

Cryptic lineages in Neotropical freshwaters: an integrative approach reveals a new species of *Megalonema* (Siluriformes: Pimelodidae) from the upper Paraná River basin

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A new species, previously identified as *Megalonema platanum*, is described as *Megalonema tinga* from the Paranapanema River basin, based on morphological (morphometry and meristic) and DNA-barcoding analyses. Body proportions based on 28 measurements in 25 specimens of *M. tinga* and 10 of *M. platanum* showed a high degree of overlap. However, an analysis of 15 measurements of *M. tinga* (n = 28) and *M. platanum* (n = 13), using sheared principal components analysis, applied to the covariance matrix of logarithmized morphometric variables, supported differentiation between the two species. The meristic analysis showed that *M. tinga* has fewer gill rakers in the first ceratobranchial (six to eight) than *M. platanum* (nine to 11), a character ontogenetically stable. COI-based species delimitation (ASAP, mPTP, and GMYC) also indicated species-level differentiation, separating supposed *M. platanum* into two groups, one of which is the new species. The new species is also distinguished from other *Megalonema* species by morphological or molecular features.

Keywords: Cytochrome c oxidase subunit I, Gill rakers, Integrative taxonomy, Multivariate morphometrics, Species complex.

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Uma nova espécie, anteriormente identificada como *Megalonema platanum*, é descrita como *Megalonema tinga* da bacia do rio Paranapanema, com base em análises morfológicas (morfometria e merística) e de codificação de barras de DNA. Proporções corporais, baseadas em 28 medições em 25 espécimes de *M. tinga* e 10 de *M. platanum*, apresentaram alto grau de sobreposição. No entanto, uma análise de 15 medições de *M. tinga* (n = 28) e *M. platanum* (n = 13), usando análise de componentes principais com distorção dos eixos (Shear), aplicada à matriz de covariância das variáveis morfométricas logaritmizadas, apoiou a diferenciação entre as duas espécies. A análise merística mostrou que *M. tinga* possui menos rastros branquiais no primeiro ceratobranquial (seis a oito) do que *M. platanum* (nove a onze), um caráter ontogeneticamente estável. A delimitação de espécies baseada em COI (ASAP, mPTP e GMYC) também indicou diferenciação em nível de espécie, separando o suposto *M. platanum* em dois grupos, sendo um deles a nova espécie. A nova espécie também se distingue de outras espécies de *Megalonema* por características morfológicas ou moleculares.

Palavras-chave: Citocromo c oxidase subunidade I, Complexo de espécies, Morfometria multivariada, Rastros branquiais, Taxonomia integrativa.

INTRODUCTION

Pimelodidae Swainson, 1838 is a family of catfishes predominantly associated with large Neotropical river systems. Within this family, *Megalonema* Eigenmann, 1912 comprises seven valid species distributed in the Magdalena, Essequibo, Orinoco, Amazonas, and Paraná river basins, as well as in Lake Maracaibo (Fricke *et al.*, 2026). Members of the genus are known by various vernacular names across their range, including ballo and ballito (Galvis *et al.*, 1997), mandi-branco and mandi-prata (Britto, 2003), espalha-brasa and mandi-João-duro (Santos *et al.*, 2004), mandi-panema (Rocha, Zuanon, 2013), fidalgo (Deprá *et al.*, 2022), and cassie (Taphorn *et al.*, 2022). They are consumed, particularly as stews, and constitute an important component of the local cuisine (Deprá *et al.*, 2022).

Megalonema was described to include *Pimelodus platycephalum* Eigenmann, 1912, from the Essequibo River basin in Guyana, established as the type species by original designation. The genus is diagnosed by a distinctive combination of characters, including the dorsal surface of the head covered by thin skin; upper jaw extending beyond the lower jaw, partially exposing the premaxillary tooth band, which lacks a pointed posterolateral projection; absence of vomerine teeth; absence of dorsal- and pectoral-fin spines; slightly flattened barbels; and a long, narrow occipital process not reaching the predorsal plate (Eigenmann, 1912; Britski, 1972). The caudal fin is deeply forked. Additional features include a relatively long adipose-fin base, approximately twice the length of the anal-fin base, and a generally homogeneous light yellow-ochre coloration, without conspicuous dark spots, although a faint ocellus may be present at the base of the dorsal caudal-fin lobe (Eigenmann, 1912; Britski *et al.*, 1999), and sometimes in the ventral lobe base.

Phylogenetically, Lundberg *et al.* (2011) and Silva *et al.* (2024) supported *Megalonema* as the sister of *Cheirocerus* Eigenmann, 1917, with the former study placing that clade as the sister of one containing *Aguarunichthys* Stewart, 1986, *Calophysus* Müller & Troschel, 1843, *Luciopimelodus* Eigenmann & Eigenmann, 1888, *Pimelodina* Steindachner, 1876 and *Pinirampus* Bleeker, 1858. Silva *et al.* (2024) supported the same sister clade but did not analyze *Aguarunichthys*. Lundberg, Dahdul (2008) recognized a putatively monophyletic lineage within the genus and proposed the subgenus *Eretmomegalonema* to include *M. amaxanthum* Lundberg & Dahdul, 2008, *M. orixanthum* Lundberg & Dahdul, 2008, and *M. xanthum* Eigenmann, 1912. This clade is supported by features shared by both other *Megalonema* species and the family Pimelodidae. The phylogenetic positions of the remaining species, however, remain insufficiently investigated.

Four species of *Megalonema* are currently recorded from Brazil: *M. pauciradiatum* Eigenmann in Driver, 1919, described from the Paraguay River basin; *M. platanum* (Günther, 1880), described from the Río de la Plata basin, but widely distributed in Paraná River basin (Ota *et al.*, 2018; Dagosta *et al.*, 2024); *M. platycephalum* Eigenmann, 1912, reported from the Amazon and Tocantins river basins (Rocha, Zuanon, 2013; Ohara *et al.*, 2017); and *M. amaxanthum*, described from the Amazon basin (Lundberg, Dahdul, 2008). Since the genus was established, species identification has been problematic, largely due to pronounced morphological similarity among congeners. Moreover, the possibility of unrecognized diversity cannot be dismissed. For instance, specimens identified as *M. platycephalum* from the Amazon and Tocantins basins warrant further scrutiny, given that the species' type locality is the Essequibo River basin.

The same problem occurs with *M. platanum* in the upper Paraná River basin. The species of Tibagi River basin was identified as *M. platanum* (Shibatta *et al.*, 2002), but a more encompassing examination of specimens deposited in the ichthyological collection of the Museu de Zoologia da Universidade Estadual de Londrina (MZUEL) revealed subtle morphological variation between populations from the Paranapanema River basin (upper Paraná River basin) and the Miranda River (upper Paraguay River basin). These observations underscore the need for a comprehensive comparative analysis. Accordingly, the present study evaluates morphometric, meristic, and molecular variation among these populations and specimens from the lower Paraná River basin to assess their taxonomic status within *Megalonema*. The results support the recognition of a new species from the upper Paraná River basin, particularly from the Paranapanema River basin, which is formally described herein.

