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Original article

Revalidation and redescription of *Steindachnerina nigrotaenia* and redescription of *S. insculpta* (Characiformes: Curimatidae)

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Steindachnerina nigrotaenia is resurrected from the synonym of *S. brevipinna* and considered a valid species. The previous designation of the lectotype of *S. nigrotaenia* is considered invalid and a new lectotype is designated herein. *Steindachnerina nigrotaenia* and *S. insculpta* are redescribed based on type specimens and on additional material from the rio Paraguai and the upper rio Paraná basins, respectively. The two species can be separated by the number of scales of the lateral line and of the transverse series and by phylogenetic analyses of molecular data.

Keywords: Ostariophysi, Neotropical fishes, Systematics, Taxonomy.

Steindachnerina nigrotaenia é retirada da sinonímia de *S. brevipinna* e considerada uma espécie válida. A designação do lectótipo de *S. nigrotaenia* é considerada inválida e um novo lectótipo é aqui designado. *Steindachnerina nigrotaenia* e *S. insculpta* são redescritas com base no material tipo e em exemplares adicionais das bacias do rio Paraguai e alto rio Paraná, respectivamente. As duas espécies se diferenciam pelo número de escamas da linha lateral e da série transversal e por análises filogenéticas de dados moleculares.

Palavras-chave: Ostariophysi, Peixes neotropicais, Sistemática, Taxonomia.

Introduction

The characiform family Curimatidae includes eight genera, two of which concentrate more than half of the species in the family, *Cyphocharax* Fowler, 1906, and *Steindachnerina* Fowler, 1906. Of the 24 valid species of *Steindachnerina*, four species occur in southern South America in the La Plata system: *S. biornata* (Braga & Azpelicueta, 1987), *S. brevipinna* (Eigenmann & Eigenmann, 1889), *S. conspersa* (Holmberg, 1891), and *S. insculpta* (Fernández-Yépez, 1948). Both *S. biornata* and *S. conspersa* appear at the base of the phylogeny of the genus with significant morphological differences when compared to the other two species, whereas *S. brevipinna* and *S. insculpta* has similar morphologies and are close related species (Vari, 1991; Melo *et al.*, 2018). Vari (1991) provided a valuable progress in the systematics of the genus by analyzing many type specimens that enable him to complete the taxonomic revision and phylogeny of *Steindachnerina*. However, there is a putative conflict in the number of valid species in the rio Paraguai (two, *S. conspersa* and *S. brevipinna*) and the number of observed morphotypes in that region (three). The available name for the third species is *Steindachnerina nigrotaenia* (Boulenger, 1902), currently placed in synonym of *S. brevipinna* by Vari (1991). The history behind the types of *Curimatus nigrotaenia* explains the reasons of the mistaken synonymy.

Early in the 20th century, the Director of the Museo Civico di Storia Naturale of Genova (MSNG) entrusted to Dr. George A. Boulenger of the British Museum (Natural History) (BMNH) a collection of fishes and reptiles collected by Dr. F. Silvestri in 1900 in Brazil, Paraguay and Argentina. One among several fish species described by Boulenger (1902) based on that material was *Curimatus nigrotaenia* Boulenger, 1902, a curimatid from the rio Coxipó, state of Mato Grosso, Brazil, upper Paraguai basin. The species was mainly characterized by the possession of 43 or 44 scales in the lateral line, 7.5 to 8.5 series of scales between the lateral line and dorsal-fin origin and six series of scales between the lateral line and pelvic-fin origin, supplemented by a dark, longitudinal stripe along midlateral surface of the body extending onto middle rays of the caudal fin. Boulenger did not mention any dark spot on the basal portion of the middle

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dorsal-fin rays, a distinct feature present in many species of curimatid fishes. These characters accurately discriminated *C. nigrotaenia* from other curimatids known at that time from the rio Paraguai basin. Silvestri's collection was partially returned to the MSNG, but, as reported by Boulenger (1902: 284), some of the specimens were retained at the BMNH. However, Boulenger did not indicate how many individuals of each species were retained at the BMNH versus returned to the MSNG.

Vari (1991) redefined *Steindachnerina*, to incorporate various species previously assigned to *Curimatus* Oken, 1817 (= *Curimata* Bosc, 1817), including *Curimatus nigrotaenia*. After examining five specimens at the BMNH labeled as syntypes of *C. nigrotaenia* under catalog number BMNH 1902.2.10:30, Vari (1991:100) observed that the features of these specimens corresponded to those of *Steindachnerina brevipinna* described from Río de la Plata, Rosario, Argentina. The putative type specimens of *C. nigrotaenia* had 34 to 35 scales in the lateral line series from the supracleithrum to the hypural joint, 5.5 scales between the lateral line and dorsal-fin origin, 4.5 scales between the lateral line and anal-fin origin, a prominent midlateral dark stripe and a dark spot on the basal portion of the middle rays of the dorsal fin. As a result, Vari (1991:100) treated *C. nigrotaenia* as a junior synonym of *S. brevipinna*, designated the largest specimen as the lectotype of *C. nigrotaenia*, and transferred the other four putative syntypes to BMNH 1989.2.2:3-6 as paralectotypes.

However, the data presented by Boulenger (1902) in the original description disagreed substantially from the data collected by Vari (1991) when he examined the specimens. At that time, Vari (1991:100) considered it impossible to determine whether the original data published by Boulenger contained typographical errors or Boulenger's counts were incorrect. In addition, he assumed that Boulenger "failed to describe the prominent dark spot on the basal portion of the middle rays of the dorsal fin in the relatively small-sized syntypes" he examined. However, he did not discuss the possibility of a curatorial error at BMNH, resulting in the wrong specimens being placed in the syntype jar for *Curimatus nigrotaenia*.

After the revision of Vari (1991), one of us (HAB) suspected the occurrence of an error due to several morphological differences observed in the two morphotypes collected in the rio Paraguai. Despite Vari's conclusions, Britski (1996) maintained *Steindachnerina nigrotaenia* as a valid species in a brief communication in a regional meeting for biologists, and in the two volumes of the manual of fishes from the Pantanal Matogrossense (Britski *et al.,* 1999; 2007), suspecting that the specimens examined by Vari (1991) at the BMNH were not the syntypes of the species, but actually specimens of *S. brevipinna* incorrectly labeled as syntypes of *S. nigrotaenia*. Additionally, the ICZN (Case 3307) received in 2004 a proposal of conservation of usage of the name *Curimatus nigrotaenia* (= *S. nigrotaenia*) by designation of a new lectotype, proposed by Britski and Vari, without any resolution.

In this context, we present complete redescriptions of the two species taking into account that specimens of *Steindachnerina nigrotaenia* and *S. insculpta* were mixed in the redescription under the name of *S. insculpta* by Vari (1991), and that the description of *Curimatus nigrotaenia* by Boulenger (1902), the redescriptions by Britski *et al*. (1999; 2007), as well as the original description of *Cruxentina insculpta* by Fernández-Yépez (1948) are very abridged and/or incomplete. In summary, the purpose of this paper is to (1) revalidate *Steindachnerina nigrotaenia* (Boulenger, 1902), (2) designate a new lectotype for the species, and (3) redescribe both *S. nigrotaenia* and *S. insculpta* based on new morphological and molecular data from both species.

Material and Methods

Morphology. To resolve the curatorial issues involving *Steindachnerina nigrotaenia*, we examined the type specimens deposited at the Natural History Museum of London (BMNH) and at the Museo di Storia Naturale of Genova (MSNG), and additional material from recent field collections of *S. brevipinna*, *S. insculpta* and *S. nigrotaenia*. Measurements were made with digital calipers to the nearest 0.1 mm. Counts and measurements were taken on the left side of specimens whenever possible. Lateral line scales were counted from the supracleithrum to caudal fin, including those overlying the hypural plate and extending to the base of median caudal-fin rays, which we also report separately. Counts of total vertebrae were usually taken from radiographs, the fused PU1+U1 was considered a single bone, and the vertebrae incorporated into the Weberian apparatus were counted as four elements.

Subunits of the head are presented as proportions of head length (HL). Head length itself and measurements of body parts are given as proportions of standard length (SL). Greatest body depth was taken at the dorsal-fin origin. In the counts of median-pectoral and pelvic fins, the unbranched rays are indicated by lower case roman numerals, and the branched-fin rays as Arabic numerals. Meristic data are given in the description with parentheses indicating the frequency of each count and asterisks indicating counts of holotype or lectotype specimens.

