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**Taxonomy and Phylogeny of the Neotropical fish genus *Hemibrycon* Günther, 1864**

**(Ostariophysi: Characiformes: Characidae)**

**Vinicius de Araújo Bertaco**

**Orientador: Dr. Luiz Roberto Malabarba**

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## Resumo

As espécies do gênero *Hemibrycon* Günther (1864) são revisadas e redescritas com base na análise do material tipo e exemplares adicionais. *Hemibrycon* é considerado monofilético e relacionado ao Clado A *sensu* Malabarba & Weitzman (2003) com base na análise de 123 caracteres e 45 táxons. No total, 21 espécies de *Hemibrycon* são reconhecidas, incluindo cinco novas espécies. *Hemibrycon* n. sp. 1 da bacia superior do rio Ucayali, Peru; *Hemibrycon* n. sp. 2 de pequenos rios de drenagens costeiras do Mar do Caribe, Colômbia; *Hemibrycon* n. sp. 3 e *Hemibrycon* n. sp. 4 da porção média da bacia do rio Magdalena, Colômbia, e *Hemibrycon* n. sp. 5 da bacia superior do rio Madre de Dios, Peru. Estas espécies distinguem-se, principalmente, pelo padrão de colorido e número de raios ramificados da nadadeira anal, de escamas da linha lateral e de dentes no maxilar. A área de distribuição do gênero é ampliada para a bacia do baixo rio Tocantins, Brasil, com a ocorrência de *H. surinamensis* nessa bacia, sendo o primeiro registro da espécie para este país. A posição taxonômica de *Bryconamericus decurrens* e *Hemibrycon orcesi* é discutida. Novos sinônimos são propostos para algumas espécies de *Hemibrycon*: *H. coxeyi* é sinônimo júnior de *H. polyodon*, *H. carrilloi* é sinônimo júnior de *H. dariensis* e *H. guppyi* é sinônimo júnior de *H. taeniurus*. É fornecida uma chave de identificação para as espécies examinadas de *Hemibrycon*.

## Abstract

The species of the genus *Hemibrycon* Günther (1864) are reviewed and redescribed based on their type series and additional specimens. *Hemibrycon* is hypothesized to be monophyletic and related to Clade A genera *sensu* Malabarba & Weitzman (2003) based on the analysis of 123 characters including 45 taxa. A total of 21 species are recognized in *Hemibrycon*, including five new species. *Hemibrycon* n. sp. 1 from the upper río Ucayali drainage, Peru; *Hemibrycon* n. sp. 2 from small rivers of the Caribbean Sea coastal drainages of Colombia; *Hemibrycon* n. sp. 3 and *Hemibrycon* n. sp. 4 from the middle río Magdalena basin, Colombia, and *Hemibrycon* n. sp. 5 from the upper río Madre de Dios, Peru. These species are distinguished among themselves mainly in the color pattern and number of branched anal-fin rays, lateral line scales, and maxillary teeth. The known geographical distribution of the genus is enlarged reaching the lower río Tocantins basin, Brazil, with the occurrence of *H. surinamensis* in this area, the first record of the species for that country. The taxonomic status of *Bryconamericus decurrens* and *Hemibrycon orcesi* is discussed. New synonymies are proposed for some species of *Hemibrycon*: *H. coxeyi* is a junior synonym of *H. polyodon*, *H. carrilloi* is a junior synonym of *H. dariensis*, and *H. guppyi* is a junior synonym of *H. taeniurus*. An identification key to the examined species of *Hemibrycon* is provided.

## Apresentação

Esta tese é apresentada conforme as Normas do Programa de Pós-Graduação em Zoologia da Pontifícia Universidade Católica do Rio Grande do Sul - PUCRS.

A tese está estruturada em forma de dois artigos científicos redigidos em inglês, um já publicado na *Neotropical Ichthyology*. É apresentado um resumo em português. As tabelas e figuras estão no final do texto do Capítulo I. O periódico escolhido para a publicação desse capítulo foi *Neotropical Ichthyology*, revista da Sociedade Brasileira de Ictiologia com periodicidade trimestral. Os artigos científicos foram redigidos conforme as instruções para os autores do periódico escolhido.

Neste estudo foi realizada uma revisão e redescrição das espécies incluídas no gênero *Hemibrycon* Günther, 1864 com base na análise do material tipo e exemplares adicionais e uma análise filogenética das relações de *Hemibrycon* com representantes do Clado A proposto por Malabarba & Weitzman (2003) e outros gêneros de Characidae (Capítulo I). O gênero *Hemibrycon* é diagnosticado com base em sinapomorfias relacionadas a caracteres osteológicos e de morfologia externa e relacionado aos gêneros do Clado A *sensu* Malabarba & Weitzman (2003).

Um total de 21 espécies é reconhecido para o gênero *Hemibrycon*, incluindo cinco novas espécies. *Hemibrycon* n. sp. 1 da bacia superior do rio Ucayali, Peru; *Hemibrycon* n. sp. 2 de pequenos rios de drenagens costeiras do Mar do Caribe, Colômbia; *Hemibrycon* n. sp. 3 e *Hemibrycon* n. sp. 4 da porção média da bacia do rio Magdalena, Colômbia, e *Hemibrycon* n. sp. 5 da bacia superior do rio Madre de Dios, Peru. Estas espécies distinguem-se, principalmente, pelo padrão de colorido e número de raios ramificados da nadadeira anal, escamas da linha lateral e dentes no maxilar. A área de distribuição do gênero é ampliada para a bacia do baixo rio Tocantins, Brasil, com a ocorrência de *H. surinamensis* nessa bacia, sendo o primeiro registro da espécie para este país. A posição taxonômica de *Bryconamericus decurrens* Eigenmann e *Hemibrycon orcesi* Böhlke é discutida. Novos sinônimos são propostos para algumas espécies de *Hemibrycon*: *H. coxei* Fowler é sinônimo de *H. polyodon* Günther, *H. carrilloi* Dahl é sinônimo de *H. dariensis* Meek & Hildebrand e *H. guppyi* Regan é sinônimo de *H. taeniurus* Gill. É fornecida uma chave de identificação para as espécies examinadas de *Hemibrycon*.

No Capítulo II é apresentado um artigo publicado em 2007 na *Neotropical Ichthyology* sobre a descrição de uma espécie nova de *Hemibrycon*, *H. divisorensis*, da porção superior da bacia do rio Ucayali, Sierra del Divisor, Peru. Esse artigo foi desenvolvido durante o curso de doutorado e em colaboração com pesquisadores do Peru.



## **CAPÍTULO I**

## Taxonomy and Phylogeny of the Neotropical fish genus *Hemibrycon* Günther, 1864 (Ostariophysi: Characiformes: Characidae)

### Abstract

The genus *Hemibrycon* Günther, 1864 is revised and diagnosed based on synapomorphies described from osteological and external morphology. The species included in the genus are reviewed and redescribed based on their type series and additional specimens. *Hemibrycon* is hypothesized to be monophyletic and related to Clade A genera *sensu* Malabarba & Weitzman (2003). A total of 21 species are recognized in *Hemibrycon*, including five new species: *Hemibrycon* n. sp. 1 from the upper río Ucayali drainage, Peru; *Hemibrycon* n. sp. 2 from small rivers of the Caribbean Sea coastal basins of Colombia; *Hemibrycon* n. sp. 3 and *Hemibrycon* n. sp. 4 from the middle río Magdalena basin, Colombia; and *Hemibrycon* n. sp. 5 from the upper río Madre de Dios, Peru. *Hemibrycon* species are distinguished among themselves mainly by the color pattern and number of branched anal-fin rays, lateral line scales, and maxillary teeth. The distribution area of the genus is enlarged reaching the lower rio Tocantins basin, Brazil, with the occurrence of *H. surinamensis* in this area, the first record of the species for that country. The taxonomic status of *Bryconamericus decurrens* and *Hemibrycon orcesi* is discussed. New synonymies are proposed for some species of *Hemibrycon*: *H. coxeyi* is a junior synonym of *H. polyodon*, *H. carrilloi* is a junior synonym of *H. dariensis*, and *H. guppyi* is a junior synonym of *H. taeniurus*. An identification key to the examined species of *Hemibrycon* is provided.

### Resumo

O gênero *Hemibrycon* Günther, 1864 é revisado e diagnosticado com base em sinapomorfias relacionadas a caracteres osteológicos e de morfologia externa. As espécies

incluídas no gênero são revisadas e redescritas com base na análise do material tipo e exemplares adicionais. *Hemibrycon* é considerado monofilético e relacionado ao Clado A *sensu* Malabarba & Weitzman (2003). No total, 21 espécies de *Hemibrycon* são reconhecidas, incluindo cinco novas espécies: *Hemibrycon* n. sp. 1 da bacia superior do rio Ucayali, Peru; *Hemibrycon* n. sp. 2 de pequenos rios de drenagens costeiras do Mar do Caribe, Colômbia; *Hemibrycon* n. sp. 3 e *Hemibrycon* n. sp. 4 da porção média da bacia do rio Magdalena, Colômbia; e *Hemibrycon* n. sp. 5 da bacia superior do rio Madre de Dios, Peru. As espécies do gênero distinguem-se, principalmente, pelo padrão de colorido e número de raios ramificados da nadadeira anal, escamas da linha lateral e dentes no maxilar. A área de distribuição do gênero é ampliada para a bacia do baixo rio Tocantins, Brasil, com a ocorrência de *H. surinamensis* nesta bacia, o primeiro registro da espécie para este país. A posição taxonômica de *Bryconamericus decurrens* e *Hemibrycon orcesi* é discutida. Novos sinônimos são propostos para algumas espécies de *Hemibrycon*: *H. coxeyi* é sinônimo de *H. polyodon*, *H. carrilloi* é sinônimo de *H. dariensis* e *H. guppyi* é sinônimo de *H. taeniurus*. É fornecida uma chave de identificação para as espécies examinadas de *Hemibrycon*.

**Key words:** South America, freshwater fishes, Amazon basin, Fin hooks, *Boehlkea*, *Bryconamericus*.

## Introduction

*Hemibrycon* is a genus of Neotropical characid fishes which comprises 21 valid species (Table 1) with up to 117.3 mm standard length, occurring in the rivers of the Pacific basins in Panama, coastal basins of the Caribbean sea in Colombia, lago Maracaibo and rio Orinoco in Venezuela, rivers of Trinidad and Tobago, coastal basins of French Guiana and Suriname, lower rio Tocantins basin, Brazil, and upper rio Amazonas in Bolivia, Brazil, Peru

and Ecuador (Lima *et al.*, 2003; Román-Valencia & Ruiz-C., 2007; present study) (Figs. 1 and 2).

The genus *Hemibrycon* was proposed by Günther (1864), as a subgenus of *Tetragonopterus* Cuvier (1816), and diagnosed in key by “cleft of the mouth of moderate width, and the entire edge of the maxillary denticulated”. *Tetragonopterus polyodon* Günther was designated as the type species. *Hemibrycon* was extensively revised by Eigenmann (1927), whose accounts still constitute the single complete review of the genus. Publications on *Hemibrycon* subsequent to Eigenmann's revision, usually involves only description of new species occurring in restricted geographic areas of South America (*e.g.* Román-Valencia *et al.*, 2006; Bertaco *et al.*, 2007).

Eigenmann (1917, 1927), diagnosed *Hemibrycon* based on the “caudal fin naked, premaxillary with two series of teeth, inner series with four teeth, infraorbital 2 in contact with the lower limb of the preopercle, adipose fin present, anal fin moderate or long, gill-rakers simple, teeth along the greater part or along the entire edge of the maxillary”. None of the characters is unique to the genus and most of them are plesiomorphic within Characidae.

Géry (1966) proposed the recognition of a subtribe Hemibryconini (Tetragonopteridi) to a group of Tetragonopterinae with only four inner premaxillary teeth, frequently associated with a great development of the third infraorbital, and, quite often, the irregular implantation of the outer premaxillary row of teeth. Géry's Hemibryconini consisted of *Hemibrycon*, *Boehlkea* Géry, *Bryconacidnus* Myers, *Bryconamericus* Eigenmann, *Ceratobranchia* Eigenmann, *Coptobrycon* Géry, *Knodus* Eigenmann, *Microgenys* Eigenmann, *Nematobrycon* Eigenmann, *Piabarchus* Myers, *Rhinopetitia* Géry and *Rhinobrycon* Myers. Another subtribe, Creagrutini, included *Creagrutus* Günther, *Creagrudite* Myers (= *Creagrutus*) and *Piabina* Reinhardt, by the possession of heavier teeth, the prominent snout, and premaxilla with three tooth rows.

The genus *Hemibrycon* was included in a phylogenetic analysis for the first time by Lucena (1993). The author used *Hemibrycon* (= *H. surinamensis*) in his phylogenetic analysis of the family Characidae, and recognized *Hemibrycon* as sister group of a clade formed by remaining Characidae genera, including some representatives of the Clade A *sensu* Malabarba & Weitzman, and Alestidae based on four synapomorphies, one of them exclusive for the Clade [numbered 92]: presence of teeth with more of one cup on dentary.

Malabarba & Weitzman (2003) recognized *Hemibrycon* as belonging to a large monophyletic clade inside Characidae (therein named Clade A), based on the putative derived presence of four teeth in the inner series of the premaxilla and reduced number of dorsal-fin rays (ii,8). Additionally, they considered *Hemibrycon* and *Boehlkea* as apparently the most basal genera in that clade, by lacking all specializations related to insemination, development of caudal- and/or anal-fin glands or the jaw and teeth modifications related to the ventral position of the mouth, as observed in the remaining genera and species of Clade A. The Clade A includes the subfamilies Glandulocaudinae plus Stevardiinae and the genera *Hemibrycon*, *Attonitus* Vari & Ortega, *Boehlkea*, *Bryconacidnus*, *Bryconamericus*, *Caiapobrycon* Malabarba & Vari, *Ceratobranchia*, *Creagrutus*, *Cyanocharax* Malabarba & Weitzman, *Hypobrycon* Malabarba & Malabarba, *Knodus*, *Microgenys*, *Monotocheirodon* Eigenmann & Pearson, *Odontostoechus* Gomes, *Othonocheirodon* Myers, *Piabarchus*, *Piabina*, *Rhinobrycon* and *Rhinopetitia*.

Calcagnotto *et al.* (2005) provided a hypothesis of relationships among characiform fishes based on nuclear and mitochondrial genes of 135 taxa, and in part corroborated the monophyly of the Clade A proposed by Malabarba & Weitzman (2003), represented by *Bryconamericus*, *Creagrutus*, *Gephyrocharax* Eigenmann, *Hemibrycon*, *Knodus* and *Mimagoniates* Regan, and also supported a basal position of the genera *Brycon* and *Bryconops* Kner in Characidae. The only specimen of *Hemibrycon* used in the Calcagnotto's

analysis was tentatively identified as *Hemibrycon* cf. *beni* (AMNH 233328). This specimen was collected in the río Coronel at Amboró National Park, Ichilo, Santa Cruz, Bolivia. The river drainage of this region corresponds to río Mamoré drainage (río Madeira drainage), where *Hemibrycon jelskii* is found based on this study. This specimen was not analyzed.

Weitzman *et al.* (2005) described a new inseminating species and genus of the Characidae, *Bryconadenos tanaothoros*, as a member of the characid Clade A and closely related to *Attonitus*. Those authors suggest that Clade A is a tentative phylogenetic hypothesis needing further investigation, and that histology and ultrastructure analysis of sperm cells may be useful for an evaluation of the phylogenetic significance of insemination in characids included in that clade.

Ferreira (2007) recognized *Hemibrycon* sp. (= *H. jelskii*), *Bryconamericus novae*, *Cregrutus meridionalis* and *Piabina argentea*, forming a large monophyletic clade including *Knodus* and other Clade A genera, in her phylogenetic analysis of the genus *Knodus*.

The genus *Hemibrycon* is herein phylogenetically diagnosed and its species are revised. The species of the genus are redescribed based on type series and new specimens when available, and five new species are described. An identification key to the examined species of *Hemibrycon* is presented.

### **Taxonomic history of *Hemibrycon* species**

Günther (1864) proposed *Hemibrycon* as subgenus of *Tetragonopterus* Cuvier (1816) in his key, differing from the remaining Characidae genera by “cleft of the mouth of moderate width; the entire edge of the maxillary denticulated”, and described the type species, *Tetragonopterus (Hemibrycon) polyodon* Günther, based on only one specimen from Guayaquil, Ecuador. Eigenmann (1909) considered *Hemibrycon* as a separate genus of *Tetragonopterus*, and listed *Hemibrycon polyodon* as the type species of the monotypic genus.

Anterior to the genus description, Gill (1858) described *Poecilurichthys taeniurus* from Trinidad Island. This species was transferred to *Tetragonopterus* by Günther (1864), and moved to *Hemibrycon* by Eigenmann (1909).

Lütken (1875) described *Tetragonopterus (Hemibrycon) trinitatis* from Trinidad Island, West Indies. Eigenmann (1927) made a revision of the genus and considered this species a junior synonym of *H. taeniurus* Gill.

Steindachner (1877) described *Tetragonopterus jelskii* from Monterico (Peru), and in 1882 proposed *Tetragonopterus huambonicus* from Huambo (Peru), and furnished short descriptions for both species. Eigenmann (1910) transferred both species to *Hemibrycon* and listed *H. huambonicus* as synonym of the type species of the genus, *H. polyodon*. Eigenmann (1922) did not list *H. huambonicus* or *H. jelskii* in his key of fish species from Peru, and in 1927, redescribed both species and revalidated *H. huambonicus*. Later, subsequent authors as Géry (1962, 1977) placed in doubt the validity of *H. huambonicus* and maintained the species in a questionable synonym with *H. polyodon*.

In the twentieth century, Regan (1906), in his study of freshwater fishes of Trinidad, described *Tetragonopterus guppyi* for “Glenside Estate stream, at the foot of the n. range of hills, Trinidad I., West Indies”, Trinidad and Tobago. Three years later, Eigenmann (1909) transferred this species to *Hemibrycon*, and in 1927 redescribed the species in his revision of the genus.

Eigenmann (1913) studying the freshwater fishes from Colombia, described four species of *Bryconamericus*: *B. tolimae* for Ibagué (upper río Magdalena basin), *B. dentatus* for Piedra Moler (upper río Cauca drainage), *B. decurrens* for Soplaviento (lower río Magdalena basin), and *B. or Hemibrycon boquiae spec. nov.? [sic]* for Boquia (upper río Cauca drainage). All species were described based on more than fifteen specimens in the type series, except for *B. dentatus*, that was described based on two specimens. Eigenmann (1922)

provided a key to the species of *Hemibrycon* and transferred all these species to this genus. In 1922, Eigenmann changed the species name from *H. boquiae* to “*H. boquillae*” in his key to *Hemibrycon* species, without comments about the new spelling, and cited the locality “Boquilla”. According to Eschmeyer (1998), Eigenmann unexplained the new name or misspelled for *B. boquiae* listing the same type specimens. Eigenmann (1927) redescribed the species with the original nomenclature, *H. boquiae*, and listed *H. boquillae* in the synonym. Román-Valencia (2001) redescribed *H. boquiae* based on new specimens and recognized the endemism of the species for the upper rio Cauca drainage, Colombia. Román-Valencia (2004) redescribed *Hemibrycon tolimae* based on four paratypes of the sixteen type specimens designated by Eigenmann (1913) and additional material, and referred the species to the genus *Bryconamericus*. That author redescribed the species in *Bryconamericus* based on the occurrence of teeth in most of the maxillary length. Maldonado *et al.* (2005) presented some features, biological information, distribution and a list of lots of *B. tolimae* deposited in ichthyological collections.

Eigenmann in Eigenmann *et al.* (1914), described *Hemibrycon colombianus* to the río San Gil [middle río Magdalena basin], Santander, Colombia, based mainly on two specimens as reported by authors “Very largely described from the two largest specimens”, although they had listed sixteen type specimens.

In the study of freshwater fishes from Panama, Meek & Hildebrand (1916) described *H. dariensis*. The authors designated one specimen as type (65 mm of length) from rio Yape, rio Tuira basin [Pacific drainage], Panama, but in the description commented that 66 specimens were analyzed from rio Tuira basin.

Eigenmann (1922) proposed *Hemibrycon tridens* based on one specimen from rio Apurimac at Uruhuasi (= Curuhuasi, Peru), diagnosed by few characters in his key to *Hemibrycon* species. Only in 1927, Eigenmann presented the original description for this



species, and designated the type specimen (65 mm of length). After Eigenmann, no additional specimens of *H. tridens* have been found.

Pearson (1924) described *Hemibrycon beni* for the Miguilla and La Paz rivers, altitude of 3,080 feet, Espia, Bolivia (rio Beni drainage).

Eigenmann (1927), in the single revision available for the genus *Hemibrycon*, described *H. helleri* from the rio Comerciato, rio Urubamba drainage, Peru. The species name homage Edmund Heller, the collector of the type specimens. An identification key to *Hemibrycon* species, including the new species, reasonable description of the new species and drawings of types and dentition of species included in the genus were presented in that work.

Myers (1930) in his study of fishes from the upper rio Meta drainage in Colombia, described *Hemibrycon metae* based on one specimen (80 mm of SL) from Guaicaramo, rio Guavio. The author commented that the new species is rather similar to *H. dentatus* and *H. decurrens*, but differs in some morphometric and meristic features.

Fowler (1943) described *Hemibrycon coxeyi* based on one specimen from rio Pastaza drainage, rio Marañon drainage, Hacienda Las Mascota, Ecuador. The species name homage Mr. W. Judson Coxey, the collector of the type specimens. Böhlke (1958) and Géry (1962, 1977) suspected that *H. coxeyi* was a synonym of *H. huambonicus* and/or *H. polyodon*, due to the similarity between the species and by their occurrence approximately in the same area. Oyakawa in Lima *et al.* (2003) placed *H. coxeyi* as provisional synonym of *H. polyodon*.

Schultz (1944) described *Hemibrycon jabonero* as subspecies of *H. dentatus*, from the río Chama at Estanques, Mérida, Venezuela. The author recognized *H. jabonero* as a subspecies of *H. dentatus* on the basis of the lateral line curved, and provided a key to subspecies of *Hemibrycon* from Venezuela: *H. dentatus dentatus* and *H. dentatus metae*. In the original description, Schultz listed 712 paratypes plus the holotype, but provided body

proportional measurements for the holotype and one paratype. Géry (1962) recognized all these taxa as species of *Hemibrycon*.

Böhlke (1958) described *Hemibrycon orcesi* [sic] for “Río Macuma, Provincia de Santiago-Zamora, Ecuador”, based on the holotype and three paratypes. According to the author, he described the species provisionally in *Hemibrycon*, but the new species has caudal-fin scaled and disagree with Eigenmann’s definition of *Hemibrycon*. The species name homage Dr. Gustavo Orcés. Géry (1962) also suspected that *H. orcesi* could represent a new genus related to *Hemibrycon*, but clearly different from it.

Dahl (1960) described *Hemibrycon carrilloi* from the quebrada La Noche, tributary of upper rio Atrato, Colombia, based on the holotype, although he had listed four paratypes. The species name homage Dr. Jorge Carrillo. *Hemibrycon carrilloi* was not listed by Géry (1962, 1977).

Boeseman (1960) in his work “The freshwater fishes of the island of Trinidad”, redescribed *H. taeniurus* and *H. guppyi*, and presented a detailed comparison between the types of these species. According to the author, they differ basically in the orbital diameter, interorbital width and head length, but he doubted the significance of these differences due to limited material of non-comparable body size. However, he maintained both species as valid.

Géry (1962) described *Hemibrycon surinamensis* from the rio Paramacca drainage, Suriname based on specimens from his particular fish collection. Taxonomic status of the genus, pattern of distribution of the included species, and a key of identification to sixteen species of *Hemibrycon* were presented in this work. The author also provided several drawings of skull skeleton, caudal fin, and a radiographed specimen of the new species.

Dahl in Dahl & Medem (1964) described *Hemibrycon velox* in a mimeographed paper by “Departamento de Investigaciones Ictiológicas y Faunísticas de la CVM”, a governmental institution of Colombia. The species was described from quebrada Caña Fina, río Verde del

Sinu, Colombia. Dahl (1971) presented a key of identification and drawings of six species of *Hemibrycon* from north of Colombia, including *H. velox*. Géry (1977) did not include *H. velox* in his key for *Hemibrycon* species.

Maldonado *et al.* (2005) in their field guide “Peces de Los Andes de Colombia” identified six species of *Hemibrycon*, and provided for each species a brief description, synonymy, distribution, biological and ecological information, drawings of entire specimens, and records of the species in ichthyological collections.

In the 21<sup>st</sup> century Román-Valencia *et al.* (2006) described *Hemibrycon pautensis* from rio Paute (a tributary of the río Santiago drainage, rio Marañon drainage), Ecuador. The authors also recognized specimens of *H. polyodon* from this river, and compared the new species with some species of *Hemibrycon*. The presented diagnosis is insufficient for the recognition of the new species separately from other species of the genus.

Román-Valencia & Ruiz-C. (2007) described *Hemibrycon microformaa* from the upper río Atrato basin in Colombia. They used the body size as principal character to distinguish the new species from remaining *Hemibrycon* species. According to the authors, the specimens of *H. microformaa* are smaller than 31 mm SL, and possess a dentition similar to *Creagrutus* species. In the same work, they provided an identification key to six species of *Hemibrycon* from Colombia, including a new combination for a species described in *Boehlkea*, *H. fredcochui* (Géry, 1966). No comments were made by the authors to justify the new combination. Additionally, they described the presence of the supraorbital bone in *H. microformaa* and in other species of the genus.

Bertaco *et al.* (2007) described a new species of *Hemibrycon*, *H. divisorensis*, from río Ucayali basin, Sierra del Divisor, Peru. The authors recorded by the first time in a species of the genus *Hemibrycon* the presence of bony hooks in all fins, except the caudal-fin, in males of *H. divisorensis*, a character not observed by previous authors. Also, they fully disagree that

*Hemibrycon* species have a supraorbital bone as recorded by Román-Valencia in his descriptions of *Hemibrycon* species.

## **Material and Methods**

Counts were taken as described by Fink & Weitzman (1974), with the exception of the number of scale rows below lateral line which were counted from the scale row ventral to the lateral line to the scale row nearest the first pelvic-fin ray. Vertebral counts, supraneurals, gill-rakers of first arch, teeth and procurrent caudal-fin-ray counts were taken from cleared and stained specimens (c&s) prepared according to the method of Taylor & Van Dyke (1985). Tooth counts were also taken in some alcohol preserved specimens. Vertebral counts include the four vertebrae integrated in the Weberian apparatus and the terminal centrum was counted as one vertebra. Osteological terminology is that used by Weitzman (1962). Teeth and bone SEM (scanning electronic microscope) photos were taken from dissected cleared and stained specimens.

Measurements were taken point to point with an electronic caliper on the left side of specimens when possible. All measurements other than SL are expressed as a percentage of SL except subunits of the head, which are recorded as a percentage of head length.

Morphometric data for the type series of each species and non-type specimens are presented separately in tables. Data for primary types are given between parentheses followed by the range, mean and number of specimens counted in the description of each species.

Proposed hypotheses of phylogenetic relationship among studied taxa followed the phylogenetic method of Hennig (1966), as discussed by Wiley (1981). The most parsimonious hypothesis of character distribution is the principle to create the cladogram. Outgroup comparison are used to hypothesize ingroup character polarity. Phylogenetic analyses were performed with TNT 1.0 (Goloboff *et al.*, 2005), and WinClada 1.00.08 (Nixon, 1999-2002)

using NONA (Goloboff, 1993-1999). The algorithms utilized were the traditional heuristic search and the new technology with sectorial searches and tree fusing (Goloboff, 1999). No difference was found between the results of these algorithms thus are presented heuristic results. All transformation series were considered unordered. Character optimization followed accelerated transformation model (ACCTRAN) considered more consistent with the concepts of homology and synapomorphy (de Pinna, 1991). The bootstrap values (Felsenstein, 1985) were calculated using 1000 replicates to the nodes support. The matrix of character distribution (Table 2) included data from examined species of *Hemibrycon* and outgroup characids. A list of comparative material is given at the end of the text.

The analysis included all examined *Hemibrycon* species, representatives of Clade A genera proposed by Malabarba & Weitzman (2003; figs. 2 and 11; Figs. 21 and 22), and representatives of other characid groups (Aphyocharacinae, Characinae, Cheirodontinae, Rhoadsinae, Stethaprioninae, plus *insertae sedis* Characidae genera). The analysis was rooted using *Brycon pesu*. *Brycon* Müller & Troschel (1844) has been considered hypothetically a basal genus of the Characidae that retain a supraorbital bone (Malabarba & Weitzman, 2003; Weitzman & Malabarba, 1998). Some *Hemibrycon* species were not included in the phylogenetic analysis due to the lack of non-type specimens available in the scientific collections for clearing and staining such as *Hemibrycon beni*, *H. decurrens*, *H. orcesi*, *H. tridens*, or due to their recent description as *H. pautensis* and *H. microformaa*. *Hemibrycon colombianus* and *Boehlkea fredcochui* could not be obtained on loan.

Specimens examined belong to the following institutions: ANSP, Academy of Natural Sciences, Philadelphia; BMNH, Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; FMNH, Field Museum of Natural History, Chicago; IAvHP, Instituto Alexander von Humboldt, Villa de Leyva; ICNMHN, Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá; IMCN,

Museo Departamental de Ciencias Naturales - INCIVA, Cali; INHS, Illinois Natural History Survey, Illinois; KU, University of Kansas, Kansas; INPA, Instituto Nacional de Pesquisa Amazônia, Manaus; MCNG, Museo de Ciencias Naturales, Guanare; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MCZ, Museum of Comparative Zoology, Cambridge; MHNG, Muséum d'Histoire Naturelle, Geneva; MHNUC, Museo de Historia Natural de la Universidad del Cauca, Popayán; MNHN, Museum National d'Histoire Naturelle, Paris; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; NMW, Naturhistorisches Museum, Vienna; NRM, Swedish Museum of Natural History, Stockholm; ROM, Royal Ontario Museum, Toronto; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C.; ZMA, Universiteit van Amsterdam, Zoölogisch Museum, Amsterdam, and ZMUC, Kobenhavns Universitet Zoologisk Museum, Copenhagen. List of examined specimens of each species includes in this order: catalog number; total number of specimens in that lot, followed by the number of c&s specimens in parentheses when available, standard length range, sex for holotypes, collecting locality, coordinates, and date. Collectors are given for type series of each species. List of comparative material includes in this order: catalog number; total number of specimens in that lot (and number of c&s specimens in parentheses when available), standard length range, and collecting locality. The synonymy provided for each species contains only papers that contain taxonomic changes or and/or illustrate characters.

Gonads were obtained from specimens deposited in institutional fish collections. These were probably fixed in 10% formalin and stored in 70% ethanol prior to sectioning. I removed ovaries and testes from one side, dehydrated in 99% ethanol, and infiltrated and embedded in glycol methacrylate. Saggital sections were made at 0.5  $\mu\text{m}$  with microtome,

mounted on glass slides, and stained either with toluidine blue and alizarin-red. For scanning electron microscopy (SEM), the pieces of mature testes of some *Hemibrycon* species were dehydrated in ethanol series, dried in a critical point dryer, and scattered upon a carbon tape of the stub and viewed with a scanning electron microscope.

Gill gland observations in males and females were made through light microscopy under stereomicroscope. When verified the presence of a gill gland, the first gill arch from one side was removed, dehydrated in ethanol series and critical point dryer. The gill arch was fixed upon the stub with a carbon tape, coated with gold in a sputter-coater, and viewed with a scanning electron microscope (SEM).

## **Results**

### **Character Description and Analysis**

Characters are grouped under separate headings according to the region of the body to which they are associated, and listed from anterior to posterior regions of body. Consistency index obtained for each character is given between parentheses along with their descriptions. All characters are treated as unordered in the analysis.

### DENTITION

According to Weitzman & Malabarba (1998) the tooth number and tooth shape have long been used in defining genera and subfamilies, and for identification of particular species of Characiformes. The authors believed that the use of these characters in diagnosing families, subfamilies and genera in diverse groups of Characidae have originated a series of polyphyletic groups. However, they also suggested that these characters must be used together

with additional characters. I have tentatively listed 26 characters related to teeth and jaw bones.

Character 1 (CI = 0.25) - Number of premaxillary tooth rows [Lucena, 1993: Chs. 38-39; Buckup, 1998: Ch. 32; Malabarba, 1998: Ch. 55; Zanata, 2000: Ch. 42; Bertaco, 2003: Ch. 75; Benine, 2004: Ch. 27; Zanata & Vari, 2005: Ch. 57; Bührnheim, 2006: Ch. 35; Ferreira, 2007: Ch. 36]: (0) 3 rows; (1) 2 rows (Fig. 3); (2) 1 row.

A single regular tooth row in the premaxilla was hypothesized as a synapomorphy for the Cheirodontinae by Malabarba (1998). The state 0 is found in *Brycon* and *Piabina* among examined taxa. Zanata (2000) considered the presence of three tooth rows in premaxilla as one of the synapomorphies that corroborates the monophyly of *Brycon*.

Character 2 (CI = 0.33) - Number of teeth in the inner series of premaxilla [Bertaco, 2003: Ch. 76; Serra, 2003: Ch. 57; Benine, 2004: Ch. 29; Zanata & Vari, 2005: Ch. 61; Ferreira, 2007: Ch. 37]: (0) five to six teeth; (1) four teeth (Fig. 3).

All *Hemibrycon* species have four teeth in the inner series of premaxilla. Among taxa examined, the state 1 also occurs in all representatives of Clade A, except *Hysteronotus megalostomus*. This species has 5-6 teeth (state 0) in the inner series of premaxilla, as also previously observed by Weitzman & Thomerson (1970).

The number of teeth in the inner series of premaxilla has been used since Eigenmann (1917) to diagnose some characid genera (Malabarba & Weitzman, 2003). Géry (1966) proposed the recognition of the Hemibryconini, as a subtribe of Tetragonopterinae based on the presence of four teeth in the inner series of the premaxilla, among other characters. Malabarba & Weitzman (2003) recognized a putative monophyletic group of characids (Clade



A) based on the presence of four teeth in the inner series of premaxilla along with the reduced number of dorsal-fin rays (ii,8).

Character 3 (CI = 0.14) - Tooth cusp number in the inner series of premaxilla [Malabarba, 1998: Ch. 72; Bührnheim, 2006: Ch. 40]: (0) one to three cusps; (1) all tricuspidate; (2) three to five cusps (Fig. 3); (3) five to eight cusps.

Tooth morphology is highly variable among characids, mainly in relation to cusp number, ranging from conical to multicuspidate (Malabarba, 1998). In the *Hemibrycon* species occurs the states 2 and 3.

Character 4 (CI = 0.16) - Arrangement of outer teeth row of premaxilla: (0) all teeth aligned in the distal portion (Fig. 3); (1) teeth not aligned in the distal portion (Fig. 4).

Géry (1966) proposed the recognition of the subtribe Hemibryconini by the irregular implantation of the outer premaxillary row of teeth, among other characters. Chernoff & Machado-Allison (1990) disagreed with Géry's statement that the outer premaxillary teeth in some genera included in Hemibryconini, including *Hemibrycon*, are irregularly placed, and distinct from those genera not included in the subtribe.

Among *Hemibrycon* species analyzed, the outer row teeth of premaxilla can be aligned (state 0) or not aligned (state 1). Serra & Langeani (2006) suggested that the presence of the not aligned teeth in the premaxilla outer row as been one of the characters to form a group of *Bryconamericus* species, *B. exodon*, *B. stramineus* and *B. turiuba*.

Character 5 (CI = 0.50) - Basal portion of the teeth of the inner row of premaxillary teeth [Ferreira, 2007: Ch. 41]: (0) basal and distal portions similar (Fig. 3); (1) smaller than distal portion (see fig. 2, *Odontostilbe fugitiva* in Bührnheim & Malabarba, 2006:173).

The state 1 represents a synapomorphy for the Clade 10, and Clade E.

Character 6 (CI = 0.33) - Position of ascending process of the premaxilla: (0) located on the anterior extremity of premaxilla and aligned at vertical through insertion of second tooth of the inner row of the premaxilla; (1) located on the anterior extremity of premaxilla and aligned at vertical through insertion of first tooth of the inner row of the premaxilla (Fig. 3); (2) located on the midcentral region of premaxilla and just after the second tooth of the inner row of the premaxilla (see fig. 2, *Odontostilbe fugitiva* in Bührnheim & Malabarba, 2006:173).

Character 7 (CI = 0.33) - Size of ascending process of the premaxilla: (0) smaller than width of premaxilla (Fig. 3); (1) similar or larger than width of premaxilla; (2) reduced to a small bone projection (less 1/3 of premaxilla length) (see fig. 2, *Odontostilbe fugitiva* in Bührnheim & Malabarba, 2006:173).

Character 8 (CI = 0.20) - Number of maxillary teeth in adult specimens [Weitzman & Menezes, 1998: Ch. 42; Vari & Harold, 2001: Ch. 7]: (0) 21 to 35; (1) 11 to 20; (2) six to 10; (3) one to five.

Weitzman & Menezes (1998) found three character states for this tooth count, one to four (state 0), five to seven (state 1) and 18 to 30 (state 2) maxillary teeth. Those authors observed that most of the examined outgroup characids and glandulocaudines have less than seven maxillary teeth, and that the state 2 was present in Xenrobryconini members. Vari & Harold (2001) recognized two character states for the number of maxillary teeth in *Piabina argentea* (2 to 5), a range found in most *Creagrutus* species, except in *C. cracentis*, *C. gephyrus* and *C. maxillaris* (8 to 12). Malabarba & Weitzman (2003) considered *Hemibrycon*

and *Boehlkea* as apparently the most basal genera in that clade A due to the presence of a long completely toothed maxilla, among other features. The states 1 and 2 are found in *Hemibrycon* species.

Character 9 (CI = 0.23) - Number of cusps of first maxillary tooth: (0) tricuspidate (Fig. 3); (1) pentacuspoid; (2) multicuspoid (more than five cusps) (see fig. 2, *Odontostilbe fugitiva* in Bührnheim & Malabarba, 2006: 173); (3) conical.

Among *Hemibrycon* species the first maxillary tooth is always tricuspidate (state 0) or pentacuspoid (state 1).

Character 10 (CI = 0.25) - Relative size of tooth cusps of the maxillary teeth: (0) central cusp longer than lateral cusps (Fig. 3); (1) all cusps of similar size.

All species of *Hemibrycon* have the midcentral cusp longer than lateral cusps in the maxillary teeth (state 0). The state 1 is found in *Bryconadenos tanaothoros*, *Knodus meridae* (Clade A characids), and *Odontostilbe fugitiva* and *Rhoadsia altipinna*.

Character 11 (CI = 0.11) - Shape of maxillary teeth: (0) shape of teeth variable along the maxilla (Fig. 3); (1) shape of teeth uniform along the maxilla.

The maxillary teeth of all *Hemibrycon* species present variable shape along this bone (state 0), but this character also observed in outgroup taxa.

Character 12 (CI = 0.22) - Relative size of the anterior portion of the maxilla articulated with premaxilla: (0) very short, one fourth or more of the maxillary free portion length (see fig. 51, *Cyanocharax alburnus* in Malabarba & Weitzman, 2003:142); (1) short, approximately one

third of the maxillary free portion length (Fig. 3); (2) long, approximately half-length of the maxillary free portion.

Character 13 (CI = 0.25) - Maxillary teeth: (0) maxillary teeth without space between teeth (or different of state 1); (1) first teeth of maxilla without space, and remaining teeth with space between teeth (Fig. 3).

Character 14 (CI = 0.16) - Size of maxillary teeth: (0) teeth gradually decreasing in length from first to last (Fig. 3); (1) teeth not decreasing in length from first to last.

Character 15 (CI = 0.33) - Relative size of the anterior toothed portion of the maxillary [Lucena, 1993: Ch. 44]: (0) larger than edentulous portion (Fig. 3); (1) smaller than edentulous portion (see fig. 2, *Odontostilbe fugitiva* in Bührnheim & Malabarba, 2006:173); (2) portions of similar size.

The edentulous portion of maxillary is always smaller than toothed portion, and is here considered a synapomorphy for the genus, but also found among other Clade A characids, as for example *Bryconamericus* spp. The state 0 also occur in the remaining taxa examined as *Brycon pesu*, *Charax stenopterus*, *Hollandichthys multifasciatus*, *Nematobrycon palmeri*, *Nematocharax venustus*, *Pseudochalceus lineatus*, *Rachoviscus* spp., and *Rhoadsia altipinna*.

Character 16 (CI = 0.16) - Dorsal profile of the maxilla: (0) convex (Fig. 5b); (1) slightly concave (see fig. 2, *Odontostilbe fugitiva* in Bührnheim & Malabarba, 2006:173); (2) straight (Fig. 5a).

The maxillary dorsal profiles of all *Hemibrycon* species is straight (state 2), and is considered a not exclusive synapomorphy for the genus, but is found in some outgroup taxa.

Character 17 (CI = 0.18) - Maxillary length [Buckup, 1998: Ch. 34]: (0) posterior border of maxillary reaching to distal portion of infraorbital 2; (1) posterior border of maxillary reaching to 2/3 of length of infraorbital 2; (2) posterior border of maxillary not surpassing the infraorbital 1.

Zanata & Vari (2005) also observed a longer maxilla in *Charax*, among other taxa. Among outgroup taxa, a small maxilla (state 2) was observed in *Carlastyanax aurocaudatus*.

Character 18 (CI = 0.33) - Number of large teeth in dentary of adult specimens: (0) 4 to 5 (Malabarba & Weitzman, 2003: fig. 51); (1) 3 (Fig. 3); (2) 2; (3) almost all teeth similar size (see fig. 2, *Odontostilbe fugitiva* in Bührnheim & Malabarba, 2006: 173).

All *Hemibrycon* species have the three anteriormost dentary teeth larger followed by medium sized tooth, and a number variable of teeth with 1-3 cusps or conical.

Character 19 (CI = 0.50) - Shape of larger dentary teeth [Malabarba, 1998: Ch. 56; Ferreira, 2007: Ch. 52]: (0) not pedunculated (Fig. 3); (1) pedunculated, largely expanded (see fig. 2, *Odontostilbe fugitiva* in Bührnheim & Malabarba, 2006: 173).

The pedunculated and largely expanded teeth are found in members of the Cheirodontinae, here represented by *Odontostilbe fugitiva*. Among Clade A characids examined, the pedunculated teeth occur in *Knodus meridae* and *Othonocheirodus* sp. The teeth of all *Hemibrycon* species are not pedunculated.

Character 20 (CI = 0.23) - Number of cusps of the larger dentary teeth [Vari & Harold, 2001: Ch. 18]: (0) five to seven cusps; (1) three to five cusps (Fig. 3); (2) all tricuspidate; (3) conical.

Character 21 (CI = 0.25) - Disposition of dentary teeth [Zanata & Vari, 2005: Ch. 85]: (0) teeth divided in two groups, teeth larger anteriorly and smaller posteriorly (Fig. 3); (1) all teeth of similar size (see fig. 2, *Odontostilbe fugitiva* in Bührnheim & Malabarba, 2006: 173).

Zanata & Vari (2005) observed that the posterior teeth of dentary are abruptly smaller than anteriormost teeth in *Astyanax*, *Charax*, *Brycon*, *Bryconops*, *Tetragonopterus* and *Triportheus*, a condition also observed in this study for the first four taxa.

Character 22 (CI = 0.25) - Relative size of the posterior edentulous portion of the dentary [Ferreira, 2007: Ch. 51]: (0) smaller than toothed portion (Fig. 3); (1) larger than toothed portion (see fig. 2, *Odontostilbe fugitiva* in Bührnheim & Malabarba, 2006: 173); (2) both portions of similar size (see fig. 9, *Bryconadenos tanaothoros* in Weitzman *et al.*, 2005: 341).

The edentulous portion of the dentary is smaller than toothed portion in all *Hemibrycon* species.

Character 23 (CI = 0.33) - Profile of dorsal border of dentary: (0) concave where the larger teeth are inserted and convex along the region where remaining teeth are inserted (Fig. 3); (1) all border concave; (2) all border straight (see fig. 4, *Nematocharax venustus* in Weitzman *et al.*, 1986: 341).

All *Hemibrycon* species have the profile of dorsal border of dentary concave where the larger teeth are inserted and convex along the region where remaining teeth are inserted. The state 1 was found only in *Othonocheirodus* sp.

Character 24 (CI = 0.16) - Alignment of distal border (cutting border) of dentary teeth: (0) distal border of dentary teeth not aligned (Fig. 3); (1) distal border of dentary teeth aligned (see fig. 2, *Odontostilbe fugitiva* in Bührnheim & Malabarba, 2006: 173).

Character 25 (CI = 0.22) - Alignment of dentary and premaxilla in lateral view: (0) premaxilla positioned anterior to dentary; (1) dentary and premaxilla aligned (isognathous); (2) dentary positioned anterior to premaxilla (prognathous).

Character 26 (CI = 0.17) - Number of interdigitating articulations of dentary symphysis [Ferreira, 2007: Ch. 50]: (0) six; (1) five; (2) four; (3) three.

*Hemibrycon* species have four or five interdigitating articulations in the dentary symphysis.

## CRANIUM

Character 27 (CI = 0.16) - Length of supraoccipital process [Bertaco, 2003: Ch. 24; Serra, 2003: Ch. 18; Benine, 2004: Ch. 19; Ferreira, 2007: Ch. 28]: (0) very short, not reaching anterodorsal region of neural complex; (1) short, reaching and/or slightly surpassing the anterodorsal region of neural complex; (2) very long, exceeding the anterodorsal region of neural complex.

Benine (2004) observed a larger supraoccipital process in deep bodied species, as observed in this study (state 2) in *Poptella brevispina*, *Astyanax* spp., *Pseudochalceus lineatus*, *Charax stenopterus* and *Rhoadsia altipinna*. The state 1 represents a synapomorphy for Clade H9, which includes *Hemibrycon* species

Character 28 (CI = 0.25) - Shape of nasal bone [Ferreira, 2007: Ch. 17]: (0) tubular with laminar bony flange (Fig. 6a); (1) tubular without laminar bony flange (Fig. 6b).

The nasal bone is present in all characiforms, except in *Lepidarchus* (Alestidae), and represents a synapomorphy for this genus (Zanata & Vari, 2005). In the majority of the Characiformes the nasal bone corresponds only to a tube, but in some taxa examined in this study it shows a laminar bony flange.

Character 29 (CI = 0.16) - Anterior portion of nasal bone [Lucena, 1993: Ch. 32; Benine, 2004: Ch. 6; Zanata & Vari, 2005: Ch. 18; Ferreira, 2007: Ch. 18]: (0) not reaching the lateral projection of mesethmoid (Fig. 6a); (1) surpassing the lateral projection of mesethmoid (Fig. 6b).

Character 30 (CI = 0.10) - Frontal fontanel [Lucena, 1993: Ch. 7; Buckup, 1998: Ch. 9; Serra, 2003: Ch. 1; Zanata & Vari, 2005: Ch. 36]: (0) absent; (1) present.

The absence of a frontal fontanel was interpreted as derived by Lucena (1993) and proposed by that author as a synapomorphy for the clade consisting of *Alestes*, *Brycon*, *Chalceus*, *Hemigrammopetersius* and *Hydrocynus*. Among examined taxa, the absence of a frontal fontanel was observed only in *Brycon pesu*.

Character 31 (CI = 0.12) - Length of the frontal fontanel [Vari & Harold, 2001: Ch. 37; Benine, 2004: Ch. 9; Zanata & Vari, 2005: Ch. 36; Ferreira, 2007: Ch. 24]: (0) reaching the ethmoid bone; (1) not reaching the ethmoid bone.

Vari & Harold (2001) considered the absence of contact between the frontal bones anterior to frontal fontanel a plesiomorphy for *Creagrutus*.



Character 32 (CI = 0.14) - Rhinosphenoid [Buckup, 1998: Ch. 7; Bertaco, 2003: Ch. 20; Zanata & Vari, 2005: Ch. 31]: (0) absent; (1) present.

Bertaco (2003) observed the absence of rhinosphenoid in *Hollandichthys*, *Rachoviscus*, *Astyanax lineatus* and *Aphyocharax anisitsi*. Chernoff & Machado-Allison (1990:266) considered the loss of the rhinosphenoid a potentially derived condition in *Ceratobranchia* Eigenmann (1914). Zanata & Vari (2005) recognized that the rhinosphenoid is absent in all examined members of the Alestidae. They also commented that this ossification is present in diverse characiform groups including many subunits of the New World family Characidae. Serra & Langeani (2006) observed the rhinosphenoid in *Bryconamericus exodon* as also observed in this study.

Character 33 (CI = 0.20) - Shape of head and body: (0) head not massive and heavy, usually narrow, and thin body; (1) head massive and heavy, and heavy body (usually elongate).

Eigenmann (1921, 1927) diagnosed *Astyanax scabripinnis* and five subspecies based on the elongate body, and head heavy. The body shape characters used by Eigenmann to diagnose *Astyanax scabripinnis* are apparently common to *Astyanax*-like forms living in fast current streams (Bertaco & Malabarba, 2001; Bertaco & Lucena, 2006). Vari & Siebert (1990) when proposed *Bryconamericus pectinatus*, recognized the body similarities of this species with *Carlastyanax aurocaudatus* due the massive heads and heavy bodies, among other features.

Among *Hemibrycon* species two groups are recognized based mainly in the shape of head, corresponding to states 0 and 1 (see the figures of *Hemibrycon* species for comparison).

#### ANTORBITAL, INFRAORBITAL AND SUPRAORBITAL BONES

Character 34 (CI = 0.50) - Supraorbital bone [Lucena, 1993: Ch. 26; Buckup, 1998: Ch. 21; Bertaco, 2003: Ch. 13; Serra, 2003: Ch. 21; Benine, 2004: Ch. 5; Zanata & Vari, 2005: Ch. 2]: (0) present; (1) absent.

The presence of the supraorbital is a primitive condition in Characidae, and is found in species of *Brycon*, *Bryconops*, *Salminus* Agassiz (1829), *Triportheus* Cope (1872), *Lignobrycon* Eigenmann & Myers (1929), *Clupeocharax* Pearson (1924) and *Engraulisoma* Castro (1981). The absence of the supraorbital has been used to delimit a lineage within Characidae (Malabarba & Weitzman, 2003). Among examined characids the supraorbital bone is present only in the outgroup species of *Brycon* and *Bryconops*. All species of the Clade 2 lack the supraorbital bone.

Character 35 (CI = 0.33) - Number of infraorbital bones [Lucena, 1993: Ch. 28; Bertaco, 2003: Ch. 14]: (0) six (Fig. 7a); (1) five (Fig. 7b); (2) four (Fig. 7c).

In the state 1, presence of 5 infraorbitals can be due to the fusion of third and fourth infraorbitals, or loss of one of these bones. The hypothesis of fusion (IO3 + IO4) is based on the position of the third infraorbital, positioned along all posteroventral portion of the orbit, originally occupied by the IO3 and IO4. All *Hemibrycon* species have six infraorbital bones (state 0).

Character 36 (CI = 1.00) - Infraorbital 6 [Weitzman & Malabarba, 1999: Ch. 18; Bertaco, 2003: Ch. 15; Serra, 2003: Ch. 27; Ferreira, 2007: Ch. 5]: (0) present (Fig. 7a-b); (1) absent (Fig. 7c).

Infraorbital bone reduction and apparent loss are common in small and miniature characiforms of divergent clades (Weitzman & Fink, 1983). Weitzman & Malabarba (1999) observed this character in *Spintherobolus* species and *Grundulus bogotensis* (Humboldt), and

suggested the infraorbital loss as a synapomorphy for *Spintherobolus*. The loss of the IO6 is a derived condition in Characidae, and occurs only in *Rachoviscus* (state 1). The sixth infraorbital is an independent bone located in lateral surface of cranium (just below the frontal) above the sphenotic spine or pterosphenotic. The infraorbital 6 possess a laterosensory canal that is connected with the laterosensory canal of the parietal bone.

Character 37 (CI = 0.33) - Anterior portion of infraorbital 1: (0) broad, with an anterior laminar bone projection from the bony tube of the laterosensory canal (Fig. 7b); (1) narrow, reduced to the bony tube of laterosensory canal (Fig. 7a).

Character 38 (CI = 0.20) - Infraorbital 1 and lateral ethmoid: (0) posterior portion of infraorbital 1 anterior to lateral ethmoid; (1) posterior portion of infraorbital 1 at alignment with lateral ethmoid; (2) posterior portion of infraorbital 1 posterior to lateral ethmoid.

Character 39 (CI = 0.14) - Position of antorbital bone: (0) anterior portion not contacting infraorbital 1; (1) anterior portion contacting infraorbital 1.

Character 40 (CI = 0.33) - Shape of antorbital [Vari & Harold, 2001: Ch. 28; Bertaco, 2003: Ch. 12; Ferreira, 2007: Ch. 3]: (0) short, anterior and posterior portions similar; (1) elongate, anterior portion broad and posterior portion narrow; (2) elongate, anterior and posterior portions similar.

According to Vari & Harold (2001) the antorbital in *Creagrutus* and *Piabina* is typically elongate, as confirmed here in *Piabina argentea*. All *Hemibrycon* species have an elongate antorbital with anterior portion broad and posterior portion narrow (state 1), also observed in *Bryconamericus exodon* (see fig. 5 in Serra & Langeani, 2006:6).

## HYOMANDIBULAR ARCH

Character 41 (CI = 0.12) - Shape of palatine bone [Ferreira, 2007: Ch. 76]: (0) square or rectangular (Fig. 8a); (1) middle portion narrow (Fig. 8b).

Ferreira (2007) observed a square or rectangular palatine bone (state 0) in all *Knodus* species and in most taxa included in her analysis, as also recognized in almost taxa of this study.

Character 42 (CI = 1.00) - Position of palatine bone [Ferreira, 2007: Ch. 75]: (0) without contact with mesopterygoid (Fig. 8a); (1) in contact with mesopterygoid (Fig. 8c).

Character 43 (CI = 0.25) - Foramen in the palatine bone [Ferreira, 2007: Ch. 74]: (0) absent (Fig. 8b-c); (1) present (Fig. 8a).

Bührnheim (2006) analyzed the shape of palatine of the Cheirodontinae and other characids, and only pointed that *Hemibrycon* sp. (= *H. jelskii*) and *Diapoma* have a conspicuous central fenestra on palatine. Serra & Langeani (2006) described a large fenestra located in the anterior and medial portion of the palatine bone in *Bryconamericus exodon*, and found a similar fenestra in *Hemibrycon boquiae* as observed in this study. Furthermore, those authors suggested that the presence of the perforated palatine bone can be a possible synapomorphy for the Clade A *sensu* Malabarba & Weitzman, 2003.

In the *Hemibrycon* species occurs the two states. Among outgroup taxa the presence of foramen in the palatine bone (state 1) is found in *Bryconamericus* species.

Character 44 (CI = 0.25) - Posterior region of metapterygoid [Lucena, 1993: Ch. 57; Vari & Harold, 2001: Ch. 23; Benine, 2004: Ch. 43; Ferreira, 2007: Ch. 67]: (0) with a concavity (Fig. 9d); (1) with an opening nearly or totally closed (Fig. 9a-c).

The posterior region of metapterygoid can present a concavity or foramen where is located a blood vessel (Vari & Harold, 2001). In this analysis it was observed a variation on the degree of development of the metapterygoid concavity, as also observed in *Creagrutus* species by Vari & Harold (2001) and in *Knodus* species by Ferreira (2007).

Character 45 (CI = 0.25) - Position of the fenestra in the posterior region of metapterygoid [Ferreira, 2007: Ch. 68]: (0) median (Fig. 9a); (1) inferior.

Character 46 (CI = 0.25) - Posterodorsal region of metapterygoid: (0) concave (Fig. 9a); (1) straight, without concavity (Fig. 9b).

Character 47 (CI = 0.16) - Shape of ectopterygoid bone [Benine, 2004: Ch. 40; Ferreira, 2007: Ch. 62]: (0) broad and abruptly narrow in the posterior portion (Fig. 8a); (1) elongate and gradually narrow in the posterior portion.

The state 0 was considered a synapomorphy for *Knodus* by Ferreira (2007), as confirmed in *Knodus meridae* in this study. All *Hemibrycon* species have ectopterygoid bone broad and abruptly narrow in the posterior portion. This state was also observed in other taxa included in this analysis.

Character 48 (CI = 0.25) - Posteroventral region of ectopterygoid and anterodorsal region of quadrate: (0) ectopterygoid clearly surpassing the superior edge of quadrate (Fig. 9d); (1) ectopterygoid slightly surpassing the superior edge of quadrate (Fig. 8a); (2) ectopterygoid not reaching the superior edge of quadrate (Fig. 8b).

Character 49 (CI = 0.20) - Articular-quadrate joint [Bertaco, 2003: Ch. 7]: (0) situated approximately on the vertical passing through the center of the orbits; (1) situated anterior to a vertical passing through the center of the orbits; (2) situated posterior to vertical passing through the center of the orbits.

Character 50 (CI = 0.16) - Dorsal stem of quadrate [Bertaco, 2003: Ch. 11; Ferreira, 2007: Ch. 73]: (0) broad and long (Fig. 9a); (1) broad and short (Fig. 9b); (2) narrow and elongate (Fig. 9c).

The quadrate is a laminar bone that lies over dorsal surface of the preopercle. This bone possesses three stems: one superior (or dorsal) stem contacting the metapterygoid, and two posterior slender stems projected backward (Weitzman, 1962).

Ferreira (2007) in her analysis identified the same character states for the dorsal stem of quadrate.

Character 51 (CI = 0.14) - Dorsal profile of anterior stem of quadrate: (0) straight or smoothly convex, not divided in two sections (Fig. 9a); (1) divided in two sections (Fig. 9b).

Character 52 (CI = 0.33) - Shape of the fenestra located between quadrate and metapterygoid bones [Lucena, 1993: Ch. 60; Lucena & Menezes, 1998: Ch. 15; Bertaco, 2003: Ch. 9; Benine, 2004: Ch. 45; Zanata & Vari, 2005: Ch. 102; Ferreira, 2007: Ch. 70]: (0) oval, horizontally elongated (Fig. 9a-c); (1) rounded, approximately circular (Fig. 9d).

All *Hemibrycon* species and the majority of outgroup taxa possess a metapterygoid-quadrate fenestra oval (horizontally elongated), except *Bryconops melanurus*, *Charax stenopterus*, *Hollandichthys multifasciatus*, and *Pseudochalceus lineatus*, also observed by

Bertaco (2003). According to Vari (1979) the presence of the metapterygoid-quadrate fenestra horizontally elongated can be considered a plesiomorphic condition for Characiformes.

Character 53 (CI = 0.14) - Posterodorsal margin of opercle [Bertaco, 2003: Ch. 31]: (0) nearly straight or smoothly concave (Fig. 10a); (1) strongly concave (Fig. 10b); (2) convex (Fig. 10c).

Character 54 (CI = 0.40) - Dorsal borders of the hyomandibular and opercle: (0) dorsal border of opercle more elevated than that of the hyomandibular (Fig. 10a); (1) opercle and hyomandibular dorsal borders nearly aligned; (2) dorsal border of opercle below that of the hyomandibular.

Character 55 (CI = 0.20) - Dorsal surface of parasphenoid: (0) strongly concave; (1) straight or smoothly concave.

#### BRANCHIAL APPARATUS

Character 56 (CI = 0.12) - Gill gland on first arch in mature males: (0) absent; (1) present (Fig. 11).

The gill gland is formed by glandular tissue and modified gill filaments. It was first reported to *Corynopoma riisei* (Burns & Weitzman, 1996), and later described to other stevardiine genera (Bushman *et al.*, 2002), some members of the subfamily Cheirodontinae (Oliveira, 2003; Bührnheim & Malabarba, 2006), in males of *Aphyocharax anisitsi* (Gonçalves *et al.*, 2005) and in sexually active males of *Bryconadenos tanaothoros* (Weitzman *et al.*, 2005). The gill gland was found in most species of *Hemibrycon*, except in *H. polyodon*, *H. dentatus*, *Hemibrycon* n. sp. 1, *Hemibrycon* n. sp. 2, and *Hemibrycon* n. sp. 3

possible due to the small samples of males. In *Hemibrycon* species, the gill gland comprises the anteroventral portion of the first gill arch, usually including about 10 gill filaments. Bührnheim (2006) also reported the gill gland in males of *Hemibrycon* sp. (= *H. jelskii*).

Character 57 (CI = 0.16) - Length of basihyal [Bertaco, 2003: Ch. 33]: (0) short; (1) elongate (Fig. 12b).

Character 58 (CI = 0.11) – Shape of basihyal [Benine, 2004: Ch. 54; Ferreira, 2007: Ch. 82]: (0) distal region broad, more than two times wider than proximal region (Fig. 12a); (1) narrow, one or two times wider than proximal region (Fig. 12b).

All examined species of *Hemibrycon* have the distal region of basihyal narrow, one or two times wider than proximal region, except in *Hemibrycon divisorensis*, *Hemibrycon* n. sp. 1, and *Hemibrycon* n. sp. 4.

Character 59 (CI = 0.15) - Urohyal bone [Benine, 2004: Ch. 51; Ferreira, 2007: Ch. 79]: (0) bony flange extending more than two thirds of bone length; (1) bony flange extending to half-length of bone; (2) bony flange restrict to anterior portion of bone.

Character 60 (CI = 0.25) - Length of gill rakers of first gill arch [Benine, 2004: Ch. 55; Bührnheim, 2006: Ch. 87-88]: (0) longer, when depressed reaching the base of two adjacent gill rakers (Fig. 11); (1) very long, when depressed reaching the base of three or more adjacent gill rakers; (2) short, when depressed reaching the base of the adjacent gill raker.

*Bryconadenos tanaothoros*, *Carlastyanax aurocaudatus*, *Knodus meridae*, *Othonocheirodus* sp., and *Piabina argentea* have short gill rakers in the first gill arch (state



0). *Astyanax* spp., *Bryconops melanurus*, *Poptella brevispina*, *Rhoadsia altipinna* and examined members of Stevardiinae have very long gill rakers.

Character 61 (CI = 0.28) - Number of gill rakers of upper branch of first gill arch [Bührnheim, 2006: Ch. 89]: (0) 10 to 14; (1) six to nine (Fig. 11); (2) four to five.

The high number of gill rakers of the upper branch of first gill arch (state 0) is found in *Astyanax* spp., *Brycon pesu*, *Landonia latidens*, *Poptella brevispina*, and *Rhoadsia altipinna*. All *Hemibrycon* species and the most outgroup taxa have six to nine gill rakers (state 1). The smallest number of gill rakers (state 2) is found in few examined taxa (*Carlastyanax aurocaudatus*, *Charax stenopterus*, and *Hysteronotus megalostomus*).

Character 62 (CI = 0.33) - Number of gill rakers on lower branch of first gill arch [Bührnheim, 2006: Ch. 90]: (0) 12 to 16; (1) eight to 11 (Fig. 11); (2) five to seven.

The high number of gill rakers on the lower branch of the first gill arch (state 0) is found in *Astyanax* spp., *Brycon pesu*, *Landonia latidens*, and *Poptella brevispina*. All *Hemibrycon* species and most outgroup taxa have eight to 11 gill rakers (state 1). The reduced number of gill rakers (state 2) is found in few examined taxa (*Bryconadenos tanaothoros*, *Carlastyanax aurocaudatus*, and *Piabina argentea*).

Bührnheim (2006) in her analysis of Cheirodontinae, observed 13-14 inferior gill rakers in *Brycon pesu*. This condition also was observed here.

Character 63 (CI = 1.00) - Size of gill rakers of the upper branch of first gill arch: (0) length increases gradually from first to last gill raker (Fig. 11); (1) length increases abruptly from first to last gill raker; (2) gill rakers of similar size.

In *Carlastyanax aurocaudatus* the gill rakers have similar size (state 2). In *Charax stenopterus* and *Hollandichthys multifasciatus* the gill rakers increase abruptly from first to last (state 1).

Character 64 (CI = 1.00) - Number of gill rakers in the hypobranchial bone: (0) two to three; (1) only one.

Among examined taxa only *Aphyocharax pusillus* and *Carlastyanax aurocaudatus* have one gill raker in the hypobranchial (state 1).

Character 65 (CI = 1.00) - Shape of the anteriormost branchiostegal ray in males [Bührnheim, 2006: Ch. 77]: (0) ventral border nearly straight (Fig. 13a); (1) ventral border concave on the anterior half length (Fig. 13b).

This character was first observed by Bührnheim (2006) in his analysis of members of the Cheirodontinae. The author identified a concavity in the anteriormost branchiostegal ray forming a hole ventrally on head exactly near the most ventral portion of the gill gland of the first gill arch. Also, the author recognized that this osseous modification can be related to the gill gland, and facilitate the excretion. According to Bührnheim (2006), the gill gland is present in all Cheirodontinae members, except in little taxa, but the modifications in the branchiostegal ray is not present in all members of this subfamily.

Among *Hemibrycon* species included in the analysis, it was not possible to verify the presence of this character in *Hemibrycon* n. sp. 1 due the absence of males.

Character 66 (CI = 0.33) - Basibranchial 4 [Lucena, 1993: Ch. 74; Benine, 2004: Ch53; Bührnheim, 2006: Ch. 82]: (0) totally cartilaginous; (1) partially ossified, central piece osseous.

Bührnheim (2006) recognized the state 1 as a unique synapomorphy to support a broad clade comprising *Hemibrycon* (= *H. jelskii*), *Diapoma*, and members of Cheirodontinae, *Aphyocharacidium*, *Phenacogaster*, *Astyanax*, *Aphyocharax*, and *Carlana*.

Lucena (1993) observation of the basibranchial 4 in the *Hemibrycon metae* (= *H. surinamensis*) agrees with the present study.

## DORSAL FIN

Character 67 (CI = 0.33) - Number of dorsal fin rays: (0) ii+9; (1) ii+8.

The usual characid dorsal fin-rays count is two anterior unbranched rays plus nine branched rays. Malabarba & Weitzman (2003) recognized a putative monophyletic clade, Clade A, including *Hemibrycon*, based on the derived presence of two anterior unbranched rays plus eight branched rays. All *Hemibrycon* species have ten (ii+8) dorsal-fin rays. The number of elements in the dorsal-fin skeleton of characid fishes rarely varies. Among examined taxa, the state 1 was found only in the members of Clade A, been recognized as a synapomorphy for this Clade, like proposed previously by Malabarba & Weitzman (2003).

The derived condition (state 1) also was found in *Carlastyanax aurocaudatus* as also observed by Malabarba & Weitzman (2003).

Character 68 (CI = 0.50) - Relative position of the dorsal fin [Benine, 2004: Ch. 65; Ferreira, 2007: Ch. 92]: (0) dorsal-fin origin located anterior to vertical through anal-fin origin; (1) dorsal-fin origin located posterior or in the vertical through anal-fin origin.

The dorsal-fin origin located posterior or in the vertical through anal-fin origin is found only in *Charax stenopterus* and *Hysteronotus megalostomus*.

Character 69 (CI = 0.12) - Relative position of the last dorsal-fin ray [Ferreira, 2007: Ch. 93]: (0) located anterior or in the vertical through anal-fin origin; (1) located posterior to vertical through anal-fin origin.

In all *Hemibrycon* species the dorsal fin base located posterior to vertical through anal-fin origin (state 1), except in *H. helleri* and *Hemibrycon* n. sp. 3 (state 0).

Character 70 (CI = 0.50) - Anterior dorsal-fin rays in males [Bertaco, 2003: Ch. 36; Cardoso, 2003: Ch. 28]: (0) not elongate; (1) elongate.

The presence of the anterior dorsal-fin rays elongate in males (state 1) is found in *Nematobrycon palmeri*, *Nematocharax venustus* (see fig. 1 in Weitzman *et al.*, 1986), *Odontostilbe fugitiva* (Bührnheim, 2006), and in larger specimens of *Pseudochalceus lineatus* (Bertaco, 2003) and *Rhoadsia altipinna* (Cardoso, 2003).

Malabarba (1998) proposed the elongation of dorsal-fin rays as a synapomorphy to *Odontostilbe*. Later, Bührnheim (2006) recognized this elongation as a synapomorphy to a clade formed by species of *Odontostilbe* and *Holoshesthes*. Recently, the elongation of dorsal- and pelvic-fin rays in males was used to diagnose *Astyanax fasciatus* by Melo & Buckup (2006).

#### ADIPOSE FIN

Character 71 (CI = 0.10) - Adipose fin origin: (0) located between last sixth and seventh caudal vertebrae; (1) located between last eighth and ninth caudal vertebrae.

#### PECTORAL FIN

Character 72 (CI = 0.25) - Total number of pectoral-fin rays: (0) 12 to 16; (1) 10 to 11.

All species of *Hemibrycon* have 12 to 16 pectoral-fin rays, except *Hemibrycon* n. sp. 1 that possess 10-11 pectoral-fin rays.

Character 73 (CI = 0.11) - Shape of postcleithrum 1: (0) broad, and with upper portion larger than lower; (1) elongate, and with upper and lower portions of similar size.

Character 74 (CI = 0.25) - Anteroventral bony projection of postcleithrum 1: (0) absent; (1) present.

The anteroventral bony projection of postcleithrum 1 is absent in all examined species of *Hemibrycon*. This bony projection is found only in *Bryconadenos tanaothoros*, *Bryconamericus exodon*, *Charax stenopterus* and *Rhoadsia altipinna*.

Character 75 (CI = 0.16) – Relative size of postcleithrum 2: (0) larger than half-length of postcleithrum 3 (Fig. 14c); (1) approximately equal to half-length of postcleithrum 3 (Fig. 14a); (2) smaller than half-length of postcleithrum 3 (Fig. 14b).

Character 76 (CI = 0.16) - Laminar bony flange on postcleithrum 3 [Bertaco, 2003: Ch. 42; Benine, 2004: Ch. 69; Zanata & Vari, 2005: Ch. 135; Bührnheim, 2006: Ch. 98; Ferreira, 2007: Ch. 86]: (0) absent (Fig. 14b); (1) present (Fig. 14a, c).

