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Description of a new species of glass knifefish genus *Eigenmannia* (Gymnotiformes: Sternopygidae) from the upper rio Paraná basin, based on anatomical, karyotypic, and molecular evidences

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A new species of *Eigenmannia* is described from the upper rio Paraná basin based on morphological and molecular data. It is distinguished for all congeners by a unique combination of morphometrics, meristics, osteological characters, a significant COI genetic divergence that ranges from 4.9 to 15.2%, and its karyotype. An osteological description for the new species is provided, the geographic distribution of *Eigenmannia* species in the upper rio Paraná basin is commented on, and the use of karyotype information in taxonomic studies is discussed.

Keywords: Biodiversity, Electric fish, Integrative taxonomy, Karyotype, Osteology.

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Uma espécie nova de *Eigenmannia* é descrita da bacia do alto rio Paraná, com base em dados morfológicos e moleculares. Distingue-se de todas as congêneres por uma combinação única de caracteres morfométricos, merísticos, osteológicos, uma significativa divergência genética que varia de 4,9 a 15,2%, e pelo seu cariótipo. Uma descrição osteológica para a nova espécie é fornecida, a distribuição geográfica das espécies de *Eigenmannia* na bacia do alto rio Paraná é comentada, e o uso da informação do cariótipo em estudos taxonômicos é discutido.

Palavras-chave: Biodiversidade, Cariótipo, Osteologia, Peixes elétricos, Taxonomia integrativa.

INTRODUCTION

Eigenmannia Jordan & Evermann, 1896, comprising the glass knifefishes, is the most species-rich genus of Sternopygidae, with 31 valid species (Fricke *et al*., 2023). They can be diagnosed from the other sternopygids by the optic nerve thicker than the olfactory nerve and by the presence of "epipleurals" at vertebrae 7–9 (Dutra *et al*., 2021). The species of *Eigenmannia* are small to medium-sized fishes (maximum 30 cm in length to the end of the anal fin), which can generate weak electric organ discharges (ranging from 100 Hz to 780 Hz) used for communication and food detection (Crampton, Albert, 2006). Glass knifefishes have an omnivorous diet, with a tendency to insectivore (Alves-Gomes, 1997; Giora *et al*., 2005). Due to their translucent appearance, these fishes are appreciated in the aquarium trade (Albert, 2003).

Eigenmannia species are distributed from the Río Tuíra in Panama to the Río La Plata basin in Argentina (Dutra *et al*., 2017; Ferraris *et al*., 2017), with its highest diversity being found in the Amazon basin, with ten valid species (Dagosta, de Pinna, 2019), followed by the Paraná-Paraguay basin with six species (Peixoto *et al*., 2015, 2020; Campos-da-Paz, Queiroz, 2017). This latter is formed by three main rivers, the rio Paraná, the rio Paraguay, and the rio Uruguay (Brea, Zucol, 2011). The rio Paraná, which is formed by the confluence of the rio Paranaíba and rio Grande, extends through the southern region of Brazil and Argentina (Brea, Zucol, 2011). In this basin, the upper rio Paraná region stands out, which includes the entire stretch upstream of the old Sete Quedas waterfall, currently flooded by the Itaipu reservoir (Graça, Pavanelli, 2007).

In the region of the upper rio Paraná basin, four *Eigenmannia* species have their occurrence historically recorded. *Eigenmannia trilineata* Lopez & Catello, 1966 and *E. virescens* (Valenciennes, 1836) were widely recorded for the South America, including upper rio Paraná (*e.g*., Castro *et al*., 2003; Langeani *et al*., 2007), however, Peixoto *et al*. (2015) restricted their distribution to lower rio Paraná and Río La Plata. In the same study, these authors described *E. guairaca* Peixoto, Dutra & Wosiacki, 2015 from a tributary of the rio Paranapanema. Later, Peixoto *et al*. (2020) described *E. dutrai* Peixoto, Pastana & Ballen, 2020 for the upper rio Paraná basin and ratified the absence of *E. trilineata* and *E. virescens* in the region.

Several studies have reported on the high diversity of karyotypes and a wide chromosomal system of sex in *Eigenmannia* species from the upper rio Paraná basin (Foresti *et al*., 1981; Almeida-Toledo *et al*., 1984, 1988, 1996, 2000, 2001, 2002; Moysés *et al*., 2005, 2010; Sene *et al*., 2014). The differences in karyotype, including sex chromosomes, may have contributed to species divergence, functioning as a reproductive isolation mechanism (Silva *et al*., 2015). On the other hand, molecular data of *Eigenmannia* in the rio Paraná basin provided by several authors (Pereira *et al*., 2011, 2013; Frantine-Silva *et al*., 2015; Díaz *et al*., 2016; Tagliacollo *et al*., 2016; Bagley *et al*., 2019; Janzen *et al*., 2022), have never been used to investigate the species diversity of the genus in the area.

During the investigation of *Eigenmannia* specimens from the upper rio Paraná basin, we detected the presence of an undescribed species for the area described here. Information on mitochondrial DNA and karyotype in the literature also supports describing the new species.

MATERIAL AND METHODS

Morphological analysis. All measurements were taken point-to-point to the nearest 0.1 mm with digital calipers under a stereomicroscope, preferably on the left side. Measurements and counts followed Peixoto *et al*. (2015). Measurements reported as a percentage of total length and length to end of anal-fin base are given only for specimens without damage or regeneration. In the description, frequencies are given in parentheses after each count and an asterisk indicates counts for the holotype. The nomenclature of stripes follows Peixoto *et al*. (2015) and Peixoto, Wosiacki (2016), as illustrated by Dutra *et al*. (2022, fig. 1).

Osteological data were obtained via specimens cleared and stained according to Taylor, Van Dyke (1985) or via microcomputed tomography (μCT scan). Utilized parameters for μCT scan follow Peixoto *et al*. (2019). Osteological terminology follows Weitzman (1962) with summarized modifications by Vari (1995) and Dutra *et al*. (2021). Precaudal vertebrae include four vertebrae of the Weberian complex plus all remaining vertebrae without fully developed hemal spines. Transitional vertebrae are post-Weberian precaudal vertebrae lacking both pleural ribs and hemal spines (Hopkins, 1991). Non-type specimens correspond to those not used in the description but provide complementary information on the distributional records of the new species.

Alignment and barcoding divergence. Twenty *Eigenmannia* sequences of cytochrome oxidase (COI) from Paraná basin available in Genbank (Tab. 1) were aligned in Geneious Prime 2022.0.1 using the MUSCLE algorithm (Edgar, 2004). To contextualize the results of the morphological species delimitation, we estimated barcoding divergence in Mega version 11.0.10 (Tamura *et al*., 2021) using the Kimura 2-parameter model (Kimura, 1980). To assure the accuracy of the molecular dataset, identification for available sequences in Genbank was checked via direct voucher examination or photographs available in BOLD System whenever possible.

Abbreviations. Institutional abbreviations follow Sabaj (2020, 2022). Abbreviations used in the text are CS = cleared and counterstained specimens, CT = x-ray microcomputed tomography scanned, HL = head length, and LEA = length to end of anal-fin base.

RESULTS

Eigenmannia catira, new species

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(Figs. 1–8; Tab. 2)

Eigenmannia trilineata (non López & Castello, 1966). —Pereira *et al*., 2013:16 (additional file, barcode, voucher LBP 4653). —Frantine-Silva *et al*., 2015:1232 (barcode, no voucher available).

Eigenmannia sp. —Sene *et al*., 2014:303 (karyotype, voucher LBP 12304).

Eigenmannia virescens (non Valenciennes, 1836). —Tagliacollo *et al*., 2016:26 (phylogenetic study, voucher LBP 9671).

FIGURE 1 | *Eigenmannia catira*, holotype, MZUSP 129263, 132.7 mm LEA, São Paulo, Córrego do Schmidt, a tributary of the rio Grande, upper rio Paraná basin. **A.** Left lateral view of the head; **B.** Left lateral view of the body.

Holotype. MZUSP 129263, 132.7 mm LEA, CT, córrego do Schmidt, tributary of rio Grande, upper rio Paraná basin, Santa Albertina, São Paulo, Brazil, 20°01'30"S 50°43'47"W, 30 Nov 2016, M. Cardoso Junior.

Paratypes. All from Brazil, upper rio Paraná basin. **Mato Grosso do Sul State:** LBP 2647 (6, 85.7–135.3 mm LEA), rio Baia, Bataiporã, 22°43'03.2"S 53°17'27.6"W, 5 Mar 2005, R. Teixeira, E. Martinez, G. França & L. Paiva. LBP 3103 (7, 75.4–115.3 mm LEA), rio Baia, Bataiporã, 22°43'19.4"S 53°17'11.3"W, 13 Oct 2005, R. Teixeira, G. França & L. Paiva. LBP 4653 (15+2CS, 78.4–85.3 mm LEA), rio Baia, Taquarussu, 22°43'46.2"S 53°19'04.2"W, 10 May 2007, R. Devidé, L. Paiva, E. Martinez & V. Cruz. LBP 9621 (4, 86.9–106.7 mm LEA), riacho de Engano, Angélica, 22°02'37.5"S 53°43'38.8"W, 19 Jun 2010, R. Devidé, M. Pazian, F. Roxo & G. Silva. LBP 9650 (27+3 CS, 53.6–97.5 mm LEA), rio Ivinhema, Angélica, 22°02'52.3"S 53°41'38.1"W, 20 Jun 2010, R. Devidé, M. Pazian, F. Roxo & G. Silva. LBP 9671 (3, 57.0–77.7 mm LEA), unamed stream, Ivinhema, 22°15'29.5"S 53°48'38.7"W, 20 Jun 2010, R. Devidé, M. Pazian, F. Roxo & G. Silva. LBP 9773 (12, 76.6–137.8 mm LEA), rio Papagaio, Nova Andradina, 21°53'48.1"S 53°47'25.1"W, 22 Jul 2010, R. Devidé, M. Pazian, F. Roxo & G. Silva. MZUSP 88455 (1, 126.4 mm LEA), córrego do Palmito below bridge of MS-262 road,

TABLE 1 | Data of 22 *Eigenmannia* COI sequences from rio Paraná basin available in Genbank utilized in this study. Institutional abbreviations follow Sabaj (2020, 2022).

