

# A new species of *Knodus* (Characiformes: Characidae: Stevardiinae) from the rio Aripuanã, rio Madeira basin, Brazil



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A new species of the characid genus *Knodus* is described from the rio Aripuanã (rio Madeira basin). It can be distinguished from its congeners by its very low body depth, the presence of tri- to pentacuspoid teeth on the outer premaxillary series, with the median cuspoid larger than the lateral ones, the teeth of the inner premaxillary series pentacuspoid, distinctly larger than those of the outer series, the maxillary teeth tri- to pentacuspoid, with the median cusp slightly larger than the lateral ones, the four anteriormost dentary teeth pentacuspoid, the smaller posterior teeth tri- to pentacuspoid, a complete lateral line with 36–38 scales, 3 longitudinal scale series from pelvic fin origin to lateral line, and 11–12 circumpeduncular scales. The new species is also compared to *incertae sedis* species of ‘*Bryconamericus*’ from northern South America since phylogenetic studies suggest a closer relationship of those species with *Knodus*.

**Keywords:** *Bryconamericus*, Distribution, Neotropical Fish, Systematics, Taxonomy.

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Uma nova espécie de um caracídeo do gênero *Knodus* é descrita do rio Aripuanã (bacia do rio Madeira). Esta espécie se distingue de suas congêneres por possuir o corpo muito estreito, a presença de dentes tri- a pentacúspides na série externa do pré-maxilar, com a cúspide mediana ligeiramente maior que as cúspides laterais, dentes da série interna pentacúspide, distintamente maiores que os da série externa, dentes do maxilar tri- a pentacúspides com a cúspide central discretamente maior que as laterais, os quatro dentes mais anteriores do dentário pentacuspidados, os dentes mais posteriores tricuspidados a pentacuspidados, a linha lateral completa com 36–38 escamas, 3 séries longitudinais de escamas entre a origem da nadadeira pélvica e a linha lateral, e 11–12 séries longitudinais de escamas circumpedunculares. A nova espécie é comparada com espécies *incertae sedis* de '*Bryconamericus*' do norte da América do Sul uma vez que estudos filogenéticos sugerem a próxima relação daquelas espécies com *Knodus*.

**Palavras-chave:** *Bryconamericus*, Distribuição, Peixes Neotropicais, Sistemática, Taxonomia.

## INTRODUCTION

The speciose genus *Knodus* Eigenmann, 1911 currently includes 28 valid species (Fricke *et al.*, 2020) of small-sized fishes (30 to 90 mm SL; van der Sleen *et al.*, 2018), mainly occurring in the Amazon basin, but with representatives distributed in all main drainages of cis-Andean South America (Lima *et al.*, 2004; Ferreira, Netto-Ferreira, 2010; Esguícero, Castro, 2014). The traditional diagnosis of *Knodus* from other Characidae is very similar to that of *Bryconamericus* Eigenmann, 1907 in its broad sense. Both genera are recognized based on a generalized combination of characters following the Eigenmannian classification scheme (Eigenmann, 1917). Besides being plesiomorphic characters within the Stevardiinae or the Characidae (Malabarba, Weitzman, 2003; Weitzman *et al.*, 2005; Mirande, 2010), a considerable plasticity has been documented within both genera for each of the diagnostic characters, and the sole character allowing the distinction from each other is based on the presence of scales covering half the extent of caudal-fin rays in *Knodus*, or being restricted to the base of that fin in *Bryconamericus* (Eigenmann, 1911; Schultz, 1944; Ferreira, Netto-Ferreira, 2010; Esguícero, Castro, 2014; Dagosta, Netto-Ferreira 2015). Despite presenting a broad variation (Schultz, 1944), the extent of scales onto caudal-fin rays has been oversimplified into a binary character (caudal fin “scaled” or not), causing ambiguous interpretations of various authors, which resulted in conflicting opinions concerning the allocation of the species to the proper genus, also recurrent in other speciose Characidae genera (*i.e.* *Hyphessobrycon* Durbin, 1907 *vs.* *Hemigrammus* Gill, 1858; *Astyanax* Baird, Girard, 1854 *vs.* *Moenkhausia* Eigenmann, 1913).

Given the controversy involving the extent of caudal fin squamation distinguishing *Bryconamericus* and *Knodus*, some authors have rejected its validity as a diagnostic character between these genera, or even proposing the synonymy of *Knodus* with *Bryconamericus* (*i.e.* Schultz, 1944; Taphorn, 1992; Román-Valencia, 2000, 2003, 2005; Román-Valencia

*et al.*, 2009). Contradicting that proposal, Thomaz *et al.* (2015) and Mirande (2019) formally corroborated the distinction of *Knodus* and *Bryconamericus* as separate lineages, justifying the maintenance of both genera as valid members of the Diapomini.