MATERIAL AND METHODS

Morphometry. The measurements for the analysis of body proportions were obtained point-to-point using a digital caliper with a precision of 0.01 mm, then rounded to 0.1 mm. The measures were as follows: (1) standard length (SL): from the tip of the snout to the base of the caudal fin, at the posterior boundary of the hypural plate; (2) head length (HL): from the tip of the snout to the edge of the opercular bone; (3) maxillary-barbel length: from the base to the posterior extremity; (4) inner mental barbel length: from the base to the posterior extremity; (5) outer mental barbel length: from the base to the posterior extremity; (6) body depth: vertical that starts at the belly and ends just before

the dorsal fin; (7) pre-dorsal length: from the tip of the snout to the origin (anterior margin) of the dorsal fin; (8) dorsal-fin base length: from the origin to the insertion (posterior margin) of the dorsal-fin base; (9) first dorsal-fin ray length: from the base to the distal end; (10) dorsal fin to adipose fin length: between the insertion of the dorsal fin and the origin of the adipose fin; (11) pre-adipose length: from the tip of the snout to the origin of the adipose fin; (12) adipose-fin base length: from the origin to the posterior insertion of the fin; (13) adipose-fin depth: vertical that passes from the base to the highest point of the fin; (14) pre-pectoral length: from the tip of the snout to the base of the first ray of the pectoral fin; (15) first pectoral-fin ray length: from the base to the distal extremity; (16) pre-pelvic length: from the tip of the snout to the anterior margin of the pelvic fin; (17) transverse distance between pelvic fins: distance between the anteriormost base of pelvic fins; (18) first pelvic-fin ray length: from the base to the distal extremity; (19) pre-anal length: from the tip of the snout to the origin of anal fin; (20) Anal-fin base length: from the origin to the posterior insertion of the anal fin; (21) caudal peduncle length: length between the posterior insertion of the anal fin and the posterior margin of the caudal peduncle, at the posterior limit of the hypural plate; (22) caudal peduncle depth: least depth of caudal peduncle; (23) eye diameter: length of the eye horizontally; (24) interorbital distance: shorter distance between the upper margins of the bony orbit; (25) Snout length: from the tip of the snout to the anterior rim of the eye; (26) head depth: depth at vertical through posterior margin of the eye; (27) head width: transverse distance between the most distal edges of the opercular bones; (28) mouth width: the distance between the angles of the mouth. Measurements related to the body, including the head length, were presented as proportions of the standard length, and those contained in the head were related to the head length (except for barbel lengths).

Multivariate morphometrics. The following morphometric characters were selected for the sheared principal components analysis, due to the limitation imposed by the program used (MacLeod, 1990): 1. Standard length; 2. Head length; 3. Pre-dorsal length; 4. Dorsal-fin base length; 5. Pre-ventral length; 6. Anal-fin base length; 7. Body depth; 8. Caudal peduncle depth; 9. Eye diameter; 10. Interorbital distance; 11. Snout length; 12. Adipose-fin base length; 13. Head width; 14. Head depth; 15. Mouth width.

For the multivariate morphometric analyses, sheared principal components analysis (SPCA) was employed to discriminate variation related to size and shape. According to Humphries *et al.* (1981), the first principal component represents overall size, with all variables positively correlated with this axis, whereas subsequent components primarily reflect shape variation. However, because some size-related variation may still be retained in the remaining components, a modified approach termed “shear” was adopted (Humphries *et al.*, 1981). This method adjusts (*i.e.*, shears) the axes according to the first component to remove size effects, transforming the original measurement matrix into an orthogonal basis of independent vectors and thereby enhancing the detection of shape-related differences. All analyses were performed using the “Shear” program developed by MacLeod (1990).

Counts. The meristic characters examined were: 1. Number of dorsal-fin rays; 2. Number of pectoral-fin rays; 3. Number of pelvic-fin rays; 4. Number of anal-fin rays (only the externally visible ones); 5. Number of principal caudal-fin rays; and 6.

Number of rakers on the first gill arch, recorded separately for the epibranchial and ceratobranchial. Meristic data are presented in the descriptions as frequency distributions, with values for the holotype indicated by an asterisk in parentheses.

Morphometric and meristic data for *M. platycephalum* were compiled from the literature (Eigenmann, 1912; Torrico-Destre *et al.*, 2024), as were corresponding data for *M. pauciradiatum* (Eigenmann, 1919) and *M. psammium* (Schultz, 1944). To assess a possible correlation between the number of gill rakers and the size (SL) of the specimens, Spearman's non-parametric correlation coefficient (ρ) was used, which is based on ranks rather than absolute values. The Past statistical package (Hammer *et al.*, 2001) was used for this analysis.

Osteology. Osteological characters were examined from cleared and stained (Dingerkus, Uhler, 1977) or radiographed specimens. The total vertebrae include the Weberian complex counted as five and the complex caudal vertebrae (PU1+U1) counted as one.

DNA Barcode and species delimitation. Twenty-nine COI gene sequences from *Megalonema* obtained from Barcode of Life Data System (BOLD) were used in genetic analyses. Of these, three were from *M. platycephalum* (ADK5242), seven were from *M. platanum* (ACY8268), and 19 were from *M. tinga* (ACG7093) (see Tab. S1 for a complete list). To test the new species hypothesis, four species delimitation methods were applied: intra- and interspecific genetic distance (Kimura 2-parameter model; Kimura, 1980; Tab. S2); the Generalized Mixed Yule-Coalescent model (GMYC; Pons *et al.*, 2006; Zhang *et al.*, 2013; Fujisawa, Barraclough, 2013); Assemble Species by Automatic Partitioning (ASAP; Puillandre *et al.*, 2021); the multi-rate Poisson Tree Processes model (mPTP) (Kapli *et al.*, 2017). The genetic distance (Kimura 2-parameter model) was calculated in MEGA v. 12 (Kumar *et al.*, 2024), and GMYC analysis was used to generate an ultrametric tree using Bayesian inference in BEAST v. 1.10.5 under a strict molecular clock and a birth-death model. The analysis was run for 10 million generations using the HKY+I+G model. Convergence was verified in TRACER v. 1.7.2 (ESS>200), and trees were summarized in TreeAnnotator and visualized in FigTree. The GMYC and mPTP analyses were performed online at <http://species.h-its.org/ptp/> and <https://mptp.h-its.org/#/tree>, respectively. ASAP analyses were performed using ASAPy v. 0.1.2 software with default parameters.

Type-series determination. The type-series of *M. tinga* was determined cautiously, as it was restricted to samples from the Tibagi River basin, given the possibility of integrating information from the morphological and molecular analyses. Thus, samples from other locations, identified solely by morphological or molecular data (without a voucher specimen), did not constitute the type series and were classified as "Non-types".

Characters of the *M. pauciradiatum* holotype from the California Academy of Sciences (CAS-ICH 63672) were analyzed from photographs and radiographs available through <https://researcharchive.calacademy.org/research/ichthyology/collection/index.asp?xAction=getrec&close=true&LotID=63672>. Institutional abbreviations follow Sabaj (2025).

RESULTS

Megalonema tinga, new species

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(Fig. 1; Tab. 1)

Megalonema platanus. —Shibatta *et al.*, 2002:418 (Short characterization, Tibagi River basin). —Brito, 2003:73 (Illustration and short characterization, Parapanema River basin).

Holotype. MZUEL 24550, 234.6 mm SL, Tibagi River, near the mouth of the Apucarantina River, Tamarana, Paraná, Brazil, 23°47'31.45"S 50°53'42.05"W, 20 Feb 2001, M. Caetano Filho.



FIGURE 1 | *Megalonema tinga*, holotype, MZUEL 24550, 234.6 mm SL, Tibagi River, Tamarana, Paraná, Brazil. Scale bar = 5 cm.

TABLE 1 | Morphometric variables of the *Megalonema tinga* from the upper Paraná River basin and *M. platanum* from the Paraná River and upper Paraguay River basin. Minimum and maximum values of body proportions (averages in parentheses) include all specimens. N = number of specimens.

