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Original Article

Fish diversity in the rivers that drain the Baixada Maranhense and the Mearim basin in northeastern Brazil

Diversidade de peixes dos rios que drenam a Baixada Maranhense e bacia do Mearim no Nordeste do Brasil

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Abstract

The Baixada Maranhense Environmental Protection Area of the Brazilian state of Maranhão encompasses a biologically rich region that includes the basins of four principal rivers, the Mearim, Pericumã, Pindaré, and Turiaçu, which form a complex of wetlands. The present study provides a comprehensive inventory of the fish fauna of the rivers that drain the Baixada Maranhense based on the identification of voucher specimens that were deposited in a scientific collection. Expeditions were conducted between 2014 and 2020. The inventory identified a total of 100 fish species representing 79 genera, 34 families, and 11 orders, which are found in both freshwater and estuarine environments. Six (*Potamotrygon orbignyi*, *Leporinus piau*, *Moenkhausia loweae*, *Serrasalmus spilopleura*, *Pachypops fourcroi* and *Peckoltia greedoi*) of the 100 taxa identified here are considered to be new records for one or more of the basins surveyed during this study, based on the existing data, while four – *Colossoma macropomum*, *Megaleporinus macrocephalus*, *Cichla* sp. and *Cichla kelberi* – are not native. The most speciose orders were the Siluriformes and Characiformes, while the most diverse families were the Loricariidae, Characidae, Auchenipteridae, Cichlidae, and Serrasalmidae. These data are consistent with the findings of most of the previous studies of freshwater ecosystems in the Neotropical region, in particular those of the rivers of Maranhão. The results of the present study represent an important advance in the understanding of the diversity of the fish fauna of the Mearim, Pericumã, Pindaré, and Turiaçu rivers, which are still poorly studied, and have likely had their diversity underestimated up to now.

Keywords: species list, fish fauna, taxonomy, hydrographic basin.

Resumo

A Área de Proteção Ambiental da Baixada Maranhense do estado brasileiro do Maranhão abrange uma região biologicamente rica que engloba as bacias de quatro rios principais, Mearim, Pericumã, Pindaré e Turiaçu, formando um complexo de áreas inundáveis. O presente estudo fornece um inventário abrangente da ictiofauna de rios que drenam a Baixada Maranhense a partir da identificação de espécimes com material testemunho depositados em coleção científica. As expedições foram realizadas entre 2014 e 2020. O inventário identificou um total de 100 espécies de peixes representando 79 gêneros, 34 famílias e 11 ordens que são encontradas em ambientes de água doce e estuarinos. Dos 100 táxons identificados, seis (*Potamotrygon orbignyi*, *Leporinus piau*, *Moenkhausia loweae*, *Serrasalmus spilopleura*, *Pachypops fourcroi* e *Peckoltia greedoi*) são considerados novo registros para uma ou mais das drenagens aqui levantadas, em comparação com os dados existentes, enquanto quatro: *Colossoma macropomum*, *Megaleporinus macrocephalus*, *Cichla* sp. e *Cichla kelberi* não são nativos. As ordens mais especiosas foram Siluriformes

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e Characiformes, enquanto as famílias mais diversas foram Loricariidae, Characidae, Auchenipteridae, Cichlidae e Serrasalmidae. Esses dados corroboram a maioria dos outros estudos de ecossistemas de água doce da região Neotropical, em particular o dos rios do Maranhão. Os resultados do presente estudo representam um avanço importante no conhecimento da diversidade da fauna de peixes dos rios Mearim, Pericumã, Pindaré e Turiaçu, que ainda são pouco estudados e provavelmente com uma diversidade subestimada.

Palavras-chave: lista de espécies, ictiofauna, taxonomia, bacias hidrográficas.