Those authors also suggest drastic modifications on the composition of both genera, considering several species of ‘*Bryconamericus*’ would be more closely related to *Eretmobrycon* Fink, 1976, *Hemibrycon* Günther, 1864, *Hypobrycon* Malabarba, Malabarba, 1994, *Knodus*, *Nantis* Mirande, Aguilera, Azpelicueta, 2006, and *Odontostoechus* Gomes, 1947 (Thomaz *et al.*, 2015; Mirande, 2019) than to *Bryconamericus* in the *strict sense*. That genus, on the other hand, would be restricted to *B. exodon* Eigenmann, 1907 and *B. stramineus* Eigenmann, 1908, considering the hypothesis of Mirande (2019), with several species from northern South America yet to be investigated, and, therefore, *incertae sedis* in Stevardiinae. In addition to the inclusion of cis-andean species previously assigned to *Bryconamericus* (i.e. *K. alpha* (Eigenmann, 1914), *K. cinarucuense* (Román-Valencia, Taphorn, Ruiz-C. 2008), *K. deuterodonoides* (Eigenmann, 1908), among others), the current composition of *Knodus*, as suggested by Thomaz *et al.* (2015), also comprises *Bryconadenos* Weitzman, Menezes, Evers, Burns, 2005, *Rhinopetitia* Géry, 1964 (see comments in Netto-Ferreira *et al.*, 2016, Netto-Ferreira, Vari, 2017; Menezes, Netto-Ferreira, 2019), and likely *Phallobrycon* Menezes, Ferreira, Netto-Ferreira, 2009. Despite such taxonomic adjustments in the composition of those genera, no morphological diagnoses were provided, thus not allowing accurate generic allocation of the species not included in both studies or new to science.

In the present contribution, a new species tentatively assigned to *Knodus* from the rio Aripuanã in the rio Madeira basin is described. The new species is also compared to representatives of *Bryconamericus* from northern South America, since the composition of both genera is likely to be further modified in future studies, considering the possible closer relationship between ‘*Bryconamericus*’ from northern South America with *Knodus*, suggested by the aforementioned studies (Thomaz *et al.*, 2015; Mirande, 2019).

## MATERIAL AND METHODS

Counts and measurements are those described in Fink, Weitzman (1974) and Menezes, Weitzman (1990) except for the number of longitudinal scale series below the lateral line, which are counted from the pelvic-fin origin to the lateral line. To determine the disposition and number of *radii* on body scales, a scale was taken from the third horizontal series down from the dorsal-fin base to the lateral line. Numbers of vertebrae and vertebral elements, supraneurals, procurrent caudal-fin rays, teeth cusps and unbranched anal-fin rays were obtained from 5 cleared and stained (CS) specimens prepared according to Taylor, Van Dyke (1985). Vertebral counts include the vertebrae of the Weberian apparatus as four elements, as well as the complex caudal ossification PU1+U1 with the associated hypural bone and “half vertebra” counted as a single element. Institutional abbreviations follow Ferraris (2007). Meristic characters are presented in the descriptions, with the range of each count followed by their frequency in parentheses, and an asterisk (\*) indicating the values of the holotype. In determining the position of the last supraneural, and dorsal- and anal-fin pterygiophores in relation to neural spines, counts of the vertebral centra, include those that are part of the Weberian apparatus.

## RESULTS

*Knodus angustus*, new species

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(Figs. 1–5, Tab. 1)

**Holotype.** MZUSP 122222, female 36.0 mm SL, Brazil, Amazonas, Apuí, Prainha Nova beach in rio Aripuanã at end of road BR-174, 7°13'49.15"S 60°39'3.56"W, 05 Oct 2016, O. T. Oyakawa, W. Ohara, T. Teixeira & M. Pastana.

**Paratypes.** MZUSP 124932, 70 (19.0–36.0 mm SL, 5, 31.0–36.0 mm SL C&S), UFRGS 28150, 5 (24.0–30.5 mm SL) collected with holotype.

**Diagnosis.** *Knodus angustus* is distinguished from most congeners, except *K. figueredoi* Esguícero, Castro, 2014, *K. heteresthes* (Eigenmann, 1908), *K. longus* Zarske, Géry, 2006, *K. meridae* Eigenmann, 1911, *K. mizquae* (Fowler, 1943), *K. moenkhausii* (Eigenmann, Kennedy, 1903), and *K. victoriae* (Steindachner, 1907) by its very low body depth (20.0–25.2% SL *vs.* above 30% SL). The new species can be further distinguished from *K. caquetae* Fowler, 1945, *K. cinarucense* (data from Román-Valencia *et al.*, 2008), *K. hypopterus* (Fowler, 1943), *K. smithi* (Fowler, 1913), *K. gamma* Géry, 1972, and *K. jacunda* (Fowler, 1913) (data from Fowler, 1913) by having fewer anal-fin branched rays (15–19 *vs.* 20–27 branched rays); from *K. shinahota* Ferreira, Carvajal, 2007 by the presence of 3 scales below the lateral line (*vs.* 5–6 scales); from *K. alpha*, *K. breviceps* (Eigenmann, 1908), *K. chapadae* (Fowler, 1906), *K. ortegasae* (Fowler, 1943), *K. pasco* Zarske, 2007, and *K. septentrionalis* Géry, 1972 by having 5 longitudinal scale series from dorsal-fin origin to lateral line (*vs.* 4 in *K. ortegasae* and *K. septentrionalis* (data from Géry, 1972); and 6 in *K. breviceps*, *K. chapadae*, and *K. alpha* (data from Eigenmann *et al.*, 1914, and Ferreira, 2007); and 7 in *K. pasco* (data from Zarske, 2007); from *K. delta* Géry, 1972 and *K. borki* by having a complete lateral line with 36–38 perforated scales (*vs.* incomplete lateral line with 8–12 and 6–14 perforated



**FIGURE 1** | *Knodus angustus*, MZUSP 122222, female. 36 mm SL, Brazil, Amazonas, rio Aripuanã, tributary of rio Madeira.

