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Knodus shinahota (Characiformes: Characidae) a new species from the río Shinahota, río Chapare basin (Mamoré system), Bolivia

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Knodus shinahota, new species, is described from río Shinahota, a tributary of the upper rio Mamoré basin, Província de Tiraque, Cochabamba State, Bolivia. The new species can be distinguished from all congeners except *K. chapadae* and *K. geryi* by having six rows of scales between the lateral line and the dorsal-fin origin (*vs* 4 or 5 rows of scales in the other species). *Knodus shinahota* differs from *K. chapadae* by possessing more rows of scales between the lateral line and the pelvic-fin origin (5 *vs* 3½ or 4, respectively) and more lateral line scales (38-41 *vs* 36-38, respectively). It differs from *K. geryi* by possessing more rows of scales between the lateral-line and the pelvic-fin origin (5 *vs* 4, respectively); fewer branched anal-fin rays (17-20 *vs* 15-17, respectively), and by lacking the two symmetric, large, dark, blotches on the basal portions of the caudal-fin lobes that characterize *K. geryi*.

Knodus shinahota, espécie nova, é descrita do río Shinahota, um afluente do alto da bacia do rio Mamoré, Província de Tiraque, Estado de Cochabamba, Bolívia. A espécie nova pode ser distinguida de todas as suas congêneres exceto *K. chapadae* e *K. geryi* por ter seis fileiras de escamas entre a linha lateral e a origem da nadadeira dorsal (*vs* 4 ou 5 fileiras de escamas nas demais espécies). *Knodus shinahota* difere de *K. chapadae* por possuir mais fileiras de escamas entre a linha lateral e a origem da nadadeira pélvica (5 *vs* 3½ ou 4, respectivamente) e mais escamas na linha lateral (38-41 *vs* 36-38, respectivamente). Difere de *K. geryi* por possuir mais fileiras de escamas entre a linha lateral e a origem da nadadeira pélvica (5 *vs* 4, respectivamente); menos raios ramificados na nadadeira anal (17-20 *vs* 15-17, respectivamente), e pela falta das duas grandes manchas escuras, simétricas, basalmente nos lobos da nadadeira caudal que caracteriza *K. geryi*.

Key words: South America, Systematics, Neotropical, Amazon basin.

Introduction

Knodus Eigenmann, 1911, is a genus of the Characidae that consists of 20 valid species (Lima *et al*., 2003; Lima *et al*., 2004; Zarske & Géry, 2006; Ferreira & Lima, 2006). *Knodus* species occur in the Paraná-Paraguay, Parnaíba, São Francisco, and Amazonas basins, with the greatest diversity of the genus in the latter drainage system. The monophyly of *Knodus* has been disputed, and the genus was considered a synonym of *Bryconamericus* by some authors (see Lima *et al*., 2004, for a discussion of the topic). Currently, the presence of scales on the basal portion of the caudal fin in the species of *Knodus* is the sole feature used to distinguish that genus from *Bryconamericus*.

Knodus was recently considered within Characidae as *incertae sedis* (Lima *et al*., 2003), and until now no phylogenetic hypothesis has been proposed concerning the monophyly or lack thereof of the genus. Only two phylogenetic studies, one based on osteology (Malabarba & Weitzman, 2003) and the second on molecular data (Calcagnotto *et al*., 2005), included *Knodus*. According to Malabarba & Weitzman (2003), *Knodus* belongs to a clade that also includes the subfamily Glandulocaudinae and *Attonitus*, *Boehlkea*, *Bryconacidnus*, *Bryconamericus*, *Caiapobrycon*, *Ceratobranchia*, *Creagrutus*, *Cyanocharax*, *Hemibrycon*, *Hypobrycon*, *Microgenys*, *Monotocheirodon*, *Odontostoechus*, *Othonocheirodus*, *Piabarcus*, *Piabina*, *Rhinobrycon* and *Rhinopetitia*. In the study by Calcagnotto *et al*. (2005), *Knodus* was a member of a clade that also included *Bryconamericus*, *Creagrutus*, *Hemibrycon*, and two genera of the Glandulocaudinae (*Gephyrocharax* and *Mimagoniates*). The interrelationships among the species of *Knodus* remain uncertain. In light of the uncertainty as to the monophyly and relationship of *Knodus* we describe the new

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species of *Knodus* using Eigenmann's (1918) original concept of the genus. According to Eigenmann, *Knodus* is characterized by the combination of the presence of the expanded second infraorbital that is in contact ventrally with the horizontal limb of the preopercle, two rows of teeth on the premaxilla, with four teeth present on the inner tooth row, a caudal fin that is scaled basally, and a slightly decurved lateral line.