Weitzman (1962) described the third postcleithrum shape like a spine bone, and situated below second postcleithrum. According to Bertaco (2003), Benine (2004), and Ferreira (2007) some characid taxa have a laminar bony flange on postcleithrum 3, usually located in the median portion of this bone.

Among *Hemibrycon* species, the laminar bony flange on postcleithrum 3 is absent in *H. metae*, *Hemibrycon* n. sp. 1, and *Hemibrycon* n. sp. 3.

According to Serra & Langeani (2006), the postcleithrum 3 is a sinuous and elongate bone with approximately the same width in all its length in most characiforms. Those authors recognized the presence of a posterior convex projection on the postcleithrum 3 (here named as laminar bony flange) as a synapomorphy for the Serrasalminae plus characids that lack the supraorbital bone and its absence as a synapomorphy for Clade A genera *sensu* Malabarba & Weitzman (2003).

By parsimony, the postcleithrum 3 bearing a laminar bony flange resulted in the consensus cladogram as a synapomorphy of all non-clade A characid genera lacking the supraorbital (Clade 3), except *Aphyocharax pusillus* and *Carlastyanax aurocaudatus* that are grouped among clade A genera.

The laminar bony flange, however, has been detected in several *Hemibrycon* species, being considered a synapomorphy of the Clade H2, with a reversion in *Hemibrycon metae*.

Character 77 (CI = 0.22) - Upper tip of postcleithrum 3: (0) below dorsal border of posterior stem of the scapula (see fig. 12, *Bryconamericus exodon* in Serra & Langeani, 2006); (1) aligned with dorsal border of posterior stem of the scapula (Fig. 15b); (2) above dorsal border of posterior stem of the scapula (Fig. 15a, c).

According to Weitzman (1962) the postcleithrum 3 is located below of postcleithrum 2 and posterior to scapula bone. In the *Hemibrycon* species the upper tip of postcleithrum can be aligned with dorsal border of posterior stem of the scapula (state 1) or above that point (state 2).

Character 78 (CI = 0.25) - Posteroventral margin of cleithrum [Benine, 2004: Ch. 68; Ferreira, 2007: Ch. 83]: (0) strongly concave (Fig. 15a); (1) smoothly concave or sinuous (Fig. 15c).

The cleithrum is a large and developed bone with the posterolateral portion exposed, and is located just after subopercle and opercle (Weitzman, 1962).

Only two states were found in this analysis, as observed by Ferreira (2007). All *Hemibrycon* species have the posteroventral margin of cleithrum strongly concave, as observed in *Aphyocharax pusillus*, *Bryconadenos tanaothoros*, *Brycon pesu*, *Bryconamericus exodon*, *Carlasyanax aurocaudatus*, and *Piabina argentea*.

Character 79 (CI = 0.25) - Profile of posteroventral border of cleithrum (above pectoral-fin origin): (0) convex or near straight (Bertaco, 2003: fig. 12); (1) smoothly concave (Fig. 15a); (2) strongly concave (Fig. 15d).

Character 80 (CI = 0.16) - Dorsolateral border of posterior laminar projection of cleithrum: (0) slightly convex or straight (Fig. 15a); (1) concave (Fig. 15b); (2) strongly concave (Fig. 15d).

Character 81 (CI = 0.66) - Profile of posterior laminar projection of cleithrum just above the pectoral-fin origin: (0) convex (Fig. 15a); (1) slightly sharp-pointed (Fig. 15d); (2) nearly straight (Bertaco, 2003: fig. 12).

Character 82 (CI = 0.09) - Posteroventral bony projection of coracoid: (0) present (Fig. 15c); (1) absent (Fig. 15a).

#### PELVIC FIN

Character 83 (CI = 0.28) - Total number of pelvic-fin rays [Lucena, 1993: Ch. 95; Buckup, 1998: Ch. 63; Malabarba, 1998: Ch. 14; Weitzman & Malabarba, 1999: Ch. 19; Bertaco,

2003: Ch. 57; Benine, 2004: Ch. 70; Zanata & Vari, 2005: Ch. 138; Ferreira, 2007: Ch. 88]: (0) eight; (1) seven; (2) six.

According to Weitzman (1962) the majority of characids have eight pelvic-fin rays. All species of *Hemibrycon* have eight pelvic-fin rays, except *Hemibrycon* n. sp. 1 with seven pelvic-fin rays. Weitzman & Malabarba (1999) pointed out that a low number of the pelvic-fin rays occurs in certain miniature or small sized characiforms, e.g. *Priocharax* Weitzman & Vari, and according to those authors, *Spintherobolus broccae* Myers.

Character 84 (CI = 0.23) - Location of pelvic bone [Weitzman & Menezes, 1998: Ch. 20; Benine, 2004: Ch. 73]: (0) anterior tip of pelvic bone occurs in region ventral to ventral tips of third and fourth pleural ribs; (1) anterior tip of pelvic bone occurs in region ventral to ventral tips of second and third pleural ribs; (2) anterior tip of pelvic bone occurs in region ventral to ventral tips of first and second pleural ribs; (3) anterior tip of pelvic bone occurs in region ventral to ventral tips anterior of first pleural ribs.

Character 85 (CI = 0.50) - Location of the dorsal longitudinal crest of pelvic bone [Benine, 2004: Ch. 71; Ferreira, 2007: Ch. 89]: (0) located near the external border of pelvic bone (Fig. 16a); (1) located near to median portion of pelvic bone (Fig. 16b).

The pelvic bones are elongate structures and parallel along belly floor (Weitzman, 1962) that present a longitudinal crest located in near the external border or near to median portion. The state 1 was found only *Charax stenopterus* and *Poptella brevispina*. Benine (2004) and Ferreira (2007) recognized three character states for this structure. According to Benine (2004) the position of longitudinal crest of pelvic bone can be related with the body depth, not observed in this study.



Character 86 (CI = 0.20) - Anterior portion of pelvic bone [Bertaco, 2003: Ch. 56; Benine, 2004: Ch. 75]: (0) broad, with lateral expansion on the inner surface (Fig. 16a); (1) narrow, without lateral expansion on the inner surface (Fig. 16b).

Among *Hemibrycon* species only *Hemibrycon* n. sp. 2 has the anterior portion of pelvic bone narrow, without lateral expansion on the inner surface (state 1). This state also observed in *Bryconops melanurus*, *Charax stenopterus*, *Mimagoniates rheocharis* and *Piabina argentea*.

Character 87 (CI = 0.16) - Posterior bony projection of ischiac process: (0) short and curve; (1) elongate.

All *Hemibrycon* species present a short and curve bony projection on ischiac process (state 0), except *Hemibrycon taeniurus* and *Hemibrycon* n. sp. 1., also observed in most outgroup taxa.

Character 88 (CI = 0.16) - Anterior bony projection of ischiatic process: (0) absent (Fig. 16b); (1) present (Fig. 16a).

All *Hemibrycon* species present an anterior bony projection on ischiac process (state 1), also observed in most outgroup taxa.

#### ANAL FIN

Character 89 (CI = 0.20) - Number of branched anal-fin rays [Lucena, 1993: Ch. 103; Buckup, 1998: Chs. 65-66; Weitzman & Menezes, 1998: Ch. 35; Weitzman & Malabarba, 1999: Ch. 20; Benine, 2004: Ch. 78]: (0) 12 to 22; (1) 23 to 34; (3) 37 to 48.

Buckup (1998) utilized two character states for anal-fin ray counts, anal fin short with 13 or fewer rays, and anal fin long with at least 19 rays. This author also commented that the

significance of the difference between these two character states has been discussed by Weitzman (1964) and Géry (1972). Weitzman & Menezes (1998) coded this character also in two states, more than eighteen and eighteen or fewer branched anal-fin rays. As pointed by Weitzman & Malabarba (1999) the number of anal-fin rays in the Characidae is quite variable. Those authors recognized as primitive the presence of 15 or more branched anal-fin rays as found in the apparently most primitive American characid species such the species of *Brycon*. The reduced number of branched anal-fin rays (13-16) was suggested as a synapomorphy to *Spintherobolus* (Weitzman & Malabarba, 1999).

In this study three character states are recognized for anal-fin ray counts. Among all examined taxa, the state 0 was assigned to only two *Hemibrycon* species (*Hemibrycon* n. sp. 2, 20-24, mean = 22.1, and *H. helleri*, 19-23, mean = 21.7) and one outgroup taxa (*Bryconamericus exodon*, 20-24, mean = 22.0, in Serra & Langeani, 2006) based on the mean of the anal-fin rays count.

Character 90 (CI = 0.50) - Elongation of the last anal-fin rays of males [Bertaco, 2003: Ch. 60]: (0) absent; (1) present.

This elongation is found in males of *Hollandichthys multifasciatus*, *Pseudochalceus lineatus*, and *Nematobrycon palmeri* as previously recognized by Bertaco (2003). See figs. 23-30, *Hollandichthys multifasciatus* in Bertaco (2003:132-139).

Character 91 (CI = 0.14) - Lobe in the anterior portion of the anal fin of males: (0) absent (Fig. 28); (1) present (see fig. 2, *Bryconadenos tanaothoros* in Weitzman *et al.*, 2005: 334).

The presence of a developed lobe in the anterior portion of anal-fin of males is found in *Aphyocharax pusillus*, *Bryconadenos tanaothoros*, *Carlastyanax aurocaudatus*, *Diapoma speculiferum*, and *Nematobrycon palmeri*.

## CAUDAL FIN

Character 92 (CI = 0.16) - Extension of the caudal fin squamation [Ferreira, 2007: Ch. 114]: (0) extended to the caudal-fin base, with three or less scale vertical rows; (1) extended beyond of the caudal-fin base, with four or more vertical rows of scales.

The species of *Hemibrycon* have four to five or six vertical rows of scales in the caudal fin (state 1). Among outgroup, this character is found in *Knodus meridae* (see fig. 13 in Weitzman *et al.*, 2005:346) examined members of Stevardiinae, *Nematocharax venustus*, and *Poptella brevispina*.

Character 93 (CI = 0.33) - Large scales on the caudal-fin lobes: (0) absent; (1) present (Fig. 17).

*Hemibrycon* species possess one large scale in the proximal portion of each caudal-fin lobe. Among examined taxa this character is found only in *Bryconamericus peruanus* and *Othonocheirodus* sp.

Character 94 (CI = 0.25) - Size of the caudal-fin scales [Ferreira, 2007: Ch. 116]: (0) scales with the same size of those of the caudal peduncle; (1) scales smaller than those of the caudal peduncle; (2) scales larger than those of the caudal peduncle (Fig. 17).

The scales found in the caudal-fin of *Hemibrycon* species are larger than those of the caudal peduncle (state 2). This character also occurs in *Carlastyanax aurocaudatus*, *Diapoma speculiferum* and *Hysteronotus megalostomus*.

Character 95 (CI = 0.50) - Caudal-fin gland [Weitzman & Menezes, 1998: Ch. 9; Ferreira, 2007: Ch. 117]: (0) absent; (1) present.

Among examined taxa, the presence of a caudal-fin gland is found only in members of the Stevardiinae and Glandulocaudinae, as previously recognized and discussed by Weitzman *et al.* (2005).

#### FIN BONY HOOKS

Character 96 (CI = 0.33) - Bony hooks in mature males [Bührnheim, 2006: Ch. 138]: (0) present in pelvic- and anal-fin rays; (1) present in all fins rays, except caudal-fin.

Mature males of *Hemibrycon* species possess bony hooks on rays of all fins, except the caudal fin (state 1). This character was not coded for *Hemibrycon* n. sp. 1 due to the lack of examined males, and was informed as state 0 for *H. dentatus*, but the examination of additional male specimens is needed to confirm this state for this species. Among Clade A\* genera, the state 1 was found only in *Hemibrycon* species. Among remaining characids, the state 1 occurs only in *Nematocharax venustus* and *Odontostilbe fugitiva*.

The presence of hooks on the anal- and pelvic-fin rays and sometime caudal-fin rays of males is often found in several genera and subfamilies of the Characidae (Azpelicueta & Garcia, 2000; Malabarba & Weitzman, 2003), and usually represents a secondary sexual character. However, the occurrence of bony hooks in all fins, including dorsal, caudal, and pectoral fins of males is uncommon in characids. Recently, Gonçalves *et al.* (2005) observed a positive correlation between mean gonadosomatic index of maturing and mature males and the number of anal-fin rays bearing hooks in *Aphyocharax anisitsi*, suggesting these hooks develop along with testes maturation, and once developed are retained by the males.

Bührnheim (2006) recognized the presence of bony hooks in all fins rays as uniquely derived feature for a clade formed by two species of *Holoshesthes*.

Character 97 (CI = 0.22) - Distribution of bony hooks in the anal-fin rays of mature males [Bertaco, 2003: Ch. 64]: (0) starting in the last unbranched and distributed along anterior branched rays; (1) starting in the last unbranched and distributed along near all branched rays; (2) distributed only in the anterior branched rays.

Presence of hooks in the anal fin is a character widespread in Characidae, showing some specializations that have been useful in diagnosing some included taxa. The putative primitive condition regarding their distribution along the anal fin is its presence starting in the last unbranched and/or first branched anal-fin rays (Malabarba, 1998). Almost all *Hemibrycon* species have bony hooks present in the last unbranched and distributed along near all branched rays, except in *Hemibrycon* n. sp. 3 (state 0) and *H. divisorensis* (state 2). This character was not coded for *Hemibrycon* n. sp. 1 by the lack of examined males. In the *Hemibrycon* species the bony hooks are more developed in the anteriormost anal-fin rays and smaller in the remaining rays.

The specimens examined of *Brycon pesu* had no hooks on fins, but these are present in other *Brycon* species, according to Lima (2001). Since presence of hooks depends on the examination of mature specimens, this character was not informed for *B. pesu*. Also it was not observed hooks on pelvic and anal fins of specimens of *Carlastyanax aurocaudatus*, *Landonia latidens*, *Nematobrycon palmeri*, *Othonocheirodus* sp., *Pseudochalceus lineatus* and *Rhoadsia altipinna*.

Character 98 (CI = 0.12) - Distribution of bony hooks along anal-fin rays of mature males [Malabarba, 1998: Ch. 27; Bührnheim, 2006: Ch. 147]: (0) distributed along distal two third of length of anal-fin rays; (1) distributed along distal half or distal third portion of anal-fin rays.

Malabarba (1998) considered the occurrence of bony hooks along anal-fin rays along distal half or distal third portion of anal-fin rays (state 1) a synapomorphy for a clade formed by *Macropsobrycon*, *Compsura*, *Saccoderma* and an undescribed genus of the Cheirodontinae. Bührnheim (2006) also considered this character a synapomorphy for a tribe of the Cheirodontinae, the Compsurini. All *Hemibrycon* species have bony hooks distributed along distal two third of length of anal-fin rays (state 0).

Character 99 (CI = 0.33) - Distribution of bony hooks on the anal-fin rays of males [Malabarba, 1998: Ch. 25; Cardoso, 2003: Ch. 30; Bührnheim, 2006: Ch. 145]: (0) anal-fin hooks paired, bilaterally symmetrical; (1) anal-fin hooks unpaired, bilaterally asymmetrical, and with irregular arrangements.

The males of all *Hemibrycon* species have bony hooks paired and bilaterally symmetrical on the anal-fin rays. This character is found in most outgroup taxa, except in *Aphyocharax pusillus*, *Bryconamericus exodon*, *Nematocharax venustus* and *Odontostilbe fugitiva*.

#### PROCURRENT CAUDAL-FIN RAYS

Character 100 (CI = 0.20) - Location of base of the first dorsal procurrent caudal-fin ray: (0) located posterior to the last caudal vertebra; (1) located anterior to the last caudal vertebra.

The base of the first dorsal procurrent caudal-fin ray is located anterior to the last caudal vertebra in all *Hemibrycon* species, except in *Hemibrycon jabonero* (state 1). The state 1 also was found only in *Bryconadenos tanaothoros*, *Knodus meridae*, *Mimagoniates rheocharis*, and *Poptella brevispina*.

Character 101 (CI = 0.16) - Number of dorsal procurrent caudal-fin rays: (0) 10 to 15 (usually 11 to 12); (1) 8 to 10 (usually 8 to 9).

Among some taxa included in the analysis a small overlapping in the range of dorsal procurrent caudal-fin rays was found, but it was possible to recognize two character states: 10 to 15 (state 0) and 8 to 10 (state 1) based on the means of these counts.

## VERTEBRAE

Character 102 (CI = 0.25) - Number of total vertebrae [Vari & Harold, 2001: Ch. 56; Benine, 2004: Ch. 57; Ferreira, 2007: Ch. 100]: (0) 38 to 43; (1) 33 to 37.

The low number of vertebrae was proposed by Harold & Vari (1994) and Vari & Harold (2001) as a synapomorphy for two Trans-Andean *Creagrutus* species. According to Vari & Harold (2001) the Cis-Andean *Creagrutus* species and *Piabina argentea* have 34 to 43 vertebrae, as observed in this study for *P. argentea*. *Hemibrycon* species have a higher number of total vertebrae (state 1) when compared with the examined taxa of Clade A, except in *Bryconamericus* spp. with 38 total vertebrae.

Character 103 (CI = 0.29) - Number of vertebrae before the first dorsal-fin pterygiophore (including Weberian Apparatus vertebrae) [Benine, 2004: Ch. 58; Ferreira, 2007: Ch. 102]: (0) nine; (1) ten; (2) eleven; (3) twelve; (4) thirteen; (5) fourteen.

The first dorsal-fin pterygiophore is situated between neural spines of the precaudal vertebrae. According to Ferreira (2007), the position of first dorsal-fin pterygiophore can indicate the dorsal fin position and the number of vertebrae. The author found a large variation in the position of first dorsal-fin pterygiophore relative to precaudal vertebrae, also observed in this analysis.

## SUPRANEURALS

Character 104 (CI = 0.50) - Position of the first supraneural [Bertaco, 2003: Ch. 91; Zanata & Vari, 2005: Ch. 122]: (0) anterior to the neural spine of fourth vertebra; (1) posterior to the neural spine of fourth vertebra.

The first supraneural in the *Hemibrycon* species and in most outgroup taxa is always posterior to the neural spine of fifth vertebra. Only *Brycon pesu*, *Bryconops melanurus* and *Bryconamericus exodon* have the first supraneural positioned anteriorly to the neural spine of the fourth vertebra.

Zanata & Vari (2005) observed the absence of supraneural anterior to neural spine associated with fourth vertebrae in *Astyanax*, *Charax*, *Cheirodon*, *Crenuchus*, *Hoplias* and *Tetragonopterus*. In this analysis, I also observed this character in *Astyanax* spp. and *Charax stenopterus*.

Character 105 (CI = 0.16) - Shape of supraneurals: (0) dorsal and ventral portions similar (Fig. 18a); (1) dorsal portion larger than ventral (Fig. 18b).

The supraneural bones are similar to the proximal radials of the dorsal fin (Weitzman, 1962), and usually the dorsal portion is larger than ventral (state 1) as observed in all *Hemibrycon* species and some outgroup taxa.

Character 106 (CI = 0.12) - Number of supraneurals: (0) six to nine; (1) three to five.

All species of *Hemibrycon* have a high number of supraneurals, six to nine (state 0), also observed in outgroup taxa.

Character 107 (CI = 0.11) - Laminar bony projections developed in the distal portions of the supraneurals: (0) absent (Fig. 18a); (1) present (Fig. 18b).



The supraneurals bones are much similar the proximal radials of the dorsal fin (Weitzman, 1962), and with usually with laminar bony projections in the distal portions, but some examined taxa this character can be absent (state 0), corresponding only a “tube” shape.

#### LATERO SENSORIAL SYSTEM

Character 108 (CI = 0.66) - Extent of the laterosensory canal of the lateral line [Zanata & Vari, 2005: Ch. 163; Bührnheim, 2006: Ch. 114]: (0) extending by almost all the length of middle caudal-fin rays; (1) extending to half-length of middle caudal-fin rays; (2) extending next to base of middle caudal-fin rays.

According to Bührnheim (2006) the laterosensory canal of the lateral line extending onto the caudal fin usually remains in cleared and stained specimens, conspicuously between the 10<sup>th</sup> and 11<sup>th</sup> principal caudal-fin rays. A condition also observed in this study.

In all *Hemibrycon* species, the laterosensory canal of the lateral line extends to half-length of middle caudal-fin rays.

Character 109 (CI = 0.25) - Lateral line [Malabarba, 1998: Ch. 60; Weitzman & Menezes, 1998: Ch. 16; Weitzman & Malabarba, 1999: Ch. 25; Cardoso, 2003: Ch. 33; Bührnheim, 2006: Ch. 153]: (0) complete; (1) incomplete.

The reduction of lateral line has been used often in defining characid genera since Eigenmann (*e.g.* 1915, 1917). Weitzman & Fink (1983) discussed laterosensory reduction in small characids and noted that its loss is often correlated with small size and has evolved several times in small characids. The lateral line reduction to 2 to 6 scales was proposed as a possible synapomorphy for the *Spintherobolus* species by Weitzman & Malabarba (1999).

All species of *Hemibrycon* have complete lateral line. The incomplete lateral line occurs in *Charax stenopterus*, *Pseudochalceus lineatus*, *Rhoadsia altipinna*, *Hollandichthys multifasciatus*, *Nematobrycon palmeri*, and *Rachoviscus* spp.

Character 110 (CI = 0.16) - Number of scales between the lateral line and dorsal-fin origin: (0) 6 to 10; (1) 4 to 5.

The smaller number of scales (state 1) was found in the taxa with relative low body depth and elongate body as *Bryconadenos tanaothoros*, *Bryconamericus exodon*, *Cyanocharax alburnus*, *Diapoma speculiferum*, *Knodus meridae*, *Odontostilbe fugitiva*, *Othonocheiroidus* sp., and *Piabina argentea*. All *Hemibrycon* examined species have 6 to 10 scales above lateral line (state 0).

#### COLOR PATTERN

Character 111 (CI = 0.33) - Humeral spot [Malabarba, 1998: Ch. 64; Weitzman & Malabarba, 1999: Ch. 1; Bührnheim, 2006: Ch. 157]: (0) present; (1) absent.

The absence of humeral spot was recognized as a synapomorphy for the subfamily Cheirodontinae by Malabarba (1998). Weitzman & Malabarba (1999) pointed that the absence of a humeral spot occurs in relative few characiform species, and suggested that this character occurred independently in certain characids. All *Hemibrycon* species have a humeral spot. Among outgroup taxa *Bryconops melanurus*, *Charax stenopterus*, and *Odontostilbe fugitiva* lack a humeral spot.

Character 112 (CI = 0.33) - Number of humeral spots [Bertaco, 2003: Ch. 86; Cardoso, 2003: Ch. 35]: (0) one; (1) two.

Bertaco (2003) found an ontogenetic variation in the number of humeral spots in juveniles and adults of *Hollandichthys* species. This character was not observed in *Hemibrycon* species. All *Hemibrycon* species have only one humeral spot. Among outgroup taxa only *Astyanax jacuhiensis*, *Nematocharax venustus*, *Poptella brevispina* and *Rhoadsia altipinna* possess two humeral spots (state 1).

Character 113 (CI = 0.16) - Size of humeral spot: (0) along 2 to 3 horizontal series of scales; (1) along 4 to 6 horizontal series of scales; (2) along 7 to 9 horizontal series of scales.

Among *Hemibrycon* species there are three character states. The smallest humeral spot is found only *Hemibrycon* n. sp. 1 (Fig. 54; state 0), and the largest humeral spot is found in *Hemibrycon jelskii* (Fig. 31) and *Hemibrycon helleri* (Fig. 45) (state 2). In the remaining species of genus occurs the state 1.

Character 114 (CI = 0.50) - Longitudinal stripes [Bertaco, 2003: Ch. 85]: (0) absent; (1) present.

Among examined taxa, the longitudinal stripes are present in *Hollandichthys multifasciatus*, and *Pseudochalceus lineatus*, as previously observed by Bertaco (2003). This character was used as one of the features to distinguish *Hollandichthys multifasciatus* from remaining characid genera (Bertaco, 2003).

Character 115 (CI = 0.40) - Adipose-fin color pattern: (0) adipose-fin unpigmented or hyaline; (1) adipose-fin densely pigmented; (2) only anterior portion of the adipose-fin densely pigmented.

The outgroup taxa, and *Hemibrycon* species have the adipose fin hyaline (state 0), except *Hemibrycon helleri* (Fig. 45) and *Hemibrycon* n. sp. 5 (Fig. 62). The anterior portion

of the adipose-fin densely pigmented is found only in *Hollandichthys multifasciatus*, being considered here an autapomorphy for the species.

Character 116 (CI = 0.11) - Anal-fin border pigmented forming a dark stripe: (0) absent; (1) present.

Almost all species of *Hemibrycon* have the anal-fin border pigmented forming a dark stripe (state 1), except *H. polyodon* (Fig. 27) and *Hemibrycon* n. sp. 1 (Fig. 54).

Character 117 (CI = 0.11) - Conspicuous caudal-peduncle spot [Cardoso, 2003: Ch. 37]: (0) absent; (1) present.

The *Hemibrycon* species have a caudal-fin spot.

Character 118 (CI = 1.00) - A wide black asymmetrical spot covering base of caudal-fin rays: (0) absent; (1) present.

The presence of a wide black asymmetrical spot covering base of caudal-fin rays is considered a synapomorphy for *Hemibrycon divisorensis* (see figs. 1 and 2 in the Chapter II) and *H. surinamensis* (Figs. 51-52).

Character 119 (CI = 0.14) - Middle caudal-fin rays: (0) unpigmented; (1) pigmented.

All species of *Hemibrycon* possess the middle caudal-fin rays dark pigmented, a character also found in outgroup taxa.

Character 120 (CI = 0.50) - Caudal-fin lobes: (0) one or two densely pigmented lobes; (1) unpigmented.

The occurrence of caudal-fin lobes pigmented is found in *Brycon pesu*, and *Bryconamericus exodon* (see fig. 1 in Serra & Langeani, 2006:3), and of the superior caudal-fin lobe pigmented in *Bryconops melanurus*.

Character 121 (CI = 0.10) - Distal tips of rays just above and below to middle caudal-fin rays densely pigmented: (0) absent; (1) present.

The presence of distal tips of rays just above and below to middle caudal-fin rays densely pigmented is found only in *Hemibrycon dariensis* (Figs. 42-43), being considered an autapomorphy for the species.

#### OTHER CHARACTERS

Character 122 (CI = 0.33) - Pseudotympanum [Malabarba, 1998: Ch. 1; Zanata & Vari, 2005: Ch. 199]: (0) absent; (1) present.

According to Malabarba (1998) the pseudotympanum is characterized by presence of a large and nearly triangular hiatus of muscles covering the anterior chamber of the swim bladder between the first and second pleural ribs. This character was interpreted as a synapomorphy for the subfamily Cheirodontinae by Malabarba (1998). Among examined taxa, the pseudotympanum is found only in *Charax stenopterus*, *Odontostilbe fugitiva*, and *Rhoadsia altipinna*. In this analysis it was considered only absence (state 0) or presence (state 1) of pseudotympanum, but in the Characidae there are various forms and degrees of muscle reduction over the anterior portion of the swim bladder as observed by Malabarba (1998), Vari & Zanata (2005).

Character 123 (CI = 0.20) - Insemination [Malabarba, 1998: Ch. 70; Weitzman & Menezes, 1998: Ch. 2; Bührnheim, 2006: Ch. 168]: (0) absent; (1) present.

Most characiforms appears to be externally fertilized (Burns *et al.*, 1998). In Characidae, insemination occurs in Stevardiinae (here represented by *Diapoma speculiferum*, *Hysteronotus megalostomus*, and *Landonia latidens*), in a tribe of the Cheirodontinae (Compsurini), and some other characid genera (*e.g.* *Attonitus*, *Creagrutus*, *Knodus*, *Bryconamericus pectinatus* and *Brittanichthys axelrodi*) (Burns *et al.*, 1995; Burns & Weitzman, 2005).

Histological analysis of mature ovaries of the *Hemibrycon* species demonstrates the absence of spermatozoa within the ovary, and histological analyses of testis confirm the occurrence of spherical sperm nuclei (aquasperm; Fig. 19), characteristic of externally fertilizing characids (Tables 3-4).

### **Phylogenetic relationships of *Hemibrycon***

The Cladogram of Figure 20 shows the strict consensus tree obtained from 65 equally parsimonious trees (CI = 0.22; RI = 0.52) achieved through the analysis of 123 characters from 45 taxa (Table 2). The analysis of 17 of 21 species (see Material and Methods) of *Hemibrycon* allows the recognition of the genus as monophyletic based on one exclusive synapomorphy and eleven non-exclusive synapomorphies. *Hemibrycon* is recognized as a member of the characid Clade A as previously proposed by Malabarba & Weitzman (2003) (see Figs. 21 and 22).

*Hemibrycon* Clade forms a polytomy with two groups formed by *Bryconamericus peruanus* plus *Bryconamericus* sp. (Clade K), and *Diapoma speculiferum*, *Hysteronotus megalostomus* plus *Mimagoniates rheocharis* (Clade L).

The strict consensus tree of 65 most parsimonious trees obtained showed *Bryconops melanurus* as a basal clade, sister group to the remaining characids (Clade 2). These were split in two large clades, one including all representatives of the Clade A *sensu* Malabarba &

Weitzman (2003) plus *Aphyocharax pusillus* and *Carlastyanax aurocaudatus*, herein also named as Clade A\*, and the other (Clade 3) including all remaining examined genera. Characters and states at each node of the cladogram are presented in Table 5.

Synapomorphies of *Hemibrycon* and internal clades according to Acctran optimization:

### ***Hemibrycon* Clade**

Synapomorphies:

- Antermost branchiostegal ray in males with ventral border concave on the anterior half length (Ch. 65.1; Fig. 13b).
- Number of maxillary teeth in adult specimens (Ch. 8.2). The *Hemibrycon* species have 6 to 10 (state 2) and 11 to 20 (state 1) maxillary teeth. Among Clade A taxa the large number of maxillary teeth was independently acquired in *Cyanocharax alburnus*, *Bryconamericus peruanus* and *Mimagoniates rheocharis*.
- First teeth of maxilla without space, and remaining teeth with space between teeth (Ch. 13.1; Fig. 3). Among Clade A taxa the state 1 is an exclusive synapomorphy for *Hemibrycon*. This condition was independently acquired in *Nematobrycon palmeri*, *Nematocharax venustus*, *Pseudochalceus lineatus* and *Rachoviscus crassiceps*.
- Posterior portion of infraorbital 1 finishing posterior to alignment with lateral ethmoid (Ch. 38.2).
- Posteroventral margin of cleithrum strongly concave (Ch. 78.0; Fig. 15a). This condition was independently acquired in *Bryconamericus exodon*, and in the Clade G.
- Number of branched anal-fin rays (Ch. 89.0). Among *Hemibrycon* species, the basal species *Hemibrycon* n. sp. 1, *Hemibrycon* n. sp. 2, and *Hemibrycon* n. sp. 3 have less branched anal-

fin rays (state 0) and with reversal in *Hemibrycon helleri*. The remaining *Hemibrycon* species possess 23 to 34 branched anal-fin rays (state 1).

- Large scales presents on the caudal-fin lobes (Ch. 93.1; Fig. 17). This condition was independently acquired in *Bryconamericus peruanus* and *Othonocheirodus* sp.

- Presence of bony hooks in all fins rays, except caudal-fin, in mature males (Ch. 96.1). Character not coded for *Hemibrycon* n. sp. 1 and *H. dentatus*. This condition was independently acquired in *Nematocharax venustus* and *Odontostilbe fugitiva*.

- The dorsal profile of maxillary in *Hemibrycon* species is always straight (Ch. 16.2; Fig. 5a). Among Clade A\* taxa this condition was independently acquired in Clade C, except *Othonocheirodus* sp. and Clade I. The state 2 was independently acquired in *Astyanax jacuhiensis*, *Poptella brevispina*, *Pseudochalceus lineatus*, *Nematocharax venustus*, and Clade 9.

- Frontal fontanel not reaching the ethmoid bone (Ch. 30.1). The frontal fontanel reaching the ethmoid bone (state 0) in clade H2 represents a reversion. The state 1 is extremely variable, and was independently acquired by several times among non-*Hemibrycon* taxa.

- The postcleithrum 2 approximately half-length of postcleithrum 3 (Ch. 75.1; Fig. 14a). The postcleithrum 2 smaller than half-length of postcleithrum 3 (state 2) in *Hemibrycon huambonicus*, *H. metae* and *H. taeniurus* represent a subsequent and independent transformation. The state 1 was independently acquired in *Bryconadenos tanaothoros*, *Knodus meridae*, Clade 4, *Pseudochalceus lineatus*, and Clade 9.

- Superior portion of supraneurals larger than inferior (Ch. 105.1; Fig. 18a). The state 1 was independently acquired in *Bryconamericus exodon*, *Bryconamericus* sp., Clade I, and in the Clade 3, except in Clade 9.

### ***Hemibrycon* n. sp. 1**



Autapomorphies:

- Premaxilla outer row teeth not aligned in the distal portion (Ch. 4.1).
- Metapterygoid fenestra located in the posteroventral region of bone (Ch. 45.1).
- Dentary-quadrato joint situated approximately on the vertical passing through the center of the orbits (Ch. 49.0).
- Total number of pectoral-fin rays 10 to 11 (Ch. 72.1).
- Upper tip of postcleithrum 3 aligned with dorsal border of posterior stem of the scapula (Ch. 77.1).
- Total number of pelvic-fin rays (Ch. 83.1).
- Humeral spot with 2 to 3 horizontal series of scales (Ch. 113.0).

### ***Hemibrycon* Clade H1**

Synapomorphies:

- Presence of head massive and heavy and heavy body (usually elongate) (Ch. 33.1).
- Basihyal bone narrow; one or two times wider than proximal region (Ch. 58.1).
- Posterior bony projection of ischiatic process short and curve (Ch. 87.0).
- Thirteen vertebrae before the first dorsal-fin pterygiophore (Ch. 103.4).
- Anal-fin border pigmented forming a dark stripe (Ch. 116.1).

### ***Hemibrycon* n. sp. 3**

Autapomorphies:

- Premaxilla inner series teeth with five to eight cusps (Ch. 3.3).
- Posterior border of maxillary reaching to 2/3 of length of infraorbital 2 (Ch. 17.1).
- Dorsal fin base located anterior or in the vertical through anal-fin origin (Ch. 69.0).

### ***Hemibrycon* Clade H2**

Synapomorphies:

- Five interdigitating articulations in the dentary symphysis (Ch. 26.1).
- Frontal fontanel reaching the ethmoid bone (Ch. 31.0).
- Dorsal stem of quadrate narrow and elongate (Ch. 50.2).
- Presence of laminar bony flange on postcleithrum 3 (Ch. 76.1).
- Bony hooks of anal-fin rays of mature males starting in the last unbranched and distributed along near all branched rays (Ch. 97.1).
- Laminar bony projections developed in the distal portions of supraneurals (Ch. 107.1).

### ***Hemibrycon* n. sp. 2**

Autapomorphies:

- Adipose fin origin located between last sixth and seventh caudal vertebrae (Ch. 71.0).
- Posteroventral bony projection of coracoid absent (Ch. 82.1).
- Anterior portion of pelvic bone narrow, without lateral expansion on the inner surface (Ch. 86.1).
- Adipose-fin densely pigmented (Ch. 115.1).

### ***Hemibrycon* Clade H3**

Synapomorphies:

- Dorsal profile of anterior stem of quadrate divided in two sections (Ch. 51.0).
- Posterodorsal margin of opercle nearly straight or smoothly concave (Ch. 53.0).
- Presence of gill gland on first arch in mature males (Ch. 56.1).
- Presence of an anterior bony projection in the ischiatic process (Ch. 89.1).

#### ***Hemibrycon n. sp. 4***

Autapomorphies:

- Premaxilla inner series teeth with five to eight cusps (Ch. 3.3).
- Larger dentary teeth with five to seven cusps (Ch. 20.0).
- Presence of foramen in the palatine bone (Ch. 43.1).
- Basihyal elongate (Ch. 57.1).
- Distal region of basihyal broad, more than two times wider than proximal region (Ch. 58.0).

#### ***Hemibrycon Clade H4***

Synapomorphies:

- First maxillary tooth tricuspidate (Ch. 9.0).
- Posterior border of maxillary reaching to 2/3 of length of infraorbital 2 (Ch 17.1).
- Posterior portion of infraorbital 1 finishing at alignment with lateral ethmoid (Ch. 38.1).

#### ***Hemibrycon huambonicus***

Autapomorphies:

- Outer row teeth of premaxilla not aligned in the distal portion (Ch. 4.1).
- 11 to 20 maxillary teeth in adult specimens (Ch. 8.1).
- Posterior border of maxillary reaching to 2/3 of length of infraorbital 2 (Ch. 17.1)
- Postcleithrum 2 smaller than half-length of postcleithrum 3 (Ch. 75.2).
- Upper tip of postcleithrum 3 aligned with dorsal border of posterior stem of the scapula (Ch. 77.1).

#### ***Hemibrycon polyodon***

Autapomorphies:

- Four interdigitating articulations in the dentary symphysis (Ch. 26.2)
- Absence of gill gland on first arch in mature males (Ch. 56.0)
- Postcleithrum 1 broad, and with upper portion larger than lower (Ch. 73.0).
- Upper tip of postcleithrum 3 aligned with dorsal border of posterior stem of the scapula (Ch. 77.1)
- Absence of anal-fin border pigmented (Ch. 116.0).

### ***Hemibrycon* Clade H5**

Synapomorphies:

- 11 to 20 maxillary teeth in adult specimens (Ch. 8.1).
- Posterior portion of infraorbital 1 finishing posterior to alignment with lateral ethmoid (Ch. 38.2)
- Dorsal stem of quadrate broad and short (Ch. 50.0).
- Absence of laminar bony projections in the distal portions of supraneurals (Ch. 107.0).
- Adipose-fin densely pigmented (Ch. 115.1).

### ***Hemibrycon helleri***

Autapomorphies:

- Dorsal fin base located anterior or in the vertical through anal-fin origin (Ch. 69.0).
- 12 to 22 branched anal-fin rays (Ch. 89.0).
- Dorsal procurrent caudal-fin rays 8 to 10 (usually 8 to 9) (Ch. 101.1).
- Humeral spot along 7 to 9 horizontal series of scales (Ch. 113.2).

### ***Hemibrycon* n. sp. 5**

Autapomorphies:

- Premaxilla inner series teeth with five to eight cusps (Ch. 3.3)
- Outer row teeth of premaxilla not aligned in the distal portion (Ch. 4.1)
- Posteroventral bony projection of coracoid absent (Ch. 82.1)

### ***Hemibrycon* Clade H6**

Synapomorphies:

- Four interdigitating articulations in the dentary symphysis (Ch. 26.2)
- Presence of the foramen in the palatine bone (Ch. 43.1).
- Adipose fin origin located between last sixth and seventh caudal vertebrae (Ch. 71.0).
- 12 vertebrae before the first dorsal-fin pterygiophore (including Weberian Apparatus vertebrae) (Ch. 103.3).

### ***Hemibrycon boquiae***

- No autapomorphies were found. See diagnosis of this species.

### ***Hemibrycon* Clade H7**

Synapomorphies:

- Premaxilla inner series teeth with five to eight cusps (Ch. 3.3).
- Outer row teeth of premaxilla not aligned in the distal portion (Ch. 4.1).
- Head no massive and heavy, usually narrow and lanky, and thin body (Ch. 33.0).

### ***Hemibrycon dariensis***

Autapomorphies:

- The presence of distal tip of rays just above and below to middle caudal-fin rays densely pigmented is found only in *Hemibrycon dariensis*, being considered an autapomorphy for the species (Ch. 121.1).
- Dorsal profile of anterior stem of quadrate divided in two sections (Ch. 51.1).
- Posterodorsal margin of opercle strongly concave (Ch. 53.1).

### ***Hemibrycon dentatus***

Autapomorphies:

- First maxillary tooth pentacuspoid (Ch. 9.1).
- Larger dentary teeth with five to seven cusps (Ch. 20.0).
- Absence of gill gland on first arch in mature males (Ch. 56.0).
- Presence of the bony hooks in pelvic- and anal-fin rays in mature males (Ch. 96.0).

### ***Hemibrycon metae***

Autapomorphies:

- Outer row teeth of premaxilla aligned in the distal portion (Ch. 4.0).
- First maxillary tooth pentacuspoid (Ch. 9.1).
- Five interdigitating articulations in the dentary symphysis (Ch. 26.1).
- Postcleithrum 2 smaller than half-length of postcleithrum 3 (Ch. 75.2).
- Absence of laminar bony flange on postcleithrum 3 (Ch. 76.0).

### ***Hemibrycon Clade H8***

Synapomorphies:

- 11 to 20 maxillary teeth in adult specimens (Ch. 8.1).
- Postcleithrum 1 broad, and with upper portion larger than lower (Ch. 73.0).

***Hemibrycon jabonero***

Autapomorphies:

- Five interdigitating articulations in the dentary symphysis (Ch. 26.1).
- Presence of head massive and heavy, and heavy body (usually elongate) (Ch. 33.1).
- First dorsal procurrent caudal-fin ray located anterior to the last caudal vertebra (Ch. 100.1).
- Thirteen vertebrae before the first dorsal-fin pterygiophore (including Weberian Apparatus vertebrae) (Ch. 103.4).

***Hemibrycon Clade H9***

Synapomorphy:

- Five interdigitating articulations in the dentary symphysis (Ch. 26.1).

***Hemibrycon taeniurus***

Autapomorphies:

- Inner series teeth of premaxilla with three to five cusps (Ch. 3.2).
- Posterior region of metapterygoid with a concavity (Ch. 44.0).
- Adipose fin origin located between last eighth and ninth caudal vertebrae (Ch. 71.1).
- Postcleithrum 2 smaller than half-length of postcleithrum 3 (Ch. 75.2).
- Upper tip of postcleithrum 3 aligned with dorsal border of posterior stem of the scapula (Ch. 77.1).
- Posterior bony projection of ischiatic process elongate (Ch. 87.1).

***Hemibrycon Clade H10***

Synapomorphies:

- Posterior border of maxillary reaching to distal portion of infraorbital 2 (Ch. 17.0).
- Eleven vertebrae before the first dorsal-fin pterygiophore (Ch. 103.2).

### ***Hemibrycon jelskii***

Autapomorphies:

- Larger dentary teeth with five to seven cusps (Ch. 20.0).
- Postcleithrum 1 elongate, and with similar portions (Ch. 73.1).
- Humeral spot along 7 to 9 horizontal series of scales (Ch. 113.2).

### ***Hemibrycon Clade H11***

Synapomorphies:

- The presence of a wide black asymmetrical spot covering base of caudal-fin rays is considered a synapomorphy for *Hemibrycon divisorensis* and *H. surinamensis* (Ch. 118.1).
- Five interdigitating articulations in the dentary symphysis (Ch. 26.1).
- Dorsal stem of quadrate broad and long (Ch. 50.0).
- Posterodorsal margin of opercle strongly concave (Ch. 53.1).

### ***Hemibrycon divisorensis***

Autapomorphies:

- Absence of gill gland on first arch in mature males (Ch. 56.0).
- Basihyal elongate (Ch. 57.1).
- Distal region of basihyal broad, more than two times wider than proximal region (Ch. 58.0).
- Bony hooks in the anal-fin rays of mature males distributed only in the anterior branched rays (Ch. 97.2).



### *Hemibrycon surinamensis*

Autapomorphies:

- Inner series teeth of premaxilla with three to five cusps (Ch. 3.2).
- Dorsal profile of anterior stem of quadrate divided in two sections (Ch. 51.1).
- Absent of posteroventral bony projection of coracoid (Ch. 82.1).

### Taxonomic revision of *Hemibrycon*

#### *Hemibrycon* Günther, 1864

*Hemibrycon* Günther, 1864:318 (diagnosed in key), 330 (type species: *Tetragonopterus (Hemibrycon) polyodon* Günther by monotypy; original description; type locality: Guayaquil). -Eigenmann, 1910:432 (type species: *Hemibrycon polyodon*, distribution). - Meek & Hildebrand, 1916:285 (redescription, type species: *Hemibrycon polyodon*). - Eigenmann, 1927:401 (redescription, type species: *Hemibrycon polyodon*), 402-403 (distribution, key to species of the genus). -Eigenmann & Allen, 1942:215-216 (redescription, type species: *Hemibrycon polyodon*, distribution). -Géry, 1962:65-68 (distribution of the genus), 68-69 (taxonomic position of the genus).

**Diagnosis.** *Hemibrycon* is diagnosed from remaining characid genera by synapomorphies listed above.

**Distinguishing characters.** *Hemibrycon* is distinguished from all Clade A\* genera, except from *Boehlkea*, by the possession of the maxilla fully toothed in adult specimens. *Hemibrycon* differs from *Boehlkea* by lobes of caudal-fin naked vs scaled, lateral line complete vs

incomplete, and larger total number of vertebrae (36 vs 38-43). Other characters useful for recognition of *Hemibrycon* are (1) maxilla fully toothed in adult specimens (except from *Boehlkea*); (2) the presence of two unbranched and eight branched dorsal-fin rays; (3) absence of caudal- and anal-fin glands or specialized organs; (4) presence of a clearly anterior mouth with unspecialized teeth, as well as the absence of a ventrally-located mouth; (5) absence of insemination; (6) presence of bony hooks on dorsal, anal, pelvic, and pectoral fins of males; and (7) presence of three anteriormost dentary teeth larger, with 5-7 cusps, followed by medium sized tooth with 3-5 cusps, and 7-13 teeth with 2-3 cusps or conical.

**Distribution.** The species of *Hemibrycon* occur in the Pacific slope basins of Panama (river basins between San Pablo and Tuirar rivers), coastal basins of Caribbean sea in Colombia and Venezuela, upper río Orinoco basins and lago Maracaibo in Venezuela, river basins in Trinidad and Tobago, coastal basins of French Guiana and Suriname, lower rio Tocantins basin, Brazil, and upper Amazonas Rivers drainages in Bolivia, Brazil, Ecuador, and Peru (Figs. 1-2).

Through that vast region, the species are most abundant in moderately to swiftly flowing water bodies. Alike this broad distribution of the *Hemibrycon* species it is notable its altitudinal range compared to that of most characiform genera, extending from near sea level at various sites on the continent to nearly 2000 m in Colombia and Peru.

#### **Key to the species of *Hemibrycon* Günther, 1864**

- 1a. Humeral spot extending over 7 to 9 horizontal series of scales ..... 2
- 1b. Humeral spot extending over 2 to 6 horizontal series of scales ..... 3

- 2a. 19 to 23 branched anal-fin rays (Fig. 23); 6 to 12 scales in the scale sheath along anal-fin base; 16 to 18 predorsal scales ..... *H. helleri* (upper rio Ucayali drainage, Peru)
- 2b. 25 to 30 branched anal-fin rays (Fig. 23); 13 to 28 scales in the scale sheath along anal-fin base; 12 to 16 predorsal scales ..... *H. jelskii* (upper portions of rivers Marañon, Ucayali, Madeira-Mamoré drainages in Bolívia, Brazil and Peru)
- 3a. Small humeral spot and extending over 2 to 3 horizontal series of scales (Fig. 54); total number of pelvic fin rays 7; 3 to 4 scale rows below lateral line ..... *Hemibrycon n. sp. 1* (upper rio Ucayali drainage, Peru)
- 3b. Humeral spot extending over 4 to 6 horizontal series of scales; total number of pelvic fin rays 8; 4 to 9 scale rows below lateral line ..... 4
- 4a. Presence of a wide black asymmetrical spot covering base of caudal-fin rays and extending along entire length of caudal-fin rays 9 to 12-13 ..... 5
- 4b. Absence of a wide black asymmetrical spot covering base of caudal-fin rays ..... 6
- 5a. Presence of a black band in the lower half of the caudal peduncle from the region above the last anal-fin rays to the caudal-fin base; scale sheath along anal-fin base with 17 to 22 scales; total number of gill rakers 20 to 22 ..... *H. divisorensis* (rio Ucayali drainage, Peru)
- 5b. Absence of a black band in the lower half of the caudal peduncle from the region above the last anal-fin rays to the caudal-fin base; scale sheath along anal-fin base with 12-17 scales; total number of gill rakers 19 to 20 ..... *H. surinamensis* (coastal basins of French Guiana and Suriname, and lower rio Tocantins basin, Brazil)

6a. Distal tip of rays just above and below to middle caudal-fin rays densely dark pigmented (Figs. 41-42) .....	<i>H. dariensis</i> (Pacific slope basins of Panama, and Atrato and Sinú River basins in Colombia)	
6b. Distal tip of rays above and below to middle caudal-fin rays unpigmented .....		7
7a. Branched anal-fin rays 15 to 20 (Fig. 23) .....		8
7b. Branched anal-fin rays 21 to 34 (except <i>H. tolimae</i> with 19-23; Fig. 23) .....		10
8a. Lateral line scales 39 (Fig. 24); 6 scale rows above of the lateral line; premaxilla inner row with tri- to pentacuspoid teeth .....	<i>H. tridens</i> (upper rio Ucayali drainage, Peru)	
8b. Lateral line scales 42 to 53 (Fig. 24); 6 scale rows above of the lateral line; premaxilla inner row with penta- to heptacuspoid teeth .....		9
9a. Lateral line scales 44 to 53 (mean = 47.3); branched anal-fin rays 15 to 19 (usually 16-18); 16-18 scales around caudal-peduncle .....	<i>H. beni</i> (rio Beni drainage, Bolivia)	
9b. Lateral line scales 42 to 46 (mean = 44.0); branched anal-fin rays 18 to 20 (usually 19); 14-16 scales around caudal-peduncle .....	<i>Hemibrycon n. sp. 3</i> (middle rio Magdalena basin, Colombia)	
10a. 44 to 58 lateral line scales (except <i>H. polyodon</i> 42 to 45; Fig. 24); 8 to 10 scales above of the lateral line .....		11
10b. 39 to 43 lateral line scales (Fig. 24); 6 to 8 scales above of the lateral line .....		15
11a. 28 to 34 branched anal-fin rays (Fig. 23); 14 to 16 scales around caudal-peduncle; 5 to 6 scales below of the lateral line .....	<i>H. dentatus</i> (upper rio Cauca drainage, Colombia)	

11b. 20 to 28 branched anal-fin rays (Fig. 23); 16 to 20 scales around caudal-peduncle; 6 to 9 scales below of the lateral line .....	12
12a. 47 to 58 lateral line scales; scale sheath along anal-fin base with 7 to 15 scales; 20 to 24 branched anal-fin rays .....	<i>H. colombianus</i> (middle rio Magdalena basin, Colombia)
12b. 42 to 47 lateral line scales; scale sheath along anal-fin base with 14 to 31 scales; 24 to 28 branched anal-fin rays (except <i>H. huambonicus</i> 22 to 27) .....	13
13a. First teeth of maxilla pentacuspitate; 21 to 22 gill rakers in the first arch .....	<i>Hemibrycon n. sp. 4</i> (middle rio Magdalena basin, Colombia)
13b. First teeth of maxilla tricuspidate; 18 to 20 gill rakers in the first arch .....	14
14a. Caudal peduncle scales 18 to 20; head length 22.0-26.0% of SL; maxillary length 45.2-52.6% of HL; branched anal-fin rays 22 to 27 (usually 24) .....	<i>H. huambonicus</i> (rio Huallaga drainage, Peru)
14b. Caudal peduncle scales 16; head length 20.9-22.9% of SL; maxillary length 43.7-45.6% of HL; branched anal-fin rays 24 to 28 (usually 26) .....	<i>H. polyodon</i> (rio Pastaza drainage, Ecuador)
15a. First maxillary tooth pentacuspitate .....	16
15b. First maxillary tooth tricuspidate .....	17

- 16a. 20 to 24 branched anal-fin rays; 16 to 18 gill rakers in the first arch; scale sheath along anal-fin base with 6 to 10 scales..... *Hemibrycon n. sp. 2* (Caribbean coastal basins in Sierra Nevada de Santa Marta, Colombia)
- 16b. 25 to 31 branched anal-fin rays; 19 to 21 gill rakers in the first arch; scale sheath along anal-fin base with 9 to 19 scales..... *H. metae* (rio Orinoco basin, Venezuela and Colombia)
- 17a. Adipose fin densely dark pigmented; humeral spot extending over 6 horizontal series of scales; 17 to 18 gill rakers in the first arch ..... *Hemibrycon n. sp. 5* (upper rio Madre de Dios drainage, Peru)
- 17b. Adipose fin hyaline; humeral spot extending over 4 to 5 horizontal series of scales; 19 to 21 gill rakers in the first arch ..... 18
- 18a. 14 scale rows around caudal-peduncle ..... 19
- 18b. 16 to 18 scale rows around caudal-peduncle ..... 20
- 19a. Humeral spot extending over 5 to 6 horizontal series of scales; premaxillary inner row teeth with 5 to 7 cusps; total number of vertebrae 39 to 40; lateral line scales 39 to 43 (usually 40) ..... *H. jabonero* (rivers drainages of lago Maracaibo basin, Venezuela)
- 19b. Humeral spot extending over 4 horizontal series of scales; premaxillary inner row teeth with 5 cusps; total number of vertebrae 41 to 43; lateral line scales 40 to 44 (usually 42) ..... *H. boquiae* (upper rio Cauca drainage, Colombia)

- 20a. 19 to 23 branched anal-fin rays; 4 to 8 maxillary teeth; 8 to 9 supraneurals  
 ..... *H. tolimae* (upper rio Magdalena basin, Colombia)
- 20b. 25 to 29 branched anal-fin rays; 7 to 15 maxillary teeth; 5 to 7 supraneurals  
 ..... *H. taeniurus* (rivers of Island Trinidad, Trinidad and Tobago)

***Hemibrycon polyodon* (Günther, 1864)**

Figs. 26-27

*Tetragonopterus (Hemibrycon) polyodon* Günther, 1864:330 (original description; type locality: Guayaquil). -Boulenger, 1898:3 (río Santiago, western Ecuador).

*Tetragonopterus (H.) polyodon*. -Lütken, 1875:234 (“Guyaquil”).

*Hemibrycon polyodon*. Eigenmann, 1909:313 (listed, Guayaquil). -Eigenmann, 1910:432 (listed; distribution: Western Ecuador and Peru). -Eigenmann, 1922:152-153 (in key; habitat: Western and eastern slopes of Ecuador). -Eigenmann, 1927:409-410 (redescription; distribution: Coastal streams of Ecuador, and comments about type locality). -Fowler, 1943:2 (comparison with *Hemibrycon coxeyi*). -Géry, 1962:66 (map with distribution), 69 (comparison with *H. coxeyi* and *H. huambonicus*). -Géry, 1977:379 (in key, synonyms *H. coxeyi* and *H. huambonicus*?). -Ortega & Vari, 1986:8 (listed, Peru). -Lima *et al.*, 2003:130 (holotype: BMNH 1858.7.25.41; distribution: Amazon River basin).

*Hemibrycon coxeyi* Fowler, 1943: 1-3, fig. 1 (original description; holotype: ANSP 70155; type locality: Hacienda Las Mascota, mouth of the río Pastaza, drainage of the Marañon, Ecuador). -Böhlke, 1958:24-25 (comments about type locality). -Géry, 1962:66 (distribution, probably synonym with *H. huambonicus*), 69 (comparison with *H. polyodon*

and *H. huambonicus*). -Géry, 1977:379 (in key, “synonym of *H. polyodon*?”). -Böhlke, 1984:45 (type catalog). -Lima *et al.*, 2003:130 (provisional synonym of *Hemibrycon polyodon* Eigenmann). [NEW SYNONYM]

**Material examined.** *Hemibrycon polyodon*, BMNH 1858.7.25.41, 70.4 mm SL, holotype, female, Guayaquil [Ecuador]. *Hemibrycon coxeyi*, ANSP 70155, 86.0 mm SL, holotype (x-ray), female, Hacienda Mascota, río Topo, a tributary of the río Pastaza, drainage of the río Marañon, Napo-Pastaza, Ecuador, 1°25'S 78°11'W, Apr 1931, W. J. Coxey, JC31-MRP-4.

**Non-type specimens. Ecuador, río Marañon drainage:** KU 19978, 1, 45.7 mm SL, río Alpayacu 1 km E Mera, Pastaza, approx. 1°27'S 78°5'W, 23 Jul 1968, G. R. Smith. KU 19992, 3, 31.0-78.2 mm SL, río Negro, tributary of río Pastaza 1 km W of río Negro Twp., Tungurahua, approx. 1°24'S 78°13'W, 26 Jul 1968, G. R. Smith & J. D. Lynch. KU 19995, 2, 27.7-29.3 mm SL, río Pastaza above río Negro, Tungurahua, approx. 1°24'S 78°13'W, 26 Jul 1968, G. R. Smith & J. D. Lynch. KU 20004, 42 of 84 (2 c&s), 15.5-72.3 mm SL, N shore río Pastaza below río Negro (town), Tungurahua, approx. 1°24'S 78°13'W, 26 Jul 1968, G. R. Smith & J. D. Lynch.

**Diagnosis.** *Hemibrycon polyodon* is distinguished from most species of the genus, except from *H. boquiae*, *H. dariensis*, *H. divisorensis*, *H. huambonicus*, *H. jabonero*, *H. jelskii*, *H. metae*, *H. surinamensis*, *H. taeniurus*, and *Hemibrycon* n. sp. 4, by the number of branched anal-fin rays (24-28 vs 15-24 and 28-34; Fig. 23). It differs from *H. boquiae*, *H. dariensis*, *H. divisorensis*, *H. jelskii*, *H. surinamensis* and *H. taeniurus* by the number of lateral line scales (42-45 vs 39-42; Fig. 24); from *H. jabonero* by the number of caudal peduncle scales (16 vs 14), and number of scales below lateral line (6 vs 4-5); from *H. metae* by the number of cusps of premaxillary inner teeth (3-5 vs 5-7), caudal peduncle length (14.4-16.6 vs 11.1-14.8% SL),



and head length (20.9-22.9 vs 22.1-25.0% SL). Furthermore, *H. polyodon* can be distinguished from *H. surinamensis* and *H. divisorensis* by absence of a wide black asymmetrical spot covering base of caudal-fin rays; from *H. jelskii* by the size of humeral spot (5-6 vs 7-9 horizontal series of scales), and by the number of maxillary teeth (4-10 vs 8-17; Fig. 25); from *H. dariensis* by the absence of pigment in the distal tip of rays just above and below to middle caudal-fin rays vs densely pigmented. *Hemibrycon polyodon* is very similar to *H. huambonicus*, but it differs by the number of caudal peduncle scales (16 vs 18-20), and number of scales above lateral line (8 vs 8-10), head length (20.9-22.9 vs 22.0-26.0% SL), and maxillary length (43.7-45.6 vs 45.2-52.6% HL).

**Description.** Morphometric data for *H. polyodon* summarized in Table 6. Largest male 74.9 mm SL, largest female 69.5 mm SL. Body compressed and moderate elongate; greatest body depth anterior to dorsal-fin origin. Dorsal profile of head slightly convex. Dorsal body profile convex from occipital bony to base of last dorsal-fin ray; straight from this point to adipose-fin origin. Ventral profile of head nearly straight to slightly convex. Ventral body profile convex from pectoral-fin origin to pelvic-fin origin, and straight to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head small. Mouth terminal, mouth slit nearly at horizontal through middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 45 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 3-5, tricuspid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 3-5 cusps, with central cusp twice or three times longer and broader than

other cusps. Maxilla fully toothed with 4-10 (Fig. 25) uni- to tricuspid teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5 cusps, followed by medium sized tooth with 3-5 cusps, and 7-9 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps (Fig. 3). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 15); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located approximately to middle of SL and posterior to vertical through pelvic-fin origin. Profile of distal margin of dorsal fin nearly straight. Males with bony hooks in distal one-third of first to fifth branched rays. Adipose-fin located at vertical through insertion of two last anal-fin rays.

Anal-fin rays iii-v,24-28 (one with 24 and one with 28, mean = 26.2, n = 14, Fig. 23). Anal-fin profile convex in males and nearly straight in females. Anal-fin origin approximately at vertical through middle dorsal-fin base. Anal-fin rays of males bearing one pair of developed bony hooks along posterolateral border of each segment of lepidotrichia, along last unbranched ray and all branched rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-12 (mean = 11.1, n = 15). Pectoral-fin tip reaching pelvic-fin origin in males. Males with bony hooks on distal portion of unbranched and all branched rays. Pelvic-fin rays i,6,i (n = 15). Pelvic-fin origin located 5-6 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males usually bearing 1 developed bony hook per segment of lepidotrichia along ventromedial border of all branched rays.

Caudal fin forked with 19 principal rays without bony hooks (n = 15); lobes similar in size. Caudal-fin base with few scales. Dorsal procurrent rays 12. Ventral procurrent rays 11 (n = 2).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series

42-45 (mean = 44.4, n = 14, Fig. 24). Scale rows between dorsal-fin origin and lateral line 8 (n = 15); scale rows between lateral line and pelvic-fin origin 6 (n = 15). Predorsal scales 15-17, arranged in regular series (mean = 15.9, n = 13). Scales rows around caudal peduncle 16 (n = 14). Triangular modified scale on pelvic-fin origin extends posteriorly covering 2-3 scales. Scale sheath along anal-fin base with 14-23 scales in single series, extending to base of 15<sup>th</sup> to 24<sup>th</sup> branched rays.

Precaudal vertebrae 18-19; caudal vertebrae 22-24; total vertebrae 40-43. Supraneurals 7-9. Gill-rakers on upper limb of outer gill arch 7-8, and on lower limb 11-13 (n = 5).

**Color in alcohol.** The holotype was totally depigmented, except the middle caudal-fin rays. Color based on the non-type specimens. General ground body color yellowish. Dorsal portion of head and body with concentration of dark chromatophores. Dorsolateral portion of head and body with scattered dark chromatophores. Midlateral body silvery. One large and vertical black humeral spot, located over fourth to sixth lateral line scales and extending over 6-7 horizontal series of scales, including lateral line. Midlateral dark stripe extending from humeral region to middle caudal-fin rays, broad in caudal peduncle. Abdominal region almost devoid of dark chromatophores. Dorsal, caudal, and anal fins with scattered dark chromatophores. Pectoral, pelvic and adipose fins hyaline (Fig. 27).

**Sexual dimorphism.** Males of *Hemibrycon polyodon* are easily recognized by the presence of bony hooks on the dorsal-, pectoral-, anal- and pelvic-fin rays. Males and females also slightly differ in proportional pectoral- and pelvic-fin lengths (Table 6) and in anal-fin shape, which is convex in males and nearly straight in females. Gill glands were not found on first gill arch in males and females.

**Distribution.** *Hemibrycon polyodon* is known from the río Pastaza, río Marañón drainage, and upper río Amazonas basin, Ecuador (Fig. 1).

**Remarks on the type locality of *Hemibrycon polyodon*.** Günther (1864) described *Tetragonopterus polyodon* based on a single specimen from Guayaquil, Ecuador. Eigenmann (1927:409-410) in his revision of the genus, assigned the distribution of *H. polyodon* as “Coastal streams of Ecuador”, also stated that “It is more than probable that the types were shipped from Guayaquil but were collected at a considerable elevation in the interior of Ecuador or Peru”.

**Remarks on the type locality of *Hemibrycon coxeyi*.** Fowler (1943:2) described *H. coxeyi* based on one of three specimens collected by Mr. W. Judson Coxey in 1931 in Ecuador. The author provided the exact locality according to Coxey trip: “All these specimens are from the basin of the Río Pastaza, in Tungurahua, where he spent sometime on the river at the Hacienda Las Mascota”. Fowler recognized that *H. coxeyi* was nearly related to *H. polyodon* from the Pacific slope of Ecuador, but he was unable to identify the new species as *H. polyodon* based on Günther’s description. Böhlke (1958:24-25) doubted the type locality of *H. coxeyi* reported by Fowler (“Hacienda Las Mascota, mouth of the Rio Pastaza, basin of the Rio Maranon, Ecuador”) and in footnote cited a reference to the location: “Annals Entomol. Soc. America, vol. 34, no. 4, Dec. 1941, p. 848”. According to Böhlke, this reference places Hacienda Las Mascota at a point far removed from mouth of the Pastaza (1°25’S 78°11’W), a station occupied on several occasions for some length of time by Coxey. The exact location of mouth of the río Pastaza is about 4°52’S 76°21’W according to Böhlke and current maps. Latter, Géry (1962:66) discussing about the distribution of the known forms of *Hemibrycon*, commented that *H. coxeyi* is probably a synonym of *H. huambonicus*, and *H. polyodon* comes

very probably from the same area of these species. According to Oyakawa in Lima *et al.* (2003) the type locality should be amended to “Ecuador, Napo-Pastaza, Hacienda Mascota, río Topo, a tributary of río Pastaza, 1°25’S 78°11’W”.

The type localities of *H. polyodon* and *H. coxei* were inexact, but can be in some place of río Pastaza drainage, a relatively large tributary to the left margin of río Marañon, upper río Amazonas basin, in Ecuador.

A comparison of the holotypes of *H. polyodon* and *H. coxei*, and new specimens from río Pastaza drainage failed to reveal any differences in examined meristic and morphometric features or other characters. *Hemibrycon coxei* is, therefore, considered a junior synonym of *H. polyodon*, an action anteriorly suggested by Géry (1962).

**Remarks of holotype of *Hemibrycon coxei*.** The holotype of *Hemibrycon coxei* is badly preserved, lacking several body scales, with dorsal fin and snout broken, and body completely depigmented. Only some measurements were taken, as fins length (except dorsal fin), body and caudal peduncle depth, and caudal peduncle length. All scales and fin ray counts were taken, except for the count of anal-fin scale sheath.

### ***Hemibrycon taeniurus* (Gill, 1858)**

Fig. 28

*Poecilurichthys taeniurus* Gill, 1858:418 (original description; type locality: Island of Trinidad).

*Tetragonopterus taeniurus*. -Günther, 1864:317 (new combination, Trinidad). -Regan, 1906:383-384 (plate xxii, fig. 4, redescription, Trinidad).

*Tetragonopterus (Hemibrycon) trinitatis* Lütken, 1875:234 (original description; type locality: Trinidad Island, West Indies). -Eigenmann, 1927:412 (synonym of *H. taeniurus* Gill, Trinidad). -Boeseman, 1960:91 (synonym of *H. taeniurus* Gill). -Nielsen, 1974:47 (= *Hemibrycon taeniurus* Gill, Syntypes: ZMUC 962, 963, 966-968, Trinidad). -Eschmeyer, 1998:1701 (Syntypes: ZMUC 962-963 (2), ZMUC 966-968 (3), Trinidad I., West Indies). -Lima *et al.*, 2003:159 (*Species Inquirenda* in Characidae).

*Hemibrycon taeniurus*. -Eigenmann, 1909:327 (new combination). -Eigenmann, 1910:432 (listed; habitat: Trinidad). -Eigenmann, 1927:402 (in key), 412 (plate 39, fig. 2; distribution: Trinidad). -Boeseman, 1960:80 (in key), 91-92 (redescription). -Géry, 1962:66-67 (distribution). -Géry, 1977:379 (Trinidad). -Lima *et al.*, 2003:130 (Western Trinidad Island).

*Tetragonopterus guppyi* Regan, 1906:384 (original description; 5 type specimens 65-85 mm TL; type locality: Glenside Estate stream, at the foot of the n. range of hills, Trinidad I.).  
[NEW SYNONYM]

*Hemibrycon guppyi*. -Eigenmann, 1909:327 (new combination; listed; distribution: Trinidad). -Eigenmann, 1910:432 (listed; distribution: Trinidad). -Eigenmann, 1927:402 (in key), 411-412 (redescription; distribution: Trinidad). -Boeseman, 1960:80 (in key), 92-94 (redescription; comparison with *H. taeniurus*; distribution: Trinidad). -Géry, 1962:66-67 (distribution). -Géry, 1977:379 (Trinidad). -Lima *et al.*, 2003:129 (Glenside Estate stream, Trinidad Island).

*Hemibrycon guppil* [error]. -Eigenmann, 1910:432 (listed; distribution: Trinidad). -Eigenmann, 1927:402 (in key), 411-412 (redescription, distribution: Trinidad).

**Material examined. Syntypes.** *Hemibrycon taeniurus*, ZMUC 962-963, 2, 42.0-50.6 mm SL, ZMUC 966-968, 3, 33.0-45.0 mm SL, Island of Trinidad, Trinidad. *Hemibrycon guppyi*, BMNH 1906.6.23.13-17, 5, 46.3-73.4 mm SL, Trinidad (Fig. 29).

**Non-type specimens. Trinidad and Tobago, Trinidad Island:** AMNH 215239, 11 of 22 (2 c&s), 57.4-81.8 mm SL, AMNH 215301, 5 of 10, 57.1-71.2 mm SL, M. N. Feinberg. CAS 70076, 3, 44.1-87.3 mm SL, West Indies, Guppy. INHS 40083, 2, 36.9-40.5 mm SL, río Quare, río Cunapo drainage, 1 km E Valencia on road to Arima, St. Andrew County, approx. 10°39'N 61°13'W, 31 Jan 1997, L. M. Page & C. W. Ronto. MCNG 8199, 3 of 5 (1 c&s), 53.4-66.1 mm SL, río Guanapo, 21 Jun 1983. ROM 61651, 1, 65.8 mm SL, from a few streams of freshwater, 10°25'00"N 61°8'00"W, J. S. Kenny. USNM 290408, 2 (x-ray), 49.4-53.8 mm SL, río Maracas, Jul-Aug 1987, M. Alkins-Koo. USNM 290413, 2 (x-ray), 58.1-65.0 mm SL, río Matura, 23 Jul 1987, M. Alkins-Koo.