scales (data from Géry, 1972 and Zarske, 2008); from *K. dorsomaculatus* Ferreira, Netto-Ferreira, 2010 by the lack of a dark dorsal-fin blotch (*vs.* dark blotch present); from *K. geryi* Lima, Britski, Machado, 2004 by the lack of dark pigmentation on the caudal-fin lobes (*vs.* caudal-fin lobes distinctly pigmented). *Knodus angustus* further differs from *K. deuterodonoides* by having 3 scale series between the pelvic-fin origin and the lateral line series (*vs.* 4 series); from *K. tiquiensis* Ferreira, Lima, 2006 by the lack of expansion of anal-fin rays (*vs.* anteriormost rays expanded with thickened integument until the sixth branched ray); and from *K. tanaothoros* (Weitzman, Menezes, Evers, Burns, 2005) and *K. weitzmani* (Menezes, Netto-Ferreira, Ferreira, 2009) by the lack of modified glandular tissue on the anal-fin lobe (*vs.* glandular tissue present). Finally, *Knodus angustus* can be distinguished from *K. figueredoi*, *K. heteresthes*, *K. meridae*, *K. mizquae*, *K. moenkhausii*, and *K. victoriae* by having 11–12 circumpeduncular scales (*vs.* 13–14); and from *K. longus* by the presence of 11–13 predorsal scales and the presence of a faint longitudinal stripe (*vs.* 17–18 predorsal scales and the presence of a conspicuous dark stripe (data from Zarske, Géry, 2006).

**Description.** Morphometric data of holotype and paratypes in Tab. 1. Body comparatively small (largest examined specimen 73 mm SL). Head and body elongate and laterally compressed; greatest body depth at dorsal-fin origin. Profile distinctly convex from upper jaw to posterior nostril, slightly convex from latter point to dorsal-fin origin, straight along dorsal-fin base, slightly concave from latter point to adipose-fin origin, and slightly concave to nearly straight from latter point to anterior most dorsal procurrent caudal-fin ray. Ventral body profile convex from tip of lower jaw to isthmus, nearly straight from that point to vertical through pectoral-fin origin, convex from latter point to pelvic-fin origin, and straight from that point to anal-fin origin, and straight along anal-fin base and concave along caudal peduncle.

Mouth sub-terminal; lower jaw short, included in upper jaw when mouth closed. Posterior tip of maxilla reaching vertical through anterior border of orbit. Outer premaxillary series with 4(29), 5\*(39), or 6(12) tri- to pentacuspoid teeth; inner series with 4(80) pentacuspoid teeth, larger than those of outer series (Fig. 2). Maxillary with 2(25), 3\*(50), or 4(5) teeth; anterior teeth largest, pentacuspoid, posterior tri- to pentacuspoid (Fig. 2). Dentary with 4(80) large pentacuspoid teeth anteriorly, followed by 3(7), 4(32), 5\*(37), or 6(3) smaller tri- to pentacuspoid teeth abruptly decreasing in size posteriorly (Fig. 2). First gill arch with external and internal series of gill-rakers; external series with 14(4), 15(23), 16\*(44), 17(8), or 18(1) gill-rakers. Branchiostegal rays 4(5), 3 originating on anterior and 1 on posterior ceratohyal.

Scales cycloid, two *radii* present, originating at focus and vertically opposed to each other. Lateral line complete with 36(35), 37(39), or 38\*(6) perforated scales. Predorsal scales 11(10), 12(65), or 13\*(5). Scale series between lateral line and dorsal-fin origin 5(80); series between lateral line and pelvic-fin origin 3(80); circumpeduncular scales 11(2) or 12\*(78). Single series of scales with sinuous posterior borders forming sheath along base of all anal-fin rays.

Pectoral-fin rays i,7,i(1), i,8,iii(6), i,9,i(2), i,9,ii(42), i,9,iii(2), i,10,i\*(9), i,10,ii(12), or i,11,i(1). Distal tip of longest pectoral-fin ray not reaching vertical through pelvic-fin origin when addressed to body. Pelvic-fin rays i,6,i\*(80), tip of fin falling short of anal-fin origin. Supraneurals 5(1), or 6(4), located anterior to spines of 5<sup>th</sup> to 9<sup>th</sup>(3) or

10<sup>th</sup>(2) vertebral centra; rod-shaped, or with discrete anteroposterior lamellar expansions of dorsal portion. Dorsal-fin rays ii,7,i,\*(80). First dorsal-fin pterygiophore inserting behind neural spine of 11<sup>th</sup>(5) vertebral centrum. Distal margin of extended dorsal fin straight to slightly convex. Dorsal-fin origin closer to caudal-fin base than to snout tip. Dorsal-fin ray terminus at vertical through base of third unbranched anal-fin ray. Anal-fin rays iii,15(6), 16(19), 17(39), 18(\*15), or 19(1), posterior-most ray adnate. Anal fin with short, inconspicuous lobe anteriorly, including last unbranched ray plus first 5–6 branched rays. Distal margin of anal fin concave. First anal-fin pterygiophore inserting behind haemal arch of centra 16<sup>th</sup>(2) or 17<sup>th</sup>(3). Adipose fin present. Principal caudal-fin rays i,9,8,i(31). Dorsal and ventral procurrent caudal-fin rays 10(2), 11(1) or 12(2), respectively. Total vertebrae 36(5).

