerais, rio Verde Grande on highway from Montes Claros to Janaúba, 20 Jul 1993, R. E. Reis, *et al.* MCP 34350, 6, (15.1-29.6 mm SL), Minas Gerais, São Francisco, rio Peruaçu, Fabião I district, 30 Jul 2003, M. Brito & B. Nogueira. MNRJ 13437, 57, (15.4-25.6 mm SL), São Francisco, Minas Gerais, Itacarambi, rio Peruaçu, affluent of the rio São Francisco left margin, Januária/Itacarambi, 18 Aug 1990, D. F. Moraes Jr. & J. C. de Oliveira. MNRJ 13447, 9, (11.5-25.4 mm SL), Minas Gerais, Manga, lagoa de Mocambinho, right margin of the rio São Francisco, 19 Oct 1989, J. C. de Oliveira. MZUSP 54626, 22 (16.6-24.9 mm SL), Bahia, Bom Jesus da Lapa, rio das Rãs (= rio Carnaíba), 69 km South of Bom Jesus da Lapa on highway to Malhada, 18 Jul 1993, R. E. Reis *et al.* MZUSP 58800, 12, (20.6-29.8 mm SL), Bahia, São Desidério,

rio São Desidério, on highway BR-135, 7 Jul 1998, O. T. Oyakawa, *et al.* USNM 355774, 7, (21.0-23.5 mm SL), Minas Gerais, Montes Claros, rio Verde, between Francisco Sá and Montes Claros, 23 Jul 1994, Exp. MZUSP/USNM/UFSCAR. USNM 356661, 46, (20 mc: 10 males 24.8-28.3 mm SL, 10 females 26.1-30.5 mm SL), Minas Gerais, Missões, stream in a farm close to Missões, 21 Jul 1994, Exp. MZUSP/USNM/UFSCAR. **Lower São Francisco basin:** MCP 31018, 6 mc, (27.0-29.6 mm SL), Pernambuco, rio Pageu in Floresta, 23 Jul 2002, C. A. S. Lucena, *et al.* MZUSP 51376, 16 (13.2-25.4 mm SL, 4 mc 23.2-25.4 mm SL), Bahia, Campo Formoso, rio Salitre, on highway to Lage *ca.* 40 km East from Lage, Poços de Doce, 4 Jan 1997, F. C. T. Lima & P. Gerhard.

***Compsura* Guaporé n. sp., new species**

Figs. 6-9

Holotype. MCP (not catalogued), 29.8 mm SL, Brazil, Mato Grosso, Vila Bela da Santíssima Trindade, affluent of the left margin of rio Guaporé, 3 Feb 2010, F. Jerep, F. R. Carvalho & V. A. Bertaco, (ex-UFRGS 12014).

Paratypes. Brazil, Mato Grosso, Vila Bela da Santíssima Trindade. MZUSP 37663, 3 c&s of 123 (21, 21.7-26.3 mm SL), rio Guaporé, Cais da Balsa, 23 Set - 10 Oct 1984, J. C. Garavello & Polonoroeste team, CNPq. UFRGS 12012, 7 (25.8-28.8 mm SL), affluent of the left margin of rio Guaporé, 3 Feb 2010, F. Jerep, F. R. Carvalho & V. A. Bertaco. UFRGS 12013, 16 (24.9-29.3 mm SL), rio Guaporé, 3 Feb 2010, F. Jerep, F. R. Carvalho & V. A. Bertaco. UFRGS 12014, 12 (27.3-29.8 mm SL), affluent of the left margin of rio Guaporé, 3 Feb 2010, F. Jerep, F. R. Carvalho & V. A. Bertaco. UFRJ 0416, 12 (19.2-26.4 mm SL), rio Guaporé, 17 Oct 1989, K. Tanizaki & S. Kullander.

Diagnosis. *Compsura* Guaporé n. sp. is distinguished from the other species of *Compsura* by the number of branched anal-fin rays (19-22, mean = 20.2; n = 50 vs. 15-20, mean = 17.4; n = 207 in *C. heterura* and 16-19, mean = 18.1; n = 20 in *C. Araguaia* n. sp.). *Compsura* Guaporé n. sp. is also distinguished from *C. heterura* by the absence of a conspicuous dorsal-fin spot, caudal-peduncle spot reaching the dorsal and ventral peduncle

edge, and by the modification in size and shape of the last two lateral line scales, instead of the last three in *C. heterura*.

Description. Morphometrics given in Table 2. Body slightly elongate and compressed, deepest at dorsal-fin origin. Dorsal profile convex from snout tip to posterior end of supraoccipital process, convex from that point to dorsal-fin origin, slightly convex along dorsal-fin base, straight or slightly convex from end of dorsal-fin base to adipose-fin origin. Dorsal and ventral caudal-peduncle profile straight to slightly concave. Ventral profile convex from dentary anterior end to pelvic-fin insertion, straight (on females) to deeply concave (on mature males) until anal-fin origin, straight (on females) to slightly convex (on males) on anal-fin base. Snout short, mouth terminal, in horizontal line through pupil ventral border.

Premaxilla with 4(1) to 5(2) teeth bearing 9(3) cusps, aligned and similar in size. Maxilla short, not reaching vertical line through orbit anterior edge, bearing 2(1) to 3(2) with 7(2) to 9(1) cusps. Dentary with 4(3) aligned heptacuspoid teeth similar in size, followed by teeth decreasing in size posteriorly 1(2) or 2(1) smaller heptacuspoid teeth, 1(3) penta- or tricuspoid tooth (Fig. 7).

Dorsal-fin origin slightly posterior to vertical through pelvic-fin origin, on middle of body. Dorsal-fin rays ii, 9*(49). Adipose-fin origin at vertical line through third to fourth last anal-fin ray insertion. Anal-fin origin slightly posterior to last dorsal-fin ray insertion; anterior rays longer than posterior ones; distal profile deeply concave on females, slightly concave to slightly convex on mature males. Anal-fin rays iii*(50), 19(10), 20(25), 21*(12), 22(3); last unbranched until nineteenth branched anal-fin ray of mature or maturing males bearing small and retrorse hooks, often associated to hypertrophied whitish tissue (Fig. 8). Hooks placed from middle length to near distal tip of anal-fin rays, attached at posterior margin, usually posterior branch of branched portion, bent over lateral surface, and directed anteriorly to anal-fin frontal margin, larger on most anterior and most posterior anal-fin rays. One, rarely two, hooks per anal-fin ray segment. Pectoral-fin rays i, 8(1), 9*(26), 10(21), 11(2); longest rays surpassing pelvic-fin insertion. Pelvic-fin insertion anterior to vertical line passing through dorsal-fin origin. Pelvic-fin rays i, 6(11), 7*(38), 8(1); branched rays bearing 1-2 unilateral ventromedial antrorse hooks per ray segment on

mature males. Caudal fin with 17(1) to 19*(47) principal rays; 9(1), 10(2) dorsal procurrent caudal-fin rays; 9(3) ventral procurrent caudal-fin rays.

Lateral line series 31(1), 32*(4), 33(14), 34(22), 35(9) scales; 5(1), 6(1), 7(5), 8(20), 9*(22), 10(1) perforated scales. Scale rows between dorsal-fin insertion and lateral line 5*(24) to 6(26); scale rows between lateral line and pelvic-fin insertion 4*(47) to 5(1). Predorsal scales 9(12), 10*(29), 11(8), 12(1); postdorsal scales 8(4), 9(22), 10*(24); scale rows around caudal peduncle 12(8), 13(2), 14*(40). Last scales of longitudinal series over base of caudal-fin modified in shape and size; scales hypertrophied on mature males, forming scale pouch in lower caudal-fin lobe (see caudal organ description, Fig. 9).

Mature males with gill gland on first branchial arch. Gill rakers on first branchial arch, 2(3) on hypobranchial, 7(4) on ceratobranchial, 4(3) on epibranchial. Supraneurals 4(3). Precaudal vertebrae 11(1), 12(2). Caudal vertebrae 17(1), 18(1), 19(1).

Pseudotympanum as large muscular hiatus between first and second pleural ribs, limited dorsally by *lateralis superficialis* muscle, posteriorly by naked anterior face of second pleural rib, posteroventrally by *obliquus inferioris* muscle, anteroventrally by *obliquus superioris* muscle.

Color in alcohol. Overall body color varying from whitish to medium yellowish in preserved specimens (Fig. 6a-b). Head dark brownish dorsally. Region of infraorbitals 3-5 and opercular apparatus silvery on freshly preserved specimens and yellowish on older ones. Dark melanophores more densely scattered around nares, lips, dorsal surface of head, and more sparsely over body. Humeral spot absent, however humeral region darkened due to presence of pseudotympanum. Melanophores distributed at posterior margin of scales in dorsal and dorsolateral regions of body, resulting in a slight reticulated color pattern on flank. Dark line extending laterally on body, starting narrower near vertical through dorsal-fin origin and widening posteriorly till merging with caudal spot. Sometimes this line silvery. Caudal region with melanophores distributed along the myoseptum of *epaxialis* and *hypaxialis* muscles. Caudal spot round, reaching dorsal or ventral margins of caudal peduncle, with posterior extension over middle caudal-fin rays. All fins hyaline with scattered melanophores. Dorsal fin distal portion with higher concentration of

melanophores. Anal fin on mature males with higher concentration of melanophores at distal margin, forming dark distal stripe.

Color in life. Overall body and head color pattern semitransparent with silvery shades (Fig. 6c). Lateral body band silvery. Melanophores distribution pattern as described in color in alcohol. Dorsal, anal, caudal and pelvic fins yellowish on females. Mature males with dorsal and caudal fins reddish, anal and pelvic fins yellowish to orangish.

Sexual dimorphism. Mature males can be differentiated from females by the presence of hooks on pelvic and anal fins. Males also present the anal-fin rays more elongated than on females, gradually decreasing in size posteriorly, conferring to the fin a straight to slightly convex distal profile, in contrast to the deeply concave profile of the females' anal fin. The pelvic fin reaches the anal-fin origin only on mature males. Mature males tend to present a knob-shaped hypertrophied tissue ventrally to the anal opening, and the urogenital papilla is hypertrophied, resembling a ladle. The scales modified in shape over the caudal-fin base of the mature males are more developed in size and modified in shape on males than on females (see discussion); these scales are associated to hypertrophied tissue structuring a caudal pouch in the lower lobe of the fin (Fig. 9). The color pattern of the fins also differs between males and females, mature males have a higher amount of melanophores at the distal portion of the anal-fin rays, which results in a dark band along the distal margin of this fin. The color of the fins also varies between males and females, while the dorsal, anal, pelvic and caudal fins are yellowish on females, on males the pelvic and anal fins are orangish, and the dorsal and caudal fins are reddish. The modification of the branchial filaments of the first branchial arch into a gill gland is also found only in mature males.

Distribution. *Compsura* Guaporé n. sp. is known from the rio Guaporé and its tributaries in the surroundings of the municipality of Vila Bela da Santíssima Trindade, State of Mato Grosso, Brazil (Fig. 5).

***Compsura Araguaia* n. sp., new species**

Figs. 10-11

Holotype. MCP (not catalogued), 23.5 mm SL, Brazil, Mato Grosso, Porto Alegre do Norte, rio Araguaia basin, rio Xavantino 16 km South of Porto Alegre do Norte, in BR 158 between Posto da Mata and Porto Alegre do Norte, 11°01'30"S 51°38'47"W, 27 Oct 2005, J. F. P. Silva, (ex - MCP 44542).

Paratypes. All from Brazil. MCP 44524, 7 (13.2-21.0 mm SL), Mato Grosso, Porto Alegre do Norte, rio Araguaia basin, rio Xavantino ca 16 km South of Porto Alegre do Norte in BR 158 between Posto da Mata and Porto Alegre do Norte, 11°01'30"S 51°38'47"W, 21 Apr 2006, J. F. P. Silva. MCP 44525, 1 (19.2 mm SL), Mato Grosso, Porto Alegre do Norte, rio Araguaia basin, rio Ribeirãozinho, 11°19'10"S 51°39'45"W, 21 Apr 2006, J. F. P. Silva. MCP 44528, 1 (20.2 mm SL), Mato Grosso, Porto Alegre do Norte, rio Araguaia basin, córrego Pium, 11°53'58"S 51°39'26"W, 20 Apr 2006, J. F. P. Silva. MCP 44542, 2 c&s of 7 (18.2-23.8 mm SL), Mato Grosso, Porto Alegre do Norte, rio Araguaia basin, rio Xavantino, 16 km South of Porto Alegre do Norte in BR 158 between Posto da Mata and Porto Alegre do Norte, 11°01'30"S 51°38'47"W, 27 Oct 2005, J. F. P. Silva. UFRJ 1529, 2 (24.2-26.1 mm SL), stream 98 km West of Jussara, Goiás, W. Costa, F. Autro, E. Vicente, M. Britto & R. D'Arrigo. UFRJ 1558, 2, (22.2-26.1 mm SL), stream 98 km West of Jussara, Goiás, 30 Aug 1993, W. Costa, F. Autro, E. Vicente, M. Britto & R. D'Arrigo.

Diagnosis. *Compsura* Araguaia n. sp. is distinguished from *C. heterura* by the absence of a conspicuous dorsal-fin spot, by the caudal-peduncle spot reaching the dorsal and ventral peduncle edge (*vs.* not reaching), and by the modification in size and shape of the last two lateral line scales (*vs.* three in *C. heterura*). From *Compsura* Guaporé n. sp., *C. Araguaia* n. sp. is diagnosed by the lower number of branched anal-fin rays (16-19, mean = 18.1; n = 20 *vs.* 19-22, mean = 20.2; n = 50 in *C. Guaporé* n. sp.).

Description. Morphometrics given in Table 2. Body slightly elongate and compressed, deepest at dorsal-fin origin. Dorsal profile convex from snout tip to posterior end of supraoccipital process, convex from that point to dorsal-fin origin, straight to slightly convex from that point to end of dorsal-fin base, straight or slightly convex from end of

dorsal-fin base to adipose-fin origin. Dorsal and ventral caudal-peduncle profile slightly concave. Ventral profile convex from dentary anterior end to pelvic-fin insertion, straight to slightly concave until anal-fin origin, straight to slightly convex on anal-fin base. Snout short, mouth terminal, on horizontal line projected through middle of pupil.

Premaxilla with 4(1) to 5(1) teeth bearing 9(2) cusps, aligned and similar in size. Maxilla short, not reaching vertical line through orbit anterior edge, bearing 2(2) heptacuspoid teeth. Dentary with 4(2) aligned heptacuspoid teeth similar in size, followed by teeth decreasing in size posteriorly 1(2) hexacuspoid tooth, 1(1) tricuspid tooth, 1(2) conical tooth (Fig. 11).

Dorsal-fin origin slightly posterior to vertical through pelvic-fin origin, on middle of body. Dorsal-fin rays ii, 9*(20). Adipose-fin origin at vertical line through first to third last anal-fin ray insertion. Anal-fin origin slightly posterior to last dorsal-fin ray insertion; anterior rays longer than posterior ones; distal profile concave on females, slightly concave on maturing males. Anal-fin rays iii*, 16(2), 17*(2), 18(9), 19(7); one not fully mature male with last unbranched until fourteenth branched anal-fin ray of mature or maturing males bearing small and retrorse hooks. Hooks placed from middle length to near the distal tip of anal-fin rays, attached at posterior margin, usually posterior branch of branched portion. One hook per anal-fin ray segment. Pectoral-fin rays i, 8(4), 9*(13), 10(3); longest rays surpassing pelvic-fin insertion. Pelvic-fin insertion anterior to vertical line passing through dorsal-fin origin. Pelvic-fin rays i, 7*(20); first four branched rays bearing 1 unilateral ventromedial antrorse hook per ray segment on one not fully mature male. Caudal fin with 18(1), 19*(19) principal rays; 12(1), 13(1) dorsal procurrent caudal-fin rays; 9(1), 10(1) ventral procurrent caudal-fin rays.

Lateral line series 31*(7), 32(8), 33(5) scales; 6*(6), 7(6), 8(5), 9(1) perforated scales. Scale rows between dorsal-fin insertion and lateral line 5*(19) to 6(1); scale rows between lateral line and pelvic-fin insertion 4*(20). Predorsal scales 9(1), 10*(11), 11(6), 12(2); postdorsal scales 8(3), 9(13), 10*(4); scale rows around caudal peduncle 11(1), 12*(18), 14(1). Last scales of longitudinal series over base of caudal-fin modified in shape and size; scales hypertrophied on mature males, probably forming scale pouch in lower caudal-fin lobe on fully mature males (see discussion).

Mature males with gill gland on first branchial arch. Gill rakers on first branchial arch, 2(2) on hypobranchial, 7(2) on ceratobranchial, 4(1), 5(1) on epibranchial. Supraneurals 4(2). Precaudal vertebrae 12(2). Caudal vertebrae 18(2). Pseudotympanum as large muscular hiatus between first and second pleural ribs, limited dorsally by *lateralis superficialis* muscle, posteriorly by naked anterior face of second pleural rib, posteroventrally by *obliquus inferioris* muscle, anteroventrally by *obliquus superioris* muscle.

Color in alcohol. Overall body color varying from whitish to light to dark yellowish in preserved specimens (Fig. 10). Head dark brownish dorsally. Region of infraorbitals 3-5 and opercular apparatus silvery on freshly preserved specimens and yellowish on old preserved ones. Dark melanophores more densely scattered around nares, lips, dorsal surface of head, and more sparsely scattered over body. Humeral spot absent, humeral region darkened due to presence of pseudotympanum. Melanophores distributed at posterior margin scales in dorsal and dorsolateral regions of body, resulting in slight reticulated color pattern on flank. Dark narrow line extending laterally on body, starting at vertical through dorsal-fin origin, ending just before caudal spot. Sometimes this line silvery. Caudal region with melanophores distributed along myosepta of *epaxialis* and *hypaxialis* muscles. Caudal spot round, reaching dorsal or ventral margins of caudal peduncle, with posterior extension over middle caudal-fin rays. All fins hyaline with scattered melanophores. Dorsal fin distal portion with higher concentration of melanophores. Anal fin with higher concentration of melanophores at distal margin.

Sexual dimorphism. Mature males can be differentiated from females by the presence of hooks on pelvic and anal fins. Males also present the anal-fin rays more elongated than on females, gradually decreasing in size posteriorly, conferring to the fin a slightly concave to straight distal profile, in contrast to the deeply concave profile of the females' anal fin. The scales modified in shape over the caudal-fin base are more developed in size and modified in shape on males than on females (see discussion). The color pattern of the fins also differs between males and females; mature males have a higher amount of melanophores at the distal portion of the anal-fin rays, forming a dark band along the distal margin of this fin.

The modification of the branchial filaments of the first branchial arch into a gill gland is also found only in males.

Distribution and habitat remarks. Records of *Compsura* Araguaia n. sp. are restrict to the rio Araguaia tributaries. The disrupted distribution in the upper part of the basin (Jussara, Goiás) and in the median portion (Porto Alegre do Norte, Mato Grosso) is probably related to insufficient collections in the rio Araguaia tributaries. A recent expedition in the municipality of Jussara in order to recollect this species was unsuccessful during the 2010 rainy season, maybe a consequence of the high degree of siltation observed in the rio Araguaia small tributaries.

Remarks on “*Compsura*” *gorgonae*. Meek & Hildebrand (1916) placed *Cheirodon gorgonae* (Fig. 12) in *Compsura* due to the presence of modified scales on the lower lobe of the caudal fin, a feature at that time, not very common among the cheirodontinae species. In fact, the modified scales over the caudal-fin lower lobe of “*Compsura*” *gorgonae* are derived from the same longitudinal series of the *Compsura* caudal-organ scales: last one or two scales from LL; last two scales from LV1; and last two scales from LV2. However, on mature males of “*C.*” *gorgonae*, the hypertrophy of the correspondent scales results in a caudal organ structurally different. Instead of one pouch-like structure with an internal chamber found in *Compsura*, the scales in “*C.*” *gorgonae* are independently modified, unattached distally, and laterally bent, forming a series of two to three pockets associated to hypertrophied tissue (probably glandular tissue). A study concerning the relationships of the compsurini species (Jerep & Malabarba, Chapter I in manuscript) has shown that “*Compsura*” *gorgonae* is more close related to the Central American compsurini “*Odontostilbe*” *dialeptura* and “*O.*” *mitoptera* than to any other species of the tribe, corroborating previous hypothesis quoting as convergent the presence of a caudal organ on *Compsura heterura* and “*Compsura*” *gorgonae* (see introduction; López, 1972; Fink & Weitzman, 1974). Further taxonomic arrangement for this species is being treated in another work (Jerep & Malabarba, Chapter IV in manuscript).

Discussion

The detailed function of the caudal organ in *Compsura* is not entirely clear, but some hypotheses can be inferred based on previous studies regarding another group of characids, which also present secondary sexual dimorphism in the caudal fin of males, like the Glandulocaudinae (*sensu* Weitzman & Menezes, 1998). Nelson (1964) was the first to hypothesize the caudal organ of the glandulocaudines as a pheromone dispersor, which was classified by Weitzman & Fink (1985) in two general hypothetical functional categories. The first category is based on the enlargement of a caudal scale, which may work as a “diaphragm scale pump”. This scale pump could be passive, when not associated to specialized musculature (present in *Argopleura* and *Iotabrycon*), or active, when associated to specialized musculature, as found in *Xenobrycon*, *Scopaeocharax*, and *Tytocharax*. The second category of pump mechanism would be constituted by modified rays, scales and hypertrophied glandular tissue, present in *Glandulocauda* and *Mimagoniates*. The species of *Compsura* do not present any modification in the shape of the caudal fins, additionally, although slightly larger and longer posteriorly in the region of the caudal organ, the muscles *interradialis* are not attached to any scale. The caudal organ in *Compsura* fits better in the Weitzman & Fink (1985) definition of the “passive scale pump”, in which a passive pumping of pheromone from the pouch is caused by the tail beating of the males. Just as described by Weitzman & Fink (1985) to *Corynopoma*, *Hysteronotus*, and *Gephyrocharax*, the movement of the tail promotes the movement of the scales, drawing water in and out of the pouch, over the glandular tissue. The behavior of “tail beating” described by Nelson (1964) and Weitzman & Fink (1985) for some glandulocaudines was observed in mature males of *Compsura heterura* in aquarium (FCJ pers. obs.). During this behavior, the male of *Compsura heterura* was placed anteriorly to the female, while beating his tail rhythmically in front of her snout, corroborating the observation of Weitzman & Fink (1985) quoting this behavior to be present in other characiforms as well.

In *Compsura*, the caudal organ is located in the base of the caudal fin, more developed in the lower lobe of the caudal fin of mature males. The last scales from LD1 and LD2, sometimes the LD3 in the upper caudal-fin lobe of *Compsura heterura*, are modified in shape, slightly enlarged in comparison to the common body scales, and present their posterior border free. Sometimes, this arrangement is associated to a small amount of

hypertrophied tissue, forming a small pouch-like structure, generally collapsed in preserved material. The portion of the caudal organ situated over the middle and lower caudal-fin rays is formed by the last three scales from the LL, last two scales from LV1, and the last two scales from LV2 in *Compsura heterura*, and only by the last two scales from the LL, and last scale from LV1 and LV2 in *Compsura Araguaia* n. sp. and *C. Guaporé* n. sp. (Figs. 4, 9). These scales are modified in shape, enlarged in size, and strongly attached to each other. The enlarged scales from LL and LV1, that forms the upper portion of the lower part of the caudal organ, are dorsally and posterodorsally attached to the caudal-fin rays 10 to 13 (in *C. heterura* and *C. Araguaia* n. sp.) or 8 to 12 (in *C. Guaporé* n. sp.) by hypertrophied tissue (supposable glandular), mostly developed from the interradiial membrane. The posteroventral border of the last scales from LV1, and the posterior border of the last LV2, are free, allowing the pouch to open over the 13th to the 19th caudal-fin rays. The ventral portion of the caudal organ is constituted by the last modified scales from the LV2. The pouch consists of an epidermal invagination between the caudal-fin rays and the scales, with posterior to posteroventral opening and ending anteriorly by a wall of hypertrophied tissue, apparently glandular. Anteriorly to the bottom of the pouch, there is an internal chamber, placed between the modified scales and the caudal-fin rays. The chamber occupies the lower portion of the caudal organ and extends dorsally until the upper portion of the organ. The chamber is delimited anteriorly by the posterior attachment of the modified scales that compose the caudal organ, and posteriorly by the bottom of the pouch, a wall of hypertrophied tissue that connects the modified scales (roof of the chamber) to the caudal-fin rays (floor of the chamber). On old preserved specimens, the wall of tissue between the pouch and the chamber presents some small openings, raising some doubts whether they are natural or whether the wall was damaged. On recently preserved specimens, we were not able to find any opening do to the large amount of hypertrophied tissue in the wall and inside the pouch. The skin flaps just posterior to pouch opening are more developed on mature males than on females and juveniles. The muscles *interradialis* are also more developed and extended posteriorly under the last modified LV1 scale, between the principal caudal-fin rays 11 to 14 in *Compsura heterura* and 7 or 8 to 13 in *C. Araguaia* n. sp. and *C. Guaporé* n. sp. No ray modification is present.

The genus *Compsura* is herein characterized by its singular caudal-fin organ among the Cheirodontinae, formed at least by the last two scales from the LL, last scale from LV1, and last scales from LV2 (Figs. 4, 9). These scales are modified in shape, hypertrophied in size, and form the roof of the pouch-like structure which presents a posterior opening. Among the cheirodontinae, only the compsurini genera *Macropsobrycon*, *Saccoderma*, and the species “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura* and “*Odontostilbe*” *mitoptera* also present some kind of modified scales in the caudal fin, nevertheless the presence of a caudal organ as a pouch-like structure is only found in *Compsura* and *Saccoderma*. The caudal organ in *Saccoderma*, which were also called “caudal pouch” by Eigenmann (1915) and “dermal sac” by Schultz (1944), is formed by modified scales from the LV1 and LV2, not presenting any scale from the LL series as a component of the caudal organ. Another difference between the caudal organs of these two genera is the presence of accessory scales posteriorly to the chamber attached to the caudal-fin rays, a feature which seems to be an autapomorphy of *Saccoderma* (fig. 33 from Eigenmann, 1915; fig. 44 from Schultz, 1944).

The species of Compsurini have very conspicuous sexual dimorphism, generally associated to the presence of hooks on fins, enlarged modified scales or hypertrophied tissue in the caudal fin, shape of the anal fin, and in some cases, differences in the shape of the urogenital papilla. The mature males of *Compsura* present a knob-shaped hypertrophied tissue just anteroventral to the anal opening, as well as an urogenital papilla more hypertrophied on males of *Compsura* than on other non-compsurini cheirodontines mature males (Fig. 13). The hypertrophy of the male urogenital papilla was also observed, although in a lesser development degree, in “*Compsura*” *gorgonae*, and in mature males of the species of *Kolpotocheirodon*. However, on the contrary to *Compsura*, not only the males of *Kolpotocheirodon* present hypertrophy of the urogenital papilla, but also the adult females, in which the papillae are modified in two ventrally expanded laminae with a ventral slit-shaped opening.

The new species herein described are included in *Compsura* for presenting the synapomorphies of the genus. The caudal organ arrangement and the pattern of hooks in the anal fin are some of the most remarkable characters that diagnose its species. Among the compsurin genera there are two evident patterns of hook distribution in the anal fin: hooks

restricted to the most anterior anal-fin rays; and hooks distributed on most of the anal-fin rays, being larger in the anterior portion of the fin and in the last branched rays, and smaller in the median rays. The first pattern is found in *Macropsobrycon*, *Kolpotocheiroidon*, and *Saccoderma*, while the second pattern is shared by *Compsura* and the Compsurini from Central America: “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura*, and “*O.*” *mitoptera*. *Acinocheiroidon melanogramma* is the only compsurini species in which the hooks and their distribution resemble the pattern found in *Odontostilbe* and *Cheiroidon* species, whose hooks are directed to the anal-fin base instead of to the anterior of the anal-fin ray, and gradually decrease in number-per-ray posteriorly. The shape of the anal-fin hooks in *Acinocheiroidon* was found to be a reversion inside the Compsurini (Malabarba, 1998, referred as new genus and new species B).

According to the phylogenetic analysis of the Compsurini presented by Jerep & Malabarba (in manuscript, Chapter I), *Compsura* Araguaia n. sp. is sister group of *C. Guaporé* n. sp. and *C. heterura*. The only synapomorphy grouping *C. Guaporé* n. sp. and *C. heterura* is the absence of the sixth infraorbital anterior lamella (Ch. 11: 0). However, *Compsura* Araguaia n. sp. and *C. Guaporé* n. sp. also share some characters still not explored cladistically, for example, they have same amount of scales from the LL, LV1 and LV2 composing the caudal organ (respectively two, one and one *vs.* three, two and two in *C. heterura*), as well as a general color pattern more similar to each other than to *C. heterura*, like the absence of a conspicuous dorsal-fin spot and deep caudal-fin spot. *Compsura heterura* is the species with larger geographical distribution, occurring along all the rio São Francisco basin and coastal rivers from the Northeast of Brazil. *Compsura* Guaporé n. sp. is only known to the upper portion of the rio Guaporé, and *C. Araguaia* n. sp. was registered for the upper and middle portion of the rio Araguaia basin. Presumably *Compsura* Araguaia n. sp. has a larger distribution in the basin, and these disrupted records are resulted from deficient sampling efforts.

Comparative material. *Acinocheiroidon melanogramma*: ANSP 176238, paratypes, 7, 21.9-26.2 mm SL, Brazil, Minas Gerais, rio Jequitaiá drainage. *Aphyodite grammica*: FMNH, holotype, 24.3 mm SL, Guiana, Konawaruk. MZUSP 29874, 20, 21.9-26.9 mm SL, Brazil, rio Negro. *Brittanichthys axelrodi*: MCP 14931, 17, 16.3-22.2 mm SL, 3 c&s,

Brazil, Boa Vista, rio Negro. *Cheirodon australe*: USNM 084317, paratypes, 12, 28.4-49.8 mm SL, Chile, Los Lagos region at Puerto Varas. *Cheirodon dialepturus*: USNM 208524, holotype, 26.8 mm SL, Panama, Veraguas, río San Pedro basin. *Cheirodon galusdai*: USNM 084319, paratypes, 10, 30.6-52.3 mm SL, Chile, río Locomilla at San Xavier. *Cheirodon gorgonae*: USNM 64094, holotype, 22.1 mm SL, Panama, Canal Zone, small seepage pool below spillway of the reservoir dam at Gorgona. MCP 11989, 7 (23.1-29.1 mm SL) Panamá, río Caimito at Chorrera falls, in backwater above dam, 17 Aug 1962, H. Loftin. MCP 16132, 36 (13.8-26.8 mm SL, 2 mc and c&s 23.2-26.8 mm SL), Panama, Darien, río Meteti, Pan Americana ca. 40 km nnw of Yaviza (Chucunaque system), 24 Feb 1985, W. C. Starnes *et al.* MCP 27060, 1 (19.7 mm SL), Panama, Darién, Tuira, río Tuira, between Calle Larga and Pinogana, 18 Feb 1985, L. Lundberg *et al.* MCP 27064, 1 (25.8 mm SL), Panama, Panama, Caribbean, río Frijoles, Nortf of Gamboa (río Chagres basin), 26 Feb 1985, W. C. Starnes *et al.* MCP 27065, 57 (21.0-23.6 mm SL), Panamá, Darien, Tuira, río Tuira close to Boca de Cupé, 18 Feb 1985, W. C. Starnes *et al.* MCP 27070, 32 (20.0-23.9 mm SL), Panamá, Darién, Tuira, río Pirre, 16 Feb 1985, L. Lundberg *et al.* MCP 27093, 3 (21.3-22.2 mm SL), Panamá, Darién, Tuira, río Pirre in Pijibasal, 23 Feb 1985, L. Lundberg *et al.* *Cheirodon kiliani*: USNM 227310, paratype, 1, 25.2 mm SL. Valdivia-Chile, río Cau-Cau. *Cheirodon microdon*: FMNH 57867, holotype, 32.2 mm SL, Brazil, Cáceres, rio Ibicuhy. *Cheirodon micropterus*: CAS 59780, holotype, 23.9 mm SL, Brazil, Pará, rio Amazonas drainage at Santarém. *Cheirodon mitopterus*: USNM 208539, holotype, 34.6mm SL, Panama, Cocle, río Tucue, tributary of río Cocle del Norte. *Cheirodon notomelas*: FMNH 57829, holotype, 28.2 mm SL, Brazil, Miguel Calmone. *Cheirodontops geayi*: USNM 121507, holotype, 35.5 mm SL, Venezuela, Estado de Aragua, río Guarico. *Holesthes heterodon* (= *Serrapinnus heterodon*): CAS 117522, paratypes, 4, 32.2-36.5 mm SL, Brazil, Minas Gerais, rio Grande, Jaguará. *Kolpotocheirodon figueiredoi*: MCP 22345, paratypes, 25.1-30.5 mm SL, rio Pratinha, Iraquara. *Kolpotocheirodon theloura*: MCP 11161, paratype, 25.9 mm SL, ribeirão do Gama, just above, the mouth of ribeirão Taquara. *Leptobrycon jatuaranae*: MCP 14936, 17, 20.8-25.1 mm SL, 3 c&s, Brazil, Amazonas, rio Negro. *Microchemobrycon guaporensis*: FMNH 57926, holotype, 29.1 mm SL, Brazil, Maciel, rio Guaporé. *Odontostilbe hastatus*: FMNH 56383, holotype, 30.2 mm SL, Colombia, Soplaviento. *Oligobrycon microstomus*: holotype, 31.0 mm SL, Brazil, Jacarehy

on rio Parahyba. *Oxybrycon* sp.: MCP 33105, 8, 13.7-14.9 mm SL, 2 c&s, Venezuela, Titi lagoon, upper Orinoco basin. *Parecbasis cyclolepis*: FMNH 56677, holotype, 56.3 mm SL, Brazil, rio Madeira. MZUSP 26146, 7, 40.3-53.5 mm SL, Peru, Ucayali, río Ucayali. *Pristella aubynei*: FMNH 52698, 34.9 mm SL, British Guiana. *Prodontocharax alleni*: CAS 117472, holotype, 32.8 mm SL, Peru, Ucayali, río Amazonas basin. *Prodontocharax melanotus*: CAS 59793, holotype, 44.9 mm SL, Bolivia, La Paz, río Amazonas drainage at Tumupasa. *Pseudocheiroduon affinis*: CAS 117516, paratype, 32.1-35.4 mm SL, Panama, rio Gatun, at Gatun. *Saccoderma melanostigma*: USNM 121519, holotype, 26.7 mm SL, Venezuela, río San Juan, South of Mene Grande. *Spintherobolus broccae*: FMNH 58864, paratype, 18.7 mm SL, Brazil, Rio de Janeiro. *Spintherobolus papilliferus*: FMNH 104802, holotype, 32.9 mm SL, Brazil, São Paulo, Alto da Serra. *Thrissobrycon pectinifer*: SU 16944, holotype, 26.8 mm SL, Brazil, Cucuhy, rio Negro. MCP 14932, 12, 26.4-30.2 mm SL, 3 c&s, Brazil, rio Arirara.

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Literature Cited

- Bührnheim, C. M. & L. R. Malabarba. 2006. Redescription of the type species of *Odontostilbe* Cope, 1870 (Teleostei: Characidae: Cheirodontinae), and description of three new species from the Amazon basin. *Neotropical Ichthyology*, 4(2): 167-196.
- Burns, J. R., S. H. Weitzman & L. R. Malabarba. 1997. Insemination in eight species of cheirodontine fishes (Teleostei: Characidae: Cheirodontinae). *Copeia* 1997: 433-438.
- Eigenmann, C. H. 1915. The Cheirodontinae, a subfamily of minute characid fishes of South America. *Memoirs of the Carnegie Museum*, 7(1): 1-99.
- Fink, W. L. & S. H. Weitzman. 1974. The so-called Cheirodontin fishes of Central America with descriptions of two new species (Pisces: Characidae). *Smithsonian Contributions to Zoology*, 172: 1-46.
- Géry, J. 1960. Contributions to the study of characoid fishes. II. The generic position of *Hyphessobrycon innesi* and *Cheirodon axelrodi*, with a review of the morphological affinities of some Cheirodontinae (Pisces, Cypriniformes). *Bulletin of Aquatic Biology*, 2(12): 1-18.
- Géry, J. 1965. Poissons characoides sud-américains du Senckenberg Museum, II. Characidae et Crenuchidae de l'Igarape Preto (Haute Amazonie). *Senckenbergiana Biologica*, 46(1): 11-45.
- Géry, J. 1977. Characoids of the world. T.F.H. Publications, Neptune City, 672p.
- Gonçalves, T. K., M. A. Azevedo, L. R. Malabarba & C. B. Fialho. 2005. Reproductive biology and development of sexually dimorphic structures in *Aphyocharax anisitsi* (Ostariophysi: Characidae). *Neotropical Ichthyology*, 3(3): 433-438.
- Javonillo, R., L. R. Malabarba, S. H. Weitzman & J. R. Burns. 2010. Relationships among major lineages of characid fishes (Teleostei: Ostariophysi: Characiformes), based on molecular sequence data. *Molecular Phylogenetics and Evolution*, 54: 498-511.
- López, M. I. 1972. Contribución al estudio de los peces Cheirodontinae (Familia Characidae) de Cost Rica y Panama: generos *Compsura* y *Pseudocheirodon*. *Revista de Biología Tropical*, 20(1): 93-129.
- Malabarba, L. R. 1998. Monophyly of the Cheirodontinae, characters and major clades (Ostariophysi: Characidae). Pp. 193-233. In: Malabarba, L. R., R. E. Reis, R. P. Vari, Z. M.

- S. Lucena & C. A. S. Lucena (Eds.). *Phylogeny and Classification of Neotropical Fishes*. Porto Alegre, Edipucrs, 603p.
- Malabarba, L. R. 2003. Subfamily Cheirodontinae (Characins, tetras). Pp. 215-221. In: R. E. Reis, S. O. Kullander & C. J. Ferraris (Eds.). *Check list of the freshwater fishes of South and Central America*. Porto Alegre, Edipucrs, 729p.
- Malabarba, L. R. & S. H. Weitzman. 1999. A new genus and species of South American fishes (Teleostei: Characidae: Cheirodontinae) with a derived caudal fin, including comments about inseminating cheirodontines. *Proceedings of the Biological Society of Washington*, 112(2): 410-432.
- Malabarba, L. R. & S. H. Weitzman. 2000. A new genus and species of inseminating (Teleostei: Characidae: Cheirodontinae: Compsurini) from South America with uniquely derived caudal-fin dermal papillae. *Proceedings of the Biological Society of Washington*, 113(1): 269-283.
- Meek, S. E. & S. F. Hildebrand. 1916. The fishes of the freshwaters of Panama. *Field Museum of Natural History, Zoological Series*, 10(15): 217-374.
- Mirande, J. M. 2009. Weighted parsimony phylogeny of the family Characidae (Teleostei: Characiformes). *Cladistics*, 25: 574–613.
- Mirande, J. M. 2010. Phylogeny of the family Characidae (Teleostei: Characiformes): from characters to taxonomy. *Neotropical Ichthyology*, 8(3): 385-568.
- Nelson, K. 1964. Behavior and morphology in the Glandulocaudine fishes (Ostariophysi, Characidae). *University of California Publications in Zoology*, 75(2): 59-152.
- Schultz, L. P. 1944. The fishes of the family Characinidae from Venezuela, with descriptions of seventeen new forms. *Proceedings of the United States National Museum* 95 (3181): 235-367.
- Taylor, W. R. & G. C. van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9(2): 107-119.
- Weitzman, S. H. & S. V. Fink. 1985. Xenobryconin phylogeny and putative pheromone pumps in glandulocaudine fishes (Teleostei: Characidae). *Smithsonian Contributions to Zoology*, 421: 1-121.
- Weitzman, S. H. & N. A. Menezes. 1998. Relationships of the tribes and genera of the Glandulocaudinae (Ostariophysi: Characiformes: Characidae) with a description of a new

genus, *Chrysobrycon*. Pp. 171-192. In: Malabarba, L. R., R. E. Reis, R. P. Vari, Z. M. S. Lucena & C. A. S. Lucena (Eds.). *Phylogeny and Classification of Neotropical Fishes*. Porto Alegre, Edipucrs, 603p.

Table 1. Morphometric data for *Compsura heterura* (H = holotype; A = coastal drainages; B = rio São Francisco drainage).

	A						B				
	H	N	Min	Max	Mean	SD	N	Min	Max	Mean	SD
Standard length (mm)	28.7	205	19.0	32.1	26.2	-	54	21.7	30.5	26.0	-
Percents of Standard Length											
Head length	25.5	205	23.8	29.5	26.8	1.1	54	25.5	30.6	27.2	1.2
Bony Head length	25.4	205	23.4	28.8	26.1	1.0	54	24.6	28.6	26.3	0.9
Snout-anal distance	66.3	205	63.5	74.4	67.8	1.5	54	65.0	73.0	68.1	1.4
Snout-dorsal distance	52.1	205	47.7	66.5	52.5	1.6	54	44.8	69.4	52.9	2.9
Snout-pelvic distance	46.9	205	45.1	52.3	48.2	1.3	54	45.6	51.9	48.5	1.4
Snout-pectoral distance	26.9	205	24.2	29.7	27.0	1.0	54	25.3	31.7	27.8	1.4
Dorsal-fin base length	14.5	205	12.6	15.8	14.2	0.7	54	13.3	16.0	14.4	0.6
Anal-fin base length	23.9	205	21.7	27.4	24.5	1.1	54	22.4	27.4	25.1	1.1
Length of caudal peduncle	15.4	205	10.6	16.8	13.4	1.0	54	10.2	16.0	13.0	1.0
Depth of caudal peduncle	14.6	205	11.7	16.2	13.7	0.8	54	12.2	15.2	13.7	0.8
Body depth at dorsal-fin	39.2	205	31.5	42.8	36.1	2.0	54	33.9	40.3	37.4	1.6
Dorsal-fin length	30.3	197	25.6	32.8	29.2	1.4	51	25.9	32.5	29.6	1.7
Pelvic-fin length	18.3	205	15.8	22.8	18.3	1.5	54	15.9	30.5	18.9	2.2
Pectoral-fin length	20.3	204	16.7	28.1	20.8	1.5	52	17.5	24.8	20.5	1.5
Percents of Head Length											
Snout length	26.6	205	21.2	30.0	25.9	1.8	54	24.6	30.0	27.1	1.3
Upper Jaw length	24.7	205	20.3	32.0	26.7	1.6	54	23.4	30.7	27.0	1.5
Horizontal orbit diameter	37.9	205	34.1	44.0	38.2	1.9	54	34.6	41.8	38.5	1.6
Interorbital width	33.1	205	27.8	35.2	31.4	1.4	54	27.2	34.4	31.4	1.3

Table 2. Morphometric data for *Compsura* sp. n. Guaporé and *Compsura* sp. n. Araguaia (H = holotype).

	<i>Compsura</i> sp. n. Guaporé						<i>Compsura</i> sp. n. Araguaia					
	H	N	Min	Max	Mean	SD	H	N	Min	Max	Mean	SD
Standard length (mm)	29.8	50	21.7	29.8	25.4	-	23.5	20	18.2	26.2	21.9	-
Percents of Standard Length												
Head length	24.8	50	23.9	27.5	25.7	0.9	25.4	20	24.8	27.7	25.9	0.8
Bony Head length	26.1	50	23.3	27.5	25.6	0.9	24.4	20	24.0	26.8	25.5	0.8
Snout-anal distance	63.6	50	62.3	70.3	65.4	1.7	66.1	20	62.8	71.2	65.5	1.9
Snout-dorsal distance	51.0	50	49.7	54.0	52.0	1.1	52.5	20	50.0	55.8	51.9	1.3
Snout-pelvic distance	45.2	50	45.2	49.6	47.4	1.0	49.3	20	44.7	49.3	47.4	1.1
Snout-pectoral distance	25.9	50	24.5	29.1	26.3	0.8	25.8	20	24.9	27.9	26.2	0.9
Dorsal-fin base length	14.7	50	12.4	15.9	14.3	0.7	13.8	20	13.3	15.5	14.4	0.7
Anal-fin base length	29.5	50	25.2	30.2	28.2	1.1	27.1	20	25.0	27.9	26.4	0.8
Length of caudal peduncle	10.0	50	10.0	13.8	11.9	0.8	13.1	20	10.5	13.4	12.5	0.7
Depth of caudal peduncle	14.4	50	10.2	14.7	12.1	0.9	11.1	20	10.3	12.8	11.3	0.7
Body depth at dorsal-fin	36.4	50	32.9	39.3	35.3	1.2	30.1	20	29.5	36.1	31.6	2.0
Dorsal-fin length	31.4	41	27.5	33.0	29.6	1.2	27.3	20	25.1	32.5	28.7	1.9
Pelvic-fin length	25.8	50	15.8	25.8	19.4	2.0	17.8	20	16.1	20.9	18.1	1.4
Pectoral-fin length	20.6	50	15.5	20.7	18.3	1.3	19.4	20	14.9	21.5	17.6	1.8
Percents of Head Length												
Snout length	30.8	50	24.6	31.8	27.6	1.6	26.2	20	23.5	27.4	26.0	1.1
Upper Jaw length	30.4	50	23.3	30.4	26.8	1.5	25.5	20	22.2	26.5	24.4	1.4
Horizontal orbit diameter	40.0	50	36.1	44.5	40.1	2.0	41.4	20	37.5	44.9	41.2	1.7
Interorbital width	36.4	50	31.5	37.3	34.4	1.3	33.7	20	30.8	34.1	32.3	1.1

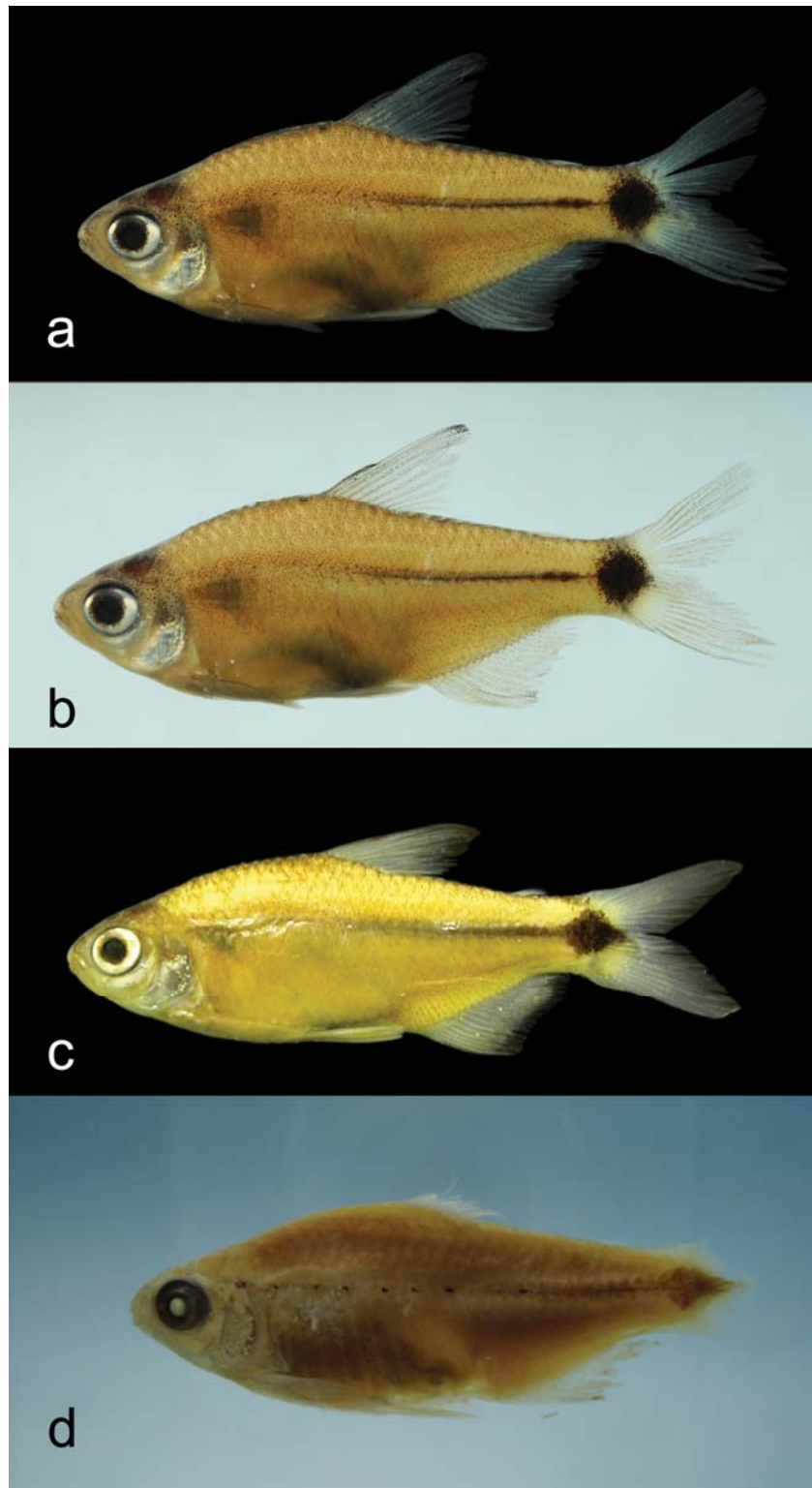


Fig. 1. *Compsura heterura*, (a, b) ANSP 171994, 25.8 mm SL; (c) UFRGS 12004, 29.7 mm SL; (d) FMNH 57825, 28.7 mm SL, holotype.

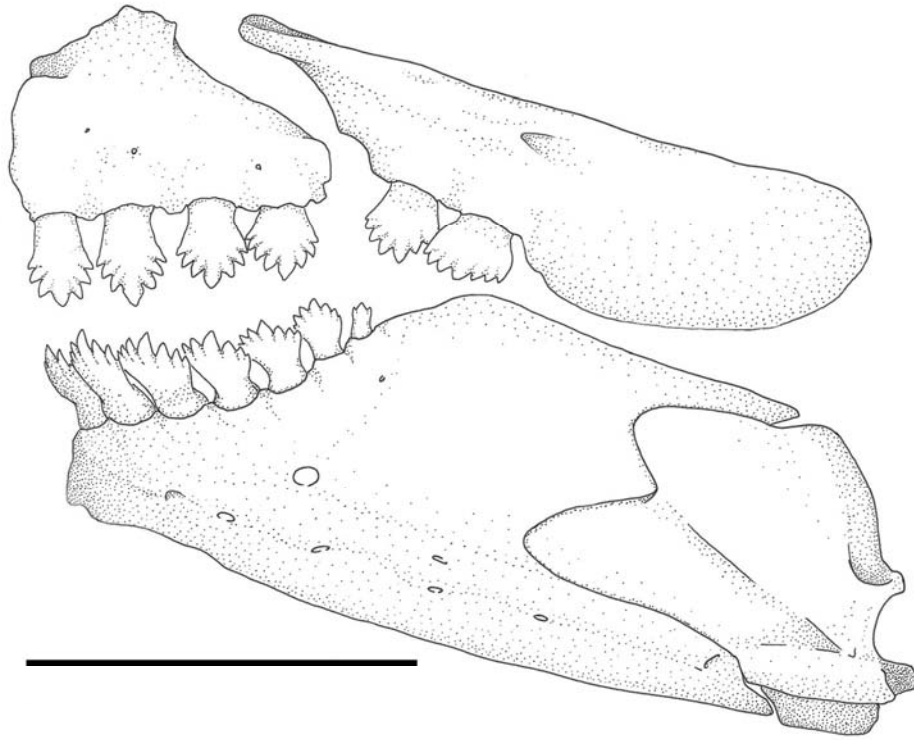


Fig. 2. Premaxilla, maxilla and dentary of *Compsura heterura*, MCP 17093, 28.0 mm SL. Scale bar = 1 mm.

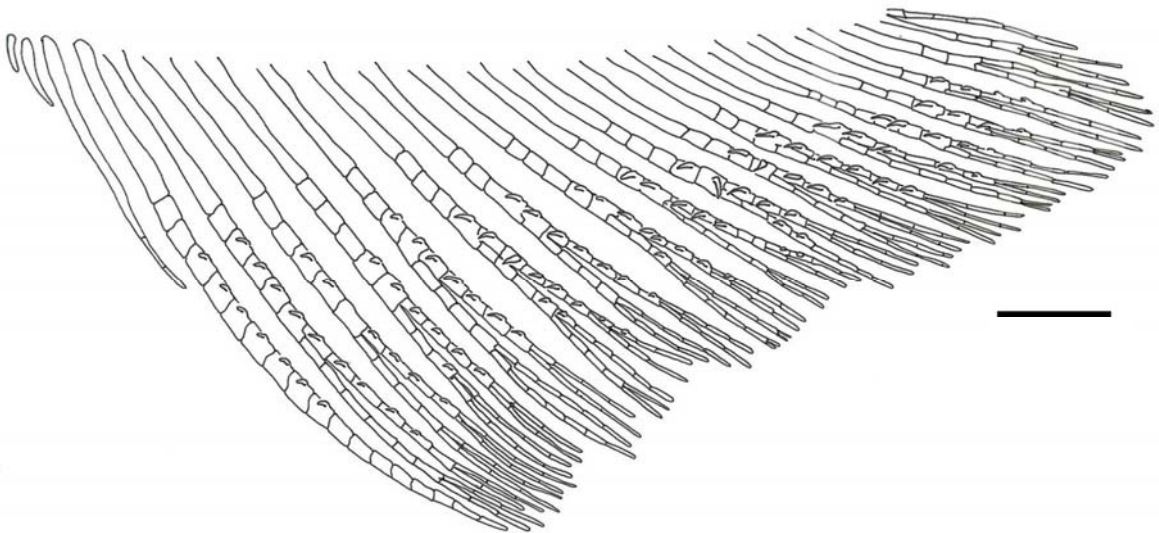


Fig. 3. Anal fin of *Compsura heterura* MCP 30939, 27.7 mm SL. Scale bar = 1 mm.

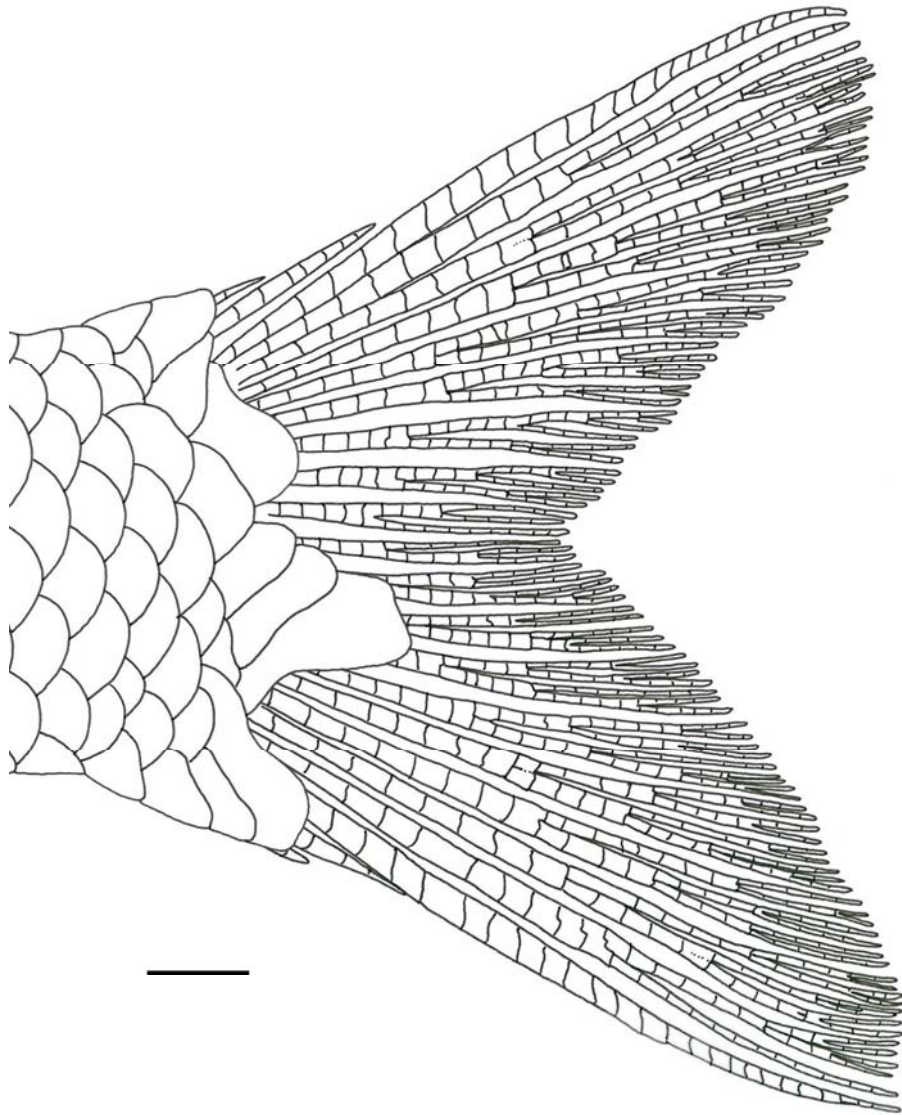


Fig. 4. Caudal fin of *Compsura heterura*, male, MCP 30939, 27.7 mm SL. Scale bar = 1 mm.

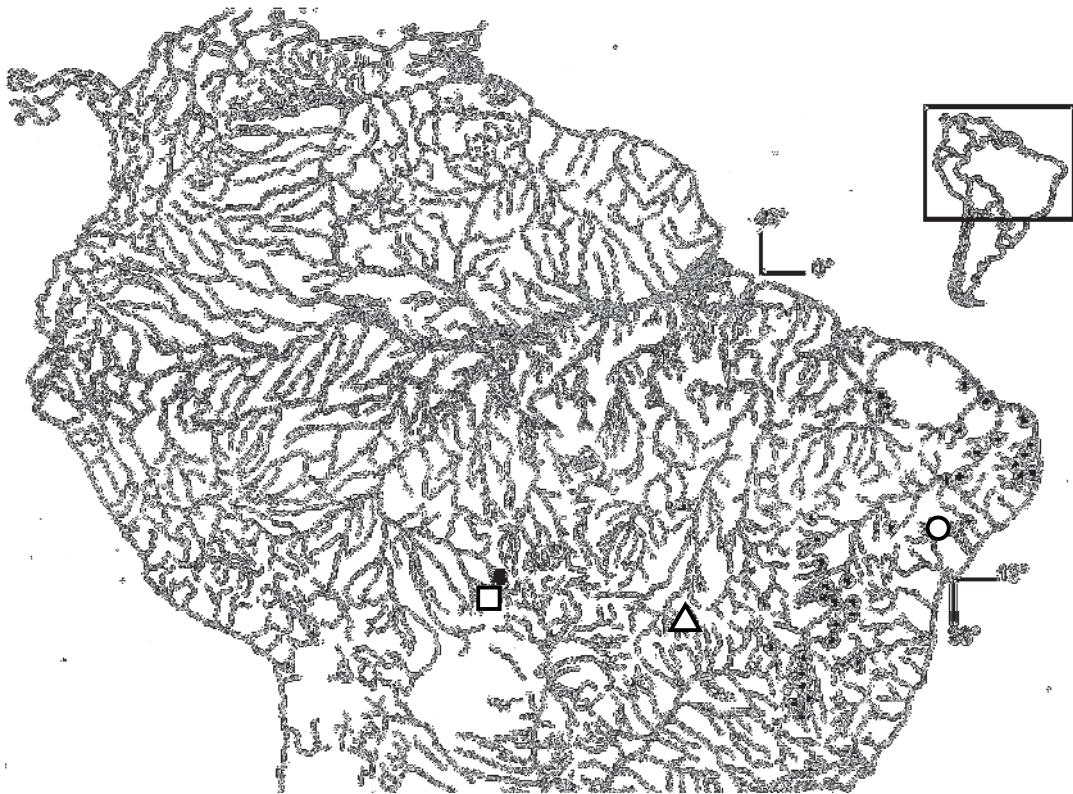


Fig. 5. Map of distribution for *Compsura heterura* (dots, empty circle = type locality), *Compsura Araguaia* n. sp. (triangles, empty triangle = type locality), and *Compsura Guaporé* n. sp. (squares, empty square = type locality).

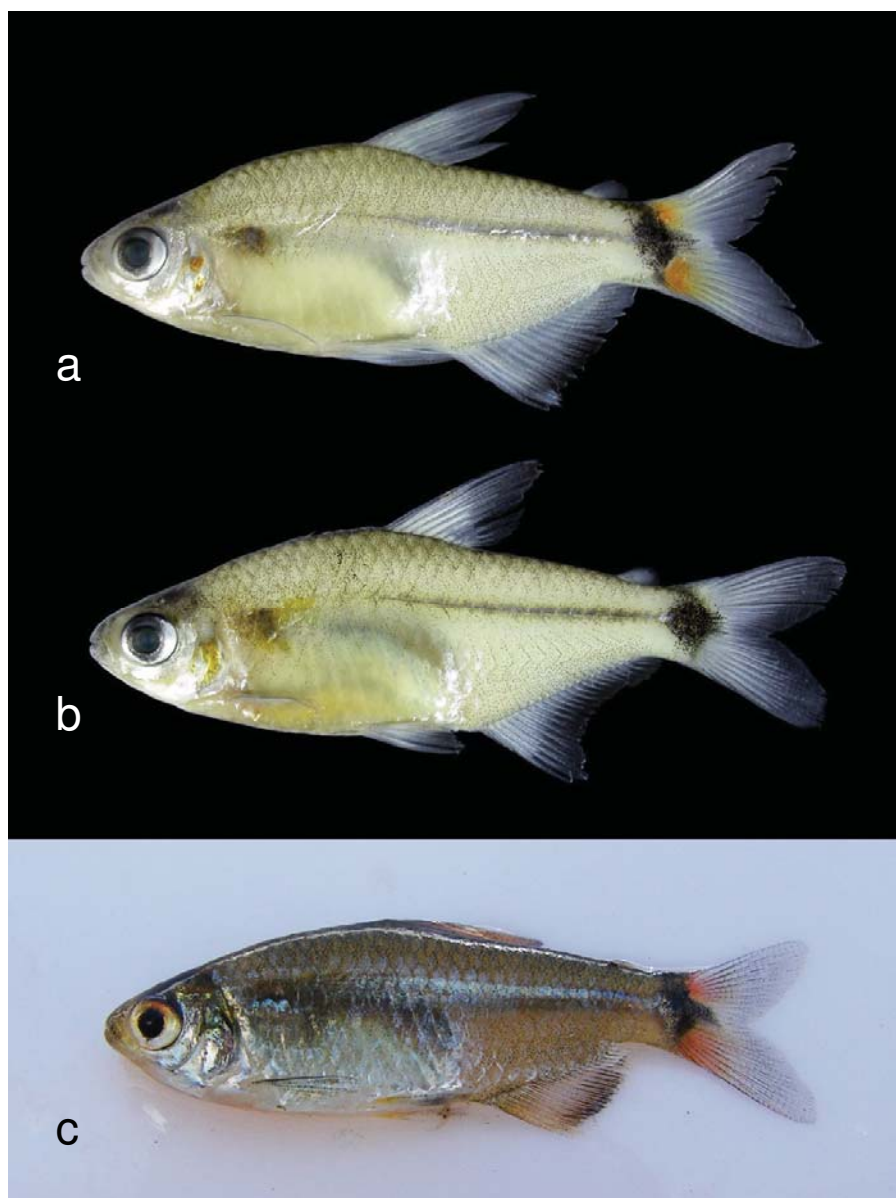


Fig. 6. *Compsura* Guaporé n. sp., (a) holotype UFRGS (uncatalogued), male, 29.8 mm SL; (b) UFRGS 12014 paratype, female, 29.4 mm SL; (c) UFRGS 12014, male, 28.2 mm SL, color just after fixation.

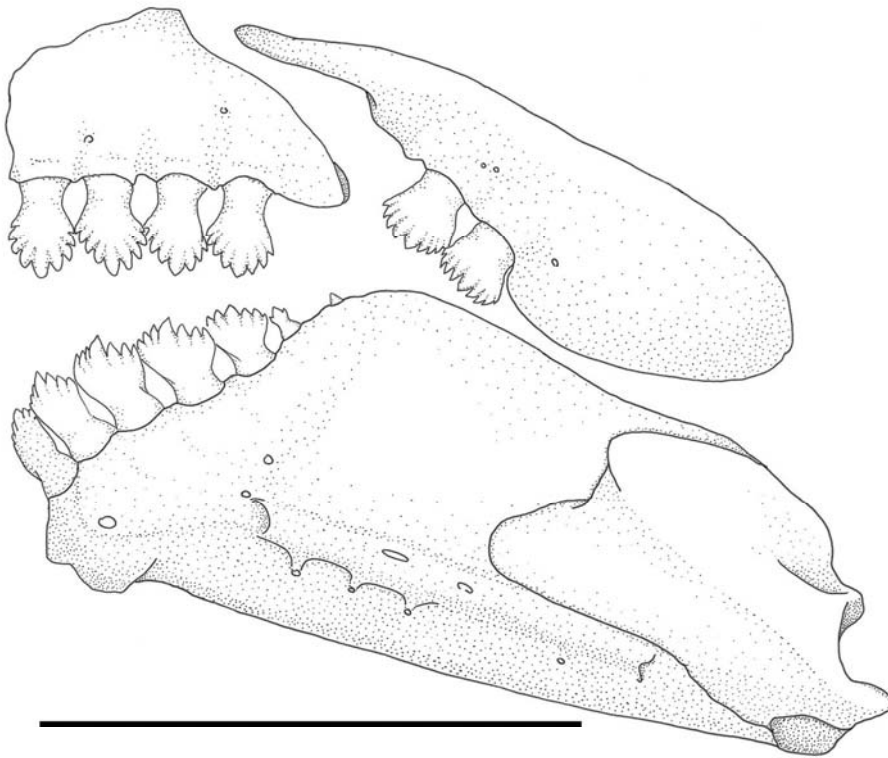


Fig. 7. Premaxilla, maxilla and dentary of *Compsura* Guaporé n. sp., MZUSP 37663, 24.1 mm SL. Scale bar = 1 mm.

