

Taxonomy of *Ixinandria* Isbrücker & Nijssen (Loricariidae: Loricariinae) based on morphological and molecular data

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The genus *Ixinandria* was described in 1979 to include *I. steinbachi* from the upper río Juramento in northern Argentina and *I. montebelloi* from the upper río Bermejo in southern Bolivia. We used a multivariate morphometric analysis (Principal Components Analysis) and a molecular comparison of the Cytochrome Oxidase I gene to investigate variation among distinct populations from the known distribution range of both species. We conclude that the populations are not significantly distinct and do not deserve separate species recognition, and we place *I. montebelloi* in the synonymy of *I. steinbachi*.

O gênero *Ixinandria* foi descrito em 1979 para incluir *I. steinbachi* do alto rio Juramento no norte da Argentina e *I. montebelloi* do alto rio Bermejo no sul da Bolívia. Utilizamos análise morfométrica multivariada (Análise de Componentes Principais) e uma comparação molecular do gene Citocromo Oxidase I para investigar a variação entre populações distintas da área de distribuição de ambas as espécies. Concluimos que as populações não são significativamente distintas e não merecem reconhecimento como espécies separadas, e colocamos *Ixinandria montebelloi* na sinonímia de *I. steinbachi*.

Key words: Neotropical, Synonymy, río Juramento; río Bermejo; río Pilcomayo.

Introduction

Ixinandria Isbrücker & Nijssen, 1979 was described to accommodate two species, *Loricaria steinbachi* Regan, 1906, the type species, and *Canthopomus montebelloi* Fowler, 1940. *Ixinandria* was considered by the authors to be very close to *Rineloricaria* Bleeker, 1862, and diagnosed on the basis of the absence of abdominal plates, the degree of development of odontodes, and the shape of the head in sexually mature males (Isbrücker, 1979). Isbrücker (1979) placed *Ixinandria* in the subtribe Rineloricariina, which also included *Spatuloricaria* Schultz, 1944, *Dasylicaria* Isbrücker & Nijssen, 1979, and *Rineloricaria*. The validity of *Ixinandria* or its relationships with other loricariines were never further investigated.

Loricaria steinbachi was placed in the subgenus *Rhineloricaria* by Eigenman (1911), a few years after its original description, and remained as *Rineloricaria* until it was moved to *Ixinandria* by Isbrücker (1979). On the other hand, *Canthopomus montebelloi* remained mostly unnoticed until Isbrücker's (1979) new combination by its inclusion in the genus *Ixinandria*.

Loricaria steinbachi was described from the río Juramento basin, a tributary to the río Salado drainage, near Cachi, Salta, Argentina, at an elevation of 2,500 meters above sea level, based on three specimens. Isbrücker (1979) later designated the larg-

est of those three syntypes as the lectotype. *Canthopomus montebelloi* was described from tributaries of the upper río Bermejo at the Monte Bello Farm in Tarija, southern Bolivia, based on the holotype only, also from high elevation.

The validity of those species was later questioned by Isbrücker (1981a), who suggested that they might represent a single species. In this paper, we revised the two species and placed *Ixinandria montebelloi* in the synonymy of *I. steinbachi*, based on both morphological and molecular evidence.

Material and Methods

The morphometric variables were measured with a digital caliper (0.1 mm precision). The measurements and counts follow Isbrücker & Nijssen (1978), except the following: Counts of lateral plates with coalesced keels and the measurement of cleithral width were made according to Reis & Pereira (2000); and eye diameter was measured according to Isbrücker (1973). Names and counts of lateral plate rows and rostral plates follow Schaefer (1997). Osteological observations were made on specimens cleared and stained (c&s) prepared according to the method of Taylor & Van Dyke (1985).

We used Principal Components Analysis (PCA) to investigate morphometric variation among four distinct populations of *Ixinandria*, encompassing the area of distribution of both *I. steinbachi* and *I. montebelloi*. A total of 30 morphometric

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variables (Table 1) was taken from 73 specimens representing comparable size ranges: a population from the río Juramento basin, upper río Salado drainage, type-locality of *Ixinandria steinbachi* (n=16, 58.2–91.6 mm SL), a population from the upper río Bermejo drainage in northern Argentina (n=18, 56.4–112.8 mm SL), a population from the upper río Bermejo in southern Bolivia, type-locality of *Ixinandria montebelloi* (n=37, 68.9–100.3 mm SL), and two specimens from the upper río Pilcomayo in Bolivia (n=2, 72.7 and 76.6 mm SL). Principal components analysis was performed on the co-variance matrix of the 30 log-transformed measurements. Factor scores were plotted for the PC II, III and IV, interpreted to represent size-free shape (Bookstein, 1989).

In the lists of material museum abbreviations and catalog number are presented first, followed by the number of specimens in that lot, size range, number and size range of measured specimens in parentheses, and locality. Institutional abbreviations are according to Reis *et al.* (2003), with the addition of Museo de Ciencias Naturales, Universidad Nacional de Salta, Salta (MCNI), and Universidad Mayor de San Simón, Cochabamba (UMSS).

Scanning electronic micrographs were made at the Facultad de Ciencias Naturales y Museo (Universidad Nacional de La Plata) and Centro de Microscopia e Microanálises (Pontificia Universidade Católica do Rio Grande do Sul).

For molecular analyses we used tissue samples from six localities as follows: 12 specimens from two localities in the río Arenales, tributary to the río Juramento near Salta, Argentina; 10 specimens from the río La Caldera and arroyo Lesser, tributaries to the río Bermejo near Salta, Argentina; and 11 specimens from the río Gaudalquivir and río Camacho, tributaries to the río Bermejo near Tarija, Bolivia. In addition, we used sequences from two outgroup species taken from GenBank (*Apistoloricaria ommation* EU359403 and *Rineloricaria* sp. EU359461).

From total genomic DNA extracted from ethanol-preserved tissue using the QIAmp tissue kit (Qiagen, Hilden, Germany), we amplified and sequenced a 709 basepair fragment of the mitochondrial Cytochrome Oxidase I gene, using the primers LCO1490 and HCO2198 (Hebert *et al.* 2003). Each PCR was carried out in 20 μ l reactions with the following concentrations: 1x Invitrogen PCR buffer (Invitrogen, São Paulo), 1.5–2.5 mM MgCl₂, 0.2% Triton, 200 μ M of each dNTP, 0.025 U/ μ l Taq polymerase (Invitrogen, São Paulo), 0.2 μ M of each primer and up to 2 μ l of DNA solution.

We used a non-standard protocol for this primer pair with an initial denaturation step of 1 min at 96°C followed by 40 cycles of 94°C for 30s, annealing at 50°C for 20s, 48°C for 5s, 46°C for 5s, 44°C for 5s, 42°C for 5s, 40°C for 20s and extension at 72°C for 1 min. This was followed by a final 3 min at 72°C extension step. Amplification success was evaluated on GelRed™ (BioTium, São Paulo) or ethidium bromide-stained agarose gels (Sambrook *et al.* 1989). PCR products were purified using PEG8000, ExoSAP-IT® (USB) or the ilustra™ GFX PCR and Gel Band Purification Kit (GE Healthcare, Buckinghamshire, UK). Sequencing was done using the

DYEnamic™ ET dye terminator kit (GE Healthcare, São Paulo) read in a MegaBace1000 sequencer. Sequences were edited and combined using BioEdit 7.0.1 (Hall 1999).

