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Redescription and osteology of *Hyphessobrycon compressus* (Meek) (Teleostei: Characidae), type species of the genus

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The type-species of *Hyphessobrycon* is redescribed and its osteology provided. *Hyphessobrycon compressus* is distinguished from its congeners by the 41-48 (mode 45) scales in the longitudinal series; 7-9 (mode 9) scales rows between the dorsal-fin origin and the lateral line, and absence of predorsal scales. Additional useful characters include the lack of spots on the body, a dorsal fin with a black spot, and an anal fin with two large, conspicuous hooks, and several other small hooks. *Hyphessobrycon milleri* is proposed as a junior synonym of *H. compressus*. The osteology of *H. compressus* is discussed in detail together with comments about phylogenetic relationships of *Hyphessobrycon sensu stricto*.

A espécie-tipo de *Hyphessobrycon* é redescrita, junto com sua descrição osteológica. *Hyphessobrycon compressus* é distinguido dos seus congêneres por possuir 41-48 (moda 45) escamas na série longitudinal, 7-9 (moda 9) séries de escamas entre a origem da nadadeira dorsal e a linha lateral, e pela ausência de escamas pré-dorsais. Caracteres adicionais úteis incluem a ausência de máculas no flanco, nadadeira dorsal com mácula preta e nadadeira anal com dois ganchos ósseos grandes e conspícuos e vários outros pequenos. *Hyphessobrycon milleri* é proposto como sinônimo júnior de *H. compressus*. A osteologia de *H. compressus* é discutida em detalhe, junto com comentários sobre as relações filogenéticas de *Hyphessobrycon sensu stricto*.

Keywords: Characiformes, *Hyphessobrycon compressus milleri*, *Hyphessobrycon sensu stricto*, Rosy tetra clade, Systematics.

Introduction

The Neotropical region shows a high degree of freshwater fish diversity (Reis, 2013). Almost all Neotropical fishes are endemic to this biogeographic region, as are several of their families (e.g., all New World characiform families sensu Oliveira et al., 2011, except for Alestidae) and at least one order (Gymnotiformes). Characidae (herein treated sensu Mirande, 2010) is the richest family of the Characiformes, but its intra and interspecific relationships remain unclear, with different alternative proposed hypotheses (Mirande, 2009, 2010; Javonillo et al., 2010; Oliveira et al., 2011). The most problematic genera in the Characidae are Astyanax Baird & Girard, Bryconamericus Eigenmann, Hemigrammus Gill, Hyphessobrycon Durbin, and Moenkhausia Eigenmann, all of which have been repeatedly considered to be polyphyletic.

Hyphessobrycon [from the Greek $\dot{v}\phi\dot{\eta}\sigma\sigma\omega v = \text{smaller}$, and $\beta \rho \nu \chi \omega = \text{to gnash the teeth, from } Brycon Müller &$ Troschel, a genus of the Characidae (Eigenmann, 1918:172)] was proposed by Durbin (in Eigenmann, 1908) as a subgenus of Hemigrammus with a short diagnosis: "this genus is a Hemigrammus with a naked caudal". The type species, by original designation, is *Hyphessobrycon compressus* (Meek, 1904), from El Hule, Oaxaca, río Papaloapan basin, Mexico, established by Durbin (in Eigenmann, 1908) together with the description of six new species: H. bentosi Durbin, H. compressus milleri Durbin, H. copelandi Durbin, H. melazonatus Durbin, H. panamensis Durbin, and H. serpae Durbin [(= H. eques (Steindachner)]. Eigenmann (1917) subsequently presented a key to the "The American Characidae", including more characters for the recognition of *Hyphessobrycon*: the lateral line is incompletely pored; the premaxillary teeth are in two series with five teeth

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in the inner series; the second (= third infraorbital sensu Weitzman, 1962) is separated from the preopercle ventrally; the presence of few maxillary teeth; a naked caudal fin, and the presence of an adipose fin. Eigenmann (1917) also commented, in a pre-cladistic context, that some of the genera diagnosed by these characters are possibly polyphyletic. In agreement with Eigenmann's first insight, Hyphessobrycon and other species-rich genera, such as Astyanax, Hemigrammus, and Moenkhausia, are now recognized as polyphyletic (Weitzman & Palmer, 1997; Mirande, 2010; Malabarba et al., 2012). In fact, the species of Hyphessobrycon demonstrate variation in form, color pattern, and size, including some species that do not share all of the characters proposed by Eigenmann (1917) to define the genus. For example, the lateral line is completely pored in some specimens of H. anisitsi (Eigenmann), H. auca Almirón, Casciotta, Bechara & Ruíz Díaz, H. luetkenii (Boulenger), and H. santae (Eigenmann); the adipose fin is absent in H. negodagua Lima & Gerhard, and H. taurocephalus Ellis; and a pseudotympanum is present in H. arianae Uj & Géry and H. elachys Weitzman.

Géry (1977) proposed artificial groups for the species of *Hyphessobrycon* and considered *H. compressus* to be a part of "the *Hy. compressus* group ("true" *Hyphessobrycon*) [sic]". This group contains the type species along with *H. milleri*, suggested by Géry (1977) as "the adult stage of *H. compressus*".

Weitzman & Palmer (1997) tentatively proposed the "rosy tetra clade", a group within *Hyphessobrycon* in which most species have deep, laterally compressed bodies; are usually less than approximately 40 mm SL as adults; have sexually active males with large, high dorsal fins, and elongate anterior anal-fin lobes in many species; and a mostly red or reddish brown body. Carvalho (2011) tested the monophyly of the "rosy tetra clade" within a phylogeny of the Characidae (*sensu* Mirande, 2010) and delimited a monophyletic group that includes most of the species cited by Weitzman & Palmer (1997) including *H. compressus*.

Hyphessobrycon compressus, as type species of genus, is "the name-bearing type of a nominal genus" (article 67.1 - International Comission on Zoological Nomenclature (ICZN), 1999). Consequently, it is crucial to known in detail the morphology and other characters of this species in order to understand intra generic phylogenetic relationships. We herein provide a detailed description of the osteology, morphometric, and meristic data for H. compressus, a poorly-known species and type species of one of the most species-rich genera of the Neotropical region.

Material and Methods

Measurements and counts follow Fink & Weitzman (1974) and Carvalho *et al.* (2010). Measurements were made point-to-point with a digital caliper on the left side of the specimen whenever possible, and are presented as percents of standard length (SL) or head length (HL). Counts, in the

description, are followed by their frequency in parentheses. including data for type and non-type specimens. An asterisk indicates the count of holotype of *Hyphessobrycon* compressus. The osteological description is based on 11 cleared and stained (c&s) specimens prepared according to Taylor & Van Dyke (1985). Osteological terminology followed Weitzman (1962), with modifications suggested by previous authors, i.e., anterior ceratohyal instead of ceratohyal (Zanata & Vari, 2005), posterior ceratohyal instead of epihyal (Zanata & Vari, 2005), autopalatine instead of palatine (Datovo & Vari, 2013), mesethmoid instead of ethmoid (Fink & Fink, 1981), vomer instead of prevomer (Zanata & Vari, 2005), and intercalar instead of opisthotic (Zanata & Vari, 2005). Vertebral counts included the four vertebrae of the Weberian apparatus and the fused PU1+U1 centra of the caudal skeleton as a single element. The patterns of circuli and radii were defined from scales sampled from the region between the lateral line and the insertion of pelvic fin. Catalog numbers are followed by the total number of specimens, number of specimens measured and counted in parentheses, and SL range of all specimens of the lot. In "Material examined" catalog numbers are followed by the total number of specimens, number of specimens measured and counted in parentheses, and SL range of all specimens of the lot (including c&s specimens, if any), when possible. Comparative material examined included also those material listed in Carvalho et al. (2010). Carvalho & Langeani (2013), and Carvalho et al. (2014). Institutional abbreviations followed Reis et al. (2003), with the addition of UFRGS - Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre. We follow the results of Malabarba et al. (2012: table 1) and Carvalho et al. (2014) for phylogenetic data and discussion according to matrix and characters of Mirande (2010).

Results

Hyphessobrycon compressus (Meek, 1904) Figs. 1-6; 9-22

Hemigrammus compressus Meek, 1904: 87, fig. 25 [original description, type locality: El Hule (Obispo), Oaxaca, río Papaloapan basin, Mexico].-Miller, 1907: 23 [listed].

Hyphessobrycon compressus milleri Durbin, in Eigenmann, 1908: 100 [original description, type locality: Los Amates, Guatemala]. NEW SYNONYM.

Hyphessobrycon compressus.-Durbin, in Eigenmann, 1908 [proposal of subgenus Hyphessobrycon and designation of Hemigrammus compressus Meek as type species].-Eigenmann, 1910: 436-437 [distribution].-Eigenmann, 1918: 172, 176, plate 24, fig. 1, plate 79, fig. 14 [redescription, analysis of types].-Géry, 1966: 223, 230, fig. 9, with legend in fig. 13 [analysis of holotype, figure of maxilla of one paratype and suggestion that genus could be restricted to its type species].-Géry, 1977: 478, 486 [image of jaws of one paratype; comments about genus Hyphessobrycon and its type species;

H. milleri as possibly junior synonym of H. compressus].-Zarske & Géry, 1997: 308, 310 [listed].-Weitzman & Palmer, 1997: 225-226 [comments about genus Hyphessobrycon and its type species; comparison with Hyphessobrycon milleri].-Lucena, 2003: 93 [comments about relationships of H. compressus with other species of Hyphessobrycon].-Miller, 2005: 157-158 [distribution and habitat].

Hyphessobrycon milleri.-Eigenmann, 1918: 177-178: (redescription, type designation).-Weitzman & Palmer, 1997: 226 (as possible synonym of *H. compressus*).

Diagnosis. Hyphessobrycon compressus is distinguished from all congeners by the number of scales in the longitudinal series (41-48, mode 45, vs. less than 40 on other species); the number of scales rows between the dorsal-fin origin and the lateral line (7-9, mode 9, vs. 6 or less, rarely 7), and the absence of predorsal scales (vs. scales present). Furthermore, H. compressus can be recognized by the

combination of a lack of humeral spots on body, presence of conspicuous bony hooks in anal fin (two large and several small), and hooks absent on pelvic fin.

Description. Morphometric data summarized in Table 1. Small size, maximum of 36.4 mm SL and 46.5 mm total length (AMNH 32275). Body compressed, moderately high, greatest body depth at vertical through dorsal-fin origin. Head profile triangular and rounded anteriorly from lateral view. Dorsal profile of head slightly convex anteriorly, nearly straight from posterior nostril to tip of supraoccipital spine. Dorsal profile of body slightly convex from posterior tip of supraoccipital to base of last dorsal-fin ray, then straight to adipose-fin origin. Ventral profile of body convex from tip of lower jaw to pelvic-fin origin, slightly convex from that point to anal-fin origin, and straight and posterodorsally slanted along of anal-fin base. Dorsal and ventral profile of caudal peduncle straight to slightly concave.



Fig. 1. Hyphessobrycon compressus, holotype, FMNH 4641, 31.2 mm SL, male, río Papaloapan, Oaxaca, Mexico. © FMNH Division of Fishes.





Fig. 2. *Hyphessobrycon compressus*, paratypes: (a) BMNH 1905.12.6.4-5, male, 31.5 mm SL; (b) MHNG 2181.076, male, 29.2 mm SL; (c) USNM 204387, male, 31.3 mm SL. Photos by James Maclaine (BMNH), Phillipe Wagneur (MHNG), and Sandra Raredon (USNM).

Mouth terminal, premaxillary dentary and approximately same length. Maxilla extending posteroventrally to anterior one-third of orbit almost to contact between second and third infraorbitals, and running approximately at 45 degree angle relative to longitudinal axis of body. Premaxilla short, approximately one-third size of maxilla (Figs. 3b, 4). Nostrils close to each other, anterior opening small and circular, posterior opening twice as large. Nostrils separated by skin flap almost covering posterior nostril. Frontals not united anteriorly, with a triangular fontanel; parietal fontanel large, extending from epiphyseal bar to supraoccipital spine. Eyes moderate in size, without conspicuous adipose evelid.

Premaxillary teeth in two rows: outer row with 1(46), 2(78), or 3*(19), uni- to tricuspid teeth; inner row with 6(89), 7*(55), or 8(4) tricuspid teeth (Figs. 3b, 4). Dentary with 4*(24), 5(96), or 6(30) large, tricuspid teeth, followed by 7(2), 8(3), 9(2), 10(2), or 11(1) smaller, conical teeth,

gradually becoming smaller than largest anterior tooth (Fig. 3c). Dorsal border of maxilla relatively straight. Maxilla with 3(27), 4(54), 5(35), 6*(18) or 7(6) tricuspid teeth along anteroventral margin (Fig. 3a). Central cusp the longest on all teeth.

Scales cycloid, relatively small, with few *radii* (2-7). *Circuli* distinct anteriorly and marginally (dorsal and ventral). Lateral line incompletely pored, pored portion extending to vertical through pelvic-fin origin, nearly straight. Perforated lateral-line scales 5(10), 6(32), 7(46), 8*(26), or 9(8). Longitudinal scales series including pored scales 41(15), 42(15), 43(19), 44(8), 45(13), 46*(11), 47(4), or 48(1). Scales rows between dorsal-fin origin and lateral line 7(6), 8(48), or 9*(67). Scales rows between lateral line and pelvic-fin origin 6(32), 7*(80), or 8(7). Predorsal scales absent. Scale sheath along anal-fin base with 3(2), 4(11), 5*(18), or 6(12) scales in single row. Circumpeduncular scales 16(15), 17*(38), or 18(11). Axillary scale present, approximately same size as body scales.