Variables	Holotype	N	<i>M. tinga</i>	N	<i>M. platanum</i>
1. Standard length (mm)	234.6	25	61.2–249.3 (129.8±51.6)	13	106.1–240.2 (160.9±50.6)
Proportions of standard length					
2. Head length	27.5	25	26.1–29.7 (27.8±0.9)	13	26.8–29.0 (27.7±0.7)
3. Maxillary-barbel length	55.1	23	55.1–117.7 (85.2±19.9)	12	59.0–96.6 (75.9±10.8)
4. Inner-mental-barbel length	15.5	23	12.8–25.2 (18.0±3.4)	12	13.1–27.0 (17.0±3.8)
5. Outer-mental-barbel length	26.4	23	24.1–48.2 (36.4±7.8)	12	28.3–40.9 (32.7±3.7)
6. Body depth	19.2	25	15.8–20.7 (17.3±1.1)	13	16.9–22.3 (19.8±1.7)
7. Pre-dorsal length	38.2	25	33.8–40.3 (36.6±1.5)	13	34.6–39.1 (36.3±1.3)
8. Dorsal-fin base length	12.5	25	11.7–13.1 (12.5±0.4)	13	12.2–14.5 (13.3±0.8)
9. First dorsal-fin ray length	22.3	20	18.0–27.2 (24.2±2.4)	12	20.7–28.0 (25.2±1.9)
10. Dorsal fin to adipose fin length	18.8	23	14.3–24.1 (17.7±2.1)	12	14.6–18.9 (16.2±1.3)
11. Pre-adipose length	71.3	23	60.9–71.6 (65.0±2.8)	12	56.7–68.4 (63.7±2.9)
12. Adipose-fin base length	21.9	25	20.3–26.4 (23.0±1.5)	13	23.9–27.8 (25.8±1.4)
13. Adipose-fin depth	5.1	23	4.1–6.9 (5.7±0.7)	12	2.8–9.0 (5.8±1.5)
14. Pre-pectoral length	26.2	23	16.8–27.3 (24.9±2.0)	12	21.0–27.6 (24.9±2.1)
15. First pectoral-fin ray length	20.0	23	18.1–21.7 (20.2±1.14)	12	18.2–22.6 (19.8±1.3)
16. Pre-pelvic length	48.6	25	45.6–50.5 (48.3±1.2)	13	45.5–51.1 (48.6±1.7)
17. Distance between pelvic fins	13.2	23	10.0–19.0 (12.4±2.3)	12	11.0–13.7 (12.5±0.8)
18. First pelvic-fin ray length	16.8	23	14.3–21.4 (18.3±1.7)	12	14.7–20.1 (18.1±1.5)
19. Pre-anal length	72.2	23	67.9–76.4 (72.8±2.2)	12	63.2–78.8 (72.4±4.1)
20. Anal-fin base length	10.7	25	9.5–13.0 (11.4±0.9)	13	10.3–12.7 (11.5±0.8)
21. Caudal-peduncle length	17.1	23	12.5–20.3 (16.6±1.7)	11	15.6–23.4 (17.4±2.1)
22. Caudal-peduncle depth	8.2	25	7.2–8.8 (7.9±0.3)	13	7.7–9.2 (8.3±0.4)
Proportion of head length					
23. Eye diameter	14.8	25	14.7–25.0 (20.0±2.8)	13	12.0–20.6 (16.5±2.8)
24. Interorbital distance	31.2	25	23.1–31.2 (26.5±1.9)	13	24.2–30.3 (27.1±1.9)
25. Snout length	50.2	25	42.6–52.4 (46.0±2.5)	13	44.2–50.5 (48.1±2.1)
26. Head depth	43.1	25	36.9–51.5 (42.0±3.0)	13	38.2–50.6 (42.4±3.4)
27. Head width	19.6	25	16.4–19.7 (18.1±0.9)	13	16.3–21.3 (18.9±1.4)
28. Mouth width	51.1	25	43.8–55.0 (48.3±3.3)	13	44.6–56.0 (49.9±3.5)

Paratypes. Brazil, Paraná State: MZUEL 1763, 4, 97.6–223.2 mm SL, collected with the holotype; MZUEL 55, 3, 129.8–222.1 mm SL, Tibagi River, Sapopema, 23°56'31.59"S 50°43'47.41"W, 5 May 1990, UEL staff (ECPUEL); MZUEL 82, 1, 141.3 mm SL, Tibagi River, Sapopema, 23°56'31.59"S 50°43'47.41"W, Mar 1990, ECPUEL; MZUEL 1030, 1, 87.0 mm SL, Tibagi River, Londrina (Limoeiro), 23°20'25.10"S 51°00'52.23"W, 23 Apr 1997, ECPUEL; MZUEL 1337, 3, 103.3–106.0 mm SL, Tibagi River, Sapopema, 23°56'31.59"S 50°43'47.41"W, 26 Sep 1997, ECPUEL; MZUEL 1669, 3, 94.6–96.3 mm SL, Tibagi River, Assaí (Cebolão), 23°28'49.39"S 50°55'15.65"W, 20 Nov 1998, M. L. Orsi & E. S. Silva; MZUEL 1782, 5, 87.8–139.5 mm SL, Tibagi River, Sapopema, 23°56'31.59"S 50°43'47.41"W, 9 Nov 2000, O. A. Shibatta & M. L. Orsi; MZUEL 1824, 3, 61.2–98.6 mm SL, Tibagi River, Londrina (Limoeiro), 23°20'25.10"S 51°00'52.23"W, 6 Apr 2000, ECPUEL; MZUEL 2712, 3, 162.8–249.3 mm SL, Tibagi River, A. M. Geahl; MZUEL 2592, 1, 81.4 mm SL, Tibagi River, Tamarana, 23°47'31.45"S 50°53'42.05"W, ECPUEL, 9 Jan 2002; MZUEL 9474, 1, 158.2 mm SL, Laranjinha River, near its mouth, tributary of rio das Cinzas, 23°01'53.9"S 50°26'51.9"W, 13 Dec 2010, B. A. Galindo *et al.*; NUP 26946 (ex MZUEL 954), 1, 123.8 mm SL, Tibagi River, Londrina (Limoeiro), 23°20'25.10"S 51°00'52.23"W, 26 Mar 1997, ECPUEL.

Non-types. Brazil. Goiás State: NUP 1155, 16 of 18 (2 *M. platanum*), 72.2–221.2 mm SL, Corumbá reservoir, Corumbá River tributary, Caldas Novas, boundary with Pires do Rio, 17°43'36.23"S 48°29'59.79"W, 9 Apr 1999, Nupelia; NUP 1156, 6, 217.7–230.2 mm SL, Corumbá reservoir, Corumbá River tributary, Caldas Novas, boundary with Pires do Rio, 17°43'36.23"S 48°29'59.79"W, 9 Apr 1999, Nupelia. Minas Gerais State: DZSJRP 18629, 1, 209.0 mm SL, Paranaíba River, UHE-São Simão downstream, 19°02'19.44"S 50°30'02.12"W, A. C. L. Rego, no date. Paraná State: NUP 1704, 1 of 2 specimens (1 *M. platanum*), 150.8 mm SL, Piquiri River, tributary of Paraná River, Mariluz, boundary of Formosa do Oeste, 24°11'48"S 53°19'20"W, 15 Jun 1987, Nupelia.

Diagnosis. *Megalonema tinga* is distinguished from *M. xanthum*, *M. amaxanthum*, and *M. orixanthum* by having a non-elongated pelvic fin and basipterygium (*vs.* elongated). It can be separated from *M. pauciradiatum* by the presence of 11 or 12 anal-fin rays (*vs.* 9). *Megalonema tinga* presents 6 to 8 gill rakers on the first ceratobranchial, a lower number than *M. platanum* (9 to 11) and *M. psammium* (10 or 11). In comparison with *M. platycephalum*, *M. tinga* shows a larger eye diameter (14.7–25.0% *vs.* 11.3–13.1% of SL), a shorter dorsal-fin base length (11.7–13.1% *vs.* 13.7–15.4% of SL), and a shorter adipose-fin base length (20.3–26.4% *vs.* 26.0–28.5% of SL). On average, it is further distinguished from *M. platanum* by a larger eye diameter (mean $20.0 \pm 2.8\%$ *vs.* $16.5 \pm 2.8\%$ of HL) and a smaller body depth ($17.3 \pm 1.1\%$ *vs.* $19.8 \pm 1.7\%$ of SL).

Description. Morphometric data in Tab. 1. Head small relative to body, dorsoventrally depressed. Dorsal profile nearly straight from snout tip to dorsal-fin origin; from dorsal-fin origin to adipose-fin end almost straight, slightly descending, with a subtle break at adipose-fin origin. Ventral profile slightly convex, nearly straight from anterior margin of lower jaw to anal-fin insertion. Caudal peduncle with dorsal and ventral profiles slightly concave.