In the synonymies for each species, localities are presented as in the original citation, followed by the corrected or modern equivalent (in parentheses) if the case. Institutional abbreviations are: Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CAS); Laboratório de Biologia e Genética de Peixes, Universidade Estadual Paulista, Botucatu (LBP); Museu Nacional do Rio de Janeiro, Rio de Janeiro (MNRJ); Museo Civico di Storia Naturale de Genova, Genova (MSNG); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP); Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Universidade Estadual de Maringá, Maringá (NUP); Naturhistorisches Museum Wien, Vienna (NMW).

Molecular analysis. Nineteen specimens of *Steindachnerina* were included in the molecular analysis: five specimens of *S. brevipinna* from rio Paraná, five specimens of *S. insculpta* from the main rio Paraná above the Itaipu dam and rio Tietê, eight specimens of *S. nigrotaenia* from the upper rio Paraguai, and one specimen of *S. elegans* from the rio São Francisco to root the tree. Sequences of ten out of nineteen specimens were obtained from Genbank (Tab. 1).

Tab. 1. Taxon, voucher, locality information and Genbank accession numbers of specimens of *Steindachnerina* analyzed in the molecular approach.

Taxon	Voucher	Specimen	Locality	City, State	Country	Genbank
Steindachnerina brevipinna	LBP 6690	32153	Rio Paraná	Marilena, Paraná	Brazil	GU701503
Steindachnerina brevipinna	LBP 6690	32154	Rio Paraná	Marilena, Paraná	Brazil	GU701502
Steindachnerina brevipinna	LBP 6690	32155	Rio Paraná	Marilena, Paraná	Brazil	GU701501
Steindachnerina brevipinna	LBP 6690	32156	Rio Paraná	Marilena, Paraná	Brazil	GU701505
Steindachnerina brevipinna	LBP 6690	32157	Rio Paraná	Marilena, Paraná	Brazil	GU701504
Steindachnerina insculpta	LBP 3192	19389	Rio Tietê, Rio Paraná	Conchas, São Paulo	Brazil	JN989237
Steindachnerina insculpta	LBP 3192	19390	Rio Tietê, Rio Paraná	Conchas, São Paulo	Brazil	JN989238
Steindachnerina insculpta	LBP 5207	26343	Rio Paraná	Porto Rico, Paraná	Brazil	JN989236
Steindachnerina insculpta	LBP 6671	32081	Rio Paraná	Marilena, Paraná	Brazil	JN989239
Steindachnerina insculpta	LBP 19770	32158	Rio Paraná	Marilena, Paraná	Brazil	GU701506
Steindachnerina nigrotaenia	LBP 5636	27395	Rio Paraguai	Cuiabá, Mato Grosso	Brazil	MK495705
Steindachnerina nigrotaenia	LBP 8573	43355	Rio Paraguai	Barra do Bugres, Mato Grosso	Brazil	MK495709
Steindachnerina nigrotaenia	LBP 9818	45230	Rio Paraguai	Miranda, Mato Grosso do Sul	Brazil	MK495701
Steindachnerina nigrotaenia	LBP 9818	45231	Rio Paraguai	Miranda, Mato Grosso do Sul	Brazil	MK495706
Steindachnerina nigrotaenia	LBP 9818	45232	Rio Paraguai	Miranda, Mato Grosso do Sul	Brazil	MK495702
Steindachnerina nigrotaenia	LBP 9818	45233	Rio Paraguai	Miranda, Mato Grosso do Sul	Brazil	MK495703
Steindachnerina nigrotaenia	LBP 9818	45234	Rio Paraguai	Miranda, Mato Grosso do Sul	Brazil	MK495707
Steindachnerina nigrotaenia	LBP 9862	45408	Rio Paraguai	Miranda, Mato Grosso do Sul	Brazil	MK495704
Steindachnerina elegans	LBP 8272	38329	Rio São Francisco	Jaíba, Minas Gerais	Brazil	MK495708

For the three newly sequenced individuals, genomic DNA was extracted from muscle tissues preserved in 95% ethanol with a DNeasy Tissue kit (Qiagen Inc.; http://www.qiagen.com) according to the manufacturer's instructions. Partial sequences of the mitochondrial gene *cytochrome oxidase c subunit I* were obtained by polymerase chain reaction (PCR) using the primers described by Melo *et al.* (2011). Total volume included 12.5 µl with 9.075 µl of double-distilled water, 1.25 µl 5x buffer, 0.375 µl MgCl2 (50mM), 0.25 µl dNTP mix, 0.25 µl of each primer at 10 µM, 0.05 µl Platinum Taq DNA polymerase enzyme (5 units/µl, Invitrogen; www.invitrogen.com) and 1.0 µl genomic DNA (10–50 ng). The PCR program consisted of an initial denaturation (4 min at 95º C) followed by 30 cycles of chain denaturation (30 s at 95ºC), primer hybridization (30–60 s at 52ºC), and nucleotide extension (45 s at 72ºC). Amplicons were visualized through 1% agarose gel, and used to perform the sequencing reaction using dye terminators (BigDye™ Terminator v 3.1 Cycle Sequencing Ready Reaction Kit, Applied Biosystems), and purified through ethanol precipitation. Samples were then loaded onto an automatic sequencer ABI 3130-Genetic Analyzer (Applied Biosystems) at the São Paulo State University, Botucatu, Brazil.

Consensus sequences were assembled and edited in Geneious v7.1.9 (Kearse *et al.*, 2012) and aligned with Muscle (Edgar, 2004) under default parameters. The index of substitution saturation in asymmetrical (Iss.cAsym) and symmetrical (Iss.cSym) topologies were estimated using Dambe v5.3.38 (Xia, 2013) and the best-fit model of nucleotide evolution was obtained in Mega v7.0 (Tamura *et al.*, 2013). We ran a neighbor-joining tree (NJ) using the Tamura-Nei distance model and generated 1,000 non-parametric bootstrap replicates in Geneious (Kearse *et al.*, 2012), and a maximum likelihood (ML) tree with 1,000 non-parametric bootstraps using GTR-GAMMA, the single model implemented in RAxML HPC2 on XSEDE v8.2.10 (Stamatakis, 2014) on the Cipres webserver (Miller *et al.*, 2010).

Results

The analyses of morphological and molecular data strongly support the recognition of three species of the same clade in the La Plata basin: *Steindachnerina brevipinna* (rio Paraná and rio Paraguai), *S. insculpta* (upper rio Paraná) and *S. nigrotaenia* (upper rio Paraguai), supplemented by *S. conspersa* and *S. biornata*. The synonymization of *S. nigrotaenia* was caused by previous curatorial mistakes that guided Vari (1991) to recognize only one species.

After finding the syntype of *Curimatus nigrotaenia* retained at the BMNH by Boulenger (1902) who assigned it the term "type", the following notes *in literis* were received from James Maclaine, curator of the British Museum of Natural History, explaining the erroneous changes that took place with materials in that fish collection: "A) BMNH 1902.2.10.30 *Curimatus nigrotaenia*, SYNTYPE (1). – mistakenly placed into jar for BMNH 1917.11.2.7 *Curimatus morawhannae* SYNTYPE (1); B) BMNH 1911.10.31.479-483 *Curimatus morawhannae* SYNTYPES (5) – mistakenly placed into jar for BMNH 1902.2.10.30 *Curimatus nigrotaenia*, SYNTYPE (1); subsequently examined by Richard Vari and synonymized and separated into a lectotype (BMNH 1902.2.10.30) and paralectotypes (given new number BMNH 1989.2.23.3-6); the above two lots can be seen in the annotations in Günther's Catalogue of Fishes; C) BMNH 1917.11.2.7 *Curimatus morawhannae* SYNTYPE (1) – mistakenly placed into jar for BMNH 1911.10.31.479-482 *Curimatus morawhannae* SYNTYPES." This explanation provided by James Maclaine also allowed the correction of some BMNH catalogue numbers published by Vari (1991:87) about syntypes of *Curimatus morawhannae*.

Analysis of the three syntypes of *Curimatus nigrotaenia* deposited at the MSNG with the BMNH syntypes has confirmed that the material now in London was incorrectly curated. The still well-preserved syntypes at MSNG entirely fit Boulenger's description and differ from the BMNH "syntypes" studied by Vari (1991). Furthermore, we have successfully found the "type" of *C. nigrotaenia*, which was wrongly deposited in a jar labeled *Curimatus morawhannae* Eigenmann, 1912, under the number BMNH 1917.11.2:7 (see paragraph above). Data taken from this "type" agree entirely with the original description of *C. nigrotaenia*. The specimen of *C. nigrotaenia* registered under the number BMNH 1902.2.10.30 by Boulenger also had already been cataloged in Günther's Catalogue of Fishes (museum catalog, vol. 5, pp. 288a) of the BMNH. That finding also revealed that Boulenger retained only one specimen of *C. nigrotaenia* (labeled as "type") at the BMNH, and not five syntypes as mentioned by Vari (1991). The number of syntypes sent back to MSNG was not specified by Boulenger, but by Tortonese (1961: 184), in his catalogue of types deposited at the MSNG mentioning three syntype specimens. Overall, the clearly morphological differences between *Steindachnerina brevipinna* and the syntypes of *C. nigrotaenia* at MSNG and BMNH illustrate that the synonymization was incorrect, and support the recognition of *S. nigrotaenia* as a valid species.