ID	Voucher	Locality	Genbank	Reference
E. catira	LBP 4653	Rio Baía	GU701794.1	Pereira *et al.* (2013)
E. catira	LBP 4653	Rio Baía	GU701795.1	Pereira *et al.* (2013)
E. catira	LBP 4653	Rio Baía	GU701797.1	Pereira *et al.* (2013)
E. catira	LBP 4653	Rio Baía	GU701798.1	Pereira *et al.* (2013)
E. catira	LBP 4653	Rio Baía	GU701801.1	Pereira *et al.* (2013)
E. catira	–	Rio Paranapanema	KM897459.1	Frantine-Silva *et al.* (2015)
E. catira	LBP 9671	Ivinhema	KR491594.1	Tagliacollo *et al.* (2016)
E. dutrai	CIUnB 931	Córrego Serandi	MK464069.1	Bagley *et al.* (2019)
E. guairaca	LBP 2576	Rio Capivara	GU701791.1	Pereira *et al.* (2013)
E. guairaca	LBP 2576	Rio Capivara	GU701792.1	Pereira *et al.* (2013)
E. guairaca	LBP 2576	Rio Capivara	GU701793.1	Pereira *et al.* (2013)
E. guairaca	LBP 2576	Rio Capivara	GU701796.1	Pereira *et al.* (2013)
E. trilineata	MACN uncat.	Esteros del Riachuelo	ON303371.1	Janzen *et al.* (2022)
E. virescens	–	Rio Paraná	KU288845.1	Díaz *et al.* (2016)
E. virescens	–	Rio Paraná	KU288846.1	Díaz *et al.* (2016)
E. virescens	–	Rio Paraná	KU288847.1	Díaz *et al.* (2016)
E. virescens	–	Rio Paraná	KU288848.1	Díaz *et al.* (2016)
E. virescens	MAG ICT 182	Rio Paraná	KU288899.1	Díaz *et al.* (2016)
E. virescens	MAG ICT 183	Rio Paraná	KU288900.1	Díaz *et al.* (2016)
E. virescens	MAG ICT 184	Rio Paraná	KU288901.1	Díaz *et al.* (2016)
E. virescens	MAG ICT 185	Rio Paraná	KU288902.1	Díaz *et al.* (2016)

TABLE 2 | Morphometry of the examined specimens of *Eigenmannia catira*. N = number of samples analyzed, SD = standard deviation.

	Holotype	Range	N	Mean	SD
Total length (mm)	164.9	57.8–285.8	27	–	–
Length to end of anal fin (mm)	132.7	43.8–217.2	31	–	–
Head length (mm)	15.8	7.1–25.5	35	–	–
Caudal-filament length (mm)	39.6	12.6–84.4	27	–	–
Percents of length to end of anal fin					
Caudal-filament length	29.8	13.3–41.1	27	28.5	7.6
Body depth at pectoral fin	15.9	14.9–19.4	31	17.3	1.2
Body depth at anal fin	14.4	12.2–18.4	30	15.3	1.5
Body width	5.1	4.2–7.8	31	6.0	0.7
Pre-anal distance	15.0	13.8–19.9	30	16.8	1.4
Pre-pectoral distance	12.9	12.7–16.7	31	14.4	0.9
Anal-fin length	80.8	79.8–91.0	30	84.0	2.7
Pectoral-fin length	8.1	7.2–13.5	31	9.8	1.4
Snout to anus	6.9	5.4–15.0	30	9.2	2.1
Head length	11.9	11.7–16.2	31	13.1	0.9
Percents of head length					
Head width at opercle	54.6	53.3–73.0	35	58.2	4.3
Head width at orbits	44.9	41.8–58.4	35	47.9	4.0
Head depth at supraoccipital	80.5	74.3–90.0	35	83.8	3.7
Head depth at orbits	64.5	54.6–71.9	35	62.4	3.9
Snout length	29.1	27.3–33.6	35	29.9	1.5
Snout to posterior naris distance	20.8	18.8–25.9	35	22.2	1.9
Posterior naris to orbit distance	8.1	3.5–12.0	35	7.3	1.8
Postorbital distance	55.3	50.6–64.9	35	55.3	3.5
Opercular opening	26.2	22.6–40.9	34	29.8	3.8
Internarial width	15.1	12.0–21.5	35	17.0	2.2
Internasal distance	9.1	7.5–15.7	35	10.4	1.7
Interorbital distance	35.0	29.4–38.8	35	34.5	2.3
Orbital diameter	20.3	14.5–24.5	35	19.8	2.3
Maxilla length	23.4	14.4–25.2	35	19.4	2.7
Oral width	19.7	15.5–22.7	35	19.3	1.8
Percents of caudal-filament length					
Caudal-filament width	1.1	0.7–8.2	21	1.8	1.8
Caudal-filament depth	7.2	4.1–16.5	21	7.9	2.7

near Fazenda Santa Ângela, Três Lagoas, 20°49'57.67"S 51°47'55.20"W, 24 Sep 2003, O. Oyakawa, J. Birindelli & C. Kikuchi. **Paraná State:** NUP 12450 (7, 63.0–80.9 mm LEA), Ressaco do Bilé at Ilha Mutum, Porto Rico, 22°45'13"S 53°17'09"W, 8 Oct 2011, F. Souza. **São Paulo State:** LBP 12304 (1, 123.2 mm LEA), rio Hortelã, Botucatu, 22°55'23.2"S 48°32'40.4"W, 27 Jan 2011, R. Devidé, J. Alves & R. Utsonomia. MZUSP 83398 (3, 168.4–217.2 mm LEA), rio Tietê below UHW Bariri, Bariri, 22°08'50"S 48°45'06"W, 3 Nov 2003, A. Akama. MZUSP 102856 (1, 136.5 mm LEA), rio do Peixe, Ribeirão dos Índios, 21°41'59"S 51°31'32"W, 14 Oct 2008, P. Hollanda-Carvalho & R. Caires. MZUSP 121047 (20+3CS, 86.1–103.2 mm LEA), collected with the holotype.

Non-types. All from Brazil, upper rio Paraná basin. **Mato Grosso do Sul State:** INPA 35360 (1, 109.6 mm LEA), córrego Piravevê, tributary of rio Ivinhema, Angélica, 22°13'59"S 53°47'02"W, 17 Dec 2010, M. Rocha & T. Carvalho. LBP 9664 (1, 47.2 mm LEA), unnamed stream, Angélica, 22°13'59.9"S 53°47'02.6"W, 20 Jun 2010, R. Devidé, M. Pazian, F. Roxo & G. Silva. MCP 45909 (2, 64.0–87.6 mm LEA), rio Guiraí, Novo Horizonte do Sul, 22°38'23.9"S 54°00'25.3"W, 16 Dec 2010, M. Rocha. MCP 45940 (2, 87.4–98.1 mm LEA), rio Guiraí, Novo Horizonte do Sul, 22°40'22"S 53°51'39"W, 16 Dec 2010, M. Rocha. MZUEL 13379 (1, 102.5 mm LEA), rio Verde, Brasilândia, 21°02'14"S 52°08'46"W, 19 Jan 2011, P. da Silva. MZUEL 14488 (43, 26.1–126.6 mm LEA), córrego Piraveve, tributary of rio Ivinhema, Angélica, 22°14'19.3"S 54°04'08.8"W, 13 Jan 2016, M. Rocha, J. Birindelli, F. Jerep, E. Santana, Y. Suarez & F. Ferreira. NUP 3201 (4, 70.5–138.0 mm LEA), lagoa do Guaraná, Taquarussu, 22°43'S 53°19'W, 20 Sep 2003, H. Júlio Jr. NUP 10713 (3, 29.3–142.7 mm LEA), lagoa Ventura, Taquarussu, 22°51'24"S 53°36'01"W, 18 Nov 2004, NUPELIA team. NUP 12674 (8, 99.2–159.3 mm LEA), lagoa Finado Raimundo, tributary of rio Ivinhema, Taquarussu, 22°47'57"S 53°32'29"W, 18 Nov 2004, NUPELIA team. NUP 12687 (7, 94.7–121.8 mm LEA), lagoa dos Patos, tributary of rio Ivinhema, Taquarussu, 22°49'33"S 53°33'09"W, 16 Nov 2006, NUPELIA team. NUP 12702 (1, 143.1–170.1 mm LEA), lagoa Finado Raimundo, tributary of rio Ivinhema, Taquarussu, 22°47'57"S 53°32'29"W, 17 Dec 2007, NUPELIA team. NUP 12713 (2, 115.5–110.5 mm LEA), NUP 12736 (1, 116.3 mm LEA), lagoa dos Patos, tributary of rio Ivinhema, Taquarussu, 22°49'33"S 53°33'09"W, 17 Dec 2007, NUPELIA team. NUP 12723 (23, 67.6–104.4 mm LEA), lagoa dos Patos, tributary of rio Ivinhema, Taquarussu, 22°49'33"S 53°33'09"W, 20 Jun 2005, NUPELIA team. NUP 12724 (1, 93.8 mm LEA), NUP 12751 (3, 67.3–74.7 mm LEA), lagoa dos Patos, tributary of rio Ivinhema, Taquarussu, 22°49'33"S 53°33'09"W, 23 Aug 2005, NUPELIA team. NUP 12735 (3, 82.1–100.5 mm LEA), lagoa dos Patos, tributary of rio Ivinhema, Taquarussu, 22°49'33"S 53°33'09"W, 16 Nov 2006, NUPELIA team. NUP 12760 (1, 88.0 mm LEA), lagoa dos Patos, tributary of rio Ivinhema, Taquarussu, 22°49'33"S 53°33'09"W, 13 Feb 2008, NUPELIA team. NUP 12767 (2, 70.9–82.9 mm LEA), lagoa Finado Raimundo, tributary of rio Ivinhema, Taquarussu, 22°47'57"S 53°32'29"W, 26 Jul 2005, NUPELIA team. **Minas Gerais State:** NUP 14027 (2, 129.6–134.0 mm LEA), rio Paranaíba, Tupaciguara, 18°21'21"S 48°40'52"W, 16 Jul 1974, J. Silva, I. Rocinski & D. Marzulo. **Paraná State:** NUP 362 (1, 110.5 mm LEA), ribeirão São Pedro, São Pedro do Paraná, 22°45'S 53°15'W, Mar 1991, C. Pavanelli *et al.* NUP 7876 (2, 91.3–85.3 mm LEA), rio Paracaí, São Jorge do Patrocínio, 23°39'01"S 53°56'36"W, 14 Jul 2009, NUPELIA team. NUP 7878 (1, 140.8 mm LEA), rio Paracaí, São Jorge do Patrocínio, 23°39’24”S 53°54’23”W, 13 Jul 2009, NUPELIA team. NUP 7913 (2, 112.5–138.1 mm LEA), rio Paracaí, São Jorge do Patrocínio, 23°39’30”S 53°55’10”W, 13 Jul 2009, NUPELIA team. NUP 7918 (2, 103.4–117.8 mm LEA), rio Paracaí, São Jorge do Patrocínio, 23°39’30”S 53°55’10”W, 13 Jul 2009, NUPELIA team. NUP 7939 (3, 91.4–90.8 mm LEA), rio Paracaí, São Jorge do Patrocínio, 23°39’01”S 53°56’36”W, 14 Jul 2009, NUPELIA team. NUP 14371 (7, 110.8–124.3 mm LEA), Ressaco do Leopoldo, Porto Rico, 22°45’24”S 53°16’08”W, 5 Dec 2004, H. Júlio Jr. **São Paulo State:** MZUSP 24563 (1, 90.8 mm LEA), fazenda Edgardia, Botucatu, 22°53’S 48°27’W, 27 Sep 1974, F. C. M. B. Botucatu.