Sequences were aligned using Clustal X 1.83 (Thompson *et al.*, 1997) with the standard settings. PAUP*4.0b10 (Swofford, 2001) was used to analyze the data with respect to the parsimony and the maximum likelihood criteria. For the maximum parsimony (MP) analysis we used the tree-bisection-reconnection (TBR) search algorithm with 1000 replicates in which taxa were added randomly to the starting tree. All characters were treated as unordered and transformations were assigned equal weight. Nodal support was evaluated with 1000 nonparametric bootstrap pseudoreplicates (Felsenstein, 1985) using the TBR search algorithm on a starting tree to which taxa were added randomly. Multiple optimal topologies were summarized through consensus methods. The maximum likelihood (ML) analysis was done using the TVM+G model found with Modeltest 3.7 (Posada & Crandall, 1998). Nodal support was evaluated with 1000 nonparametric bootstrap pseudoreplicates.

A haplotypic network was calculated using Network 4.5.0.0 (Bandelt *et al.*, 1999). An Analysis of Molecular Variance (AMOVA) and a fixation index (F_{ST}) analysis were calculated using Arlequin 3.11 (Excoffier *et al.*, 2005). Mega 3.1 (Kumar *et al.*, 2004) was used to calculate sequence divergences using Kimura-2-parameter (K2P) distance.

Results

Multivariate analysis. The resulting first principal component included a large proportion of the total variance (78.6%) and all variable loadings were positive and varied little in magnitude, suggesting that it represents a general size factor. Plots of factor scores of principal component II vs. III grouped specimens into four broadly overlapping clusters (Fig. 1). PC II and III included 4.5 and 4.0% of the total variance, respectively. Measurements with heavier loadings on PC II are anal-fin spine length (0.395), body width at dorsal-fin origin (-0.416) and body depth at dorsal-fin origin (-0.434); on PC III are dorsalmost principal caudal-fin ray (-0.407), ventralmost principal caudal-fin ray (-0.386) and eye diameter (0.395). Plots of factor scores of PC II vs. IV also grouped specimens into four overlapping clusters (Fig. 1). PC IV included 2.5% of the total variance and heavier loadings on PC IV were on thoracic length (0.247) and internareal width (-0.487).

Molecular analysis. We obtained an alignment with 35 sequences with 709 contiguous nucleotides. The character matrix contained 42 parsimony-informative characters. The MP analysis resulted in 26 equally parsimonious trees with a length of 151 steps. Their summarized strict consensus tree is shown in Fig. 2. The single best tree found in the ML analysis has a -ln L score of -1643.94356 and is shown in Fig. 3.

Based on the geographic distances we considered our samples to be from three populations: Juramento (río Arenales), Bermejo 1 (río Caldera and arroyo Lesser) and Bermejo 2 (río

Gaudalquivir and río Camacho). The Network showed the population Bermejo 2 separated from Juramento and Bermejo 1 which, in turn, could not be separated (Fig. 4).

The AMOVA showed that the sequences from the samples from Tarija are significantly different ($p=0.0000$) from the other samples. The samples from Salta did not show any significant difference ($p=0.39640 \pm 0.0243$). Our sequences showed an average K2P distance of 1.1%.

***Ixinandria* Isbrücker & Nijssen, 1979**

Ixinandria Isbrücker & Nijssen, in Isbrücker, 1979: 87 and 91, figs. 1-4. Type species: *Loricaria steinbachi* Regan, 1906, by original designation. Gender: feminine.

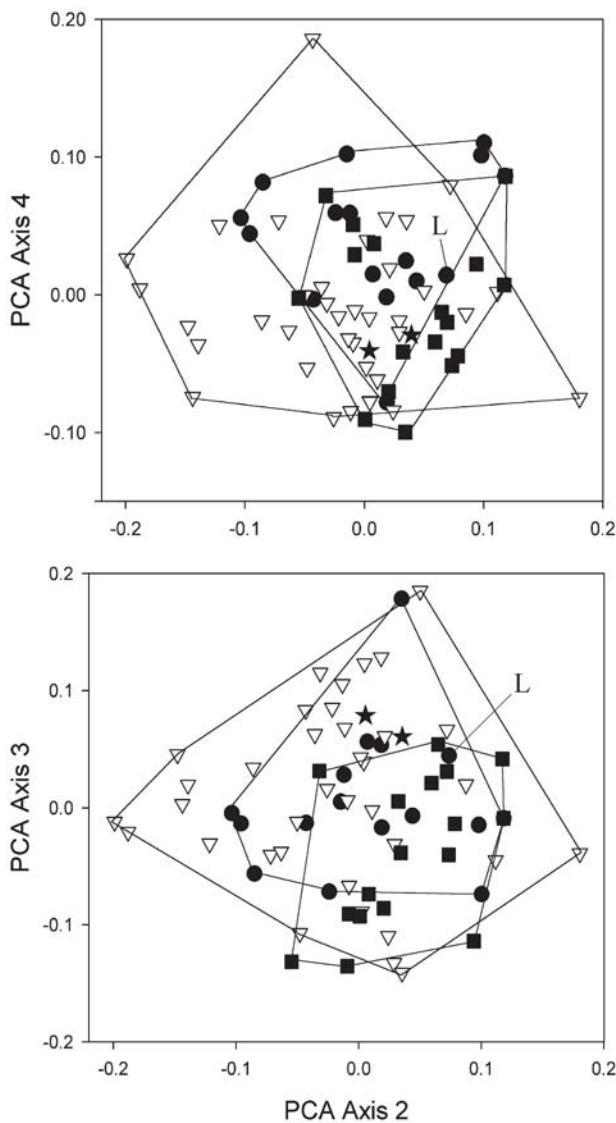


Fig. 1. Plots of factor scores of principal component analysis of four populations of *Ixinandria steinbachi*. Dot, río Juramento basin; Square, southern upper río Bermejo basin; triangle, northern upper río Bermejo basin; and Star, río Pilcomayo. L = lectotype.

Diagnosis. Among loricariines *Ixinandria* is most similar to *Rineloricaria* and can be distinguished from most genera by the total lack of abdominal plates, including the preanal plate. *Hartiella* and a few species of *Harttia* also have the abdomen completely devoid of plates, and can be distinguished from *Ixinandria* by having 12 branched caudal-fin rays (vs. 10 in *Ixinandria*) and by the absence of postorbital notch, which is present in *Ixinandria*. Species of *Crossoloricaria*,