Vari's (1991:100) designation of the lectotype of *Curimatus nigrotaenia* should be considered invalid because the lot from which he separated the specimen was incorrectly labeled as the syntype series of *C. nigrotaenia*. As specified in the ICZN (1999: Art. 74.2), "If it is demonstrated that a specimen designated as a lectotype was not a syntype, it loses its status of lectotype". Günther's citation of BMNH 1902.2.10.30 as a "type" for *C. nigrotaenia* is similarly invalid because "the mere citation of 'Type' or equivalent expression, … or in an unpublished catalogue of a museum, or on a label, is not necessarily evidence that a specimen is or is fixed as any of the kinds of types referred in this Chapter." (ICZN, 1999: Art. 72.4.7). Consequently, we herein formally designate the specimen of *C. nigrotaenia* retained by Boulenger (1902) at the British Museum (BMNH 1902.2.10.30) as the new lectotype for *Steindachnerina nigrotaenia*, with the three syntypes at the Museo Civico di Storia Naturale of Genova (MSNG 14859) becoming paralectotypes. This is likely the same specimen considered by Günther when assembling his catalog of types, but definitely not the same specimen that Vari previously assigned to that catalog number.

How the "type" of *Curimatus nigrotaenia* was deposited in a jar labeled as *C. morawhannae* in the collection at the BMNH is an issue that possibly we will never know, but surely we cannot attribute this action to Boulenger when describing the species, because *C. morawhannae* was described in 1912 by Carl H. Eigenmann based on specimens from Guyana and, obviously, paratypes were sent to the British Museum after the description of the species (1912). So, this error should be credited to someone who worked with the type specimens of *C. nigrotaenia* and *C. morawhannae* afterwards, but before Vari's examination.

Molecular analysis. Molecular results also support the recognition of *Steindachnerina nigrotaenia*. The matrix contained 675 bp with 48 polymorphic sites (7.1%), and 98.6% pairwise identity. Nucleotide frequencies corresponded to 22.9% adenine, 28.4% cytosine, 18.2% guanine, and 30.6% thymine/uracil. We did not find any saturation in the dataset. Tab. 1 includes voucher information, locality, and Genbank accession numbers. Both neighbor-joining analysis (not shown) and the maximum likelihood approach returned the same topology (Fig. 1). Results revealed a clear separation among samples of *S. insculpta* from the rio Paraná and the group *S. brevipinna*/*S. nigrotaenia* from rio Paraná and rio Paraguai, respectively. The eight specimens of *S. nigrotaenia* from the upper rio Paraguai (including one topotype from rio Coxipó) appear genetically closer to the five specimens of *S. brevipinna* from the rio Paraná. These results demonstrate that *S. nigrotaenia* clearly differs genetically from the morphologically similar *S. insculpta*, but much less from *S. brevipinna* which also occurs in the rio Paraguai. It appears that both *S. brevipinna* and *S. nigrotaenia* did accumulate morphological differences but not in the mitochondrial DNA. The sum of evidence allows us to redescribe *S. nigrotaenia* from the rio Paraguai basin, and *S. insculpta* from the upper rio Paraná basin.

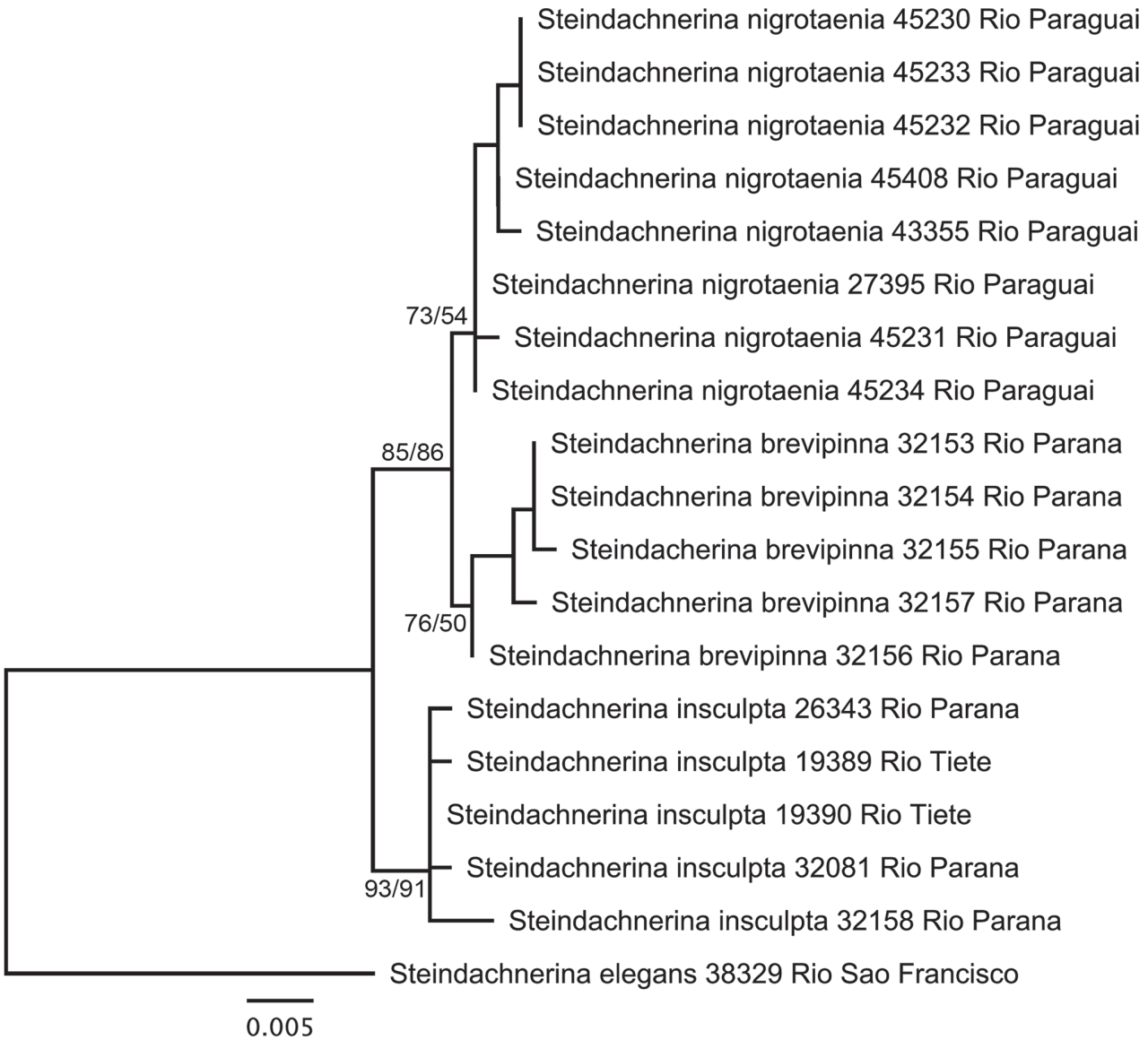

Fig. 1. Best maximum likelihood tree based on partial sequences of the mitochondrial gene cytochrome oxidase c subunit I among samples of *Steindachnerina nigrotaenia*, *S. insculpta* and *S. brevipinna*. Numbers near nodes represent bootstrap values of maximum likelihood/neighbor-joining analyses.

***Steindachnerina nigrotaenia* (Boulenger, 1902)**

Fig. 2, Tab. 2

Curimatus nigrotaenia Boulenger, 1902:2 [type-locality: Mato Grosso, rio Coxipó].-Eigenmann, 1910:421 [reference].-Vari, 1989, tables 2, 3 [assignment to *Steindachnerina*].-Tortonese, 1961:184 [Catalog: three syntypes].-Litz & Koerber, 2014:9 [Check list; synonym of *Steindachnerina brevipinna*].

Curimata nigrotaenia.-Fernández-Yépez, 1948:73 [reference].-Fowler, 1950:288 [literature compilation].-Fowler, 1975:369 [reference].-Ringuelet, 1975:72 [Argentina, rio Paraguai system].

Steindachnerina nigrotaenia.-Britski, 1996:74 (previous resurrection).-Britski *et al.*, 1999:72 [diagnose in key; shortened description; text-figure; Pantanal do Mato Grosso].-Britski *et al.*, 2007: 96 [diagnose in key; shortened description; text figure; Pantanal do Mato Grosso].-Polaz *et al.*, 2014:125 [list of species from Parque Nacional do Pantanal Matogrossense].