Diagnosis. *Eigenmannia catira*, a member of the *E. trilineata* species-group (*sensu* Dutra *et al*., 2021), differs from *E. macrops* and the *E. humboldtii* species-group by the presence of lateral line stripe (*vs*. absence). The new species is further distinguished from *E. macrops* by the eye diameter corresponding to 14.5–24.5% HL (*vs.* 26.4–29.7% HL), and the caudal filament corresponding to 13.3–41.9% LEA (*vs*. 67.5–79.3% LEA). It can be further distinguished from the *E. humboldtii* species-group by the anal fin hyaline (*vs.* anal-fin margin distinctly darkened).

Eigenmannia catira differs from all other species of the *E. trilineata* species-group, except *E. antonioi* Peixoto, Dutra & Wosiacki, 2015, *E. cacuria* Dutra, Ramos & Menezes, 2022, *E. desantanai* Peixoto, Dutra & Wosiacki, 2015, *E. guairaca*, *E. lorenata* Waltz & Albert, 2018, *E. magoi* Herrera-Collazos, Galindo-Cuervo, Maldonado-Ocampo & Rincón-Sandoval, 2020, *E. matintapereira* Peixoto, Dutra & Wosiacki, 2015, *E. microstoma* (Reinhardt, 1852), *E. muirapinima* Peixoto, Dutra & Wosiacki, 2015, *E. pavulagem* Peixoto, Dutra & Wosiacki, 2015, *E. sayona* Peixoto & Waltz, 2017, *E. trilineata*, and *E. zenuensis* Herrera-Collazos, Galindo-Cuervo, Maldonado-Ocampo & Rincón-Sandoval, 2020, by having a terminal mouth (*vs*. subterminal). The new species differs from the aforementioned species by the following combination of characters: (1) lateral line stripe extending from first perforated lateral line scale to distal portion of caudal filament (*vs*. lateral line stripe restricted to last two thirds of body in *E. cacuria*); (2) superior midlateral stripe absent (*vs*. present in *E. antonioi*, *E. cacuria*, *E. desantanai*, *E. guairaca*, *E. lorenata*, *E. magoi*, *E. microstoma*, *E. muirapinima*, *E. pavulagem*, *E. sayona*, *E. trilineata*, and *E. zenuensis*); (3) ii,12–14 pectoral-fin rays (*vs*. ii,16–17 in *E. matintapereira*); (4) 174–209 anal-fin rays (*vs*. 151–170 in *E. guairaca*, and 216–222 in *E. matintapereira*); (4) 13–22 premaxillary teeth (*vs*. 8–12 in *E. antonioi*, 24–25 in *E. desantanai*, 9–10 in *E. guairaca*, 32 in *E. magoi*, 8–10 in *E. muirapinima*, 31–33 in *E. trilineata*, and 31–34 in *E. zenuensis*); (6) 10–19 dentary teeth (*vs*. 21–23 in *E. desantanai*, 35–39 in *E. magoi*, 25–27 in *E. matintapereira*, 23 in *E. trilineata*, and 56–60 in *E. zenuensis*); (7) 7–12 endopterygoid teeth (*vs*. 14–15 in *E. desantanai*, and 16–17 in *E. trilineata*); (8) all dentary teeth similar in size (*vs*. dentary teeth increasing in size along dentigerous surface in *E. antonioi*, *E. cacuria*, *E. loretana*, *E. muirapinima*, *E. pavulagem*, and *E. sayona*); (9) basibranchial 1 unossified (*vs*. ossified in *E. sayona*); and (10) 13–14 precaudal vertebrae (*vs*. 15 in *E. guairaca*). *Eigenmannia catira* can also be diagnosed from *E. dutrai* and *E. guairaca* by having 2n = 36 (*vs*. 2n = 38 or 2n = 38, XY in *E. dutrai*, and 2n = 28 or 2n = $31/32\text{–}X_1X_1X_2X_2\text{-}X_1X_2Y$ in *E. guairaca* – data from Sene *et al*., 2014: tab. 1, see discussion).

Barcoding divergence. The overall mean distance among *Eigenmannia* species from Paraná basin was 10.1%. The lowest genetic distance between *E. catira* and any other *Eigenmannia* species from rio Paraná was 4.9% (from *E. dutrai* and *E. virescens*), followed by 13.9% from *E. guairaca*, and 15.2% from *E. trilineata* (Tab. 3).

Description. Body shape and pigmentation are shown in Fig. 1, and the morphometric data in Tab. 2. Largest examined specimen 222.2 mm LEA. Body elongate and distinctly compressed laterally. Greatest body depth at vertical through distal tip of pectoral fin. Dorsal profile of body slightly convex from snout tip to vertical through anal-fin terminus. Ventral profile of body slightly convex from mandibular symphysis to end of anal fin. Caudal filament short.

Head laterally compressed, greatest width at opercular region, greatest depth at nape. Dorsal profile of head convex from snout tip to nape. Ventral profile of head slightly convex from tip of lower jaw to isthmus. Snout rounded in lateral view. Mouth terminal. Mouth rictus at vertical through a point between anterior and posterior nares or vertical through posterior nostril. Anterior nostril tube-like, closer to snout tip than to anterior margin of eye. Posterior nostril round, closer to anterior margin of eye than to snout tip. At horizontal line, posterior nostril at horizontal through dorsal margin of eye or slightly above. Eye small, circular, completely covered by skin, on anterior one-half of HL, laterally oriented. Branchial membranes joined at isthmus. Anus adjacent to urogenital papilla, shifting ontogenetically from vertical through posterior to anterior margin of opercle. Urogenital papilla not developed in specimens under 103.2 mm LEA.

Scales cycloid and small, extending from posterior most part of head to vertical through tip of caudal filament, present on mid-dorsal region of body. Scales above lateral line at vertical through end of pectoral fin 9(1), 10*(4), 11(2), 12(5), or 13(5). Anterior most perforated lateral-line scale along vertical through pectoral-fin origin. Lateral-line scales to vertical through base of last anal-fin ray 107–136(n = 25; 113*). Pectoral-fin rays ii,12(5), ii,13*(11), ii,14(9), or ii,15(1). Distal pectoral-fin margin straight. Total anal-fin rays 174–209(n = 20; 179*). Anal-fin origin along vertical through pectoral-fin insertion or slightly posterior. Distal margin of anal fin slightly convex. First unbranched rays tiny, subsequent rays progressively increasing in size toward first branched rays. Branched rays of nearly equal length except for posterior most rays that progressively decrease in length.

TABLE 3 | Average barcoding divergence (%) among species of the *Eigenmannia* in rio Paraná basin based on the Kimura two-parameters model using COI data matrix. Values in bold refer to intraspecific distance within each species. Values above the diagonal refer to standard deviation.

	E. catira	*E. dutrai*	*E. guairaca*	*E. trilineata*	*E. virescens*
E. catira	**0.011**	0.007	0.006	0.007	0.007
E. dutrai	0.049	–	0.127	–	0.003
E. guairaca	0.139	0.127	–	0.002	0.002
E. trilineata	0.152	0.145	0.050	–	0.003
E. virescens	0.049	0.030	0.127	0.145	**0.005**

Coloration in alcohol. Body ground coloration cream. Body with two layers of chromatophores. Outer layer covered by dark chromatophores gradually more spaced ventrally. Chromatophores more concentrated on perforated scales forming lateral line stripe. Lateral line stripe tapering from first perforated scale until end of caudal filament. Superior midlateral stripe absent. Inner layer of pigmentation formed by multiple, small bars of dark chromatophores situated between the musculature associated with anal-fin pterygiophores. Dark individual bars in combination forming two stripe-like patterns. Inferior midlateral stripe inconspicuous, tapering from vertical through tip of pectoral-fin when adpressed on body to last anal-fin pterygiophore. Anal-fin base stripe conspicuous approximately one third as depth as orbital diameter, tapering from vertical through tip of pectoral-fin when adpressed on body to last anal-fin pterygiophore. Head covered by dark chromatophores, more concentrated on dorsal region gradually more spaced ventrally. Pectoral and anal fins hyaline with scattered dark chromatophores overlying fin rays.

Jaws. Premaxilla somewhat retangular-shaped, relative length of premaxilla twice as long as its width. Anterolateral process on premaxilla about one third of anterior margin of bone. Premaxilla with 13(1), 14(1), 17*(2), 18(1), 20(2), 21(1), or 22(2) villiform teeth arranged in two (2), or three*(7) rows. Teeth firmly, but not fully ankilosed, attached to ventral surface of premaxilla. Maxilla edentulous, slender, and slightly curved posteriorly. Descending blade of maxilla narrower than its dorsal most portion. Anterior hook-like process on maxilla present. Cartilaginous autopalatine connecting posterior cartilage of maxilla to endopterygoid.

Dentary as long as lower jaw depth, with 10(2), 12(1), 15(1), 16(2), 17(2), or 19*(2) villiform teeth arranged in one (3), or two*(6) rows. All teeth similar in size along dentigerous surface, which extends beyond anterior limit of Meckel's cartilage. Coronoid process ossified, ventrally curved in its posterior end. Meckel's cartilage rectangular shaped, its anterior portion approximately as wide as posterior portion. Coronomeckelian bone 20% of length of Meckel's cartilage. Angulo-articular with a narrow crest on posterolateral surface. Retroarticular small, roughly rectangular, located at posteroventral margin of anguloarticular. Retroarticular not included in socket that receives condyle of quadrate (Figs. 2–3).