**Coloration in alcohol.** Ground color pale yellowish to brown. Color pattern poorly counter shaded. Upper portion of head from tip of snout to end of supraoccipital spine and predorsal scales only slightly more pigmented, and somewhat darker than lateral and ventral portions of body; minute dark chromatophores scattered around eye extending laterally over maxilla, first, second, fourth, fifth and sixth infraorbitals, upper half of third infraorbital, upper half of opercle and interopercle; anterior part of lower jaw with scattered dark chromatophores. Postorbital portion of the head

**TABLE 1** | Morphometric data for *Knodus angustus*, new species. Values for the holotype included in number and range of female specimens. SD = standard deviation. P = significance of comparison between variable in male and female specimens.

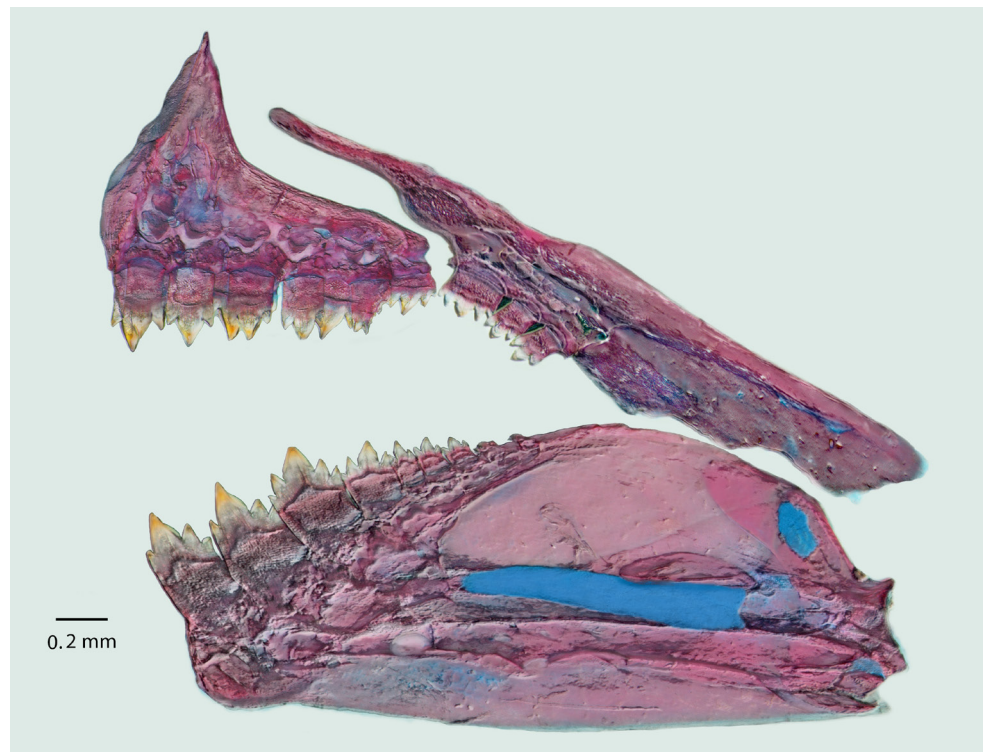
| Characters                            | Males    |    |           |      |     | Females |           |      |     |       |
|---------------------------------------|----------|----|-----------|------|-----|---------|-----------|------|-----|-------|
|                                       | Holotype | n  | range     | mean | SD  | n       | range     | mean | SD  | p     |
| Standard length                       | 36.0     | 10 | 22.0-32.1 | 29.3 | 3.0 | 70      | 19.0-36.0 | 27.6 | 3.7 |       |
| <b>Percentages of Standard length</b> |          |    |           |      |     |         |           |      |     |       |
| Depth at dorsal-fin origin            | 22.2     | 10 | 21.4-23.6 | 22.8 | 1.0 | 70      | 20.0-25.2 | 22.7 | 1.1 | 0.056 |
| Snout to dorsal-fin origin            | 52.7     | 10 | 51.0-54.5 | 52.7 | 1.0 | 70      | 51.0-54.8 | 52.7 | 0.8 | 0.099 |
| Snout to pectoral-fin origin          | 23.0     | 10 | 22.6-25.0 | 23.6 | 1.0 | 70      | 22.0-25.4 | 23.7 | 0.8 | 0.085 |
| Snout to pelvic-fin origin            | 48.6     | 10 | 44.4-48.6 | 46.2 | 1.0 | 70      | 44.0-50.0 | 47.0 | 1.1 | 0.196 |
| Snout to anal-fin origin              | 63.8     | 10 | 60.3-63.6 | 61.8 | 1.0 | 70      | 60.0-65.0 | 62.0 | 1.1 | 0.156 |
| Caudal peduncle depth                 | 10.2     | 10 | 09.3-10.8 | 10.1 | 0.4 | 70      | 09.2-11.1 | 10.0 | 0.4 | 0.068 |
| Pectoral-fin length                   | 19.4     | 10 | 19.0-21.4 | 20.4 | 0.8 | 70      | 19.0-21.6 | 20.5 | 0.6 | 0.117 |
| Pelvic-fin length                     | 13.8     | 10 | 13.0-14.7 | 14.0 | 0.4 | 70      | 12.0-15.1 | 14.1 | 0.6 | 0.143 |
| Dorsal-fin base length                | 11.1     | 10 | 09.8-11.4 | 10.4 | 0.6 | 70      | 09.8-12.3 | 10.7 | 0.5 | 0.269 |
| Dorsal-fin height                     | 20.5     | 10 | 21.0-22.7 | 21.3 | 0.6 | 70      | 20.0-23.1 | 21.2 | 0.7 | 0.075 |
| Anal-fin base length                  | 23.0     | 10 | 22.0-26.2 | 23.8 | 1.1 | 70      | 22.0-26.1 | 23.4 | 0.8 | 0.515 |
| Anal-fin lobe length                  | 14.7     | 10 | 15.6-18.2 | 16.5 | 0.8 | 70      | 14.7-18.0 | 17.0 | 0.8 | 0.099 |
| Eye to dorsal-fin origin              | 38.8     | 10 | 36.2-39.3 | 38.0 | 1.0 | 70      | 36.0-40.4 | 38.6 | 1.0 | 0.192 |
| Dorsal-fin origin to caudal-fin base  | 51.3     | 10 | 46.7-51.7 | 49.3 | 1.5 | 70      | 45.0-51.8 | 49.3 | 1.3 | 0.106 |
| Bony head length                      | 24.8     | 10 | 24.0-25.3 | 24.8 | 0.5 | 70      | 24.0-26.7 | 25.3 | 0.6 | 0.177 |
| <b>Percentages of Head length</b>     |          |    |           |      |     |         |           |      |     |       |
| Horizontal eye diameter               | 38.9     | 10 | 35.1-40.0 | 37.5 | 1.4 | 70      | 34.0-40.5 | 37.8 | 1.4 | 0.266 |
| Snout length                          | 25.9     | 10 | 23.4-28.2 | 26.4 | 1.5 | 70      | 23.0-28.5 | 26.0 | 1.3 | 0.135 |
| Least interorbital width              | 33.7     | 10 | 32.5-35.6 | 34.0 | 1.1 | 70      | 31.0-36.5 | 34.0 | 1.3 | 0.184 |
| Upper jaw length                      | 38.9     | 10 | 34.6-41.0 | 37.2 | 1.7 | 70      | 34.0-40.5 | 37.2 | 1.6 | 0.229 |