**Diagnosis.** *Hemibrycon taeniurus* is distinguished from most species of the genus, except from *H. boquiae*, *H. dariensis*, *H. divisorensis*, *H. huambonicus*, *H. jabonero*, *H. jelskii*, *H. metae*, *H. polyodon*, *H. surinamensis* and *Hemibrycon* n. sp. 4, by the number of branched anal-fin rays (25-29 vs 15-24, Fig. 23). It differs from *H. huambonicus*, and *Hemibrycon* n. sp. 4 by the number of lateral line scales (40-42 vs 43-48, Fig. 24); from *H. surinamensis* and *H. divisorensis* by the absence of a wide black asymmetrical spot covering base of caudal-fin rays; from *H. jelskii* by size of humeral spot (4-5 vs 7-9 horizontal series of scales), and the number of sheath along anal-fin base (10-15 vs 13-28); from *H. jabonero* by the number of caudal peduncle scales (16 vs 14), and the number of scales below lateral line (5-6 vs 4-5); from *H. dariensis* by the number of cusps of premaxilla inner row teeth (5 vs 5-7), and by the absence of pigment in the distal tip of rays just above and below to middle caudal-fin rays; from *H. boquiae* by the total number of vertebrae (39-41 vs 41-43), and the number of scales

above lateral line (8 vs 6-7); and from *H. polyodon* by the number of lateral line scales (40-42 vs 42-45), number of sheath along anal-fin base (10-15 vs 14-23), and by the size of humeral spot (4-5 vs 6-7 horizontal series of scales). *Hemibrycon taeniurus* is rather similar the *H. metae*, but can be distinguished by the number of maxillary teeth and cusps (7-15 tricuspidate vs 3-11 tri- to pentacuspitate, Fig. 25), number of cusps of inner row premaxillary teeth (5 vs 5-7), and by the smaller humeral spot size (4-5 vs 5-6 horizontal series of scales).

**Description.** Morphometric data for *H. taeniurus* summarized in Table 7. Largest male 65.1 mm SL, largest female 81.8 mm SL. Body compressed and moderately elongate; greatest body depth anterior to dorsal-fin origin. Dorsal profile of head slightly convex. Dorsal body profile convex from occipital bony to base of last dorsal-fin ray; straight from this point to adipose-fin origin. Ventral profile of head slightly convex. Ventral body profile convex from pectoral-fin origin to pelvic-fin origin, and straight to slightly convex to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head small. Mouth terminal, mouth slit nearly at horizontal through middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 45 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 4-6, tricuspid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 5 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla fully toothed with 7-15 (Fig. 25) uni- to tricuspid teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5 cusps, followed by medium sized tooth with 3-5 cusps, and 10-13 teeth with 1-3 cusps or conical; central cusp in all teeth two to three



times longer and broader than other cusps (Fig. 30). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 39); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located posterior to middle of SL and posterior to vertical through pelvic-fin origin. Profile of distal margin of dorsal fin nearly straight to slightly concave. Males with bony hooks in distal one-third of first branched rays. Adipose-fin located at vertical through insertion of last anal-fin rays.

Anal-fin rays ii-vi,26-29 (rarely 25, mean = 27.0, n = 39, Fig. 23). Anal-fin profile slightly concave in males and females. Anal-fin origin approximately at vertical through insertion in the last dorsal fin rays. Anal-fin rays of males bearing one pair of developed bony hooks along posterolateral border of each segment of lepidotrichia, along last unbranched ray and twelfth to fifth branched rays, and small bony hooks on remaining rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-12 (mean = 11.1, n = 39). Pectoral-fin tip surpassing pelvic-fin origin in males and nearly reaching in females. Males with bony hooks on distal portion of unbranched and all branched rays. Pelvic-fin rays i,6,i (rarely i,7, n = 39). Pelvic-fin origin located 4-5 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males usually bearing 1 small bony hook per segment of lepidotrichia along ventromedial border of all branched rays.

Caudal fin forked with 19 principal rays without bony hooks (n = 39); lobes similar in size. Caudal-fin base have a few scales. Dorsal procurrent rays 11-13, and ventral procurrent rays 10-12 (n = 7).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 40-42 (mean = 40.5, n = 39, Fig. 24). Scale rows between dorsal-fin origin and lateral line 8 (n = 39); scale rows between lateral line and pelvic-fin origin 5-6 (mean = 5.6, n = 39).

Predorsal scales 13-16, arranged in regular series (mean = 14.0, n = 36). Scales rows around caudal peduncle 16 (n = 38). Triangular modified scale on pelvic-fin origin extends posteriorly covering 2-3 scales. Scale sheath along anal-fin base with 10-15 scales in single series, extending to base of most anterior branched rays.

Precaudal vertebrae 17-18; caudal vertebrae 22-24; total vertebrae 39-41 (n = 7). Supraneurals 5-7 (n = 7). Gill-rakers on upper limb of outer gill arch 7-8, and on lower limb 11-13 (n = 25).

**Color in alcohol.** Holotype without chromatophores. Color based on non-type specimens. General ground body color yellowish. Dorsal portion of head and body with concentration of dark chromatophores. Dorsolateral portion of head and body with scattered dark chromatophores. One large and vertical black humeral spot, located over third to fifth lateral line scales and extending over 4-5 horizontal series of scales, including lateral line. Midlateral dark stripe extending from humeral region to middle caudal-fin rays, broad in the caudal peduncle. Abdominal region almost devoid of dark chromatophores. Dorsal and caudal fin with dark pigmentation diffuse and anal fin with small black chromatophores along its border forming narrow stripe. Pectoral, pelvic and adipose fins hyaline (Fig. 28).

**Sexual dimorphism.** Males of *Hemibrycon taeniurus* are easily recognized by the presence of bony hooks on the dorsal-, pectoral-, anal- and pelvic-fin rays. Males and females slightly differ in proportional pectoral- and pelvic-fin lengths and body depth (Table 7). Mature males with gill gland on first gill arch, covering the first branchial filaments (Table 4).

**Distribution.** *Hemibrycon taeniurus* is known from river basins from West Trinidad Island, Trinidad and Tobago (Fig. 1).

**Remarks.** Theodore Gill described *Poecilurichthys taeniurus* in 1858 when he traveled to the West Indian Islands. In his original description of *P. taeniurus* Gill (1858:418-419) did not provide a catalog number nor museum name for the type material, but the author remarked that “specimens of most of the species which are being described have been deposited in the museum of the Smithsonian Institution, and in the private cabinets of Messrs. Stewart and Brevoort”. Vari & Howe (1991) report no type specimens of *P. taeniurus* in the Smithsonian catalog of type specimens of Characiformes.

Later in 1875, Christian Lütken redescribed *Tetragonopterus taeniurus* (Gill) and described *Tetragonopterus (Hemibrycon) trinitatis* from Trinidad. Lütken did not explain to which museum belong the specimens used in his descriptions. According to Lütken (1875:234) a glass of tetragonopters from Trinidad, that Mr. Riise obtained from Dr. (?Hr.) Gill at his return from that island, classified as *Brevortia* [sic] *taeniata* Gill, contained two specimens of *T. taeniurus* (Gill), and seven specimens of a form that looks closely related to *Tetragonopterus*. These seven specimens were found to lack the dark humeral spot, and to have a maxilla equipped with small teeth in a greater part of its length, being referred by Lütken to the subgenus *Hemibrycon*, as *T. (H.) trinitatis*.

Regan (1906:383-384) redescribed *T. taeniurus* based on two specimens from Trinidad, reporting that received one specimen from the Copenhagen Museum as *T. trinitatis*, commenting: “Gill’s description of *T. taeniurus* is, so far it goes, perfectly applicable to *T. trinitatis*, and there can be but little doubt of their identify”. In the same work, Regan proposed a new species, *H. guppyi*, from Trinidad Island, and presented the only possible differences between these species: “*H. taeniurus* has diameter of eye 2.5 in the HL and a little greater than interorbital width, and *H. guppyi* has diameter of eye 3-3.5 in the HL and less than interorbital width”.

In the catalog of fish types of Zoological Museum of Copenhagen, Nielsen (1974) reported the five syntypes of *Tetragonopterus trinitatis* (ZMUC 962, 963, 966-968), referring the species as a synonym of *Hemibrycon taeniurus* (Gill). Lütken worked at ZMUC from 1852 to 1899 (Alves & Pompeu, 2001) and probably the specimens were carried by him for that institution or donated by Gill.

Boeseman (1960) in “The fresh-water fishes of the island of Trinidad” provided a table with some distinct characters for *H. taeniurus* and *H. guppyi*. Boeseman (1960) and Géry (1962, 1977) distinguished these species by head length, orbital diameter and interorbital width, and commented that (Boeseman, 1960:93) “These differences, though apparently sufficient for specific discrimination, left some room for doubt, especially since the variability in the discriminative characters still remained to be determined”, but decided to maintain *H. guppyi* as a separate species from *H. taeniurus*, although knowing that analysis was limited by the small number of specimens and mostly by not comparable sizes of the specimens available of each nominal species.

The syntypes of *H. taeniurus* are somewhat damaged with some caudal-fin rays broken and lacking several body scales. The dentition is preserved. The syntypes of *H. guppyi* (Fig. 29) are in good condition for all body measurements. I have analyzed the type series of *H. taeniurus* and T. Carvalho and R. Reis (MCP) analyzed the types of *H. guppyi* when visited the BMNH. I have compared the data of these species and did not find significant differences to distinguish the two species. Only the snout length in *H. guppyi* is slightly large than the syntypes of *H. taeniurus*. This difference can be related to the observed differences in the standard length range between the type series of the two species (Table 7). New specimens from Trinidad were analyzed and no significant differences were found when compared with the type series of both species. Since there are no diagnostic features to

support the recognition of two species, *H. guppyi* is herein considered a junior synonym of *H. taeniurus*.

***Hemibrycon jelskii* (Steindachner, 1875)**

Fig. 31

*Tetragonopterus jelskii* Steindachner, 1875:40 (original description), 42 (type locality: Monterico in Peru [Monterrico, Departamento de Ayacucho, río Ucayali drainage, Peru]).

*Hemibrycon jelskii*. -Eigenmann, 1910:432 (new combination). -Eigenmann, 1927:402 (in key), 412-413 (redescription; distribution: central Peru, east slope, 2723 feet). -Eigenmann & Allen, 1942:218 (species cited; distribution: Eastern slopes of central Peru). -Fowler, 1945:147 (Peru, Huambo, río Marañón). -Fowler, 1948:98-99 (upper Amazonas, Peru). -Géry, 1962:66 (map distribution), 78 (in key, Peru). -Géry, 1977:379 (in key, Peru and Ecuador?). -Ortega & Vari, 1986:8 (listed). -Lima *et al.*, 2003:130 (Monterico [Peru], Remac River drainage near Lima; erroneously reported).

**Material examined. Syntypes.** NMW 57548, 2, 99.7-101.7 mm SL (x-ray); NMW 57551, 4, 57.0-68.5 mm SL (x-ray); NMW 57554, 5, 69.4-90.6 mm SL (x-ray), río Ucayali drainage, approx. 12°28'S 73°54'W, Monterrico, Department of Ayacucho, Peru.

**Non-type specimens. Peru, río Ucayali drainage:** ANSP 143281, 2, 41.9-43.5 mm SL, río Tono at Hacienda San Jorge, 4 km W on road from Patria, Cusco, approx. 12°53'S 71°27'W, 17 Jul 1977, R. Horwitz. ANSP 143282, 1, 32.5 mm SL, mouth of río Carbon, below Atalaya on N/S road, Cusco-Madre de Dios, approx. 12°53'S 71°20'W, 18 Jul 1977, R. Horwitz. ANSP 143285, 1, 41.3 mm SL, near Atalaya, N bank tributary of río Carbon about 3 km upstream from Huacarpay-Shintuya Road ford, Madre de Dios-Cusco, approx. 12°54'S

71°21'W, 18 Jul 1977, R. Horwitz. ANSP 143274, 1, 42.6 mm SL; ANSP 143286, 1, 79.8 mm SL; ANSP 143288, 3, 46.8-82.8 mm SL; ANSP 143289, 2, 42-84.4 mm SL, río Hospital about 2 km W of Patria on N/S road, Cusco, approx. 12°53'S 71°20'W, 14-15 Jul 1977, R. Horwitz. ANSP 180772, 1, 68.6 mm SL, río Igoritoshiari, río Urubamba drainage, road crossing north of Kiteni, Cusco, 12°26'56"S 73°00'59"W, 21 Jul 2004, M. Sabaj *et al.* MUSM 2958, 4 of 6, 52.6-63.8 mm SL, río Huacamayo, Aguaytía, Padre Abad, Ucayali, approx. 9°2'S 75°30'W, 24 Nov 1983, H. Ortega & J. Cánepa. MUSM 17261, 20 of 62, 26.5-46.6 mm SL, río Urubamba, Shepahua, Ucayali, approx. 11°10'S 73°00'W, 6 Jun 1998, H. Ortega *et al.* MUSM 19562, 20 of 64, 46.1-69.0 mm SL, middle portion of quebrada John, río Pacuya, Cordillera Azul Norte, Ucayali, Loreto, approx. 7°20'S 75°40'W, 24 Aug 2000, P. de Rham.

**Peru, río Marañon drainage:** MUSM 2166, 10 of 25, 54.2-81.9 mm SL, tributary of río Huancabamba, between Pucará and Guabel, Jaen, Cajamarca, approx. 5°56'S 79°15'W, 9 Jul 1986, E. Holm *et al.* MUSM 19145, 20 of 70, 38.9-67.9 mm SL, quebrada Chumab, CCNN Paski, río Cenepa, CCA río Marañon, Condarcanqui, Amazonas, 4°33'5"S 78°11'3"W, 25 Sep 2001, M. Hidalgo. MUSM 21343, 20 of 82, 33.9-60.4 mm SL, quebrada Capitán Ponce, CCA río Alto Cenepa, Cenepa, Condarcanqui, Amazonas, 3°47'28"S 78°22'19"W, 15 Nov 2003, B. Rengifo & M. Velásquez. ROM 52240, 50 of 205 (3 c&s), 25.1-87.8 mm SL, approx. 74 km W of road going N to Jean, between Pucara and Guabel, Huancabamba river tributary, 5°56'00"S 79°15'00"W, 8 Jul 1986, E. Holm & J. Patalas.

**Peru, río Madre de Dios drainage:** ANSP 143275, 1, 30.0 mm SL, río Alto Madre de Dios, about 15 km upstream from Boca Manu, Madre de Dios, approx. 12°19'S 70°58'W, R. Horwitz. ANSP 143277, 24 (3 c&s), 22.7-35.8 mm SL, Pilcopata River, wire ferry, 3 km above Pilcopata, Cusco, 12°56'30"S 71°24'W, 16 Jun 1977, R. Horwitz. ANSP 143278, 1, 39.4 mm SL, at Shintuya, río Alto Madre de Dios, Madre de Dios, approx. 12°40'S 71°11'W, 1-3 Aug 1977, R. Horwitz. ANSP 180778, 1, 71.3 mm SL, río Nusiniscato, río Inambari drainage, road crossing

between Quince Mil and Pto. Leguia, Cusco, 13°11'17"S 70°34'5"W, 26 Jul 2004, M. Sabaj *et al.* ANSP 180779, 3, 38.1-45.0 mm SL, río Inambari and mouth of quebrada Hondonado, upstream of Puerto Mazuko, Cusco, 13°6'23"S 70°24'44"W, 27 Jul 2004, M. Sabaj *et al.* CAS 70386, 11 of 18, 70.5-90.4 mm SL, tributary to río Tambopata at Pampa Grande, ca 12 mi below San Ignacio, ca 3,000 ft. elev., Puno, approx. 14°5'S 69°00'W, 5 Nov 1951, H. H. Heller. MUSM 3759, 8 of 25, 43.9-85.0 mm SL, quebrada Culli, upper río Madre de Dios, Erika, Manu, Madre de Dios, approx. 12°10'S 71°00'W, 5 Sep 1988, M. Hidalgo *et al.* MUSM 11080, 8 of 11, 36.6-78.6 mm SL, quebrada Ebebahuaeji, río Candamo, Sandia, Puno, 13°14'56"S 70°00'35"W, 31 Mar 1997, F. Chang. MUSM 24302, 10 of 22, 26.5-37.3 mm SL, río Amiguillos, CCA río Loa Amigos, Manu, Madre de Dios, 12°25'37"S 70°17'33"W, 18 Jun 2004, M. Hidalgo *et al.* MUSM 26409, 20 of 66, quebrada Yanamayo, Quincemil, río Araza drainage, Camanti, Quispicanchi, Cusco, 13°16'54"S 70°47'4"W, 21 Oct 2005, M. Hidalgo. MUSM 26776, 2 of 8, 79.6-88.3 mm SL, río Araza drainage, San Lorenzo, Camanti, Quispicanchi, Cusco, 13°13'5"S 70°31'39"W, 25 Oct 2005, M. Hidalgo. MUSM 26785, 20 of 53, 36.8-96.9 mm SL, quebrada Ilahuala, río Araza drainage, San Lorenzo, Camanti, Quispicanchi, Cusco, 13°13'2"S 70°31'48"W, 25 Oct 2005, M. Hidalgo. ROM 66370, 9, 39.2-57.2 mm SL, Tambopata-Candamo Reserved Zone, Puno, left bank, large stream, 13°21'2"S 69°38'58"W, Tavera river tributary, 17 Aug 1992, F. Chang. **Bolivia, río Beni drainage:** CAS 70079, 11, 46.9-82.2 mm SL, río Popoi, a tributary of upper río Beni, Beni, Sep 1921, N. E. Pearson. CAS 70081, 18, 30.3-46.0 mm SL, 30 miles northwest of Rurrenabaque, Tumapasa, La Paz, approx. 14°10'S 67°30'W, Dec 1921, N. E. Pearson. MNHN 1989.1417, 2, 50.7-59.1 mm SL, río San Juanito, Yacuma, Beni, approx. 15°10'S 67°4'W, Jul 1982, L. Loubens. **Bolivia, río Chapare drainage:** MCP 35019, 17, 42.1-66.8 mm SL, arroyo del Hotel el Puente, Villa Tunari, Chapare, Cochabamba, 16°59'6"S 65°24'45"W, 10 Nov 2003, T. Oberdorff *et al.* MCP 35020 4, 37.4-57.7 mm SL, río Espiritu

Santo, Villa Tunari, Chapare, Cochabamba, 16°58'20"S 65°24'48"W, 14 Sep 2002, F. Carvajal *et al.* MCP 35021, 10, 40.1-63.5 mm SL, río Espiritu Santo, Chocolatal, Chapare, Cochabamba, 17°3'51"S 65°38'50"W, 20 Feb 2003, F. Carvajal *et al.* MCP 35022, 21, 36.3-46.0 mm SL, río Chipiriri, Chipiriri, Chapare, Cochabamba, 16°53'33"S 65°24'44"W, 20 Sep 2002, F. Carvajal *et al.* MNHN 1989.1418, 20, 35.3-75.5 mm SL, río Espiritu Santo, Villa Tunari, Cristal Mayu, approx. 17°3'S 65°38'W, Jun 1983, L. Loubens. MZUSP 27827, 4, 53.7-73.0 mm SL, río Espiritu Santo, Villa Tunari, Cristal Mayu, approx. 17°3'S 65°38'W, 24 Jun 1983, Conv. Pisc. ORSTOM-UTB. **Brazil, rio Guaporé drainage:** MCP 37754, 5, 26.0-36.1 mm SL, affluent of rio Galera, Pontes e Lacerda, Mato Grosso, 14°39'12"S 59°26'46"W, 12 Jul 2004, R. E. Reis *et al.* MCP 38177, 67 (5 c&s), 18.0-42.4 mm SL, stream Retiro at road BR 174, tributary of rio Guaporé, Nova Lacerda, Mato Grosso, 14°48'7"S 59°19'24"W, 12 Jul 2004, V. A. Bertaco *et al.*

**Diagnosis.** *Hemibrycon jelskii* can be distinguished from all species of the genus by the size of humeral spot (7-9 vs 3-7 horizontal series of scales), and from most species by the number of scales in scale sheath along anal-fin base (13-28 vs 5-17), except from *H. dentatus*, *H. polyodon*, *H. huambonicus*, *H. divisorensis*, and *Hemibrycon* n. sp. 4. It differs from *H. dentatus*, *Hemibrycon* n. sp. 4, and *H. huambonicus* by the number of lateral line scales (40-43 vs 43-50, Fig. 24), and from *H. polyodon* by the number of maxillary teeth (8-17 vs 4-10). *Hemibrycon jelskii* is distinguished from *H. divisorensis* by the number of scales below lateral line (5-7 vs 4-5), and by the absence of a wide black asymmetrical spot covering base of caudal-fin rays.

**Description.** Morphometric data for *H. jelskii* summarized in Table 8. Largest male 77.9 mm SL, largest female 101.7 mm SL. Body compressed and moderately elongate; greatest body



depth anterior to dorsal-fin origin. Dorsal profile of head nearly straight to slightly convex, and slightly concave in the occipital region. Dorsal body profile convex from occipital bony to base of last dorsal-fin ray; straight from this point to adipose-fin origin. Ventral profile of head nearly straight to slightly convex. Ventral body profile convex from pectoral-fin origin to pelvic-fin origin and straight to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head small. Mouth terminal, mouth slit nearly at horizontal through below middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 45 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 3-6, tri- to pentacuspoid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 5 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla fully toothed with 8-17 (Fig. 25) uni- to tricuspid teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5-7 cusps, followed by medium sized tooth with 3-5 cusps, and 8-10 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps (Fig. 32). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 224); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located approximately to middle of SL and posterior to vertical through pelvic-fin origin. Males with bony hooks in distal one-third of first branched rays. Profile of distal margin of dorsal fin nearly straight to slightly concave. Adipose-fin located at vertical through insertion of last anal-fin rays.

Anal-fin rays iii-v,25-30 (mean = 26.7, n = 224, Fig. 23). Anal-fin profile slightly concave in males and nearly straight in females. Anal-fin origin approximately at vertical through insertion in the last dorsal fin rays. Anal-fin rays of males bearing one pair of bony hooks along posterolateral border of each segment of lepidotrichia, along last unbranched ray and all branched rays, usually to fifth branched rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-13 (mean = 11.0, n = 224). Pectoral-fin tip reaching pelvic-fin origin only in males. Males with bony hooks on distal portion of unbranched and all branched rays. Pelvic-fin rays i,6,i or i,7 (n = 224). Pelvic-fin origin located 6-7 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males usually bearing 1 small bony hook per segment of lepidotrichia along ventromedial border of all branched rays.

Caudal fin forked with 19 principal rays (n = 224). Caudal-fin base have a few scales. Dorsal procurrent rays 10-13, and ventral procurrent rays 10-13 (n = 16).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 40-43 (mean = 41.3, n = 221, Fig. 24). Scale rows between dorsal-fin origin and lateral line 7-9 (mean = 7.9, n = 224); scale rows between lateral line and pelvic-fin origin 5-7 (mean = 5.9, n = 224). Predorsal scales 13-17, arranged in regular series (mean = 14.6, n = 218). Scales rows around caudal peduncle 16 (n = 220). Triangular modified scale on pelvic-fin origin extends posteriorly covering 2-3 scales. Scale sheath along anal-fin base with 13-28 scales in single series, extending to base of most branched rays.

Precaudal vertebrae 16-18; caudal vertebrae 21-23; total vertebrae 38-40 (n = 21). Supraneurals 6-8 (n = 22). Gill-rakers on upper limb of outer gill arch 7-9, and on lower limb 12-14 (n = 26).

**Color in alcohol.** General ground body color brown yellowish. Dorsal portion of head and

body with concentration of dark chromatophores. Dorsolateral portion of head and body with scattered dark chromatophores. One vertical black humeral spot, located over fourth to sixth lateral line scales and extending over 7-9 horizontal series of scales, including lateral line. Midlateral stripe silvery. Midlateral dark stripe extending from humeral region to middle caudal-fin rays, broad in the caudal peduncle. Abdominal region almost devoid of dark chromatophores. Dorsal and caudal fin with dark pigmentation diffuse and anal fin with small black chromatophores along its border forming narrow stripe. Pectoral, pelvic and adipose fins hyaline (Fig. 31).

**Sexual dimorphism.** Males of *Hemibrycon jelskii* are easily recognized by the presence of bony hooks in dorsal, anal, pelvic and pectoral fin rays. Males and females also slightly differ in proportional pectoral- and pelvic-fin lengths and body depth (Table 8), and in anal-fin shape, slightly concave in males and nearly straight in females. Mature males with gill gland on first gill arch, covering the first branchial filaments (Fig. 11c, Table 4).

**Distribution.** *Hemibrycon jelskii* is widespread in the upper portions of río Marañon, río Ucayali, and headwaters rivers of río Madeira-Mamoré drainages in Bolivia, Brazil and Peru (Fig. 2).

**Remarks of type locality of *Hemibrycon jelskii*.** The specimens on which Steindachner (1875:42) proposed *Tetragonopterus jelskii* were collected at “Monterico”, Peru by Prof. Jelski. According to Stephens & Traylor (1983:137), the exact site of the locality reported by Taczanowski (1884:73) as “Monterico” has been the subject of differing opinions. Those authors suggest that the type locality is probably Monterrico (approx. 12°28’S 73°54’W) in the Department of Ayacucho, Peru. The river or basin next this locality is the río Apurimac

that belong the río Ucayali drainage, and not río Remac drainage near Lima as reported in Lima *et al.* (2003:130). I analyzed eleven specimens of the 22 syntypes deposited in the NMW. The specimens are relatively in good condition and only one specimen examined had the caudal-fin broken.

**Geographic variation.** Several population samples of *Hemibrycon jelskii* were examined during this study from upper portions of the río Marañon, and río Ucayali drainages, and upper tributaries of the río Madeira-Mamoré drainage. *Hemibrycon jelskii* is herein recognized based on the combination of following characters: larger number of maxillary teeth (8 to 17), larger number of scales in the scale sheath along anal-fin base (13 to 28), a larger humeral spot (7-9 horizontal series of scales), and larger number of branched anal-fin rays (25-30). All these values, except the number of anal-fin rays, are uncommon among *Hemibrycon* species. The humeral spot is a little narrow in the syntype specimens.

All specimens fit within the range of meristic and morphometric data of the syntype specimens examined, except the orbital diameter. The orbital diameter of types is smaller than that found in all population samples of the species, but this seems to be related to the large body size of the type specimens (Table 8). Among 11 syntypes analyzed, nine are larger than 70 mm SL. No significant differences in counts were found between populations of *H. jelskii*.

The population from the río Beni has a slightly larger head length compared with syntypes, but overlapping with the ranges observed in population samples from the río Ucayali, type locality of the species. This difference is due to distinct standard length of specimens between populations. The río Chapare population has a prepectoral distance slightly larger than that observed in the syntypes, but when compared with Ucayali population this difference disappear (Table 8).

Further collections from those river drainages are necessary to determine whether there is any significant difference between the populations.

***Hemibrycon huambonicus* (Steindachner, 1882)**

Figs. 33-34

*Tetragonopterus huambonicus* Steindachner, 1882:177 (original description, type locality: Huambo).

*Hemibrycon huambonicus*. -Eigenmann, 1910:432 (new combination, synonym of *H. polyodon*). -Eigenmann, 1927:402 (in key), 410-411 (redescription, mountain streams of the eastern slope of Peru and the Beni drainage). -Eigenmann & Allen, 1942:216-218 (redescription, distribution). -Fowler, 1945:147 (Peru, río Marañón). -Fowler, 1948:98 (upper Amazonas, Peru, Bolivia). -Géry, 1962:66 (map distribution), 78 (in key [*polyodon huambonicus?*], río Huambo, Peru, Ecuador?; río Beni?). -Géry, 1977:379 (in key, Peru and Ecuador?). -Ortega & Vari, 1986:8 (listed). -Lima *et al.*, 2003:130 (Huambo [Peru], syntypes NMW 57531, distribution).

**Material examined. Syntype.** NMW 57531, 87.0 mm SL (x-ray), male, Huambo, Peru. [río Huambo, Huanuco, approx. 9°39'S 74°56'W, río Pachitea and río Ucayali drainage].

**Non-type specimens. Peru, río Huallaga drainage:** CAS 70082, 5, 64.1-95.2 mm SL, río Huallaga at Ambo (or Tambo), ca. 7,500 ft. elev., Departament Huanuco, approx. 10°8'S 76°10'W, 26-29 Oct 1918, W. R. Allen, Irwin Exp. CAS 70085, 6, 59.9-86.1 mm SL, río Huallaga at Huanuco, ca. 6,000 ft. elev., Departament Huanuco, approx. 9°55'S 76°13'W Oct 1918, W. R. Allen, Irwin Exp. CAS 70089, 51, 30.7-81.2 mm SL, río Tingo (=río Higueros) into río Huallaga from the NW at Huanuco, Huanuco, approx. 9°55'S 76°13'W, 16-25 Oct

1918, W. R. Allen. CAS 70090, 24, 43.0-85.3 mm SL, CAS 70091, 89, 42.7-94.4 mm SL, Huancachupa creek, a tumultuous small stream from the eastern slope of the central cordillera to río Huallaga a league above Huanuco, ca. 6,000 ft. elev., Huanuco, approx. 9°55'S 76°13'W, 16-25 Oct 1918, W. R. Allen. CAS 70092, 14, 42.0-73.1 mm SL, large creek/small river arising from río Huallaga above Cayumba rapids, Chumatagua, approx. 9°27'S 75°58'W, 1 Oct 1918, W. R. Allen, Irwin Exp. CAS 70093, 6 of 7, 37.1-84.3 mm SL, Chachara and Ford on lower río Chinchao (into río Huallaga above Cayumba rapids), Pedra Blanca, approx. 9°27'S 75°58'W, 2 Oct 1918, W. R. Allen, Irwin Exp. ICNMHN 7317, 73, 32.6-109.9 mm SL, provincia de Leoncio Prado, Parque Nacional Tingo Maria, Departament Huanuco, approx. 9°18'S 75°59'W, May 2003, M. Galtier. MUSM 10565, 2 of 3, Huanuco, río Huallaga, río Cayumba, río Marañon drainage, km 495, 9°32'00"S 76°00'00"W, 29 Sep 1996, P. de Rham & F. Chang. **Peru, río Marañon drainage:** CAS 44355, 1, 57.9 mm SL, río Crisnejas near its junction with upper río Paipay, at Paipay, Cajamarca, approx. 7°25'S 78°10'W, Aug 1923, N. E. Pearson. CAS 70083, 2, 52.5-53.5 mm SL, on the intercordilleran río Marañon at 3,500 ft. elev., Balsas, Amazonas, approx. 6°50'S 77°58'W, Jul 1923, N. E. Pearson. CAS 70086, 25, 52.6-82.4 mm SL, Cajamarca, río Paipay into río Crisnejas near its junction with upper río Marañon, approx. 7°20'S 77°45'W, small deeply entrenched stream ca. 4,000 ft. elev., Jul 1923, N. E. Pearson. ROM 52238, 40 of 85, 25.6-94.5 mm SL, approx. 74 km W of road going N to Jean, between Pucara and Guabel, Huancabamba river tributary, río Marañon drainage, 5°56'00"S 79°15'00"W, 8 Jul 1986, E. Holm & J. Patalas. ROM 55366, 21 of 47, 24.6-62.1 mm SL, approx. 14 km W of Bagua, Marañon river tributary, 5°41'00"S 78°39'00"W, 1 Jul 1986, E. Holm *et al.* ROM 55406, 60 of 603 (3 c&s), 35.1-105.6 mm SL, 2 km NW from the junction of the road to Chachapoyas and the road to Bagua, Utcubamba river tributary, río Marañon drainage, 6°13'00"S 77°54'00"W, 29 Jun 1986, E. Holm *et al.*

**Diagnosis.** *Hemibrycon huambonicus* is distinguished from most species of the genus, except from *H. beni*, *H. dentatus*, *H. decurrens*, *H. helleri*, *H. polyodon*, *Hemibrycon* n. sp. 3 and *Hemibrycon* n. sp. 4, by the number of lateral line scales (44-48 vs 34-43 and 47-58 in *H. colombianus*, Fig. 24). It differs from *H. beni*, *Hemibrycon* n. sp. 3, *H. dentatus* and *H. decurrens* by the number of branched anal-fin rays (22-27 vs 15-19, 18-20, 28-31 and 28-34, respectively, Fig. 23); from *H. helleri* by the number of scales in scale sheath along anal-fin base (17-26 vs 6-12) and the number of scale rows above lateral line (8-10 vs 7-8); and from *Hemibrycon* n. sp. 4 by the number of maxillary teeth (7-13 vs 4-9), the number of scales around caudal peduncle (18-20 vs 16-18), and maxilla length (45.2-52.6 vs 40.1-47.8% HL). *Hemibrycon huambonicus* is rather similar to *H. polyodon*, but it differs by the number of caudal peduncle scales (18-20 vs 16), number of scales above lateral line (8-10 vs 8), head length (22.0-26.0 vs 20.9-22.9% SL), and maxillary length (45.2-52.6 vs 43.7-45.6% HL).

**Description.** Morphometric data for *H. huambonicus* summarized in Table 9. Largest male 87.0 mm SL, largest female 109.9 mm SL. Body compressed and elongate; greatest body depth anterior to dorsal-fin origin. Dorsal profile of head nearly straight to slightly convex. Dorsal body profile convex from occipital bony to base of last dorsal-fin ray; straight from this point to adipose-fin origin. Ventral profile of head slightly convex. Ventral body profile convex from pectoral-fin origin to pelvic-fin origin and straight to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head heavy (massive) and relatively small. Mouth terminal, mouth slit nearly at horizontal through below middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 45

degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 4-6, tricuspid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 5 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla fully toothed with 7-13 (Fig. 25) uni- to tricuspid teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5 cusps, followed by medium sized tooth with 3-5 cusps, and 7-10 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps (Fig. 35). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 64); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located approximately to middle of SL and posterior to vertical through pelvic-fin origin. Males with bony hooks in distal one-third of first branched rays. Profile of distal margin of dorsal fin nearly straight to slightly concave. Adipose-fin located at vertical through insertion of two last anal-fin rays.

Anal-fin rays iii-v,22-27 (mean = 24.7, n = 64, Fig. 23). Anal-fin profile slightly concave in males and nearly straight in females. Anal-fin origin approximately at vertical through insertion in the last dorsal fin rays. Anal-fin rays of males bearing one pair of developed bony hooks along posterolateral border of each segment of lepidotrichia, usually along last unbranched ray and first twelve branched rays. Only two males (syntype and non-type male) possess bony hooks in all anal-fin rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-12 (mean = 10.8, n = 64). Pectoral-fin tip surpassing pelvic-fin origin in males, and reaching in females. Males with bony hooks on distal portion of unbranched and all branched rays. Pelvic-fin rays i,6,i or i,7 (n = 64). Pelvic-fin origin located



4-5 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males usually bearing 1 small bony hook per segment of lepidotrichia along ventromedial border of all branched rays.

Caudal fin forked with 19 principal rays (n = 64); lobes in similar size. First third of caudal-fin scaled. Dorsal procurrent rays 11, and ventral procurrent rays 11-12 (n = 4).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 44-48 (mean = 45.3, n = 64, Fig. 24). Scale rows between dorsal-fin origin and lateral line 8-10 (mean = 8.7, n = 64); scale rows between lateral line and pelvic-fin origin 6-7 (mean = 6.6, n = 64). Predorsal scales 15-19, arranged in regular series (mean = 16.8, n = 62). Scales rows around caudal peduncle 18-20 (n = 64). Triangular modified scale on pelvic-fin origin extends posteriorly covering 2-3 scales. Scale sheath along anal-fin base with 17-26 scales in single series, extending to base to 18<sup>th</sup> to 24<sup>th</sup> branched rays.

Precaudal vertebrae 20-21; caudal vertebrae 22-24; total vertebrae 42-43 (x-ray of syntype). Supraneurals 8-9. Gill-rakers on upper limb of outer gill arch 7-8, and on lower limb 11-12 (n = 12).

**Color in alcohol.** General ground body color brown yellowish. Dorsal portion of head and body with concentration of dark chromatophores. Dorsolateral portion of head and body with scattered dark chromatophores. One vertical black humeral spot, located over fourth to sixth lateral line scales and extending over 5-6 horizontal series of scales, including lateral line. Caudal peduncle and middle caudal-fin rays dark pigmented. Abdominal region almost devoid of dark chromatophores. Dorsal, adipose and caudal fin with dark pigmentation diffuse, and pectoral and pelvic fins hyaline (Figs. 33-34).

**Sexual dimorphism.** Males of *Hemibrycon huambonicus* are easily recognized by the presence of bony hooks in dorsal, anal, pelvic and pectoral fin rays. Males and females also slightly differ in proportional pectoral- and pelvic-fin lengths and body depth (Table 9), and in anal-fin shape, slightly concave in males and nearly straight in females. Mature males with gill gland on first gill arch, covering the first branchial filaments (Table 4).

**Distribution.** *Hemibrycon huambonicus* is known from río Huambo, río Crisnejas and río Tingo, all tributaries of río Huallaga drainage, and río Marañon drainage, upper río Amazonas basin, Peru (Fig. 1).

**Remarks of type locality of *Hemibrycon huambonicus*.** The original description of *H. huambonicus* provided by Steindachner (1882) is relatively brief, with the type locality reported only for Huambo (Peru). In Peru, there are two possible localities for Huambo: (1) río Huambo, San Martín, Peru, approx. 7°4'S 77°10'W, upper río Huallaga drainage, and (2) río Huambo, Huanuco, approx. 9°39'S 74°56'W, río Pachitea and río Ucayali drainage. All lots analyzed and identified as *H. huambonicus* are from río Huallaga and río Marañon drainages.

**Geographic variation.** The population of *H. huambonicus* from río Marañon drainage has the smaller number of scale sheath along anal-fin base than *H. huambonicus* from río Huallaga drainage (7-13, mean = 10.1, n = 80 vs 17-26, mean = 21.9, n = 60), and smaller slightly maxillary length (39.5-48.9 vs 45.2-52.6% HL, Table 9), respectively. However, no other significant difference was found between these populations for the recognition of a distinct species.

***Hemibrycon boquiae* (Eigenmann, 1913)**

Fig. 36

*Bryconamericus boquiae* Eigenmann, 1913:20 (originally published as “*Bryconamericus* or *Hemibrycon boquiae* spec. nov?”), original description, type locality: Boquia).

*Hemibrycon boquillae*. -Eigenmann, 1922:152-153 (misspelled or unjustifiably emended, in key, nomenclature change due change locality name for Boquilla, distribution: Cauca Valley).

*Hemibrycon boquiae*. -Eigenmann, 1927:402 (in key), 409 (type material examined, distribution: Boquia, at the western foot of Mt. Tolima, Colombia). -Géry, 1962:66 (map distribution), 78 (in key, upper Cauca drainage, Colombia). -Dahl, 1971:153 (in key), 155 (distribution: Alto Cauca). -Géry, 1977:379 (distribution: río Cauca in Colombia). -Ibarra & Stewart, 1987:43 (holotype FMNH 56259 (CM 5059), Colombia: Boquia). -Román-Valencia, 2001: 28-30 (redescription with base non-type specimens). -Lima *et al.*, 2003:129 (holotype FMNH 56259, distribution: upper Cauca River drainage). -Maldonado-Ocampo *et al.*, 2005:71-72 (description, distribution, list of type specimens, non-type specimens examined), 310 (map 40).

**Material examined. Holotype.** FMNH 56259, 43.0 mm SL, female (x-ray), Colombia, Quindío, Boquia, upper río Cauca drainage, 4°38'44"N 75°35'3"W, altitude 1857 m, C. H. Eigenmann. **Paratypes.** FMNH 56260, 10 (3 x-ray), 31.3-45.0 mm SL, CAS 44332, 10, 29.4-40.9 mm SL, same data of the holotype.

**Non-type specimens. Colombia, upper río Cauca drainage, río Magdalena basin:** IAvHP 7762, 29, 57.5-87.5 mm SL, río San Rafael, altitude 1520 meters, Risaralda, 5°5'42"N 75°58'9"W, 20 Aug 2004, J. Maldonado *et al.* IMCN 2495, 10, 63.4-93.9 mm SL, río

Barragán, Pijao, Quindío, approx. 4°25'S 75°40'W, 30 Nov 2002, S. Usma *et al.* IMCN 1076, 10, 57.3-83.8 mm SL, quebrada Boquia, Salento, Quindío, approx. 4°38'N 75°50'W, 17 Jul 2002, S. Usma *et al.* MHNUC 820, 1 of 3, 53.0 mm SL, quebrada Boquilla, vereda Boquilla via Salento, tributary of upper río Cauca, Quindío, approx. 4°40'N 75°34'W, 30 Nov 2003.

**Diagnosis.** *Hemibrycon boquiae* is distinguished from most species of the genus, except from *H. dariensis*, *H. divisorensis*, *H. huambonicus*, *H. jabonero*, *H. metae*, *H. polyodon*, *H. surinamensis*, *H. taeniurus*, *Hemibrycon* n. sp. 4 and *Hemibrycon* n. sp. 5, by the number of branched anal-fin rays (23-28 vs 15-23 or 28-34, Fig. 23). It can be also distinguished from *H. huambonicus*, *H. polyodon*, and *Hemibrycon* n. sp. 4 by the number of scales rows below lateral line (4-5 vs 6-7). It differs from *H. huambonicus* and *Hemibrycon* n. sp. 4 by the number of lateral line scales (40-44 vs 43-48); from *H. dariensis*, *H. taeniurus*, *H. jabonero* and *H. metae* by the number of cusps of inner row premaxillary teeth (5 vs 5-7); from *H. surinamensis* and *H. divisorensis* by the absence of a wide black asymmetrical spot covering the base of caudal-fin rays and extending along entire length of middle caudal-fin rays; from *H. polyodon* by the number of scales above lateral line (6-7 vs 8-9); from *Hemibrycon* n. sp. 5 by the total number of vertebrae (39-40 vs 41-43) and the number of cusps of the inner row premaxillary teeth (5 vs 5-7); from *H. taeniurus* by the total number of vertebrae (41-43 vs 39-41), and the number of scales above lateral line (6-7 vs 8). Furthermore, *H. boquiae* can be distinguished from *H. dariensis* by the absence of pigment in the distal tip of rays just above and below to middle caudal-fin rays vs densely pigmented.

**Description.** Morphometric data for *H. boquiae* summarized in Table 10. Largest male 72.4, largest female 93.9 mm SL. Body compressed and moderately elongate; greatest body depth anterior to dorsal-fin origin. Dorsal profile of head slightly convex. Dorsal body profile

convex from occipital bony to base of last dorsal-fin ray; straight from this point to adipose-fin origin. Ventral profile of head nearly straight to slightly convex. Ventral body profile convex from pectoral-fin origin to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head small. Mouth terminal, mouth slit nearly at horizontal through middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 45 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 3-5, tricuspid teeth with central cusp slightly longer, usually aligned teeth; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 4-5 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla fully toothed with 7-11 (Fig. 25) uni- to tricuspid teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5 cusps, followed by medium sized tooth with 3 cusps, and 5-10 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps (Fig. 37). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (one with ii,9, n = 43); first unbranched ray approximately one-half length of second ray. Males and females with bony hooks in distal one-third of first branched rays. Dorsal-fin origin located approximately to middle of SL and posterior to vertical through pelvic-fin origin. Profile of distal margin of dorsal fin nearly straight to slightly concave. Adipose-fin located at vertical through insertion of last anal-fin rays.

Anal-fin rays iii-v,23-28 (mean = 25.4, n = 46, Fig. 23). Anal-fin profile nearly straight in males and concave in females. Anal-fin origin approximately at vertical through insertion in the last dorsal fin rays. Anal-fin rays of males and females bearing one pair of

small bony hooks along posterolateral border of each segment of lepidotrichia, along last unbranched ray and all branched rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-12 (mean = 11.1, n = 42). Pectoral-fin tip reaching pelvic-fin origin in males. Males and females with bony hooks on distal portion of unbranched and all branched rays. Pelvic-fin rays i,6,i or i,7 (n = 39). Pelvic-fin origin located 4-5 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males and females usually bearing 1 small bony hook per segment of lepidotrichia along ventromedial border of all branched rays.

Caudal fin forked with 19 principal rays without bony hooks (n = 36); lobes similar in size. Caudal-fin base with a few scales until half of lobes, following by one large scales in each lobe. Dorsal procurrent rays 11, and ventral procurrent rays 11-12 (n = 2).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 40-44 (mean = 42.2, n = 31, Fig. 24). Scale rows between dorsal-fin origin and lateral line 6-7 (mean = 6.2, n = 31); scale rows between lateral line and pelvic-fin origin 4-5 (mean = 4.8, n = 31). Predorsal scales 12-15, arranged in regular series (mean = 13.8, n = 31). Scales rows around caudal peduncle 14 (n = 30). Triangular modified scale on pelvic-fin origin extends posteriorly covering 2-3 scales. Scale sheath along anal-fin base with 10-16 scales in single series, extending to base of most anterior branched rays.

Precaudal vertebrae 18-19; caudal vertebrae 22-24; total vertebrae 41-43 (n = 4). Supraneurals 6-8 (n = 4). Gill-rakers on upper limb of outer gill arch 7-8, and on lower limb 11-12 (n = 4).

**Color in alcohol.** Type material without chromatophores. Color based on the non-type specimens. General ground body color brown yellowish. Dorsal portion of head and body

with concentration of black chromatophores. Dorsolateral portion of head and body with scattered black chromatophores. One large and vertical black humeral spot, located over fourth to fifth lateral line scales and extending over 4-5 horizontal series of scales, including lateral line. Midlateral dark stripe extending from humeral region to middle caudal-fin rays, broad in the caudal peduncle. Abdominal region almost devoid of dark chromatophores. Dorsal and caudal fin with dark pigmentation diffuse and anal fin with small black chromatophores along its distal third forming a stripe. Pectoral, pelvic and adipose fins hyaline (Fig. 36). Some specimens examined three years after fixation in formalin (IAVHP 7762) yet presented the dorsal and caudal-fin base red-orange pigmented.

**Sexual dimorphism.** Mature males and females of *Hemibrycon boquiae* possess small bony hooks on the dorsal-, anal-, pelvic-, and pectoral-fin rays. Mature males with gill gland on first gill arch, covering first branchial filaments. Males and females slightly differ in proportional body depth and pelvic-fin lengths (Table 10) and in anal-fin shape, which is concave in females and nearly straight in males. Twelve dissected mature females (IMCN lots, 68.7-93.9 mm SL) present small bony hooks in the most of anal-, pectoral-, and pelvic-fin rays, and in the first dorsal-fin rays, a character unusual in the characids.

**Distribution.** *Hemibrycon boquiae* is known only from upper río Cauca drainage, río Magdalena basin, Colombia (Fig. 1).

**Remarks on the type material of *Hemibrycon boquiae*.** Type series in very bad condition. The specimens are crooked, with broken fins and lacking body scales. In the brief original description Eigenmann already commented that the type specimens were in very bad condition. It was not possible to make some measurements and counts in the holotype and

paratypes. Eigenmann, 1913:20 designated the holotype (CM 5059, now FMNH 56259) and 21 paratypes (CM 5059, 10, now FMNH 56260, and IU 12831, 10 or 11, now CAS 44332). Eigenmann possibly included the holotype in the paratypes counts.

Román-Valencia (2001:29) redescribed *H. boquiae* based only in non-type material (11 specimens) collected at type locality: “Quebrada Boquia”, affluent of the río Quindío, alto río Cauca, Vereda Boquia, Municipio de Salento, Departamento del Quindío, Colombia. Román-Valencia compared *H. boquiae* with *Bryconamericus caucanus* but did not provide a diagnosis for that species. In the discussion, *H. boquiae* was compared only with *H. dentatus*, and it was not distinguished from the remaining species of the genus.

I have analyzed the type and non-type material and compared with data presented by Román-Valencia, and found some scales and rays counts do not agree with those reported in the redescription. The variation in number of lateral line scales found is 40-44 *versus* 38-42 reported by Román-Valencia; number of branched anal-fin rays 23-28 *versus* 23-26; and number of pelvic-fin rays i,6,i or i,7 *versus* ii,6.

### ***Hemibrycon dentatus* (Eigenmann, 1913)**

Fig. 38

*Bryconamericus dentatus* Eigenmann, 1913:19 (original description, type locality: Piedra Moler). -Ibarra & Stewart, 1987:18 (holotype FMNH 56253 (CM 5054), Colombia: Piedra de Moler). -Vari & Howe, 1991:10 (USNM 79175, 3 paratypes, Colombia, Paila).  
*Hemibrycon dentatus*. -Eigenmann, 1922:152-153 (new combination; in key; distribution: Piedra Moler; Paila; Cali; upper río Cauca and Atlantic side of the Cordillera of Bogotá). -Eigenmann, 1927:403 (in key), 414-415 (original description repeated; type specimens examined; distribution: upper río Cauca and ?Atlantic side of the Cordillera east of



Bogotá). -Géry, 1962:66 (map distribution), 78 (in key; upper Cauca drainage, Colombia). -Dahl, 1971:153 (in key), 155 (distribution: Alto Magdalena, Alto Cauca, Alto San Jorge, río Cesar y río Orihueca). -Géry, 1977:379 (distribution: río Cauca in Colombia). -Lima *et al.*, 2003:129 (holotype FMNH 56253; distribution: Cauca River drainage, upper San Jorge, Cesar, and Orihueca Rivers). -Maldonado-Ocampo *et al.*, 2005:73-74 (description, distribution, list of type specimens, non-type specimens examined).

*Hemibrycon dentatus dentatus*. -Schultz, 1944:362-363 (table 27, in key, non-type material examined).

**Material examined. Colombia, upper río Cauca drainage, río Magdalena basin:**

**Holotype.** FMNH 56253, 76.6 mm SL, female, Piedra de Moler, approx. 4°44'N 75°55'W, 22 Feb 1912, C. H. Eigenmann. **Paratypes.** CAS 39543, 4 of 5, 61.4-90.1 mm SL, 31.25 miles up river from Cartago, río Paila into río Cauca, Paila, Valle del Cauca, approx. 4°20'N 76°5'W, 25-26 Feb 1912, C. H. Eigenmann. CAS 39544, 7, 57.6-73.2 mm SL, río Viejo, east of Cartago, río Cauca drainage, Quindío, 21 Feb 1912, C. H. Eigenmann. CAS 39545, 1, 34.1 mm SL, Cali, 3°27'10"N 76°23'30"W, 29 Feb - 3 Mar 1912. FMNH 56252, 1 of 5 (x-ray), 96.0 mm SL, Paila, approx. 4°20'N 76°5'W, 25 Feb 1912, C. H. Eigenmann. FMNH 69709, 3 of 8, 67.9-80.1 mm SL, Paila, approx. 4°20'N 76°5'W, 26 Feb 1912, C. H. Eigenmann. USNM 79175, 3 of 4 originally (x-ray), 64.8-80.5 mm SL, Paila, approx. 4°20'N 76°5'W, 28 Aug 1917, C. H. Eigenmann.

**Non-type specimens. Colombia (upper río Cauca drainage, río Magdalena basin):** IMCN 282, 4, 82.0-100.8 mm SL, río Ovejas, Suarez, Cauca, 3°5'N 76°42'W, Nov 1995, S. Usma. IMCN 3036, 2, 68.9-75.8 mm SL, río Coltarina, Ansermanuevo, Valle del Cauca, approx. 4°42'N 75°57'W, Feb 1999, A. Ortega-Lara *et al.* MHNG 1226.53, 1, 128.5 mm SL, El

Tambo, Prov. Cauca, alt. 1700m, upper río Cauca drainage, approx. 2°25'N 76°49'W, Aug 1952, ach. K. von Sneidern.

**Diagnosis.** *Hemibrycon dentatus* is distinguished from most species of the genus, except from *H. beni*, *H. huamponicus*, *Hemibrycon* n. sp. 3 and *Hemibrycon* n. sp. 4 by the number of lateral line scales (45-50 vs 34-44 and 47-58 in *H. colombianus*, Fig. 24). It differs from *H. beni*, *H. colombianus*, *Hemibrycon* n. sp. 3 and *Hemibrycon* n. sp. 4 by the number of branched anal-fin rays (28-34 vs 15-28, Fig. 23). Furthermore, *H. dentatus* differs from all species listed above by the number of cusps of inner row premaxillary teeth (5-7 vs 5).

**Description.** Morphometric data for *H. dentatus* summarized in Table 11. Largest male 80.1 mm SL, largest female 96.0 mm SL. Body compressed and moderately elongate; greatest body depth anterior to dorsal-fin origin. Dorsal profile of head slightly concave to nearly straight. Dorsal body profile convex from occipital bony to base of last dorsal-fin ray; straight from this point to adipose-fin origin. Ventral profile of head slightly convex. Ventral body profile convex from pectoral-fin origin to pelvic-fin origin, and nearly straight to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head small. Mouth terminal, mouth slit nearly at horizontal through middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 60 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 4-5, tri- to pentacuspoid teeth with central cusp slightly longer, and with the first and last teeth unaligned, distal tip of teeth dislocated forward; inner row teeth 4, gradually decreasing in length from first to third teeth

and last smaller; with 5-7 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla toothed with 3-9 (Fig. 25) tri- to pentacuspoid teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5-7 cusps, followed by medium sized tooth with 5 cusps, and 7-9 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps (Fig. 4). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 25); first unbranched ray approximately one-half length of second ray. Dorsal fin without bony hooks. Dorsal-fin origin located posterior to middle of SL and posterior to vertical through pelvic-fin origin. Profile of distal margin of dorsal fin nearly straight to slightly concave. Adipose-fin located at vertical through insertion of last anal-fin rays.

Anal-fin rays iii-vi,28-34 (mean = 29.9, n = 26, Fig. 23). Anal-fin profile concave in males and nearly straight to slightly concave in females. Anal-fin origin approximately at vertical through insertion in the last dorsal fin rays. Anal-fin rays of males bearing one pair of small bony hooks along posterolateral border of each segment of lepidotrichia, along last unbranched ray and eighth to twelfth branched rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-13 (mean = 11.5, n = 26). Pectoral-fin tip reaching pelvic-fin origin in both sexes. Pectoral fin without bony hooks. Pelvic-fin rays i,6,i or i,7(n = 26). Pelvic-fin origin located 6-7 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males usually bearing 1 small bony hook per segment of lepidotrichia along ventromedial border of all branched rays.

Caudal fin forked with 19 principal rays without bony hooks (n = 26); lobes similar in size. Caudal-fin base have a few scales. Dorsal procurrent rays 11-12, and ventral procurrent rays 10-12 (n = 8).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 45-50 (mean = 46.5, n = 26, Fig. 24). Scale rows between dorsal-fin origin and lateral line 7-9 (mean = 7.9, n = 26); scale rows between lateral line and pelvic-fin origin 5-6 (mean = 5.5, n = 26). Predorsal scales 14-17, arranged in regular series (mean = 16.1, n = 26). Scales rows around caudal peduncle 14-16 (mean = 15.5, n = 26). Triangular modified scale on pelvic-fin origin extends posteriorly covering 3-4 scales. Scale sheath along anal-fin base with 15-31 scales in single series, extending to base of most anterior branched rays.

Precaudal vertebrae 18; caudal vertebrae 24-25; total vertebrae 42-43 (n = 8). Supraneurals 8-9 (n = 8). Gill-rakers on upper limb of outer gill arch 7-9, and on lower limb 12-14 (n = 8).

**Color in alcohol.** General ground body color brown yellowish. Dorsal portion of head and body with concentration of dark chromatophores. Dorsolateral portion of head and body with scattered dark chromatophores. One large and vertical black humeral spot, located over third to fifth lateral line scales and extending over 4-5 horizontal series of scales, including lateral line. Midlateral dark stripe extending from humeral region to middle caudal-fin rays, broad in the caudal peduncle. Abdominal region almost devoid of dark chromatophores. Dorsal and caudal fin with dark pigmentation diffuse and anal fin with small black chromatophores along its border forming narrow stripe. Pectoral, pelvic and adipose fins hyaline (Fig. 38). Holotype with midlateral body silvery.

**Sexual dimorphism.** Males of *Hemibrycon dentatus* are easily recognized by the presence of bony hooks on the anal- and pelvic-fin rays. Males and females also slightly differ in proportional pectoral- and pelvic-fin lengths and body depth (Table 11), and in anal-fin shape,

concave in males and nearly straight to slightly concave in females. Mature males without gill gland on first gill arch.

**Distribution.** *Hemibrycon dentatus* is known only from upper río Cauca drainage, río Magdalena basin, Colombia (Fig. 1).

***Hemibrycon tolimae* (Eigenmann, 1913)**

Fig. 39

*Bryconamericus tolimae* Eigenmann, 1913:18 (original description, type material, type locality: Ibagué). -Román-Valencia, 2004:23-26 (new combination, redescription, paratypes examined: FMNH 56258, 4 of 7; distribution: restrict for río Combeima, Ibagué, río Magdalena basin, Colombia). -Maldonado-Ocampo *et al.*, 2005:61-62 (description, type locality: río Combeima, Tolima; list of type specimens, non-type specimens examined).

*Hemibrycon tolimae*. -Eigenmann, 1922:152-153 (new generic combination, in part, in key, distribution: Ibagué; various localities on the western slope of the Cordillera of Bogotá). -Eigenmann, 1927:402 (in key), 404-405 (in part, description original repeated, type specimens examined, distribution: mountain streams of Colombia on both the eastern and western slopes of the río Magdalena basin; Pacific slope). -Géry, 1962:66 (map distribution), 77 (in key, río Magdalena, Colombia). -Dahl, 1971:153 (in key), 154 (distribution: Alto Magdalena, Santander, río Cesar, Alto San Jorge y en ríos Piedras, Manzanares, Gaira (Minca), etc. de la Sierra Nevada de Santa Marta). -Géry, 1977:379 (distribution: río Magdalena in Colombia). -Ibarra & Stewart, 1987:19 (holotype FMNH

56257 (CM 5057), Colombia: Ibagué). -Lima *et al.*, 2003:130 (holotype FMNH 56257, distribution: upper Magdalena River basin).

**Material examined. Upper río Magdalena basin: Holotype.** FMNH 56257, 90.6 mm SL, female (x-ray), río Combeima, Ibagué, Tolima, Colombia, approx. 4°27'N 75°14'W, C. H. Eigenmann. **Paratypes.** FMNH 56258, 7 (x-ray), 47.2-81.4 mm SL, CAS 44357, 8, 40.8-91.6 mm SL, río Combeima, 4250 feet, Ibagué, Tolima, Colombia, C. H. Eigenmann.

**Non-type specimens. Colombia, upper río Magdalena basin:** CAS 70098, 9, 35.6-48.0 mm SL, FMNH 56772, 9, 33.4-40.2 mm SL, quebrada Chamisal, between Honda and Facatativa, Cundinamarca, approx. 4°49'N 74°22'W, 1913, M. Gonzales. CAS 70102, 2, 49.1-67.6 mm SL, FMNH 56769, 1, 63.9 mm SL, quebrada El Guadual, Tolima, approx. 4°24'N 75°23'W, 1913, M. Gonzales. CAS 70103, 10, 31.5-50.2 mm SL, FMNH 56652, 1, 40.8 mm SL, quebrada de Suescum, río Magdalena basin (?), Santander or Cundinamarca, 1913, M. Gonzales. CAS 132084, 1, 70.9 mm SL, Fusagasuga, Cundinamarca, approx. 4°21'N 74°27'W, N. Maria. FMNH 56770, 1, 70.5 mm SL, quebrada Chimbe, Cundinamarca, approx. 4°55'N 74°28'W, M. Gonzales. FMNH 56771, 1, 59.1 mm SL, quebrada Sayeta, M. Gonzales.

**Diagnosis.** *Hemibrycon tolimae* is distinguished from all species of the genus, except from *H. colombianus*, *H. helleri*, *H. huambonicus*, *Hemibrycon* n. sp. 1, *Hemibrycon* n. sp. 2, *Hemibrycon* n. sp. 3 and *Hemibrycon* n. sp. 5, by the number of branched anal-fin rays (19-23 vs 15-19 or 24-34, Fig. 23). *Hemibrycon tolimae* differs from *H. colombianus* and *H. huambonicus* by the number of lateral line scales (40-43 vs 47-58 and 44-48, respectively, Fig. 24). It differs from *H. helleri* by the number of scale around caudal peduncle (14-16 vs 16-18), and the number of maxillary teeth (4-8 vs 8-13); from *Hemibrycon* n. sp. 2 by the

number of scales horizontal rows above lateral line (6-8 vs 8-9), and the number of scale around caudal peduncle (14-16 vs 16-18); from *Hemibrycon* n. sp. 1, *Hemibrycon* n. sp. 2, *Hemibrycon* n. sp. 3 by the number of cusps of the inner row teeth (5-7 vs 5); from *Hemibrycon* n. sp. 5 by the number of maxillary teeth (4-8 vs 8-14) and the total number of gill rakers (19-21 vs 17-18). Furthermore, *H. tolimae* can be distinguished from *Hemibrycon* n. sp. 1 by the number of scales rows below lateral line (5-6 vs 3-4), and from *Hemibrycon* n. sp. 3 by the number of lateral line scales (40-43 vs 42-46).

**Description.** Morphometric data for *H. tolimae* summarized in Table 12. Largest male 68.0 mm SL, largest female 91.6 mm SL. Body compressed and moderately elongate; greatest body depth anterior to dorsal-fin origin. Dorsal profile of head nearly straight to slightly convex, and concave in the occipital region. Dorsal body profile convex from occipital bony to base of last dorsal-fin ray; straight from this point to adipose-fin origin. Ventral profile of head nearly straight to slightly convex. Ventral body profile convex from pectoral-fin origin to pelvic-fin origin and straight to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head small. Mouth terminal, mouth slit nearly at horizontal through below middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 60 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 3-5, tricuspid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 5-7 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla toothed with 4-8 (Fig. 25) tri- to pentacusp teeth, with central cusp

longer. Three anteriormost dentary teeth larger, with 5 cusps, followed by medium sized tooth with 3-5 cusps, and 4-5 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps. All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 28); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located approximately to middle of SL and posterior to vertical through pelvic-fin origin. Males with bony hooks in distal one-third of first to seventh branched rays. Profile of distal margin of dorsal fin nearly straight to slightly concave. Adipose-fin located at vertical through insertion of last anal-fin rays.

Anal-fin rays ii-v,19-23 (mean = 21.6, n = 28, Fig. 23). Anal-fin profile slightly concave in males and nearly straight in females. Anal-fin origin approximately at vertical through insertion in the last dorsal fin rays. Anal-fin rays of males bearing one pair of bony hooks along posterolateral border of each segment of lepidotrichia, along last unbranched ray and eleventh to fifth branched rays, and small bony hooks in the tip of last rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-12 (mean = 11.2, n = 28). Pectoral-fin tip not reaching pelvic-fin origin in males and females. Males with bony hooks on distal portion of unbranched and all branched rays. Pelvic-fin rays i,6,i or i,7 (rarely i,7,i, n = 28). Pelvic-fin origin located 4-5 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males usually bearing 1 small bony hook per segment of lepidotrichia along ventromedial border of second to eighth branched rays.

Caudal fin forked with 19 principal rays without bony hooks (n = 28); lobes similar in size. Males with bony hooks in the distal tip of middle caudal-fin rays. Caudal-fin base have a few scales. Dorsal procurrent rays 10-12, and ventral procurrent rays 10-11 (n = 7).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series



40-43 (mean = 42.0, n = 28, Fig. 24). Scale rows between dorsal-fin origin and lateral line 6-8 (mean = 6.9, n = 28); scale rows between lateral line and pelvic-fin origin 5-6 (mean = 5.8, n = 28). Predorsal scales 14-18, arranged in regular series (mean = 15.5, n = 25). Scales rows around caudal peduncle 14-16 (mean = 14.8, n = 28). Triangular modified scale on pelvic-fin origin extends posteriorly covering 2-3 scales. Scale sheath along anal-fin base with 5-14 scales in single series, extending to base of most anterior branched rays.

Precaudal vertebrae 19-20; caudal vertebrae 20-21; total vertebrae 39-41 (n = 8). Supraneurals 8-9 (n = 8). Gill-rakers on upper limb of outer gill arch 7-8, and on lower limb 11-13 (n = 11).

**Color in alcohol.** General ground body color brown yellowish. Dorsal portion of head and body with concentration of dark chromatophores. Dorsolateral portion of head and body with scattered dark chromatophores. One vertical black humeral spot, located over third to fifth lateral line scales and extending over 4 horizontal series of scales, including lateral line. Midlateral stripe silvery. Midlateral dark stripe extending from humeral region to middle caudal-fin rays, broad in the caudal peduncle. Abdominal region almost devoid of dark chromatophores. Dorsal and caudal fin with dark pigmentation diffuse and anal fin with small black chromatophores along its border forming narrow stripe. Pectoral, pelvic and adipose fins hyaline (Fig. 39).

**Sexual dimorphism.** Males of *Hemibrycon tolimae* are easily recognized by the presence of bony hooks in all fins rays. Males and females also slightly differ in anal-fin shape, which is slightly concave in males and nearly straight in females. Mature males with gill gland on first gill arch, covering the first branchial filaments.

**Distribution.** *Hemibrycon tolimae* is known from upper río Magdalena basin, Colombia (Fig. 1).

**Remarks.** Román-Valencia (2004) redescribed *Bryconamericus tolimae* analyzing only four paratypes (FMNH 56258) and some lots non-types from río Combeima, upper río Magdalena basin, Ibagué, Tolima, Colombia. That author presented an inadequate diagnosis for the species and his morphometric data are doubtful. The author based on the number of maxillary teeth (2-6) to redescribed the species in *Bryconamericus* genus. I analyzed all type series of *B. tolimae* and this species possess 4-8 maxillary teeth (Fig. 25), a character uncommon for *Bryconamericus* species, but often found in the *Hemibrycon* species.

#### ***Hemibrycon colombianus* Eigenmann, 1914**

Fig. 40

*Hemibrycon colombianus* Eigenmann, in Eigenmann, Henn & Wilson, 1914:8 (original description, type locality: río San Gil, Santander, Colombia). -Eigenmann, 1922:152-153 (in key, distribution: Santander). -Eigenmann, 1927:402 (in key), 407-408 (original description repeated, type specimens examined, distribution: mountain streams of Santander, Colombia). -Géry, 1962:66 (distribution: near Bogotá), 77 (in key). -Dahl, 1971:153 (in key), 154 (drawing of the one specimen). -Ibarra & Stewart, 1987:43 (catalog of types FMNH). -Lima *et al.*, 2003:129 (holotype FMNH 56653 [ex CM 5470], distribution: San Gil River, Santander). -Maldonado-Ocampo *et al.*, 2005:73 (description, distribution, list of type specimens, non-types specimens examined).

**Material examined. Colombia, Santander, middle río Magdalena basin: Holotype.**

FMNH 56653, female (x-ray), 84.0 mm SL, río San Gil, approx. 6°33'S 73°8'W, 1913, M. Gonzales. **Paratypes.** CAS 44350, 1, 83.8 mm SL, same data of holotype. CAS 44351, 1, 60.7 mm SL, FMNH 56654, 1, 46.2 mm SL, río Piedras, 1913, M. Gonzales. CAS 44352, 1, 41.8 mm SL, FMNH 56655, 1, 46.8 mm SL, quebrada Deoca Monte, 6°9'45"N 72-73°35'35"W, 1913, M. Gonzales. CAS 44353, 5, 28.3-42.8 mm SL, FMNH 56656, 5 (x-ray), 26.3-38.0 mm SL, quebrada Mararari, 1913, M. Gonzales.

**Non-type specimens. Colombia, middle río Magdalena basin: IAvHP 2942, 4 of 6, 52.5-**

62.3 mm SL, quebrada El Cobre, río Suarez, Boyacá, approx. 6°27'S 72°42'W, 26 Jun 1995, V. Ortiz. IAvHP 3130, 26, 31.3-108.0 mm SL, río Moniquira and río Suarez, Santander, approx. 6°46'S 73°12'W, 11 Sep 1995, V. Ortiz. IAvHP 3132, 24, 54.4-93.1 mm SL, río Moniquira, río Suarez and quebrada El Cobre, approx. 6°27'S 72°42'W, 20 Jun 1995, V. Ortiz.

**Diagnosis.** *Hemibrycon colombianus* is distinguished from all species of the genus, except from *H. helleri*, *H. huambonicus*, *H. jabonero*, *H. tolimae*, *Hemibrycon* n. sp. 2 and *Hemibrycon* n. sp. 5, by the number of branched anal-fin rays (20-25 vs 15-19 or 24-34, Fig. 23). *Hemibrycon colombianus* differs from all these species by the number of lateral line scales (47-58 vs 39-48), and the number of scales horizontal rows below lateral line (7-9 vs 4-7). Furthermore, *H. colombianus* differs from *H. huambonicus* by the number of scale sheath along anal-fin base (7-15 vs 17-26), and the number of cusps of the inner row teeth (5-7 vs 5).

**Description.** Morphometric data for *H. colombianus* summarized in Table 13. Largest male 93.1 mm SL, largest female 108.0 mm SL. Body compressed and moderately elongate; greatest body depth anterior to dorsal-fin origin. Dorsal profile of head slightly convex.

Dorsal body profile convex from occipital bony to base of last dorsal-fin ray; straight from this point to adipose-fin origin. Ventral profile of head nearly straight to slightly convex. Ventral body profile convex from pectoral-fin origin to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head small. Mouth terminal, mouth slit nearly at horizontal through middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 45 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 4-5, tricuspid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 5-7 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla fully toothed with 4-10 (Fig. 25) uni- to pentacusp teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5 cusps, followed by medium sized tooth with 3-5 cusps, and 7-10 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps. All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 37); first unbranched ray approximately one-half length of second ray. Dorsal fin without bony hooks. Dorsal-fin origin located approximately to middle of SL and posterior to vertical through pelvic-fin origin. Profile of distal margin of dorsal fin nearly straight to slightly concave. Adipose-fin located at vertical through insertion of last anal-fin rays.

Anal-fin rays iii-v,21-24 (rarely 20 or 25, mean = 22.3, n = 37, Fig. 23). Anal-fin profile slightly convex in males and concave in females. Anal-fin origin approximately at vertical through insertion in the last dorsal fin rays. Anal-fin rays of males bearing one pair of

small bony hooks along posterolateral border of each segment of lepidotrichia, along last unbranched ray and ninth to tenth branched rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-13 (mean = 11.5, n = 37). Pectoral-fin tip reaching pelvic-fin origin in males. Pectoral fin without bony hooks. Pelvic-fin rays i,6,i or i,7 (n = 37). Pelvic-fin origin located 6-7 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males usually bearing 1 small bony hook per segment of lepidotrichia along ventromedial border of second to sixth branched rays.