Suspensorium and opercular apparatus. Endopterygoid roughly triangular with well-developed dorsally directed process, half as long as its length, attached to anterior portion of orbitosphenoid. Relative length of anterior portion of endopterygoid, as long as its depth. Ventral surface of endopterygoid with small, pointed, conical teeth on arranged in one (6), or two (2) rows at anterior portion. Endopterygoid teeth seven (3), eight (1), nine*(4), 11(1) or 12(2). Quadrate roughly trapezoidal in shape, with a posteroventral process that articulates with preopercle and symplectic; its condyle extending anteroventrally from base and articulating with anguloarticular (Fig. 3). Metapterygoid slightly trapezoidal, relative length of metapterygoid as long as its largest depth. Symplectic elongate and triangular, located in a medial crest of preopercle and posteroventral portion of quadrate. Relative length of symplectic two thirds as long as hyomandibula. Hyomandibula at roughly 90° to horizontal line through long axis of head. Neurocranial articulatory head roughly three times wider than ventral margin.

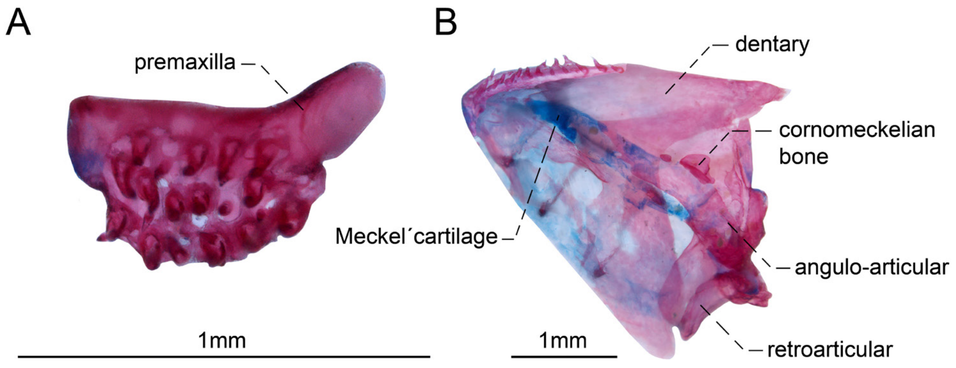

FIGURE 2 | Jaws of *Eigenmannia catira*, paratype, MZUSP 121047. **A.** Premaxilla, right side, ventral view, anterior on top; **B.** Lower jaw, inverted image, left side, medial view, anterior on left.

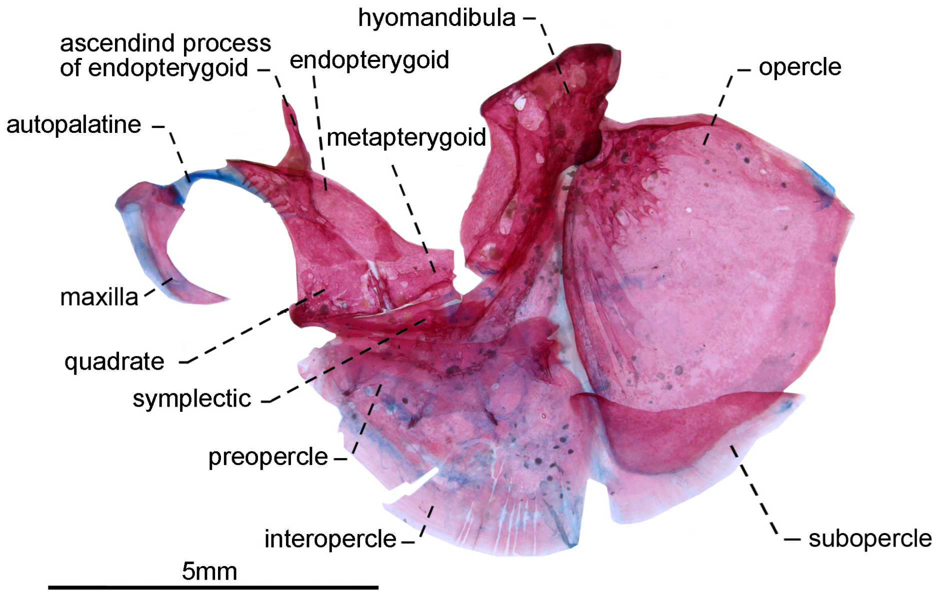

FIGURE 3 | Maxilla, suspensorium and opercular series of *Eigenmannia catira*, paratype, MZUSP 121047, inverted image, left side, medial view, anterior on left.

Laminar anterior shelf from widest hyomandibula point to anteroventral margin. Main axis of hyomandibula forming an angle of nearly 40° in relation to its dorsal margin. Condyle that receives the opercular distinct from main body of hyomandibula and directed posteroventrally. Posterodorsal portion of hyomandibula extending posteriorly to condyle that receives opercular socket. Posterodorsal margin of hyomandibula with a large foramen in which recurrent ramus of the anteroventral part of the anterior lateral line nerve passes before extending to body.

Preopercle crescent-shaped with five bony arches corresponding to laterosensory canal along its lateral surface. Interopercle fan-shaped, with posterodorsal expansion and margins rounded. Opercle roughly triangular, dorsal margin convex, with a pointed anterodorsal process. Subopercle sickle-shaped, tapering posterodorsally, forming concave dorsal profile. Subopercle and interopercle becoming membranous distally.

Cephalic lateral line system. Canals of nasal, antorbital and infraorbitals 1+2 to 4 enlarged and half-pipe shaped. Infraorbitals 1+2 with three bony arches. Depth of posterodorsal laminar expansion of infraorbitals 1+2 half as long as its length. Infraorbitals 3 and 4 closely associated. Fifth and sixth infraorbitals slender and tubular. Mandibular canal and preopercular canals enlarged and half-pipe shaped. Mandibular canal with three poorly ossified bony arches fused along lateroventral surface of dentary. Preopercular with four ossified bony arches. Supraorbital canal robust, forming a highly ossified shelf-like structure fused to frontal bone. Connection between infraorbital and supraorbital canal on sphenotic process. Otic and extrascapular canals slender and tubular shaped. Extrascapular slender and tubular located on joint of parietal, pterotic and epioccipital (Figs. 4–5).

Hyoid arch. Head of urohyal is anteriorly expanded with two short anterolateral arms each articulating with hypohyal dorsal. Body of urohyal with two contralateral ridges conferring a diamond shape. Free urohyal blade somewhat as long as urohyal body. Dorsal hipohyal somewhat rounded in shape not visible in lateral view. Ventral hipohyal somewhat triangular in shape with socket that contacts urohyal. Anterior ceratohyal rectangular. Posterior ceratohyal triangular, its relative length as long as ventral hypohyal. Branchiostegal rays five (5). First and second branchiostegal thin. Third to fifth branchiostegal spatulated. First to fourth branchiostegal rays attached to anterior ceratohyal. Fifth branchiostegal ray attached to posterior ceratohyal (Fig. 6).

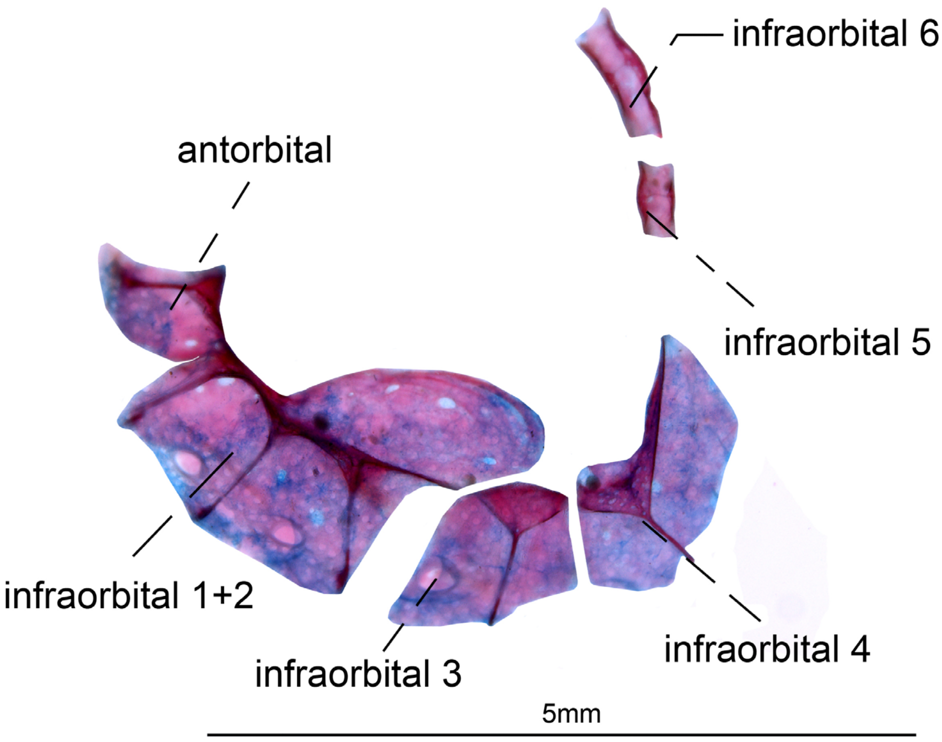

FIGURE 4 | Infraorbitals of *Eigenmannia catira*, paratype, MZUSP 121047, left side, lateral view, anterior on left.

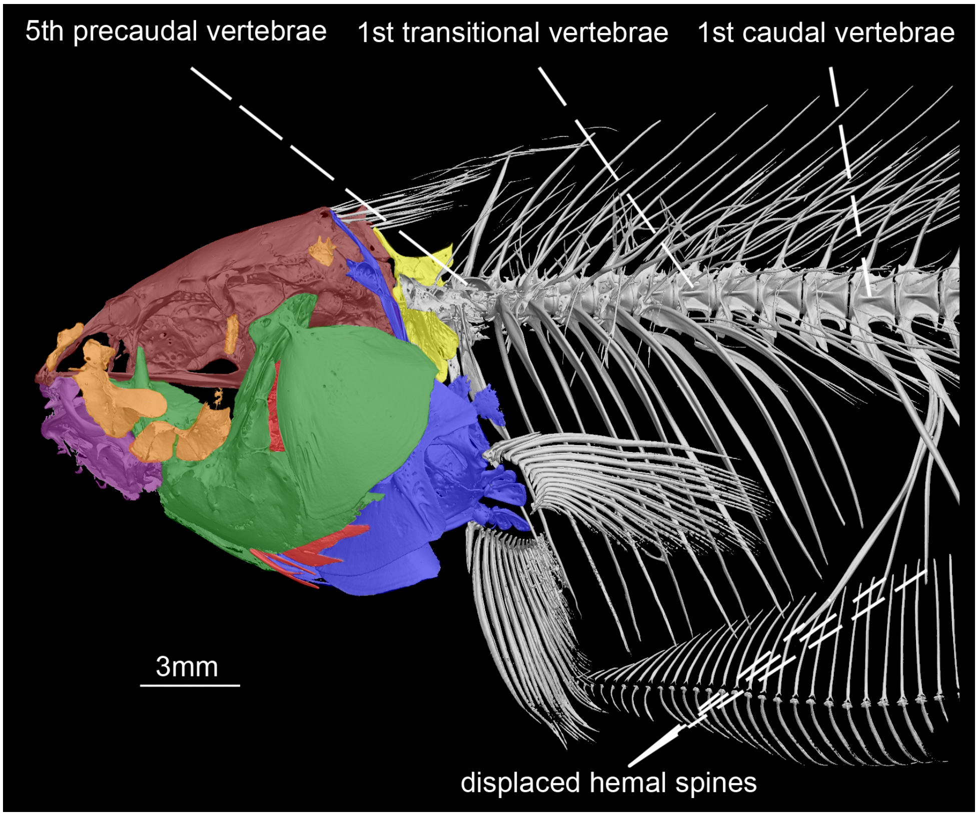

FIGURE 5 | Microcomputed tomography of head and body cavity of *Eigenmannia catira*, MZUSP 129263, holotype, left side, lateral view, anterior on left. Colors represent major subdivisions of bone complexes: jaws (purple), nasal, infrorbitals and extraexcapular (orange), suspensorium and opercular series (green), branchial and hyoid arches (red); neurocranium (garnet), Weberian apparatus (yellow), and pectoral girdle (blue).