The new species described herein is the fourth species of *Knodus* reported from the upper Madeira-Mamoré basin. We provide comparisons between the new species and the remaining three congeners from that basin and also with *Bryconamericus bolivianus*, the only species of that genus known from the upper Madeira-Mamoré basin.

Material and Methods

Institutional abbreviations follow Leviton *et al*. (1985) with the addition of LIRP, Laboratório de Ictiologia de Ribeirão Preto, Departamento de Biologia da FFCLRP, Universidade de São Paulo, Ribeirão Preto, Brazil; and UMSS, Universidad Mayor de San Simón, Facultad de Ciencias y Tecnología, Unidad de Limnología y Recursos Acuáticos, Laboratorio de Ictiología, Cochabamba, Bolivia.

Counts and measurements follow Fink & Weitzman (1974) except for counts of the horizontal scale rows below the lateral line which were counted to the pelvic-fin insertion because this region presents a minor degree of deformation making counts more precise. In Table 1, standard length (SL) is expressed in mm and all other measurements are expressed as percentage of SL, except for subunits of the head which are expressed as percentages of head length (HL). Counts are presented in the description, followed by frequency of particular values in parentheses. Asterisks indicate values of the holotype. Counts of vertebrae and supraneurals were taken from cleared and stained (c&s) paratypes. Counts of total vertebral include the four vertebrae of the Weberian apparatus and the terminal centrum. Specimens were cleared and stained following the method of Taylor & Van Dyke (1985). Osteological terminology follows Weitzman (1962) with the modifications listed by Vari & Harold (2001). Comparisons were based on the examination of type-specimens of species of *Knodus* made by the first author, with the exception of *Bryconamericus bolivianus* and *K. longus*, in which case the comparison was based on photographs of the holotype and data provided in the original description.

With objective of verifying the presence of insemination, tissue samples for histology were removed from specimens initially fixed in 10% formalin and subsequently transferred to 70% ethanol. Tissue samples were dehydrated in an ethanol series, embedded in paraffin, sectioned at 6 µm and stained with hematoxylin and eosin.

Knodus shinahota, new species

Fig. 1

Holotype. LIRP 5722 (33.7 mm SL, male), río Shinahota, approximately 150 m upriver from under bridge of new Cochabamba-Santa Cruz road, río Chapare basin (rio Mamoré system), town of Shinahota, Província de Tiraque, Cochabamba, Bolivia, 16º59'34"S 65º15'4"W, F. M. Carvajal, L. Córdova & C. Flores, 6 Sep 2002.
Paratypes. LIRP 5723, 7, 29.6-36.9 mm SL (4, 31.9-36.9 mm SL, c&s), MZUSP 91630, 3, 33.1-34.0 mm SL, and UMSS 935, 12, 29.4-35.0 mm SL, collected with holotype.

Diagnosis. *Knodus shinahota* can be distinguished from all congeners except *K. chapadae* and *K. geryi* by having six rows of scales between the lateral line and the dorsal-fin origin (*vs* 4 or 5 rows of scales in the other species). *Knodus shinahota* differs from *K. chapadae* by possessing more rows of scales between the lateral line and the pelvic-fin origin (5 *vs* 3½ or 4, respectively) and more lateral line scales (38-41 *vs* 36-38, respectively). *Knodus shinahota* differs from *K. geryi*

Fig. 1. *Knodus shinahota*, holotype, LIRP 5722, 33.7 mm SL (male): Bolivia, río Shinahota, río Chapare basin, rio Mamoré system. Photo by Alexandre C. Ribeiro.

by possessing more rows of scales between the lateral line and the pelvic-fin origin (5 *vs* 4, respectively); fewer branched anal-fin rays (17-20 *vs* 15-17, respectively), and in lacking the two symmetric, large, dark, blotches that are present on the base of the caudal-fin lobes in *K. geryi*.

Description. Morphometric and meristic data for holotype and paratypes presented in Table 1.