Caudal fin forked with 19 principal rays without bony hooks (n = 36); lobes similar in size. Caudal-fin base have a few scales. Dorsal procurrent rays 11, and ventral procurrent rays 11-12 (n = 4).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 47-58 (mean = 51.5, n = 34, Fig. 24). Scale rows between dorsal-fin origin and lateral line 8-10 (mean = 9.0, n = 36); scale rows between lateral line and pelvic-fin origin 7-9 (mean = 7.6, n = 36). Predorsal scales 16-20, arranged in regular series (mean = 18.1, n = 35). Scales rows around caudal peduncle 16-20 (mean = 17.3, n = 34). Triangular modified scale on pelvic-fin origin extends posteriorly covering 2-3 scales. Scale sheath along anal-fin base with 7-15 scales in single series, extending to base of most anterior branched rays.

Precaudal vertebrae 18-19; caudal vertebrae 22-23; total vertebrae 40-42 (n = 6). Supraneurals 6-7 (n = 2). Gill-rakers on upper limb of outer gill arch 6-7, and on lower limb 12 (n = 7).

**Color in alcohol.** Type material depigmented. Color based on non-type specimens. General ground body color brown yellowish. Dorsal portion of head and body with concentration of dark chromatophores. Dorsolateral portion of head and body with scattered dark

chromatophores. One large and vertical black humeral spot, located over fourth to fifth lateral line scales and extending over 5-6 horizontal series of scales, including lateral line. Midlateral dark stripe extending from humeral region to middle caudal-fin rays, broad in the caudal peduncle. Abdominal region almost devoid of dark chromatophores. Dorsal and caudal fin with dark pigmentation diffuse and anal fin with small black chromatophores along its border forming narrow stripe. Pectoral, pelvic and adipose fins hyaline (Fig. 40).

**Sexual dimorphism.** Males of *Hemibrycon colombianus* are easily recognized by the presence of bony hooks on the anal- and pelvic-fin rays. Males and females also slightly differ in proportional pectoral- and pelvic-fin lengths and body depth (Table 13), and in anal-fin shape, which is slightly convex in males and concave in females. Mature males lack gill gland on first gill arch.

**Distribution.** *Hemibrycon colombianus* is known only from río Sogamoso drainage, middle río Magdalena basin, Colombia (Fig. 1).

**Remarks.** All type specimens designated by Eigenmann are in good conditions. I have analyzed the holotype and six paratypes of the type series of *Bryconamericus plutarcoi* Román-Valencia (2001) from alto río Suárez, middle río Magdalena basin. Five paratypes of this species belong to *Hemibrycon colombianus*. Only the holotype and one paratype seem to belong to “*B. plutarcoi*”. The type locality of *B. plutarcoi* is the same or very near that of the *H. colombianus*.

### ***Hemibrycon dariensis* Meek & Hildebrand, 1916**

Figs. 41-42

*Hemibrycon dariensis* Meek & Hildebrand, 1916:285-286 (original description, type locality: río Yape, río Tuira Drainage, Panama). -Eigenmann, 1922:152-153 (in key, distribution: río Yape, Tuira Drainage). -Eigenmann, 1927:403 (in key), 413-414 (description, two paratypes examined: 15335 IU; distribution: río Tuira Drainage, Panama). -Géry, 1962:66 (distribution: río Tuira in Panama), 69-70 (comparison with species of genus), 78 (in key). -Géry, 1977:379 (Panama). -Ibarra & Stewart, 1987:43 (catalog of types FMNH). -Vari & Howe, 1991:23 (USNM 78594, 8 paratypes). -Lima *et al.*, 2003:129 (holotype: FMNH 8947, distribution: Yape River in Tuira River drainage).

*Hemibrycon carrilloi* Dahl, 1960:467-468 (original description, types, drawing of holotype, type locality: quebrada Lá Noche, tributary to the upper Atrato, Pavarandó, Baudó system, Colombia). -Cala, 1981:3 (catalog of types ICNMHN, "Holotypus destruido? Paratypus ICNMHN 126, 29, 31, 50 mm longitude standard, Colombia, Chocó, Pavarandó, sist. río Baudó, 23 noviembre 1959, G. Dahl"). -Maldonado-Ocampo *et al.*, 2005:72 (description, distribution, list of type specimens and material examined). -Lima *et al.*, 2003:129 (Holotype: whereabouts unknown, distribution: Upper Atrato River basin). [NEW SYNONYM]

**Material examined. Panama, Darién, río Tuira basin, Pacific slope basin: Holotype.**

FMNH 8947, female, 49.9 mm SL (x-ray), río Yape, approx. 8°5'N 77°35'W, 6 Mar 1912.

**Paratypes.** CAS 44343, 4, 38.8-49.5 mm SL, río Yape, approx. 8°5'N 77°35'W, 6 Mar 1912,

S. E. Meek & S. F. Hildebrand. FMNH 12661, 8, 51.4-66.5 mm SL, FMNH 12662, 1, 40.8 mm SL, río Capetí, Cana, 5 Mar 1912. FMNH 12663, 1, 62.1 mm SL, río Grande, Cana, 3 Mar 1912. FMNH 12664, 1, 55.9 mm SL, río Satigante, Cana, 1 Mar 1912. FMNH 12665-12670, 6, 32.4-53.6 mm SL, same data of holotype. FMNH 12671, 3, 39.4-51.0 mm SL,

FMNH 12672, 3, 37.0-53.2 mm SL, boca de Cupe, approx. 8°3'N 77°35'W, 28 Feb 1912.  
FMNH 12673, 2, 51.0-54.8 mm SL, río Cupe, Cituro, approx. 8°5'N 77°35'W, 25 Feb 1912.  
FMNH 12674, 3, 40.5-53.9 mm SL, río Aruza, Aruza, approx. 8°5'N 77°38'W, 26 Feb 1912.  
USNM 78594, 8 (x-ray), 29.1-45.3 mm SL, same data of holotype.

**Non-type specimens. Panama, Darién, Pacific slope basin, río Tuira basin:** ANSP 151226, 12, 31.0-42.9 mm SL, river 156.5 km E Bayano bridge, 3 Feb 1983, D. Fromm & D. Weber. MCP 25491, 6 (1 c&s), 30.3-52.5 mm SL, río Pucuro about 3-4 km above mouth of río Tuira, 8°00'00"N 77°31'00"W, 17 Feb 1985, W. C. Starnes *et al.* MCP 27066, 1, 27.9 mm SL, río Tuira, 2-3 km above Pinogana, Pinogana, 8°7'00"N 77°42'00"W, 19 Feb 1985, W. C. Starnes *et al.* MCP 27072, 12 (1 c&s), 20.2-45.2 mm SL, río Pirre, above El Real, El Real, 8°6'00"N 77°45'00"W, 16 Feb 1985, B. Chernoff *et al.* MCP 27074, 18 (1 c&s), 24.4-42.1 mm SL, río Pucuro, above mouth of río Tuira, Pucuro, 8°00'00"N 77°32'00"W, 18 Feb 1985, W. C. Starnes *et al.* MCP 27094, 2, 31.0-33.4 mm SL, río Peresinico, below Renare, above Pigibasal (affluent of río Pirre), 8°1'00"N 77°45'00"W, 23 Feb 1985, B. Chernoff *et al.* USNM 078591, 2, 37.5-42.7 mm SL, río Tuira, boca de Cupe, approx. 8°3'N 77°35'W, 28 Feb 1912, Meek & Hildebrand. USNM 078593, 7, 38.1-48.3 mm SL, río Aruza, Aruza, approx. 8°5'N 77°38'W, 26 Feb 1912, Meek & Hildebrand. USNM 310567, 5, 29.2-49.9 mm SL, río Membrillo, Colon, approx. 8°41'N 77°41'W, 22 Mar 1967, Battelle, NW Lab. USNM 310572, 14, 20.0-55.1 mm SL, río Uruseca, 2 mi above El Real, approx. 8°7'N 77°45'W, 26 Feb 1967, Battelle, NW Lab. USNM 310574, 8, 42.0-71.1 mm SL, río Sambu, approx. 7°52'N 78°5'W, 25 Mar 1967, Battelle, NW Lab. USNM 310575, 13, 28.4-55.6 mm SL, río Mortí at hydro station, approx. 8°54'N 77°53'W, 16 Mar 1967, Battelle, NW Lab. **Los Santos (río La Villa drainage):** ANSP 99923, 7, 30.2-57.3 mm SL, río Estibana at bridge shortly before entering Macaracas, approx. 7°45'N 80°33'W, 30 Sep 1961, H. G. Loftin & E. L. Tyson. **Veraguas (río Martí Grande basin):** ANSP 99901, 1, 60.5 mm SL, river at bridge



about 17 mi W of Santiago on road to Soná, approx. 8°3'N 81°6'W, 28 Jan 1962, H. G. Loftin *et al.* USNM 310580, 3, 40.1-48.9 mm SL, río Martin Grande, 4 mi south of Santiago on Montijo road, approx. 8°4'N 81°1'W, 14 Jan 1962, H. Loftin *et al.* **Río San Pablo basin:** USNM 310582, 4, 38.3-53.9 mm SL, creek 3 mi W of Soná on Inter American Highway, approx. 8°1'N 81°18'W, 29 Oct 1961, H. Loftin *et al.* **Río Santa Maria basin:** USNM 310565, 27, 20.5-43.9 mm SL, río Conaca, 16 mi E of Santiago, approx. 8°7'N 80°46'W, 25 Feb 1962, H. G. Loftin *et al.* USNM 327266, 37, 38.1-88.6 mm SL, creek 1 mi S of Santa Fe, approx. 8°32'N 81°5'W, 9 Feb 1962, H. G. Loftin *et al.* **Coclé (Pacific slope basin):** USNM 078590, 8, 52.3-63.3 mm SL, río Grande, Cana, approx. 8°25'N 80°30'W, 3 Mar 1912, Meek & Hildebrand. USNM 310571, 7, 17.5-39.3 mm SL, río Estância at bridge on Inter American Highway about 3 mi W of Antón, Antón, approx. 8°25'N 80°17'W, 14 Oct 1961, H. G. Loftin *et al.* USNM 310560, 13, 15.6-46.1 mm SL, creek 5 mi E of Natá on Inter American Highway, approx. 8°22'N 80°36'W, 15 Oct 1961, H. G. Loftin *et al.* USNM 310569, 8, 26.4-38.3 mm SL, río Grande basin, río Cocle at road just outside la Pintada, approx. 8°35'N 80°27'W, 23 Mar 1962, H. G. Loftin. **Panama (río Bayano or Chepo basin):** USNM 293215, 14 (9 x-ray), 37.0-57.1 mm SL, río Terables, Pan American Highway ca 17 km E Chepo, approx. 9°14'N 78°58'W, 25 Feb 1985, W. C. Starnes *et al.* USNM 350168, 4, 32.9-74.9 mm SL, creek 1 mi W of el Llano on Inter American Highway, approx. 9°14'N 78°57'W, 17 Mar 1962, H. G. Loftin *et al.* **Colombia, Chocó (lower río Atrato basin):** IAvHP 7156, 22, 46.4-70.6 mm SL, río El Tigre, Unguia, 8°5'15"N 77°5'15"W, 25 Jul 2005, J. Maldonado *et al.* IAvHP 7237, 9, 45.5-76.8 mm SL, río Unguia abajo de la bocatoma del acueducto, Unguia, 8°3'36"N 77°7'21"W, 24 Jul 2005, J. Maldonado *et al.* IMCN 223, 2, 49.6-54.1 mm SL, IMCN 221, 2, 63.3-96.9 mm SL, río Cutí, Unguia, Chocó, approx. 8°12'N 77°2'W, Aug 1995, S. Usma *et al.* USNM 260699, 4, 23.8-33.0 mm SL, río Salado near Teruita, Chocó, Colombia, 8 Feb 1968, H. Loftin. USNM 327221, 7, 56.5-72.3 mm SL, creek into río Jurado,

about five min. Heli-flight downstream fr. Moutains, 31 Aug 1967, H. G. Loftin. **Colombia, Córdoba (río Sinú basin):** CAS 149497, 5, 34.6-60.5 mm SL, middle río Sinú basin, 16 Jan 1957, G. Dahl. NRM 16280, 1, 52.9 mm SL, río Verde, upper río Sinú.

**Diagnosis.** *Hemibrycon dariensis* distinguished from all species of genus by possessing the distal tip of rays just above and below to middle caudal-fin rays densely pigmented (Figs. 41-42) vs unpigmented. Furthermore, *Hemibrycon dariensis* distinguished from *H. beni*, *H. colombianus*, *H. helleri*, *H. taeniurus*, *H. tolimae*, *H. tridens*, *Hemibrycon* n. sp. 1, *Hemibrycon* n. sp. 2, and *Hemibrycon* n. sp. 3 by the number of branched anal-fin rays (24-28 vs 15-24, Fig. 23). It differs from *H. decurrens*, *H. dentatus*, *H. huambonicus*, and *Hemibrycon* n. sp. 4 by the number of lateral line scales (39-41 vs 42-48, Fig. 24); from *H. divisorensis* and *H. surinamensis* by the absence of a wide black asymmetrical spot covering the base of caudal-fin rays and extending along entire length of middle caudal-fin rays; from *H. jelskii*, *H. boquiae*, and *H. taeniurus* by the number of cusps of the inner row teeth (5-7 vs 5), and from *H. jelskii* by the size of humeral spot (5-6 vs 7-9 horizontal series of scales); from *H. jabonero* by the number of scales rows above and below lateral line (7-8 vs 6-7 and 5-6 vs 4-5); and from *H. metae* by the lateral line scales (39-41 vs 40-43). It also differs from *H. boquiae* by the number of total vertebrae (38-39 vs 41-43). *Hemibrycon dariensis* differs from *H. polyodon* by prepelvic distance (42.1-47.2 vs 39.9-41.9% SL), and by caudal peduncle length (10.7-13.2 vs 14.4-16.6% SL), and from *Hemibrycon* n. sp. 5 by the total number of gill rakers (19-21 vs 17-18).

**Description.** Morphometric data for *H. dariensis* summarized in Table 14. Largest male 58.6 mm SL, largest female 66.6 mm SL. Body compressed and moderately elongate; greatest body depth anterior to dorsal-fin origin. Dorsal profile of head slightly convex. Dorsal body

profile convex from occipital bony to base of last dorsal-fin ray; straight from this point to adipose-fin origin. Ventral profile of head nearly straight to slightly convex. Ventral body profile convex from pectoral-fin origin to pelvic-fin origin, and straight to slightly convex to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head small. Mouth terminal, mouth slit nearly at horizontal through middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 45 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 3-5, tri- to pentacusp teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 5-7 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla fully toothed with 3-11 (Fig. 25) uni- to tricuspid teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5 cusps, followed by medium sized tooth with 3-5 cusps, and 9-12 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps (see fig. 10 in Malabarba & Weitzman, 2003:85). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 79); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located posterior to middle of SL and posterior to vertical through pelvic-fin origin. Profile of distal margin of dorsal fin nearly straight to slightly concave. Males with bony hooks in distal one-third of first to fifth branched rays. Adipose-fin located at vertical through insertion of last anal-fin rays.

Anal-fin rays ii-v,25-28 (two with 24, mean = 26.3, n = 79, Fig. 23). Anal-fin profile slightly convex in males and nearly straight in females. Anal-fin origin approximately at vertical through insertion in the last dorsal fin rays. Anal-fin rays of males bearing one pair of

small bony hooks along posterolateral border of each segment of lepidotrichia, along last unbranched ray and eighth to tenth branched rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-13 (mean = 11.1, n = 79). Pectoral-fin tip reaching pelvic-fin origin in males. Males with bony hooks on distal portion of unbranched and all branched rays. Pelvic-fin rays i,6,i (n = 79). Pelvic-fin origin located 4-5 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males usually bearing 1 small bony hook per segment of lepidotrichia along ventromedial border of second to seventh branched rays.

Caudal fin forked with 19 principal rays without bony hooks (n = 78); lobes similar in size. Caudal-fin base have a few scales. Dorsal procurrent rays 11-12, and ventral procurrent rays 10-11 (n = 18).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 39-41 (mean = 40.1, n = 64, Fig. 24). Scale rows between dorsal-fin origin and lateral line 7-8 (mean = 7.8, n = 74); scale rows between lateral line and pelvic-fin origin 5-6 (mean = 5.6, n = 74). Predorsal scales 14-17, arranged in regular series (mean = 14.5, n = 51). Scales rows around caudal peduncle 14-16 (mean = 15.4, n = 51). Triangular modified scale on pelvic-fin origin extends posteriorly covering 2-3 scales. Scale sheath along anal-fin base with 8-15 scales in single series, extending to base of most anterior branched rays.

Precaudal vertebrae 16-17; caudal vertebrae 21-23; total vertebrae 38-39 (n = 20). Supraneurals 6-8 (n = 20). Gill-rakers on upper limb of outer gill arch 7-8, and on lower limb 12-13 (n = 12).

**Color in alcohol.** Type material without chromatophores. Color based on the non-type specimens. General ground body color yellowish. Dorsal portion of head and body with concentration of dark chromatophores. Dorsolateral portion of head and body with scattered

dark chromatophores. Midlateral body silvery. One large and vertical black humeral spot, located over fourth to sixth lateral line scales and extending over 5-6 horizontal series of scales, including lateral line. Midlateral dark stripe extending from humeral region to middle caudal-fin rays, broad in the caudal peduncle. Distal tip of rays just above and below of the middle caudal-fin rays with small black chromatophores. Abdominal region almost devoid of dark chromatophores. Dorsal and caudal fin with dark pigmentation diffuse and anal fin with small black chromatophores along its border forming narrow stripe. Pectoral, pelvic and adipose fins hyaline (Figs. 41-42).

**Sexual dimorphism.** Males of *Hemibrycon dariensis* are easily recognized by the presence of bony hooks on the dorsal-, pectoral-, anal- and pelvic-fin rays. Males and females also slightly differ in proportional body depth (Table 14), and in anal-fin shape, which is slightly convex in males and nearly straight in females. Mature males with gill gland on first gill arch, covering the first branchial filaments (Table 4).

**Distribution.** *Hemibrycon dariensis* is known from río Tuira, río Chepo or Bayano, río Santa Maria, río Martí Grande and río San Pablo basins, Pacific slope basins, Panama, and río Atrato and río Sinú basins, Caribbean Sea coastal basins, Colombia (Fig. 1).

**Remarks.** *Hemibrycon dariensis* populations from río Bayano, río San Pablo, río Martí Grande and Santa Maria basins (all isolated rivers from Pacific basins) possess some small differences from río Tuira population. They have a larger number of scale rows above and below lateral line (8-9 vs 7-8 and 6-7 vs 5-6, respectively), and a larger number of scales around caudal-peduncle (16-18 vs 14-16), but no other significant difference was found to recognize these populations as distinct species.

Males and females from río Atrato strongly differ in body depth (Table 14). These females also differ in body depth of those females from río Tuira basin, but not differ from type series of *H. dariensis*. This difference can be due to the larger standard length of those specimens than Panama specimens.

**Remarks from *Hemibrycon carrilloi*.** In the original description of *Hemibrycon carrilloi*, Dahl (1960:467) neglected to provide the catalog numbers for the holotype and paratypes of the species. Cala (1981:3) in his catalog of types of the ICNMHN reported that the holotype was apparently destroyed (without catalog number) and four paratypes (ICNMHN uncat., 126, 29, 31, 50 mm SL). I visited the Instituto de Ciencias Naturales to analyze some lots of *Hemibrycon*, but was not able to examine the paratypes of *H. carrilloi* because they were on loan to Román-Valencia. I recognized three *Hemibrycon* populations from río Atrato basin and compared with the populations of *H. dariensis* from Panama basins, and did not found significant differences between these populations. Furthermore, the specimens from río Atrato basin also had the distal tip of fin rays just above and below to middle caudal-fin rays densely pigmented as found in *H. dariensis*.

### ***Hemibrycon tridens* Eigenmann, 1922**

Fig. 43

*Hemibrycon tridens* Eigenmann, 1922:152 (species described in key, distribution: extralimital, río Apurimac at Uruhuasi). -Eigenmann, 1927:402 (in key), 403-404 (pl. 96, fig. 3, original description, distribution: Uruhuasi, southeastern Peru; holotype 13723 IU). -Eigenmann & Allen, 1942:216 (holotype 13723 IU, Uruasi, southern Peru). -Fowler,

1945:146 (Peru, río Apurimac). -Fowler, 1948:99 (fig. 106, type locality, distribution: alto Amazonas, sudeste do Peru). -Ortega & Vari, 1986:8 (checklist of freshwater fishes from Peru). Lima *et al.*, 2003:130 (holotype: CAS 44358 [ex IU 13723], distribution: upper Amazon River basin).

**Material examined. Holotype.** CAS 44358, 51.5 mm SL, male (x-ray), Peru, 24 leagues from Cusco, Curuhuasi, province of Aymaraes, Department of Apurimac, F. Rosenberg.

**Diagnosis.** *Hemibrycon tridens* is distinguished from all species of the genus, except from *H. beni* by the small number of branched anal-fin rays (17 vs 18-34, Fig. 23). *Hemibrycon tridens* differs from *H. beni* by the number of lateral line scales (39 vs 44-53, Fig. 24). Furthermore, it differs from *H. beni* by the number of scale rows above and below lateral line (6 and 5 vs 7-8 and 6-8, respectively).

**Description.** Morphometric data for *H. tridens* summarized in Table 15. Largest male 51.5 mm SL. Body compressed and elongate; greatest body depth anterior to dorsal-fin origin. Dorsal profile of head convex. Dorsal body profile convex from occipital bony to base of last dorsal-fin ray; straight from this point to adipose-fin origin. Ventral profile of head slightly convex. Ventral body profile convex from pectoral-fin origin to pelvic-fin origin, and straight to slightly convex to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head relatively small. Mouth sub-terminal, mouth slit nearly at horizontal through inferior margin

of eye. Maxilla long and slightly curved, aligned at angle of approximately 45 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 5 tricuspid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 3-5 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla fully toothed with 12 (Fig. 25) tricuspid teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5 cusps, followed by medium sized tooth with 3 cusps, and 8 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps. All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8, first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located posterior to middle of SL and posterior to vertical through pelvic-fin origin. Profile of distal margin of dorsal fin slightly concave. Dorsal fin without bony hooks. Adipose-fin located at vertical through insertion posterior to last anal-fin ray.

Anal-fin rays iii,17 (Fig. 23). Anal-fin profile slightly nearly straight. Anal-fin origin approximately at vertical through insertion in the last dorsal fin rays. Anal-fin rays of male bearing one pair of small bony hooks along posterolateral border of each segment of lepidotrichia, along last unbranched ray and sixteenth branched rays. Hooks located along anteriormost branch and proximal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10. Pectoral-fin tip surpassing pelvic-fin origin. Pectoral fin without bony hooks. Pelvic-fin rays i,6,i. Pelvic-fin tip nearly reaching anal-fin origin. Pelvic-fin origin located 4 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of male bearing 1 small bony hook per segment of lepidotrichia along ventromedial border of second to seventh branched rays.

Caudal fin forked with 19 principal rays without bony hooks; lobes similar in size.



Caudal-fin base with a few scales. Dorsal procurrent rays 10, and ventral procurrent rays 10 (holotype x-ray).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 39 (Fig. 24). Scale rows between dorsal-fin origin and lateral line 6; scale rows between lateral line and pelvic-fin origin 5. Predorsal scales 14, arranged in regular series. Scales rows around caudal peduncle 14.

Precaudal vertebrae 18; caudal vertebrae 22; total vertebrae 40. Supraneurals 5 (holotype x-ray). Gill-rakers on upper limb of outer gill arch 5, and on lower limb 10.

**Color in alcohol.** Holotype bad preserved. Humeral and caudal peduncle spot not evident. Base of caudal fin and middle rays black pigmented. Distal half of dorsal fin with dark pigmentation, and caudal and anal fin with dark pigmentation diffuse. Pectoral and pelvic fins hyaline (Fig. 43). Body yellowish. Left side of holotype has three black spots due fixation or conservation process. Eigenmann (1927:404) described the color pattern “A dark lateral band, caudal spot, and middle caudal rays dusky; distal parts of dorsal and anal and outer part of caudal lobes dusky; margin of lower caudal lobe dusky”.

**Sexual dimorphism.** Male of *Hemibrycon tridens* is easily recognized by the presence of bony hooks on the anal- and pelvic-fin rays. No gill gland was observed on first gill arch.

**Distribution.** *Hemibrycon tridens* is known from río Apurimac, upper río Ucayali drainage, Curuhuasi, Peru (Fig. 1).

**Remarks.** Eigenmann (1922:152) proposed *Hemibrycon tridens* based on one specimen only, diagnosed in his key to *Hemibrycon* species. Only in 1927, Eigenmann presented a full

description, and designated IUM 13723, now CAS 44358, as the type specimen. The type specimen is the only known specimen. The type locality provided by Eigenmann (1922) for *H. tridens* was “Rio Apurimac at Uruhuasi”. According to Hernán Ortega from MUSM (pers. comm.), the correct type locality of *H. tridens* is the río Apurimac at Curuhuasi, upper río Ucayali drainage. He believed that Eigenmann erroneously wrote “Uruhuasi” instead of Curuhuasi.

***Hemibrycon beni* Pearson, 1924**

Fig. 44

*Hemibrycon beni* Pearson, 1924:42-43 (original description; type material; type locality: Espia and río Colorado, lower Bopi, Bolivia), 62-63 (pl. 2, fig. 6, cotype). -Eigenmann, 1927:402 (in key), 407 (redescription; type specimen examined; distribution: Espia and río Colorado, lower Bopi). -Fowler, 1948:96 (fig. 101; type locality; distribution: alto Amazonas, Bolivia). -Géry, 1962:65-66 (distribution on map; fig. 1), 77 (key). -Vari & Howe, 1991:23 (type catalog USNM).

**Material examined. Syntypes.** CAS 44333, 29 (1 x-ray), 24.1-56.0 mm SL, CAS 44334, 60, 27.4-81.4 mm SL, USNM 117543, 2 (x-ray), 31.6-42.1 mm SL, where ríos La Paz and Miguilla join to form río Bopi, río Beni drainage, elev. 3,080 ft., Espia, La Paz, Bolivia, approx. 16°16'S 67°12'W, Jul 1921, N. E. Pearson.

**Non-type specimens.** CAS 44335, 6, 22.5-24.8 mm SL, río Colorado, tributary to lower río Bopi 10 miles above Huachi (=San Miguel de Huachi?), Mulford Exploration of the Amazon Basin, La Paz, Bolivia, approx. 16°5'S 67°12'W, Sep 1921, N. E. Pearson.

**Diagnosis.** *Hemibrycon beni* is distinguished from all species of the genus, except from *H. microformaa*, *H. tridens*, *Hemibrycon* n. sp. 1 and *Hemibrycon* n. sp. 3 by the small number of branched anal-fin rays (15-19 vs 20-34, Fig. 23). *Hemibrycon beni* differs from these species (except from *Hemibrycon* n. sp. 3) by the larger number of lateral line scales (44-53 vs 34-42, Fig. 24). It differs from *Hemibrycon* n. sp. 3 by the number of scale rows below lateral line (6-8 vs 5-6), number of scales rows around caudal peduncle (16-18 vs 14-16), and the total number of vertebrae (38-39 vs 41).

**Description.** Morphometric data for *H. beni* summarized in Table 15. Largest male 81.4 mm SL, largest female 34.3 mm SL. Body compressed and moderately elongate; greatest body depth usually anterior to dorsal-fin origin. Dorsal profile of head straight to slightly convex. Dorsal body profile convex from occipital bony to base of last dorsal-fin ray; straight from this point to adipose-fin origin. Ventral profile of head convex. Ventral body profile convex from pectoral-fin origin to pelvic-fin origin, and straight to slightly convex to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head small. Mouth terminal, mouth slit nearly at horizontal through below middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 45 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 4-5, tricuspid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 5 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla fully toothed with 7-14 (Fig. 25) uni- to tricuspid teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 3-5 cusps, followed by medium sized

tooth with 3 cusps, and 8-9 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps. All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (one with ii,7 and iii,8; n = 30); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located posterior to middle of SL and posterior to vertical through pelvic-fin origin. Profile of distal margin of dorsal fin convex. Dorsal fin without bony hooks. Adipose-fin located at vertical through insertion of last or posterior to last anal-fin ray.

Anal-fin rays iii-iv,16-18 (rarely 15 or 19, mean = 17.0, n = 35, Fig. 23). Anal-fin profile slightly convex in males and nearly straight in females. Anal-fin origin approximately at vertical through insertion in the last dorsal fin rays. Anal-fin rays of males bearing one pair of small bony hooks along posterolateral border of each segment of lepidotrichia, usually along last unbranched ray and third to fourth branched rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-11 (mean = 10.0, n = 33). Pectoral-fin tip reaching pelvic-fin origin in all specimens. Pectoral fin without bony hooks. Pelvic-fin rays i,6,i (one with i,5,i, n = 33). Pelvic-fin origin located 5-6 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males usually bearing 1 small bony hook per segment of lepidotrichia along ventromedial border of second to eighth branched rays.

Caudal fin forked with 19 principal rays without bony hooks (n = 33); lobes similar in size. Caudal-fin base with a few scales in the half-length, followed by one large scale in each lobe. Caudal fin without bony hooks. Dorsal procurrent rays 10-11, and ventral procurrent rays 11 (n = 2, x-ray).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 44-53 (mean = 47.3, n = 32, Fig. 24). Scale rows between dorsal-fin origin and lateral line 7-8

(mean = 7.7, n = 33); scale rows between lateral line and pelvic-fin origin 6-8 (mean = 6.8, n = 33). Predorsal scales 17-20, arranged in regular series (mean = 18.4, n = 33). Scales rows around caudal peduncle 16-18 (mean = 16.4, n = 32). Triangular modified scale on pelvic-fin origin extends posteriorly covering 2 scales. Scale sheath along anal-fin base with 5-8 scales in single series, extending to base of most anterior branched rays.

Precaudal vertebrae 18-19; caudal vertebrae 20; total vertebrae 38-39 (n = 3). Supraneurals 7 (n = 1, x-ray). Gill-rakers on upper limb of outer gill arch 6, and on lower limb 10-11 (n = 4).

**Color in alcohol.** Dorsal portion of head and body dark brown. Dorsolateral portion of body with scattered dark chromatophores. Midlateral body silvery. One small and vertical black humeral spot, located over third to fourth lateral line scales and extending over 1-2 horizontal series of scales including lateral line, and some times over the first horizontal series below lateral line. Base of caudal fin and middle rays black pigmented. Abdominal region almost devoid of dark chromatophores. Dorsal, adipose, and caudal fin with dark pigmentation diffuse and anal fin with small black chromatophores along its border forming narrow stripe. Caudal peduncle without spot. Pectoral and pelvic fins hyaline (Fig. 44). Body yellowish.

**Sexual dimorphism.** Males of *Hemibrycon beni* are easily recognized by the presence of bony hooks on the anal- and pelvic-fin rays. Males and females also slightly differ in proportional body depth (Table 15), and in anal-fin shape, which is slightly convex in males and nearly straight in females. Gill gland not found on first gill arch.

**Distribution.** *Hemibrycon beni* is known from río Beni drainage, río Madeira basin, where ríos La Paz and Miguilla join to form río Bopi, Espia, La Paz, Bolivia (Fig. 1).

**Remarks on the type material.** *Hemibrycon beni* was described by Nathan Pearson with basis in the material collected by the Mulford Expedition, Bolivia, in 1921. In the original description, Pearson designated 48 syntypes in good condition plus 58 syntypes (all specimens from IU 17321, now CAS 44333, 29 and CAS 44334, 60) that were dried during shipment to Indiana University, and listed as additional material 6 more specimens (IU 17347, now CAS 44335). Later, 2 syntypes were donated to USNM 117543 and 16 syntypes to UMMZ 66504 (both ex IU 17321). This last lot was not analyzed. All specimens of the lot CAS 44334 were very dried, but had reasonable condition for analysis. The remaining syntypes are in good condition.

***Hemibrycon helleri* Eigenmann, 1927**

Fig. 45

*Hemibrycon helleri* Eigenmann, 1927:402 (in key), 406 (pl. 96, fig. 2; original description; type material; type locality: río Comerciato, río Urubamba drainage; non-types listed from río Crisnejas [error, specimens refer to *H. huambonicus*]). -Géry, 1962:66 (distribution: río Urubamba), 77 (in key, distribution: río Urubamba, Peru). -Eigenmann & Allen, 1942:216 (18 types without catalog number, río Comerciato; 17611 IU, Paipay, río Crisnejas [error, specimens refer to *H. huambonicus*]; 16047 IU Santa Ana creek). -Fowler, 1943:2 (comparison with *H. coxeyi*). -Fowler, 1948:97 (fig. 104, distribution: alto Amazonas, río Urubamba, Peru). -Ortega & Vari, 1986:8 (type catalog). -Ibarra & Stewart, 1987:43 (three paratypes from FMNH; río Comerciato, Peru). -Lima *et al.*, 2003:129 (distribution: Amazon River basin, Urubamba, Comerciato, and Crisnejas [erroneous distribution] rivers in Peru).

**Material examined (see remarks below). Holotype.** MCZ 31565, (x-ray), 82.7 mm SL, río Comerciato, a small tributary of middle río Urubamba, 30 miles above the Pongo de Mainique, Cusco, Peru, 1,800 ft. elev., approx. 12°28'S 73°7'W, 1910-1915, E. Heller (Yale-National Geographic Expedition). **Paratypes.** CAS 44354, 5, 39.6-72.0 mm SL, FMNH 58439, 3 (x-ray), 36.4-78.5 mm SL, MCZ 30980, 1 (x-ray), 83.8 mm SL, MCZ 30981, 8 (x-ray), 46.1-79.2 mm SL, collected with the holotype.

**Non-type specimens. Peru, Cusco, río Urubamba drainage:** ANSP 180775, 4 (1 c&s), 53.3-81.1 mm SL, quebrada Rosariomayo, west of Quelluono on road to Kiteni, 12°46'28"S 72°39'6"W, 19 Jul 2004, M. Sabaj *et al.* ANSP 180777, 2, 20.4-72.4 mm SL, río Amaybamba, southeast of Quillabamba on road to Ollantaytambo, 12°59'55"S 72°31'24"W, 17 Jul 2004, M. Sabaj *et al.* ANSP 180780, 1, 23.5 mm SL, Yanayaku Grande, tributary of río Urubamba, southeast of Quillabamba on road to Ollantaytambo, 12°59'49"S 72°32'16"W, 17 Jul 2004, M. Sabaj *et al.* CAS 70077, 15, 27.5-81.5 mm SL, río de Santa Ana, creek entering middle río Urubamba at ca. 3000-3400 ft. elev., the farthest point reached by the Eigenmann's on río Urubamba, approx. 12°52'S 72°43'W, 15 Nov 1918, C. H. Eigenmann.

**Diagnosis.** *Hemibrycon helleri* is distinguished from all species of the genus, except from *H. colombianus*, *H. huambonicus*, *H. jabonero*, *H. tolimae*, *Hemibrycon* n. sp. 2, and *Hemibrycon* n. sp. 5, by the number of branched anal-fin rays (19-23 vs 15-19 or 24-34, Fig. 23). *Hemibrycon helleri* differs from *H. colombianus*, *Hemibrycon* n. sp. 2 and *Hemibrycon* n. sp. 5 by the number of lateral line scales (42-45 vs 47-58, 39-42 and 40-42, respectively, Fig. 24). It differs from *H. huambonicus* by the number of scale sheath along anal-fin base (6-12 vs 17-26), and the number of scales rows above lateral line (8-10 vs 7-8); from *H. jabonero* by the number of scales rows above lateral line (7-8 vs 6-7), number of scales around caudal

peduncle (16-18 vs 14), and by the number of cusps of the inner row teeth (5 vs 5-7), and from *H. tolimae* by the number of maxillary teeth (8-13 vs 4-8) and the number of cusps of the inner row teeth (5 vs 5-7). *Hemibrycon helleri* is rather similar to *Hemibrycon* n. sp. 5, but further differs by the number of scales around caudal peduncle (16-18 vs 14), anal-fin base (25.1-29.3 vs 28.0-34.4% of SL), the number of predorsal scales (16-18 vs 13-17), total number of vertebrae (41-43 vs 39-40), and the number of dorsal procurrent rays (8-10 vs 10-12) and ventral procurrent rays of caudal fin (9-10 vs 10-12). The number of branched anal-fin rays distinguish *H. helleri* from *H. huamponicus* and *H. jabonero* (19-23, mean = 21.7, n = 37 vs 22-27, mean = 24.7, n = 64 and 22-28, mean = 25.1, n = 85).

**Description.** Morphometric data for *H. helleri* summarized in Table 16. Largest male 78.6 mm SL, largest female 81.6 mm SL. Body compressed and moderately elongate; greatest body depth anterior to dorsal-fin origin. Dorsal profile of head straight to slightly convex. Dorsal body profile convex from occipital bony to base of last dorsal-fin ray; straight from this point to adipose-fin origin. Ventral profile of head nearly straight to slightly convex. Ventral body profile convex from pectoral-fin origin to pelvic-fin origin, and straight to slightly convex to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head small. Mouth terminal, mouth slit nearly at horizontal through middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 45 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 3-5, tricuspid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and



last smaller; with 4-5 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla fully toothed with 8-13 (Fig. 25) uni- to tricuspid teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5 cusps, followed by medium sized tooth with 3 cusps, and 7-9 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps (Fig. 46). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 33); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located posterior to middle of SL and posterior to vertical through pelvic-fin origin. Profile of distal margin of dorsal fin nearly straight to slightly concave. Males with bony hooks in distal one-third of first branched rays. Adipose-fin located at vertical through insertion of last or posterior to last anal-fin ray.

Anal-fin rays ii-v,19-23 (mean = 21.7, n = 37, Fig. 23). Anal-fin profile slightly convex in males and nearly straight in females. Anal-fin origin approximately at vertical through insertion in the last dorsal fin rays. Anal-fin rays of males bearing one pair of small bony hooks along posterolateral border of each segment of lepidotrichia, along last unbranched ray and twelfth to sixteenth branched rays. One male paratype had bony hooks in all anal-fin branched rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-11 (mean = 10.5, n = 27). Pectoral-fin tip reaching pelvic-fin origin in males. Males with bony hooks on distal portion of unbranched and all branched rays. Pelvic-fin rays i,6,i (n = 30). Pelvic-fin origin located 4-5 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males usually bearing 1 small bony hook per segment of lepidotrichia along ventromedial border of fourth to eighth branched rays.

Caudal fin forked with 19 principal rays without bony hooks (n = 30); lobes similar in size. Caudal-fin base with a few scales in the half-length, followed by one large scale in each

lobe. Dorsal procurrent rays 8-10, and ventral procurrent rays 9-10 (n = 12).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 42-45 (mean = 42.9, n = 23, Fig. 24). Scale rows between dorsal-fin origin and lateral line 7-8 (mean = 7.9, n = 35); scale rows between lateral line and pelvic-fin origin 5-6 (mean = 5.8, n = 35). Predorsal scales 15-18, arranged in regular series (mean = 16.5, n = 34). Scales rows around caudal peduncle 16-18 (mean = 17.0, n = 27). Triangular modified scale on pelvic-fin origin extends posteriorly covering 2-3 scales. Scale sheath along anal-fin base with 6-12 scales in single series, extending to base of most anterior branched rays.

Precaudal vertebrae 19-21; caudal vertebrae 22-23; total vertebrae 41-43 (n = 13). Supraneurals 6-7 (n = 13). Gill-rakers on upper limb of outer gill arch 6-7, and on lower limb 10-11 (n = 11).

**Color in alcohol.** Type material without chromatophores. Color based on the non-type specimens. General ground body color yellowish. Dorsal portion of head and body with dense concentration of dark chromatophores. Dorsolateral portion of head and body with scattered dark chromatophores. Midlateral body silvery. One large and vertical black humeral spot, located over fourth to sixth lateral line scales and extending over 7-8 horizontal series of scales, including lateral line. Midlateral dark stripe extending from humeral region to middle caudal-fin rays, broad in the caudal peduncle. Abdominal region almost devoid of dark chromatophores. Adipose fin densely dark pigmented. Dorsal and caudal fin with dark pigmentation diffuse and anal fin with small black chromatophores along its border forming narrow stripe. Pectoral and pelvic fins hyaline (Fig. 45).

**Sexual dimorphism.** Males of *Hemibrycon helleri* are easily recognized by the presence of bony hooks on the dorsal-, pectoral-, anal- and pelvic-fin rays. Males and females also slightly

differ in proportional body depth (Table 16), and in anal-fin shape, which is slightly convex in males and nearly straight in females. Mature males with gill gland on first gill arch, covering the first branchial filaments.

**Distribution.** *Hemibrycon helleri* is known from río Comerciato, and río Urubamba, upper río Ucayali drainage, Cusco, Peru (Fig. 1).

**Remarks.** Eigenmann (1927: 406) described *Hemibrycon helleri* and designated the holotype (13565) and 17 paratypes (7439 C., 13754 I.) from río Comerciato, Peru. Later, Eigenmann & Allen (1942: 216) listed the type material but did not provided the catalog number for types of *H. helleri*, but only listed 18 type specimens along with their lengths, and type locality. Böhlke (1953) in his catalog of types from Stanford University did not list types of *H. helleri*. Ibarra & Stewart (1987:43) listed three paratypes of *H. helleri* but did not provide the catalog number of FMNH specimens. Eschmeyer (1998:717) listed two possible lots as holotype: ?MCZ 31565 (1) or MCZ 30980 (1), and paratypes: CAS 44354 [ex IU 13754] (5) and FMNH 58439 (3). Lima *et al.* (2003: 129) also presented two catalog numbers for the holotype of *H. helleri*.

Based on a search in the web site of MCZ fish collection some lots of *H. helleri* were discovered. Among these lots, the type specimens designated by Eigenmann in the original description were found. According to Eigenmann (1927) the holotype has 100 mm of size that can be confirmed for the specimen of lot MCZ 31565 (Paulo Petry, pers. comm.). The lots MCZ 30980 (1), and MCZ 30981 (8) are the paratypes that were lacking to complete the type series of *H. helleri*. Paulo Petry analyzed and provided the morphometric data of these lots. Based on these data set and fish images I can to confirm that these specimens are part of the type series of *Hemibrycon helleri*.

***Hemibrycon metae* Myers, 1930**

Fig. 47

*Hemibrycon metae* Myers, 1930:68-69 (original description; diagnosis; holotype SU 23727; type locality: Guaiacaramo, río Guavio, Colombia).

*Hemibrycon dentatus metae*. -Schultz, 1944:362-363 (table 27; in key; new subspecies; non-type material examined).

*Hemibrycon metae*. -Böhlke, 1953:24 (type catalog; holotype SU 23727). -Géry, 1962:66 (distribution: (río Guavia) belongs to the Orinoco-basin), 78 (in key; distribution: upper Orinoco basin). -Géry, 1977:379 (in key; distribution: Upper Orinoco basin). -Lima *et al.*, 2003:130 (holotype SU 23727; distribution: Upper Meta River basin).

**Material examined. Holotype.** CAS 123727 (ex-SU 23727), 77.2 mm SL, female (x-ray), at junction of río Guavio and río Upía, río Meta drainage, río Orinoco basin, Guaiacaramo, Colombia, approx. 4°43'N 73°2'W, Jan 1928, H. A. Maria.

**Non-type specimens. Venezuela, río Orinoco basin, río Apure drainage:** INHS 27766, 30 of 51, 29.4-45.8 mm SL, caño Curito at Ruta 5, Barinas, 7°58'41"N 71°00'5"W, 7 Jan 1992, L. M. Page *et al.* INHS 31851, 12, 27.0-44.5 mm SL, río La Yuca 17 km N Barinas, Barinas, 8°46'00"N 70°15'00"W, 31 Dec 1993, D. C. Taphorn *et al.* INHS 61270, 22 of 28, 30.7-61.4 mm SL, río Santa Barbara 3 km NE Santa Barbara, Barinas, 7°50'14"N 71°11'14"W, 7 Jan 1992, L. M. Page *et al.* MCNG 98, 10 of 27, 34.4-43.9 mm SL, 1 km al S carretera 5, via Cd Bolivia, Barinas, 8°20'8"N 70°31'4"W, 13 Jun 1979, D. C. Taphorn. MCNG 5646, 17 of 54, 29.5-47.0 mm SL, río Tucupido en Las Canoas, bastante arriba de la presa aproximadamente a 300 msnm, Portuguesa, 9°3'00"N 70°5'30"W, 18 Mar 1982, D. C. Taphorn *et al.* MCNG 6759, 23 of 73 (3 c&s), 25.5-49.5 mm SL, río Tinaco, carretera entre Tinaco y Tinaquillo,

entre San Carlos e Valencia, Cojedes, Tinaco, 9°48'10"N 68°23'50"W, 3 Feb 1982, D. C. Taphorn & C. Lilyestron. MCNG 7923, 12 of 64 (2 c&s), 44.5-71.6 mm SL, caño Grande en Finca Cano Grande, Barinas, Pedraza, 8°24'10"N 70°39'25"W, 7 Dec 1982, D. C. Taphorn & C. Lilyestron. USNM 121466, 18, 35.6-50.5 mm SL, río Guárico and tributaries between San Sebastian and San Casemiro, Aragua, approx. 9°57'N 67°11'W, 12 May 1942, L. P. Schultz *et al.* USNM 121467, 12 of 117, 42.7-72.8 mm SL, río Torbes, 1 km above Táriba, Tachira, approx. 7°40'N 72°15'W, 31 Mar 1942, L. P. Schultz. **Colombia, Meta (río Meta drainage):** IAvHP 2973, 7, 53.1-76.0 mm SL, quebrada Palmicha, afluente del río Unete, Casanare, approx. 5°10'N 72°30'W, 1 Aug 1984, F. Rodriguez. IAvHP 3122, 10, 47.6-93.0 mm SL, quebrada Chichaca afluente del río Cachiza, Aguazul, Casanare, approx. 5°15'N 72°29'W, 1 Mar 1994, F. Rodriguez. IAvHP 3322, 10, 51.3-70.0 mm SL, quebrada Guamalera, Yopal, Casanare, approx. 5°21'N 72°23'W, 1 Aug 1993, M. Camargo. IAvHP 3628, 25, 45.0-70.6 mm SL, río Unete, Casanare, approx. 5°10'N 72°30'W, 1 Aug 1993. IAvHP 3632, 65, 45.0-86.8 mm SL, ríos Tocaria, Charte and Cravo Sur drainages, approx. 5°20'N 72°20'W, 18 Aug 1995. NRM 23991, 1, 48.8 mm SL, caño Candelaria tributary to río Negro, about 20 km SW of Villavicencio, approx. 4°5'N 73°42'W, 10 Jan 1988, A. Silfvergrip. NRM 23993, 1, 67.3 mm SL, caño Union tributary to río Ocoa, where crossed by road Villavicencio - Acacias, approx. 4°00'N 73°43'W, 6 Jan 1988, A. Silfvergrip. **Venezuela (Golfo de Cariaco or Golfo de Paria coastal basin):** USNM 228563, 16 of 21, 38.3-52.4 mm SL, Sucre, Clavellino Reservoir Sucre, 29 Sep 1979, M. F. Huq. MCNG 17030 (3 c&s), 17035 (3 c&s), 16796. CAS 70096, 58, 35.0-64.9 mm SL, Miranda, río Tiquirito at Concejo, a tributary of the Tuy River, 1 Aug 1918, A. S. Pearse. FMNH 105860, 52, 21.4-46.7 mm SL, Venezuela, Monagas, río Azuma at edge of municipio Punceres on road to Caripito (Golf Paria basin), 8 Aug 1985, A. Machado. MNHN 1920.0002, 1, 67.4 mm SL, col. Serre, Venezuela.

**Diagnosis.** *Hemibrycon metae* is distinguished from most species of the genus, except from *H. boquiae*, *H. dariensis*, *H. dentatus*, *H. divisorensis*, *H. huambonicus*, *H. jabonero*, *H. jelskii*, *H. polyodon*, *H. surinamensis*, *H. taeniurus* and *Hemibrycon* n. sp. 4, by the number of branched anal-fin rays (25-31 vs 15-24, Fig. 23). It differs from *H. dentatus*, *H. huambonicus*, and *Hemibrycon* n. sp. 4 by the number of lateral line scales (40-43 vs 43-50, Fig. 24); from *H. surinamensis* and *H. divisorensis* by the absence of a wide black asymmetrical spot covering base of caudal-fin rays; from *H. jelskii* by the size of humeral spot (5-6 vs 7-9 horizontal series of scales), and by the number of maxillary teeth (3-11 vs 7-17, Fig. 25); from *H. jabonero* by the number of caudal peduncle scales (16 vs 14), and the number of scales below lateral line (5-7 vs 4-5); from *H. dariensis* by the lateral line scales (40-43 vs 39-41), and by the absence of pigment in the distal tip of rays just above and below to middle caudal-fin rays; from *H. boquiae* by the total number of vertebrae (39-41 vs 41-43), and by the number of cusps of premaxilla inner row teeth (5-7 vs 5); and from *H. polyodon* by the number of cusps of premaxilla inner row teeth (5-7 vs 3-5), caudal peduncle length (11.1-14.8 vs 14.4-16.6% SL), and head length (22.1-25.0 vs 20.9-22.9% SL). *Hemibrycon metae* is rather similar the *H. taeniurus*, but can be distinguished by the number of maxillary teeth and cusps (3-11 tri- to pentacuspitate vs 7-15 tricuspitate), number of cusps of inner row premaxillary teeth (5-7 vs 5), and by the smaller humeral spot size (5-6 vs 4-5 horizontal series of scales).

**Description.** Morphometric data for *H. metae* summarized in Table 17. Largest male 79.7 mm SL, largest female 93.1 mm SL. Body compressed and moderately elongate; greatest body depth anterior to dorsal-fin origin. Dorsal profile of head slightly convex. Dorsal body profile convex from occipital bony to base of last dorsal-fin ray; straight from this point to adipose-fin origin. Ventral profile of head slightly convex. Ventral body profile convex from

pectoral-fin origin to pelvic-fin origin, and straight to slightly convex to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head small. Mouth terminal, mouth slit nearly at horizontal through middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 45 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 4-5, tri- to pentacuspoid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 5-7 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla fully toothed with 3-11 (Fig. 25) uni- to pentacuspoid teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5 cusps, followed by medium sized tooth with 3-5 cusps, and 8-10 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps (Fig. 48). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 104); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located posterior to middle of SL and posterior to vertical through pelvic-fin origin. Profile of distal margin of dorsal fin nearly straight to slightly concave. Males with bony hooks in distal one-third of first branched rays. Adipose-fin located at vertical through insertion of last anal-fin rays.

Anal-fin rays ii-vi,25-30 (rarely 24 or 31, mean = 27.4, n = 104, Fig. 23). Anal-fin profile slightly concave in males and females. Anal-fin origin approximately at vertical through insertion in the last dorsal fin rays. Anal-fin rays of males bearing one pair of small bony hooks along posterolateral border of each segment of lepidotrichia, along last

unbranched ray and eighth to twelfth branched rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-13 (mean = 11.4, n = 104). Pectoral-fin tip surpassing pelvic-fin origin in males and nearly reaching in females. Males with bony hooks on distal portion of unbranched and all branched rays. Pelvic-fin rays i,6,i (rarely i,7,i or i,6, n = 104). Pelvic-fin origin located 4-5 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males usually bearing 1 small bony hook per segment of lepidotrichia along ventromedial border of second to eighth branched rays.

Caudal fin forked with 19 principal rays without bony hooks (n = 104); lobes similar in size. Caudal-fin base have a few scales. Dorsal procurrent rays 11-12, and ventral procurrent rays 10-11 (n = 5).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 40-43 (mean = 41.6, n = 89, Fig. 24). Scale rows between dorsal-fin origin and lateral line 7-8 (mean = 7.8, n = 103); scale rows between lateral line and pelvic-fin origin 5-6 (rarely 7, mean = 5.9, n = 103). Predorsal scales 14-16, arranged in regular series (mean = 14.7, n = 94). Scales rows around caudal peduncle 16 (n = 96). Triangular modified scale on pelvic-fin origin extends posteriorly covering 2-4 scales. Scale sheath along anal-fin base with 9-19 scales in single series, extending to base of most anterior branched rays.

Precaudal vertebrae 17-18; caudal vertebrae 22-24; total vertebrae 39-41 (n = 6). Supraneurals 6-8 (n = 6). Gill-rakers on upper limb of outer gill arch 7-8, and on lower limb 12-13 (n = 19).

**Color in alcohol.** Holotype without chromatophores. Color based on the non-type specimens. General ground body color yellowish. Dorsal portion of head and body with concentration of dark chromatophores. Dorsolateral portion of head and body with scattered dark



chromatophores. One large and vertical black humeral spot, located over third to fifth lateral line scales and extending over 5-6 horizontal series of scales, including lateral line. Midlateral dark stripe extending from humeral region to middle caudal-fin rays, broad in the caudal peduncle. Abdominal region almost devoid of dark chromatophores. Dorsal and caudal fin with dark pigmentation diffuse and anal fin with small black chromatophores along its border forming narrow stripe. Pectoral, pelvic and adipose fins hyaline (Fig. 47).

**Sexual dimorphism.** Males of *Hemibrycon metae* are easily recognized by the presence of bony hooks on the dorsal-, pectoral-, anal- and pelvic-fin rays. Males and females also slightly differ in proportional pectoral- and pelvic-fin lengths, and body depth (Table 17). Mature males with gill gland on first gill arch, covering the first branchial filaments (Fig. 11b, Table 4).

**Distribution.** *Hemibrycon metae* is known from río Orinoco basin, Venezuela and Colombia, and Caribbean coastal basins of Venezuela (Fig. 1).

**Remarks.** *Hemibrycon metae* was proposed by Myers (1930) from río Guavio, río Meta drainage, Guaiacaramo, Colombia based only in the holotype. I have compared the populations from río Meta and río Apure, two large rivers from río Orinoco basin, and found no differences in meristic and morphometric characters.

In this study some *Hemibrycon* populations were identified from coastal basins of Venezuela, Golfo de Paria. All these specimens are smaller than 51.3 mm SL, being smaller than río Orinoco specimens, and difficult to compare regarding body measurements. In relation the scales and maxillary teeth number, this population is more similar to *H. metae* than *H. taeniurus* from Trinidad Island. Samples of large specimens from coastal basins of

Venezuela are necessary to confirm whether those populations are indeed conspecific. However, I tentatively assign the examined specimens from that area to *H. metae*.

***Hemibrycon jabonero* Schultz, 1944**

Fig. 49

*Hemibrycon dentatus jabonero* Schultz, 1944:363, fig. 55 (type locality: río Chama at Estanques, Estado de Mérida, Venezuela; in key; type material listed), 364-366 (original description). -Boeseman, 1960:91-92 (comparison with the subspecies of Schultz). -Nijssen *et al.*, 1988:18 (type catalog ZMA). -Vari & Howe, 1991:23 (type catalog USNM).

*Hemibrycon jabonero*. -Géry, 1962:66 (distribution map; comments about subspecies of Schultz), 70 (Table 1: data of paratypes), 78 (in key). -Géry, 1977:379 (in key). -Lima *et al.*, 2003:130 (holotype: USNM 121455; distribution: Maracaibo Lake basin). -Maldonado-Ocampo *et al.*, 2005: 74-75 (description; distribution; list of type specimen).

**Material examined. Venezuela, Mérida (lago Maracaibo basin, coll. L. P. Schultz):**

**Holotype.** USNM 121455, female (x-ray), 95.1 mm SL, río Chama at Estanques, approx. 8°50'N 71°37'W, 3 Apr 1942. **Paratypes.** MHNG 2182.54, 4, 69.1-100.3 mm SL, MHNG 2182.55, 6, 52.0-62.5 mm SL, USNM 121456, 20 of 601, 56.8-117.2 mm SL, ZMA 102.112, 2 of 10, 77.1-105.4 mm SL, río Gonzáles, tributary of río Chama at La Gonzáles, approx. 8°45'N 71°35'W, 29 Mar 1942. USNM 121457, 11, 26.0-49.5 mm SL, río Jimellas 12 km east of Motatám, tributary of río Motatán, approx. 9°24'N 70°36'W, 24 Mar 1942. USNM 121458, 2, 47.4-57.1 mm SL, USNM 121459, 4, 23.1-36.7 mm SL, río Palmar near Totuma, about 100 km southwest of Maracaibo, approx. 10°25'N 71°55'W, 21 Feb 1942. USNM

121460, 42 (13 x-ray), 38.9-86.7 mm SL. USNM 121461, 1, 53.2 mm SL, río Táchira 7 km north of San Antonio, río Catatumbo system, approx. 9°10'N 72°30'W, 1 Apr 1942. USNM 121463, 9 (x-ray), 31.3-59.5 mm SL, río San Pedro at bridge, Motatán system, approx. 9°24'N 70°36'W, 20 Mar 1942. USNM 121464, 2, 22.6-49.3 mm SL, río Motatán 8 km below Motatán, approx. 9°24'N 70°36'W, 24 Mar 1942. USNM 121465, 25, 26.3-65.3 mm SL, río Motatán 4 km above Motatán, approx. 9°24'N 70°36'W, 25 Mar 1942.

**Non-type specimens. Venezuela, lago Maracaibo basin:** INHS 34889, 29 of 36, 28.0-54.5 mm SL, río Negro and tributary 16 km W Machiques, Zulia, 10°2'56"N 72°40'57"W, 1 Feb 1995, D. C. Taphorn *et al.* INHS 60374, 31 of 50, 21.2-58.8 mm SL, caño Mimbos 2 km S La Victoria, Trujillo, 9°19'44"N 70°50'75"W, 6 Jan 1991, D. C. Taphorn *et al.* **(Coastal basins):** MCNG 4609, 25 of 173, 21.9-37.4 mm SL, zona carbonifera del alto río Guasare, pequeño caño dentro del area de la mina, Zulia, Mara, approx. 11°3'N 72°2'W, 11 Oct 1981, D. C. Taphorn *et al.* MCNG 4634, 21 of 123, 23.3-30.8 mm SL, alto río Guasare, zona carbonifera del alto río Guasare, parte Sur de la mina abierta, Zulia, Mara, approx. 11°3'N 72°2'W, 11 Oct 1981, D. C. Taphorn *et al.* MCNG 4648, 21 of 110, 24.1-30.2 mm SL, zona carbonifera del alto río Guasare, caño cerca del campamento Carichuana, Zulia, Mara, approx. 11°3'N 72°2'W, 11 Oct 1981, D. C. Taphorn *et al.*

**Diagnosis.** *Hemibrycon jabonero* is distinguished from *H. beni*, *H. tridens*, *Hemibrycon* n. sp. 1, and *Hemibrycon* n. sp. 3 by the larger number of branched anal-fin rays (22-28 vs 15-21, Fig. 23), and from *H. dentatus*, and *H. decurrens* by the smaller number of branched anal-fin rays (28-34, Fig. 23). It differs from *H. colombianus*, *H. dentatus*, *H. decurrens*, *H. huambonicus* and *Hemibrycon* n. sp. 4 by the number of lateral line scales (39-43 vs 43-55, Fig. 24), and from *H. divisorensis* and *H. surinamensis* by the absence of a wide black asymmetrical spot covering the base of caudal-fin rays and extending along entire length of

middle caudal-fin rays. *Hemibrycon jabonero* differs from *H. jelskii* by the size of humeral spot (5-6 vs 7-9 horizontal series of scales), and by the number of scales above and below lateral line (6-7 vs 7-9 and 4-5 vs 6-7); from *H. boquiae* by the total number of vertebrae (39-40 vs 41-43) and the number of cusps of premaxilla inner teeth (5-7 vs 5); from *H. metae* and *H. taeniurus* by the number of caudal peduncle scales (14 vs 16), and the number of scales below lateral line (4-5 vs 5-7); from *H. dariensis* and *H. polyodon* by the number of scales below lateral line (4-5 vs 5-6), and from *H. polyodon* by the number of scales above lateral line (6-7 vs 8), and from *Hemibrycon* n. sp. 5 by the number of scales horizontal rows below lateral line (4-5 vs 5-6), and by the total number of gill rakers (19-21 vs 17-18);

**Description.** Morphometric data for *H. jabonero* summarized in Table 18. Largest male 85.3 mm SL, largest female 117.3 mm SL. Body compressed and moderately elongate; greatest body depth anterior to dorsal-fin origin. Dorsal profile of head nearly straight to slightly convex, and slightly concave in occipital bone region. Dorsal body profile convex from occipital bony to base of last dorsal-fin ray; straight from this point to adipose-fin origin. Ventral profile of head nearly straight to slightly convex. Ventral body profile convex from pectoral-fin origin to pelvic-fin origin, and straight to slightly convex to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head small. Mouth terminal, mouth slit nearly at horizontal through middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 45 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 4-6, tricuspid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and

last smaller; with 5-7 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla fully toothed with 3-15 (Fig. 25) uni- to tricuspid teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5 cusps, followed by medium sized tooth with 3-5 cusps, and 8-10 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps (Fig. 50). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 85); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located approximately to middle of SL and posterior to vertical through pelvic-fin origin. Profile of distal margin of dorsal fin nearly straight to slightly concave. Males with bony hooks in distal one-third of first to fifth branched rays. Adipose-fin located at vertical through insertion of last anal-fin rays.

Anal-fin rays ii-v,23-27 (rarely 22 or 28, mean = 25.1, n = 85, Fig. 23). Anal-fin profile slightly convex in males and nearly straight in females. Anal-fin origin approximately at vertical through insertion in the last dorsal fin rays. Anal-fin rays of males bearing one pair of small bony hooks along posterolateral border of each segment of lepidotrichia, along last unbranched ray and eighth to tenth branched rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-13 (mean = 12.4, n = 80). Pectoral-fin tip reaching pelvic-fin origin in males. Males with bony hooks on distal portion of unbranched and all branched rays. Pelvic-fin rays i,6,i (n = 78). Pelvic-fin origin located 3-4 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males usually bearing 1 small bony hook per segment of lepidotrichia along ventromedial border of second to seventh branched rays.

Caudal fin forked with 19 principal rays without bony hooks (n = 85); lobes similar in size. Caudal-fin base have a few scales. Dorsal procurrent rays 10-13, and ventral procurrent rays 10-12 (n = 18).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 40-42 (rarely 39 or 43, mean = 40.8, n = 71, Fig. 24). Scale rows between dorsal-fin origin and lateral line 6-7 (mean = 6.8, n = 77); scale rows between lateral line and pelvic-fin origin 4-5 (mean = 5.0, n = 76). Predorsal scales 13-16, arranged in regular series (mean = 14.1, n = 69). Scales rows around caudal peduncle 14 (rarely 16, mean = 14.1, n = 69). Triangular modified scale on pelvic-fin origin extends posteriorly covering 2-3 scales. Scale sheath along anal-fin base with 8-14 scales in single series, extending to base of most anterior branched rays.

Precaudal vertebrae 16-17; caudal vertebrae 22-23; total vertebrae 38-40 (n = 19). Supraneurals 6-7 (n = 19). Gill-rakers on upper limb of outer gill arch 7-8, and on lower limb 12-13 (n = 10).

**Color in alcohol.** Type material without chromatophores. Color based on the non-type specimens. General ground body color yellowish. Dorsal portion of head and body with concentration of dark chromatophores. Dorsolateral portion of head and body with scattered dark chromatophores. Midlateral body silvery. One large and vertical black humeral spot, located over third to fifth lateral line scales and extending over 5-6 horizontal series of scales, including lateral line. Midlateral dark stripe extending from humeral region to anterior portion of caudal peduncle, and black from this point to middle caudal-fin rays. Abdominal region almost devoid of dark chromatophores. Dorsal, adipose and caudal fin with dark pigmentation diffuse and anal fin with small black chromatophores along its border forming narrow stripe. Pectoral and pelvic fins hyaline (Fig. 49).

**Sexual dimorphism.** Males of *Hemibrycon jaborero* are easily recognized by the presence of bony hooks on the dorsal-, pectoral-, anal- and pelvic-fin rays. Males and females also slightly

differ in proportional pectoral- and pelvic-fin lengths and body depth (Table 18), and in anal-fin shape, which is slightly convex in males and nearly straight in females. Mature males with gill gland on first gill arch, covering the first branchial filaments (Fig. 11a, Table 4).

**Distribution.** *Hemibrycon jabonero* is known from rivers tributaries from lago Maracaibo basin, and rio Guasare drainage, coastal basins, Venezuela (Fig. 1).

### ***Hemibrycon surinamensis* Géry, 1962**

Figs. 51-52

*Hemibrycon surinamensis* Géry, 1962:66 (map with distribution, fig. 1), 71 (diagnosis; fig. 2 - holotype; type locality: browns creek, - km. 114 of the railroad Paramaribo-Dam, Paramaracca river basin, Surinam), 72-75 (original description), 78 (in key). -Nijssen *et al.*, 1982:18 (catalog of types ZMA). -Planquette *et al.*, 1996:242 (biology of species; distribution). -Lima *et al.*, 2003:130 (holotype: ZMA 104188 [ex Géry M.107.1], distribution: coastal basins of French Guiana and Suriname).

**Material examined. Paratypes.** MHNG 2182.59, 1 of 2, 57.1 mm SL, brown creek sur 114 km railroad Paramacca River basin, Suriname, 6 Nov 1960 (origin ZMA). MNHN 1980.1435, 1, 53.3 mm SL, Suriname, Nov 1960, H. P. Pijpers. ZMA 100.347, 4 of 7, 55.0-64.8 mm SL, Paramacca river basin, Browns creek, 8 km NW of Browns weg Village, km 14 of the railroad Paramaribo-Dam, Suriname, 6 Nov 1960, H. P. Pijpers.

**Non-type specimens. French Guiana:** MHNG 2179.27, 2, 74.6-76.3 mm SL, crique Cochou, environ de Saul, Maroni, 7 Jun 1983, Durantou & Demarty (coll. J. Géry 107). MHNG 2279.28, 12 (2 c&s), 51.5-91.5 mm SL, bassin Mana, eau claire environ de Saül,

1983, Duranton & Demarty (coll. Géry 107). MHNG 2182.61, 3, 53.2-80.2 mm SL, crique Balatés, Maroni River drainage. MHNG 2182.62, 2, 35.8-73.6 mm SL, crique Balatés, 9 Oct 1979, P. Planquette (coll. J. Géry 107). MHNG 2182.63, 6, 29.5-75.5 mm SL, riviere Conté, crique Blanche, 3 Oct 1979, J. Géry & P. Planquette (coll. Géry 0107). MNHN 1989.0046, 1, 43.3 mm SL, crique Japigny, río Approuague drainage, Cayenne, Meunier at Pascal Boujard, Nov 1988. MNHN 1994.0094, 1, 38.5 mm SL, Arataye River, Approuague River drainage, Saut parare, Cayenne, approx. 4°2'0"N 52°42'0"W, Meunier at Pascal Boujard, Nov 1988. MNHN 1998.1780, 2, 59.8-72.0 mm SL, Tampoc, approx. 3°20'N 53°45'W, río Maroni drainage, Filet Haut, St. Laurent du Maroni, 26 Nov 1998, P. Keith & P. Y. Le Bail. MNHN 1998.1931, 11, 35.5-77.1 mm SL, Grand Inini, Maroni River drainage, St. Laurent du Maroni, 27 Sep 1997, P. Y. Le Bail *et al.* MNHN 2001.1944, 8, 26.2-37.4 mm SL, crique Blanche, Comté River drainage, Cayenne, 3 Oct 1979, coll. Inconnu. MNHN 2001.2513, 13, 23.4-37.1 mm SL, Approuague River drainage, Decouverte, Cayenne, 10 Nov 2003, H. Weber. MNHN 2002.3511, 10, 69.8-88.7 mm SL, Alama, Maroni River drainage, Mitaraka, St. Laurent du Maroni, 2°18'26"N 54°34'31"W, 17 Oct 2002, G. Keith. MNHN 2004.1199, 2, 35.4-39.6 mm SL, Petit Approuague, Orapu River drainage, Cayenne, 9 Nov 2003, H. Weber. **Suriname:** MHNG 1553.54-58, 5, 46.8-77.3 mm SL, Torrent rocheux dans le Brownsberg national Parck, Oct 1976, P. de Rham. MHNG 2182.57, 1, 52.6 mm SL, Maroni creek, 7 Jul 1949, M. Boeseman (coll. Géry M. 58). MHNG 2182.64, 1, 69.5 mm SL, torrent rocheux ds le Brownsberg National Park, Feb 1977 (coll. J. Géry 107). MHNG 2279.80, 1, 69.6 mm SL, Maroni, crique grand fossé, env. de Saul, 7 Jun 1983, Duranton & Demanty (coll. J. Géry 107). ZMA 107.232, 11, 49.0-74.2 mm SL, district Saramacca, Coppename River on northern slope of Wilhelmina Mountains, approx. 3°49'N 56°57'W, 17 May 1967, H. Nijssen. ZMA 107.275, 4, 53.2-82.9 mm SL, Kamaloea (= Saloea) Creek at right bank of Marowijne River, 9 km SE of Gran Creek, district Marowijne, 24 Apr 1967, H. Nijssen, Suriname Expedition



1966/Æ67. **Brazil, Pará (lower río Tocantins basin):** MZUSP 30529, 23 of 26 (3 c&s), 32.7-87.1 mm SL; MCP 17074, 1 c&s, 51.9 mm SL, río Itacaiúnas, Caldeirão, 15 Oct 1983, M. Goulding. MZUSP 30530, 5, 44.9-68.8 mm SL, río Itacaiúnas, estrada de Ferro, 10 km leste do N-4, approx. 5°52'S 50°32'W, 13 Oct 1983, M. Goulding. MZUSP 31840, 1, 77.5 mm SL, río Itacaiúnas, Igarapé Pojuca, Caldeirão, Serra dos Carajás, approx. 5°52'S 50°32'W, 5 Oct 1983, M. Goulding.