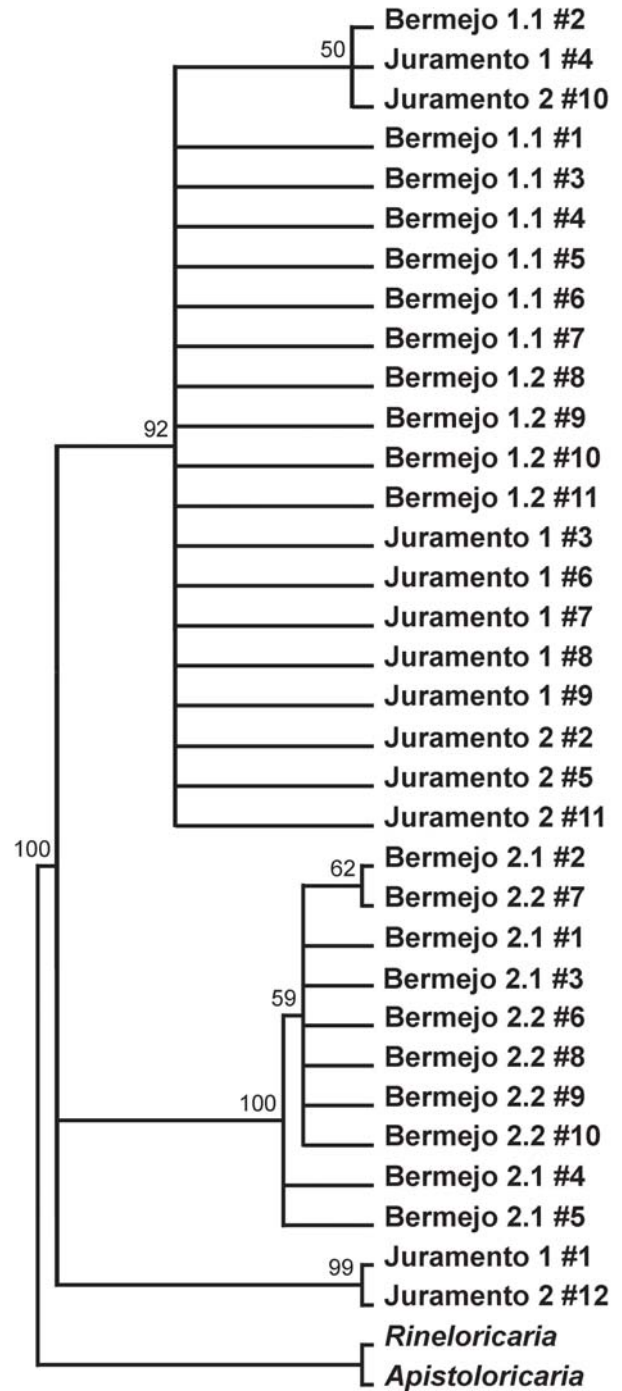


Fig. 2. Strict consensus of the 26 best trees from the maximum parsimony analysis. Tree length: 151. Numbers above branches are values from 1000 bootstrap replications.

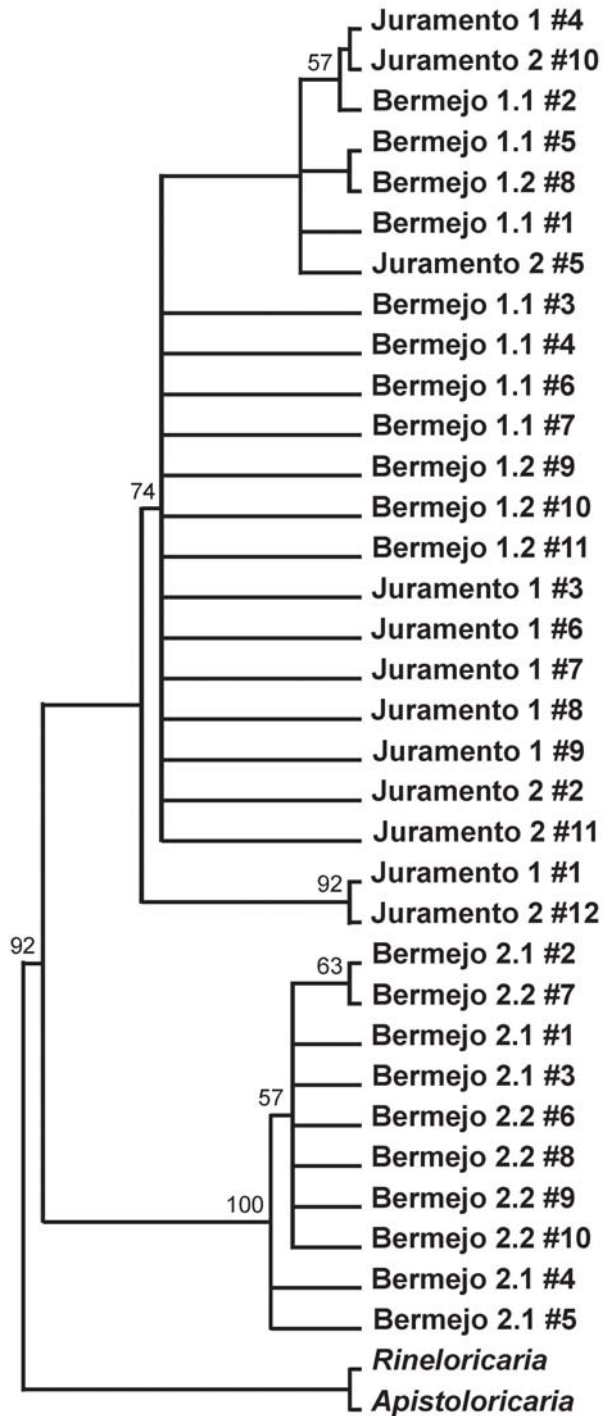


Fig. 3. Best tree from maximum likelihood analysis. $-\ln L=1643.94356$. Numbers above branches are values from 1000 bootstrap replications.

Spatuloricaria, and *Loricaria* sometimes lack a preanal plate, but small abdominal plates are present. Some species of *Rineloricaria* have a naked abdomen, but a preanal plate is always present, except in *R. setepovos*. This species, however, has a caudal-fin filament and 3-4 premaxillary teeth. *Ixinandria* can also be distinguished from other loricariines by the shape and number of premaxillary teeth. *Ixinandria*

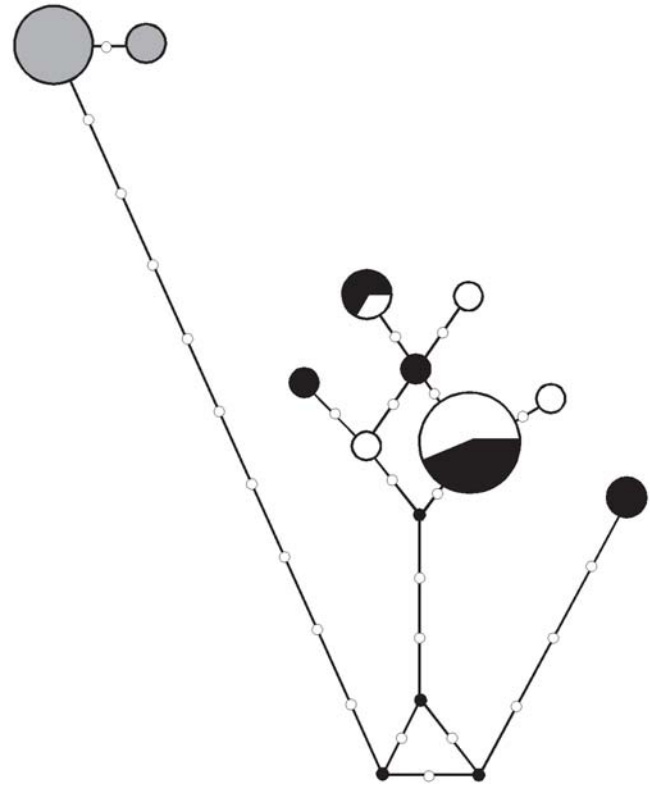


Fig. 4. Minimum spanning network of *Ixinandria steinbachi* haplotypes. Distances correlate to the number of mutations in the sequence as marked by open dots. Circle size corresponds to frequency of haplotypes. White: Juramento, black: Bermejo 1, grey: Bermejo 2.

has wide and almost symmetrical tooth cusps, and up to 18 teeth in each premaxilla (vs. premaxilla with up to 13 narrow and clearly asymmetrical teeth in other loricariines, except *Rineloricaria aequalicuspis* which has up to 15 narrow teeth with nearly symmetrical cusps, and some hartiini, which also have many asymmetrical premaxillary teeth).