Body laterally compressed, largest specimen 37.0 mm SL. Greatest body depth situated at dorsal-fin origin. Dorsal profile of head distinctly convex from margin of upper lip to tip of supraoccipital spine. Dorsal profile of body convex from tip of supraoccipital spine to dorsal-fin origin; straight along dorsal-fin base; straight from posterior terminus of dorsal-fin base to adipose-fin insertion, and slightly concave from latter point to caudal-fin origin. Ventral profile of body convex from tip of lower jaw to anal-fin insertion. Anal-fin base straight to slightly concave. Ventral profile of caudal peduncle slightly concave.

Dorsal-fin rays ii,8* (23). Length of first unbranched dorsal-fin ray less than one-half length of second unbranched ray. Dorsal-fin origin located at middle of SL and posterior to vertical through pelvic-fin origin. First dorsal-fin pterygiophore inserted posterior to neural spine of 11th (4) vertebra. Adipose fin present, its origin located at vertical through base of last anal-fin ray. Pectoral-fin rays i,8 (3), 9* (16), 10 (4),i. Pelvic-fin rays i,6,i* (23). Anal fin with five unbranched rays followed by 18 (7), 19* (10) or 20 (6) branched rays. First anal-fin pterygiophore inserted posterior to hemal spine of 16th (4) vertebra. Caudal fin forked; lobes similar in size. Principal caudal-fin rays i,17,i* (23).

Mouth terminal. Premaxilla extending slightly anterior of vertical through anterior limit of dentary. Premaxilla with two rows of teeth (Fig. 2). Outer tooth row aligned in gentle arch, with 4* (18) or 5 (5) tricuspid teeth, with median cusps largest. Inner premaxillary tooth row with 4 teeth. Symphyseal tooth in row with four cusps and remaining teeth with five cusps. Maxilla with 2 (4) or 3* (19) teeth; teeth with seven cusps with median cusps slightly more developed. Dentary with four large teeth with five cusps followed by 2 (3), 3* (16) or 4 (4) smaller teeth with three to five cusps.

Scales cycloid. Lateral line complete, with 36 (5), 37* (15) or 38 (3) perforated scales. Six rows of scales between dorsal-fin origin and lateral line. Five rows of scales between lateral line and pelvic fin. Predorsal scales 11* (4), 12 (13) or 13 (6). Circumpeduncular scales 14* (23). Single row of six to nine scales extending along base of anal fin. Basal portion of caudal-fin lobes covered with scales.

First gill arch with 7* (14) or 8 (9) gill rakers on hypobranchial and ceratobranchial, 4* (23) rakers on epibranchial and 1* (23) raker on cartilage between ceratobranchial and epibranchial. Four (4) branchiostegal rays; 3 (4) on anterior ceratohyal and 1 (4) on posterior ceratohyal. Vertebrae 36 (4). Supraneurals 4 (4).

Sexual dimorphism. Sexually mature males easily recognized by presence of hooks on anal-fin rays, by possession of proportionally longer pectoral and pelvic fins, by tip of pectoral fin reaching pelvic-fin origin, and by tip of pelvic fin reaching anal-fin origin.

Anal-fin hooks small, slightly curved dorsally, with one or two hooks on each ray segment along posterior margin of ray. Hooks more numerous on longest unbranched to seventh to ninth branched rays. Longest unbranched ray with 10 to 12 hooks limited to central portion of ray. Branched rays with hooks distributed along entire fin margin. One to four hooks located basal to split of ray and 9 to 20 hooks distal

Table 1. Morphometric data of *Knodus shinahota* (n= 23).

	Holotype	Paratypes		
		Range	Mean	*SD*
Standard length (mm)	33.7	29.4-36.9	-	-
Percents of standard length				
Body depth	33.8	32.3-36.2	34.1	0.9
Head length	24.1	23.0-27.1	24.9	1.2
Head depth	22.0	21.8-25.6	23.9	0.9
Snout to dorsal-fin origin	50.8	50.5-56.8	52.7	1.4
Snout to pelvic-fin origin	45.9	43.1-49.6	45.8	1.5
Pelvic-fin insertion to anal-fin origin	11.9	11.6-14.4	13.2	0.8
Caudal peduncle length	10.8	10.0-12.4	11.1	0.6
Dorsal-fin length	12.8	11.9-15.1	13.3	0.7
Anal-fin length	29.1	27.1-31.7	28.9	1.1
Length of longest pectoral-fin ray	23.0	21.2-26.9	23.2	1.4
Length of longest pelvic-fin ray	15.5	14.0-18.2	15.6	1.1
Length of longest dorsal-fin ray	24.5	24.6-29.9	27.1	1.3
Length of longest anal-fin ray	21.7	18.1-24.5	21.0	1.6
Percents of head length				
Orbital diameter	41.0	37.2-42.5	39.7	1.6
Snout length	23.2	21.7-27.1	23.8	1.3
Interorbital width	33.3	30.8-35.8	33.4	1.3