Mouth wide; lips laterally expanded. Dorsal mandible longer than ventral; premaxillary dentigerous plate slightly exposed anteriorly. Anterior nostril small, tubular, just beyond upper jaw margin; posterior nostril wider, oval, lateromedially elongate. Eye large, elliptical, longer than deep, with free orbital margin, dorsally positioned at approximately mid-head length. Cranial skeleton (Fig. 2A), with mesethmoid almost straight anteriorly, with shallow concavity, articulated posteriorly with lateral ethmoid. Lateral ethmoid dorso-anteriorly articulated with infraorbital 1 and ventro-anteriorly with mesethmoid and laterally with autopalatine by synchondrosis. Lateral ethmoid posteriorly enlarged, forming part of orbit. Frontal anteriorly thin, elongated, articulated with mesethmoid; posteriorly articulated with sphenotic and supraoccipital. Wide nasal concavity formed by mesethmoid, lateral ethmoid, frontal, and infraorbital 1. Sphenotic elongated, articulated medially with frontal, and posteriorly with supraoccipital and pterotic, completing posterior rim of orbit. Pterotic length and width similar, articulated anteriorly with sphenotic, medially with supraoccipital, and posteriorly with posttemporal. Posttemporal wider than long, articulated medially with supraoccipital and laterally with supracleithrum. Supraoccipital wider than long, occipital process thin, pointed, separated from the pre-dorsal plate by a small distance. Premaxillary dentigerous plate thin, curved, width approximately uniform along length, posterior tip slightly rounded; five rows of villiform teeth (Fig. 2B).

Maxillary barbel, when adpressed, reaching pelvic fin, not surpassing distal tip of pelvic fin; outer mental barbel surpassing pelvic-fin base; inner mental barbel reaching beyond opercular opening, not attaining pectoral-fin base. Opercle wavy free margin; posterior tongue-like expansion.

Weberian complex (Fig. 2C) with anterior and posterior fourth vertebra parapophyses interconnected dorsally by concave bony lamina receiving dorsal face of gas bladder, ventrally by narrow bridge (ventral flange of compound centrum). Fourth and fifth vertebrae with open aortic canal. Fifth vertebra articulated with fourth by serrated suture.

Dorsal fin approximately triangular, i,6(22)* rays; first branched ray longest. Pectoral girdle arched, cleithrum dorsal region nearly vertical, wider dorsally than ventrally, with dorsal process articulated with posttemporal; posterior cleithral process indistinct, shallow and rounded; ventral cleithrum nearly horizontal, laminar, anteriorly articulated with coracoid and medially with its opposite counterpart. Coracoid slimmer than cleithrum articulated with arched mesocoracoid. Two wide radials, with anterior and posterior border approximately rounded, articulated with pectoral girdle and pectoral-fin rays (Fig. 2D). Pectoral fin triangular, posterior margin falcate, i,11(10), i,12(5), i,13(7)* rays; first branched ray longest. Pelvic fin triangular, posteromedial margin rounded, i,5(22)* rays. Basipterygium (Fig. 2E) roughly triangular, with two anterior (anterolateral and anteromedial) and one posterior (ischiatric) processes. Adipose fin elongated, anterior portion deeper, posterior portion free. Anal fin trapezoidal, distal margin concave when extended, iii,9(21)*, ii,10(1) rays. Anal fin with twelve proximal radials, first articulated with three rudimentary rays, last bifurcated, articulated with two rays; distal radials between (Fig. 2F). Caudal fin forked; base deeper than caudal peduncle; upper lobe slightly more pointed than lower lobe; lower lobe slightly wider than upper lobe; i,7,8,i(25)* rays.