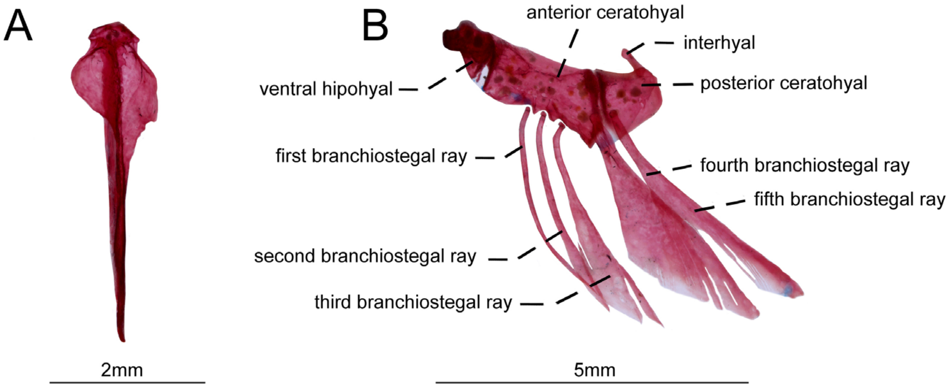

FIGURE 6 | Hyoid apparatus of *Eigenmannia catira*, paratype, MZUSP 121047. **A.** Urohyal, ventral view, anterior on top; **B.** Hyoid arch, inverted image, right side, lateral view anterior on left.

Branchial arches. All gill rakers short and unossified attached on anterior margin of each branchial arch. Pair of tiny spine shape ossicles present at base of each gill raker. Gill rakers on first branchial arch nine (1), 10(3), or 11(3). Basihyal somewhat triangular in shape, anterior portion twice as wide as its posterior portion. First basibranchial unossified, round in shape. Second and third basibranchials thin and ossified. Fourth basibranchial unossified and somewhat hexagonal in shape. Fifth basibranchial unossified and trapezoidal in shape, posterior margin twice as large as anterior margin. All hypobranchials with ossified and cartilaginous portion. First hipobranchial triangular. Second and third hipobranchials somewhat rectangular in shape. Ceratobranchials 1 to 4 retangular shape. First ceratobranchial longest, ceratobranchials 2 to 4 gradually decreasing in size. Ceratobranchial 5 supports lower pharyngeal plate, which anchors eight (1), nine (3), 10(2), or 11*(1) teeth (Fig. 7).

Epibranchials 1 to 4 ossified. Epibranchials 1 to 3 rectangular shaped. First epibranchial longest, second and third epibranchials gradually decreasing in size. Third epibranchial with posterior spine shaped process. Fourth epibranchial somewhat Y-shaped. Fifth epibranchial cartilaginous, tiny, articulating with both posterior arms of fourth epibranchials. Pharyngobranchials 1 to 3 ossified. First and second pharyngobranchial ovoid. Third pharyngobranchial triangular in shape with cartilaginous anterior portion. Fourth pharyngobranchial cartilaginous and rectangular in shape. Upper pharyngeal plate between fourth pharyngobranchial and fourth epibranchial. Upper pharyngeal plate with four (1), six (2), seven (7), or nine*(3) teeth.

Neurocranium. Mesethmoid oriented at about 45° angle from vomer, until reaching anterior margin of frontals; anterior portion with small lateral process. Frontal convex in lateral profile, about 60% as long as skull. Antorbital process of frontal present. Antorbital portion of frontal shorter than half-length of orbit. Anterior portion of anterior fontanelle limited by contralateral posterior processes of mesethmoid and completely surrounded by frontals. Posterior fontanelle about 90% as long as anterior fontanelle. Anterior one third of posterior fontanelle surrounded by frontals, posterolateral portion by parietals and posterior edge by supraoccipital. Parietal contacts frontal anteriorly, supraoccipital posteriorly, epioccipital and pterotic laterally (Fig. 5).

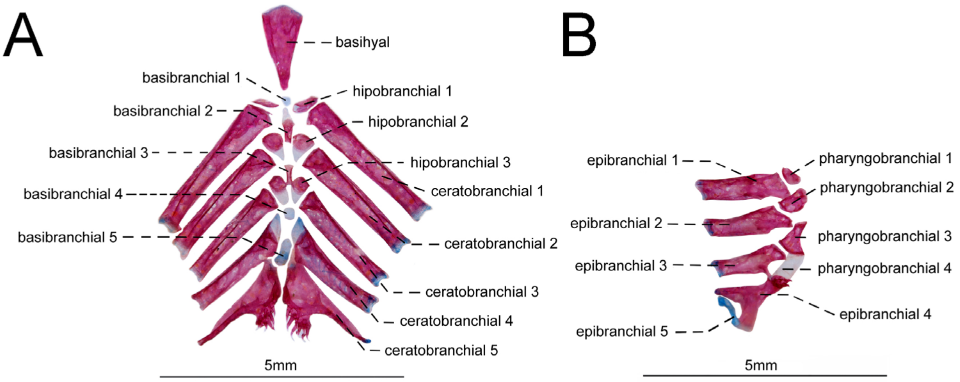

FIGURE 7 | Branchial arches of *Eigenmannia catira*, paratype, MZUSP 121047. **A.** Dorsal view, anterior on top; **B.** Ventral view anterior on top.

Lateral ethmoid a small element Y-shaped positioned in a vertical thought contact between mesethmoid and frontals; connected ventrally to parasphenoid by a connective tissue and to frontals by two strong and short ligaments. Posterodorsal process of lateral ethmoid shorter than main axis of this bone. Orbitosphenoid connected dorsally to neurocranium and posteriorly separated from pterosphenoid by a segment of cartilage. Entire ventral surface of orbitosphenoid contacting dorsal margin of parasphenoid. Pterosphenoid contacts orbitosphenoid anteriorly, and associates with frontal dorsally. Pterosphenoid contacts parasphenoid only posteroventrally, with its anteroventral surface not contacting dorsal margin of parasphenoid, forming a lateral fenestra.

Vomer arrow shaped anteriorly, with small anterior processes on each side, becoming larger posteriorly and diverging in two posterior processes, contacting anterior margin of parasphenoid. Posterior process of vomer shorter than vomer largest width. Anterior portion of vomer, which corresponds to distance from its anterior margin to the anteriormost contact with the endopterygoid, is longer than its posterior portion, which extends from the anteriormost contact with the endopterygoid until posteriormost margin of this bone. Anteriorly, parasphenoid reaches posterior portion of vomer, posteriorly surrounding ventral margin of prootics and ventral surface of basioccipital. Antorbital portion of parasphenoid shorter than its orbital portion. At its posterolateral portion, parasphenoid contacts posteroventral margin of pterosphenoid through a tapered lateral process; and dorsally contacts orbitosphenoid entirely.

Sphenotic somewhat triangular with anterior process that extends from its anterodorsal to its anteroventral margins. Sphenotic contacts pterosphenoid anteriorly, frontal anterodorsally, pterotic posterodorsally, prootic posteroventrally, and parasphenoid only at its ventralmost tip. Prootic contacts basioccipital, exoccipital, pterotic, sphenotic and pterosphenoid through cartilage filled sutures, and directly contacts to parasphenoid. Prootic with single prominent foramen. Pterotic form posterolateral portion of skull roof, and contacts prootic and exoccipital ventrally, epioccipital posteriorly, parietal dorsally, frontal anterodorsally and sphenotic anteriorly. Parietal, epioccipital, and pterotic bones in contact, posttemporal fossa absent.

Supraoccipital contacts parietal anteriorly and epioccipital posterolaterally, extending dorsally to dorsal margin of parietal. Epioccipital form posterodorsal corner of neurocranium and contacts supraoccipital medially. Exoccipital contacts basioccipital ventrally, pterotic anterodorsally, prootic anteriorly, and epioccipital posterodorsally. Internally, basioccipital and exoccipitals form a pair of chambers for cf. asteriscus otoliths; and pterotics and prootics allocate a pair of *cf. lapillus* otoliths located anterodorsally to basioccipital and exoccipitals chambers. Baudelot's ligament partially ossified.

Pectoral fin and girdle. Cleithrum somewhat half-moon shaped. Cleithral ridge not limiting anterodorsal border of this bone. Posterior process of cleithrum approximately triangular. Postcleithrum thin and discoid. Supracleithrum fused with posttemporal and lying at posterolateral surface of neurocranium at epioccipitals and pterotic sutures. Baudelot's ligament partially ossified. Coracoid with long anteroventral process that contacts cleithral ridge at anteriormost portion of cleithrum. Mesocoracoid absent. Scapula with large foramen. Radials 1 and 2 independents. Radials 3 and 4 co-ossified. Pectoral-fin tip not beyond body cavity (Fig. 8).