***Ixinandria steinbachi* (Regan, 1906)**

Fig. 5

Loricaria steinbachi Regan, 1906: 97. Type locality: Salta, Argentina. - Eigenmann, 1911: 414 (listed under subgenus *Rhineloricaria*). - Pozzi, 1945: 275 (Jujuy). - Arratia *et al.*, 1983: 54 and 82 (Jujuy; río Bermejo). - Arratia & Menu Marque, 1984: 517 (reference).

Loricaria (Rhineloricaria) steinbachi. - Gosline, 1945: 102 [listed]. - Gomes, 1947: 24 [reference]. - Ringuélet & Arámburu, 1962: 53 [Argentina]. - Ringuélet *et al.*, 1967: 411, 413 [description and distribution in Argentina].

Ixinandria steinbachi. - Isbrücker, 1979: 91, 113 [new combination, lectotype designation]. - Isbrücker, 1980: 103 [reference]. - Isbrücker, 1981a: VI,75 [reference, discussion]. - Isbrücker, 1981b: 89 [reference]. - López *et al.*, 1987: 31 [listed, Argentina]. - Burgess, 1989: 417 [reference]. - Fernández, 1996: 22 [Ledesma, Jujuy and Rosario de Lerma,

Salta]. - Monasterio de Gonzo *et al.*, 1998: 133-139 [trophic ecology]. - Isbrücker, 2001: 29 [reference]. - Nieva *et al.*, 2001: 85 [La Ciénaga, río Arias, río Juramento basin, Salta]. - Barros *et al.*, 2001: 9 [density in the río Arenales, Salta]. - Monasterio de Gonzo, 2002: 11-18 [description and comparison of dentition of three loricariids]. - López *et al.*, 2002: 7 & 60 [endemism in the Subtropical Potamic Axis ecoregion]. - López *et al.*, 2003: 45 [listed]. - Ferraris, 2003: 336 [listed]. - Menni, 2004: 195, 198 [río Aguas Negras, Ledesma, Jujuy, and río Rosario at 48 km of Salta, habitat]. - Monasterio de Gonzo, 2003: 191-192 [distribution and redescription]. - Menni *et al.*, 2005: 34, 38 [río Aguas Negras and río Juramento basin]. - López & Miquelarena, 2005: 530, 534 [Paranoplatensean distribution, endemism in western South America]. - Monasterio de Gonzo *et al.*, 2005: 36-41 [abundance and detritivorous trophic habits in río Popayán, Parque Nacional el Rey, Salta]. - Monasterio de Gonzo *et al.*, 2005: 26 [distribution, listed to río Bermejo, río Juramento and río Dorado del Valle]. - Liotta, 2006: 365 [distribution]. - Covain & Fisch-Müller, 2007: 31 [distribution, habitat, sexual dimorphism, and reproductive habits]. - Ferraris, 2007: 263 [listed, distribution, and remarks].

Canthopomus montebelloi Fowler, 1940: 55, fig. 10 [NEW SYNONYM]. Type locality: Monte Bello, Tarija, Bolivia. - Böhlke, 1984: 123 [type catalog]. - Gosline, 1945: 83 [listed]. - Gosline, 1947: 108 [reference].

Ixinandria montebelloi. - Isbrücker, 1979: 87 [new combination]. - Isbrücker, 1980: 103 [reference]. - Isbrücker, 1981a: VI,75 [reference, discussion]. - Burgess, 1989: 417 [reference]. - Isbrücker, 2001: 29 [reference]. - Ferraris, 2003: 336 [reference]. - Armbruster, 2004: 46, 66 & 68 [phylogeny of family Loricariidae]. - López & Miquelarena, 2005: 534 [endemism in western South America]. - Ferraris, 2007: 263 [listed, distribution].

Diagnosis. As for the genus

Description. Morphometric data in Table 1. Head and body strongly depressed. Trunk and caudal peduncle becoming more compressed caudally. Dorsal profile of body convex from snout to end of supraoccipital, straight or slightly convex from supraoccipital to dorsal-fin spine, straight from dorsal fin to one or two plates before caudal fin. Upper edge of orbit not raised. Scarcely developed triangular postorbital notch.

Outline of head rounded in dorsal view. Head strongly flattened in mature males. Paired anterior postrostral and cheek plates scarcely developed ventrally. Odontodes curved, conical, and pointed, densely covering head, trunk, and fin rays, making fish somewhat hispid. Body odontodes scarcely distributed and grouped centrally in plates (Fig. 6). Thick skin sometimes covering plates partially, hiding plate limits and covering odontodes. Snout tip with big globular protuber-

Table 1. Descriptive morphometrics of *Ixinandria steinbachi* of four distinct populations. Values are given as percents of standard length or of head length. Lec = Lectotype of *Loricaria steinbachi*, SD = standard deviation.

Character	río Juramento basin n=16				río Bermejo Argentina n=18				río Bermejo Bolivia n=37				río Pilcomayo n=2			
	Lec	Low	High	Mean	SD	Low	High	Mean	SD	Low	High	Mean	SD	Low	High	Mean
Standard length (mm)	84.5	58.16	91.6	75.0	-	56.37	112.8	76.5	-	68.9	100.3	82.0	-	72.7	76.6	74.7
	Percents of standard length															
Predorsal length	41.5	39.3	42.3	40.6	0.98	36.4	42.5	40.0	1.55	38.2	43.0	40.9	1.25	38.5	42.1	40.3
Postdorsal length	61.0	57.5	63.4	61.3	1.59	59.8	64.9	62.3	1.41	59.3	65.0	62.2	1.43	60.7	63.3	62.0
Postanal length	42.5	40.9	47.9	44.8	1.95	43.2	49.0	46.1	1.64	40.7	48.3	44.7	1.63	45.0	47.3	46.1
Dorsal-fin spine length	21.3	19.1	23.8	21.7	1.38	17.9	26.1	22.3	1.82	18.1	24.6	21.1	1.63	20.0	23.5	21.8
Anal-fin spine length	18.3	16.8	19.6	18.3	0.93	15.8	22.7	19.3	1.48	14.6	20.4	17.6	1.30	16.0	18.8	17.4
Pectoral-fin spine length	21.9	19.1	23.1	20.8	1.24	15.9	23.8	20.7	1.94	16.6	22.7	20.1	1.65	19.0	21.7	20.4
Pelvic-fin spine length	21.2	17.9	21.2	19.3	0.91	15.7	21.7	19.0	1.47	16.6	21.6	19.4	1.21	17.1	19.4	18.2
Uppermost caudal-fin ray	16.7	14.1	19.9	15.5	4.38	15.7	21.4	18.1	1.42	14.0	19.9	17.0	1.52	14.4	15.5	15.0
Lowermost caudal-fin ray	16.7	14.0	18.8	13.8	5.53	13.9	19.6	16.9	1.55	13.6	19.4	16.3	1.18	14.0	15.3	14.6
Thoracic length	22.5	16.1	22.5	18.7	1.69	16.1	19.2	18.1	0.77	16.3	21.3	18.3	1.31	17.2	19.1	18.2
Abdominal length	18.7	16.4	21.1	18.9	1.27	17.1	22.1	19.3	1.32	17.7	22.0	19.9	1.23	20.1	20.1	20.1
Cleithral width	24.5	22.0	25.8	24.2	1.00	21.8	25.6	23.9	1.16	22.4	27.6	24.8	1.25	23.3	26.4	24.9
Depth of caudal peduncle	3.4	2.3	3.4	2.8	0.26	2.3	3.2	2.7	0.23	2.5	3.8	3.0	0.28	2.7	2.8	2.8
Width of caudal peduncle	5.1	4.2	5.9	5.0	0.46	4.3	5.6	4.8	0.39	4.1	5.9	5.0	0.38	4.3	4.7	4.5
Pelvic-fin origin to caudal-fin	59.4	59.4	65.4	62.7	1.71	61.7	68.1	64.7	1.65	58.8	69.1	63.2	2.23	65.7	67.0	66.4
Snout tip to pelvic-fin origin	43.2	36.1	43.2	38.6	2.19	34.7	42.0	37.0	1.69	34.1	42.0	38.2	1.79	35.2	36.3	35.7
Body width at dorsal fin origin	21.3	17.3	24.0	21.3	1.93	16.8	24.8	20.5	1.74	18.9	28.5	23.2	2.27	19.1	19.8	19.4
Body depth at dorsal fin origin	-	12.3	17.3	14.1	4.12	10.0	18.4	15.6	2.07	12.2	21.3	16.9	2.20	14.1	14.6	14.3
Body width at anal-fin origin	14.2	13.2	16.6	14.8	1.04	11.1	15.7	14.1	1.26	13.5	19.7	15.7	1.33	14.2	14.2	14.2
Body depth at anal-fin origin	9.9	9.8	12.9	10.8	0.73	9.8	16.6	11.3	1.77	10.1	12.6	11.3	0.60	9.7	10.7	10.2
Head length	28.7	26.0	28.7	27.1	0.93	24.9	29.0	26.6	0.98	24.2	29.8	27.4	1.24	25.4	26.8	26.1
	Percents of head length															
Head depth	50.1	45.5	61.4	53.7	4.59	50.7	64.3	55.3	3.62	45.6	65.6	55.7	4.67	48.2	50.3	49.3
Snout length	57.5	50.3	59.6	54.7	2.64	51.5	56.3	54.8	1.36	49.7	62.2	55.6	2.26	52.3	56.2	54.2
Interorbital width	31.3	25.3	31.3	28.8	1.61	25.8	30.3	28.7	1.48	25.0	30.3	27.4	1.06	28.2	28.3	28.3
Internareal width	10.3	7.3	11.7	9.2	1.21	8.4	12.2	10.1	0.90	6.4	12.7	10.1	1.32	11.3	11.7	11.5
Orbit diameter including notch	14.8	13.4	20.1	15.8	1.89	14.5	20.1	17.5	1.56	14.8	19.8	16.9	1.45	15.7	16.1	15.9
Orbit diameter excluding notch	10.1	8.4	14.6	10.7	1.41	10.0	12.8	11.4	0.72	9.7	13.2	11.4	0.94	11.8	11.8	11.8
Premaxillary ramus	17.6	13.3	17.9	15.9	1.41	14.8	18.8	16.9	1.02	13.9	19.5	17.0	1.24	16.8	17.6	17.2
Width of lower lip	65.9	51.9	66.5	60.8	4.26	59.0	70.2	63.3	3.13	58.0	84.1	71.3	5.59	70.8	71.8	71.3