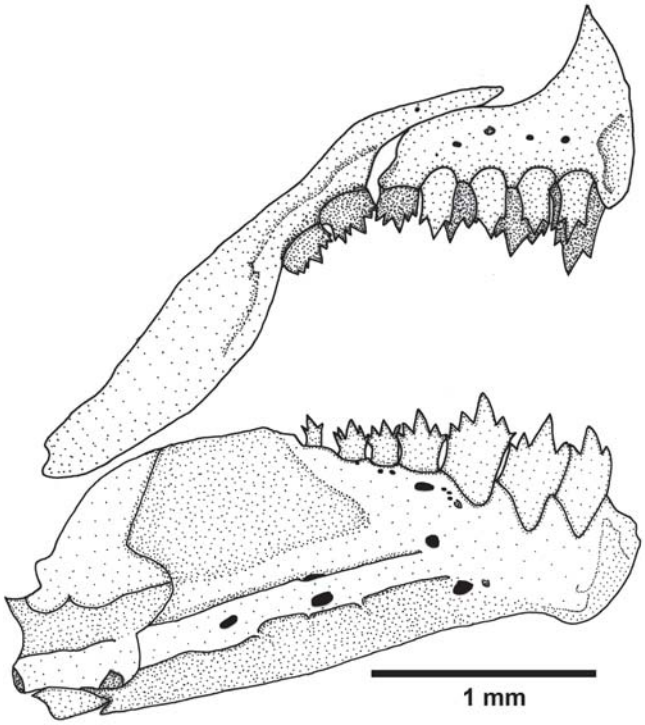

Fig. 2. *Knodus shinahota*, paratype, LIRP 5723, 38.9 mm SL. Upper and lower jaws, right side, lateral view.

that point. All pelvic-fin rays with hooks. Pelvic-fin hooks small, curved, and distally-projected, with one or two hooks per ray segment along both anterior and posterior margins of rays. Three to 12 hooks located basal to first split of ray and nine to 15 hooks distal of that point.

Color in alcohol. Overall ground coloration yellowish tan. Specimens retaining guanine on body and head silvery in these areas. Dorsal surface of head and lips with dense concentration of dark chromatophores. Scattered dark chromatophores covering dorsal one-third of opercle along with fifth and sixth infraorbitals. Dark chromatophores concentrated on scales of dorsal portion of body, mainly along scale margins. Concentration of chromatophores decreasing progressively from middorsal region to lateral line where dark pigmentation limited to margins of scales. Scales below lateral line without chromatophores along margins. One narrow, vertically-elongate humeral mark present over second or third lateral line scale; extending more than two series of scales dorsal to lateral line and one scale ventral of lateral line. Humeral mark is darkest immediately above lateral line and more diffuse dorsal and ventral of that area. Diffuse midlateral stripe on body extending from humeral mark to onto middle caudal-fin rays. Pectoral, pelvic and caudal fins hyaline, with scattered, dark chromatophores outlining rays. Dark chromatophores more concentrated along margin of distal portions of membranes of anal and dorsal fins. Adipose fin hyaline, with small, dark chromatophores concentrated over center of fin.

Histological analysis. No evidence of insemination was found. Examined females of *K. shinahota* lack spermatozoa inside ovary. The spermatozoa nucleus was rounded.

Distribution. Known only from the type locality (Fig. 3).

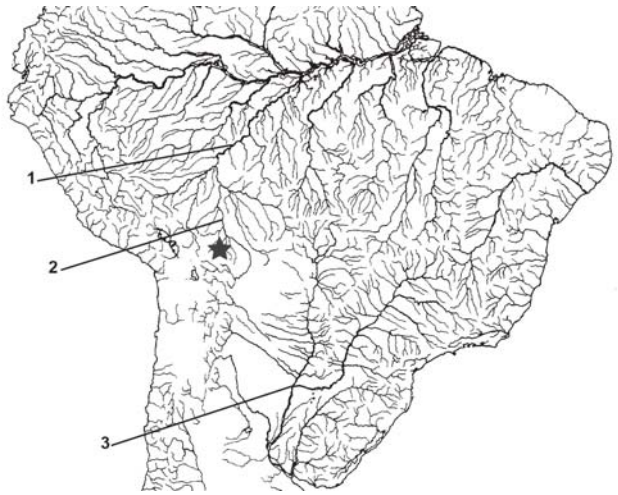

Fig. 3. Map of South America, star indicates the approximate position of the type locality of *Knodus shinahota*; 1, rio Madeira; 2, rio Mamoré; 3, rios Paraná-Paraguay.