Steindachnerina insculpta.-Vari, 1991:71 [in part, material from rio Paraguai basin, not from upper rio Paraná basin].-Aguilera *et al.*, 2018:1018 [Argentina: río San Francisco, Bermejo river basin, Jujuy, and Madrejón El Divisadero, Bermejo river basin, Salta].

Steindachnerina brevipinna.-Vari, 1991:97 [in part, material from Mato Grosso, upper rio Paraguai].

?*Curimata nasa*.-Géry *et al.*, 1987:425, fig. 41 [material from arroyo Trementina, rio Paraguai basin].

Fig. 2. a. *Steindachnerina nigrotaenia*, lectotype of *Curimatus nigrotaenia*, BMNH 1902.2.10.30, 43.5 mm SL, Brazil, Mato Grosso, rio Coxipó, upper rio Paraguai; **b.** LBP 1477, 43.4 mm SL, Brazil, Mato Grosso do Sul, Coxim, rio Taquari, upper rio Paraguai.

Diagnosis. *Steindachnerina nigrotaenia* can be distinguished from all congeners, except *S. binotata* (Pearson, 1924), *S. biornata*, *S. dobula* (Günther, 1868), *S. hypostoma* (Boulenger, 1887), *S. insculpta*, *S. leucisca* (Günther, 1868), *S. notograptos* Lucinda & Vari, 2009, and *S. varii* Géry, Planquette, Le Bail, 1991, by possessing an unpigmented dorsal fin (*vs*. a dorsal fin with a spot of dark pigmentation on the basal portion of the middle rays). *Steindachnerina nigrotaenia* has 43 to 48 perforated scales in the lateral line series running from the supracleithrum to the middle rays of the caudal fin, differing from *S. binotata*, *S. leucisca* and *S. notograptos*, which have 50 or more perforated scales in that series and from *S. biornata* and *S. varii* which have fewer than 40 perforated scales in the lateral line series. *Steindachnerina nigrotaenia* differs from *S. hypostoma* by possessing a relatively shallower body with greatest body depth 24-27% of SL (*vs*. 29-34% of SL). *Steindachnerina nigrotaenia* differs from *S. dobula* and *S. varii* by having a dark midlateral stripe extending from the rear of the opercle posteriorly onto middle rays of caudal fin (*vs*. dark midlateral stripe beginning posterior to a vertical line through the dorsal-fin origin, and continuing posteriorly to the middle rays of the caudal fin). *Steindachnerina nigrotaenia* differs from the very similar *S. insculpta* by the generally higher number of perforated scales along the lateral line series (43 to 48, 45 most frequent, *vs*. 40 to 45, 42 most frequent and 44 and 45 in only 1.3% of specimens examined for this feature, respectively; Fig. 3), by the total number of scale rows in the transverse series from the dorsal-fin origin to the pelvic-fin base (13 to 16, 14 most frequent, *vs*. 12 to 14, 12 most frequent and 13.5 and 14 in only 6.4% and 1.3% of specimens examined for this feature, respectively; Fig. 4). *Steindachnerina nigrotaenia* can also be discriminated from congeners by a combination of the following features: multiple lobulated fleshy processes on the roof of the oral cavity, absence of a wide, flattened prepelvic region of the body, possession of 43 to 48 perforated scales in the lateral line series, 13 to 16 scales in the transversal series, lack of a dark spot on the basal portions of the dorsal fin and the presence of a dark midlateral stripe along the lateral surface of the body.

Description. Morphometric data of lectotype, paralectotypes and other specimens are summarized in Tab. 2. Body relatively elongate, somewhat compressed. Dorsal profile of head slightly convex anteriorly, straight from the line above orbit to rear of head. Dorsal profile of body straight or very slightly convex from rear of head to origin of dorsal fin; straight at dorsal-fin base; straight from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body transversely rounded anteriorly, with indistinct median keel immediately anterior to dorsal fin, smoothly rounded transversely posterior to dorsal fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle. Prepelvic region obtusely flattened, with median series of scales proximate to pelvic-fin origin, median series irregularly arranged anteriorly. Barely discernable median keel posterior to pelvic-fin origin.

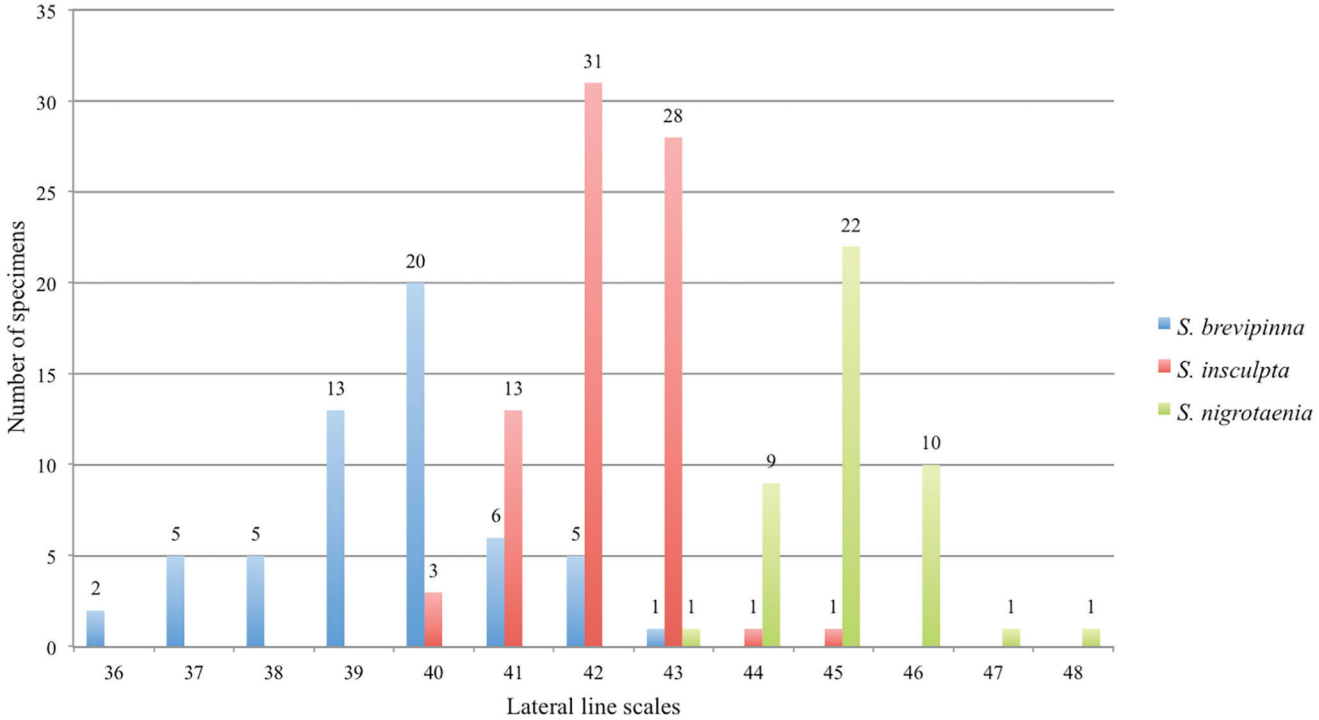

Fig. 3. Histogram of number of lateral-line scales against number of specimens of *Steindachnerina brevipinna*, *S. insculpta* and *S. nigrotaenia*.