Fig. 5. *Ixinandria steinbachi*, UMSS 215, 100.3 mm SL, male, río Orosas, Aniceto Arce, Province of Tarija, río Bermejo basin, Bolivia.

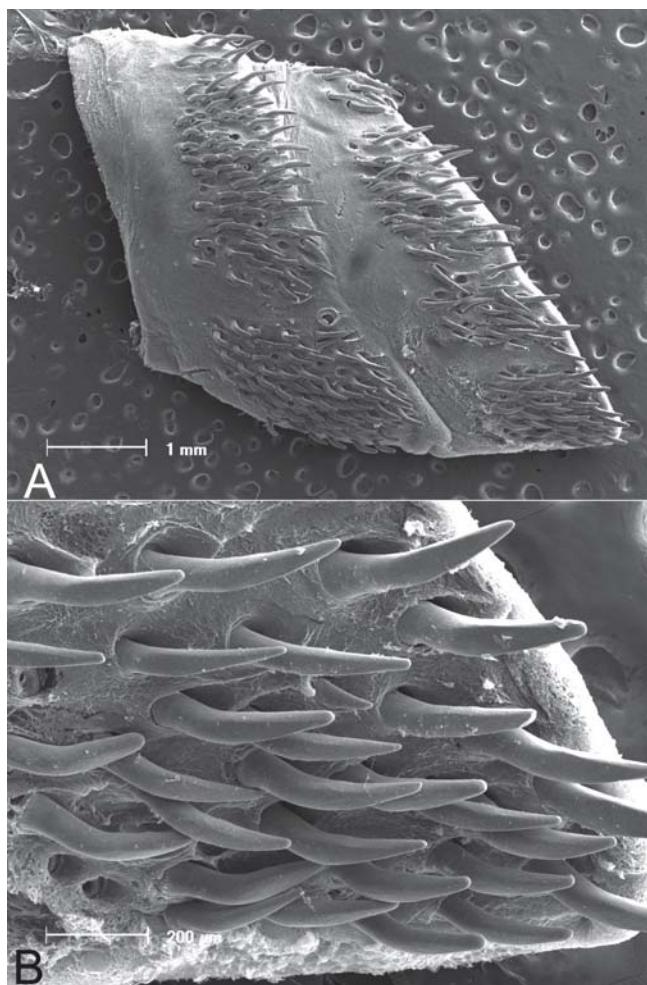


Fig. 6. Scanning electron micrographs of the body odontodes of *Ixinandria steinbachi* (MCNI 99, 65.9 mm SL). A) Two plates of the median and mid-ventral lateral series with odontodes; B) detail of odontodes.

ance of naked skin. This roundish naked area not reaching most anterior pore of infra-orbital ramus of sensory canal. Gill opening small. Mouth big and roundish. Lower lip margin with short digitiform papillae. Upper lip well developed, folded inwards with row of globular papillae. Big globular papillae arranged in regular rows on surface of lips. Numerous small globular papillae on mouth roof, bigger posteriorly. Maxillary barbel very small, mostly coalesced with lower lip. Teeth bilobed, with wide cusps, mesial more developed and slightly longer than lateral (Fig. 7). Premaxilla with six to 18 (mean=12.4, n=71) teeth in functional series. Dentary with six to 15 (mean=10.3, n=46) teeth in functional series.

Abdomen completely naked, except for lateral abdominal plates. Preanal plate absent. Two to 11 (mean= 7.0, n= 72) lateral abdominal plates on each side. 27 to 32 (mean=29.4, n=72) plates in median lateral series, with well developed keels formed by hypertrophied odontodes. Five lateral series, sometimes broken and appearing to have six or seven lateral series; only posterior portion of median and midventral series with keels. Keels coalesced in last seven to 12 rings (mean=9.5,