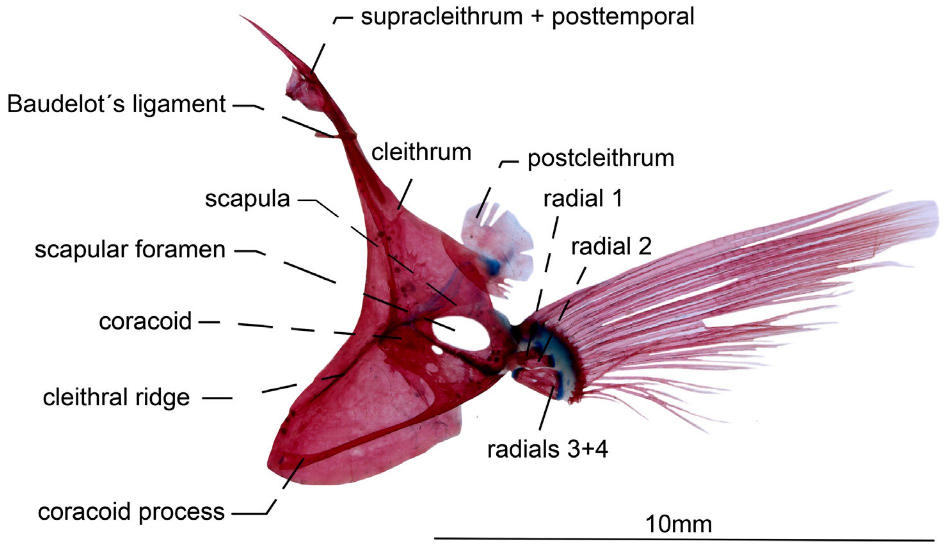

FIGURE 8 | Pectoral girdle and fin of *Eigenmannia catira*, paratype, MZUSP 121047, inverted image, right side, medial view, anterior on left.

Weberian complex. Supraneural with long anterior process that contacts supraoccipital. Scaphium somewhat triangular in shape. Intercalarium tiny located between scaphium and tripus. Tripus elongated. Parapophysis of second and fourth vertebra in contact and ventrally curved. Neural arch of third vertebrae well developed. Neural spine of fourth vertebra long and spine shaped (Fig. 5).

Axial skeleton. Precaudal vertebrae 13(6), or 14*(4). Transitional vertebrae three (2), four*(7), or five (1). Pleural ribs six (4), or seven*(6). Relative length of two anteriormost post-Weberian ribs approximately as long as abdominal cavity depth. Displaced hemal spines two (1), three*(6), or four (3). Relative size of hemal spine of 26th to 30th vertebrae longer than its associated pterygiophore (Fig. 5).

Intermuscular bones at 7–9th vertebrae. Epineurals highly branched. Rami arranged in several directions conferring a stellate shape for these elements. Epicentrals unbranched. "Epipleurals" present (Fig. 5).

Karyotype. Diploid chromosome number 2n = 36 (Sene *et al*., 2014).

Etymology. The epithet "*catira*" is in reference to a popular dance in Brazilian folklore performed by herdsmen and farmers in the areas of influence of the "sertaneja" culture in São Paulo and Mato Grosso do Sul states, which includes the occurrence area of the new species occurs. A noun in apposition.

Geographical distribution. *Eigenmannia catira* is known from rio Grande, rio Ivinhema, rio Paraná, rio Paranaíba, rio do Peixe, and rio Tietê, upper rio Paraná basin, Brazil (Fig. 9).

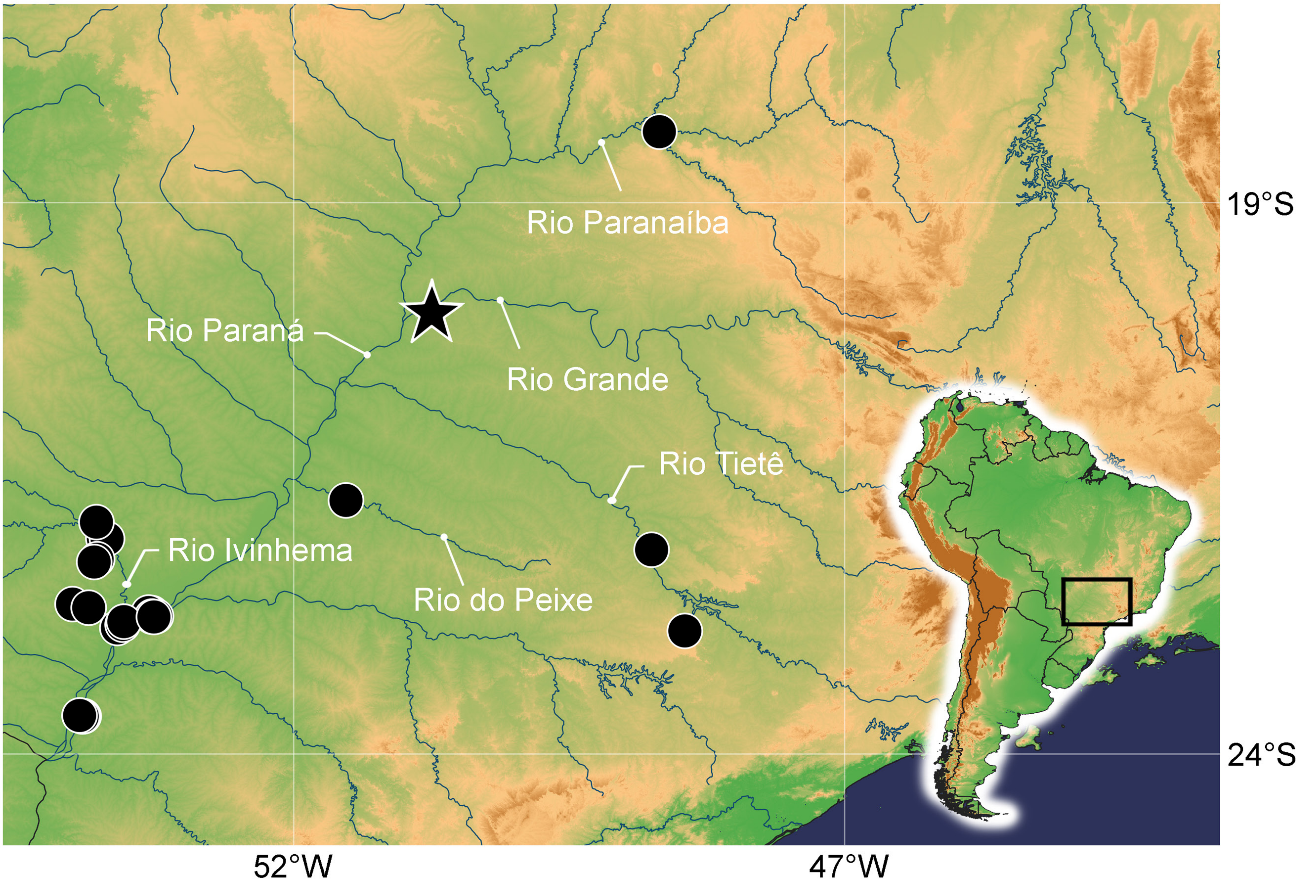

FIGURE 9 | Map of southeastern South America shows the distribution of *Eigenmannia catira* (black star for type-locality) in the upper rio Paraná basin, Brazil.

Conservation status. *Eigenmannia catira* has a relatively broad distribution, widespread in the upper rio Paraná basin. Therefore, according to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Subcommittee, 2022), *E. catira* can be classified as Least Concern (LC).

DISCUSSION

During the revision of *Eigenmannia* from the upper rio Paraná basin, we recognized four species: *E. catira*, *E. dutrai*, *E. guairaca*, and *E. trilineata*. *Eigenmannia guairaca*, which was described from two localities in a tributary of rio Paranapanema (Peixoto *et al*., 2015), turned out to be a widespread species in the upper rio Paraná basin, occurring in tributaries of the left bank of the rio Paraná, such as rio Paranaíba, rio Grande, rio Tietê and rio Paranapanema, and in the rio Paraná. A similar scenario was recorded for *E. dutrai*, which was described from rio Grande, rio Tietê and rio Paranapanema (Peixoto *et al*., 2020), and had its geographic distribution expanded to the upper portion of rio Paranaíba basin at rio Corumbá, and the rio Paraná. In turn, *E. trilineata* was described for the rio de La Plata basin (López, Castello, 1966), posteriorly recorded in the upper rio Paraná basin (Langeani *et al*., 2007; Oyakawa, Menezes, 2011), and more recently restricted again to the lower rio Paraná and rio de La Plata (Peixoto *et al*., 2015). The present analysis ratifies the presence of *E. trilineata* in the upper rio Paraná basin, occurring in rio Tietê, rio Grande, rio Paraná (see Comparative material).

In the upper rio Paraná basin, several studies provided cytogenetic information on *Eigenmannia* populations (Foresti *et al*., 1981; Almeida-Toledo *et al*., 1984, 1988, 1996, 2000, 2001, 2002; Moysés *et al*., 2005, 2010; Henning *et al*., 2008; Sene *et al*., 2014). Among these, we analyzed the voucher specimens of Almeida-Toledo *et al*. (1984, 1996) and Sene *et al*. (2014), assigning the different karyotype formula to three valid species: 2n = 36 to *E. catira*, 2n = 38 or 2n = 38, XY to *E. dutrai*, and 2n = 28 or 2n = 31/32–$X_1X_1X_2X_2$-X_1X_2Y to *E. guairaca*. The presence of two karyotypes in *E. dutrai* and *E. guairaca* could be evidence of cryptic diversity under these names. However, a detailed morphological analysis of a massive number of *E. dutrai* and *E. guairaca* specimens did not detect any diagnostic feature between populations of *E. dutrai* nor between populations of *E. guairaca*. Therefore, we took a more conservative taxonomic approach regarding these two species that present two different karyotypes formula each, considering that differences in the number and shape of chromosomes have not yet resulted in changes in the morphology that would allow the recognition of each karyotype formula as an independent species. On the other hand, the previous population assigned with diploid number 2n = 36 (see Sene *et al*., 2014) was revealed to be a new species based on several morphological traits that allow us to diagnose it from *E. dutrai* and *E. guairaca* (see Diagnosis), and by having a high genetic distance from all other *Eigenmannia* species from the rio Paraná basin.

Karyotype information was previously applied in the description of *Gymnotus* species such as *G. sylvius* Albert & Fernandes-Matioli, 1999 and *G. capanema* Milhomem, Crampton, Pierczeka, Shetka, Silva & Nagamachi, 2012 (Albert *et al*., 1999; Milhomem *et al*., 2012), being reliable information that provides additional evidence to support the description of these species. However, such methodology is rarely applied in taxonomic studies of Neotropical knifefishes. For instance, the present paper is the first that includes karyotype information as additional evidence to support the description of a new species in *Eigenmannia*, even knowing of extensive literature with this information (Foresti *et al*., 1981; Almeida-Toledo *et al*., 1984, 1985, 1988, 1996, 2000, 2001, 2002; Moysés *et al*., 2005, 2010; Henning *et al*., 2008; Silva *et al*., 2009, 2015; Nirchio *et al*., 2014; Sene *et al*., 2014). Thus, the description of *E. catira* reinforces the karyotype information available in cytogenetics as a valuable source of information for taxonomic studies.