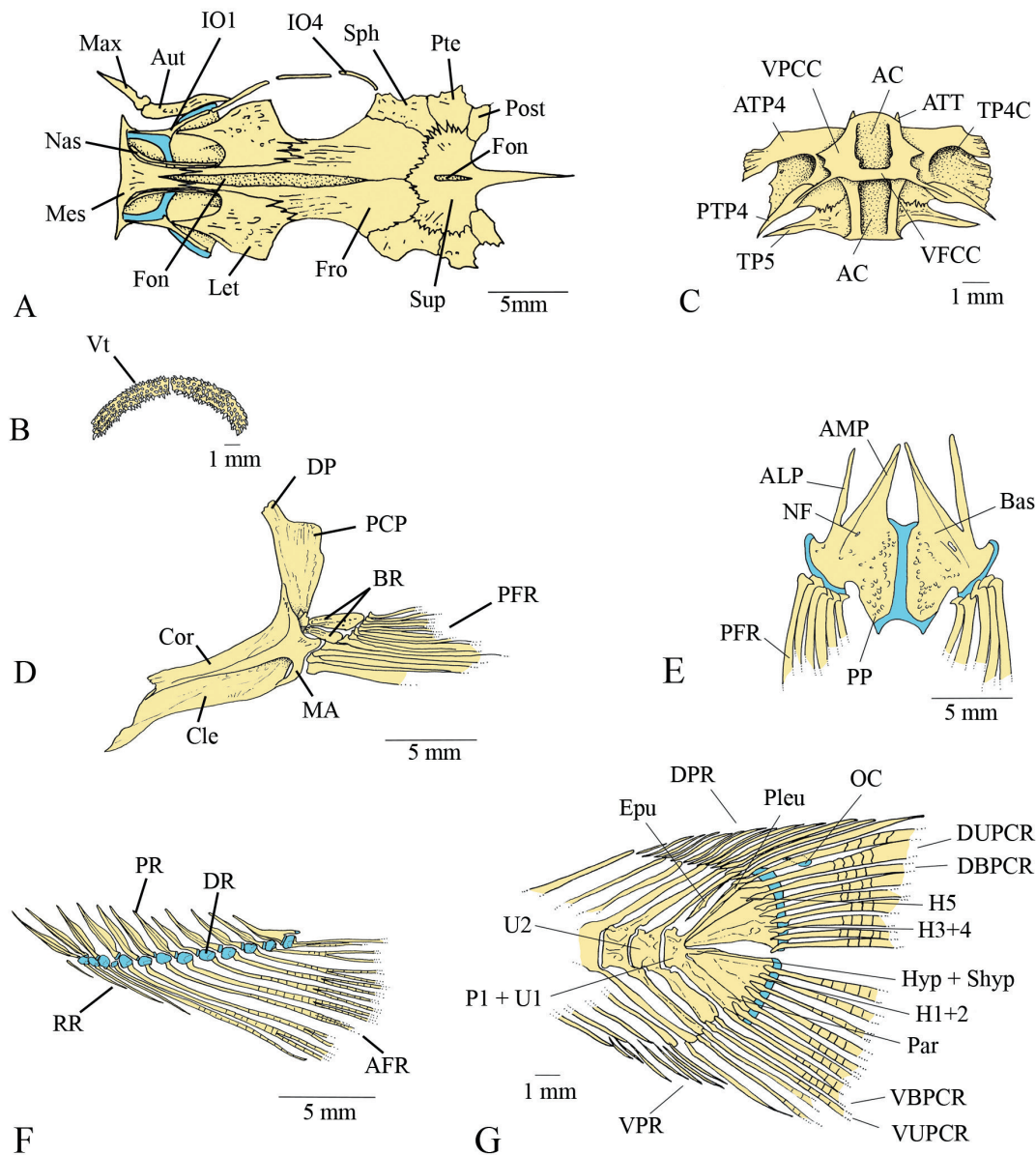


FIGURE 2 | Selected parts of *Megalonema tinga* skeleton. **A.** Cranium dorsal view; **B.** Premaxillary dentigerous plate ventral view; **C.** Weberian complex ventral view; **D.** Pectoral girdle dorsal view; **E.** Pelvic girdle dorsal view; **F.** Anal fin lateral view; **G.** Caudal-fin and supporting elements lateral view. Abbreviations: AC = aortic canal; ALP = anterolateral process; AFR = anal-fin ray; AMP = anteromedial process; ATP4 = anterior process of vertebrae 4; ATT = anterior tip of tripus; Aut = autopalatine; Bas = basipterygium; BR = Basal radials; Cle = cleithrum; Cor = coracoid; DBPCR = Dorsal branched principal caudal-fin ray; DP = dorsal process; DPR = dorsal procurent rays; DR = distal radial; DUPCR = dorsal unbranched principal caudal-fin ray; Epu = epural; Fon = fontanel; Fro = frontal; IO1 = infraorbital 1; IO4 = infraorbital 4; MA = mesocoracoid arch; Max = maxilla; H1+2 = hypural 1+2; H3+4 = hypural 3+4; H5 = hypural 5; Hyp+Shyp = hypurapophysis+secondary hypurapophysis; Let = lateral ethmoid; Mes = mesethmoid; Nas = nasal; NF = neural foramen; OC = opisthural cartilage; Par = parhypural; PCP = posterior cleithral process; PFR = pelvic-fin rays; Pleu = pleurostyle; PFR = pectoral-fin rays; PP = posterior process (ischial); Post = posttemporal; PR = proximal radial; Pte = pterotic; PTP4 = posterior transverse process of vertebrae 4; P1+U1 = preural 1 + ural1 centra; Pvr = pelvic-fin ray; RR = rudimentary ray; Sph = sphenotic; Sup = supraoccipital; TP4C = concavity of transverse process 4 (gas bladder capsule); TP5 = transverse process of vertebrae 5; U2 = Ural centrum 2; VBPCR = Ventral branched principal caudal-fin ray; VFCC = ventral flange of compound centrum; VPCC = ventral plate of compound centrum; VPR = ventral procurent ray; Vt = villiform tooth; VUPCR = ventral unbranched principal caudal-fin ray. Bones are colored yellow, and cartilages are colored blue.

Post-Weberian vertebrae 41(2) or 42(4)*, totaling 47 or 48 vertebrae. Complex caudal vertebrae (Fig. 2G) with triangular preural 1 + ural 1 centra, fused with wide parhypural, triangular hypural 1+2, articulated with hypural 3+4, and hypural 5 (hypural 3+4 and hypural 5 free), and fused with narrow pleurostyle; free, elongated, narrowly triangular epural dorsally.

Gill rakers on first branchial arch elongated, epibranchial 3(27)*, 4(1) rakers, ceratobranchial 6(1), 7(11), 8(15)* rakers. Pleural ribs 12(6)*. Lateral line complete.

Coloration in alcohol. Head and trunk dorsal region light yellow ochre; trunk becoming paler ventrally. Dorsal snout with dark brown longitudinal stripes, slightly concave, one laterally and one medially to the anterior and posterior nares. Short dark brown stripe posterior to maxillary barbel origin. Pectoral and pelvic fins translucent light ochre; dorsal fin translucent light ochre with melanocytes dispersed posteriorly; caudal fin dorsal lobe base with a faint dark brown spot; ventral lobe membranes with melanocytes.

Geographical distribution. Widely distributed in the upper Paraná River basin (Fig. 3). The presence in Argentina, in the lower Paraná River basin, revealed by molecular analysis, may be a consequence of the absence of a current geographic barrier. See Discussion for further comments.

Ecological notes. This species occurs in the middle Tibagi River, a region characterized by high topography and steep slopes (locally known as Serra do Cadeado; Maack, 2002). In this area, the river flows through deep canyons with rocky substrates and high-energy rapids. However, the new species was primarily associated with sandy substrates in backwaters and depositional zones. This psammophilous behavior suggests a specialized niche within the main river channel.

Conservation status. *Megalonema tinga* is widely distributed in the Upper Paraná River basin and, according to the IUCN criteria, can be primarily classified as Least Concern (LC). However, its populations are increasingly threatened by habitat loss from the construction of hydroelectric dams throughout the basin, which convert lotic environments into reservoirs and fragment river stretches. For instance, specimens were captured in the lotic stretches of the Tibagi River but not at its mouth, under the influence of the Capivara power plant reservoir. Furthermore, the species occurs in syntopy with its sibling species, *M. platanum*, which has expanded its range and may represent a potential competitor in these modified environments. Although the specific impacts of this interaction are currently unquantified, the combination of environmental degradation and interspecific competition warrants future monitoring to ensure the species long-term persistence.

Etymology. The specific epithet *tinga* comes from the old Tupi, the classical Brazilian indigenous language, and means “white” (Navarro, 2013), alluding to the species’ whitish coloration. It is treated here as a noun in apposition.

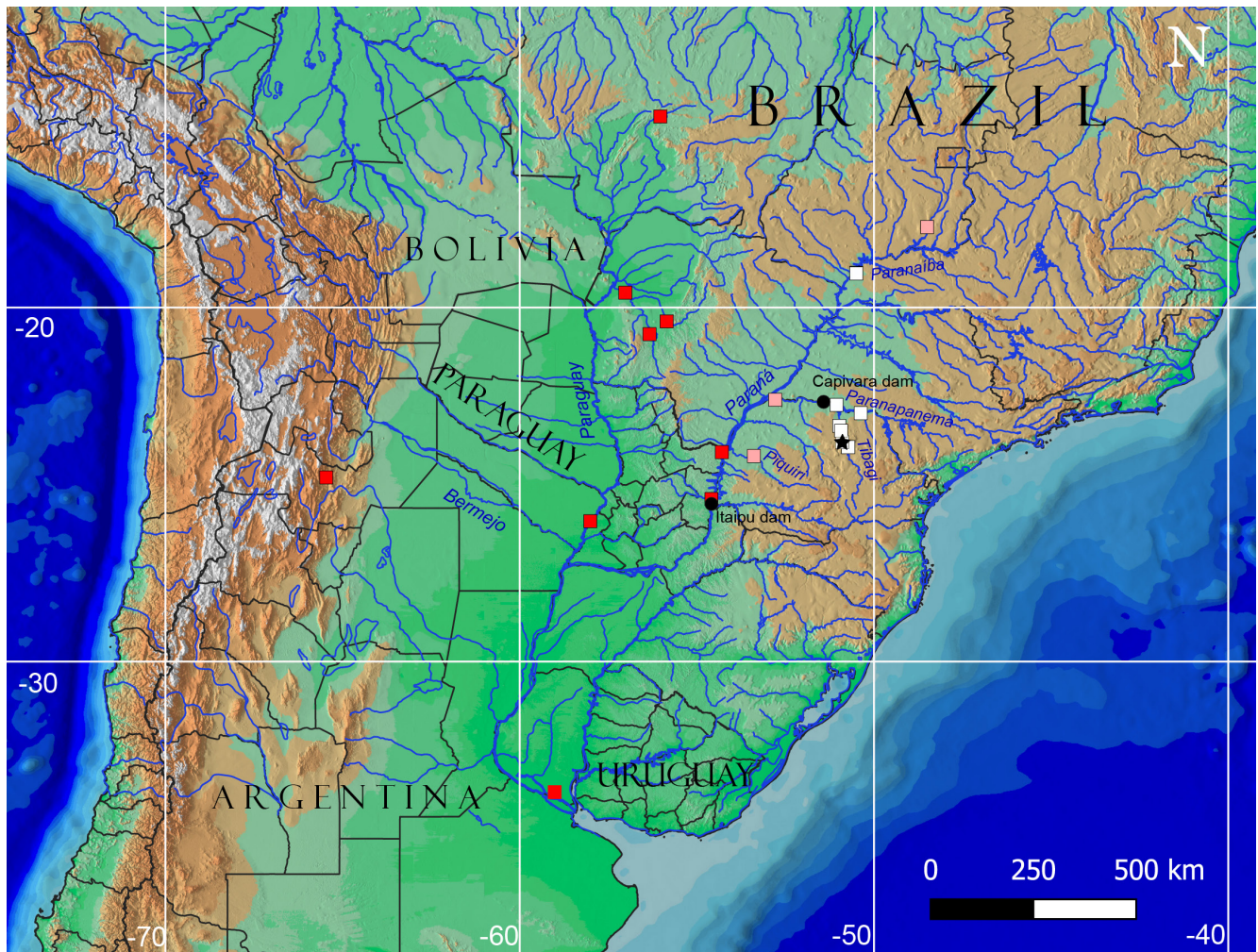


FIGURE 3 | Geographic distribution of *Megalonema tinga* and *M. platanum* in the Paraná River basin, according to the examined material. White squares represent *M. tinga*, black star is the type locality of *M. tinga*, pink squares are the sites where *M. tinga* and *M. platanum* occur in syntopy, red squares represent *M. platanum*, dark blotches are hydroelectric dams.