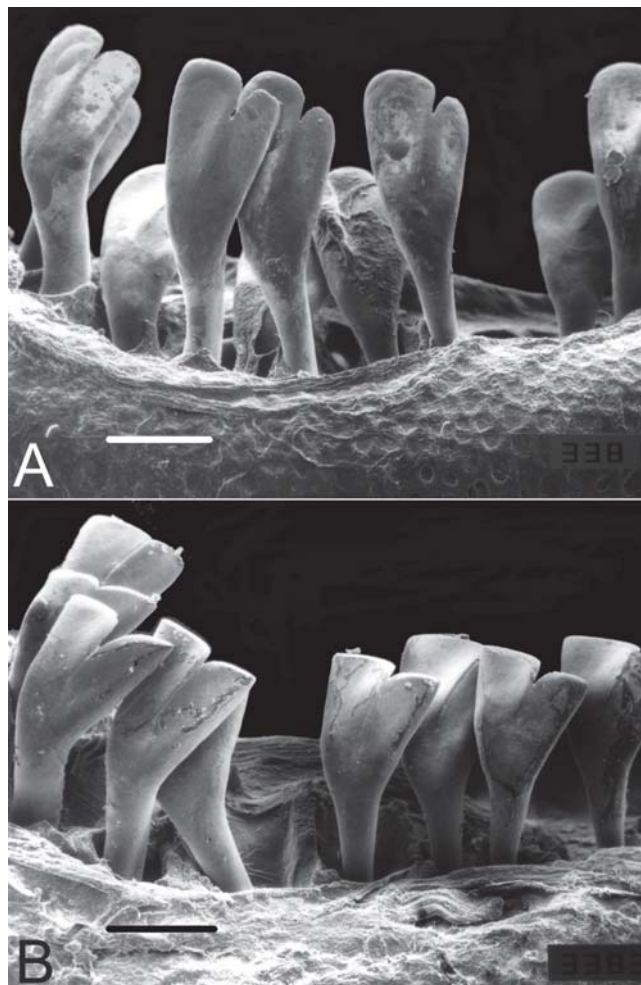


Fig. 7. Scanning electron micrographs of premaxillary teeth of *Ixinandria steinbachi*, showing sexual dimorphism in teeth cusps. A) MCNI 419, 69.3 mm SL, male; B) MCNI 419, 71.1 mm SL, female. Scale 700 μ m.

n=72). Middorsal series with 5-10 plates (mean=7.8, n=9) (better visible in cleared and stained material). Entire body with thick skin between the plates, especially in the lateral series. Predorsal plates usually arranged in irregular pattern, not forming rows. Supraoccipital and predorsal plates without keels. Transversal diameter of nasal capsule equal or slightly larger than eye diameter including notch (better visible in cleared and stained material).

Posterior margin of dorsal fin straight or slightly rounded, generally with first or second branched ray longest. Tip of dorsal fin, when depressed, reaching third or fourth (exceptionally fifth) plate posterior to fin insertion. Dorsal-fin spinelet absent. Posterior margin of pectoral fin convex, first or second branched ray longest, reaching to or slightly beyond pelvic-fin origin. Posterior margin of pelvic fin rounded; first or second branched ray longest, reaching to or falling slightly short of anal-fin origin. Posterior margin of anal fin rounded, with longest first or second (rarely) branched ray. Tip of anal fin, when depressed, reaching fifth or sixth plate posterior to fin insertion; three or four ventral plates along its base. Pos-

terior margin of caudal fin truncated or slightly concave. Upper and lower unbranched rays never extending as filament. Two or three supracaudal plates covering base of caudal-fin rays, median plate sometimes absent.

Color in alcohol. Background color of dorsal surface of head and body dark brown with five darker transverse bars; first one inconspicuous on supraoccipital, others distributed between origin of dorsal fin and caudal fin. Last three bars sometimes continuing across ventral surface and forming dark brown rings. Some specimens with black spots on head and snout. Dorsal fin with dark gray circular spots. Pectoral and pelvic fins yellowish with dark circular spots. Sensorial pores on head and beginning of lateral canal pigmented with black. Ventral surface of body light brown in naked regions. Anal and caudal fins with dark dots arranged in bars on branched and unbranched rays. Ventral plates darkened around anal-fin base.

Color in life. Background color of head and body light brown with five dark brown transverse bars distributed as described above. Other markings as described above (Fig. 8).

Sexual dimorphism. Males with head wide and flattened; long hypertrophied odontodes on sides of head and on upper side of branched pectoral-fin rays; short odontodes on remaining of dorsal surface of body, especially on predorsal region; unbranched pectoral-fin ray hypertrophied. Papillae in mouth cavity more numerous in males than in females. Outer margin of tooth cusps straight in females, rounded in males (Fig. 7).

Ontogeny. Many structures vary ontogenetically in *Ixinandria steinbachi*. The premaxilla, dentary, and the pectoral girdle are ossified in a specimen of 17.2 mm SL, the smallest individual we were able to examine. At that size the pelvic girdle was not developed, the lateral abdominal plates and plates on the head and predorsal region were not formed. The lateral series of plates were represented by small platelets with one or two odontodes each.

In a specimen of 28.2 mm SL the pelvic girdle, the lateral connecting bone, the nuchal plate, and the neurocranium are totally ossified. The plates on the head are represented by scarce odontodes and the lateral series of plates are almost entirely formed from the posterior region to level of the dorsal fin. Three small lateral abdominal plates are forming laterally on the abdomen, with one or few odontodes each.

Distribution and habitat. Upper río Juramento basin, río Salado drainage in Salta (Argentina), upper río Bermejo in northwestern Argentina and southern Bolivia, and upper río Pilcomayo in southern Bolivia (Fig. 9). Its presence in the río Pilcomayo is herein reported for the first time. *Ixinandria steinbachi* was caught in fast flowing waters between 15 and 65 cm depth, especially in places with filamentous algae, in mountainous areas at altitudes ranging from around 200 to 2900 meters a.s.l.. The minimum altitude where it was recorded is 210 m a.s.l. in the río Rosario, 48 km from the city of Salta. This



Fig. 8. Living specimen of *Ixinandria steinbachi* from the río Arenales near Salta, Argentina, November 2007. Photo by CAC.

species lives in fast flowing and highly oxygenated waters, with stony bottom, usually hiding under the stones during the day. Under 2200 m a.s.l. one species of *Hypostomus*, *Heptapterus mustelinus*, and some characids and other loricarids were found occurring syntopically with *I. steinbachi* (Menni, 2004).

Discussion

The principal components analysis of morphometric traits failed to discriminate clusters among the four populations of *Ixinandria* being investigated, indicating that morphology is highly homogeneous and suggesting no species-level separation. However, small morphological differences were found between specimens of populations from the río Bermejo in southern Bolivia and the río Bermejo in Argentina (Baritú National Park) when compared to specimens from other tributaries to the río Bermejo and río Juramento basins in Argentina. These

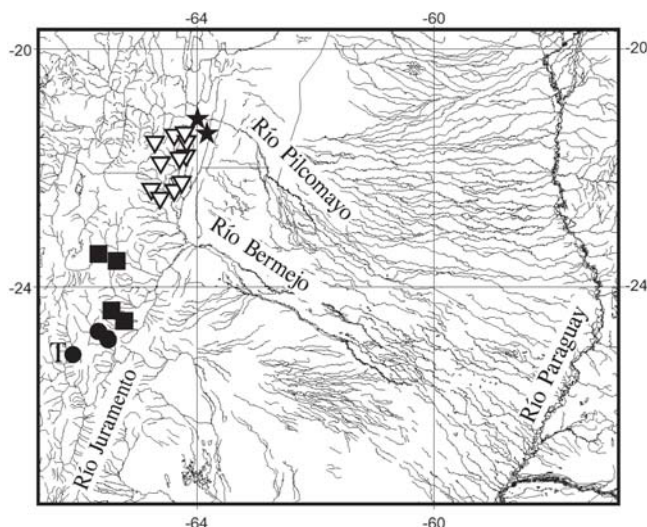


Fig. 9. Distribution of *Ixinandria steinbachi*. Dot, río Juramento basin; Square, southern upper río Bermejo drainage; triangle, northern upper río Bermejo basin; and Star, río Pilcomayo. Each symbol can represent more than one lote or locality. (T=Type locality).

small differences are degree of development of odontodes along the sides of the head in mature males, width of the pectoral-fin spine, and size of the naked skin area at the tip of the snout. These differences, however, are difficult to interpret and mostly overlap when many specimens are analysed, and are not enough to warrant species level separation.