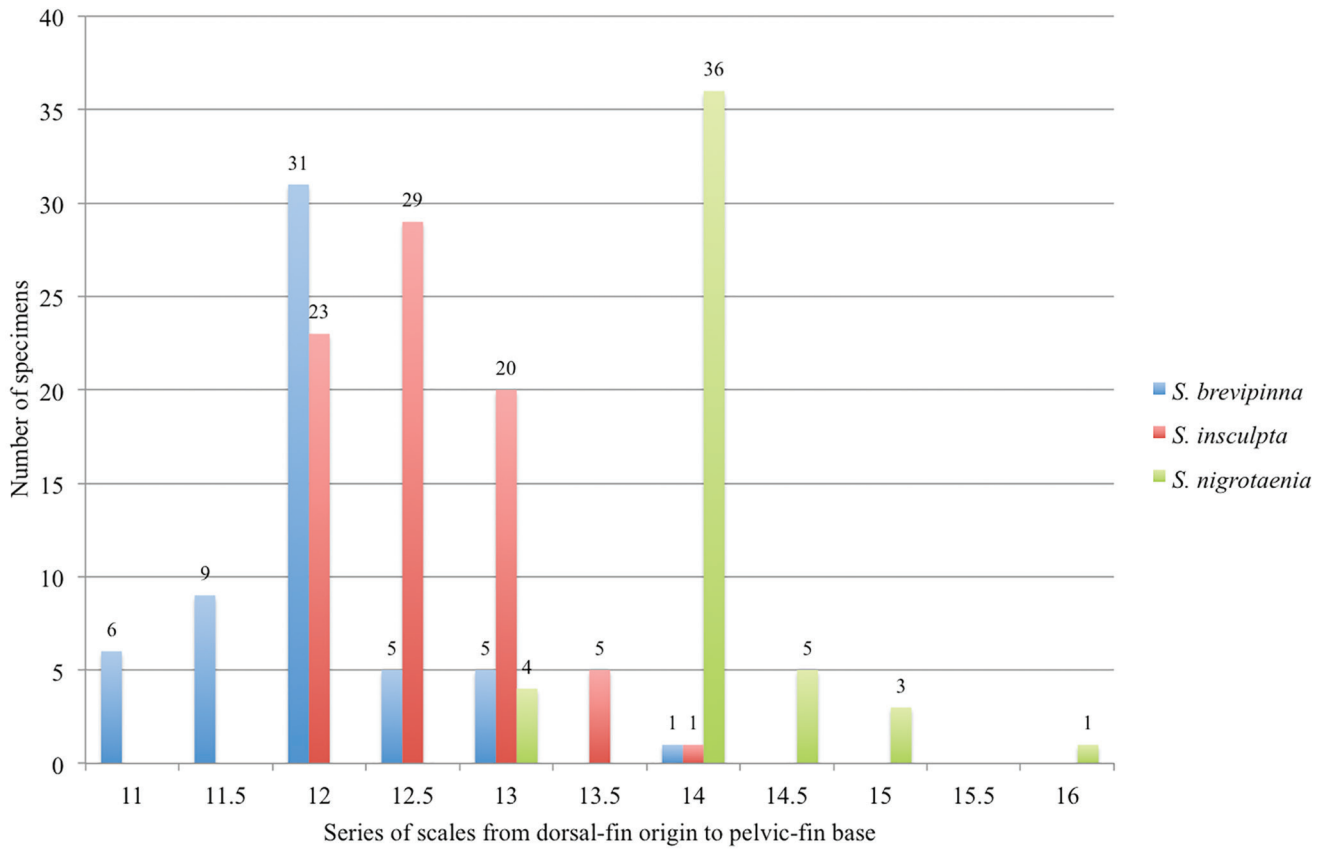

Fig. 4. Histogram of number of series of scales from dorsal-fin origin to pelvic-fin base against number of specimens of *Steindachnerina brevipinna*, *S. insculpta* and *S. nigrotaenia*.

Tab. 2. Morphometric data for *Steindachnerina nigrotaenia* and *S. insculpta*. N = number of specimens. SD = Standard deviation. Range of each species includes the lectotype of *S. nigrotaenia* (BMNH 1902.2.10.30) and the paratype of *S. insculpta* (MZUSP 1376), respectively.

	Steindachnerina nigrotaenia					*Steindachnerina insculpta*				
	Lectotype	N	Range	Mean	SD	Paratype	N	Range	Mean	SD
Standard length (mm)	43.5	44	37.0-90.3	63.4	-	105.0	78	42.6-108.1	75.6	-
Percentages of standard length										
Body depth	26.5	44	25.0-33.8	28.8	1.5	29.5	78	25.6-34.1	30.1	1.7
Caudal peduncle depth	11.0	44	10.3-11.7	11.0	0.3	11.7	78	10.8-12.4	11.7	0.4
Head length	32.0	44	25.7-32.5	29.0	1.7	18.9	78	25.6-30.2	28.1	0.8
Predorsal distance	47.2	44	44.3-49.7	46.8	1.2	46.8	78	43.3-49.7	46.2	1.2
Prepelvic distance	51.9	44	48.8-55.4	52.4	1.4	54.9	78	48.8-58.0	52.1	1.6
Pectoral-fin length	15.2	44	15.0-20.0	18.1	0.9	17.9	78	15.6-19.8	18.0	0.9
Pelvic-fin length	19.9	44	18.0-22.3	19.7	0.9	19.6	78	15.5-21.8	19.0	1.2
Percentages of head length										
Eye diameter	32.4	44	27.6-34.9	30.5	1.8	27.7	78	26.3-33.5	29.8	1.7
Snout length	34.5	44	30.1-35-6	32.9	1.3	35.1	78	29.7-38.9	34.1	1.7
Interorbital distance	33.1	44	31.7-43.2	38.0	2.2	39.7	78	38.3-44.8	41.0	1.8

Dorsal-fin margin rounded; anteriormost rays three to 3.5 times the length of ultimate ray. Pectoral-fin margin acute, extending one-half to two-third the distance to origin of pelvic fin in smaller adults, barely beyond that point in largest specimens examined. Pelvic-fin margin acute; pelvic fin extending about one half the distance to origin of anal fin. Caudal fin forked. Adipose fin well developed. Anal fin emarginate, anteriormost branched rays 2.5 to three times the length of ultimate ray.

Head profile pointed; upper jaw distinctly longer, mouth inferior; buccopharyngeal complex on roof of the oral cavity in adults consisting of multiple lobulated fleshy bodies; nostrils very close, anterior circular, posterior crescent-shaped with aperture closed by thin flap of skin separating nares; adipose eyelid present, more developed anteriorly, with broad, vertically ovoid opening over center of eye.

Pored lateral-line scales from supracleithrum to medial caudal-fin rays 43(1), 44(9), 45*(22), 46(10), 47(1) or 48(1), 2 to 3 over caudal-fin base; series of scales from dorsal-fin origin to lateral line 6(8), 7*(31) or 8(5); series of scales from lateral line to pelvic-fin base 6*(39), 6.5(3) or 7(2); total series of scales from dorsal fin to base pelvic-fin base 13(4), 14*(36), 14.5(5), 15(3) or 16(1); series of scales from lateral line to first ray of anal fin 5*(6), 5.5(8) or 6(29); circumpeduncular scales 16*(36), 17(1), 18(3) or 20(3); predorsal scales 11*(13), 12(19) or 13(10); scales from dorsal fin to adipose fin 12*(7), 13(17), 14(16) or 15(3); scales from adipose fin to caudal fin 8(3), 9(10), 10(19), 11(8) or 12*(2); prepelvic scales 18(1), 19(8), 20*(10), 21(12), 22(5), 23(4) or 24(1); scales from pelvic fin to anus 8*(13), 9(21), 10(7) or 11(2); scales from anus to anterior margin of anal fin 2(4), 3(31) or 4*(9); scales from posterior margin of anal fin to anteroventral margin of caudal fin 8(1), 9(6), 10(16), 11*(16) or 12(2). All scales of lateral line pored with canals in scales straight.

Dorsal-fin rays ii,8,ii*; pectoral-fin rays i,12(3), i,13(7), i,14*(20), i,15(9) or i,16(4); pelvic-fin rays i,8*(41) or i,9(3); anal-fin rays ii-iii,5,ii(2) or ii-iii,6,ii*(42); caudal--fin rays i,8,9,i*(38). Total vertebrae 28(8) or 29 (2).

Coloration in alcohol. Overall coloration of specimens retaining guanine on scales silvery to silvery golden, darker on dorsal portions of head and body. Ground coloration of specimens lacking guanine on scales tan to yellow, darker dorsally, with irregular patch of dark pigmentation extending from rear of orbit across opercle; degree of intensity of dark pigmentation and extent of patch variable among individuals. Irregular, dark longitudinal stripe extending along lateral line from supracleithrum to base of middle caudal-fin rays. Stripe slightly wider posteriorly, continuous posteriorly with dusky stripe on middle caudal-fin rays. Stripe in adults continuous, about one scale wide; not as well developed in juveniles, consisting of discrete spots surrounding pores of lateral line. Caudal-fin with stripe more prominent on the anterior portion of rays. Anterior margin and distal portions of dorsal fin typically dusky in adults. Ventral lobe and dorsal rays of dorsal lobe of caudal fin dusky. All caudal-fin rays outlined by small chromatophores on membranes. Adipose fin dusky distally. Dorsal fin with dusky anterior region in many specimens, without any discrete spot on middle rays. Other fins hyaline.

Sexual dimorphism. Secondary sexual characters were not found.

Geographical distribution. *Steindachnerina nigrotaenia* is distributed along the rio Paraguai basin (Fig. 5).