Table 1. Morphometric data for *Hyphessobrycon compressus*. H¹ = holotype of *Hyphessobrycon compressus* (FMNH 4641); H² = holotype of *Hyphessobrycon compressus milleri* (CAS 70115). N = number of specimens, SD = Standard Deviation.

| | | | Paratypes | | | | | Non-types | | | |
|------------------------------------|-------|-------|-----------|------------------|--------|-----|-----|-----------|------|-----|--|
| | H^1 | H^2 | N | Range | Mean | SD | N | Range | Mean | SD | |
| Standard length (mm) | 31.2 | 31.3 | 26 | 26.6-35.7 | 30.0 | - | 130 | 19.7-36.4 | 28.5 | - | |
| | | | Perc | ents of Standard | Length | | | | | | |
| Body depth | 39.0 | 41.0 | 26 | 36.2-40.7 | 38.7 | 1.2 | 130 | 29.0-41.6 | 35.2 | 2.8 | |
| Head length | 28.6 | 28.4 | 26 | 26.6-30.4 | 28.1 | 0.8 | 130 | 25.9-31.1 | 27.9 | 0.9 | |
| Head depth | 29.4 | 32.9 | 26 | 27.9-31.4 | 29.8 | 1.0 | 130 | 25.2-33.3 | 28.6 | 1.3 | |
| Predorsal length | 58.0 | 56.8 | 26 | 53.4-59.5 | 55.8 | 1.4 | 130 | 51.6-60.0 | 54.7 | 1.4 | |
| Prepelvic length | 47.1 | 49.0 | 26 | 45.7-50.2 | 47.6 | 1.2 | 130 | 44.0-51.3 | 47.1 | 1.3 | |
| Pelvic fin to anal distance | 14.6 | 14.6 | 26 | 11.4-17.4 | 14.4 | 1.1 | 130 | 11.6-18.7 | 14.5 | 1.0 | |
| Caudal peduncle depth | 10.3 | 10.6 | 23 | 9.2-10.8 | 10.0 | 0.5 | 130 | 8.0-11.2 | 9.4 | 0.6 | |
| Dorsal-fin base length | 13.9 | 14.3 | 26 | 12.9-14.5 | 13.8 | 0.5 | 130 | 12.0-15.8 | 13.6 | 0.8 | |
| Anal-fin base length | 33.9 | 31.8 | 25 | 29.0-35.7 | 32.8 | 1.4 | 130 | 29.0-37.1 | 33.1 | 1.4 | |
| Pectoral-fin length | 22.5 | 20.7 | 25 | 19.0-23.1 | 21.3 | 1.1 | 130 | 17.6-24.1 | 21.3 | 1.4 | |
| Pelvic-fin length | 19.7 | 20.7 | 25 | 18.6-22.8 | 20.8 | 1.0 | 129 | 17.0-22.7 | 19.7 | 1.4 | |
| Dorsal-fin length | 29.5 | - | 19 | 22.0-32.8 | 29.9 | 2.2 | 117 | 24.4-34.0 | 30.0 | 1.7 | |
| Anal-fin length | 19.1 | - | 19 | 20.1-25.5 | 22.7 | 1.5 | 122 | 19.9-28.0 | 23.4 | 1.8 | |
| Caudal peduncle length | 12.8 | 14.8 | 23 | 12.3-14.8 | 13.3 | 0.6 | 130 | 11.2-16.0 | 13.0 | 0.9 | |
| Dorsal fin to adipose-fin distance | 34.3 | 32.6 | 26 | 31.7-36.6 | 34.6 | 1.2 | 129 | 30.1-37.9 | 34.5 | 1.3 | |
| Eye to dorsal-fin origin | 43.1 | 41.4 | 26 | 33.4-43.4 | 41.3 | 2.0 | 130 | 36.4-45.6 | 39.7 | 1.5 | |
| Dorsal origin to caudal origin | 50.0 | 50.5 | 23 | 50.5-55.6 | 52.4 | 1.3 | 130 | 39.1-54.3 | 51.4 | 1.7 | |
| | | | Pe | rcents of Head I | ength | | | | | | |
| Interorbital width | 26.2 | 31.3 | 26 | 26.4-30.0 | 28.0 | 0.9 | 130 | 25.6-35.6 | 28.9 | 1.5 | |
| Snout length | 21.7 | 23.3 | 26 | 18.1-25.2 | 23.1 | 1.4 | 130 | 20.0-24.8 | 22.5 | 1.0 | |
| Orbital diameter | 42.1 | 37.2 | 22 | 37.9-44.8 | 40.1 | 2.0 | 127 | 38.3-46.4 | 42.9 | 1.8 | |
| Upper jaw length | 43.3 | 41.3 | 25 | 40.9-51.7 | 44.4 | 2.0 | 129 | 36.3-47.2 | 42.2 | 2.2 | |

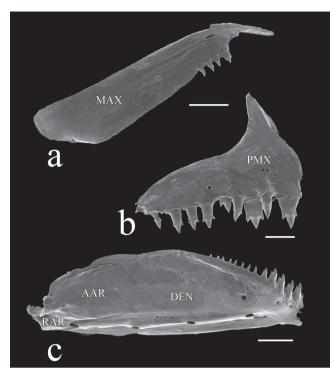


Fig. 3. *Hyphessobrycon compressus*, UFRGS 9683, female, 32.2 mm SL, right lateral view of (**a**) maxilla, (**b**) premaxilla, and (**c**) dentary. AAR = anguloarticular; DEN = dentary; MAX= maxilla; PMX = premaxilla; RAR = retroarticular. Scale bars of (**a**, **c**) = 0.5 mm and (**b**) = 0.2 mm.

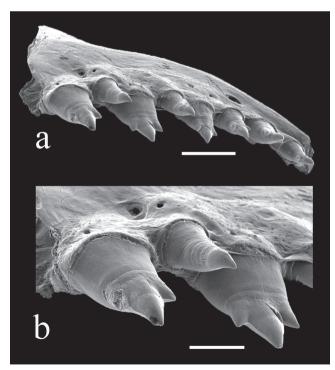


Fig. 4. Hyphessobrycon compressus, UFRGS 9683, female, 30.9 mm SL, ventrolateral view of premaxillary teeth in left premaxilla. (a) inner and outer row of premaxillary teeth, (b) detail of tooth form and alignment. Scale bars of (a) = 0.2 mm and (b) = 0.1 mm.

Dorsal-fin rays ii,8(3), 9*(141), or 10(1); first unbranched ray approximately 45% of second ray. Dorsal-fin origin at midlength of body or posterior to that point, at vertical through anterior one-third of pelvic-fin base. Base of last dorsal-fin ray at or slightly posterior of vertical through tip of pelvic fin; posterior to anal-fin origin. Tip of longest ray of adpressed dorsal fin extends to adipose-fin origin. Adipose fin slightly semicircular distally, greatest dimension less than orbital diameter; adipose-fin origin between base of fourth and fifth posteriormost branched anal-fin rays; its posterior tip extending to vertical through branched anal-fin end. Pectoral fin with i,10(16), 11*(82), 12(45), or 13(12) rays. Tip of pectoral fin extending beyond to pelvic-fin origin; profile slightly pointed and greatest medially (its base from vertical through opercular bony to horizontal through end portion of third infraorbital). Pelvic fin with i,6(2), 7*(145), or 8(5) rays. Pelvic-fin origin located anterior to vertical through dorsalfin origin; tip of pelvic fin extending to fourth branched analfin ray. Anal-fin rays iii*(71), iv(74), or v(7), 20(3), 21(2), 22*(45), 23(56), 24(35), or 25(13). Anal fin of males with large bony hooks; hooks absent in females. Anal-fin base nearly straight with first unbranched ray sometimes under muscles, but evident in cleared and stained specimens. Last unbranched ray and first two branched largest; remaining rays gradually decreasing in length to sixth branched ray; seventh through last rays approximately of same length. Caudal fin forked, lobes slightly rounded, similar in size, with i,9/8,i*(123) or i,10/8,i(1) rays. Caudal fin naked, other than for scales restricted to base. Basal scales same size as body scales. Dorsal procurrent caudal-fin rays 11(9) or 13(2). Ventral procurrent caudal-fin rays 8(4) or 9(6).

Branchiostegal rays 4(11). First gill arch with 8(1) or 9(1) gill rakers on epibranchial, 1(11) between epibranchial and ceratobranchial, 12(2) on ceratobranchial, and 2(7) or 3(1) on hypobranchial. Precaudal vertebrae 15(6) or 16(4). Caudal vertebrae 17(1), 18(9), or 19(1). Total vertebrae 33(7) or 34(3). Supraneurals 4(1) or 5(9), filiform, other than for some dorsal expansion.

Color in alcohol. Overall body color uniform greyish, yellowish to dusky, with scattered chromatophores uniformly distributed. Body without spots on longitudinal stripe. Inconspicuous, narrow longitudinal line along where epaxial and hypaxial muscles meet. Abdominal region usually less pigmented than remainder body. Iris black. Opercle, preopercle, and interopercle sometimes silvery. Dorsal fin with conspicuous black spot; spot more densely pigmented on proximal half of anterior rays. Spot extending to sixth branched ray and sometimes extending to distal tip of first branched rays. Dorsal and anal fins almost completely dark in mature males, with dense chromatophores concentration. Females with pigmentation less intense at half of anterior dorsal-fin rays and proximal length of anal-fin rays. Pectoral-, pelvic-, adipose-, and caudal fins normally dark gray or dark brown with scattered chromatophores on rays and interradial membrane. Some specimens with dark gray median caudal-fin rays (Figs. 1-2).

Color in life. Overall body color dark silvery to dusky (in reproductive males) dependent on conditions (stress, reproductive condition) (Greenfield & Thomerson, 1997) or light olivaceous (Meek, 1904). Caudal fin yellowish to reddish. Caudal peduncle without spot. Dorsal fin black,

chromatophores more densely concentrated along proximal half of anterior dorsal rays. This pattern sometimes observed on all fins. Pelvic fin darkish gray. Anal fin with brown or black stripe along midlength of rays; stripe extending along all of anal fin in mature males (Greenfield & Thomerson, 1997) (Fig. 5).

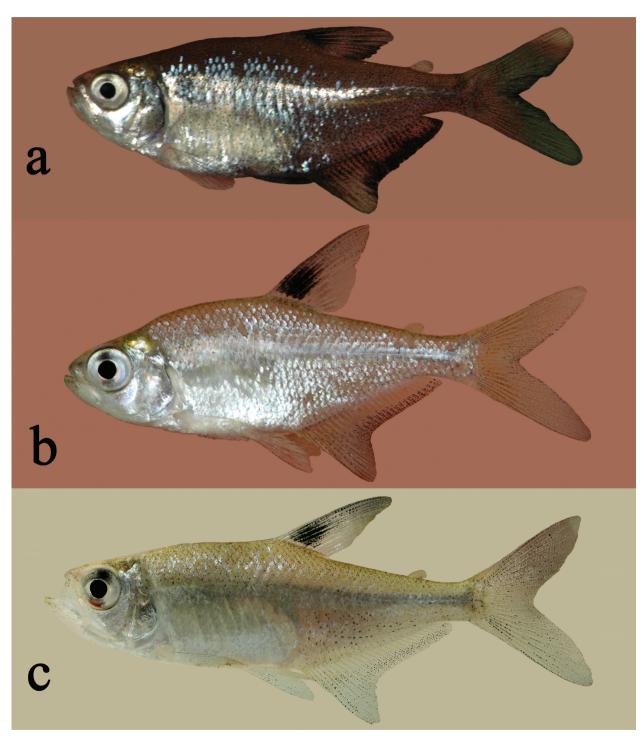


Fig. 5. Hyphessobrycon compressus just after collection, not preserved, left view: (a) nuptial male individual displaying darker color pattern, collected in drainage of río Coatzacoalcos basin, Veracruz Province, Mexico; (b) female from río Usumacinta basin, Chiapas Province, southern Mexico. (c) female from river near Teapa, Tabasco, Mexico. Background of images were edited and differences in fins color are due to back ground color of original images, normally made on hand. © Photos (a-b) by Marco Endruweit and (c) by Michael Tobler.

Sexual dimorphism. Mature males can be distinguished from females by the presence of bony hooks on anal fin and by the slightly less concave anterior distal margin of anal fin. Males over 28.0 mm SL have small, slightly developed bony hooks. Males larger than 32.0 mm SL have two pairs of large bony hooks. The first pair is larger, retrorse, fishhooklike and normally located at midlength of last unbranched ray. Length of hook larger than that of ray segment, with posterior tip of hook extending to adjacent ray. Second pair of large bony hooks slightly smaller than first and located immediately before first ramification of branched analfin ray. Small bony hooks (size smallest that ray segment) present on unbranched ray and anterior six branched rays of anal fin. Hooks located on distal portion of ray after ray ramification with one pair of bony hooks by ray segment. Tissue developed around large bony hooks of anal fin (Fig. 6). Gill glands (sensu Burns & Weitzman, 1996) on first gill arch in males and females were not macroscopically evident.

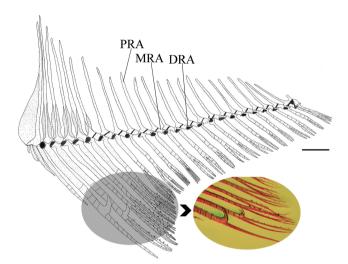


Fig. 6. *Hyphessobrycon compressus*, UFRGS 9683, male, 31.2 mm SL, anal fin and detail of bony hooks, left lateral view. DRA = distal radial; MRA = medial radial, and PRA = proximal radial. Scale bar = 1 mm.

Distribution. Hyphessobrycon compressus is distributed in many independent Atlantic slope rivers and streams of southern of Mexico, Belize, and Guatemala, an area known as Middle America (sensu Winker, 2011), in the Usumacinta Province (sensu Miller, 1966, fig. 3) (Fig. 7). It is the most northerly distributed species of Hyphessobrycon. Although there are numerous isolated populations within this range, our analysis revealed they together constitute an unique species without detected variations in meristic and morphometric data among these populations.

Common names. The species is commonly known as *billium*, Mayan tetra (Belize), Maya tetra, *sardinita plateada* (Mexico), *vihersulkatetra* (Finland), *pepesca*, *sardine* (Alvarado *et al.*, 2005; Froese & Pauly, 2014).

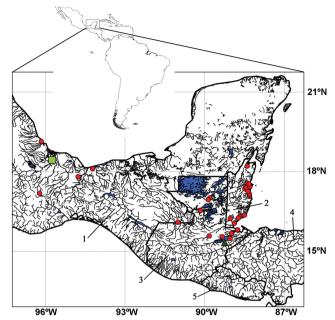


Fig. 7. Geographic distribution of *Hyphessobrycon compressus*. Green light square represent approximate locality of *Hemigrammus compressus* holotype and dark green triangle represent approximate locality of *Hyphessobrycon compressus milleri* holotype. Some symbols can represent more than one lot or locality. 1) Mexico, 2) Belize, 3) Guatemala, 4) Nicaragua, and 5) El Salvador.

Ecological notes. Hyphessobrycon compressus seems to be most frequently found in wetlands, where it is associated with macrophytes, over sandy and muddy substrates (Greenfield & Thomerson, 1997). It is rather sensitive to stress and dies quickly after capture (Endruweit, 2013). In a pool on right side of the road MEX 307, Nuevo Orizaba - Nuevo Reforma, río Usumacinta basin, Mexico, it was abundant in lentic water, with plenty of shade along the margin due to overhanging branches. The water was two meters maximum depth, without aquatic macrophytes, but with terrestrial vegetation hanging into the pool. The bottom was gravel 5 mm, loam and the water highly turbid and greenish (Endruweit, 2013). Mature males have an intense black color to the fins, especially the dorsal and anal fins, but it rapidly loose the coloration after removal of the water, becoming pale as females (Endruweit, 2013) (Fig. 5c). The species is commercialized in the aquarium trade (Alvarado et al., 2005).

Remarks. In the original description of *Hemigrammus compressus*, Meek (1904) mentioned only the type (F.C.M. 4641, now FMNH 4641), though there is a range of values for some measurement and meristic data in the description, *e.g.*, "(...) A. 25 to 27; scales 45 to 48; (...) the lateral line incomplete, on the 4 to 10 anterior scales (...) [*sic*]". Eigenmann (1918), in the brief redescription of this species, examined eight specimens in three lots: IU

10798 and IU 11126 (now combined in CAS 70114, with five specimens and MCZ 29911, with two specimens), and IU 10929 (now CAS 70116, with one specimen, and with doubts about the locality of collection of this lot and collector), all from Mexico, collected by S. E. Meek. There are, however, no records for these specimens (CAS 70114, CAS 70116, and MCZ 29911) as types.