The molecular analysis was similarly not able to discriminate the population from the upper río Juramento basin, type locality of *Ixinandria steinbachi*, from that in the the upper río Bermejo in Salta, Argentina. A significant difference, however, was found between the population in the río Bermejo in Salta and that in the tributaries to the same river in Tarija, Bolivia, type locality of *Ixinandria montebelloi*. This difference, however, is smaller than those usually found among species clearly distinct and is not enough to warrant separate species recognition. The mean K2P distance between our sequences was 1.1%, which falls within the typical range of intraspecific K2P distance in COI sequences of up to 2%, much smaller than the average distance of 9.9% of distinct, congeneric species (Ward *et al.*, 2005).

An explanation for the differences found could be that the samples represent three separate populations of the same species, what corroborates the morphologic results. The differences between the populations from the río Bermejo in Salta and in Tarija could be explained by the geographic distance (>350 km) between the two sample localities. To test this hypothesis, samples from areas between the present collection stations and from the río Pilcomayo basin would be necessary. In summary, the results of the molecular analysis do not adequately support the discrimination of the populations and therefore the separation of the two species.

Both morphometric and molecular results make sense from the geological point of view. Andean orogeny and climate have had profound influence on the biota of the Central Cor-

dillera in northeastern Argentina and southern Bolivia. The geological and climatic development during the late Tertiary and early Quaternary have had a significant impact on the establishment of orographic barriers and the regulation and distribution of rain in this region and, as a consequence, on the establishment and continuous changing of hydrographic drainages (Alonso *et al.*, 2006).

The presence of a single species of *Ixinandria* in the three river drainage basins can be explained by the fact that the Pilcomayo, Bermejo, and Juramento rivers had been connected and separated several times during the Quaternary, as indicated by the superposition of their alluvial fans (Iriando, 1993). One example of documented river capture is the río La Caldera, presently a tributary to the río Bermejo basin that formerly used to cross the area where today the city of Salta is located draining towards the south and emptying into the río Arenales, itself a tributary to the río Juramento (Monasterio de Gonzo, 2003). Because of early Quaternary tectonism the río La Caldera changed its direction and become a tributary to the río Mojotoro, in the upper río Bermejo basin. A considerable similarity in the catfish fauna between the río Juramento and the río Bermejo drainage basins was reported by Monasterio de Gonzo *et al.* (1994). The geographic distribution of *Ixinandria steinbachi*, encompassing the upper portions of the Pilcomayo, Bermejo, and Juramento rivers, is very similar to the distributions of *Parodon carrikeri*, *Oligosarcus bolivianus*, *Corydoras micracanthus*, *Loricaria tucumanensis* (Liotta, 2006), and *Jenynsia alternimaculata* (Ghedotti, 1998).

The only citation of *Ixinandria steinbachi* for a river outside the known range of the species is that of Gomes (1947), who listed a species of *Rineloricaria* from the río Maquiné in northeastern Rio Grande do Sul State, southern Brazil, as *Loricaria (Rineloricaria) steinbachi*, based on 18 young specimens deposited at the UMMZ. That species was later found to be new and described as *Rineloricaria aequalicuspis* by Reis & Cardoso (2001).

The diagnosis of *Ixinandria* is based on a completely naked abdomen, which has no abdominal plates ventral to the lateral abdominal plates. Only one specimen out of 242 examined in this study, from the río Juramento basin (MCNI 1225), has small platelets on the central portion of the abdomen. Even in this specimen, a preanal plate is lacking. The validity of the genus *Ixinandria* is a question beyond the scope of this study, and will remain unanswered until a broad phylogenetic analysis of the loricariines can be performed.

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Material examined. *Ixinandria steinbachi*. **Argentina: Salta: río Juramento basin:** BMNH 1906.5.31.37 (84.5 mm SL), lectotype, Departamento Cachi, elevation 2,500m a.s.l. (25°06'15"S 66°11'16"W). BMNH 1906.5.31.38-39 (2, 58.2-66.4 mm SL), paralectotypes, same data as lectotype. MCNI 99, 10+2 c&s, 56.2-91.6 mm SL (9, 71.7-91.6 mm SL), río Calchaqui, Departamento Cachi (25°07'30"S 66°09'57"W). MCNI 419, (4, 69.1-76.6 mm SL), río Arenales at field station 2, Departamento Capital (24°48'34"S 65°25'18"W). MCNI 854, 4, 75.2-85.0 mm SL, río Calchaqui, Departamento Cachi (25°07'42"S 66°09'46"W). MCNI 1225, 2, 75.6-77.3 mm SL, río Arenales, Departamento Capital, elevation 1219 m a.s.l., (24°47'43.9"S 65°28'2.5"W). MCP 41303, 27+5 c&s, 33.9-69.9 mm SL, río Arenales, Departamento Capital (approx. 24°46'S 65°28'W). **Argentina: Salta: río Bermejo basin:** MCNI 186, 1, 68.2 mm, río Mojotoro, Departamento La Caldera (approx. 24°41'S 65°17'W). MCNI 198, 6, 61.4-91.5 mm SL (2, 74.8-87.4 mm SL), El Gallinacito, Departamento La Caldera (25°41'00.9"S 65°18'48.7"W). MCNI 220, 3, 58.7-73.5 mm SL (2, 59.5-74.3 mm SL), río La Caldera, Departamento La Caldera (approx. 24°41'S 65°17'W). MCNI 331 (2 c&s, 56.4-60.6 mm SL), río Mojotoro, Departamento La Caldera (24°42'21"S 65°15'16"W). MCNI 415, (1, 76.4 mm SL) and MCP 41918, 6, 39.5- 89.4 mm SL (2, 69.3-89.4 mm SL), río La Caldera, Departamento La Caldera (24°36'22"S 65°22'39"W). MCNI 519, 12, 58.8-74.0 mm SL, río La Caldera, Departamento La Caldera (approx. 24°37'S 65°23'W). MCNI 585 (4, 73.8-112.8 mm SL), río Castellanos, Departamento Capital (24°41'58"S 65°28'45"W). MCNI 1122, 5, 65.3-78.9 mm SL, río Baritú, Departamento Santa Victoria (22°30'11"S 64°45'30"W). MCNI 1130, 2, 89.1-100.7 mm SL, arroyo Vallecito, Departamento Santa Victoria (22°20'00"S 64°45'21"W). **Argentina: Jujuy: río Bermejo basin:** ILPLA 1677, 4, 40.2-85.8 mm SL (2, 78.1-85.8 mm SL) creek tributary to río Grande near Tilcara (approx. 23°34'S 65°22'W). ILPLA 1678, (2, 71.7-86.8 mm SL), río Grande north of Tilcara (approx. 23°25'S 65°44'W). MACN-Ict 3157, 9, 26.6-94.5 mm SL, río Grande. **Bolivia: Tarija Province: río Bermejo basin:** ANSP 68832, 1, 72.9 mm SL, holotype of *Canthopomus montebelloi* (not measured for morphometric comparisons because of bad state of preservation), Monte Bello, río Bermejo. UMSS 210, 4, 27.6-68.8 mm SL, río Salinas, O'Connor (21°38'42"S 64°9'8"W). UMSS 211, 12, 24.8-69.8 mm SL (1, 69.7 mm SL), río Say Kan, O'Connor (21°46'27"S 64°5'24"W). UMSS 214, 41 + 1 c&s, 35.3-89.4 mm SL (14, 68.9-89.4 mm SL), río Emborozú (21°56'08"S 64°41'21"W). UMSS 215, 22 + 6 c&s. 16.8-100.5 mm SL (10, 82.1-100.3 mm SL), río Orosas, Aniceto Arce (21°56'8"S 64°41'21"W). UMSS 216, 7, 46.2-77.3 mm SL (2, 76.1-76.7 mm