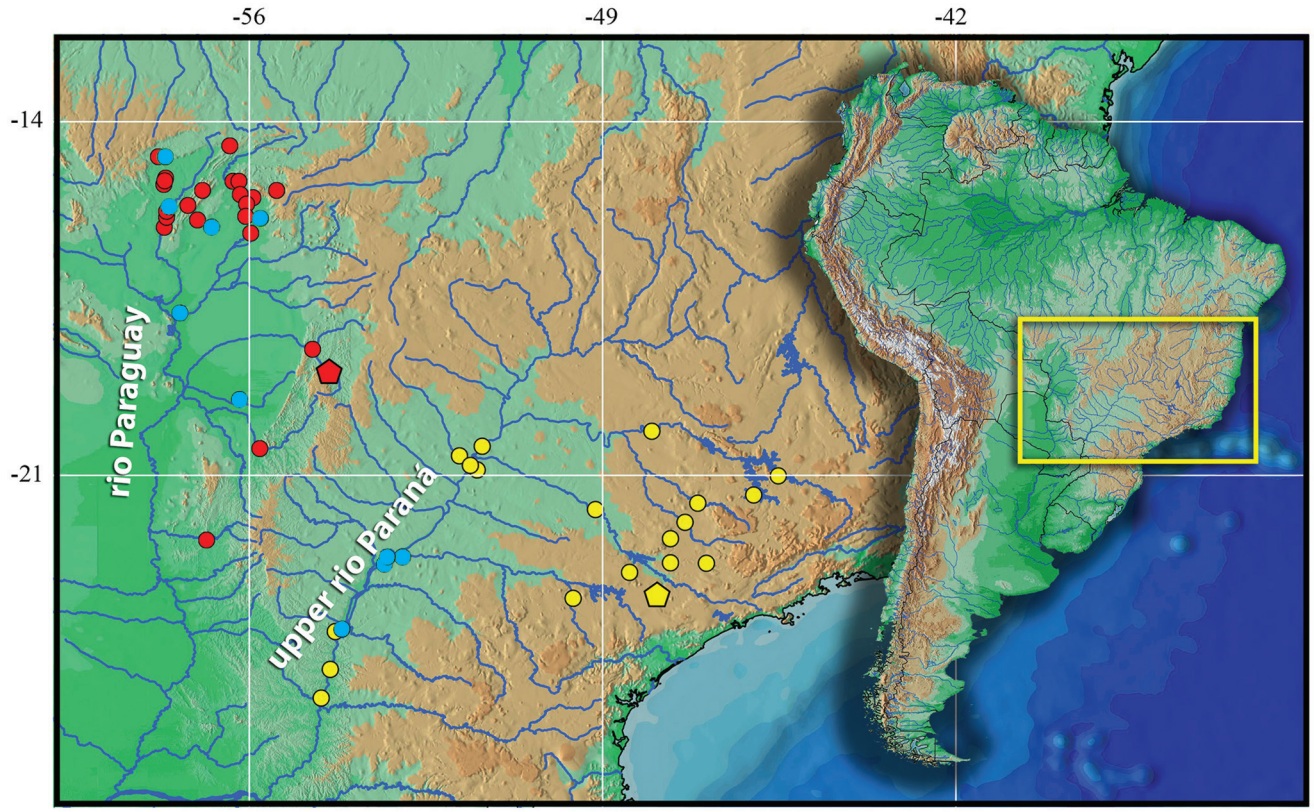

Fig. 5. Distribution map of *Steindachnerina brevipinna* in both rio Paraná and rio Paraguai (green), *S. nigrotaenia* in the rio Paraguai (red), and *S. insculpta* in the upper rio Paraná (yellow). Pentagons indicate type localities. Some symbols represent more than one collecting locality.

Material examined. All from Brazil, rio Paraguai basin. BMNH 1902.2.10.30, 43.5 mm SL, Mato Grosso, rio Coxipó, F. Silvestri. Lectotype of *Curimatus nigrotaenia* (designated herein). MSNG 14859, 3, 42.7, 51.2, 52.2 mm SL, same data as lectotype. Paralectotypes of *Curimatus nigrotaenia* (designated herein). MNRJ 11206, 3, 59.8-85.7 mm SL, Mato Grosso, Acorizal, rio Acorizal at bridge along road from Acorizal to Baús. MNRJ 11207, 1, 102.0 mm SL, Mato Grosso, Acorizal, ribeirão Baús. MNRJ 11214, 1, not measured, Mato Grosso, Acorizal, ribeirão Tangará, along road from Acorizal to Cuiabá. MZUSP 4383, 3; MZUSP 4449, 1, 39.2 mm SL, Mato Grosso, Santo Antonio do Leverger, rio Cuiabá. MZUSP 21512, 16, Mato Grosso, Cuiabá, rio Coxipó da Ponte, 15°38'S 56°03'W. MZUSP 21656, 6, Mato Grosso, Santo Antonio do Leverger, rio Cuiabá. MZUSP 21662, 2, Mato Grosso, Barão do Melgaço, rio Cuiabá, Boca do Croará, 16°11'S 55°57'W. MZUSP 38015, 2, Mato Grosso, Cáceres, Porto Limão. MZUSP 38079, 1, Mato Grosso do Sul, Coxim, rio Taquari, Ilha da Goiaba, 18°30'00"S 54°45'00"W. MZUSP 40068, 4, Mato Grosso do Sul, Aquidauana, rio Aquidauana, Baia da Onça or Jatobá, Fazenda Alegrete, 20°28'00"S 55°48'00"W. MZUSP 45476, 9, Mato Grosso, rio Paraguai at Cáceres and vicinities. MZUSP 47762, 130, Mato Grosso, Barão de Melgaço, rio Cuiabá. MZUSP 54139, 1, rio Apa, small bay of the river. MZUSP 56234, 1, Mato Grosso, Chapada dos Guimarães, rio Casca. MZUSP 59541, 41, Mato Grosso do Sul, Corumbá, rio Vermelho, Fazenda Xaroes, 19°36'73"S 56°55'42"W. MZUSP 74361, 4, Mato Grosso, Santo Antonio do Leverger, rio Cuiabá, 3 km from the town. MZUSP 75480, 2, Mato Grosso, Cáceres, ribeirão das Flexas, along road from Cáceres to Cuiabá at about 69 km E of Cáceres. MZUSP 78750, 3, Mato Grosso, Porto Estrela, rio Saloba, along road at Estação Ecológica da Serra das Araras, 15°39'03"S 57°13'29"W. MZUSP 78845, 1, Mato Grosso, Diamantino, downstream of waterfall in the rio Paraguai, 14°28'32"S 56°23'32"W. MZUSP 78946, 1, Mato Grosso, Santo Antonio do Leverger, rio Cuiabá. MZUSP 87785, 2, Mato Grosso, Tangará da Serra, rio Sepotuba, salto Maciel, 15°55'59"S 57°39'00" W. MZUSP 89954, 2, Mato Grosso, rio Sepotuba. MZUSP 90075, 8, Mato Grosso, Curvelândia, lower rio Sepotuba, 15°53'34"S 57°38'44"W. MZUSP 90181, 14, Mato Grosso, lower rio Sepotuba. MZUSP 90422, 27, Mato Grosso, Curvelândia, rio Sepotuba, 15°46'07"S 57°38'54"W. MZUSP 90702, 3, Lambari d'Oeste, rio Sepotuba, at mouth of a creek, 15°10'00"S 57°41'00"W. MZUSP 91014, 1, Barra do Bugres, rio Sepotuba, 15°06'52"S 57°39'57"W. MZUSP 91060, 2, Cáceres, rio Sepotuba, artificial lagoon downstream of the bridge, 15°14'08"S 57°41'46"W. LBP 5636, 1 (tissue 27395), Mato Grosso, Cuiabá, rio Coxipó, rio Paraguai. LBP 8573, 1 (tissue 43355), Mato Grosso, Barra do Bugres, rio Paraguai. LBP 9818, 6 (tissues 45230–45234, Mato Grosso do Sul, Miranda, rio Paraguai. LBP 9862, 1 (tissue 45408), Mato Grosso do Sul, Miranda, rio Paraguai.

Steindachnerina insculpta (Fernández-Yépez, 1948)

Fig. 6, Tab. 2

Cutimata elegans Amaral Campos, 1945:46 [Brazil: rio Mogi Guaçu].-Britski, 1972:83 [Brazil, São Paulo, rio Paraná basin]. -Foresti *et al.*, 1974:249 [karyotypes].-Nomura, 1977:727 [Brazil: rio Mogi-Guaçu; meristic].-Nomura, Taveira, 1979:331 [life history].

Cruxentina insculpta Fernández-Yépez, 1948:53, figs. 27, 28 [type-locality: Brazil: São Paulo, rio Tatuhy (= Tatuí); autorship cited as Amaral Campos].-Britski, 1969:200, 203 [correction of originally cited authorship, depositary and collector; meristic and morphometrics].-Fowler, 1975:368 [reference].-Vari, 1989, tables 2, 3 [assignment to *Steindachnerina*].