Géry (1966) presented some data for the holotype of Hemigrammus compressus and mentioned the existence of paratypes, but did not list them (one is MHNG 2181.076; this specimen is cited and jaws illustrated in Géry, 1966: 223, but figure legend is mislabeled as Ceratobranchia binghami; the same figure is presented in Géry, 1977: 486 and labelled as a paratype of Hyphessobrycon compressus). In the catalog of FMNH fish types, Henn (1928) did not cite any types to H. compressus. Grev (1947), in turn, listed the holotype and 34 paratypes (23 from El Hule and 11 from Obispo). Ibarra & Stewart (1987) mentioned the holotype and 28 paratypes, from two localities (río Papaloapan and río Obispo). Both, Grev (1947) and Ibarra & Stewart (1987) did not mention the catalog number (with respective specimens number) for these types.

Information added to jar FMNH 105930 by Géry (November 1965) suggested that these specimens could be members of Astyanax. Marilyn Weitzman, in a subsequent analysis, confirmed Géry's information and inserted an undated note identifying the specimens as Astyanax sp. We identify these specimens as Astyanax cf. mexicanus. Vari & Howe (1991) commented that the two specimens in USNM 55728 (probably ex FMNH 4662, now missing – S. Raredon, pers. comm.) are two paratypes of Hemigrammus compressus (26.0-29.5 mm SL). Eschmeyer (2014) listed the holotype and 36 paratypes of Hemigrammus compressus as: BMNH 1905.12.6.4-5 (2); FMNH 4642 (17), FMNH 4662 (11); FMNH 105930 (ex FMNH 4642 - 2); MCZ 29911 (ex IU 11126 - 2), and USNM 55728 (2, missing). All these lots were collected by Meek in March and April 1903. According to ICZN (1999), Articles 72.4.1 and 72.4.1.1., all these specimens may be, in fact, paratypes of Hemigrammus compressus. Furthermore, we add also for type series two lots of California Academy of Science (CAS 70114 and 70116) and one lot at the National Museum of Natural History, Smithsonian Institution (USNM 204387). These were collected by Meek during March-April 1903, as described by Meek (1904), and should therefore be also considered paratypes of *H. compressus*.

Lima et al. (2003) mentioned the holotype of *Hyphessobrycon compressus milleri* as "whereabouts unknown". The specimen is housed in the California Academy of Sciences (CAS) and it was with an old identification label of *Hemigrammus compressus* (Fig. 8). The old collection number in the jar (IU 11255) was metallic and oxidized over time, impregnating the entire specimen with a ferrous color. After careful examination,

we found that the holotype of *Hyphessobrycon compressus* milleri is, indeed, a mature male of H. compressus, with two large bony hooks and black anal fin along its entire length (Fig. 8). The dense chromatophore concentration in this specimen proposed by Durbin, in Eigenmann (1908), as diagnostic for the species, is rather one of the characteristics of mature males of Hyphessobrycon compressus. Furthermore, the jaw length of the holotype of Hyphessobrycon compressus milleri ("maxillary considerably less than the length of the eye" [sic]), is also observed in H. compressus, as is the form of the third infraorbital ("second suborbital covering two-thirds of cheek, otherwise as in *H. compressus*" [sic]) (compare Figs. 1 and 8). Eigenmann (1918) suggested also that Hyphessobrycon milleri is very close to H. compressus, but deferred in having the dorsal-fin spot extending for entire fin.

Meristic data of the holotype of Hyphessobrycon compressus milleri are: ii,9 dorsal fin rays; caudal fin broken; iv,22 anal-fin rays, broken in some parts; i,7 pelvic-fin rays; i,11 pectoral-fin rays; 9 perforated lateral line scales; 46 scales in longitudinal series; 18 circumpeduncular scales; 9 scales rows between dorsalfin origin and lateral line; 7 scales rows between lateral line and pelvic-fin-origin; 4 scales in sheath along anal-fin base; predorsal scales absent in distinct series; 4 maxillary teeth; 2 premaxillary teeth in outer series; 7 premaxillary teeth in inner series; 6 dentary teeth; all tricuspid teeth. Second specimen of Hyphessobrycon milleri (= H. compressus), collected with the holotype but not cited in the original description, was also analyzed and is listed as non-type material of Hyphessobrycon compressus (CAS) 70113).

Osteological description

Neurocranium. Mesethmoid (Figs. 9-11). Median unpaired bone situated anterodorsally in neurocranium, with lateral portion adjacent to nasal; relatively flat and approximately trapezoidal; anterior portion rounded, bearing conical forward-projection to forming anteriormost portion of neurocranium; posterior margin with small notch, smooth or slightly wavy, with medial small triangular notch continuous with frontal fontanel; posteriorly posterolaterally contacting frontal; positioned dorsally to vomer; anterior third with two wing-like triangular lateral processes, overlying vomer.

Vomer (Figs. 10-11). Median unpaired bone, situated anteriorly in neurocranium, toothless, and approximately "T" shaped in frontal view; anterior margin concave and posterior region pointed. Anterior portion with adjacent cartilage along its dorsal and ventral margins; bordered ventrally by parasphenoid and anteriorly forming the roof of the mouth or palate; bordered anteriorly by mesethmoid and posteroventrally by lateral ethmoid.

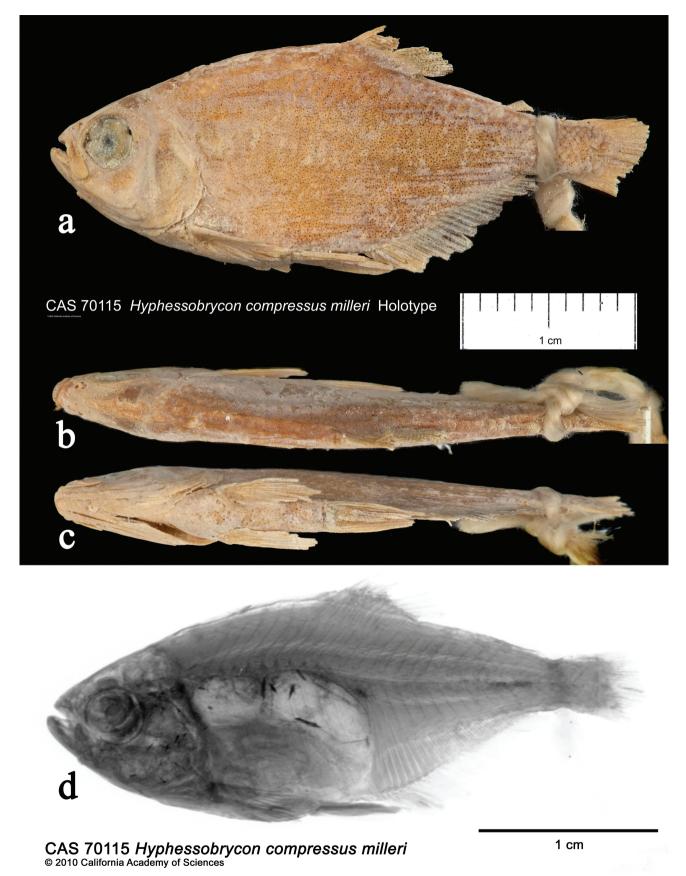


Fig. 8. *Hyphessobrycon compressus milleri*, holotype, CAS 70115, 31.3 mm SL, male, Los Amates, Guatemala. Views (a) left lateral, (b) dorsal, (c) ventral, and (d) radiograph of holotype. Photos by © California Academy of Sciences.

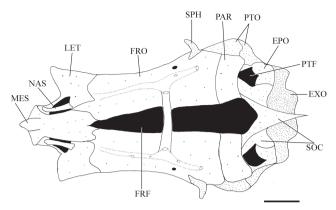


Fig. 9. Hyphessobrycon compressus, UFRGS 9683, 31.2 mm SL, male, neurocranium in dorsal view, anterior to left. EPO = epioccipital; EXO = exoccipital; FRF = frontal fontanel; FRO = frontal; LET = lateral ethmoid; MES = mesethmoid; NAS = nasal; PAR = parietal; PTF = posttemporal fossa; PTO = pterotic; SOC = supraoccipital; SPH = sphenotic. Scale bar = 1 mm.

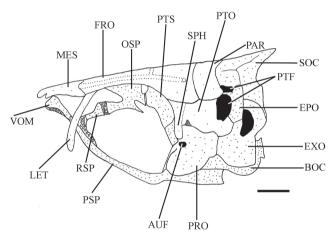


Fig. 10. *Hyphessobrycon compressus*, UFRGS 9683, 31.2 mm SL, male, neurocranium in left lateral view, anterior to left. AUF = auditory foramen; BOC = basioccipital; EPO = epioccipital; EXO = exoccipital; FRO = frontal; LET = lateral ethmoid; MES = mesethmoid; OSP = orbitosphenoid; PAR = parietal; PRO = prootic; PSP = parasphenoid; PTF = posttemporal fossa; PTO = pterotic; PTS = pterosphenoid; RSP = rhinosphenoid; SOC = supraoccipital; SPH = sphenotic; VOM = vomer. Scale bar = 1 mm.

Lateral ethmoid (Figs. 9-11). Paired bone, anteroposteriorly flat with lateral profile convex in dorsal view and with anteromedial bony projection; bordered anterodorsally by antorbital, ventrally by infraorbital 1 and posteriorly by orbit; bordered posterodorsally by frontal and dorsomedially by mesethmoid. Lateral ethmoid with bony extension posteromedially reaching anterior portion of parasphenoid near vomer; bony extension contacts ventromedial portion of rhinosphenoid.

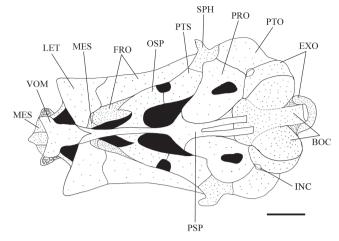


Fig. 11. *Hyphessobrycon compressus*, UFRGS 9683, 31.2 mm SL, male, neurocranium in ventral view, anterior to left. BOC = basioccipital; EXO = exoccipital; FRO = frontal; INC = intercalar; LET = lateral ethmoid; MES = mesethmoid; OSP = orbitosphenoid; PRO = prootic; PSP = parasphenoid; PTO = pterotic; PTS = pterosphenoid; SPH = sphenotic; VOM = vomer. Scale bar = 1 mm.

Frontal (Figs. 9-11). Paired bone covering circa 70% of dorsal surface of neurocranium; anteromedial portion contacting mesethmoid and anteroventrally overlying lateral ethmoid, with limited sculpturing on dorsal surface; posteriorly contacting parietal and laterally sphenotic. Frontal bordered anteroventrally by lateral ethmoid. posteroventrally by sphenotic and pterotic, ventromedially by orbitosphenoid and pterosphenoid. Each frontal medially delimits lateral border of cranial fontanel; fontanel divided in two by epiphyseal bar: anterior and posterior fontanels of approximately equal lengths. Anterior frontal fontanel elongate and approximately triangular; anterior portion bordered by posterior portion of mesethmoid. Posterior portion of cranial fontanel approximately rectangular and also separating parietals. Dorsolateral surface of frontal bears portion of cephalic laterosensory system which extends from anterior portion along median portion of bone, towards, but not contacting parietal. Proximate to epiphyseal bar canal has dorsomedial branch directed towards bar. Ventrally frontal with thin laminar expansion that connects with dorsal surface of orbitosphenoid and pterosphenoid.

Parietal (Figs. 9-10). Paired relatively trapezoid bones, slightly convex anteriorly and concave posteriorly. Bordered anteriorly by frontal, posteriorly by epioccipital and supraoccipital and ventrolaterally by pterotic. Parietals separated by approximately rectangular parietal fontanel. Small sculpturing sometimes present on dorsal surface. Parietal anteriorly overlap frontal and posteromedially overlap anterior region of supraoccipital. Parietal laterosensory branch absent.

Supraoccipital (Figs. 9-10). Median unpaired bone situated posterodorsally in neurocranium. Bordered anterodorsally by parietal and delimiting posterior margin of parietal fontanel. Bordered ventrolaterally by epioccipital and ventrally by exoccipital. "V" shaped in dorsal view, with posteriorly pointing indentation forming acute angle and supraoccipital spine.

Epioccipital (Figs. 9-10). Paired bone situated posteriorly in neurocranium; bordered anteriorly by parietal and pterotic; dorsally by supraoccipital; ventromedially by exoccipital and pterotic. Bony anterior projection of epioccipital toward parietal and pterotic divides the posttemporal fossa into dorsal and ventral portions: small dorsal portion about half diameter of ventral portion; bordered dorsally by supraoccipital, anteriorly by parietal and posteriorly by epioccipital. Ventral portion bordered laterally by pterotic and ventromedially by exoccipital and epioccipital.

Exoccipital (Figs. 9-11). Paired bone forming posteroventral portion of neurocranium; bordered dorsally by supraoccipital; laterally by ventromedial portion of epioccipital, and laterally by posteroventral portion of pterotic. Posteroventral portion of exoccipital with convex lateral projection, forming dorsolateral part of lagenar capsule. Ventral portion of capsule formed by basioccipital. *Magnum* foramen in dorsolateral portion of lagenar capsule serves for passage of tenth cranial nerve (*vagus*).

Intercalar (Fig. 11). Small, and thin, oval shaped paired bone, overlying narrow part of exoccipital and pterotic and with anterior portion near prootic.

Basioccipital (Figs. 10-11). Median unpaired ventrally positioned bone, forming posteroventral base of neurocranium. Lateral region globular and anteroventral portion laminar. Bordered dorsally by exoccipital, anteroventrally by parasphenoid; ventrolaterally by prootic and posteriorly by first vertebra. Anterior portion of basioccipital form ventral portion of lagenar capsule and posterior region forming saccular capsules for *asteriscus* otolith.

Pterotic (Figs. 9-11). Paired bone situated posterolaterally in neurocranium. Bordered anteriorly by sphenotic, anterodorsally by frontal, posterodorsally by parietal; ventrally by prootic and exoccipital. Anteroventrally pterotic overly hyomandibula, and posteriorly inferior posttemporal fossa of epioccipital. Pterotic bears two cylindrical elevations corresponding to pterotic branch of cephalic system and lateral projection of tubule of horizontal semicircular canal, extending from its anterodorsal margin to its posteroventral margin. Anteroventral portion of pterotic continuous with hyomandibular fossa of sphenotic. Dorsal and ventral portions of pterotic with some small foramina.

Sphenotic (Figs. 9-11). Paired bone, approximately quadrangular from lateral view and narrowing ventromedially into laminar sphenotic spine, distally contacts infraorbital 6. Sphenotic situated ventral to frontal and normally contacting frontal laterosensory system. Sphenotic bordered anteriorly by pterosphenoid, ventrally by prootic and posteriorly by pterotic. Medially portion of each sphenotic bears part of anterior vertical semicircular canals which extends along dorsoventral axis of bone.