Comparative material examined. In addition to the comparative material examined listed in Dutra *et al*. (2014, 2017, 2018, 2021, 2022), the following species were examined. All from upper rio Paraná basin. *Eigenmannia dutrai*: MZUSP 125788 (holotype, 203.8 mm LEA), LBP 471 (2 paratypes, 172.3–203.7 mm LEA), córrego Canta Galo. MZUSP 49383 (2 paratypes, 102.0–162.9 mm LEA), córrego das Araras. MZUSP 87940 (4 paratypes, 112.7–130.0 mm LEA), corrégo da Lapa. MZUSP 118377 (1 paratype, 145.6 mm LEA), córrego do Canta Galo. CI-UFLA 276 (7, not measured), rio Grande at UHE Itutinga. CI-UFLA 819 (1, not measured), rio Paranaíba. LBP 4800 (2, 203.5– 277.2 mm LEA), rio Paranapanema. LBP 6266 (1, 81.5 mm LEA), rio Muzambinho. LBP 8366 (11, 64.2–101.2 mm LEA), rio Araras. LBP 11215 (1, 201.6 mm LEA), calha do Baiano. LBP 11246 (1, 147.6 mm LEA), lagoa da Usina. LBP 12307 (26, 62.1–141.5 mm LEA), LBP

30070 (3, 65.8–121.4 mm LEA), rio Mogi-Guaçu. LBP 12308 (5, 104.6–135.4 mm LEA), ribeirão Claro. LBP 12309 (21, 135.0–203.8 mm LEA), rio Mogi Guaçu. LBP 13303 (2, 159.6–206.2 mm LEA), rio Paranapanema. LBP 13926 (1, 96.7 mm LEA), unnamed stream at Cássia. LBP 15284 (1, 175.7 mm LEA), rio Taquari. LBP 17326 (4, 164.4– 312.7 mm LEA), rio Paranapanema. LBP 18913 (1, 128.7 mm LEA), rio Piraí. LBP 18929 (1, 135.7 mm LEA), rio Piraí. LBP 23595 (9, 39.3–98.6 mm LEA), stream tributary of rio Sapucaí. LBP 26599 (4, 66.7–188.4 mm LEA), ribeirão Fortaleza. LBP 28499 (3, 108.2–146.9 mm LEA), unnamed stream. LBP 30017 (10, 119.3–212.5 mm LEA), rio Jaguari. MCNIP 2052 (1, 204.7 mm LEA), rio Araguari. MCNIP 2408 (1, 241.4 mm LEA), PCH Tamboril. MCNIP 2560 (1, 172.3 mm LEA), rio Araguari. MNRJ 19944 (1, 141.8 mm LEA), córrego da Prata. MNRJ 12192 (3, 42.0–66.7 mm LEA), córrego Alegre. MNRJ 12194 (2, 28.4–41.0 mm LEA), córrego Água Limpa. MNRJ 12195 (4, 43.5–70.3 mm LEA), córrego das Contendas. MNRJ 12197 (5, 98.8–163.6 mm LEA), córrego do Moquem. MNRJ 16976 (15, 40.4–121.4 mm LEA), MNRJ 16987 (1, 112,5– mm LEA), MNRJ 17007 (15, 102.7–181.13 mm LEA), ribeirão dos Coelhos. MNRJ 17069 (1, 59.1 mm LEA), ribeirão Itapecirica. MNRJ 17200 (1, 178,7– mm LEA), rio Grande near Itutinga. MNRJ 19942 (1, 103.1 mm LEA), ribeirão Imburuçu. MNRJ 19944 (1, 141.8 mm LEA), córrego da Prata. MNRJ 20008 (4, 23.8–93.9 mm LEA), córrego da Cascatinha. MNRJ 27443 (2, 220.4–215.4 mm LEA), rio Paranapanema. MNRJ 31784 (1, 67.9 mm LEA), córrego Antinha. MNRJ 37188 (1, 96.5 mm LEA), rio Alambari. MNRJ 46498 (2, 157.5–194.4 mm LEA), rio da Prata. MNRJ 47142 (1, 231.5 mm LEA), rio Veríssimo. MNRJ 47176 (1, 244.0 mm LEA), rio Veríssimo. MZUEL 61 (1, 243.7 mm LEA), rio Tibagi. MZUEL 62 (1, 232.5 mm LEA), rio Tibagi. MZUEL 63 (2, 208.5–211.7 mm LEA), MZUEL 64 (1, 171.3 mm LEA), MZUEL 65 (1, 241.9 mm LEA), MZUEL 66 (2, 196.1–200.0 mm LEA), rio Tibagi. MZUEL 1277 (7, 141.2–200.8 mm LEA), MZUEL 1278 (5, 126.9–205.8 mm LEA), ribeirão Três Bocas. MZUEL 1383 (1, 150.7 mm LEA), rio Tibagi. MZUEL 1876 (1, 151.7 mm LEA), rio Paranapanema at mouth of ribeirão Vermelho. MZUEL 2705 (4, 84.9–110.1 mm LEA), rio Verde. MZUEL 2736 (1, 205.4 mm LEA), MZUEL 2741 (1, 183.4 mm LEA), MZUEL 2780 (2, 153.0–161.5 mm LEA), MZUEL 3292 (1, 244.1 mm LEA), rio Paranapanema. MZUEL 4685 (3, 147.2–238.8 mm LEA), rio Taquara. MZUEL 5846 (4, 78.8–103.3 mm LEA), ribeirão Pouso Alegre. MZUEL 5853 (1, 66.2 mm LEA), córrego da Sola. MZUEL 4980 (1, 152.4– mm LEA), MZUEL 11453 (10, 127.0–217.9 mm LEA), MZUEL 11454 (2, 138.4–165.7 mm LEA), MZUEL 11455 (19, 97.7–229.67 mm LEA), MZUEL 11456 (1, 56.5 mm LEA), MZUEL 11457 (3, 124.7–208.8 mm LEA), MZUEL 11458 (5, 94.2–172.6 mm LEA), MZUEL 11459 (2, 121.0–140.1 mm LEA), MZUEL 11460 (2, 139.6–161.0 mm LEA), MZUEL 11462 (1, 168– mm LEA), MZUEL 11463 (1, 173.9 mm LEA), MZUEL 14582 (1, 87.9 mm LEA), MZUEL 14630 (5, 147.4–233.2 mm LEA), MZUEL 15517 (1, 151.0 mm LEA), MZUEL 15522 (1, 86.8 mm LEA), MZUEL 18196 (9, 96.2–160.3 mm LEA), ribeirão Três Bocas. MZUEL 8722 (2, 106.8–148.3 mm LEA), ribeirão Centenário. MZUEL 13530 (1, 102.8 mm LEA), córrego Quinze. MZUEL 14315 (1, 93.1 mm LEA), córrego Água Branca. MZUEL 17082 (6, 112.8–134.1 mm LEA), rio Tibagi. MZUEL 19022 (13, 91.9–164.1 mm LEA), rio Paraná at arquipélago da Ilha Grande. MZUEL 19292 (1, 103.8 mm LEA), córrego Areia. MZUEL 19902 (1, 149.5 mm LEA), rio Aguapeí. MZUEL 20625 (1, 162.7 mm LEA), rio Mogi Guaçu. MZUSP 2660 (1, 200.0 mm LEA), rio Grande. MZUSP 2662 (1, 173.0 mm LEA), rio Mogi-Guaçu. MZUSP 2663 (2, not measured), Piracicaba. MZUSP 22463 (1, 196.0 mm LEA), MZUSP 22476 (2, 94.9–146.6 mm LEA), MZUSP 22477 (8, 104.3–197.8 mm LEA), rio Corumbataí. MZUSP 22587 (2, not measured), Dam at São José do Rio Preto. MZUSP 22624 (2, 112.8–142.7 mm LEA), rio Paraná. MZUSP 22653 (1, 131.3 mm LEA), rio Corumbataí. MZUSP 22748 (5, 157.7–257.5 mm LEA), fazenda Pau D'Alho. MZUSP 22759 (2, 71.2–143.9 mm LEA), rio Corumbataí. MZUSP 22943 (3, 124.4–147.4 mm LEA), rio Mogi-Guaçu. MZUSP 23085 (68, 69.8–196.2 mm LEA), rio Paraná at Ilha Solteira. MZUSP 23119 (2, 92.9–141.6 mm LEA), córrego do Bueno. MZUSP 23155 (1, not measured), córrego do Diogo. MZUSP 24452 (68, 70.3–173.4 mm LEA), rio Paraná at Ilha Solteira. MZUSP 24667 (23, 88.4–131.1 mm LEA), MZUSP 24983 (2, 99.9–100.8 mm LEA), Piracicaba. MZUSP 27740 (3, 187.1–225.0 mm LEA), represa de Furnas. MZUSP 36997 (8, 115.4–