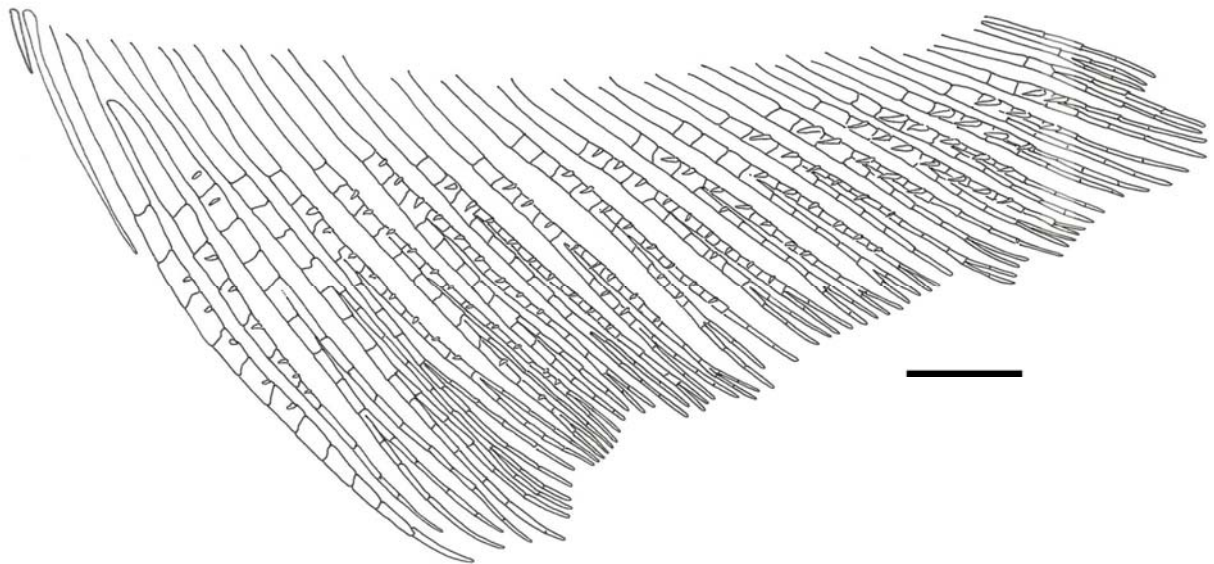


Fig. 8. Anal fin of *Compsura* Guaporé n. sp. UFRGS 12014, male, 28.9 mm SL. Scale bar = 1 mm.

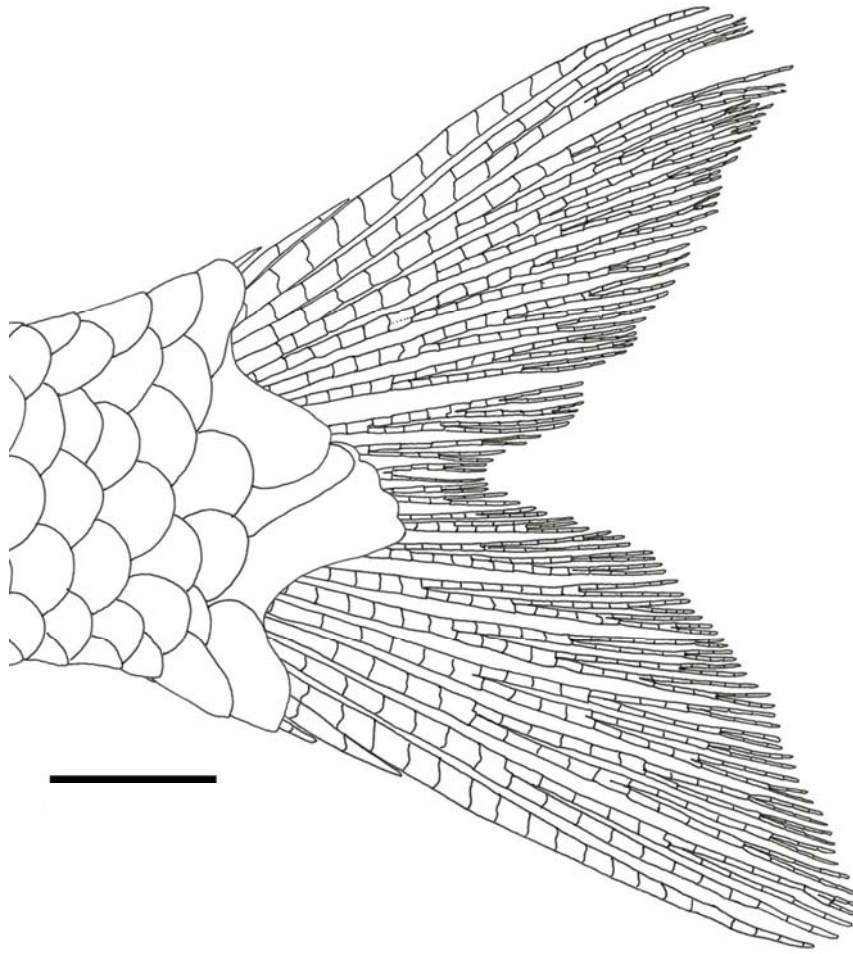


Fig. 9. Caudal fin of *Compsura* Guaporé n. sp., male, UFRGS 12014, male, 28.9 mm SL.
Scale bar = 1 mm.



Fig. 10. *Compsura Araguaia* n. sp., (a) UFRJ 1558, male, 22.2 mm SL; (b) UFRJ 1558, female, 26.1 mm SL.

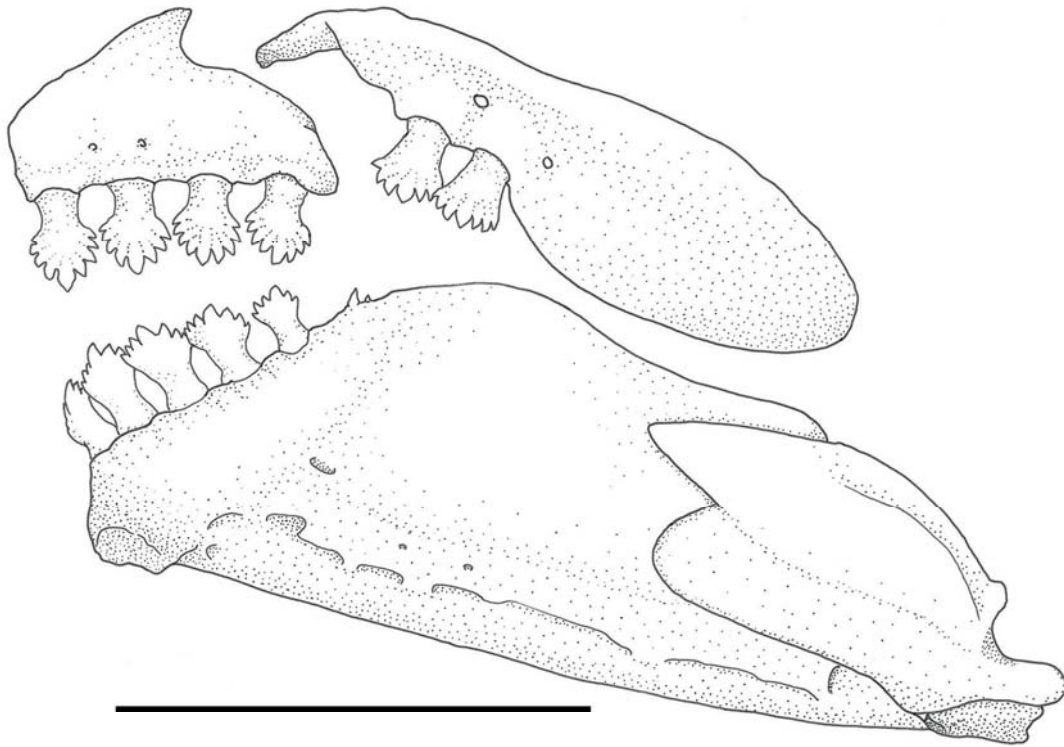


Fig. 11. Premaxilla, maxilla and dentary of *Compsura Araguaia* n. sp., MCP 44542, 18.2 mm SL. Scale bar = 1 mm.



Fig. 12. "*Compsura*" *gorgonae* ANSP 151219, 27.5 mm SL.

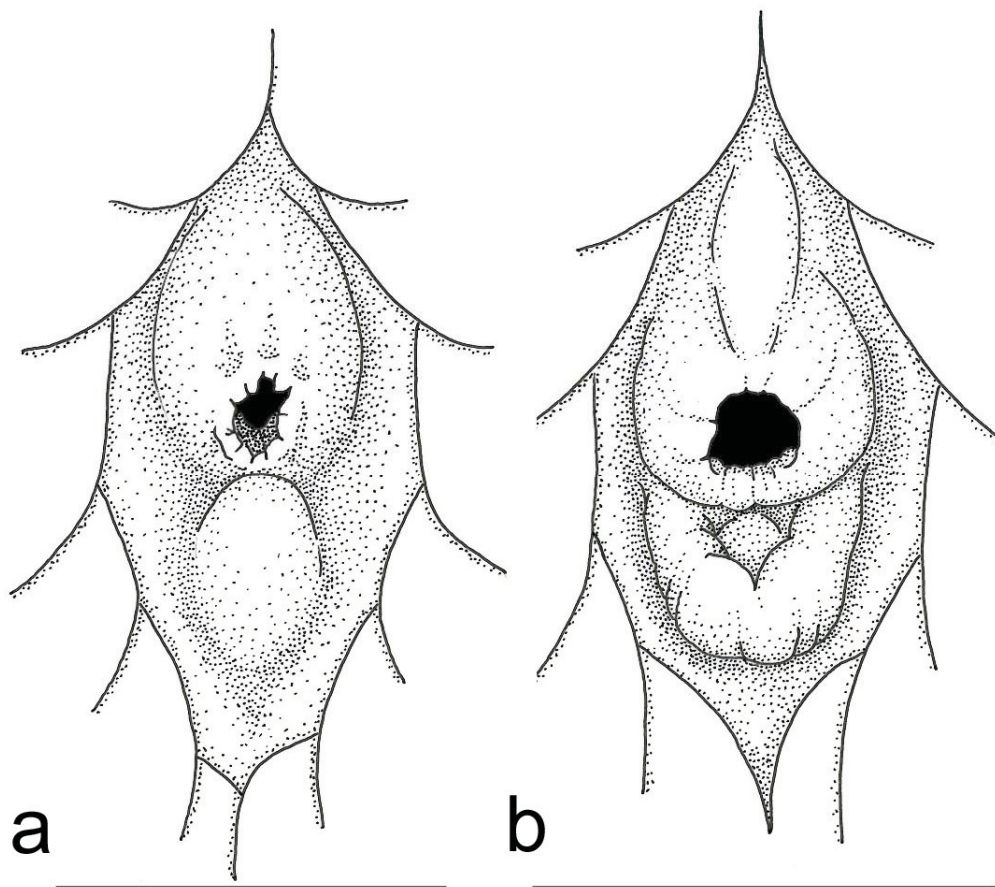


Fig. 13. Urogenital papillae of mature males of *Serrapinnus calliurus* MCP 19414, 31.4 mm SL (**a**); and *Compsura heterura* MCP 31368, 25.6 mm SL (**b**). Scale bar = 1 mm.

CAPÍTULO III

Revision of the genus *Macropsobrycon* Eigenmann, 1915 (Characidae: Cheirodontinae: Compsurini)

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Abstract

The cheirodontine genus *Macropsobrycon* is redefined and considered monotypic based on the morphological analysis of its type species. The type species, *M. uruguayanae*, is redescribed based on samples from the entire known geographical distribution of the species. *Macropsobrycon* is diagnosed by the following autapomorphies: (1) a small and elongate black spot is present on the proximal half of the second unbranched dorsal-fin ray; (2) presence of a small black spot on the base of unbranched anal-fin rays; (3) presence of a hypertrophied caudal-fin scale on ventral lobe of mature males; (4) 12th and 13th principal caudal-fin rays of males with robust retrorse hooks anteriorly directed at their branched portion; (5) 14th to 18th principal caudal-fin rays of males with feeble and flexible spinelets along their proximal length, and harder and anteriorly directed spinelets along its distal length; (6) 12th and 13th principal caudal-fin rays of males distant from each other, with the fin membrane between these contiguous rays bearing hypertrophied tissues. Sexually dimorphic characters of *M. uruguayanae* are further described and the relationships of the species with the remaining Compsurini are discussed.

Resumo

O gênero *Macropsobrycon* de Cheirodontinae é redefinido e considerado monotípico com base na análise morfológica da espécie tipo. A espécie-tipo, *M. uruguayanae*, é redescrita com base em amostras de toda a distribuição geográfica conhecida da espécie. *Macropsobrycon* é diagnosticado pelas seguintes autapomorfias: (1) presença de uma

mancha negra pequena e alongada na metade proximal do segundo raio não ramificado da nadadeira dorsal; (2) presença de uma pequena mancha negra na base dos raios não ramificados da nadadeira anal; (3) presença de uma escama hipertrofiada no lobo ventral da nadadeira caudal dos machos maduros; (4) porção ramificada dos 12° e 13° raios principais da nadadeira caudal dos machos, com ganchos robustos e retrorsos direcionados anteriormente; (5) 14° ao 18° raios principais da nadadeira caudal dos machos com “espinhos” frágeis e flexíveis ao longo de sua porção proximal, mais duros e anteriormente direcionados ao longo da porção distal; (6) 12° e 13° raios principais da nadadeira caudal dos machos espaçados, com a membrana entre eles portando tecido hipertrofiado. Caracteres de dimorfismo sexual secundário de *M. uruguayanae* são descritos e as relações da espécie com outros Compsurini são discutidas.

Key words: Systematics, Taxonomy, Neotropical, Sexual dimorphism.

Introduction

Historical review. Eigenmann (1915) described *Macropsobrycon*, containing a single species, *M. uruguayanae*, in the subfamily Cheirodontinae. In the Eigenmann's early concept of this subfamily (now corresponding to Aphyocharacinae + Aphyoditeinae + Cheirodontinae + Paragoniatinae + some *incertae sedis* characid genera), the Cheirodontinae diagnosis was presented in a topic “Generalized type of the subfamily” in which he referred the conspicuous small body size, the single tooth series, and the teeth with “lateral notches” [cusps] for these characids. Actually, the multicuspid teeth and the presence of one tooth series in the premaxilla and dentary have been the main characters used in subsequent years to diagnose the Cheirodontinae among characids. In the end of the description of *M. uruguayanae*, notably Eigenmann considered that its conical teeth would “place it outside the subfamily”, but also stated that its relationships [to Cheirodontinae] are “unmistakable”. He further considered *Macropsobrycon* related to *Parecbasis* Eigenmann, *Aphyodite* Eigenmann, *Leptobrycon* Eigenmann, and possibly to some *Megalampodus* Eigenmann, all genera currently removed from Cheirodontinae (Malabarba, 1998), differing from *Parecbasis* by having fainter dentition and incomplete lateral line, from *Aphyodite* by having the caudal fin naked and well developed pseudotympanum, and from *Leptobrycon* by having the anal fin longer.

Although consistent, Eigenmann's description was incomplete in some aspects as the color pattern of the dorsal and anal fins, and neither mentioned the complex caudal-fin structures present on mature males. He still affirmed that scales were "apparently absent from caudal" causing uncertainty about the presence of them on the caudal fin.

Géry (1960), reviewing the morphological affinities of some Cheirodontinae, placed *Macropsobrycon* in an "intermediate section" of the subfamily, among with 13 genera characterized by the presence of slender conical or tricuspid teeth, fourth infraorbital not developed, and presence of an adipose fin. In that paper, Géry split this "section" in three smaller groups, situating *Macropsobrycon* with some other "degenerate or specialized species" of the genera *Parecbasis*, *Leptobrycon*, *Aphyodite*, and *Thrissobrycon* Böhlke, based on the shared presence of an elongated body, conical teeth reduced in number and size (at least on the maxillary), and a thicker and blade-like maxillary. Géry still briefly distinguished *Macropsobrycon* from these other genera by the presence of a superior mouth, postorbitals (infraorbitals 4 and 5) not developed, fontanel short, lateral line incomplete, caudal naked, pseudotympanum and some interhaemals (caudal-fin procurrent rays) present; and described the shape of the *Macropsobrycon* premaxillary and mesethmoid (dermethmoid in that paper) bones as identical to those of the representatives of the "tricuspid cheirodontines" group, where the premaxillary is asymmetric with a high ascending process and low horizontal process, and the mesethmoid pointed.

Géry (1965) also included *Macropsobrycon* in his phenetic diagram with the representatives of the sub-tribe Aphyoditeini, suggesting that the genus could be the "junction" between the subgroup formed by *Prodontocharax* Eigenmann & Pearson, *Hyphessobrycon stigmatias* Fowler, and *Microschemobrycon* Eigenmann; and the subgroups formed by *Parecbasis*, *Aphyodite*, *Leptobrycon*, and *Brittanichthys* Géry. Later on Géry (1972) proposed an updated phenetic diagram for the Aphyoditeini, where *Macropsobrycon* was grouped with *Aphyodite* representing a major group with *Brittanichthys*, *Leptobrycon* and *Thrissobrycon*. In this work, Géry also emphasized the differences between *Aphyocharax melanotus* [sic] and *Macropsobrycon uruguayanae*, disagreeing with Eigenmann's (1915) suggestion about a possible close relationship between these species, and proposed the new combination *Microschemobrycon melanotus* (Eigenmann).

The genus remained monotypic up to Géry (1973) describes *Macropsobrycon xinguensis* in a revisionary study of the "Aphyoditeina" species from the Amazon basin.

Géry (1973) quoted several differences between *M. uruguayanae* and *M. xinguensis*, like, for instance, the absence of a humeral hiatus in his new species, as well as the presence of partially scaled caudal-fin lobes, tricuspid teeth (vs. conical), dorsal-fin in front of mid-body, number of branched anal-fin rays (17-18 vs. 19-22 in *M. uruguayanae*), number of perforated lateral line scales (8 vs. 5-6 in *M. uruguayanae*), and a different caudal color pattern. The placement of the new species in *Macropsobrycon* was considered by Géry a “conservative solution”, taken “provisory”, once both species have similar characters like feeble teeth, toothless maxillary and incomplete pored lateral line. Géry (1977) arranged the Cheirodontinae in two major groups: the Cheirodontinae *sensu stricto*, and the “allied genera”. The group represented by the “allied genera” was split in three tribes: Henochilini, Probolodini, and Grundulini. His former Aphyoditeina, including the *Macropsobrycon* species, was treated in this paper as the “Aphyodite-group”, inside the tribe Grundulini together with the *Grundulus*-group and the *Pristella*-group.

Reproductive biology. Little was known about the biology and reproductive characters of *Macropsobrycon* up to Burns *et al.* (1997) analysed histological sections of *Macropsobrycon uruguayanae*, as well as of some other cheirodontines, and found *M. uruguayanae* to be inseminating, presenting elongated spermatozoa also known as introsperm. Burns *et al.* (1998) carried out transmission electron microscopy on some inseminating characid species belonging to the subfamilies Aphyocharacinae, Glandulocaudinae (now part of Stevardiinae *sensu* Miranda, 2010), and Cheirodontinae, represented by *M. uruguayanae*. The same authors described briefly the spermatozoa ultrastructure of *M. uruguayanae*, and through new ultrastructural characters supported Malabarba’s (1998) hypothesis of independent development of insemination in the Glandulocaudinae and in the inseminating Cheirodontinae (now Compsurini). Later on the sperm ultrastructure of *M. uruguayanae* was described in detail by Oliveira *et al.* (2008), and its reproductive biology and gill gland development by Azevedo *et al.* (2010), making *M. uruguayanae* the best known cheirodontine in terms of reproductive aspects to date.

Systematics and relationships. In a phylogenetic study Malabarba (1998) defined Cheirodontinae *sensu stricto* and demonstrated cladistically that in the former systematic arrangement of the subfamily the species were artificially grouped, and

several genera and species were then removed from that taxon. *Macropsobrycon uruguayanae*, sharing the main synapomorphies with the other members of the subfamily, was kept in the more restricted group of the Cheirodontinae as part of a new inseminating tribe, Compsurini. On the other hand, *M. xinguensis* was considered *species incertae sedis* in Characidae, since it does not present all of the synapomorphies of the subfamily (Malabarba, 1998; Reis *et al.* 2003). The genus *Macropsobrycon* was further diagnosed by Malabarba (1998) based on four characters: (1) presence of a large space bearing hypertrophied tissue between the twelfth and thirteenth caudal-fin rays; (2) small and flexible spines present along the proximal portion of the lower lobe principal caudal-fin rays; (3) jaw teeth elongated and conical or tricuspid [modified herein, see diagnosis of *Macropsobrycon*]; and (4) the dorsal-fin strongly black-pigmented along the mid-length of the second unbranched and first 5 branched rays [modified herein, see diagnosis of *Macropsobrycon*], and weakly pigmented along their distal portion.

Secondary sexual characters of *M. uruguayanae* have been briefly discussed by Malabarba & Weitzman (1999, 2000) and Malabarba *et al.* (2004) in comparison to *Acinocheirodon melanogramma* Malabarba & Weitzman, *Kolpotocheirodon theloura* Malabarba & Weitzman, and *Kolpotocheirodon figueiredoi* Malabarba, Lima & Weitzman, respectively.

Mirande (2009, 2010) proposed a hypothesis of relationships among characid representatives and a new classification. Although the genus *Macropsobrycon* was kept in Cheirodontinae, none of its species were included in his analysis. Most recently, Javonillo *et al.* (2010) developed a phylogenetic study within the Characidae based on molecular sequenced data of a number of genera and species. The results showed *M. uruguayanae* as part of the Cheirodontinae in accordance with previous phylogenetic analysis based on morphological data, and *M. xinguensis* as sister group of *Hyphessobrycon herbertaxelrodi* Géry, inside a large clade including several *incertae sedis* Characidae genera distant from the Cheirodontinae clade.

Despite of the works regarding the relationships and reproductive biology of *Macropsobrycon uruguayanae*, the range of its geographical distribution, its morphological variation, and the secondary sexual dimorphism on its caudal fin, were never assessed. *Macropsobrycon uruguayanae* was described based on six specimens collected by Haseman in the río Uruguay basin [Uruguaiana and Cacequi, Rio Grande do Sul State], nevertheless the species has been collected in an wider geographical

range, encompassing the rio Negro basin (a tributary on the lower part of rio Uruguai), and the laguna dos Patos system in Rio Grande do Sul, Brazil and Uruguay. It is often misidentified as a *Heterocheiroduon* species, which present the same geographical distribution and similar body shape. Herein the genus *Macropsobrycon* is redefined based on new morphological characters related to its sexual dimorphism, and its type species *M. uruguayanae* redescribed based on specimens from all its geographical range, which allowed the study of the morphological variation among populations from different drainages. The secondary sexual characters found in the caudal fin of mature males are detailed reviewed and firstly described.

Material and Methods

Counts and measurements were taken according to Fink & Weitzman (1974), whenever possible on the left side of the specimens. Measures were taken point-to-point straight-line with a 0.01 precision caliper. Head length is defined as the distance between the tip of the snout and the posterior margin of subopercle (Bührnheim & Malabarba, 2006). Total vertebrae number includes the four vertebrae of the Weberian apparatus, and the terminal “half centrum” (Malabarba & Weitzman, 1999). Gill rakers were counted on first branchial arch, and the gill raker located at the junction of the ceratobranchial and the epibranchial was referred to the epibranchial count. The counts of vertebrae, supraneurals, teeth, and gill rakers were based on radiographs and cleared and stained (c&s) specimens following Taylor & van Dyke (1985) protocol. Scanning Electron Microscope (SEM) images were obtained from the jaws. Drawings of the anal fin, caudal fin, and scales were prepared in a stereomicroscope with camera lucida.

Sex identification of specimens was based on Gonçalves *et al.* (2005) and Bührnheim & Malabarba (2006), where males and females are recognized by dissection, or by the presence of sexual dimorphism, like anal and caudal-fin hooks, in specimens with similar size in the same sample. Specimens smaller than the smallest specimen showing sexual dimorphism in each lot are termed as unsexed, as well as specimens belonging to lots where sexual dimorphism is absent.

The redescription and the statistical and histological analysis were based on specimens from museum collections listed in the material examined, which abbreviations are: ANSP - Academy of Natural Sciences of Philadelphia, Philadelphia, USA; CAS - California Academy of Sciences, San Francisco, USA; FMNH - Field

Museum of Natural History, Chicago, USA; MCP - Museu de Ciências e Tecnologia, PUCRS, Porto Alegre, Brazil; MZUSP - Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; UFRGS - Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; and USNM - National Museum of Natural History, Smithsonian Institution, Washington D.C., USA. Other abbreviations are given along with the number of specimens: m - morphometric and meristic, c&s - cleared and stained.

Statistical analyses. Principal Component Analysis (PCA) was used to investigate morphometric variation among *Macropsobrycon uruguayanae* populations from three river basins: río Uruguay basin, rio Negro basin (a tributary of the lower rio Uruguai), and laguna dos Patos basin. The program PAST version 2.04 (Hammer *et al.*, 2001) was used for PCA analysis, the measures were logarithmically transformed. Considering that generally the first principal component mostly accounts for size variation (Strauss, 1985), a linear correlation was performed between the PC1 scores and the standard length values of the analysed specimens to test this hypothesis. A simple Multivariate Analysis of Variance (MANOVA) on the PC2 and PC3 scores, grouped by drainage, was also performed. The morphometric variable “dorsal-fin length” was not included on the PCA analysis once this data was missing for several specimens with the dorsal fin broken.

Results

Macropsobrycon Eigenmann, 1915

Macropsobrycon Eigenmann, 1915: 16 [key to Cheirodontinae species]; 48 [diagnosis; type species by original designation and monotypy: *Macropsobrycon uruguayanae* Eigenmann, 1915:]. -Géry, 1960: 2, 5, 9, 14 [placement in an unnamed group of degenerated of very specialized species with reduced conical teeth]. -Géry, 1965 [listed in a new subtribe of Cheirodontidi [sic], the Aphyoditeini]. -Géry, 1972: 15-18 [inclusion in Aphyoditeini]. -Géry, 1977: 594 [in key to Aphyoditeina genera and species]. -Malabarba, 1998: 218 [phylogenetic diagnosis and relationships to cheirodontine genera; included in the new tribe Compsurini]. -Malabarba & Weitzman, 1999: 424 [comparison with *Acinocheirodon melanogramma*]. -Malabarba *et al.*, 2003: 217 [listed in Cheirodontinae]. -Mirande, 2009: 8, 11 [listed as Cheirodontinae]. -

Javonillo *et al.*, 2010: 505-507 [relationships within Characidae]. -Mirande, 2010: 528, 531-532 [listed as Cheirodontinae].

Diagnosis. Distinguished from other genera of the Compsurini by the jaw teeth elongate and conical or rarely bicuspid. *Macropsobrycon* is further diagnosed from all characid species except the Cheirodontinae by the presence of cheirodontine synapomorphies (see discussion), and from all cheirodontine genera by the following autapomorphies: (1) a small and elongate black spot is present on the proximal half of the second unbranched dorsal-fin ray, corresponding to the distal half of the first unbranched dorsal-fin ray, sometimes extending over the first unbranched ray and corresponding region of the first branched ray [modified from Malabarba, 1998; originally stated as, black pigmentation along the mid-length of the second unbranched and first 5 branched rays]; (2) presence of a small black spot on the base of unbranched anal-fin rays; (3) presence of a hypertrophied caudal-fin scale on ventral lobe of mature males; (4) 12th and 13th principal caudal-fin rays of males with robust retrorse hooks anteriorly directed at their branched portion; (5) 14th to 18th principal caudal-fin rays of males with feeble and flexible spinelets along their proximal length, and harder and anteriorly directed spinelets along its distal length; and (6) 12th and 13th principal caudal-fin rays of males distant from each other, with the fin membrane between these contiguous rays bearing hypertrophied tissues.

***Macropsobrycon uruguayanae* Eigenmann, 1915**

Figs. 1-7

Macropsobrycon uruguayanae Eigenmann, 1915: 48 [original description; dentition figured; type locality Cacequi, Rio Grande do Sul, Brazil, rio Uruguay drainage]. -Henn, 1928: 59 [type material listed from Carnegie Museum]. -Ibarra & Stewart, 1987: 54 [type material listed from Field Museum of Natural History]. -Ringuelet, 1967 [listed as freshwater fish from Argentina]. -Géry, 1972: 15-18 [inclusion in Aphyoditeini]. -Géry, 1973: 108-109 [compared to *Macropsobrycon xinguensis*]. -Géry, 1977: 594 [in key to Aphyoditeina genera and species]. -Malabarba 1989: 136 [listed to laguna dos Patos drainage]. -Burns *et al.*, 1997: 434 [listed as inseminating species]. -Malabarba, 1998: 218 [phylogenetic diagnosis of the genus and placement in Compsurini]. -Burns *et al.*, 1998: 242 [short description of sperm ultrastructure]. -Malabarba & Weitzman,

1999: 416, 427 [comparison with *Acinocheirodon melanogramma*]. -Malabarba & Weitzman, 2000: 270, 279-280 [comparison with *Kolpotocheirodon theloura*]. -López *et al.*, 2003: 31 [listed from Argentina]. -Malabarba *et al.*, 2003: 217 [listed in Cheirodontinae]. -Quagio-Grassiotto *et al.*, 2003: 41 [sperm morphology compared to other characiforms]. -Menni, 2004: 78 [listed from Argentina]. -Malabarba *et al.*, 2004: 324-325 [comparison with *Kolpotocheirodon figueiredoi*]. -Malabarba, 2007: 37 [listed in Cheirodontinae]. -Pecio *et al.*, 2007: 458 [sperm morphology compared along with other inseminating characids]. -Oliveira *et al.*, 2008: 691-697 [description of sperm ultrastructure and comparison to inseminating characids]. -Bührnheim *et al.*, 2008: 671 [referred as bearing conical teeth]. -Miquelarena *et al.*, 2008: 78 [listed from Argentina]. -Javonillo *et al.*, 2010: 505-507 [relationships within Characidae]. -Azevedo *et al.*, 2010: 87-96 [reproductive biology and gill gland development].

Diagnosis. Same as the genus.

Description. Morphometrics given in Table 1. Body slightly elongate and compressed, deepest at dorsal-fin origin. Dorsal profile convex from snout tip to dorsal-fin origin, straight or slightly convex from that point to adipose-fin origin. Ventral profile convex from snout tip to pelvic-fin insertion, straight or somewhat concave up to anal-fin origin, straight to slightly convex on anal-fin base. Caudal-peduncle profile slightly concave dorsally and ventrally. Snout short, mouth slightly superior above horizontal line projected through pupil dorsal border and below horizontal line projected through orbit dorsal edge.

Premaxilla slender with 3(1), 4(1), 5(11), 6(14) or 7(4) conical teeth, aligned and similar in size; ascending process wide and square shaped. Maxilla toothless, wide, arched, with distal tip reaching or surpassing vertical line projected through orbit anterior edge. Dentary with 4(2), 5(8), 6(13), 7(4), 8(2) or 10(2) aligned teeth; teeth conical, rarely bicuspid; four medial teeth larger with similar size, following teeth smaller decreasing in size laterally (Fig. 2).

Dorsal-fin origin slightly posterior to vertical through middle of standard length. Dorsal-fin rays ii, 8-10 (mean = 9.0, n = 120). Adipose-fin origin at vertical line through last anal-fin ray insertion. Anal-fin origin slightly anterior to last dorsal-fin ray insertion; anterior rays longer than posterior ones; distal profile more convex on females than on males. Anal-fin rays iii-v, 17-22 (mean = 23.8, n = 121); last unbranched up to

ninth anal-fin branched ray of mature or maturing males bearing small retrorse hooks (Fig. 3). Hooks placed from middle length to near the distal tip of anal-fin rays, attached at posterior margin and usually posterior branch in branched portion, bent over lateral surface, and directed anteriorly to anal-fin frontal margin. One or two hooks per anal-fin ray segment. Pectoral-fin rays i, 10-12 (mean = 10.6, n = 121); longest rays surpassing pelvic-fin insertion. Pelvic-fin insertion anterior to vertical line through dorsal-fin origin. Pelvic-fin rays i, 7; all of them bearing 1-2 unilateral ventromedial antrorse hooks per segment on mature males. Caudal fin with 18-20 (mean = 19.0, n = 121) principal rays. Principal caudal-fin rays 12th and 13th bearing recurved strong hooks anteriorly directed on branched portions, usually dorsally; principal caudal-fin rays 14th to 18th bearing posteriorly directed feeble spinelets along proximal portion, and anteriorly directed bony hooks along mid- and distal portions of fin rays on mature males (Fig. 4).

Lateral line incomplete, with 3-8 (mean = 6.1, n = 91) perforated scales. Total scales at lateral line series 30-37 (mean = 33.6, n = 120) scales. Scale rows between dorsal-fin insertion and lateral line 5; scale rows between lateral line and pelvic-fin insertion 2-4 (mean = 3.2, n = 121). Predorsal scales 10-16 (mean = 12.9, n = 119); postdorsal scales 7-10 (mean = 8.2, n = 121); scales rows around caudal peduncle 12-14 (mean = 13.8, n = 121). Last scales of lateral scale rows with higher radii number on adult males than other body scales. Last scale of scale row below lateral line larger and posteriorly hypertrophied on mature males, with distal margin reaching or slightly overlapping most proximal caudal-fin ray spinelets (Figs. 5-6).

Mature males with gill gland on first branchial arch (Fig. 7). Gill rakers of first branchial arch 1.5 times longer than rakers from remaining branchial arches, not bearing denticles, 3(2), 4(2) on hypobranchial, 13(3), 14(1) on ceratobranchial, 7(4) on epibranchial. Supraneurals 4(1), 5(15), 6(74), 7(115), 8(28), 9(2). Total vertebrae 29(1), 30(35), 31(179), 32(35). Precaudal vertebrae 12(4), 13(227), 14(20).

Pseudotympanum as large muscular hiatus between first and second pleural ribs, limited dorsally by the *lateralis superficialis* muscle, posteriorly by naked anterior face of second pleural rib, posteroventrally by *obliquus inferioris* muscle, anteroventrally by *obliquus superioris* muscle.

Color in alcohol. Overall body color varying from light yellowish in fresh preserved specimens to pale brownish on old preserved specimens (Fig. 1a,c). Head black to dark

brownish dorsally. Region of infraorbitals 3-5 and opercular apparatus silvery on freshly preserved specimens and yellowish on older ones. Dark melanophores surround nares, lips, and anterior margin of orbit. Mentonian region dark due to high concentration of melanophores. Humeral spot absent. Dorsal and dorsolateral portion of body with melanophores distributed at posterior margin of the scales. Thin dark line extending laterally on body, from posterior region of pseudotympanum to caudal spot. Posterior portion of this line sometimes silvery. Caudal region with few melanophores distributed in oblique lines along myoseptum of *epaxialis* and *hypaxialis* muscles. Ventral region with higher concentration of melanophores around pelvic-fin insertion in mature males. All fins hyaline with scattered melanophores, except dorsal fin with a small elongated spot between distal tip of first unbranched ray and midpoint of second unbranched ray. Anal fin with an elongated small spot at base of unbranched anal-fin rays. Males with higher concentration of melanophores at distal margin of anal fin than females. Caudal spot round, not reaching dorsal and ventral margins of caudal peduncle, and not extending over middle caudal-fin rays; not conspicuous on some specimens.

Color in life. Overall body and head color pattern silvery to whitish (Fig. 1b). Lateral body band silvery. All the fins are hyaline with few scattered melanophores, and a small dark spot present at the dorsal and anal fin as described above.

Sexual dimorphism. Mature males can be differentiated from adult females by the presence hooks on pelvic, anal and caudal-fin rays (Figs. 3-5). Males also present the the gill filaments from the first branchial developed into a gill gland (Fig. 7), due to the fusion of adjacent gill filaments by expansion of the epithelium that covers it (Azevedo *et al.*, 2010). The last scale of the scale row below the lateral line is also larger and more developed in males than females (Fig. 6b). Although the females also present a homologous scale relatively large when compared to other cheirodontine species, it is still smaller than that observed in males. Mature males also have a higher number of melanophores at the distal portion of the anal-fin rays forming a tenuous dark band along the distal margin of the anal fin that it is not seen in females. The ventral profile of the anal fin also differs between males and females, being less concave on males.

Habitat and ecological notes. *Macropsobrycon uruguayanae* is usually found in natural flooded ponds and/or small lagoons with direct and active connection to rivers

or streams. This kind of habitat is strongly affected along the area of distribution of this species by its extensive use to rice cultivation. The species is inseminating with reproductive biology detaily described by Azevedo *et al.* (2010).

Distribution and geographical variation. Records of *Macropsobrycon uruguayanae* are known from Rio Grande do Sul State in southern of Brazil, Província de Entre Ríos in Argentina (Demonte & Arias, 2005; Miquelarena *et al.*, 2008), and Uruguay. Its geographical distribution encompasses the río Uruguay basin, rio Negro basin (large tributary of the lower río Uruguay), and laguna dos Patos drainage (Fig. 8).

The PCA analysis provided some morphological differences among the populations from the three studied drainages. The PC1 represented 72.5% of the variance, however it was found a correlation of 0.96 between its scores and the standard length values, showing to be most affected by the size. The PC2 and PC3 represented respectively 6.2% and 4.7% of the variance. The PC2 showed a trend of separation between the specimens from rio Negro and from río Uruguay basins. The individuals from rio Negro presented relatively smaller snout length and trends to bigger horizontal orbit diameter than the río Uruguay representatives. Morphological differences between *Macropsobrycon uruguayanae* from laguna dos Patos basin and rio Negro basin were evidenced by the PC3. The laguna dos Patos basin specimens presented somewhat larger caudal peduncle length and upper jaw length, and relatively smaller anal-fin base length than specimens from rio Uruguay basin (Fig. 9). The MANOVA analysis of the PC2 and PC3 scores did not succeed in discriminating the three populations.

Material Analyzed.

Macropsobrycon uruguayanae. **Type material.** Holotype: FMNH 57910, 36.0 mm SL, Brazil, Cacequy (= Cacequi), 1 Feb 1909, J. D. Haseman. Paratypes: FMNH 57911, 4, 14.4-35.5 mm SL, Brazil, Cacequy (= Cacequi), 1 Feb 1909, J. D. Haseman. FMNH 57912, 21.3 mm SL, Brazil, Cacequy (= Cacequi), 5 Feb 1909, J. D. Haseman. **Non-type material.** **Laguna dos Patos system**, Brazil, Rio Grande do Sul: MCP 8421, 1 (m, male, 34.7 mm SL), arroio Capané at bridge on BR 290, tributary of rio Jacuí, 24 Oct 1982, C. A. S. Lucena & L. R. Malabarba. MCP 9245, 6 (2m, males, 34.8-40.6 mm SL, 3, unsexed, 39.2-40.8 mm SL, 1 c&s, 32.4 mm SL), backwater of rio Jacuí, road between Santa Maria and Vera Cruz, 16 Sep 1983, C. A. S. Lucena *et al.* MCP 11997, 11 (4m, males, 32.4-39.8 mm SL, 6m, females, 31.1-39.2 mm SL, 1, unsexed, 30.9 mm

SL, 1 c&s, female, 32.4 mm SL), arroio Francisquinho on highway BR 290 between Butiá and Rio Pardo, rio Jacuí basin, 24 Oct 1982, C. A. S. Lucena & L. R. Malabarba. MCP 19410, 1 (unsexed, 22.3 mm SL), lakes on left margin of rio Jacuí, at bridge on road connecting BR 290 to Cachoeira do Sulpicará, 22 Jan 1996, L. R. Malabarba *et al.* MCP 20900, 87 (6m, males, 29.3-33.0 mm SL, 2m, females, 35.5-39.6 mm SL, 66, unsexed, 10.5-36.6 mm SL, 6 c&s, males, 24.6-34.2 mm SL, 2 c&s, females 33.2-35.1 mm SL, 1 c&s, unsexed, 23.4 mm SL), stream on rio Jacuí basin, at bridge on road between São Gabriel and Tiarajupuçá, 14 Jan 1997, L. R. Malabarba *et al.* MCP 37579, 2 (1m, male, 36.1 mm SL, 1m, female, 33.7 mm SL), Taim, Lago do Nicola, Jun 2004, A. Garcia. UFRGS 2244, 3 (unsexed, 22.9-24.7 mm SL) Rio Grande, Estação Ecológica do Taim, 8 May 1981, R. E. Reis & J. R. Stehmann. UFRGS 2245, 2 (1m, female, 34.0, 1, unsexed, 33.2 mm SL), between Taim and Mirim, channel parallel to BR 471 near a pump building in Estação Ecológica do Taim, 21 Apr 1979, L. Jardim & L. Chomenko. UFRGS 2306, (5m, females, 30.7-36.4 mm SL), between Rio Grande and Mirim, right margin of BR 471 on Arroio Taim road, Estação Ecológica do Taim, 7 Dec 1979, N. Menezes *et al.* UFRGS 2307, 3 (m, females, 33.0-35.2 mm SL), same locality as UFRGS 2306, 7 Jul 1979, P. A. Buckup. UFRGS 5604, 5 (4m, males, 34.2-35.4 mm SL, 1m, female, 34.0 mm SL), Barra do Ribeiro, arroio Ribeiro, bridge on road to Barra do Ribeiro, 19 Oct 1999. USNM 268449, 3 (2m, males, 31.3-32.0 mm SL, 1m, female, 37.3 mm SL), arroio Sarandi at stream under road crossing on road between Pelotas and Jaguarão, tributary of Lago Mirim North of arroio Grande, 14 Dec 1972, N. Menezes *et al.* **Rio Negro basin**, Brazil, Rio Grande do Sul: MCP 11932, 1 (unsexed, 25.4 mm SL), Bagé, arroio on BR 153 km 33 between Bagé and Aceguá, 25 Oct 1982, C. A. S. Lucena & L. R. Malabarba. MCP 11938, 6 (3m, males, 28.0-28.6 mm SL, 1m, female, 31.0 mm SL, 2, unsexed, 19.5-23.4 mm SL) rio Negro, bridge on highway BR 293, between Bagé and Aceguá, 25 Oct 1982, C. A. S. Lucena & L. R. Malabarba. UFRGS 8383, 2 (1m, female, 38.9 mm SL, 1, unsexed, 25.5 mm SL) Bagé, sanga Cinco Salsos, BR 153 between Aceguá and Bagé, 29 Mar 2006, L. R. Malabarba *et al.* UFRGS 8430, 18 (8m, males, 30.6-32.4 mm SL, 3m, females, 28.2-34.8 mm SL, 5, unsexed, 28.2-31.3 mm SL, 1 c&s, male, 31.3 mm SL), Bagé, rio Negro on highway BR 153 between Aceguá and Bagé, 29 Mar 2006, L. R. Malabarba *et al.* Uruguay, Cerro Largo: ANSP 168826, 20 (20.5-34.5 mm SL), Uruguay, Depto. Cerro Largo, pool at 10 m of rio Negro, Arreteria, 19 may 1984, C. A. S. Lucena & C. Chagas. MCP 11936, 120 (8m, males, 31.6-35.5 mm SL, 13m, females, 28.7-35.7 mm SL, 92, unsexed, 22.9-32.4

mm SL, 4 c&s, males, 30.2 mm SL, 5 c&s, females, 30.0-31.7 mm SL, 4 c&s, unsexed, 21.5-25.6 mm SL), same data as ANSP 168826. Uruguay, Rivera: UFRGS 7277, 2 (1m, male, 31.2 mm SL, 1m, female, 39.3 mm SL), rio Negro in the bridge on highway 44, 27 May 2005, L. R. Malabarba *et al.* Uruguay, Rio Negro: UFRGS 7421, 1 (m, female, 39.3 mm SL), on bridge in Pasos del Toros, rio Negro, 28 May 2005, L. R. Malabarba *et al.* **Rio Uruguay basin**, Brazil, Rio Grande do Sul: MCP 11810, 1 (unsexed, 20.9 mm SL), rio Uruguai, 10 Nov 1987, J. Bertoletti *et al.* MCP 11921, 4 (unsexed, 17.9-20.4 mm SL), rio Ibicuí-Mirim at rio Toropi mouth, 3 Jan 1983, UFSM. MCP 11922, 4 (unsexed, 18.9-22.5 mm SL), rio Ibicuí-Mirim at mouth on rio Santa Maria, 14 Jan 1983, UFSM - Universidade Federal de Santa Maria. MCP 11923, 3 (unsexed, 24.1-36.7 mm SL), rio Ibicuí-Mirim on rio Toropi mouth, 3 Jan 1983, UFSM. MCP 11924, 1 (unsexed, 22.8 mm SL), rio Santa Maria, 26 Oct 1982, C. A. S. Lucena & L. R. Malabarba. MCP 11925, 3 (unsexed, 32.7-35.1 mm SL), rio Ibicuí-Mirim on rio Santa Maria mouth, 14 Jan 1983, UFSM. MCP 11926, 7 (6m, males, 28.4-32.2 mm SL, 1m, female, 32.2 mm SL), São Francisco de Assis, rio Jaguari, 15 Sep 1983, C. A. S. Lucena *et al.* MCP 11927, 11 (unsexed, 24.6-35.9 mm SL), rio Ibicuí-Mirim, at road connecting Santa Maria to São Pedro, at 20 km far from Santa Maria, 20 Mar 1982, UFSM. MCP 11928, 36 (unsexed, 21.2-35.3 mm SL), rio Santa Maria, at BR 293, km 246, section Dom Pedrito/Santana do Livramento, 26 Oct 1982, C. A. S. Lucena & L. R. Malabarba. MCP 11929, 16 (5m, males, 31.2-33.6 mm SL, 2m, females, 31.5-31.9 mm SL, 9, unsexed, 30.6-33.26 mm SL), sanga on road Santa Maria/Mata, 13 Sep 1983, C. A. S. Lucena *et al.* MCP 11930, 10 (unsexed, 25.5-32.0 mm SL), Ponto 2, 8 Apr 1983, UFSM. MCP 11931, 51 (unsexed, 21.4-33.5 mm SL), rio Santa Maria on BR 293, km 246, section Dom Pedrito/Santana do Livramento, 26 Oct 1982, C. A. S. Lucena & L. R. Malabarba. MCP 11933, 1 (unsexed, 27.6 mm SL), rio Santa Maria, on BR 293, km 246, section Dom Pedrito/Santana do Livramento, 26 Oct 1982, C. A. S. Lucena & L. R. Malabarba. MCP 11934, 5 (unsexed, 26.1-34.4 mm SL), rio Ibicuí-Mirim, 10 Jun 1986, UFSM. MCP 11935, 6 (unsexed, 24.0-25.9 mm SL), Itaquí, mouth of rio Ibicuí at rio Uruguai, 19 Nov 1984, L. R. Malabarba & R. E. Reis. MCP 11937, 208 (6m, males, 31.8-33.9 mm SL, 7m, females, 29.6-34.4 mm SL, 191, unsexed, 21.8-34.4 mm SL, 4 c&s, males, 27.8-32.8 mm SL), rio Santa Maria on BR 293, km 246, section Dom Pedrito/Santana do Livramento, 26 Oct 1982, C. A. S. Lucena & L. R. Malabarba. MCP 11939, 223 (219, unsexed, 21.4-34.8 mm SL, 1 c&s, male, 30.1 mm SL, 3 c&s, females, 32.4-35.1 mm SL), rio Santa Maria on BR 293, km 246, section Dom Pedrito/Santana

do Livramento, 26 Oct 1982, C. A. S. Lucena & L. R. Malabarba. MCP 11998, 6 (1, males, 38.0 mm SL, 5, females, 36.5-44.6 mm SL), Santa Maria, pools on margin of rio Vacacai, 12 Sep 1983, C. A. S. Lucena *et al.* MCP 14158, 4 (2, unsexed, 37.6-39.5 mm SL), arroio Santo Antonio, at road Rosário do Sul/Santana do Livramento, 13 Dec 1989, C. Weber *et al.* MCP 14205, 1 (unsexed, 34.5 mm SL), pools on margin of rio Santa Maria, road Dom Pedrito/Santana do Livramento, 14 Dec 1989, C. Weber *et al.* MCP 15336, 7 (unsexed, 26.2-28.4 mm SL), Uruguaiana, affluent of rio Uruguay at PUC, 26 Feb 1991, E. Q. Chiva. MCP 16393, 2 (unsexed, 21.0-26.2 mm SL), São Marcos, marginal lake on Formosa beach, affluent of rio Uruguai, 11 Dec 1992, P. H. Wimberger *et al.* MCP 16399, 12 (unsexed, 20.9-28.8 mm SL), São Marcos, marginal lake on Formosa beach, affluent of rio Uruguay, 11 Dec 1992, P. H. Wimberger *et al.* MCP 18365, 86 (1m, male, 32.8 mm SL, 6m, females, 33.0-34.7 mm SL, 77, unsexed, 13.5-34.6 mm SL, 2c&s, females, 29.7-35.2 mm SL), São Marcos, marginal lake on Formosa beach, affluent of rio Uruguai, 21 Nov 1995, J. F. Pezzi *et al.* MCP 19602, 1 (unsexed, 27.7 mm SL), pool near Olaria on low land along side rio Santa Maria, BR 290, 15 Jan 1997, L. R. Malabarba *et al.* MCP 23660, 7 (2m, males, 31.3-31.6 mm SL, 4m, females, 30.2-32.7 mm SL, 1, unsexed, 28.0 mm SL), Uruguaiana, Sanchuri dam, 21 Jul 1999, R. C. Beheregaray. MCP 40723, 1 (unsexed, 20.9 mm SL), rio Touro Passo, 17 Oct 1985, C. A. S. Lucena *et al.*

Discussion

Relationships and characters defining *Macropsobrycon*.

Macropsobrycon uruguayanae presents most of the synapomorphies described by Malabarba (1998) to diagnose the Cheirodontinae: the peculiar pseudotympanum (see Ch. 1 of Malabarba 1998: 199), the lack of a humeral spot, and a single tooth row with teeth aligned and similar in shape and cusp number. The absence of the fourth synapomorphy - teeth multicuspid, pedunculate, largely expanded and distally compressed - was found by Malabarba (1998) to be apomorphically reversed in *M. uruguayanae*, which presents conical teeth. The only other cheirodontines that present conical teeth are included in a monophyletic clade hypothesized by Bührnheim *et al.* (2008), belonging to the tribe Cheirodontini, and composed by *Amazonspinther dalmata* Bührnheim, Carvalho, Malabarba & Weitzman plus *Spintherobolus* species.

When describing some deviations from the cheirodontine generalized type, Eigenmann (1915) included *Macropsobrycon* in a group of genera with “three-pointed”

teeth (p. 7), but in his picture of the types and variation of teeth in the Cheirodontinae (fig. 1, a-b¹, p. 9), and in the description of the genus *Macropsobrycon* and its type species (p. 48), Eigenmann only mentioned the presence of conical teeth, with few of them bearing a lateral notch. Géry (1960, 1965, 1972, 1973, and 1977) as well as Malabarba (1998, Ch. 56-0) considered that *M. uruguayanae* bears conical teeth. From 34 c&s specimens of *M. uruguayanae* only two relatively large females (MCP 18365, 35.2 mm SL; MCP 11939, 32.4 mm SL) presented one single tooth on the dentary bearing an evident lateral notch; the remaining specimens presented conical teeth both on the dentary and premaxillary.

Mature males of *Macropsobrycon uruguayanae* present several modifications associated with the secondary sexual system, such as presence of gill gland, caudal-fin hooks, and hypertrophy of the last body scales over the base of the caudal-fin rays. The occurrence of elaborate structural modifications associated with sexual dimorphism was hypothesized by Weitzman & Malabarba (1998) to be directly related to the existence of complex courtship behavior and/or the process of insemination. *Macropsobrycon uruguayanae* was recognized as an inseminating species by Burns *et al.* (1997), its sperm ultrastructure studied by Oliveira *et al.* (2008), and its gill gland development and reproductive biology described by Azevedo *et al.* (2010), but nothing is known about its courtship behavior.

Among characids, the presence of modified scales in the caudal fin is a feature known to occur in the inseminating species of the Stevardiinae, and Compsurini. Notwithstanding, recent morphological and molecular based phylogenies encompassing representatives of these groups have shown that they belong to distinct and distant evolutionary lineages in Characidae, denoting that both the modified caudal-fin structures and the associated inseminating process are homoplastic and have evolved independently in Compsurini and in some Stevardiinae representatives (Malabarba, 1998; Weitzman & Menezes, 1998; Malabarba & Weitzman, 2003; Calcagnotto *et al.* 2005; Weitzman *et al.*, 2005; Menezes *et al.*, 2008; Mirande, 2009, 2010; Javonillo *et al.*, 2010).

Among the Compsurini fishes, *Compsura heterura* Eigenmann, “*Compsura*” *gorgonae* (Evermann & Goldsborough), “*Odontostilbe*” *dialeptura* (Fink & Weitzman), “*O*”. *mitoptera* (Fink & Weitzman), *Saccoderma hastata* (Eigenmann), and *S. melanostigma* Schultz, present modified caudal-fin scales. “*Odontostilbe*” *dialeptura* and “*O*”. *mitoptera* have a cluster of small scales over the base of the middle caudal-fin

rays (Fink & Weitzman, 1974: fig. 3). These scales are feebler than the body scales, and are usually missing at specimens from museums. In *Compsura* species, *Saccoderma hastata* and *S. melanostigma* the modified scales are as strong as the body scales and firmly attached to the skin. These scales are placed at the lower lobe of the caudal fin, and compose one or more pouches associated to the hypertrophied tissue. The modified scales of *M. uruguayanae* are also present over the lower caudal-fin lobe, but they do not form any kind of pouch structure even on fully mature males. The largest scale of *M. uruguayanae* (Fig. 6b) has several radii; it is feebler than the common body scales, and generally is missing on preserved mature males. This scale enlargement associated to the modified shape of the scale of the lower caudal-fin lobe of *M. uruguayanae* is unique and autapomorphic for the genus and species.

Among cheirodontines, the presence of hooks at the caudal-fin rays is a character shared by most compsurin species including *Macropsobrycon uruguayanae*, *Acinocheirodon melanogramma*, “*Odontostilbe*” *dialeptura*, *Saccoderma hastata*, and *S. melanostigma*. Mature males of *M. uruguayanae* have hooks and spinelets from the 12th to the 18th caudal-fin rays. The hooks found on the 12th and 13th principal caudal-fin rays are restricted to the terminal branches of these rays, they are large, thick, retrorse, laterally and sometimes ventrally curved, and directed toward the caudal-fin base, while the spinelets are fragile and distributed along most length of the 14th to 18th principal caudal-fin rays (Figs. 4-5). The presence of these spinelets is unique among compsurins and an autapomorphy of *M. uruguayanae*.

Possible homologies of the hooks found in the 12th to the 13th caudal-fin rays of *Macropsobrycon uruguayanae* with remaining compsurin genera deserve further investigation, considering they vary in shape, size, and location. Mature males of *Acinocheirodon melanogramma* also present distinct hooks on the distal portion of 13th and 14th caudal-fin rays, but in this case, the caudal-fin hooks are longer, straight, angled dorsoanteriorly, and are borne by thickened ray segment (Malabarba & Weitzman 1999: 416-418, figs. 4-6). The caudal-fin hooks in “*Odontostilbe*” *dialeptura* are distributed from the 12th to the 15th principal rays and in *Saccoderma hastata*, and *S. melanostigma* from the 13th to the 18th rays (rarely on 19th), and on these species the hooks can be found along all the length of the rays. They have similar size all over the fin and are dorsoanteriorly directed in “*Odontostilbe*” *dialeptura*, and mostly retrorse and anteriorly directed in *Saccoderma* species. Besides this variation, the shape and distribution of the hooks in *M. uruguayanae* differ from all other compsurin.

The variation of color patterns among cheirodontines is not great. In spite of some species presenting notable marks on the dorsal fin such as *Amazonspinther dalmata*, *Odontostilbe pequirá* (Steindachner, 1882), *Prodontocharax melanotus* Pearson, 1924 and *Serrapinnus notomelas* (Eigenmann, 1915), or on the anal fin as some species of *Spintherobolus* Eigenmann, 1911 and *Amazonspinther dalmata*, most of the cheirodontines present basically a narrow longitudinal line at the body, a caudal spot, and scattered melanophores all over the dorsal, anal and caudal fins. As stated by Malabarba (1998), all the Compsurini share a dark distal border on the anal fin due to the higher concentration of melanophores in that region, a character more conspicuous on fully mature males. Eigenmann (1915) cited the presence of “an ovate dark spot on middle caudal peduncle” for *Macropsobrycon uruguayanae*, but neglects the small dark bars present between the first two unbranched dorsal-fin rays, and between the bases of the last two unbranched anal-fin rays (see color pattern description). The presence of these small spots on the anteriormost dorsal- and anal-fin rays is apomorphic, but it is also found in other Compsurini from South America. *Acinocheirodon melanogramma* and *Compsura heterura* also have a dark bar between the first and second unbranched rays of dorsal and anal fin from about the distal tip of first to about midlength of the second fin ray. *Kolpotocheirodon figueiredoi* also present a dorsal-fin spot, but in this species it is located posteriorly, between midlengths of the first and second, and second and third branched rays; and both *Kolpotocheirodon* species possess a dark bar at the midlength of the first branched anal-fin ray (Malabarba & Weitzman, 2000; Malabarba *et al.*, 2004). None of the trans-Andean Compsurini species possess any conspicuous bars as found on cis-Andean species.

Another peculiar color pattern of *Macropsobrycon uruguayanae* is the presence of a high concentration of melanophores anteriorly to- and around the pelvic-fin insertion in mature males. The melanophores are mainly scattered over the pelvic-girdle muscles, in a very similar pattern to that found in *Kolpotocheirodon figueiredoi*, as described by Malabarba *et al.* (2004: fig. 8). Mature males of *Kolpotocheirodon theloura* also present the respective ventral region darker than in females and immature males, but in this species the melanophores seem to be distributed along the contacting edge between the muscles *arrector ventralis pelvici* and *abductor superficialis pelvici*.

We found that “*Macropsobrycon*” *xinguensis* lacks the synapomorphies discussed above for Cheirodontinae, Compsurini, and even those characters shared

between *M. uruguayanae* and the other genera of Compsurini. “*Macropsobrycon*” *xinguensis* also lacks all autapomorphies proposed for *Macropsobrycon*, and thus does not belong to this genus, tribe and subfamily. Relationships of “*M*”. *xinguensis* will be dealt in a separate paper, with a new set of comparative taxa and characters than those discussed herein.

Macropsobrycon uruguayanae is the only Compsurini representative to occur in the Uruguay and laguna dos Patos basins. Other cheirodontines present in these systems are: *Cheirodon ibicuiensis* Eigenmann, 1915, *C. interruptus* (Jenyns, 1842), *Heterocheirodon yatai* (Casciotta, Miquelarena & Protogino, 1992), *H. jacuiensis* Malabarba & Bertaco, 1999, *Odontostilbe pequirá* (Steindachner), and *Serrapinnus calliurus* (Boulenger, 1900) (Malabarba, 2003, 2007). These Cheirodontini species can be readily distinguished from *M. uruguayanae* by the presence of expanded and distally compressed pedunculate teeth, and absence of any modifications at the caudal fin, like hooks or hypertrophied scales.

Comparative material. *Acinocheirodon melanogramma*: ANSP 176238, 7 paratypes, 21.9-26.2 mm SL, Brazil, Minas Gerais, rio Jequitaiá drainage. *Aphyodite grammica*: FMNH, holotype, 24.3 mm SL, Guiana, Konawaruk. MZUSP 29874, 20, 21.9-26.9 mm SL, Brazil, rio Negro. *Brittanichthys axelrodi*: MCP 14931, 17, 16.3-22.2 mm SL, 3 c&s, Brazil, Boa Vista, rio Negro. *Cheirodon australe*: USNM 84317, 12 paratypes, 28.4-49.8 mm SL, Chile, Los lagos Region at Puerto Varas. *Cheirodon dialepturus*: USNM 208524, holotype, 26.8 mm SL, Panama, Veraguas, rio San Pedro basin. *Cheirodon galusdae*: USNM 084319, 10 paratypes, 30.6-52.3 mm SL, Chile, Rio Locomilla at San Xavier. *Cheirodon gorgonae*: USNM 64094, holotype, 22.1 mm SL, Panama, Canal Zone, small seepage pool below spillway of the reservoir dam at Gorgona. *Cheirodon kiliani*: USNM 227310, 1 paratype, 25.2 mm SL. Valdivia-Chile, rio Cau-Cau. *Cheirodon microdon*: FMNH 57867, holotype, 32.2 mm SL, Brazil, Caceres, rio Ibicuhy. *Cheirodon micropterus*: CAS 59780, holotype, 23.9 mm SL, Brazil, Para, rio Amazonas drainage at Santarem. *Cheirodon mitopterus*: USNM 208539, holotype, 34.6mm SL, Panama, Cocle, rio Tucue, tributary of rio Cocle del Norte. *Cheirodon notomelas*: FMNH 57829, holotype, 28.2 mm SL, Brazil, Miguel Calmone. *Cheirodontops geayi*: USNM 121507, holotype, 35.5 mm SL, Venezuela, Estado de Aragua, rio Guarico. *Compsura heterura*: FMNH 57825, holotype, 28.7 mm SL, Brazil, rio Itapicuru, Queimadas. *Holesthes heterodon* (= *Serrapinnus heterodon*):

CAS 117522, 4 paratypes, 32.2-36.5 mm SL, Brazil, Minas Gerais, rio Grande, Jaguará. *Leptobrycon jatuaranae*: MCP 14936, 17, 20.8-25.1 mm SL, 3 c&s, Brazil, Amazonas, rio Negro. *Macropsobrycon* " *xinguensis*: MCP 34546, 26, 18.6-29.1 mm SL, 3 c&s, Brazil, Mato Grosso, Nova Canaã do Norte, rio Kaiapá. *Microschemobrycon guaporensis*: FMNH 57926, holotype, 29.1 mm SL, Brazil, Maciel, rio Guaporé. *Odontostilbe hastatus*: FMNH 56383, holotype, 30.2 mm SL, Colombia, Soplaviento. *Oligobrycon microstomus*: holotype, 31.0 mm SL, Brazil, Jacarehy on Rio Parahyba. *Oxybrycon* sp.: MCP 33105, 8, 13.7-14.9 mm SL, 2 c&s, Venezuela, Titi lagoon, upper Orinoco basin. *Parecbasis cyclolepis*: FMNH 56677, holotype, 56.3 mm SL, Brazil, rio Madeira. MZUSP 26146, 7, 40.3-53.5 mm SL, Peru, Ucayali, río Ucayali. *Pristella aubyni*: FMNH 52698, holotype, 34.9 mm SL, British Guiana. *Prodontocharax alleni*: CAS 117472, holotype, 32.8 mm SL, Peru, Ucayali, río Amazonas basin. *Prodontocharax melanotus*: CAS 59793, holotype, 44.9 mm SL, Bolivia, La Paz, rio Amazonas drainage at Tumupasa. *Pseudocheirodon affinis*: CAS 117516, 10 paratypes, 32.1-35.4 mm SL, Panama, río Gatun, at Gatun. *Saccoderma melanostigma*: USNM 121519, holotype, 26.7 mm SL, Venezuela, río San Juan, South of Mene Grande. *Spintherobolus broccae*: FMNH 58864, 1 paratype, 18.7 mm SL, Brazil, Rio de Janeiro. *Spintherobolus papilliferus*: FMNH 104802, holotype, 32.9 mm SL, Brazil, São Paulo, Alto da Serra. *Thrissobrycon pectinifer*: SU 16944, holotype, 26.8 mm SL, Brazil, Cucuhy, rio Negro. MCP 14932, 12, 26.4-30.2 mm SL, 3 c&s, Brazil, rio Arirara.

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Literature Cited

- Azevedo, M. A., L. R. Malabarba & J. R. Burns. 2010. Reproductive biology and development of gill glands in the inseminating characid, *Macropsobrycon uruguayanae* Eigenmann, 1915 (Cheirodontinae: Compsurini). *Neotropical Ichthyology*, 8(1): 87-96.
- Bührnheim, C. M., T. P. Carvalho, L. R. Malabarba & S. H. Weitzman. 2008. A new genus and species of characid fish from the Amazon basin - the recognition of a relictual lineage of characid fishes (Ostariophysi: Cheirodontinae: Cheirodontini). *Neotropical Ichthyology*, 6(4): 663-678.
- Bührnheim, C. M. & L. R. Malabarba. 2006. Redescription of the type species of *Odontostilbe* Cope, 1870 (Teleostei: Characidae: Cheirodontinae), and description of three new species from the Amazon basin. *Neotropical Ichthyology*, 4(2): 167-196.
- Burns, J. R., S. H. Weitzman, K. R. Lange & L. R. Malabarba. 1998. Sperm ultrastructure in characid fishes (Teleostei: Ostariophysi). Pp. 235-244. In: Malabarba, L. R., R. E. Reis, R. P. Vari, Z. M. S. Lucena, & C. A. S. Lucena (Eds.). *Phylogeny and Classification of Neotropical Fishes*. Porto Alegre, Edipucrs, 603p.
- Burns, J. R., S. H. Weitzman & L. R. Malabarba. 1997. Insemination in eight species of cheirodontine fishes (Teleostei: Characidae: Cheirodontinae). *Copeia*, 1997: 433-438.
- Calcagnotto, D., S. A. Schaefer & R. DeSalle. 2005. Relationships among characiform fishes inferred from analysis of nuclear and mitochondrial gene sequences. *Molecular Phylogenetics and Evolution*, 36(1): 135-153.
- Demonte, L. D. & J. D. Arias. 2005. Ictiofauna de afluentes de los ríos Paraná y Uruguay em la Provincia de Entre Ríos, Argentina. *Temas de la Biodiversidad del Litoral II, Insugeo – Miscelanea*, 14: 355-366.
- Eigenmann, C. H. 1915. The Cheirodontinae, a subfamily of minute characid fishes of South America. *Memoirs of the Carnegie Museum*, 7(1): 1-99.
- Fink, W. L. & S. H. Weitzman. 1974. The so-called Cheirodontin fishes of Central America with descriptions of two new species (Pisces: Characidae). *Smithsonian Contributions to Zoology*, 172: 1-46.
- Géry, J. 1960. Contributions to the study of characoid fishes. II. The generic position of *Hyphessobrycon innesi* and *Cheirodon axelrodi*, with a review of the morphological affinities of some Cheirodontinae (Pisces - Cypriniformes). *Bulletin of Aquatic Biology*, 2(12): 1-18.
- Géry, J. 1965. Poissons characoides sud-américains du Senckenberg Museum, II. Characidae et Crenuchidae de l'Igarape Preto (Haute Amazonie). *Senckenbergiana Biologica*, 46(1): 11-45.