with disperse chromatophores forming a discrete darker pigmentation from the infraorbitals 5 and 6, and opercle to the pectoral girdle. Dark chromatophores onto distal margins of scales, distinctly lighter at focus; scattered dark chromatophores on lower part of body below lateral line series, darker above anal-fin base. A vertically elongate humeral blotch present onto scales of 3 to 4 longitudinal series, becoming narrower downward (Fig. 1). Diffuse stripe with scattered chromatophores present on the body, from vertical through pectoral-fin midline to caudal-fin base, becoming more conspicuous near vertical through anal-fin origin, being slightly enlarged over caudal peduncle (Fig. 1). All fins hyaline with scattered dark chromatophores on intervening membranes.

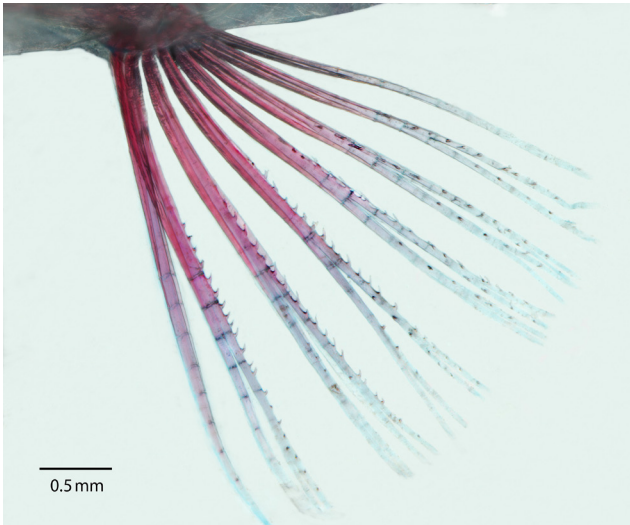
**Sexual dimorphism.** Mature males of *Knodus angustus* present bilateral hooks on first unbranched and the following six branched pelvic-fin rays (Fig. 3). Bilateral bony hooks present on last unbranched plus four to six anteriormost branched anal-fin rays (Fig. 4). Mature males also with a gill gland on the lower portion of the first gill arch involving 8 gill filaments. Hooks and gill gland absent on mature females.

**Etymology.** The species epithet *angustus* is from the Latin, meaning “narrow” in allusion to the narrowness of the body of this species. An adjective.

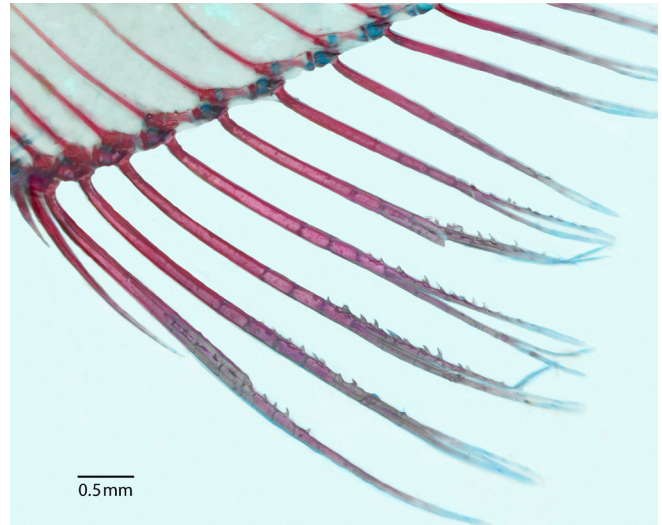
**Geographical distribution.** *Knodus angustus* is known so far from the rio Aripuanã, a tributary of the rio Madeira, Amazonas, Brazil (Fig. 5).