Etymology. The specific name, *shinahota*, is in reference to the río Shinahota, the type locality. A noun in apposition.

Ecological notes. The río Shinahota is a typical Andean piedmont drainage, with medium water velocity and with the substrate composed primarily of gravel and pebbles. In some years the river has an intermittent flow. The riparian forest is degraded and, the river is polluted by domestic waste.

Discussion

Three *Knodus* species (*K. mizquae*, *K. longus* and *K. smithi*) that occur in the Madeira-Mamoré system were compared with *K. shinahota*. *Knodus mizquae* and *Knodus longus* occur in tributaries of the río Beni, Bolivia. *Knodus mizquae* differs from *K. shinahota* in the number rows of scales above and below the lateral line (5 and 3½-4 in *K. mizquae vs* 6 and 5 in *K. shinahota*), in the head length (22.5-28.0 % SL in *K. mizquae vs* 32.3-36.2 % SL in *K. shinahota*), and in the number of cusps on the maxillary teeth (5 in *K. mizquae vs* 7 in *K. shinahota*). *Knodus longus* differ from *K. shinahota* in the number of anal-fin branched rays (15-16 in *K. longus vs* 18-20 in *K. shinahota*), perforated scales in the lateral line (41-42 in *K. longus vs* 36-38 in *K. shinahota*), and in number of predorsal scales (17-18 in *K. longus vs* 11-13 in *K. shinahota*). *Knodus smithi* was described from a small tributary of the rio Madeira near Porto Velho, Brazil, and differs from *K. shinahota* in the number of branched anal-fin rays (25-26 in *K. smithi vs* 17-20 in *K. shinahota*), in the number of scale series above and below the lateral line (5 and 4 in *K. smithi vs* 6 and 5 in *K. shinahota*), in the number of cusps on the maxillary teeth (5 in *K. smithi vs* 7 in *K. shinahota*), in the number of cusps on the teeth of the inner row of the premaxilla (7 in *K. smithi vs* 5 in *K. shinahota*), in the distance between the snout and pelvic-fin origin (41.9-43.3% SL in *K. smithi vs* 43.1-49.6% SL in *K. shinahota*), in the caudal-peduncle length (8.8-10.6% SL in *K. smithi vs* 10.0-12.4% SL in *K. shinahota*) and in the interorbital width (35.3-37.2% HL in *K. smithi vs* 30.8-35.8% HL in *K. shinahota*).

As noted in the Introduction, some authors consider *Knodus* as a synonym of *Bryconamericus* and we consequently extend our comparisons of *Knodus shinahota* to the members of *Bryconamericus* that occur in the rio Madeira basin. *Bryconamericus bolivianus* that occurs in upper Madeira basin (río Beni) belongs to the *B. diaphanus* group as defined by Géry (1977). The *B. diaphanus* group is characterized by the presence of 15-25 branched anal-fin rays and 4-6 transverse scales above the lateral line. *Bryconamericus bolivianus* has a shallower body than *K. shinahota* (22.3% SL in *B. bolivianus vs* 32.3-36.2% SL in *K. shinahota*), and fewer branched anal-fin rays (15-16 in *B. bolivianus vs* 18-20 in *K. shinahota*), the number of maxillary teeth (4-5 in *B. bolivianus vs* 2-3 in *K. shinahota*), and the number of scale series above (to origin of the dorsal fin) and below (to origin of the pelvic fin) the lateral line (4 and 2½-3 in *B. bolivianus vs* 6 and 5 in *K. shinahota*).

Weitzman *et al*. (2005) commented on insemination in an undescribed *Knodus* species. According to those authors *Knodus meridae*, the type-species of the genus is non-inseminating species. In that same study they also suggested that inseminating species of *Knodus* are related to some glandulocaudines, stevardiines, and other inseminating characids belonging to Clade A of Malabarba & Weitzman (2003). *Knodus shinahota* is non-inseminating, as is the case *K. meridae*.