Curimata elegans.-Gomes, Monteiro, 1955:88, 103, 129 [São Paulo, Pirassununga; occurrence in flowing and still waters].-Oliveira *et al.*, 1988:594 [in part, Brazil, São Paulo, rio Mogi-Guaçu and Botucatu; not Minas Gerais, Três Marias; chromosome counts].

Pseudocurimata elegans elegans.-Godoy, 1975: 88, 103, 129, fig. 132A, 133 [Brazil: São Paulo, rio Mogi-Guassu; life history data; meristic and morphometrics; not cited occurrence in drainage basins other than upper rio Paraná].

Steindachnerina insculpta.-Venere, Galetti Júnior, 1989:18, 19, fig. 19 [upper rio Paraná basin, rio Mogi-Guaçu and rio Passa-Cinco; karyotype information].-Vari, 1991:71 [in part Brazil, material from upper rio Paraná basin above Sete Quedas; not from rio Paraguai system and from Goiás]. -Koerber *et al.*, 2017:16 [reference; type locality mistakenly referred to as being in Venezuela].

?*Curimata nasa*.-Géry *et al.*, 1987:425, fig. 41 [material from arroyo Porooco and Itaipu Lake, rio Paraná basin].

Fig. 6. *Steindachnerina insculpta*, LBP 11381, 78.7 mm SL, Brazil, São Paulo, Birigui, Rio Tietê, upper Rio Paraná.

Diagnosis. *Steindachnerina insculpta* can be distinguished from congeners, except *S. binotata*, *S. biornata*, *S. dobula*, *S. hypostoma*, *S leucisca*, *S. nigrotaenia*, *S. notograptos*, and *S. varii* by possessing a plain dorsal fin (*vs.* dorsal fin with a spot of dark pigmentation on the basal portion of the middle rays). *Steindachnerina insculpta* has 40 to 45 scales in the lateral line series, differing from *S. binotata*, *S. leucisca*, *S. hypostoma*, *S. notograptos*, and *S. gracilis* which have 46 or more scales and from *S. biornata* which has 31 to 34 scales in the lateral line series. *Steindachnerina insculpta* differs from *S. dobula* and *S. varii* by having a dark midlateral stripe extending from rear of opercle posteriorly onto middle rays of caudal fin (*vs.* dark midlateral stripe beginning posterior to vertical line from dorsal-fin origin). *Steindachnerina insculpta* differs from the very similar *S. nigrotaenia* by the lower modal number of perforated scales in the lateral line series (40 to 45, 42 most frequent *vs.* 43 to 48, 45 most frequent and 43 in only 2.27% of specimens examined for this feature; Fig. 3), and by the total number of scale rows in the transverse series from the dorsal-fin origin to the pelvic-fin base (12 to 14, 12.5 most frequent, 13.5 and 14 less frequent *vs.* 13 to 16, 14 most frequent; 13 in only 8.16% of specimens examined for this feature; Fig. 4). *Steindachnerina insculpta* can also be discriminated from its congeners by a combination of the following features: multiple lobulated fleshy processes on the roof of the oral cavity, absence of a wide, flattened prepelvic region of the body, 40 to 45 scales on the lateral line, 12 to 14 scales on the transversal series, lack of a dark spot on basal portions of the dorsal fin and the presence of a dark midlateral stripe along the body.

Description. Morphometric data of *Steindachnerina insculpta* are summarized in Tab. 2. Body relatively elongate, somewhat compressed. Dorsal profile of head very slightly convex anteriorly, straight from above orbit to rear of head. Dorsal profile of body straight or very slightly convex

from rear of head to origin of dorsal fin; straight at base of dorsal fin; straight from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body transversely rounded anteriorly, with indistinct median keel immediately anterior to dorsal fin, smoothly rounded transversely posterior to dorsal fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle. Prepelvic region obtusely flattened, with median series of scales proximate to pelvic-fin origin, median series less regularly arranged anteriorly. Median keel barely discernable posterior to pelvic-fin origin.

Dorsal-fin margin rounded; anteriormost rays three to three and half times length of ultimate ray. Pectoral-fin margin acute, extending one-half to two-third distance to origin of pelvic fin in smaller adults, barely beyond that point in the largest examined specimens. Pelvic-fin margin acute; pelvic fin extending about one-half distance to origin of anal fin. Caudal fin forked. Adipose fin well developed. Anal fin emarginate, anteriormost branched rays two and one-half to three times the length of ultimate ray.

Head pointed in profile; upper jaw distinctly longer, mouth inferior; buccopharyngeal complex on roof of oral cavity in adults consisting of multiple lobulated fleshy bodies; nostrils very close, anterior circular, posterior crescent-shaped with aperture closed by thin flap of skin separating nares; adipose eyelid present, more developed anteriorly, with broad, vertically ovoid opening over center of eye.

Total pored lateral-line scales 40 (3), 41(13), 42(31), 43(28), 44(1) or 45(1); two to three scales over caudal fin. Longitudinal series of scales from dorsal-fin origin to lateral line 6(51), 6.5(23) or 7(4); longitudinal series of scales from lateral line to base of pelvic fin 5(26), 5.5(49) or 6(3); total lateral series from dorsal-fin origin to pelvic-fin base 12(23), 12.5(29), 13(20), 13.5(5) or 14(1); longitudinal series of scales from lateral line to first ray of anal fin 4.5(9) or 5(69); circumpeduncular scales 16(77) or 17(1); predorsal scales 10(7), 11(38), 12(17) or 13(5); scales from end of dorsal fin to adipose fin 12(6), 13(34) or 14(37); scales from end of adipose fin to anteriormost dorsal caudal-fin ray 8(3), 9(14), 10(35), 11(16) or 12(4); prepelvic scales 19(3), 20(11), 21(26), 22(11), 23(15) or 24(4); scales from pelvic fin to anus 7(5), 8(23), 9(38), 10(10) or 11(1); scales from anus to anal-fin origin 2(8), 3(51) or 4(2); scales from end of anal fin to anteriormost ventral caudal-fin ray 9(13), 10(37), 11(19) or 12(4); all scales of lateral line pored, canals in scales of lateral line straight.

Dorsal-fin rays ii-iii,8,ii(76); pectoral-fin rays i,12(2), i,13(17), i,14(40), i,15(18) or i,16(1); pelvic-fin rays i,7(1), i,8(76) or i,9(1); anal-fin rays ii-iii,6,ii(76) or iii5,ii(1); caudal-fin rays i,8,9,i(78). Total vertebrae 28(8) or 29(3).

Coloration in alcohol. Overall coloration of specimens retaining guanine on scales silvery to silvery golden, darker on dorsal portions of head and body. Ground coloration of specimens lacking guanine on scales tan to yellow, darker dorsally, with irregular patch of dark pigmentation extending from rear of orbit across opercle; degree of intensity of dark pigmentation and extent of patch variable among individuals. Irregular, dark longitudinal stripe extending along lateral line from supracleithrum to base of middle caudal-fin rays. Stripe slightly wider posteriorly, continuous posteriorly with dusky stripe on middle caudal-fin rays. Stripe in adults continuous, about one scale wide; not as well developed in juveniles, consisting of discrete spots surrounding pores of lateral line. Caudal-fin stripe more prominent on anterior portion of rays. Anterior margin and distal portions of dorsal fin typically dusky in adults. Ventral lobe and dorsal rays of dorsal lobe of caudal fin dusky. All caudal-fin rays outlined by small chromatophores on membranes. Adipose fin dusky distally. Dorsal fin with dusky anterior region in many specimens, without any discrete spot on middle rays. Other fins hyaline.

Sexual dimorphism. Secondary sexual characters were not found.

Geographical distribution. *Steindachnerina insculpta* is restricted to the upper rio Paraná basin (Fig. 5).