**Diagnosis.** *Hemibrycon surinamensis* is distinguished from all other species of the genus by the presence of a wide black asymmetrical spot covering base of caudal-fin rays and extending along entire length of caudal-fin rays 9 to 12-13 (Figs. 51-52), except from *H. divisorensis*. *Hemibrycon surinamensis* differs from *H. divisorensis* by the absence of a black band in the lower half of the caudal peduncle from the region above the last anal-fin rays to the caudal-fin base, and by the smaller number of scale sheath along anal-fin base (15-16 vs 17-22). Furthermore, it is distinguished from most species of the genus by the number of the scale rows below lateral line (4-5 vs 5-9), except from *H. jabonero*, *Hemibrycon* n. sp. 1, and *H. divisorensis*. It differs from *Hemibrycon* n. sp. 1 by the number of branched anal-fin rays (25-28 vs 18-21), and from *H. jabonero* by the number of cusps of premaxilla inner row teeth (5 vs 5-7).

**Description.** Morphometric data for *H. surinamensis* summarized in Table 19. Largest male 80.2 mm SL, largest female 91.5 mm SL. Body compressed and moderately elongate; greatest body depth usually anterior to dorsal-fin origin. Dorsal body profile convex from nostril to dorsal-fin origin, slightly concave in supraoccipital spine; posteroventrally slanted at dorsal-fin base; straight from last dorsal-fin ray to adipose-fin origin. Ventral profile of head convex. Ventral body profile slightly convex to nearly straight from pectoral-fin origin to pelvic-fin

origin, and straight to slightly convex to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle short, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head small. Mouth terminal. Maxilla long and slightly curved, aligned at angle of approximately 45 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 4-6, tricuspid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 5 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla toothed with 7-14 (Fig. 25) tricuspid teeth (rarely pentacuspoid), except for last four or five conical teeth, with central cusp longer. Three or 4 anteriormost dentary teeth larger, with 5 cusps, followed by medium sized tooth with 3-5 cusps, and 8-10 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps (Fig. 53). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii, 8 (n = 67); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located posterior to middle of SL and posterior to vertical through pelvic-fin origin. Profile of distal margin of dorsal fin slightly concave. Adipose-fin located approximately at vertical through insertion of last three or four anal-fin ray.

Anal-fin rays iii-iv, 26-27 (rarely 25 or 28, mean = 26.5, n = 67, Fig. 23). First unbranched ray normally only apparent in cleared and stained specimens. Anal-fin profile slightly concave in females and males. Anal-fin origin posterior to vertical through base of last dorsal-fin ray. Anal-fin rays of males bearing one pair of small, elongate, retrorse bony hooks along posterolateral border of each segment of lepidotrichia, usually along last unbranched ray and twelve anterior branched rays; hooks more numerous along second

through seventh branched rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i, 10-12 (mean = 10.9, n = 67). Pectoral-fin tip reaching pelvic-fin origin in males but not in females. Pelvic-fin rays i, 7 (one with i, 8; n = 67). Pelvic-fin origin located anterior to vertical through dorsal-fin origin. Pelvic fin of males usually bearing 1 retrorse bony hook per segment of lepidotrichia along ventromedial border of second to ninth branched rays.

Caudal fin forked with 19 principal rays without bony hooks (n = 67); lobes similar in size. Dorsal procurrent rays 10-11, and ventral procurrent rays 9-11 (n = 6).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 39-41 (mean = 40.1, n = 62, Fig. 24). Scale rows between dorsal-fin origin and lateral line 6-7 (mean = 6.8, n = 67); scale rows between lateral line and pelvic-fin origin 4-5 (mean = 4.5, n = 67). Predorsal scales 12-15, arranged in regular series (mean = 13.1). Scales rows around caudal peduncle 14. Triangular modified scale on pelvic-fin origin extends posteriorly covering 2-3 scales. Scale sheath along anal-fin base with 12-17 scales in single series, extending to base of eighth to fourteenth branched rays.

Precaudal vertebrae 16-17; caudal vertebrae 21-22; total vertebrae 38-39 (n = 10). Supraneurals 6-7 (n = 6). Gill-rakers on upper limb of outer gill arch 7-9, and on lower limb 11-12 (n = 12).

**Color in alcohol.** Dorsal and dorsolateral portion of head and body pigmented dark brown. One black humeral spot narrow, larger and vertically elongate, located over fifth to sixth lateral line scales and extending over 5-6 horizontal series of scales, including lateral line. Midlateral body stripe broad silvery extending from humeral region to caudal peduncle. A wide black spot covering base of caudal-fin rays and extending about median rays. Dorsal fin

with dark pigmentation diffuse, and anal fin with small black chromatophores along its border forming narrow stripe in some specimens. Other fins without distinctive marks (Figs. 51-52). Body yellowish.

**Sexual dimorphism.** Males of *Hemibrycon surinamensis* are easily recognized by the presence of bony hooks on the dorsal-, anal-, pelvic-, and pectoral-fin rays. Males and females also slightly differ in proportional pectoral- and pelvic-fin lengths, and body depth (Table 19). Mature males with gill gland on first gill arch, covering the first branchial filaments.

**Distribution.** *Hemibrycon surinamensis* is known from coastal basins of French Guiana and Suriname (Paramacca and Maroni basin), and from rio Itacaiúnas, lower rio Tocantins basin, Pará, Brazil (Fig. 1).

**Remarks.** J. Géry described *Hemibrycon surinamensis* in 1962 from the basin of Paramacca River, Suriname, based on his particular fish collection. Géry designated only a lot with catalog number (ZMA 100347, 1 paratype), and the remaining lots numbered according with his particular fish's collection (Holotype Nr. M. 107,1; and 9 paratypes Nr. M. 107.2-11, except Nr. 4). Later, the holotype was donated to ZMA and received a catalog number (ZMA 104188), and the paratypes were distributed to MHNG and MNHN fish collection (see material examined above). Planquette *et al.* (1996) collected several specimens and lots of *H. surinamensis* in some river basins from French Guiana, as the Maroni, Approuague, Comté and Mana. In the 1980 decade, Michael Goulding makes several collecting expeditions in the Amazon basin, including the rio Tocantins. Most of the fishes collected by Goulding are located at MZUSP, but a large portion has not been cataloged. I have analyzed the lots of *Hemibrycon* collected by Goulding in 1983 in the rio Itacaiúnas, lower rio Tocantins basin

and concluded that is the same species from Suriname and French Guiana, *H. surinamensis* (see Table 19). No significant difference was found between the Suriname/French Guiana and Tocantins populations. Some species or genera of Characidae also possess a similar distribution just as *H. surinamensis*, e.g. *Roebioxodon geryi* and *Exodon paradoxus* (see comments about the distribution in Lucena & Lucinda, 2004).

### ***Hemibrycon divisorensis* Bertaco, Malabarba, Hidalgo & Ortega, 2007**

*Hemibrycon divisorensis* was recently described by Bertaco *et al.*, 2007, from upper río Ucayali drainage, Peru, and it is not repeated here. See the Chapter II for diagnosis and original description of species.

#### ***Hemibrycon* n. sp. 1**

Fig. 54

**Holotype.** MUSM uncat., 44.4 mm SL, Peru, Ucayali, Padre Abad, Aguaytía, río Aguaytía, río Negro, upper río Ucayali drainage, 9°2'34"S 75°30'45"W, 2 Nov 1999, P. de Rham & F. Chang.

**Paratypes.** MUSM 15845, 39 of 207 (3 c&s), 24.5-42.4 mm SL, collected with the holotype.

**Diagnosis.** *Hemibrycon* n. sp. 1 is distinguished from all *Hemibrycon* species by the small size of humeral spot (2-3 vs 5-9 horizontal series of scales, including lateral line), lower number of scale rows below of the lateral line (3-4 vs 4-8), total number of pelvic-fin rays (7 vs 8), and by the total number of gill rakers in the first arch, except *H. tridens* (14-16 vs 17-23). Furthermore, *Hemibrycon* n. sp. 1 differs from most species by the smaller number of

anal-fin rays (18-21 vs 21-34, Fig. 23), except from *H. beni*, *H. helleri*, *H. tridens* and *Hemibrycon* n. sp. 3. It differ from *H. beni*, *H. helleri* and *Hemibrycon* n. sp. 3 by the number of lateral line scales (40-42 vs 44-53, 42-44 and 42-46, respectively, Fig. 24), the number of row scales below (3-4 vs 6-8, 5-6 and 6, respectively) and above (6-7 vs 7-8 and 8, respectively) of the lateral line; from *H. tridens* by the number of scales below of lateral line (3-4 vs 5), larger depth body (30.0-33.6 vs 23.6% SL), larger caudal peduncle depth (11.0-13.6 vs 7.7% SL), and larger anal-fin base (26.6-30.4 vs 23.7% SL).

**Description.** Morphometric data for *Hemibrycon* n. sp. 1 summarized in Table 20. Largest specimen 44.4 mm SL. Body compressed and moderately elongate; greatest body depth usually anterior to dorsal-fin origin. Dorsal profile of head nearly straight. Dorsal body profile convex from occipital bony to dorsal-fin origin; posteroventrally slanted at dorsal-fin base; straight from last dorsal-fin ray to adipose-fin origin. Ventral profile of head convex. Ventral body profile convex from pectoral-fin origin to pelvic-fin origin, and straight to slightly convex to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle short, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head relatively small. Mouth terminal, mouth slit nearly at horizontal through below middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 45 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 4-6, tricuspid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 5 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla fully toothed with 7-11 (Fig. 25) tri- to pentacusp teeth, except for last three or four conical teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5

cusps, followed by medium sized tooth with 3 cusps, and 12-13 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps (Fig. 55). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 20); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located posterior to middle of SL and posterior to vertical through pelvic-fin origin. First dorsal-fin pterygiophore inserted between the neural spines of eleventh to twelfth vertebrae (n = 3). Profile of distal margin of dorsal fin convex. Adipose-fin located at vertical through insertion of last or posterior to last anal-fin ray.

Anal-fin rays iii-iv,18-20 (rarely 21, mean = 19.5, n = 20, Fig. 23). Anal-fin profile slightly concave in all specimens. First anal-fin pterygiophore inserted between the haemal spine of last precaudal vertebra and the first caudal vertebrae. Anal-fin origin approximately at vertical through insertion in the middle dorsal fin.

Pectoral-fin rays i,9-10 (mean = 9.5, n = 20). Pectoral-fin tip reaching pelvic-fin origin. Pelvic-fin rays i,5,i (n = 15) or i,6 (n = 5). Pelvic-fin origin located 3-4 predorsal scales anterior to vertical through dorsal-fin origin.

Caudal fin forked with 19 principal rays (n = 20); lobes similar in size. Basal portion of caudal-fin lobes covered with irregular scales and smaller than those of the body, following by one larger scale in each lobe. Dorsal procurrent rays 12-13, and ventral procurrent rays 12-14 (n = 3).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 40-42 (mean = 41.1, n = 16, Fig. 24). Scale rows between dorsal-fin origin and lateral line 6-7 (mean = 6.4, n = 18); scale rows between lateral line and pelvic-fin origin 3-4 (mean = 3.9, n = 18). Predorsal scales 14, arranged in regular series (n = 18). Scales rows around caudal peduncle 14 (n = 18). Triangular modified scale on pelvic-fin origin extends posteriorly covering 2-3 scales. Scale sheath along anal-fin base with 7-10 scales in single series,

extending to base of most anterior branched rays.

Precaudal vertebrae 17; caudal vertebrae 23-24; total vertebrae 40-41. Supraneurals 6-7 (n = 3). Gill-rakers on upper limb of outer gill arch 5-6, and on lower limb 9-10 (n = 5).

**Color in alcohol.** Dorsal portion of head and body with dense concentration of dark chromatophores. Dorsal and dorsolateral portion of caudal peduncle near caudal fin base densely pigmented. Dorsolateral portion of body with scattered dark chromatophores. Snout and upper portion of maxilla densely pigmented. Infraorbitals and opercle with scattered dark chromatophores. Midlateral body silvery and dark pigmented. One small black humeral spot, located over third to fourth lateral line scales and extending over 1-2 horizontal series of scales, some times including lateral line. Base of caudal fin and middle rays black pigmented. Abdominal region almost devoid of dark chromatophores. Dorsal, adipose, anal and caudal fin with dark pigmentation diffuse. Pectoral and pelvic fins hyaline (Fig. 54). Body yellowish.

**Sexual dimorphism.** None of the type specimens examined had hooks on fins or any other apparent sexually dimorphic features. Also not found gill gland on first arch.

**Distribution.** *Hemibrycon* n. sp. 1 is known only from río Aguaytía, upper río Ucayali drainage, Ucayali, Peru (Fig. 2).

### ***Hemibrycon* n. sp. 2**

Fig. 56



**Holotype.** ICNMHN uncat., male, 55.4 mm SL, Colombia, Magdalena, Sierra Nevada de Santa Marta, quebrada El Congo, 500 msnm, Caribbean coastal basin, 1 Sep 2001, Y. López & P. Pulido.

**Paratypes. Colombia, Caribbean coastal basin, río Ranchería basin:** IAvHP 28, 50, 25.5-81.0 mm SL, río Ranchería, La Guajira, Colombia, approx. 11°00'N 72°45'W, 25 Aug 1981, MB/GSR. ICNMHN 5748, 7, 53.9-73.7 mm SL, Magdalena, Sierra Nevada de Santa Marta, río Córdoba, 450 msnm, approx. 11°15'N 74°5'W, Feb-Jun 2002, Y. López & P. Pulido. ICNMHN 6439, 7 (2 c&s), 35.6-53.1 mm SL, collected with the holotype. ICNMHN 6931, 4, 69.4-80.4 mm SL, Magdalena, Sierra Nevada de Santa Marta, río Manzanares, approx. 11°15'N 74°10'W, Feb 2002, Y. López & P. Pulido. ICNMHN 9655, 28, 34.5-79.3 mm SL, La Guajira, Distracción, Chorreras, El Cercado, río Ranchería, approx. 10°54'N 72°53'W, 2 May 2004, C. Castellanos. ICNMHN 10834, 8 of 134, 65.3-72.9 mm SL, La Guajira, Distracción, Chorreras, El Cercado, río Ranchería, approx. 10°54'N 72°53'W, 27 Oct 2004, C. Castellanos & P. Sánchez.

**Non-type specimens.** NRM 16268, 2, 58.4-61.3 mm SL, Colombia, Magdalena, quebrada Tamocal, tributary of the río Manzanares, approx. 11°15'N 74°10'W, Ex. Coll. Museum, Cartagena/DED: R.Olsson.

**Diagnosis.** *Hemibrycon* n. sp. 2 is distinguished from all species of the genus, except from *H. colombianus*, *H. helleri*, *H. huambonicus*, *H. jabonero*, *H. tolimae* and *Hemibrycon* n. sp. 5, by the number of branched anal-fin rays (20-24 vs 15-19 or 24-34, Fig. 23). *Hemibrycon* n. sp. 2 differs from *H. colombianus*, *H. helleri*, and *H. huambonicus* by the number of lateral line scales (39-42 vs 42-55, Fig. 24). It differs from *H. tolimae* by the number of scale rows above lateral line (8-9 vs 6-8), caudal peduncle depth (11.8-15.4 vs 11.1-12.9% SL), and the anal-fin base (28.7-34.4 vs 25.4-29.8% SL), and from *Hemibrycon* n. sp. 2 by the number of

scales around caudal peduncle (16-18 vs 14), and the number of maxillary teeth (6-9 vs 8-14). *Hemibrycon* n. sp. 2 is very similar to *H. jabonero* but can be distinguished by the larger number of scales rows around caudal peduncle (16-18 vs 14), larger number of scale rows above lateral line (8-9 vs 6-7), smaller number of branched anal-fin rays (20-24 vs 23-27), and larger caudal peduncle depth (11.8-15.4 vs 10.0-12.7% SL).

**Description.** Morphometric data for *Hemibrycon* n. sp. 2 summarized in Table 21. Largest male 81.4 mm SL, largest female 81.1 mm SL. Body compressed and moderately elongate; greatest body depth usually anterior to dorsal-fin origin. Dorsal profile of head slightly convex. Dorsal body profile convex from occipital bony to dorsal-fin origin; posteroventrally slanted at dorsal-fin base; straight from last dorsal-fin ray to adipose-fin origin. Ventral profile of head convex. Ventral body profile convex from pectoral-fin origin to pelvic-fin origin, and straight to slightly convex to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle short, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head relatively small. Mouth terminal, mouth slit nearly at horizontal through middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 45 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 3-5, tricuspid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 5 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla toothed with 6-9 (Fig. 25) tri- to pentacusp teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5 cusps, followed by 1-2 medium sized teeth with 3-5 cusps, and 4-5 teeth with 1-3 cusps or conical; central cusp in all teeth two to three

times longer and broader than other cusps (Fig. 57). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 42); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located posterior to middle of SL and posterior to vertical through pelvic-fin origin. First dorsal-fin pterygiophore inserted between the neural spines of thirteenth to fourteenth vertebrae (n = 2). Profile of distal margin of dorsal fin slightly convex. Adipose-fin located at vertical through insertion of last anal-fin rays.

Anal-fin rays iii-iv,20-24 (mean = 22.3, n = 42, Fig. 23). Anal-fin profile concave in males and slightly concave in females. First anal-fin pterygiophore inserted between the haemal spine of last precaudal vertebra and the first caudal vertebrae (n = 2). Anal-fin origin approximately at vertical through insertion of middle dorsal fin. Anal-fin rays of males bearing one pair of developed bony hooks along posterolateral border of each segment of lepidotrichia, usually along last unbranched to eighth or ninth anterior branched rays; hooks more numerous along third through sixth branched rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-12 (mean = 11.2, n = 42). Pectoral-fin tip surpassing pelvic-fin origin in males and reaching in females. Males with small bony hooks on distal portion of unbranched and all branched rays. Pelvic-fin rays i,6,i (n = 42). Pelvic-fin origin located 4-5 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males surpassing anal-fin origin in males and near reaching in females. Pelvic fin of males usually bearing 1 larger bony hook per segment of lepidotrichia along ventromedial border of the second to sixth branched rays.

Caudal fin forked with 19 principal rays without bony hooks (n = 42); lobes similar in size. Basal portion of caudal-fin lobes covered with irregular scales and smaller than those of the body, following by one larger scale in each lobe. Dorsal procurrent rays 11, and ventral

procurent rays 11-12 (n = 2).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 39-42 (mean = 40.5, n = 42, Fig. 24). Scale rows between dorsal-fin origin and lateral line 8-9 (mean = 8.2, n = 42); scale rows between lateral line and pelvic-fin origin 5-6 (mean = 5.5, n = 42). Predorsal scales 13-18, arranged in regular series (mean = 15.3, n = 42). Scales rows around caudal peduncle 16-18 (mean = 17.3, n = 42). Triangular modified scale on pelvic-fin origin extends posteriorly covering 2-3 scales. Scale sheath along anal-fin base with 6-10 scales in single series, extending to base of most anterior branched rays.

Precaudal vertebrae 17-18; caudal vertebrae 21; total vertebrae 38-39. Supraneurals 7 (n = 2). Gill-rakers on upper limb of outer gill arch 6-7, and on lower limb 10-11 (n = 7).

**Color in alcohol.** Dorsal portion of head and body pigmented dark brown. Dorsolateral portion of body with scales bordered by dark pigment and forming reticulate pattern. Snout and upper portion of maxilla densely pigmented. Infraorbitals and opercle with scattered dark chromatophores. One small black humeral spot, located over third to fifth lateral line scales and extending over 5-6 horizontal series of scales, including lateral line. Base of caudal fin and middle rays black pigmented. Abdominal region almost devoid of dark chromatophores. All fins with dark pigmentation diffuse. Anal fin with small black chromatophores along its border forming narrow stripe. (Fig. 56). Body yellowish.

**Sexual dimorphism.** Males of *Hemibrycon* n. sp. 2 are easily recognized by the presence of bony hooks on the dorsal-, pectoral-, anal-, and pelvic-fin rays (see Description). Males and females also differ in proportional pelvic-fin length, body depth (Table 21), and profile of anal-fin base, which is concave in males and nearly straight in females. Mature males with gill gland on first gill arch, covering the first branchial filaments.

**Distribution.** *Hemibrycon* n. sp. 2 is known from río Ranchería, río Cordoba, and río Manzanares, Caribbean Sea coastal basin of Sierra Nevada de Santa Marta, Colombia (Fig. 2).

### *Hemibrycon* n. sp. 3

Fig. 58

**Holotype.** ICNMFHN uncat., female, 76.7 mm SL, Colombia, Santander, río Luisito, río Sogamoso drainage, río Magdalena basin, approx. 6°5'S 73°12'W, 29 Jan 1980, G. Galvis *et al.*

**Paratypes.** ICNMFHN 753, 4 (1 c&s), 29.7-77.3 mm SL, collected with the holotype. ICNMFHN 6736, 12, 15.0-86.4 mm SL, Colombia, Santander, río Luisito, río Virofín, quebrada la Cristata, 1750 m elev., río Sogamoso drainage, approx. 6°5'S 73°12'W, 29 Nov 1978, G. Galvis *et al.*

**Diagnosis.** *Hemibrycon* n. sp. 3 is distinguished from all species of the genus, except from *H. beni*, *H. tridens*, and *Hemibrycon* n. sp. 1, by the small number of branched anal-fin rays (18-20 vs 20-34, Fig. 23). *Hemibrycon* n. sp. 3 differs from these species (except from *H. beni*) by the number of lateral line scales (42-46 vs 34-42, Fig. 24). It differs from *H. beni* by the number of scale rows below lateral line (5-6 vs 6-8), number of scales rows around caudal peduncle (14-16 vs 16-18), and the total number of vertebrae (41 vs 38-39). Further, it can be distinguished from *H. beni* by the smaller number of lateral line scales (42-46 vs 44-53). Furthermore, it differs from *Hemibrycon* n. sp. 1 by the larger number of scale rows below lateral line (5-6 vs 3-4), and by the total number of pelvic-fin rays (8 vs 7).

**Description.** Morphometric data for *Hemibrycon* n. sp. 3 summarized in Table 22. Largest

male 77.8 mm SL, largest female 88.3 mm SL. Body compressed and moderately elongate; greatest body depth usually anterior to dorsal-fin origin. Dorsal profile of head slightly convex. Dorsal body profile convex from occipital bony to dorsal-fin origin; posteroventrally slanted at dorsal-fin base; straight from last dorsal-fin ray to adipose-fin origin. Ventral profile of head convex. Ventral body profile convex from pectoral-fin origin to pelvic-fin origin, and straight to slightly convex to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle short, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head relatively small. Mouth terminal, mouth slit nearly at horizontal through middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 60 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 3-5, tricuspid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 5-7 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla toothed with 6-9 (Fig. 25) uni- to pentacusp teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5 cusps, followed by medium sized tooth with 3-5 cusps, and 8-10 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps (Fig. 59). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 11); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located approximately to middle of SL and posterior to vertical through pelvic-fin origin. First dorsal-fin pterygiophore inserted between the neural spines of thirteenth to fourteenth vertebrae (n = 1). Profile of distal margin of dorsal fin nearly straight. Adipose-fin located at vertical through insertion of last anal-fin ray.

Anal-fin rays iii-v,18-20 (mean = 19.3, n = 14, Fig. 23). Anal-fin profile slightly concave in all specimens. First anal-fin pterygiophore inserted between the haemal spine of first and second caudal vertebrae. Anal-fin origin approximately at vertical through insertion of last dorsal fin ray. Anal-fin rays of males bearing one pair of small bony hooks along posterolateral border of each segment of lepidotrichia, usually along last unbranched to eighth anterior branched rays; hooks more numerous along fourth through fifth branched rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,11-12 (mean = 11.5, n = 11). Pectoral-fin tip not reaching pelvic-fin origin in males and females. Pelvic-fin rays i,6,i or i,7 (n = 11). Pelvic-fin origin located 3-4 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males usually bearing 1 small bony hook per segment of lepidotrichia along ventromedial border of the second to sixth branched rays.

Caudal fin forked with 19 principal rays without bony hooks (n = 11); lobes similar in size. Basal portion of caudal-fin lobes covered with irregular scales and smaller than those of the body, following by one larger scale in each lobe. Dorsal procurrent rays 12, and ventral procurrent rays 12 (n = 1).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 42-46 (mean = 44.0, n = 11, Fig. 24). Scale rows between dorsal-fin origin and lateral line 8 (n = 11); scale rows between lateral line and pelvic-fin origin 5-6 (mean = 5.9, n = 11). Predorsal scales 15-18, arranged in regular series (mean = 16.2, n = 11). Scales rows around caudal peduncle 14-16 (mean = 14.9, n = 11). Triangular modified scale on pelvic-fin origin extends posteriorly covering 3 scales. Scale sheath along anal-fin base with 6-9 scales in single series, extending to base of most anterior branched rays.

Precaudal vertebrae 18; caudal vertebrae 23; total vertebrae 41. Supraneurals 9. Gill-rakers on upper limb of outer gill arch 7, and on lower limb 11 (n = 1).

**Color in alcohol.** Dorsal portion of head and body dark brown pigmented. Dorsolateral portion of body with scales bordered by dark pigment, forming reticulate pattern. Snout and upper portion of maxilla densely pigmented. Infraorbitals and opercle with scattered dark chromatophores. One small black humeral spot, located over third to fourth lateral line scales and extending over 3-4 horizontal series of scales, including lateral line. Base of caudal fin and middle rays black pigmented. Abdominal region almost devoid of dark chromatophores. All fins with dark pigmentation diffuse. Anal fin with small black chromatophores along its border forming narrow stripe (Fig. 58). Body yellowish.

**Sexual dimorphism.** Males of *Hemibrycon* n. sp. 3 are easily recognized by the presence of small bony hooks on the anal-, and pelvic-fin rays (see Description). Males lack the gill gland on first arch.

**Distribution.** *Hemibrycon* n. sp. 3 is known only from río Virolin, río Sogamoso drainage, middle río Magdalena basin, Colombia (Fig. 2).

#### ***Hemibrycon* n. sp. 4**

Fig. 60

**Holotype.** ICNMFN uncat., female, 74.0 mm SL, río La Miel, tributary of middle río Magdalena basin, Caldas, Norcasia, Colombia, approx. 5°34'N 74°53'W, 1 May 1988, G. Galvis.

**Paratypes.** Colombia, middle río Magdalena basin, río La Miel drainage: IAvHP 8444, 2, 46.5-60.8 mm SL, río Tajasos tributary of río La Miel, Samaná, Caldas, 5°23'32"N 74°56'7"W, 1 Mar 2006, L. Garcia & J. Bogotá. IAvHP 8445, 4, 43.9-64.7 mm SL, same data



of the IAvHP 8444, 1 Dec 2005. ICNMHN 2990, 4 (1 c&s), 48.0-77.4 mm SL, collected with the holotype. ICNMHN 10397, 16, 30.0-78.9 mm SL, río Manso, La Punta, tributary of río La Miel, Norcasia, Caldas, approx. 5°34'N 74°53'W, Sep 2002, C. A. Cipamocha & N. Luque. ICNMHN 15551, 31, 36.0-88.3 mm SL, río Manso, La Punta, tributary of río La Miel, Norcasia, Caldas, approx. 5°34'N 74°53'W, 24 Jan 2006, P. Sánchez.

**Non-type specimens. Colombia, middle río Magdalena basin:** ANSP 93221, 4 of 5, 65.4-75.1 mm SL, Honda, Tolima, approx. 5°12'N 74°45'W, Nov 1940, C. Miles. ICNMHN 3675, 6 (1 c&s), 41.4-85.9 mm SL, río Dormilón, San Luis, Antioquia, 6°2'42"N 74°59'48"W, 19 May 1987, G. Galvis *et al.*

**Diagnosis.** *Hemibrycon* n. sp. 4 is distinguished from all other species of the genus, except from *H. boquiae*, *H. dariensis*, *H. divisorensis*, *H. huambonicus*, *H. jabonero*, *H. jelskii*, *H. metae*, *H. polyodon*, *H. surinamensis*, and *H. taeniurus*, by the number of branched anal-fin rays (24-28 vs 15-24 and 28-34 in *H. decurrens* and *H. dentatus*, Fig. 23). It differs from all these species (except *H. huambonicus* and *H. polyodon*) by the number of lateral line scales (43-47 vs 38-43, Fig. 24). *Hemibrycon* n. sp. 4 can be distinguished from *H. huambonicus* by the number of maxillary teeth (4-9 vs 7-13, Fig. 25), number of scales around caudal peduncle (16-18 vs 18-20), and maxilla length (40.1-47.8 vs 45.2-52.6% HL), and from *H. polyodon* by the head length (22.3-26.8 vs 20.90-22.9% SL), prepelvic distance (41.5-47.8 vs 39.9-41.9% SL), and prepectoral distance (22.8-27.9 vs 21.0-23.5% SL). Furthermore, *Hemibrycon* n. sp. 4 differs from *H. dariensis* by the absence of pigment in the distal tip of rays just above and below to middle caudal-fin rays; and from *H. divisorensis* and *H. surinamensis* by the absence of a wide black asymmetrical spot covering base of caudal-fin rays.

**Description.** Morphometric data for *Hemibrycon* n. sp. 4 summarized in Table 23. Largest

male 74.7 mm SL, largest female 88.3 mm SL. Body compressed and moderately elongate; greatest body depth anterior to dorsal-fin origin. Dorsal profile of head over nostrils slightly convex, and in supraoccipital bone concave. Dorsal body profile convex from occipital bony to base of last dorsal-fin ray; straight from this point to adipose-fin origin. Ventral profile of head nearly straight to slightly convex. Ventral body profile convex from pectoral-fin origin to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head small. Mouth terminal, mouth slit nearly at horizontal through middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 50 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 4-6, tri- to pentacuspoid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 5-7 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla toothed with 4-9 (Fig. 25) uni- to pentacuspoid teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5-7 cusps, followed by medium sized tooth with 3-5 cusps, and 8-10 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps (Fig. 61). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 27); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located slightly posterior to middle of SL and posterior to vertical through pelvic-fin origin. First dorsal-fin pterygiophore inserted between the neural spines of thirteenth to fourteenth vertebrae (n = 2). Profile of distal margin of dorsal fin nearly straight to slightly concave. Males with bony hooks in distal one-third of first to fifth branched rays. Adipose-fin located at vertical through insertion of last anal-fin rays.

Anal-fin rays iii-v,24-28 (mean = 26.3, n = 27, Fig. 23). Anal-fin profile slightly convex in males and concave in females. First anal-fin pterygiophore inserted between the haemal spine of the first and second caudal vertebrae (n = 2). Anal-fin origin approximately at vertical through insertion in the last dorsal fin rays. Anal-fin rays of males bearing one pair of small bony hooks along posterolateral border of each segment of lepidotrichia, along last unbranched ray and eighth to seventh branched rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-11 (mean = 10.7, n = 27). Pectoral-fin tip surpassing pelvic-fin origin in males, and reaching in females. Males with small bony hooks on distal portion of unbranched and almost all branched rays. Pelvic-fin rays i,6,i or i,7 (n = 27). Pelvic-fin origin located 4-5 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males usually bearing 1 small bony hook per segment of lepidotrichia along ventromedial border of second to sixth branched rays.

Caudal fin forked with 19 principal rays without bony hooks (n = 27); lobes similar in size. Caudal-fin base have a few scales. Dorsal procurrent rays 10-11, and ventral procurrent rays 9-11 (n = 2).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 43-47 (mean = 43.4, n = 27, Fig. 24). Scale rows between dorsal-fin origin and lateral line 8-9 (mean = 8.5, n = 27); scale rows between lateral line and pelvic-fin origin 6-7 (mean = 6.4, n = 27). Predorsal scales 13-17, arranged in regular series (mean = 15.7, n = 27). Scales rows around caudal peduncle 16-18 (mean = 16.6, n = 25). Triangular modified scale on pelvic-fin origin extends posteriorly covering 2-3 scales. Scale sheath along anal-fin base with 13-25 scales in single series, extending to base of most anterior branched rays.

Precaudal vertebrae 17-18; caudal vertebrae 23-24; total vertebrae 40-41 (n = 2). Supraneurals 7-8 (n = 2). Gill-rakers on upper limb of outer gill arch 8-9, and on lower limb

13 (n = 2).

**Color in alcohol.** Dorsal and dorsolateral portion of head and body densely pigmented dark brown. Snout and upper portion of maxilla densely pigmented. Infraorbitals and opercle with scattered dark chromatophores. One large black humeral spot, located over third to sixth lateral line scales and extending over 5-6 horizontal series of scales, including lateral line. Midlateral body densely pigmented. Abdominal region almost devoid of dark chromatophores. Caudal-fin peduncle and middle rays black pigmented. Dorsal and caudal fin with dark pigmentation diffuse and anal fin with small black chromatophores along its border forming narrow stripe. Pectoral, pelvic and adipose fins hyaline (Fig. 60).

**Sexual dimorphism.** Males of *Hemibrycon* n. sp. 4 are easily recognized by the presence of bony hooks on the dorsal-, pectoral-, anal-, and pelvic-fin rays (see Description). Mature males with gill gland on first gill arch, covering the first branchial filaments (Fig. 11d, Table 4).

**Distribution.** *Hemibrycon* n. sp. 4 is known from middle río Magdalena basin, in the La Miel and Dormilón Rivers, Colombia (Fig. 2).

#### ***Hemibrycon* n. sp. 5**

Fig. 62

**Holotype.** ANSP uncat., male, 59.6 mm SL, second stream W of end of dirt track off km 143.9 on Huacarpay-Shintuya road, near Patria, Asuncion, Cusco, Peru, approx. 12°57'S 71°25'W, 6-7 Jul 1977, R. Horwitz.

**Paratypes. Peru, Cusco, upper río Madre de Dios drainage, río Alto Madre de Dios:**

ANSP 143290, 12 (3 c&s), 26.4-39.0 mm SL, ANSP 143293, 10, 24.1-34.0 mm SL, ANSP 143307, 6, 25.4-35.2 mm SL, río Pilcopata, wire ferry, 3 km above Pilcopata, 12°53'30"S 71°24'00"W, 16 Jul 1977, R. Horwitz. ANSP 143291, 1, 37.2 mm SL, río Hospital, moderate stream, 2 km W of Patria on N/S road, approx. 12°53'S 71°27'W, 12 Jul 1977, R. Horwitz. ANSP 143294, 4 (x-ray), 28.0-76.0 mm SL, ANSP 143300, 2, 38.5-79.3 mm SL, ANSP 143306, 5, 34.0-81.5 mm SL, ANSP 143312, 10 (x-ray), 28.2-48.2 mm SL, ANSP 143317, 5, 28.0-76.0 mm SL, collected with the holotype. ANSP 151478, 1, 35.0 mm SL, ANSP 151497, 4, 28.8-68.7 mm SL, second stream W of end of dirt track off km 143.9 on Huacarpay-Shintuya road, near Patria, Asuncion, 12°57'30"S 71°21'30"W, 5-10 Jul 1977, R. Horwitz. ANSP 151526, 2, 34.1-37.2 mm SL, río Pilcopata, wire ferry, 3 km above of Pilcopata, approx. 12°56'S 71°24'W, 16-17 Jun 1977, R. Horwitz.

**Non-type specimens. Peru, río Madre de Dios drainage, río Inambari drainage:**

ANSP 180770, 3 of 4 (1 c&s), 57.1-71.9 mm SL, tributary of río Araza, vicinity of Quince Mil, 13°18'52"S 70°49'13"W, 25 Jul 2004, M. Sabaj *et al.* MUSM 26299, 20 of 40, 48.2-87.3 mm SL, río Araza, río Inambari drainage, Sirihua, Camanti, Quispicanchi, Cusco, 13°24'5"S 70°53'57"W, 17 Oct 2005, M. Hidalgo. MUSM 26776, 4 of 8, 43.4-70.9 mm SL, río Araza, río Inambari drainage, San Lorenzo, Camanti, Quispicanchi, Cusco, 13°13'5"S 70°31'39"W, 25 Oct 2005, M. Hidalgo. MUSM 26802, 20 of 97, 28.3-51.1 mm SL, quebrada Huaca, río Inambari drainage, Huañuna, Ayapata, Carabaya, Puno, 13°12'16"S 70°22'26"W, 25 Oct 2005, M. Hidalgo.

**Diagnosis.** *Hemibrycon* n. sp. 5 is distinguished from all species of the genus, except from *H. boquiae*, *H. colombianus*, *H. helleri*, *H. huamponicus*, *H. jabonero*, *H. tolimae* and *Hemibrycon* n. sp. 2, by the number of branched anal-fin rays (21-25 vs 15-21 or 25-34, Fig.

23). *Hemibrycon* n. sp. 5 differs from *H. boquiae* by the total number of vertebrae (39-40 vs 41-43, Fig. 24), the number of cusps of the inner row premaxillary teeth (5-7 vs 5); from *H. colombianus* and *H. helleri* by the number of lateral line scales (40-42 vs 47-58 and 42-45, respectively), from *Hemibrycon* n. sp. 2 by the number of scales around caudal peduncle (14 vs 16-18), and the number of maxillary teeth (8-14 vs 6-9). It differs from *H. huambonicus* by the number of scale sheath along anal-fin base (6-10 vs 17-26), and the number of scales rows above lateral line (7-8 vs 8-10); from *H. jabonero* by the number of scales rows below lateral line (5-6 vs 4-5), and by the total number of gill rakers (17-18 vs 19-21); from *H. tolimae* by the number of maxillary teeth (8-14 vs 4-8) and the total number of gill rakers (17-18 vs 19-21). *Hemibrycon* n. sp. 5 is rather similar to *H. helleri*, but further differs by the number of scales around caudal peduncle (14 vs 16-18), anal-fin base (28.0-34.4 vs 25.1-29.3% of SL), number of predorsal scales (13-16 vs 16-18), total number of vertebrae (39-40 vs 41-43), and the number of dorsal procurrent rays (10-12 vs 8-10) and ventral procurrent rays of caudal fin (10-12 vs 9-10). The number of branched anal-fin rays also can distinguish *Hemibrycon* n. sp. 5 from *H. helleri* (21-25, mean = 22.9, n = 52 vs 19-23, mean = 20.9, n = 37, Fig. 23).

**Description.** Morphometric data for *Hemibrycon* n. sp. 5 summarized in Table 24. Largest male 59.7 mm SL, largest female 81.5 mm SL. Body compressed and elongate; greatest body depth anterior to dorsal-fin origin. Dorsal profile of head straight to slightly convex. Dorsal body profile convex from occipital bony to base of last dorsal-fin ray; straight from this point to adipose-fin origin. Ventral profile of head nearly straight to slightly convex. Ventral body profile convex from pectoral-fin origin to pelvic-fin origin, and straight to slightly convex to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head small. Mouth terminal, mouth slit below at horizontal through middle of eye. Maxilla long and slightly curved, aligned at angle of approximately 45 degrees to longitudinal body axis, with ventral border convex and anterodorsal border slightly concave.

Premaxilla with two tooth rows; outer row with 3-5, tricuspid teeth with central cusp slightly longer; inner row teeth 4, gradually decreasing in length from first to third teeth and last smaller; with 5-7 cusps, with central cusp twice or three times longer and broader than other cusps. Maxilla fully toothed with 8-14 (Fig. 25) uni- to tricuspid teeth, with central cusp longer. Three anteriormost dentary teeth larger, with 5 cusps, followed by medium sized tooth with 3 cusps, and 7-9 teeth with 1-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps (Fig. 63). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 54); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located approximately to middle of SL and posterior to vertical through pelvic-fin origin. Profile of distal margin of dorsal fin nearly straight to slightly concave. Males with bony hooks in distal one-third of first branched rays. Adipose-fin located at vertical through insertion of last anal-fin rays.

Anal-fin rays iii-v,21-25 (mean = 22.9, n = 54, Fig. 23). Anal-fin profile slightly convex to nearly straight both sexes. Anal-fin origin approximately at vertical through insertion in the last dorsal fin rays. Anal-fin rays of males bearing one pair of small bony hooks along posterolateral border of each segment of lepidotrichia, along last unbranched ray and almost all branched rays. Hooks usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-12 (mean = 10.5, n = 54). Pectoral-fin tip not reaching pelvic-fin origin in both sexes. Males with bony hooks developed on distal portion of unbranched and

all branched rays. Pelvic-fin rays i,6,i or i,7 (n = 54). Pelvic-fin origin located 4-5 predorsal scales anterior to vertical through dorsal-fin origin. Pelvic fin of males usually bearing 1 small bony hook per segment of lepidotrichia along ventromedial border in all branched rays.

Caudal fin forked with 19 principal rays without bony hooks (n = 54); lobes similar in size. Caudal-fin base with a few scales in the half of lobes, following by one large and round scale in each lobe. Dorsal procurrent rays 8-10, and ventral procurrent rays 9-10 (n = 12).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 40-42 (mean = 41.2, n = 54, Fig. 24). Scale rows between dorsal-fin origin and lateral line 7-8 (mean = 7.3, n = 51); scale rows between lateral line and pelvic-fin origin 5-6 (mean = 5.9, n = 52). Predorsal scales 13-16, arranged in regular series (mean = 14.8, n = 50). Scales rows around caudal peduncle 14 (n = 48). Triangular modified scale on pelvic-fin origin extends posteriorly covering 2-3 scales. Scale sheath along anal-fin base with 6-10 scales in single series, extending to base of most anterior branched rays.

Precaudal vertebrae 19-21; caudal vertebrae 22-23; total vertebrae 41-43 (n = 13). Supraneurals 6-7 (n = 13). Gill-rakers on upper limb of outer gill arch 6-7, and on lower limb 10-11 (n = 11).

**Color in alcohol.** General ground body color yellowish. Dorsal portion of head and body with dense concentration of dark chromatophores. Dorsolateral portion of head and body with scattered dark chromatophores. Midlateral body silvery. One large and vertical black humeral spot, located over third to sixth lateral line scales and extending over 6-7 horizontal series of scales, including lateral line. Midlateral dark stripe extending from humeral region to middle caudal-fin rays, broad in the caudal peduncle. Abdominal region almost devoid of dark chromatophores. Adipose fin densely dark pigmented. Dorsal and caudal fin with dark pigmentation diffuse and anal fin with small black chromatophores along its border forming



narrow stripe. Pectoral and pelvic fins hyaline (Fig. 62).

**Sexual dimorphism.** Males of *Hemibrycon* n. sp. 5 are easily recognized by the presence of bony hooks on the dorsal-, pectoral-, anal- and pelvic-fin rays. Mature males with gill gland on first gill arch, covering the first branchial filaments.

**Distribution.** *Hemibrycon* n. sp. 5 is known from río Alto Madre de Dios drainage, and río Inambari drainage, both from upper río Madre de Dios drainage, Peru (Fig. 2).

**Remarks.** The río Alto Madre de Dios is a headwater river that joins río Manu in the río Madre de Dios drainage. The río Inambari is a left affluent of the río Madre de Dios below the confluence of río Alto Madre de Dios and río Manu. The Inambari population shows a larger number of branched anal-fin rays than río Alto Madre de Dios population (21-25 vs 24-26), respectively, but there is a notable overlapping in this count. None other significant differences were found in the counts and morphometric features between these populations. However, we tentatively assign the examined specimens from Inambari population to *Hemibrycon* n. sp. 5.

#### **Taxonomic status of *Bryconamericus decurrens* Eigenmann, 1913**

*Bryconamericus decurrens* was described by Eigenmann (1913) based on the holotype (CM 5055, now FMNH 56255, Fig. 64) and one paratype (IU 12829, now CAS 39542) from the río Magdalena basin, Colombia. Eigenmann in his brief original description for species, described as having six teeth on the maxillary on half or a little less than half maxillary length, a character also used herein for distinguish *Hemibrycon* from *Bryconamericus*, as also recognized previously by Vari & Siebert (1990), Román-Valencia (1998, 2000). The type

locality is situated in the lower río Magdalena basin, on the Canal del Dique, coordinates of Canal del Dique on road between Cartagena and Calamar, approx. 10°09'N 75°17'W (see Miles, 1947:152; Dahl, 1971:156).

During this study, no additional specimens of *B. decurrens* were found for analysis, only type material. More specimens from that locality are necessary to confirm what genus is more appropriate for that species. However, *Bryconamericus decurrens* is herein recognized in *Bryconamericus* mostly by the lower number of maxillary teeth (5-6), and distributed only in the first third of maxilla.

The following scales and ray counts are found in type specimens of *B. decurrens*: dorsal-fin rays ii,8 or i,9; anal-fin rays iv-v,28-31; lateral line scales 43-44; scale rows above the lateral line 9, and scale rows below 6-7; scales rows around caudal peduncle 16-18. Dentition: premaxilla with two tooth rows; outer row with 4-5, tri- to pentacuspoid teeth; inner row teeth 4 with 5-7 cusps; maxilla with 5-6 tri- to pentacuspoid teeth. The holotype is a male (56.7 mm SL), and the paratype is a female (50.9 mm SL). Both type specimens are in good condition, but almost depigmented.

#### **Taxonomic status of *Hemibrycon orcesi* Böhlke, 1958**

*Hemibrycon orcesi* was described by Böhlke (1958) based on the holotype and three paratypes from río Macuma, Provincia de Santiago-Zamora, Ecuador (Fig. 65, ANSP 75904, paratype, female, 44.6 mm SL). According to the author, the species was proposed provisionally in *Hemibrycon* because that the species has the lobes of the caudal-fin scaled and disagree with Eigenmann's definition for *Hemibrycon*. In 1962, Géry also suspected that *H. orcesi* can be a new genus related to *Hemibrycon*, but clearly different from it.

The type specimens examined of *H. orcesi* possess the caudal fin scaled or with scale marks to proximal half of lobes, a character not found in *Hemibrycon* species. Also, in all

those specimens some body scales are lacking, and all are not in good preservation conditions, thus it is not possible to know if the lateral line is incomplete or complete. Böhlke (1958:27) when described a lateral line complete to *H. orcesi* comments that “though all lateral line counts were interrupted by areas where scales were missing”. Also, Böhlke comments “although the caudal scalation of all the present specimens is damaged to some extent, some specimens (most notably the holotype) still possess scales which extend more than half-way out on the caudal lobes”.

The species of *Hemibrycon* and *Boehlkea* share a large number of teeth in the maxilla, as observed in the types of *H. orcesi* (13-14 uni- to pentacuspoid teeth) and *B. fredcochui* Géry (14-15 uni- to tricuspoid teeth). *Boehlkea* differs from *Hemibrycon* by the presence of scales in the caudal fin lobes, lateral line interrupted, and low total number of vertebrae (36 vs 38-43). Furthermore, *Hemibrycon orcesi* possess some features uncommon for *Hemibrycon* species, as 34 to 35 lateral line scales; 36 to 37 total vertebrae; color pattern of dorsal, anal and ventral fins densely pigmented, and lobes of caudal fin scaled.

I have analyzed the holotype and one paratype of *Boehlkea fredcochui*, and the caudal-fin presented small scales to half of upper and lower lobes, lateral line interrupted with 14 perforated scales plus 23 remaining scales (last scales perforated or unperforated), and 37 scales in the longitudinal series. Further, *H. orcesi* differs from *B. fredcochui* by number of the branched anal-fin rays (17-18 vs 24-25), pelvic-fin rays (8 vs 7), lateral line scales (34-35 vs 37), and scale rows above of the lateral line (6-7 vs 5), and color pattern and by some body measurements.

After the original description of Böhlke, no other specimen is known as *H. orcesi*, only the type material. According to the features presented here I can assume that *H. orcesi* is possibly more related to *Boehlkea* than to *Hemibrycon*. Due to the lack of non-type specimens from *B. fredcochui* and *H. orcesi* to morphological analysis, it was not possible to resolve the

taxonomic status of *H. orcesi*. The systematics of *Boehlkea* is still unresolved and lacks a phylogenetic diagnosis for this genus.

#### **Taxonomic status of *Hemibrycon velox* Dahl (1964)**

Dahl (1964:68) did not provide a catalog number nor museum name for the type material of *Hemibrycon velox*, but only listed a type specimen “un ejemplar de 60 mm de largo esquelético...” and “Paratipos, 54”. George Dahl worked in the “Departamento de Investigaciones Ictiológicas y Faunísticas de la CVM” and together with Federico Medem has done an inventory of the aquatic fauna from río Sinú basin. This study was published as a mimeographed paper by that governmental institution. In this paper five new species were described: *H. velox*, *Bryconamericus icelus*, *Gephyrocharax sinuensis*, *Pimelodella reyesi* and *Gambusia (Toluichthys) meadi*. The last species was considered a species Inquirenda in Poeciliidae (Lucinda, 2003). All type specimens of these species were whereabouts unknown or apparently destroyed (Cala, 1981, 1987; Eschmeyer, 1998). Cala (1981) in his catalog of types of the ICNMHN reported: “Unfortunately part of the Dahl’s & Mile’s types in Colombia has been lost or destroyed”. Later, Cala (1987:79) confirmed that almost all types of Colombian species described by Dahl were lost and destroyed by negligence and departure that author to other institution.

I have analyzed some specimens designated as paratypes of *H. velox* (7 of 11 SMF 21300) and *B. icelus* (7 of 15 SMF 16284) deposited in the Natural History Museum Senckenberg, the only museum with type specimens cataloged. The exam revealed that all paratypes belong only a species, probably *B. icelus*. The original descriptions of these species includes several features that are useful to their recognition, just as counts of the all fin rays and scales, color pattern and for type specimen the body measurements. Most of the features in these specimens agreed with the information presented in the original description of *B.*

*icelus*. It seems possible that type specimens or labels were changed by mistake before the transport for the museum. No other possible type specimens of *Hemibrycon velox* were found in the collection of fishes of SMF (H. Zetsche and F. Krupp, pers. comm.).

New *Hemibrycon* specimens from río Sinú basin in collection are rare. I have analyzed only six specimens from this river and I was unable to find significant differences between the populations from river basins of Panama and río Atrato basin in Colombia. Furthermore, the specimens from río Sinú basin also have the distal tip of rays just above and below to middle caudal-fin rays densely pigmented as found in specimens from *H. dariensis*. Additional samples from the río Sinú basin are necessary to decide whether *H. velox* is a valid species or junior synonymy of *H. dariensis*.

#### **Taxonomic status of *Hemibrycon pautensis* Román-Valencia, Ruiz C. & Barriga, 2006**

*Hemibrycon pautensis* was described by Román-Valencia, Ruiz C. & Barriga (2006) based on specimens collected in río Paute, a tributary of the río Santiago drainage, río Marañón drainage, Ecuador. The río Santiago is nearly located to río Pastaza, both affluent of left margin of río Marañón drainage, in Peru and Ecuador, where also occur *Hemibrycon polyodon*, the type species of the genus.

In the original description, one of the characters presented in the diagnosis of *H. pautensis* was not found in the species of *Hemibrycon* analyzed in this study: six to seven vs eight to nine branched dorsal-fin rays. Another character used by authors, branched anal fin rays (27-28) can be easily found in several species of genus that were not compared in diagnosis. On the other hand, the authors presented in the work (text and table) different values for counts of anal- and dorsal- fin rays, number of maxillary teeth and vertebrae for that species. Also, the authors commented that the supraorbital bone is found in *H. pautensis*, and other *Hemibrycon* species, but this bone is absent in all species of *Hemibrycon* examined.

Analyzing the characters presented in the diagnosis and in the description of *H. pautensis* it is not possible to distinguish this species from *H. polyodon*, also found in the río Santiago drainage according to those authors. I believe that *H. pautensis* is possibly a synonym of *H. polyodon*, but it is necessary an analysis of all type series of the species for the recognition of a synonym or a distinct species.

#### **Comments about *Hemibrycon microformaa* Román-Valencia & Ruiz C, 2007**

*Hemibrycon microformaa* was described by Román-Valencia & Ruiz C. (2007) based on sixteen specimens collected in the upper río Atrato basin, Caribbean Sea basin river in Colombia. In the original description, the authors used the body size (smaller than 31 mm SL) to distinguish the new species from all *Hemibrycon* species. No other *Hemibrycon* species analyzed have this body size; all are larger than 31 m SL.

Another character used by authors, the number of branched anal fin rays (14-16) is not common among the species of the genus, except in *H. beni* (15-19) and *H. tridens* (17). *Hemibrycon beni* and *H. tridens* differs from *H. microformaa* by lateral line scales (44-53 and 39 vs 33-37, respectively). On the other hand, the authors comment that the supraorbital bone is present in *H. microformaa*, and in other *Hemibrycon* species. This bony is absent in all species of *Hemibrycon* examined.

Román-Valencia & Ruiz C. (2007) commented that *H. microformaa* can be one species of genus *Creagrutus*, *C. affinis*, due to the presence of some characters similar to those of that genus, but furnished several differences between *H. microformaa* and *C. affinis*, the only species of the genus that occur in the río Atrato basin.

Analyzing the characters presented in the diagnosis and in the description of *H. microformaa* it is possible that this is a new species of *Boehlkea* or another Characid genus. The only known species of *Boehlkea*, *B. fredcochui*, was described from upper río Amazonas,

around Leticia, Brazil (inexact type locality), also have small body size, and a small total number of vertebrae as *H. microformaa*. *Boehlkea fredcochui* proposed by Géry (1966), presents an incomplete lateral line, maxilla toothed, and caudal-fin scaled. According to those authors, *H. microformaa* has lateral complete and caudal fin naked, but maxilla toothed. It was not possible to analyze the type series of this species to recognize it as belonging to *Hemibrycon*.

Other *Hemibrycon* species described from the río Atrato basin is *H. carrilloi* Dahl (1960), with a larger number of branched anal-fin rays than *H. microformaa*, among other distinct characters. *Hemibrycon carrilloi* is a synonym of *H. dariensis* according to this study.

In the same work, Román-Valencia & Ruiz C. (2007) provided an incomplete taxonomic key to *Hemibrycon* species of Colombia, lacking *H. dentatus*, *H. carrilloi*, and *H. velox*, but including *Boehlkea fredcochui* as a *Hemibrycon* species, without explanation of the reasons of this new allocation. I have analyzed the holotype and one paratype of *Boehlkea fredcochui* and it is here maintained in a separate genus until additional specimens are available for a taxonomic review and phylogenetic analysis.

### **Gonadal and gill gland analysis of *Hemibrycon* species**

A total of 12 ovaries of ten species of *Hemibrycon* were analyzed histologically (Table 3). Almost all examined gonads removed from females preserved in fish collections were not satisfactorily preserved and rendered poorly informative histological slides. Although no sperm were observed, this information must be viewed with caution. Burns & Weitzman (2005: 110) mentioned that *Hemibrycon* genus appears to be externally fertilizing based mainly on the absence of sperm in mature ovaries. Ovaries and testes from *Hemibrycon dariensis* (USNM 293215) and *H. metae* (USNM 121466, 121467) were analyzed by John Burns (pers. comm.) and no sperm were found inside ovaries. Scanning electron micrographs

of testis of 12 *Hemibrycon* species showed all sharing a spherical sperm nuclei or aquasperm, typical of the species with externally fertilizing, or not inseminating (Table 4). So far, available information support *Hemibrycon* species as externally fertilized.

The gill gland was found only in sexually mature males (Fig. 11, Table 4). Gill glands were also observed in the first branchial arch on males of *H. boquiae*, *H. tolimae*, and *Hemibrycon* n. sp. 5 through light microscopy under stereomicroscope, therefore the scanning electron micrographs from these species was not made. Gill glands were not found on first gill arch of *H. beni*, *H. colombianus*, *H. dentatus*, *H. polyodon*, *H. tridens*, and *Hemibrycon* n. sp. 1 due to the small specimen samples or absence of males.

#### **Comments about the distribution of *Hemibrycon* species**

Most species of the genus *Hemibrycon* occur in the upper portions of the Amazon and Orinoco tributaries, and in the río Magdalena basin, in both sides of Andes. Some species are distributed in the rivers of northern region of South America between the lower rio Tocantins (rio Itacaiúnas drainage), Brazil, and Pacific slope basins of Panama from río Tuira to río San Pablo, including the river basins in Trinidad and Tobago. As observed by Géry (1962) *Hemibrycon* species have a peculiar distribution in the Amazon basin, and are confined to the periphery of the basin, inhabiting the upper portions of their tributaries. They are found usually in mountain streams with clear and fast water, and do not live in the slow running rivers of the lowlands (Géry, 1962). This pattern is similar and largely congruent with the distribution given to the species of the genera *Roeboides* Günther by Lucena (1998; 2000), *Creagrutus* Günther by Harold & Vari (1994), and Vari & Harold (2001), and partially similar with the distribution of the species of *Knodus* Eigenmann by Ferreira (2007). All species of *Hemibrycon* from the Trans-Andean basins are different species from those in



rivers east of the Andean Cordilleras, a situation found in other groups of fishes taxonomically revised, e. g. *Creagrutus*.

The distribution pattern of *Hemibrycon metae*, found in the río Orinoco basin and river basins of Caribbean Sea versant of northern Venezuela, is congruent with those found in *Creagrutus melasma* and *C. taphorni* (see Vari & Harold, 2001), and partially similar with the distribution of *Knodus meridae* (see Ferreira, 2007) and *Odontostilbe pulchra* (see Bührnheim & Malabarba, 2007).

*Hemibrycon jabonero* has a small geographical distribution in the tributaries of the lago Maracaibo basin and river basins of the Gulf of Venezuela. Common patterns of distribution between these drainages have been found for some species of *Creagrutus* as *C. hildebrandi*, *C. maracaiboensis* and *C. paralacus* (see Vari & Harold, 2001). According to Lundberg *et al.*, (1998), the species endemism found in the lago Maracaibo is strongly related to progressive reduction of marine influences in the Late Tertiary, a period during which the major drainage systems on the continent began to approximate their present form.

*Hemibrycon surinamensis* was originally described to Atlantic coastal rivers of Suriname and posteriorly found in coastal rivers of French Guyana (Géry *et al.*, 1991), also occurs in the lower rio Tocantins basin, Brazil according to this study. *Roebioxodon geryi* (see Lucena & Lucinda, 2004) has a similar distribution pattern, but widespread in the largest tributaries of the rio Amazonas (rios Xingu and Tapajós), and rio Tocantins.

One of the main tributaries of the rio Amazonas basin, the río Ucayali drainage, Peru, possess a high degree of endemism of *Hemibrycon* species. *Hemibrycon divisorensis*, *H. helleri*, *H. tridens* and *Hemibrycon* n. sp. 1 occur only in the upper portion of this river basin, a distribution pattern partially similar to *Creagrutus changae*, *C. pila* (see Vari & Harold, 2001), and *Attonitus ephimeros* and *A. irisae* (see Vari & Ortega, 2000).

*Hemibrycon jelskii* has a widespread distribution in the upper río Ucayali, río Marañon, and headwater of the rio Madeira-Mamoré drainage. The populations herein recognized as belonging to this species need to be revised in full detail and more collections from some of these rivers drainages are necessary to determine the actual distribution of the species. No other characid was found with the geographic distribution similar to *Hemibrycon jelskii*.

*Hemibrycon polyodon* is known only from río Pastaza drainage, a tributary of río Marañon drainage, Ecuador. *Brycon coxeyi* shows a similar distribution pattern in the rio Pastaza drainage, but also occurs in other tributaries of río Marañon drainage in Ecuador (see Lima, 2001). No other characid was found with a geographical distribution similar to *H. polyodon*.

Two *Hemibrycon* species occur in the tributaries of the upper portions of río Madeira drainage, southeastern of Peru, including a new species (*Hemibrycon* n. sp. 5). *Hemibrycon beni* is known only from upper río Beni drainage, where ríos La Paz and Miguilla join to form río Bopi, Espia, La Paz, Bolivia, a distribution pattern similar to *Creagrutus beni* (see Vari & Harold, 2001). *Hemibrycon* n. sp. 5 is found only in the upper río Madre de Dios drainage, a distribution pattern similar that found to *Attonitus bounites* (see Vari & Ortega, 2000), *Bryconamericus pectinatus* (see Vari & Siebert, 1990), and *Creagrutus unguis* (see Vari & Harold, 2001).

Some of the Trans-Andean species of *Hemibrycon* show distribution patterns similar mainly with *Creagrutus* species. *Hemibrycon boquiae* and *H. dentatus* are found only upper río Cauca drainage in Colombia, a distribution pattern partially similar to *Creagrutus brevipinnis* and *C. caucanus* (see Harold & Vari, 1994), and *Carlasyanax aurocaudatus* (see Ruiz-C. & Román-Valencia, 2006). *Hemibrycon tolimae* is found in the upper río Magdalena basin in Colombia, likewise *Creagrutus magdalenae* (see Harold & Vari, 1994) and

*Bryconamericus huilae* (see Román-Valencia, 2003). *Hemibrycon colombianus* and *Hemibrycon* n. sp. 3 are sympatric with *Bryconamericus plutarcoi* Román-Valencia, all known only from the río Sogamoso drainage, a tributary of middle río Magdalena basin, Colombia. *Hemibrycon* n. sp. 4, is found in two tributaries of the middle río Magdalena basin, and *Hemibrycon* n. sp. 2 occurs in small rivers of Caribbean coastal basin on the region of Sierra Nevada de Santa Marta, Colombia. *Triportheus magdalenae* is found only río Magdalena basin (see Malabarba, 2004). No taxa were found with geographic distribution similar to *Hemibrycon* n. sp. 2.

*Hemibrycon dariensis* is found in river basins of Pacific slope from Panama (between the ríos Tuirá and San Pablo basin), and río Atrato and río Sinú basins in Colombia, a distribution pattern partially similar with *Bryconamericus zeteki* (pers. obs.), *Creagrutus affinis* (see Vari & Harold, 2001) and *Roeboides occidentalis* (see Lucena, 2000), but the last also occurs in the Pacific versant of Colombia. No *Hemibrycon* species was found in the rivers of the Pacific versant of Colombia.

## **Discussion**

Phylogenetic studies of the family Characidae have been customarily problematic, due to the high occurrence of homoplasies among species included in this family as observed by Lucena (1993) or among subfamilies or genera as evidenced by Zanata (2000), Benine (2004), Bührnheim (2006), and Ferreira (2007). The high occurrence of homoplasies is also evidenced in the present study (CI = 0.22), where diverse characters that are variable and potentially informative to hypothesize *Hemibrycon* phylogeny are also found among other taxa. According to Klassen *et al.* (1991) the value of consistence index is related to the number of homoplasies in the analysis, *i.e.*, large values of CI correspond to small number of homoplasies. Archie (1989) discussed that the consistence index value will be smaller as more

taxa or characters are added in the analysis. The low CI observed may be related in part to the number of taxa (45) and characters (123) in the present analysis. According to Lucena (1993) the complexity of group analyzed and the evolutionary history of characters can contribute for low consistency index value.

A high number of characters presented low consistency indexes: 83.7% of the 123 characters used in the analysis have CI below 0.40, and among these 41.7% have CI smaller than 0.20. The consistence index is used to reveal the homoplasies and estimate confidence levels about the employed characters. Although most characters presented low CI values in the analysis, the bootstrap values observed in supporting the different branches in the consensus tree demonstrates a higher confidence in the support of some branches than others. Although all characters defining the *Hemibrycon* Clade are found outside the genus, the bootstrap value recovered to this clade is 77, showing a reasonable confidence level in supporting the monophyly of *Hemibrycon* (Fig. 20). Except for *Hemibrycon* and internal clades, only clades 1, 4, 5, 9, K, L, and M showed in Figure 20 presented bootstrap values higher than 50.

Malabarba and Weitzman (2003) recognized *Hemibrycon* as belonging to a large monophyletic clade inside Characidae (Clade A), based on the putative derived presence of four teeth in the inner series of the premaxilla and reduced number of dorsal-fin rays (ii,8). Additionally, they considered *Hemibrycon* and *Boehlkea* as apparently the most basal genera in that clade, by lacking all specializations related to insemination, development of caudal-and/or anal-fin glands or the jaw and teeth modifications related to the ventral position of the mouth, as observed in the remaining genera and species of Clade A. The genus *Boehlkea* was not included in the analysis due to the lacking of specimens available for clearing and staining. In the present hypothesis the Clade A of Malabarba and Weitzman (2003) is recognized as monophyletic based on three exclusive synapomorphies: presence of four teeth

in the inner series of premaxilla (Ch. 2.1), ii+8 dorsal-fin rays (Ch. 67.1), and profile strongly concave in the posteroventral border of cleithrum (Ch. 79.1).

*Cyanocharax alburnus* was found basal within Clade A\*, similar to that found in the hypothesis presented by Ferreira (2007) among on inseminating Clade A genera.

In the present hypothesis *Aphyocharax pusillus* and *Carlastyanax aurocaudatus* formed a group (Clade I) included in the Clade A\*. *Carlastyanax aurocaudatus* is herein recognized as a possible member of Clade A, possessing four teeth in the inner row of the premaxilla (Ch. 2.1) and ii+8 dorsal-fin rays (Ch. 67. 1). *Aphyocharax pusillus* has ii+9 dorsal-fin rays (Ch. 67.0) and a single regular tooth row in the premaxilla (Ch. 1.2). The inclusion of this taxon in the Clade A may be related to the Character 2 not coded.

The comparative analysis of all available material of *Hemibrycon* allows the recognition of 21 species in the genus, including five new species and three new synonyms (not included *H. microformaa* and *H. pautensis*). Since Eigenmann (1927) no extensive revision was made for the species included in *Hemibrycon*, only new species were described from restrict drainages or localities. Some *Hemibrycon* species were not possible to resolve the taxonomic status due to the lack or inexistence of available material in ichthyologic collections that permit to discover the real limit of character range of each species (see specific comments above).

Almost all species of the genus *Hemibrycon* inhabit headwater rivers or stream from upper portion of drainages basins located mainly in the north of South America. The five new species proposed here live in these environments, supporting the recognition of areas of elevated endemism. New collection efforts along these areas are extremely necessary and recommended for the recognition of new species of *Hemibrycon* and the proposition of new areas of environmental preservation. Vari & Malabarba (1998) pointed to a series of paramount initiatives for understand the diverse Neotropical ichthyofauna, one being

extensive surveys of the ichthyofauna in the vast under sampled regions of South and Central America.

Weitzman *et al.* (2005: 344) suggested that detailed investigations of the histology and ultrastructure of sperm cells are necessary for a useful evaluation of the phylogenetic significance of insemination in characids included in Clade A. I agree with that, but testis properly fixed for TEM (Transmission Electronic Microscopy) analyses of the ultrastructure of sperm cells and mature ovaries for histological examination were not available. I have made SEM preparations of testis of some species of *Hemibrycon* (Table 4), and all examined species have a typical aquasperm with a spherical to slightly ovoid nucleus suggesting the species are not inseminating.

Recently, Román-Valencia and collaborators (2006, 2007) described two species of *Hemibrycon*, *H. pautensis* and *H. microformaa*. I did not analyze any specimen from these species, and maintained them in the genus (see comments above). According to Román-Valencia & Ruiz-C. (2007), a supraorbital bone is found in *H. boquiae*, *H. microformaa*, *H. orcesi*, *H. pautensis* and *H. polyodon*, and its presence would not support the inclusion of *Hemibrycon* among Clade A genera of Malabarba & Weitzman (2003). The supraorbital, however, is absent in the all species of *Hemibrycon* analyzed in this study.

Mature males of almost all examined *Hemibrycon* species possess bony hooks in rays in all fins, except in the caudal fin, as reported for the first time for the genus in *H. divisorensis* by Bertaco *et al.* (2007). The presence of hooks on the anal- and pelvic-fin rays and sometime caudal-fin rays of males is often found in several genera and subfamilies of the Characidae (Azpelicueta & Garcia, 2000; Malabarba & Weitzman, 2003), and usually represent a secondary sexual character. However, the occurrence of bony hooks in all fins, including dorsal, caudal, and pectoral fins in males is uncommon in characids. Recently, some

characids species have been described with bony hooks on rays of all fins in males (Bertaco *et al.*, 2007).

Some analyzed females of *Hemibrycon boquiae* present small bony hooks in the anal-fin rays, an uncommon character in Characidae. Among characids, bony hooks in females are recorded only on the pelvic-fin rays of species of *Cheirodon*, and were considered a synapomorphy (Malabarba, 1998). According to that author, these bony hooks are not developed in size as described for males, and sometimes they are visible only in large females, as observed here only in *Hemibrycon boquiae*.