Comparative Examined Material. *Bryconamericus beta*: FMNH 56648, holotype, 43.2 mm SL, Colombia, Sucre, Villavicencio; FMNH 56649, paratypes, 40.2-47.8 mm SL, same data as preceding. *Knodus albolineatus*: NMW 83365:1, syntype, 70.1 mm SL, Brazil, Piquirão, Amazonas. *Knodus breviceps*: MCZ 20692, syntypes, 52.0-66.8 mm SL, Brazil, Goiás, exact locality unknown, probably in rio Tocantins or rio Paraná basins. *Knodus chapadae*: ANSP 21828, holotype, 59.1 mm SL, Brazil**,** Mato Grosso, near Santa Anna da Chapada, headwaters of rio Paraguai, upper rio Paraguai basin; ANSP 21829, paratype, 42.6 mm SL, same data as preceding. *Knodus calliurus*: ZMB 23684, holotype, 33.2 mm SL, Brazil, Pará, rio Capim basin. *Knodus caquetae*: ANSP 71670, holotype, 50.0 mm SL and ANSP 71671, paratype, 38.1 mm SL, Colombia, Caquetá, Morelia, río Caquetá basin. *Knodus delta*: ZMH 1473, holotype, 34.0 mm SL, Ecuador, Napo, Puerto Napo, upper Amazon River basin. *Knodus gamma*: ZMH 1861, holotype, 48.5 mm SL and ZMH 2211, paratypes, 46.7-48.2 mm SL, Ecuador, río Villano, río Cururay tributary, upper Amazon River basin. *Knodus geryi*: MZUSP 83354, holotype, 63.4 mm SL, Brazil, Mato Grosso, Barra dos Bugres, rio do Peixe, tributary of rio Cabaçal, fazenda Entre Rios, at bridge, 14º55'0"S, 58º27'24"W; MZUSP 78863, paratypes, 18.4-64.8 mm SL, same data as preceding. *Knodus heteresthes*: MCZ 89966, syntypes, 25.3-39.0 mm SL, Brazil, Pará, rio Tapajós basin; USNM 120247, syntype, 38.5 mm SL, same data as preceding. *Knodus hypopterus*: ANSP 70505, holotype, 32.5 mm SL, Colombia, Caqueta, Florência, río Orteguasa. *Knodus jacunda*: ANSP 39292, holotype, 22.1 mm SL, Brazil, Rondônia, near Porto Velho, rio Madeira. *Knodus meridae*: BMNH 1908.5.29.148, holotype, 44.0 mm SL, Venezuela, Mérida, río Orinoco basin. *Knodus mizquae*: ANSP 69176, holotype, 32.2 mm SL, Bolivia, Cochabamba, Ele Ele, 5.000 feet elevation, río Mizque; ANSP 69178-69191, paratypes, 23.4-32.8 mm SL, Bolivia, same data as preceding. *Knodus moenkhausii*: CAS 55104, paratypes, 23.5-28.7 mm SL and CAS 55103, paratype, 36.1 mm SL, Paraguay, Paraná/de La Plata basin, stream close to Arroyo Trementina; AMNH 1463, paratypes, 26.6-30.0 mm SL, Paraguay, Arroyo Trementina, close to río Aquino, Canigi; FMNH 52601, paratype, 31.9-33.0 mm SL, Paraguay, Arroyo Trementina. *Knodus orteguasae*: ANSP 70504, holotype, 55.6 mm SL, Colombia, Caqueta, Florência, río Orteguasa. *Knodus savannensis*: USNM 196088, holotype, 30.4 mm SL, Brazil, Tocantins, município de Itacajá, between Rio Manoel Alves Pequeno and Rio Vermelho, rio Tocantins basin. *Knodus septentrionalis*: ZMH 2261, holotype, 50.1 mm SL, Ecuador, río Capotazo, río Pastaza tributary. *Knodus smithi*: ANSP 39293, holotype, 25.2 mm SL, Brazil, Rondônia, near Porto Velho, rio Madeira; ANSP 39294-39297, paratypes, 18.5-24.0 mm SL, same data as preceding. *Knodus tiquiensis*: MZUSP 88059, holotype, 72.6 mm SL, Brazil, Amazonas, rio Tiquié, Indian village of Caruru, cachoeira do Caruru, 0º16'28.9"N 69º54'53.6"W. *Knodus victoriae*: NMW 57823, syntypes, 29.02-44.6 mm SL, Brazil, Maranhão, Victoria, rio Parnaíba basin.

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