- Géry, J. 1972. Corrected and supplemented descriptions of certain Characoid fishes described by Henry W. Fowler, with revisions of several of their genera. *Studies on the Neotropical Fauna*, 7: 1-35.
- Géry, J. 1973. New and little-known Aphyoditeina (Pisces, Characoidei) from the Amazon basin. *Studies on the Neotropical Fauna*, 8: 81-137.
- Géry, J. 1977. *Characoids of the world*. T.F.H. Publications, Neptune City, 672p.
- Gonçalves, T. K., M. A. Azevedo, L. R. Malabarba & C. B. Fialho. 2005. Reproductive biology and development of sexually dimorphic structures in *Aphyocharax anisitsi* (Ostariophysi: Characidae). *Neotropical Ichthyology*, 3(3): 433-438.
- Hammer, Ø. & D. A. T. Harper. 2005. PAST: Paleontological Statistics Software Package for Education and Data Analysis, version 1.93. Available at <http://folk.uio.no/ohammer/past/>.
- Javonillo, R., L. R. Malabarba, S. H. Weitzman & J. R. Burns. 2010. Relationships among major lineages of characid fishes (Teleostei: Ostariophysi: Characiformes), based on molecular sequence data. *Molecular Phylogenetics and Evolution*, 54: 498-511.
- Malabarba, L. R. 1998. Monophyly of the Cheirodontinae, characters and major clades (Ostariophysi: Characidae). Pp. 193-233. In: Malabarba, L. R., R. E. Reis, R. P. Vari, Z. M. S. Lucena & C. A. S. Lucena (Eds.). *Phylogeny and Classification of Neotropical Fishes*. Porto Alegre, Edipucrs, 603p.
- Malabarba, L. R. 2003. Subfamily Cheirodontinae (Characins, tetras). Pp. 215-221. In: Reis, R. E.; S. O. Kullander & C. J. Ferraris (Eds.). *Check list of the freshwater fishes of South and Central America*. Porto Alegre, Edipucrs, 729p.
- Malabarba, L. R. 2007. Family Characidae: Cheirodontinae. Pp. 36-38. In: Buckup, P. A., N. A. Menezes & M. S. Ghazzi (Eds.). *Catálogo das espécies de peixes de água doce do Brasil*. Série Livros 23 Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, 195p.
- Malabarba, L. R., F. C. T. Lima & S. H. Weitzman. 2004. A new species of *Kolpotocheirodon* (Teleostei: Characidae: Cheirodontinae: Compsurini) from Bahia, northeastern Brazil, with a new diagnosis of the genus. *Proceedings of the Biological Society of Washington*, 117(3): 317-329.
- Malabarba, L. R. & S. H. Weitzman. 1999. A new genus and species of South American fishes (Teleostei: Characidae: Cheirodontinae) with a derived caudal fin, including

- comments about inseminating cheirodontines. *Proceedings of the Biological Society of Washington*, 112(2): 410-432.
- Malabarba, L. R. & S. H. Weitzman. 2000. A new genus and species of inseminating fish (Teleostei: Characidae: Cheirodontinae: Compsurini) from South America with uniquely derived caudal-fin dermal papillae. *Proceedings of the Biological Society of Washington*, 113(1): 269-283.
- Malabarba, L. R. & S. H. Weitzman. 2003. Description of a new genus with six new species from southern Brazil, Uruguay and Argentina, with a discussion of a putative characid clade (Teleostei: Characiformes: Characidae). *Comunicações do Museu de Ciências e Tecnologia, PUCRS, Série Zoologia*, 16(1): 67-151.
- Menezes, N. A., A. C. Ribeiro, S. H. Weitzman & R. Torres. 2008. Biogeography of Glandulocaudinae (Teleostei: Characiformes: Characidae) reviewed: phylogenetic patterns, historical geology and genetic connectivity. *Zootaxa*, 1726: 33-48.
- Miquelarena, A. M., J. E. Mantinián & H. L. López. 2008. Peces de la Mesopotamia Argentina (Characiformes: Characidae: Cheirodontinae). *Temas de la Biodiversidad del Litoral III, Insugeo – Miscelanea*, 17: 51-90.
- Mirande, J. M. 2009. Weighted parsimony phylogeny of the family Characidae (Teleostei: Characiformes). *Cladistics*, 25: 574–613.
- Mirande, J. M. 2010. Phylogeny of the family Characidae (Teleostei: Characiformes): from characters to taxonomy. *Neotropical Ichthyology*, 8(3): 385-568.
- Oliveira, C. L. C., J. R. Burns, L. R. Malabarba & S. H. Weitzman. 2008. Sperm ultrastructure in the inseminating *Macropsobrycon uruguayanae* (Teleostei: Characidae: Cheirodontinae). *Journal of Morphology*, 269: 691-697.
- Pecio, A., J. R. Burns & S. H. Weitzman. 2007. Comparison of spermiogenesis in the externally fertilizing *Hemigrammus erythrozonus* and the inseminating *Corynopoma riisei* (Teleostei: Characiformes: Characidae). *Neotropical Ichthyology*, 5(4): 457-470.
- Quagio-Grassiotto, I., M. C. Gameiro, T. Schneider, L. R. Malabarba & C. Oliveira. 2003. Spermiogenesis and spermatozoa ultrastructure in five species of the Curimatidae with some considerations on spermatozoal ultrastructure in the Characiformes. *Neotropical Ichthyology*, 1(1): 35-45.
- Reis, R. E., S. O. Kullander & C. J. Ferraris (Eds.). 2003. Check List of the Freshwater Fishes of South and Central America. Porto Alegre, Edipucrs, 729p.

- Strauss, R. E. 1985. Evolutionary allometry and variation in body form in the South American catfish genus *Corydoras* (Callichthyidae). *Systematic Zoology*, 34: 381-396
- Taylor, W. R. & G. C. van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9(2): 107-119.
- Weitzman, S. & L. R. Malabarba. 1998. Perspectives about the phylogeny and classification of the Characidae (Teleostei: Characiformes). Pp. 161-170. In: Malabarba, L. R., R. E. Reis, R. P. Vari, Z. M. S. Lucena & C. A. S. Lucena (Eds.). *Phylogeny and Classification of Neotropical Fishes*. Porto Alegre, Edipucrs, 603p.
- Weitzman, S. H., N. A. Menezes, H-G. Evers & J. R. Burns. 2005. Putative relationships among inseminating and externally fertilizing characids, with a description of a new genus and species of Brazilian inseminating fish bearing an anal-fin gland in males (Characiformes: Characidae). *Neotropical Ichthyology*, 3(3): 329-360.

Table 1. Morphometric data of *Macropsobrycon uruguayanae*.

	Holotype	N	Min	Max	Mean	SD
Standard length (mm)	36.1	121	28.0	40.6	32.9	-
Percents of standard length						
Head length	23.5	121	21.3	27.3	24.2	1.1
Bony head length	20.3	121	19.0	24.1	21.7	0.8
Snout-anal fin distance	62.9	121	59.2	65.9	62.6	1.5
Snout-dorsal fin distance	53.4	121	50.3	56.9	54.2	1.3
Snout-pelvic fin distance	46.6	121	42.4	49.8	45.6	1.3
Snout-pectoral fin distance	25.4	121	24.5	29.5	26.8	1.0
Dorsal-fin base length	12.1	120	10.4	14.2	12.4	0.7
Anal-fin base length	28.9	121	22.7	28.9	26.0	1.4
Length of caudal peduncle	14.6	121	13.9	18.6	16.2	1.0
Depth of caudal peduncle	11.7	121	9.7	13.5	11.7	0.8
Body depth at dorsal-fin	31.8	121	27.3	35.2	30.9	1.4
Dorsal-fin length	25.6	113	23.3	30.1	26.5	1.2
Pelvic-fin length	14.7	120	14.0	17.7	15.9	0.8
Pectoral-fin length	23.3	120	19.5	25.9	22.4	1.3
Percents of head length						
Snout length	23.6	121	20.2	28.6	23.8	1.6
Upper Jaw length	36.6	121	29.3	38.5	34.5	1.8
Horizontal orbit diameter	37.4	121	30.8	42.9	36.4	2.8
Interorbital width	25.1	121	23.6	32.2	27.4	1.5

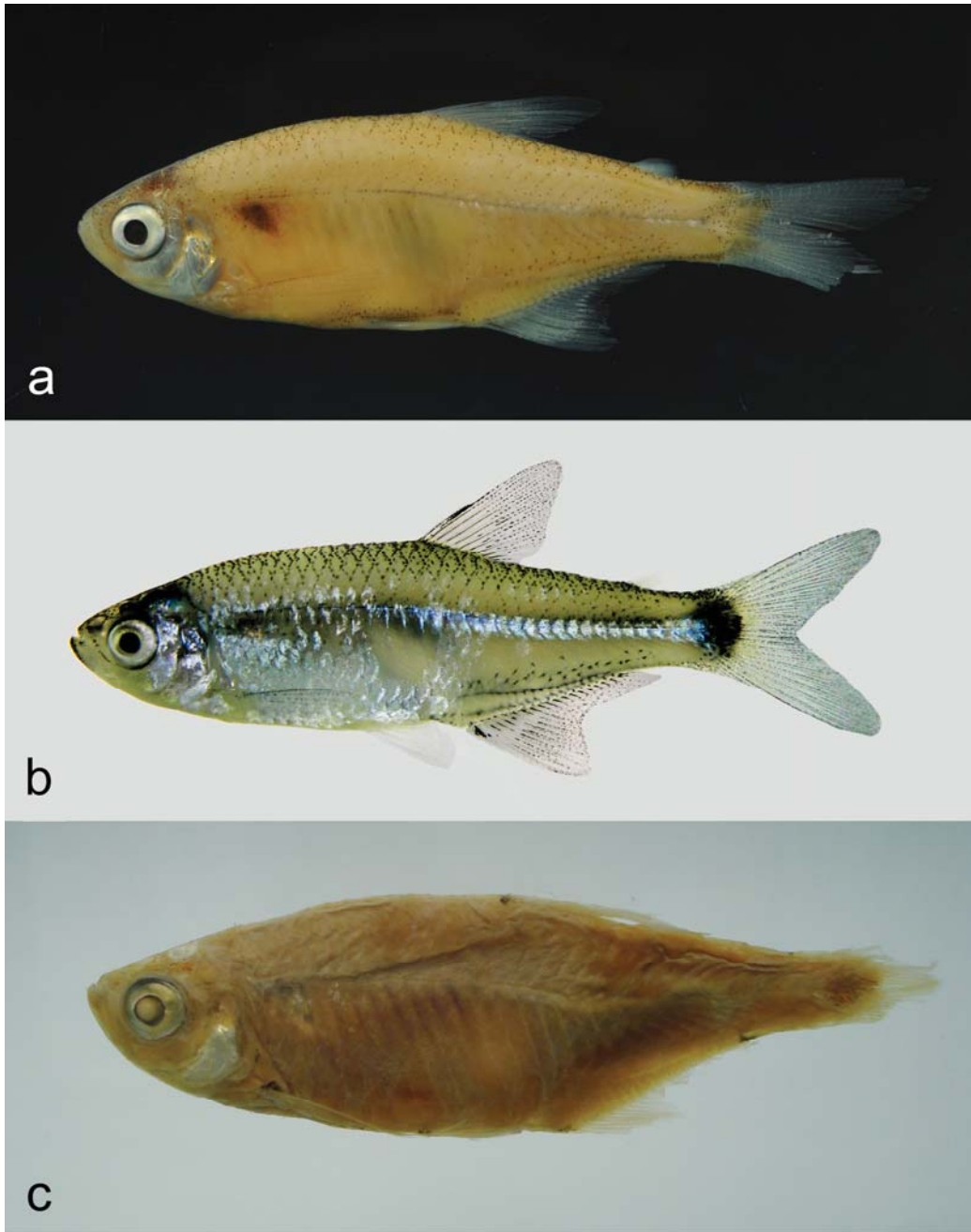


Fig. 1. *Macropsobrycon uruguayanae*, (a) ANSP 168826, 32.8 mm SL, Uruguay, Depto. Cerro Largo, pool of rio Negro; (b) specimen alive, not preserved; (c) holotype, FMNH 57910, 36.0 mm SL, Brazil, Cacequy, río Uruguay basin.

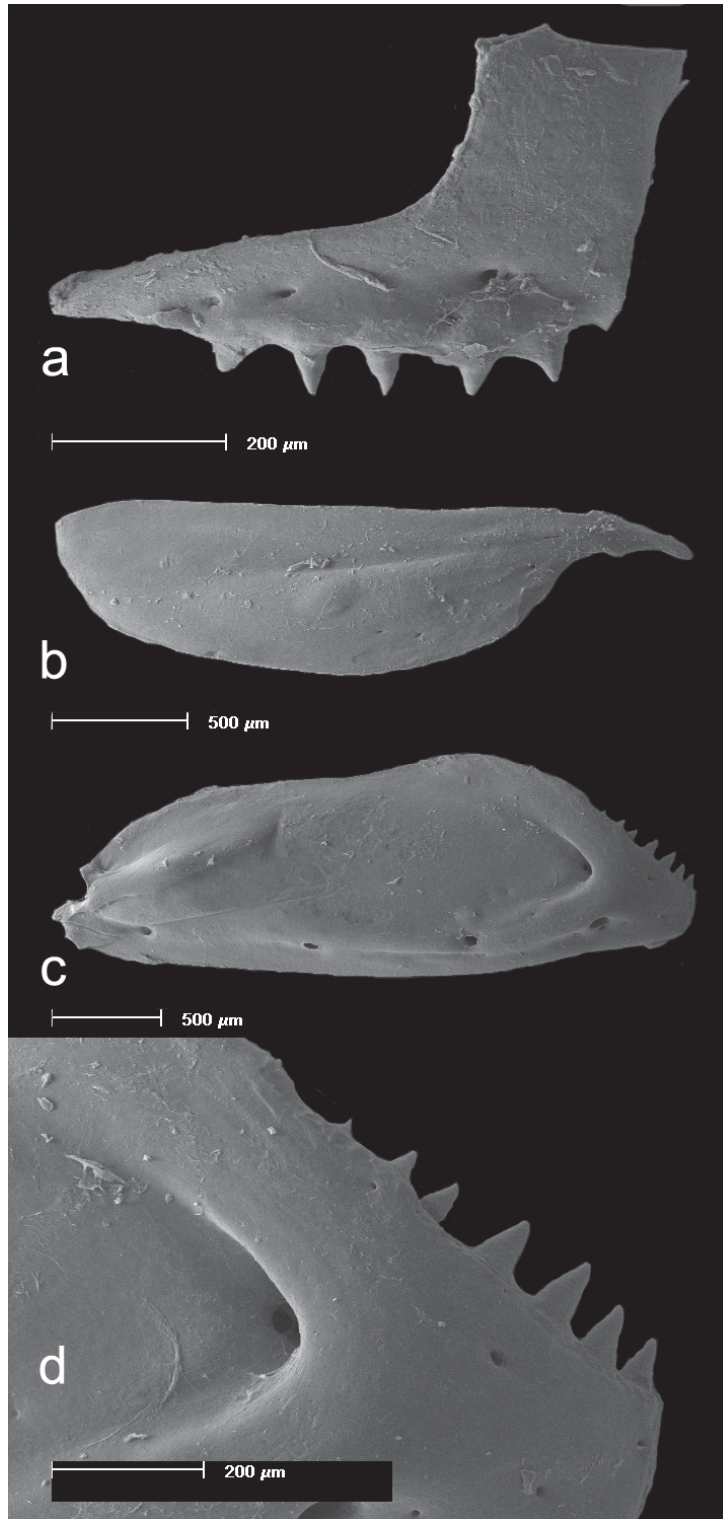


Fig. 2. *Macropsobrycon uruguayanae*, MCP 20900, 27.9 mm SL; scanning electron microscopy (SEM) images showing right side premaxillary (**a**), maxillary (**b**), and dentary (**c**), with detail of the teeth (**d**).

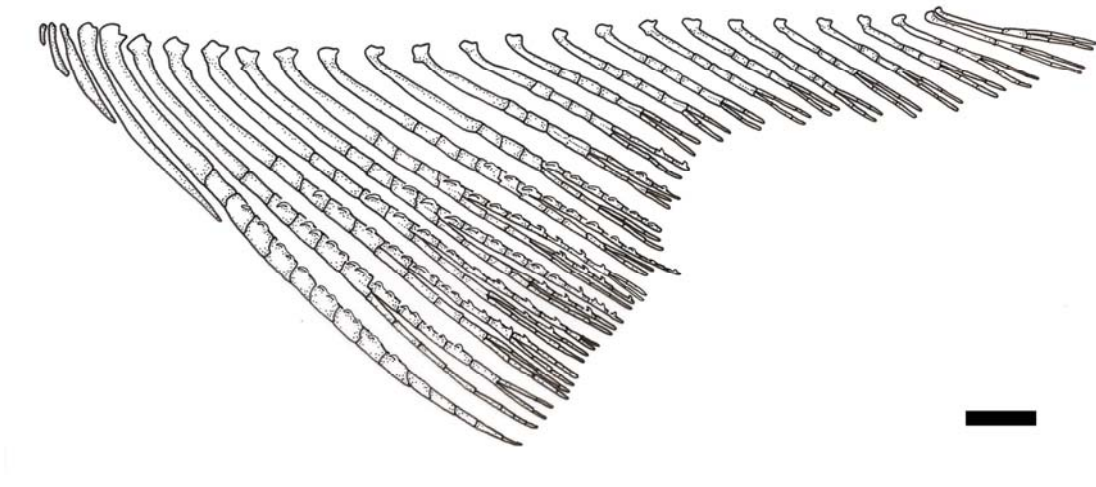


Fig. 3. *Macropsobrycon uruguayanae*, mature male, MCP 20900, 34.2 mm SL, left side lateral view of anal fin showing anal-fin hooks shape and distribution. Scale bar = 1 mm.

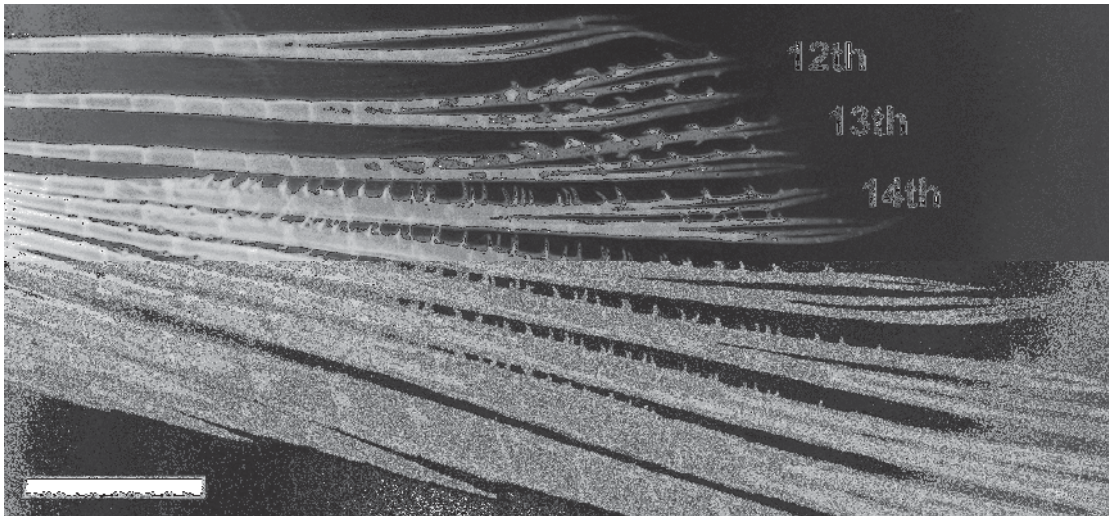


Fig. 4. *Macropsobrycon uruguayanae*, mature male, MCP 20900, 34.2 mm SL, left side lateral view of the caudal-fin lower lobe, hook distribution. Scale bar = 1 mm.

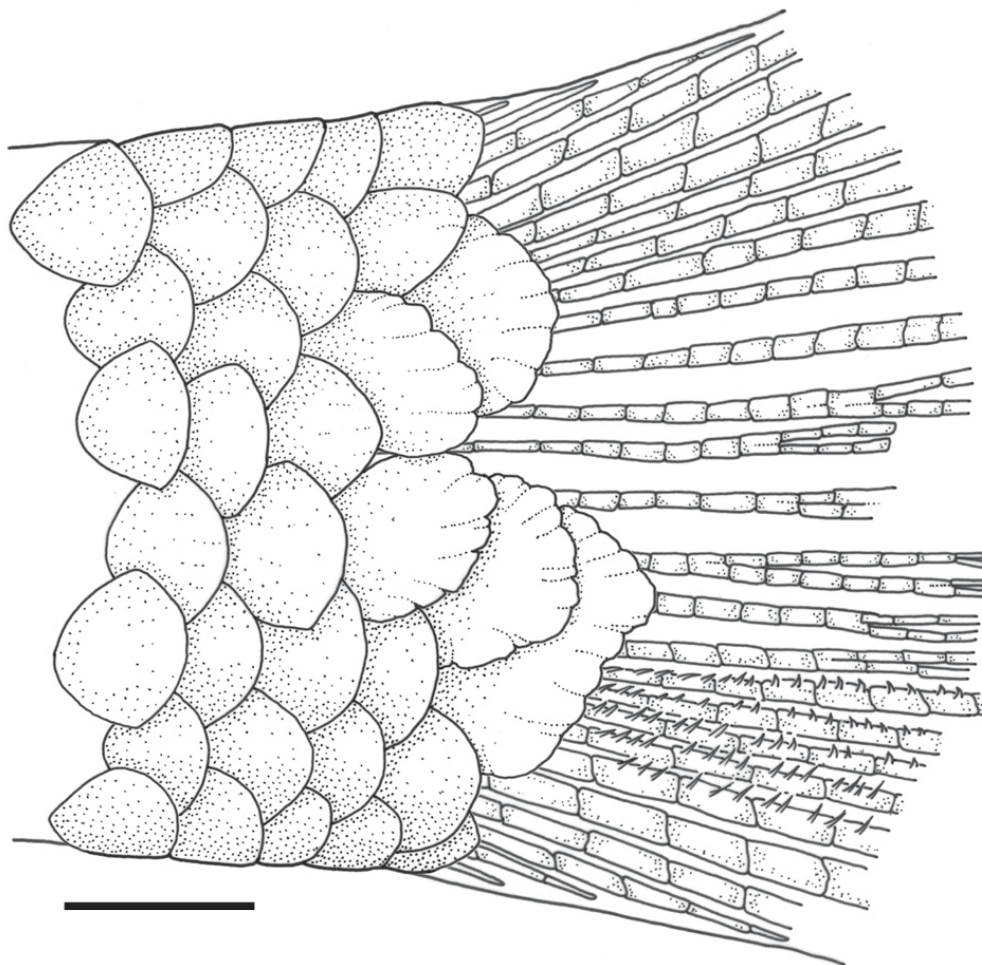


Fig. 5. *Macropsobrycon uruguayanae*, mature male, MCP 20900, 34.2 mm SL, left side lateral view of the terminal portion of the caudal peduncle and caudal-fin base, showing modified scales and distribution of the “spinelets” on the caudal-fin rays. Scale bar = 1 mm.

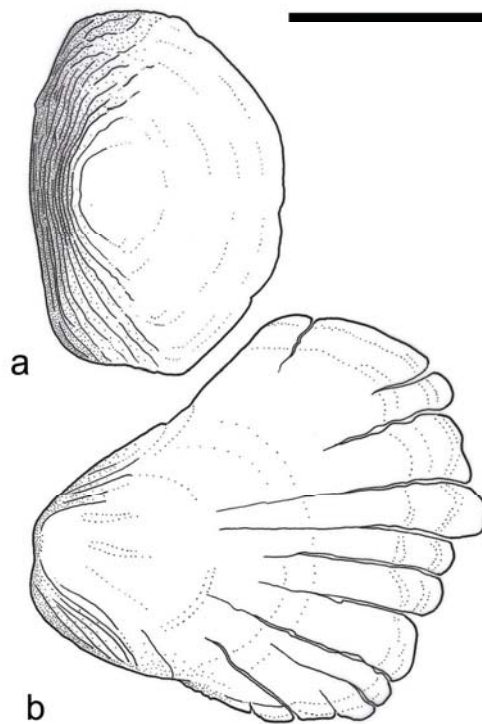


Fig. 6. *Macropsobrycon uruguayanae*, mature male, MCP 20900, 34.2 mm SL, left side, lateral view, (a) lateral body scale and hypertrophied caudal-fin scale. Scale bar = 1 mm.

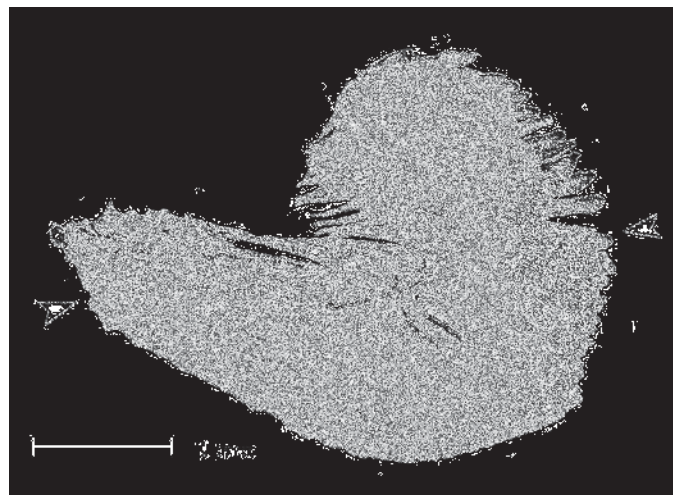


Fig. 7. *Macropsobrycon uruguayanae*, mature male, MCP 11939, 34.2 mm SL; scanning electron micrograph (SEM) of the first gill arch left side, showing the gill gland delimited by the arrows head.

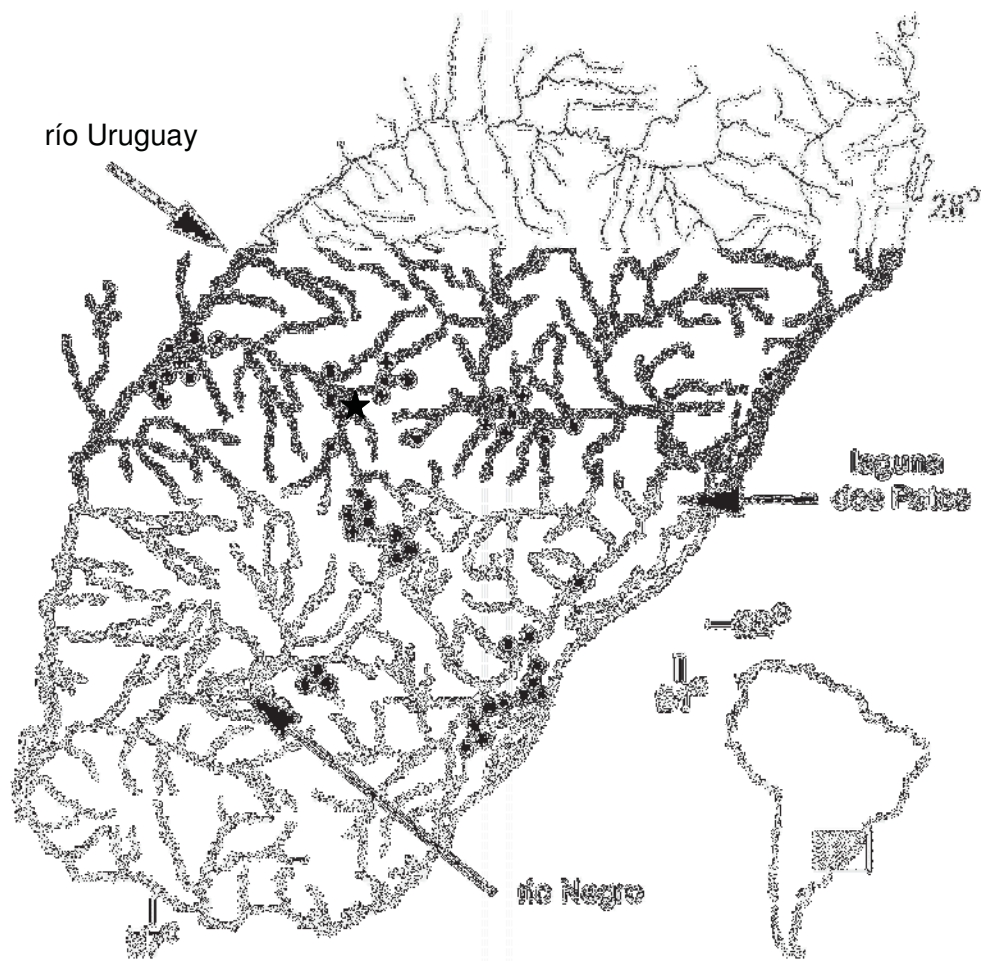


Fig. 8. Geographic distribution of *Macropsobrycon uruguayanae*, one dot can represent more than one locality or lots. The star represents the type locality.

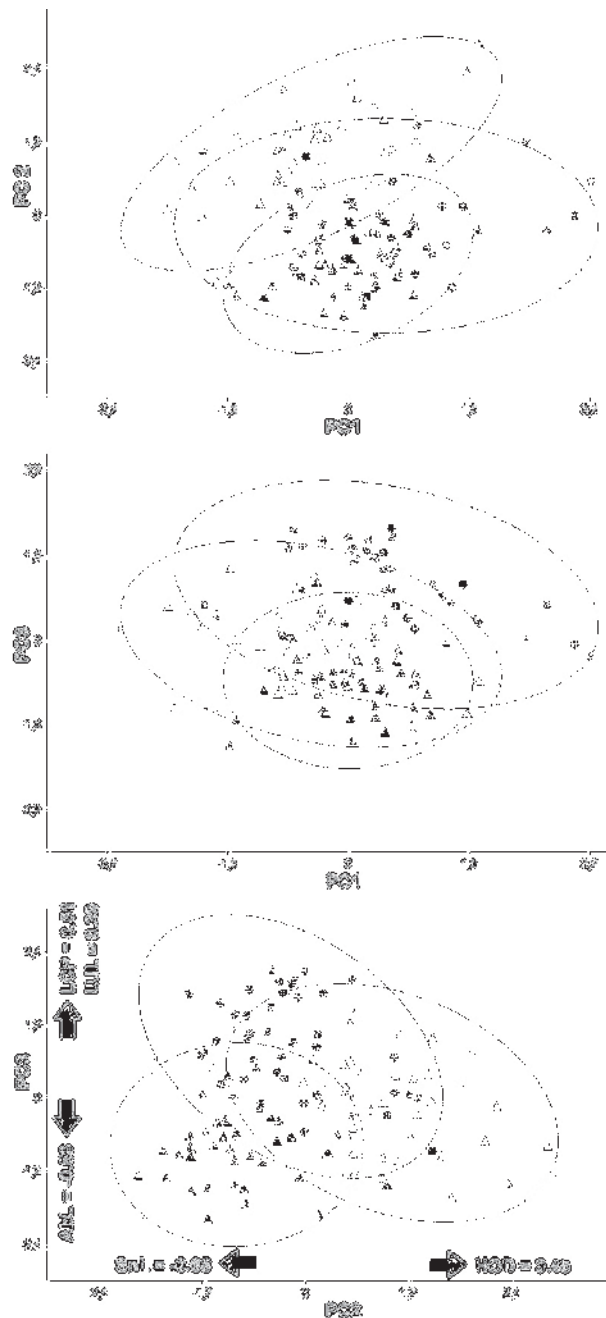


Fig. 9. Principal component analysis of *Macropsobrycon uruguayanae* from three different basins: laguna dos Patos basin (dots), río Uruguay basin (filled triangles), and río Negro basin (empty triangles); based on the 18 morphometric variables listed in Table 1, except dorsal-fin length. Ellipses correspond to 95% confidence ellipses. The largest loadings are indicated on the second and third principal components (PC2, PC3), where AbL = anal-fin base length; HOD = horizontal orbit diameter; LCP = length of caudal-peduncle; SnL = snout length; UJL = upper jaw length.

CAPÍTULO IV

A revisionary study of the trans-Andean Compsurini (Characidae: Cheirodontinae): description of a new genus and review of the *Saccoderma* Schultz, 1944

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Abstract

Compsurini is a group of inseminating cheirodontines whose species are geographically distributed from Central America to southern South America. Herein, trans-Andean species of the tribe are revised, and a new genus of Compsurini is described based on characters related to secondary sexual dimorphism and ultrastructural morphology of the spermatozoa. The new genus hosts the Central American species “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura*, and “*O.*” *mitoptera*, which were until now in provisory genera. The genus *Saccoderma* and its species, *S. hastata* and *S. melanostigma*, which inhabits respectively several Colombian drainages and the río Maracaibo basin in Venezuela, are redescribed including their caudal organ morphology. *Saccoderma falcata* and *S. robusta* are considered junior synonyms of *S. hastata*.

Resumo

Compsurini é um grupo de queirodontíneos inseminadores cujas as espécies são geograficamente distribuídas da América Central ao Sul da América do Sul. Aqui, as espécies trans-andinas da tribo são revisadas, e um novo gênero de Compsurini é descrito com base em caracteres relacionados ao dimorfismo sexual secundário e morfologia ultraestrutural dos espermatozoides. O novo gênero abriga as espécies já descritas da América Central “*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura* e “*O.*” *mitoptera*, as

quais estavam até o momento em gêneros provisórios. O gênero *Saccoderma* e suas espécies, *S. hastata* e *S. melanostigma*, as quais habitam respectivamente diversas drenagens da Colômbia e a bacia do rio Maracaibo na Venezuela, são redescritos incluindo a morfologia de seu órgão caudal. *Saccoderma falcata* e *S. robusta* são considerados sinônimos juniores de *S. hastata*.

Key words: Systematics, Taxonomy, Neotropical region, Caudal organ.

Introduction

The Compsurini is a monophyletic group with eighteen species remarkably recognized by hosting the inseminating species of Cheirodontinae, characterized by the presence of spermatozoa in the ovaries of females (Burns, Weitzman & Malabarba, 1997) and by the common presence of unusual secondary sexual dimorphism associated to the caudal fin, resembling partially some species of the Stevardiinae with caudal glands (Malabarba & Weitzman, 1999; Malabarba & Weitzman, 2000; Malabarba, Lima & Weitzman, 2004). The tribe was erected by Malabarba, Weitzman & Burns (in Malabarba, 1998) as a result of the cladistic analysis of the cheirodontine species, which also defined the tribe Cheirodontini, and the *incertae sedis* genera in Cheirodontinae.

At the present, the species belonging to the tribe are: *Acinocheirodon melanogramma* Malabarba & Weitzman, *Compsura heterura* Eigenmann, *Kolpotocheirodon figueiredoi* Malabarba, Lima & Weitzman, *K. theloura* Malabarba & Weitzman, *Macropsobrycon uruguayanae* Eigenmann, *Saccoderma falcata* Dahl, *S. hastata* (Eigenmann), *S. melanostigma* Schultz, *S. robusta* Dahl, and three species from Central America, “*Compsura*” *gorgonae* (Evermann & Goldsborough), “*Odontostilbe*” *dialeptura* (Fink & Weitzman) and “*Odontostilbe*” *mitoptera* (Fink & Weitzman). To investigate the relationship among the Cheirodontinae, Malabarba (1998) used only the type species of the aforementioned genera of Compsurini, and although recognized as compsurini integrants, the species from Central America did not receive new generic assignment due to the need of a deeper investigation.

The compsurini species are distributed from the Uruguay to South of Costa Rica, however only the *Saccoderma* species and the Central American compsurin species

“*Compsura*” *gorgonae*, “*Odontostilbe*” *dialeptura*, and “*Odontostilbe*” *mitoptera* occur in trans-Andean basins.

The genus *Saccoderma* was erected by Schultz (1944) in a revisionary work on the family “Characinidae” (present Characiformes) from the Venezuela. Schultz created the genus based on the singular modified caudal-fin scales of *Saccoderma melanostigma*, his new species designated as the “genotype” (type species) of the genus. Schultz also included in the genus the species *Odontostilbe hastata* Eigenmann (1913), described to the río Atrato basin in Colombia, redescribed and illustrated by Eigenmann (1915), due to the presence of a similar “dermal sac” on the caudal fin. *Saccoderma melanostigma* was detailed described based on a large number of specimens, however the species’s diagnose was poorly based on the tenuous differences on the dorsal-, anal- and caudal-fins color pattern. Posteriorly, Dahl (1955) described two more Colombian species, *Saccoderma falcata* from several tributaries of río Sinú and río Pechilín, and *S. robusta*, from the Pulgas, Nain and Chibogadó, tributaries of río Sinú (treated as *S. falcatum* and *S. robustum* in Dahl, 1971). These species were described altogether with several other species of the río Sinú, however Dahl did not designate any catalog number to any analysed specimens along with the original description or subsequent works (Dahl, 1958, 1971; Dahl & Medem, 1964; Dahl, Medem & Henao, 1964). The only reference is that the described species “form part of a collection at present in the Liceo Bolívar in Sincelejo” (Dahl, 1955: 12). Posteriorly, Dahl (1958) restricted the geographic distribution of *S. falcata* to the río Pechilín basin, and *S. robusta* to the río Sinú basin.

Some additional morphological information about the genus was given by Fink & Weitzman (1974), who illustrated the dentition of *Saccoderma hastata* and presented a detailed illustration of the holotype’s caudal fin, showing the arrangement of the modified scales as well as the distribution of the caudal-fin hooks. Fink & Weitzman (1974) also quoted the presence of immature *Saccoderma* specimens among other cheirodontine species collected in Panama (SU 48851), indicating a wider geographical range for the genus. After a while, *Saccoderma hastata* was considered synonym to *S. melanostigma* by Galvis *et al.* (1997), who considered the difference in color pattern between the species not valuable to separate them. Notwithstanding, *S. hastata* was considered a valid species in

subsequent works (Malabarba & Weitzman, 1999; Malabarba & Weitzman, 2000; Malabarba, 2003; Maldonado-Ocampo *et al.*, 2005).

“*Compsura*” *gorgonae* (Evermann & Goldsborough) was described as an integrant of *Cheirodon*, due to its incomplete lateral line. The species possesses a series of modified scales on the lower caudal fin lobe, also called pouch scales. Based on the similarity of the modified scales forming pouches in the caudal fin those of to *Compsura heterura*, Meek & Hildebrand (1916) transferred the species to *Compsura* Eigenmann. The distribution of the species and its morphological variation was detailed studied by López (1972), who raised questions about the congenerity of these species in front of the large distance between their areas of occurrence. In a review of the cheirodontine fishes from Central America, Fink & Weitzman (1974) described two new species from Panama, *Cheirodon dialepturus* and *Cheirodon mitopterus*. Despite of the presence of modified scales over the middle caudal-fin rays, the presence of hooks in the caudal fin of *C. dialepturus*, and completely pored lateral line in *C. mitopterus*, at the time used to defined the genus *Odontostilbe*, the authors decided to place their new species and *Compsura gorgonae* in *Cheirodon*; a conservative position taken in front of the instability and unknown cladistic significance of the characters in use at that time to define the genera *Cheirodon*, *Compsura*, and *Odontostilbe*. With the definition of *Cheirodon* supported by phylogenetic methods, the Central America compsurini were kept in the provisory genera *Compsura* and *Odontostilbe* (Malabarba, 1998; Malabarba, 2003), until a better understanding of their relationships was available.

Herein we describe a new genus to host the Central American compsurini species based on the phylogeny of the tribe; define the genus *Saccoderma*, redescribe its species and update their geographical distribution. The taxonomic status of *Saccoderma falcata* and *S. robusta* are also commented.

Material and Methods

Counts and measurements were taken according to Fink & Weitzman (1974), as possible on the left side of the specimens. Measures were taken point-to-point straight-line with a 0.01 precision caliper. The head length measure is defined as the distance between the tip of the snout and the posterior margin of subopercle (Bührnheim & Malabarba, 2006). Total

vertebrae number includes the four vertebrae of the Weberian apparatus, and the terminal “half centrum” (Malabarba & Weitzman, 1999). The gill rakers were counted from the first branchial arch, and the gill raker in the junction of the ceratobranchial and the epibranchial was counted referred to the epibranchial count. The counts of vertebrae, supraneurals, teeth, and gill rakers were based on cleared and stained (c&s) specimens, according to Taylor & van Dyke’s (1985) protocol. Drawings of the jaws, anal fin, caudal fin, and scales were prepared in a stereomicroscope with camera lucida.

The following abbreviations are given to identify the longitudinal series of scales in the lateral region of the fish body: LL - lateral line series of scales; LD1 - longitudinal series of scales above LL; LD2 - longitudinal series of scales above LD1; LD3 - longitudinal series of scales above LD2; LV1 - longitudinal series of scales below LL; and LV2 - longitudinal series of scales below LV1.

The sex identification of specimens was based on Gonçalves *et al.* (2005) and Bührnheim & Malabarba (2006), where males and females are recognized by dissection, or by the presence of sexual dimorphism in specimens with similar size in the same sample. Specimens smaller than the smallest specimen showing sexual dimorphism in each lot are termed as unsexed, as well as specimens belonging to lots where sexual dimorphism is absent.

Material from the following institutions were analyzed in this study: AMNH - American Museum of Natural History, New York, USA; ANSP - Academy of Natural Sciences of Philadelphia, Philadelphia, USA; CAS - California Academy of Sciences, San Francisco, USA; FMNH - Field Museum of Natural History, Chicago, USA; ICNMHN - Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá, Colombia; INHS - Illinois Natural History Survey, Champaign, USA; MCP - Museu de Ciências e Tecnologia PUCRS, Porto Alegre, Brazil; MHNG - Muséum d’Histoire Naturelle, Geneve, Switzerland; MZUSP - Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; SU – Stanford University, Palo Alto, USA; UFRGS - Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; UF - Florida Museum of Natural History, Florida, USA; UMMZ - University of Michigan Museum of Zoology, Ann Arbor, USA; and USNM - National Museum of Natural History, Smithsonian Institution,

Washington D.C., USA. Abbreviations given along with the number of specimens are the following: mc - morphometric and meristic.

Diagnosis given in the text are taken from the phylogeny of Compsurini presented by Jerep & Malabarba (in manuscript, Chapter 1). The species allocated in the “New Genus” were detailly described by Fink & Weitzman (1974), and will not be redescribed here.

Results

“New Genus” from Central America

Type species: *Cheirodon gorgonae* Evermann & Goldsborough, 1909: 99; by present designation.

Diagnosis. The “New Genus” is diagnosed from all characid species by the presence of the cheirodontine synapomorphies, and from all cheirodontine genera by the following synapomorphies: supraorbital laterosensory canal not continuous to the pterotic laterosensory canal [Ch. 42: 1]; caudal fin modified scales not forming a pouch [Ch. 220: 0]; skin flaps restricted to the first third of the caudal-fin ray length [Ch. 226: 0]; caudal peduncle dorsal and ventral margins convex, with scales and skin non-attached to *hipaxialis* muscles, resulting in an internal chamber between them [Ch. 240: 1]; centriolar complex outside the nuclear fossa [Ch. 273: 0]; nucleus anterior border asymmetric, clearly oblique to the longest axis of the nucleus [Ch. 276: 1]; and vesicles located after the mitochondria, in the basal region of the midpiece and along the cytoplasmic collar in one side of the nucleus [Ch. 278: 1].

Distinguishing characters. The “New Genus” can also be characterized among the cheirodontines by the presence of retrorse hooks anteriorly directed in the anal fin, bigger and more numerous in the most anterior and most posterior branched anal-fin rays, last anal-fin rays elongated on mature males, and additional scales with reduced size and modified shape over the middle and lower caudal-fin rays not forming a pouch.

“New Genus” *gorgonae* (Evermann & Goldsborough, 1909), new combination

Figs. 1-2, 18a

Cheirodon gorgonae Evermann & Goldsborough, 1909: 99 [original description, type illustration, type locality Gorgona, Canal Zone, Panamá]; 100 [teeth illustration, comparative measurements].-Fink & Weitzman, 1974: 4, 5 [valid as *Cheirodon gorgonae*]; 14-18 [redescription and comparison to Cheirodontinae, figs. 8-10].

Compsura gorgonae (Evermann & Goldsborough). -Meek & Hildebrand, 1916: 226, 229, 231 [geographical distribution update]; 273 [valid as *Compsura gorgonae*]. -López, 1972 [morphological variation and geographical distribution]. -Géry, 1977: 575 [treated *Compsura gorgonae*, listed as strict sense Cheirodontinae]. -Vari & Howe, 1991: 14 [type material listed from National Museum of Natural History]. -Burns, 1997 [listed as inseminating species]. -Malabarba, 1998 [included in the new tribe Compsurini]. -Malabarba & Weitzman, 1999: 427 [comparison to *Acinocheirodon melanogramma*]. -Malabarba & Weitzman, 2000: 280 [comparison to *Kolpotocheirodon theloura*]. -Malabarba, 2003: 216 [listed in Cheirodontinae]. -Malabarba, Lima & Weitzman, 2004: 324 [comparison to *Kolpotocheirodon figueiredoi*]. -Javonillo, Burns & Weitzman, 2007: 30 [spermatozoa comparison to *Brittanichthys*].

Diagnosis. According to the phylogenetic analysis of the Compsurini (Jerep & Malabarba, in manuscript, Chapter I), the following characters were found to be autapomorphies of “New Genus” *gorgonae*: nasal bone straight [Ch. 23: 0]; absence of the quadrate anteroventral foramen [Ch. 110: 0]; modified caudal-fin scales forming pockets [Ch. 219: 1] (Fig. 2); muscle *interradialis* thicker between the caudal-fin rays 11 to 15 [Ch. 243: 1]; maxilla not extending posteriorly the vertical line through the ventral limit of the lateral ethmoid [Ch. 55: 1]; and maxilla without a longitudinal groove [Ch. 56: 0].

Distinguishing characters. “New Genus” *gorgonae* can also be distinguished from the other species of the genus by presenting incomplete lateral line (*vs.* complete in “New Genus” *mitopterus*), and the absence of hooks in the caudal-fin rays (*vs.* present in “New

Genus” *dialepturus*) (Fig. 2). For additional morphological data see Fink & Weitzman (1974). Female specimens can also be diagnosed from other species of the genus by the presence of scales modified in shape over the base of the lower caudal-fin lobe, although those scales are not hypertrophied as observed in males.

Distribution. Records of “New Genus” *gorgonae* are restricted to the Panama, on both Atlantic and Pacific drainages, syntopically with “New Genus” *dialepturus* and “New Genus” *mitopterus* (Fig. 3).

Analyzed material. “New Genus” *gorgonae*. **Type material:** USNM 64094, holotype (mc 22.1 mm SL), Panama, Canal Zone, small seepage pool below spillway of the reservoir dam at Gorgona, 7 Feb 1908, A. Jennings. USNM 64095, paratypes, 4 mc (19.9-21.1 mm SL), Panama, Canal Zone, small seepage pool below spillway of the reservoir dam at Gorgona, 7 Feb 1908, A. Jennings. USNM 127086, paratypes, 3 (1 mc, 19.8 mm SL), Panama, Gorgona, C. Z. seepage pool below spillway, 7 Feb 1908, A. Jennings. **Non-type material:** ANSP 99865, 97 (14.8-24.5 mm SL), Panama, Panama Province, creek into río Caimito 8 mi from Chorrera on Nuevo Emperador road, 17 Aug 1962, H. G. Loftin & E. L. Tyson. ANSP 104039, 9 (1 female 23.3 mm SL, 8 males 23.0-25.5 mm SL), Panama, Panama Province, río Perequete at bridge on Interamerican Highway East of Capira, 24 Mar 1962, H. G. Loftin. ANSP 146796, 1 (27.5 mm SL), Panama, Panama Province, pool at culvert 0.3 km S of bridge at Las Cañitas, 26 Feb 1981, D. Fromm. ANSP 146803, 1 male (20.6 mm SL), Panama, Panama Province creek on road to Arensa near shore of Lake Gatun, 13 Mar 1981, D & P. Fromm. ANSP 151208, 1 (24.9 mm SL), Panama, Darién, drying up pool 140.4 km E Bayano bridge, 3 Feb 1983, D. Fromm & D. Weber. ANSP 151209, 2 (1 male 23.9 mm SL, 1 female 24.0 mm SL), Panama, río Darién at Canclon (or Canclum) 166.4 km E Bayano bridge, 3 Feb 1983, D. Fromm & D. Weber. ANSP 151219, 4 (1 unsexed 16.9 mm SL, 2 females 27.9-29.2 mm SL, 1 male 27.3 mm SL), Panama, Panama Province, small stream at Interamerican Highway about 7.6 km W of Bayano bridge, 31 Jan 1983, D. Fromm & D. Weber. ANSP 151222, 1 (25.9 mm SL), Panama, Darién, river 156.5 km E Bayano bridge, 3 Feb 1983, D. Fromm & D. Weber. CAS 6823, 10 (juveniles 16.8-18.5 mm SL), Panama, La Jagua Hunting Club (Pacific Slope), 9-10

February 1935, S. F. Hildebrand. CAS 69193, 2 (males 23.0-24.3 mm SL), Panama, Canal Zone, río Gatun at Monte Liria, 27 Mar 1911, Meek & Hildebrand. CAS 69229, 1 (male 18.9 mm SL), Panama, Canal Zone, río Trinidad at Agua Clara, 10 March 1911, Meek & Hildebrand. CAS 150891, 4 mc (1 male 27.5 mm SL, 3 females 26.6-28.0 mm SL), Panama, Canal Zone, *ca.* 2 mi SE of Gamboa, on E side of the Canal, 09°7'N 794°1'W, Jan 1954, Gen. T. D. White & L. Coman. FMNH 12958, 1 (male 24.5 mm SL), Panama, Canal Zone, Paraiso, 3 Mar 1911, Meek & Hildebrand. FMNH 12959, 6 (unsexed 22.1-23.8 mm SL), Panama, río Mamoni or río Calobre, date unknown, Meek & Hildebrand. FMNH 12960, 6 (unsexed 25.9-27.5 mm SL), Panama, río Calobre, 18 Mar 1911, Meek & Hildebrand. FMNH 12961, 1 (male 26.4 mm SL), Panama, río Chorrera, 10 Apr 1911, Meek & Hildebrand. FMNH 12962, 1 (unsexed 24.3 mm SL), Panama, río Marte Anarde, 22 Apr 1911, Meek & Hildebrand. FMNH 12963, 1 (unsexed 26.4 mm SL), Panama, creek near Chorrera, 11 Apr 1911, Meek & Hildebrand. FMNH 12964, 1 (unsexed 23.1 mm SL), Panama, Largateria creek, 9 Mar 1911, Meek & Hildebrand. FMNH 12965, 4 (unsexed 24.0-25.4 mm SL), Panama, Canal Zone, río Missimbi, Empire, 2 Apr 1912, Meek & Hildebrand. FMNH 12966, 2 (1 unsexed 22.3 mm SL, 1 male 25.0 mm SL), Panama, río o Chagres, Alhajuela, 21 Feb 1911, Meek & Hildebrand. FMNH 12967, 23 (unsexed 18.9-27.1 mm SL), Panama, Canal Zone, Agua Clara, 10 Mar 1911, Meek & Hildebrand. FMNH 12968, 34 (unsexed 22.4-25.6 mm SL), Panama, Canal Zone, río Gatun, Monte Liria 27 Mar 1911, Meek & Hildebrand. FMNH 12969, 2 mc (males 27.4-28.5 mm SL), Panama, Canal Zone, río Gatun, Monte Liria, 28 Mar 1911, Meek & Hildebrand. FMNH 12971, 2 (unsexed 25.3-27.0 mm SL), Panama, Darien, río Aruza, Aruza, 26 Feb 1912, Meek & Hildebrand. FMNH 12972, 2 (unsexed 26.2-26.5 mm SL), Panama, Darien, Aruza, río Aruza, 27 Feb 1912, Meek & Hildebrand. FMNH 12973, 21 (unsexed 22.6-26.4 mm SL), Panama, Canal Zone, río Frijoles, 19 Mar 1911, Meek & Hildebrand. FMNH 12974, 3 (males 27.9-29.2 mm SL), Panama, Darien, río Yape, 6 Mar 1912, Meek & Hildebrand. FMNH 12975, 6 (unsexed 17.6-24.1 mm SL), Panama, Limon Creek, Alhajuela, 26 Feb 1911, Meek & Hildebrand. FMNH 17730, 1 (male 24.75 mm SL), Panama, Canal Zone, Gatun Lake, Baro Colorado Island, 20 Dec 1928, Crane Pacific Expedition. FMNH 36720, 9 (8 mc 22.2-26.3 mm SL), Panama, Madden dam road, small creek tributary to río Chagres, 14 Feb 1935, S. F. Hildebrand. FMNH 55257, 2 (males 24.7-25.4 mm SL), Canal

Zone, río Frijoles, 1911-12, Meek & Hildebrand. MCP 11988, 3 c&s (23.7-28.5 mm SL), Panama, río Caimito at Chorrera falls, in backwater above dam, 17 Aug 1962, H. Loftin. MCP 11989, 7 (23.1-29.1 mm SL) Panamá, río Caimito at Chorrera falls, in backwater above dam, 17 Aug 1962, H. Loftin. MCP 16132, 36 (13.8-26.8 mm SL, 2 mc and c&s 23.2-26.8 mm SL), Panama, Darien, río Meteti, Pan Americana *ca.* 40 km nnw of Yaviza (Chucunaque system), 24 Feb 1985, W. C. Starnes *et al.* MCP 27060, 1 (19.7 mm SL), Panama, Darién, Tuira, río Tuira, between Calle Larga and Pinogana, 18 Feb 1985, L. Lundberg *et al.* MCP 27064, 1 (25.8 mm SL), Panama, Panama, Caribbean, río Frijoles, North of Gamboa (río Chagres basin), 26 Feb 1885, W. C. Starnes *et al.* MCP 27065, 57 (21.0-23.6 mm SL), Panamá, Darien, Tuira, río Tuira close to Boca de Cupé, 18 Feb 1985, W. C. Starnes *et al.* MCP 27070, 32 (20.0-23.9 mm SL), Panamá, Darién, Tuira, río Pirre, 16 Feb 1985, L. Lundberg *et al.* MCP 27093, 3 (21.3-22.2 mm SL), Panamá, Darién, Tuira, río Pirre in Pijibasal, 23 Feb 1985, L. Lundberg *et al.* MHNG 2232.67, 1 (26.8 mm SL), Panama, affluent du río Bayano prés de Maje, Jul 1983, Géry. MHNG 2369.45, 1 of 4 (27.2 mm SL), Panamá, río Caimito of Chorrera falls, in backwater above dam, 17 Aug 1962, Loftin (ex-USNM 210548) MHNG 2661.014, 3 (19.5-24.2 mm SL), Panamá, río Paripiti, affluent du río Bayano, 4 Feb 1994, P. de Rham. MHNG 2661.015, 6 (20.8-21.7 mm SL), Panamá, río Piritiz, affluent of río Bayanu, 30°03'23"N 28°39'31.5"W, 11 Mar 2000, P. de Rham & J. C. Nourussat. MZUSP 17196, 5 (21.5-23.3 mm SL), Panamá, Provincia de Panamá, río Cabra, Nov 1965, H. Britski. MZUSP 41085, 5 (18.6-22.6 mm SL), Panamá, Provincia de Panamá, Chepo, río Mamoni, Dec 1965, H. Britski. SU 24298, 2 mc (1 male 23.8 mm SL, 1 female 26.2 mm SL), Panama, Barro Colorado, Gatun Lake, 20 Dec 1928, Herre. SU 24767, 32 (16 males 20.0-25.6 mm SL, 13 females 20.5-25.5 mm SL, 3 juveniles 17.8-19.6 mm SL), Panama, Gatun Lake, 18 Mar 1930, Zschokke & Blackwelder. UMMZ 92123, 20 (24.7-27.2 mm SL) Panama, Canal Zone, Gatun L., Barro Colorado Id. (from Asbestos House), 15 Sep 1929, W. N. Bougham. UMMZ 180736, 1 (23.5 mm SL), Panama, Barro Colorado island, Gatun lake, Canal Zone (prob. Chapman 4 1/2), 6 Aug 1940, N. Scrimshaw & T. Sanders. UMMZ 180769, 34 (20.3-28.8 mm SL), Panama, Barro Colorado island, Gatun lake, Canal Zone (bay near Shannon trail), Jul 1936, C. L. Turner. UMMZ 199421, 6 (16.4-22.6 mm SL), Panama, Panama Province along Inter-American highway, *ca.* 7 1/2 mi E of turnoff to Pecora, 12 Feb 1972, J. Strauch family. UMMZ

217271, 2 (22.1-24.7 mm SL), Panama, Darien, mouth of a small creek flowing into río Chucunaque just below mouth of río Cancion, río Tuyra drainage, 28 Jun 1961, H. Heatwole & F. Torres. UMMZ 217292, 15 (21.4-25.5 mm SL), Panamá, Darien, Ox-bow, 1 km downstream from mouth of río Cancion (into río Chucunaque), 30 m from river, río Tuyra drainage, 4 Jul 1961, O. J. Sexton & F. Torres. USNM 78688, 3 (2 males 23.1- 24.6, 1 unsexed 23.9 mm SL), Panama, Aqua Clara, C. Z., 10 Mar 1911, S. Meek & S. Hildebrand. USNM 78693, 2 mc (1 male 26.3 mm SL, 1 female 30.7 mm SL), río Chorrera, Chorrera, Panama, 10 Apr 1911, S. Meek & S. Hildebrand. USNM 109254, 4 mc (1 male 25.9 mm SL, 3 female 27.1-28.9 mm SL), Panama, C.Z. Madden Lake río Boqueron (above lake in current), 12 Feb 1935, S. Hildebrand. USNM 109255, 5 (23.6-26.2 mm SL, 4 mc, 1 male 23.6 mm SL, 3 females 24.3-25.6 mm SL), Panama, río Cocoli-Miraflores Lake, Canal Zone, 1 Apr 1937, S. Hidebrand. USNM 208521, 1 mc (male 26.9 mm SL), Panama, Panama, creek about 2 mi E of El Llano Rd. 17 Mar 1962, H. Loftin. USNM 208542, 4 mc (3 males 26.8-28.4 mm SL, 1 female 29.6 mm SL), Panama, Panama Province, creek about 5 mi West of El Llano, 17 Mar 1962, H. Loftin & C. Kupfer. USNM 208543, 17 (24.4-26.5 mm SL, 10 mc, 5 males 25.7-27.6 mm SL, 5 females 23.7-28.1 mm SL), Panama, Canal Zone, creek about 2 mi E. of Nueva Emperador road, 17 Aug 1962, H. Loftin *et al.* USNM 210548, 36 (27.1-28.7 mm SL, 4 mc, 3 males 27.1-28.4 mm SL, 2 females 27.4-28.7 mm SL), Panama, río Caimito at Chorrera Falls, in backwater above dam, 17 Aug 1962, H. Loftin *et al.* USNM 218357, 2 (males 26.5-27.4 mm SL), Panama, río Calobre, 18 Mar 1911, S. Meek & S. Hildebrand. USNM 293214, 24 (23.4-27.0 mm SL), Panama, Darien Prov., río Pucuro just above confl. with río Tuira (Pacific), 8°00'N 77°32'W, 16-18 Feb 1985, W. C. Starnes *et al.* USNM 325269, 3 (1 male 25.1 mm SL, 2 unsexed 22.4-23.4 mm SL), Panama stream near el llano, Bayano basin, 20 May 1979, D. Kramer.

“New Genus” *dialepturus* (Fink & Weitzman, 1974), new combination

Figs. 4-5

Cheirodon dialepturus Fink & Weitzman, 1974: 3 [key for cheirodontine species from Central America]; 5-18 [description, compared to other cheirodontines from Central

America]; 6 [holotype picture]; 7 [dentition picture]; 8 [caudal fin picture]; 9-10 [non-types photographs]. -Géry, 1977: 570 [listed in key to *Cheirodon* species]. -Nijssen *et al.*, 1982: 16 [type catalogue]. -Böhlke, 1984: 45 [type catalogue]. -Ibarra & Stewart, 1987: 23 [type catalogue]. -Vari & Howe 1991: 14 [type catalogue].

Compsura dialeptura (Fink & Weitzman). -Bussing, 1998: 103 [valid as *Compsura dialeptura*].

Compsura gorgonae (not Evermann & Goldsborough). -Nelson, 1964: 62, 71, 74, 129 [listing, caudal morphology, discussion of possible relationships]. -Bussing, 1967: 211, 214, 241 [listed, compared to *Pseudocheirodon*, photograph]. -López, 1972: 93-129 [compared to *Cheirodon* species, morphological variation, distribution].

Odontostilbe dialeptura (Fink & Weitzman). -Burns, 1997: 434 [listed as *Odontostilbe dialeptura*, inseminating species]. -Malabarba *in* Reis *et al.*, 2003: 217 [valid as *Odontostilbe dialeptura*]. -Malabarba, Lima & Weitzman, 2004: 324 [caudal fin comparison to other compsurini]. -Bührnheim & Malabarba, 2006: 193 [not in *Odontostilbe*].

"*Odontostilbe*" *dialeptura* (Fink & Weitzman). -Malabarba, 1998: 216 [valid as "*Odontostilbe*" *dialeptura*, included in the new tribe Compsurini]. -Malabarba & Weitzman, 1999: 427 [valid as "*Odontostilbe*" *dialeptura*]. -Malabarba & Weitzman, 2000: 270, 280 [caudal fin comparison to other compsurini].

Diagnosis. According to the phylogenetic analysis of the Compsurini (Jerep & Malabarba, in manuscript), the following characters were found to be autapomorphies of "New Genus" *dialepturus*: ectopterygoid not contacting the quadrate [Ch. 107: 0]; three posteriormost ventral procurrent caudal-fin rays hypertrophied on mature males, distal tips expanded, forming a small keel in the ventral profile of the caudal fin [Ch. 207: 1]; absence of skin flaps over the 18th to 19th principal caudal-fin rays [Ch. 230: 0]; presence of hypertrophied skin flaps associated to whitish tissue in the caudal fin [Ch. 231: 1] (Fig. 6); and caudal fin bearing hooks on the lower lobe [Ch. 184: 1] (Fig. 5).

Distinguishing characters. "New Genus" *dialepturus* can also be distinguished from the other species of the genus by the absence of caudal-fin scales forming pockets in the lower

lobe (*versus* present in “New Genus” *gorgonae*); and incomplete lateral line (*vs.* present in “New Genus” *mitopterus*). For additional morphological data see Fink & Weitzman (1974).

Distribution. “New Genus” *dialepturus* is mainly distributed on the Pacific coastal rivers from Panama, syntopically with “New Genus” *gorgonae* and “New Genus” *mitopterus*. However, there is also one record of the species for the río Sinú in Colombia (CAS 149505) and three records for the surroundings of Puntarenas in Costa Rica (ANSP 164244, UMMZ 245729, USNM 210990) (Fig. 7).

Analyzed material. “New Genus” *dialepturus*. **Type material:** USNM 208524, holotype (26.8 mm SL), Panama, Veraguas, río San Pedro basin, creek at bridge, 12 mi. West of Santiago on road to Sona, 28 Jan 1962, H. Loftin *et al.* USNM 208523, paratypes, 132 (10 mc, 5 males 27.0-28.7 mm SL, 5 females 26.8-28.3 mm SL), Panama, Veraguas, río San Pedro basin, creek at bridge, 12 mi. West of Santiago on road to Sona, 28 Jan 1962, H. Loftin *et al.* ANSP 121989, paratypes, 2 mc (1 male 28.7 mm SL, 1 female 27.8 mm SL), Panama, Veraguas Province, río San Pedro basin, creek at bridge 12 mi. West of Santiago on road to Sona, 28 Jan 1972, H. Loftin *et al.* FMNH 71702, 2 paratypes (1 male 28.3 mm SL, 1 female 27.3 mm SL), Panama, Veraguas Province, río San Pedro basin, creek at bridge 12 miles west of Santiago on road to Sona, 28 Jan 1962, H. Loftin *et al.* **Non-type material.** **Colombia:** CAS 149505, 14 (13.3-23.7 mm SL), Colombia, Cordoba, Sinú, Betanci, a large lake and its outlet into río Sinú *ca.* midway between Monteria & Tierra Alta, 16 Jan 1956, G. Dahl. **Costa Rica:** ANSP 164244, 4 (20.7-30.1 mm SL), Costa Rica, Puntarenas Prov. brook at Inter American Highway 2 km N of Ciudad Neill, 10 Mar 1989, D. Fromm. UMMZ 245729, 16 (22.8-31.8 mm SL), Costa Rica, Puntarenas, Quebrada Tinajam río Coto drainage, 2 Aug 1992, D. Reznick. USNM 210990, 4 (17.0-31.3 mm SL), Costa Rica, Puntarenas Province, 7 km southeast of Villa Neily on IAH (Inter American Highway), 28 Feb 1973, W. Bussing *et al.* **Panamá:** ANSP 146811, 4 (unsexed 15.4-17.2 mm SL), Panama, Panama Province, pool at culvert 22 km N of Chepo, 26 Feb 1981, D. Fromm. ANSP 146812, 1 (unsexed 22.8 mm SL), Panama, Chiriqui Province, brook 500 m from Inter American Highway on road to Gualaca, 2 Mar 1981, D. & P. Fromm. ANSP 146818, 1 (unsexed 26.5 mm SL), Panama, Veraguas Province, culvert pool 3 km above

San Francisco on Santa Fe road, 9 Mar 1981, D. & P. Fromm. ANSP 146880, 6 (20.1-25.6 mm SL), Panama, Chiriqui Province 2 km from Gualaca on road to discharge tunnel of Fortiera Hydro Project, 2 Mar 1981, D. & P. Fromm. ANSP 146905, 4 (2 unsexed 18.8-26.3 mm SL, 2 males 26.8-27.4 mm SL), Panama, Chiriqui Province Río la Pata at IAH, 4 Mar 1981, D. & P. Fromm. ANSP 146906, 1 (female 30.3 mm SL), Panama, Chiriqui Province 9 km from IAH on Boquete Rd., 3 Mar 1981, D. & P. Fromm. ANSP 151203, 2 (males 28.4-31.0 mm SL), Panama, Chiriqui, stream 29 km S of Inter-American Highway on Canoas-Puerto Armuelles road, 28 Jan 1983, D. Fromm & D. Weber. ANSP 151204, 7 (26.0-29.6 mm SL), Panama, Chiriqui, Canal between Santa Maria and Progreso about 11 km S of Inter-American Highway, 28 Jan 1983, D. Fromm & D. Weber. ANSP 151207, 24 (12.5-24.5 mm SL), Panama, Chiriqui, small creek about 2.2 km WNW of Gualaca, 29 Jan 1983, D. Fromm & D. Weber. ANSP 158996, 4 (1 male 26.0 mm SL, 1 female 27.5 mm SL, 2 unsexed 17.5-18.6 mm SL), Panama, Panama Province, río Bejuco, on IAH, 1973. INHS 53202, 10 of 66 (26.3-31.4 mm SL), Panama, Chiriqui, Quebrada Gallina, río Corcha, 9 km E Chiriqui, on highway 1, 08°24'08"N 82°14'24"W, 9 Sep 1999, L. M. Page & S. M. Phelps. INHS 53205, 10 of 28 (24.4-31.3 mm SL), Panamá, Coclé, río Coclé del Sur, 1 km S la Pintada, 08°34'03"N 80°25'58"W, 11 Sep 1999, L. M. Page & S. M. Phelps. INHS 53215, 10 of 25 (17.6-27.5 mm SL), Panama, Chiriqui, río Chiquiri, 3 km E Guayaba, 08°26'13"N 82°19'08"W, 9 Sep 1999, L. M. Page & S. M. Phelps. MCP 11992, 5 c&s (18.2-29.5 mm SL), Panamá, Herrera province, creek about 4 mi up road from junction with chitre-div. road, 21 Oct 1961, H. Loftin & E. Tyson, ex-USNM 208534. MCP 11993, 15 (21.3-28.3 mm SL), Panamá, Herrera province, creek about 4 mi up road from junction with chitre-div. road, 21 Oct 1961, H. Loftin & E. Tyson, ex-USNM 208534. MCP 16131, 36 (22.8-33.0 mm SL), Panama, Chiriqui Province, creek 5 mi W of David on IAH, 2 Dec 1961, H. Loftin & E. Tyson, ex-USNM 208522. MZUSP 17207, 26 (20.1-34.1 mm SL), Panamá, David, río Riacuas, Dec 1965, H. Britski. MZUSP 41084, 12 (20.0-24.5 mm SL), Panamá, Santiago, Riacho de las Palmas, Dec 1965, H. Britski. MZUSP 41086, 4 (23.8-27.1 mm SL), Panamá, Coclé, río Grande, Dec 1965, H. Britski. MZUSP 53249, 2 (28.1-28.4 mm SL), Panamá, Chirugui, David, riacho *ca.* 20 km do mun. de David, 3 Jan 1998, A. Akama & R. A. Guerra. USNM 208508, 19 (27.1-29.9 mm SL, 2 c&s 27.6-27.9 mm SL), Panamá, Chiriqui Province, la Concepcion on IAH, 26 Jun 1964, R. H. Goodyear.