Prootic (Figs. 10-11). Paired bone of complex laminar form bordering posteroventral margin of eye socket. Bordered anterodorsally by pterosphenoid and sphenotic, posterodorsally by pterotic, ventrally by parasphenoid, and posteriorly by exoccipital and basioccipital. Ventrally, with relatively large foramen (auditory foramen), ventrally sometimes with additional smaller opening. Anterodorsal surface with laminar projection contacting posteroventral surface of pterosphenoid. Prootic ventrally bordered by posterior portion parasphenoid with thickening of prootic anteroventrally.

Parasphenoid (Figs. 10-11). Unpaired elongate median bone, situated along ventralmost portion of neurocranium. Bordered anteriorly by vomer, posterodorsally by prootic and basioccipital. Parasphenoid with median ventral keel ventrally anterior to area of contact with prootic; posteroventrally it bears two laminar processes that may bifurcate distally. Mid-anterior portion of parasphenoid larger than mid-posterior portion of bone.

Pterosphenoid (Figs. 10-11). Paired laminar bone, trapezoidal from lateral view, with irregular margins, and composing together with orbitosphenoid and rhinosphenoid part of the dorsal portion of ocular cavity. Bordered dorsally by frontal, posteriorly by sphenotic, posteroventrally by prootic and anteriorly by orbitosphenoid. Small foramen of trochlear nerve present at junction of orbitosphenoid with pterosphenoid. Small foramina sometimes present on surface of bone.

Orbitosphenoid (Figs. 10-11). Unpaired median bone situated in ventromedial portion of neurocranium under frontal and posterior to mesethmoid. Bordered anterodorsally by frontal and posteriorly by pterosphenoid. With laminar process extending ventrally towards anterior of neurocranium, broad posteriorly and narrowing anteriorly. Dorsal portion broader than ventral region, with lateral wings in ventral view and anterior portion narrower.

Rhinosphenoid (Fig. 10). Small unpaired laminar bone approximately trapezoid-shape, with dorsal portion slightly concave and ventral portion relatively straight. Posterior portion relatively higher than anterior. Bordered anteriorly by medial projection of lateral ethmoid along

cartilage joint; posteriorly by orbitosphenoid, also with cartilage. Lacks dorsal expansion forming bony bridge among olfactory nerve.

Nasal (Fig. 9). Paired tubular bone along anterolateral margin of neurocranium, and parallel to mesethmoid. Bordered anteriorly by premaxilla and posteriorly by frontal. Each nasal carries a portion of laterosensory system (nasal branch), continuation of supraorbital branch in frontal. Anterior and posterior portions of nasal with circular openings.

Asteriscus otolith (Fig. 12). Paired bilaterally symmetrical calcareous concretion and largest otolith in ostariophysans. Round to ovoid with small projections along its border, except for inner margin. Otolith lies in capsule formed by exoccipital and basioccipital. Other otoliths (lapillus and sagitta) could not be observed and presented because of their thin nature.

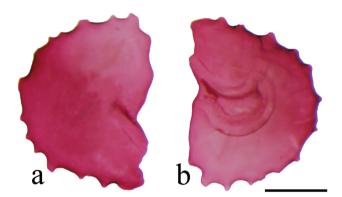


Fig. 12. *Hyphessobrycon compressus*, UFRGS 9683, 30.7 mm SL, female, *asteriscus* otolith, (a) left, ventral view and (b) right, dorsal view. Scale bar = 0.5 mm.

Infraorbital series. Antorbital (Fig. 13). Paired flat bone. Antorbital is slender dorsally and slightly expanded ventrally. Situated between the lateral ethmoid and posterior opening of the nostril just above infraorbital 1, with ventral terminations at horizontal through dorsal border of maxilla.

Infraorbitals (Fig. 13). *Hyphessobrycon compressus* has normally six flattened infraorbitals (IO) surrounding orbit.

Infraorbital 1 (IO1) small, relatively trapezoid, with anteroventral margin bordered by maxilla. Its anterodorsal margin varying from straight to approximately rounded; ventral margin extending to anterior margin of lateral ethmoids. IO1 with small openings in surface but without laterosensory canal segment.

Infraorbital 2 (IO2) larger than IO1; form overall trapezoid, with anterior margin anterodorsally inclined; posterior portion twice as high as anterior portion. Narrow laterosensory canal running along dorsal margin of posterodorsal border.

Infraorbital 3 (IO3) largest element in series; with posteroventral border slightly rounded and anteroventral margin irregular. Anterior portion of IO3 overlies mesopterygoid, metapterygoid, and quadrate; posterior portion overlies symplectic and part of hyomandibula; ventral portion overlies anterior arm of preopercle. Ventralmost portion not contacting laterosensory canal of the preopercle. Laterosensory canal running along anterodorsal margin of bone.

Infraorbital 4 (IO4) approximately trapezoidal with laterosensory canal limited to anteroventral portion. IO4 situated over central portion of hyomandibular.

Infraorbital 5 (IO5) approximately same height IO4, but anteroposteriorly narrower. Dorsal and ventral margins rounded. IO5 situated over anterior half of hyomandibular, and posteroventrally in contact with sphenotic.

Infraorbital 6 (IO6) relatively elongate, rounded dorsally and ventrally and overlying hyomandibula; adjacent to dorsal margin of lateral wing of sphenotic. No laterosensory canal present.

Infraorbitals 4, 5, and 6 variable in form and presence: IO4, IO5, and IO6 sometimes absent; IO4 and IO5 may be fused and separate from IO6, or IO4, IO5, and IO6 fused.

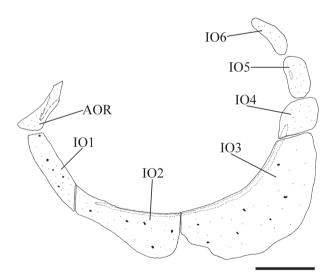


Fig. 13. *Hyphessobrycon compressus*, UFRGS 9683, 31.1 mm SL, female, antorbital and infraorbital series, left lateral view, anterior to left. AOR = antorbital; IO (1 to 6) = infraorbitals. Scale bar = 1 mm.

Jaws. Upper jaw. Premaxilla (Figs. 3b, 4). Paired robust bone, at anterior of skull; dorsally narrow and ventrally expanded, with teeth along ventral margin. Bordered posteriorly by mesethmoid and nasals, and laterally by maxilla. Approximately triangular in lateral view. Bears two rows of teeth, almost overlapping along tooth bases. Outer row teeth usually unicuspid, slightly shorter or almost same size as teeth of inner series; when tricuspid, lateral cusps small. Outer row tooth bases juxtaposed or almost along base of inner row teeth; median cusps of

outer row teeth not aligned. Inner row teeth tricuspid, with central cusp about two or three times length of lateral cusps, usually aligned. Replacement teeth situated behind teeth of inner row.

Maxilla (Fig. 3a). Approximately laminar, and trapezoid to quadrangular paired bone; except near anterior margin, overall relatively rounded. Bordered anteriorly by premaxilla and posterodorsally by antorbital and IO1; ventral half of maxilla overlaps dentary. Anteroventral portion bears normally tricuspid (sometimes unicuspid) teeth. First tooth of maxilla located near last tooth of inner row of premaxilla.

Lower jaw. Dentary (Fig. 3c). Rather robust and long paired bone. Dorsally convex and ventrally almost straight. Bordered posteriorly by anguloarticular and retroarticular; dorsally by maxilla and IO2; posteromedially by coronomeckelian. Laterosensory system with some ventral openings running along ventrolateral surface. Horizontal host bony bridge, bordered anteriorly by dentary, anguloarticular, and Meckelian cartilage at midlength of bone. Small, laminar coronomeckelian near anguloarticular. Single tooth row on dentary. Anteriormost teeth tricuspid, largest, then gradually decreasing posterior to fourth or fifth tooth, then followed by small unicuspid teeth. Central cusp two to three times the size of lateral cusps, and curved inwardly towards mouth. Replacement teeth located behind largest teeth.

Anguloarticular (Fig. 3c). Paired bone forming posterior portion of lower jaw. Anterior portion highest, with median concavity anteriorly. Posterior margin slightly rounded with ventral concavity. Bordered anteriorly by dentary, posteroventrally by retroarticular, posteriorly by quadrate via condyle and anteromedially by coronomeckelian. Laterosensory system canal segment communicates posteriorly with preopercular canal.

Retroarticular (Fig. 3c). Paired variably shaped bone (triangle, trapezoid), slightly larger than coronomeckelian. Bordered anteroventrally by dentary, dorsally by anguloarticular and posteriorly by interopercle.

Coronomeckelian bone. Paired small, relatively oval bone with pointed margin, situated on medial portion of anguloarticular and Meckelian cartilage (like in Mirande, 2010, fig. 58).

Suspensorium. Metapterygoid (Fig. 14). Paired largely laminar hourglass-shaped bone, with posteromedial foramen and small ovoid openings near hyomandibular. Bordered anteriorly by mesopterygoid, anteroventrally by quadrate, posterodorsally by hyomandibular and posteroventrally by symplectic. Anterior portion sometimes with foramen on the inner surface of the bone.

Mesopterygoid (Fig. 14). Paired laminar bone, approximately triangular in form. Bordered anteriorly by autopalatine, ventrally by ectopterygoid and posteriorly by metapterygoid and quadrate. Narrow anteriorly and wide posteriorly. Ventrolateral margin running parallel to ectopterygoid. Infraorbitals 2 and 3 overlap with posteroventral portion of mesopterygoid.

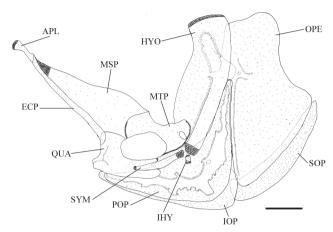


Fig. 14. *Hyphessobrycon compressus*, UFRGS 9683, 31.2 mm SL, male, suspensorium in left lateral view, anterior to left. APL = autopalatine; ECP = ectopterygoid; HYO= hyomandibula; IHY = interhyal; IOP = interopercle; OPE = opercle; POP = preopercle; QUA = quadrate; SOP = subopercle; SYM = symplectic; MSP = mesopterygoid; MTP = metapterygoid. Scale bar = 1 mm.

Ectopterygoid (Fig. 14). Paired flat, narrow toothless bone, adjacent to mesopterygoid. Bordered anteriorly by autopalatine and posteriorly by quadrate. Gradually narrows anteriorly. Along with mesopterygoid forms anteroventral bone wall of orbital region and posteromedial wall of oral cavity.

Autopalatine (Fig. 14). Paired small, laminar, edentulous, relatively trapezoidal bone. Bordered anteriorly by premaxillae anterolateral of vomer; posteriorly by ectopterygoid and mesopterygoid.

Hyomandibular (Fig. 14). Paired elongate, laminar bone. Bordered dorsally by neurocranium, proximate to pterotic, sphenotic, and prootic; posterodorsally by opercle, ventrally by metapterygoid, symplectic, and interhyal. Posterodorsal margin adjacent to anterior margin of preopercles reinforced (two-thirds of ventral portion), posterior one-third with convex projection bordered by anterodorsal portion of preopercle (ventral half) and opercle (dorsal half).

Quadrate (Fig. 14). Paired slightly laminar bone. Bordered anterodorsally by mesopterygoid and metapterygoid along thin portion, posterodorsally by metapterygoid also along thin region; anteroventrally by anguloarticular, ventromedially by preopercle and interopercle, posteroventrally by symplectic

and metapterygoid. Anterior portion large, posterior narrow in form recumbent "L", with convex posteroventral process.

Symplectic (Fig. 14). Paired cylindrical, elongate, relatively straight bone. Anterior half bordered by quadrate and posterodorsal half by preopercle. Firmly attached anteriorly to quadrate.

Opercular Series. Opercle (Fig. 14). Paired bone, higher than long. Dorsal margin slightly posterodorsally inclined. Posterior margin slightly concave posterodorsally, then convex, and then straight, nearly to posteroventrally. Anterior margin relatively straight throughout its length; posterior margin extending to cleithrum; bordered anteriorly by hyomandibular and preopercle; ventrally by interopercle and subopercle. Medial bony ridge present at margin of anterior one-third (like in Mirande, 2010: fig. 75).

Subopercle (Fig. 14). Paired approximately trapezoidal bone, dorsally concave and ventrally convex, with posterior portion relatively pointed to rounded and posterodorsally inclined. Anterior margin straight. Dorsal portion underlying the opercle and anterior region of interopercle.

Interopercle (Fig. 14). Paired approximately triangular bone, anterior portion narrow and posterior margin straight to slightly convex. Overlies ventral portion of preopercle.

Preopercle (Fig. 14). Paired half-moon shaped bone, with anterior and posterior portions relatively pointed. Dorsal and ventral portions with slight surface sculpturing. Laterosensory canal with irregular margins running through middle portion of bone. Three to five openings present in ventral portion of laterosensory canal. Dorsal portion of canal between hyomandibular and opercle; ventral portion overlying interopercle.

Hyoid arch. Interhyal (Figs. 14-15a). Paired small cylindrical bone, with cartilaginous inner portion. Bordered ventrally by anterior portion of hyomandibular and posteriorly by symplectic, anteriorly by posterior portion of ceratohyals and posteriorly by hyomandibular and symplectic.

Posterior ceratohyal (Fig. 15a). Paired flat, approximately triangular bones, with rounded margins. Elongate oval foramen present anteromedially, associated with canal extending into dorsomedial portion of anterior ceratohyal. Bordered anteriorly by anterior ceratohyal and posteriorly by interhyal. Ventromedially connected with fourth branchiostegal ray.

Anterior ceratohyal (Fig. 15a). Paired approximately trapezoidal bone, anteriorly narrower; concave along dorsal and ventral margins, with two notches along ventral margin. Bordered anteriorly by dorsal and ventral hypohyal and

posteriorly by posterior ceratohyal. First two branchiostegal rays anteromedially connected to small grooves along ventral margin (grooves barely apparent in some specimens); third branchiostegal ray posteriorly near posterior ceratohyal, ventral to medial surface of ceratohyal.

Dorsal and ventral hypohyal (Fig. 15a). Paired small bone. Dorsal hypohyal relatively ovoid, bordered ventrally by ventral hypohyal and posteriorly by anterior ceratohyal. Ventral hypohyal in shape of inverted "Y". Bordered dorsally by basihyal and by anterior portion of first basibranchials. Bifurcate ventral portion bordered anteriorly by dorsal portion of dorsal hypohyal and anterior portion of anterior ceratohyal and posteriorly by anteroventral portion of anterior ceratohyal. Small oval opening present internally in ventral hypohyal.

Branchiostegal rays (Fig. 15a). Four paired flat bones, bordered dorsally by ceratohyals (first three by anterior ceratohyal and last by posterior ceratohyal). Rays gradually increasing in length from posteriorly last. Convex ventral portions of rays lie along isthmus. Posterior margin of third and fourth branchiostegals reaching posteriorly to pectoral girdle.

Urohyal (Fig. 15b). Unpaired, approximately triangular flat bone. Posterior portion with large median groove and concave; anterior portion approximately trapezoidal. Ventromedially portion flattened, and contacting basibranchials.