**Comparative specimens examined.** *Aphyocharax pusillus*, MCP 32769, 69 (5 c&s), 32.1-50.1 mm SL, rio solimões at Içé Island, Alvarães, Amazonas, Brazil. *Astyanax jacuhiensis*, MCP 37026, 5, 43.9-82.1 mm SL, arroio Alexandrino, tributary of rio Ijuí, rio Uruguay basin, Salvador das Missões, Rio Grande do Sul, Brazil; MCP 34719, 2 of 27 c&s, 49.2-50.1 mm SL, lago Guaíba at Ponta da Cadeia, Porto Alegre, Rio Grande do Sul, Brazil. *Astyanax aff. fasciatus*, MCP 18675, 24, 47.7-98.8 mm SL, tributary of rio Jacuí, Rio Pardo, Rio Grande do Sul, Brazil; MCP 21293, 21 (3 c&s), 63.9-71.8 mm SL, lageado do Gringo, Agudo, Rio Grande do Sul, Brazil. *Bryconadenos tanaothoros*, MCP 30516, 106 (5 c&s), 16.0-32.1 mm SL, córrego Tatu about 14 km at Cláudia, rio Xingu drainage, Cláudia, Mato Grosso, Brazil. *Brycon pesu*, MCP 23298, 27, 33.3-70.3 mm SL, rio Tocantins, Miracema, Tocantins, Brazil; MCP 23299, 2 of 3 c&s, 65.4-66.6 mm SL, rio Amazonas basin, south rio Capim and marginal pool, about 56 km W Paragonominas, Pará, Brazil. *Bryconops melanurus*, MCP 41772, 12, 92.0-117.5 mm SL, tributary of rio Madeira, Humaitá, Amazonas, Brazil; MCP 15807, 46 (3 c&s), 40.2-82.2 mm SL, stream at 13 km S of Nova Olímpia, Barra dos Bugres, Mato Grosso, Brazil. *Bryconamericus exodon*, MNHNP 431, 49 (2 c&s), 29.4-40.5 mm SL, rio Paraguay about 5 km N of the Bahia Negra, Alto Paraguay, Paraguay. *Bryconamericus*

*peruanus*, MUSM 6158, 10 of 25 (2 c&s), 48.1-65.0 mm SL, río Comaninas, río Marañón drainage, Condorcanqui, Amazonas, Peru. *Bryconamericus* sp., MUSM 28772, 20 of 68 (3 c&s), 31.1-49.6 mm SL, río Mayo, Moyobamba, San Martín, Peru. *Carlastyanax aurocaudatus*, IMCN 891, 7, 38.1-63.1 mm SL, río Quindío, upper río Cauca drainage, Armenia, Colombia; MCP 41717, 6 (2 c&s), 20.2-45.0 mm SL, parte alta zanjón Bagazal, upper río Cauca drainage, Finca Izquande, Buenos Aires, Cauca, Colombia. *Charax stenopterus*, MCP 9037, 20 (1 c&s), 63.5 mm SL, río Santa María at BR 293, Dom Pedrito, Rio Grande do Sul, Brazil; MCP 14784, 15, 49.5-78.5 mm SL, lago Guaíba, Porto Alegre, Rio Grande do Sul, Brazil. *Cyanocharax alburnus*, MCP 9100, 1 c&s, 55.0 mm SL, rio Jacuí, Soledade, Rio Grande do Sul, Brazil; MCP 40492, 29, 45.8-58.0 mm SL, rio Cadeia, Santa Maria do Herval, Rio Grande do Sul, Brazil. *Diapoma specularum*, MCP 26564, 12 (4 c&s), 33.8-49.5 mm SL, arroio Caemborá, rio Jacuí drainage, Nova Palma, Rio Grande do Sul, Brazil. *Hollandichthys multifasciatus*, MZUSP 35237, 20 of 38 (3 c&s), 32.8-90.0 mm SL, stream near of the Paranapiacaba, upper rio Tietê drainage, Santo André, São Paulo, Brazil. *Hysteronotus megalostomus*, MCP 33741, 9 (1 c&s), 29.7-40.8 mm SL, rio Peruaçu, rio São Francisco basin, Januária, Minas Gerais, Brazil. *Knodus meridae*, ANSP 165613, 30 of 73 (2 c&s), 31.1-46.3 mm SL, río Orinoco, about 7 km S of Puerto Ayacucho, Amazonas, Venezuela. *Landonia latidens*, CAS 55299, 16, 22.2-32.5 mm SL, MZUSP 49195, 1 c&s of 12 alc., 36.5 mm SL, río Daule, 200 m above Colimes, Guayas, Ecuador. *Mimagoniates rheocharis*, MCP 29273, 74 (3 c&s), 39.1-52.9 mm SL, arroio Molha Coco, rio Mampituba basin, Praia Grande, Santa Catarina, Brazil. *Nematobrycon palmeri*, CAS 70883, 43 (2 c&s), 10.2-28.2 mm SL, rio Condoto, tributary of rio San Juan, Departamento Choco, Colombia; MHNG 2182.86, 7 (2 c&s), 25.0-30.2 mm SL, Colombia (aquarium center). *Nematocharax venustus*, MCP 17773, 8 (1 c&s), 25.6-51.7 mm SL, rio Branco, Arataca, Bahia, Brazil; MCP 17987, 29 (3 c&s), 15.9-44.7 mm SL, tributary of rio Pratas at São José, Buerarema, Bahia,



Brazil. *Odontostilbe fugitiva*, INPA 18506, 10 of 50 (1 c&s), 22.2-33.9 mm SL, paran do Xiborena, rio Solimes drainage, Amazonas, Brazil; MZUSP 77844, 2 c&s, 36.9-40.0 mm SL, ro Pastaza, Pastaza, Ecuador; INPA 18465, 73 (4 c&s), 30.8-36.1 mm SL, rio Solimes, Ilha de Marchantaria, Manaus, Amazonas, Brazil; INPA 18510, 100, 16.5-28.9 mm SL, rio Solimes, Manaus, Amazonas, Brazil. *Othonocheirodus* sp., USNM 216717, 11 (2 c&s), 31.6-45.8 mm SL, backwater of ro Zamora 12 km NE of Zamora, Zamora-Chinchipe, Ecuador. *Piabina argentea*, MCP 16862, 30 (5 c&s), 22.5-47.3 mm SL, rio Peruau, rio So Francisco basin, Januria, Minas Gerais, Brazil. *Poptella brevispina*, MCP 10969, 2 c&s, 45.4-59.0 mm SL, tributary of rio Trombetas; MCP 22931, 42, 38.8-50.3 mm SL, tributary of rio Guama, Concrdia do Par, Par, Brazil. *Pseudochalceus lineatus*, ANSP 75905, 1, 42.4 mm SL, ro Santiago, Esmeraldas, Ecuador; ANSP 75906, 1, 80.2 mm SL, ro Toachi near Santo Domingo of Los Colorados, Pichincha, Ecuador; ANSP 75907, 1, 48.4 mm SL, ro Cupa, Esmeraldas, Ecuador; MCZ 48730, 2, 37.3-61.2 mm SL, tributary of ro Branco, Pichincha, Ecuador; USNM 287747, 5 (1 c&s), 24.6-43.7 mm SL, ro Chirape tributary of ro Guayllabama, R. Esmeraldos de Paraiso, Ecuador. *Rachoviscus crassiceps*, MCP 37987, 8, 22.3-36.0 mm SL, stream at So Francisco do Sul, Santa Catarina; MZUSP 18564, 8 (1 c&s), 18.6-23.4 mm SL, praia de Brejatuba, Guaratuba, Paran, Brazil; MZUSP 35732, 3 (1 c&s), 13.6-14.5 mm SL; MHNG 2188.72, 1, 14.1 mm SL, praia de Guaratuba, Guaratuba, Paran, Brazil. *Rachoviscus graciliceps*, MHNG 2514.34, 4 (1 c&s), 13.8-16.6 mm SL, stream at 13 km S of Prado, Bahia, Brazil; MZUSP 38366, 6 (1 c&s), 11.5-19.3 mm SL, tributary of ro So Jos, Reserva Florestal de Soretama, Esprito Santo, Brazil; MZUSP 90590, 20 (3 c&s), 22.3-29.0 mm SL, stream L at road Santa Luzia, Canasvieiras, Bahia, Brazil. *Rhoadsia altipinna*, FMNH 79077, 48 (1 c&s), 67.0-89.1 mm SL, Estacion Biologica ro Palenque, Esmeraldas, Ecuador; MCZ 131525, 16 (1 c&s), 65.5-86.0 mm SL, ro Esmeraldas drainage, Esmeraldas, Ecuador. **Examined specimens not included in matrix analysis:** *Boehlkea*

*fredcochui*, ANSP 111675, holotype, male (x-ray), 39.3 mm SL, upper Amazon, Paramount Aquarium via Tropicarium Frankfurt am Main, 1956; ANSP 111668, paratype, male, 31.8 mm SL, upper Amazon from surroundings of Leticia, Colombia, Paramount Aquarium import via Herbert R. Axelrod, 1964. *Bryconamericus andresoi*, CAS 70099, 40 of 192 paratypes, 30.5-66.9 mm SL, Colombia, Narino, creek into río Juanambu, a tributary of upper río Patia at Mancha Bajoi, 18 Mar 1913, A. W. Henn; FMNH 56567, 5 paratypes, 49.7-63.7 mm SL, Colombia, los llanas de Sandona, 9 Mar 1913, A. W. Henn. *Bryconamericus caucanus*, CAS 39510, 29 paratypes, 31.2-58.4 mm SL, Colombia, Dept. Quindio, rio Cauca drainage, Piedra Moler bridge over the rio Viejo, east of Cartago, 21 Feb 1912, C. H. Eigenmann. *Bryconamericus decurrens*, FMNH 56255, holotype (x-ray), 56.7 mm SL, male, Colombia, Bolivar, Soplaviento; CAS 39542, paratype, 50.9 mm SL, Colombia, Bolivar, Soplaviento, town on the Dique de Cartagena between Cartagena and Calamar, approx. 10°09'N 75°17'W, 11-13 Jan 1912, C. H. Eigenmann. *Bryconamericus emperador*, MCP 27090, 6 (2 c&s), 40.6-47.3 mm SL, rio Pucuro, 3-4 km above confluence of the rio Tuira, Pucuro, Darién, Panama. *Bryconamericus icelus*, SMF 16284, 6 of 15 paratypes, 42.8-55.3 mm SL, several tributaries of río Manso, río Sinú basin, Colombia, 18 Apr 1964, F. Flores & C. Velásquez. *Bryconamericus peruanus*, MUSM 6158, 10 of 25 (2 c&s), 48.1-65.0 mm SL, río Comaninas, río Marañon drainage, Condorcanqui, Dept. Amazonas, Peru, 4°2'S 78°20'W, 19 Jul 1994, H. Ortega. *Bryconamericus plutarcoi*, ICNMHN 4886, holotype, 51.3 mm SL, ICNMHN 4887, 6 paratypes, 54.9-68.8 mm SL, quebrada Santa Rosa, río Suárez drainage, middle río Magdalena basin, Santander, Colombia, 6°26'9"N 73°18'56"W, 2 Feb 1971, P. Cala. *Bryconamericus zeteki*, USNM 109263, 9 of 52 paratypes, 45.8-69.1 mm SL, USNM 109264, 9 of 32 paratypes, 51.1-66.2 mm SL, creek in El Valle, Pacific Slope, Panama. *Eretmobrycon bayano*, USNM 213843, 9 of 14 paratypes, 42.5-55.3 mm SL, pool in small stream about 19 km along road from El Llano to Carti, río Bayano basin, Panama, 10 Mar 1973, J. D. McPhail

& R. Dressler. *Hemibrycon orcesi*, USNM 164064, holotype, male (x-ray), 47.4 mm SL, río Macuma, northern tributary of upper río Morona, upper Amazon, altitude 550-650 m, Santiago-Zamora, Ecuador, 2°07-13'S 77°35-47'W, Apr 1953, B. Pazmino; ANSP 75904, 2 paratypes (x-ray), 44.2-45.5 mm SL, USNM 175128, paratype (x-ray), 48.7 mm SL, collected with the holotype. *Hemibrycon velox*, SMF 21300, 7 of 11 paratypes, 34.7-52.7 mm SL, several tributaries between Chibogodó to río Manso, río Sinú basin, Colombia, 1 May 1962, C. Velásquez.

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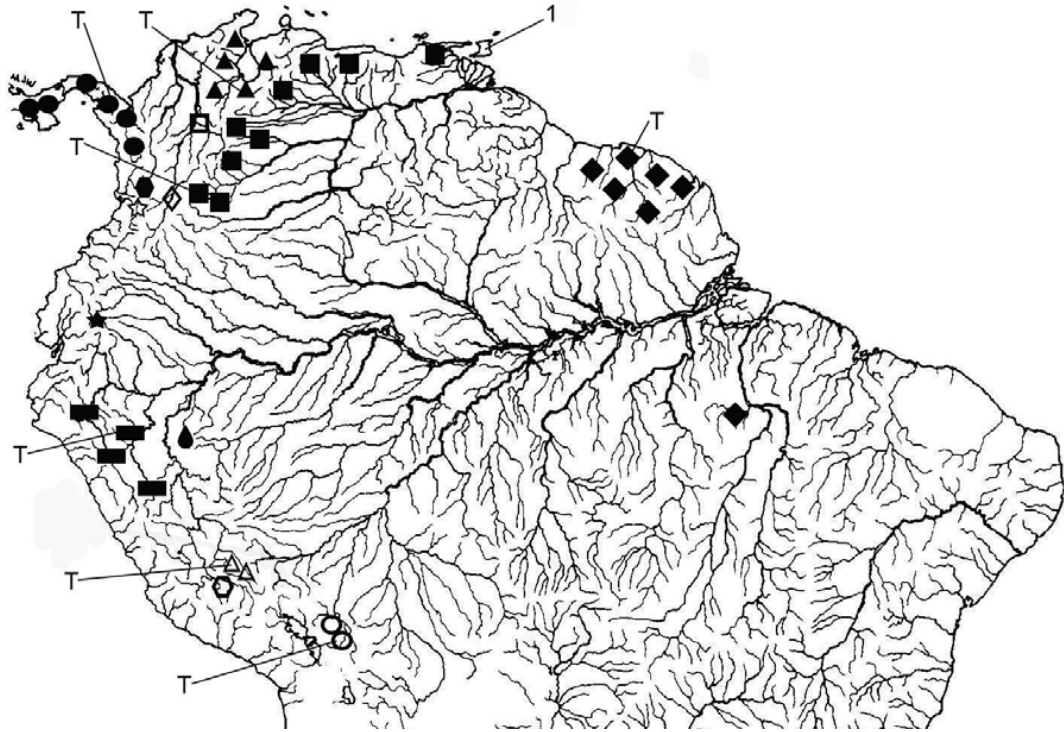
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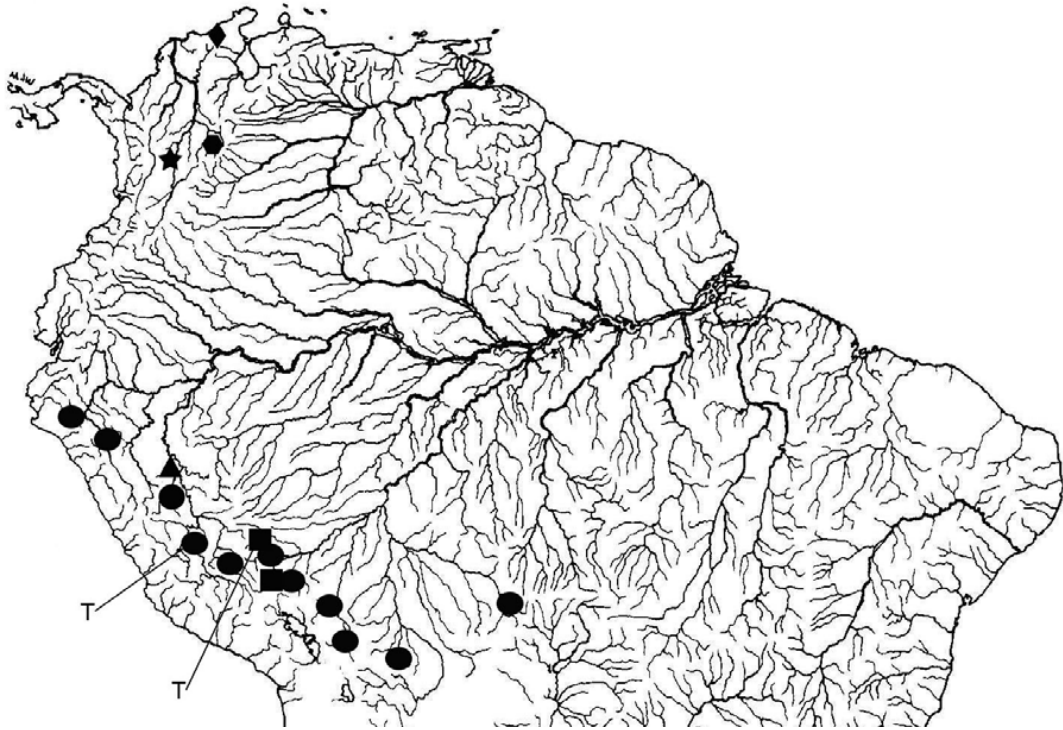
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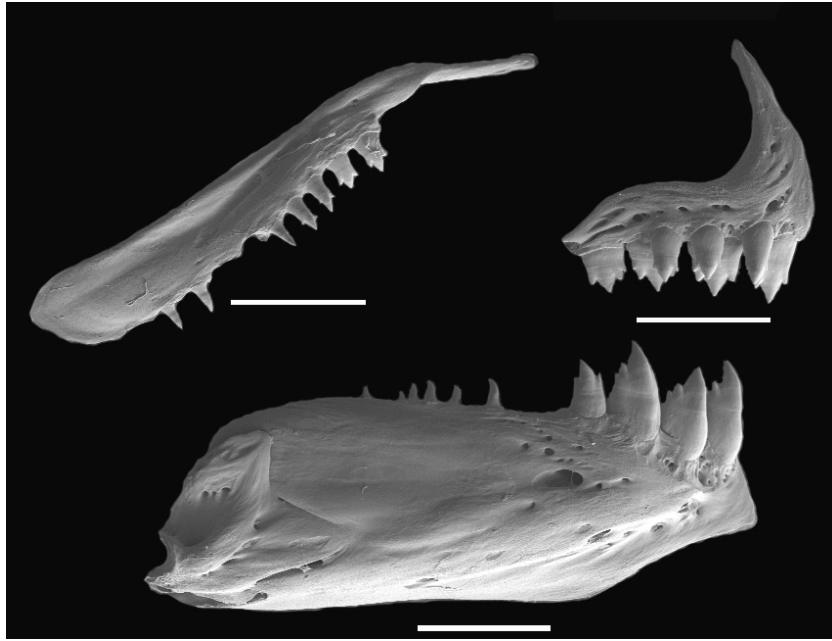
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**Fig. 1.** Map of central and northern South America showing geographic distribution of *Hemibrycon polyodon* (solid star), *H. taeniurus* (1 - Trinidad Island), *H. huambonicus* (rectangle), *H. boquiae* (open star), *H. dentatus* (solid hexagon), *H. tolimae* (open diamond), *H. colombianus* (open square), *H. dariensis* (solid dots), *H. tridens* (open hexagon), *H. beni* (open dots), *H. helleri* (open triangles), *H. metae* (solid squares), *H. jabonero* (solid triangles), *H. surinamensis* (solid diamonds), and *H. divisorensis* (solid gout). Some symbols represent more than one lot or locality of specimens. T = type locality of each species.



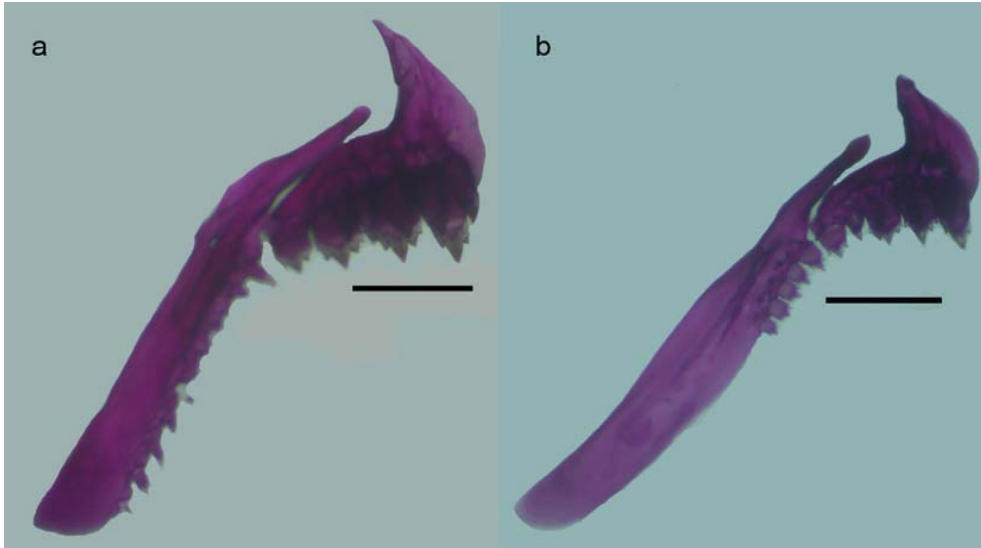
**Fig. 2.** Map of central and northern South America showing geographic distribution of *Hemibrycon jeslkii* (solid circles), *Hemibrycon* n. sp. 1 (triangle), *Hemibrycon* n. sp. 2 (diamond), *Hemibrycon* n. sp. 3 (hexagon), *Hemibrycon* n. sp. 4 (star), and *Hemibrycon* n. sp. 5 (squares). Some symbols represent more than one lot or locality of specimens. T = type locality of each species.



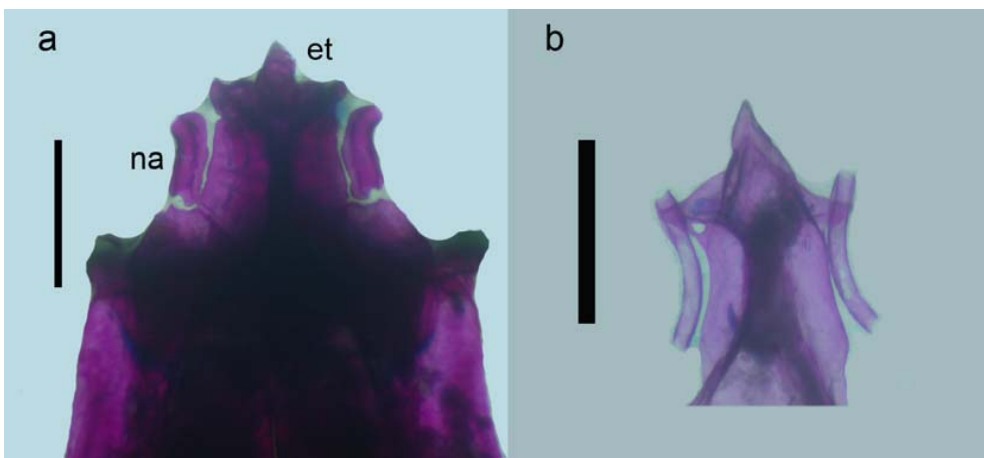
**Fig. 3.** *Hemibrycon polyodon*, KU 20004, female, 52.5 mm SL. Scanning electron micrograph of right side upper and lower jaws. Scale bars = 1 mm.



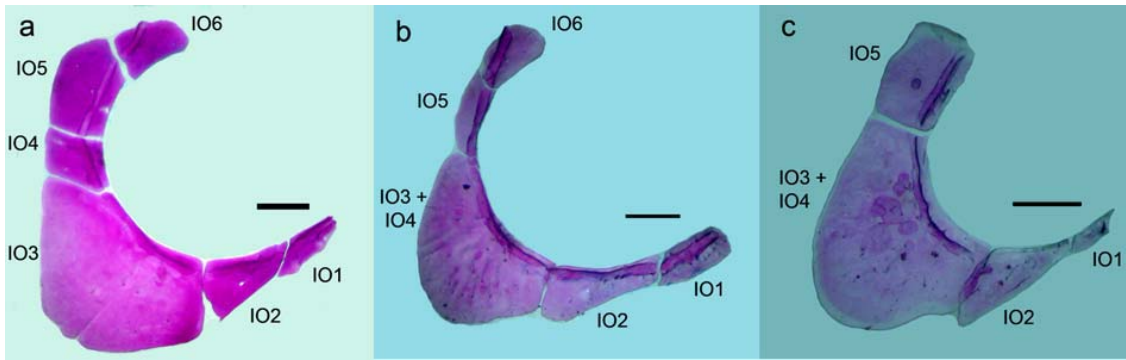
**Fig. 4.** *Hemibrycon dentatus*, IMCN 282, female, 82.0 mm SL. Scanning electron micrograph of right side upper and lower jaws. Scale bars = 1 mm.



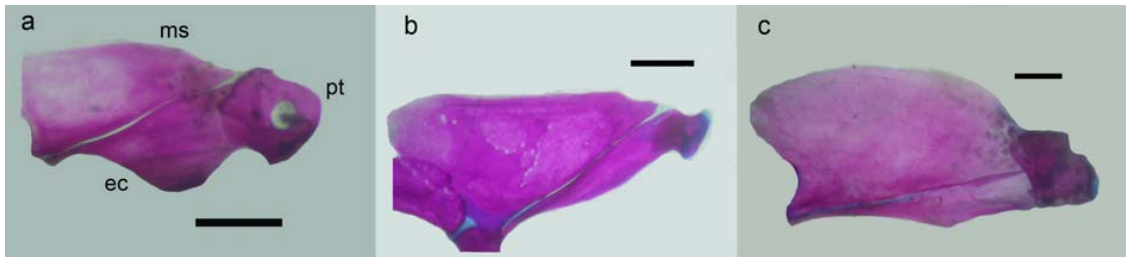
**Fig. 5.** Premaxilla and maxilla. Lateral views: a- *Hemibrycon surinamensis*, MZUSP 30529; b- *Diapoma speculiferum*, MCP 26564. Bars = 1 mm.



**Fig. 6.** Nasal bones (na) and anterior portion of ethmoid (et). Dorsal views: a- *Aphyocharax pusillus*, MCP 32769; b- *Bryconadenos tanaothoros*, MCP30516. Bars = 1 mm.

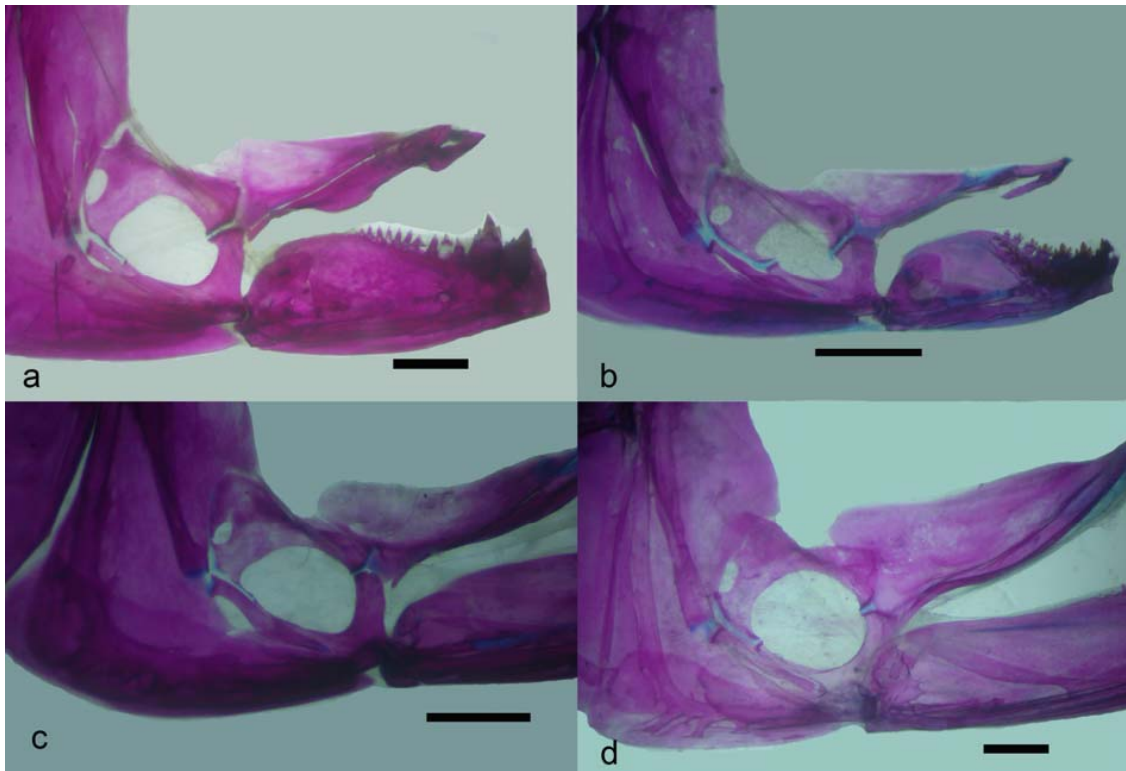


**Fig. 7.** Infraorbital bones (io). Lateral views: a- *Hemibrycon surinamensis*, MZUSP 30529; b- *Nematocharax venustus*, MCP 17773; c- *Rachoviscus crassiceps*, MCP37987. Bars = 1 mm.

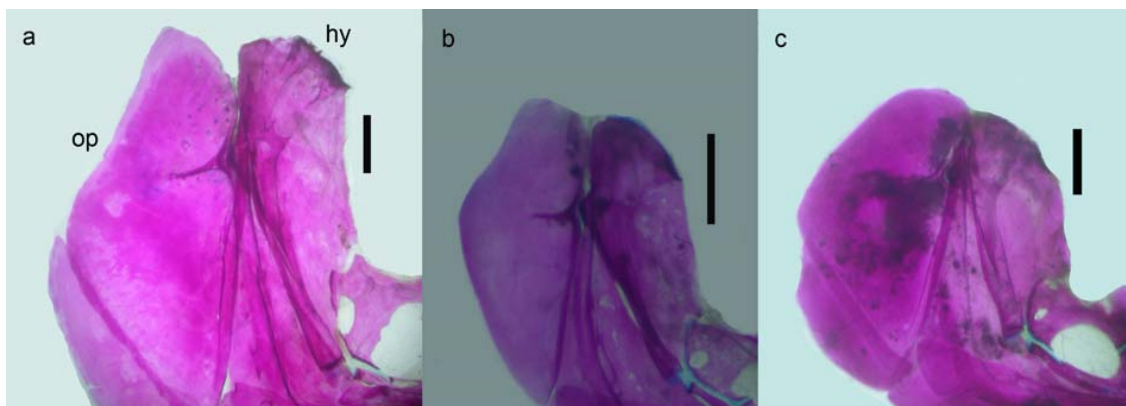


**Fig. 8.** Palatine (pt), mesopterygoid (ms), and ectopterygoid (ec) bones. Dorsal views: a- *Hemibrycon surinamensis*, MZUSP 30529; b- *Astyanax* aff. *fasciatus*, MCP 21293; c- *Hollandichthys multifasciatus*, MZUSP 35237. Bars = 1 mm.

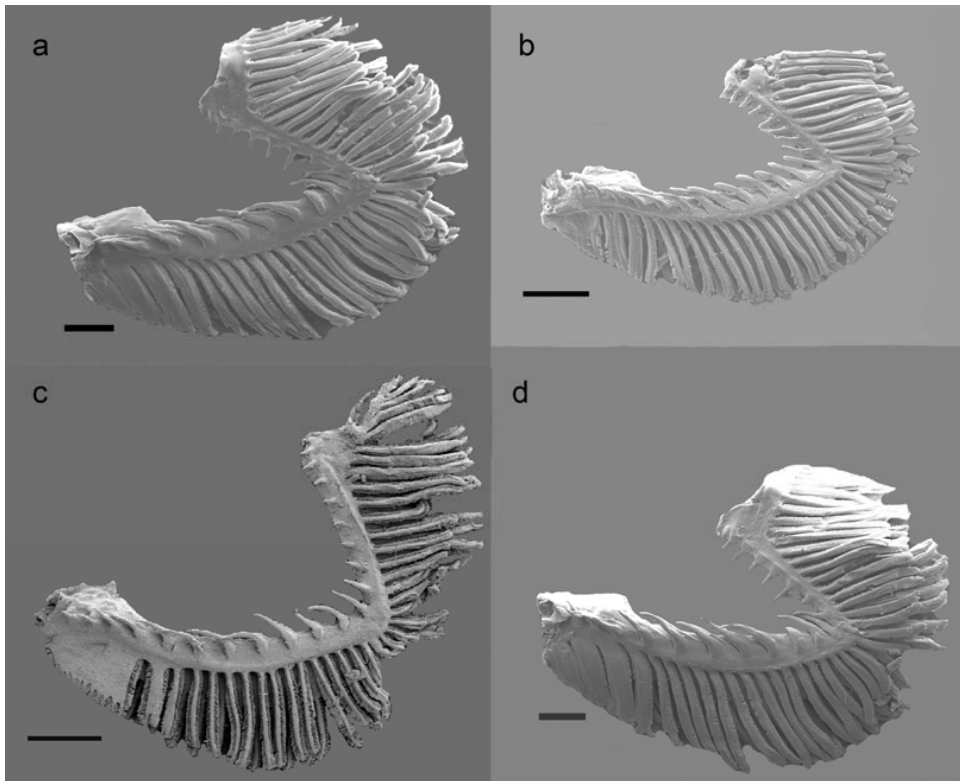




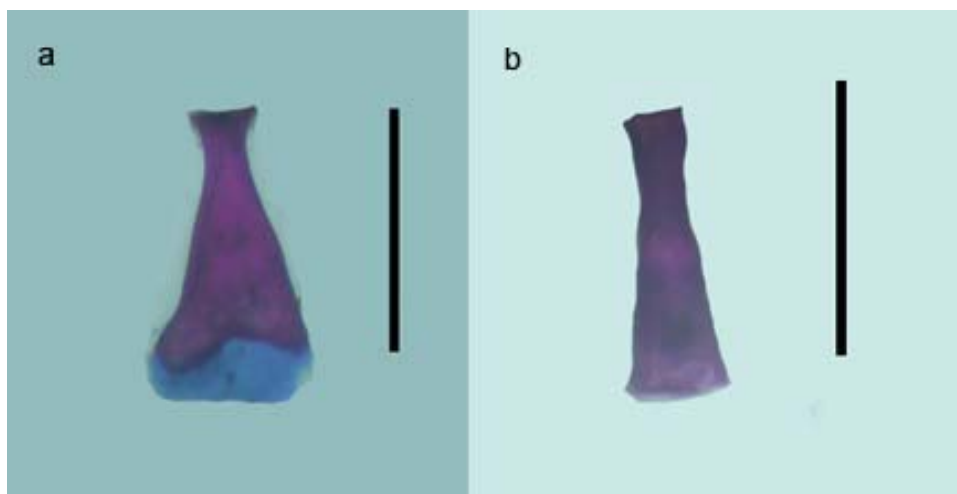
**Fig. 9.** Suspensory apparatus. Lateral views: a- *Hemibrycon surinamensis*, MZUSP 30529; b- *Bryconadenos tanaothoros*, MCP30516; c- *Diapoma speculiferum*, MCP 26564; d- *Bryconops melanurus*, MCP 15807. Bars = 1 mm.



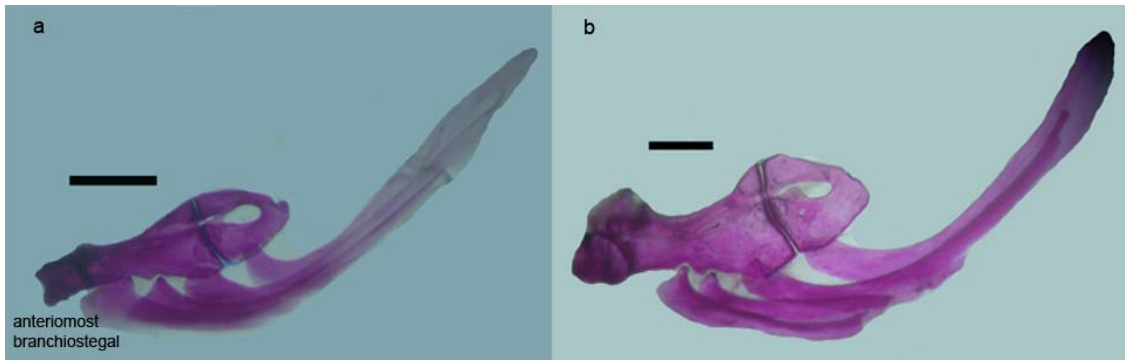
**Fig. 10.** Opercle (op) and hyomandibular (hy) bones. Lateral views of the right side: a- *Hemibrycon huambonicus*, ROM 55406; b- *Bryconadenos tanaothoros*, MCP30516; c- *Aphyocharax pusillus*, MCP 32769.



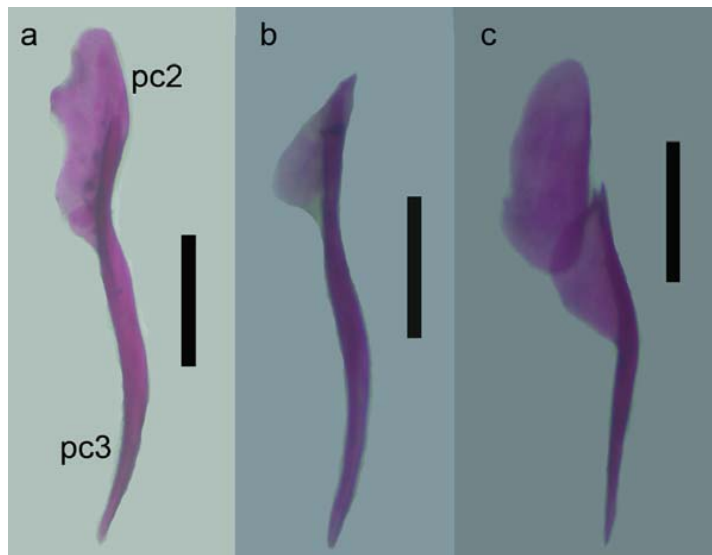
**Fig. 11.** First gill arch. Lateral view of the left side of *Hemibrycon jabonero*, USNM 121456 (a); *Hemibrycon metae*, MCNG 5646 (b); *Hemibrycon jelskii*, MCP 35022 (c); *Hemibrycon* n. sp. 4, ANSP 93221 (d). Bars = 1 mm.



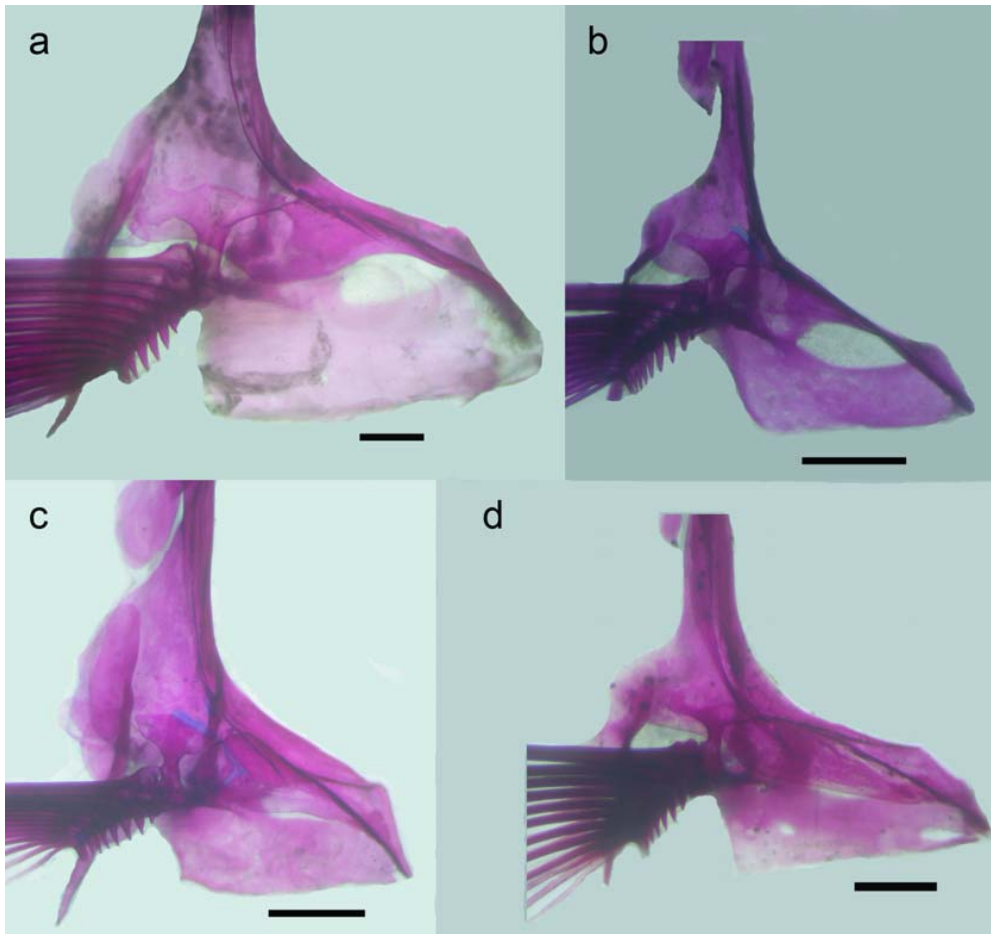
**Fig. 12.** Basihyal bone. Dorsal views: a- *Diapoma speculiferum*, MCP 26564; b- *Hemibrycon metae*, MCNG 7923. Bars = 1 mm.



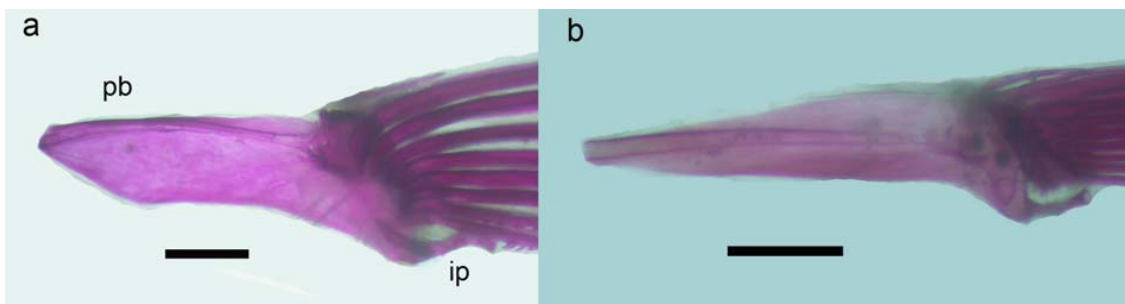
**Fig. 13.** Branchiostegal bones of males. Lateral views of the left side: a- *Diapoma speculiferum*, MCP 26564; b- *Hemibrycon huambonicus*, ROM 55406. Bars = 1 mm.



**Fig. 14.** Postcleithrum 2 (pc2) and 3 (pc3) bones. Lateral views of the right side: a- *Hemibrycon surinamensis*, MZUSP 30529; b- *Hemibrycon metae*, MCNG 7923; c- *Nematocharax venustus*, MCP 17987.



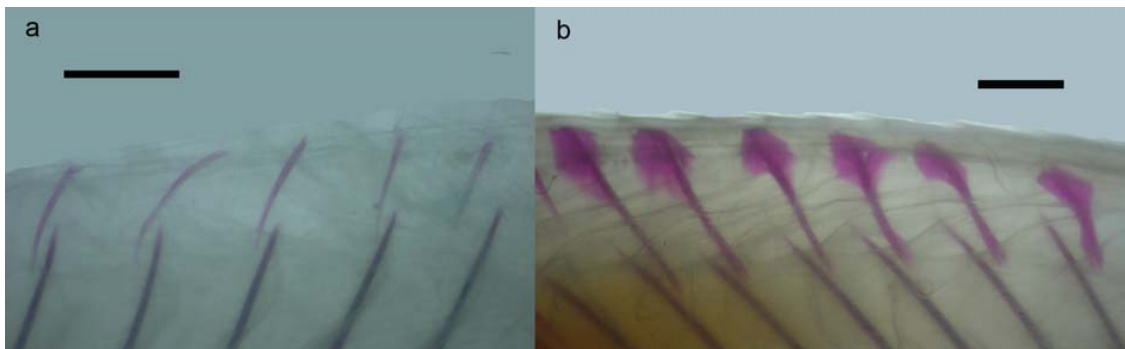
**Fig. 15.** Right pectoral girdle and fin origin of *Hemibrycon* n. sp. 4, ICNMHN 3675 (a); *Bryconadenos tanaothoros*, MCP30516 (b); *Nematoccharax venustus*, MCP 17987 (c); *Piabina argentea*, MCP 16862 (d).



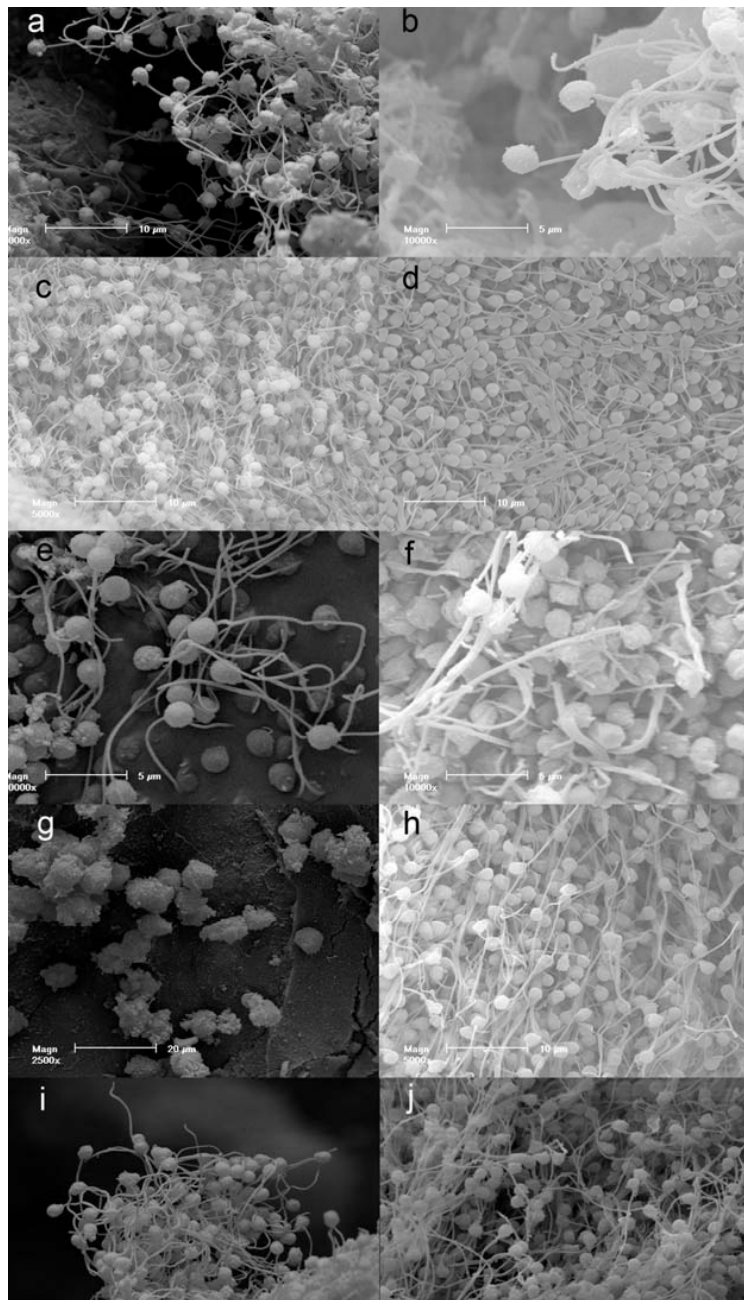
**Fig. 16.** Right pelvic girdle of *Hemibrycon huambonicus*, ROM 55406 (a); *Poptella brevispina*, MCP 10969 (b). Pelvic bone (pb); ischiac process (ip). Medial views. Bars = 1 mm.



**Fig. 17.** Caudal fin of the left side of *Hemibrycon boquiae*, IMCN 1076, 80.1 mm SL.



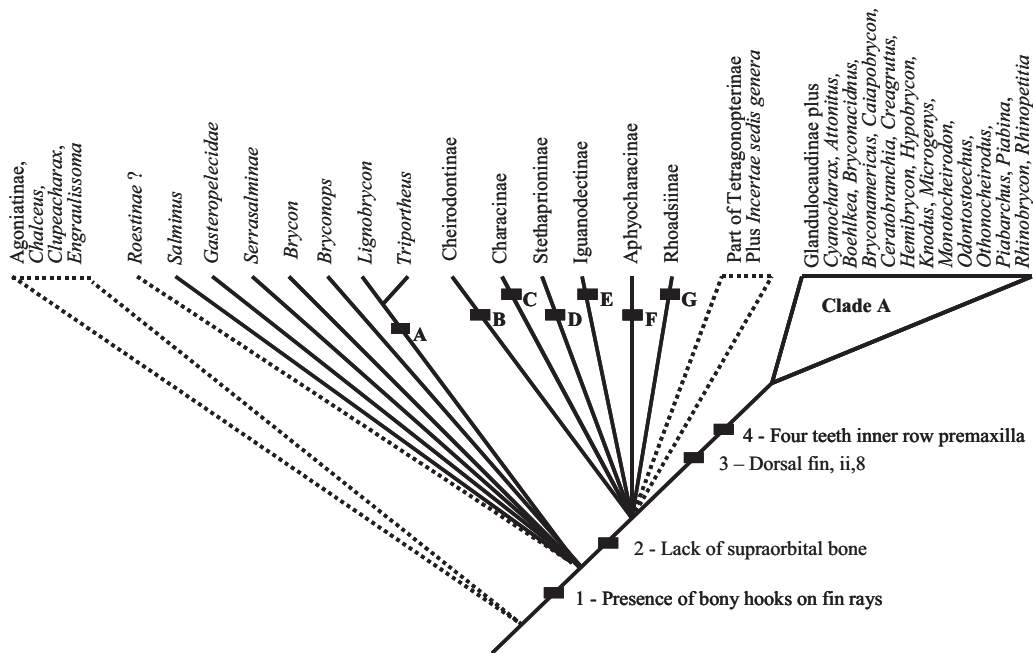
**Fig. 18.** Supraneural bones. Lateral views: a- *Diapoma speculiferum*, MCP 26564; b- *Hemibrycon surinamensis*, MZUSP 30529. Bars = 1 mm.



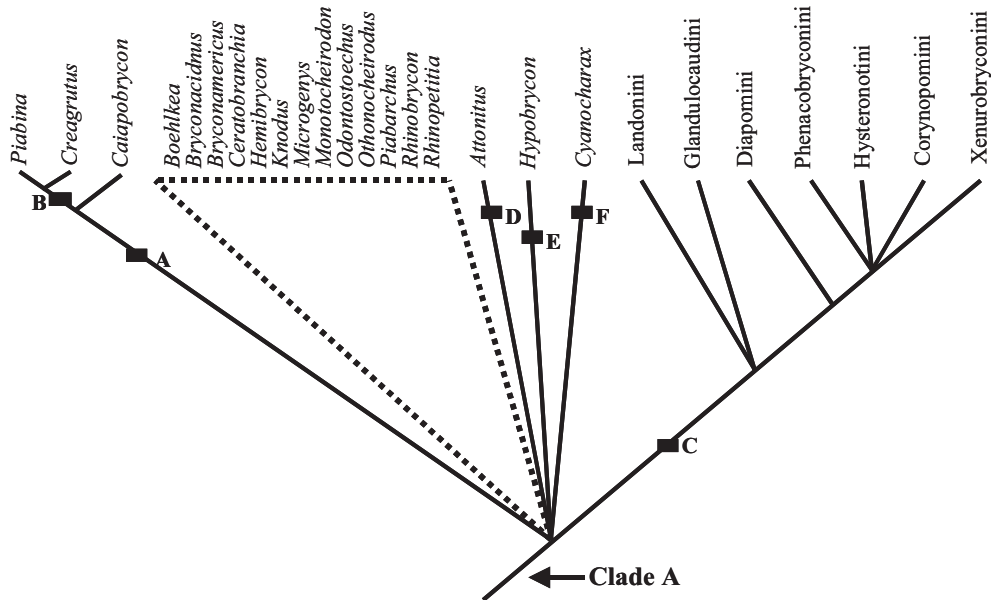
**Fig. 19.** Spermatozoa: a- *Hemibrycon dariensis* (USNM 327266, 57.5 mm SL); b- *Hemibrycon divisorensis* (MUSM 28040, 68.4 mm SL); c- *Hemibrycon huambonicus* (USNM 086794, 44.7 mm SL); d- *Hemibrycon jabonero* (USNM 121456, 76.6 mm SL); e- *Hemibrycon jelskii* (MUSM 19562, 57.1 mm SL); f- *Hemibrycon metae* (USNM 228563, 50.3 mm SL); g- *Hemibrycon surinamensis* (MHNG 227928, 56.1 mm SL); h- *Hemibrycon taeniurus* (USNM 290413, 58.1 mm SL); i- *Hemibrycon* n. sp. 4 (ANSP 93221, 65.4 mm SL); j- *Hemibrycon* n. sp. 3 (ICNMHN 753, 74.8 mm SL). Scanning electron micrographs.



**Fig. 20.** Strict consensus tree of 65 most equally parsimonious trees showing the interrelationships among *Hemibrycon* species and related taxa obtained from the analysis of 123 characters. Tree Length = 775, Consistency Index = 0.22, Retention Index = 0.52. Bootstrap values below the node.

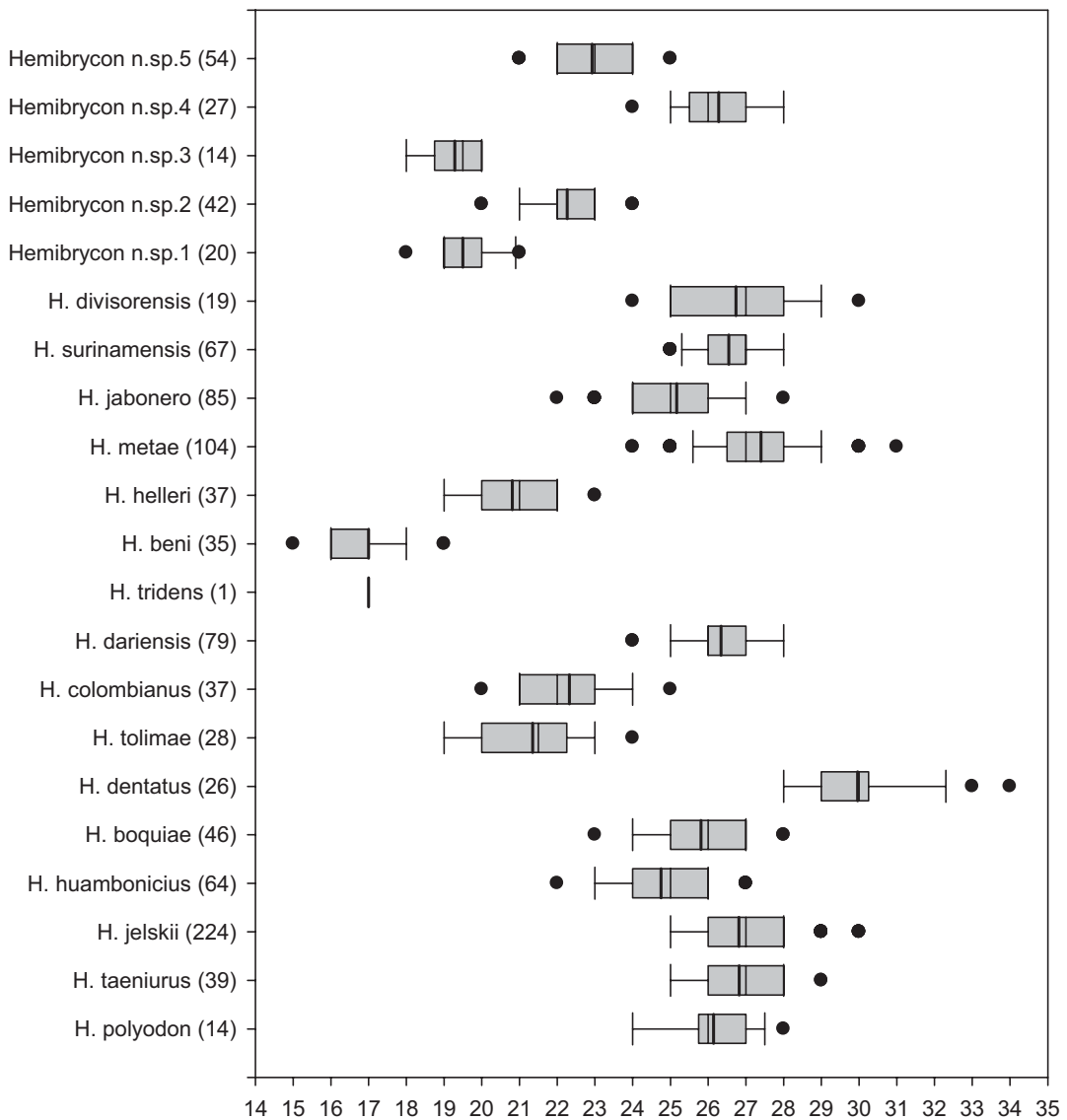


**Figure 21.** Cladogram proposed by Malabarba & Weitzman (2003: fig. 2) showing the current knowledge on the relationships of characids, gasteropelecids and roestines. See Malabarba & Weitzman (2003: 75) for more details.

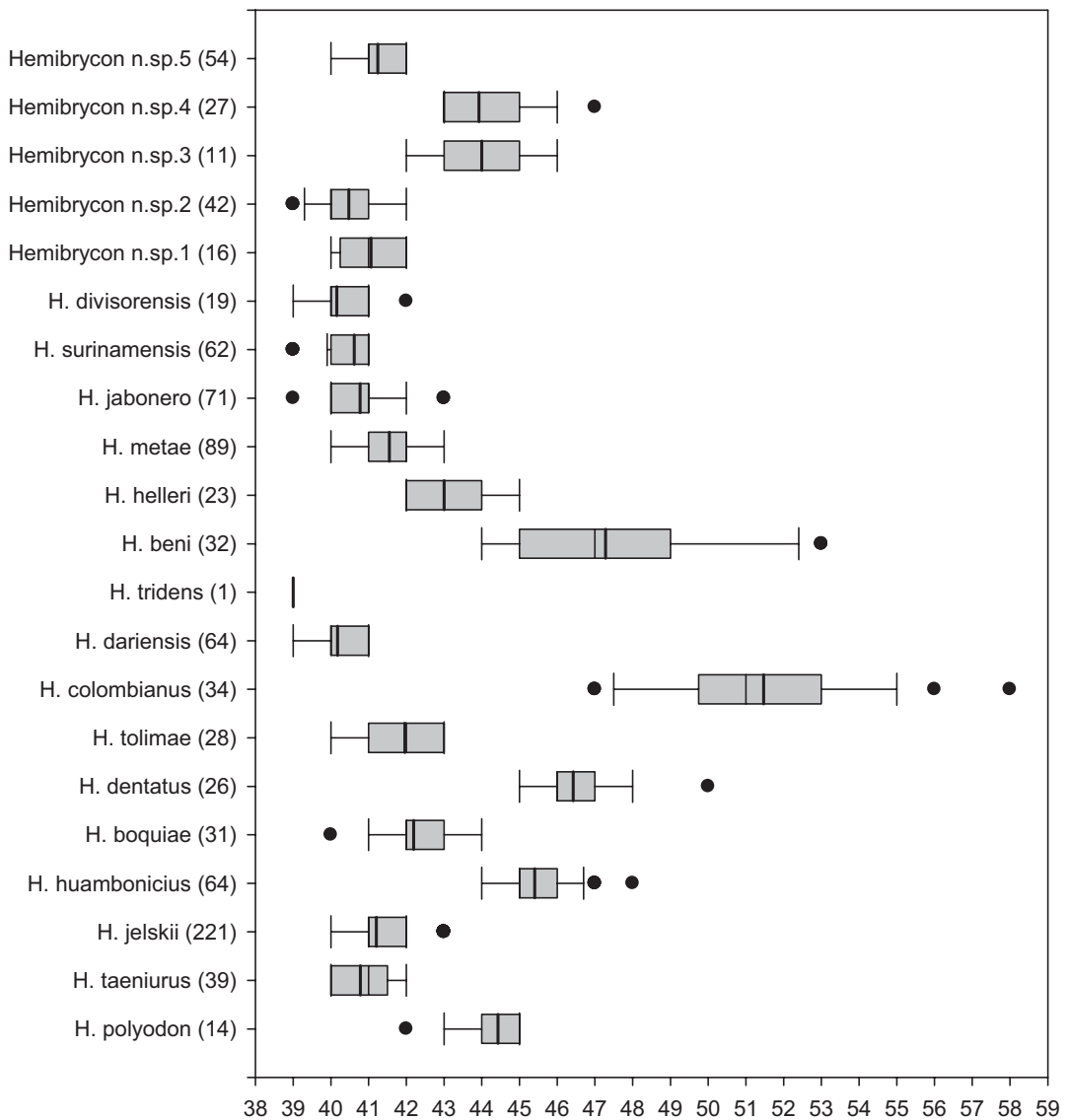


**Figure 22.** Cladogram depicting known relationships of the Clade A proposed by Malabarba & Weitzman (2003: fig. 11). See Malabarba & Weitzman (2003: 87) for more details.

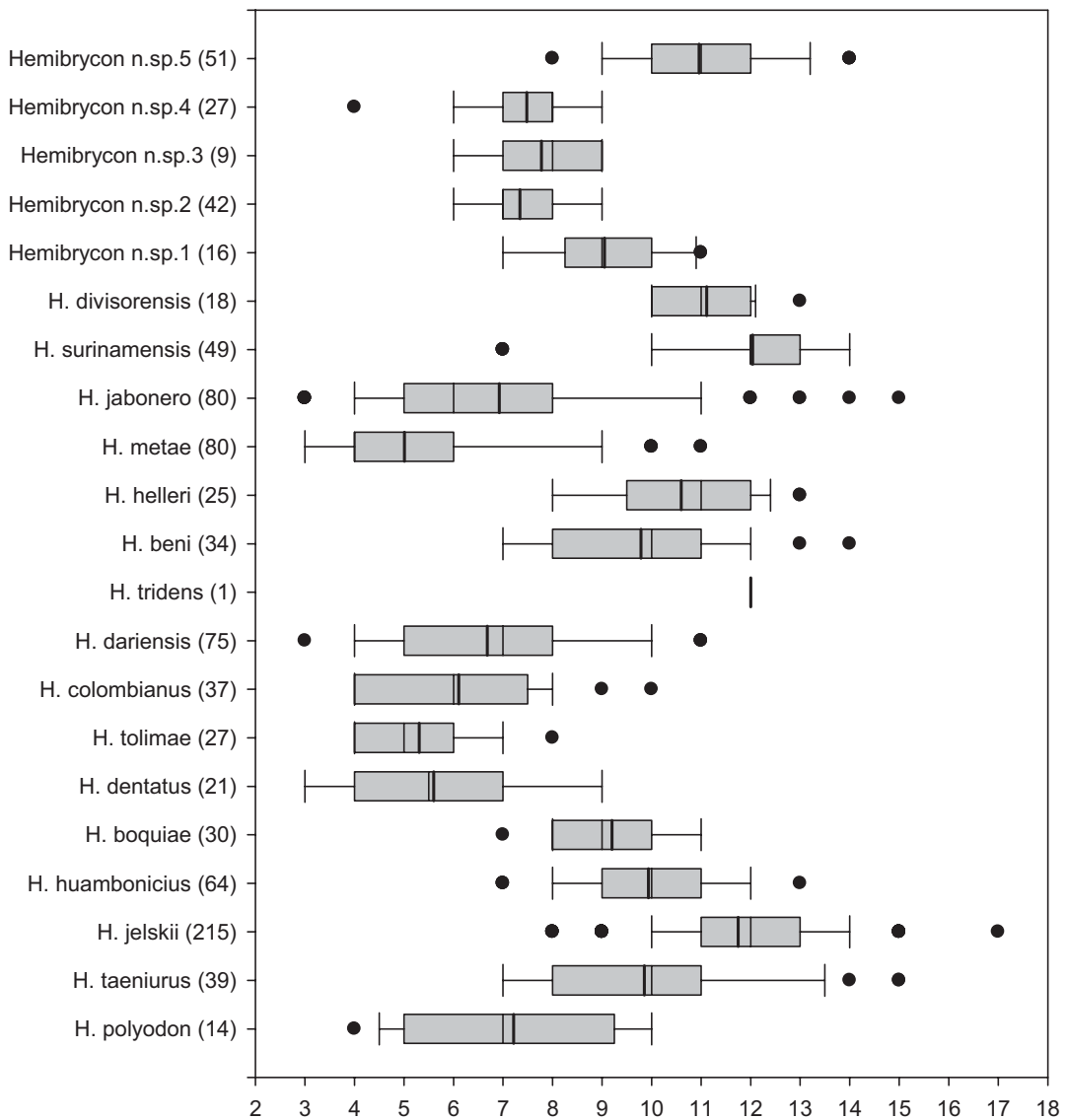




**Fig. 23.** Tukey box plots of the number of branched anal-fin rays in species of *Hemibrycon*. Mean represented by thick vertical bar, and 25<sup>th</sup> and 75<sup>th</sup> percentiles as lateral borders of box plots. Error bars represent 10<sup>th</sup> and 90<sup>th</sup> percentile points. Circles represent values found below 10<sup>th</sup> and above 90<sup>th</sup> percentile points. Number of the analyzed specimens between parentheses.



**Fig. 24.** Tukey box plots of the number of lateral line scales in species of *Hemibrycon*. Mean represented by thick vertical bar, and 25<sup>th</sup> and 75<sup>th</sup> percentiles as lateral borders of box plots. Error bars represent 10<sup>th</sup> and 90<sup>th</sup> percentile points. Circles represent values found below 10<sup>th</sup> and above 90<sup>th</sup> percentile points. Number of the analyzed specimens between parentheses.



**Fig. 25.** Tukey box plots of the number of maxillary teeth in species of *Hemibrycon*. Mean represented by thick vertical bar, and 25<sup>th</sup> and 75<sup>th</sup> percentiles as lateral borders of box plots. Error bars represent 10<sup>th</sup> and 90<sup>th</sup> percentile points. Circles represent values found below 10<sup>th</sup> and above 90<sup>th</sup> percentile points. Number of the analyzed specimens between parentheses.



**Fig. 26.** *Hemibrycon polyodon*, BMNH 1858.7.25.41, holotype, female, 70.4 mm SL, Guayaquil, Ecuador.



**Fig. 27.** *Hemibrycon polyodon*, KU 20004, male, 71.2 mm SL, río Pastaza basin, Ecuador.



**Fig. 28.** *Hemibrycon taeniurus*, AMNH 215239, male, 68.5 mm SL, Island of Trinidad, Trinidad and Tobago.



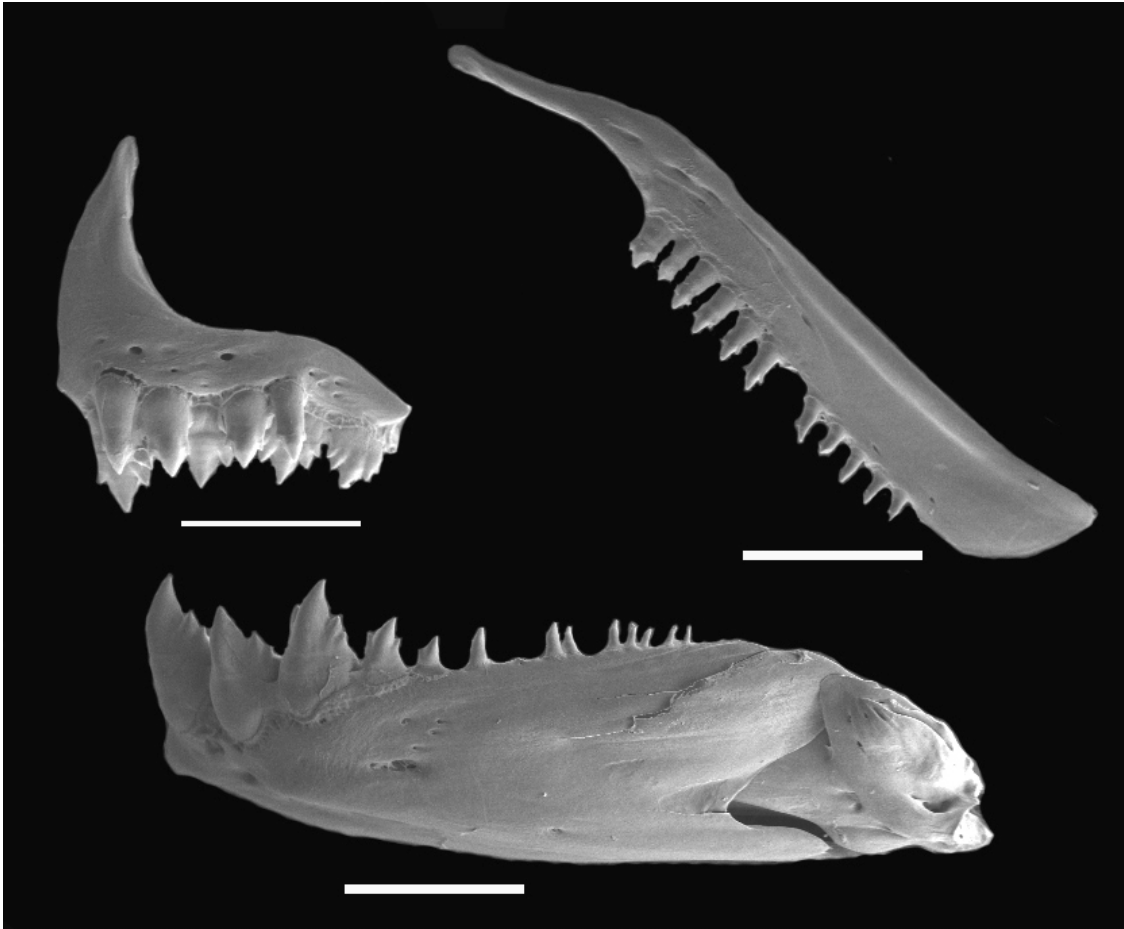
**Fig. 29.** *Hemibrycon guppyi*, BMNH 1906.6.23.13-17, syntype, female, 73.4 mm SL, Island of Trinidad, Trinidad and Tobago.



**Fig. 30.** *Hemibrycon taeniurus*, MCNG 8199, female, 57.5 mm SL. Scanning electron micrograph of right side upper and lower jaws. Scale bars = 1 mm.



**Fig. 31.** *Hemibrycon jelskii*, MUSM 19562, male, 69.0 mm SL, upper río Ucayali basin, Peru.



**Fig. 32.** *Hemibrycon jelskii*, MUSM 19562, male, 52.1 mm SL. Scanning electron micrograph of right side upper and lower jaws. Scale bars = 1 mm.



**Fig. 33.** *Hemibrycon huambonicus*, NMW 57531, syntype, male, 87.0 mm SL, upper río Ucayali basin, Huambo, Peru.



**Fig. 34.** *Hemibrycon huambonicus*, ROM 55406, female, 83.4 mm SL, upper río Ucayali basin, Peru.



**Fig. 35.** *Hemibrycon huambonicus*, ROM 55406, male, 70.0 mm SL. Scanning electron micrograph of right side upper and lower jaws. Scale bars = 1 mm.





**Fig. 36.** *Hemibrycon boquiae*, IMCN 1076, male, 62.4 mm SL, upper río Cauca basin, Colombia.



**Fig. 37.** *Hemibrycon boquiae*, IMCN 1076, female, 68.7 mm SL. Scanning electron micrograph of right side upper and lower jaws. Scale bars = 1 mm.