USNM 208509, 1 c&s of 20 (26.2 mm SL), Panama, Veraguas, creek 1 mi S of río Santa Maria bridge on São Francisco road, 14 Jan 1962, H. Loftin. USNM 208510, 17 (10 males 27.5-30.6 mm SL, 2 females 28.4-29.4 mm SL, 3 unsexed 25.0-26.4 mm SL, 2 c&s 27.9-30.5 mm SL), Panama, Chiriqui Province, creek 15 mi W of Concepcion on IAH, 2 Dec 1961, H. Loftin & E. Tyson. USNM 208511, 12 (27.8-30.2 mm SL, 2 c&s 27.5-32.0 mm SL), Panama, Panama Province, río Corona at bridge on IAH, 3 mi E of San Carlos, 11 Mar 1962, H. Loftin & E. Hislop. USNM 208512, 17 (26.0-29.9 mm SL, 2 c&s 28.6-29.9 mm SL), Panama, Veraguas Province, río San Pablo basin, creek 2 mi W of río San Pablo bridge on new IAH section from Santiago, 4 Jan 1962, H. Loftin, E. Tyson & R. Condon. USNM 208522, 58 (7 mc, 4 males 29.2-32.2 mm SL, 3 females 28.6-33.0 mm SL), Panama, Chiriqui Province, creek 5 mi. W of David on IAH, 2 Dec 1961, H. Loftin & E. Tyson. USNM 208525, 16 (11 males 27.0-31.4 mm SL, 4 females 28.5-29.5 mm SL, 1 unsexed 25.32 mm SL), Panama, Veraguas, río Cobre at bridge on new IAH section from Santiago, 4 Jan 1962, H. Loftin *et al.* USNM 208527, 95 (26.4-32.9 mm SL), Panamá, Chiriqui Province, río Chorcha at bridge on IAH E of town of Chiriqui, 1 Dec 1961, H. Loftin & E. Tyson. USNM 208530, 2 mc (males 29.9-32.2 mm SL), Panama, Panama Province, río Las Lajas at bridge on IAH E of San Carlos, 24 Mar 1962, H. Loftin. USNM 208533, 5 (males 28.5-29.53 mm SL), Panama, Comoro del Barú Province, large irrigation canal by road 8 mi. N. of Puerto Armuelles, Chiriqui, 15 Apr 1962, H. Loftin & E. Tyson. USNM 208534, 93 (18.2-29.4 mm SL), Panamá, Herrera province, creek about 4 mi up Pese road from junction with Chitre-div. road, 21 Oct 1961, H. Loftin & E. Tyson. USNM 208535, 10 (22.5-26.6 mm SL, 3 mc, 2 males 29.9-34.5 mm SL, 1 female 30.6 mm SL), Panama, Chiriqui Province, río Esti, about 1 mi N of Gualaca, 16 Dec 1961, H. Loftin & E. Tyson. USNM 208537, 2 c&s of 83 (28.2-32.4 mm SL), Panama, Chiriqui Province, creek on IAH, less than one-fourth mile from San Felix bridge, 18 Nov 1961, H. Loftin & E. Tyson. USNM 208552, 16 (15.0-29.6 mm SL), Panama, Coclé, río Grande basin, creek of río Coclé about 5 mi N of Penonome on road to La Pintada, 23 Mar 1962, H. Loftin. USNM 209488, 8 (19.5-28.2 mm SL, 4 mc, 3 males 27.8-28.2 mm SL, 1 female 27.4 mm SL), Panama, drainage ditch at city limits of Gualaca, 16 Dec 1961, H. Loftin & E. Tyson. USNM 209491, 3 mc (1 male 32.2 mm SL, 2 unsexed 27.9-30.9 mm SL), Panama, creek 2 mi. W of Concepcion on Inter-American Highway, 2 Dec 1961, H. Loftin & E. Tyson.

USNM 209492, 119 (20.0-32.9 mm SL), Panama, creek 5 mi W of David on Inter-American Highway, 2 Dec 1961, H. Loftin & E. Tyson. USNM 209494, 3 (1 male 26.9 mm SL, 2 unsexed 24.1-25.6 mm SL), Panama, Los Santos Province, río Mariabe, 4 mi. North of río Pedosi on Hwy, 29 Sep 1961, H. Loftin & E. Tyson. USNM 209495, 23 (23.6-27.6 mm SL), Panama, Cocle Province, río Grande basin, swampy creek on Inter-American Highway about 2 mi. E of Nata, 15 Oct 1961, H. Loftin & E. Tyson. USNM 209497, 1 (28.2 mm SL), Panama, creek about 14 mi. S of Divisa on Chitre road, 20 Oct 1961, H. Loftin & E. Tyson. USNM 209498, 3 mc (males 27.3-29.3 mm SL), Panama, río San Pablo basin, Veraguas Province, río Santa Clara at bridge on new Inter-American Highway Section from Santiago, 7 mi. E of R. Cobre bridge, 4 Jan 1962, H. Loftin *et al.* USNM 209500, 68 (13 mc, 3 males 26.4-27.7 mm SL, 10 females 24.3-27.8 mm SL), Panama creek off road about 7 mi up road, from its junction with Inter-American Highway, 21 Oct 1961, H. Loftin & E. Tyson. USNM 209502, 21 (5 males 26.1-28.9 mm SL, 12 females 26.2-28.6 mm SL, 4 unsexed 22.1-24.9 mm SL), Panama, río Estibana at bridge shortly before entering Macaracas, 30 Sep 1961, H. Loftin & E. Tyson. USNM 209510, 117 (14.4-31.2 mm SL), Panama, creek dammed to form farm pond about 8 mi. up Pese road from junction with Chitre-Divisa road, 21 Oct 1961, H. Loftin & E. Tyson. USNM 209517, 20 (11 unsexed 21.6-27.7 mm SL, 1 female 30.8 mm SL, 8 males 28.1-32.4 mm SL), Panama, creek 12 mi. W of David on Inter-American Highway, Dec 1961, H. Loftin & E. Tyson. USNM 209520, 2 c&s of 107 (26.0-30.6 mm SL), Panama, creek into río Jacaque and the río Jacaque near San Lorenzo at farm of Dr. Alvarez, 9 Dec 1961, H. Loftin & E. Tyson. USNM 209521, 91 (16.8-29.5 mm SL), Panama, Veraguas, río San Pedro basin, river at bridge about 17 mi. W of Santiago on rd. to Sona, 28 Jan 1962, H. Loftin & R. Yerger. USNM 209523, 19 (24.3-30.0 mm SL), Panama, río Coton at bridge on Inter-American Highway about 5 mi. W of San Carlos, 11 Mar 1962, H. Loftin & E. Heslop. USNM 209525, 2 c&s of 26 (26.3-26.7 mm SL), Panama, Panama Province, río Arenal at bridge on IAH E. of San Carlos, 13 Oct 1961, H. Loftin & E. Tyson. USNM 209526, 61 (10 mc, 5 males 32.7-34.2 mm SL, 5 females 30.5-34.7 mm SL, 2 c&s 31.2-34.7 mm SL), Panama, creek at bridge 7 mi up Boquete road from David, 16 Dec 1961, H. Loftin & E. Tyson. USNM 209527, 2 c&s of 61 (25.3-26.8 mm SL), Panama, creek about 6 mi S of divisa on Chitre road, 20 Oct 1961, H. Loftin & E. Tyson. USNM 210551, 4 mc (1 male 26.1 mm

SL, 3 females 27.0-28.5 mm SL), Panama, Chiriqui, 10.6 mi from Pan-American Hwy on road to Estero Rico, ditch crossing graded roadbed, 4 Jul 1968, R. Gibbs. USNM 210552, 14 (8 males 25.1-29.2 mm SL, 1 female 26.2 mm SL, 5 unsexed 22.7-24.5 mm SL), Panama, Chiriqui Province, río Chiriqui Viejo basin, river 1 mi N of Progreso on road from Inter-American Highway to Armuelles, 15 Apr 1962, H. Loftin & E. Tyson. USNM 244658, 32 (18.3-31.5 mm SL), Panamá, Veraguas Province, río Martin Grande, 4 mi south of Santiago on Montijo road, 14 Jan 1962, H. Loftin *et al.* USNM 348763, 1 mc (male 31.0 mm SL), Panama, Veraguas Province, creek crossing Colobre to la Yeguada road, not far above Colobre, 08°19'58"N 80°49'56"W, 17 Mar 1997, D. Fromm & P. Fromm.

“New Genus” *mitopterus* (Fink & Weitzman, 1974), new combination

Figs. 8-9

Cheirodon mitopterus Fink & Weitzman, 1974: 3 [key for cheirodontine species from Central America]; 12-18 [description, compared to other cheirodontines from Central America]; 12 [holotype picture]; 13 [dentition picture]. -Nijssen *et al.*, 1982: 16 [type catalogue]. -Böhlke, 1984: 51 [type catalogue]. -Vari & Howe 1991: 14-15 [type catalogue].

Compsura gorgonae (not Evermann & Goldsborough). -López, 1972: 101 [listed to río Cocle del Norte]; 106 [discussion of lateral-line length].

Compsura mitoptera (Fink & Weitzman). -Bussing, 1998: 104 [valid as *Compsura mitoptera*].

Odontostilbe mitoptera (Fink & Weitzman). -Burns, 1997: 434 [listed as *Odontostilbe mitoptera*, inseminating species]. -Malabarba *in* Reis *et al.*, 2003: 218 [valid as *Odontostilbe mitoptera*]. -Malabarba, Lima & Weitzman, 2004: 324 [caudal fin comparison to other compsurini]. -Bührnheim & Malabarba, 2006: 193 [not in *Odontostilbe*].

"*Odontostilbe*" *mitoptera* (Fink & Weitzman). -Malabarba, 1998: 216 [valid as "*Odontostilbe*" *mitoptera*, included in the new tribe Compsurini]. -Malabarba & Weitzman, 1999: 411, 427 [valid as "*Odontostilbe*" *mitoptera*]. -Malabarba & Weitzman, 2000: 270, 280 [caudal fin comparison to other compsurini].

Diagnosis. According to the phylogenetic analysis of the Compsurini (Jerep & Malabarba, in manuscript), the following characters were found to be autapomorphies of “New Genus” *mitopterus*: elongation of the second dorsal-fin ray on males [Ch. 137: 1]; elongation of the unbranched pectoral-fin ray on males [Ch. 148: 1]; elongation of the unbranched pelvic-fin ray on males [Ch. 150: 1]; lateral line completely pored [Ch. 210: 0]; dorsal-fin melanophores concentrated on the distal portion of the fin [Ch. 250: 1]; and supraorbital laterosensory canal continuous to the pterotic laterosensory canal [Ch. 42: 0].

Distinguishing characters. “New Genus” *mitopterus* can also be distinguished from the other species of the genus by the absence of caudal-fin rays bearing hooks (*vs.* present in “New Genus” *dialepturus*) (Fig. 9), and the absence of modified scales forming pockets in the lower lobe of the caudal fin (*vs.* present in “New Genus” *gorgonae*). For additional morphological data see Fink & Weitzman (1974).

Distribution. “New Genus” *mitopterus* is known for the Atlantic and Pacific drainages from Panama, syntopically with “New Genus” *dialepturus* and “New Genus” *gorgonae*; and also for a single record in Costa Rica (MCP 14713, ex-ANSP 140649) (Fig. 10).

Analyzed material. “New Genus” *mitopterus*. **Type material:** USNM 208539, holotype (34.6 mm SL), Panama, Cocle, río Tucue, trib. of río Cocle del Norte, at junction of river and between Tucue and Tambo, 28 Aug 1972, J. Mcphail. USNM 208513, paratypes, 8 (7 mc 28.4-33.0 mm SL), Panama, Cocle Province, río Tucue, tributary of río Cocle del Norte, at junction of river and road between Tucue and Tamba, 28 Aug 1972, J. Mcphail. ANSP 121987, paratype (30.1 mm SL), Panama, Cocle Province, río Tucue, tributary of río Cocle del Norte, 28 Aug 1972, J. D. McPhail. **Non-type material:** INHS 62732, 23 (25.4-32.7 mm SL), Panama, stream, río Arriero basin, 3.5 mi NNW Escobal, 7 mi SW Gatun Locks, 1 Aug 1977, R. L. Mayden & M. E. Braasch. MCP 14713, 5 (3, 19.2-21.7 mm SL, 2 c&s 19.7-27.3 mm SL), Costa Rica, río Claro-Golfito road just East of Bar Roded, 28 Feb 1979, D. & P. Fromm (ex-ANSP 140649). MCP 16130, 3 (28.3-29.5 mm SL), Panama, Coclé, río Tambo, near Tambo and Toubre in headwaters of río Coclé del Norte, 15 Sep 1962, H.

Loftin & W. Kupfer. MCP 16133, 2 (30.4-34.7 mm SL), Panama, stream near Toabre road (either the río Toabre or a small tributary of it, near Tambo (drainage río Coclé del Norte), Sep 1972, R. Drassier. MZUSP 16840, 2 (28.1-31.5 mm SL), Panama, Coclé Province, río del Norte basin, río Tucue near village at Tucue in headwaters of río Coclé del Norte, 15 Sep 1962, H. Loftin & W. Kosan (from USNM 208540). USNM 208514, 11 (25.2-33.8 mm SL, 6 mc 25.7-33.8 mm SL), Panama, Cocle, río Tambo, near Tambo and Toubre in headwaters of río Cocle del Norte, 15 Sep 1962, H. Loftin, W. Kupfer. USNM 208541, 9 (27.6-33.3 mm SL), Panama, stream near Toabre road (either the río Toabre or a small tributary of it, near Tambo (río Coclé del Norte drainage), Sep 1972, R. Drassier. USNM 348761, 1 mc (30.2 mm SL), Panama, tributary of río Cocle del Sur, Northeast of la Pintada, above Colobre, 08°39'12"N 80°19'26"W, 1 Mar 1997, D. Fromm & P. Fromm. USNM 348762, 1 mc (29.7 mm SL), Panama, tributary of río Cocle del Sur, Northeast of la Pintada, above Colobre, 08°39'12"N 80°19'26"W, 1 Mar 1997, D. Fromm & P. Fromm.

The caudal organ of the “New Genus”. The “New Genus” encompasses the compsurini species which present scales modified in size and shape over the caudal fin, but not forming a pouch-like structure associated with an internal chamber as found in *Compsura*, *Saccoderma*, and *Compsurini* n. sp. Purus. The scales in “New Genus” are not deeply attached to each other structuring a single caudal organ; instead, they are independently modified and associated to hypertrophied tissue. In “New Genus” *dialepturus* and “New Genus” *mitopterus* the last body scales marginating the caudal-fin base are reduced in size, slightly extending over the middle caudal-fin rays in the midline. The modified scales in the midline are slightly elongated posteriorly, longer than deeper, while the ones bordering the base of the caudal lobes are deeper than longer. In “New Genus” *dialepturus*, the scales of the midline are attached to the interradial skin flaps, which are hypertrophied proximally, and reduced in size distally. In “New Genus” *mitopterus* the interradial skin flaps are more developed in the proximal portion of the upper and lower caudal-fin lobes, however they are not attached to the modified scales just bordering that region. “New Genus” *dialepturus* is the only species of the genus that present caudal-fin hooks in the 12 to 15-16 principal rays. The hooks are placed in the dorsal surface of these rays, approximately at their distal half/third, and are curved anteriorly. Generally, the hooks are associated to whitish tissue

on their surroundings. Another feature only found in “New Genus” *dialepturus* is the conspicuous spacement between the principal caudal-fin rays 15 to 16, and 16 to 17. This spacement is more remarked on mature males, when the interradiial membrane is whitish by the presence of hypertrophied tissue and the skin flaps above and below the 16th caudal-fin ray are also hypertrophied.

In “New Genus” *gorgonae*, the scales are modified in shape and size in the base of the lower and upper caudal fin-lobes, being strongly developed in the lower lobe of mature males. In the upper lobe, the last scales from LD1 and LD2, and sometimes the LD3 are modified in shape, slightly enlarged in comparison to the common body scales, and present their posterior border free. Generally they are distally associated to a small amount of hypertrophied tissue, sometimes forming a small pocket-like structure usually collapsed in preserved material. The cluster of modified caudal scales situated over the base of the lower caudal-fin rays is formed by the last one or two scales from the LL, last two scales from the LV1, and the last two scales from LV2 (Fig. 2). The modified scales from the LL and LV1 are somewhat elongated dorsoposteriorly and present their dorsal margin attached to the fin by tissue, and the modified scales from the LV2 somewhat elongated ventroposteriorly, with ventral margin attached to the fin by tissue. The distal border of these scales are free, convex, slightly mobile, and raised laterally, leaving an open space underneath each scale with direct contact with the water. Differently from *Compsura*, there is no internal chamber placed between the modified scales and the caudal-fin rays, nor there is hypertrophied tissue in the pockets opening. The skin flaps just posterior to the modified scales are more developed on mature males than on females and juveniles. The muscles *interradiialis* are also slightly more developed and extended posteriorly between the principal caudal-fin rays 11 to 14. No ray modification is present (Fig. 2).

***Saccoderma* Schultz, 1944**

Saccoderma Schultz, 1944: 245 [key for genera from Venezuela]; 314 [description, conferring *Saccoderma melanostigma* as “genotype” by original designation]. Dahl, 1955: 17 [assigned to río Sinú, describing two new species]. -Dahl, 1958: 24 [assigned to río Sinú]. -Dahl, 1964: 51 [key of species from río Sinú]; 64 [listed to río Sinú]. -

Dahl, 1965: 48 [assigned to río San Jorge]. -Géry, 1965: 14 [comparison with *Brittanichthys*]. -Dahl, 1971: 131 [listed to North of Colombia]. -Fink & Weitzman, 1974: 3 [key for cheirodontines from Central America]; 33 [assigned to Central America, illustration of the holotype and dentition]; 34 [illustration of the caudal scales]. -Géry, 1977: 546 [key to Cheirodontinae strict sense]; 574 [comparison to *Compsura*]. -Malabarba, 1998: 199, 203, 216, 217, 218, 219 [phylogenetic diagnosis and relationships to cheirodontine genera; included in the new tribe Compsurini]. -Malabarba & Weitzman, 1999: 427, 428 [comparison with *Compsura*]. -Malabarba & Weitzman, 2000: 280, 281 [caudal organ comparison with *Compsura*]. -Malabarba, 2003: 219 [listed in Cheirodontinae]. -Malabarba, Lima & Weitzman, 2004: 325 [dorsal-fin spot comparison]. -Mirande, 2009: 8 [listed in Cheirodontinae]. -Mirande, 2010: 531 [listed in Cheirodontinae].

Diagnosis. *Saccoderma* is diagnosed from all characid species by the presence of cheirodontine synapomorphies, and from all cheirodontine genera by the following apomorphies: anteromedial process of the mesethmoid well-developed, extending between premaxillae and reaching anteriorly the tooth bearing border of the premaxillae [Ch. 15: 0]; maxilla dorsal profile slightly concave [Ch. 59: 1]; lower branch of the anguloarticular elongate, reaching or falling short to the line through the toothed portion of the dentary [Ch. 73: 1]; first to third most lateral premaxillary teeth larger than the preceding ones [Ch. 76: 1]; longer axis of the anteriormost dentary teeth perpendicular to the longer axis of the dentary [Ch. 96: 0]; dentary teeth with 5 medial cusps larger, nearly equal in size [Ch. 103: 2]; dentary teeth with 5 medial cusps aligned in row with other teeth cusps, forming a continuous cutting edge [Ch. 104: 2]; caudal-fin rays 12 and 13 ventrally curved on mature males [Ch. 182: 1]; lateral line scales completely pored [Ch. 210: 0]; laterosensory canal extending beyond the half-length of the middle caudal-fin rays [Ch. 212: 2]; one or two elongate modified scales on the distal portion of the middle caudal-fin rays [Ch. 217: 1]; muscle *interradialis* extending posteriorly between the caudal-fin rays [Ch. 241: 1]; intrasperm nucleus elongated [Ch. 268: 1]; toothless portion of the maxilla extended, more than two times longer than the tooth bearing portion of the maxilla [Ch. 62: 3]; posterior branched anal-fin rays with same size or smaller than median branched rays on mature

males [Ch. 156: 0]; anal-fin hooks restricted to the i+5 anal-fin rays [Ch. 170: 2]; and caudal-fin rays on the lower lobe with hooks [Ch. 184: 1] (Jerep & Malabarba, in manuscript, Chapter I).

Distinguishing characters. *Saccoderma* can also be distinguished from the other cheirodontine genera by the presence of complete lateral line; dentary teeth composed anteriorly by three large pedunculated teeth with the five medial cusps enlarged and aligned in row with other teeth cusps, forming a continuous cutting edge; presence of caudal-fin rays bearing hooks; presence of a pouch-like caudal organ in the lower lobe of the caudal fin; and presence of elongated scales attached over the middle caudal-fin rays.

***Saccoderma hastata* (Eigenmann, 1913)**

Figs. 11-12

Odontostilbe hastatus Eigenmann, 1913: 27 [original description; type locality Soplaviento, Colombia]. -Eigenmann, 1915: 5 [comments on enlarged caudal-fin scales]; 10 [discussion about relationship]; 12 [listed in table of distribution]; 91 [distribution range to Magdalena and Atrato basins, description, illustration of caudal fin]; plate XVI [figure 1, illustration]. -Henn, 1928: 59 [type catalogue].

Saccoderma hastata (Eigenmann). -Schultz, 1944: 314 [valid as *Saccoderma hastata*]; 315 [discussion about caudal-fin scales]; 316 [present in comparison table of counts]; 318 [present in key for *Saccoderma* species]. -Dahl, 1955: 17 [in key for *Saccoderma* species from Colombia]. -Dahl, 1964: 64 [feeding comparison with *Saccoderma robusta* and *S. falcata*]. -Dahl, 1965: 48 [listed to río San Jorge]. -Fink & Weitzman, 1974: 33 [recorded to Panama, Veraguas, holotype photograph, dentition illustration]; 34 [holotype caudal fin illustration]. -Ibarra & Stewart, 1987: 61 [type catalogue]. -Vari & Howe, 1991: 32 [type catalogue]. -Galvis, Mojica & Camargo, 1997: 53 [synonym of *Saccoderma melanostigma*]. -Malabarba & Weitzman, 1999: 427 [valid as *Saccoderma hastata*, comparison with Compsurini about caudal-fin hooks]. -Malabarba & Weitzman, 2000: 280 [valid as *Saccoderma hastata*, comparison with

Compsurini about caudal-fin hooks]. -Malabarba, Lima & Weitzman, 2004: 324 [caudal-fin hooks comparison with Compsurini].

Saccoderma hastatum (Eigenmann). -Dahl, 1971: 131 [listed as *Saccoderma hastatum* to North of Colombia].

Saccoderma hastatus (Eigenmann). -Malabarba in Reis *et al.*, 2003: 219 [listed as Cheirodontinae, valid as *Saccoderma hastatus*]. -Maldonado-Ocampo *et al.*, 2005: 87 [description, biology and distribution]; 269 [illustration].

Diagnosis. *Saccoderma hastata* can also be distinguished from *S. melanostigma* by the ascending portion of the preopercle lateral system canal short, reaching the posterior articular surface of the hyomandibular condyle [Ch. 114: 1]; and by the presence of melanophores homogenously distributed over the dorsal fin and along all the distal portion of the anal fin (*vs.* melanophores concentrated on the distal portion of the dorsal fin and on the anterior portion of the distal margin of the anal fin).

Description. Morphometrics and counts given in Table 1. Body slightly elongate and compressed, deepest at dorsal-fin origin. Dorsal profile convex from snout tip to dorsal-fin origin, straight or slightly convex from that point to end of dorsal-fin base, straight or slightly convex from end of dorsal-fin base to adipose-fin origin. Dorsal and ventral caudal-peduncle profile slightly concave. Ventral profile convex from dentary anterior end to pelvic-fin insertion, straight to deeply concave (on mature males) until anal-fin origin, straight along anal-fin base. Snout short, mouth terminal, between horizontal lines projected through pupil ventral and dorsal borders.

All teeth pedunculated, aligned in one tooth row. Premaxilla with 2(9) slightly larger teeth bearing 7(9) cusps followed by 3(9) teeth bearing 7(5), 8(1) to 9(3) cusps. Maxilla reaching vertical line through orbit anterior edge, bearing 2(9) teeth bearing 7(8), 8(5), 9(1), or 11(1) cusps. Dentary with 3(9) large heptacuspoid teeth similar in size, with five central cusps expanded, aligned, forming cutting edge, followed by teeth decreasing in size posteriorly, none or 1(6) heptacuspoid, none or 1(6) pentacuspoid, none or 1(6) tricuspoid, 1(4), 2(4), 4(1) conical teeth (Fig. 12).

Dorsal-fin origin slightly posterior to vertical through pelvic-fin origin, on middle of body. Dorsal-fin rays ii, 8(2), 9(100). Adipose-fin origin at vertical line through third to fourth last anal-fin ray insertion. Anal-fin origin slightly posterior to last dorsal-fin ray insertion; anterior rays longer than posterior ones; distal profile deep concave on females, slightly concave to straight on mature males. Anal-fin rays iii to iv, 16(3), 17(43), 18(39), 19(17); last unbranched until fifth branched anal-fin rays, rarely sixth, of mature or maturing males bearing small and retrorse hooks, often associated to hypertrophied whitish tissue (Fig. 13). Hooks placed from middle length to near the distal tip of anal-fin rays, attached at posterior margin, usually posterior branch of branched portion, bent over lateral surface, directed anteriorly to anal-fin frontal margin. One to two hooks per anal-fin ray segment. Pectoral-fin rays i, 9(20), 10(65), 11(16); longest rays surpassing pelvic-fin insertion. Pelvic-fin insertion anterior to vertical line passing through dorsal-fin origin. Pelvic-fin rays i, 6(1), 7(101); all of them bearing 1-2 unilateral ventromedial antrorse hooks per ray segment on mature males. Caudal fin with 18(4), 19(94), 20(2) principal rays; 10(6), 11(1), 12(2) dorsal procurrent caudal-fin rays; 9(4), 10(4), 11(1) ventral procurrent caudal-fin rays. Caudal-fin hooks retrorse, anteriorly directed, distributed along distal half or third of 13th to 18th caudal-fin rays, rarely along 11th, 12th, and 19th (Fig. 14).

Lateral line completely pored 31(1), 32(7), 33(30), 34(44), 35(17), 36(3) scales. Scale rows between dorsal-fin insertion and lateral line 5(83), 6(18); scale rows between lateral line and pelvic-fin insertion 3(8), 4(85). Predorsal scales 9(4), 10(43), 11(53), 12(2); postdorsal scales 7(2), 8(35), 9(50), 10(13), 11(2); scale rows around caudal peduncle 14(100), 16(2). Last scales of longitudinal series above lateral line series modified in shape and size; scales hypertrophied on mature males, forming scale pouch in lower caudal-fin lobe (see caudal organ description, Fig. 14).

Mature males with gill gland on first branchial arch. Gill rakers on first branchial arch, 2(9) on hypobranchial, 10(9) on ceratobranchial, 6(9) on epibranchial, 1(9) on pharyngobranchial. Supraneurals 4(7) to 5 (2). Precaudal vertebrae 15(1), 16(7), 17(1). Caudal vertebrae 17(1), 18(4), 19(4). Pseudotympanum as large muscular hiatus between first and second pleural ribs, limited dorsally by *lateralis superficialis* muscle, posteriorly by naked anterior face of second pleural rib, posteroventrally by *obliquus inferioris* muscle, anteroventrally by *obliquus superioris* muscle.

Color in alcohol. Overall body color varying from light to pale yellowish (Fig. 11). Head dusk to dark brownish dorsally. Region from 2nd to 5th infraorbital and opercular apparatus silvery. Several small dark melanophores more densely scattered around nares, lips, maxillary, anterior margin of orbit, dorsal surface of head, and more sparsely over body. Overall iris color silvery. Humeral spot absent, however humeral region darkened due to presence of pseudotympanum. Melanophores distributed at posterior margin of scales in dorsal and dorsolateral regions of body, resulting in slight reticulated pattern. Dark melanophores scattered over body, except ventral region from lower jaw articulation to urogenital papillae. Melanophores distributed in narrow line along the longitudinal line. Caudal peduncle with higher concentration of melanophores in elliptical caudal black spot, sometimes extending posteriorly over base of middle caudal-fin rays, narrowing posteriorly conferring itself lanceolate shape, not reaching dorsal or ventral margins of caudal peduncle. Few melanophores following miosepta of muscles *hypaxialis* at lower lateral side of caudal region. Dorsal, caudal, pectoral and pelvic fins hyaline with scattered melanophores at interradiial membrane and bordering margins of rays. Anal fin also hyaline, with scattered melanophores more concentrated at distal margin on mature males (Fig. 11).

Color in life. Overall body and head color pattern semitransparent with silvery to whitish shades. Melanophores distribution pattern as described in color in alcohol. Dorsal and anal fins orangish, caudal fin orangish on lower lobe and reddish on upper lobe (Maldonado-Ocampo *et al.*, 2005).

Sexual dimorphism. Mature males differ from females by the presence of hooks on pelvic, anal, and caudal fins. Males present the anal-fin profile less concave than on females due to the slightly elongation of the middle and posterior anal-fin rays. The pelvic fin reaches the anal-fin origin on mature males, and falls short on females. The scales modified in shape over the caudal-fin base are more developed in size on males than on females, and are associated to hypertrophied tissue structuring a caudal pouch in the lower lobe of the fin. The anal-fin color pattern also differs between males and females, once mature males have a higher amount of melanophores at the distal portion of the anal-fin rays, which results in a

tenuous dark band along the distal margin of the fin. The mature males also present modification of the branchial filaments of the first branchial arch into a gill gland, that is absent on females. The ventral profile between the pelvic-fin insertion and the anal-fin origin is deeply concave on mature males, and straight to convex on females.

Distribution. *Saccoderma hastata* is recorded for the río Atrato, río Magdalena, río Sinú, and río Pechelin drainages, and also for several costal drainages from the Atlantic (Fig. 15). Fink & Weitzman (1974) registered some specimens of *Saccoderma* for the Central America, Panama, Veraguas (SU 48851), however still immature to confirm specific identity. Ringuelet (1975), also listed the species (*Odontostilbe hastata* in that work) to municipality of Salta in Argentina, followed by López *et al.* (2003) and Menni (2004), notwithstanding, this record is based on the misidentification of specimens of *Odontostilbe microcephala* (J. M. Mirande, pers. com.).

Remarks on *Saccoderma falcata* Dahl, 1955 and *S. robusta* Dahl, 1955. The status of the *Saccoderma* species described by Dahl (1955) from tributaries of río Sinú and río Pechilín is a mystery. There is no type designation in any accessible work from Dahl, nor specimens registered as type material in any institution in or outside Colombia. Dahl described both species as possessing pseudotympanum, a caudal sac in the lower lobe of the caudal fin, complete lateral line, humeral spot absent, as well as four “comb-like” teeth in the dentary, all of them are features found in the genus. However, *Saccoderma falcata* was also characterized as presenting ii,8 dorsal-fin rays, i,10-12 pelvic-fin rays, seven teeth in the premaxilla, one in the maxilla, and absence of hooks in the males anal fin; and *S. robusta* as presenting ii,7-ii,8 dorsal-fin rays, six teeth not aligned in the premaxilla, maxilla toothless and 38-39 scales on the lateral line. These data are strongly different from the morphological characters found in *S. hastata* and *S. melanostigma*. The *Saccoderma* species recognized in the present work have at least two teeth in the maxilla, at most five teeth in the premaxilla (rarely 6), and at most 36 scales in the lateral line; furthermore all cheirodontines have ii,9 rays in the dorsal fin, i, 6-7 rays in the pelvic fin, as well as aligned teeth in the premaxilla. After a while, Dahl (1971) presented illustrations of his species that badly resembles a cheirodontinae (*S. falcatum* and *S. robustum* in that paper) in which the

number of lateral line scales and the number of dorsal- and anal-fin rays match with the original description, however the number of pelvic-fin rays seems to be smaller than i,10-12 in *S. falcata*. Several lots, most collected by Dahl, and identified by himself as *Saccoderma falcata* (CAS 149503, collected in 1955 in the type locality), and *S. robusta* (CAS 149505 collected in 1956, CAS 149506 collected in 1957, and MHNG 1066.039 to MHNG 1066.042, all from río Sinú basin) were analyzed for this study and none of those specimens match, or fit, in Dahl's diagnosis for his species, being actually individuals of "New Genus" *dialepturus* (CAS 149505), and *S. hastata* (CAS 149503, CAS 149506). The Eschmeyer & Fricke (2011) digital catalog lists the lots MHNG 1066.039 to MHNG 1066.042 as paratypes of *Saccoderma robusta*, however the analysis of some of these specimens showed they are also specimens of *S. hastata*. Furthermore, they were collected in 1962, seven years after the description of *S. robusta*, and could not be considered paratypes. Considering the uncertainty of the diagnosis elaborated by Dahl for his new species, the absence of type material, and Dahl misidentifications of *Saccoderma hastata* as *S. falcata* and *S. robusta*, we herein consider the last two species as junior synonyms of *Saccoderma hastata*.

Analyzed material. *Saccoderma hastata*. **Type material:** FMNH 56383, holotype, 30.2 mm SL, Colombia, Soplaviento, 11 January 1912, C. H. Eigenmann. FMNH 56300, paratypes, 9 (24.3-27.0 mm SL, 1 c&s 24.1 mm SL), Colombia, Bernal creek, 28 Jan 1912, C. H. Eigenman. FMNH 69555, paratypes, 3 (23.7-25.7 mm SL), Colombia, Bernal creek, near Honda. 28 Jan 1912, C. H. Eigenmann. USNM 79223, paratypes, 2 mc (26.6-27.4 mm SL), Colombia, Bernal creek, Columbia, C. Eigenmann. **Non-type material. Río Magdalena basin:** ANSP 139460, 2 (23.4-25.1 mm SL), Colombia, Caldas, río Miel ca 12 km downstream from San Miguel, 05°25'N 75°00'W, 24 Mar 1973, J. E. Bohlke *et al.* ANSP 139487, 177 (21.9-29.2 mm SL, 3 c&s 28.0-29.7 mm SL), Colombia, Caldas, oxbow of río Miel at hacienda Sonadora approximately 8 km from San Miguel, 23 Mar 1973, Böhlke, Smith-Vaniz, Saul. ANSP 140817, 127, (35 mc 21.8-26.3 mm SL), Colombia, Caldas, small tributary of río Miel, 6.8 km (by road) downstream from San Miguel, 05°25'N 75°00'W, 24 Mar 1973, J. E. Bohlke *et al.* CAS 70902, 2 (15.3-25.0 mm SL), Colombia, Bolivar, Soplaviento, town on the Dique de Cartegena between Cartegena

and Calamar, 11-13 Jan 1912, C. H. Eigenmann. CAS 70919, 9 (24.3-28.3 mm SL), Colombia, Tolima, río Magdalena basin, Bernal Creek, near Honda, 28 Jan 1912, C. H. Eigenmann. CAS 150374, 5 (22.8-25.8 mm SL), Colombia, Caldas, río Magdalena basin, at or near junction of ríos Samana La Miel, near La Dorada, 27 Feb 1957, T. D. White & J. N. Reynolds. CAS 150379, 1 (male 27.7 mm SL), Colombia, río Magdalena system, at or near junction of R. Samana & R. La Miel, near La Dorada, 05°29'N 74°40'W, 27 Feb 1957, T. D. White & J. N. Reynolds. CAS 150381, 1 (23.2 mm SL), Colombia, Caldas, río Magdalena basin, at or near junction of río Samana La Miel, near La Dorada, 27 Feb 1957, T. D. White & J. N. Reynolds. CAS 150386, 1 (24.8 mm SL), Colombia, Caldas, río Magdalena basin, at or near junction of ríos Samana La Miel, near La Dorada, 27 Feb 1957, T. D. White & J. N. Reynolds. FMNH 56301, 1 (24.4 mm SL), Colombia, Calamar, Cienega, Jan 1912, C. H. Eigenmann. FMNH 56302, 1 (21.2 mm SL), Colombia, Soplaviento, 11-13 Jan 1912, C. H. Eigenmann. ICNMHN 1464, 9 (23.6-27.6 mm SL, 2 c&s 25.6-26.7 mm SL), Colombia, Caldas, Samaná, Norcasia, Quebrada la Libertad, río la Miel, vertiente del Magdalena, 7 Nov 1988, P. Cala *et al.* ICNMHN 2455, 9 (18.2-24.6 mm SL), Colombia, Tolima, Honda, quebrada El Perico, río Magdalena, 1 Feb 1977, G. Galvis. ICNMHN 6478, 23 (15.6-28.6 mm SL, 5 mc 25.1-28.4 mm SL, 1 c&s 25.1 mm SL), Colombia, Boyacá, Boyacá, Romero, Snía las Quinchas, quebrada la Fiebre, río Magdalena, 1 Apr 2001, J. I. Mojica & C. A. Cipamocha. SU 49504, 4 (18.1-21.2 mm SL), Colombia, Bolivar, Pozo del Chorro, Sincelejo, 20 Aug 1954, G. Dahl. **Río Atrato basin:** AMNH 5328, 5 (19.7-21.2 mm SL), Colombia, Choco, río Truanto, 1913, Landon-Fisher Expedition, H. W. Henn. CAS 70909, 48 (15.6-25.7 mm SL, 5 mc 22.1-23.1 mm SL, 2 c&s 22.2-22.9 mm SL), Colombia, Chocó, río Truanto, Atrato basin, 1913, C. Wilson. CAS 70918, 18 (20.6-21.7 mm SL, 6 mc 23.5-24.9 mm SL), Colombia, Chocó, río Atrato basin, Quibdo, town at junction of río Quito and río Atrato, 1913, C. Wilson. FMNH 56551, 1 mc (24.2 mm SL), Colombia, Ceterqui, 1913, C. E. Wilson. FMNH 56552, 37 (17.2-22.0 mm SL, 5 mc 22.0-24.2 mm SL), Colombia, Truanto, 1913, C. E. Wilson. FMNH 56572, 6 (16.7-19.5 mm SL, 3 mc 22.9-24.9 mm SL), Colombia, Quibdo, 1913, C. E. Wilson. ICNMHN 1334, 11 (17.5-20.5 mm SL, 3 mc 22.2-23.8 mm SL), Colombia, Choco, Cienaga Aguaciara, Atrato, cuenca Atrato, 3 Jan 1988, E. Puentes & C. Roman-Valencia. ICNMHN 1563, 2 (16.9-18.3 mm SL), Colombia, Chocó, Boca río Neguá, río Atrato, 26

Jan 1988, C. Román-Valencia. ICNMHN 3118, 3 (18.3-20.6 mm SL, 1 mc 26.7 mm SL), Colombia, Antioquia, Chigorodó via Medellín, Chigorodó, río Juradó, Atrato cuenca, 14 Dec 1990, R. Román-Valencia & L. Suárez. MCP 16169, 13 (20.0-22.6 mm SL, 2 mc 23.1-23.3 mm SL), Colombia, Antioquia, Uraba, Quebrada Polín, afl. río Guapá, sist. río León en la vía a Barranquillita, 13 Jan 1991, C. Román-Valencia & L. Suarez. USNM 210549, 16 (20.2-22.9 mm SL, 2 mc 23.1-23.2 mm SL, 1 c&s 22.8 mm SL), Colombia, Choco, Río Pavarando, tributary of río Salaquí, 10 Feb 1968, H. G. Loftin. USNM 311062, 19 (18.1-22.1 mm SL), Colombia, Choco, río Saladonear Teresita, 8 Feb 1968, H. Loftin. USNM 358165, 2 mc (2 mc 24.7-26.4 mm SL), Colombia Choco, río Ucati at Acandi, 9 Feb 1968, H. Loftin. **Río Sinú basin:** CAS 149506, 32 (18.1-25.0 mm SL, 19 mc 22.8-26.1 mm SL, 3 c&s 24.6-26.1 mm SL), Colombia, Cordoba, río Sinu, Chibogado, brook ca. 20 mi above Tierra Alta, at foot of Las Angosturas, a long series of rapids, 17 Jan 1957, G. Dahl. ICNMHN 2056, 10 mc (29.0-31.2 mm SL, 1 c&s 31.1 mm SL), Colombia, Cordoba, Ciénega de Lorica, río Sinú, 1 May 1992, J. I. Mojica & F. Rodríguez. MHNG 1066.039-1066.042, 2 of 4 (23.0-23.2 mm SL), Colombia, Cordoba, río Verde, Sinú, 30 Mar 1962, B. Mechler. MHNG 2172.91, 1 mc (1 mc 28.1 mm SL), Colombia, Cordoba, Chibogadi, middle río Sinu, 17 Jan 1957, G. Dahl. USNM 175308, 16 (17.8-23.6 mm SL, 8 mc 23.3-25.3 mm SL), Colombia, Chibogado, Sinú Cordoba, 17 Jan 1957, G. Dahl. USNM 175320, 9 (13.9-20.4 mm SL, 2 mc 23.7-24.4 mm SL), Colombia, Betanci, Cordoba, Sincelejo, 16 Jan 1956, G. Dahl. **Río Pechelin basin:** CAS 149503, 15 (10.4-26.5 mm SL), Colombia, Bolivar, Pechelin, río Pechelin drainage, a small stream reduced to pools in dry season from hills near Ovejas, it flows to Golfo de Morrequillo at Tolu, 14 Aug 1955, G. Dahl & Gonzales. ICNMHN 1050, 3 mc (30.7-33.5 mm SL), Colombia, Sucre, arroyo Pechelin, Costa Caribe. **Caribe coastal drainage:** ANSP 139177, 1 mc (26.0 mm SL), Colombia, Magdalena, Quebrada de Aguja, 40 km SE Santa Marta, 4 Dec 1976, F. W. Saul. ICNMHN 787, 19 mc (23.4-27.2 mm SL, 1 c&s 25.0-25.3 mm SL), Colombia, Guajira, Ciénega, Garrapatero, Cuenca Costa Caribe, 11 Sep 1981, T. Viel & E. Cordero. MCP 20695, 5 mc (24.0-28.2 mm SL), Colombia, Guajira, Riohacha, río Rancheria, 23 Mar 1988, G. Holand.

***Saccoderma melanostigma* Schultz, 1944**

Figs. 13-14, 16-17, 18b

Saccoderma melanostigma Schultz, 1944: 314 [type species of *Saccoderma*]; 315 [holotype illustration, tooth illustration, caudal fin illustration, type locality río San Juan, Mene Grande, Motatán system]; 316 [description]; 318 [key to *Saccoderma* species]. - Böhlke, 1953: 26 [type catalogue]. -Nijssen *et al.*, 1982: 24 [type catalogue]. -Vari & Howe, 1991: 38-39 [type catalogue]. -Burns, Weitzman & Malabarba, 1997: 434 [listed as inseminating species]. -Malabarba, 1998: 233 [listed as analysed material]. -Galvis, Mojica & Camargo, 1997: 53 [listed to Catatumbo]. -Malabarba *in* Reis *et al.*, 2003: 219 [listed as Cheirodontinae].

Diagnosis. *Saccoderma melanostigma* can be distinguished from *S. hastata* by short lateral ridge of the anguloarticular upper portion, not reaching its anterior end [Ch. 71: 2]; by the dorsal-fin scattered melanophores concentrated on the distal portion of the fin [Ch. 245: 1]; and by the melanophores of the anal fin only concentrated in the distal portion of the most anterior rays.

Description. Morphometrics and counts given in Table 1. Body slightly elongate and compressed, deepest at dorsal-fin origin. Dorsal profile convex from snout tip to dorsal-fin origin, straight or slightly convex from that point to end of dorsal-fin base, straight or slightly convex from end of dorsal-fin base to adipose-fin origin. Dorsal and ventral caudal-peduncle profile slightly concave. Ventral profile convex from dentary anterior end to pelvic-fin insertion, straight to deeply concave (on mature males) until anal-fin origin, straight along anal-fin base. Snout short, mouth terminal, between horizontal lines projected through pupil ventral and dorsal borders.

All teeth pedunculated, aligned in one tooth row. Premaxilla with 2(2) to 3(1) slightly larger teeth bearing 7(3) cusps followed by 3(3) teeth bearing 8(1) to 9(2) cusps. Maxilla reaching vertical line through orbit anterior edge, bearing 2(2) to 3(1) teeth bearing 5(1), 7(2), 8(1), 10(1) or 11(1) cusps. Dentary with 3(3) large heptacuspoid teeth similar in size, with five central cusps expanded, aligned, forming cutting edge, followed by teeth decreasing in size posteriorly, 2(3) heptacuspoid, 1(2) pentacuspoid, 1(1) to 2(3) tricuspoid, 2(1) conical tooth (Fig. 17).

Dorsal-fin origin slightly posterior to vertical through pelvic-fin origin, on middle of body. Dorsal-fin rays ii, 9(32), 10(1). Adipose-fin origin at vertical line through third to fourth last anal-fin ray insertion. Anal-fin origin slightly posterior to last dorsal-fin ray insertion; anterior rays longer than posterior ones; distal profile deep concave on females, slightly concave to straight on mature males. Anal-fin rays iii-iv, 17(6), 18(16), 19(9), 20(2); last unbranched until fifth branched anal-fin ray, rarely sixth, of mature or maturing males bearing small and retrorse hooks, often associated to hypertrophied whitish tissue (Fig. 13). Hooks placed from middle length to near distal tip of anal-fin rays, attached at posterior margin, usually posterior branch of branched portion, bent over lateral surface, directed anteriorly to anal-fin frontal margin. One to two hooks per anal-fin ray segment. Pectoral-fin rays i, 10(10), 11(21), 12(2); longest rays surpassing pelvic-fin insertion. Pelvic-fin insertion anterior to vertical line passing through dorsal-fin origin. Pelvic-fin rays i, 7(33); all of them bearing 1-2 unilateral ventromedial antrorse hooks per ray segment on mature males. Caudal fin with 19(33) principal rays; 10(1), 12(2) dorsal procurrent caudal-fin rays; 8(1), 10(2) ventral procurrent caudal-fin rays. Caudal-fin hooks retrorse, anteriorly directed, distributed along distal half or third of 13th to 18th caudal-fin rays, rarely along 19th.

Lateral line completely pored 32(2), 33(12), 34(15), 35(3) scales. Scale rows between dorsal-fin insertion and lateral line 5(29), 6(4); scale rows between lateral line and pelvic-fin insertion 3(2), 4(31). Predorsal scales 9(1), 10(20), 11(11), 12(1); postdorsal scales 8(6), 9(22), 10(5); scale rows around caudal peduncle 14(33). Last scales of longitudinal series above lateral line series modified in shape and size; scales hypertrophied on mature males, forming scale pouch in lower caudal-fin lobe (see caudal organ description, Fig. 14).

Mature males with gill gland on first branchial arch. Gill rakers on first branchial arch, 1(3) on hypobranchial, 11(2), 12(1) on ceratobranchial, 5(1), 6(2) on epibranchial, 1(3) on pharyngobranchial. Supraneurals 4(3). Precaudal vertebrae 16(3). Caudal vertebrae 17(1), 18(2). Pseudotympanum as large muscular hiatus between first and second pleural ribs, limited dorsally by *lateralis superficialis* muscle, posteriorly by naked anterior face of second pleural rib, posteroventrally by *obliquus inferioris* muscle, anteroventrally by *obliquus superioris* muscle.

Color in alcohol. Overall body color varying from light to pale yellowish (Fig. 16). Head dusk to dark brownish dorsally. Region from 2nd to 5th infraorbital and opercular apparatus silvery. Several small dark melanophores more densely scattered around nares, lips, maxillary, anterior margin of orbit, dorsal surface of head, and more sparsely over body. Overall iris color silvery. Humeral spot absent, however humeral region darkened due to presence of pseudotympanum. Melanophores distributed at posterior margin of scales in dorsal and dorsolateral regions of body, resulting in a slight reticulated pattern. Dark melanophores scattered over body, except ventral region from lower jaw articulation to urogenital papillae. Melanophores distributed in narrow line along the longitudinal line. Caudal peduncle with higher concentration of melanophores forming elliptical caudal black spot, sometimes extending posteriorly over the base of the middle caudal-fin rays, narrowing posteriorly conferring itself lanceolate shape, not reaching dorsal or ventral margins of caudal peduncle. Few melanophores following miosepta of muscles *hypaxialis* at lower lateral side of caudal region. Caudal, pectoral and pelvic fins hyaline with scattered melanophores at interradiial membrane and bordering margins of rays. Dorsal and anal fins also hyaline, with scattered melanophores only concentrated at anterior portion of distal margin of those fins on mature males (Fig. 16).

Color in life. Overall body and head color pattern semitransparent with silvery to whitish shades. Melanophores distribution pattern as described in color in alcohol. Dorsal and anal fins orangish to reddish, caudal fin reddish only on proximal portion of the upper lobe (Galvis, Mojica & Camargo, 1997).

Sexual dimorphism. Mature males differ from females by the presence of hooks on pelvic, anal, and caudal fins (Figs. 13, 14). Mature males present the anal-fin profile less concave than on females due to the slightly elongation of the median and posterior anal-fin rays. The pelvic fin reaches anal-fin origin on mature males, and falls short on females. The scales modified in shape over the caudal-fin base are more developed in size on males than on females, and are associated to hypertrophied tissue structuring a caudal pouch in the lower lobe of the fin (Fig. 14). The ventral profile between the pelvic-fin insertion and the anal-

fin origin is deeply concave on mature males, and straight to convex on females. The anal-fin color pattern also differs between males and females, once mature males have a higher concentration of melanophores at the distal portion of the anal-fin anteriormost rays, which results in a tenuous dark spot in that region. The mature males also present modification of the branchial filaments of the first branchial arch into a gill gland, that is absent on females.

Distribution. *Saccoderma melanostigma* is known for several tributaries of the lago Maracaibo drainage, in Venezuela (Fig. 15).

Analyzed material. *Saccodermma melanostigma*. **Type material:** USNM 121519, holotype (26.7 mm SL), Venezuela, río San Juan near bridge, tributary of río Motatan, South of Mene Grande, 17-20 Mar 1942, L. Schults, G. Zuvage & W. Phelps. USNM 121522, paratypes, 24 (10 mc, 5 males 27.0-28.7 mm SL, 5 females 28.5-29.5 mm SL), Venezuela, Cienago del Guanavana about 10 km N of Sinamaica, 11 Mar 1942, L. Schultz. USNM 121524, paratypes, 3 mc (2 females 28.2-29.5 mm SL, 1 male 23.6 mm SL), Venezuela, Cano 1/2 mile West of Sanamaica, 11 Mar 1942, L. Schultz. USNM 121525, paratypes, 19, (24.6-27.6, 10 mc, 3 males 24.6-27.0 mm SL, 7 females 24.7-27.6 mm SL), Venezuela, río San Juan near bridge, tributary of río Motatan, South of Mene Grande, 17-20 Mar 1942, L. Schultz. USNM 121528, paratypes, 98, Venezuela, río Negro below mouth of río Yasa, Maracaibo basin, 2 Mar 1942, L. Schultz. USNM 121529, paratypes, 9 (25.1-26.1, 6 mc, 5 males 25.1-26.1 mm SL, 1 female 25.4 mm SL), Venezuela, Zulia, río Palmar at bridge 70 km S.W. of Maracaibo, 6 Mar 1942, L. Schultz. SU 18145, paratypes, 6 (22.5-24.9 mm SL), Venezuela, río Negro, below mouth of río Yasa, Maracaibo basin, 2 Mar 1942, L. P. Schultz. UMMZ 145025, paratypes, 4 (24.0-25.0 mm SL), Venezuela, río Palmar near Totuma about 100 km Southwest of Maracaibo, Maracaibo basin, 21 Feb 1942, Schultz. **Non-type material:** ANSP 150061, 6 (18.7-22.2 mm SL), Venezuela, Quebrada Sargento tributary of río Simon, 70 km NW Maracaibo, 5 Apr 1938, F. F. Bond. CAS 66936, 89 (19.8-25.9 mm SL), Venezuela, Zulia, Río Apon at Machiques, 30 Mar 1938, F. F. Bond. FMNH 85280, 22 (17.4-28.4 mm SL, 3 mc 23.8-26.1 mm SL, 3 c&s 23.8-25.6 mm SL), Venezuela, Zulia, río Guasare at El Paso, somewhere west San Felipe, Zuba W shore of Lake Maracaibo in the mountains, 26 Aug 1975, D. C. Hicks, D. C. Taphorn, V.

H. Sabril, Lilyestrom. INHS 35362, 13 of 25 (19.1-26.6 mm SL), Venezuela, Zulia, Caño Taguara, río Santa Ana, Lago Maracaibo drainage, 18 km N Puerto Catatumbo, 09°17'22"N 72°32'49"W, 2 Feb 1995, D. C. Taphorn *et al.* INHS 35426, 25 of 45 (18.1-22.7 mm SL), Venezuela, Zulia, río Negro, río Santa Ana, Lago Maracaibo drainage, 8 km SW Alturitas, 09°41'30"N 72°25'47"W, 2 Feb 1995, D. C. Taphorn *et al.* INHS 35459, 4 of 26 (18.4-18.7 mm SL), Venezuela, Zulia, río Santa Rosa, río Santa Ana, Lago Maracaibo drainage, 09°39'06"N 72°35'00"W, 1 Feb 1995, D. C. Taphorn *et al.* INHS 35535, 10 of 71 (19.2-23.8 mm SL), Venezuela, Zulia, río Chama, Lago Maracaibo drainage, Puerto Chama, 08°51'21"N 71°39'58"W, 31 Jan 1995, D. C. Taphorn *et al.* INHS 55462, 10 of 12 (23.7-27.4 mm SL), Venezuela, Zulia, Caño el Padre, río Onla, río Escalante, Lago Maracaibo drainage, 19 Dec 1999, J. W. Armbruster *et al.* INHS 60028, 4 of 7 (24.5-25.7 mm SL), Venezuela, río Riecito, río Maticora, Caribbean Sea drainage, town of Goajira, Falcón, 10°37'N 70°43'W, 11 Jan 1991, D. C. Taphorn *et al.* INHS 60457, 7 of 15 (21.4-26.8 mm SL), Venezuela, Zulia, río Palmar, Lago Maracaibo drainage, 5 km south of Machines, 9 Jan 1991, D. C. Taphorn *et al.* UF 23802, 5 (25.1-26.0 mm SL), Venezuela, Zulia, Municipio Bartolome de las Casas, río Negro bridge, D. C. Taphorn. USNM 228324, 2 (24.3-26.1 mm SL), Venezuela, Zulia, río Limon, 25 Mar 1974, C. Lilyestrom. USNM 228325, 7 (23.6-26.4 mm SL), Venezuela, Zulia, río Yasa, Libertad Edo, 3 Jul 1974.

The caudal organ of *Saccoderma*. *Saccoderma hastata* and *S. melanostigma* present the same caudal organ structure and arrangement (Fig. 14). The modified scales in *Saccoderma* are placed in the base of the upper and lower caudal-fin lobes, however only the scales from the lower lobe are conspicuously increased in size and modified in shape forming the caudal organ itself on mature males. In the upper lobe, the last scales from the LD1 and LD2 are modified in shape. The last LD1 scale is deeper and shorter than the previous body scales, and the last scale from the LD2 has generally its dorsoposterior portion elongated posteriorly. The distal border of those scales is free, however no hypertrophied tissue association with the scales was observed in any specimen. The caudal organ itself is formed by the last two scales from the LV1 and the last two scales from LV2 (Fig. 14). Those four scales are enlarged and strongly attached to each other. The dorsal border of the LV1 scales and the ventral border of the LV2 scales are attached to the caudal fin rays by tissue. The

posterior border of the last LV1 and LV2 scales is free, forming the opening of the pouch. Marginating the upper limit of the pouch opening, there is a scale elongated posteriorly, generally attached to over the 12th and 13th principal caudal-fin rays, extending posteriorly almost until the distal forth of these rays. This elongated scale has its borders free, and it is attached to the caudal fin by its central portion, and not by its borders as the usual. Generally there is a large amount of whitish hypertrophied tissue associated to this scale. Sometimes mature males may present additional smaller elongated scales associated to the main one, posteriorly or dorsally placed. The 12th and 13th principal caudal-fin rays under the elongated scale are ventrally curved and closer to each other than any other caudal-fin ray. Marginating the lower limit of the pouch opening there is a skin flap from the 19th principal caudal-fin ray, which is attached to the ventral border of the last LV2 scale and extends posteriorly. The interradiation membrane skin flaps just posterior to the pouch opening are slightly larger on mature males than the corresponding skin flaps on females. The pouch consists of an epidermal invagination between the caudal-fin rays and the scales, with posterior to posteroventral opening and ending anteriorly by a wall of hypertrophied tissue, apparently glandular. In the bottom of the pouch, there is an internal chamber, placed between the modified scales and the caudal-fin rays. The chamber is delimited anteriorly by the posterior attachment of the modified scales that compose the caudal organ, and posteriorly by the bottom of the pouch, a wall of hypertrophied tissue that connects the modified scales (roof of the chamber) to the caudal-fin rays (floor of the chamber). In old preserved specimens, the wall of tissue between the pouch and the chamber is absent, or when present may have some small openings, raising some doubts whether they are natural or whether the wall is damaged. On recently preserved specimens, we were not able to find any opening due to the large amount of hypertrophied tissue in the wall and inside the pouch. The muscles *interradialis* are also more developed under the caudal organ, but are not extended posteriorly between the caudal-fin rays as found in “New genus” *gorgonae*. No attachment between muscles and scales was observed. Hooks are in the dorsolateral surface of the rays, anteriorly curved, and associated to hypertrophied whitish tissue. Hooks usually distributed along the distal half or third of the 13th to 18th principal caudal-fin rays, less frequently found from the 12th to the 19th.

Discussion. The “New Genus” and *Saccoderma* are the only compsurin genera whose species inhabit the Central America and the Colombian and Venezuelan trans-Andean drainages. According to Jerep & Malabarba (in manuscript) phylogeny of the Compsurini, “New Genus” is close related to *Saccoderma*, as sister group.

Most of the synapomorphies of “New Genus” is related to the caudal organ morphology and to some ultrastructural aspects of the spermatozoa. Among the Compsurini, the presence of caudal fin modified scales not forming a pouch [Ch. 217: 0] is only found in the “New Genus” species and *Macropsobrycon uruguayanae*. However the modification presented by the scales in *M. uruguayanae* are very tenuous when compared to what is seen in “New Genus”. In *M. uruguayanae* the modified scales are located in the base of the caudal-fin lower lobe, while they are found in the midline of the caudal-fin base in “New Genus” *dialepturus* and “New Genus” *mitopterus*; and although they are enlarged in size, they do not form pockets, as described to “New Genus” *gorgonae*.

The “New Genus” presents the dorsal and ventral margins of the caudal peduncle deeply convex on mature males [Ch. 236: 1]. Under microscope, it is possible to see that the caudal-peduncle scales and skin are not attached to the *hipaxialis* muscles, resulting in an internal chamber-like space between them. A similar condition is also found on mature males of *Kolpotocheirodon*, Compsurini n. sp. Letícia, and Compsurini n. sp. Yurimaguas, however it seems to have been independently acquired by those genera (Jerep & Malabarba, in manuscript).

The spermatozoa morphology of the “New Genus” species presents some unique features among the Cheirodontinae, like the anterior border of the nucleus asymmetric, clearly oblique to the longest axis of the nucleus [Ch. 270: 0 > 1] (Fig. 18a), and vesicles located after the mitochondria, in the basal region of the midpiece and along the cytoplasmic collar in one side of the nucleus [Ch. 272: 0 > 1]. The spermatozoa in the other Compsurini fishes presents the anterior border of the nucleus round or truncated, and absence of vesicles in the located only after the mitochondria in the basal region of the midpiece, even the genera that, like the “New Genus”, do not present nuclear rotation like *Acinocheirodon* and *Saccoderma* (Fig. 18b).

Saccoderma is readily diagnosed from all characid species by the unique caudal organ presented by the mature males (see caudal organ description). The presence of a

pouch-like structure with an internal chamber formed by tissue is only found in *Saccoderma*, *Compsura*, and *Compsurini* n. sp. Purus. Nevertheless the caudal organ in those genera is composed by different scales arranged in different ways. While the organ in *Saccoderma* is formed exclusively by modified scales from the LV1 and LV2 series, in *Compsura* and *Compsurini* n. sp. Purus some enlarged scales from the LL also integrate the organ. The presence of an elongated scale limiting the caudal organ dorsally is also exclusive to *Saccoderma*.

In the description of *Saccoderma melanostigma*, Schultz (1944) diagnosed his species from *S. hastata* by tenuous differences related to the melanophores distribution in the dorsal and anal fins, caudal spot shape, and position of the pelvic fin. According to Schultz, *S. melanostigma* only presents black pigments in the first fourth to fifth branched rays of dorsal and anal fins (*vs.* black pigment cells distributed along the outer third of nearly all the branched rays of these fins in *S. hastata*), posterior margin of the caudal spot round and not extending over the middle caudal-fin rays (*vs.* caudal spot pointed posteriorly, ending over the middle caudal-fin rays), and “pelvic insertion equidistant between snout tip and base of last anal ray to half a snout length behind the anal base” (*vs.* equidistant between tip of snout and a snout length behind the base of anal fin). For this comparison, Schultz quoted that only two specimens of *Saccoderma hastata* (USNM 79223) were used, however the analysis of a larger number of specimens from both species corroborates in part with Schultz observations. Although neither meristic variables nor proportional measurements were useful to separate the species (Table 1), the difference in the distribution of melanophores in the dorsal and anal fins was conservative among the specimens of *S. hastata* and *S. melanostigma*, being useful to distinguish them. The color pattern of the fins was more restricted to the distal tip of the anteriormost rays in *Saccoderma melanostigma* than in *S. hastata*, however this character is sometimes masked in old preserved specimens by the loss of pigments from the melanophores. The caudal spot shape stated by Schultz as diagnostic for the species was variable enough to do not distinguish both species, once its posterior portion varied from pointed to abruptly round among its representatives according to the size and time of preservation.