Body proportions. Analysis of body proportions (Tab. 1) revealed overlap among all traits, indicating that this analysis was not very sensitive in differentiating the two species. However, *M. platanum* showed higher averages on most variables than *M. tinga*. Only the distance from the dorsal fin to the adipose fin and the adipose-fin depth showed similar values.

Multivariate morphometrics analysis. The first component retained 98.3% of the variance in the original data, and all eigenvalues were positive, indicating that the components are representative of the size. The second component retained 0.5%, and the third, 0.3%. The discrimination between *M. tinga* and *M. platanum* occurred in the second principal component (Fig. 4). The variables with the highest weight were eye diameter, interorbital distance, and pre-dorsal distance (negative sign), characterizing *M. tinga* and adipose-fin base length, body depth, head length, and anal-fin base length in *M. platanum* (Tab. 2).

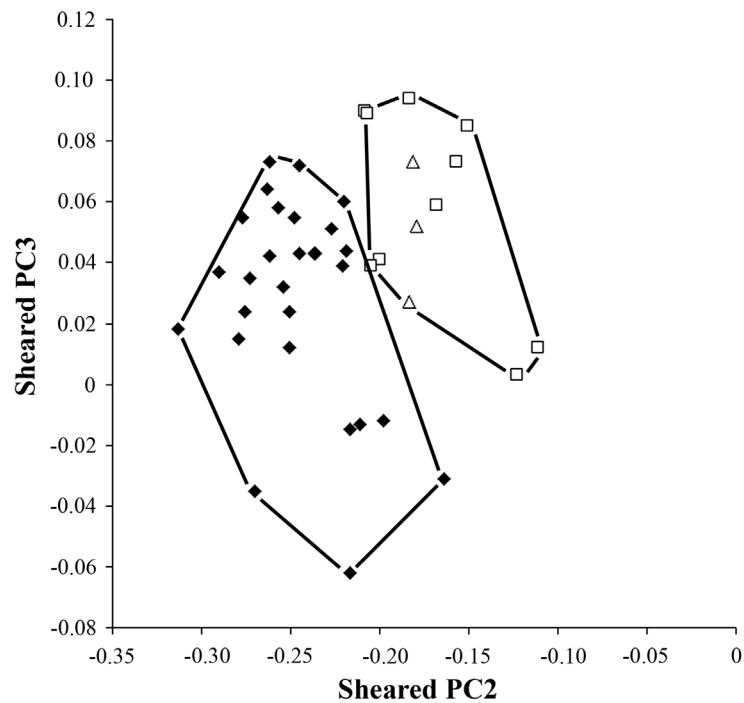


FIGURE 4 | Scatterplot of individual scores on the second and third sheared axes of Principal component analysis of combined samples of *Megalonema tinga* (n = 28; black diamonds), and *M. platanum* from Paraná (n = 3; open triangles), and upper Paraguay rivers basins (n = 10; open squares).

TABLE 2 | Variables loadings of Sheared (S) principal components analysis of combined samples of *Megalonema tinga* from the Paranapanema River basin (n = 28) and *M. platanum* from the Paraná (n = 3) and upper Paraguay (n =10) rivers basins.

Variables	PC1	S2	S3
1. Standard length	0.252572	-0.141969	-0.051801
2. Head length	0.249637	-0.166863	0.062850
3. Pre-dorsal length	0.257557	-0.280541	0.160215
4. Dorsal-fin base length	0.265645	0.141716	0.030348
5. Pre-ventral length	0.257417	-0.133686	0.078148
6. Anal-fin base length	0.224209	0.192546	-0.075017
7. Body depth	0.295475	0.327359	0.116930
8. Caudal-peduncle depth	0.263935	0.081410	0.221077
9. Eye diameter	0.132151	-0.604602	-0.162064
10. Interorbital distance	0.286445	-0.308989	0.263675
11. Snout length	0.283470	-0.107121	0.107079
12. Adipose-fin base length	0.265079	0.375737	0.455645
13. Head width	0.274839	0.100421	-0.348625
14. Head depth	0.252119	0.238699	-0.404494
15. Mouth width	0.272486	0.059421	-0.540637

Counts. The only difference between *M. tinga* and *M. platanum* was the number of gill rakers on the first ceratobranchial. In *M. tinga*, the value ranged from six to eight rakers, whereas in *M. platanum* it ranged from nine to 11, without overlapping, allowing it to be used as a diagnostic character. Also, the number of gill rakers does not have a significant correlation with the standard length (Spearman (ρ) = 0.068091; p = 0.73065), confirming the ontogenetic stability of this diagnostic character.

Delimitation of species by molecular analysis. The delimitation species analysis (ASAP, GMYC, and mPTP) consistently recovered the new species as a distinct operational taxonomic unit, separating *M. platanum* into two groups, one of which belongs to the new species *M. tinga* (Figs. 5, S3, S4, S5). The genetic distance between these two groups varies between 2.0 to 2.4%, while that between the two groups with *M. platycephalum* varies between 2.6 to 3.0%. The mean distance between *M. platanum* and *M. platycephalum* is 3.05%; between *M. platanum* and *M. tinga* is 2.05%; and between *M. platycephalum* and *M. tinga* is 2.7%. The intrapopulation distance varied from 0.0% (*M. platycephalum*), 0.08% (*M. tinga*), and 0.1% (*M. platanum*).

Among the previously identified species, one individual, identified as *Megalonema* sp. from the Amazon basin, is closely related to *M. platycephalum*, indicating the need to correct the name in the database. In addition, a specimen identified as *M. argentina* (MacDonagh, 1938; currently valid as *Pinirampus argentina*) and two specimens of *M. platanum* from the lower Paraná River were nested with others of *M. tinga*. This may indicate that *M. tinga* is not currently restricted to the upper Paraná River basin.