155.3 mm LEA), Cachoeira de Emas. MZUSP 38883 (4, 164.7–207.0 mm LEA), rio Paranaíba. MZUSP 39950 (2, 73.6–78.8 mm LEA), represa de Água Vermelha. MZUSP 42629 (2, 103.0–109.2 mm LEA), rio Corumbataí. MZUSP 46024 (1, 93.4 mm LEA), córrego do Machadinho. MZUSP 47774 (1, 73.8 mm LEA), rio Meia Ponte. MZUSP 49365 (18, 82.3–143.6 mm LEA), córrego da Barrinha. MZUSP 49500 (1, 122.1 mm LEA), córrego Sujo. MZUSP 52934 (2, 57.9–61.3 mm LEA), rio da Bocaína. MZUSP 58599 (1, 140.8 mm LEA), rio Jaguari. MZUSP 79687 (1, 163.7 mm LEA), córrego do Moinho. MZUSP 79858 (1, 119.4 mm LEA), ribeirão Corrente. MZUSP 83683 (3, 167.4–229.0 mm LEA), rio Corumbataí. MZUSP 84644 (1, not measured), rio Sorocaba. MZUSP 88479 (1, 76.3 mm LEA), ribeirão Passa Cinco. MZUSP 88651 (1, 183.2 mm LEA), rio Pardo. MZUSP 108078 (1, 160.8 mm LEA), rio Verde. NUP 82 (2, 69.2–136.5 mm LEA), rio Capivara. NUP 470 (1, 228.7 mm LEA), rio Corumbá. NUP 1158 (71, 78.8–218.7 mm LEA), Corumbá reservoir. NUP 1278 (2, 26.1–89.9 mm LEA), ribeirão Bocaina. NUP 1326 (5, 131.1–145.5 mm LEA), rio Corumbá. NUP 1330 (1, 162.1 mm LEA), Corumbá reservoir. NUP 2684 (1, 245.2 mm LEA), Capivara reservoir. NUP 8576 (3, 20.5–66.2 mm LEA), córrego do Retiro. NUP 8777 (1, 238.4 mm LEA), Corumbá reservoir. NUP 9028 (1, 75.1 mm LEA), córrego Forquilha. NUP 9165 (1, not measured), NUP 9171 (1, 132.8 mm LEA), Assis Chateaubriant reservoir. NUP 12663 (2, 161.0–161.1 mm LEA), NUP 12679 (5, 101.2–137.1 mm LEA), lagoa dos Patos, tributary of rio Ivinhema. NUP 13842 (2, 145.6–148.1 mm LEA), rio Veríssimo. NUP 13875 (2, 172.6–167.5 mm LEA), rio Paranaíba. NUP 13887 (2, 111.3–141.3 mm LEA), NUP 13917 (2, 142.4–163.2 mm LEA), ribeirão das Antas. NUP 13929 (2, 186.0–216.3 mm LEA), NUP 13932 (2, 153.0–157.1 mm LEA), NUP 14058 (2, 160.0–171.5 mm LEA), ribeirão da Caridade. NUP 13988 (2, 154.6–173.7 mm LEA), rio Paranaíba. NUP 14015 (2, 140.3–205.5 mm LEA), Itumbiara reservoir. NUP 14021 (2, 153.0–153.1 mm LEA), ribeirão das Antas. NUP 14031 (2, 166.2–172.5 mm LEA), rio Veríssimo. NUP 14075 (2, 182.7–191.5 mm LEA), córrego Água Suja. NUP 21044 (1, 108.5 mm LEA), rio Pelame. *Eigenmannia guairaca*: MPEG 31307 (holotype, 133.3 mm LEA), MPEG 31165 (paratypes, 1+1CS, 115.7 mm LEA), NUP 6467 (paratypes, 8+1CS, 81.4–135.8 mm LEA), riacho Água do Ó, tributary of rio Paranapanema. LBP 319 (24, 65.8–149.9 mm LEA), LBP 1301 (8, 91.3–141.6 mm LEA), LBP 3687 (1, 96.8 mm LEA), LBP 12306 (88, 32.7–130.6 mm LEA), LBP 30080 (3, 108.7–119.2 mm LEA), rio Araquá. LBP 1144 (1, 155.1 mm LEA), LBP 1149 (2, 96.2–111.1 mm LEA), LBP 14582 (2, 105.7–119.2 mm LEA), rio Capivara. LBP 3385 (3, 109.2–134.6 mm LEA), rio Capivarinha. LBP 8927 (9, 86.5–147.7 mm LEA), córrego Fazenda Água Mole. LBP 9179 (6, 90.2–144.6 mm LEA), rio Itararé. LBP 11221 (2, 102.5–111.8 mm LEA), lagoa Cabeça de Boi. LBP 11394 (1, 58.4 mm LEA), córrego Goulart. LBP 12305 (12, 78–144.6 mm LEA), rio Mogi-Guaçu. LBP 19707 (1, 112.6 mm LEA), rio Piraí. LBP 26493 (1, 130.0 mm LEA), ribeirão Sucuri. LBP 26503 (5, 46.0–110.7 mm LEA), córrego Água Grande. LBP 28498 (2, 144.7–174.1 mm LEA), LBP 30071 (1, 133.1 mm LEA), unnamed stream. LBP 28501 (5, 105.4–146.1 mm LEA), unnamed stream. LBP 28760 (1, 108.9 mm LEA), córrego Água Boa. MNRJ 24208 (1, 106.7 mm LEA), rio Água Fria. MNRJ 29815 (1, 103.1 mm LEA), córrego da Inácia. MNRJ 36885 (1, 65.7 mm LEA), fazenda Edgardia. MNRJ 39399 (1, 85.5 mm LEA), Paranapanema dam at fazenda Regina. MZUEL 103 (3, 46.4–60.2 mm LEA), rio Tibagi. MZUEL 1757 (1, 145.1 mm LEA), ribeirão Jacutinga. MZUEL 1758 (1, 123.7– mm LEA), rio Tibagi. MZUEL 1759 (32, 50.0–118.9 mm LEA), MZUEL 2775 (16, 38.3–115.0 mm LEA), ribeirão Palmital. MZUEL 2276 (1, 65.4 mm LEA), rio Congonhas. MZUEL 2389 (1, 137.8 mm LEA), ribeirão Pau D'Alho. MZUEL 2529 (1, 67.8 mm LEA), MZUEL 2533 (1, 101.4 mm LEA), rio São João. MZUEL 2750 (3, 55.7–79.6 mm LEA), rio Inhumas. MZUEL 3463 (1, 97.2 mm LEA), MZUEL 16489 (1, 125.0 mm LEA), MZUEL 16494 (1, 74.2 mm LEA), rio Paranapanema at Canoas dam. MZUEL 6525 (1, 103.7 mm LEA), MZUEL 6534 (1, 111.3 mm LEA), MZUEL 6551 (1, 101.7 mm LEA), MZUEL 8943 (2, 150.1–154.0 mm LEA), MZUEL 8974 (1, 51.8 mm LEA), ribeirão Couro do Boi. MZUEL 14326 (3, 26.4–115.2 mm LEA), córrego Tujuri. MZUEL 14447 (3, 49.6–89.8 mm LEA), tributary of rio Tujuri. MZUEL 21752 (1, 59.8 mm LEA), ribeirão Centenário. MZUEL 21754 (1, 126.6 mm LEA), córrego Piraveve. MZUSP 22363 (1, 101.0 mm LEA), rio Veado. MZUSP 22602 (49+5CS, 53.5–122.5 mm LEA), rio Corumbataí. MZUSP 22516 (3, 45.0–115.3 mm LEA), stream tributary of Laranja Azeda. MZUSP 22549 (5, 62.4–94.1 mm LEA), lago São Vicente. MZUSP 22738 (1, 56.6 mm LEA), MZUSP 22922 (1, 72.8–103.3 mm LEA), córrego do Pinheiro. MZUSP 23086 (4, 68.2–102.7 mm LEA), rio Paraná at represa de Ilha Solteira. MZUSP 24353 (1, 103.1 mm LEA), córrego do Bueno. MZUSP 23774 (4, 68.8–84.7 mm LEA), córrego do Machadinho. MZUSP 24563 (4, 59.1–96.2 mm LEA), MZUSP 24571 (1, 66.0 mm LEA), córrego da fazenda Edgardia. MZUSP 24663 (8, 72.7–86.6 mm LEA), unnamed stream. MZUSP 24666 (1, 94.5 mm LEA), Cachoeira de Emas. MZUSP 24984 (1, 107.2 mm LEA), São Paulo. MZUSP 35362 (5, 26.4–86.1 mm LEA), MZUSP 35368 (4, 71.6–96.2 mm LEA), rio Araguá. MZUSP 35803 (1, 66.4 mm LEA), fazenda do Dendosho. MZUSP 36996 (2, 66.3–82.4 mm LEA), MZUSP 36998 (8, 83.3–102.3 mm LEA), Botucatu. MZUSP 39813 (3, 103.1–107.8 mm LEA), rio Alambari. MZUSP 39829 (7, 44.3–89.6 mm LEA), MZUSP 39842 (2, 32.2–71.1 mm LEA), MZUSP 39859 (3, 42.6–85.8 mm LEA), rio Alambari. MZUSP 39876 (1, 88.2 mm LEA), rio Capivara. MZUSP 42624 (1, 104.3 mm LEA), rio Tietê. MZUSP 43115 (1, 96.7 mm LEA), rio Turvo. MZUSP 49229 (1, 129.4 mm LEA), unnamed stream. MZUSP 49385 (12+3CS, 69.5–130.8 mm LEA), córrego das Araras. MZUSP 51337 (1, 65.6 mm LEA), unnamed stream. MZUSP 74754 (2, 38.3–81.3 mm LEA), córrego Luciano. MZUSP 79857 (1, 101.3 mm LEA), rio Jacaré. MZUSP 83428 (1, 91.9 mm LEA), córrego Catingueiro. MZUSP 84278 (2, 45.5–98.6 mm LEA), fazenda Santa Paula. MZUSP 88415 (11, 30.3–82.7 mm LEA), córrego Taboca. MZUSP 88455 (1, 117.9 mm LEA), córrego do Palmito. MZUSP 102839 (3, 72.8–86.6 mm LEA), unnamed stream at Teodoro Sampaio. NUP 9381 (3, 47.0–86.4 mm LEA), córrego Rosário. NUP 16151 (1, 101.9 mm LEA), córrego Água Boa. NUP 16509 (1, 90.2 mm LEA), rio Baía. NUP 17019 (16, 19.9–124.0 mm LEA), córrego Itauna. NUP 17114 (12, 78.5–143.8 mm LEA), riacho Água do Ó. NUP 18769 (1, 131.8 mm LEA), rio São Camilo. NUP 18966 (4, 109.1–127.6 mm LEA), riacho São Pedro. NUP 22465 (2, 68.9–91.6 mm LEA), córrego Taquari. *Eigenmannia trilineata*: MZUEL 8375 (1, 46.9 mm LEA), rio do Tigre. MZUEL 13379 (1, 102.5 mm LEA), rio Verde. MZUEL 13471 (1, 94.0 mm LEA), rio Pardo. MZUEL 14488 (43, 26.1–126.6 mm LEA), córrego Piraveve. MZUSP 79303 (1, 120.6 mm LEA), rio Jacaré-Guaçú. NUP 421 (12, 94.0–120.1 mm LEA), rio Paraná at Porto Rico. NUP 1707 (11, 117.6–235.8 mm LEA), rio Piquiri. NUP 1733 (3, 60.9–103.2 mm LEA), riacho Caracu. NUP 1751 (16, 76.2–103.3 mm LEA), Itaipu reservoir. NUP 1909 (1, 134.1 mm LEA), Itaipu reservoir. NUP 7025 (1, 153.0 mm LEA), rio Ocoí. NUP 7027 (2, 152.7–187.3 mm LEA), arroio Guaçu. NUP 7569 (2, 120.9–157.7 mm LEA), lagoa Fechada. NUP 19082 (1, 55.9 mm LEA), arroio Carvoraci.

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Vinicius de Carvalho Cardoso: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing-original draft, Writing-review and editing.

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ETHICAL STATEMENT

This study was carried out under the approval of the Animal Care and Use Committee (ACUC) of the Instituto de Biociências, Universidade de São Paulo (Project #226/2015; CIAEP #01.0165.2014).

COMPETING INTERESTS

The author declares no competing interests.

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