1. Introduction

The northern Brazilian state of Maranhão covers a total area of 331,983.29 km^2 (Brasil, 2002; Porto et al., 2019), which encompasses phytogeographic and climatological features that reflect the transition between the northern (Amazon) and northeastern regions of Brazil. The state has a number of major rivers, lacustrine basins, and subterranean reservoirs (Maranhão 2002, 2011, 2016). The Baixada Maranhense Environmental Protection Area, located in the northern mesoregion of the state, is a wetland of considerable international importance, and has been designated as one of the Brazilian Ramsar sites (Nunes et al., 2011; Ramsar, 2022). The Baixada Maranhense encompass a vast region with a rich biodiversity, in particular of fish, encompassing major rivers, such as the Aurá, Mearim, Pericumã, Pindaré, and Turiaçu, which form a complex of wetlands (Castro and Dourado 2011; Nunes et al., 2011; Silva et al., 2015b).

Fish are the most diverse and abundant vertebrates, with a total of 36,532 valid species worldwide (Fricke et al., 2023b). The Neotropical region, which includes South America and part of Central America, has the most diverse freshwater fish fauna found anywhere on the planet, comprising more than 6,200 valid species (Birindelli and Sidlauskas, 2018; Albert et al., 2020), of which, 5,160 are from South America (Reis et al., 2016) and of these, 3,523 are present in Brazil (Froese and Pauly, 2023). This enormous fish diversity has attracted considerable interest from the scientific community, which has led to significant advances in the understanding of the evolution and diversification of these organisms (Birindelli and Sidlauskas, 2018; Albert et al., 2020; Cassemiro et al., 2023). Even so, research on the freshwater fish fauna of the Neotropics is still relatively incipient (Albert et al., 2020), and the data available for many river basins are still far from complete (Reis et al., 2003, 2016).

The fish fauna of the Brazilian state of Maranhão has been the subject of a number of different studies over the past few decades, which have made advances in the areas of taxonomy, the systematics of both species and groups, including the description of new taxa, the composition of communities, geographic distributions, and biogeography (Piorski et al., 1998, 2003, 2008, 2017; Soares, 2005; Castro et al., 2010; Barros et al., 2011; Birindelli et al., 2011; Castro and Dourado, 2011; Ottoni, 2011; Fraga et al., 2012; Almeida et al., 2013; Ramos et al., 2014; Ribeiro et al., 2014; Lima et al., 2015, 2019; Matavelli et al., 2015; Melo et al., 2016; Nascimento et al., 2016; Guimarães et al., 2018, 2020a, b, c, 2021; Abreu et al., 2019; Almeida et al., 2019; Brito et al., 2019; Teixeira et al., 2019; Oliveira et al., 2020, 2022; Saraiva et al., 2021; Silva et al., 2021; Dutra et al., 2022; Vieira et al., 2023). Based on a review of the published data, Koerber et al. (2022) recorded a total of 263 species of freshwater fish for the state of Maranhão. Even so, a number of lacunas still exist in the understanding of the true diversity of the freshwater fish of the state (Ramos et al., 2014; Koerber et al., 2022).

The few studies available on the fish fauna of the rivers that form the Baixada Maranhense have been based on the compilation of published records, with no revision or updating of the taxonomic status of the species listed (Castro and Dourado, 2011). In a previous study, Piorski et al. (2003) listed 36 species for the Pindaré and Turiaçu rivers, based primarily on observations of the fishing practises of indigenous populations. Soares (2005) subsequently reported the occurrence of 60 species in the Mearim River. During an extensive, long-term inventory of the Pindaré River, Guimarães et al. (2020a) identified 101 species, and later listed 130 species for the Mearim basin (Guimarães et al., 2020c). In the most recent study of the Pindaré River, Guimarães et al. (2021) catalogued 102 species, of which 32 are listed as official fishery resources or are authorized for capture as ornamental fish. These authors reinforce the need for further, more detailed taxonomic studies to better define the diversity of fish that inhabit these poorly-studied drainages, which is almost certainly underestimated. By contrast, the Pericumã and Turiaçu rivers have received virtually no attention from researchers, with practically no data being available, which reinforces the need for further studies in these basins. Recent studies in molecular taxonomy that focused on the tributaries of the Mearim (Silva et al., 2021) and Turiaçu (Teixeira et al., 2019) rivers identified 26 and 30 species, respectively, confirming the endemism of some taxa to the drainages of the Brazilian northeastern and others with Amazonian characteristics.