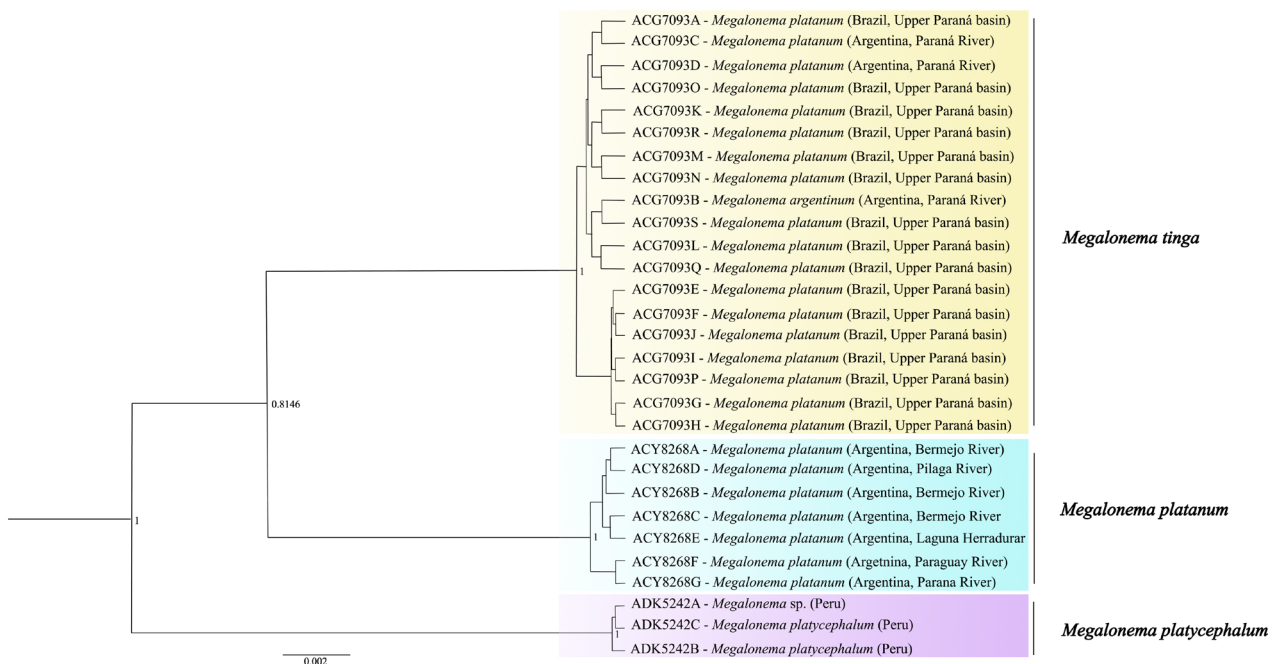


FIGURE 5 | Phylogenetic relationship of *Megalonema* species based on COI sequences. The colors represent the groups of species delimited by mPTP, ASAP, and GMYC. The codes represent Bold Systems accession numbers (with letters added to distinguish the specimens), and the names are those listed in that database. New identifications of the species are bold in the right of the figure. The scale bar represents the unity of time elapsed between branch events (nodes).

DISCUSSION

Systematic position and osteological considerations. *Megalonema tinga* exhibits all synapomorphies proposed for *Megalonema* by Lundberg, Dahdul (2008), including characters associated with the Weberian complex, the gas bladder, and the dark spot embedded in the caudal fin. The species also shares with *M. xanthum* (as illustrated in Driver, 1919) a large nasal capsule formed between the mesethmoid and lateral ethmoid, laterally circumscribed by the lacrimal (= infraorbital 1). In addition, the basipterygium of *M. tinga* is approximately as long as wide, indicating that the species does not belong to the subgenus *Eretmomegalonema*.

The caudal skeleton of *M. tinga* further contributes relevant information to the comparative morphology of Luciopimelodinae. In this species, the parhypural remains free from hypurals 1+2, a condition interpreted here as plesiomorphic because these elements are separated during early ontogeny in some Siluriformes, such as *Ictalurus punctatus* (Rafinesque, 1818) (Kubicek, 2022) and *Lophiosilurus alexandri* Steindachner, 1876 (Shibatta *et al.*, 2021). A similar condition is also present in *Steindachneridion scriptum* (Miranda Ribeiro, 1918), regarded as the sister group of the remaining Pimelodidae. In contrast, fusion between the parhypural and hypurals 1+2 occurs in *Iheringichthys labrosus* Lütken, 1874 (Shibatta, Souza-Filho, 2025), representing a derived condition within the family.

Limitations of traditional taxonomy in *Megalonema*. Comparison of the examined material with the diagnostic characters traditionally employed in identification keys for Luciopimelodinae (Eigenmann in Driver, 1919) revealed substantial limitations in reliably delimiting species within *Megalonema*. Most diagnostic traits, particularly body proportions, broadly overlapped among the analyzed specimens. Some characters, such as the relationships between eye diameter and snout length, eye diameter and head length, and the number of anal-fin rays, conform to the traditional concept of *Megalonema platanum*. Consequently, populations from the upper Paraná and upper Paraguay river basins have historically remained under a single taxonomic identity, masking cryptic diversity within the genus.

Integrative evidence supporting *Megalonema tinga*. Multivariate analyses of morphometric data proved essential for detecting morphological differentiation among the species. Univariate comparisons revealed tendencies toward lower body depth and larger eye diameter in *M. tinga* from the Tibagi River relative to *M. platanum* from the Paraná and Paraguay rivers, although extensive overlap limited the diagnostic utility of individual measurements. In contrast, principal component analysis strengthened the evidence for differentiation and additionally indicated shorter adipose-fin base length and a greater interorbital distance in *M. tinga*. Although subtle, these differences demonstrate the utility of multivariate approaches for recognizing distinct lineages in morphologically conservative groups such as *Megalonema* species.

The limitations of traditional morphometric characters become particularly evident when contrasted with the molecular results. Specimens from the Tibagi River formed a distinct lineage from populations identified as *M. platanum* from the Paraná and Paraguay river basins, despite substantial overlap observed in many external morphological traits.

These molecular data provide independent evidence that at least two evolutionary lineages have historically been treated as *M. platanum* and support the recognition of the Tibagi population as a distinct species, herein described as *Megalonema tinga*.

Chromosomal data reported by Carvalho *et al.* (2011) further reinforce this interpretation. Although populations from the Tibagi River and the lower Paraná River in Argentina share the same diploid number ($2n = 54$; karyotype formula $24m + 16sm + 2st + 12a$), specimens from the Tibagi River possess a small acrocentric supernumerary chromosome with centromeric heterochromatin, whereas individuals from the lower Paraná River exhibit heterochromatic blocks at both chromosomal ends in some chromosome pairs. These cytogenetic differences are congruent with the molecular and morphometric evidence and indicate a history of evolutionary independence between the populations. Taken together, morphometric, molecular, and cytogenetic datasets consistently support the hypothesis that the Tibagi population represents a distinct lineage, herein recognized as *Megalonema tinga*.

Historical biogeography and species delimitation. The distributional pattern observed for *M. platanum* and *M. tinga* provides additional support for their recognition as distinct evolutionary lineages. *Megalonema platanum* is broadly distributed throughout the upper Paraguay basin, where *M. tinga* is unknown, whereas *M. tinga* occurs in several tributaries of the upper Paraná basin, including the upper Paranapanema basin, where *M. platanum* has not been recorded despite extensive ichthyological surveys. This reciprocal distribution pattern, together with the morphological and molecular differences documented herein, is consistent with the hypothesis that these taxa represent independently evolving species rather than geographically structured populations of a single widespread taxon.

Conversely, specimens of *Megalonema* from the lower Paraná River in Argentina and the upper Paraguay River were morphometrically indistinguishable and shared highly similar DNA barcode sequences, supporting their identification as *M. platanum*, originally described from the lower Paraná River near the Río de la Plata (Günther, 1880). The occurrence of *M. platanum* in the upper Paraguay basin, together with its morphological and molecular similarity to populations from the lower Paraná River, also suggests a long-term historical connection between these basins. In contrast, the consistent differentiation observed in upper Paraná populations indicates prolonged geographic isolation and an independent evolutionary history for *M. tinga*.

The occurrence of both species in portions of the upper Paraná River basin requires a different interpretation. *M. platanum* was originally described from the lower Paraná basin, and the available morphological and molecular evidence indicate that specimens from the upper Paraguay basin are conspecific with populations from the type locality and adjacent portions of the lower Paraná drainage. Consequently, the presence of *M. platanum* in the upper Paraná basin may represent a relatively recent range expansion. The inundation of the Sete Quedas waterfalls following the formation of the Itaipu Reservoir eliminated one of the most important historical barriers between the lower and upper Paraná basins, creating opportunities for dispersal and faunal exchange among previously isolated fish assemblages. Under this scenario, the current occurrence of *M. platanum* in the upper Paraná basin is more parsimoniously interpreted as secondary contact with *M. tinga* rather than evidence of a long-term history of sympatry.

The congruence among morphological, molecular, and biogeographic evidence strongly supports the recognition of *M. tinga* as a distinct species. In particular, the absence of *M. tinga* from the upper Paraguay basin and of *M. platanum* from the upper Paranapanema basin provides independent geographic evidence consistent with the existence of two separate evolutionary lineages. Although broader geographic sampling may further refine our understanding of the phylogeographic history and dispersal dynamics of *M. platanum* within the Paraná basin, the taxonomic conclusions presented herein are not dependent upon such data. Rather, the available evidence consistently supports the interpretation that *M. platanum* and *M. tinga* represent distinct species with largely non-overlapping historical distributions, whose current coexistence in portions of the upper Paraná basin is likely a consequence of recent hydrographic changes and secondary range expansion.