**Fig. 38.** *Hemibrycon dentatus*, IMCN 282, female, 99.4 mm SL, upper río Cauca basin, Colombia.



**Fig. 39.** *Hemibrycon tolimae*, FMNH 56257, holotype, female, 90.6 mm SL, río Combeima, Ibagué, Tolima, Colombia.



**Fig. 40.** *Hemibrycon colombianus*, IAvHP 3132, female, 65.1 mm SL, middle río Magdalena basin, Colombia.



**Fig. 41.** *Hemibrycon dariensis*, FMNH 8947, holotype, female, 49.9 mm SL, río Tuira basin, Panama.



**Fig. 42.** *Hemibrycon dariensis*, MCP 27072, female, 45.2 mm SL, río Tuira basin, Panama.



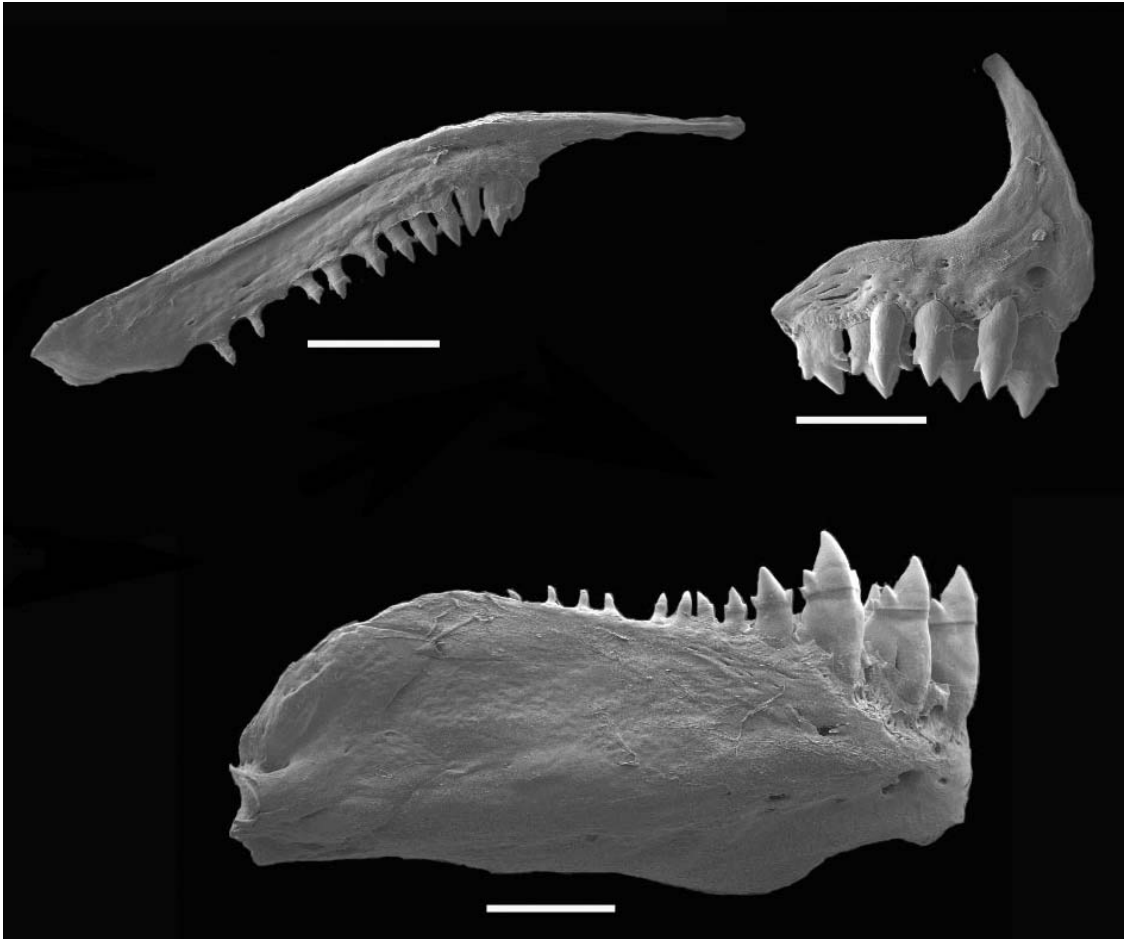
**Fig. 43.** *Hemibrycon tridens*, CAS 44358, holotype, 51.5 mm SL, male, upper río Ucayali basin, Peru.



**Fig. 44.** *Hemibrycon beni*, CAS 44333, syntype, male, 56.0 mm SL, upper río Beni basin, Bolivia.



**Fig. 45.** *Hemibrycon helleri*, ANSP 180775, female, 66.6 mm SL, upper río Ucayali basin, Peru.



**Fig. 46.** *Hemibrycon helleri*, ANSP 180775, female, 66.6 mm SL. Scanning electron micrograph of right side upper and lower jaws. Scale bars = 1 mm.



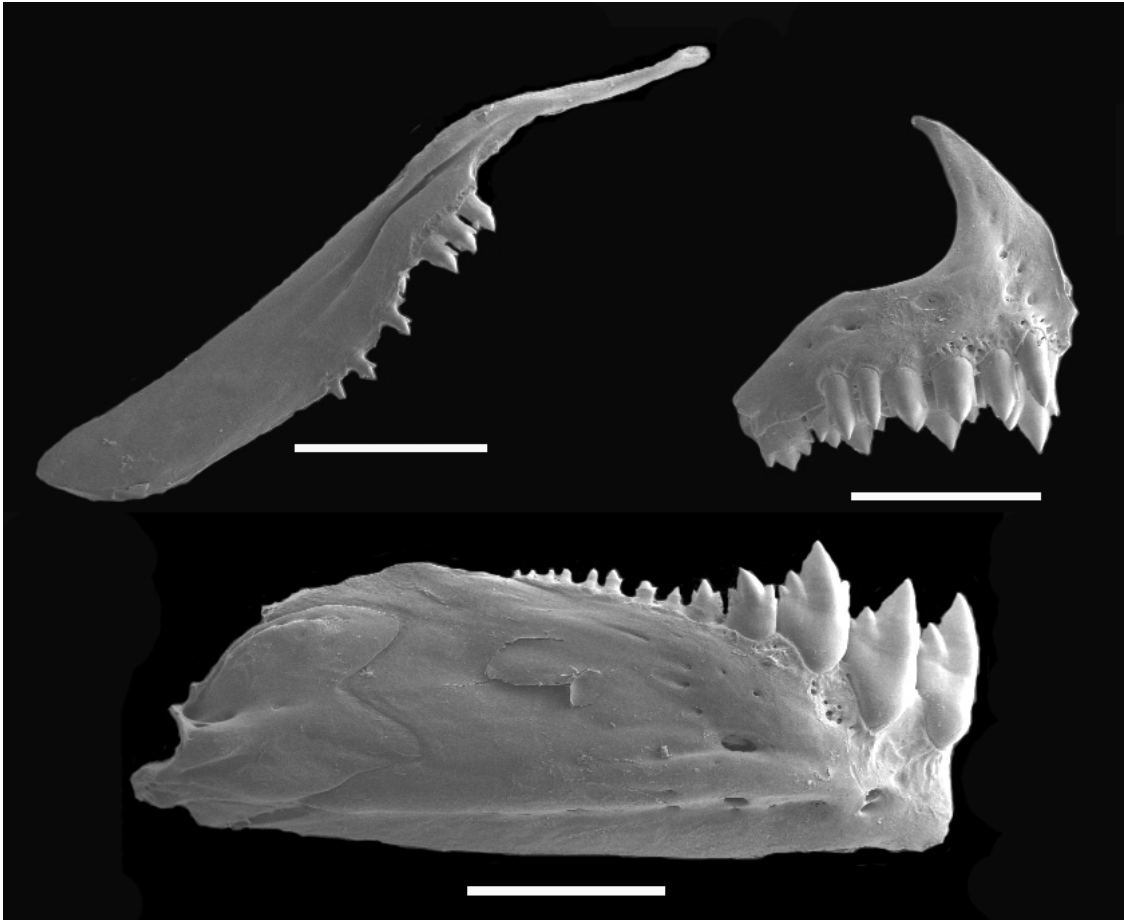
**Fig. 47.** *Hemibrycon metae*, INHS 61270, female, 61.4 mm SL, río Apure basin, Venezuela.



**Fig. 48.** *Hemibrycon metae*, MCNG 17030, female, 39.8 mm SL. Scanning electron micrograph of right side upper and lower jaws. Scale bars = 1 mm.



**Fig. 49.** *Hemibrycon jabonero*, INHS 34889, female, 46.2 mm SL, Lago Maracaibo basin, Venezuela.



**Fig. 50.** *Hemibrycon jabonero*, INHS 34889, female, 46.2 mm SL. Scanning electron micrograph of right side upper and lower jaws. Scale bars = 1 mm.



**Fig. 51.** *Hemibrycon surinamensis*, ZMA 100347, paratype, female, 65.0 mm SL, río Paramacca basin, Suriname.



**Fig. 52.** *Hemibrycon surinamensis*, ZMA 107232, male, 74.2 mm SL, rio Coppename basin, Saramacca, Suriname.



**Fig. 53.** *Hemibrycon surinamensis*, MHNG 227928, male, 58.9 mm SL. Scanning electron micrograph of right side upper and lower jaws. Scale bars = 1 mm.





**Fig. 54.** *Hemibrycon* n. sp. 1, MUSM uncat., holotype, female, 44.4 mm SL, upper río Ucayali basin, Peru.



**Fig. 55.** *Hemibrycon* n. sp. 1, MUSM 15845, paratype, female, 35.7 mm SL. Scanning electron micrograph of right side upper and lower jaws. Scale bars = 1 mm.



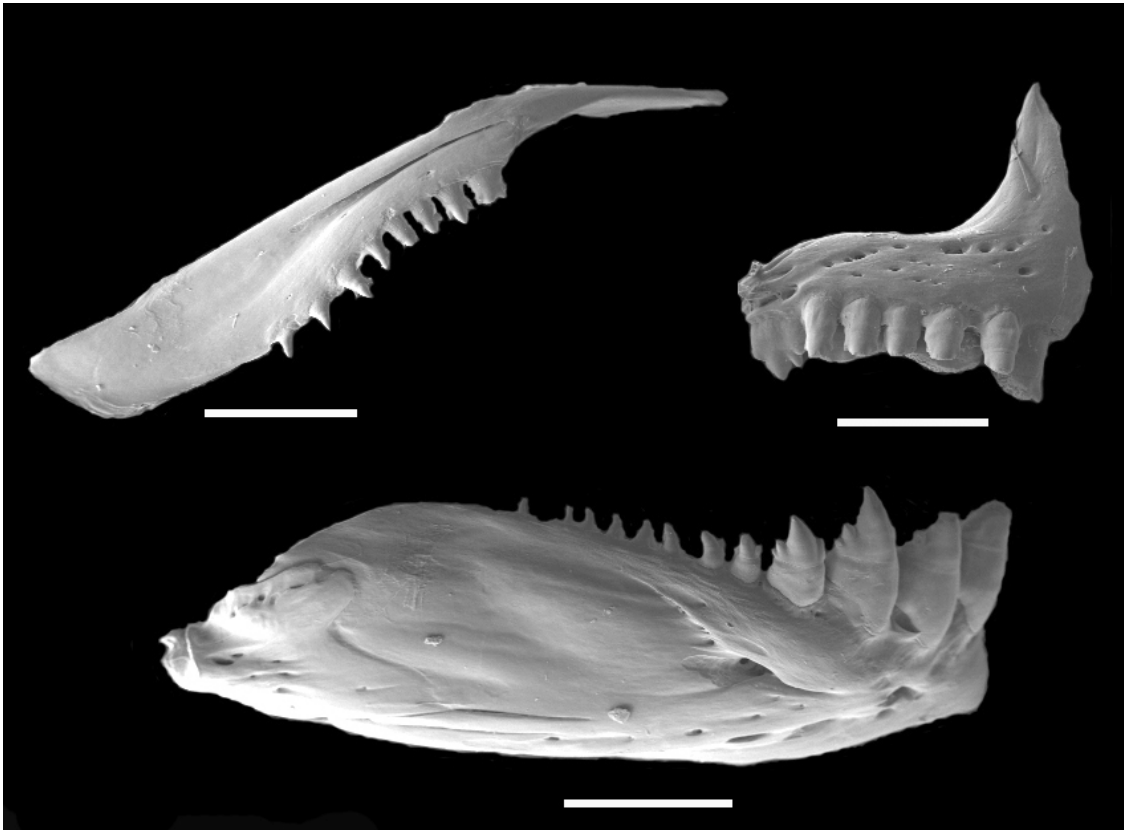
**Fig. 56.** *Hemibrycon* n. sp. 2, ICNMHN uncat., holotype, male, 55.4 mm SL, Caribbean coastal drainage on the region of Sierra Nevada de Santa Marta, Colombia.



**Fig. 57.** *Hemibrycon* n. sp. 2, ICNMHN 6439, paratype, male, 47.7 mm SL. Scanning electron micrograph of right side upper and lower jaws. Scale bars = 1 mm.



**Fig. 58.** *Hemibrycon* n. sp. 3, ICNMHN uncat., holotype, female, 76.7 mm SL, middle río Magdalena basin, Colombia.



**Fig. 59.** *Hemibrycon* n. sp. 3, ICNMHN 753, paratype, female, 58.0 mm SL. Scanning electron micrograph of right side upper and lower jaws. Scale bar = 1 mm.



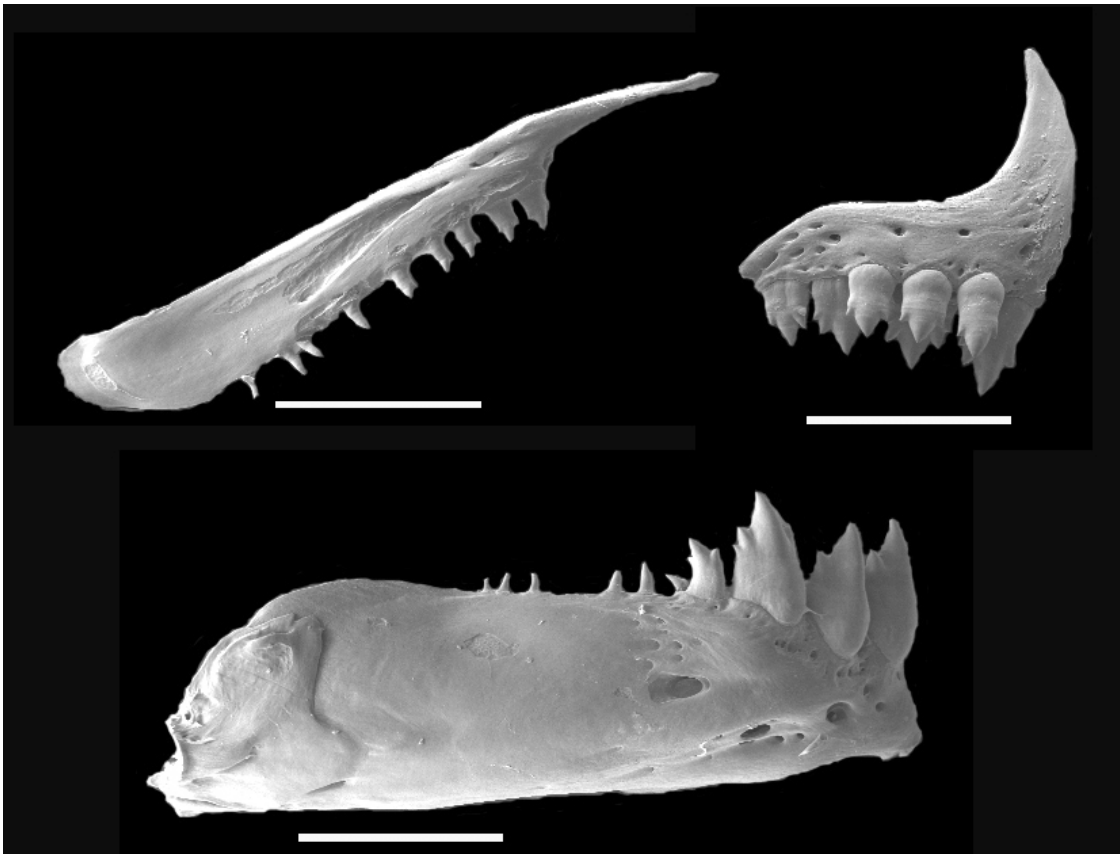
**Fig. 60.** *Hemibrycon* n. sp. 4, ICNMHN uncat., holotype, female, 74.0 mm SL, middle río Magdalena basin, Colombia.



**Fig. 61.** *Hemibrycon* n. sp. 4, ICNMHN 3675, female, 68.1 mm SL. Scanning electron micrograph of right side upper and lower jaws. Scale bars = 1 mm.



**Fig. 62.** *Hemibrycon* n. sp. 5, ANSP uncat., holotype, male, 59.6 mm SL, upper río Madre de Dios basin, Peru.



**Fig. 63.** *Hemibrycon* n. sp. 5, ANSP 143290, paratype, female, 39.2 mm SL. Scanning electron micrograph of right side upper and lower jaws. Scale bars = 1 mm.



**Fig. 64.** *Bryconamericus decurrens*, FMNH 56255, holotype, male, 56.7 mm SL, lower río Magdalena basin, Colombia.



**Fig. 65.** *Hemibrycon orcesi*, ANSP 75904, paratype, female, 44.6 mm SL, río Macuma, upper río Morona basin, Ecuador.

**Table 1.** Nominal species assigned herein to *Hemibrycon* and recognized species according to the results of this study. Nominal species are cited as in original description and arranged by year of publication. <sup>1</sup>Román-Valencia, 2004, redescribed the species in *Bryconamericus*, but it is recognized herein as belonging to *Hemibrycon*. <sup>2</sup>Species not analyzed in this study, but temporally assigned for *Hemibrycon* until analyze the type series (See specific comments above).

Nominal species	Assignment herein
<i>Poecilurichthys taeniurus</i> Gill, 1858	<i>Hemibrycon taeniurus</i>
<i>Tetragonopterus polyodon</i> Günther, 1864	<i>Hemibrycon polyodon</i>
<i>Tetragonopterus (Hemibrycon) trinitatis</i> Lütken, 1875	<i>Hemibrycon taeniurus</i>
<i>Tetragonopterus jelskii</i> Steindachner, 1877	<i>Hemibrycon jelskii</i>
<i>Tetragonopterus huambonicus</i> Steindachner, 1882	<i>Hemibrycon huambonicus</i>
<i>Tetragonopterus guppyi</i> Regan, 1906	<i>Hemibrycon taeniurus</i>
<i>Bryconamericus</i> or <i>Hemibrycon boquiae</i> Eigenmann, 1913	<i>Hemibrycon boquiae</i>
<i>Bryconamericus dentatus</i> Eigenmann, 1913	<i>Hemibrycon dentatus</i>
<i>Bryconamericus tolimae</i> Eigenmann, 1913	<i>Hemibrycon tolimae</i> <sup>1</sup>
<i>Hemibrycon colombianus</i> Eigenmann, 1914	<i>Hemibrycon colombianus</i>
<i>Hemibrycon dariensis</i> Meek & Hildebrand, 1916	<i>Hemibrycon dariensis</i>
<i>Hemibrycon boquillae</i> Eigenmann, 1922	<i>Hemibrycon boquiae</i>
<i>Hemibrycon tridens</i> Eigenmann, 1922	<i>Hemibrycon tridens</i>
<i>Hemibrycon beni</i> Pearson, 1924	<i>Hemibrycon beni</i>
<i>Hemibrycon helleri</i> Eigenmann, 1927	<i>Hemibrycon helleri</i>
<i>Hemibrycon metae</i> Myers, 1930	<i>Hemibrycon metae</i>
<i>Hemibrycon coxeyi</i> Fowler, 1943	<i>Hemibrycon polyodon</i>
<i>Hemibrycon dentatus jabonero</i> Schultz, 1944	<i>Hemibrycon jabonero</i>
<i>Hemibrycon carrilloi</i> , Dahl 1960	<i>Hemibrycon dariensis</i>
<i>Hemibrycon surinamensis</i> Géry, 1962	<i>Hemibrycon surinamensis</i>
<i>Hemibrycon velox</i> Dahl, 1964	<i>Hemibrycon dariensis</i>
<i>Hemibrycon divisorensis</i> Bertaco, Malabarba, Hidalgo & Ortega, 2007	<i>Hemibrycon divisorensis</i>
<i>Hemibrycon pautensis</i> Román-Valencia, 2006	<i>Hemibrycon pautensis</i> <sup>2</sup>
<i>Hemibrycon microformaa</i> Román-Valencia & Ruiz-C., 2007	<i>Hemibrycon microformaa</i> <sup>2</sup>
<i>Hemibrycon</i> n. sp. 1	new species
<i>Hemibrycon</i> n. sp. 2	new species
<i>Hemibrycon</i> n. sp. 3	new species
<i>Hemibrycon</i> n. sp. 4	new species
<i>Hemibrycon</i> n. sp. 5	new species





Table 2. Continue.

	1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 3 3 4 4 4 4																																																			
	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	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
<i>Knodus meridae</i>	1	1	3	0	1	1	0	3	2	1	1	2	0	1	1	2	1	3	1	0	1	0	2	1	1	1	0	1	1	1	1	1	0	1	0	0	1	0	0	1	0	0	1	0	0							
<i>Landonia latidens</i>	1	1	2	0	1	1	1	3	?	?	1	0	0	1	2	2	1	3	?	?	1	0	2	1	2	3	1	1	0	1	0	0	0	1	2	?	1	2	0	1	1	0	0	0	0							
<i>Mimagoniates rheocharis</i>	1	1	1	0	0	1	1	2	0	0	1	1	0	0	1	0	1	0	0	2	0	0	0	0	2	2	1	1	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0					
<i>Nematobrycon palmeri</i>	1	0	2	0	0	1	0	2	0	0	0	0	1	1	0	1	1	1	0	1	0	0	0	0	1	3	1	1	0	1	1	1	0	1	1	?	0	0	1	1	1	0	0	0	0	0						
<i>Nematocharax venustus</i>	1	0	3	0	1	0	0	2	2	0	0	0	1	1	0	2	1	0	1	0	0	0	2	1	1	3	1	1	1	1	1	1	0	1	0	0	0	0	1	2	1	0	0	0	0	0						
<i>Odontostilbe fugitiva</i>	2	?	?	?	1	2	2	3	2	1	1	1	0	1	1	1	1	3	1	0	1	1	2	1	1	3	1	1	0	1	1	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0					
<i>Othonocheirodus sp.</i>	2	?	?	?	1	0	2	3	1	0	1	0	0	1	2	0	0	3	1	1	1	0	1	0	0	3	1	1	0	1	1	0	0	1	0	0	1	0	0	1	2	0	1	0	0	0						
<i>Piabina argentea</i>	0	0	1	0	0	1	1	3	0	0	0	1	0	1	1	2	1	2	0	2	0	2	2	0	0	1	0	1	0	1	1	1	1	0	1	0	0	0	0	1	2	1	0	0	0	0						
<i>Poptella brevispina</i>	1	0	2	0	0	1	0	3	0	0	0	1	0	0	1	2	1	0	0	1	0	0	0	0	1	0	2	1	1	1	0	1	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0					
<i>Pseudochalceus lineatus</i>	1	0	1	0	0	1	0	2	1	0	1	0	1	1	0	2	1	0	0	1	0	0	0	0	1	3	2	1	0	1	1	1	1	1	1	1	?	0	2	1	1	1	0	0	0	0						
<i>Rachoviscus crassiceps</i>	2	?	?	?	?	0	0	0	1	3	0	1	0	1	1	0	2	1	0	0	2	0	1	0	0	2	3	0	1	0	1	0	0	0	1	2	1	0	2	0	2	0	0	0	0	0						
<i>Rachoviscus graciliceps</i>	2	?	?	?	?	0	0	0	2	3	0	0	0	1	0	2	1	0	0	2	0	0	0	0	2	3	0	1	0	1	1	0	0	1	2	1	0	2	0	2	0	0	0	0	0	0						
<i>Rhoadsia altipinna</i>	2	?	?	?	1	2	2	1	2	1	0	0	?	1	0	1	1	0	1	0	0	0	0	0	1	2	2	0	0	1	1	1	0	1	1	?	0	0	?	?	?	1	0	0	0	0						

Table 2. Continue.

	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	7	8	8	8	8	8	8			
	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	1	2	3	4	5	6	7	8	9	0	1	2	3	4
<i>Hemibrycon boQUIAE</i>	1	1	0	0	0	1	1	2	0	0	0	0	0	1	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	1	0	1	1	2	0	1	0	0	0	0	1	
<i>Hemibrycon dariensis</i>	1	1	0	0	0	1	1	2	1	0	1	0	0	1	0	1	1	0	0	1	1	1	0	1	0	0	0	1	0	1	1	2	0	1	0	0	0	0	0	0	1	
<i>Hemibrycon dentatus</i>	1	1	0	0	0	1	1	2	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	1	0	1	1	2	0	1	0	0	0	0	0	1	
<i>Hemibrycon divisorensis</i>	1	1	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1	0	1	1	0	0	1	1	0	1	0	0	0	0	0	1	1	2	0	1	0	0	0	0	1	
<i>Hemibrycon helleri</i>	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	1	0	0	0	1	0	1	1	2	0	1	0	0	0	0	0	0	1		
<i>Hemibrycon huambonicus</i>	0	1	0	0	0	1	1	2	0	0	0	0	0	1	0	1	1	0	1	1	0	0	1	1	0	1	0	1	0	1	0	2	1	0	1	0	0	0	0	1		
<i>Hemibrycon jabonero</i>	1	1	0	0	0	1	1	2	0	0	0	0	0	1	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	0	1	1	2	0	1	0	0	0	0	1		
<i>Hemibrycon jelskii</i>	1	1	0	0	0	1	1	2	0	0	0	0	0	1	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	1	0	1	1	2	0	1	0	0	0	1		
<i>Hemibrycon metae</i>	1	1	0	0	0	1	1	2	0	0	0	0	0	1	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	1	0	2	0	2	0	1	0	0	0	1		
<i>Hemibrycon polyodon</i>	0	1	0	0	0	1	1	2	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	0	1	0	1	0	0	0	1	1	1	0	1	0	0	0	0	1		
<i>Hemibrycon surinamensis</i>	1	1	0	0	0	1	1	0	1	0	1	0	0	1	0	1	1	0	0	1	1	0	1	0	0	0	0	0	0	1	1	2	0	1	0	0	1	0	1			
<i>Hemibrycon taeniurus</i>	1	0	0	0	1	1	2	0	0	0	0	0	1	0	1	1	0	1	1	0	0	1	1	0	1	0	1	0	0	0	2	1	0	1	0	0	0	0	1			
<i>Hemibrycon n. sp. 1</i>	0	1	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Hemibrycon n. sp. 2</i>	0	1	0	0	0	1	1	2	1	0	1	0	0	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	1	0	1	1	2	0	1	0	0	1	0	1		
<i>Hemibrycon n. sp. 3</i>	0	1	0	0	0	1	1	0	1	0	1	0	0	0	1	1	0	1	1	0	0	1	1	0	0	0	1	0	1	0	1	0	2	0	1	0	0	0	0	1		
<i>Hemibrycon n. sp. 4</i>	1	1	0	0	0	1	1	2	0	0	0	0	0	1	1	0	1	0	1	1	0	0	1	1	0	1	0	1	0	1	0	1	1	2	0	1	0	0	0	1		
<i>Hemibrycon n. sp. 5</i>	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	1	0	1	0	1	1	2	0	1	0	0	1	0	1	
<i>Aphyocharax pusillus</i>	0	1	0	0	1	1	1	1	0	2	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	1	1	1	0	0	0
<i>Astyanax jacuhiensis</i>	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	1	0	0	0	0	0	2		
<i>Astyanax aff. fasciatus</i>	0	1	0	0	1	0	1	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	1	0	0	0	0	0	1		
<i>Bryconadenos tanaothoros</i>	0	1	0	1	1	2	1	1	0	1	1	0	1	1	0	0	2	1	2	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	0	2	1	0	1	0	1	
<i>Brycon pesu</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	0	0	0	0	0	0	0	0	0	0	0	
<i>Bryconops melanurus</i>	0	0	0	1	1	0	2	2	1	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	1	1	0	0	0	0	
<i>Bryconamericus exodon</i>	1	1	0	0	2	1	1	1	0	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	0	0	1	2	0	0	0	2	1	0	0	0	0	0	
<i>Bryconamericus peruanus</i>	1	1	0	0	2	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	1	1	0	1	0	0	0	1	0	2	0	2	1	1	0	0	1	0	1
<i>Bryconamericus sp.</i>	1	1	0	0	1	1	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	1	1	0	1	0	0	0	1	0	2	1	2	1	1	0	0	1	0	1	
<i>Carlastyanax aurocaudatus</i>	0	1	0	0	2	1	1	0	0	0	1	1	0	0	1	1	0	2	2	2	1	0	0	1	0	1	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	
<i>Charax stenopterus</i>	0	1	1	1	1	0	1	0	1	1	1	1	1	0	0	0	1	0	2	1	1	0	0	0	0	1	1	0	0	0	1	1	0	1	2	1	0	0	0	1	0	3
<i>Cyanocharax alburnus</i>	0	1	0	0	1	2	1	1	1	0	0	0	0	0	1	2	0	1	1	0	0	0	1	1	0	1	0	1	0	0	0	2	0	2	1	2	1	0	1	1	0	
<i>Diapoma speculiferum</i>	0	1	0	1	0	1	0	2	1	0	1	2	0	1	0	0	2	1	1	1	0	0	0	1	1	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Hollandichthys multifasciatus</i>	0	1	0	0	1	0	2	0	1	1	0	1	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	2	1	0	0	2	0	2	1	0	1	
<i>Hysteronotus megalostomus</i>	0	1	0	1	0	2	1	2	1	0	1	1	0	1	1	0	1	1	2	1	0	0	0	1	1	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	

Table 2. Continue.

	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	7	7	7	7	8	8	8	8	8				
	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	1	2	3	4	5	6	7	8	9	0	1	2	3	4				
<i>Knodus meridae</i>	0	1	0	0	0	2	1	1	1	0	0	1	0	0	0	0	1	2	1	1	0	0	0	1	1	0	0	0	1	1	1	0	1	0	0	1	2	1	0	1	0	0				
<i>Landonia latidens</i>	0	1	0	0	1	0	1	1	1	0	1	1	0	1	0	1	0	1	0	0	0	0	0	1	0	0	1	0	1	1	1	0	0	2	1	2	1	2	0	0	1	0	1			
<i>Mimagoniates rheocharis</i>	0	1	0	1	0	2	1	1	1	0	1	1	1	?	0	0	0	0	1	0	0	0	0	1	?	1	1	0	0	1	?	?	2	0	2	1	1	1	0	0	1	2				
<i>Nematobrycon palmeri</i>	0	0	0	0	1	0	1	2	1	0	1	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	1	1	?	1	1	0	0	1	2	1	0	0	0	1	1	2				
<i>Nematocharax venustus</i>	0	1	1	0	1	0	0	1	1	0	1	1	1	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	2	1	1	0	0	1	0	2	
<i>Odontostilbe fugitiva</i>	0	1	0	0	1	1	1	1	1	0	1	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	2	1	2	1	1	0	0	0	0	1	0	0	1		
<i>Othonocheirodus sp.</i>	0	1	0	0	0	2	2	1	1	0	0	1	0	0	0	0	2	2	1	1	0	0	0	1	1	0	0	0	1	1	1	0	2	1	2	1	1	0	0	1	0	0	1	0	0	
<i>Piabina argentea</i>	0	1	0	0	0	2	1	1	1	0	0	1	1	0	0	0	2	2	1	2	0	0	0	1	1	0	0	0	1	0	1	0	2	0	0	0	2	0	1	1	0	0	1	0	0	
<i>Poptella brevispina</i>	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	1	0	1	1	2	1	0	0	0	0	0	2		
<i>Pseudochalceus lineatus</i>	0	1	0	0	1	0	0	0	1	1	0	1	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	1	1	2	1	0	0	0	1	1
<i>Rachoviscus crassiceps</i>	0	0	1	0	1	1	0	1	0	0	1	1	1	0	0	1	1	0	1	1	0	0	0	1	0	0	1	0	0	0	1	0	1	1	2	1	0	0	0	0	2	0	0	2	0	
<i>Rachoviscus graciliceps</i>	0	0	1	0	1	1	0	1	0	0	1	1	1	0	0	1	1	0	1	1	0	0	0	1	0	0	1	0	0	0	1	0	1	1	2	1	0	0	0	0	2	1	0	0	2	1
<i>Rhoadsia altipinna</i>	0	1	0	0	1	0	2	1	1	0	0	1	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	1	1	?	0	2	1	0	0	0	0	0	?	

Table 2. Continue.

	1 1																																								
	8	8	8	8	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9																	
	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	1	2	3												
<i>Hemibrycon boQUIAE</i>	0	0	0	1	1	0	0	1	1	2	0	1	1	0	0	0	0	0	3	1	1	0	1	1	0	0	0	0	1	0	0	1	1	0	1	1	0	0	0		
<i>Hemibrycon dariensis</i>	0	0	0	1	1	0	0	1	1	2	0	1	1	0	0	0	0	0	3	1	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	1	0	1	1	0	0
<i>Hemibrycon dentatus</i>	0	0	0	1	1	0	0	1	1	2	0	0	1	0	0	0	0	0	3	1	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	1	0	1	1	0	0
<i>Hemibrycon divisorensis</i>	0	0	0	1	1	0	0	1	1	2	0	1	2	0	0	0	0	0	2	1	1	0	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0	
<i>Hemibrycon helleri</i>	0	0	0	1	0	0	0	1	1	2	0	1	1	0	0	0	1	0	4	1	1	0	0	1	0	0	0	2	0	1	1	1	0	1	1	0	0	0	0		
<i>Hemibrycon huambonicus</i>	0	0	0	1	1	0	0	1	1	2	0	1	1	0	0	0	0	4	1	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	1	0	1	1	0	0	
<i>Hemibrycon jABONERO</i>	0	0	0	1	1	0	0	1	1	2	0	1	1	0	0	1	0	4	1	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	1	0	1	1	0	0	
<i>Hemibrycon jelskii</i>	0	0	0	1	1	0	0	1	1	2	0	1	1	0	0	0	0	2	1	1	0	1	1	0	0	0	2	0	0	1	1	0	1	1	0	1	1	0	0	0	
<i>Hemibrycon metae</i>	0	0	0	1	1	0	0	1	1	2	0	1	1	0	0	0	0	3	1	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	1	0	1	1	0	0	
<i>Hemibrycon polyodon</i>	0	0	0	1	1	0	0	1	1	2	0	1	1	0	0	0	0	4	1	1	0	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0	
<i>Hemibrycon surinamensis</i>	0	0	0	1	1	0	0	1	1	2	0	1	1	0	0	0	0	2	1	1	0	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0		
<i>Hemibrycon taeniurus</i>	0	0	1	1	0	0	1	1	2	0	1	1	0	0	0	0	3	1	1	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0	
<i>Hemibrycon n. sp. 1</i>	0	0	1	1	0	0	0	1	1	2	0	?	?	0	0	0	0	3	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0		
<i>Hemibrycon n. sp. 2</i>	0	1	0	1	0	0	0	1	1	2	0	1	1	0	0	0	0	4	1	1	0	1	1	0	0	0	0	1	0	1	1	1	0	1	1	0	1	0	0	0	
<i>Hemibrycon n. sp. 3</i>	0	0	0	1	0	0	0	1	1	2	0	1	0	0	0	0	0	4	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Hemibrycon n. sp. 4</i>	0	0	0	1	1	0	0	1	1	2	0	1	1	0	0	0	0	4	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Hemibrycon n. sp. 5</i>	0	0	0	1	1	0	0	1	1	2	0	1	1	0	0	0	0	4	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Aphyocharax pusillus</i>	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	1	3	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Astyanax jacuhiensis</i>	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	1	1	0	0	1	1	0	1	1	0	1	1	0	0	
<i>Astyanax aff. fasciatus</i>	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Bryconadenos tanaothoros</i>	0	0	1	1	0	0	1	0	0	0	0	2	1	0	1	0	1	2	1	0	0	0	1	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	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Bryconops melanurus</i>	0	1	1	1	1	0	0	0	?	0	0	0	1	0	0	0	2	0	0	0	0	1	0	0	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Bryconamericus exodon</i>	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	3	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Bryconamericus peruanus</i>	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0	1	0	4	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Bryconamericus sp.</i>	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	3	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Carlastyanax aurocaudatus</i>	0	0	1	1	0	0	1	0	0	2	0	0	?	?	?	0	0	1	1	1	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Charax stenopterus</i>	1	1	1	1	2	0	0	0	?	0	0	0	1	0	0	0	1	0	1	1	1	1	?	1	0	1	?	?	0	0	0	0	0	0	0	0	0	0	0		
<i>Cyanocharax alburnus</i>	0	0	1	1	0	0	0	0	0	0	0	2	1	0	0	0	3	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Diapoma speculiferum</i>	0	0	1	1	1	0	1	1	0	2	1	0	1	1	0	0	1	3	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Hollandichthys multifasciatus</i>	0	0	1	0	1	1	0	0	0	1	0	0	1	1	0	0	1	2	1	1	0	1	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Hysteronotus megalostomus</i>	0	0	1	1	1	0	0	1	0	2	1	0	0	1	0	0	0	?	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	



**Table 3.** Specimens of *Hemibrycon* species with ovaries histological examined.

Species	Museum Number	Sex	Standard length (mm)
<i>Hemibrycon dariensis</i>	USNM 327221	Mature female	72.3
<i>Hemibrycon huambonicus</i>	ROM 55406	Mature female	85.8
<i>Hemibrycon jaborero</i>	USNM 121456	Mature female	88.1
<i>Hemibrycon jelskii</i>	MCP 35022	Immature female?	41.8
	MUSM 26785	Mature female	96.9
<i>Hemibrycon metae</i>	USNM 228563	Immature female?	43.8
<i>Hemibrycon surinamensis</i>	MHNG 227928	Mature female	74.2
<i>Hemibrycon taeniurus</i>	AMNH 215239	Mature female	58.6
	MCNG 8199	Mature female	57.5
<i>Hemibrycon</i> n. sp. 3	ICNMHN 0753	Mature female	77.3
<i>Hemibrycon</i> n. sp. 4	ICNMHN 3675	Female	82.6
<i>Hemibrycon</i> n. sp. 5	MUSM 26299	Mature female	75.8

**Table 4.** Specimens of *Hemibrycon* species with testes and gill arch analyzed under scanning electron microscope.

Species	Museum Number	Sex	Standard length (mm)	Gill gland	Sperm nuclei
<i>Hemibrycon dariensis</i>	USNM 327266	Male	57.5	Present	Spherical
	USNM 327221	Male	63.8	Present	Spherical
<i>Hemibrycon divisorensis</i>	MUSM 28040	Male	68.4	Absent	Spherical
	MUSM 28040	Male	62.7	Absent	Spherical
<i>Hemibrycon helleri</i>	ANSP 180775	Male	53.3	Present	Spherical
<i>Hemibrycon huambonicus</i>	USNM 086794	Male	44.7	Present	Spherical
<i>Hemibrycon jaborero</i>	USNM 121456	Male	76.6	Present	Spherical
<i>Hemibrycon jelskii</i>	MUSM 19562	paratype Male	57.1	Present	Spherical
	MUSM 19145	Male	63.1	Present	Spherical
	MCP 35022	Male	44.8	Present	Spherical
<i>Hemibrycon metae</i>	MCNG 5646	Male	44.3	Present	Spherical
	USNM 228563	Male	50.3	Present	Spherical
	MCNG 17035	Male	42.4	Present	Spherical
<i>Hemibrycon surinamensis</i>	MHNG 227928	Male	56.1	Present	Spherical
<i>Hemibrycon taeniurus</i>	USNM 290413	Male	58.1	Present	Spherical
<i>Hemibrycon</i> n. sp. 2	ICNMHN 6439	Male	40.4	Absent	Spherical
<i>Hemibrycon</i> n. sp. 3	ICNMHN 0753	Male	74.8	Absent	Spherical
<i>Hemibrycon</i> n. sp. 4	ANSP 93221	Male	75.1	Present	Spherical

**Table 5.** Characters and possible states assigned for each hypothesized Clade and terminal taxon. \*Characters ambiguous, optimized with ACCTRAN procedures.

Clade or taxon	Character	State	Consistency Index
<i>Brycon pesu</i>	18*	1	0.33
Clade 1	1*	1	0.25
	8*	3	0.20
	9*	1	0.23
	15*	1	0.33
	16*	1	0.16
	25*	1	0.22
	26*	2	0.17
	28*	1	0.25
	30*	1	0.10
	32*	1	0.14
	34*	1	0.50
	39*	1	0.14
	40*	1	0.33
	41*	1	0.12
	47*	1	0.16
	49*	1	0.20
	51*	1	0.14
	58*	1	0.11
	59*	1	0.15
	61*	1	0.28
	62*	1	0.33
	71*	1	0.10
	77*	2	0.22
	78*	1	0.25
	87*	1	0.16
	88*	1	0.16
	89*	1	0.20
	98*	1	0.12
	108*	1	0.66
	117*	1	0.11
<i>Bryconops melanurus</i>	3*	3	0.16
	11	1	0.11
	22	2	0.25
	25*	2	0.22
	38	2	0.20
	46	1	0.25
	49	2	0.20
	50	2	0.16
	52	1	0.33
	60	1	0.25
	79	1	0.25
	86	1	0.20
	103	2	0.29
	111	1	0.33
	119	1	0.14
Clade 2	17	1	0.18
	20	1	0.23
	27*	1	0.16
	44	1	0.25
	53*	1	0.14
	66	1	0.33
	69	1	0.12
	73*	1	0.11

**Table 5.** Continue.

	104	1	0.50
	120	1	0.50
Clade 3	9*	0	0.23
	71*	0	0.10
	76	1	0.16
	84*	1	0.23
	88*	0	0.16
	94*	1	0.25
	102	1	0.25
	103	0	0.29
	105	1	0.16
	106	1	0.12
	107*	1	0.11
	113*	1	0.16
Clade 4	6	1	0.33
	12	1	0.22
	16*	2	0.16
	27*	2	0.17
	31	0	0.12
	60	1	0.25
	61	0	0.28
	62	0	0.33
	75	1	0.16
	84*	2	0.23
	97	1	0.22
	112*	1	0.33
<i>Poptella brevispina</i>	26	0	0.17
	51	0	0.14
	53*	0	0.14
	59*	0	0.15
	71*	1	0.10
	85	1	0.50
	91	1	0.14
	92	1	0.16
	100	1	0.20
	117*	0	0.11
Clade 5	9*	1	0.23
	22	1	0.25
	37	1	0.33
	69	0	0.12
	73*	0	0.11
	94*	0	0.25
	98	0	0.12
	116	1	0.11
	119	1	0.14
<i>Astyanax jacuhiensis</i>	12	2	0.22
	32	0	0.14
	41	0	0.12
	47	0	0.16
	101	1	0.16
<i>Astyanax</i> aff. <i>fasciatus</i>	3	3	0.14
	16*	1	0.16
	20	0	0.23
	50	1	0.16
	84*	1	0.23
	102	0	0.25
	103	1	0.29
	106	0	0.12



**Table 5.** Continue.

	112*	0	0.33
	113*	0	0.16
Clade 6	1*	2	0.25
	3*	1	0.14
	8	1	0.20
	14	1	0.16
	15	0	0.33
	20*	2	0.23
	26	3	0.17
	29	0	0.16
	35*	1	0.33
	40*	2	0.33
	54	1	0.40
Clade 7	109	1	0.25
	1*	1	0.25
	6	1	0.33
	8*	2	0.20
	13	1	0.25
	20*	1	0.23
	40*	1	0.33
	59*	0	0.15
	70	1	0.50
	82	1	0.09
	83	1	0.28
	90	1	0.50
	107*	0	0.11
	113*	0	0.16
	116	1	0.11
<i>Nematobrycon palmeri</i>	3*	2	0.14
	18	1	0.33
	44	0	0.25
	50	2	0.16
	57	1	0.16
	72	1	0.25
	84	2	0.23
	94*	0	0.25
	101	1	0.16
	117*	0	0.11
<i>Pseudochalceus lineatus</i>	119	1	0.14
	9	1	0.23
	11*	1	0.11
	16	2	0.16
	27*	2	0.16
	33	1	0.20
	38	2	0.20
	49	0	0.20
	52	1	0.33
	53	0	0.14
	75	1	0.16
	87	0	0.16
	89	0	0.20
	103	1	0.29
Clade 8	114	1	0.50
	14	0	0.16
	17	0	0.18
	23	2	0.33
	26	0	0.17
	28	0	0.25

**Table 5.** Continue.

	32	0	0.20
	42	1	1.00
	52	1	0.33
	55	1	0.20
	63	1	1.00
	66	0	0.33
<i>Charax stenopterus</i>	8*	0	0.20
	9	3	0.23
	11*	1	0.11
	18	3	0.33
	20	3	0.23
	21	1	0.25
	24	1	0.16
	26*	2	0.17
	27*	2	0.16
	31	0	0.12
	45	1	0.25
	46	1	0.25
	58	0	0.11
	61	2	0.28
	68	1	0.50
	74	1	0.25
	82	1	0.09
	84	3	0.23
	85	1	0.50
	86	1	0.20
	88	1	0.16
	89	2	0.20
	111	1	0.33
	122	1	0.33
<i>Hollandichthys multifasciatus</i>	1*	1	0.25
	16	0	0.16
	38	2	0.20
	39	0	0.14
	49	2	0.20
	53	0	0.14
	81	2	0.66
	83	2	0.28
	90	1	0.50
	97	1	0.22
	103	2	0.29
	106	0	0.12
	114	1	0.50
	115	2	0.40
	116	1	0.11
	117	0	0.11
	123	1	0.20
Clade 9	9*	3	0.23
	16	2	0.16
	25	2	0.22
	27	0	0.16
	32	0	0.14
	35	2	0.33
	36	1	1.00
	38	2	0.20
	39	0	0.14
	41	0	0.12
	44	0	0.25

**Table 5.** Continue.

	45	1	0.25
	48	1	0.25
	49	0	0.20
	50	1	0.16
	51	0	0.14
	55	1	0.20
	75	1	0.16
	83	2	0.28
	97	2	0.22
	101	1	0.16
	103	4	0.29
	105	0	0.16
	106	0	0.12
	107*	0	0.11
	113	0	0.16
	115	1	0.40
	117*	0	0.11
	123	1	0.20
<i>Rachoviscus crassiceps</i>	11	1	0.11
	13	1	0.25
	22	1	0.25
	31	0	0.12
	84	0	0.23
<i>Rachoviscus graciliceps</i>	8*	2	0.20
Clade 10	3	3	0.14
	5*	1	0.50
	6*	2	0.33
	7	2	0.33
	9*	2	0.23
	10*	1	0.25
	19	1	0.50
	20	0	0.23
	23*	2	0.33
	24*	1	0.16
	35*	0	0.33
	50	1	0.16
	59*	0	0.15
	69	0	0.12
	70	1	0.50
	79*	1	0.25
	88	1	0.16
	91*	1	0.14
	96	1	0.33
	99	1	0.33
	109*	0	0.25
	112	1	0.33
	122*	1	0.33
<i>Nematocharax venustus</i>	1*	1	0.25
	6*	0	0.33
	7*	0	0.33
	8*	2	0.20
	10*	0	0.25
	13	1	0.25
	16	2	0.16
	29	1	0.16
	45	1	0.25
	49	0	0.20
	55	1	0.20

**Table 5.** Continue.

	82	1	0.09
	84	2	0.23
	92	1	0.16
	98	0	0.12
	107*	0	0.11
	108	2	0.66
	116	1	0.11
	119	1	0.14
	122*	0	0.33
<i>Odontostilbe fugitiva</i>	8	3	0.20
	11	1	0.11
	12	1	0.22
	15	1	0.33
	18	3	0.33
	21	1	0.25
	22	1	0.25
	40	1	0.33
	41	0	0.12
	48	1	0.25
	54	0	0.40
	56	1	0.12
	58	0	0.11
	73	0	0.11
	75	2	0.16
	89	0	0.20
	91*	0	0.14
	110	1	0.16
	111	1	0.33
<i>Rhoadsia altipinna</i>	23*	0	0.33
	24	0	0.16
	26	2	0.17
	27*	2	0.16
	28	0	0.25
	35*	1	0.33
	49	2	0.20
	53	0	0.14
	59	1	0.15
	60	1	0.25
	61*	0	0.28
	74	1	0.25
	76	0	0.16
	79*	0	0.25
	87	0	0.16
	94*	0	0.25
	103	1	0.29
	109*	1	0.25
	113*	2	0.16
	117*	0	0.11
Clade A	2	1	0.33
	41*	0	0.12
	48	2	0.25
	50*	1	0.16
	67	1	0.33
	75	2	0.16
	79	2	0.25
	80	1	0.16
	82*	1	0.09
	89*	0	0.20

**Table 5.** Continue.

	110*	1	0.16
<i>Cyanocharax alburnus</i>	8	2	0.20
	22	1	0.25
	29	0	0.16
	53*	0	0.14
	59	2	0.15
	73*	0	0.11
	83	1	0.28
	97	2	0.22
	117*	0	0.11
Clade B	6	1	0.33
	12	1	0.22
	27*	0	0.16
	37	1	0.33
	39	0	0.14
	47	0	0.16
	58	0	0.11
	98*	0	0.12
	119	1	0.14
Clade C	11	1	0.11
	14	1	0.16
	16	2	0.16
	25*	0	0.22
	54	1	0.40
	59*	0	0.15
	77	0	0.22
	78*	0	0.25
<i>Bryconamericus exodon</i>	4	1	0.16
	43	1	0.25
	73*	0	0.11
	74	1	0.25
	82	0	0.09
	94*	1	0.25
	99	1	0.33
	104	0	0.50
	105	1	0.16
	107	1	0.11
	120	0	0.50
Clade D	12	2	0.22
	23	2	0.33
	53*	0	0.14
	60	2	0.25
	69	0	0.12
	102	1	0.25
	103	2	0.29
	106*	1	0.12
Clade E	5	1	0.50
	18	3	0.33
	19	1	0.50
	21	1	0.25
	24*	1	0.16
	26*	1	0.17
	72	1	0.25
	78*	1	0.25
	92	1	0.16
	97*	1	0.22
<i>Knodus meridae</i>	3	3	0.14
	9	2	0.23

**Table 5.** Continue.

	10	1	0.25
	20	0	0.23
	25*	1	0.22
	59	1	0.15
	75	1	0.16
	88	0	0.16
	100	1	0.20
	119	0	0.14
Clade F	7*	1	0.33
	12	0	0.22
	15	2	0.33
	26	3	0.17
	27	1	0.16
	29	0	0.16
	32	0	0.14
	38	2	0.20
	76	1	0.16
	77	2	0.22
	80*	0	0.16
	123*	1	0.20
<i>Landonia latidens</i>	25*	2	0.22
	31	0	0.12
	35	2	0.33
	41	1	0.12
	47	1	0.16
	48	0	0.25
	53	1	0.14
	56	1	0.12
	58	1	0.11
	60	1	0.25
	61	0	0.28
	62	0	0.33
	67	0	0.33
	69	1	0.12
	73	0	0.11
	84	1	0.23
	87	0	0.16
	89	1	0.20
	95	1	0.50
	106*	0	0.12
	110	0	0.16
	117	0	0.11
<i>Othonocheirodus</i> sp.	1	2	0.25
	6	0	0.33
	7*	2	0.33
	16	0	0.16
	17	0	0.18
	23	1	0.33
	24*	0	0.16
	49	2	0.20
	59	2	0.15
	79	1	0.25
	93	1	0.33
	103	3	0.29
Clade G	22	2	0.25
	62	2	0.33
	71*	0	0.10
	91	1	0.14

**Table 5.** Continue.

	98*	1	0.12
<i>Bryconadenos tanaothoros</i>	10	1	0.25
	14	0	0.16
	25*	1	0.22
	46	1	0.25
	53*	1	0.14
	56	1	0.12
	57	1	0.16
	74	1	0.25
	75	1	0.16
	77	1	0.22
	84	1	0.23
	97	2	0.22
	100	1	0.20
	106*	0	0.12
	116	1	0.11
	123	1	0.20
Clade H	2	0	0.33
	9	0	0.23
	18	2	0.33
	20	2	0.23
	29	0	0.16
	39*	1	0.14
	40*	2	0.33
	41*	1	0.12
	55	1	0.20
	59*	2	0.15
	80*	0	0.16
	81*	1	0.66
<i>Piabina argentea</i>	1	0	0.25
	3	1	0.14
	7	1	0.33
	11	0	0.11
	12	1	0.22
	26	1	0.17
	37	0	0.33
	71*	1	0.10
	86	1	0.20
Clade I	98*	0	0.12
	16	0	0.16
	28	0	0.25
	35	2	0.33
	58	1	0.11
	64	1	1.00
	66	0	0.33
	79*	0	0.25
	99*	1	0.33
	103	1	0.29
	105	1	0.16
	107	1	0.11
	110	0	0.16
	117	0	0.11
	119	0	0.14
<i>Aphyocharax pusillus</i>	1	2	0.25
	8	1	0.20
	12	0	0.22
	14	0	0.16
	18	3	0.33

**Table 5.** Continue.

	21	1	0.20
	24	1	0.16
	25	1	0.22
	26	3	0.17
	41*	0	0.12
	47	1	0.16
	48*	1	0.25
	53	2	0.14
	59*	0	0.15
	60	0	0.25
	62	1	0.33
	67	0	0.33
	79*	1	0.25
	80	1	0.16
	82	0	0.09
	88	0	0.16
	101	1	0.16
	103*	3	0.29
	106*	0	0.12
<i>Carlastyanax aurocaudatus</i>	17	2	0.18
	20	0	0.23
	22	0	0.25
	23	0	0.33
	27	1	0.16
	32	0	0.14
	33	1	0.20
	39*	0	0.14
	40*	1	0.33
	51	0	0.14
	61	2	0.28
	63	2	1.00
	69	1	0.12
	75	0	0.16
	81	0	0.66
	83	2	0.28
	84	1	0.23
	94	2	0.25
	108	2	0.66
	113	1	0.16
	115	1	0.40
	116	1	0.11
Clade J	15*	0	0.33
	17	0	0.18
	18	1	0.33
	31*	0	0.12
	38	1	0.20
	48*	1	0.25
	50*	0	0.16
	71*	0	0.10
	79	1	0.25
	80*	0	0.16
	84*	1	0.23
	89*	1	0.20
	92*	1	0.16
	94*	2	0.25
	110*	0	0.16
	113*	1	0.16
Clade K	11	1	0.11



**Table 5.** Continue.

	26	1	0.17
	43	1	0.25
	53*	0	0.14
	57	1	0.16
	92*	0	0.16
	94*	0	0.25
	101	1	0.16
	116	1	0.11
<i>Bryconamericus peruanus</i>	8	2	0.20
	27	1	0.16
	48*	2	0.25
	91	1	0.14
	93	1	0.33
	103	4	0.29
<i>Bryconamericus</i> sp.	12	2	0.22
	17	1	0.18
	76	1	0.16
	98*	1	0.12
	105	1	0.16
	107	1	0.11
Clade L	15*	1	0.33
	46	1	0.25
	50	2	0.16
	54*	1	0.40
	56	1	0.12
	60*	1	0.25
	80*	1	0.16
	83	1	0.28
	84*	0	0.23
	91*	1	0.14
	95	1	0.50
	98*	1	0.12
	123	1	0.20
<i>Diapoma speculiferum</i>	22	2	0.25
	49	0	0.20
	54*	2	0.40
	59	2	0.15
	77	1	0.22
	97	1	0.22
	102	1	0.25
	110	1	0.16
	113*	0	0.16
Clade M	3	1	0.14
	9	0	0.23
	18	0	0.33
	20	2	0.23
	25	2	0.22
	48*	2	0.25
	68	1	0.50
	72	1	0.25
	84*	2	0.23
	103*	5	0.29
<i>Hysteronotus megalostomus</i>	2	0	0.33
	14	1	0.16
	31*	1	0.12
	32	0	0.14
	38	2	0.20
	39	1	0.14

**Table 5.** Continue.

	57	1	0.16
	61	2	0.28
	91*	0	0.14
<i>Mimagoniates rheocharis</i>	7	1	0.33
	8	2	0.20
	11	1	0.11
	16	0	0.16
	17	1	0.18
	27	1	0.16
	29*	0	0.16
	34	0	0.50
	50	1	0.16
	55	1	0.20
	59	0	0.15
	60	0	0.25
	62	0	0.33
	82	0	0.09
	86	1	0.20
	92*	0	0.16
	100	1	0.20
	109	1	0.25
	113	2	0.16
<i>Hemibrycon</i> Clade	8	2	0.20
	13	1	0.25
	16	2	0.16
	31*	1	0.12
	38	2	0.20
	65*	1	1.00
	75	1	0.16
	78	0	0.25
	89*	0	0.20
	93	1	0.33
	96*	1	0.33
	105	1	0.16
<i>Hemibrycon</i> n. sp. 1	4	1	0.16
	45	1	0.25
	49	0	0.20
	72	1	0.25
	77	1	0.25
	83	1	0.28
	113*	0	0.16
Clade H1	33	1	0.20
	58	1	0.11
	71*	1	0.10
	82*	0	0.09
	87	0	0.16
	103	4	0.29
	116	1	0.11
<i>Hemibrycon</i> n. sp. 3	3	3	0.14
	17	1	0.18
	69	0	0.12
Clade H2	26	1	0.17
	31*	0	0.12
	50	2	0.16
	76	1	0.16
	97	1	0.22
	107	1	0.11
<i>Hemibrycon</i> n. sp. 2	71*	0	0.10

**Table 5.** Continue.

	82*	1	0.09
	86	1	0.20
	115	1	0.40
Clade H3	51	0	0.14
	53	0	0.14
	56	1	0.12
	89	1	0.20
<i>Hemibrycon</i> n. sp. 4	3	3	0.14
	20	0	0.23
	43	1	0.25
	57	1	0.16
	58	0	0.11
Clade H4	9	0	0.23
	17	1	0.18
	38	1	0.20
<i>Hemibrycon huambonicus</i>	4	1	0.16
	8	1	0.20
	17	0	0.18
	75	2	0.16
	77	1	0.22
<i>Hemibrycon polyodon</i>	26	2	0.17
	56	0	0.12
	73	0	0.11
	77	1	0.22
	116	0	0.11
Clade H5	8	1	0.20
	38	2	0.20
	50	0	0.16
	107	0	0.11
	115	1	0.40
<i>Hemibrycon helleri</i>	69	0	0.12
	89	0	0.20
	101	1	0.16
	113	2	0.16
<i>Hemibrycon</i> n. sp. 5	3	3	0.14
	4	1	0.16
	82	1	0.09
Clade H6	26	2	0.17
	43	1	0.25
	71	0	0.10
	103	3	0.29
<i>Hemibrycon boquiae</i>	-	-	-
Clade H7	3	3	0.14
	4	1	0.16
	33	0	0.20
<i>Hemibrycon dariensis</i>	51	1	0.14
	53	1	0.14
	121	1	0.10
<i>Hemibrycon dentatus</i>	9	1	0.23
	20	0	0.23
	56	0	0.12
	96	0	0.33
<i>Hemibrycon metae</i>	4	0	0.16
	9	1	0.23
	26	1	0.17
	75	2	0.16
	76	0	0.16
Clade H8	8	1	0.20

**Table 5.** Continue.

	73	0	0.11
<i>Hemibrycon jaborero</i>	26	1	0.17
	33	1	0.20
	100	1	0.20
	103	4	0.29
Clade H9	27	1	0.16
<i>Hemibrycon taeniurus</i>	3	2	0.14
	44	0	0.25
	71	1	0.10
	75	2	0.16
	77	1	0.22
	87	1	0.16
Clade H10	17	0	0.18
	103	2	0.29
<i>Hemibrycon jelskii</i>	20	0	0.23
	73	1	0.11
	113	2	0.16
Clade H11	26	1	0.17
	50	0	0.16
	53	1	0.14
	118	1	1.00
<i>Hemibrycon divisorensis</i>	56	0	0.12
	57	1	0.16
	58	0	0.11
	97	2	0.22
<i>Hemibrycon surinamensis</i>	3	2	0.14
	51	1	0.14
	82	1	0.09

**Table 6.** Morphometric data of holotype (H) of *Hemibrycon polyodon* (BMNH 1858.7.25.41) from Guayaquil, Ecuador, and non-types from tributary of río Pastaza, río Marañon basin (KU 19978, 19992, 20004). The range includes the holotype. m, males; f, females.

	H	Non-types		
		n	Range	Mean
Standard Length (mm)	69.5	7	45.7-78.3	64.1
Percents of Standard length				
Predorsal distance	51.5	7	49.5-51.5	50.6
Prepelvic distance	40.6	7	39.9-41.9	40.7
Prepectoral distance	23.5	7	21.0-23.5	22.2
Preanal distance	55.7	7	53.7-58.0	55.7
Depth at dorsal-fin origin (m)	-	4	27.7-33.8	30.1
Depth at dorsal-fin origin (f)	30.6	3	26.0-30.6	28.3
Caudal peduncle depth	11.7	7	11.0-12.9	11.6
Caudal peduncle length	16.1	7	14.4-16.6	15.5
Anal-fin base	29.3	7	29.3-35.9	32.8
Dorsal-fin length	22.3	7	21.7-24.9	22.9
Pelvic-fin length (m)	-	4	13.1-15.5	14.7
Pelvic-fin length (f)	14.7	3	13.2-14.7	13.7
Pectoral-fin length (m)	-	4	19.9-21.3	20.6
Pectoral-fin length (f)	21.2	3	19.0-21.2	20.3
Head length	22.2	7	20.9-22.9	21.8
Percents of Head length				
Snout length	22.5	7	20.7-23.5	22.0
Upper jaw length	45.4	7	43.7-45.6	44.6
Orbital diameter	33.2	7	29.5-34.1	32.0
Interorbital width	32.1	7	32.1-35.3	33.9

**Table 7.** Morphometric data of syntypes of *Hemibrycon guppyi* (= *H. taeniurus*, BMNH 1906.6.23.13-17), and syntypes of *H. taeniurus* (ZMUC 962-963, ZMUC 966-968), and non-types of *H. taeniurus* (AMNH 215239, 215301; INHS 40083; MCNG 8199; ROM 61651; USNM 290408, 290413) from Island of Trinidad, Trinidad and Tobago. m, males; f, females.

	<i>H. guppyi</i>			<i>H. taeniurus</i>					
	Syntypes			Syntypes			Non-types		
	n	Range	Mean	n	Range	Mean	n	Range	Mean
Standard Length (mm)	5	46.3-73.4	57.5	5	33.0-50.6	42.1	26	36.9-81.8	62.4
Percents of Standard length									
Predorsal distance	5	49.5-55.5	52.0	5	51.6-55.7	53.4	26	47.6-52.4	50.6
Prepelvic distance	5	38.8-42.7	41.1	5	41.2-46.4	43.7	26	39.2-46.5	42.9
Prepectoral distance	5	22.8-23.9	23.4	5	22.0-24.2	23.0	26	20.8-24.0	22.2
Preanal distance	5	54.6-59.8	57.4	5	54.4-60.7	58.2	26	53.9-61.9	58.4
Depth at dorsal-fin origin (m)	2	31.4-32.3	31.9	3	29.4-30.8	30.0	6	28.8-33.2	30.5
Depth at dorsal-fin origin (f)	3	33.3-35.5	34.3	2	31.9-33.3	32.6	20	30.1-39.1	35.0
Caudal peduncle depth	5	11.8-12.7	12.3	5	10.0-11.2	10.6	26	10.8-12.9	11.7
Caudal peduncle length	5	12.0-14.2	13.2	5	12.7-14.0	13.3	26	11.6-15.0	13.1
Anal-fin base	5	32.0-34.9	33.2	5	31.8-34.5	33.4	26	31.7-36.2	33.9
Dorsal-fin length	5	22.5-24.4	23.3	5	22.1-24.2	23.7	26	22.2-26.1	23.9
Pelvic-fin length (m)	2	15.1-15.3	15.2	3	14.7-16.7	15.5	6	13.7-15.3	14.6
Pelvic-fin length (f)	3	13.2-15.0	14.4	2	14.1-14.5	14.3	20	12.3-15.3	14.2
Pectoral-fin length (m)	2	19.9-20.1	20.0	3	20.7-21.6	21.3	6	19.7-21.4	20.4
Pectoral-fin length (f)	3	18.3-20.5	19.5	2	21.0-21.4	21.2	20	19.0-22.2	20.6
Head length	5	21.8-23.3	22.5	5	22.9-24.7	23.8	26	21.0-23.6	22.3
Percents of Head length									
Snout length	5	23.4-26.8	24.8	5	21.8-24.5	23.0	26	19.5-24.6	22.3
Upper jaw length	5	42.7-47.9	44.5	5	45.4-50.0	47.7	26	42.5-47.3	45.6
Orbital diameter	5	33.6-38.6	36.4	5	35.0-36.8	36.1	26	29.4-37.3	32.5
Interorbital width	5	31.6-32.9	32.3	5	31.4-32.5	32.0	26	31.3-35.5	33.3

**Table 8.** Morphometric data of syntypes of *Hemibrycon jelskii* (NMW 57548, 57551, 57554) and non-types from rio Ucayali basin, Peru (ANSP180772; MUSM 2958, 17261, 19562; MHNG 218265), from rio Chaparre basin, Bolivia (MCP 35019, 35020, 35021, 35022; MZUSP 27827; MNHN 1989.1418), from rio Madre de Dios basin, Cochabamba, Bolivia (MUSM 3759, 11080, 26409, 26785; ROM 66370), from rio Huancabamba, rio Marañon basin, Peru (MUSM 2166; ROM 52240), and from rio Beni basin, Bolivia (CAS 70081; MNHN 1989.1417). m, males; f, females.

	Syntypes						Non-types											
	Rio Ucayali basin			Rio Ucayali basin			Rio Chaparre basin			Rio Madre de Dios basin			Rio Marañon basin			Rio Beni basin		
	n	Range	Mean	n	Range	Mean	n	Range	Mean	n	Range	Mean	n	Range	Mean	n	Range	Mean
Standard Length (mm)	11	57.0-101.7	77.9	17	37.4-69.0	55.7	75	36.3-75.5	50.1	37	39.2-96.9	62.5	33	52.3-87.8	70.3	14	37.2-59.1	42.4
Percents of Standard length																		
Predorsal distance	11	50.2-54.6	51.9	17	49.5-53.5	51.3	75	49.9-56.3	52.5	37	48.3-62.1	51.7	33	49.1-53.9	52.2	14	50.4-56.6	52.3
Prepelvic distance	11	39.3-43.1	41.6	17	41.8-44.1	43.1	75	41.2-47.3	44.2	37	40.0-45.6	43.4	33	41.5-45.3	43.3	14	40.8-46.8	43.4
Prepectoral distance	11	19.8-23.7	21.6	17	22.8-26.0	24.0	75	21.7-27.0	24.3	37	21.5-26.1	24.0	33	20.9-23.4	22.4	14	23.9-25.9	24.7
Preanal distance	11	55.2-60.5	58.4	17	55.7-59.7	58.0	75	54.1-63.7	59.8	37	55.0-61.5	59.0	33	55.2-61.0	58.9	14	54.8-64.5	57.9
Depth at dorsal-fin origin (m)	4	30.2-32.7	31.2	9	32.4-35.3	33.6	42	28.1-36.5	32.2	16	30.1-37.8	34.3	7	30.3-35.6	33.9	8	28.1-33.0	29.9
Depth at dorsal-fin origin (f)	7	33.7-37.9	36.0	8	30.7-36.5	34.2	33	29.8-37.6	34.6	21	32.7-38.8	35.1	26	32.4-38.7	35.8	6	30.0-34.4	32.1
Caudal peduncle depth	11	11.5-13.7	12.9	17	11.1-13.4	12.5	75	10.6-13.6	12.3	37	11.5-13.7	12.4	33	11.3-13.6	12.5	14	10.4-11.8	11.0
Caudal peduncle length	11	12.6-15.0	13.9	17	11.4-13.4	12.5	74	10.7-14.5	12.7	37	11.1-14.1	13.0	33	10.6-15.0	13.0	14	10.1-14.7	12.8
Anal-fin base	11	31.4-36.2	33.8	17	33.4-36.8	34.6	75	29.7-35.2	33.0	37	31.4-37.1	33.9	33	31.9-36.0	34.3	14	30.6-36.4	33.2
Dorsal-fin length	11	21.0-25.2	23.7	17	23.7-26.1	25.2	74	21.7-26.4	23.8	37	23.0-27.4	24.8	33	23.2-27.4	25.3	14	23.0-26.8	24.2
Pelvic-fin length (m)	4	15.1-15.4	15.2	9	14.8-17.0	15.7	42	14.3-17.3	15.4	16	14.8-17.0	15.7	7	15.0-16.1	15.5	8	14.6-17.0	15.5
Pelvic-fin length (f)	7	13.2-15.0	14.2	8	13.7-15.5	14.6	33	12.7-15.4	14.4	21	13.9-15.4	14.7	26	13.1-16.4	14.7	6	13.5-14.9	14.5
Pectoral-fin length (m)	4	20.6-21.7	21.1	9	21.2-23.0	22.0	42	20.2-23.3	21.6	16	20.5-23.2	21.9	7	20.5-22.6	22.0	8	20.0-25.0	21.6
Pectoral-fin length (f)	7	19.1-21.4	20.4	8	20.5-22.9	21.5	33	19.2-23.4	20.9	21	19.4-22.4	21.0	26	19.0-24.3	21.6	6	20.5-22.7	21.3
Head length	11	21.1-23.6	22.2	17	22.4-24.6	23.3	42	21.7-25.9	23.5	37	20.9-24.9	23.2	33	20.8-23.4	22.2	14	23.3-25.9	24.5
Percents of Head length																		
Snout length	11	21.0-24.3	22.5	17	19.5-23.9	21.2	75	19.8-25.1	22.5	37	20.2-24.8	22.3	33	19.3-24.1	21.5	14	20.7-24.3	22.5
Upper jaw length	11	43.3-49.7	46.7	17	45.6-49.4	47.4	75	42.0-52.8	45.7	37	44.5-48.8	46.5	33	40.6-46.8	43.8	14	43.7-50.1	47.2
Orbital diameter	11	26.2-31.9	28.6	17	31.2-37.2	33.2	75	27.9-39.3	33.4	37	29.6-37.9	33.8	33	30.2-34.3	31.9	14	32.6-35.5	33.5
Interorbital width	11	31.9-39.3	35.1	17	31.3-36.3	33.3	75	29.0-35.5	32.3	37	32.2-37.3	34.3	33	30.6-35.5	33.3	14	30.5-33.6	31.7

**Table 9.** Morphometric data of syntype of *Hemibrycon huambonicus* from Huambo, Peru (NMW 57531), and non-types from upper río Huallaga basin (CAS 70082, 70085, 70089, 70091-93; ICNMHN 7317), and from upper río Marañón basin (CAS 70083, 70086; ROM 55238, 55406, 55366). m, males; f, females.