**FIGURE 2** | *Knodus angustus*, MZUSP 124932, C&S, jaws and dentition, lateral view, left side, anterior at left.



**FIGURE 3** | *Knodus angustus*, MZUSP 124932, sexually mature male; pelvic-fin rays, ventral view, left side showing pelvic-fin hooks.



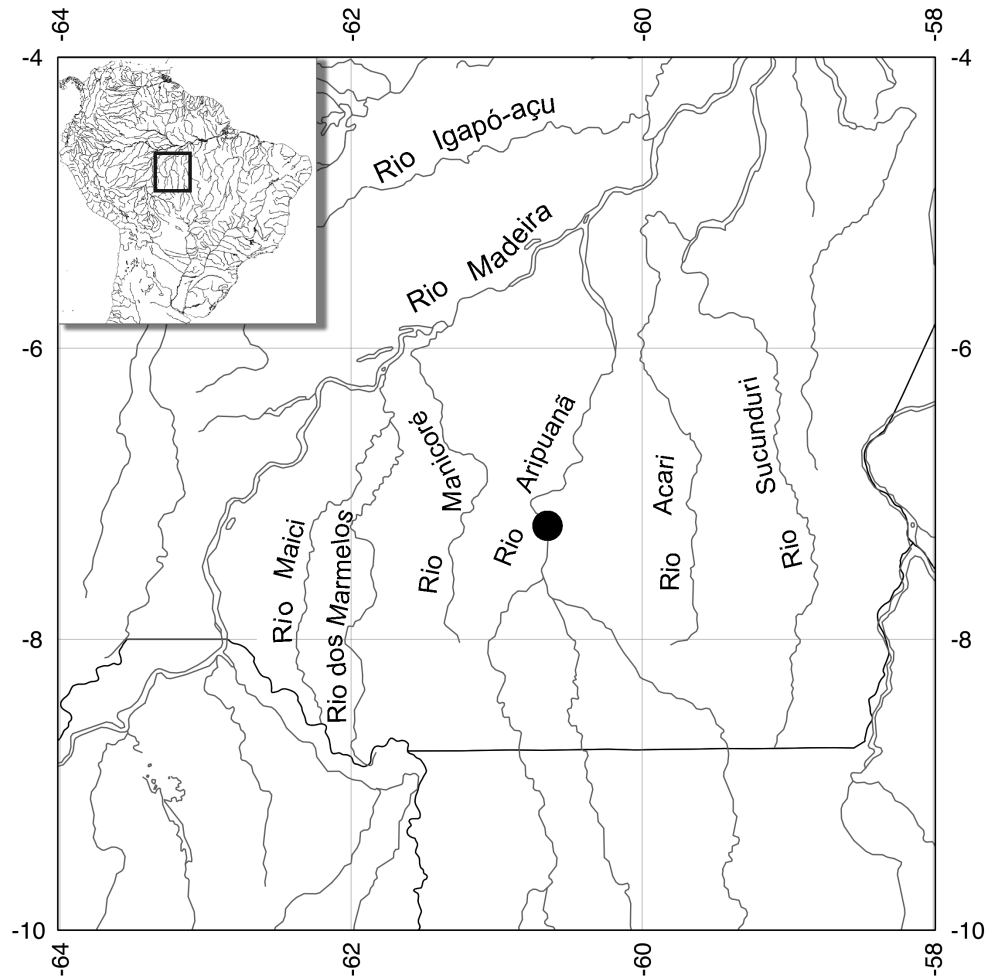
**FIGURE 4** | *Knodus angustus*, MZUSP 124933, sexually mature male; anal-fin rays, lateral view, left side showing pelvic-fin hooks.

**Conservation status.** Although *Knodus angustus* is known only from its type locality in the rio Aripuanã, the area where the specimens were sampled is adjacent to the Floresta Nacional do Aripuanã. Despite the recent, on-going deforestation peak in the Brazilian Amazon, it is likely that anthropic impacts on the forest will take several years to generate impacts on the population of *K. angustus*, therefore, the species is classified herein as Least Concern (LC) according to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Subcommittee, 2019).

## DISCUSSION

The present allocation of the new species in *Knodus* is based both on the presence of scales covering over one third of caudal-fin rays, following the Eigenmannian classification scheme, but also in the strong evidence provided by Thomaz *et al.* (2015) and Miranda (2019) that small Stevardiinae from the Amazon basin and cis-Andean northern South America fitting the general diagnosis for *Knodus* and *Bryconamericus* would be more closely related to *Knodus meridae*. That relationship pattern was largely corroborated by García-Melo *et al.* (2019) with most samples originating from cisandean Northern South America being nested with species of *Knodus*, the only exception being the specimens identified as ‘*Bryconamericus*’ *pachacuti* Eigenmann, 1927 from the Amazon, which grouped with *Bryconamericus*. That result contradicts the hypotheses of Thomaz *et al.* (2015) and Miranda (2019), in which ‘*B.*’ *pachacuti* grouped with *Attonitus* Vari, Ortega, 2000. Considering the oversimplified phylogenetic framework of García-Melo *et al.* (2019), lacking representatives of several Diapomini genera (*i.e.* *Attonitus*, *Diapoma* Cope, 1984, *Odontostoechus*, *Piabarchus* Myers, 1928), and the effect of taxon sampling in phylogenetic trees topology, the close relation of ‘*B.*’ *pachacuti* with *B. exodon* may be an analytical artifact.