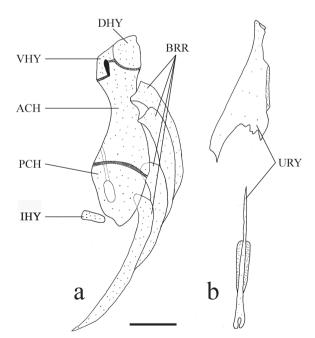


Fig. 15. *Hyphessobrycon compressus*, UFRGS 9683, 31.2 mm SL, male, (a) left hyoid skeleton in dorsal view, and (b) left lateral and dorsal views of urohyal. ACH = anterior ceratohyal; BRR = branchiostegal ray; DHY = dorsal hypohyal; IHY = interhyal; PCH = posterior ceratohyal; URY = urohyal; VHY = ventral hypohyal. Scale bar = 1 mm.

Branchial arches. Basihyal (Fig. 16). Unpaired elongate, relatively cylindrical bone with anterior portion expanded and cartilaginous. Bordered posteriorly by first basibranchial and by anterodorsal portion of anterior ceratohyal. Anterior tip of basihyal is anteriormost portion of branchial arch.

Pharyngobranchials (Fig. 16a). Small bones at anterior limit of each epibranchial. First pharyngobranchial variable in form (triangular, trapezoidal, quadrangular) with cartilaginous caps on anterior and posterior margins. Second pharyngobranchial approximately triangular, with 1-3 very small conical teeth ventrally. Third pharyngobranchial variable in form (triangular, trapezoidal) with teeth along anteroventral half. Fourth pharyngobranchial trapezoidal, cartilaginous, with teeth ventrally, forming the upper pharyngeal plate. Pharyngobranchials gradually increase in size from first to fourth.

Epibranchials (Fig. 16a). Elongated bones of variable form. First three elongate, fourth broad, forming the dorsal portion of each branchial arch. First two epibranchials longest, with uncinate process; third epibranchial with small lateral process in its posterior third; fourth epibranchial with pronounced lateral process, approximately triangular. Gill rakers present on all epibranchials. Epibranchial articulate ventrally with ceratobranchials and medially with pharyngobranchials.

Ceratobranchials (Fig. 16a). Elongate narrow bones of similar form and forming major ventral portion of gill arches. Articulate anteriorly with corresponding hypobranchial and posteriorly with epibranchial (except fifth element). Ceratobranchials gradually decrease in length posteriorly last. First two ceratobranchials with one series of gill rakers and last two with two rows. Dorsolateral row about twice the length of ventrolateral row. Fifth ceratobranchial largest, with gill rakers along anterodorsal margin and with anteroventral half formed by triangular process bearing tiny conical teeth dorsally.

Hypobranchials (Fig. 16a). Small paired, trapezoidal shaped bone with three in series. First hypobranchial with small concavity dorsally and articulated with first basibranchial and first ceratobranchial. Second hypobranchial with more pronounced concavity anterodorsally, and articulated with second basibranchial and second ceratobranchial. Third hypobranchial smaller and narrower anteriorly articulated with third basibranchial and third ceratobranchial. All hypobranchials rakers on ventral surface.

Gill rakers (Fig. 16b). Setiform/conical, with calcified bases on all gill arches. Rakers increase in length from posterior of epibranchial to medial of ceratobranchial and then gradually decreasing thereafter. Small denticles covering ventral half of each raker.

Basibranchials (Fig. 16a). Unpaired, narrow, cylindrical bones with four elements in series situated along median of gill arch. Bordered anteriorly by basihyal and posteromedially by first hypobranchial. Second basibranchial larger than first and bordered anteriorly by first basibranchial and posteriorly by third basibranchial. Elongate third basibranchial, approximately same length as second basibranchial, gradually narrowing posteriorly. Bordered anteriorly by second basibranchial and posteriorly by fourth basibranchial. Fourth basibranchial smallest in series and surrounded by a cartilaginous structure extending to lower pharyngeal plate; bordered anteriorly by third basibranchial and posteriorly by fourth ceratobranchial; cartilaginous plate gradually narrowing posteriorly.

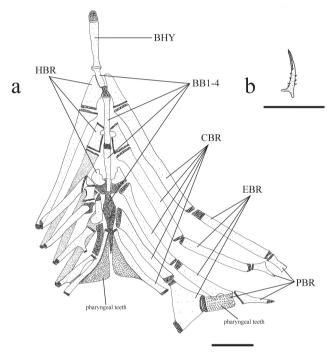


Fig. 16. *Hyphessobrycon compressus*, UFRGS 9683, 31.2 mm SL, male, (a) branchial skeleton in dorsal view, and (b) detail of second branchial raker of epibranchial 1. BB1-4 = basibranchials 1-4; BHY = basihyal; CBR = ceratobranchial (1-5); EBR = epibranchials (1-4); HBR = hypobranchials; PBR = pharyngobranchials (1-4). Scale bar = 1 mm.

Weber apparatus (Fig. 17). Neural complex approximately triangular with concave posterior margin; base contact third and fourth neural arches. First and second neural arches modified to components of Weberian apparatus. Neural arch 3 short but horizontally elongate and situated below of neural complex with transverse process. Fourth neural arch with posterodorsal concavity, immediately below of neural spine. Tip of first neural spine (corresponding to fourth vertebra), toward posterior portion of neural complex. Tripus triangular, convex along margins and with angular corners. Claustrum small, rather reniform with pointed tips and situated under the scaphium. Scaphium ovoid,

posterodorsally inclined, and situated anterior to third neural arch. Intercalarium elongate and relatively pointed anteriorly and posteriorly; dorsally concave ventrally convex, and about three times size of claustrum.

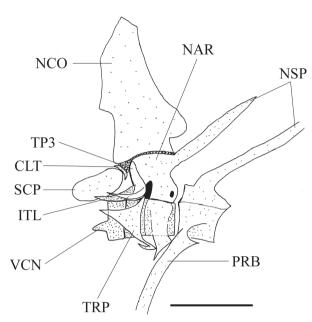


Fig. 17. *Hyphessobrycon compressus*, UFRGS 9683, 31.2 mm SL, male, Weberian apparatus in left lateral view, anterior to left. CLT = claustrum; ITL = intercalarium; NAR = neural arch; NCO = neural complex of Weberian apparatus; NSP = neural spine of fourth and fifth vertebrae; PRB = pleural rib; SCP = scaphium; TP3 = transverse process of third vertebra; TRP = tripus; VCN = vertebral centrum. Scale bar = 1 mm.

Vertebral column. Precaudal vertebrae (Fig. 18a). Precaudal vertebrae bear neural spine, neural canal, vertebral centrum, and associated with pleural ribs. Fifth to 14th or 15th vertebrae of similar form with one pair of neural prezygapophyses and one pair of neural postzygapophyses, one neural arch, one neural spine, and associated with pleural ribs. Haemal arch with haemal canal of 15th or 16th vertebra associated with small pleural rib. Pleural ribs expanded dorsally, and bordered gradually by lateral surface of each parapophysis then narrowing ventrally.

Caudal vertebrae (Fig. 18b). Each caudal vertebrae formed by neural spine, neural canal, vertebral centrum, haemal canal, and haemal spine. Sixteenth or 17th through 29th or 30th vertebra of similar form with one pair of neural prezygapophyses and one pair of neural postzygapophyses. Last four caudal vertebrae with diminute pre- and postzygapophyses.

Intermuscular bones (Fig. 18). Epineurals between the neural spines range in number between 27(4), 28(1) to 29(4), first through third epineurals not forked, fourth to 24th forked anteriorly, and posterior elements to the hypural plate elongate and flattened. Epipleurals haemal intermuscular

bones 17(1), 18(6), or 19(2) with first and second elongate and not forked; third to 10th anteriorly forked, and posterior elements to hypural plate elongate, and flattened.

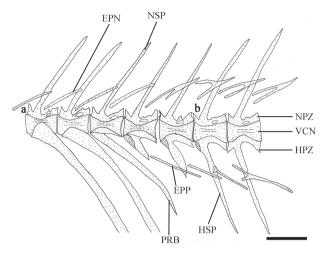


Fig. 18. *Hyphessobrycon compressus*, UFRGS 9683, 31.1 mm SL, female, posterior precaudal and anterior caudal vertebrae in left lateral view, (a) precaudal vertebrae and (b) caudal vertebrae.; EPN = epineural; EPP = epipleural; HPZ = haemal postzygapophysis; HSP = haemal spine; NPZ = neural postzygapophysis; NSP = neural spine; PRB = pleural rib; VCN = vertebral centrum. Scale bar = 1 mm.

Pectoral girdle. Posttemporal (Fig. 19). Paired flat, approximately triangular bone, with slightly wavy to straight margins in dorsal portion narrowing and overlying posttemporal fossa of epioccipital. Posttemporal bordered ventrally by dorsal portion of supracleithrum; ventrally with spiniform bony process on medial surface contacting limits of epioccipital and exoccipital.

Extrascapular (Fig. 19). Paired flat small bones bearing branch of laterosensory system along almost half its width, and continuing to supracleithrum. Dorsal portion of extrascapular overlying epioccipital and adjacent to posterior margin of posttemporal. Ventral portion bordered by ventral portion of posttemporal.

Supracleithrum (Fig. 19). Paired flattened to elongated, approximately trapezoidal bone, with dorsal portion concave and slightly rounded. Bordered anteriorly by ventral portion of posttemporal and ventrally by cleithrum and ventral region by postcleithrum 1. Laterosensory system extending through its central portion.

Cleithrum (Fig. 19). Paired bone and largest in pectoral girdle, situated posterior of subopercle and opercle. Anterior margin flattened and concave. Posterior margin wavy along half ventral. Anterior portion thin and elongate. Bordered anteriorly by supracleithrum and postcleithrum 1, posteroventrally by coracoid, mesocoracoid and scapulum, and posteromedially by postcleithrum 2.

Postcleithrum (Fig. 19). Paired flattened bone with three on each side of body. Postcleithrum 1 and 2 approximately ovoid, although of variable form. Postcleithrum 1 connecting anteriorly with supracleithrum and anterodorsally with cleithrum. Postcleithrum 2 elongate, with rounded margins. Median dorsal portion of postcleithrum 3 with lateral laminar expansion. Postcleithrum 2 connected dorsally with cleithrum and ventrally with postcleithrum 3. Postcleithrum 3 connected dorsally with postcleithrum 2. Postcleithrum 1 separate from postcleithra 2 and 3.

Mesocoracoid (Fig. 19a). Paired narrow and elongate bone, with thin dorsal portion and pentagonal ventral region. Dorsal portion underlying to cleithrum. Bordered ventrally by coracoids and scapulum.

Coracoid (Fig. 19). Paired flattened bone with straight ventral and anterior margins and undulated posterior edge. Concave along anterodorsal half. Bordered posterodorsally by mesocoracoid and scapulum. Contralateral coracoids united ventrally.

Scapulum (Fig. 19a). Paired relatively thick, "T" shaped bone, with pentagonal dorsal portion. Bordered dorsally by cleithrum and posteriorly by proximal radials of pectoral

fin, coracoid, and mesocoracoid. Posteroventral margin connected with proximal radials and first unbranched ray of pectoral fin. Small foramina passing throughout bone.

Distal and proximal radials of pectoral fin (Fig. 19a). Paired, flattened to thick bone, relatively trapezoid to irregular forms. Four pairs. Anterior tip of the first to third proximal radials contacting or reaching nearly to scapulum, fourth proximal radial lying near of coracoid. Posterior margin of all proximal radials contacting distal radials. First proximal radial largest, somewhat square, overlying the scapulum with three cylindrical projections posteriorly. Second, third, and fourth proximal radials circular/ovoid and approximately of equals length and shape. First through third distal radials of same size. Fourth distal smaller, about half the diameter of others. Distal radials contacting with the pectoral-fin rays.

Pelvic girdle and fin (Fig. 20). Pelvic bone paired, elongate, approximately triangular, situated on ventral portion of body. Anterior portion pointed with cylinder proximate to lateral border. Ischiatic process situated posteroventrally, with margins formed by narrow cartilaginous tube. Contralateral pelvic bones connected by ischiatic processes. Rays decreasing gradually in length laterally. No bony hooks on pelvic-fin rays.

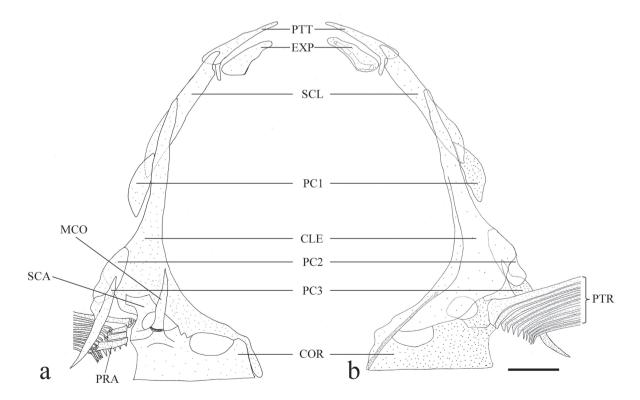


Fig. 19. *Hyphessobrycon compressus*, UFRGS 9683, 31.2 mm SL, male, pectoral girdle in (a) medial view, anterior to right, and (b) lateral view, anterior to left. CLE = cleithrum; COR = coracoid; EXP = extrascapular; MCO = mesocoracoid; PC1 = postcleithrum 1; PC2 = postcleithrum 2; PC3 = postcleithrum 3; SCA = scapulum; SCL = supracleithrum; PRA = proximal radial; PTR = pectoral-fin rays; PTT = posttemporal. Scale bar = 1 mm.

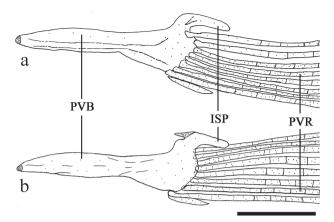


Fig. 20. Hyphessobrycon compressus, UFRGS 9683, 31.1 mm SL, female, pelvic girdle in (a) ventral view of right pelvic fin and (b) dorsal view of left pelvic fin, anterior to left. ISP = ischiatic process; PVB = pelvic bone; PVR = pelvic-fin rays. Scale bar = 1 mm.

Dorsal fin (Fig. 21). Dorsal fin formed by proximal, median, and distal radials, and unbranched and branched rays. Proximal radials elongate. First proximal radial anteroventrally bifurcated between 10th and 11th precaudal vertebrae. Proximal radials with lateral anteromedial expansion, gradually decreasing in length posteriorly, and bordered dorsally by median radials. Medial radials approximately square, bordered ventrally by proximal radials and dorsally by distal radials. Distal radials ovoid; some with dorsally-pointed projection, and bordered by dorsalfin rays. First unbranched dorsal-fin ray approximately half length of second ray. Second unbranched ray and first branched ray largest in fin, other gradually decreasing in length to the last ray. Supraneurals 4(2) or 5(7), filiform, sometimes with enlarged dorsal portion; dorsal and ventral portions cartilaginous.