Comparative material. *Acinocheiroidon melanogramma*: ANSP 176238, paratypes, 7, 21.9-26.2 mm SL, Brazil, Minas Gerais, rio Jequitaiá drainage. *Aphyodite grammica*: FMNH, holotype, 24.3 mm SL, Guiana, Konawaruk. MZUSP 29874, 20, 21.9-26.9 mm SL, Brazil, rio Negro. *Brittanichthys axelrodi*: MCP 14931, 17, 16.3-22.2 mm SL, 3 c&s, Brazil, Boa Vista, rio Negro. *Cheiroidon australe*: USNM 084317, paratypes, 12, 28.4-49.8 mm SL, Chile, Los Lagos region at Puerto Varas. *Cheiroidon dialepturus*: USNM 208524, holotype, 26.8 mm SL, Panama, Veraguas, río San Pedro basin. *Cheiroidon galusdae*: USNM 084319, paratypes, 10, 30.6-52.3 mm SL, Chile, río Locomilla at San Xavier. *Cheiroidon gorgonae*: USNM 64094, holotype, 22.1 mm SL, Panama, Canal Zone, small seepage pool below spillway of the reservoir dam at Gorgona. *Cheiroidon kiliani*: USNM 227310, paratype, 1, 25.2 mm SL. Valdivia-Chile, río Cau-Cau. *Cheiroidon microdon*: FMNH 57867, holotype, 32.2 mm SL, Brazil, Caceres, rio Ibicuhy. *Cheiroidon micropterus*: CAS 59780, holotype, 23.9 mm SL, Brazil, Pará, rio Amazonas drainage at Santarém. *Cheiroidon mitopterus*: USNM 208539, holotype, 34.6 mm SL, Panama, Cocle, río Tucue, tributary of río Cocle del Norte. *Cheiroidon notomelas*: FMNH 57829, holotype, 28.2 mm SL, Brazil, Miguel Calmone. *Cheiroidontops geayi*: USNM 121507, holotype, 35.5 mm SL, Venezuela, Estado de Aragua, río Guarico. *Compsura heterura*: FMNH 57825, holotype, 28.7 mm SL, Brazil, rio Itapicuru, Queimadas. *Holesthes heterodon* (= *Serrapinnus heterodon*): CAS 117522, paratypes, 4, 32.2-36.5 mm SL, Brazil, Minas Gerais, rio Grande, Jaguará. *Kolpotocheiroidon figueiredoi*: MCP 22345, paratypes, 25.1-30.5 mm SL, rio Pratinha, Iraquara. *Kolpotocheiroidon theloura*: MCP 11161, paratype, 25.9 mm SL, ribeirão do Gama, just above, the mouth of ribeirão Taquara. *Leptobrycon jatuaranae*: MCP 14936, 17, 20.8-25.1 mm SL, 3 c&s, Brazil, Amazonas, rio Negro. *Microchemobrycon guaporensis*: FMNH 57926, holotype, 29.1 mm SL, Brazil, Maciel, rio Guaporé. *Odontostilbe hastatus*: FMNH 56383, holotype, 30.2 mm SL, Colombia, Soplaviento. *Oligobrycon microstomus*: holotype, 31.0 mm SL, Brazil, Jacarehy on rio Parahyba. *Oxybrycon* sp.: MCP 33105, 8, 13.7-14.9 mm SL, 2 c&s, Venezuela, Titi lagoon, upper Orinoco basin. *Parecbasis cyclolepis*: FMNH 56677, holotype, 56.3 mm SL, Brazil, rio Madeira. MZUSP 26146, 7, 40.3-53.5 mm SL, Peru, Ucayali, río Ucayali. *Pristella aubynei*: FMNH 52698, 34.9 mm SL, British Guiana. *Prodontocharax alleni*: CAS 117472, holotype, 32.8 mm SL, Peru, Ucayali, río Amazonas basin. *Prodontocharax melanotus*:

CAS 59793, holotype, 44.9 mm SL, Bolivia, La Paz, río Amazonas drainage at Tumupasa. *Pseudocheirodon affinis*: CAS 117516, paratype, 32.1-35.4 mm SL, Panama, rio Gatun, at Gatun. *Saccoderma melanostigma*: USNM 121519, holotype, 26.7 mm SL, Venezuela, río San Juan, South of Mene Grande. *Spintherobolus broccae*: FMNH 58864, paratype, 18.7 mm SL, Brazil, Rio de Janeiro. *Spintherobolus papilliferus*: FMNH 104802, holotype, 32.9 mm SL, Brazil, São Paulo, Alto da Serra. *Thrissobrycon pectinifer*: SU 16944, holotype, 26.8 mm SL, Brazil, Cucuhy, rio Negro. MCP 14932, 12, 26.4-30.2 mm SL, 3 c&s, Brazil, rio Arirara.

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Literature Cited

- Bührnheim, C. M. & L. R. Malabarba. 2006. Redescription of the type species of *Odontostilbe* Cope, 1870 (Teleostei: Characidae: Cheirodontinae), and description of three new species from the Amazon basin. *Neotropical Ichthyology*, 4(2): 167-196.
- Burns, J. R., S. H. Weitzman & L. R. Malabarba. 1997. Insemination in eight species of cheirodontine fishes (Teleostei: Characidae: Cheirodontinae). *Copeia* 1997: 433-438.
- Dahl, G. 1955. An ichthyological reconnaissance of the Sinu River. *Revista Linneana*, 1 (1): 11-19.
- Dahl, G. 1958. Los peces del río Sinú – Informe preliminar. Publicación de la secretaría de agricultura y Ganadería de Córdoba. Montería. 9-47p.

- Dahl, G. 1971. Los peces del norte de Colombia. Instituto de Desarrollo de los Recursos Naturales Renovables (INDERENA), Bogota. xvii + 391p.
- Dahl, G. & F. Medem. 1964. Informe sobre la fauna acuatica del Rio Sinu. I Parte. Los Peces y la Pesca del Rio Sinu. Corporacion Autonoma Regional de los Valles del Magdalena y del Sinu -CVM-. Departamento de Investigaciones Ictiologicas y Faunisticas. 109 p.
- Dahl, G., F. Medem & A. Ramos Henao. 1964. El "Bocachico" contribución al estudio de su biología y de su ambiente. Departamento de Pesca de la Corporación Autónoma Regional de los Valles del Magdalena y del Sinú, 144p.
- Eigenmann, C. H. 1915. The Cheirodontinae, a subfamily of minute characid fishes of South America. *Memoirs of the Carnegie Museum*, 7(1): 1-99.
- Eschmeyer, W. N. & R. Fricke, R. 2011. Catalog of Fishes electronic version (5 May 2011). <http://research.calacademy.org/ichthyology/catalog/fishcatmain.asp>
- Fink, W. L. & S. H. Weitzman. 1974. The so-called Cheirodontin fishes of Central America with descriptions of two new species (Pisces: Characidae). *Smithsonian Contributions to Zoology*, 172: 1-46.
- Galvis, G., J. I. Mojica & M. Camargo. 1997. Peces del Catatumbo - Asociación Cravo Norte, Santafé de Bogotá, D.C., 188p.
- Gonçalves, T. K., M. A. Azevedo, L. R. Malabarba & C. B. Fialho. 2005. Reproductive biology and development of sexually dimorphic structures in *Aphyocharax anisitsi* (Ostariophysi: Characidae). *Neotropical Ichthyology*, 3(3): 433-438.
- López, M. I. 1972. Contribución al estudio de los peces Cheirodontinae (Familia Characidae) de Cost Rica y Panama: generos *Compsura* y *Pseudocheirodon*. *Revista de Biología Tropical*, 20(1): 93-129.
- López, H. L. , A. M. Miquelarena & R. C. Menni. 2003. Lista comentada de los peces continentales de la Argentina. *ProBiotA - Serie Técnica y Didáctica*. 5: 1-85.
- Malabarba, L. R. 1998. Monophyly of the Cheirodontinae, characters and major clades (Ostariophysi: Characidae). Pp. 193-233. In: Malabarba, L. R, R. E. Reis, R. P. Vari, Z. M. S. Lucena & C. A. S. Lucena (Eds.). *Phylogeny and Classification of Neotropical Fishes*. Porto Alegre, Edipucrs, 603p.

- Malabarba, L. R. 2003. Subfamily Cheirodontinae (Characins, tetras). Pp. 215-221. In: R. E. Reis; S. O. Kullander & C. J. Ferraris (Eds.). Check list of the freshwater fishes of South and Central America. Porto Alegre, Edipucrs, 729p.
- Malabarba, L. R., F. C. T. Lima & S. H. Weitzman. 2004. A new species of *Kolpotocheirodon* (Teleostei: Characidae: Cheirodontinae: Compsurini) from Bahia, northeastern Brazil, with a new diagnosis of the genus. Proceedings of the Biological Society of Washington, 117(3): 317-329.
- Malabarba, L. R. & S. H. Weitzman. 1999. A new genus and species of South American fishes (Teleostei: Characidae: Cheirodontinae) with a derived caudal fin, including comments about inseminating cheirodontines. Proceedings of the Biological Society of Washington, 112(2): 410-432.
- Malabarba, L. R. & S. H. Weitzman. 2000. A new genus and species of inseminating (Teleostei: Characidae: Cheirodontinae: Compsurini) from South America with uniquely derived caudal-fin dermal papillae. Proceedings of the Biological Society of Washington, 113(1): 269-283.
- Maldonado-Ocampo, J. A., A. Ortega-Lara, J. S. Usma O., G. Galvis V., F. A. Villa-Navarro, G. L. Vasquez, S. Prada-Pedrerros & C. Ardila R. 2005. Peces de los Andes de Colombia. Instituto de Investigaciones de Recursos Biológicos “Alexander von Humboldt”. Bogotá, Colombia. 346p.
- Menni, R. C. 2004. Peces y ambientes en la Argentina continental. Monografías del Museo Argentina Ciencias Natureles, Buenos Aires. 5: 1-316.
- Meek, S. E. & S. F. Hildebrand. 1916. The fishes of the freshwaters of Panama. Field Museum of Natural History, Zoological Series, 10(15): 217-374.
- Schultz, L. P. 1944. The fishes of the family Characinidae from Venezuela, with descriptions of seventeen new forms. Proceedings of the United States National Museum, 95(3181): 235-367.
- Taylor, W. R. & G. C. van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium, 9(2): 107-119.

Table 1. Morphometric and meristic data for *Saccoderma hastata* and *S. melanostigma*. Ray counts correspond only to the branched rays.

	<i>Saccoderma hastata</i>					<i>Saccoderma melanostigma</i>				
	N	Min	Max	Mean	SD	N	Min	Max	Mean	SD
Standard length (mm)	102	21.8	30.2	24.4	-	33	23.6	29.5	26.6	-
Percents of Standard Length										
Head length	102	24.2	29.6	27.0	1.01	33	24.9	27.6	26.2	0.69
Bony Head length	102	23.0	27.4	25.3	0.89	33	23.2	26.8	24.8	0.86
Snout-anal distance	102	59.1	72.9	65.2	2.17	33	61.7	69.0	65.6	1.75
Snout-dorsal distance	102	47.7	56.4	51.9	1.73	33	49.0	55.6	51.1	1.32
Snout-pelvic distance	102	44.7	53.0	47.8	1.43	33	43.7	52.1	47.5	1.61
Snout-pectoral distance	102	24.6	30.0	27.3	1.13	33	25.1	28.6	26.5	0.82
Dorsal-fin base length	102	11.6	16.6	14.1	0.80	33	13.2	15.8	14.3	0.69
Anal-fin base length	102	21.3	29.1	25.5	1.35	33	23.4	28.0	25.4	0.96
Length of caudal peduncle	102	11.7	17.1	14.2	1.22	33	13.7	18.2	15.4	1.00
Depth of caudal peduncle	102	9.6	15.0	11.9	1.06	33	10.7	13.9	12.0	0.76
Body depth at dorsal-fin	102	27.2	35.9	32.1	2.13	33	28.8	41.2	33.6	2.35
Dorsal-fin length	87	26.1	31.9	29.2	1.31	32	24.3	33.3	29.8	1.46
Pelvic-fin length	101	14.0	21.7	18.6	1.46	33	17.3	20.2	18.7	0.84
Pectoral-fin length	102	11.6	24.7	21.3	1.50	33	19.9	23.4	21.6	0.75
Percents of Head Length										
Snout length	102	22.4	28.9	25.8	1.23	33	22.9	28.7	25.1	1.51
Upper Jaw length	102	26.3	36.1	30.7	1.92	33	28.4	36.8	33.2	1.75
Horizontal orbit diameter	102	33.3	44.1	38.1	1.85	33	37.0	43.7	39.6	1.50
Interorbital width	102	25.9	33.5	29.4	1.51	33	27.9	33.7	30.8	1.28
Counts										
Lateral line	102	31	36	33.8	0.95	32	32	35	33.6	0.76
Lateral line perforated scles	102	31	36	33.7	0.97	32	32	35	33.6	0.76
Lateral line to dorsal fin	102	5	6	5.2	0.38	33	5	6	5.1	0.33
Lateral line to anal fin	102	3	5	3.9	0.30	33	3	4	3.9	0.24
Pre-dorsal scales	102	9	12	10.5	0.61	33	9	12	10.4	0.60
Pos-dorsal scales	102	7	11	8.8	0.77	33	8	10	9.0	0.59
Anal-fin base scales	102	8	14	10.4	0.91	32	10	13	11.0	0.82
Scales rows on CP	102	14	16	14.0	0.28	33	14	14	14.0	0.00
Dorsal-fin rays	102	8	9	9.0	0.14	33	9	10	9.0	0.17
Anal-fin rays	102	16	19	17.7	0.78	33	17	20	18.2	0.82
Pectoral-fin rays	102	9	11	10.0	0.60	33	10	12	10.8	0.56
Pelvic-fin rays	102	6	7	7.0	0.10	33	7	7	7.0	0.00
Caudal-fin rays	100	18	20	19.0	0.25	33	19	19	19.0	0.00

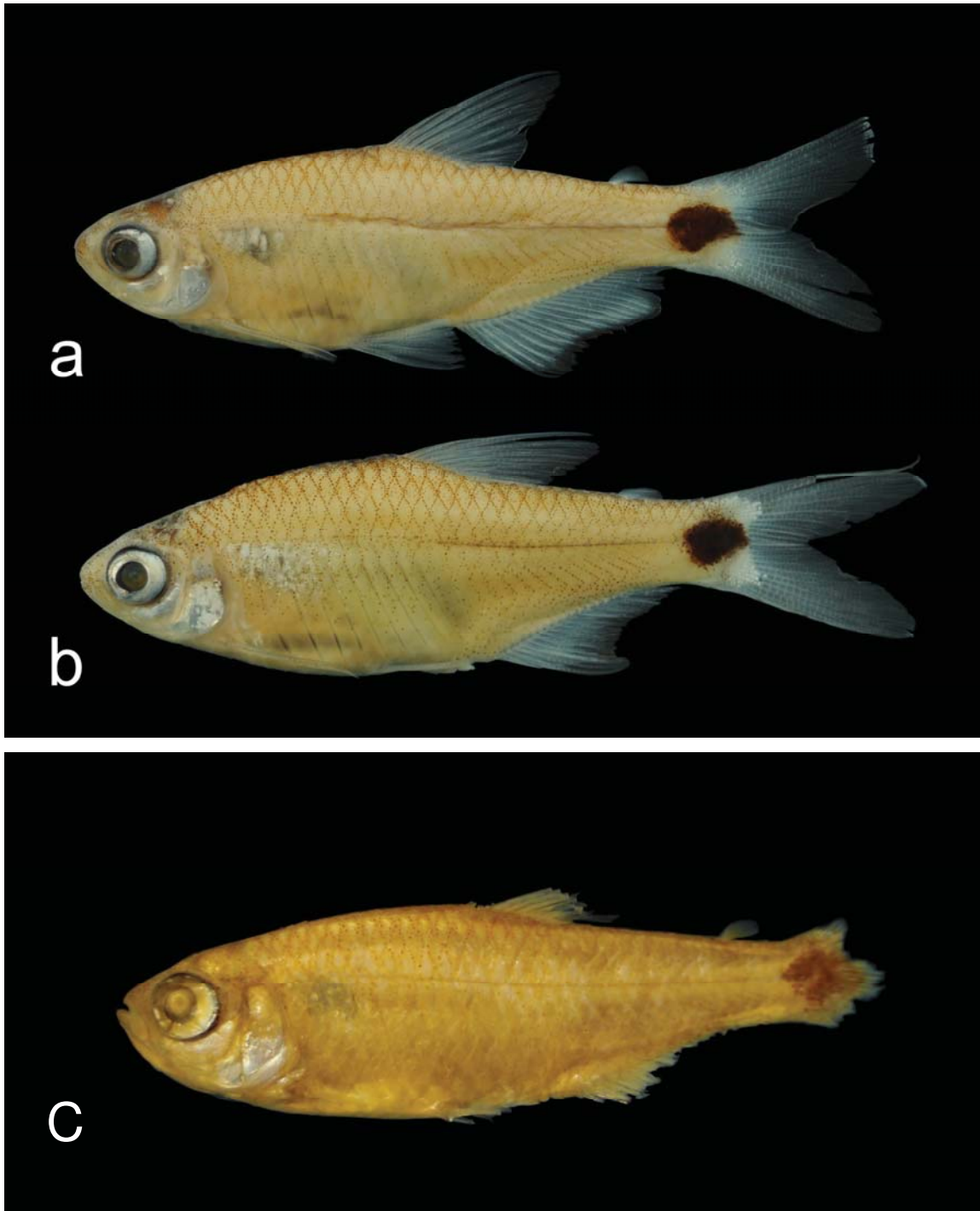


Fig. 1. “New Genus” *gorgonae*, (a) ANSP 151219, male, 27.5 mm SL; (b) ANSP 151219, female, 28.7 mm SL; (c) USNM 64094, holotype, 22.1 mm SL.

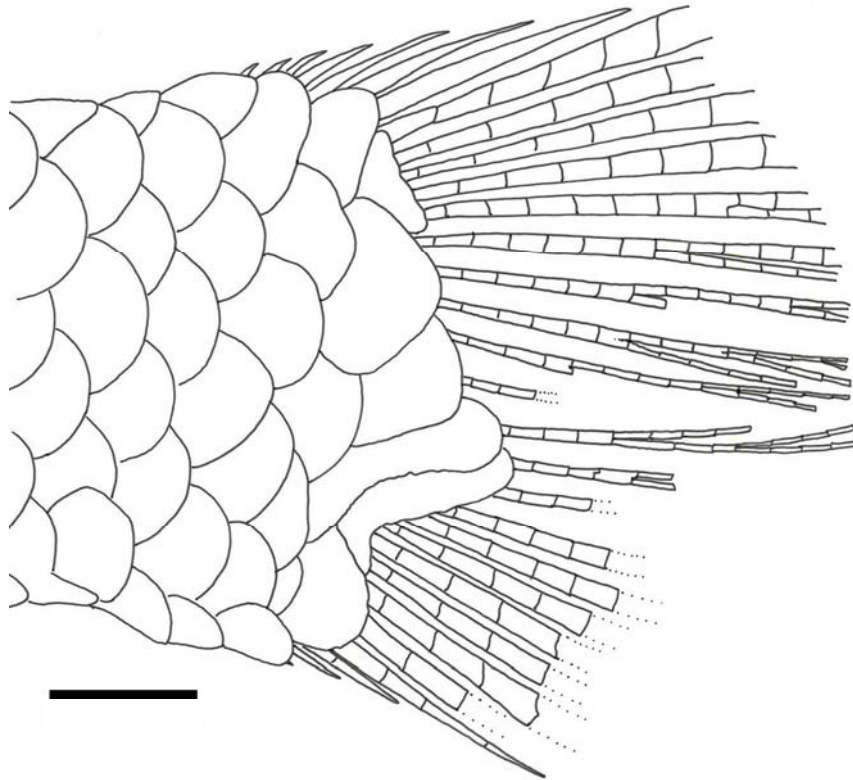


Fig. 2. “New Genus” *gorgonae* caudal fin, USNM 208543, male, 25.9 mm SL. Scale bar = 1 mm.

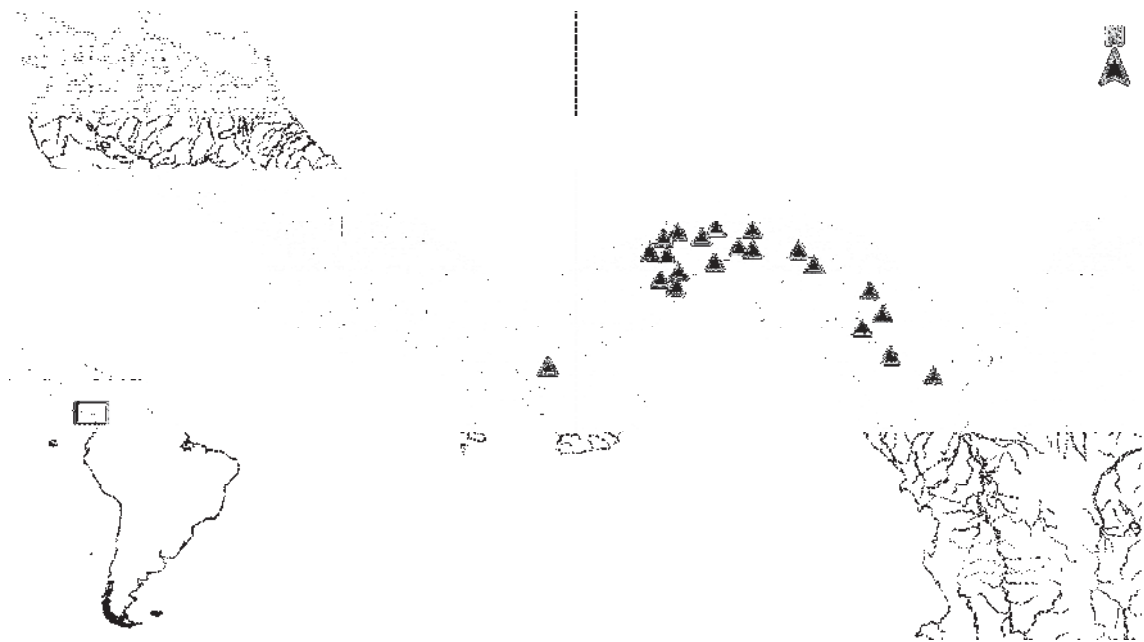


Fig. 3. Map of distribution for “New Genus” *gorgonae*. Symbols may represent more than one lot or locality.



Fig. 4. “New Genus” *dialepturus*, (a) ANSP 146905, male, 27.9 mm SL; (b) USNM 208524, holotype, 28.0 mm SL.

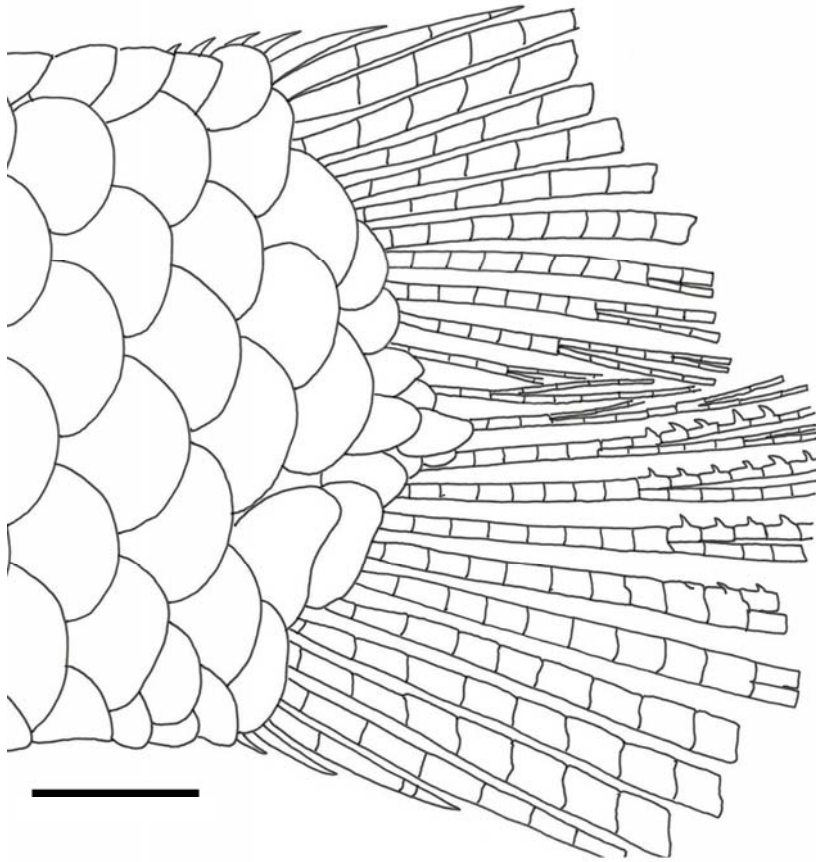


Fig. 5. Caudal fin illustration of “New Genus” *dialepturus*, USNM 209509, male, 31.9 mm SL, showing modified scales over the base of the middle caudal-fin rays. Scale bar = 1 mm.



Fig. 6. Whitish tissue surrounding anal and caudal-fin hooks in “New Genus” *dialepturus*, ANSP 146905, 27.9 mm SL.



Fig. 7. Map of distribution for “New Genus” *dialepturus*. Symbols may represent more than one lot or locality.

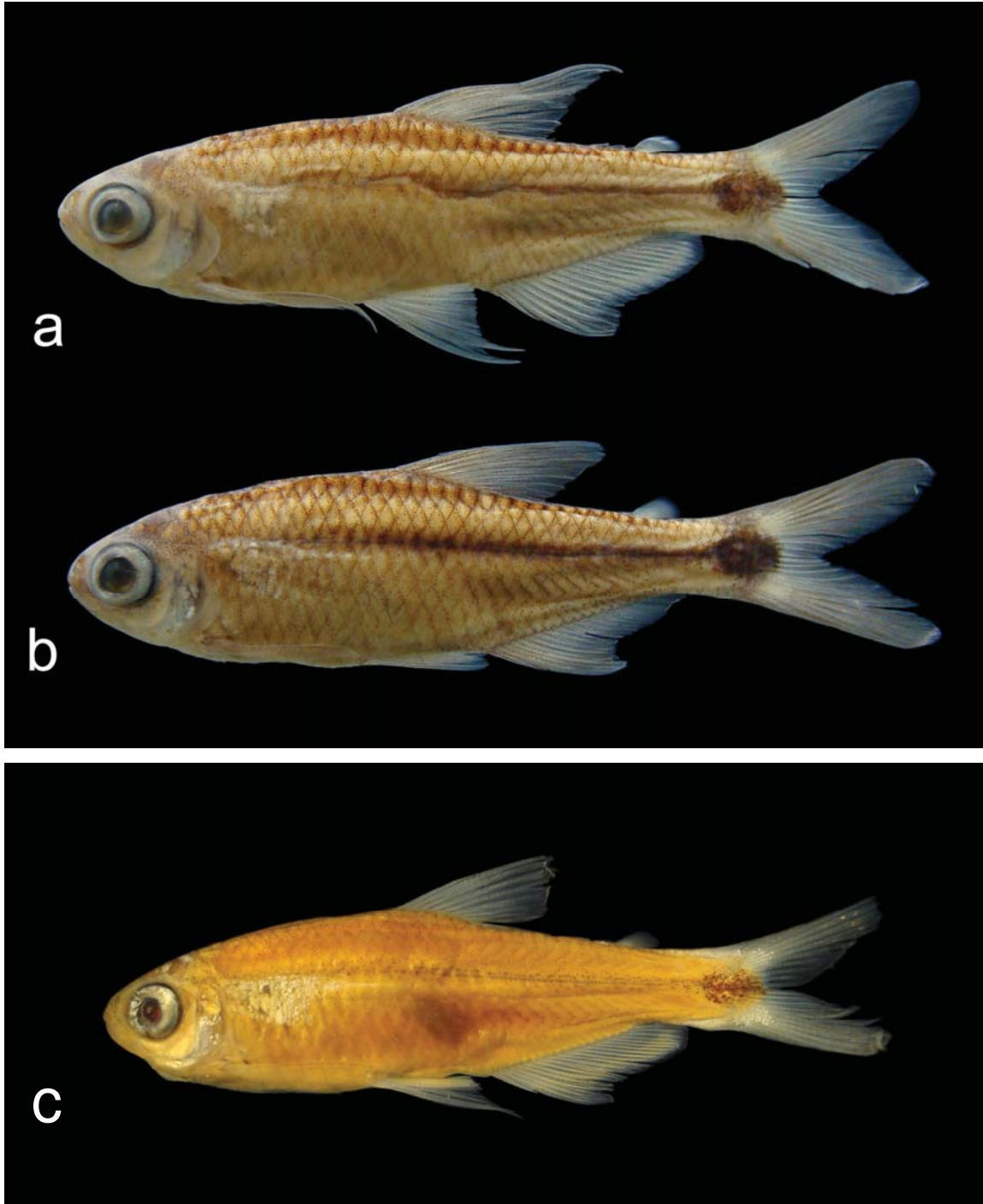


Fig. 8. “New Genus” *mitopterus*, (a) USNM 208541, paratype, male, 30.5 mm SL; (b) USNM 208541, paratype, female, 31.1 mm SL; (c) USNM 208539, holotype, male, 35.1 mm SL.

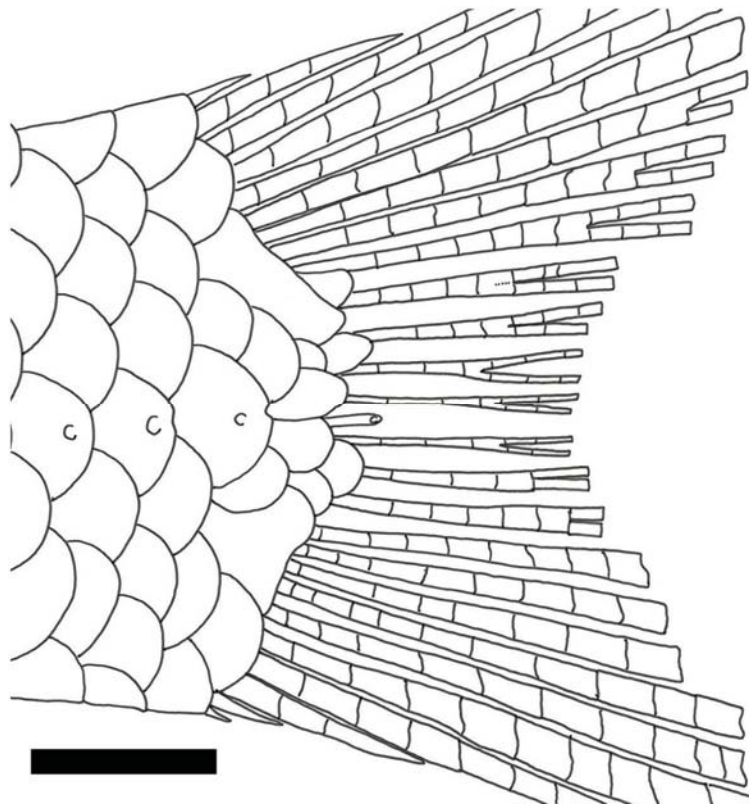


Fig. 9. Caudal fin illustration of “New Genus” *mitopterus*, MCP 16133, male, 30.5 mm SL, showing modified scales over the base of the middle caudal-fin rays. Scale bar = 1 mm.

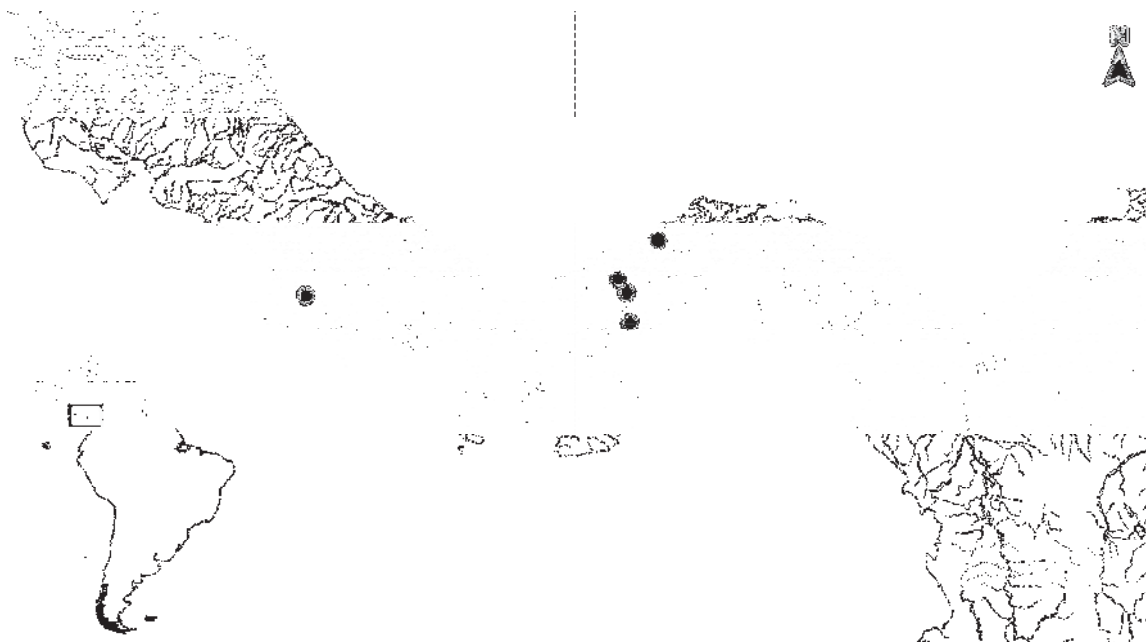


Fig. 10. Map of distribution for “New Genus” *mitopterus*. Symbols may represent more than one lot or locality.

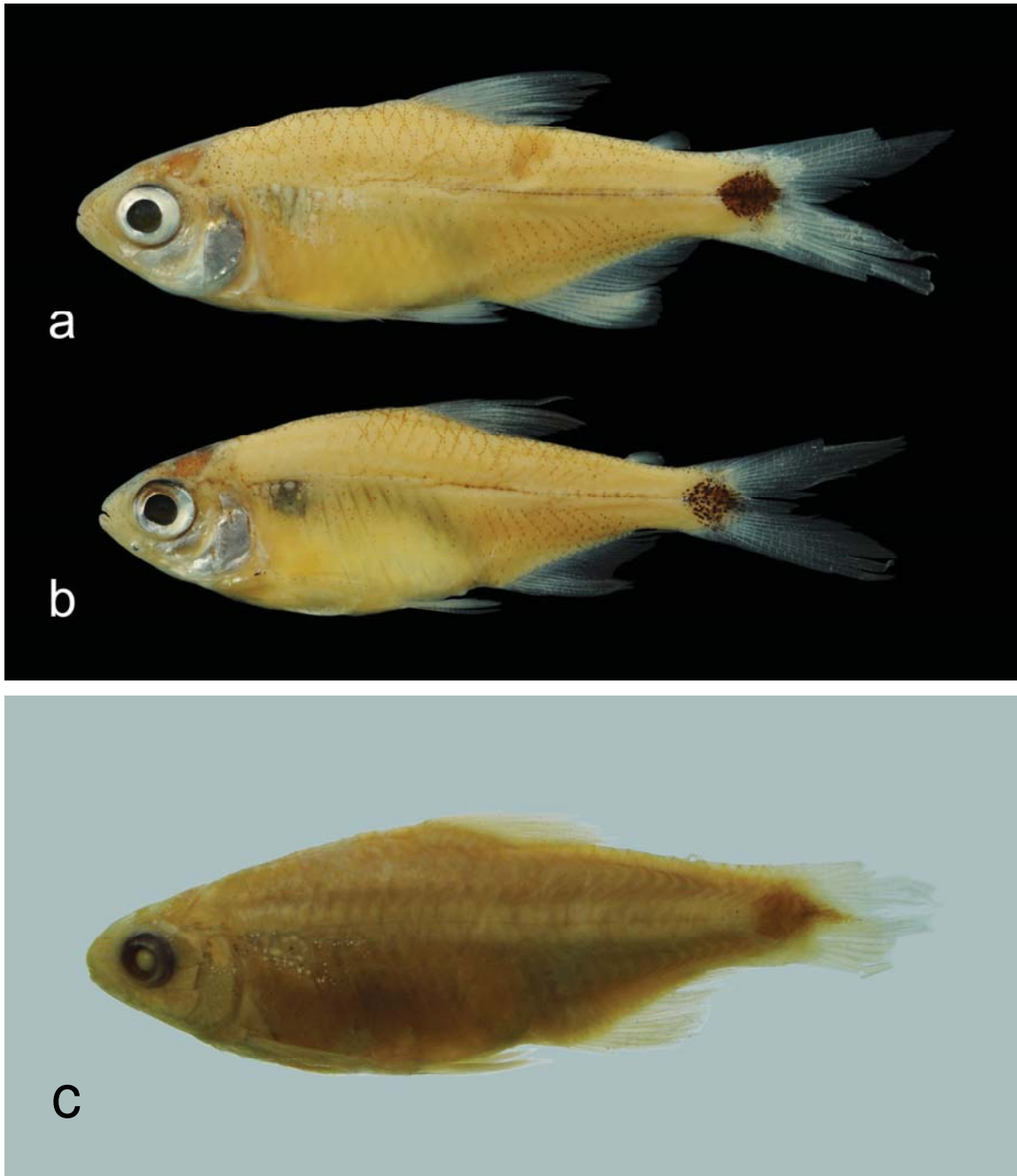


Fig. 11. *Saccoderma hastata*, (a) ANSP 140817, male, 26.2 mm SL; (b) ANSP 140817, female, 24.2 mm SL; (c) FMNH 56383, holotype, male, 30.2 mm SL.

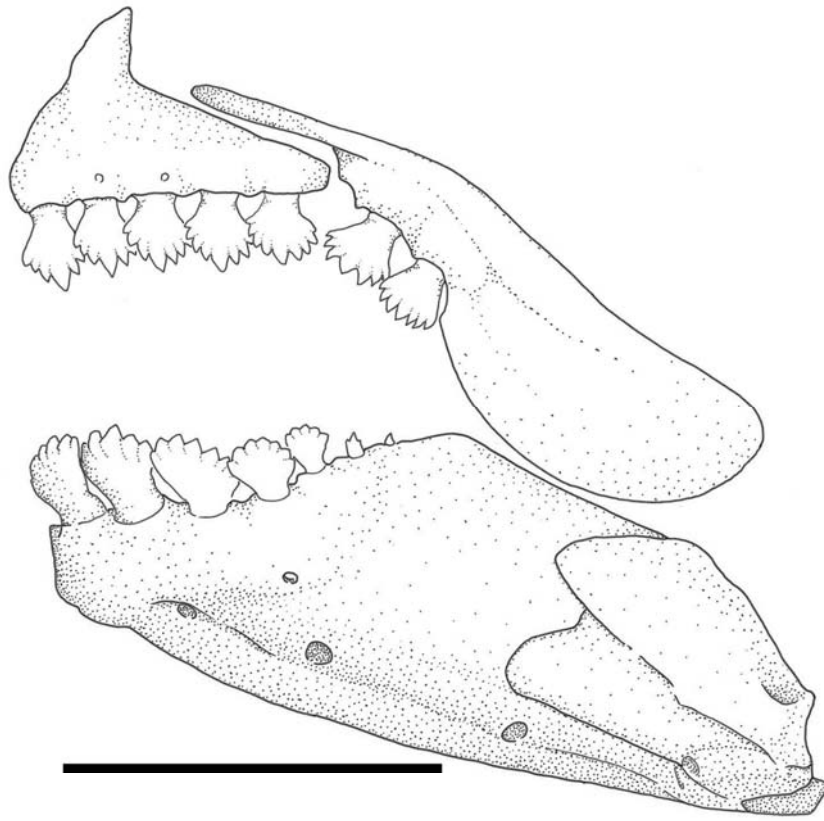


Fig. 12. Premaxilla, maxilla and dentary of *Saccoderma hastata*, ICN 1464, 25.6 mm SL.
Scale bar = 1 mm.

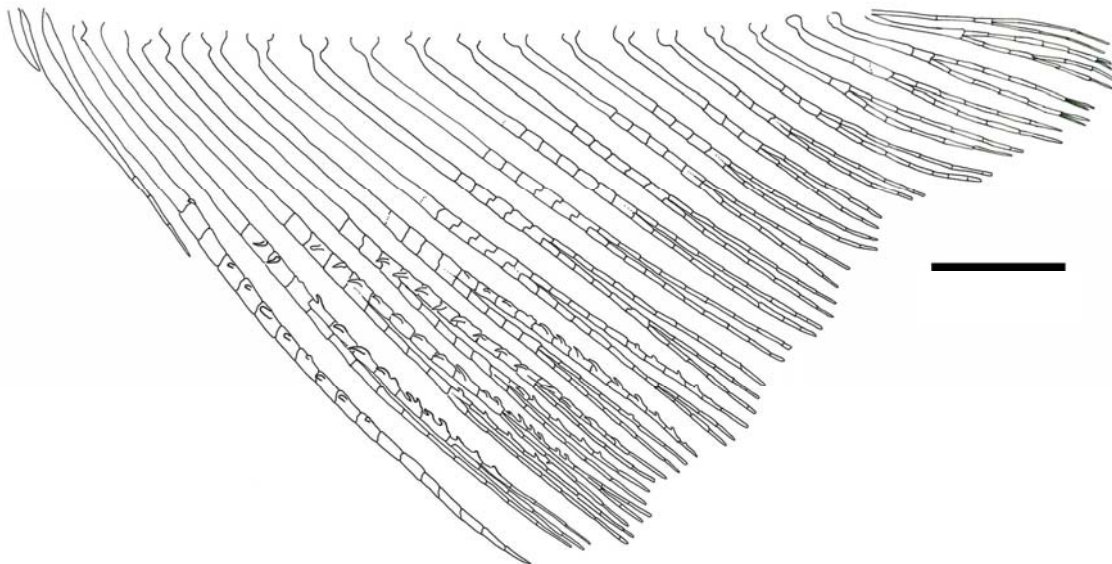


Fig. 13. Anal fin illustration of *Saccoderma melanostigma*, USNM 121522, 28.1 mm SL.
Scale bar = 1 mm.

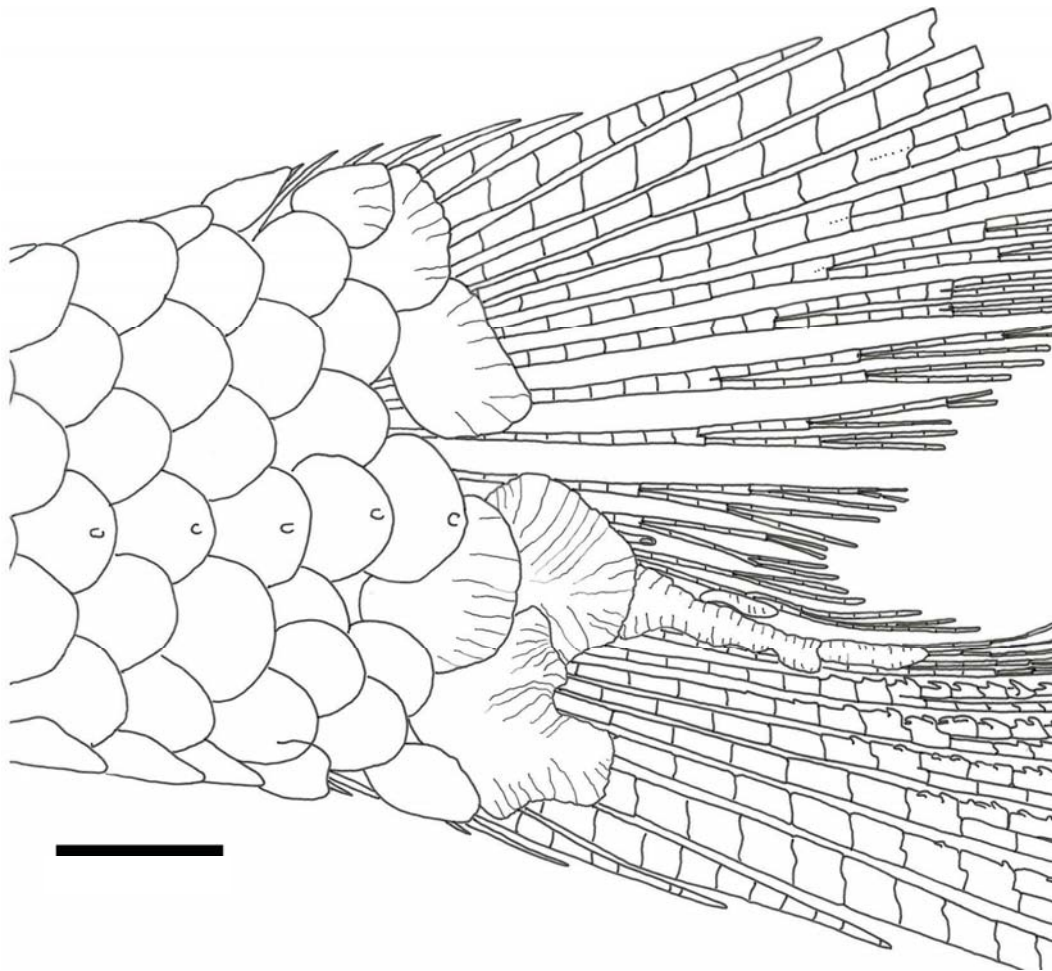


Fig. 14. Caudal fin illustration of *Saccoderma melanostigma*, USNM 121522, 28.1 mm SL, showing modified scales over the caudal-fin lower lobe. Scale bar = 1 mm.

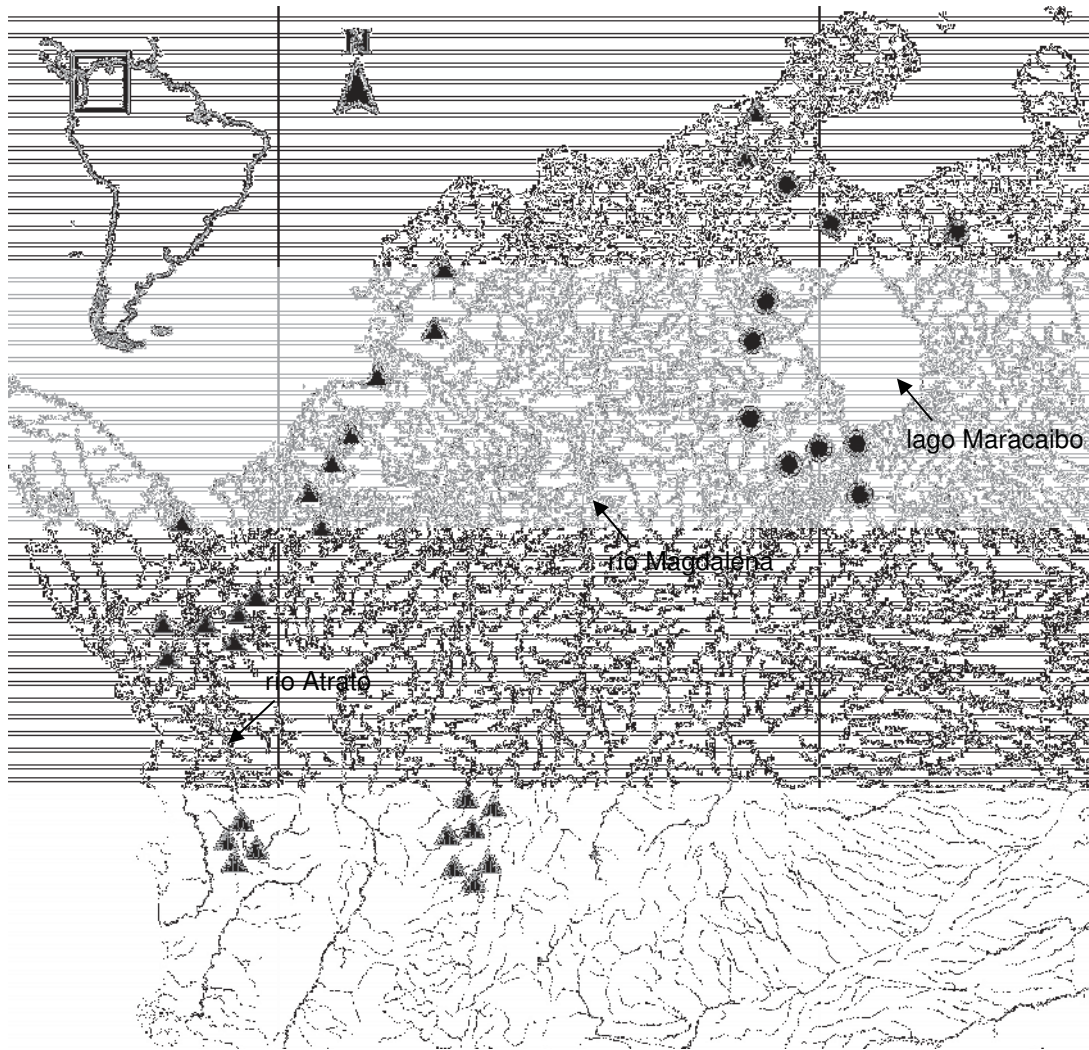


Fig. 15. Map of distribution for *Saccoderma hastata* (triangles) and *S. melanostigma* (dots). Symbols may represent more than one lot or locality.

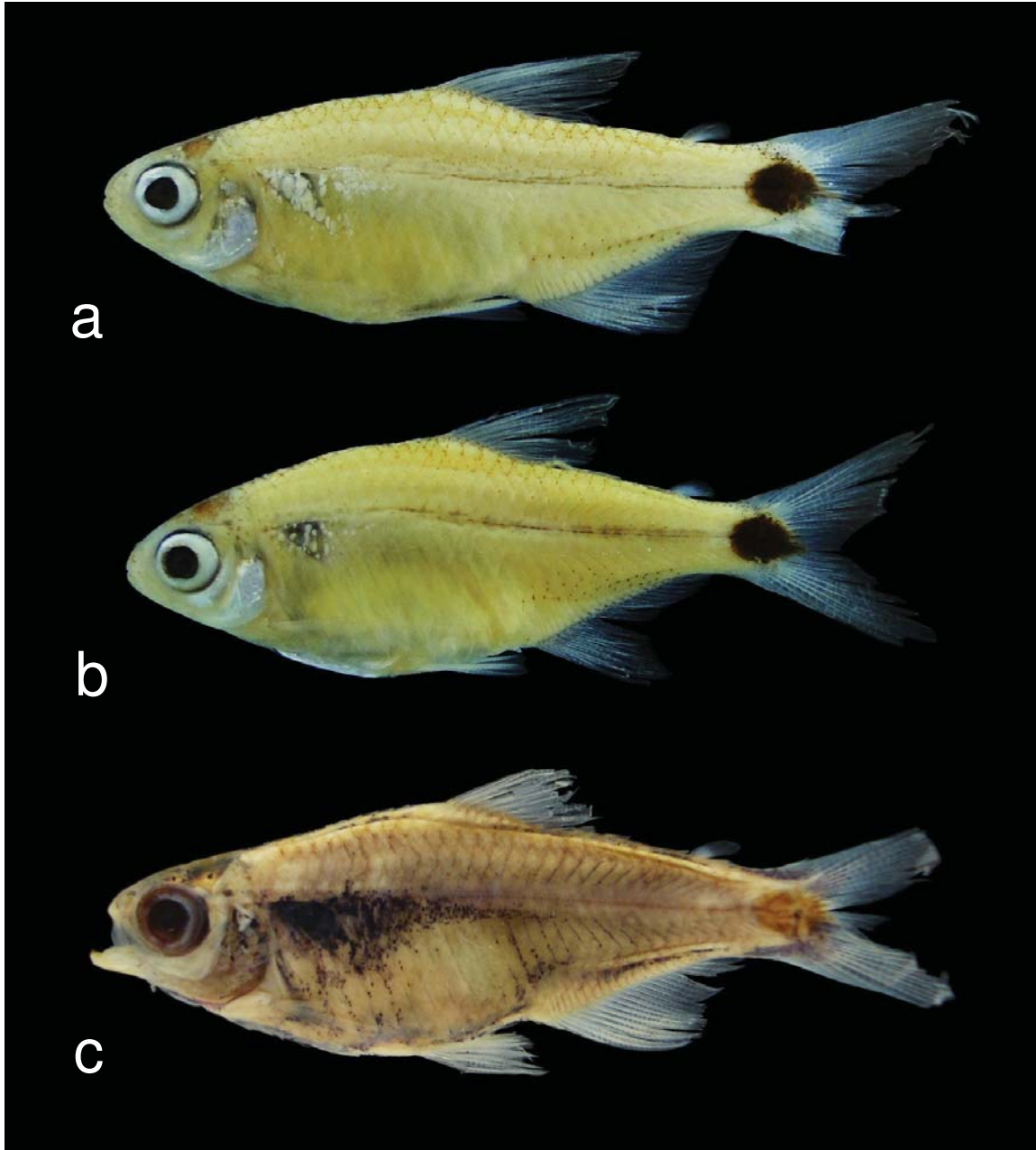


Fig. 16. *Saccoderma melanostigma*, (a) INHS 55462, male, 27.7 mm SL; (b) INHS 55462, female, 26.7 mm SL; (c) USNM 121519, holotype, male, 26.7 mm SL.

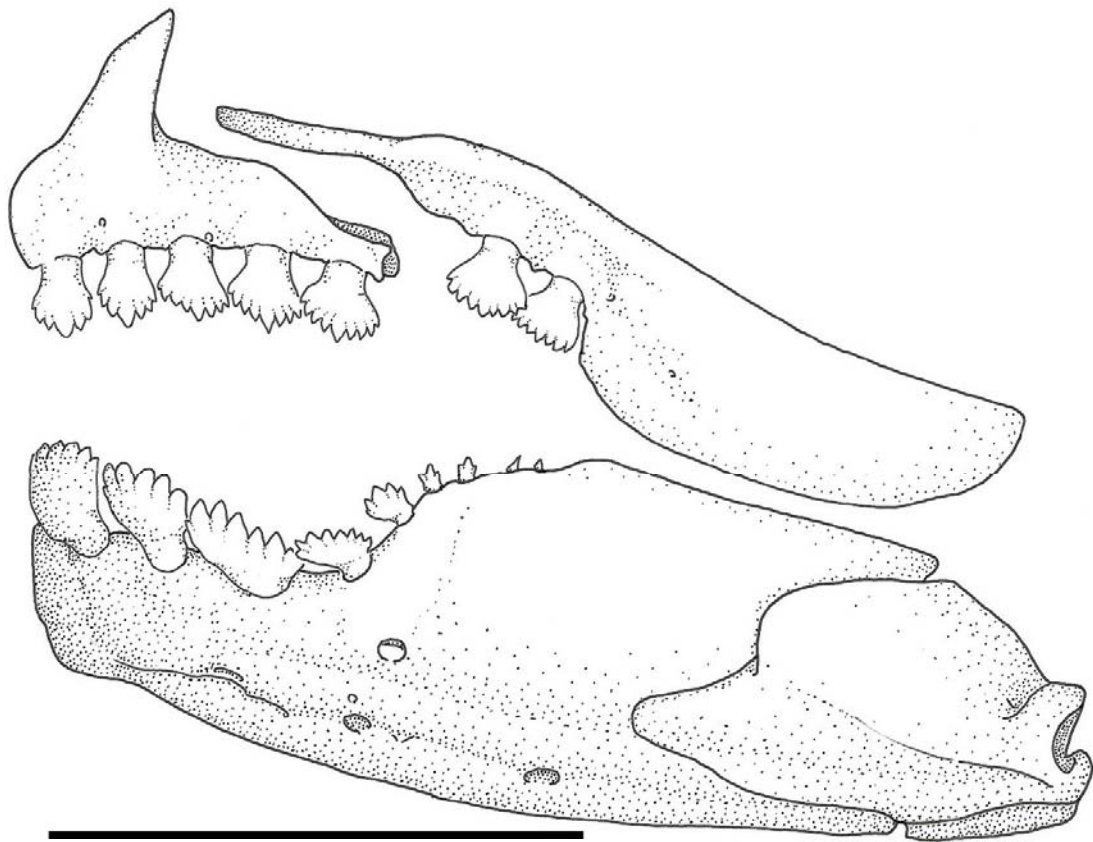


Fig. 17. Premaxilla, maxilla and dentary of *Saccoderma melanostigma*, FMNH 85280, 23.8 mm SL. Scale bar = 1 mm.

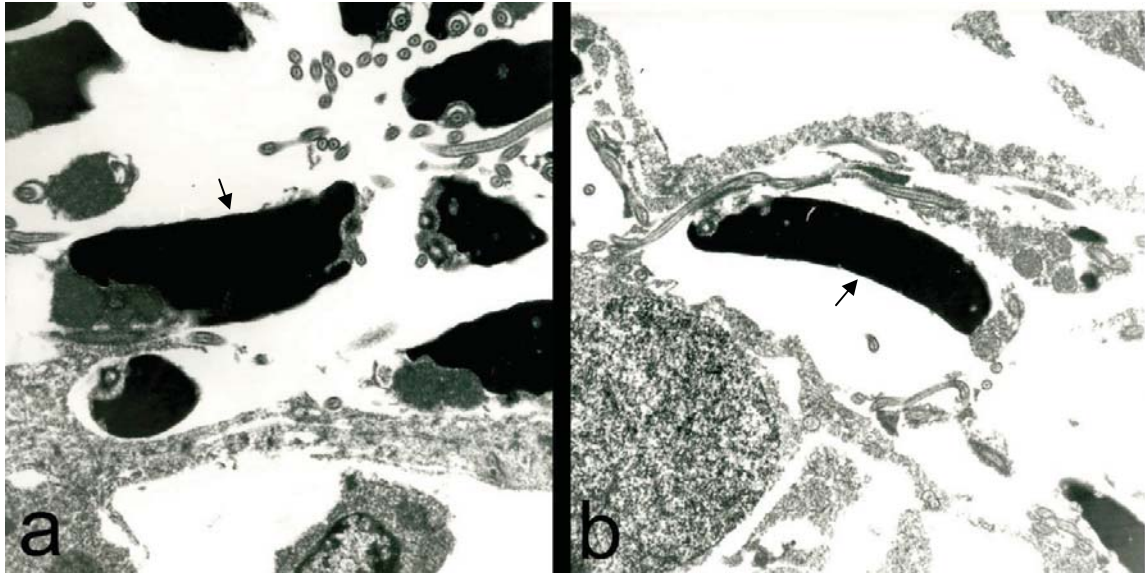


Fig. 18. Longitudinal sections through mature spermatozoa of the inseminating compsurins (a) “New Genus” *gorgonae* (USNM 293214) and (b) *Saccoderma melanostigma* (CAS 66936). Arrows point nucleus of the spermatozoa. Zoom 3400x.

CAPÍTULO V

Description of three genera and six new species of Compsurini (Characidae: Cheirodontinae) from the upper Amazon basin

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Abstract

Three genera and six new species of Compsurini from the Amazon basin are herein described. “New Genus A” Cuzco n. sp., from the upper río Madre de Díos and upper río Ucayali basins, and “New Genus A” Tingo n. sp., from the río Ucayali basin, are diagnosed from all compsurin by the absence of sexual dimorphism in the caudal fin. The former species differs from the latter by having anal-fin hooks dorsally directed, instead of anteriorly directed, as usually found in the Compsurini. “New Genus B” Purus n. sp., from the upper rio Purus basin, is diagnosed by the presence of a caudal pouch formed by modified scales from the LL and LV1 in association to caudal-fin hooks posteriorly directed. “New Genus C” Leticia n. sp. from rio Amazonas in Colombia, is diagnosed by the presence of anal-fin hooks dorsally bent and the presence of none or one single tricuspid tooth in the maxilla. The presence of hooks anteriorly directed on the i,1-4 anal-fin rays distinguishes “New Genus C” Napo n. sp., from the río Napo, upper río Huallaga, and upper río Ucayali basins, from all the compsurini. The sixth species, “New Genus C” Yurimaguas n. sp., only known from a small tributary of the rio Amazonas, inland from Yurimaguas, Peru, is distinguished by the presence of hooks on the 8th to 18th principal caudal-fin rays.

Resumo

Três gêneros e seis species novas de Compsurini da bacia amazônica são aqui descritas. “Gênero Novo A” Cuzco n.sp., das bacias do alto río Madre de Díos e do alto río Ucayali, e “Gênero Novo A” Tingo n. sp., da bacia do río Ucayali basin, são diagnosticados dos demais Compsurini pela ausência de dimorfismo sexual na nadadeira caudal. A primeira espécie, difere da segunda por ter os ganchos da nadadeira anal direcionados dorsalmente, ao invés de direcionados anteriormente, como comumente encontrado nos Compsurini. “Gênero Novo C” Leticia n. sp. do rio Amazonas na Colombia, é diagnosticada pela presença de ganchos da nadadeira anal direcionados dorsalmente e pela ausência de dentes na maxila, ou presença de um único dente tricuspíado. A presença de ganchos direcionados anteriormente nos raios i,1-4 da nadadeira anal distingue “Gênero Novo C” Napo n. sp., presente nas bacias do río Napo, alto río Huallaga, e alto río Ucayali, de todos os Compsurini. “Gênero Novo B” Purus n. sp., da bacia alto rio Purus, é diagnosticado pela presença de uma bolsa caudal formada por escamas modificadas da LL e LV1 em associação a ganchos direcionados posteriormente da nadadeira caudal. A sexta espécie, “Gênero Novo C” Yurimaguas n. sp., apenas conhecida para um pequeno tributário do rio Amazonas, Peru, é distinguida pela presença de ganchos nos raios principais 8 a 18 da nadadeira caudal.

Key words: Systematics, Taxonomy, Neotropical region.

Introduction

The Cheirodontinae is a group of small characid fishes widely distributed throughout the Neotropical region (Fig. 1a). Two tribes were recognized by Malabarba (1998) in the subfamily, Cheirodontini Eigenmann and Compsurini Malabarba, Weitzman & Burns, being the latter the one which includes the inseminating cheirodontines (Burns, Weitzman & Malabarba, 1997). At the moment, Compsurini hosts twelve species remarkably recognized by the presence of secondary sexual dimorphism on the caudal fin, usually related to the hypertrophy of soft tissue, presence of papillae, presence of hooks on the rays, and/or scales modified in shape and size (Malabarba & Weitzman, 1999; Malabarba & Weitzman, 2000; Malabarba, Lima & Weitzman, 2004).

The compsurin species are distributed from the South of Brazil and Uruguay to the South of Costa Rica, where *Macropsobrycon uruguayanae* Eigenmann, inhabits the laguna dos Patos system and rio Uruguai basin; *Kolpotocheirodon theloura* Malabarba & Weitzman, from the upper Paraná basin; *Kolpotocheirodon figueiredoi* Malabarba, Lima & Weitzman, from the rio Paraguaçu basin in Northeast of Brazil; *Acinocheirodon melanogramma* Malabarba & Weitzman, from the rio São Francisco and rio Jaquitinhonha basins; *Compsura heterura* Eigenmann, from the rio São Francisco basin and coastal rivers from Northeast of Brazil; *Saccoderma falcata* Dahl, *S. hastata* (Eigenmann), *S. melanostigma* Schultz, and *S. robusta* Dahl, from Colombian drainages and Lago Maracaibo basin; “*Compsura*” *gorgonae* (Evermann & Goldsborough), “*Odontostilbe*” *dialeptura* (Fink & Weitzman), and “*Odontostilbe*” *mitoptera* (Fink & Weitzman) from Central America, in the Panama and South of Costa Rica drainages. No species is known from the Amazon basin, what characterises a large gap in the geographic distribution of the tribe (Fig. 1b).

A review of the cheirodontine species from the Amazon basin revealed the presence of eight new species of Compsurini, most of them from the upper portion of the main tributaries of the basin, bringing a new comprehension about the real geographic distribution of the compsurins (Fig. 1c). Two of these species belongs to *Compsura* Eigenmann, they are from the rio Araguaia and upper rio Guaporé basins and will be described elsewhere with a complete review of the genus. The other six species are from headwaters of the río Madre de Díos, rio Purus, río Ucayali, río Huallaga, and río Napo, and belong to three new genera described herein. A taxonomic key for the Compsurini species is also presented.

Material and Methods

Counts and measurements were taken according to Fink & Weitzman (1974), as possible on the left side of the specimens. Measures were taken point-to-point straight-line with a 0.01 precision caliper. The head length measure is defined as the distance between the tip of the snout and the posterior margin of subopercle (Bührnheim & Malabarba, 2006). Total vertebrae number includes the four vertebrae of the Weberian apparatus, and the terminal

“half centrum” (Malabarba & Weitzman, 1999). The gill rakers were counted from the first branchial arch, and the gill raker in the junction of the ceratobranchial and the epibranchial was counted referred to the epibranchial count. The counts of vertebrae, supraneurals, teeth, and gill rakers were based on radiographs and cleared and stained (c&s) specimens following Taylor & van Dyke (1985) protocol. The counts referred to the holotype are followed by an asterisk in the description. Drawings of the jaws, anal fin, caudal fin, and scales were prepared in a stereomicroscope with camera lucida.

The sex identification of specimens was based on Gonçalves *et al.* (2005) and Bührnheim & Malabarba (2006), where males and females are recognized by dissection, or by the presence of sexual dimorphism in specimens with similar size in the same sample. Specimens smaller than the smallest specimen showing sexual dimorphism in each lot are termed as unsexed, as well as specimens belonging to lots where sexual dimorphism is absent.

The following abbreviations are given to identify the longitudinal series of scales in the lateral region of the fish body: LL – lateral line series of scales; LV1 – longitudinal series of scales below LL; and LV2 – longitudinal series of scales below LV1. Abbreviations given along with the number of specimens are the following: mc - morphometric and meristic.

Material from the following institutions were analyzed in this study: ANSP – Academy of Natural Sciences of Philadelphia, Philadelphia, USA; CAS – California Academy of Sciences, San Francisco, USA; FMNH - Field Museum of Natural History, Chicago, USA; MCP – Museu de Ciências e Tecnologia PUCRS, Porto Alegre, Brazil; ROM - Royal Ontario Museum, Toronto, Canada; and USNM - National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

Diagnoses given in the text are based on the phylogenetic analysis of the Compsurini by Jerep & Malabarba (in manuscript).

Results

“New Genus A”

Type species: “New Genus A” Cuzco, new species.

Diagnosis. The “New Genus A” is diagnosed from all genera of Compsurini by the premaxilla without the ascending process [Ch. 51: 0 > 1].

Distribution. The species of “New Genus A” are distributed in the upper río Madre de Díos, and río Ucayali basin, Peru.

“New Genus A” Cuzco new species

Figs. 2-3

Holotype. (uncatalogued, ex-USNM 295636), male, 28.8 mm SL, Peru, Departamento Madre de Dios, Parque Nacional Manu, Pakitza and Vicinity, Oct 1987, H. Ortega.

Paratypes. USNM 295636, 14 mc (24.6-34.9 mm SL, 3 c&s 27.4-29.2 mm SL), same data of holotype. USNM 317789, 2 mc (26.1-30.0 mm SL), Peru, Department Madre de Dios, Manu, río Alto Madre de Dios basin, Quebrada, Salvación, 5 Sep 1989, H. Ortega. USNM 324067, 9 mc (29.8-34.5 mm SL) Peru, Departamento Madre de Dios, Province of Manu, side stream to río Alto Madre de Dios, about 1.5 km upstream from Erika, between Salvacion and Atalaya, 6 Sep 1988, H. Ortega *et al.* USNM 357195, 3 mc (26.3-28.5 mm SL), Peru, Cuzco, la convencion, Echarata, Sagakiato, quebrada Anuintoniato, 5 Oct 1997, M. Hidalgo

Diagnosis. “New Genus A” Cuzco n. sp. is diagnosed from all cheirodontine species by the presence of the Compsurini synapomorphies, and from all species of the tribe by the following apomorphies: anterior lamella of the sixth infraorbital lingual-shaped, expanded, and contacting the frontal supra-orbital canal until its pore [Ch. 12: 1]; orbitosphenoid with a dorsal fenestra with frontal [Ch. 37: 1]; lateral ridge of the anguloarticular short, not reaching the anterior end of the anguloarticular anterodorsal process [Ch. 71: 1]; anterior portion of the basihyal concave [Ch. 123: 1]; anal-fin hooks dorsally directed [Ch. 173: 1]; laterosensory canal extending nearly half-length of the middle caudal-fin rays [Ch. 212: 1]; and ectopterygoid posterior portion contacting the quadrate [Ch. 107: 0].

Distinguishing characters. The anal-fin hooks dorsally directed differ “New Genus A” Cuzco n. sp. from all the Compsurini, except “New Genus C” Leticia n. sp. (*vs.* anal-fin hooks anteriorly directed); the absence of caudal-fin hooks distinguishes “New Genus A” Cuzco n. sp. from “New Genus C” Leticia n. sp.