**FIGURE 5 |** Map of northern South America showing collection site of *Knodus angustus* in the rio Aripuanã, rio Madeira basin.

Besides the multiple taxonomic recombinations within the Diapomini, the aforementioned phylogenetic studies partially refute the validity of the caudal-fin squamation as a diagnostic character between *Bryconamericus* and *Knodus*, as the extended sense of *Knodus* includes a broad variation of that character, partially corroborating the criticism from several authors (Schultz, 1944; Taphorn, 1992; Román-Valencia, 2000, 2003, 2005; Román-Valencia *et al.*, 2009). In addition, as both genera lack unambiguous morphological diagnostic characters, it is not possible, at this moment, to unambiguously assign which species of ‘*Bryconamericus*’ would be, in fact, more closely related to *Knodus*.

Among the species of *Bryconamericus* from northern South America, *K. angustus* can be distinguished from ‘*Bryconamericus*’ *carlosi* Román-Valencia, 2003, ‘*B.*’ *motatanensis* Schultz, 1944, ‘*B.*’ *pachacuti*, and ‘*B.*’ *singularis* Román-Valencia, Taphorn, Ruiz-C, 2008 by the presence of 5 scales series between the lateral line and the dorsal-fin origin (*vs.* 6, data from Román-Valencia, 2003, 2005); *K. angustus* can be distinguished from ‘*Bryconamericus*’ *carlosi* Román-Valencia, 2003, ‘*B.*’ *macrophthalmus* Román-Valencia,

2003, '*B. motanensis* Schultz, 1944, '*B. pachacuti*, and '*B. singularis* Román-Valencia, Taphorn, Ruiz-C, 2008 by the presence of 4 scales series between the lateral line and the dorsal-fin origin (*vs.* 5–6, data from Román-Valencia, 2003, 2005); from '*B. charalae* Román-Valencia, 2005, '*B. diaphanus* (Cope, 1878), and '*B. orinocoense* Román-Valencia, 2003 by having more perforated lateral-line scales (36–38 *vs.* 13–33 lateral line scales in '*B. orinocoense*, data from Román-Valencia, 2003; 31–34 in '*B. charalae*, and 34 in the holotype of '*B. diaphanus*); from '*B. bucaiyensis* Román-Valencia, Ruiz-C., Taphorn, García-Alzate, 2013, '*B. cismontanus* Eigenmann, 1914, '*B. lassorum* Román-Valencia, 2002, '*B. macarena* Román-Valencia, García-Alzate, Ruiz-C., Taphorn, 2010, '*B. osgoodi* Eigenmann, Allen, 1942, and '*B. ternetzi* Myers, 1928 by having 3 scales between the pelvic-fin origin and the lateral line series (*vs.* 4–5 in '*B. cismontanus*, '*B. lassorum*, '*B. macarena*, and '*B. ternetzi*; 6 in '*B. osgoodi*, and 7 in '*B. bucaiyensis*); from '*B. bolivianum* Pearson, 1924, '*B. hyphesson* Eigenmann, 1909, and '*B. pinnavittatus* Dagosta, Netto-Ferreira, 2015 by having more branched anal-fin rays (15–19 *vs.* 11–14); from '*B. guyanensis* Zarske, Le Bail, Géry, 2010 by having the largest dentary teeth followed by smaller tri- to pentacuspide teeth gradually decreasing in size posteriorly (*vs.* large teeth followed by conical teeth abruptly decreasing in size posteriorly) and the anal-fin origin located posterior to dorsal-fin terminus (*vs.* anal-fin origin at vertical through middle dorsal fin); and from '*B. novae* by the longitudinal stripe becoming wider posteriorly (*vs.* longitudinal stripe becoming narrower posteriorly). The very low body depth, the subterminal position of the mouth, and the overall pale coloration of *Knodus angustus*, are very similar to that of representatives of *Rhinopetitia*, but the species lacks the diagnostic characters of that genus recently proposed by Menezes, Netto-Ferreira (2019).

*Knodus angustus* is the third species of the genus described from tributaries of the Rio Madeira, the other species being *K. smithi* and *K. jacunda*. The first occurs upstream of the Teotônio rapids in Porto Velho, Rondônia (Queiroz *et al.*, 2013), whereas *Knodus jacunda*, also described from near Porto Velho, is only known from the holotype and its validity is still questionable. *Knodus angustus* differs from *K. smithi* by having 3 longitudinal scale series from the lateral line to the pelvic fin-origin (*vs.* 4), 11–12 circumpeduncular scale rows (*vs.* 14); 15–19 branched anal-fin rays (*vs.* 23–27); the presence of pentacuspide teeth on the inner premaxillary series (*vs.* teeth heptacuspide); and the lateral line with 36–38 perforated scales, (*vs.* 38–40 perforated scales).