SL), río Cuesta Vieja, O'Connor (21°25'17"S 64°16'39"W). USNM 314303, 1, 44.9 mm SL, río Salinas, 3 km S of Entre Rios (approx. 21°33'S 64°10'W). USNM 314300, 17, 35.4-94.3 mm SL (5, 72.5-94.3 mm SL), río Guadalquivir, tributary to río Tarija ca. 5 km NW Tarija (approx. 21°30'S 64°46'W). CBF 6069, 2, 70.6-73.7 mm SL (1, 73.7 mm SL), río La Planchada, tributary to río Conchas, Tariquia, Arce (22°17'15"S 64°23'30"W). CBF 6071, 2, 42.9-69.7 mm SL, río Conchas, Tariquia, Arce (approx. 22°22'S 64°24'W). CBF 6100, 6, 34.6-92.1 mm SL (2, 69.0-92.1 mm SL), arroyo La Misión, Tariquia, Arce (approx. 21°48'S 64°17'W). CBF 6106, 2, 62.0-71.6 mm SL, creek near Arémbolo, Tariquia Arce (21°49'49"S 64°14'59"W). CBF 6137 (2, 73.2-73.6 mm SL), arroyo Barrial, tributary to río Chuquisaca, Entre Rios, O'Connor (21°53'30"S 64°8'15"W). **Bolivia: Tarija Province: río Pilcomayo basin:** UMSS 212 (1, 72.7 mm SL), río Serere, O'Connor (21°26'54"S 64°5'58"W). UMSS 213 (1, 76.6 mm SL), río Saladito, O'Connor (21°18'29"S 64°7'2"W).

Comparative material. *Crossoloricaria venezuelae*: UMMZ 141938, 6 paratypes, río Socuy, 3 km above mouth north of Maracaibo, Venezuela. *Dasylicaria capetensis*: FMNH 7582, holotype and USNM 78340, 1 paratype, río Capeti, Panamá. *Dasylicaria filamentosa*: FMNH 55114, 1 syntype, Calamar, Colombia; FMNH 55115, 7 syntypes and USNM 79219, 1 syntype, Boca de Certegui, Colombia. *Dasylicaria tuyrensis*: FMNH 7583, holotype, FMNH 29317-18, 2 paratypes and USNM 78341, 3 paratypes, río Tuyra, Boca de Cupe, Darien, Panama. *Dasylicaria seminuda*: FMNH 55116, 2 syntypes, Soplaviento, Colombia; FMNH 55113, syntype?, Colombia. *Fonchiichthys rupestris*: UMMZ 141939, 6 paratypes, río San Juan above bridge south of Mene Grande, Motatan System, Venezuela. *Harttia kronoi*: MCP 20148, 22 + 2 c&s, río Piedade on road from Rio Branco do Sul to Açungui ca. 26 km NNW of Rio Branco do Sul, río Ribeira drainage, Rio Branco do Sul, Paraná, Brazil (25°00'42"S 49°20'20"W). *Hemiloricaria altipinnis*: AMNH 8404, holotype, río Chico, Panama. *Hemiloricaria fallax*: ANSP 177288, 10, Essequibo River, extensive sandbar 2 km upstream from Paddle Rock campsite, Guyana (approx. 04°42'N 58°42'W); ANSP 175898, 3, clear water creek at campsite 3.1 miles from Kurupukari field station on Kurupukari-Suranama river road (approx. 04°38'N 58°42'W). *Hemiloricaria morrowi*: ANSP 68663, holotype, río Ucayali basin near Cantamana, Peru. *Hemiloricaria parva*: ANSP 53892, 1, Descalvados, Mato Grosso, Brazil. *Rineloricaria malabarbai*: MCP 9801, 1 paratype, arroio Fão, Lageado, Rio Grande do Sul, Brazil; MCP 9848, 1 paratype, río Pardinho, Santa Cruz do Sul, Rio Grande do Sul, Brazil. *Rineloricaria misionera*: MCP 35793, 3 paratypes, arroyo Liso, Cuña-Pirú valley, Departamento Cainguás, Misiones, Argentina. *Rineloricaria pareiacantha*: ANSP 67815, holotype, río Santa Lucia, Canelones, Uruguay. *Spatuloricaria caquetae*: ANSP 70527, 1 paratype, río Orteguausa, Florencia, Provincia Caqueta, Colombia. *Spatuloricaria evansii*: ANSP 180486, 1, río Yanatili near confluence with río Urubamba and town of Quello Uno, Cuzco, Peru (approx. 12°38'S 72°33'W). *Spatuloricaria fimbriata*: FMNH 55117, holotype and FMNH 55118, 1 paratype, Boca de Certegui, Colombia. *Spatuloricaria gymnogaster*: FMNH 55138, 29 paratypes, Colombia; UMMZ 141937, 15 paratypes, río Motatán, at bridge 22 km N of Motatán, Venezuela. *Spatuloricaria lagoichthys*: FMNH 42792, 5 and USNM 121097, 43 paratypes, río Socuy 3 km above mouth, río Maracaibo basin, Venezuela. *Spatuloricaria pujanensis*: FMNH 84109, 1, río San Alejandro, Peru; FMNH 84127, 2, río Sungaro Yacu, ca 2.75 hrs upstream junction of río Sungaro Yacu and río Pachitea, Peru.

Genbank and depository information for specimens included in the molecular analysis. *Ixinandria steinbachi*: **Argentina, río Juramento basin:** Juramento 1: MCNI 1222, 7, río Arenales, Departamento Capital (24°47'43.9"S 65°28'02.5"W, elevation 1185 m a.s.l.) (Genbank codes EU359426, EU559056, EU559057, EU559059, EU559060, EU559061, and EU559062). Juramento 2: MCNI 1382, 5, río Arenales, Departamento Capital (24°48'37"S 65°25'10.9"W, elevation 1185 m a.s.l.) (Genbank codes EU559055, EU559058, EU559063, EU559064, and EU559065). **Argentina, río Bermejo basin:** Bermejo 1.1: MCNI 1287, 7, río La Caldera (24°41'21.2"S 65°23'29.8"W, elevation 1252 m a.s.l.) (EU559066, EU359424, EU559067, EU559068, EU559069, EU559070, and EU559071). Bermejo 1.2: MCNI 1286, 4, arroyo Lesser (24°40'44.1"S 65°28'55.6"W) (Genbank codes EU559072, EU559073, EU559074, and EU559075). **Bolivia, río Bermejo basin:** Bermejo 2.1: UMSS GEN1707, 1, UMSS GEN1708, 1, UMSS GEN1709, 1, UMSS GEN1710, 1, and UMSS GEN1711, 1, río Gaudalquivir, tributary to río Tarija, San Lorenzo, Mendez Province (21°22'23.9"S 64°44'43.7"W) (Genbank codes EU559076, EU559077, EU559078, EU559079, and EU559080). Bermejo 2.2: UMSS GEN1712, 1, UMSS GEN1713, 1, UMSS GEN1714, 1, UMSS GEN1715, 1, and UMSS GEN1716, 1, río Camacho, tributary to río Tarija, Padcaya, Arce Province (21°42'22.0"S 64°38'51.6"W) (Genbank codes EU559081, EU359425, EU559082, EU559083, and EU559084).

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