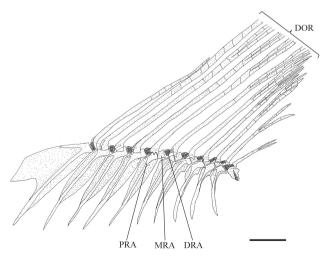


Fig. 21. *Hyphessobrycon compressus*, UFRGS 9683, 31.2 mm SL, male, dorsal fin in left lateral view. DOR = dorsal-fin rays; DRA = distal radial; MRA = medial radial; PRA = proximal radial. Scale bar = 1 mm.

Anal fin (Fig. 6). Anal fin formed by proximal, medial, and distal radials plus unbranched and branched rays. First four branched anal-fin rays lack medial radials and first three unbranched lack distal radials. Proximal radial elongate with anterior expansion of first proximal radial. First to fourth proximal radials situated between haemal spines of first and second caudal vertebrae, or first proximal radial between haemal spines of last precaudal vertebrae and second to fourth between first and second caudal vertebrae. Proximal radials bordered dorsally by medial radials. Medial radials approximately square, dorsally contacting proximal radials and ventrally distal radials. Distal radials ovoid, some dorsally pointed projections and bordered ventrally by anal-fin rays. First unbranched rays small; rays increasing in length to ultimate unbranched ray. Last unbranched ray and first two branched rays largest, other branched rays decreasing gradually in length to last branched ray. Small- to largesized bony hooks on anal-fin rays. Two pairs of large bony hooks: one on last unbranched ray and other in first branched ray. Hooks on median portion of anterior fin ray. Large hook on last unbranched ray retrorse, largest than the size of its segment. Posterior tip of hook extending to subsequent ray. Hook on first branched ray slightly slender than anterior hook, but larger than size of ray segment, and also extending to subsequent ray. Large hooks positioned midlength of ray, proximate to branched portion of rays. Small-sized hooks, smaller than the size of associated segment, on second to sixth branched ray along both anterior and posterior branches.

Caudal fin and hypural complex (Fig. 22). Caudal fin consists of dorsal and ventral procurrent rays, epurals, uroneural, hypurals, unbranched and branched caudalfin rays, and parhypural. Procurrent rays gradually increasing in length posteriorly with the first seven rays associated with neural spines of 32nd or 33rd vertebrae, three associated with two epurals, and the last associated with urostyle. Dorsal unbranched ray of caudal fin associated with sixth hypural; two branched rays with fifth hypural, two branched rays with fourth hypural, five rays with third hypural, two with second hypural; five with first hypural; one with parhypural. Ventral unbranched ray and last ventral procurrent ray associated with 32nd or 33th vertebrae, and remaining ventral procurrent rays with 31st or 32nd vertebrae. Epurals elongate, relatively cylindrical. Uroneural with anteroventrally convex neural process, with irregular anterior surface. Hypurals 1 and 3 approximately triangular, flattened. Hypurals 2 and 4, 5, and 6 approximately trapezoidal. Hypurals 2 and 4 of approximately same size, others gradually decreasing in length. Hypural 2 connected with last vertebra. Hypural 3 with anterior tip at base of uroneural, and other hypurals with free anterior margins, contacting or not uroneural (hypurals 4, 5, and 6) and parhypural (hypural 1). Parhypural with small haemal process.

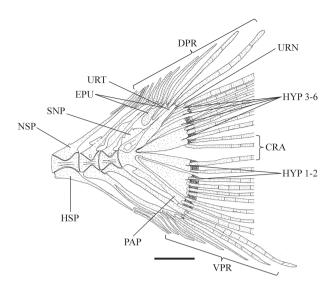


Fig. 22. *Hyphessobrycon compressus*, UFRGS 9683, 31.2 mm SL, male, caudal skeleton in left lateral view. EPU = epurals; CRA = caudal-fin rays; DPR = dorsal procurrent caudal-fin rays; HSP = haemal spine; HYP = hypurals; NSP = neural spine; PAP = parhypural; SNP = specialized neural process; URN = uroneural; URT = urostyle; VPR = ventral procurrent caudal-fin rays. Scale bar = 1 mm.

Examined material. Holotypes. *Hemigrammus compressus*, FMNH 4641, male, 31.2 mm SL, Mexico, Oaxaca, El Hule, río Papaloapan, 22 Apr 1903, S. E. Meek. *Hyphessobrycon compressus milleri*, CAS 70115 (ex IU 11255), male, 31.3 mm SL, Guatemala, Los Amates (possibly swamp 0.5 miles to the East), 17 Jan 1905, N. Miller.

Paratypes. BMNH 1905.12.6.4-5, 2 (2), male, 31.5-32.5 mm SL, Mexico, Oaxaca, Obispo, S. E. Meek. CAS 70114 (ex IU 10798, IU 11126), 5 (5), 26.6-32.0 mm SL, Mexico, Obispo, Veracruz, 23 Apr 1903. CAS 70116 (ex IU 10929), 1 (1), 31.6 mm SL, Mexico, Veracruz, Perez (probably río Tesechocán, tributary of río Papaloapan), S. E. Meek. FMNH 4642, 17 (17), 26.6-35.7 mm SL, Mexico, Oaxaca, El Hule, río Papaloapan, 22 Apr 1903, S. E. Meek. FMNH 4662, 11, 26.2-31.8 mm SL, 1 c&s, no length (disarticulated and in poor condition), Mexico, Oaxaca, Obispo, río Obispo, 23 Apr 1903, S. E. Meek. FMNH 105930 (ex FMNH 4642), 2, 28.8-30.8 mm SL, same data as FMNH 4642; MCZ 29911 (ex IU 11126), 2, 29.0-30.3 mm SL, Mexico. MHNG 2181.076, 1(1), 29.2 mm SL, same locality as FMNH 4641. USNM 55728, 2, missing, Mexico, Obispo, S. E Meek. USNM 204387, 3, males, 30.0-31.3 mm SL, 1 c&s, ca. 31.0 mm SL, Mexico, Oaxaca; El Hule, 22 Apr 1903, S. E. Meek.

Non-type material. All from Atlantic drainages. Mexico, Oaxaca: río Papaloapan drainage: UMMZ 210792, 18 of 29 (18), 27.3-31.8 mm SL (topotypes), disconnected lagoons (part of single channel) on W side of highway 145, *ca.* of two miles (3 km) S of río Papaloapan drainage. **Mexico**, Chiapas: río Usumacinta drainage: AMNH 25681, 12 of 189 (12), 19.7-25.6 mm SL, arroyo Sousa, lower 200 km above mouth in Usumacinta, 3 km

downstream from río de la Passion. AMNH 32275, 9 of 30 (9), 3 c&s, 31.7-36.4 mm SL, Guatemala, Alta Verapaz, río Chivu, 19 air km NE Cahabon, 14 air km W-SW of Chajal. ANSP 124161, 2, 25.1-30.1 mm SL, Guatemala, río Usumacinta near Sayaxche, Usumacinta Expedition. ANSP 127725, 34, 27.3-33.4 mm SL, Guatemala, río Usumacinta near Sayaxche, Usumacinta Expedition. ANSP 142724, 2, 27.3-27.4 mm SL, Guatemala, río Usumacinta, near Sayaxche. FMNH 108872, 10, 23.8-31.6 mm SL, Guatemala, Peten, río Usumacinta, small bay on río Escondido. FMNH 108875, 58, 31.0-33.3 mm SL, Guatemala, Peten, río Usumacinta, Laguna Flor de Luna. MHNG 2485.6, 13, 17.9-33.4 mm SL, Mexico, Campeche, Laguna Lacandons. MHNG 2485.007, 9, 20.0-24.8 mm SL, Mexico, Campeche, near Palizada. MHNG 2485.8, 1, 18.4 mm SL, Mexico, Tabasco, río Usumacinta, near Jonuta. Río Coatzacoalcos drainage: UMMZ 187748, 11 of 59 (11), 27.6-32.1 mm SL, Mexico, Veracruz, laguna de Tio Ramon, 17 km of Tenochtitlan, 320 m W of big bend of río Chiquito, río Coatzacoalcos. UMMZ 209579, 15 of 49 (15), 27.2-33.0 mm SL, Mexico, Veracruz, small tributary to río Tonala, on road to Agua Dulce, 1.3 mi N of city with highway 180, río Tonala to Gulf of Mexico drainage. Lake Petèn Itzà drainage: MHNG 2179.16, 8, 11.8-28.1 mm SL, Guatemala, Izabal, rio Ixlu, boundary of Honduras. UFRGS 9683 (ex UMMZ 143343), 12 of 50 (12), 6 c&s, 29.2-34.6 mm SL, Guatemala, Peten, Lago Peten along CNA airfield, near middle of S shore of shouthern arm of lake. Lake Izabal drainage: CAS 70113 (ex IU 11254), 1 (1), 26.8 mm SL, Guatemala, Los Amates (possibly swamp 0.5 mi. to the East) (topotype of *Hyphessobrycon compressus milleri*). UMMZ 197186, 3 of 63 (3), 26.2-31.6 mm SL, 2 c&s, 26.7-26.9 mm SL, Guatemala, Izabal, río Dulce, N side at mouth of río Cienega. USNM 114275, 2 of 24 (2), Guatemala, 25.1-28.1 mm SL, río Sauce, approximately 2 miles SW of El Estor at mouth in Lake Izabal. USNM 134463, 2 of 25 (2), 24.0-25.5 mm SL, Guatemala, Lake Izabal, West End. USNM 134464, 1 of 13 (1), 25.8 mm SL, Guatemala, Lake Izabal near south tributary west end. FMNH 108880, 13, 29.1-38.0 mm SL, Guatemala, Peten, río Candelaria, río Candelaria at road. **Río Sarstoon drainage:** USNM 114339, 2 of 14 (2), 24.8-26.7 mm SL, Guatemala, Jicotea Creek, tributary río Sarstoon, approximately 1/4 mile above mouth. Chetumal Bay drainage: FMNH 82260, 279, 15.9-28.9 mm SL, Belize, Orange Walk, New River Lagoon at Hillbank. USNM 389634, 10 of 42 (10), 26.4-30.2 mm SL, Belize, Kate's Lagoon. USNM 389567, 11 of 28 (11), 27.2-31.7 mm SL, Belize, Orange Walk. Belize River drainage: FMNH 82111, 24, 13.5-27.7 mm SL, Belize, Cayo, Aguacate Lagoon, tributary to Labouring Creek and Belize River, NW of Spanish Lookout. FMNH 82286, 7, 20.8-26.6 mm SL, Belize, Belize, Mexico Creek, tributary of Belize River, NW of Sand Hill on road to Crooked Tree. FMNH 82368, 5, 21.6-26.3 mm SL, Belize, Belize, Black Creek at Washing Tree, ca. 3.5 mi upriver from junction with Belize River and ca. 3 miles SW on dirt road from Crooked. FMNH 82875, 6, 21.3-25.3 mm SL, Belize, Belize, Belize River, mile 16 on Western Highway, Savanna pool. FMNH 82887, 2, 25.1-29.9 mm SL, Belize, Roaring Creek at Roaring Creek City. FMNH 82512, 16, 19.6-33.7 mm SL, Belize, Belize at churchyard, far side of river near Wood's house. FMNH 82882, 121, 22.5-32.5 mm SL, Belize, Belize, Belize River, Mussel

Creek about 13 miles NW of Hattieville. FMNH 104673, 16 of 32 (16), 23.6-26.3 mm SL, Belize, Belize, Burrell Boom swimming hole. UMMZ 190455, 3 of 47 (3), 21.6-27.7 mm SL, Belize, Belize, Hector Creek road. USNM 198815, 2 of 13 (2), 25.2-26.1 mm SL, Belize, Belize. New River Lagoon: MZUSP 28535, 21 of 25, 18.7-26.9 mm SL, Belize, Orange Walk District, Baba Creek near New River Lagoon. Progresso Lagoon: FMNH 82133, 13, 21.5-28.3 mm SL, Belize, Orange Walk, Progresso Lagoon, West shore, ca. 1 mile SW of Progresso Village (on road from Orange Walk). Monkey River drainage: FMNH 82233, 48, 14.3-28.9 mm SL, Belize, Toledo, Negra Creek, on S Highway, tributary of Monkey River, FMNH 104442, 6, 19.3-30.2 mm SL, Belize, Toledo, Machaca Creek, N. Aspinwall. Moho River drainage: FMNH 82402, 4, 22.8-27.9 mm SL, Belize, Toledo, Aguacate Creek, 5 miles E of village, 4 miles on new oil road SE out of Blue Creek Village. MZUSP 18422, 5, 22.2-26.1 mm SL, Belize, Toledo, Moho, the "Dump" at mile 13 on road between Punta Gorda and San Antonio. Mangrove Creek drainage: FMNH 82384, 23, 16.1-28.1 mm SL, Belize, Stann Creek, Mangrove Creek. Quamina Creek drainage: FMNH 82392, 19, 20.0-22.0 mm SL, Belize, Stann Creek, ditch under culvert 1.1 miles S of Quamina Creek on road to Melinda Forest Station. Sibun River drainage: FMNH 82876, 3, 24.6-26.2 mm SL, Belize, Belize, Sibun River, Sibun River, mile 13 on Western Highway, above Freetown. FMNH 82888, 4, 22.0-28.1 mm SL, Belize, Sibun River 0.5 mile upstream from Freetown. FMNH 82886, 2, 25.5-26.2 mm SL, Belize, Sibun drainage ditches along road to Roaring Creek. FMNH 82939, 8, 16.0-19.2 mm SL, Belize, Belize, Sibun River, mile 8 or more on W Highway N of highway. FMNH 82940, 3, 27.7-29.6 mm SL, Belize, Cayo, Sibun River, Richie Wood's Farm Pond 33 miles of West Highway. Grande River drainage: FMNH 82556, 18, 19.9-26.6 mm SL, Belize, Toledo, Grande River, Jacinto Creek, about 8 miles W of Punta Gorda on southern highway, río Grande drainage. Deep River drainage: FMNH 82883, 22, 17.9-22.9 mm SL, Belize, Toledo, Deep River at bridge on southern highway. Southern Lagoon drainage: FMNH 82564, 39, 18.7-30.8 mm SL, Belize, Stann Creek, Jenkins Creek, S Highway. FMNH 82884, 16, 23.3-32.9 mm SL, Belize, Stann Creek, South Stann Creek on Southern Highway. Northern Lagoon drainage: FMNH 82885, 104, 24.3-27.5 mm SL, Belize, Hector Creek at Hattieville under bridge, MHNG 2177.93, 1, 20.9 mm SL, Belize, vicinity British Honduras. Mullins River drainage: FMNH 82877, 134, 19.1-35.9 mm SL, Belize, Stann Creek, Caribbean Sea, Nelly Creek, N Mullins River.