Description. Morphometrics given in Table 1. Body slightly elongate and compressed, deepest at dorsal-fin origin. Dorsal profile convex from snout tip to vertical line through the nares, slightly convex from that point to dorsal-fin origin, straight or slightly convex along dorsal-fin base, straight or slightly convex from end of dorsal-fin base to adipose-fin origin. Dorsal and ventral caudal-peduncle profile slightly concave. Ventral profile convex from dentary anterior end to pelvic-fin insertion, straight up to anal-fin origin, deeply concave on mature males. Anal-fin base straight. Snout short, mouth terminal, at horizontal line through pupil ventral border.

All teeth pedunculated, aligned in one tooth row. Premaxilla with 4(1), 5(1), 6(1) teeth bearing 6 to 9 cusps. Maxilla reaching vertical line through orbit anterior edge, bearing 2(1), 3(1), 4(1) teeth with 5 to 7 cusps. Dentary with 3(1) to 5(2) large teeth similar in size bearing 5 to 7 cusps, followed by 3(1), 4(1), 5 (1) smaller teeth decreasing in size posteriorly bearing five to one cusp (Fig. 3).

Dorsal-fin origin slightly posterior to vertical through pelvic-fin origin, on middle of body. Dorsal-fin rays ii,9*(29). Adipose-fin origin at vertical line through third to fifth last anal-fin ray insertion. Anal-fin origin slightly posterior to last dorsal-fin ray insertion; anterior rays longer than posterior ones; distal profile deep concave on females, slightly concave to straight on mature males. Anal-fin rays iii to iv,18(2), 19*(10), 20(13), 21(4); last unbranched up to eleventh branched anal-fin ray of mature or maturing males bearing small retrorse hooks, often associated to hypertrophied whitish tissue. Hooks placed from middle length to near the distal tip of anal-fin rays, attached at posterior margin, usually on posterior branch of branched portion, bent dorsally, directed to anal-fin base. One, rarely two, hooks per anal-fin ray segment. Pectoral-fin rays i,8*(2), 9(11), 10(12), 11(4); longest rays falling short pelvic-fin insertion. Pelvic-fin insertion anterior to vertical through dorsal-fin origin. Pelvic-fin rays i,7*(29); branched rays bearing 1-2 ventromedial antrorse

hooks per ray segment on mature males. Caudal fin with 18(1), 19*(27), 20(1) principal rays; 9(1), 11(1), 12(1) dorsal procurent caudal-fin rays; 9(1), 10(1), 12(1) ventral procurent caudal-fin rays.

Lateral line scales 32(4), 33(7), 34(11), 35*(4), 36(1) scales. Perforated scales on lateral line 10 to 34 (mean = 21.1; n = 27). Scale rows between dorsal-fin insertion and lateral line 5(5), 6*(22); scale rows between lateral line and pelvic-fin insertion 4*(26), 5(1). Predorsal scales 9(2), 10(12), 11*(13), 12(2); postdorsal scales 8(4), 9*(10), 10(11), 11(4); scale rows around caudal peduncle 12(1), 14*(28).

Gill rakers of first branchial arch 10(2) on lower portion, 6(2) on upper portion. Supraneurals 4(3). Precaudal vertebrae 15(1), 16(2); caudal vertebrae 15(3). Pseudotympanum as large muscular hiatus between first and second pleural ribs, limited dorsally by *lateralis superficialis* muscle, posteriorly by naked anterior face of second pleural rib, posteroventrally by *obliquus inferioris* muscle, anteroventrally by *obliquus superioris* muscle.

Color in alcohol. Overall body color varying from light to pale yellowish (Fig. 2). Head darker dorsally. Region from 3rd to 5th infraorbital and opercular apparatus whitish to silvery. Small dark melanophores scattered around nares, lips, maxilla, margin of orbit, dorsal surface of head, and more sparsely over body. Overall iris color silvery. Humeral spot absent, humeral region darkened due to presence of pseudotympanum. Melanophores distributed at posterior margin of scales in dorsal and dorsolateral regions of body, resulting in slight reticulated pattern. Dark melanophores sparsely scattered over body, except abdominal region and from lower jaw articulation to urogenital papilla. Melanophores distributed in narrow line along longitudinal line. Caudal peduncle with higher concentration of melanophores shaping round caudal black spot, sometimes slightly extending posteriorly over base of middle caudal-fin rays, not reaching dorsal or ventral margins of caudal peduncle. Few melanophores following miosepta of muscles *hypaxialis* at lower lateral side of caudal region. Dorsal, caudal, pectoral and pelvic fins hyaline with scattered melanophores at interradiation membrane and bordering margins of rays. Anal fin also hyaline, with scattered melanophores more concentrated at distal margin on mature males (Fig. 2).

Sexual dimorphism. Mature males differ from females by the presence of hooks on pelvic and anal fins. Males present the anal-fin profile less concave than females due to the elongation of the rays. The pelvic fin falls short the anal-fin origin only on mature males. The anal fin of mature males has a higher amount of melanophores at the distal portion of the rays, which results in a tenuous dark band along the distal margin of the fin. The ventral profile between the pelvic-fin insertion and the anal-fin origin is concave on mature males, and straight to convex on females.

Distribution. There are records of “New Genus A” Cuzco n. sp. from the upper río Madre de Díos and upper río Ucayali basins (Fig. 4).

“New Genus A” Tingo new species

Figs. 5-6

Holotype. (uncatalogued, ex-ANSP 116449), male, 31.3 mm SL, Peru, Huanucu, vicinity of Tingo Maria, río Rondos, tributary of río Monzon, just above new bridge site, 29 Sep 1955, Catherwood Expedition.

Paratypes. ANSP 116449, 30 (16 males 25.9-31.4 mm SL, 9 females 26.0-33.5 mm SL, 5 unsexed 21.5-25.7 mm SL, 3 c&s), same data as for holotype. ANSP 136841, 16 (20.1-27.4 mm SL, 11 mc 23.6-27.1), Peru, Luling. ANSP 136842, 1 (male 26.5 mm SL), Peru, Huanucu, río Huallaga, Luling. ANSP 136843, 25, (5 males 26.0-31.1 mm SL, 6 females 28.2-31.9 mm SL, 4 unsexed 21.7-25.4 mm SL), Peru, Tingo Maria, Huallaga, Luling. ANSP 136844, 17 (18.0-27.1, 33 mc 23.6-27.1 mm SL), Peru, Tingo Maria, río Subte, 30 June 1966, Luling. ANSP 136846, 25, (7 males 23.5-30.9 mm SL, 18 females 24.0-33.7 mm SL), Peru, Huallaga river at Tingo Maria, Luling. ANSP 136847, 9 (2 males 27.4-28.4 mm SL, 4 females 28.9-33.9 mm SL, 3 unsexed 25.4-25.9 mm SL), Peru, Tingo Maria, Huallaga, Luling. ANSP 136848, 3 (2 males 32.1-32.7 mm SL, 1 female 32.0 mm SL), Peru, río Monzon, Huallaga, Luling. ANSP 136869, 55 (21.4-31.7 mm SL), Peru, Tingo Maria, Luling. ANSP 150175, 1 (male 26.7 mm SL), Peru, Huanucu, vicinity of Tingo Maria, río Rondos, tributary of río Monzon, just above new bridge site, 29 Sep 1955,

Catherwood Expedition. USNM 207516, 11, (6 males 26.5-28.3 mm SL, 2 females 26.5-28.3 mm SL, 3 unsexed 23.1-23.7 mm SL), Peru, Departamento Huanuco, río Huallaga, vicinity of Universidad Agraria de la Selva, Tingo Maria, 9 Aug 1966, W. C. Sherbrooke. MCP 14957, 15 (3 males 26.3-32.7 mm SL, 4 females 26.7-32.5 mm SL, 5 unsexed 22.0-25.0 mm SL; 3 C&S, 2 males 25.6-27.6 mm SL, 1 female 26.8 mm SL), Peru, Tingo Maria, Luling. MCP 14962, 10, (4 males 26.8-31.0 mm SL, 3 females 31.5-36.0 mm SL, 3 unsexed 22.7-25.3 mm SL), Peru, Loreto, Tingo Maria, Huallaga, 09°8'S 75°54'W, Luling. MCP 14951, 5 (unsexed 20.7-24.3 mm SL), Peru, río Huallaga, Luling.

Diagnosis. “New Genus A” Tingo n. sp. is diagnosed from all cheirodontine species by the presence of the Compsurini synapomorphies, and from all species of the tribe by the following apomorphies: fourth infraorbital squarish, similar in width and height [Ch. 9: 0]; fifth infraorbital broad, with expanded lateral laminae from the laterosensory canal [Ch. 10: 0]; longer axis of the anteriormost teeth nearly at the same axis of the dentary, forwardly projected [Ch. 96: 2]; dentary teeth bearing at most seven cusps [Ch. 105: 3]; postcleithrum 1 round and expanded posteriorly [Ch. 142: 0]; all anal-fin rays longer on males than on females [Ch. 154: 1]; anal-fin hooks more numerous in both anterior and posterior portions of anal fin, and reduced in the middle portion of anal fin [Ch. 170: 1]; and urogenital papilla hypertrophied on adult females [Ch. 263: 1].

Distinguishing characters. “New Genus A” Tingo n. sp. differs from all the compsurin species, except “New Genus A” Cuzco n. sp., by the absence of sexual dimorphism on the caudal fin; and from “New Genus A” Cuzco n. sp. by the presence of anteriorly directed retrorse hooks until the 14th anal-fin ray (*vs.* hooks posterodorsally directed until the 11th anal-fin ray).

Description. Morphometrics given in Table 1. Body slightly elongate and compressed, deepest at dorsal-fin origin. Dorsal profile convex from snout tip to vertical line through nostril, slightly convex from that point to dorsal-fin origin, straight or slightly convex along dorsal-fin base, straight or slightly convex from end of dorsal-fin base to adipose-fin origin. Dorsal and ventral caudal-peduncle profile straight to slightly concave. Ventral profile

convex from dentary to pelvic-fin insertion, straight up to anal-fin origin on females, deeply concave on mature males. Anal-fin base straight. Snout short, mouth terminal, at horizontal line through middle of pupil.

All teeth pedunculated, aligned in one tooth row. Premaxilla with 4(3) teeth bearing 7 to 8 cusps. Maxilla reaching vertical line through orbit anterior edge, bearing 3(3) teeth with 6 to 7 cusps, rarely posteriormost tooth with 3 cusps. Dentary with 4(3) large teeth similar in size bearing 7 to 9 cusps, followed by 2(1), 3(1), 4(1) smaller teeth decreasing in size posteriorly bearing five to one cusp (Fig. 6).

Dorsal-fin origin slightly posterior to vertical through pelvic-fin origin, on middle of body. Dorsal-fin rays ii,9*(49). Adipose-fin origin at vertical line through last or penultimate anal-fin ray insertion. Anal-fin origin slightly posterior to last dorsal-fin ray insertion; anterior rays longer than posterior ones; distal profile deep concave on females, slightly concave to straight on mature males. Anal-fin rays iii to iv,15(5), 16(21), 17(17), 18*(5); last unbranched up to fourteenth branched anal-fin ray of mature or maturing males bearing small retrorse hooks, often associated to hypertrophied whitish tissue. Hooks placed on distal third of anal-fin rays, attached at posterior margin, usually on posterior branch of branched portion, bent anteriorly, directed to anal-fin anterior margin. One hook per anal-fin ray segment. Pectoral-fin rays i,9(21), 10(25), 11*(3); longest rays reaching pelvic-fin insertion on males, falling short on females. Pelvic-fin insertion anterior to vertical line through dorsal-fin origin. Pelvic-fin rays i,7*(49); branched rays bearing one ventromedial antrorse hooks per ray segment on mature males, rarely two. Caudal fin with 18(1), 19*(47), 20(1) principal rays; 11(2), 12(1) dorsal procurrent caudal-fin rays; 6(1), 8(1), 9(1) ventral procurrent caudal-fin rays.

Lateral line scales 30(1), 31(11), 32*(26), 33(7), 34(1), 35(1) scales. Perforated scales on lateral line 7 to 18 (mean = 10.6). Scale rows between dorsal-fin insertion and lateral line 5(19), 6*(29); scale rows between lateral line and pelvic-fin insertion 4*(48). Predorsal scales 9(6), 10*(24), 11(19); postdorsal scales 8*(29), 9(12), 10(2); scale rows around caudal peduncle 14*(47), 16(1).

Mature males with gill gland on first branchial arch. Gill rakers of first branchial arch 10(1), 11(1) on the lower portion, 6(2) on upper portion. Supraneurals 4(3). Precaudal vertebrae 16(3); caudal vertebrae 16(3). Pseudotympanum as large muscular hiatus between

first and second pleural ribs, limited dorsally by *lateralis superficialis* muscle, posteriorly by naked anterior face of second pleural rib, posteroventrally by *obliquus inferioris* muscle, anteroventrally by *obliquus superioris* muscle.

Color in alcohol. Overall body color varying yellowish (Fig. 5). Head darker dorsally. Small dark melanophores scattered around nostrils, lips, maxilla, margin of orbit, dorsal surface of head, and more sparsely over body. Region from 3rd to 5th infraorbital and opercular apparatus without melanophores. Overall iris color black. Humeral spot absent, humeral region darkened due to presence of pseudotympanum. Melanophores distributed at posterior margin scales in dorsal and dorsolateral regions of body, resulting in slight reticulated pattern. Dark melanophores sparsely scattered over body, except abdominal region and from lower jaw articulation to urogenital papillae. Melanophores distributed in narrow line along longitudinal line. Caudal peduncle with higher concentration of melanophores shaping round caudal black spot, sometimes slightly extending posteriorly over base of middle caudal-fin rays, not reaching dorsal or ventral margins of caudal peduncle. Melanophores following miosepta of muscles *hypaxialis* at lower lateral side of caudal region. Dorsal, caudal, pectoral and pelvic fins hyaline with scattered melanophores at interradiation membrane and bordering margins of rays. Anal fin also hyaline, with scattered melanophores more concentrated at distal margin on mature males (Fig. 5).

Sexual dimorphism. Mature males differ from females by the presence of hooks on pelvic and anal fins. Males present the anal-fin profile less concave than females due to the elongation of the rays bearing hooks. The anal fin of mature males has more melanophores at the distal portion of the anal-fin rays, resulting in a tenuous dark band along the distal margin of the fin. The ventral profile between the pelvic-fin insertion and the anal-fin origin is concave on mature males, and straight to convex on females. A gill gland on the first branchial arch was found in some mature males.

Distribution. “New Genus A” Tingo n. sp is only known for the río Ucayali basin, Peru (Fig.4).

“New Genus B”

Type species: “New Genus B” Purus, new species.

Diagnosis. “New Genus B” is diagnosed from all genera of Compsurini by the following apomorphies: supraorbital laterosensory canal not continuous to the pterotic laterosensory canal [Ch. 42: 1]; anteromedial tooth bearing portion of dentary shorter than posterior portion [Ch. 69: 0]; lateral ridge of the anterodorsal process of the anguloarticular short, not reaching the anterior end of the anguloarticular anterodorsal process [Ch. 71: 1]; ascending laterosensory canal of the preopercle short, reaching the posterior articular surface of the hyomandibular condyle [Ch. 114: 1]; caudal-fin rays bearing hooks thickened on mature males [Ch. 183: 1]; three posteriormost ventral procurrent caudal-fin rays hypertrophied on mature males, with distal tips expanded, forming a small keel in the ventral profile of the caudal fin [Ch. 207: 1]; presence of scale modified in shape in the lower lobe of the caudal-fin [Ch. 214: 1]; muscle *interradialis* in the caudal-fin lower lobe more extended posteriorly between rays [Ch. 242: 1]; muscle *interradialis* in the caudal fin thicker and more concentrated in the ventral direction in the lower lobe [Ch. 244: 1]; urogenital papilla hypertrophied in two longitudinal skin flaps on adult females [Ch. 264: 1]; caudal-fin hooks straight. [Ch. 187: 1]; and opening of the caudal-fin pouch scale over the 13th to 18th principal caudal-fin rays [Ch. 225: 2].

Distinguishing characters. The presence of a caudal pouch formed by modified scales from the LL and LV1 in association to caudal-fin hooks posteriorly directed, diagnosis “New Genus B” from all Cheirodontinae.

Distribution. “New Genus B” are distributed in the upper río Madre de Díos, and río Ucayali basin, Peru.

“New Genus B” Purus new species

Figs. 7-12a

Holotype. MCP (uncatalogued), male, 26.1 mm SL, Brazil, Acre, Sena Madureira, affluent of rio São Pedro on BR 364, 08°59'53"S 68°53'54"W, 21 Jul 2004, A. R. Cardoso, J. P. da Silva, P. Lehmann, R. Dárrigo & V. A. Bertaco.

Paratypes. MCP 41716, 41, (14.2-28.9 mm SL, 2 c&s 23.6-25.7 mm SL), same data of holotype.

Diagnosis. Same as for the genus.

Description. Morphometrics given in Table 2. Body slightly elongate and compressed, deepest at dorsal-fin origin. Dorsal profile convex from snout tip to vertical line through nare, slightly convex up to dorsal-fin origin, straight or slightly convex along dorsal-fin base, straight or slightly convex from end of dorsal-fin base to adipose-fin origin. Dorsal and ventral caudal-peduncle profile slightly concave on females, straight to convex on mature males. Ventral body profile convex from dentary to pelvic-fin insertion, straight until anal-fin origin on females, deeply concave on mature males. Anal-fin base straight. Snout short, mouth terminal, placed around horizontal line projected through pupil ventral border.

All teeth pedunculated, aligned in one tooth row. Premaxilla with 5(1) to 6(1) heptacuspoid teeth bearing. Maxilla falling short vertical line through orbit anterior edge, bearing 3(2) penta to heptacuspoid teeth. Dentary with 6(2) large heptacuspoid teeth similar in size, followed by 3(1) to 6(1) smaller teeth decreasing in size posteriorly, bearing five to one cusp (Fig. 8).

Dorsal-fin origin slightly posterior to vertical through pelvic-fin origin, on middle of body. Dorsal-fin rays ii,9*(28). Adipose-fin origin at vertical line through third to fourth last anal-fin ray insertion. Anal-fin origin slightly posterior to last dorsal-fin ray insertion; anterior rays longer than posterior ones; distal profile concave, anterior lobe round on mature males. Anal-fin rays iii to iv,18(1), 19(1), 20(3), 21(17), 22*(6); last unbranched up to fifth branched anal-fin rays of mature or maturing males bearing small retrorse hooks, often associated to hypertrophied whitish tissue. Hooks placed from middle length to near distal tip of anal-fin rays, attached at posterolateral margin, usually on posterior branch of branched portion, bent anteriorly, directed to anal-fin anterior margin (Fig.9). One hook per

anal-fin ray segment. Pectoral-fin rays i,8(1), 9(23), 10*(4); longest rays surpassing pelvic-fin insertion only on mature males. Pelvic-fin insertion anterior to vertical line through dorsal-fin origin. Pelvic-fin rays i,7*(28); branched rays bearing one ventromedial antrorse hooks per ray segment on mature males. Caudal fin with 18(1), 19*(26), 20(1) principal rays; 11(2) dorsal procurrent caudal-fin rays; 8(2) ventral procurrent caudal-fin rays. Principal caudal-fin rays 11 to 16 thickened on midlength portion just before ray ramification. Principal caudal-fin rays 14 to 16 bearing one large hook posteriorly directed over bony expansion; branched distal region of same rays bearing several anteriorly directed hooks, dorsally placed (Figs. 10, 11).

Lateral line scales 33(3), 34(5), 35(6), 36(11), 37*(3), perforated scales 7 to 11 (mean = 8.5; n = 27). Scale rows between dorsal-fin insertion and lateral line 5(1), 6*(27); scale rows between lateral line and pelvic-fin insertion 4(2), 5*(26). Predorsal scales 10(13), 11*(10), 12(4), 13(1); postdorsal scales 8(3), 9(17), 10*(6), 11(2); scale rows around caudal peduncle 14*(28). Scales over base of lower caudal-fin lobe enlarged, modified in shape, on both sexes (Fig. 10).

Mature males with gill gland on first branchial arch. Gill rakers of first branchial arch 10(1), 11(1) on lower portion, 6(1), 7(1) on upper portion. Supraneurals 4(1), 5(1). Precaudal vertebrae 15(2); caudal vertebrae 19(2). Pseudotympanum as large muscular hiatus between first and second pleural ribs, limited dorsally by *lateralis superficialis* muscle, posteriorly by naked anterior face of second pleural rib, posteroventrally by *obliquus inferioris* muscle, anteroventrally by *obliquus superioris* muscle.

Color in alcohol. Overall body color varying from whitish to pale yellowish (Fig. 7). Head darker dorsally. Melanophores scattered around nares, lips, maxilla, margin of orbit, region between dentaries, dorsal surface of head, and more sparsely over body. Overall iris color black. Humeral spot absent, humeral region is darkened due to presence of pseudotympanum. Melanophores distributed at posterior margin of scales on dorsolateral region of body, resulting in reticulated pattern. Abdominal region with dark melanophores sparsely scattered. Ventral region from pectoral girdle to urogenital papillae without pigmentation. Melanophores distributed in narrow line along longitudinal line. Larger melanophores scattered dorsally to longitudinal line, along lateral of body. Large

melanophores placed in miosepta of muscles *hypaxialis* at lower lateral side of caudal region. Caudal peduncle with higher concentration of melanophores shaping round caudal black spot that does not extend posteriorly over base of middle caudal-fin rays. Caudal spot not reaching dorsal or ventral margins of caudal peduncle. Dorsal, caudal, pectoral and pelvic fins hyaline with scattered melanophores at interradial membrane and bordering margins of rays. Anal fin also hyaline, with scattered melanophores more concentrated at distal margin on mature males (Fig. 7).

Sexual dimorphism. Mature males differ from females by the presence of hooks on pelvic, caudal and anal fins. Pectoral fins on males reach the pelvic-fin insertion, but fall short of the pelvic-fin insertion on females. Males present the profile of the anterior lobe of the anal-fin rounded due to the elongation of the rays bearing hooks, which is concave to straight on females. The anal-fin on mature males also has a higher amount of melanophores at the distal portion, resulting in a tenuous dark band. Only mature males have the scales on the base of the lower caudal-fin lobe enlarged and modified in shape, composing a caudal organ with association to hypertrophied whitish tissue and hooks. The ventral profile between the pelvic-fin insertion and the anal-fin origin is concave on mature males, and straight to convex on females. A gill gland on the first branchial arch was found in some mature males. The urogenital papilla on females is hypertrophied, divided in two bilateral flaps of tissue extended posteroventrally (Fig. 12a).

Distribution. There is only one record of “New Genus B” *Purus n. sp.*, it is from an affluent of the rio São Pedro, from the upper rio Purus basin (Fig.4).

Remarks on the caudal organ of “New Genus B” *Purus n. sp.* Males and females of “New Genus B” *Purus n. sp.* present the last scales from the lateral line (LL) and the longitudinal series of scale below the lateral line (LV1) modified in shape, elongated posteriorly, and larger than preceding scales from the caudal peduncle. No modified scales are present in the upper caudal-fin lobe. Adult individuals from both sexes present the last scale from the LL firmly attached to the caudal fin along its dorsal margin, and firmly attached to the dorsal margin of the last scale from the LV1 along its ventral margin; while

the LV1 has its ventral margin attached to the caudal fin, and its dorsal margin attached to the LL. These last modified scales are laterally concave, not medially attached to the caudal fin, and have their posterior border free. This arrangement forms a pouch-like structure with a posterior opening, by the epidermal invagination between the caudal-fin rays and the scales. Although both sexes present the scale structure describe above, only on mature males it is much more developed, and associated to hypertrophied tissue and hooks. Specifically on mature males, the region where the modified LL scale attaches to the caudal fin is covered by hypertrophied tissue. The bottom of the pouch on mature males is formed by a wall of hypertrophied tissue, connecting the modified scales (roof of the pouch), to the caudal fin (floor of the pouch). Anteriorly to the bottom of the pouch, there is an internal chamber, also placed between the modified scales and the caudal-fin rays. The chamber is delimited anteriorly by the attachment of the modified scales that compose the caudal organ on the body, and posteriorly by the bottom of the pouch. No clear opening was found between the internal chamber and the pouch due to the large amount of hypertrophied tissue in the wall and inside the pouch. The principal caudal fin rays 11 to 16, which are directly under the LL enlarged scale, are thicked on their midlength portion, just anterior to the first ramification. Posterior to the pouch opening, there are three large hooks placed over the thickened portion of the principal caudal-fin rays 14, 15 and 16. These hooks emerge laterally from the principal caudal-fin rays, are slightly bent posteriorly, and carry a large amount of hypertrophied tissue surrounding their bases. The principal caudal-fin rays 14 to 16, rarely the 17, still carry on their distal third smaller anteriorly directed hooks, placed over the dorsolateral surface of the rays and also surrounded by hypertrophied tissue. The muscles *interradialis* attached to the principal caudal-fin rays 13, 14 and 15 are also more developed than the muscle *interradialis* associated to the other rays of the fin (Fig.10).

“New Genus C”

Type species: “New Genus C” Napo, new species.

Diagnosis. “New Genus C” is diagnosed from all genera of Compsurini by the presence of caudal-fin hooks emerging laterally from the dorsolateral surface of the caudal-fin rays [Ch. 188: 0 > 1].

Distribution. Species belonging to the “New Genus C” are found in the upper rio Amazonas, rio Napo, upper rio Huallaga, and upper rio Ucayali basin.

“New Genus C” Napo new species

Figs. 13-14

Holotype. (uncatalogued, ex-FMNH 113496), 25.3 mm SL, Ecuador, Napo State, tributary of rio Due, just at mouth on west bank, rio Aguarico drainage, 00°4'30"N 77°24'24"W, 23 Sep 1983, D. Stewart, M. Ibarra, R. Barriga.

Paratypes. FMNH 113496, 57 (11.9-31.8 mm SL, 33 mc 23.7-31.8 mm SL), same data of holotype. ANSP 149440, 30 (13.2-23.2 mm SL, 1 mc 23.3 mm SL), Ecuador, Napo, small stream *ca.* 15 mi downstream from Misahuall, 0°56'N 77°30'W, 24 August 1980, A. Mack. ANSP 149671, 54 (26.1-33.3 mm SL, 3 mc and c&s 26.3-28.7 mm SL) Peru, Huanucu, vicinity of Tingo Maria, main stream of rio Tullamayo, near Puerto Nuevo, 27 Sep 1955, Catherwood Expedition. FMNH 113495, 1 (19.4 mm SL), Ecuador, Napo, quebrada about 1.7 km SW of rio Napo bridge at Coca (first small bridge) towards Tiputini, 3 Oct 1981, D. Stewart, M. Ibarra, R. Barriga. MCP 28030, 2 (20.7-23.0 mm SL, 1 mc 23.0 mm SL), Ecuador, Napo, 17 Aug 1991, R. McDiarmid. USNM 328557, 14 (16.8-26.0 mm SL, 4 mc 23.8-26.0), Peru, Departamento Loreto, Maynas, Province of Arcadia, rio Napo, Padre Isla-Cocha Grande, 30 min downriver, 6 Nov 1993, F. Chang. USNM 328558, 15 (16.6-22.6 mm SL, 9 mc 20.0-26.0 mm SL), Peru, Departamento Loreto, Maynas, Province of Arcadia, rio Napo, 30 min downriver, Padre Isla-Cochachica, 8 Nov 1993, F. Chang. USNM 329360, 18 (15.8-25.3 mm SL, 8 mc 20.9-25.3 mm SL), Peru, Departamento Loreto, Maynas, Province of Arcadia, rio Napo, 30 min downriver, Padre Isla, Cocha Chica, 4 Nov 1993, F. Chang *et al.* USNM 357196, 3 mc (25.0-25.8 mm SL), Peru, Cuzco, la convencion, Echarate, Shivangouni - Camisca, Cocha Konkariari, 20 Oct 1997, M. Hidalgo. USNM 362030, 4 mc (25.0-29.2 mm SL), Peru, Cuzco, La Concención,

Echarata, Sagakiato, quebrada Anuintoniato, 5 Oct 1997, M. Hidalgo. USNM 379470, 1 (20.8 mm SL), Peru, Departamento Loreto, Mayanas, Province of Arcadia, río Napo, 30 min downriver, Padre Cochachica, 4 Nov 1993, F. Chang *et al.*

Diagnosis. “New Genus C” Napo n. sp. is diagnosed from all cheirodontine species by the presence of the Compsurini synapomorphies, and from all species of the tribe by two apomorphies: nasal bone straight [Ch. 23: 0]; nasal bone shorter than half the distance between the frontal anterior margin and the mesethmoid lateral wing [Ch. 25: 2]; anteromedial process of the lateral ethmoid robust [Ch. 30: 0]; and abdomen slightly concave ventrally [Ch. 239: 0].

Distinguishing characters. The presence of hooks anteriorly directed on the i,4 anal-fin rays differs “New Genus C” Napo. n. sp. from all Cheirodontinae (*vs.* hooks posterodorsally directed in Cheirodontinae and “New Genus A” Cuzco n. sp., and at least i,5 anal-fin rays bearing hooks in the remaining Compsurini).

Description. Morphometrics given in Table 2. Body slightly elongate and compressed, deepest at dorsal-fin origin. Dorsal profile convex from snout tip to vertical line through nare, slightly convex up to dorsal-fin origin, straight or slightly convex along dorsal-fin base, straight or slightly convex from end of dorsal-fin base to adipose-fin origin. Dorsal and ventral caudal-peduncle profile straight to slightly concave. Ventral profile convex from dentary anterior end to pelvic-fin insertion, straight to deeply concave (on mature males) until anal-fin origin, straight along anal-fin base. Snout short, mouth terminal, placed between horizontal lines projected through pupil ventral and dorsal borders.

All teeth pedunculated, aligned in one tooth row. Premaxilla with 3(1), 4(1), 6(1) teeth bearing seven cusps, sometimes five or eight. Maxilla not reaching vertical line through orbit anterior edge, bearing 3(3) pentacuspoid to heptacuspoid teeth. Dentary with 4(1), 5(1), 6(1) large heptacuspoid teeth similar in size, followed by 2(1), 3(1), 4(1) smaller teeth decreasing in size posteriorly, bearing five to one cusp (Fig. 14).

Dorsal-fin origin slightly posterior to vertical through pelvic-fin origin, on middle of body. Dorsal-fin rays ii,9(66). Adipose-fin origin at vertical line through third to fourth

last anal-fin ray insertion. Anal-fin origin slightly posterior to last dorsal-fin ray insertion; anterior rays longer than posterior ones; distal profile concave, anterior lobe slightly concave to straight on mature males. Anal-fin rays iii to iv, 18(2), 19(17), 20*(31), 21(13), 22(2); last unbranched up to fourth branched anal-fin rays of mature or maturing males bearing small retrorse hooks, often associated to hypertrophied whitish tissue. Hooks placed from middle length to near distal tip of anal-fin rays, attached at posterolateral margin, usually on posterior branch of branched portion, bent anteriorly, directed to anal-fin anterior margin. One hook per anal-fin ray segment. Pectoral-fin rays i, 8*(4), 9(26), 10(29), 11(6), 12(1); longest rays surpassing pelvic-fin insertion. Pelvic-fin insertion anterior to vertical line through dorsal-fin origin. Pelvic-fin rays i, 6(1), 7*(61), 8(4); branched rays bearing 1, rarely 2, ventromedial antrorse hooks per ray segment on mature males. Caudal fin with 18(1), 19*(63) principal rays; 9(1), 10(1), 11(1) dorsal procurrent caudal-fin rays; 7(2), 9(1) ventral procurrent caudal-fin rays. Caudal-fin hooks retrorse, anteriorly directed, over distal half of 12th to 18th caudal-fin rays, rarely along 10th to 19th.

Lateral line incompletely pored (63), rarely completely pored (3). Lateral line scales 31(4), 32*(25), 33(22), 34(10), 35(1), 36(1), perforated scales 6 to 15 (mean = 10.3; n = 60). Scale rows between dorsal-fin insertion and lateral line 5(33), 6*(31), 7(1); scale rows between lateral line and pelvic-fin insertion 3(3), 4*(58), 5(3). Predorsal scales 9(1), 10(18), 11*(40), 12(6); postdorsal scales 8(10), 9*(37), 10(17), 11(2); scale rows around caudal peduncle 14*(64).

Mature males with gill gland on first branchial arch. Gill rakers of first branchial arch 9(1), 10(1) on lower portion, 6(2) on upper portion. Supraneurals 3(1), 4(2). Precaudal vertebrae 16(3); caudal vertebrae 17(1), 18(2). Pseudotympanum as large muscular hiatus between first and second pleural ribs, limited dorsally by *lateralis superficialis* muscle, posteriorly by naked anterior face of second pleural rib, posteroventrally by *obliquus inferioris* muscle, anteroventrally by *obliquus superioris* muscle.

Color in alcohol. Overall body color varying from light to pale yellowish (Fig. 13). Head darker dorsally. Small dark melanophores scattered around nares, lips, maxilla, margin of orbit, dorsal surface of head, and more sparsely over body. Overall iris color black.

Humeral spot absent, humeral region is darkened due to presence of pseudotympanum. Melanophores distributed at posterior margin of scales all over body, resulting in reticulated pattern more remarkable on dorsal region of body. Abdominal region with dark melanophores sparsely scattered. Region between dentaries pigmented, from there to urogenital papillae without pigmentation. Melanophores distributed in narrow line along longitudinal line. Caudal peduncle with higher concentration of melanophores shaping slightly round caudal black spot, extending posteriorly just over base of middle caudal-fin rays, and reaching dorsal or ventral margins of caudal peduncle. Few melanophores following miosepta of muscles *hypaxialis* at lower lateral side of caudal region. Dorsal, caudal, pectoral and pelvic fins hyaline with scattered melanophores at interradial membrane and bordering margins of rays. Anal fin also hyaline, with scattered melanophores more concentrated at distal margin on mature males (Fig. 13).

Sexual dimorphism. Mature males differ from females by the presence of hooks on pelvic, caudal and anal fins. Males present the profile of the anterior lobe of the anal-fin slightly less concave than females, due to the elongation of the rays bearing hooks. The anal-fin color pattern on mature males has a higher amount of melanophores at the distal portion of the rays. The ventral profile between the pelvic-fin insertion and the anal-fin origin is concave on mature males, and straight to convex on females. A gill gland on the first branchial arch was found in some mature males.

Distribution. “New Genus C” Napo n. sp. is known to occur in the río Napo, upper río Huallaga, and upper río Ucayali basin (Fig.4).

“New Genus C” Leticia new species

Figs. 15-16

Holotype. (uncatalogued, ex-ROM ICH 56384), male, 25.3 mm SL, Colombia, río Amazonas, 5-10 mi upstream from Leticia, Lakes and Pepper Farm, Feb 1974, A. Keast.

Paratypes. ROM ICH 56384, 21 mc (24.0-26.8 mm SL, 3 c&s 24.0-26.2 mm SL), same data of holotype.

Diagnosis. “New Genus C” *Leticia* n. sp. is diagnosed from all cheirodontine species by the presence of the Compsurini synapomorphies, and from all species of the tribe by the following apomorphies: orbitosphenoid with dorsal fenestra with frontal [Ch. 37: 1]; supraorbital laterosensory canal not continuous with the pterotic laterosensory canal [Ch. 42: 1]; maxilla with a longitudinal groove just below the dorsolateral border [Ch. 56: 1]; dorsal profile of the maxilla slightly concave [Ch. 59: 1]; margin of the tooth bearing portion of the maxilla continuous to the toothless margin [Ch. 60: 0]; toothless portion of the maxilla extended, more than two times longer than the tooth bearing portion of the maxilla [Ch. 62: 3]; absence of anguloarticular anterodorsal projection [Ch. 72: 1]; premaxillary teeth not pedunculated, with tooth base enlarged [Ch. 74: 0]; cusps of the premaxillary teeth not contacting each other [Ch. 81: 0]; dentary teeth bearing five cusps [Ch. 105: 0]; absence of pelvic bone more developed on mature males [Ch. 149: 0]; anal-fin hooks dorsally directed [Ch. 173: 1]; hemal spines of preural vertebrae 2 to 5 contacting the procurrent caudal-fin rays [Ch. 178: 1]; and urogenital papilla not hypertrophied on adult females [Ch. 263: 0].

Distinguishing characters. “New Genus C” *Leticia* n. sp. can be diagnosed from all the Compsurini by the presence of anal-fin hooks dorsally directed (*vs.* hooks anteriorly directed, curved over lateral surface of the rays); and from the “New Genus A” *Cuzco* n. sp. by the presence of none or a single tricuspid tooth in the maxilla and caudal-fin hooks (*vs.* 2-4 teeth with up to five cusps and absence of caudal-fin hooks).

Description. Morphometrics given in Table 3. Body slightly elongate and compressed, deepest at dorsal-fin origin. Dorsal profile convex from snout tip to dorsal-fin origin, straight or slightly convex along dorsal-fin base, straight or slightly convex from end of dorsal-fin base to adipose-fin origin. Dorsal and ventral caudal-peduncle profile straight to slightly convex, strongly convex on mature males. Ventral profile convex from dentary anterior end to pelvic-fin insertion, straight up to anal-fin origin but concave on mature males. Anal-fin base profile convex anteriorly, straight to slightly concave posteriorly. Snout short, mouth terminal, at horizontal line through pupil dorsal border.

All teeth pedunculated, aligned in one tooth row. Premaxilla with 7(3) teeth bearing three to five cusps, most lateral tooth sometimes conical. Maxilla reaching vertical line through orbit anterior edge, toothless or bearing 1(1) tricuspid tooth. Dentary with 4(3) large pentacuspoid teeth similar in size, followed by 3(1), 5(1) or 6(1) smaller teeth decreasing in size posteriorly, bearing five to one cusp (Fig. 16).

Dorsal-fin origin slightly posterior to vertical through pelvic-fin origin, on middle of body. Dorsal-fin rays ii,9*(22). Adipose-fin origin at vertical line through fourth to fifth last anal-fin ray insertion. Anal-fin origin slightly posterior to last dorsal-fin ray insertion; anterior rays longer than posterior ones; distal profile concave. Anal-fin rays iii to iv,24(2), 25*(6), 26(4), 27(6), 28(3), 29(1); last unbranched up to fifteenth branched anal-fin rays of mature or maturing males bearing small retrorse hooks, often associated to hypertrophied whitish tissue. Hooks placed from middle length to near distal tip of anal-fin rays, attached at posterior margin, usually on posterior branch of branched portion, bent dorsally, directed to anal-fin base. One, rarely two, hooks per anal-fin ray segment. Pectoral-fin rays i,9(1), 10*(16), 11(3), 12(2); longest rays surpassing pelvic-fin insertion. Pelvic-fin insertion anterior to vertical line through dorsal-fin origin. Pelvic-fin rays i,7*(22); branched rays bearing 1, rarely 2, ventromedial antrorse hooks per ray segment on mature males. Caudal fin with 19*(21), 20(1) principal rays; 11(1), 12(1), 13(1) dorsal procurrent caudal-fin rays; 10(1), 12(2) ventral procurrent caudal-fin rays. Caudal-fin hooks retrorse, anteriorly directed, distributed along branched portion of 11th to 15th caudal-fin rays, rarely along 11th and 16th. One male with hooks on 6th and 7th principal caudal-fin rays.

Lateral line scales 32*(3), 33(8), 34(9), 35(2) scales. Perforated scales on lateral line 6(4), 7*(8), 8(2). Scale rows between dorsal-fin insertion and lateral line 5*(19), 6(3); scale rows between lateral line and pelvic-fin insertion 3(7), 4*(17). Predorsal scales 10(5), 11*(13), 12(4); postdorsal scales 8*(3), 9(8), 10(8), 11(3); scale rows around caudal peduncle 14*(22).

Gill rakers of first branchial arch 13(2), 14(1) on lower portion, 7(2), 8(1) on upper portion. Supraneurals 4(1), 5(2). Precaudal vertebrae 15(3); caudal vertebrae 19(1), 20(2). Pseudotympanum as large muscular hiatus between first and second pleural ribs, limited dorsally by *lateralis superficialis* muscle, posteriorly by naked anterior face of second

pleural rib, posteroventrally by *obliquus inferioris* muscle, anteroventrally by *obliquus superioris* muscle.

Color in alcohol. Overall body color varying from light to pale yellowish (Fig. 15). Head darker dorsally. Small dark melanophores scattered around nares, lips, maxilla, margin of orbit, dorsal surface of head, and more sparsely over body. Overall iris color black. Humeral spot absent, humeral region is darkened due to presence of pseudotympanum. Melanophores distributed at posterior margin of scales in dorsal and dorsolateral regions of body, resulting in slight reticulated pattern. Dark melanophores sparsely scattered over body, except abdominal region and from lower jaw articulation to urogenital papillae. Melanophores distributed in narrow line along longitudinal line. Caudal peduncle with higher concentration of melanophores shaping round caudal black spot, sometimes slightly extending posteriorly over base of middle caudal-fin rays, not reaching dorsal or ventral margins of caudal peduncle. Few melanophores following miosepta of muscles *hypaxialis* at lower lateral side of caudal region. Dorsal, caudal, pectoral and pelvic fins hyaline with scattered melanophores at interradiial membrane and bordering margins of rays. Anal fin also hyaline, with scattered melanophores more concentrated at distal margin on mature males (Fig. 15).

Sexual dimorphism. Mature males differ from females by the presence of hooks on pelvic, caudal and anal fins. Males present the profile of the anterior lobe of the anal-fin slightly less concave than females, due to the elongation of the rays. The anal-fin color pattern on mature males has a higher amount of melanophores at the distal portion of the anal-fin rays. The ventral profile between the pelvic-fin insertion and the anal-fin origin is concave on mature males, and straight to convex on females.

Distribution. The only known register of “New Genus C” *Leticia n. sp.* is from rio Amazonas in Colombia, on the surroundings of Leticia (Fig. 4).

“New Genus C” *Yurimaguas* new species

Figs. 17-18

Holotype. (uncatalogued, ex-CAS 71733), male, 23.1 mm SL, Peru, Departamento de Lore, río Amazon, creek in forest inland from Yurimaguas, 3-4 Nov 1920, W. R. Allen.

Paratypes. CAS 71733, 20, (21.8-25.2 mm SL, 20 mc 21.8-25.2 mm SL, 3 c&s 21.8-23.4 mm SL), same data of holotype.

Diagnosis. “New Genus C” Yurimaguas n. sp. is diagnosed from all cheirodontine species by the presence of the Compsurini synapomorphies, and from all species of the tribe by the following apomorphies: sixth infraorbital bearing an anterior lamella [Ch. 11: 0]; premaxilla without ascending process [Ch. 51: 1]; longer axis of the anteriormost dentary teeth nearly at the same axis of the dentary, forwardly projected [Ch. 96: 2]; all anal-fin rays longer on males than on females [Ch. 154: 1]; and anal-fin hooks more numerous in both anterior and posterior portions of anal fin, reduced in the middle portion of anal fin [Ch. 170: 1].

Distinguishing characters. “New Genus C” Yurimaguas n. sp. is distinguished from all cheirodontine species by the presence of hook on the 8th (rarely on 7th) to 18th principal caudal-fin rays (*vs.* absence of caudal-fin hooks, or when present distributed on the principal caudal-fin rays 13-14 in *Acinocheirodon*, 12-18 in *Macropsobrycon*, 12-15 in *Kolpotocheirodon theloura*, 14-18 in *Saccoderma*, 12-15 in “*Odontostilbe*” *dialeptura*, 11-16 in “New Genus C” Leticia n. sp., 12-18 in “New Genus C” Napo n. sp., and 14-16 in “New Genus B” Purus n. sp).

Description. Morphometrics given in Table 3. Body slightly elongate and compressed, deepest at dorsal-fin origin. Dorsal profile convex from snout tip to vertical line through nostril, slightly convex up to dorsal-fin origin, straight or slightly convex along dorsal-fin base, straight or slightly convex from end of dorsal-fin base to adipose-fin origin. Dorsal and ventral caudal-peduncle profile straight to slightly concave, strongly convex on mature males. Ventral profile convex from dentary anterior end to pelvic-fin insertion, straight until anal-fin origin, deeply concave on mature males. Anal-fin base straight. Snout short, mouth terminal, placed in horizontal line projected through middle of pupil.

All teeth pedunculated, aligned in one tooth row. Premaxilla with 5(3) teeth bearing five to seven cusps. Maxilla reaching vertical line through orbit anterior edge, bearing 2(1) or 3(2) tricuspid to pentacuspoid teeth. Dentary with 4(1), 5(1), 6(1) large pentacuspoid to heptacuspoid teeth similar in size, followed by 4(1) to 5(2) smaller teeth decreasing in size posteriorly, bearing five to one cusp (Fig. 18).

Dorsal-fin origin slightly posterior to vertical through pelvic-fin origin, on middle of body. Dorsal-fin rays ii,8(1), 9*(19). Adipose-fin origin at vertical line through fourth to fifth last anal-fin ray insertion. Anal-fin origin on vertical line of last dorsal-fin ray insertion, or slightly posterior; anterior rays longer than posterior ones; distal profile concave, slightly concave to straight on mature males. Anal-fin rays iii to iv,18(3), 19(2), 20*(13), 22(2); last unbranched up to sixteenth branched anal-fin rays of mature or maturing males bearing small retrorse hooks, often associated to hypertrophied whitish tissue. Hooks placed at distal third of anal-fin rays, attached at posterolateral margin, usually on posterior branch of branched portion, bent anteriorly, directed to anal-fin anterior margin. One hook per anal-fin ray segment, rarely two. Pectoral-fin rays i,8(2), 9(2), 10(11), 11(4); longest rays surpassing pelvic-fin insertion. Pelvic-fin insertion anterior to vertical line through dorsal-fin origin. Pelvic-fin rays i,7*(20); longest rays reaching origin of anal fin; branched rays bearing one ventromedial antrorse hooks per ray segment on mature males. Caudal fin with 18(1), 19*(12) principal rays; 11(2), 12(1) dorsal procurrent caudal-fin rays; 6(1), 8(1), 9(1) ventral procurrent caudal-fin rays. Caudal-fin hooks retrorse, anteriorly directed, over distal half of 8th to 18th caudal-fin rays.

Lateral line scales 30*(2), 31(1), 32(4), 33(7), 34(3), perforated scales 6*(4), 7(6), 8(1). Scale rows between dorsal-fin insertion and lateral line 5(7), 6*(11); scale rows between lateral line and pelvic-fin insertion 4*(15), 5(2). Predorsal scales 9*(8), 10(9), 11(3); postdorsal scales 7*(10), 8(6), 9(2); scale rows around caudal peduncle 14*(20).

Mature males with gill gland on first branchial arch. Gill rakers of first branchial arch 10(1), 11(1) on lower portion, 6(2) on upper portion. Supraneurals 4(3). Precaudal vertebrae 15(3); caudal vertebrae 18(3). Pseudotympanum as large muscular hiatus between first and second pleural ribs, limited dorsally by *lateralis superficialis* muscle, posteriorly by naked anterior face of second pleural rib, posteroventrally by *obliquus inferioris* muscle, anteroventrally by *obliquus superioris* muscle.

Color in alcohol. Few aspects of color pattern remain on species, due to their conditions of conservation. Overall body color whitish (Fig. 17). Melanophores scattered in dorsal surface of head, and more sparsely over body. Overall iris color silvery. Humeral spot absent, humeral region is darkened due to presence of pseudotympanum. Dorsolateral margin of body with melanophores distributed at posterior margin of scales, resulting in reticulated pattern. Abdominal region and region from dentaries to urogenital papillae without pigmentation. Melanophores distributed in narrow line along longitudinal line. Caudal peduncle with higher concentration of melanophores shaping a slightly round caudal black spot, extending posteriorly at least over proximal third of middle caudal-fin rays, not reaching dorsal or ventral margins of caudal peduncle. Few melanophores following miosepta of muscles *hypaxialis* at lower lateral side of caudal region. Dorsal, caudal, pectoral and pelvic fins hyaline with scattered melanophores at interradiial membrane and bordering margins of rays. Anal fin also hyaline, with scattered melanophores more concentrated at distal margin on mature males (Fig. 17).

Sexual dimorphism. Mature males differ from females by the presence of hooks on pelvic, caudal and anal fins. The pelvic fin reaches the origin of the anal fin only on males. Males present the distal profile of the anal-fin slightly less concave than females, due to the elongation of the rays bearing hooks. The anal-fin on mature males has a higher amount of melanophores at the distal portion of the rays. The ventral profile between the pelvic-fin insertion and the anal-fin origin is concave on mature males, and straight to convex on females. A gill gland on the first branchial arch was found in some mature males.

Distribution. “New Genus C” Yurimaguas n. sp. is only known from a small tributary of the río Amazonas, inland from Yurimaguas, Peru (Fig.4).

Discussion. The presence of hooks on the caudal fin of mature males is a feature present in most of the compsurins. *Acinocheiroduon melanogramma* Malabarba & Weitzman, *Kolpotocheiroduon theloura* Malabarba & Weitzman, *Macropsobrycon uruguayanae* Eigenmann, “*Odontostilbe*” *dialeptura* (Fink & Weitzman), *Saccoderma hastata*

(Eigenmann), *S. melanostigma* Schultz, and the species herein described “New Genus C” Leticia n. sp., “New Genus C” Napo n. sp., “New Genus B” Purus n. sp., and “New Genus C” Yurimaguas n. sp., are the Compsurini integrants whose adult males have hooks on the caudal-fin rays. Although shared by several species, the caudal-fin hooks vary in shape, size and distribution among the compsurins.

“New Genus C” Yurimaguas n. sp. is the compsurin species which has the higher number of caudal-fin rays bearing hooks. They are distributed along the distal half of the 8th, rarely of the 7th, to the 18th principal caudal-fin rays; while the hooks are generally restricted to the lower caudal-fin lobe on the remaining species, being distributed from the 13th and 14th in *Acinocheirodon melanogramma*, from the 12th-18th in *Macropsobrycon uruguayanae*, 12th-15th in *Kolpotocheirodon theloura*, 14th-18th in the *Saccoderma* Schultz species, 12th-15th in “*Odontostilbe*” *dialeptura*, 11th-16th in “New Genus C” Leticia n. sp., 12th-18th in “New Genus C” Napo n. sp., and from the 14th-16th in “New Genus B” Purus n. sp.

Not only the distribution of the hooks varies among the compsurin species, but also their shape. Most of the species present small hooks placed along the dorsolateral surface of the rays, slightly curved anteriorly and dorsally directed. However, in *Acinocheirodon* and “New Genus B” Purus n. sp., the hooks distally placed over the caudal-fin rays are straight, longer than the ray’s depth, and dorsoanteriorly directed (Fig. 11). In “New Genus C” Leticia n. sp. and “New Genus C” Yurimaguas n. sp. small caudal hooks arise laterally instead of dorsally from the dorsolateral surface of the rays, and are slightly bent toward the caudal-fin base. The hooks in *Saccoderma*, “*Odontostilbe*” *dialeptura* and “New Genus C” Napo n. sp. are generally anteriorly bent over the caudal-fin rays, laid down over the surface of the rays. *Macropsobrycon uruguayanae* is the compsurini species which presents the most diverse shapes of hooks in the caudal fin. The hooks on the 12th and 13th caudal-fin rays are large and anteriorly bent, facing the base of the caudal fin, while the hooks on the 14th to 18th caudal-fin rays are small, slightly curved anteriorly and dorsally directed in the distal portion of these rays, but in the proximal portion they are straight and flexible, being called “spinelets” by Malabarba (1998).

Among the characids, the presence of caudal-fin hooks is not very common. It is more frequently found in groups of species that present conspicuous secondary sexual

dimorphism. Some members of the Stevardiinae, like *Acrobrycon* Eigenman & Pearson, *Mimagoniates microlepis* (Steindachner), *M. pulcher* Menezes & Weitzman, and *M. rheocharis* Menezes & Weitzman, *Scopaeocharax* Weitzman & Fink, *Tytocharax cochui* (Ladiges), and *Xenurobrycon* Myers & Miranda Ribeiro, have caudal-fin rays bearing hooks combined with hypertrophy of scales and/or glandular tissue. The presence of caudal-fin hooks is also known for the *incertae sedis* genus *Brittanichthys* Géry. As already commented by former authors, the presence of caudal hooks in the previous species is likely homoplastic with the Compsurini caudal-hooks, once none of them present the synapomorphies of the Cheirodontinae (Weitzman & Fink, 1985; Malabarba, 1998; Malabarba & Weitzman, 1999; Weitzman *et al.*, 2005; Menezes & Weitzman, 2009).

The function of the caudal-fin hooks is not completely clear yet, however, as hypothesized by Lima & Sousa (2009) for the anal-fin hooks in some characids, the constant association of hooks with hypertrophied whitish tissue rich in club cells, suggests that the hooks may have an important function in damaging the surrounding whitish tissue by friction, rupturing and allowing the club cells to liberate their contents. Although Pfeiffer (1977) quoted the club cell rupture in Ostariophysi to be linked to the release of alarm pheromone substances, the existence of hypertrophied tissue rich in club cells associated with secondary sexual dimorphic structures, may be an indicative that the function of the pheromone released by these cells is related to the courtship behavior (Weitzman *et al.*, 2005).

“New Genus B” *Purus* n. sp. has a unusual sexually dimorphic caudal fin. The presence of a pouch scale proceeded by three large hooks surrounded by hypertrophied tissue on its opening, is autapomorphic for the species. The *Compsura* Eigenmann and *Saccoderma* species also have a scale pouch in the lower lobe of the caudal fin, however *Compsura* has no hooks in the caudal-fin rays, and the caudal-fin hooks on *Saccoderma* are small, numerous, and placed in the distal portion of the lower lobe caudal-fin rays. Another difference is that the scale pouch in “New Genus B” *Purus* n. sp. is composed dorsally by the last modified scale from the LL, and ventrally by the last modified scale from the LV1, while it is formed by the last modified scales from the LV1 and LV2 in the *Compsura* and *Saccoderma* species. This corroborates the hypothesis that the pouch scale among the Compsurini may have been independently acquired by these genera.

Artificial key for the species of Compsurini

1. Absence of the group of characters below..... **Not Cheirodontinae**
 - 1'. One tooth row in the premaxilla; premaxillary and dentary teeth pedunculated, expanded and compressed distally; pseudotympanum between the first and second pleural ribs as a large, nearly triangular hiatus on muscles covering the anterior swimbladder, limited dorsally by the *lateralis superficialis* muscle, posteriorly by a naked anterior surface of the second pleural rib, posteroventrally by the *obliquus inferioris* and anteroventrally by the *obliquus superioris* muscle; humeral spot absent..... **Cheirodontinae** (2)
 2. Anal-fin hooks on mature males directed posterodorsally; anal fin evenly pigmented on mature males and females..... **Odontostilbini** or **Cheirodontini**
 - 2'. Anal-fin hooks on mature males directed anteriorly (except *Acinocheirodon*, “New Genus A” Cuzco n. sp., and “New Genus C” Leticia n. sp.); distal margin of the anal fin densely pigmented on mature males..... **Compsurini** (3).
 3. Absence of sexual dimorphism in the caudal fin..... “**New Genus A**” 4
 - 3'. Presence of sexual dimorphism in the caudal fin (hooks or modified scales).....5
 4. Anal-fin hook posterodorsally directed; i,11 anal-fin rays bearing hooks..... “**New Genus A**” **Cuzco n. sp.** (upper río Madre de Díos and upper río Ucayali basins)
 - 4'. Anal-fin hook anteriorly directed; i,14 anal-fin rays bearing hooks..... “**New Genus A**” **Tingo n. sp.** (upper río Ucayali basin)
 5. Absence of modified caudal-fin scales on mature males (only hooks).....6
 - 5'. Presence of modified caudal-fin scales on mature males..... 11
 6. Lateral line completely pored; hypertrophied skin flaps between the 13th and 14th caudal-fin rays..... *Acinocheirodon melanogramma* (rio São Francisco and rio Jequitinhonha basins)
 - 6'. Lateral line incompletely pored.....7
 7. Maxilla toothless, rarely with one tricuspid tooth..... “**New Genus C**” **Leticia n. sp.** (upper río Amazonas)
 - 7'. Maxilla toothed, generally two or more teeth with up to five cusps.....8

8. Pineapple organ in the caudal fin of mature males; pelvic bone region pigmented; conspicuous small black spot at the midlength of the first branched anal-fin rays of males..... *Kolpotocheiroduon* (9)
- 8'. Absence of pineapple organ in the caudal fin; pelvic bone region not pigmented; absence of a conspicuous small black spot at the anterior portion of the anal fin of males10
9. Presence of hooks on the caudal fin of mature males..... *Kolpotocheiroduon theloura* (upper rio Paraná basin)
- 9'. Absence of hooks on the caudal fin of mature males..... *Kolpotocheiroduon figueiredoi* (rio Paraguaçu basin)
10. Principal caudal-fin rays 8-18 bearing hooks on mature males; i,14-16 anal-fin rays bearing hooks on mature males..... **“New Genus C” Yurimaguas n. sp.** (rio Ucayali basin)
- 10'. Principal caudal-fin rays 12-18 bearing hooks on mature males; i,4 anal-fin rays bearing hooks on mature males..... **“New Genus C” Napo n. sp.** (rio Napo, upper rio Huallaga, and upper rio Ucayali basin)
11. Presence of scale pouch in the caudal fin.....14
- 11'. Absence of scale pouch in the caudal fin.....**Compsurini from Central America** (12)
12. Presence of modified scales forming pockets in the lower caudal-fin lobe.....
“Compsura” gorgonae (Panama drainages)
- 12'. Absence of modified scales forming pockets in the lower caudal-fin lobe; presence of a group of small scales extending over the base of the middle caudal-fin rays.....13
13. Lateral line complete; first unbranched ray from pectoral and pelvic fins elongated on mature males; absence of hooks on the caudal-fin rays of males..... **“Odontostilbe” mitopterus** (Panama drainages)
- 13'. Lateral line generally incomplete; first unbranched ray from pectoral and pelvic fins not elongated on mature males; presence of hooks on the caudal-fin rays of males.....
“Odontostilbe” dialepturus (Panama drainages)
14. Lateral line completely pored; elongated scales over the 12-13 principal caudal-fin rays..... *Saccoderma* (15)
- 14'. Lateral line incompletely pored; absence of elongated scales on the caudal fin.....16

15. Melanophores equally distributed over the dorsal and anal fins.... *Saccoderma hastata* (Colombia, coastal rivers, río Atrato, río Sinú, río Pechilín, río Magdalena basins)
- 15'. Melanophores concentrated on the anterodistal region of the dorsal and anal fins.... *Saccoderma melanostigma* (Lago Maracaibo basin)
16. Caudal-fin rays bearing hooks..... “**New Genus B**” *Purus n. sp.* (upper rio Purus)
- 16'. Caudal-fin rays not bearing hooks..... *Compsura*
17. Presence of a conspicuous dark spot between the first and second unbranched dorsal-fin rays; the last three scales from the lateral line series modified in shape and size, and involved in the caudal organ structure..... *Compsura heterura* (rio São Francisco basin and coastal rivers from Northeast of Brazil)
- 17'. Absence of a conspicuous dark spot between the first and second unbranched dorsal-fin rays; the last two scales from the lateral line series modified in shape and size, and involved in the caudal organ structure.....18
18. Presence of 19-22 (mean = 20.2; n = 50) branched anal-fin rays..... *Compsura Guaporé n. sp.* (upper rio Guaporé basin)
- 18'. Presence of 16-19 (mean = 18.1; n = 20) branched anal-fin rays..... *Compsura Araguaia n. sp.* (rio Araguaia basin)

Comparative material. *Acinocheiroidon melanogramma*: ANSP 176238, paratypes, 7, 21.9-26.2 mm SL, Brazil, Minas Gerais, rio Jequitaiá drainage. *Aphyodite grammica*: FMNH, holotype, 24.3 mm SL, Guiana, Konawaruk. MZUSP 29874, 20, 21.9-26.9 mm SL, Brazil, rio Negro. *Brittanichthys axelrodi*: MCP 14931, 17, 16.3-22.2 mm SL, 3 c&s, Brazil, Boa Vista, rio Negro. *Cheiroidon australe*: USNM 084317, paratypes, 12, 28.4-49.8 mm SL, Chile, Los Lagos region at Puerto Varas. *Cheiroidon dialepturus*: USNM 208524, holotype, 26.8 mm SL, Panama, Veraguas, río San Pedro basin. *Cheiroidon galusdae*: USNM 084319, paratypes, 10, 30.6-52.3 mm SL, Chile, río Locomilla at San Xavier. *Cheiroidon gorgonae*: USNM 64094, holotype, 22.1 mm SL, Panama, Canal Zone, small seepage pool below spillway of the reservoir dam at Gorgona. *Cheiroidon kiliani*: USNM 227310, paratype, 1, 25.2 mm SL. Valdivia-Chile, río Cau-Cau. *Cheiroidon microdon*: FMNH 57867, holotype, 32.2 mm SL, Brazil, Caceres, rio Ibicuhy. *Cheiroidon micropterus*: CAS 59780, holotype, 23.9 mm SL, Brazil, Pará, rio Amazonas drainage at Santarém.

Cheirodon mitopterus: USNM 208539, holotype, 34.6mm SL, Panama, Cocle, río Tucue, tributary of río Cocle del Norte. *Cheirodon notomelas*: FMNH 57829, holotype, 28.2 mm SL, Brazil, Miguel Calmone. *Cheirodontops geayi*: USNM 121507, holotype, 35.5 mm SL, Venezuela, Estado de Aragua, río Guarico. *Compsura heterura*: FMNH 57825, holotype, 28.7 mm SL, Brazil, rio Itapicuru, Queimadas. *Holesthes heterodon* (= *Serrapinnus heterodon*): CAS 117522, paratypes, 4, 32.2-36.5 mm SL, Brazil, Minas Gerais, rio Grande, Jaguará. *Kolpotocheirodon figueiredoi*: MCP 22345, paratypes, 25.1-30.5 mm SL, rio Pratinha, Iraquara. *Kolpotocheirodon theloura*: MCP 11161, paratype, 25.9 mm SL, ribeirão do Gama, just above, the mouth of ribeirão Taquara. *Leptobrycon jatuaranae*: MCP 14936, 17, 20.8-25.1 mm SL, 3 c&s, Brazil, Amazonas, rio Negro. *Microschemobrycon guaporensis*: FMNH 57926, holotype, 29.1 mm SL, Brazil, Maciel, rio Guaporé. *Odontostilbe hastatus*: FMNH 56383, holotype, 30.2 mm SL, Colombia, Soplaviento. *Oligobrycon microstomus*: holotype, 31.0 mm SL, Brazil, Jacarehy on rio Parahyba. *Oxybrycon* sp.: MCP 33105, 8, 13.7-14.9 mm SL, 2 c&s, Venezuela, Titi lagoon, upper Orinoco basin. *Parecbasis cyclolepis*: FMNH 56677, holotype, 56.3 mm SL, Brazil, rio Madeira. MZUSP 26146, 7, 40.3-53.5 mm SL, Peru, Ucayali, río Ucayali. *Pristella aubynei*: FMNH 52698, 34.9 mm SL, British Guiana. *Prodontocharax alleni*: CAS 117472, holotype, 32.8 mm SL, Peru, Ucayali, río Amazonas basin. *Prodontocharax melanotus*: CAS 59793, holotype, 44.9 mm SL, Bolivia, La Paz, río Amazonas drainage at Tumupasa. *Pseudocheirodon affinis*: CAS 117516, paratype, 32.1-35.4 mm SL, Panama, rio Gatun, at Gatun. *Saccoderma melanostigma*: USNM 121519, holotype, 26.7 mm SL, Venezuela, río San Juan, South of Mene Grande. *Spintherobolus broccae*: FMNH 58864, paratype, 18.7 mm SL, Brazil, Rio de Janeiro. *Spintherobolus papilliferus*: FMNH 104802, holotype, 32.9 mm SL, Brazil, São Paulo, Alto da Serra. *Thrissobrycon pectinifer*: SU 16944, holotype, 26.8 mm SL, Brazil, Cucuhy, rio Negro. MCP 14932, 12, 26.4-30.2 mm SL, 3 c&s, Brazil, rio Arirara.

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Literature Cited

- Bührnheim, C. M. & L. R. Malabarba. 2006. Redescription of the type species of *Odontostilbe* Cope, 1870 (Teleostei: Characidae: Cheirodontinae), and description of three new species from the Amazon basin. *Neotropical Ichthyology*, 4(2): 167-196.
- Burns, J. R., S. H. Weitzman & L. R. Malabarba. 1997. Insemination in eight species of cheirodontine fishes (Teleostei: Characidae: Cheirodontinae). *Copeia* 1997: 433–438.
- Fink, W. L. & S. H. Weitzman. 1974. The so-called Cheirodontin fishes of Central America with descriptions of two new species (Pisces: Characidae). *Smithsonian Contributions to Zoology*, 172: 1-46.
- Gonçalves, T. K., M. A. Azevedo, L. R. Malabarba & C. B. Fialho. 2005. Reproductive biology and development of sexually dimorphic structures in *Aphyocharax anisitsi* (Ostariophysi: Characidae). *Neotropical Ichthyology*, 3(3): 433-438.
- Lima, F. C. T. & L. M. Sousa. 2009. A new species of *Hemigrammus* from the upper rio Negro basin, Brazil, with comments on the presence and arrangement of anal-fin hooks in *Hemigrammus* and related genera (Ostariophysi: Characiformes: Characidae). *Aqua, International Journal of Ichthyology*, 15(3): 153-168.
- Malabarba, L. R. 1998. Monophyly of the Cheirodontinae, characters and major clades (Ostariophysi: Characidae). Pp. 193-233. In: Malabarba, L. R., R. E. Reis, R. P. Vari, Z. M. S. Lucena & C. A. S. Lucena (Eds.). *Phylogeny and Classification of Neotropical Fishes*. Porto Alegre, Edipucrs, 603p.
- Malabarba, L. R. & F. C. T., Lima & S. H. Weitzman. 2004. A new species of *Kolpotocheirodon* (Teleostei: Characidae: Cheirodontinae: Compsurini) from Bahia,

- northeastern Brazil, with a new diagnosis of the genus. *Proceedings of the Biological Society of Washington*, 117(3): 317-329.
- Malabarba, L. R. & S. H. Weitzman. 1999. A new genus and species of South American fishes (Teleostei: Characidae: Cheirodontinae) with a derived caudal fin, including comments about inseminating cheirodontines. *Proceedings of the Biological Society of Washington*, 112(2): 410-432.
- Malabarba, L. R. & S. H. Weitzman. 2000. A new genus and species of inseminating (Teleostei: Characidae: Cheirodontinae: Compsurini) from South America with uniquely derived caudal-fin dermal papillae. *Proceedings of the Biological Society of Washington*, 113(1): 269-283.
- Menezes, N. A. & S. H. Weitzman. 2009. Systematics of the Neotropical fish subfamily Glandulocaudinae (Teleostei: Characiformes: Characidae). *Neotropical Ichthyology*, 7(3): 295-370.
- Pfeiffer, W. 1977. The distribution of fright reaction and alarm substances cells in fishes. *Copeia*, 1977(4): 653-665.
- Taylor, W. R. & G. C. van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9(2): 107-119.
- Weitzman, S. H. & L. R. Malabarba. 1998. Perspectives about the phylogeny and classification of the Characidae (Teleostei: Characiformes). Pp. 161-170. In: Malabarba, L. R., R. E. Reis, R. P. Vari, Z. M. S. Lucena & C. A. S. Lucena (Eds.). *Phylogeny and Classification of Neotropical Fishes*. Porto Alegre, Edipucrs, 603p.
- Weitzman, S. H. & S. V. Fink. 1985. Xenurobryconin phylogeny and putative pherome pumps in Glandulocaudine fishes (Teleostei: Characidae). *Smithsonian Contributions to Zoology*, 421: 1-121.
- Weitzman, S. H., N. A. Menezes, H. G. Evers & J. R. Burns. 2005. Putative relationships among Inseminating and externally fertilizing characids, with a description of a new genus and species of Brazilian inseminating fish bearing an anal-fin gland in males (Characiformes: Characidae). *Neotropical Ichthyology* 3(3): 329-360.