	Non-types						
	Syntype	Río Huallaga basin			Río Marañón basin		
		n	Range	Mean	n	Range	Mean
Standard length (mm)	87.0	63	39.5-109.9	69.5	86	32.0-107.1	69.9
Percents of Standard length							
Predorsal distance	52.5	63	26.4-54.9	51.0	86	45.6-55.2	50.6
Prepelvic distance	43.1	63	39.6-47.0	43.5	86	38.0-46.7	42.0
Prepectoral distance	22.9	63	21.7-27.3	23.9	86	19.8-25.9	22.2
Preanal distance	55.7	63	54.1-62.2	58.0	86	51.5-61.3	56.9
Depth at dorsal-fin origin (m)	32.2	16	29.7-34.1	31.4	41	27.3-32.6	29.5
Depth at dorsal-fin origin (f)	-	47	28.9-35.8	32.0	43	29.3-34.9	31.8
Caudal peduncle depth	16.2	16	11.2-15.1	12.8	86	10.7-13.6	12.3
Caudal peduncle length	15.5	47	13.5-17.9	15.4	86	13.2-18.7	15.7
Anal-fin base	33.4	63	26.3-36.1	30.9	86	27.1-37.7	32.1
Dorsal-fin length	24.1	63	22.0-26.3	23.7	85	20.4-26.9	23.3
Pelvic-fin length (m)	16.2	16	14.1-17.3	15.2	42	14.2-17.4	15.7
Pelvic-fin length (f)	-	47	12.7-17.0	14.5	44	12.7-15.8	14.2
Pectoral-fin length (m)	22.6	16	20.8-23.4	21.8	42	18.9-23.3	20.7
Pectoral-fin length (f)	-	47	19.7-25.3	22.0	44	18.7-22.6	20.4
Head length	23.5	63	22.0-26.0	24.2	86	19.7-25.4	22.4
Percents of Head length							
Snout length	21.5	63	17.7-24.3	21.6	86	19.0-25.8	21.8
Upper jaw length	45.5	63	45.2-52.6	48.5	86	39.5-48.9	44.7
Orbital diameter	25.4	63	24.2-33.9	29.1	86	26.0-35.3	30.7
Interorbital width	35.5	63	31.0-39.2	34.5	86	28.1-39.2	33.7



**Table 10.** Morphometric data of holotype (H) of *Hemibrycon boquiae* (FMNH 56259), and paratypes (CAS 44332; FMNH 56260), and non-types from upper rio Cauca basin, Colombia (IAvHP 7762; IMCN 2495, 1076). The range includes the holotype. m, males; f, females.

	Paratypes				Non-types		
	H	n	Range	Mean	n	Range	Mean
Standard Length (mm)	43.0	12	32.7-45.0	39.3	31	57.3-93.9	73.6
Percents of Standard length							
Predorsal distance	-	-	-	-	31	48.3-53.7	50.8
Prepelvic distance	-	-	-	-	31	38.5-45.6	43.7
Prepectoral distance	-	-	-	-	31	20.5-23.1	21.7
Preanal distance	-	-	-	-	31	56.4-60.9	58.4
Depth at dorsal-fin origin (m)	-	-	-	-	10	28.4-31.7	30.3
Depth at dorsal-fin origin (f)	24.4	8	22.3-27.9	25.8	21	28.6-34.1	31.5
Caudal peduncle depth	10.0	8	9.7-11.8	10.5	31	11.0-12.9	12.1
Caudal peduncle length	14.3	4	13.8-16.6	14.9	31	12.7-16.3	14.0
Anal-fin base	-	-	-	-	31	29.0-33.7	31.7
Dorsal-fin length	-	-	-	-	31	20.6-24.4	22.6
Pelvic-fin length (m)	-	-	-	-	10	12.3-13.5	13.0
Pelvic-fin length (f)	-	-	-	-	21	9.7-13.8	12.5
Pectoral-fin length (m)	-	-	-	-	10	19.5-21.6	20.5
Pectoral-fin length (f)	-	-	-	-	21	18.6-21.4	20.0
Head length	23.2	11	22.9-25.5	23.9	31	19.9-22.1	21.2
Percents of Head length							
Snout length	21.4	11	21.4-24.2	22.8	31	18.8-24.6	21.8
Upper jaw length	46.0	10	43.3-47.5	45.6	31	40.6-50.6	43.8
Orbital diameter	34.9	11	31.0-34.9	33.0	31	27.5-32.4	30.1
Interorbital width	32.2	11	32.2-36.5	34.3	31	33.2-37.6	35.3

**Table 11.** Morphometric data of holotype (H) of *Hemibrycon dentatus* (FMNH 56253), and paratypes (CAS 39543-45; FMNH 56252-53; USNM 79175), and non-types (IMCN 282, 3036) from upper río Cauca basin, Colombia. The range includes the holotype. m, males; f, females.

	Paratypes				Non-types		
	H	n	Range	Mean	n	Range	Mean
Standard Length (mm)	76.6	19	57.7-96.0	72.9	6	68.9-100.8	87.6
Percents of Standard length							
Predorsal distance	52.2	19	49.6-54.2	51.8	6	52.1-53.4	52.8
Prepelvic distance	42.3	19	38.0-57.2	43.5	6	42.2-44.7	43.6
Prepectoral distance	24.1	19	22.0-42.2	24.4	6	21.3-23.5	22.5
Preanal distance	58.3	19	54.5-61.4	58.0	6	58.8-61.6	60.3
Depth at dorsal-fin origin (m)	-	6	27.8-30.9	29.3	-	-	-
Depth at dorsal-fin origin (f)	30.8	13	25.9-32.7	29.6	6	29.9-36.0	32.7
Caudal peduncle depth	11.5	19	9.3-11.5	10.5	6	10.5-11.4	11.0
Caudal peduncle length	13.2	19	11.7-16.7	13.2	6	10.1-13.2	11.9
Anal-fin base	33.2	19	31.1-36.2	33.8	6	31.1-36.0	34.2
Dorsal-fin length	24.4	19	20.9-25.3	23.2	6	22.1-25.1	23.3
Pelvic-fin length (m)	-	6	13.2-15.4	14.4	-	-	-
Pelvic-fin length (f)	14.5	13	13.1-15.4	14.1	6	13.2-15.9	14.4
Pectoral-fin length (m)	-	6	19.2-21.8	20.6	-	-	-
Pectoral-fin length (f)	22.4	13	19.6-26.4	21.4	6	19.2-22.1	20.5
Head length	23.8	19	21.8-24.7	23.0	-	21.1-22.1	21.8
Percents of Head length							
Snout length	20.0	18	20.0-25.1	23.6	6	21.0-23.8	22.3
Upper jaw length	44.0	17	41.2-47.5	44.3	6	41.6-43.8	42.8
Orbital diameter	32.2	19	30.2-34.5	32.6	6	25.9-30.4	28.6
Interorbital width	31.2	19	30.4-34.4	32.3	6	31.1-35.2	33.2

**Table 12.** Morphometric data of holotype of *Hemibrycon tolimae* (FMNH 56257), and paratypes (CAS 44357, FMNH 56258), and non-types from upper rio Magdalena, Colombia (CAS 70102, 132084, 70098; FMNH 56772). The range includes the holotype. m, males; f, females.

	Types				Non-types		
	H	n	Range	Mean	n	Range	Mean
Standard Length (mm)	90.6	16	40.8-91.6	61.6	11	51.7-56.2	50.9
Percents of Standard length							
Predorsal distance	52.9	16	49.0-54.1	51.5	11	51.6-56.2	54.2
Prepelvic distance	47.1	16	44.1-47.9	45.4	11	43.1-47.2	45.1
Prepectoral distance	22.7	16	21.4-24.1	22.8	11	22.8-25.6	24.0
Preanal distance	65.7	16	58.3-65.7	61.1	11	58.0-64.2	60.3
Depth at dorsal-fin origin (m)	-	7	28.9-32.0	30.3	4	29.0-31.5	30.4
Depth at dorsal-fin origin (f)	33.8	9	27.8-33.8	30.5	7	27.8-33.3	29.9
Caudal peduncle depth	12.3	16	11.1-12.9	12.1	11	9.0-11.6	10.6
Caudal peduncle length	14.9	16	12.5-17.9	15.4	11	12.5-16.6	14.5
Anal-fin base	27.6	16	25.4-29.8	27.3	11	26.7-31.1	28.4
Dorsal-fin length	23.6	16	21.3-25.1	22.6	11	20.6-24.7	22.5
Pelvic-fin length (m)	-	7	11.8-13.2	12.7	7	12.3-13.8	13.0
Pelvic-fin length (f)	13.6	9	12.2-14.6	13.2	4	12.3-13.9	13.0
Pectoral-fin length (m)	-	7	18.7-20.4	19.8	7	19.6-22.0	20.6
Pectoral-fin length (f)	20.5	9	19.4-22.4	20.5	4	18.5-22.0	20.3
Head length	23.4	16	21.4-24.0	22.7	11	23.7-25.4	24.7
Percents of Head length							
Snout length	20.6	15	19.6-22.9	21.3	11	20.2-24.9	22.4
Upper jaw length	42.6	15	39.8-46.8	43.4	11	42.0-48.8	46.5
Orbital diameter	23.6	16	23.6-33.0	28.7	11	26.8-33.8	30.4
Interorbital width	34.3	16	23.8-35.1	33.3	11	30.8-34.3	32.4

**Table 13.** Morphometric data of holotype (H) of *Hemibrycon colombianus* (FMNH 56653), and paratypes (CAS 44350-53; FMNH 56654-56), and non-types from rio Sogamoso basin, middle rio Magdalena basin (IAvHP 2942, 3130, 3132). The range includes the holotype. m, males; f, females.

	Paratypes				Non-types		
	H	n	Range	Mean	n	Range	Mean
Standard Length (mm)	84.1	10	31.9-84.1	50.5	21	52.5-108.0	68.9
Percents of Standard length							
Predorsal distance	50.9	10	49.3-55.7	52.8	21	46.4-52.9	50.8
Prepelvic distance	43.6	9	43.6-48.6	46.7	21	41.0-49.7	45.2
Prepectoral distance	21.5	9	21.5-25.5	23.7	21	20.6-24.3	22.8
Preanal distance	60.0	9	60.0-64.5	62.1	21	56.3-64.2	60.0
Depth at dorsal-fin origin (m)	-	3	25.5-30.8	28.0	2	30.3-30.5	30.4
Depth at dorsal-fin origin (f)	31.7	7	27.9-32.2	29.7	19	29.1-33.2	30.5
Caudal peduncle depth	11.7	10	8.8-12.9	10.5	21	10.6-11.9	11.3
Caudal peduncle length	16.1	9	13.3-16.4	15.3	21	13.1-16.6	14.9
Anal-fin base	26.5	9	25.0-28.1	26.8	21	26.5-30.6	28.6
Dorsal-fin length	22.2	10	22.2-25.1	23.3	21	20.5-24.1	22.6
Pelvic-fin length (m)	-	3	15.0-15.7	15.4	2	14.2-14.9	14.5
Pelvic-fin length (f)	13.1	7	12.6-15.7	13.7	19	12.7-15.1	13.8
Pectoral-fin length (m)	-	3	19.8-22.4	21.4	2	20.1-21.4	20.7
Pectoral-fin length (f)	19.8	7	19.8-21.9	21.1	19	19.5-22.5	20.4
Head length	21.2	10	21.2-26.3	24.2	21	21.0-24.0	22.8
Percents of Head length							
Snout length	23.1	10	19.9-24.9	22.6	21	20.0-23.5	21.8
Upper jaw length	45.7	10	43.2-51.6	46.8	21	40.5-46.8	44.3
Orbital diameter	28.1	10	28.1-37.7	31.3	21	23.1-31.2	27.8
Interorbital width	38.0	10	26.5-38.0	31.7	21	29.1-35.0	31.5

**Table 14.** Morphometric data of holotype (H) of *Hemibrycon dariensis* (FMNH 8947), and paratypes (CAS 44343; FMNH 12661-74; USNM 78594), and non-types from río Tuira basin (ANSP 151226; MCP 25491, 27066, 27072, 27074, 27094; USNM 078591, 078593), and from rio Atrato basin (IAvHP 7156, 7237). The range includes the holotype. m, males; f, females.

	Paratypes				Non-types					
	H	n	Range	Mean	Río Tuira basin			Río Atrato basin		
					n	Range	Mean	n	Range	Mean
Standard Length (mm)	49.9	34	35.8-66.6	48.6	35	29.7-52.5	38.8	19	45.5-76.8	60.3
Percents of Standard length										
Predorsal distance	52.4	34	50.4-55.6	52.9	35	51.7-56.4	54.0	19	49.3-54.4	51.6
Prepelvic distance	45.3	34	42.1-46.0	43.7	35	42.5-47.2	44.8	19	41.0-47.3	43.9
Prepectoral distance	23.1	34	22.4-25.0	23.6	35	22.7-26.3	24.3	19	21.3-23.5	22.4
Preanal distance	76.5	34	55.3-76.5	59.6	35	57.1-62.6	59.9	19	55.9-63.9	59.4
Depth at dorsal-fin origin (m)	-	13	28.6-33.3	31.1	4	29.4-33.3	30.8	8	29.8-33.0	30.9
Depth at dorsal-fin origin (f)	34.5	21	28.3-39.8	32.3	31	27.5-34.4	30.4	11	33.7-37.4	35.1
Caudal peduncle depth	11.2	34	10.4-13.0	11.4	35	9.2-11.8	10.7	19	11.0-13.2	11.5
Caudal peduncle length	12.3	34	11.5-13.5	12.6	35	10.7-13.2	12.0	19	12.2-16.7	13.4
Anal-fin base	32.8	34	30.1-35.7	33.1	35	31.6-36.3	33.6	19	29.4-35.1	32.2
Dorsal-fin length	24.3	34	22.3-30.3	24.8	35	23.1-25.8	24.3	19	22.0-25.4	23.5
Pelvic-fin length (m)	-	13	14.2-16.4	15.3	4	14.5-15.5	15.0	8	13.6-16.2	14.8
Pelvic-fin length (f)	16.1	21	13.9-16.6	15.3	31	14.0-15.8	14.8	11	13.4-16.1	14.5
Pectoral-fin length (m)	-	13	20.5-23.5	21.6	4	21.0-22.8	22.1	8	19.9-22.7	21.1
Pectoral-fin length (f)	22.7	21	20.7-23.7	22.2	31	20.5-23.4	21.6	11	20.0-22.7	21.2
Head length	23.4	34	22.4-26.0	23.7	35	22.8-26.1	24.3	19	20.8-23.8	22.4
Percents of Head length										
Snout length	23.7	32	21.4-25.4	22.9	35	21.2-25.9	22.9	19	19.6-24.2	22.5
Upper jaw length	43.6	33	40.0-48.5	44.0	35	40.3-47.4	44.0	19	38.9-46.6	43.2
Orbital diameter	35.0	34	29.8-38.7	35.0	35	34.0-41.1	36.9	19	30.0-37.4	33.8
Interorbital width	34.2	34	29.8-38.7	35.0	35	31.2-35.7	33.1	19	33.1-36.5	34.6

**Table 15.** Morphometric data of syntypes of *Hemibrycon beni* (CAS 44333, 44334; USNM 117543) from río Beni basin, Espia, La Paz, Bolivia, and the holotype of *Hemibrycon tridens* (CAS 44358) from río Apurimac, upper río Ucayali basin, Curuhuasi, Peru. m, males; f, females.

	n	<i>H. beni</i>		<i>H. tridens</i>
		Range	Mean	
Standard Length (mm)	30	29.0-81.4	45.5	51.5
Percents of Standard length				
Predorsal distance	30	51.8-58.6	54.9	49.9
Prepelvic distance	30	41.2-51.0	45.9	39.5
Prepectoral distance	30	23.0-28.7	25.7	22.3
Preanal distance	30	60.9-67.8	63.3	57.0
Depth at dorsal-fin origin (m)	23	29.6-35.6	32.3	23.6
Depth at dorsal-fin origin (f)	7	29.4-33.1	31.2	-
Caudal peduncle depth	30	10.6-14.6	12.7	7.7
Caudal peduncle length	30	14.0-19.6	17.9	19.1
Anal-fin base	30	19.1-25.0	22.1	23.7
Dorsal-fin length	30	21.6-26.7	24.0	23.7
Pelvic-fin length (m)	23	14.8-18.2	16.3	18.2
Pelvic-fin length (f)	7	14.0-15.3	14.8	-
Pectoral-fin length (m)	23	18.8-22.1	20.4	21.7
Pectoral-fin length (f)	7	20.4-21.8	21.3	-
Head length	30	24.1-28.8	26.2	23.4
Percents of Head length				
Snout length	30	20.0-26.0	22.7	22.0
Upper jaw length	29	40.8-53.2	47.1	44.4
Orbital diameter	30	25.4-38.2	30.7	33.6
Interorbital width	30	29.1-35.3	31.9	28.6

**Table 16.** Morphometric data of paratypes of *Hemibrycon helleri* (CAS 44354; FMNH 58439), and non-types from rio Urubamba basin (ANSP 180775, 180777; CAS 70077). m, males; f, females.

	Paratypes			Non-types		
	n	Range	Mean	n	Range	Mean
Standard Length (mm)	8	36.4-78.6	53.9	11	43.3-81.6	60.9
Percents of Standard length						
Predorsal distance	7	50.8-52.7	52.0	11	50.5-54.2	52.9
Prepelvic distance	7	43.1-47.9	44.9	10	42.9-47.0	45.4
Prepectoral distance	7	22.1-25.4	23.7	10	21.4-26.7	23.5
Preanal distance	7	59.2-61.2	60.2	11	57.9-63.9	61.4
Depth at dorsal-fin origin (m)	2	30.6-30.9	30.7	2	28.7-29.6	29.2
Depth at dorsal-fin origin (f)	6	29.3-34.5	32.1	8	28.5-32.4	30.8
Caudal peduncle depth	8	11.9-14.3	12.7	11	10.5-13.3	12.2
Caudal peduncle length	8	12.4-17.0	15.6	11	14.3-16.4	15.3
Anal-fin base	8	27.3-29.3	28.2	11	25.1-29.6	27.2
Dorsal-fin length	8	20.8-24.6	22.2	5	20.4-22.7	21.4
Pelvic-fin length (m)	2	11.8-13.0	12.4	2	13.1-13.3	13.2
Pelvic-fin length (f)	6	13.5-14.3	13.9	3	13.1-14.5	13.7
Pectoral-fin length (m)	2	18.7-20.2	19.4	2	20.2-20.2	20.2
Pectoral-fin length (f)	6	19.7-21.7	20.5	3	20.4-21.5	20.8
Head length	7	22.4-25.1	23.6	11	21.9-25.3	23.5
Percents of Head length						
Snout length	7	19.9-24.6	22.1	11	19.7-23.0	21.4
Upper jaw length	7	42.1-47.6	45.4	11	43.2-49.3	46.0
Orbital diameter	7	28.4-33.5	31.1	11	25.4-32.0	28.9
Interorbital width	7	30.9-33.7	32.2	11	30.5-38.3	33.9

**Table 17.** Morphometric data of holotype (H) of *Hemibrycon metae* (CAS 123727), and non-types from rio Meta basin, Colombia (IAvHP 2973, 3122, 3322, 3628, 3632), and from rio Apure basin, Venezuela (INHS 27766, 31851, 61270; MCNG 98, 5646, 6759, 7923; NRM 23991, 23993), all from rio Orinoco basin. m, males; f, females.

	Non-types						
	Río Meta basin				Río Apure basin		
	H	n	Range	mean	n	Range	mean
Standard Length (mm)	77.2	43	51.3-93.1	67.5	97	32.4-76.7	44.5
Percents of Standard length							
Predorsal distance	50.8	43	47.4-53.3	50.6	97	48.4-56.2	52.5
Prepelvic distance	42.2	43	39.8-45.3	42.0	97	37.9-49.3	43.9
Prepectoral distance	22.5	43	21.0-24.6	22.7	97	21.7-26.2	23.6
Preal anal distance	58.4	43	53.3-60.7	57.1	97	54.7-62.1	58.1
Depth at dorsal-fin origin (m)	-	19	26.4-31.5	29.9	27	25.6-33.4	28.4
Depth at dorsal-fin origin (f)	33.5	24	29.4-37.0	32.5	70	25.6-36.5	31.5
Caudal peduncle depth	12.4	43	10.6-12.5	11.5	97	9.5-13.0	10.8
Caudal peduncle length	13.5	43	10.7-15.3	13.2	97	11.1-14.9	12.9
Anal-fin base	33.2	43	31.4-37.7	34.6	97	30.4-36.4	33.2
Dorsal-fin length	22.6	43	21.6-26.6	24.0	97	19.0-27.6	24.0
Pelvic-fin length (m)	-	19	13.4-16.5	14.7	27	13.0-15.6	14.4
Pelvic-fin length (f)	14.0	24	13.0-15.2	14.1	70	12.7-16.3	14.1
Pectoral-fin length (m)	-	19	18.8-25.8	21.5	27	19.5-22.0	21.0
Pectoral-fin length (f)	21.2	24	19.5-23.6	21.1	70	18.6-22.8	21.3
Head length	21.4	43	20.4-23.6	21.6	97	21.4-25.0	23.2
Percents of Head length							
Snout length	24.9	43	20.2-24.4	22.0	97	18.3-24.3	22.1
Upper jaw length	45.3	43	40.9-46.5	43.6	96	40.8-50.3	45.4
Orbital diameter	28.7	43	26.0-34.5	31.1	97	26.8-38.7	34.2
Interorbital width	33.1	43	30.3-35.9	32.7	97	29.6-34.7	32.4



**Table 18.** Morphometric data of holotype (H) of *Hemibrycon jaborero* (USNM 121455), and paratypes (MHNG 2182.54, 2182.55; USNM 121456-61, 121463-65; ZMA 102.112), and non-types from Lago Maracaibo basin (INHS 34889, 60374; MCNG 4609). The range includes the holotype. m, males; f, females.

	Paratypes				Non-types		
	H	n	Range	Mean	n	Range	Mean
Standard Length (mm)	95.1	74	36.1-117.3	63.0	19	32.1-58.8	41.8
Percents of Standard length							
Predorsal distance	49.3	70	46.9-54.0	51.0	19	50.8-54.3	52.5
Prepelvic distance	45.0	74	39.0-48.3	43.6	19	41.7-45.9	44.3
Prepectoral distance	23.8	74	20.3-42.2	22.7	19	21.8-25.6	24.0
Preanal distance	59.5	74	54.1-65.1	59.7	19	57.3-61.5	59.9
Depth at dorsal-fin origin (m)	-	33	25.1-32.9	29.5	-	-	-
Depth at dorsal-fin origin (f)	32.4	39	27.7-37.1	33.6	19	28.3-34.2	30.9
Caudal peduncle depth	12.2	74	10.0-12.7	11.4	19	10.4-12.0	11.0
Caudal peduncle length	14.8	74	11.6-29.7	14.4	19	11.5-14.4	12.7
Anal-fin base	29.7	73	21.9-34.8	31.2	19	29.7-33.5	31.7
Dorsal-fin length	22.3	73	13.7-27.0	24.1	19	23.1-26.0	24.5
Pelvic-fin length (m)	-	32	14.1-18.4	15.8	-	-	-
Pelvic-fin length (f)	11.9	40	11.9-22.0	14.4	19	12.2-16.4	14.9
Pectoral-fin length (m)	-	33	20.2-26.3	22.2	-	-	-
Pectoral-fin length (f)	18.5	41	18.5-24.2	21.8	19	21.3-23.8	22.4
Head length	24.4	74	21.3-25.9	22.9	19	22.8-26.1	24.3
Percents of Head length							
Snout length	23.1	74	19.3-24.8	21.9	19	19.6-24.3	22.2
Upper jaw length	46.8	73	40.4-51.5	45.6	19	41.9-51.1	46.8
Orbital diameter	25.3	74	22.9-35.6	30.5	19	31.7-38.5	36.4
Interorbital width	37.5	74	28.0-38.2	33.2	19	28.8-34.3	31.1

**Table 19.** Morphometric data of paratypes of *Hemibrycon surinamensis* (MHNG 2182.59, MNHN 1980.1435, ZMA 100.347), and non-types from coastal drainages of the Guiana and Suriname (MHNG 1553.54-58, 2179.27, 2182.57, 2182.61-64, 2279.28, 2279.80; MNHN 1989.0046, 1994.0094, 1998.1780, 1998.1931, 2002.3511; ZMA 107.232, 107.275), and from rio Tocantins basin, Brazil (MZUSP 30529, 30530). m, males; f, females.

	Paratypes			Non-types					
	n	Range	Mean	Guiana and Suriname			Rio Tocantins basin		
				n	Range	Mean	n	Range	Mean
Standard Length (mm)	7	53.3-64.8	57.5	65	33.5-91.5	64.7	20	38.6-87.1	54.3
Percents of Standard length									
Predorsal distance	7	49.5-54.2	51.0	65	48.4-55.1	51.1	20	49.2-53.0	51.5
Prepelvic distance	7	42.6-47.4	44.5	65	40.9-49.2	45.4	20	41.7-47.6	45.0
Prepectoral distance	7	23.2-25.1	24.3	65	22.3-25.8	24.2	20	22.3-26.7	24.8
Preanal distance	7	59.0-65.2	61.1	65	56.9-65.1	62.0	20	57.9-63.0	60.6
Depth at dorsal-fin origin (m)	3	31.2-32.0	32.0	19	33.1-39.5	35.5	8	31.8-38.2	34.9
Depth at dorsal-fin origin (f)	4	31.4-37.1	34.0	46	32.7-42.7	37.1	12	30.5-38.0	34.4
Caudal peduncle depth	7	9.7-12.8	11.1	65	10.0-12.9	11.7	20	10.0-12.0	10.8
Caudal peduncle length	7	9.1-13.9	11.9	65	7.5-14.1	12.3	20	11.7-14.5	12.7
Anal-fin base	7	30.8-33.4	32.0	65	29.7-35.9	32.4	20	29.0-35.2	32.6
Dorsal-fin length	7	24.4-27.5	25.3	65	22.0-26.7	24.6	20	21.8-25.7	23.9
Pelvic-fin length (m)	3	15.2-15.8	15.4	19	14.5-17.1	16.1	8	15.1-17.2	16.2
Pelvic-fin length (f)	4	15.8-17.6	16.7	46	13.9-17.6	15.6	12	13.3-16.1	15.1
Pectoral-fin length (m)	3	20.8-22.0	21.3	19	20.4-22.9	21.7	8	20.7-23.1	22.1
Pectoral-fin length (f)	4	20.7-22.9	22.2	46	19.5-24.1	21.7	12	20.7-22.3	21.3
Head length		22.4-25.3	24.0	65	21.1-25.7	23.1	20	21.9-25.1	23.3
Percents of Head length									
Snout length	7	22.9-25.1	24.2	65	21.6-27.8	23.9	20	22.2-25.2	23.6
Upper jaw length	7	45.4-48.1	46.7	65	42.7-49.8	46.7	20	43.7-49.2	47.1
Orbital diameter	7	31.9-35.6	33.9	64	30.1-37.4	33.7	20	31.1-37.9	34.7
Interorbital width	7	33.2-35.9	34.7	65	32.0-40.1	36.7	20	34.4-39.7	36.5

**Table 20.** Morphometric data of holotype (H, MUSM uncat.) and paratypes (MUSM 15845, 12 of 40) of *Hemibrycon* n. sp. 1 from upper río Ucayali basin, Peru. The range includes the holotype.

	H	Range	Mean	SD
Standard length (mm)	44.4	32.7-44.4	36.8	3.58
Percents of Standard length				
Predorsal distance	52.8	52.1-55.2	53.6	1.03
Prepelvic distance	43.9	43.6-45.7	44.8	0.75
Prepectoral distance	23.1	23.1-25.2	24.1	0.64
Preanal distance	58.9	56.5-60.5	59.1	1.09
Depth at dorsal-fin origin	32.4	30.0-33.6	31.6	1.34
Caudal peduncle depth	12.4	11.0-13.6	12.2	0.78
Caudal peduncle length	15.9	13.6-19.3	16.8	1.40
Anal-fin base	28.2	26.6-30.4	28.0	1.15
Dorsal-fin length	23.4	22.8-25.6	23.7	0.74
Pelvic-fin length	13.6	13.0-14.6	13.8	0.56
Pectoral-fin length	22.1	20.7-23.7	22.1	0.75
Head length	23.8	23.7-25.8	24.8	0.70
Percents of Head length				
Snout length	21.3	19.3-22.9	20.9	1.06
Upper jaw length	50.2	44.5-50.2	47.7	1.72
Orbital diameter	33.2	33.2-37.6	35.7	1.15
Interorbital width	34.1	32.7-35.6	34.1	0.88

**Table 21.** Morphometric data of holotype (H, ICNMHN uncat., male) and paratypes (IAvHP 28; ICNMHN 5748, 6439, 6931, 9655, 10834; n = 23) of *Hemibrycon* n. sp. 2 from the Caribbean coastal drainage, Colombia. The range includes the holotype. m, males; f, females.

	H	n	Range	Mean	SD
Standard length (mm)	55.4	42	40.1-80.1	66.3	11.16
Percents of Standard length					
Predorsal distance	53.2	42	50.6-56.9	53.3	1.36
Prepelvic distance	42.0	42	40.7-47.4	44.2	1.80
Prepectoral distance	24.7	42	22.1-26.8	23.8	1.20
Preanal distance	57.9	42	55.0-63.5	59.5	2.13
Depth at dorsal-fin origin (m)	29.4	21	27.9-34.1	30.9	1.74
Depth at dorsal-fin origin (f)	-	21	30.1-38.7	33.0	2.18
Caudal peduncle depth	14.2	42	11.8-15.4	13.5	1.00
Caudal peduncle length	13.6	42	12.0-15.4	13.6	0.88
Anal-fin base	30.3	42	28.7-34.4	31.3	1.34
Dorsal-fin length	23.6	42	21.2-25.6	23.7	0.90
Pelvic-fin length (m)	17.6	21	14.4-18.7	16.8	1.04
Pelvic-fin length (f)	-	21	14.0-16.0	15.0	0.51
Pectoral-fin length (m)	21.8	21	20.2-26.5	22.4	1.35
Pectoral-fin length (f)	-	21	21.0-23.3	22.1	0.72
Head length	24.9	42	22.1-27.0	23.6	1.18
Percents of Head length					
Snout length	21.8	42	19.9-24.4	22.1	1.09
Upper jaw length	47.2	42	43.0-49.9	46.0	1.61
Orbital diameter	31.2	42	25.1-34.4	29.6	2.13
Interorbital width	30.9	42	26.9-35.0	32.1	2.00

**Table 22.** Morphometric data of holotype (H, ICNMHN uncat., female) and paratypes (ICNMHN 0753, 6736) of *Hemibrycon* n. sp. 3 from middle río Magdalena basin, Colombia.

The range includes the holotype. m = males; f = females.

	H	n	Range	Mean	SD
Standard length (mm)	76.7	13	54.3-88.3	71.2	11.28
Percents of Standard length					
Predorsal distance	50.8	13	47.1-51.1	49.5	1.08
Prepelvic distance	43.8	13	41.5-46.3	43.5	1.45
Prepectoral distance	23.4	13	21.4-24.6	22.7	1.01
Preanal distance	59.9	13	57.8-62.1	59.5	1.31
Depth at dorsal-fin origin (m)	-	2	30.1-30.7	30.4	0.41
Depth at dorsal-fin origin (f)	30.3	11	27.1-32.3	29.6	1.29
Caudal peduncle depth	10.7	13	10.2-12.2	10.9	0.54
Caudal peduncle length	16.1	13	14.9-18.7	17.1	1.19
Anal-fin base	24.9	13	24.9-28.4	26.5	1.04
Dorsal-fin length	20.6	13	20.6-23.3	21.9	0.78
Pelvic-fin length (m)	-	2	13.4-13.5	13.5	0.09
Pelvic-fin length (f)	12.9	11	12.9-14.3	13.6	0.45
Pectoral-fin length (m)	-	2	20.1-21.1	20.6	0.71
Pectoral-fin length (f)	20.7	11	20.0-22.4	21.0	0.86
Head length	22.2	13	20.9-24.1	22.5	0.89
Percents of Head length					
Snout length	22.1	13	20.2-23.3	21.4	0.88
Upper jaw length	47.4	13	43.4-48.2	45.2	1.70
Orbital diameter	29.7	13	26.6-32.4	29.3	1.94
Interorbital width	31.8	13	29.5-33.7	31.8	1.35

**Table 23.** Morphometric data of holotype (H, ICNMHN uncat., female) and paratypes (IAvHP 8444, 8445; ICNMHN 2990, 10397, 15551) of *Hemibrycon* n. sp. 4 from rio La Miel basin, Colombia. The range includes the holotype. m, males; f, females.

	H	n	Range	Mean	SD
Standard length (mm)	74.0	27	43.9-88.3	66.3	11.79
Percents of Standard length					
Predorsal distance	54.6	27	49.5-55.8	52.9	1.38
Prepelvic distance	45.3	27	41.5-47.8	44.5	1.75
Prepectoral distance	25.2	27	22.8-27.9	24.7	1.06
Preanal distance	60.3	27	56.4-64.5	60.6	2.04
Depth at dorsal-fin origin (m)	-	7	32.2-34.8	33.6	0.88
Depth at dorsal-fin origin (f)	32.0	20	28.8-38.4	33.2	2.57
Caudal peduncle depth	10.8	27	10.2-13.2	11.8	1.05
Caudal peduncle length	13.9	27	12.0-15.2	13.5	0.76
Anal-fin base	31.2	27	25.8-35.4	31.8	2.44
Dorsal-fin length	22.8	27	21.0-24.9	23.4	0.97
Pelvic-fin length (m)	-	7	13.8-15.5	14.6	0.64
Pelvic-fin length (f)	15.6	20	13.2-15.6	14.6	0.54
Pectoral-fin length (m)	-	7	20.8-21.8	21.3	0.70
Pectoral-fin length (f)	21.1	20	20.3-22.5	21.4	0.68
Head length	24.5	27	22.3-26.8	24.0	1.15
Percents of Head length					
Snout length	22.1	27	20.4-24.7	22.2	1.22
Upper jaw length	47.5	27	40.1-47.8	43.9	1.99
Orbital diameter	30.1	27	28.6-37.0	31.5	2.06
Interorbital width	32.3	27	31.1-35.9	33.6	1.19

**Table 24.** Morphometric data of holotype (H) of *Hemibrycon* n. sp. 5 (ANSP uncat., male), and paratypes from río Alto Madre de Dios basin (ANSP 143290, 143293, 143307, 143291, 143294, 143300, 143306, 143312, 143317, 151478, 151497, 151526), and non-types from río Inambari basin (MUSM 26299, 26776, 26802), upper río Madre de Dios drainage. The range includes the holotype. m, males; f, females.

	H		Paratypes		Non-types		
		n	Range	Mean	n	Range	Mean
Standard Length (mm)	59.6	29	32.3-81.5	45.5	23	43.4-87.3	59.1
	Percents of Standard length						
Predorsal distance	51.0	29	50.1-54.8	52.7	23	48.6-53.7	51.2
Prepelvic distance	43.2	29	43.4-47.6	45.3	23	40.4-45.9	42.9
Prepectoral distance	22.0	29	20.9-25.9	23.7	23	19.9-24.1	22.3
Preanal distance	57.4	29	57.7-63.1	59.9	23	54.8-60.8	57.4
Depth at dorsal-fin origin (m)	32.1	2	32.1-32.5	32.3	12	29.1-32.7	31.0
Depth at dorsal-fin origin (f)	-	27	28.7-35.3	32.1	11	30.7-33.4	31.9
Caudal peduncle depth	14.6	29	11.1-13.9	12.7	23	12.0-13.8	12.7
Caudal peduncle length	14.6	29	10.9-15.6	14.0	23	12.3-15.1	13.7
Anal-fin base	33.2	29	28.0-32.9	30.2	23	30.0-34.4	32.3
Dorsal-fin length	23.5	29	21.9-25.3	23.6	23	21.0-23.7	22.4
Pelvic-fin length (m)	12.0	2	12.0-13.8	12.9	12	11.2-12.8	12.2
Pelvic-fin length (f)	-	27	12.1-13.6	12.9	11	11.2-13.5	12.3
Pectoral-fin length (m)	20.0	2	20.0-22.7	21.3	12	17.7-20.3	19.1
Pectoral-fin length (f)	-	27	18.9-23.0	21.1	11	18.6-21.1	19.8
Head length	22.5	29	21.9-26.3	24.5	23	20.6-24.1	22.3
	Percents of Head length						
Snout length	22.0	29	18.5-23.6	21.0	23	19.1-23.1	21.6
Upper jaw length	47.9	29	45.5-50.7	48.1	23	43.1-50.2	46.1
Orbital diameter	30.5	29	27.1-37.9	34.1	23	27.4-35.4	31.2
Interorbital width	31.3	29	29.3-36.2	32.7	23	31.3-35.9	33.7

## **CAPÍTULO II**



## A new species of *Hemibrycon* (Teleostei: Characiformes: Characidae) from the río Ucayali drainage, Sierra del Divisor, Peru

Vinicius A. Bertaco\*, Luiz R. Malabarba\*\*\*, Max Hidalgo\*\*\* and Hernán Ortega\*\*\*

A new characid species, *Hemibrycon divisorensis*, is described from the río Ucayali drainage, Loreto, Peru. The new species is distinguished from all *Hemibrycon* species by the presence of a wide black asymmetrical spot covering base of caudal-fin rays and extending along entire length of caudal-fin rays 9 to 12-13 (except from *H. surinamensis*), and a black band in the lower half of the caudal peduncle extending from the region above the last anal-fin rays to the caudal-fin base. Furthermore, it is distinguished from most species of the genus by the number of scale rows below the lateral line (4-5 vs 5-9), except *H. jabonero*, *H. microformaa*, *H. orcesi*, and *H. surinamensis*. It differs from these species by scale and fin ray counts and color pattern. The lack of a supraorbital in *Hemibrycon* species is discussed and confirmed.

Uma nova espécie de caracádeo, *Hemibrycon divisorensis*, é descrita para a bacia do río Ucayali, Loreto, Peru. A nova espécie distingue-se das demais espécies de *Hemibrycon* pela presença de uma ampla mancha preta assimétrica na base dos raios da nadadeira caudal estendida até a extremidade dos raios 9 a 12 ou 13 (exceto de *H. surinamensis*), e de uma faixa preta na metade inferior do pedúnculo caudal desde a região acima dos últimos raios da nadadeira anal até a base da nadadeira caudal. Ela distingue-se da maioria das espécies do gênero pelo número de escamas abaixo da linha lateral (4-5 vs 5-9), exceto de *H. jabonero*, *H. microformaa*, *H. orcesi* e *H. surinamensis*. Ela difere destas espécies pela contagem de escamas, raios das nadadeiras e colorido padrão. Discute-se e confirma-se a ausência do osso supraorbital em *Hemibrycon*.

**Key words:** Neotropical, Amazon basin, Taxonomy, Supraorbital, Fin hooks, *Carlastyanax*.

### Introduction

*Hemibrycon* is a Neotropical genus of characid fishes which comprises about 21 valid species, occurring in the coastal drainages of the Caribbean sea and East Pacific in Colombia, río Tuira drainage in Panama, rivers drainages in Trinidad and Tobago, río Orinoco and lago Maracaibo in Venezuela, upper río Amazonas in Bolivia, Peru, and Ecuador, and coastal drainages of French Guiana and Suriname (Lima *et al.*, 2003; Román-Valencia & Ruiz-C., 2007).

The genus *Hemibrycon* was proposed by Günther (1864), as a subgenus of *Tetragonopterus* Cuvier, differing by “cleft of the mouth of moderate width, and the entire edge of the maxillary denticulated”. *Tetragonopterus polyodon* Günther was designed as type-species. *Hemibrycon* was extensively revised by Eigenmann (1927), whose accounts still constitute the single complete review of the genus. Publications on *Hemibrycon* subsequent to Eigenmann’s revision usually in-

volves only description of new species occurring in restricted geographic areas of South America.

Eigenmann (1917, 1927) further diagnosed *Hemibrycon* based on the “caudal fin naked, premaxillary with two series of teeth, inner series with four teeth, infraorbital 2 in contact with the lower limb of the preopercle, adipose fin present, anal fin moderate or long, gill-rakers simple, teeth along the greater part or along the entire edge of the maxillary”. None of the characters are unique to the genus and most of them are plesiomorphic within Characidae or treated as putative synapomorphies of more inclusive clades containing *Hemibrycon* (Malabarba & Weitzman, 2003).

Géry (1966) grouped *Hemibrycon* along with *Boehlkea*, *Bryconacidnus*, *Bryconamericus*, *Ceratobranchia*, *Coptobrycon*, *Knodus*, *Microgenys*, *Nematobrycon*, *Piabarchus*, *Rhinobrycon*, and *Rhinopetitia*, in a new subtribe, *Hemibryconini*, consisting of a group of *Tetragonopterinae* with four inner premaxillary teeth, frequently associated with

\*Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Av. Ipiranga 6681, 90619-900 Porto Alegre, RS, Brazil. ubertaco@puers.br

\*\*Departamento de Zoologia, IB, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves, 9500, 91501-970 Porto Alegre, RS, Brazil. malabarba@ufrgs.br

\*\*\*Departamento de Ictiologia, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, PO Box 14-0434, Lima – 14, Peru. maxhhidalgo@yahoo.com, tortegat@unmsm.edu.pe

a great development of the third infraorbital, and, quite often, the irregular implantation of the outer premaxillary row of teeth. Malabarba & Weitzman (2003) recognized *Hemibrycon* as belonging to a large monophyletic clade inside Characidae (therein named Clade A), based on the putative derived presence of four teeth in the inner series of the premaxilla and reduced number of dorsal-fin rays (ii,8). Additionally, they considered *Hemibrycon* and *Boehlkea* as apparently the most basal genera in that clade, by lacking all specializations related to insemination, development of caudal- and/or anal-fin glands or the jaw and teeth modifications related to the ventral position of the mouth, as observed in the remaining genera and species of Clade A.

During a recent expedition to the Zona Reservada Sierra del Divisor, Peru, a new species of *Hemibrycon* was collected in the río Ucayali drainage and it is herein described. This is part of a systematic study of *Hemibrycon* conducted by the senior author (doctoral thesis).

### Materials and Methods

Counts were taken as described by Fink & Weitzman (1974), with the exception of number of scale rows below lateral line which were counted from the scale row ventral to lateral line to the scale row nearest the first pelvic-fin ray. Vertebral counts, supraneurals, gill-rakers, teeth, and procurrent caudal-fin-ray counts were taken from cleared and stained specimens (c&s) prepared according to the method of Taylor & Van Dyke (1985). The gill raker at the junction of the ceratobranchial and the epibranchial is included in the counting of gill rakers of lower limb. Maxillary tooth counts were taken in type specimens included in Table 1. Counts for the holotype are indicated with an asterisk. Vertebral counts include the four vertebrae integrated in the Weberian apparatus and the terminal centrum was counted as one vertebra. Scanning electron micrographs (SEM) of teeth and jaws were taken from one cleared and stained dissected specimen. Testes were removed prior to clearing and staining, dehydrated in an ethanol series until 99.5%, and critical point dried. The dried testes were placed in stub with carbon tape and split with a needle, coated with gold and carbon, and viewed with SEM.

Measurements were taken point to point with an electronic caliper from the left side of the specimens. All measurements other than SL are expressed as a percents of SL except subunits of the head, which are recorded as a percents of head length (HL).

Specimens examined belong to the following institutions: ANSP, Academy of Natural Sciences, Philadelphia; BMNH, Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; FMNH, Field Museum of Natural History, Chicago; IAvH-P, Instituto Alexander von Humboldt - Peces, Villa de Leyva; IMCN, Colección Zoológica de Referencia del Museo Departamental de Ciencias Naturales Federico Carlos Lehmann Valencia - INCIVA, Valle del Cauca, Cali; MCP, Museu de Ciências e Tecnologia, Pontificia

Universidade Católica do Rio Grande do Sul, Porto Alegre; MHNG, Muséum d'histoire naturelle, Geneva; MNHN, Muséum nationale d'histoire naturelle, Paris; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima; NMW, Naturhistorisches Museum, Wien; USNM, National Museum of Natural History, Washington D.C.; ZMA, Universitat van Amsterdam Zoologisch Museum, Amsterdam; and ZMUC, Zoological Museum, University of Copenhagen, Copenhagen.

### *Hemibrycon divisorensis*, new species

Figs. 1-3

**Holotype.** MUSM 28860, 68.2 mm SL, male, Peru, Loreto, Requena, Zona Reservada Sierra del Divisor, upper río Tapiche, quebrada en la trocha 1, río Ucayali drainage, 07°12'02"S 73°53'00"W, 20 Aug 2005, M. Hidalgo & J. F. P. da Silva.

**Paratypes.** MCP 41346, 4 (60.5-81.6 mm SL), 2 c&s (62.7-68.4 mm SL), MUSM 28040, 19, 35.0-73.0 mm SL, collected with holotype. MCP 41347, 5, 48.9-65.0 mm SL, MUSM 28039, 11 (43.0-58.0 mm SL), 1 c&s (55.9 mm SL), Peru, Loreto, Zona Reservada Sierra del Divisor, Ojo de Contaya, quebrada en la trocha 4, río Ucayali drainage, 07°06'54"S 74°35'08"W, 6 Aug 2005, M. Hidalgo & J. F. P. da Silva.

**Diagnosis.** *Hemibrycon divisorensis* is distinguished from all other species of the genus by the presence of a wide black asymmetrical spot covering the base of caudal-fin rays and extending along entire length of caudal-fin rays 9 to 12-13 (except from *H. surinamensis*), and by the presence of a black band in the lower half of the caudal peduncle from the region above the last anal-fin rays to the caudal-fin base (Figs. 1-2). Furthermore, it is distinguished from most species of the genus by the number of the scale rows below lateral line (4-5 vs 5-9), except from *H. jabonero*, *H. microformaa*, *H. orcesi*, and *H. surinamensis*. *Hemibrycon divisorensis* differs from *H. orcesi* and *H. microformaa* by the higher number of lateral line scales (39-42 vs 34-35 and 33-37, respectively) and anal-fin rays (24-30 vs 18 and 14-16, respectively), and by color pattern; from *H. jabonero* and *H. surinamensis* by the higher number of scale sheath along anal-fin base (17-22 vs 8-14 and 15-16, respectively), and number of cusps in the inner row of the premaxilla teeth (5-7 vs 5, respectively).

**Description.** Morphometric data for *Hemibrycon divisorensis* summarized in Table 1. Largest male 68.4 mm SL, largest female 81.6 mm SL. Body compressed and moderately elongate; greatest body depth usually nearly to dorsal-fin origin. Dorsal profile of head slightly convex to nearly straight. Dorsal body profile slightly convex from supraoccipital to dorsal-fin origin; posteroventrally slanted from dorsal-fin origin to adipose fin. Ventral profile of head slightly convex. Ventral body profile convex from isthmus to pelvic-fin origin, and straight to slightly convex from this point to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle slightly concave along dorsal and ventral margins.



**Fig. 1.** *Hemibrycon divisoirensis*, MUSM 28860, holotype, male, 68.2 mm SL; río Ucayali drainage, Loreto, Peru.

Snout rounded from margin of upper lip to vertical through anterior nostrils. Head small. Mouth terminal, mouth slit nearly at horizontal through middle of eye. Maxilla long, slightly curved, and aligned at angle of approximately 60 degrees to longitudinal body axis, with ventral border slightly convex to nearly straight and dorsal border slightly concave.

Premaxilla with two tooth rows; outer row teeth 4-7 (6\*), tricuspid to pentacuspoid, central cusp slightly longer; inner row teeth 4, pentacuspoid to heptacuspoid, central cusp twice or three times longer and broader than other cusps, gradually decreasing in length from first to third teeth and last tooth smallest. Maxilla fully toothed with 10-13 (11\*) tricuspid teeth with central cusp longer, except for last six or seven conical teeth. Three anteriormost dentary teeth larger, with 5-7 cusps, followed by medium sized tooth with 3-5 cusps, and 9-12 teeth with 2-3 cusps or conical; central cusp in all teeth two to three times longer and broader than other cusps (Fig. 3). All cusp tips slightly curved posteriorly towards inside of mouth.

Dorsal-fin rays ii,8 (n = 19); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located slightly posterior to middle of SL and posterior to vertical through pelvic-fin origin. First dorsal-fin pterygiophore inserted between neural spines of 11<sup>th</sup> to 12<sup>th</sup> vertebrae (n = 3). Profile of distal margin of dorsal fin slightly concave or nearly straight. Males with bony hooks on distal one-third of first to fifth branched dorsal-fin rays. Adipose-fin located approximately at vertical through insertion of last four or five anal-fin rays.

Anal-fin rays iv,25-28 (27\*, rarely 24 or 29-30, mean = 26.7, n = 19). Anal-fin profile nearly straight in males and concave in females. Anal-fin origin approximately at vertical through insertion of last two or three dorsal-fin rays. First anal-fin pterygiophore inserted between hemal spines of first and second caudal vertebrae. Anal-fin rays of males bearing one pair of small bony hooks along posterolateral border of each segment of lepidotrichia, usually along first to 12<sup>th</sup> anterior branched rays. Hooks more numerous along fourth through seventh branched rays, and usually located along posteriormost branch and distal 1/2 to 2/3 of each ray.

Pectoral-fin rays i,10-13 (11\*, mean = 11.1, n = 19). Pecto-

ral-fin tip reaching pelvic-fin origin in males, not in females. Males with bony hooks on distal portion of unbranched and all branched pectoral-fin rays. Pelvic-fin rays i,6,i (n = 11) or i,7\* (n = 8). Pelvic-fin origin located at vertical through 3-4 predorsal scales anterior to dorsal-fin origin. Pelvic fin of males usually bearing one small bony hook per lepidotrichia segment along ventromedial border of all branched rays.

Caudal fin forked with 19 principal rays (n = 19); lobes similar in size. Basal portion of caudal-fin lobes covered with somewhat irregular scales and smaller than those of body, following by one larger and round shaped scale in each lobe. Dorsal procurent rays 11 and ventral procurent rays 10-11 (n = 3).

Scales cycloid, moderately large. Lateral line complete with 39-41 scales (41\*, one specimen with 42, mean = 40.2, n = 19). Scale rows between dorsal-fin origin and lateral line 6-7 (6\*, mean = 6.5, n = 19); scale rows between lateral line and pelvic-fin origin 4-5 (5\*, mean = 4.7, n = 19). Predorsal scales 13-15, arranged in regular series (13\*, mean = 13.3, n = 19). Scale rows around caudal peduncle 14-16 (14\*, mean = 15.5, n = 19). Triangular modified scale on pelvic-fin origin posteriorly covering three scales. Scale sheath along anal-fin base with 17-22 (18\*) scales in single series, extending to base of 18<sup>th</sup> to 20<sup>th</sup> branched rays.

Precaudal vertebrae 16-17; caudal vertebrae 21-22; total vertebrae 38-39. Supraneurals 5-6 (n = 3). Gill-rakers on upper limb of outer gill arch 7-9, and on lower limb 12-14 (n = 8).

**Color in alcohol.** General body color yellowish to yellowish-brown. Dorsal and dorsolateral portions of head and body pigmented dark brown. Dorsolateral portion of body with scales bordered by dark pigment and forming reticulate pattern. One black humeral spot vertically elongate, wide in dorsal portion and narrowing ventrally; wide dorsal portion of humeral spot located over two or three scales of two scale series just above lateral line; narrow portion crossing lateral line at fourth and/or fifth scales and extending one or two scale series just below lateral line. Midlateral body silvery. Lower half portion of caudal peduncle from region above last anal-fin rays to caudal-fin base black pigmented, usually from



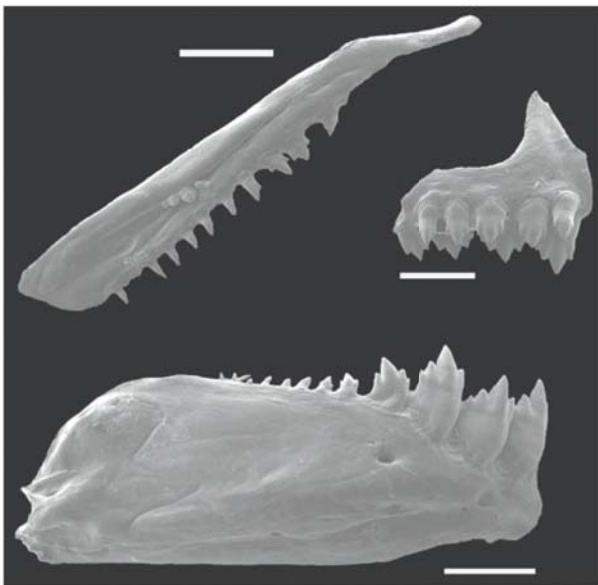
**Fig. 2.** *Hemibrycon divisorensis*, MCP 41346, paratype, female, 81.6 mm SL; río Ucayali drainage, Loreto, Peru.

the scale row bearing the lateral line to the scales near anal-fin base and ventral margin of caudal peduncle. Wide and asymmetric black spot covering base of middle caudal-fin rays and extending along entire length of caudal-fin rays 9 to 12-13. Dorsal and caudal fin with dark pigmentation diffuse. Anal fin with small black chromatophores along its border forming narrow stripe. Other fins without distinctive marks (Figs. 1-2).

**Color just after fixation.** Color pattern similar to described for alcohol preserved specimens. Specimens examined soon after fixation in formalin with dorsal and adipose fins and caudal peduncle reddish pigmented, and red spot on ventral portion of caudal-fin base.

**Sexual dimorphism.** Males of *Hemibrycon divisorensis* are easily recognized by the presence of small bony hooks on the dorsal-, anal-, pelvic-, and pectoral-fin rays (see Description). Also, males and females differ in pectoral and pelvic-fin lengths (Table 1), and anal-fin shape, which is nearly straight in males and concave in females (Figs. 1-2). Mature males do not present gill gland on first arch.

**Distribution.** *Hemibrycon divisorensis* is known only from the río Tapiche drainage, a tributary to the río Ucayali, Loreto, Peru. This locality is included in the conservation area "Zona Reservada Sierra del Divisor" recently established by the Peruvian government.



**Fig. 3.** *Hemibrycon divisorensis*, MCP 41346, paratype, male, 68.4 mm SL. Scanning electron micrograph of right side upper and lower jaws. The presence of 3-4 teeth in the midlateral of maxilla is an anomaly. Scale bar = 1 mm.

**Table 1.** Morphometric data of holotype (MCP 28860, male) and paratypes (6 of MCP 41346, 5 of MCP 41347, 4 of MUSM 28039, and 3 of MUSM 28040) of *Hemibrycon divisorensis* from the río Ucayali drainage, Loreto, Peru. The range includes the holotype. m, males (n = 6); f, females (n = 13). SD = standard deviation.

	Holotype	Range	Mean	SD
Standard length (mm)	68.2	48.9-81.6	-	-
Percents of standard length				
Predorsal distance	50.2	49.8-55.5	51.5	1.21
Prepelvic distance	43.5	43.6-47.6	45.4	0.95
Prepectoral distance	24.4	23.6-26.0	24.9	0.64
Preanal distance	59.3	59.3-63.6	61.2	1.27
Depth at dorsal-fin origin	33.0	32.9-36.2	34.3	1.09
Caudal peduncle depth	11.3	10.7-12.2	11.8	0.44
Caudal peduncle length	13.8	11.7-13.8	13.0	0.65
Anal-fin base	32.7	29.6-32.9	31.5	0.95
Dorsal-fin length	23.2	22.9-25.9	23.9	0.77
Pelvic-fin length (m)	16.4	15.9-17.1	16.4	0.45
Pelvic-fin length (f)	-	13.7-15.7	14.8	0.63
Pectoral-fin length (m)	21.1	20.6-22.9	21.7	0.79
Pectoral-fin length (f)	-	19.1-21.4	20.4	0.74
Head length	23.8	22.6-24.9	24.0	0.55
Percents of head length				
Snout length	24.7	22.4-24.7	23.3	0.61
Upper jaw length	43.8	43.8-47.7	45.8	0.97
Orbital diameter	34.6	31.7-35.5	33.8	1.28
Interorbital width	33.8	32.2-36.6	34.4	1.26

**Etymology.** The species name, *divisorensis*, is in reference to the type locality. A noun in apposition.

**Ecological notes.** The tributaries of río Tapiche where the type specimens were collected are about 2-3 m wide with crystalline water, 0.3-0.5 m deep, medium water current, sandy substrate, and with moderate amount of riparian vegetation.

**Spermatozoa.** *Hemibrycon divisorensis* has a typical aquasperm with a spherical to slightly ovoid nucleus (MCP 28040, 62.7 mm SL), suggesting that the species is non-inseminating (Burns *et al.*, 1995, 1998; Burns & Weitzman, 2005). Due to the lack of mature females, it was not possible to verify the presence of spermatozoa in the ovaries of *H. divisorensis*.

### Discussion

The new species is described in *Hemibrycon* considering the definition of the genus currently in use, proposed by Günther (1864) and further elaborated by Eigenmann (1927). The systematics of *Hemibrycon* is still unresolved and the genus lacks a phylogenetic diagnosis. Eigenmann (1917) distinguished *Hemibrycon* from *Bryconamericus* only by the “few teeth along the upper portion of the maxillary” in the latter, compared to the large toothed maxilla of the former. Román-Valencia (2000) considered *Hemibrycon* related to *Bryconamericus*, but did not present a phylogenetic evidence to support his hypothesis.

Recently, Malabarba & Weitzman (2003) recognized a putative monophyletic clade within Characidae, which includes *Hemibrycon*, along with the subfamily Glandulocaudinae (now Glandulocaudinae and Stevardiinae) and the genera *Attonitus* Vari & Ortega, *Boehlkea* Géry, *Bryconacidnus* Myers, *Bryconamericus* Eigenmann, *Caiapobrycon* Malabarba & Vari, *Ceratobranchia* Eigenmann, *Creagrutus* Günther, *Cyanocharax* Malabarba & Weitzman, *Hypobrycon* Malabarba & Malabarba, *Knodus* Eigenmann, *Microgenys* Eigenmann, *Monotocheirodon* Eigenmann & Pearson, *Odontostoechus* Gomes, *Othonocheirodon* Myers, *Piabarchus* Myers, *Piabina* Reinhardt, *Rhinobrycon* Myers, and *Rhinopetitia* Géry. Additionally, *Hemibrycon* and *Boehlkea* were considered as apparently the most basal genera in that clade, by lacking all specializations related to insemination, development of caudal and/or anal glands, or the jaw and teeth modifications related to ventral mouth, as observed in the species of the remaining genera of that clade. The species of *Hemibrycon* further differ from the species of all those genera by sharing a large number of teeth in the maxilla, as observed in the new species described herein. A taxonomic review and phylogenetic analysis of *Hemibrycon* species is in progress by the senior author, and evaluates the potential use of this and other characters in defining *Hemibrycon*.

Weitzman *et al.* (2005: 344) suggest that detailed investigations of the histology and ultrastructure of sperm cells is

necessary for a useful evaluation of the phylogenetic significance of insemination in characids included in Clade A. We agree with that, but testes properly fixed for Transmission Electronic Microscopy (TEM) analyses of the ultrastructure of sperm cells and mature ovaries for histological examination were not available. We have made SEM preparations of testes and found *H. divisorensis* has a typical aquasperm with a spherical to slightly ovoid nucleus suggesting the species is not inseminating.

According to Román-Valencia & Ruiz-C. (2007), a supraorbital bone is found in *H. boquiae*, *H. microformaa*, *H. orcesi*, *H. pautensis*, and *H. polyodon*, and its presence would not support the inclusion of *Hemibrycon* among Clade A genera of Malabarba & Weitzman (2003). The supraorbital, however, is absent in all species of *Hemibrycon* examined by one of us (VAB). The supraorbital is also described by Ruiz-C. & Román-Valencia (2006:51) in *Carlastyanax aurocaudatus* as [our translation]: long and narrow, joined laterally to the frontal, with anterior and posterior tips semi-concave and originating the supraorbital canal, flattened dorsal surface. The anteroventral surface of the supraorbital articulates to the dorsal portion of the lateral ethmoid through a band of cartilage extending from the joining of frontal and orbitosphenoid [“*hueso largo, angosto, unido lateralmente al frontal, cuyos extremos anterior y posterior semicóncavos dan lugar al canal supraorbital, superficie dorsal más plana. La superficie anteroventral del supraorbital se articula a la parte dorsal del lateroetmoide, mediante una banda de cartilago que se extiende entre la unión del frontal y el orbitoesfenoide*”]. This description corresponds to the lateralmost laminar portion of the frontal, external to the laterosensory tube that runs dorsally in the frontal. In the same paper (p.61), the supraorbital is described as an element joined to the lateral border of the frontal originating the laterosensory canal that continues in the nasal [“una estructura . . . , que al unirse al borde lateral del frontal da origen al canal laterosensorial, que se continúa con el nasal”]. The only representation of the supraorbital bone is given in a superficial sketch of a dorsal view of the skull of *Carlastyanax aurocaudatus* (Ruiz-C. & Román-Valencia, 2006:50, fig. 1), and it is shown in the same position of the lateral expansion of the frontal, external to the lateral line canal of this bone. Apparently, Ruiz-C. & Román-Valencia (2006) assumed that the laterosensory tube that runs dorsally and divides the frontal is the limit between the frontal and the ossification they interpret as a supraorbital. We have examined cleared and stained specimens of *Carlastyanax aurocaudatus* and a supraorbital is absent, likewise in the examined species of *Hemibrycon*.

*Hemibrycon divisorensis* possess a wide black asymmetrical spot covering the base of caudal-fin rays and extending to the tip of median caudal-fin rays, and a black band in the lower half of caudal peduncle from above of last anal-fin rays to caudal fin base, characters uncommon among the species of the genus. Among *Hemibrycon* species a black asymmetrical spot covering base of caudal-fin rays is found only in *H. surinamensis*, but black band in the lower half of caudal pe-

duncle is unique to *H. divisorensis*, here considered an autapomorphy to the species. All other *Hemibrycon* species have a dark midlateral body stripe extending to the tip of median caudal-fin rays, or have only the median caudal-fin rays symmetrically pigmented.

Mature males of *Hemibrycon divisorensis* possess bony hooks on rays of all fins, except the caudal fin. The presence of hooks on the anal- and pelvic-fin rays and sometime caudal-fin rays of males is often found in several genera and subfamilies of the Characidae (Azpelicueta & Garcia, 2000; Malabarba & Weitzman, 2003), and usually represents a secondary sexual character. However, the occurrence of bony hooks in all fins, including dorsal, caudal, and pectoral fins of males is uncommon in characids. Recently, Gonçalves *et al.* (2005) observed a positive correlation between mean gonadosomatic index of maturing and mature males and the number of anal-fin rays bearing hooks in *Aphyocharax anisitsi*, suggesting these hooks develop along with testes maturation, and once developed are retained by the males.

Recently some species of Tetragonopterinae (*sensu* Géry) have been described with bony hooks on rays of all fins in males, *e.g.* *Moenkhausia pankilopteryx*, and except in the caudal fin in *Astyanax elachylepis* and *Hypessobrycon hamatus* (see Bertaco & Malabarba, 2005). The presence of bony hooks on the dorsal- and pectoral-fin rays is unknown among the species of *Hemibrycon*.

Four species of *Hemibrycon* were described from the upper río Amazonas drainage in Peru: *H. jelskii* (Steindachner, 1877), *H. helleri* Eigenmann (1927), and *H. tridens* Eigenmann (1922) from río Ucayali drainage, and *H. huambonicus* (Steindachner, 1882) from río Huallaga drainage. *Hemibrycon divisorensis* differs from all these species by the number of branched anal-fin rays, number of scale rows above and below the lateral line, and number of lateral line scales.

**Comparative material.** *Astyanax aurocaudatus*, CAS 68647, 5 paratypes, río Cauca basin, Boquia, Quindío, Colombia. *Bryconamericus decurrens*, CAS 39542, paratype, town on the Dique de Cartagena between Cartagena and Calamar, Soplaviento, Bolívar, Colombia. *Bryconamericus tolimae*, FMNH 56258, 7 paratypes, río Magdalena drainage, Ibagué, Colombia. *Carlastyanax aurocaudatus*, IMCN 891, 8, río Quindío, Armenia, Colombia; MCP 41717, 4+2 c&s, río Cauca basin, Cauca, Colombia. *Hemibrycon beni*, CAS 44333, 29 syntypes, río Beni drainage, Espira, La Paz, Bolivia. *Hemibrycon boquiae*, FMNH 56260, 10 paratypes, Boquia, Colombia. *Hemibrycon carrilloi*, IAvH-P 7156, 22, río El Tigre, Unguía, río Atrato basin, Chocó, Colombia. *Hemibrycon colombianus*, CAS 44353, 5 paratypes, río Magdalena drainage, Quebrada Mararari, Santander, Colombia. *Hemibrycon dariensis*, USNM 78594, 8 paratypes, río Yape, Darien, Panama. *Hemibrycon helleri*, CAS 44354, 5 paratypes, río Comerciato, tributary of middle río Urubamba, Cuzco, Peru. *Hemibrycon jabonero*, USNM 121456, 601 paratypes, río Gonzáles, tributary of río Chama at La Gonzáles, Mérida, Venezuela. *Hemibrycon metae*, CAS 123727, holotype, at junction of río Guavio and río Upia, río Meta drainage, Guaiacaramo, Colombia. *Hemibrycon orcesi*, ANSP 75904, 2 paratypes, headwaters of río Macuma, tributary of río Morona, Ecuador. *Hemibrycon surinamensis*, MHNG 2182.59, 2 paratypes,

brownskreek sur 114 km railroad Paramacca River drainage, Suriname. MNHN 1980.1435, 1 paratype, Suriname. ZMA 100.347, 4 of 7 paratypes, Paramacca River drainage, brownskreek, km 14 of the railroad Paramaribo-Dam, Suriname. *Hemibrycon tridens*, CAS 44358, holotype, 24 leagues from Cuzco, Curuhuasi, Peru. *Tetragonopterus guppyi*, BMNH 1906.6.23.13-17, 5 syntypes, Trinidad. *Tetragonopterus huambonicus*, NMW 57531, syntype, Huambo, Peru. *Tetragonopterus jelskii*, NMW 57554, 5 syntypes, Huambo, Huánuco, Peru. *Tetragonopterus polyodon*, BMNH 1858.7.25.41, holotype, Guayaquil, Ecuador. *Poecilurichthys taeniurus*, ZMUC 966-968, 3 syntypes, Trinidad Island.

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## Conclusões Gerais

A monofilia de *Hemibrycon* é reconhecida com base na análise filogenética de 45 táxons e 123 caracteres relacionados à morfologia interna e externa. O monofiletismo de *Hemibrycon* é suportado por 12 sinapomorfias, e o gênero está relacionado aos gêneros incluídos no Clado A *sensu* Malabarba & Weitzman (2003).

As espécies de *Hemibrycon* ocorrem nas porções superiores dos rios das drenagens costeiras do mar do Caribe na Colômbia, drenagens do oceano Pacífico no Panamá, rios da Ilha de Trinidad e Tobago, rio Orinoco e lago Maracaibo na Venezuela, porções superiores dos rios da bacia do rio Amazonas na Bolívia, Brasil, Peru e Equador, drenagens costeiras da Guiana Francesa e Suriname, e na porção inferior da bacia do rio Tocantins, Brasil conforme esse estudo. A área de distribuição do gênero é ampliada para a bacia do rio Tocantins, com a ocorrência de *H. surinamensis*, o primeiro registro do gênero e espécie para este país.

São reconhecidas 21 espécies para o gênero *Hemibrycon*, incluindo cinco espécies novas, alcançando 117,3 mm de comprimento padrão. *Hemibrycon* n. sp. 1 da bacia superior do rio Ucayali, Peru; *Hemibrycon* n. sp. 2 de pequenos rios de drenagens costeiras do Mar do Caribe, Colômbia; *Hemibrycon* n. sp. 3 e *Hemibrycon* n. sp. 4 da porção média da bacia do rio Magdalena, Colômbia, e *Hemibrycon* n. sp. 5 da bacia superior do rio Madre de Dios, Peru. A posição taxonômica de *Bryconamericus decurrens* e *Hemibrycon orcesi* incluídas anteriormente em *Hemibrycon* é discutida, e comentários sobre duas espécies descritas recentemente, *H. microforma* Román-Valencia (2007) e *H. pautensis* Román-Valencia (2006), são apresentados. Novos sinônimos são propostos para algumas espécies de *Hemibrycon*: *H. coxei* é sinônimo júnior de *H. polyodon*; *H. carrilloi* é sinônimo júnior de *H. dariensis* e *H. guppyi* é sinônimo júnior de *H. taeniurus*.

Com base na análise histológica e de microscopia eletrônica de varredura dos ovários e espermatozóides, as espécies de *Hemibrycon* não são inseminadoras, pois apresentam o núcleo espermático oval (aquaesperma), característica de espécies com fertilização externa e, também, não foi encontrada célula espermática nos ovários. Os machos de algumas espécies de *Hemibrycon* apresentam glândula branquial localizada nos filamentos mais anteriores do primeiro arco branquial.

Exemplares machos maduros das espécies de *Hemibrycon* possuem pequenos ganchos nos raios das nadadeiras dorsal, peitoral, pélvica e anal. Fêmeas maduras de *Hemibrycon boquiae* podem apresentar alguns ganchos nos raios das nadadeiras anal e ventral. Ambas as características são incomuns entre os caracídeos neotropicais.