Material examined. All from Brazil, upper rio Paraná. CAS 20312, holotype of *Cruxentina insculpta*, 95.3 mm SL, São Paulo, rio Tatuhy (= Tatuí, SP). MZUSP 1376, 1, paratype of *Cruxentina insculpta*, 105.6 mm SL, rio Tatuhy (= Tatuí). USNM 295275, 5, 76.3–104.0 mm SL; MZUSP 20381, 98, Alfredo de Castilho, córrego do Moinho. USNM 295272, 5 (4, 66.7-78.4 mm SL); MZUSP 21515, 26, Miguelópolis, Volta Grande reservoir. USNM 295271, 22 (5, 51.8-87.8); MNRJ 5669, 5 (3, 74.4-81.7); MZUSP 20700, 15; MZUSP 20704, 33; MZUSP 20739, 19; MZUSP 20741, 1; MZUSP 20744, 2; MZUSP 20750, 74 (10, 80.9-90.4); MZUSP 20791, 1; BMNH 1946.12.23:97-111, 11, 69.9-79.5 mm SL, rio Mogi-Guaçu, Emas. MZUSP 20672, 36; MZUSP 20691, 17, rio Mogi-Guaçu, Cachoeira de Emas. USNM 295274, 9; MZUSP 20711,10, rio Mogi-Guaçu, Pirassununga. CAS 41729, 4 66.0-91.9 mm SL; NWW 67002, 3; NMW 68914, 2, Piracicaba, rio Piracicaba. MZUSP 20755, 64; MZUSP 20758, 37; MZUSP 20768, 1, Corumbataí, rio Corumbataí. MZUSP 21317, 10, 88.7-101.4 mm SL; USNM 295266, 2, Borborema, rio Tietê. MZUSP 21525, 1, Marimbondo, rio Grande. MZUSP 21429, 106, Ilha Solteira, rio Paraná. MZUSP 21603, 2, Pedreira, rio Jaguari. MZUSP 20865, 1, rio Pardo, usina de Limoeiro. MZUSP 21471, 1, Botucatu. Minas Gerais: MZUSP 21505, 2, Alfenas, rio Grande, Furnas reservoir. MZUSP 21502, 1, Boa Esperança, rio Grande. Mato Grosso do Sul: MZUSP 20683,15; MZUSP 20714, 84; MZUSP 20853, 18, Três Lagoas, usina de Jupiá, rio Paraná. MZUSP 20824, 1; MZUSP 20894, 1, Três Lagoas, rio Sucuriú. Paraná: MZUSP 21620, 103, rio Paraná, Guaíra, above Sete Quedas. LBP 3192, 4 (tissues 19389–19390), São Paulo, Conchas, rio Tietê; LBP 5207, 8 (tissue 26343), Paraná, Porto Rico, rio Paraná; LBP 6671, 1 (tissue 32081); LBP 19770, 1 (tissue 32158), Paraná, Marilena, rio Paraná; NUP 1424, 4; NUP 4576, 6, Guaíra, rio Paraná, Itaipu reservoir. NUP 1753, 7, Santa Helena, rio Paraná, Itaipu reservoir. NUP 7513, 4, Foz do Iguaçu, rio Paraná, Reservatório Itaipu.

Discussion

Populations of *Steindachnerina* from the rio Paraguai basin and from the upper rio Paraná basin were considered by Vari (1991:71) as belonging to a single species (*S. insculpta*) but studies carried out on these populations have allowed us to conclude that they belong to two distinct species: *S. insculpta* (upper rio Paraná basin) and *S. nigrotaenia* (rio Paraguai basin), supplemented by the very distinct *S. brevipinna* (rio Paraguai basin) (Fig. 7). Although the first two species are very similar in many morphological aspects, they might be diagnosed from each other firstly on the basis of the number of scales in the lateral line and number of scales in the transverse line, and they can be further diagnosed by *S. brevipinna* by the lack of the dark spot on basal portions of the dorsal fin, and by modal differences in the number of scales of the lateral line and of the transverse line (Figs. 3-4). Furthermore, a molecular analysis strongly supports the recognition of the three species.

Fig. 7. *Steindachnerina brevipinna*, LBP 9753, 51.6 mm SL, Brazil, Mato Grosso do Sul, Nova Andradina, upper Rio Paraná.

Vari (1991) interpreted the presence of *Steindachnerina insculpta* (= *S. nigrotaenia*) populations in the rio Paraguai basin as a result of a possible introduction of specimens originated from the upper rio Paraná. This interpretation was first a consequence of the supposition that *S. nigrotaenia* was a synonym of *S. brevipinna*, and secondarily because Vari (1991) had only a small number of specimens from the rio Cuiabá collected at that time. That small number of lots concentrated in a small area of the rio Paraguai basin and geographically distant from populations of the upper rio Paraná led him to hypothesize a human-mediated introduction to explain the disjoint distribution of what he considered to be populations of the same species (*S. insculpta*). Obviously, the present findings disprove his hypothesis, showing that he was working with two distinct species, *S. insculpta* and *S. nigrotaenia*.

Several pieces of evidence indicate a gap separating the distributions of *Steindachnerina nigrotaenia* (upper rio Paraguai and lower rio Paraná) from that of *S. insculpta* (upper rio Paraná, upriver Itaipu). Inventories in the rio Paraná below Itaipu reported neither *S. insculpta* nor *S. nigrotaenia*, and indicated, instead, the presence of *S. brevipinna, S. biornata* and *S. conspersa* (*e.g.*, López *et al.*, 2003; 2005). In addition, many species of the middle rio Paraná were incorporated to the ichthyofauna of the upper rio Paraná after the construction of the Itaipu dam (Agostinho *et al.*, 1992, 1997; Júlio Júnior *et al.*, 2009), including *S. brevipinna* that that is genetically distinct of the sympatric *S. insculpta* (Oliveira *et al.*, 2002), but no evidence of *S. nigrotaenia* in that section has been reported recently (Graça, Pavanelli, 2007; Ota *et al.*, 2018).

Specimens identified as *Curimata nasa* (Steindachner, 1882) by Géry *et al.* (1987:425) from Paraguay were considered by Vari (1991:71) to belong to *S. insculpta* (*sensu* Vari, 1991). However, the five specimens mentioned by Géry *et al.* (1987) are from different localities: two of them collected in the rio Paraguai (possibly *S. nigrotaenia*), and three other specimens in the rio Paraná basin (*S. insculpta*). Nevertheless, any definitive decision on the status of these specimens without a direct examination is premature. More recently, Koerber *et al.* (2017:16) in the checklist of fishes from Paraguay cited *S. brevipinna*, *S. conspersa* and *S. insculpta*, the latter being *S. nigrotaenia* according to the concept herein established; they also erroneously refer to the type locality of *S. insculpta* as being in Venezuela, disregarding that Britski (1969:201), and Vari (1991:72) had already clarified this question. Aguilera *et al.* (2018) also reported the first occurrence of *S. insculpta* in Argentina, which, based on their description, the species in question also represents *S. nigrotaenia*.

After the revision of *Steindachnerina* (Vari, 1991), two other species were described in the genus and another species is validated herein, then accumulating 25 species of *Steindachnerina*. Another species, *Cyphocharax corumbae* (Pavanelli & Britski, 1999) was originally described in *Steindachnerina* but recently transferred to *Cyphocharax* (Melo *et al.*, 2018). Presently, five *Steindachnerina* species are known from the rio La Plata basin (Paraná, Paraguai and Uruguai rivers): *S. brevipinna* (rio Paraná, rio Paraguai, and rio Uruguai), *S. conspersa* (rio Paraguai and lower rio Paraná), *S. nigrotaenia* (upper rio Paraguai), *S. insculpta* (upper rio Paraná), and *S. biornata* (rio Uruguai, lower rio Paraná and coastal rivers of southern Brazil).

This study resolves a long-standing question in the systematics of *Steindachnerina* and adds one more species to the ichthyofauna of the rio Paraguai. Further research might investigate the phylogenetic placement of *S. nigrotaenia* within the recently proposed *S. dobula* clade (*sensu* Melo *et al.*, 2018) and also compare morphological features of the three related species occurring in the La Plata system.

Comparative material examined. *Steindachnerina brevipinna*: LBP 659, 2, Mato Grosso, Poconé, rio Paraguai; LBP 3728, 1, Mato Grosso do Sul, Aquidauana, rio Paraguai; LBP 4665, 4, Mato Grosso do Sul, Rio Baia, rio Paraguai; LBP 5804, 15, Mato Grosso, Santo Antônio do Laverger, rio Paraguai; LBP 6690, 34 (tissues 32153-32157), Paraná, Marilena, rio Paraná; LBP 8433, 9, Mato Grosso, Tangará da Serra, rio Paraguai; LBP 8448, 5, Mato Grosso, Cáceres, rio Paraguai; LBP 9753, 45, Mato Grosso do Sul, Nova Andradina, rio Paraná; LBP 13338, 2, Mato Grosso, Poconé, rio Paraguai; NUP 1431, 4 (102.2-114.2 mm SL), Paraná, Guaíra, rio Paraná, Itaipu reservoir; NUP 2895, 62 (5, 88.3-104.5 mm SL), Paraná, Porto Rico, Ilha Porto Rico, rio Paraná, Lagoa Jenipapo. *Steindachnerina elegans*: LBP 8272, 2, Minas Gerais, Jaíba, rio Verde Grande, rio São Francisco.

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