Discussion

The type species of *Hyphessobrycon* was hypothesized by Weitzman & Palmer (1997) to belong to a group of species of the "rosy tetra clade". This group was found to be monophyletic by Mirande (2010, clade 292), but specimens of *H. compressus* were not available to Mirande (2010) and this species was not included in his analysis. Malabarba *et al.* (2012) and Carvalho *et al.* (2014) performed a new analysis including *H. compressus* and found it belongs to clade 292 of Mirande (2010), which also included *Hemigrammus*

unilineatus (Gill), Hyphessobrycon eques, H. pulchripinnis Ahl, H. socolofi, Weitzman, and Pristella maxillaris (Ulrey). In the first of the phylogenetic analyses, Hemigrammus unilineatus, the type species of that genus, was recovered within the same clade of Hyphessobrycon compressus (Malabarba et al., 2012; Carvalho et al., 2014), but in an ongoing more inclusive phylogenetic analysis Hemigrammus *unilineatus* resolves in a separate clade and does not seems to be part of *Hyphessobrycon sensu stricto*. Autapomorphies for H. compressus, according to Malabarba et al. (2012) are: the anterior paired projections of the parasphenoid are absent; a lack of pelvic-fin bony hooks in adult males; and the predorsal scales leaving a naked area anterior to the dorsal fin. Unlike other Hyphessobrycon species, H. compressus has small scales, 41-48 in a longitudinal series, and 7-9 scales above lateral line, the highest values for a species of Hyphessobrycon. Other Hyphessobrycon species normally do have no more than 40 scales in the longitudinal series that includes the lateral lines, and the scales rows between dorsal-fin origin and lateral line usually do not exceed six.

Bony hooks are relatively common sexually dimorphic structures in many members of the Characidae, including *Hyphessobrycon*. The most common condition is the presence of bony hooks on the anal and pelvic fins (Carvalho *et al.*, 2014: fig. 5; Lima & Sousa, 2009: fig. 6). *Hyphessobrycon compressus* exhibits hooks in the anal fin (two very large and several minute), but these are absent in pelvic fins. Large, conspicuous bony anal-fin hooks are found in few species, such as *Hyphessobrycon chocoensis* García-Alzate, Román-Valencia & Taphorn (García-Alzate *et al.*, 2013), *H. condotensis* Regan, *H. diancistrus* Weitzman, *H. otrynus* Benine & Lopez, *H. panamensis* Durbin, *H. savagei* Bussing, *H. sebastiani* García-Alzate, Román-Valencia & Taphorn, *Moenkhausia ceros* Eigenmann, and *M. mikia* Marinho & Langeani.

The median predorsal scales series is composed of regularly or irregularly arranged scales in a row between the supraoccipital process and the dorsal-fin origin. This is the common condition in Characidae *incertae sedis* (sensu Lima et al., 2003). Gymnocorymbus Eigenmann, however, is diagnosed by the absence of a predorsal scale series. Benine (2004) also mentioned other species in the Characidae with the same condition, e.g., Jupiaba apenima Zanata, J. pirana Zanata, J. poranga Zanata, J. yarina Zanata, Moenkhausia levidorsa Benine, besides some specimens of Astyanax aff. bimaculatus. Hyphessobrycon compressus is, however, the unique species of the genus lacking median predorsal scales.

Color patterns have been suggested convey a phylogenetic signal among recently described species of *Hyphessobrycon* (e.g., Bertaco et al., 2007; Benine & Lopes, 2008; Zanata & Camelier, 2010; Ingenito et al., 2013; Dagosta et al., 2014; Lima et al., 2014). One pattern was proposed as a putative synapomorphy for part of *Hyphessobrycon* (the "rosy tetra clade", Weitzman & Palmer, 1997) including *H. compressus*. Most *Hyphessobrycon* species have humeral spots in the

flank, but such pigmentation is missing in H. compressus and part of the "rosy tetra clade" of Weitzman & Palmer (1997). Besides of this character present in some species, the black dorsal fin and no midlateral stripe on body, may be useful in the identification of Hyphessobrycon sensu stricto, including the type species H. compressus, H. bentosi, H. copelandi, H. epicharis Weitzman & Palmer, H. eques, H. erythrostigma (Fowler), H. georgettae Géry, H. haraldschultzi Travassos, H. hasemani Fowler, H. khardinae Zarske, H. megalopterus (Eigenmann), H. micropterus (Eigenmann), H. minor, H. pulchripinnis, H. pyrrhonotus Burgess, H. rosaceus, H. roseus (Géry), H. simulatus (Géry), H. socolofi, H. sweglesi (Géry), H. takasei Géry, and H. werneri (Géry & Ui), besides 'Cheirodon' troemneri Fowler (Carvalho, 2011). Other species recently referred to the "rosy tetra clade", as H. dorsalis Zarske, H. jackrobertsi Zarske, H. paepkei Zarske, and H. pando Hein, share these characteristics, but their taxonomic status are doubtful. The more than 100 remaining species of *Hyphessobrycon* other than those in the rosy tetra clade probably will need to be assigned to other genera or new genera (Hyphessobrycon sensu lato). An example of this rearrangement is *Ectrepopterus uruguayensis* (Fowler), formerly housed in Hyphessobrycon, but that failed to group with H. compressus and was found more related to other characid taxa in a more representative and robust analysis (Malabarba et al., 2012). We may expect the same for other species currently listed in Hyphessobrycon.

The small characids, in special the *incertae sedis* (sensu Lima et al., 2003), have a conservative morphology associated to a long period of evolution of the group (Weiss et al., 2012). Morphological changes in different lineages seems to be convergent resulting in high levels of morphological homoplasies, that may be associated with small size and reduction or loss of structures, turning difficult to find robust monophyletic clades (Mirande, 2010; Mattox et al., 2013). Hyphessobrycon compressus has a skeleton similar to those described for other members of Characidae [Astyanax fasciatus (Cuvier) by Mejía-Mójica & Díaz-Pardo (1991); A. mexicanus De Filippi (type species) by Valdéz-Moreno & Contreras-Balderas (2003); Bramocharax caballeroi Contreras-Balderas & Rivera-Teillery by Valdez-Moreno & Contreras-Balderas (2009); Brycon meeki Eigenmann & Hildebrand by Weitzman (1962); Bryconamericus exodon Eigenmann (type species) by Serra & Langeani (2006); Carlastyanax aurocaudatus (Eigenmann) (type species) by Ruiz-C. & Román-Valencia (2006); Cyanogaster noctivaga Mattox, Britz, Toledo-Piza & Marinho (type species) by Mattox et al. (2013); Gymnocharacinus bergi Steindachner (type species) by Miquelarena & Arámburu (1983); Gymnocorymbus ternetzi (Boulenger) by Bogutskaya et al. (2008)]. Osteological differences among these species have been briefly discussed or debated (e.g., as table 2 of Valdez-Moreno & Contreras-Balderas, 2009), and is potentially useful in a future more comprehensive phylogenetic analysis. Overall, most differences are associated with teeth (form, number, and position), shape and position of bones,

and presence vs. absence of structures. Hyphessobrycon compressus has unique and distinctive characters among its congeners, and the understanding of synapomorphies shared with other species may provide examples of these and allow the recognition of the Hyphessobrycon sensu stricto.

Four Hyphessobrycon species are recognized valid in the Middle America and southern Mexico: H. compressus (including H. milleri as its junior synonym proposed herein), H. panamensis Durbin, H. tortuguerae Böhlke, and H. savagei Bussing. Hyphessobrycon compressus readily differs from the others in the possession of a black dorsal fin (vs. hvaline dorsal fin). Freshwater fish diversity is uneven across Central America. Miller (1966) proposed that the dispersion of the Central American "primary" freshwater fishes (Characiformes, principally) into the region occurred during the Plio-Pleistocene emergence of the Panamanian land bridge, whereas "secondary" freshwater fishes (Poeciliidae and Cichlidae, especially) dispersed and diversified in Central America during the early Cenozoic, long before the Plio-Pleistocene rise of the Isthmus of Panama (Matamoros et al., 2015). The Characidae is most diversified in lower Central America (Matamoros et al., 2015), but H. compressus occurs in the upper portion of Middle America and southern Mexico, in the Grijalva-Usumacinta, Polochic-Cahabon, and Motagua-Nombre de Dios areas of endemism (sensu Matamoros et al., 2015). Almost all species of Hyphessobrycon of the "rosy tetra clade" are in South America, and it is probable that ancients of H. compressus had a fragmentation of a widespread ancestral species or dispersed from northern South America into middle Central America, as noted for others Characiformes [Cyphocharax Fowler and Lebiasina (Valenciennes)] (Matamoros et al., 2015).

Comparative Material Examined. Specific names herein listed are according with the composition in the original description. For current status, check Catalog of Fish (Eschmeyer, 2014). Because all are types, information about localities were omitted. Carlastyanax aurocaudatus: Colombia: FMNH 56882, 45.0 mm SL, holotype of Astyanax aurocaudatus Eigenmann, 1913, Boquia; Colombia: FMNH 56883, 3, 34.0-40.5 mm SL, paratypes of Astyanax aurocaudatus Eigenmann, 1913, Boquia. Diapoma guarani: Paraguay: MHNG 2366.100, 66, 17.3-18.8 mm SL, 6 c&s, 24.1-26.1 mm SL, paratypes of Hyphessobrycon guarani Mahnert & Géry, 1987, Alto Parana Department, río Parana at Puerto Bertoni, rio Paraná basin; Paraguay: MHNG 2367.001, 34, 18.7-23.6 mm SL, paratypes of Hyphessobrycon guarani Mahnert & Géry, 1987, Alto Parana Department, Itaipu Dam, rio Paraná basin; Paraguay: MHNG 2367.002, 40, 17.5-29.8 mm SL, paratypes of Hyphessobrycon guarani Mahnert & Géry, 1987, Alto Parana Department, Itaipu Dam, rio Paraná basin; Argentina: MHNG 2367.003, 24.8 mm SL, paratypes of Hyphessobrycon guarani Mahnert & Géry, 1987, Missiones Department, río Alto Parana, rio Paraná basin; Paraguay: MNHN 1988-0467, 2, 24.8-25.3 mm SL, paratypes of *Hyphessobrycon* guarani Mahnert & Géry, 1987, Alto Parana Department, río Parana at Puerto Bertoni, rio Paraná basin; Paraguay: ZFMK 15521-15523, 3, 19.7-30.4 mm SL, paratypes of *Hyphessobrycon* guarani Mahnert & Géry, 1987, Alto Parana Department, río Parana at Puerto Bertoni, rio Paraná basin. Gymnocharacinus bergii: Argentina: NMW 69429, 61.8 mm SL, holotype of Gymnocharacinus bergi Steindachner, 1903, Southern Argentina. Hemigramus stictus: Guyana: BMNH 1911.10.31.415-417, 3, 22.2-31.5 mm SL, paratypes of Hyphessobrycon stictus Durbin, 1909, Maduni creek; Guyana: BMNH 1911.10.31.418-419, 2, 20.6-27.8 mm SL, paratypes of *Hyphessobrycon stictus* Durbin, 1909, Lama Stop-Off; Guyana: ZMA 100974, 20.0 mm SL, paratype of Hyphessobrycon stictus Durbin, 1909, BMNH 1911.10.31.418-419; Guyana: ZMA 101033, 2, 20.7-28.9 mm SL, paratypes of Hyphessobrycon stictus Durbin, 1909, BMNH 1911.10.31.418-419. Hyphessobrycon amandae: Brazil: MHNG 2280.091, 10, 15.1-19.0 mm SL, paratypes of Hyphessobrycon amandae Géry & Uj, 1987, rio das Mortes, some 100 km before its confluence of the rio Araguaia (the western border of the Ilha do Bananal), Mato Grosso State, rios Tocantins-Araguaia basin. Hyphessobrycon amapaensis: Brazil: MTD F 21447-214456, 10, 26.3-29.7 mm SL, paratypes of Hyphessobrycon amapaensis Zarske & Géry, 1998, Amapá State, about 45 km north Macapá. Hyphessobrycon anisitsi: Brazil?: ZMB 20828, 38.6 mm SL, holotype of Hyphessobrycon erythrurus Ahl, 1928, Amazonas?. Hyphessobrycon borealis: French Guiana: MNHN 2006-787, 22.2 mm SL, holotype of Hyphessobrycon borealis Zarske, Le Bail & Géry, 2006, Mana; French Guiana: MNHN 2006-0788, 30, 20.9-26.0 mm SL, paratypes of Hyphessobrycon borealis Zarske, Le Bail & Géry, 2006, Mana; French Guiana: MNHN 2006-0789, 1 of 3, 20.5 mm SL, paratypes of Hyphessobrycon borealis Zarske, Le Bail & Géry, 2006, Kaw; Brazil: MTD F 28805-28814, 10, 21.5-27.4 mm SL, paratypes of Hyphessobrycon borealis Zarske, Le Bail & Géry, 2006, Amapá State, Clevelandia, Oyapock basin; French Guiana: MTD F 28843-28852, 10, 19.4-22.9 mm SL, paratypes of Hyphessobrycon borealis Zarske, Le Bail & Géry, 2006, Mana. Hyphessobrycon coelestinus: Brazil: MHNG 2179.005, 2, 22.9-23.2 mm SL, paratypes of Hyphessobrycon coelestinus Myers, 1929, Goiás State, Lagoa Bonita, upper rio Paraná basin. Hyphessobrycon cyanotaenia: Brazil: MTD F 28760, 32.3 mm SL, holotype of Hyphessobrycon cyanotaenia Zarske & Géry, 2006, Pará State, rio Guamá; Brazil: MTD F 28761-28762, 2, 28.9-33.0 mm SL, paratypes of Hyphessobrycon cyanotaenia Zarske & Géry, 2006, Pará State, rio Gamá; Brazil: MTD F 28763-28764, 2, 23.5-26.4 mm SL, paratypes of Hyphessobrycon cyanotaenia Zarske & Géry, 2006, Pará State, rio Guamá. Hyphessobrycon ecuadoriensis: Ecuador: BMNH 1924.3.3.44-45, 2, 17.6-18.0 mm SL, paratypes of Hyphessobrycon ecuadoriensis Eigenmann & Henn, 1914, same data as BMNH 1924.3.3.44-45; Ecuador: MHNG 2179.014, 8, 18.8-25.5 mm SL, paratypes of Hyphessobrycon ecuadoriensis Eigenmann & Henn, 1914, same data as BMNH 1924.3.3.44-45; Ecuador: MNHN 1980-1439, 20.8 mm SL, paratypes of Hyphessobrycon ecuadoriensis Eigenmann & Henn, 1914, same data as BMNH 1924.3.3.44-45; Ecuador: MZUT 3554, 51, 11.7-22.4 mm SL, paratypes of Hyphessobrycon ecuadoriensis Eigenmann & Henn, 1914, same data as BMNH 1924.3.3.44-45; **Ecuador:** ZMA 113819, 20.9 mm SL, paratypes of *Hyphessobrycon ecuadoriensis* Eigenmann & Henn, 1914, same data as BMNH 1924.3.3.44-45.