Table 1. Morphometric data for “New Genus A” Cuzco n. sp. and “New Genus A” Tingo n. sp. Holotype (H) included the sample size (N).

	“New Genus A” Cuzco n. sp.						“New Genus A” Tingo n. sp.					
	H	N	Min	Max	Mean	SD	H	N	Min	Max	Mean	SD
Standard length (mm)	30.2	29	24.6	34.9	29.7	-	31.3	48	22.7	31.4	25.2	-
Percents of Standard Length												
Head length	24.2	29	23.5	26.9	24.9	0.8	24.5	48	23.5	28.0	26.2	1.0
Bony Head length	24.0	29	23.2	26.8	24.7	1.0	26.2	48	24.2	27.9	25.8	0.8
Snout-anal distance	62.6	29	59.3	68.4	63.0	2.1	64.3	48	62.7	70.5	66.2	1.6
Snout-dorsal distance	49.9	29	48.9	53.7	50.9	1.3	52.0	48	49.8	57.2	53.4	1.4
Snout-pelvic distance	44.1	29	39.6	48.8	44.8	1.9	44.8	48	43.5	48.5	46.4	1.2
Snout-pectoral distance	24.0	29	23.1	26.7	24.9	1.0	24.7	48	24.0	28.4	26.4	0.9
Dorsal-fin base length	13.6	29	12.2	15.4	13.9	0.9	13.1	48	11.3	14.8	13.2	0.8
Anal-fin base length	27.0	29	14.9	29.8	26.9	2.8	24.0	48	21.3	26.8	23.6	1.1
Length of caudal peduncle	16.3	29	10.9	17.2	14.4	1.5	16.6	48	13.7	18.7	16.6	1.1
Depth of caudal peduncle	13.7	29	10.5	14.9	12.7	1.1	14.5	48	12.7	16.6	14.4	0.8
Body depth at dorsal-fin	36.1	29	31.9	40.5	36.3	2.1	37.9	48	31.3	41.8	37.4	2.0
Dorsal-fin length	31.3	28	25.6	32.5	30.0	1.7	29.6	32	24.5	33.1	28.5	1.5
Pelvic-fin length	19.2	29	16.2	20.7	18.7	0.9	19.3	47	13.2	20.4	17.1	1.4
Pectoral-fin length	19.7	29	17.7	23.0	20.3	1.1	20.4	48	15.4	23.0	19.4	1.4
Percents of Head Length												
Snout length	29.1	29	25.3	30.7	28.1	1.2	27.2	48	22.3	28.8	25.8	1.5
Upper Jaw length	32.3	29	26.8	32.3	29.3	1.4	29.3	48	24.8	29.3	27.0	1.1
Horizontal orbit diameter	38.1	29	34.5	39.9	37.3	1.7	36.5	48	34.7	41.7	37.5	1.6
Interorbital width	34.8	29	30.4	37.0	33.2	1.5	34.2	48	29.7	36.5	32.7	1.5

Table 2. Morphometric data for “New Genus B” Purus n. sp. and “New Genus C” Napo n. sp. Holotype (H) included the sample size (N).

	“New Genus B” Purus n. sp.						“New Genus C” Napo n. sp.					
	H	N	Min	Max	Mean	SD	H	N	Min	Max	Mean	SD
Standard length (mm)	26.1	28	23	29.0	25.5	-	25.3	66	20.0	31.8	25.7	-
Percents of Standard Length												
Head length	26.5	28	24.3	27.2	26.1	0.9	26.4	66	24.1	30.5	26.2	1.2
Bony Head length	25.6	28	23.5	26.5	24.9	0.8	27.2	66	23.6	28.2	25.9	0.9
Snout-anal distance	63.0	28	62.2	66.6	64.4	1.2	65.2	66	51.0	66.9	63.9	2.2
Snout-dorsal distance	53.8	28	50.5	54.6	53.3	1.0	53.2	66	48.8	55.7	52.9	1.6
Snout-pelvic distance	45.9	28	43.8	48.2	46.1	1.1	46.7	66	44.2	50.6	46.6	1.4
Snout-pectoral distance	29.5	28	25.7	29.5	27.4	1.0	27.7	66	23.8	31.0	26.7	1.3
Dorsal-fin base length	12.4	28	11.9	14.2	13.2	0.6	14.6	66	11.3	15.2	13.9	0.9
Anal-fin base length	29.4	28	25.9	30.1	28.3	1.1	28.2	66	24.1	31.5	28.0	1.5
Length of caudal peduncle	14.2	28	12.3	15.8	14.0	1.0	13.7	66	11.0	15.8	13.4	1.0
Depth of caudal peduncle	13.5	28	11.6	14.3	13.2	0.7	12.3	66	9.4	15.0	11.9	1.0
Body depth at dorsal-fin	36.2	28	34.2	38.5	35.8	1.3	35.9	66	29.8	41.0	35.8	2.6
Dorsal-fin length	28.0	28	17.6	31.1	28.8	2.5	32.7	64	16.7	34.5	30.5	2.9
Pelvic-fin length	17.7	28	14.6	23.5	16.8	1.8	18.8	66	15.2	23.1	17.9	1.4
Pectoral-fin length	22.0	28	19.1	23.8	21.5	1.4	22.1	66	17.5	23.8	20.8	1.3
Percents of Head Length												
Snout length	23.9	28	22.6	28.7	25.6	1.8	25.7	66	21.6	30.1	26.3	2.2
Upper Jaw length	26.5	28	23.5	37.9	28.0	2.6	29.0	66	23.4	32.6	27.6	1.8
Horizontal orbit diameter	39.2	28	34.2	39.2	37.1	1.3	41.2	66	28.0	43.6	39.3	2.6
Interorbital width	36.9	28	31.8	39.2	36.2	1.7	31.3	66	24.1	34.6	30.5	2.2

Table 3. Morphometric data for “New Genus C” Leticia n. sp. and “New Genus C” Yurimaguas n. sp. Holotype (H) included the sample size (N).

	“New Genus C” Leticia n. sp.						“New Genus C” Yurimaguas n. sp.					
	H	N	Min	Max	Mean	SD	H	N	Min	Max	Mean	SD
Standard length (mm)	26.2	22	24.1	26.8	26.0	-	23.1	20	21.8	25.3	23.3	-
Percents of Standard Length												
Head length	27.1	22	25.0	28.7	26.9	1.0	28.6	20	26.5	30.1	28.4	1.0
Bony Head length	23.8	22	22.7	25.5	23.9	0.7	26.8	20	25.7	28.4	26.6	0.8
Snout-anal distance	60.0	22	57.8	64.1	61.0	2.0	63.0	20	61.2	69.3	63.5	2.0
Snout-dorsal distance	52.7	22	50.1	54.1	52.7	1.1	53.3	20	49.5	55.0	51.7	1.7
Snout-pelvic distance	47.9	22	44.1	50.5	47.5	1.7	47.7	20	43.2	51.4	46.4	1.7
Snout-pectoral distance	32.6	22	26.4	32.6	28.3	1.3	28.3	20	26.1	30.2	28.5	1.0
Dorsal-fin base length	14.2	22	11.8	16.7	13.3	1.1	15.4	10	14.0	16.6	15.5	0.6
Anal-fin base length	30.0	22	30.0	34.6	32.7	1.3	29.1	20	27.0	31.8	29.3	1.2
Length of caudal peduncle	12.1	22	10.4	14.3	12.2	0.9	13.6	20	11.1	15.2	12.9	1.0
Depth of caudal peduncle	14.7	22	11.8	14.7	12.9	0.9	14.9	20	12.7	16.4	14.7	1.3
Body depth at dorsal-fin	37.3	22	30.9	38.6	35.8	1.9	37.5	20	35.4	40.4	37.9	1.5
Dorsal-fin length	18.0	22	18.0	33.1	29.1	2.8	34.3	20	33.0	35.7	34.0	0.8
Pelvic-fin length	21.0	22	15.4	21.0	18.0	1.7	22.3	19	17.9	23.0	20.2	1.8
Pectoral-fin length	21.0	22	18.4	23.3	20.7	1.1	-	17	18.6	24.6	21.6	1.9
Percents of Head Length												
Snout length	23.1	22	21.2	26.4	24.0	1.4	26.1	20	22.5	29.0	26.2	1.4
Upper Jaw length	30.3	22	25.1	33.0	29.6	2.0	31.4	20	25.7	31.4	27.8	1.5
Horizontal orbit diameter	38.0	22	33.3	38.8	36.7	1.4	35.8	20	33.3	39.3	36.5	1.7
Interorbital width	27.8	22	25.0	29.5	27.4	1.4	31.7	20	26.5	34.8	30.7	1.8

Figures

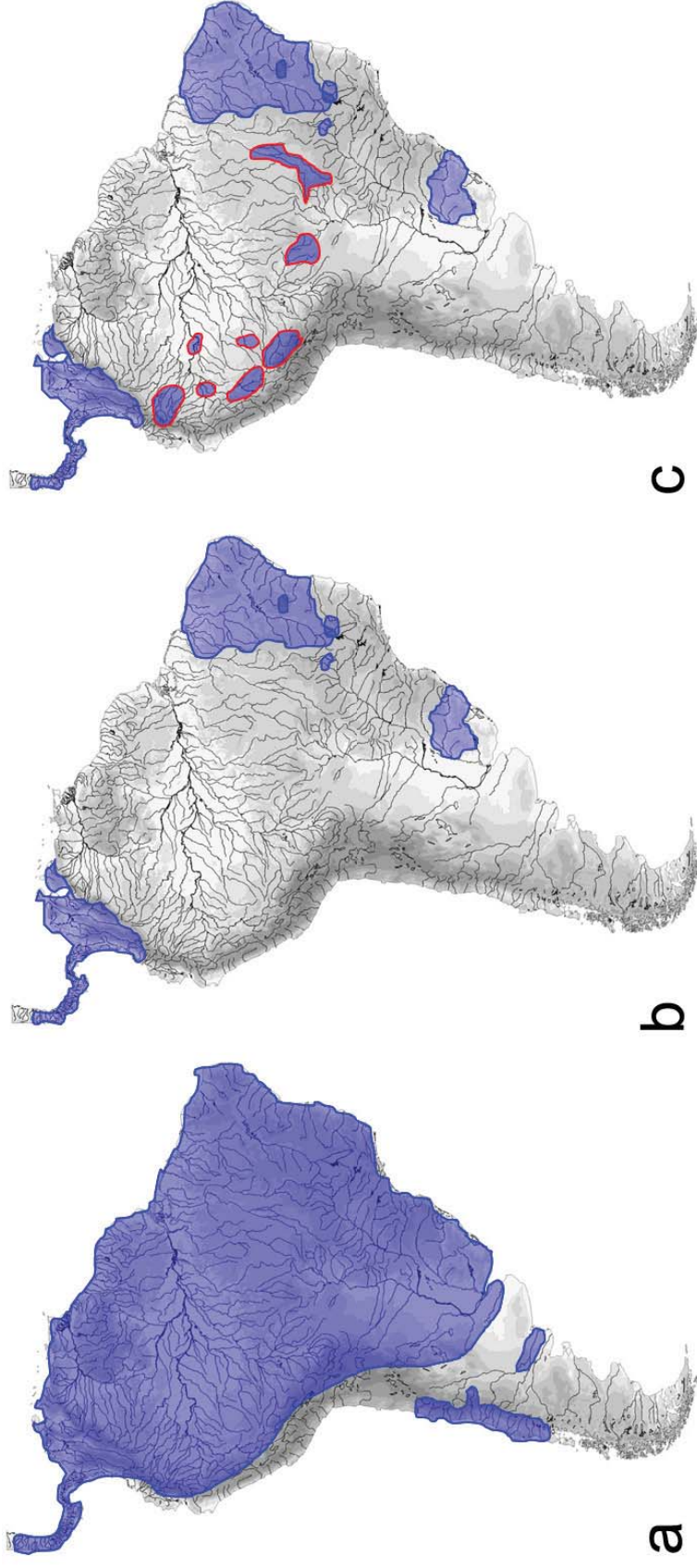


Fig. 1. Geographic distribution range of the (a) Cheirodontinae; (b) Compsurini before the present work; (c) Compsurini after the review of the tribe, along the Neotropical region. Areas delimited in red represent the new species distribution.



Fig. 2. “New Genus A” Cuzco n. sp. **(a)** uncatalogued, male, holotype, 28.8 mm SL and **(b)** female, USNM 295636 paratype, 34.9 mm SL; both from Peru, Department Madre de Dios, Parque Nacional Manu, Pakitza and Vicinity.

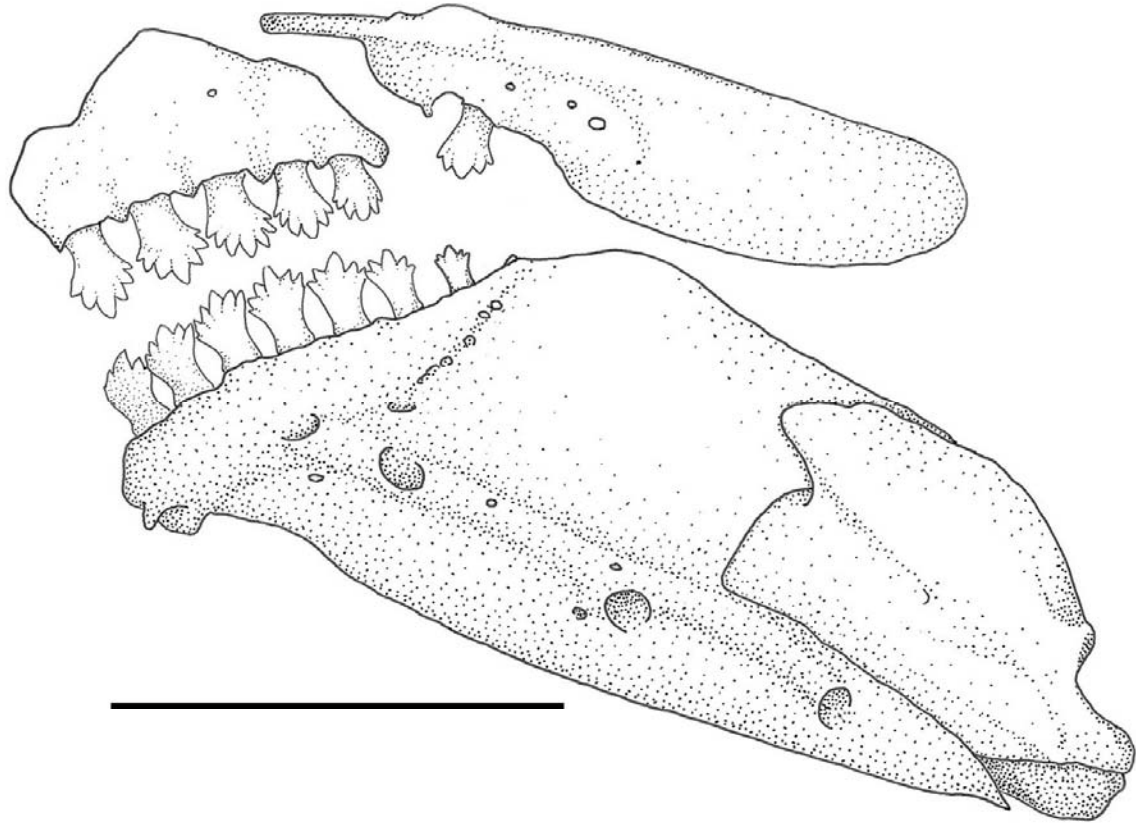


Fig. 3. Dentition and jaws morphology of “New Genus A” Cuzco n. sp.; USNM 295636 paratype, 27.4 mm SL. Scale bar = 1 mm.



Fig. 4. Geographic distribution of the new species of Compurini from the Amazon basin; “New Genus A” Cuzco n. sp (empty lozenges); “New Genus C” Leticia n. sp (triangle); “New Genus C” Napo n. sp (dark lozenges); “New Genus B” Purus n. sp (star); “New Genus C” Yurimaguas n. sp (square); “New Genus A” Tingo n. sp (dots).



Fig. 5. “New Genus A” Tingo n. sp. **(a)** uncatalogued, male, holotype, 31.3 mm SL and **(b)** ANSP 116449, paratype, female, 32.5 mm SL; both from Peru, Huanucu, Vicinity Tingo Maria, río Rondos (tributary of río Monzon), just above new bridge site.

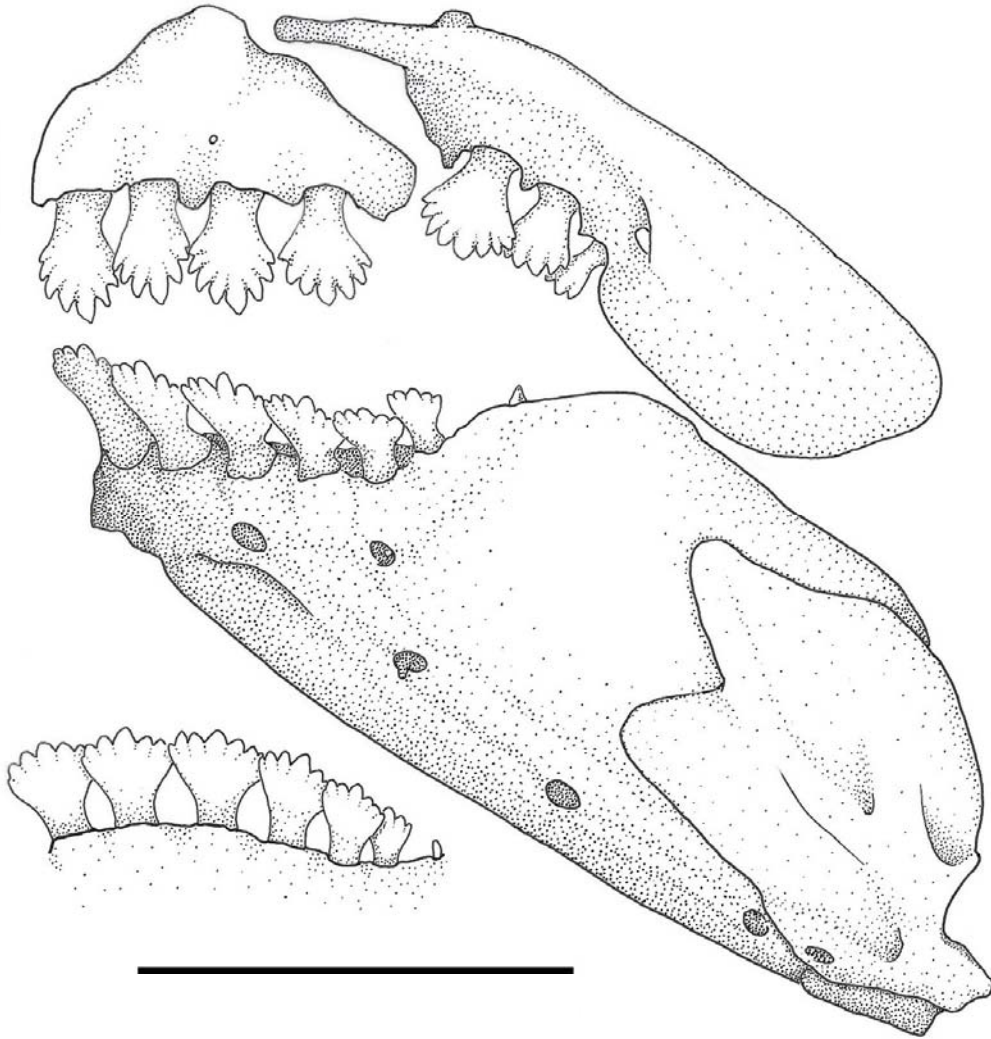


Fig. 6. Dentition and jaws morphology of “New Genus A” *Tingo* n. sp.; ANSP 116449, paratype, 27.6 mm SL. Scale bar = 1 mm.



Fig. 7. “New Genus B” Purus n. sp. **(a)** MCP uncatalogued, male, holotype, 26.1 mm SL and **(b)** MCP 41716, paratype, female, 28.3 mm SL; both from Brazil, Acre, Sena Madureira, affluent of rio São Pedro, rio Purus basin.

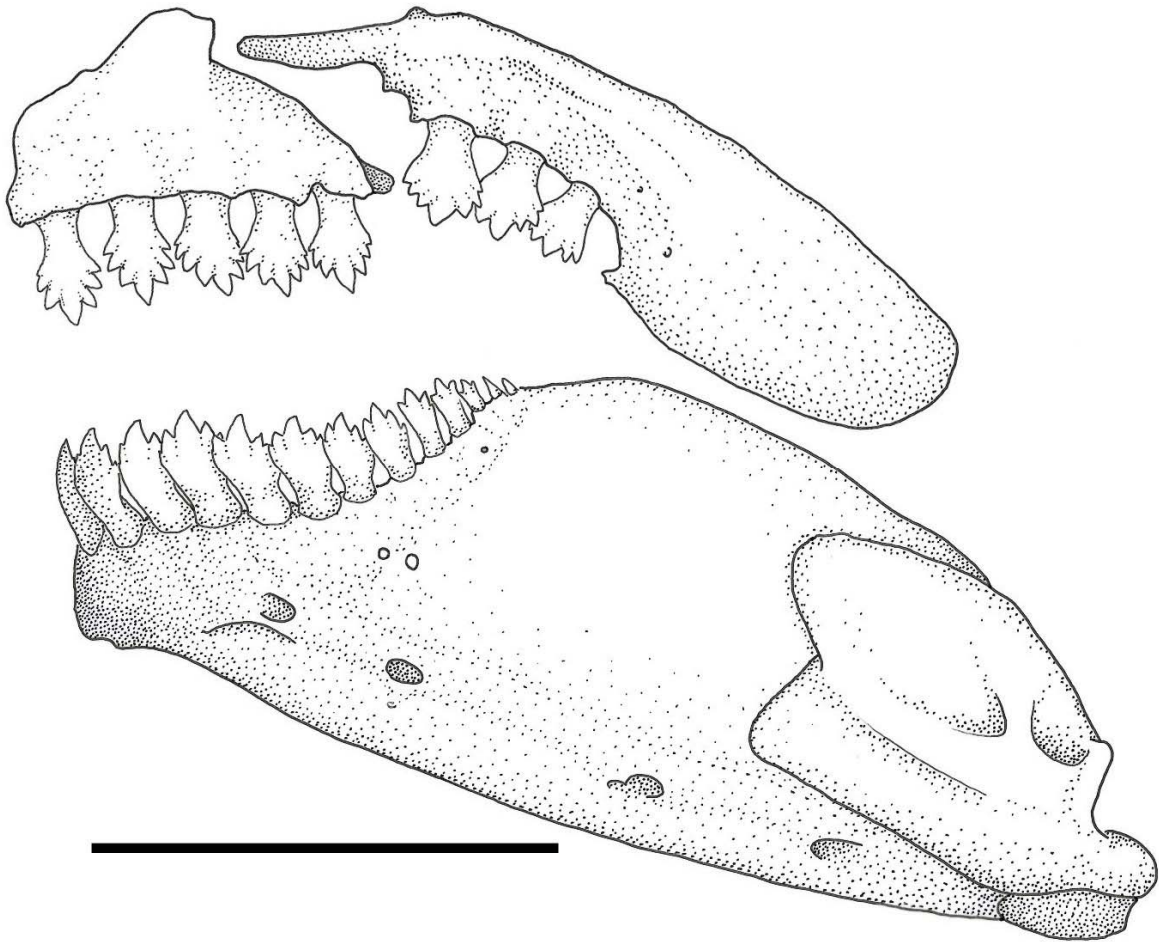


Fig. 8. Dentition and jaws morphology of “New Genus B” *Purus* n. sp.; MCP 41716, paratype, 23.6 mm SL. Scale bar = 1 mm.

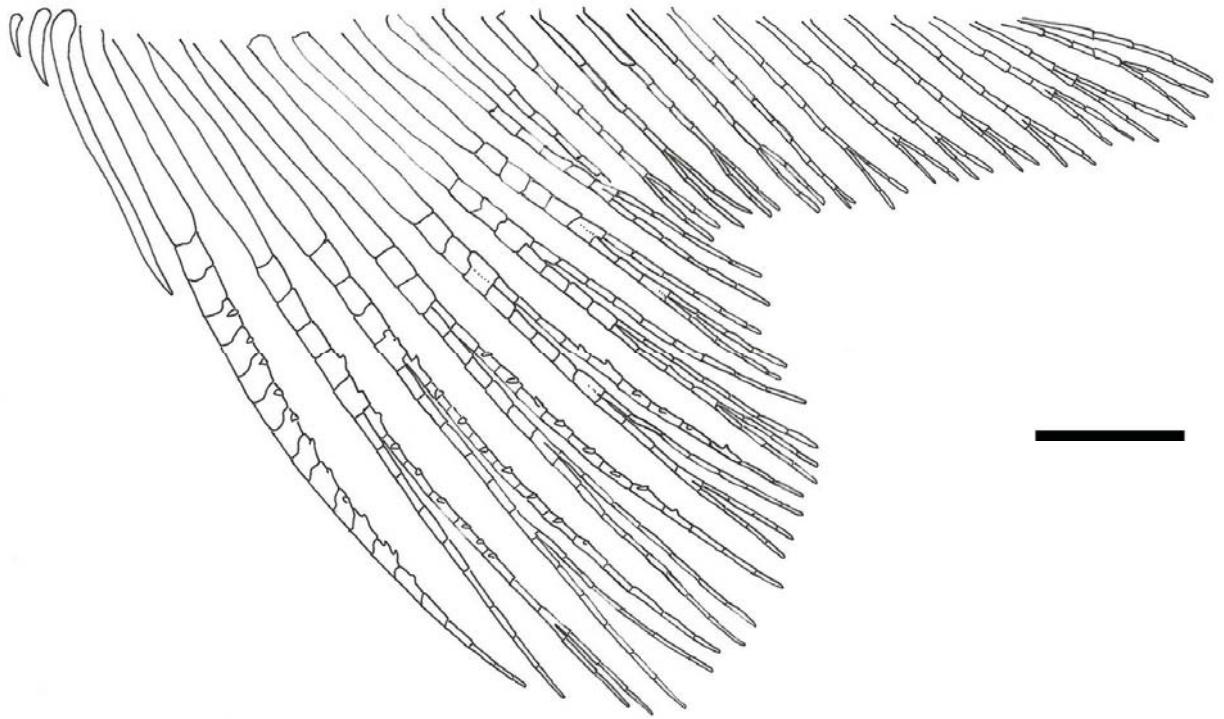


Fig. 9. Anal fin of a male specimen of "New Genus B" Purus n. sp.; MCP 41716, paratype, 25.9 mm SL. Scale bar = 1 mm.

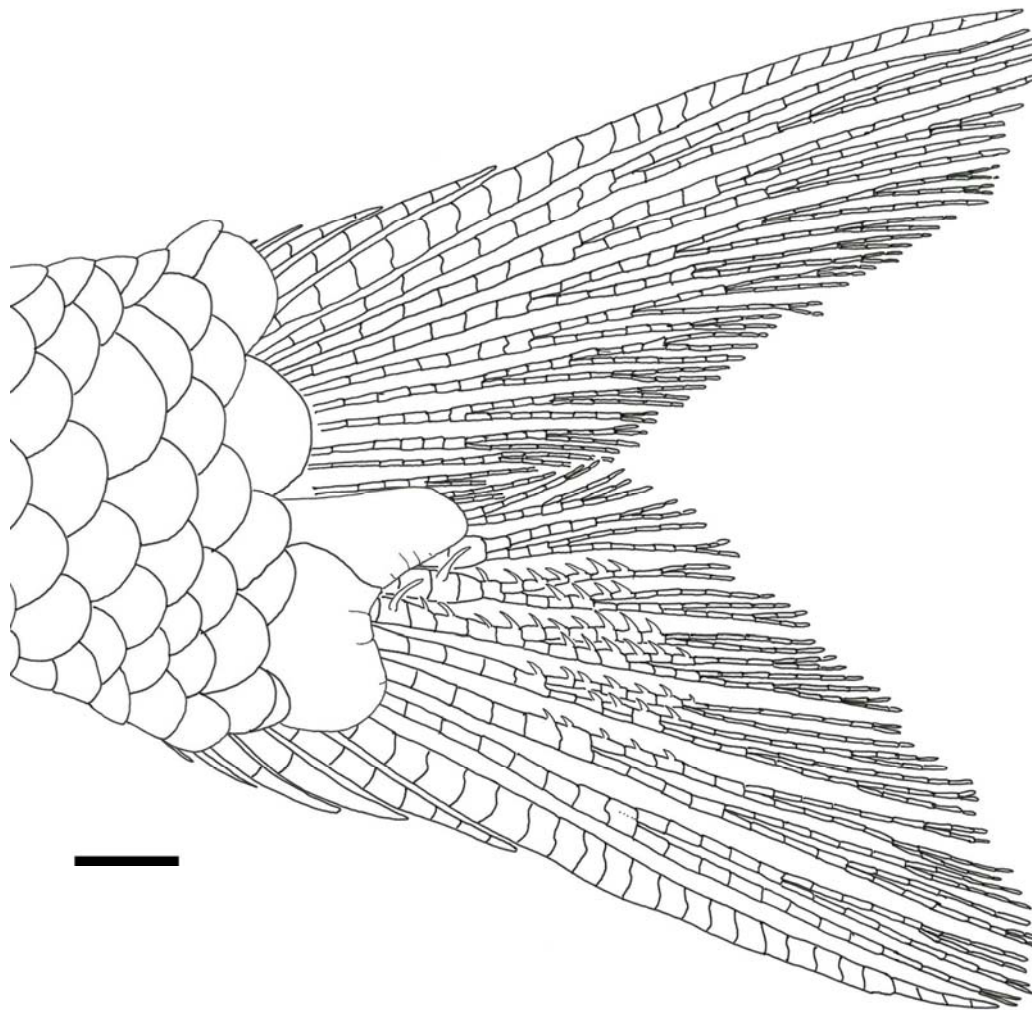


Fig. 10. Caudal fin organ of a male specimen of "New Genus B" Purus n. sp.; MCP 41716, paratype, 25.9 mm SL. Scale bars = 1 mm.

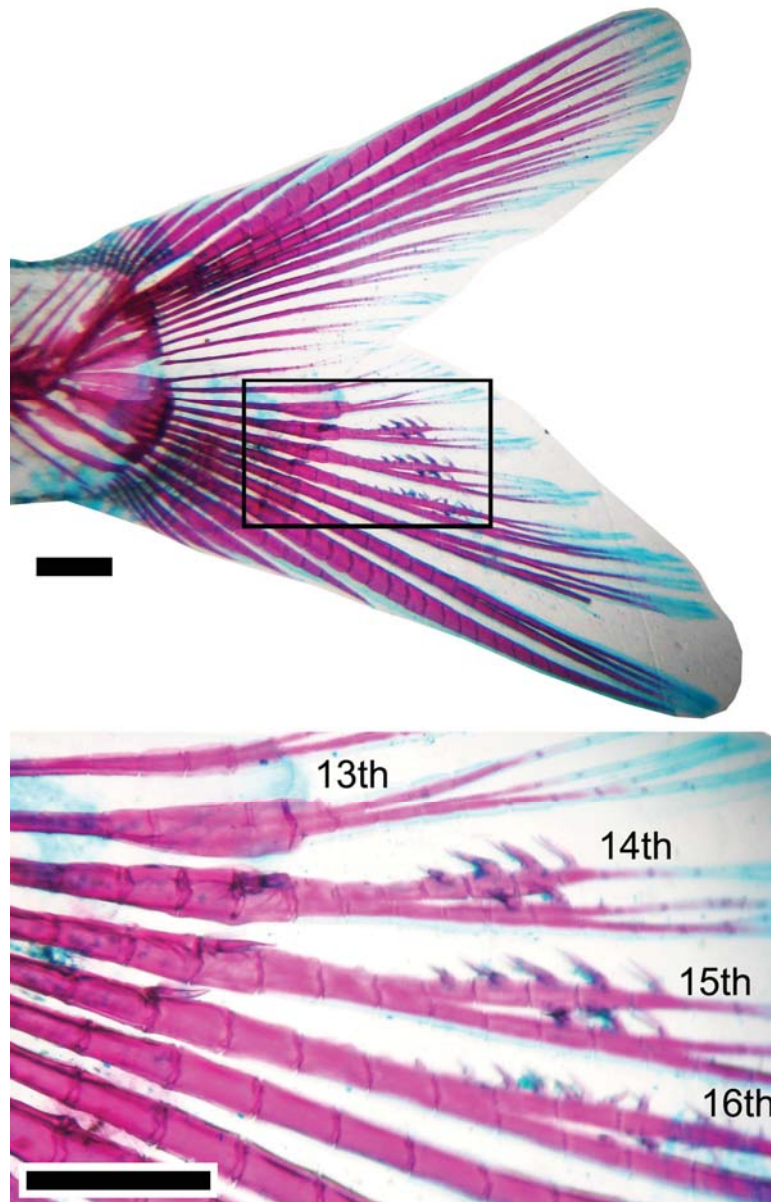


Fig. 11. Caudal fin hooks of a male specimen of “New Genus B” *Purus* n. sp.; MCP 41716, paratype, 23.6 mm SL. Scale bars = 1 mm.

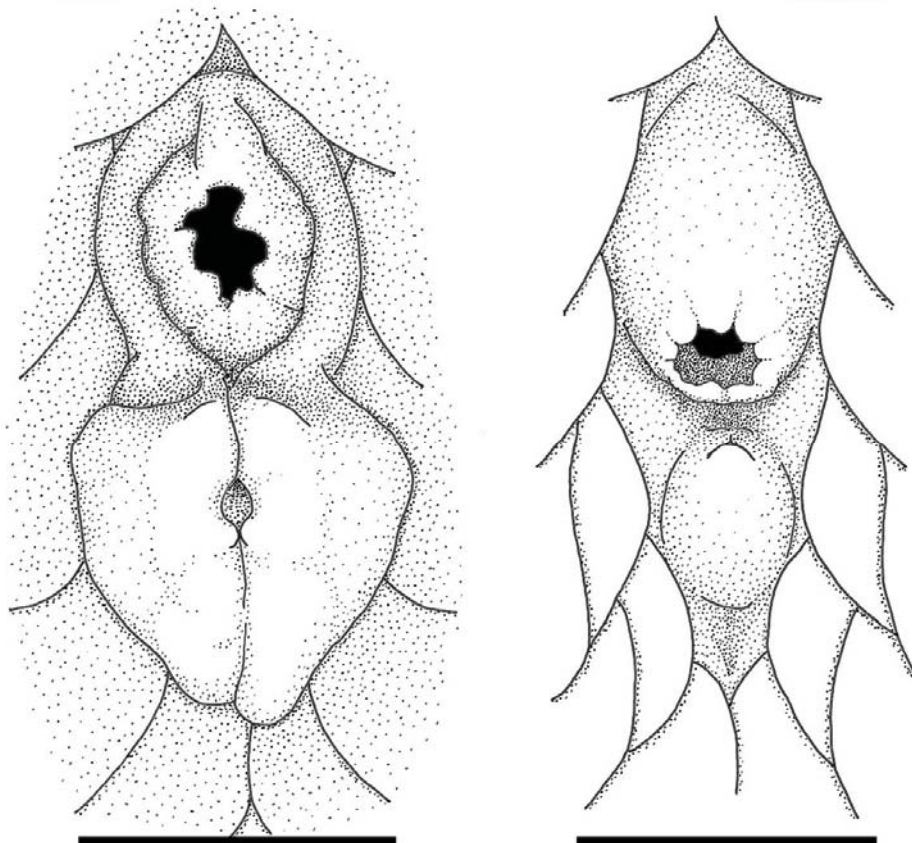


Fig. 12. Urogenital papillae area of female specimens of (a) “New Genus B” *Purus* n. sp., MCP 41716, paratype, 29.0 mm SL; and (b) *Serrapinnus calliurus*, MCP 19414, 35.2 mm SL. Scale bars = 1 mm.



Fig. 13. “New Genus C” Napo n. sp. **(a)** MCP uncatalogued, male, holotype, 25.3 mm SL and **(b)** ANSP 116449, paratype, female, 27.6 mm SL; both from Peru, Huanucu, vicinity of Tingo Maria, río Rondos, tributary of río Monzon.

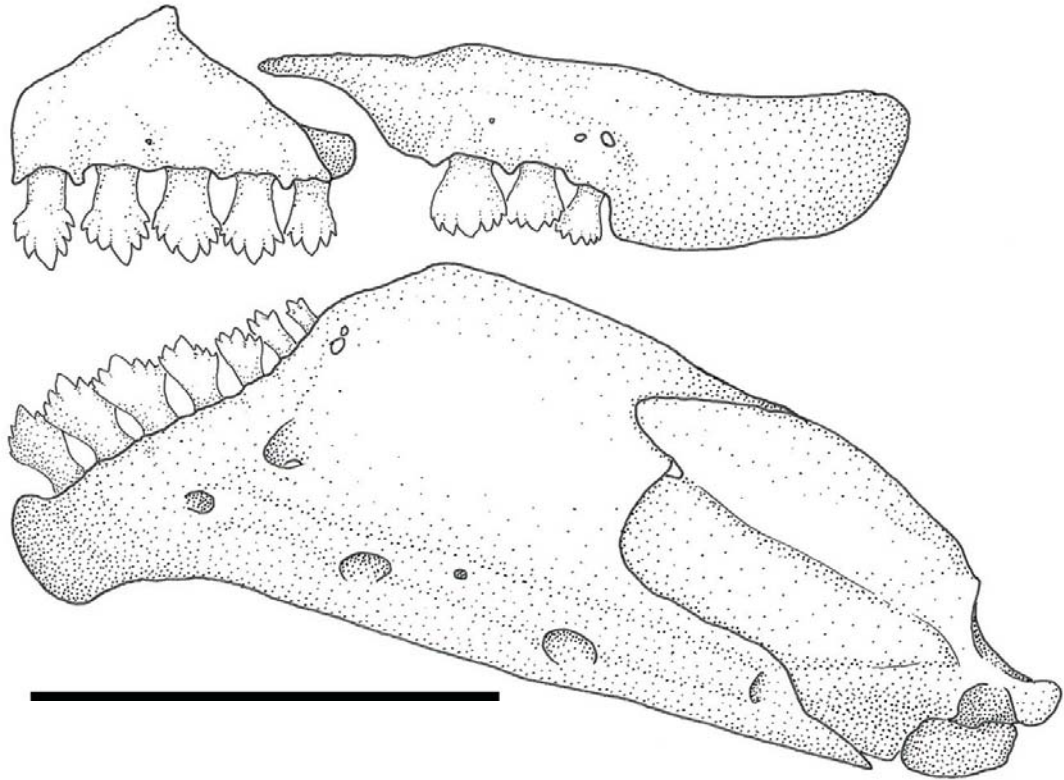


Fig. 14. Dentition and jaws morphology of “New Genus C” *Napo n. sp.*; ANSP 149671, paratype, 26.3 mm SL. Scale bar = 1 mm.



Fig. 15. “New Genus C” *Leticia* n. sp. **(a)** MCP uncatalogued, male, holotype, 25.3 mm SL and **(b)** ROM ICH 56384, paratype, female, 26.6 mm SL; both from Colombia, rio Amazonas, 5-10 mi upstream from Leticia, lakes and pepper farm.

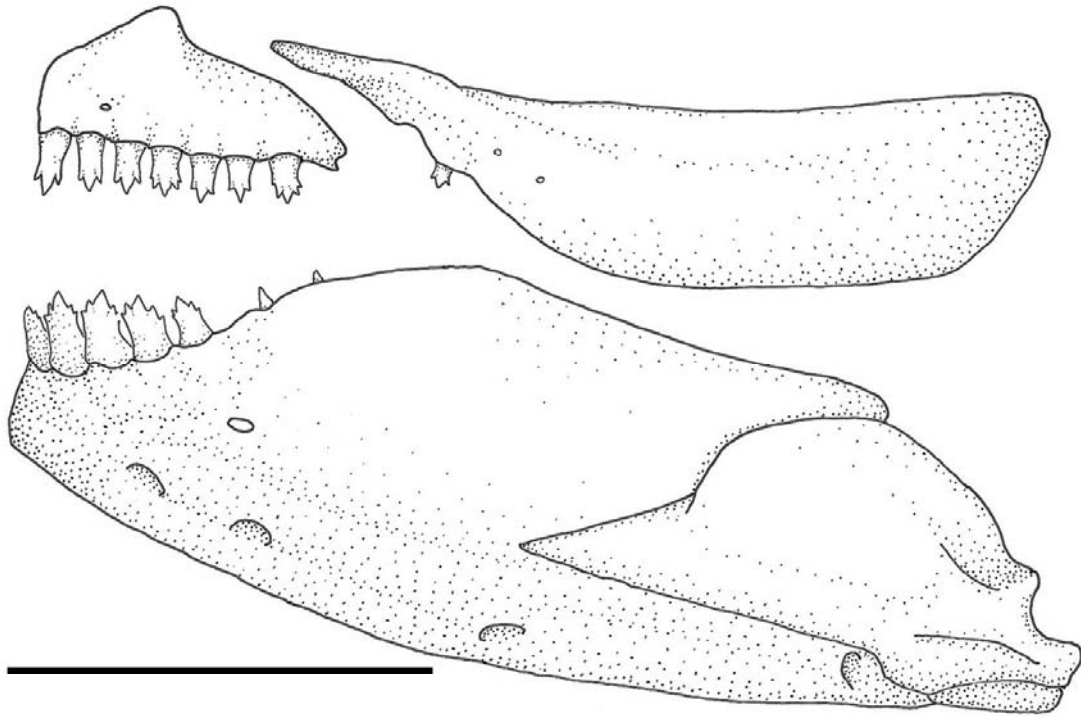


Fig. 16. Dentition and jaws morphology of “New Genus C” *Leticia* n. sp.; ROM ICH 56384, paratype, 26.2 mm SL. Scale bar = 1 mm.



Fig. 17. “New Genus C” Yurimaguas n. sp. **(a)** MCP uncatalogued, male, holotype, 23.1 mm SL and **(b)** CAS 71733, paratype, female, 25.2 mm SL; both from Peru, Departamento de Lore, río Amazonas, creek in forest inland from Yurimaguas.

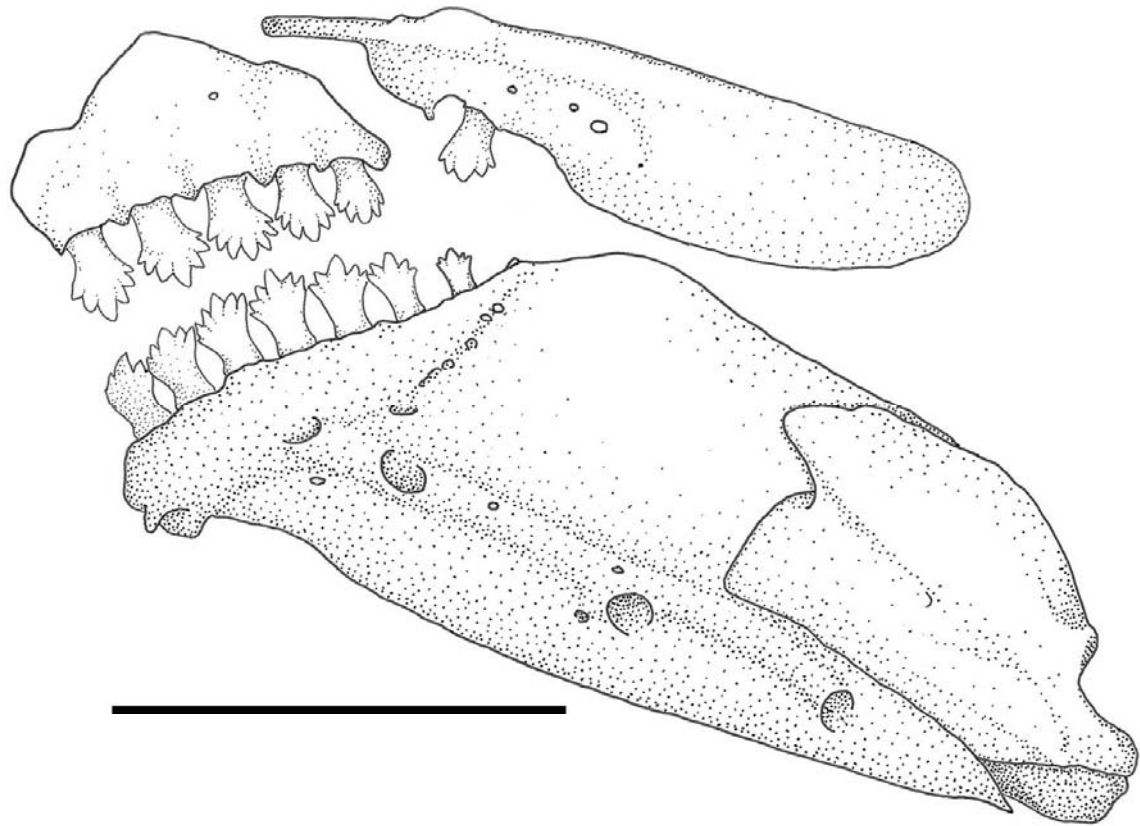


Fig. 18. Dentition and jaws morphology of “New Genus C” *Yurimaguas* n. sp.; CAS 71733, paratype, 23.4 mm SL. Scale bar = 1 mm.

CAPÍTULO VI

Redescription of *Leptobrycon xinguensis* (Géry, 1972), new combination, and phylogenetic relationships and redefinition of *Leptobrycon* (Characiformes: Characidae: Aphyoditeinae)

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Abstract

Leptobrycon xinguensis, is redescribed, its geographical distribution updated, and its relationship among characid representatives is investigated through the methods of equal weighting parsimony and implied weighting parsimony based on a matrix of 365 morphological characters and 163 taxa. The analysis showed that *M. xinguensis* is closely related to *Leptobrycon jatuaranae*, and is herein transferred to the genus *Leptobrycon*. The subfamily Aphyoditeinae is further supported as monophyletic, including (*Microschemobrycon* (*Aphyocharacidium* + *Axelrodia*) (*Aphyodite* (*Parecbasis* + *Leptobrycon*))).

Resumo

Macropsobrycon xinguensis, é redescrito, sua distribuição geográfica é atualizada, e sua relação com outros representantes de Characidae é investigada através do método de parcimônia sem pesagem e de pesagem implícita, com base em uma matriz de 365 caracteres morfológicos e 163 táxons. A análise mostra que *M. xinguensis* é proximamente relacionado com *Leptobrycon jatuaranae*, e é aqui transferido para o gênero *Leptobrycon*. A subfamília Aphyoditeinae é corroborada como monofilética, incluindo (*Microschemobrycon* (*Aphyocharacidium* + *Axelrodia*) (*Aphyodite* (*Parecbasis* + *Leptobrycon*))).

Key words: *Aphyodite*, *Macropsobrycon*, Systematics, Implied weights.

Introduction

Macropsobrycon xinguensis Géry is a small freshwater fish that inhabits some of the rio Amazonas tributaries. The species was described by Géry (1973) in a revisionary study of the “Aphyoditeina” species from the Amazon basin, placing his new species in the genus *Macropsobrycon* Eigenmann, a monotypic genus previously erected to host *Macropsobrycon uruguayanae* Eigenmann. Géry defined his decision as a “conservative solution”, taken “provisorily”, once both species share some morphological characters like feeble teeth, toothless maxilla, and lateral line incompletely pored; but also several differences: the absence of muscular hiatus in the pseudotympanum area, the scaled caudal-fin lobes, the tricuspid teeth (*vs.* conical in *M. uruguayanae*), the position of the dorsal-fin in front of mid-body, the number of branched anal-fin rays (17-18 *vs.* 19-22 in *M. uruguayanae*), the number of pored lateral line scales (8 *vs.* 5-6 in *M. uruguayanae*), and the black caudal-fin color pattern.

The relationship of the *Macropsobrycon* species with the remaining one-tooth-row small characids was non-cladistically hypothesized in several subsequent works (Eigenmann, 1915; Géry, 1960, 1965, 1972, 1973 and 1977) as detailed in Jerep & Malabarba (*in press*), and in all of these works the genus was to some extent considered related to the genera *Aphyodite* Eigenmann, *Brittanichthys* Géry, *Leptobrycon* Eigenmann, *Megalamphodus* Eigenmann, *Parecbasis* Eigenmann, and/or *Thrissobrycon* Böhlke, mainly due to the presence of small teeth with few cusps, and of a wide and usually toothless maxilla.

In the phylogenetic definition of Cheirodontinae *sensu stricto*, Malabarba (1998) concluded that *Macropsobrycon xinguensis* was not a Cheirodontinae, while *Macropsobrycon uruguayanae*, the type species of the genus, was kept as a Cheirodontinae for presenting the main synapomorphies of the subfamily, and that consequently the two species of *Macropsobrycon* were until then artificially grouped. *Macropsobrycon xinguensis* was considered species *incertae sedis* in Characidae, as well as the genera *Aphyodite*, *Brittanichthys*, *Leptobrycon*, *Megalamphodus*, *Parecbasis*, and *Thrissobrycon* mentioned above, since they did not present all of the cheirodontine synapomorphies (Malabarba, 1998; Reis *et al.*, 2003).

No phylogenetic analysis was performed with these *incertae sedis* genera or species until Mirande (2009, 2010). Among the aforementioned genera, *Aphyodite* and *Parecbasis* were included in his analysis and were classified as integrants of the

Aphyoditeinae, along with *Aphyocharacidium* Géry, *Axelrodia* Géry, and *Microschemobrycon* Eigenmann. Although not included in the analysis, the genera *Leptobrycon*, *Oxybrycon* Géry, and *Tyttobrycon* Géry were also considered Aphyoditeinae integrants, while *Brittanichthys* and *Thrissobrycon* remained classified as *incertae sedis* taxa in Characidae, and *Macropsobrycon* was treated as a Cheirodontinae.

The only systematic work including both *Macropsobrycon* species was developed by Javonillo *et al.* (2010), in his phylogenetic study of the major Characidae lineages inferred with molecular data. In this analysis *Macropsobrycon* was further corroborated as non-monophyletic. *Macropsobrycon xinguensis* was found as sister group of *Hyphessobrycon herbertaxelrodi* Géry, within a large clade hosting several *incertae sedis* genera, while *M. uruguayanae* was found within the Cheirodontinae clade. No representative of the Aphyoditeinae was included in his analysis, keeping uncertain the relationship of *M. xinguensis* with the remaining aphyoditeine genera.

In the present work we redescribe and investigate phylogenetically the relationships of *M. xinguensis* within Characidae.

Material and Methods

Counts and measurements were taken according to Fink & Weitzman (1974), as possible on the left side of the specimens. Measures were taken point-to-point straight-line with a 0.01 precision caliper. The head length measure is defined as the distance between the tip of the snout and the posterior margin of subopercle (Bührnheim & Malabarba, 2006). Total vertebrae number includes the four vertebrae of the Weberian apparatus, and the terminal “half centrum” (Malabarba & Weitzman, 1999). The gill rakers were counted from the first branchial arch, and the gill raker in the junction of the ceratobranchial and the epibranchial was counted referred to the epibranchial count. The counts of vertebrae, supraneurals, teeth, and gill rakers were based on radiographs and cleared and stained (c&s) specimens following Taylor & van Dyke (1985) protocol. Scanning Electron Microscope (SEM) images were obtained from the jaws. Drawings of the anal fin and neurocranium were prepared in a stereomicroscope with camera lucida.

The nomenclature of suprageneric groups corresponds to Miranda (2010) classification. Myological nomenclature follows Winterbottom (1974) and Datovo &

Bockmann (2010), and osteological nomenclature Weitzman (1962), with the modifications of Zanata & Vari (2005).

Material from the following institutions were analyzed in this study: ANSP - Academy of Natural Sciences of Philadelphia, Philadelphia, USA; CAS - California Academy of Sciences, San Francisco, USA; FMNH - Field Museum of Natural History, Chicago, USA; MCP - Museu de Ciências e Tecnologia, Porto Alegre, Brazil; MZUSP - Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; SU – Stanford University, Palo Alto, USA; and USNM - National Museum of Natural History, Smithsonian Institution, Washington D.C., USA. Abbreviations given along with the number of specimens are the following: m - morphometric and meristic.

Systematic analysis. In order to investigate the relationship of the *incertae sedis* species *Macropsobrycon xinguensis* among characids, a reanalysis of the Miranda (2010) matrix of characters was performed with its inclusion. The species *Macropsobrycon uruguayanae* and *Leptobrycon jatuaranae* were also included in the analysis due to their morphological similarity to *M. xinguensis*, and to assess previous hypothesis quoting *M. uruguayanae* as a Cheirodontinae and previous untested hypothesis placing *L. jatuaranae* as an Aphyoditeinae integrant (Miranda 2009, 2010). Weighted parsimony analysis were employed in the software TNT version 1.1 (Goloboff, Farris & Nixon, 2008), through the methods of new technology described in Nixon (1999) and Goloboff (1999), and discussed based on the Hennig (1966) concepts. The weighted analysis under implied weights (IW) method followed Goloboff (1993) and Miranda (2009). The implied weighted analysis was performed to estimate the relationships of the taxa herein included with the remaining characids, and also, to assess the consistency and reliability of the synapomorphies and clades proposed by Miranda (2009, 2010) for the Aphyoditeinae, with the addition of more taxa in his matrix. The analyses were set for 100 iterations and 100 replications with the methods tree-fusing, sectorial search and tree-drifting set as the default parameter presented by the software. The “k”-values used in the IW analysis were calculated according to Miranda (2009). Characters are numbered following Miranda (2010). The synapomorphies and apomorphies quoted for clades and terminal taxa in the paper are the synapomorphies and apomorphies present in the strict consensus from the most stable trees from the implied weighted analysis, summarizing the phylogenetic hypotheses presented by those trees.

Results

Systematics of *Leptobrycon xinguensis* new combination. In the present analysis, *Macropsobrycon xinguensis* was found to be sister group of *Leptobrycon jatuaranae*, and belonging to a monophyletic Aphyoditeinae, as redefined by Mirande (2009, 2010). *Macropsobrycon xinguensis* is thereafter referred as *Leptobrycon xinguensis*. *Macropsobrycon uruguayanae* was found to be integrant of the Cheirodontinae, as previously hypothesized by Malabarba (1998), and further comments on this species relationships are given in Jerep & Malabarba (in manuscript, Chapter I) and will not be repeated here.

The IW trees obtained from “k”-value equal to 12.5722 were found to be more stable than the trees resulted from the remaining “k”-values. The data concerning all the IW trees obtained from different “k”-values are shown in the Table 2. The IW analysis with “k”-value 12.5722 resulted in a total of two trees with 2201 steps (CI = 0.17; RI = 0.66). The strict consensus from those trees has 2203 steps (CI = 0.17; RI = 0.66), and represents the phylogenetic hypothesis in which the discussion is focused and all the synapomorphies and characters indexes (CI and RI) are described (Fig. 1). The character states for the species herein included in the analysis is presented in the Appendix I. The complete strict consensus tree is showed in the Appendix II. The following list of synapomorphies is restricted to the Aphyoditeinae and major clades. The reanalysis of the Mirande (2010) database with the inclusion of three taxa brought more resolution to the relationship among the aphyoditeine representatives. Some of the apomorphies defining the Aphyoditeinae and internal clades have changed in this analysis comparing to the original analysis of Mirande (2010) and are thereafter referred as “Synapomorphies only found in Mirande (2010)” and “Synapomorphies only found in the present work”.

Monophyly of Aphyoditeinae (Fig. 1, Clade A)

1. Eight or more teeth on second premaxillary row (Ch. 130: 1; ci = 0.12).
2. Size and number of anterior dentary teeth eight or more small and slender teeth in front of dentary (Ch. 142: 1; ci = 0.25).
3. Four or fewer supraneurals (Ch. 280: 0; ci = 0.07).

Synapomorphies only found in Mirande (2010):

4. Dorsal margin of lateral ethmoids aligned (Ch. 16: 0; ci = 0.14).
5. Canal of lateral line on caudal-fin membrane absent (Ch. 92: 0; ci = 0.05).

Synapomorphies only found in the present work:

6. Anterior convergence of ventral diverging lamellae with nasal septum of mesethmoid absent, or confluent near anterior end of nasal septum (Ch. 31: 0; ci = 0.09).

Autapomorphies of *Microschemobrycon casiquiare*

1. Absence of epiphyseal branch of frontoparietal laterosensory canal (Ch. 84: 1; ci = 0.33).
2. Absence of contact between ectopterygoid and anterodorsal region of quadrate (Ch. 162: 1; ci = 0.10).
3. Well developed transverse process of third vertebra neural arch, surpassing anterior margin of tripus (Ch. 219: 1; ci = 0.06).
4. *Radii* of scales converging at focus (Ch. 322: 1; ci = 0.12).

Autapomorphy only found in the present work:

5. Three or four dorsal-fin rays articulating with first dorsal pterygiophore (Ch. 266: 1; ci = 0.06).

Monophyly of *Aphyocharacidium bolivianum* and *Axelrodia lindeae* (Fig. 1, Clade B)

1. Presence of a large foramen on pterospheoid (Ch. 43: 1; ci = 1.0).
2. Anterior tip of branchiostegal rays slender (Ch. 214: 1; ci = 0.33).

Synapomorphy only found in Mirande (2010):

3. Fourth infraorbital longer dorsoventrally than longitudinally (Ch. 67: 1; ci = 0.04).

Synapomorphy only found in the present work:

4. Bony hooks on base of pelvic-fin rays of adult males as numerous as on segmented portion of rays (Ch. 313: 1; ci = 0.12).

Autapomorphies of *Aphyocharacidium bolivianum*

1. Anterior convergence of ventral diverging lamellae with nasal septum of mesethmoid confluent at posterior end of nasal septum (Ch. 31:1; ci = 0.09).
2. Presence of lateral ridge of anguloarticular (Ch. 107: 1; ci = 0.16).
3. Presence of second row of dentary teeth (Ch. 143: 0; ci = 0.09).
4. Presence of bony hooks on first pelvic-fin ray of adult males (Ch. 315: 1; ci = 0.11).

Synapomorphy only found in the present work:

5. Lateral line complete (Ch. 91: 0; ci = 0.05).

Autapomorphies of *Axelrodia lindeae*

1. Contact between frontals anteriorly to frontal fontanel absent (Ch. 21: 0; ci = 0.04).
2. Ventral coverage of third infraorbital not reaching horizontal arm of preopercle, at least anteriorly (Ch. 64: 1; ci = 0.03).
3. All premaxillary, maxillary, and dentary teeth conical, caniniform or mamilliform (Ch. 118: 0; ci = 0.12).
4. Conical, a single cusp maxillary teeth (Ch. 138: 0; ci = 0.09).
5. Dentary anterior teeth internally displaced, with dentary forming an anterior ridge (Ch. 146: 1; ci = uninformative).
6. Bony lamellae dorsal to second and third basibranchials absent (Ch. 184: 0; ci = 0.05).
7. Bony lamella dorsal to fourth basibranchial absent (Ch. 185: 1; ci = 0.06).
8. One row of gill rakers on second ceratobranchial (Ch. 193: 0; ci = 0.04)
9. Denticles on gill rakers absent (Ch. 201: 1; ci = 0.11).
10. Fifth ceratobranchial dentigerous plate rounded, with a posterior notch (Ch. 204: 0; ci = 0.14).
11. Six or less branched pelvic-fin rays (Ch. 258: 0; ci = 0.05).
12. Ventral procurrent caudal-fin rays of adult males laminar (Ch. 301: 1; ci = 0.50).
13. Ventral procurrent caudal-fin rays of adult males projected ventrally from peduncle musculature and skin (Ch. 303: 1; ci = 0.33).
14. Bony hooks on last pelvic-fin ray of adult males as numerous as in other rays (Ch. 314: 1; ci = 0.14).

Synapomorphy only found in the present work:

15. Foramen in posterior region of metapterygoid in form of incomplete arch, bordered posteriorly by hyomandibula (Ch. 168: 02; ci = 0.20).

Monophyly of *Aphyodite grammica*, *Parecbasis cyclolepis*, *Leptobrycon jatuaranae*, and *Leptobrycon xinguensis* (Fig. 1, Clade C)

1. Length of sphenotic spine projected ventrally to articulation between sphenotic and hyomandibular (Ch. 10: 1; ci = 0.10).
2. Up to three maxillary teeth (Ch. 136: 0; ci = 0.05).

3. Ten or fewer gill rakers on first hypobranchial and ceratobranchial (Ch. 196: 0; ci = 0.03).
4. Scales covering one third of caudal-fin lobes (Ch. 328: 1; ci = 0.10).

Autapomorphies of *Aphyodite grammica*

1. Absence of contact between frontals anteriorly to frontal fontanel (Ch. 21: 0; ci = 0.04).
2. Fourth infraorbital absent, fused with fifth infraorbital, or reduced and bordered posteriorly by third and fifth infraorbitals (Ch. 66: 1; ci = 0.07).
3. Process of scapula forming anterior border of scapular foramen absent (Ch. 244: 1; ci = 0.10).
4. Posterior attachment of section A1 from *adductor mandibulae* restricted or almost restricted to horizontal arm of preopercle (Ch. 332: 1; ci = 0.11).

Synapomorphy only found in Mirande (2010):

5. Ventral coverage of third infraorbital not reaching horizontal arm of preopercle, at least anteriorly (Ch. 64: 1; ci = 0.03).

Monophyly of *Parecbasis cyclolepis*, *Leptobrycon jatuaranae*, and *Leptobrycon xinguensis* (Fig.1, Clade D)

1. Presence of lateral ridge of anguloarticular (Ch. 107: 1; ci = 0.16).
2. Maxillary teeth absent (Char. 134: 0; ci = 0.06).
3. Sixteen or more gill rakers on first hypobranchial and ceratobranchial (Ch. 195: 0; ci = 0.06).

Autapomorphies of *Parecbasis cyclolepis*

1. Length of supraoccipital spine projected dorsal to, at least, middle length of neural complex of Weberian apparatus (Ch. 53: 0; ci = 0.05).
2. Two rows of gill rakers on first ceratobranchial (Ch. 192: 1; ci = 0.05).
3. Presence of laminar bony ridge on dorsal margin of abdominal ribs (Char. 224: 1; ci = 0.33).
4. Presence of “type II” transitional vertebrae, with haemal canal but without haemal spine (Ch. 229: 0; ci = 0.05).
5. Relative position of dorsal-fin anterior insertion anterior or at vertical through pelvic-fin origin (Ch. 265: 0; ci = 0.08).

6. Bony lamellae associated to supraneurals wider than main axis of supraneurals (Ch. 282: 1; ci = 0.05).

Synapomorphies only found in Mirande (2010):

7. Lateral coverage of dilator fossa by sixth infraorbital almost complete, at least in its ventral border (Ch. 69: 0; ci = 0.07).

8. Dorsal end of laterosensory canal of preopercle overlapping anterodorsal corner of opercle, in lateral view (Ch. 82: 1; ci = 0.08).

9. Presence of lateral ridge of anguloarticular (Ch. 107: 1; ci = 0.16).

10. Absence of maxillary teeth (Ch. 134: 0; ci = 0.06).

11. Palatine approximately half length of ectopterygoid, or less (Ch. 172: 0; ci = 0.05).

12. Sixteen or more gill rakers on first hypobranchial and ceratobranchial (Ch. 195: 0; ci = 0.06)

Synapomorphies only found in the present work:

13. Dorsal expansion of rhinosphenoid present (Ch. 48: 0; ci = 0.14).

14. Lateral line complete (Ch. 91: 0; ci = 0.05).

Monophyly of *Leptobrycon* (Fig. 1, Clade E)

1. Slender and developed mesethmoid anterior process between the premaxillae (Ch. 27: 0; ci = 0.20).

2. Trigemino-facialis foramen narrow as a cleft with sphenotic almost excluded from its margin (Ch. 42: 1; ci = 0.50).

3. Posterior extent of third infraorbital relatively reduced, angle of preopercle covered partially by fourth infraorbital (Ch. 65: 1; ci = 0.20).

4. Maxilla reaching posterior end of Meckelian cartilage (Ch. 100: 0; ci = 0.16).

5. Posteriormost dentary teeth separated by gaps bigger than their base width (Ch. 147: 1; ci = 0.16).

6. Presence of a foramen on the articular condyle of the quadrate (Ch. 149: 1; ci = 0.08).

7. One rows of gill rakers on second ceratobranchial (Ch. 193:0; ci = 0.04).

8. One row of gill rakers on first epibranchial (Ch. 203: 0; ci = 0.33)

9. Less than 17 branched anal-fin rays (Ch. 287: 0; ci = 0.10).

10. Contact between dorsal margin of *adductor mandibulae* and ventral margin of *dilator operculi* absent (Ch. 335: 0; ci = 0.08).

Autapomorphies of *Leptobrycon jatuaranae*

1. Bony hooks on first pelvic-fin ray of adult males (Ch. 315: 1; ci = 0.11).
2. Scales covering only the base caudal-fin lobes (Ch. 328: 0; ci = 0.10).

Autapomorphies of *Leptobrycon xinguensis*

1. Less than eight teeth in inner premaxillary row (Ch. 130: 0; ci = 0.12).
2. Fossa for inner row of replacement premaxillary teeth absent (Ch. 133: 0; ci = 0.20).
3. Foramen in the posterior region of the metapterygoid as an incomplete arch posteriorly bordered by the hyomandibula (Ch. 168: 2; ci = 0.20).
4. Absence of bony hooks on the pelvic fins (Ch. 309: 1; ci = 0.07).