Anthropogenic connectivity and recent distributional changes. With the currently available data, it is not possible to determine whether the historical distribution of *M. platanum* was naturally restricted to the lower Paraná River basin. However, prior to the flooding of the Sete Quedas Falls, 33 fish species from the lower Paraná basin were geographically isolated from those in the upper Paraná basin by this major biogeographic barrier (Júlio Jr *et al.*, 2009). The inundation of Sete Quedas following the construction of the Itaipu Hydroelectric Power Plant in 1984 removed this historical barrier, facilitating faunal exchange between previously isolated ichthyofaunas. Similar processes have been documented for several other Neotropical freshwater fishes (Júlio Jr. *et al.*, 2009). The ecological consequences of this secondary contact remain poorly understood, although competitive exclusion and hybridization have been proposed as potential outcomes (Agostinho *et al.*, 2016).

Molecular analyses further revealed that one specimen identified as *M. argentinum* and two specimens identified as *M. platanum* from Argentina, deposited in BOLD Systems, correspond to *M. tinga*. This finding suggests that *M. tinga*, currently recognized as native to the upper Paraná basin, may have expanded downstream following the loss of historical barriers and the subsequent implementation of fish transposition systems associated with the Itaipu Hydroelectric Power Plant.

Artificial connectivity promoted by hydroelectric impoundments, therefore, appears to have obscured historical species distributions within *Megalonema*, complicating taxonomic interpretation in morphologically conservative lineages. In this context, isolated tributaries such as the Tibagi River are particularly informative, as they may preserve remnants of the original upper Paraná ichthyofauna. The Tibagi River was effectively isolated from the main Paraná channel after the construction of the Capivara Hydroelectric Power Plant on the Paranapanema River in 1975, prior to the formation of the Itaipu Reservoir. This historical isolation may explain the persistence of *M. tinga* as a native upper Paraná lineage within the basin. Similar processes may have affected additional fish taxa, reinforcing the importance of the Tibagi River basin as a refuge for native upper Paraná species, except for taxa subsequently introduced through aquaculture, stocking programs, sport fishing, or the ornamental fish trade.

Taxonomic considerations on *Megalonema pauciradiatum*. No specimens attributable to *Megalonema pauciradiatum* were identified during the present morphological and molecular survey of the upper Paraguay River basin. This species is particularly relevant in the present context because, if valid, it would represent an additional species of *Megalonema* potentially distributed within the Paraná-Paraguay system, having originally been described from the upper Paraguay basin. According to Eigenmann (1919), *M. pauciradiatum* differs from congeners mainly by possessing nine anal-fin rays. However, the species appears to be extremely rare, being known only from the type series and absent from subsequent inventories of the upper Paraguay ichthyofauna (e.g., Britski *et al.*, 1999; Deprá *et al.*, 2022), as well as from 20 ichthyological collections surveyed through the SpeciesLink database. In contrast, *M. platanum* was consistently recorded in both previous studies and the present contribution.

The morphometric information provided by Eigenmann (1919) does not allow a secure distinction between *M. pauciradiatum* and *M. platanum*, since both nominal species were based on a single specimen and exhibit broadly overlapping measurements. Moreover, an apparent inconsistency in the reported adipose-fin length [4.75 (21.0% SL) in the original description *versus* 4.95 (20.2% SL) in the identification key] suggests a possible typographical error. No COI sequences attributable to *M. pauciradiatum* are currently available in GenBank or BOLD Systems, further limiting comparative analyses.

Although the absence of recent records and molecular data could suggest that *M. pauciradiatum* represents a junior synonym of *M. platanum*, photographs and radiographs of the holotype (CAS-ICH 63672) from the California Academy of Sciences, available through the Global Biodiversity Information Facility, appear to indicate a lower number of anal-fin rays than those observed in *M. platanum* specimens analyzed herein. Despite the limitations of this indirect assessment, the available evidence does not allow the *a priori* rejection of the species as valid. Instead, it may represent a rare and poorly sampled taxon in the upper Paraguay basin.

Overall, the results presented herein highlight the complexity of species delimitation within *Megalonema* and reinforce the importance of integrative taxonomic approaches combining morphology, osteology, cytogenetics, molecular evidence, and historical biogeography (e.g., Serejo-Saraiva *et al.*, 2026; Uzeda *et al.*, 2026). More broadly, this study demonstrates how anthropogenic alterations in river connectivity may obscure original distributional patterns and complicate the recognition of native lineages in Neotropical freshwater fishes.

Comparative material examined. Brazil: *Megalonema amaxanthum*. Acre: MZUEL 5488, 3, 74.3–86.0 mm SL, Acre River, beach above Dona Bela, Rio Branco, 28 Aug 2009, O. A. Shibatta. *Megalonema platanum*. Mato Grosso: NUP1042, 7, 91.4–121.8 mm SL, Manso reservoir, Manso River tributary, Rosário do Oeste, boundary with Nobres, Mato Grosso, -14.6961111000 -56.2536111000, 14 Nov 2003, Nupelia. Mato Grosso do Sul: MZUEL 1396, 1, 125.4 mm SL, Miranda River, Corumbá, May 1991, M. Caetano-Filho; MZUEL 2544, 1, 188.0 mm SL, Miranda River, Passo do Lontra, Corumbá, 7 Jul 2001, M. L. Orsi; MZUEL 2545, 4, 116.5–131.6 mm SL, Miranda River, Bonito, 19–26 Oct 1999, O. A. Shibatta & E. S. Silva; MZUEL 2546, 1, 240.2 mm SL, Aquidauana River, Aquidauana, 28 Oct – 4 Nov 2000, M. Caetano-Filho; MZUEL 2547, 1, 106.1 mm SL, Miranda River, Bonito, 27 Oct 1998, O. A. Shibatta & M. Caetano-Filho; MZUEL 2548, 4, 110.0–213.0 mm SL, Miranda River, Bonito, 19–26 Oct 1999, J. H. Leonhardt & O. A. Shibatta; MZUEL 2727, 1, 229.7 mm SL, Miranda River, Corumbá, 3 Sep 2002, H. S. Souza-Filho; DZSJRP 1183, 1, 178.4

mm SL, rio Miranda, Morro do Azeite, Fazenda Bodoquena, Miranda, 20,11722°S, 56,74639°W, V. Garutti, 21 Oct 1989. Paraná/Mato Grosso do Sul: MZUEL 2549, 3, 119.5–125.7 mm SL, Ilha Grande Archipelago, Paraná River, 31 Mar – 2 Apr 1995, O. A. Shibatta & M. Caetano-Filho. Paraná: NUP 1854, 4, 189.5–249.5 mm SL, Itaipu reservoir, Paraná River tributary, Guaíra, boundary with Foz do Iguaçu, -25.546667000 -54.5880556000, 15 Jun 1983, Nupelia; NUP 2016, 5, 145.2–272.6 mm SL, Itaipu reservoir, Paraná River tributary, Guaíra, 15 Jun 1983, Nupelia. São Paulo: DZSJRP 4463, 1, 244.4 mm SL, Paranapanema River, Rosana reservoir, 1 Jan 1992, CESP-Salto Grande; DZSJRP 4580, 1, 207.2 mm SL, Paranapanema River, Rosana reservoir, 1 Jan 1994, CESP-Salto Grande.

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AUTHORS' CONTRIBUTION

Oscar Akio Shibatta: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing-original draft, Writing-review and editing.

Hugo Sum de Souza-Filho: Data curation, Formal analysis, Investigation, Methodology, Writing-original draft.

Lenice Souza-Shibatta: Data curation, Formal analysis, Investigation, Methodology, Validation, Writing-original draft, Writing-review and editing.

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Not applicable.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

AI STATEMENT

ChatGPT was used to detect information redundancy, assess writing coherence, and revise English.

COMPETING INTERESTS

The authors declare no competing interests.

SUPPLEMENTARY MATERIAL

Supplementary Material File

Neotropical Ichthyology

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