Despite tentative, the comparisons between *K. angustus* and the species above are an attempt to facilitate the distinction between them in future studies, especially considering the great impact of recent phylogenetic hypotheses in the number of species presently included in the genus *Knodus* (Thomaz *et al.*, 2015; Mirande, 2019; García-Melo *et al.*, 2019). Although the relationships of several species from northern South America with other Stevardiinae are yet to be adequately tested, those studies also provide strong evidence suggesting the composition of *Knodus* is likely to be further adjusted by future, more comprehensive phylogenetic hypotheses.

**Comparative material examined.** *Knodus tanaothoros*: Brasil: MZUSP 85852, holotype of *Bryconadenos tanaothoros*, 41.3 mm SL. *Bryconadenos weitzmani*: Brasil: MZUSP 98666, holotype, 40.7 mm SL. *Knodus alpha*: Venezuela: AUM 54052, 2, 38.6–39.2 mm SL. Colombia: FMNH: 56648, holotype of *Bryconamericus beta*, 43.2 mm

SL; FMNH 56649, paratypes, 40.2–47.8 mm SL. *Knodus deuterodonoides*: Venezuela: INHS 60365, 9, 22.5–44.0 mm SL; INHS 55421, 11, 16.5–40.3 mm SL; INHS 28933, 4, 27.4–50.7 mm SL. *Bryconamericus macrophthalmus*: Venezuela: MBUCV 29392, holotype, 39.0 mm SL; MBUCV 11381, paratypes, 21.9–47.6 mm SL. *Bryconamericus orinocoense*: Venezuela: MBUCV 29464, holotype, 27.0 mm SL; MBUCV 25834, paratypes, 27.9–29.8 mm SL. *Bryconamericus singularis*: Venezuela: MBUCV 33029, paratypes, 21.5–24.33 mm SL. *Bryconamericus subtiliformis*: Venezuela: MBUCV 29393, holotype, 55.3 mm SL; MBUCV 29393, paratypes, 27.9–38.3 mm SL. *Bryconamericus yokiae*: Venezuela: MBUCV 29540, holotype, 65.5 mm SL; MBUCV 20273, paratypes, 27.9–56.7 mm SL. *Knodus albolineatus*: Brazil: NMW 83365:1, syntype, 70.1 mm SL. *Knodus breviceps*: Brazil: MCZ 20692, syntypes, 52.0–66.8 mm SL. *Knodus calliurus*: Brazil: ZMB 23684, holotype, 33.2 mm SL. *Knodus caquetae*: Colombia: ANSP 71670, holotype, 50.0 mm SL; ANSP 71671, paratype, 38.1 mm SL. *Knodus chapadae*: Brazil: ANSP 21828, holotype, 59.1 mm SL; ANSP 21829, paratype, 42.6 mm SL. *Knodus cinarucuense*: Venezuela: ANSP 191136, 22.8 mm SL. *Knodus delta*: Ecuador: ZMH 1473, holotype, 34.0 mm SL. *Knodus dorsomaculatus*: Brazil: MZUSP 102823, holotype, 48.0 mm SL. *Knodus figueiredoi*: Brazil: LIRP 10241, paratypes, 31.7–19.3 mm SL. *Knodus gamma*: Ecuador: ZMH 1861, holotype, 48.5 mm SL; ZMH 2211, paratypes, 46.7–48.2 mm SL. *Knodus geryi*: Brazil: MZUSP 83354, holotype, 63.4 mm SL; MZUSP 78863, paratypes, 18.4–64.8 mm SL. *Knodus heteresthes*: Brazil: MCZ 89966, syntypes, 25.3–39.0 mm SL; USNM 120247, syntype, 38.5 mm SL. *Knodus hypopterus*: Colombia: ANSP 70505, holotype, 32.5 mm SL. *Knodus jacunda*: Brazil: ANSP 39292, holotype, 22.1 mm SL. *Knodus meridae*: Venezuela: BMNH 1908.5.29.148, holotype, 44.0 mm SL. *Knodus mizquae*: Bolivia: ANSP 69176, holotype, 32.2 mm SL; ANSP 69178–69191, paratypes, 23.4–32.8 mm SL. *Knodus moenkhausii*: Paraguay: CAS 55104, paratypes 23.5–28.7 mm SL; CAS 55103, paratype, 36.1 mm SL; AMNH 1463, paratypes 26.6–30.0 mm SL; FMNH 52601, paratype, 31.9–33.0 mm SL. *Knodus nuptialis*: Brazil: MZUSP 124829, holotype, 46.5 mm SL. *Knodus ortegasae*: Colombia: ANSP 70504, holotype, 55.6 mm SL. *Knodus savannensis*: Brazil: USNM: 196088, holotype, 30.4 mm SL. *Knodus septentrionalis*: Ecuador: ZMH 2261, holotype, 50.1 mm SL. *Knodus shinahota*: Bolivia: LIRP 5722, holotype, 33.7 mm SL. *Knodus smithi*: Brazil: ANSP 39293, holotype, 25.2 mm SL; ANSP 39294–39297, paratypes, 18.5–24.0 mm SL. *Knodus tiquienensis*: Brazil: MZUSP 88059, holotype, 72.6 mm SL. *Knodus victoriae*: Brazil: NMW 57823, syntypes, 29.0–44.6 mm SL. *Moenkhausia lepidura hasemani*: Brazil: FMNH 55055, holotype, 44.4 mm SL.

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