***Leptobrycon* Eigenmann, 1915**

Type species: *Leptobrycon jatuaranae* Eigenmann, 1915: 46; by original designation.

Leptobrycon Eigenmann, 1915: 16 [original description; figured; type locality Jatuarana, Brazil]. -Böhlke, 1953: 168 [comparison to *Thrissobrycon*]. -Géry, 1960: 3 [relationships to *Parecbasis*, *Aphyodite*, *Macropsobrycon*, and *Thrissobrycon*]. -Géry, 1965: 18 [listed in Aphyoditeini]. -Géry, 1972: 16-17 [listed in Aphyoditeini]. -Géry, 1973: 81 [listed in Aphyoditeina]. -Géry, 1977: 594 [in key to Aphyoditeina genera and species]. -Malabarba, 1998: 230 [cited as genera once assigned to Cheirodontinae]. -Lima *et al.*, 2003: 144 [listed as genera *incertae sedis* in Characidae]. -Zanata & Akama, 2004: 48 [presence of a ceratohyal foramen]. -Mirande, 2009: 7 [listed in Aphyoditeinae, with question mark]. -Mirande, 2010: 528 [in Aphyoditeinae, with question mark].

Diagnosis. See list of synapomorphies given above.

Distinguishing characters. Although not found as synapomorphies for *Leptobrycon*, the following combination of characters can be further useful in distinguishing the genus from all characids: one tooth row on the premaxilla with 6-14 conical or tricuspid teeth; maxilla wide and toothless; incompletely perforated lateral line; absence of a muscular hiatus on the pseudotympanum area; first gill arch bearing 17-20 gill rakers on

the lower portion (see Discussion for detailed description and comparisons of these characters among others characids).

***Leptobrycon xinguensis* (Géry, 1973), new combination**

Figs. 2-4b, 5, 7a

Macropsobrycon xinguensis Géry, 1973: 106 [original description; holotype, head and dentition figured; type locality rio Suia Missu, Mato Grosso, Brazil, rio Xingu drainage]. -Géry, 1977: 594 [in key to Aphyoditeina genera and species]. - Malabarba, 1998: 200 [cited as integrant of Cheirodontinae *sensu lato*]. -Reis *et al.*, 2003: 104 [listed as species *incertae sedis* in Characidae].

Diagnosis. See list of synapomorphies given above.

Distinguishing characters. The combination of a peculiar black blotch in the base of the caudal-fin, the incomplete lateral line, and the presence of one tooth row on the premaxilla, distinguishes *L. xinguensis* from all characids species. Furthermore, *Leptobrycon xinguensis* can be distinguished from *L. jatuaranae* by the higher number of branched anal-fin rays (14-18 vs. 12-13), and the lower number of teeth in the premaxilla (6-9 vs. 11-13).

Description. Morphometrics given in Table 1. Body slightly elongate and compressed, deeper at dorsal-fin origin. Dorsal profile straight from snout tip to end of supraoccipital process, slightly convex from that point to dorsal-fin origin, straight to slightly convex at dorsal-fin base, convex from that point to adipose-fin origin. Ventral profile convex from snout to pelvic-fin insertion, straight or somewhat concave until anal-fin origin, straight to slightly convex along anal-fin base. Caudal-peduncle profile slightly concave dorsally and ventrally. Snout short, mouth terminal slightly superior to horizontal line projected through pupil dorsal border.

Premaxilla slender, one tooth row with 2(3), 3(1) bigger tricuspid teeth and 4(1), 5(2), 6(1) conical teeth decreasing in size posteriorly; one specimen with symphyseal tooth bearing four cusps. Teeth not aligned, third and fourth slightly placed outwards. Premaxillary ascending process pointed distally. Maxilla toothless, broad, posteriorly angulated with distal tip reaching line of orbit anterior edge. Dentary with 2(1), 3(2), or

5(1), tricuspid teeth followed by 8(2), 9(1), 10(1) conical teeth; first four bigger with similar size, last ones smaller decreasing in size posteriorly (Fig. 3).

Dorsal-fin insertion slightly posterior to vertical through middle of the body, distal profile round. Dorsal-fin rays ii, 8(2), 9(20), 10(1). Adipose-fin origin at line through last anal-fin ray insertion. Anal-fin origin posterior to last dorsal-fin ray insertion; anterior rays longer than posterior ones; distal profile more convex. Anal-fin rays iii(15), iv(8), 14(1), 15(1), 16(10), 17(10), 18(1); last unbranched until fifth anal-fin branched rays of mature or maturing males bearing two to six small and retrorse hooks (Fig. 4b). Hooks placed at distal length of anal-fin rays, attached at posterior margin, dorsally bent, and directed to anal-fin base. One or two hooks per ray segment. Pectoral-fin rays i,8(1), 10(4), 11(17), 12(1); longest rays not reaching pelvic-fin insertion. Pelvic-fin insertion slightly anterior to line of dorsal-fin origin. Pelvic-fin rays i,7 (22), 8(1); not bearing hooks. Caudal fin forked, dorsal and ventral lobes similar in size, 19(23) principal rays; 4(1), 5(3), 6(7), 7(9), 8(3) dorsal procurrent caudal-fin rays; and 5(2), 6(5), 7(12), 8(4), ventral procurrent caudal-fin rays.

Lateral line incomplete, with 7(7), 8(6), 9(3) pored scales. Total scales at lateral line 28(1), 29(1), 30(7), 31(5), 32(4) scales. Scale rows between dorsal-fin insertion and lateral line 5 (22); scale rows between lateral line and pelvic-fin insertion 3(22). Predorsal scales 9(7), 10(15), 11(1); postdorsal scales 8(7), 9(11), 10(5); scale rows around caudal peduncle 12(7), 14(17). One row of four scales covering base of anteriormost anal-fin rays, missing in most specimens. Caudal-fin lobes scaled. Scales at caudal-fin lobes smaller than body scales, placed at proximal third to proximal half of their length.

Gill rakers on first branchial arch 3(1), 4(3) on hypobranchial, 15(2), 16 (2) on ceratobranchial, 7(1), 8(1), 9(2) on epibranchial. Gill arches from first branchial arch bearing denticles along all its length; ceratobranchial rakers from first branchial arch three times longer than ceratobranchial rakers from remaining branchial arches. Gill rakers from remaining branchial arches not bearing denticles. Pseudotympanum as thin muscle layer between first and second pleural ribs, evidenced as concavity filled with adipose tissue. Infraorbital 1-6. Supraneurals 4(4). Precaudal vertebrae 12(3), 13(1); caudal vertebrae 15(1), 16(3). Spermatozoa aquasperm like (Fig. 5).

Color in alcohol. Overall body color varying from light yellowish to pale brownish on older specimens (Fig. 2). Head black to dark brownish dorsally between transversal line

through anterior edge of orbits and posterior tip of supraoccipital process. Dark melanophores surrounding nares, lips, dorsal margin of maxilla, and anterior margin of orbit. High concentration of melanophores on pseudotympanum region, but not forming a conspicuous humeral spot. Dorsal and dorsolateral portion of body with reticulated pattern due to higher concentration of melanophores at posterior margin of scales. Pores at lateral line scales surrounded by dark melanophores. Lateral side of body with scattered melanophores, except at abdominal region. Thin and dark lateral band extending posteriorly from humeral region to almost end of caudal peduncle. On older specimens this band starts just anterior to vertical line of dorsal-fin origin. Caudal peduncle spot absent, instead of that a light and unpigmented area, 1.5 scale wide and 4 scale rows deep. Caudal region along lateral side of body with few melanophores distributed along miosepta of *hypaxialis* muscles. Caudal fin with round black blotch at proximal portion, extending over all length of middle caudal-fin rays and almost half length of dorsal and ventral caudal-fin lobes. On older specimens the caudal-fin blotch keeps its intensity at the middle caudal-fin rays, but becomes fainter at upper and lower caudal-fin lobes. Remaining fins hyaline with scattered melanophores at interradial membrane following margins of rays.

Color in life. Overall body color pattern yellowish to whitish (Fig. 2c). Head and body ventral region overall color pattern silvery. Presence of golden, green and orangish hue at opercular area, parietal bones region and lateral band of body. Distal border of caudal blotch posteriorly margined by a light whitish narrow band at dorsal and ventral lobes. Black caudal blotch and melanophores distribution pattern of head, body and fins as described at color in alcohol.

Sexual dimorphism. Mature males can be differentiated from adult females and juveniles by the presence of hooks on first unbranched and anterior five branched anal-fin rays (Fig. 4b). Spermatozoa aquasperm like (Fig. 5).

Distribution. Records of *Leptobrycon xinguensis* are known from the rio Xingu and rio Tapajós basins (Fig. 6).

Discussion

Leptobrycon xinguensis is herein retreated from *Macropsobrycon* Eigenmann, 1915 and placed in *Leptobrycon* due to the presence of several synapomorphies shared with *Leptobrycon jatuaranae*, and with the genera actually included in the Aphyoditeinae. *Leptobrycon xinguensis* also lacks several morphological characters that define cladistically the genus *Macropsobrycon*, the tribe Compsurini, and the subfamily Cheirodontinae (see Malabarba, 1998: 218), further rejecting previous assignment of the species to those taxa. The spermatozoa in *L. xinguensis* is nearly spherical, aquasperm like (Fig. 5), not sharing the typical introsperm like spermatozoa observed in *Macropsobrycon uruguayanae* or other compsurins (Oliveira *et al.*, 2008). The only character state diagnosing *Macropsobrycon* that is also found in *L. xinguensis* is the presence of conical and tricuspid teeth in the jaws, but this character is likely a result of convergence.

The genus *Leptobrycon* is characterized by a series of features shared between *Leptobrycon jatuaranae* and *L. xinguensis*. One of the synapomorphies of these species is the presence of the trigemino-facialis foramen narrow as a cleft, with sphenotic almost excluded from its margin (Ch. 42: 1). Among the examined species this character was only found in the *Leptobrycon* species and in the genus *Aphyocharax*. However the *Aphyocharax* and *Leptobrycon* are not closely related, and both genera belong to different subfamilies supported by very distinct characters (Mirande, 2010).

Leptobrycon xinguensis does not have any hooks, hypertrophied tissues or modified scales at the caudal-fin as observed in the genus *Macropsobrycon* and its type species, *M. uruguayanae*. The only secondary sexual dimorphism detected in *L. xinguensis* is the presence of hooks on the last unbranched and anterior five branched anal-fin rays (Fig. 4b). These hooks are surrounded by a whitish tissue, as commonly found on the fins of characid fishes bearing hooks (as discussed by Lima & Sousa, 2009). Although *Leptobrycon xinguensis* presents scales over the caudal fin lobes, they are not hypertrophied or associated with developed tissue. The scales are numerous, decrease in size posteriorly, and are arranged following the common pattern found in most of *Hemigrammus* and *Moenkhausia* species. Among the species of Aphyoditeinae, the presence of caudal-fin scales can only be found in *Aphyodite grammica* and *Parecbasis cyclolepis*, a relatively large species (until 80 mm SL, Lima *et al.*, 2003), that presents completely pored lateral line and two rows of teeth in the dentary, being easily diagnosed from the *L. xinguensis*.

Leptobrycon xinguensis presents one tooth row on the premaxilla bearing 6-9 tricuspid or conical teeth. These teeth are not perfectly aligned as seen in the Cheirodontinae, instead, the third and fourth teeth are slightly displaced outwards (Fig. 3a). Even the smallest analyzed specimen (MZUSP 91701, 12.4 mm SL) already presents the same tooth arrangement as the adults, bringing no evidence about the evolutionary origin of this tooth arrangement. Based on the fact that two or more tooth rows in the premaxilla is being found as plesiomorphic on former phylogenetic works on characids, Malabarba (1998: 203) presented three different putative non-homologous origins for the “apomorphic” state of one tooth row. Nonetheless, no information was found to designate whether the teeth arrangement present in *L. xinguensis* is a result of an incomplete merging of two tooth rows into one, or a reduction of the external tooth row with the remaining of two teeth not perfectly aligned.

Leptobrycon xinguensis presents a very single feeding apparatus among characids. Its single feeble tooth row in the premaxilla, a well developed broad and toothless maxilla, and the elongated and relatively numerous (15-16) gill rakers in the first ceratobranchial bearing denticles, indicate that this species is probably an open-water plankton-feeding fish. This hypothesis is supported by the fact that most of the specimens here analyzed were collected in this kind of habitat. A similar feeding apparatus is also found in *Brittanichthys* spp., *Leptobrycon jatuaranae*, *Macropsobrycon uruguayanae*, and *Thrissobrycon pectinifer*. *Brittanichthys* spp. and *M. uruguayanae* present around 13-14 gill rakers in the ceratobranchial and no denticles were found on them, while *L. jatuaranae* and *T. pectinifer* present a higher number of gill rakers (17) and also denticles along all their length, as seen in *L. xinguensis*. No denticles on gill rakers were observed in the aphyoditeine species *Aphyodite grammica* (13 gill rakers on the first ceratobranchial), *Microschemobrycon* sp. (8 gill rakers on the first ceratobranchial), and *Parecbasis cyclolepis* (11 gill rakers on the first ceratobranchial), although these species may have none or few teeth in the maxilla. Regardless the number of gill rakers, the species of *Leptobrycon* share the presence of one row of gill rakers on second ceratobranchial (Ch. 193: 0), and one row of gill rakers on first epibranchial (Ch. 203: 0).

Aphyodite and *Leptobrycon* are the genera of Characidae that better resembles *Leptobrycon xinguensis*. These genera were described by Eigenmann (1912 and 1915, respectively) to host *Aphyodite grammica* from middle Essequibo, British Guiana and

Leptobrycon jatuaranae from the Amazon basin. In addition to the similar pseudotympanum constitution and the already mentioned single row of feeble conical to tricuspid tooth in the premaxilla, and wide and toothless maxilla, *Aphyodite*, *L. jatuaranae* and *L. xinguensis* share the presence of an incomplete lateral line. Nevertheless, osteologically, these genera present very distinctive characters, like the shape and placement of the premaxilla and mesethmoid bones (Fig. 7). The premaxilla in the *L. xinguensis* is very similar to *L. jatuaranae*; it is slender and feebler than the *Aphyodite* premaxilla. Its ascending process is very distinct and narrowed distally, while it is short and wide in *Aphyodite* (Fig. 7). *Leptobrycon* and *Aphyodite* also possess very different mesethmoid bones. The slender and developed mesethmoid anterior process between the premaxillae of *Leptobrycon* (Ch. 27: 0) (Fig. 7), is a reversion of the short anterior process of the mesethmoid shared by the Cheirodontinae + Aphyoditeinae (clade 285). The mesethmoid bone is elongated, straightened and forms the anterior border of the cranium fontanel in the *L. xinguensis*, meanwhile in *Aphyodite*, it is short, wide and does not contact the cranium fontanel posteriorly, once the frontal bones contact each other anteriorly. Although *L. jatuaranae* presents a very similar premaxilla and mesethmoid bone shape to *L. xinguensis*, the mesethmoid bone also does not contact the cranium fontanel (Fig. 7), a state also shared by the Aphyoditeinae *Aphyocharacidium*, *Microschemobrycon* and *Parecbasis*.

The pseudotympanum in *Leptobrycon* is not a muscular hiatus as observed in Cheirodontinae and other Characidae representatives like *Rhoadsia*, some miniature species as *Priocharax*, *Tyttobrycon*, *Xenurobrycon*, and the Characinae *Charax*, *Phenacogaster*, and *Roeboides*. As already stated by Malabarba (1998: 200), the pseudotympanum in *L. xinguensis* (*Macropsobrycon xinguensis* in that work), as well as in some other characids (*e.g. Aphyodite grammica*) is constituted by a reduction of the muscular layer between the first and second pleural ribs. In that region, the muscle *obliquus inferioris* is absent, and the *obliquus superioris* muscle layer is thinner in comparison to the same muscle in others regions of the body, which results in a concavity usually filled up with adipose tissue. Among the Aphyoditeinae (*sensu* Mirande, 2009; 2010), the same kind of pseudotympanum is found in *Aphyodite*, *Parecbasis* and in the former integrant of the group *Thrissobrycon*; the remaining genera present a muscular hiatus, sometimes very small and anterodorsally placed, as observed in *Oxybrycon* sp.

Regardless the autapomorphies presented for each of the *Leptobrycon* species, these species can also be distinguished by the absence of the fronto-parietal branch of the laterosensory canal in *Leptobrycon jatuaranae* (Fig. 7), and the low number of anal-fin rays (iii+11), although the presence of less than 17 branched anal-fin rays (Ch. 287: 0) was found to be a synapomorphy of the genus. Another important difference is the very remarkable color pattern that *L. xinguensis* owns in the caudal fin. As remarked by Géry (1973, 1977), this pattern (see color description section) is very similar to the color pattern shared by the *Moenkhausia oligolepis* species complex (Costa, 1994) in the caudal region. Another character shared between the *Leptobrycon* and the *M. oligolepis* species complex is the presence of scales covering the caudal-fin lobes; however, the *L. xinguensis* does not present the remaining non-cladistic characters that define *Moenkhausia*, like the completely pored lateral line and two tooth rows at the premaxilla. Among the Aphroditeinae species only *Parecbasis cyclolepis* presents a caudal-fin blotch restricted to the proximal portion of the caudal-fin rays that deeply resembles the *L. xinguensis* caudal-fin color pattern. Nevertheless, despite of the differences already mentioned above, both species are also diagnosed by the presence of a humeral spot in *P. cyclolepis*, a feature which is absent in *L. xinguensis*.

Material Analyzed.

Leptobrycon xinguensis: **Non-type material. All from Brazil: Rio Tapajós basin:** MCP 30905, 1 (26.8 mm SL), rio Quatro Pontes or Carmindo, Alta Floresta, Mato Grosso, 23 Jan 2002, R. E. Reis *et al.* MCP 30907, 1m (31.3 mm SL), affluent of rio Kaiapá, Nova Canaã do Norte, Mato Grosso, 22 Jan 2002, R. E. Reis *et al.* MCP 32144, 5 (4m 29.4-36.0 mm SL, 1m/c&s 36.1 mm SL), rio Kaiapá, Nova Canaã do Norte, Mato Grosso, 22 Jan 2002, R. E. Reis *et al.* MCP 34546, 26 (18.6-29.1 mm SL, 12m 26.0-29.1 mm SL, 3 c&s 28.0-29.0 mm SL), rio Kaiapá, Nova Canaã do Norte, Mato Grosso, 22 Jan 2002, R. E. Reis *et al.* ACRONYM ??? 30545, 1m (30.3 mm SL), rio Arinos, Porto dos Gaúchos, 18 Aug 1984, M. Goulding, *et al.* **Rio Xingu basin:** MCP 30906, 2m (21.1-26.6 mm SL), rio Manissamá-Miçu, Marcelândia, Mato Grosso, 27 Jan 2002, R. E. Reis *et al.* MCP 44531, 3 (21.1-27.3 mm SL), ribeirão das Traíras, Posto da Mata, Mato Grosso, 20 Apr 2006, J. P. da Silva & L. Cotrim. MZUSP 89737, 14 (20.8-26.3 mm SL), pound at right margin of rio Culuene, Paranatinga, Mato Grosso, 15 Jan 2006, A. Akama & J. L. Birindelli. MZUSP 91330, 5 (22.3-27.4 mm SL), córrego da Mata, affluent of rio Sete de Setembro, Garapu, Mato Grosso, 17 Oct 2004, AXE. MZUSP

91701, 49 (12.4-31.1 mm SL) lagoon at rio Culuene left margin, Paranatinga, Mato Grosso, 21 Aug 2006, J. L. Birindelli *et al.* MZUSP 91732, 14 (19.2-30.0 mm SL), pound at right margin of rio Culuene, Paranatinga, Mato Grosso, 21 Oct 2006, J. L. Birindelli *et al.* MZUSP 98985, 21 (26.2-36.1 mm SL), rio Von den Steinen, Nova Ubiratã, Mato Grosso, 21 Jan 2006, F. A. Machado *et al.* MZUSP 100342, 4 (20.8-26.0 mm SL), lagoon complex Tarik Yegum, rio Jatobá basin, Mato Grosso, Jul 2008, M. C. Lopes. USNM 311186, 2m (26.8-27.3 mm SL), tributary of rio Batovi, upper rio Xingu, Mato Grosso, Aug 1964, H. Schultz.

Comparative material. *Acinocheiroidon melanogramma*: ANSP 176238, paratypes, 7, 21.9-26.2 mm SL, Brazil, Minas Gerais, rio Jequitaiá drainage. *Aphyodite grammica*: FMNH, holotype, 24.3 mm SL, Guiana, Konawaruk. MZUSP 29874, 20, 21.9-26.9 mm SL, Brazil, rio Negro. *Brittanichthys axelrodi*: MCP 14931, 17, 16.3-22.2 mm SL, 3 c&s, Brazil, Boa Vista, rio Negro. *Cheiroidon australe*: USNM 084317, paratypes, 12, 28.4-49.8 mm SL, Chile, Los lagos Region at Puerto Varas. *Cheiroidon dialepturus*: USNM 208524, holotype, 26.8 mm SL, Panama, Veraguas, rio San Pedro Basin. *Cheiroidon galusdae*: USNM 084319, paratypes, 10, 30.6-52.3 mm SL, Chile, Rio Locomilla at San Xavier. *Cheiroidon gorgonae*: USNM 64094, holotype, 22.1 mm SL, Panama, Canal Zone, small seepage pool below spillway of the reservoir dam at Gorgona. *Cheiroidon kiliani*: USNM 227310, paratype, 1, 25.2 mm SL, Valdivia-Chile, rio Cau-Cau. *Cheiroidon microdon*: FMNH 57867, holotype, 32.2 mm SL, Brazil, Caceres, rio Ibicuhy. *Cheiroidon micropterus*: CAS 59780, holotype, 23.9 mm SL, Brazil, Para, rio Amazonas drainage at Santarem. *Cheiroidon mitopterus*: USNM 208539, holotype, 34.6 mm SL, Panama, Cocle, rio Tucue, tributary of rio Cocle del Norte. *Cheiroidon notomelas*: FMNH 57829, holotype, 28.2 mm SL, Brazil, Miguel Calmone. *Cheiroidontops geayi*: USNM 121507, holotype, 35.5 mm SL, Venezuela, Estado de Aragua, río Guarico. *Compsura heterura*: FMNH 57825, holotype, 28.7 mm SL, Brazil, rio Itapicuru, Queimadas. *Holesthes heterodon* (= *Serrapinnus heterodon*): CAS 117522, paratypes, 4, 32.2-36.5 mm SL, Brazil, Minas Gerais, rio Grande, Jaguará. *Leptobrycon jatuaranae*: MCP 14936, 17, 20.8-25.1 mm SL, 3 c&s, Brazil, Amazonas, rio Negro. *Microschemobrycon guaporensis*: FMNH 57926, holotype, 29.1 mm SL, Brazil, Maciel, rio Guaporé. *Odontostilbe hastatus*: FMNH 56383, holotype, 30.2 mm SL, Colombia, Soplaviento. *Oligobrycon microstomus*: holotype, 31.0 mm SL, Brazil, Jacarehy on rio Parahyba. *Oxybrycon* sp.: MCP 33105, 8, 13.7-14.9 mm SL, 2

c&s, Venezuela, Titi lagoon, upper Orinoco basin. *Parecbasis cyclolepis*: FMNH 56677, holotype, 56.3 mm SL, Brazil, rio Madeira. MZUSP 26146, 7, 40.3-53.5 mm SL, Peru, Ucayali, río Ucayali. *Pristella aubynei*: FMNH 52698, 34.9 mm SL, British Guiana. *Prodontocharax alleni*: CAS 117472, holotype, 32.8 mm SL, Peru, Ucayali, rio Amazonas basin. *Prodontocharax melanotus*: CAS 59793, holotype, 44.9 mm SL, Bolivia, la Paz, rio Amazonas drainage at Tumupasa. *Pseudocheiroduon affinis*: CAS 117516, paratype, 32.1-35.4 mm SL, Panama, rio Gatun, at Gatun. *Saccoderma melanostigma*: USNM 121519, holotype, 26.7 mm SL, Venezuela, rio San Juan, South of Mene Grande. *Spintherobolus broccae*: FMNH 58864, paratype, 18.7 mm SL, Brazil, Rio de Janeiro. *Spintherobolus papilliferus*: FMNH 104802, holotype, 32.9 mm SL, Brazil, São Paulo, Alto da Serra. *Thrissobrycon pectinifer*: SU 16944, holotype, 26.8 mm SL, Brazil, Cucuhy, rio Negro. MCP 14932, 12, 26.4-30.2 mm SL, 3 c&s, Brazil, rio Arirara.

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Literature Cited

- Böhlke, J. E. 1953. Studies on fishes of the family Characidae, No.3: A minute new herring-like characid fish genus adapted for plankton feeding, from the Rio Negro. Stanford Ichthyological Bulletin, 5: 168-170.
- Bührnheim, C. M. & L. R. Malabarba. 2006. Redescription of the type species of *Odontostilbe* Cope, 1870 (Teleostei: Characidae: Cheirodontinae), and description of three new species from the Amazon basin. Neotropical Ichthyology, 4(2): 167-196.
- Costa, W. J. E. M. 1994. Description of two new species of the genus *Moenkhausia* (Characiformes: Characidae) from the central Brazil. Zoologischer Anzeiger, 232: 21-29.

- Datovo, A. & F. A. Bockmann. 2010. Dorsolateral head muscles of the catfish families Nematogenyidae and Trichomycteridae (Siluriformes: Loricarioidei): comparative anatomy and phylogenetic analysis. *Neotropical Ichthyology*, 8(2): 193-246
- Eigenmann, C. H. 1912. The freshwater fishes of British Guiana, including a study of the ecological grouping of species, and the relation of the fauna of the plateau to that of the lowlands. *Memoirs of the Carnegie Museum*, 5(1): 1-103.
- Eigenmann, C. H. 1915. The Cheirodontinae, a subfamily of minute characid fishes of South America. *Memoirs of the Carnegie Museum*, 7(1): 1-99, pls. 1-17.
- Fink, W. L. & S. H. Weitzman. 1974. The so-called Cheirodontin fishes of Central America with descriptions of two new species (Pisces: Characidae). *Smithsonian Contributions to Zoology*, 172: 1-46.
- Géry, J. 1960. Contributions to the study of characid fishes. II. The generic position of *Hyphessobrycon innesi* and *Cheirodon axelrodi*, with a review of the morphological affinities of some Cheirodontinae (Pisces, Cypriniformes). *Bulletin of Aquatic Biology*, 2(12): 1-18.
- Géry, J. 1965. A new genus from Brazil - *Brittanichthys*. *Tropical Fish Hobbyist*, 13(6): 13-23, 61-69.
- Géry, J. 1972. Corrected and supplemented descriptions of certain Characoid fishes described by Henry W. Fowler, with revisions of several of their genera. *Studies on the Neotropical Fauna*, 7: 1-35.
- Géry, J. 1973. New and little-known Aphyoditeina (Pisces, Characoidei) from the Amazon basin. *Studies on the Neotropical Fauna*, 8: 81-137.
- Géry, J. 1977. *Characoids of the world*. T.F.H. Publications, Neptune City, 672p.
- Goloboff, P. A. 1993. Estimating character weights during tree search. *Cladistics*, 9(1): 83-91.
- Goloboff, P. A. 1999. Analyzing large data sets in reasonable times: solutions for composite optima. *Cladistics*, 15: 415-428.
- Goloboff, P. A., J. S. Farris & K. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*, 24: 774-786.
- Hennig, W. 1966. *Phylogenetic Systematics*. University of Illinois, Urbana, Illinois.
- Javonillo, R., L. R. Malabarba, S. H. Weitzman & J. R. Burns. 2010. Relationships among major lineages of characid fishes (Teleostei: Ostariophysi: Characiformes),

- based on molecular sequence data. *Molecular Phylogenetics and Evolution*, 54: 498-511.
- Lima, F. C. T., L. R. Malabarba, P. A. Buckup, J. F. P. Silva, R. P. Vari, A. Harold, R. Benine, O. T. Oyakawa, C. S. Pavanelli, N. A. Menezes, C. A. S. Lucena, R. E. Reis, F. Langeani, L. Casatti, V. A. Bertaco, C. R. Moreira & P. H. F. Lucinda. 2003. Genera *Incertae Sedis* in Characidae. Pp. 106-169. In: Reis, R. E., S. O. Kullander & C. J. Ferraris Jr. (Eds.). Check List of the Freshwater fishes of South and Central America. Porto Alegre, Edipucrs, 729p.
- Lima, F. C. T. & L. M. Sousa. 2009. A new species of *Hemigrammus* from the upper rio Negro basin, Brazil, with comments on the presence and arrangement of anal-fin hooks in *Hemigrammus* and related genera (Ostariophysi: Characiformes: Characidae). *Aqua*, International Journal of Ichthyology, 15(3): 153-168.
- Malabarba, L. R. 1998. Monophyly of the Cheirodontinae, characters and major clades (Ostariophysi: Characidae). Pp. 193-233. In: Malabarba, L. R., R. E. Reis, R. P. Vari, Z. M. S. Lucena & C. A. S. Lucena (Eds.). Phylogeny and Classification of Neotropical Fishes. Porto Alegre, Edipucrs, 603p.
- Malabarba, L. R. & S. H. Weitzman. 1999. A new genus and species of South American fishes (Teleostei: Characidae: Cheirodontinae) with a derived caudal fin, including comments about inseminatingcheirodontines. *Proceedings of the Biological Society of Washington*, 112(2): 410-432.
- Mirande, J. M. 2009. Weighted parsimony phylogeny of the family Characidae (Teleostei: Characiformes). *Cladistics*, 25: 574–613.
- Mirande, J. M. 2010. Phylogeny of the family Characidae (Teleostei: Characiformes): from characters to taxonomy. *Neotropical Ichthyology*, 8(3): 385-568.
- Nixon, K. C. 1999. The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics*, 15: 407–414.
- Oliveira, C. L. C., J. R. Burns, L. R. Malabarba & S. H. Weitzman. 2008. Sperm Ultrastructure in the Inseminating *Macropsobrycon uruguayanae* (Teleostei: Characidae: Cheirodontinae). *Journal of Morphology*, 269: 691–697.
- Reis, R. E., S. O. Kullander & C. J. Ferraris (Eds.). 2003. Check List of the Freshwater Fishes of South and Central America. Porto Alegre, Edipucrs, 729 p.
- Taylor, W. R. & G. C. Van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybiurn*, 9(2): 107-119.

- Weitzman, S. H. 1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. *Stanford Ichthyological Bulletin*, 8(1): 3-77.
- Winterbottom, R. 1974. A descriptive synonymy of the striated muscles of the Teleostei. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 125(12): 225-317.
- Zanata, A. M. & A. Akama. 2004. *Myxiops aphos*, a new characid genus and species (Characiformes: Characidae) from the rio Lençóis, Bahia, Brazil. *Neotropical Ichthyology*, 2(2): 45-54.
- Zanata, A. M. & R. P. Vari. 2005. The family Alestidae (Ostariophysi, Characiformes): a phylogenetic analysis of a trans-Atlantic clade. *Zoological Journal of the Linnean Society*, 145(1): 1–144.

Table 1. Morphometric data for *Leptobrycon xinguensis*.

	N	Min	Max	Mean	SD
Standard length (mm)	23	26.0	36.1	29.1	-
Percents of standard length					
Head length	23	26.2	30.5	28.2	1.02
Bony head length	23	23.3	26.2	24.6	0.76
Snout-anal distance	23	63.9	71.8	68.9	1.91
Snout-dorsal distance	23	48.4	52.8	50.8	1.25
Snout-pelvic distance	23	46.3	53.5	50.3	1.68
Snout-pectoral distance	23	27.1	31.7	29.3	1.09
Dorsal-fin base length	23	10.9	14.9	12.8	0.83
Anal-fin base length	23	17.1	23.6	20.5	1.30
Length of caudal peduncle	23	12.8	16.8	14.8	1.05
Depth of caudal peduncle	23	8.7	11.4	9.7	0.60
Body depth at dorsal-fin	23	23.4	30.5	26.8	1.60
Dorsal-fin length	22	24.9	28.4	26.0	1.03
Pelvic-fin length	23	15.9	20.7	18.1	1.12
Pectoral-fin length	21	16.4	21.5	18.9	1.43
Percents of head length					
Snout length	23	21.6	29.0	24.4	1.55
Upper jaw length	23	34.0	40.7	36.8	1.65
Horizontal orbit diameter	23	32.1	40.4	36.0	2.36
Interorbital width	23	23.8	29.3	26.1	1.28

Table 2. Results of the IW under different parameters. Trees used for the final phylogenetic hypothesis are in bold.

	"k"- values	Average character fit (F)	Average homoplastic steps (S)	Number of trees	Steps	Tree-fit	Best score
K1	4.88919	0.50	4.8891892	5	2255	217.16	137.80
K2	5.29662	0.52	4.8891892	4	2231	222.03	132.97
K3	5.73948	0.54	4.8891892	3	2231	226.83	128.13
K4	6.22260	0.56	4.8891892	5	2231	231.70	123.29
K5	6.75174	0.58	4.8891892	4	2229	236.55	118.45
K6	7.33378	0.60	4.8891892	4	2222	241.41	113.58
K7	7.97710	0.62	4.8891892	6	2216	246.28	108.68
K8	8.69189	0.64	4.8891892	2	2216	251.25	103.74
K9	9.49078	0.66	4.8891892	1	2205	256.23	98.76
K10	10.38953	0.68	4.8891892	2	2203	261.25	93.74
K11	11.40811	0.70	4.8891892	2	2203	266.32	88.68
K12	12.57220	0.72	4.8891892	2	2201	271.44	83.56
K13	13.91538	0.74	4.8891892	2	2197	276.62	78.37
K14	15.48243	0.76	4.8891892	2	2197	281.87	73.12
K15	17.33440	0.78	4.8891892	2	2197	287.21	67.79
K16	19.55676	0.80	4.8891892	2	2197	292.62	62.37
K17	22.27297	0.82	4.8891892	1	2193	298.15	56.85
K18	25.66824	0.84	4.8891892	1	2191	303.78	51.21
K19	30.03359	0.86	4.8891892	1	2191	309.55	45.45
K20	35.85405	0.88	4.8891892	3	2184	315.44	39.54
K21	44.00270	0.90	4.8891892	4	2182	321.53	33.46

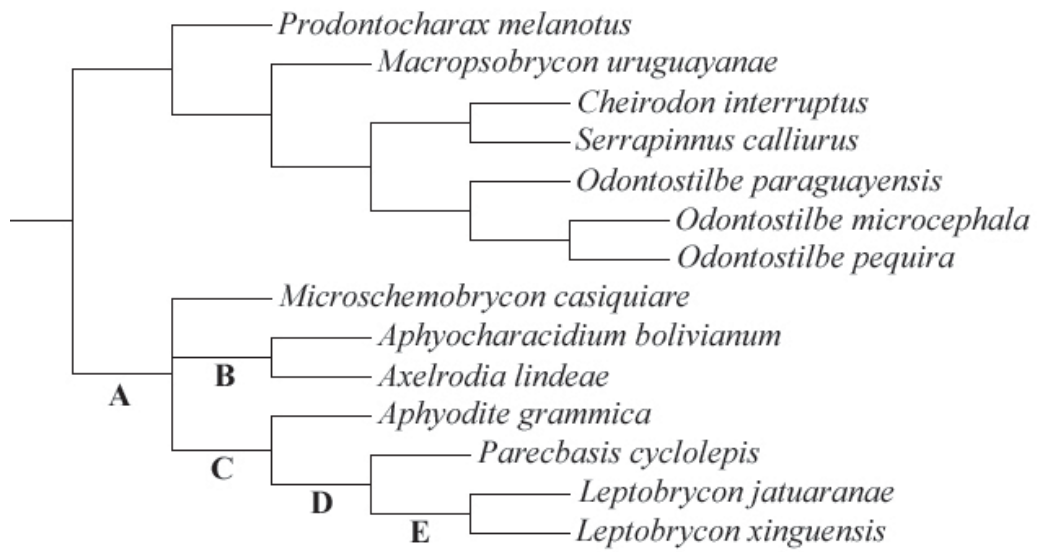


Fig. 1. Aphyoditeinae topology found in the implied weighted analysis under “k”-value = 12.5722, as part of a strict consensus tree of the Characidae phylogeny (2203 steps; CI = 0.17, RI = 0.66).

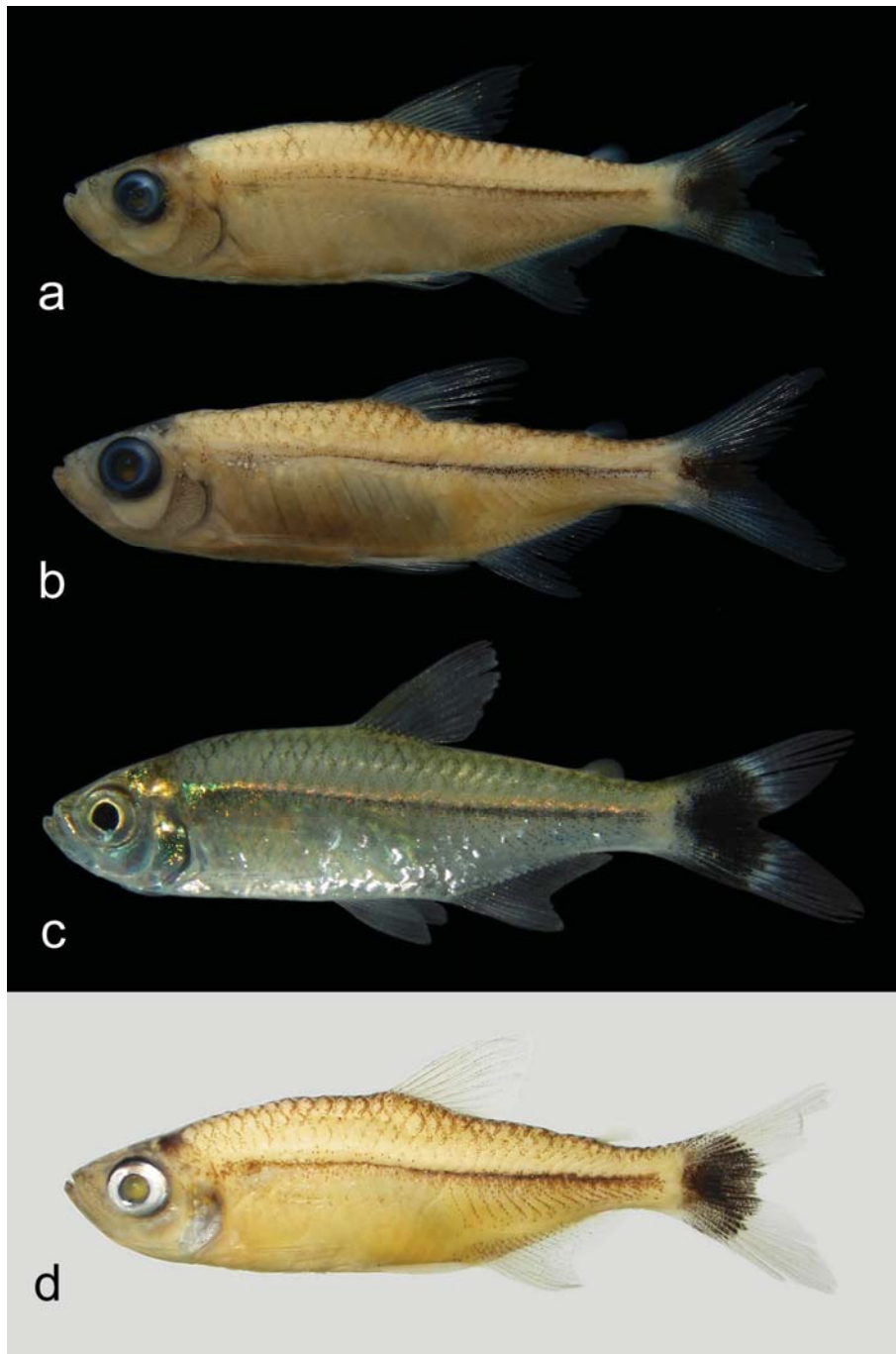


Fig. 2. Color variation on specimens of *Leptobrycon xinguensis*, (a) MCP 34546, 29.1 mm SL, (b) MCP 32144, 35.8 mm SL, (c) specimen alive (not preserved), (d) MZUSP 91701, 29.6 mm SL.

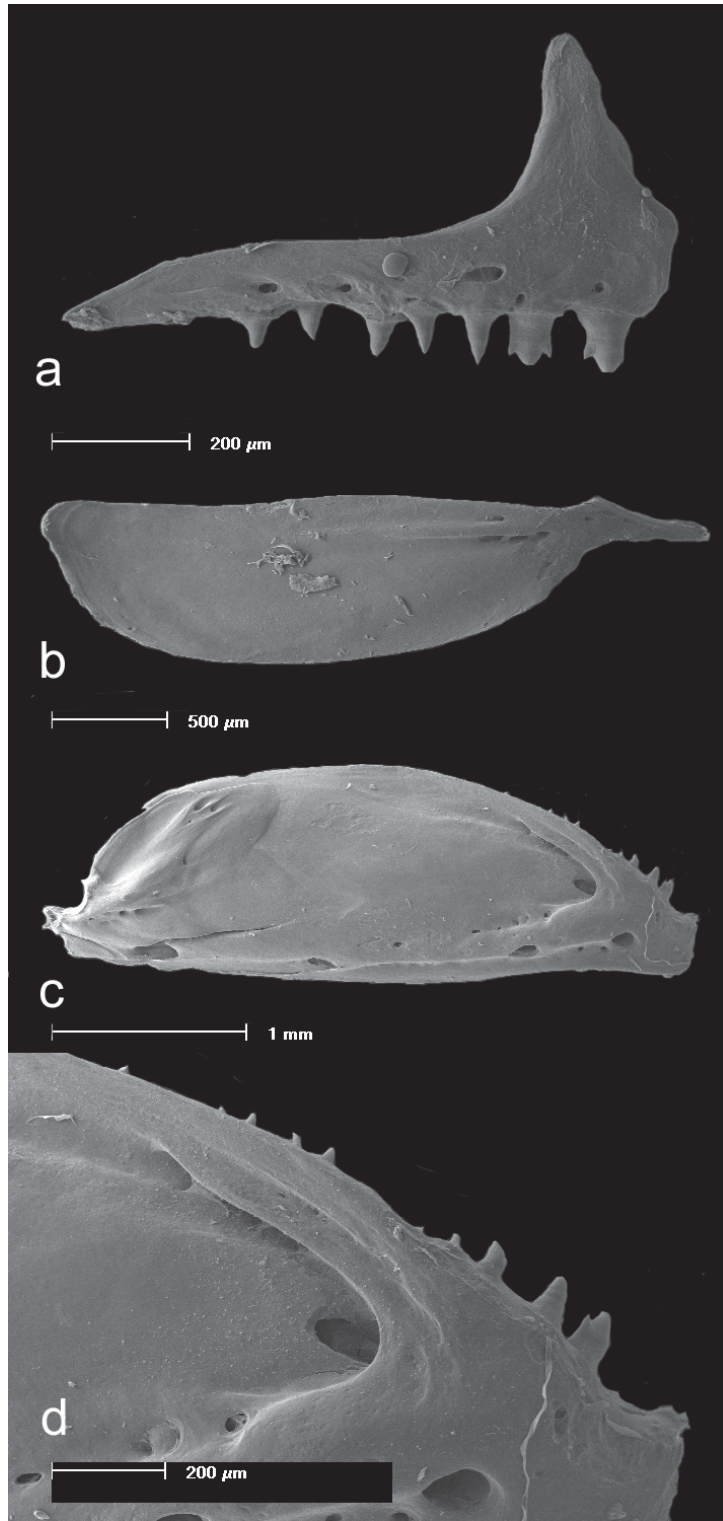


Fig. 3. Scanning micrographs showing right side jaws, lateral view, of *Leptobrycon xinguensis* MCP 34546, 28.9 mm SL; (a) premaxillary, (b) maxillary, (c) dentary, and (d) detail of dentary teeth.

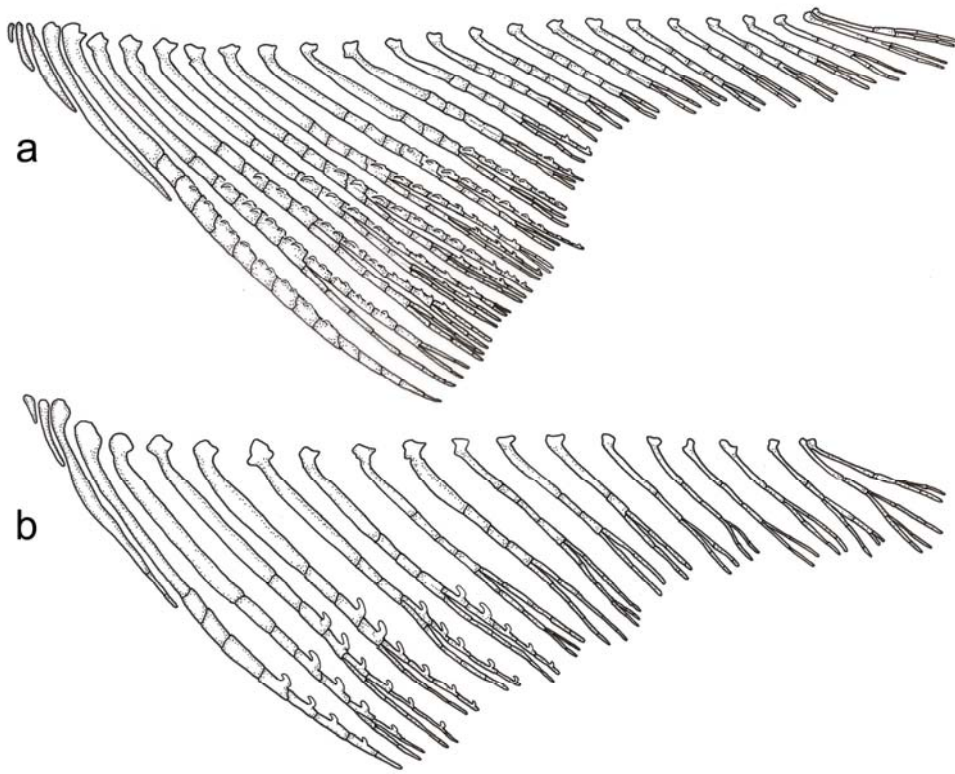


Fig. 4. Shape and distribution of anal-fin bony hooks in (a) *Macropsobrycon uruguayanae* mature male, MCP 20900, 34.2 mm SL; and (b) *Leptobrycon xinguensis* mature male, MCP 32144, 36.1 mm SL. Left side lateral view of anal fin.

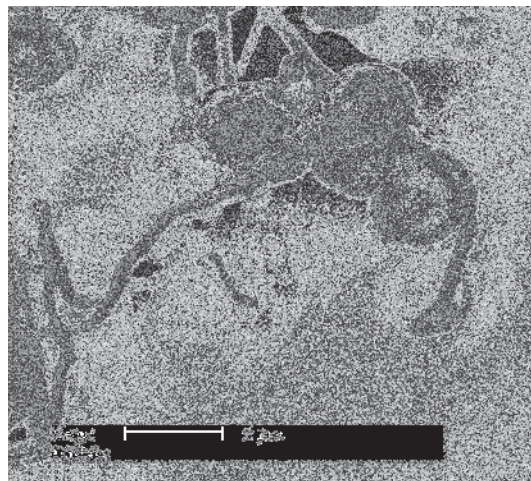


Fig. 5. Scanning micrograph showing spermatozoa shape of *Leptobrycon xinguensis*, mature male, MCP 32144, 36.1 mm SL.

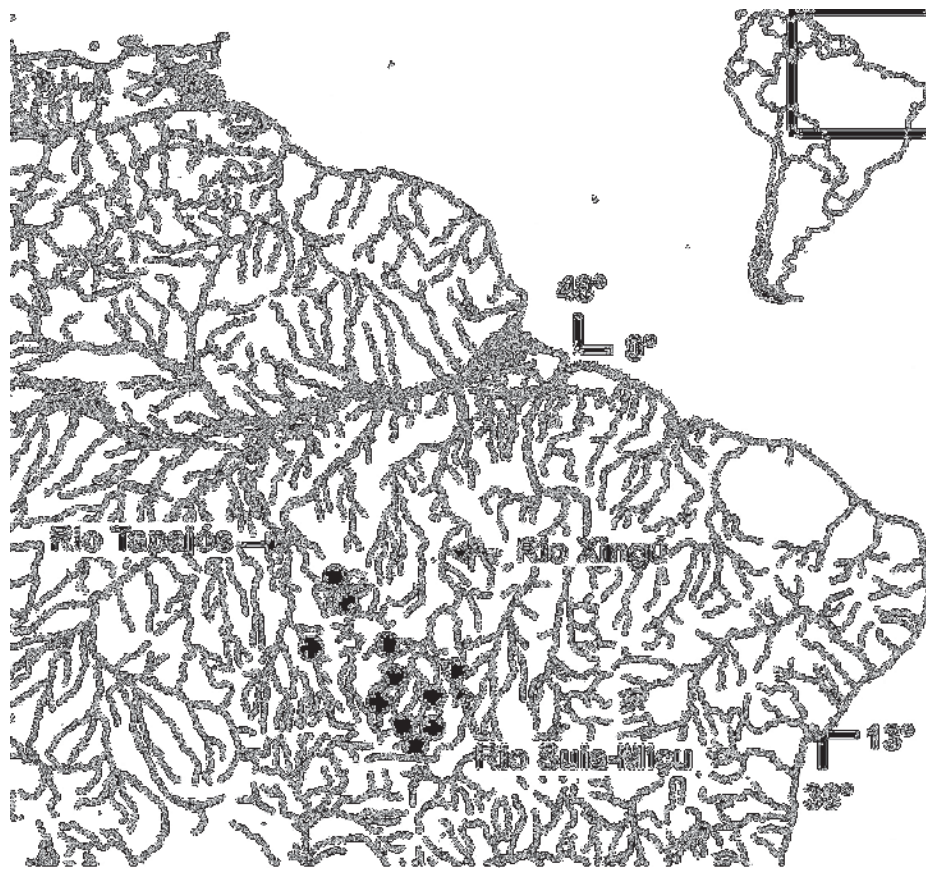


Fig. 6. Geographic distribution of *Leptobrycon xinguensis*, one dot can represent more than one locality.

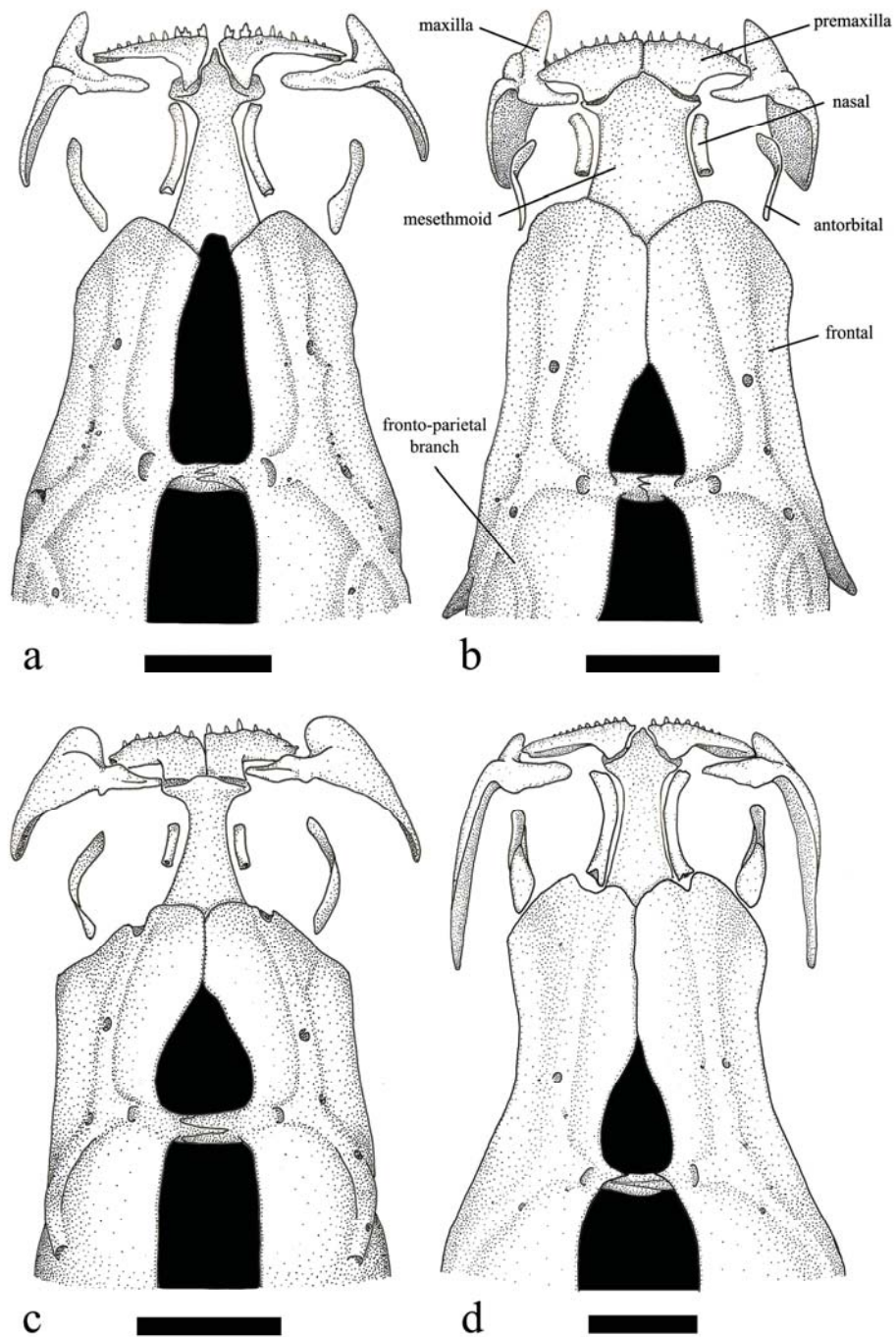


Fig. 7. Dorsal view of the anterior portion of the neurocranium: **(a)** *Leptobrycon xinguensis* MCP 34546, 29.4 mm SL; **(b)** *Aphyodite grammica* MCP 16893, 25.9 mm SL; **(c)** *Macropsobrycon uruguayanae* MCP 11939, 32.6 mm SL; **(d)** *Leptobrycon jatuaranae* MCP 14936, 23.3 mm SL. Anterior portion pointing up; scale bars = 1 mm.

Appendix I. Ordinal list of the character states of *Leptobrycon jatuaranae*, *L. xinguensis*, and *Macropsobrycon uruguayanae* according to the 365 characters present in Mirande (2010).

Leptobrycon jatuaranae:

00110010-1 / 0011000100 / 10-1100001 / 0000100100 / 0100011000 / 0110000000 /
0101101011 / ?010000000 / 0010000110 / 10 - 1 - - - 010 / 0011001000 / 1000000000 /
00 - - - 1 - - 11 / 001000 - - - 0 / 011 - 001010 / 1010000000 / 0000000101 / 100100011
/ 0010100010 / 1000100000 / 0000100001 0 0100000101 / 0100010110 / 1001000000 /
0000000001 / 0101000100 / 0001100001 / 1000010000 / 0000110000 / 0000010101 /
0000101110 / 0000100011 / 2000000010 / 00?1010000 / 0000000001 / 0000000?? /
?????

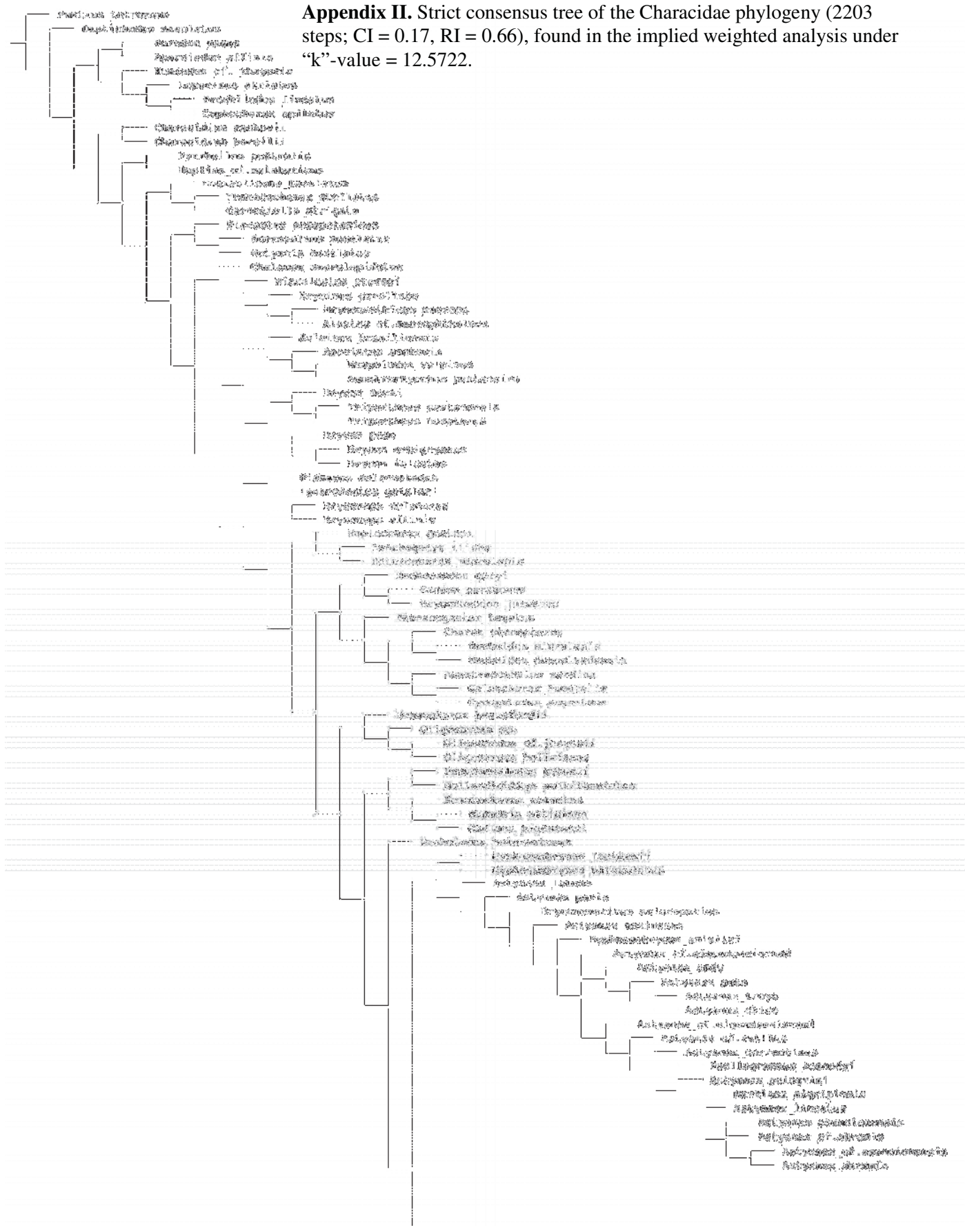
Leptobrycon xinguensis:

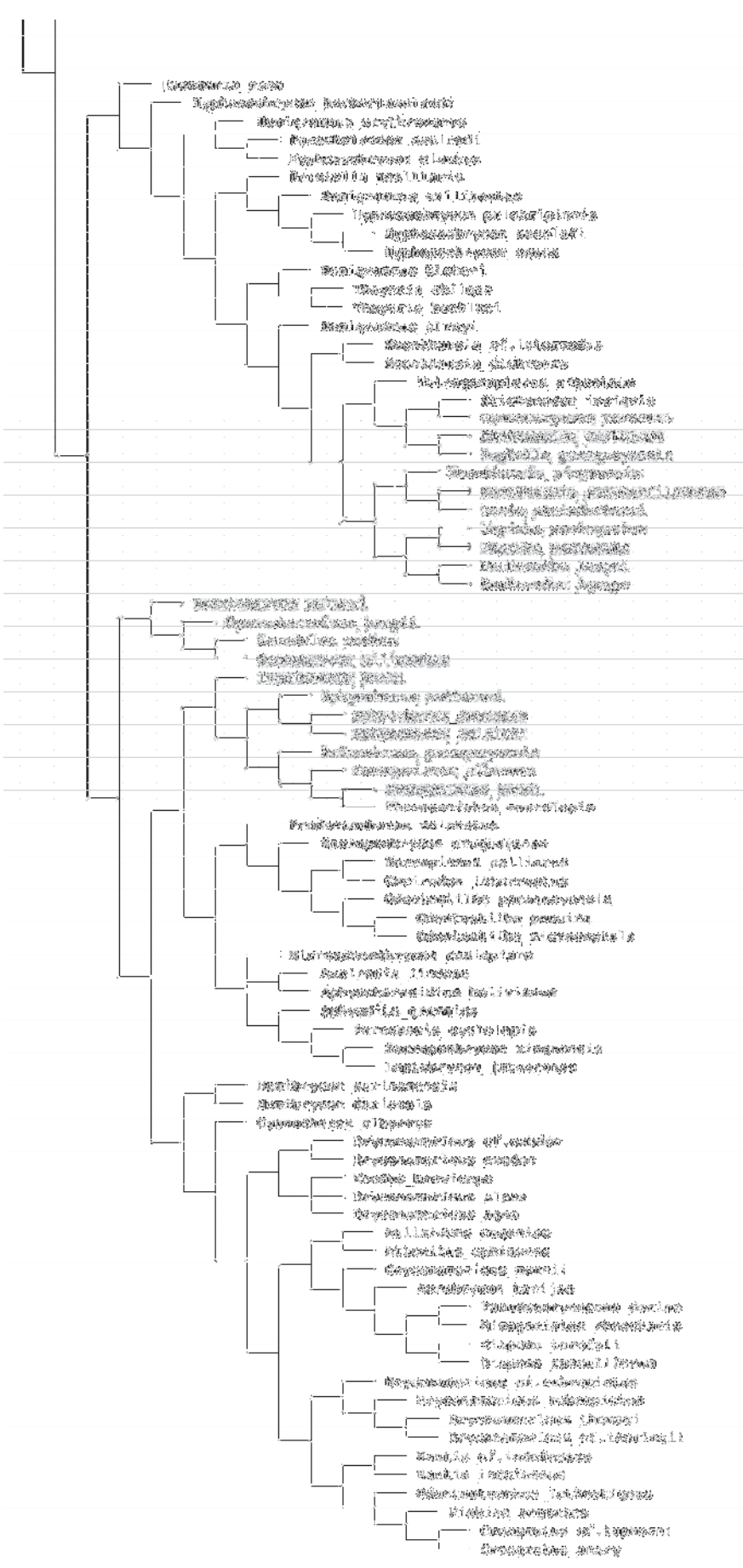
00110010 - 1 / 0011000100 / 1011100001 / 0000100100 / 0100011000 / 0110000000 /
0101101001 / ?010000000 / 0110000110 / 10 - 1 - - - 010 / 0011001000 /
1000000[0&1]00 / 00 - - - 11110 / 000000 - - - 0 / 011-001010 / 1010000000 /
0000000201 / 1101000110 / 0101000001 / 0001000000 / 0001000010 / 0100000111 /
0100010110 / 1001000000 / 0000000001 / 0101000100 / 0001100001 / 1000010000 /
0000110000 / 0000010101 / 0000101100 / 0000000011 / 2000000110 / 00?1010000 /
0000000001 / 0000000?0? / ??????

Macropsobrycon uruguayanae:

00110010 - 0 / 0011000100 / 00 - 1101001 / 1000100100 / 0000011000 / 0110000000 /
0100001011 / ?010000000 / 0010000110 / 10 - 1 - - - 010 / 0011001000 /
1000000[0&1]00 / 00 - - - 11110 / 000000 - - - 0 / 001 - 001000 / 1010000000 /
0001000201 / 0101000111 / 0101010101 / 0011000000 / 0011000010 / 0100000101 /
0100010110 / 1001000000 / 0000000001 / 0101000100 / 0001110001 / 1000010001 /
0000111000 / 0000010101 / 0000101110 / 0101100011 / 2000000010 / 00?1010010 /
0000000001 / 0100000110 / ??????

Appendix II. Strict consensus tree of the Characidae phylogeny (2203 steps; CI = 0.17, RI = 0.66), found in the implied weighted analysis under “k”-value = 12.5722.





Conclusões Gerais. A monofilia de Compsurini é confirmada com base em uma análise filogenética incluindo 101 táxons e 278 caracteres. A monofilia da subfamília Cheirodontinae, da tribo Cheirodontini, e de um clado formado pelas espécies previamente consideradas *incertae sedis* em Cheirodontinae, também são suportadas. Compsurini passa a ser suportada por seis sinapomorfias relacionadas ao dimorfismo sexual, ultraestrutura dos espermatozóides e tamanho dos processos laterais do mesetmóide. Um total de seis gêneros e 18 espécies são agora reconhecidos como integrantes de Compsurini: *Compsura* Eigenmann, 1915 com três espécies; *Macropsobrycon* Eigenmann, 1915, monotípico; *Acinocheirodon* Malabarba & Weitzman, 1999, monotípico; *Kolpotocheirodon* Malabarba & Weitzman, 2000, com duas espécies; *Saccoderma* Schultz, 1944, com duas espécies; e um novo gênero incluindo três espécies da América Central. Na hipótese de relação filogenética, as duas espécies amazônicas, Compsurini Cuzco n. sp. e Compsurini Tingo n. sp., foram designadas como grupo irmão dos Compsurini remanescentes que apresentam dimorfismo sexual na nadadeira caudal. *Acinocheirodon* e *Macropsobrycon* formaram um clado monofilético, e *Kolpotocheirodon* foi assinalado como grupo irmão de *Compsura* mais as espécies trans-andinas. De acordo com a presente hipótese, a presença de um órgão em formato de bolsa composto por escamas modificadas na nadadeira caudal surgiu independentemente mais de uma vez dentre os compsurinins: em Compsurini Purus n. sp., e posteriormente no clado agrupando *Compsura* e as espécies trans-andinas, com reversão nas espécies da América Central. Em trabalhos posteriores, a monofilia da tribo Compsurini foi suportada por caracteres relacionados a inseminação e ultraestrutura de espermatozóides; embora estas informações ainda sejam desconhecidas para algumas espécies de Compsurini, o grupo foi encontrado como natural na presente análise.