Hyphessobrycon elachys: Paraguay: BMNH 1984.12.21.2-3, 2, 13.9-14.7 mm SL, paratypes of Hyphessobrycon elachys Weitzman, 1985, San Pedro Department, río Aguaray-guazu system. Hyphessobrycon eos: Guvana: BMNH 1911.10.31.412, 31.9 mm SL, paratype of Hyphessobrycon eos Durbin, 1909, creek between Potaro Landing and Kangaruma; Guyana: MHNG 2178.086, 17.0 mm SL, paratype of Hyphessobrycon eos Durbin, 1909, Tukeit; Guyana: ZMA 100983, 23.6 mm SL, paratype of Hyphessobrycon eos Durbin, 1909, creek between Potaro Landing and Kangaruma; Guyana: ZMA 101031, 17.2 mm SL, paratype of Hyphessobrycon eos Durbin, 1909, Tukeit. Hyphessobrycon epicharis: Venezuela: MHNG 2516.56, 55, 23.1-29.5 mm SL paratypes of Hyphessobrycon epicharis Weitzman & Palmer, 1997, Río Negro Departament, río Negro basin. Hyphessobrycon eques: Paraguay: ZMB 17147, 2, 21.1-25.4 mm SL, paratypes of Hemigrammus melasopterus Eigenmann & Kennedy, 1903, Aguada, near arroyo Trementina. Hyphessobrycon frankei: Peru: MHNG 2586.031, 4, 20.5-22.8 mm SL, paratypes of Hyphessobrycon frankei Zarske & Géry, 1997, río Ucavali basin; **Peru:** MHNG 2586.032, 2, 22.4-25.7 mm SL, paratypes of Hyphessobrycon frankei Zarske & Géry, 1997, río Ucayali basin; Peru: MTD F 16599-16603, 6, 19.9-32.7 mm SL, paratypes of *Hyphessobrycon frankei* Zarske & Géry, 1997, río Ucayali basin; Peru: MTD F 17707-17730, 24, 17.2-30.8 mm SL, paratypes of Hyphessobrycon frankei Zarske & Géry, 1997. río Ucayali basin. Hyphessobrycon georgettae: Suriname: Hyphessobrycon georgetti: MHNG 2178.062, 4, 13.9-16.0 mm SL, paratypes of Hyphessobrycon georgetti Géry, 1961, Sipaliwini District, swamp creek in the Paru Savannah; ZMA 104184, 9, 14.8-16.1 mm SL, paratypes of Hyphessobrycon georgetti Géry, 1961, Sipaliwini District, swamp creek in the Paru Savannah. Hyphessobrycon gracilior: Peru: ZFMK 1329, 21.4 mm SL, holotype of Hyphessobrycon gracilior Géry, 1964, río Ucayali basin; Peru: MHNG 2150.012-2150.013, 2, 16.8-17.1 mm SL, paratypes of Hyphessobrycon gracilior Géry, 1964, río Ucayali basin; Peru: ZFMK 1330, 16.9 mm SL, paratype of Hyphessobrycon gracilior Géry, 1964, río Ucayali basin. Hyphessobrycon herbertaxelrodi: Brazil: MHNG 2178.067, 2, 23.9-30.7 mm SL, paratypes of Hyphessobrycon herbertaxelrodi Géry, 1961, Mato Grosso do Sul State, Coxim, rio Taquari, rio Paraguay basin; Brazil: SMF 5376, 24.2 mm SL, paratype of Hyphessobrycon herbertaxelrodi Géry, 1961, Mato Grosso do Sul State, Coxim, rio Taquari, rio Paraguay basin. Hyphessobrycon isiri: Argentina: MHNG 2666.080, 2, 30.5-42.1 mm SL, paratypes of Hyphessobrycon isiri Almirón, Casciotta & Koerber, 2006, Entre Ríos, río Uruguay basin. Hyphessobrycon khardinae: **Brazil:** MTD F 31212-312113, 2, 36.3-38.0 mm SL, paratypes of Hyphessobrycon khardinae Zarske, 2008, Amazonas State, rio Itaparaná, rio Purus basin; Brazil: NMW 92128, 36.8 mm SL, paratype of Hyphessobrycon khardinae Zarske, 2008, Amazonas State, rio Itaparaná, rio Purus basin; Brazil: ZMB 33796, 37.1 mm SL, paratype of Hyphessobrycon khardinae Zarske, 2008, Amazonas State, rio Itaparaná, rio Purus basin; MZUSP 98667, holotype is probably lost. Hyphessobrycon loretoensis: Peru: ZMH 59, 24.0 mm SL, lectotype of Hyphessobrycon loretoensis Ladiges, 1938, designated by Ladiges (1958:157), Loreto, upper rio Amazonas; Peru: ZMH 183, 21.0 mm SL, paralectotype of Hyphessobrycon loretoensis Ladiges, 1938, same data as ZMH 59. Hyphessobrycon minor: Guyana: BMNH 1911.10.31.409, 19.2 mm SL, paratype of Hyphessobrycon minor Durbin, 1909, Konawaruk. Hyphessobrycon nigricinctus: Peru: MTD F 28465, 34.2 mm SL, holotype of Hyphessobrycon nigricinctus Zarske & Géry, 2004. Madre de Dios, imported aquarium fish: Peru: MTD F 28457-28459, 3, 29.8-32.5 mm SL paratypes of *Hyphessobrycon* nigricinctus Zarske & Géry, 2004, Madre de Dios, imported aquarium fish; **Peru:** MTD F 28460-28461, 2, 26.3-30.6 mm SL, paratypes of Hyphessobrycon nigricinctus Zarske & Géry, 2004, Madre de Dios, imported aquarium fish; Peru: ZFMK 39847, 27.7 mm SL, paratype of Hyphessobrycon nigricinctus Zarske & Géry, 2004 Madre de Dios, imported aquarium fish. Hyphessobrycon pando: Bolivia: ZFMK 41452, 34.9 mm SL, holotype of Hyphessobrycon pando Hein, 2009, Pando Department, río Manuripi; Bolivia: MTD F 30756-30758, 3, 27.6-29.8 mm SL, paratypes of Hyphessobrycon pando Hein, 2009, Pando Department, río Manuripi; Bolivia: ZFMK 41453, 30.0 mm SL, paratype of Hyphessobrycon pando Hein, 2009, Pando Department, río Manuripi; Bolivia: ZFMK 41454, 27.2 mm SL, paratype of Hyphessobrycon pando Hein, 2009, Pando Department, río Manuripi; Bolivia: ZFMK 41455, 34.7 mm SL, paratype of Hyphessobrycon pando Hein, 2009, Pando Department, río Manuripi; Bolivia: ZFMK 41456, 31.0 mm SL, paratype of Hyphessobrycon pando Hein, 2009, Pando Department, río Manuripi. Hyphessobrycon peruvianus: Peru: ZMH 60, 28.1 mm SL, lectotype of Hyphessobrycon peruvianus Ladiges, 1938, designated by Ladiges (1958:157), Loreto Department, upper Amazon; Peru: ZMH 182, 25.5 mm SL, paralectotype of Hyphessobrycon peruvianus Ladiges, 1938, Loreto Department, upper Amazon. Hyphessobrycon procerus: Paraguay: MHNG 2385.068, 33.4 mm SL, holotype of Hyphessobrycon procerus Mahnert & Géry, 1987, Caaguazu Department, río Guyrau-gua à Ltr. Juan M. Frutos, río Paraguay basin; Paraguay: MHNG 2385.069, 4, 26.8-33.5 mm SL, paratypes of Hyphessobrycon procerus Mahnert & Géry, 1987, same data as MHNG 2385.068; Paraguay: MNHN 1988-468, 2, 23.4-25.7 mm SL, paratypes of Hyphessobrycon procerus Mahnert & Géry, 1987, same data as MHNG 2385.068; Paraguay: ZMA 119953, 2, 22.0-25.7 mm SL, paratypes of Hyphessobrycon procerus Mahnert & Géry, 1987, same data as MHNG 2385.068. Hyphessobrycon pytai: Paraguay: MHNG 2543.86, 35.3 mm SL, holotype of *Hyphessobrycon pytai* Géry & Mahnert, 1993, Caaguazu Department, affluent of río Guyrau-gua, río Monday basin; Paraguay: MHNG 2543.087, 4, 17.4-34.6 mm SL, paratypes of Hyphessobrycon pytai Géry & Mahnert, 1993, same data as MHNG 2543.86; Paraguay: MHNG 2543.088, 1 c&s, 22.8 mm SL, paratype of *Hyphessobrycon pytai* Géry & Mahnert, 1993, same data as MHNG 2543.86; **Paraguay:** MHNG 2543.089, 38.0 mm SL, paratype Hyphessobrycon pytai Géry & Mahnert, 1993, same data as MHNG 2543.86. Hyphessobrycon rosaceus: Guyana: BMHN 1911.10.31.410-411, 2, 15.8-29.8 mm SL,

paratypes of Hyphessobrycon rosaceus Durbin 1909, Gluck Island, Esseguibo River basin; Guvana: ZMA 101013, 16.2 mm SL, paratype of Hyphessobrycon rosaceus Durbin 1909, same data as BMHN 1911.10.31.410-411. Hyphessobrycon roseus: French Guiana: SMF 4784, 19.4 mm SL, holotype of Megalamphodus roseus Géry, 1960, criques near Gaa Kaba, Maroni River; French Guiana: SMF 4790, 4, 12.7-13.3 mm SL, paratypes of Megalamphodus roseus Géry, 1960, same data as SMF 4784; French Guiana: ZMA 100620, 2, 14.2-15.2 mm SL, paratypes of Megalamphodus roseus Géry, 1960, criques in the Tampoc, upper Maroni. Hyphessobrycon saizi: Colombia: MHNG 2177.045, 3, 19.4-21.7 mm SL, paratypes of Hyphessobrycon saizi Géry, 1964, río Manacacias into upper Río Meta at Restrepo; Colombia: ZMA 114206, 19.7 mm SL, paratype of Hyphessobrycon saizi Géry, 1964, same data as MHNG 2177.045. Hyphessobrycon simulatus: French Guiana: SMF 4786, 31.5 mm SL, holotype of *Pseudopristella simulata* Géry, 1960, Kourou River; French Guiana: MHNG 2172.079, 13, 14.2-21.5 mm SL, paratypes of Pseudopristella simulata Géry, 1960, Cayenne, Ile de Cayenne; French Guiana: MHNG 2172.080, 21, 13.6-25.8 mm SL, paratypes of *Pseudopristella simulata* Géry, 1960, crique near Sinnamary; French Guiana: MHNG 2172.081, 2, 32.4-37.0 mm SL, paratypes of *Pseudopristella simulata* Géry, 1960, Côte, crique Moulet in the Orapu River; French Guiana: MNHN 1980-1449, 1 of 2, 16.5 mm SL, paratype of Pseudopristella simulata Géry, 1960, crique near Sinnamary; French Guiana: SMF 4788, 2, 22.6-24.1 mm SL, paratypes of Pseudopristella simulata Géry, 1960, crique near Sinnamary; French Guiana: ZMA 100621, 6, 16.7-29.5 mm SL, paratypes of Pseudopristella simulata Géry, 1960, crique near Sinnamary; French Guiana: ZMA 113855, 2, 17.3-25.4 mm SL, paratypes of Pseudopristella simulata Géry, 1960, crique near Sinnamary; French Guiana: ZSM 26762, 2, 27.5-29.3 mm SL, paratypes of Pseudopristella simulata Géry, 1960, crique near Sinnamary. Hyphessobrycon stegemanni: Brazil: MHNG 2177.078, 2, 28.4-28.7 mm SL, paratypes of Hyphessobrycon stegemanni Géry, 1961, Tocantins State, rios Tocantins-Araguaia basin; Brazil: SMF 5302, 30.4 mm SL, paratype of Hyphessobrycon stegemanni Géry, 1961, same data as MHNG 2177.078; **Brazil:** SMF 5377, 23.2 mm SL, paratype of Hyphessobrycon stegemanni Géry, 1961, same data as MHNG 2177.078. Hyphessobrycon sweglesi: Colombia: MHNG 2172.096, 31.3 mm SL, paratype of Megalamphodus sweglesi Géry, 1961, surroundings of Leticia, upper Amazon. Hyphessobrycon takasei: Brazil: MHNG 2177.036, 19.9 mm SL, paratype of Hyphessobrycon takasei Géry, 1964, Amapá State, lower rio Amazonas. Hyphessobrycon tenuis: Peru: ZFMK 1327, 24.3 mm SL, holotype of Hyphessobrycon tenuis Géry, 1964, small creek connecting. "Zapote Cocha" and "Caño Yarina", on edge of río Pacaya, tributary of lower río Ucayali; Peru: MHNG 2150.008, 3, 17.4-24.4 mm SL, paratypes of *Hyphessobrycon* tenuis Géry, 1964, same data as ZFMK 1327; Peru: ZFMK 1328, 16.8 mm SL, paratype of Hyphessobrycon tenuis Géry, 1964, same data as ZFMK 1327; Peru: ZMA 113853, 23.5 mm SL, paratype of Hyphessobrycon tenuis Géry, 1964, same data as ZFMK 1327. Hyphessobrycon togoi: Argentina: MHNG 2679.013, 2, 65.3-65.4 mm SL, paratypes of Hyphessobrycon

togoi Miquelarena & López, 2006, Buenos Aires Province, Chascomús lagoon. Hyphessobrycon tukunai: Brazil: SMF 7209, 18.9 mm SL, holotype of Hyphessobrycon tukunai Géry, 1965, igarapé Préto, along upper Amazon, near Belem, about 60 km below Leticia; Brazil: MHNG 2177.035, 2, 18.8-19.6 mm SL, paratypes of Hyphessobrycon tukunai Géry, 1965, same data as SMF 7209; Brazil: SMF 7210, 21.2 mm SL, paratype of Hyphessobrycon tukunai Géry, 1965, same data as SMF 7209; Brazil: SMF 7211, 18.5 mm SL, paratype of Hyphessobrycon tukunai Géry, 1965, same data as SMF 7209, Hyphessobrycon vilmae: Brazil: MHNG 2177.041, 4, 26.0-27.5 mm SL, paratypes of Hyphessobrycon vilmae Géry, 1966, Mato Grosso State, upper Arinos-Juruena basin; Brazil: MNHN 1980-1440, 26.5 mm SL, paratype of Hyphessobrycon vilmae Géry, 1966, same data as MHNG 2177.041; **Brazil:** ZMA 113825, 26.3 mm SL, paratype of Hyphessobrycon vilmae Géry, 1966, same data as MHNG 2177.041. Hyphessobrycon wajat: Argentina: MHNG 2593.096, 5, 26.7-29.0 mm SL, paratypes of Hyphessobrycon wajat Almirón & Casciotta, 1999, Corrientes Province, laguna Iberá. Hyphessobrycon werneri: Brazil: MHNG 2393.097, 8, 25.0-29.0 mm SL, paratypes of Hyphessobrycon werneri Géry & Uj, 1987, Pará State, rio Guamá basin; Brazil: MNHN 1992-0351, 1 of 3, 28.6 mm SL, paratype of Hyphessobrycon werneri Géry & Uj. 1987, Pará State, rio Guamá basin. Paracheirodon simulans: Brazil: MHNG 2171.019, 15.6 mm SL, holotype of Hyphessobrycon simulans Géry, 1963, Amazonas State, Manaus, rio Purus; Brazil: MHNG 2171.20, 15.2 mm SL, paratype of Hyphessobrycon simulans Géry, 1963, same data as MHNG 2171.019; Brazil: USNM 197510, 15.7 mm SL, paratype of Hyphessobrycon simulans Géry, 1963, same data as MHNG 2171.019.

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