The present study is based primarily on an inventory of the fish species collected from the rivers that drain the Baixada Maranhense Environmental Protection Area of the state of Maranhão, which provides important advances and new insights into the aquatic biodiversity of this conservation unit. These data will also be important for the development of effective conservation strategies and measures for the management of the region's fishery resources. The species list refers to the drainages of the Mearim, Pindaré, Pericumã, and Turiaçu rivers with identified voucher specimens being deposited in a zoological collection.

2. Material and Methods

2.1. Study area

The Baixada Maranhense is located to the west of the island of São Luís, in northern Maranhão (1°59'–4°00' S, 44°21'–45°33' W; Figure 1). This area encompasses the

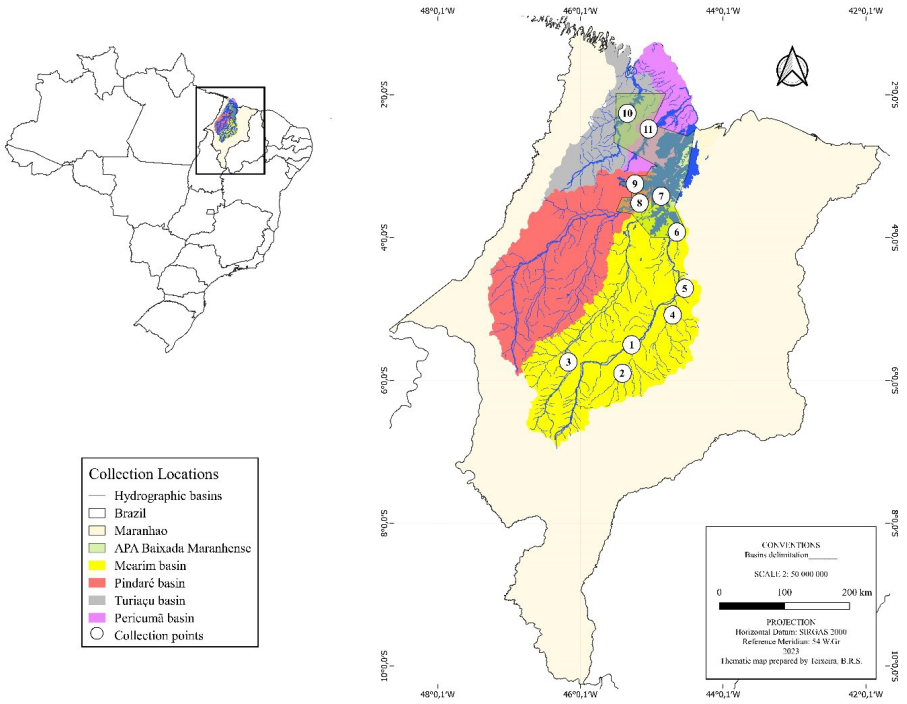

Figure 1. Sampling sites in the drainages of the Mearim, Pindaré, Turiaçu, and Pericumã rivers, in Maranhão state, Brazil . 1,5,6,7 - Mearim river; 2-Corda river; 3-Grajaú river; 4-Flores river; 8, 9-Pindaré river; 10-Turiaçu river; 11-Pericumã river.

hydrographic basins of the Mearim and Pindaré rivers, as well as the secondary basins of the Aurá, Pericumã, and Turiaçu rivers, which overflow and inundate the local floodplains on an annual cycle, forming a large number of both temporary and permanent lakes (Almeida-Funo et al., 2010).

The hydrographic basin of the Mearim River is the largest in the state of Maranhão, with a total area of 99,058.68 km^2. The principal river is the Mearim, which originates in the Serra da Menina, an upland area that includes the municipalities of Formosa da Serra Negra, Fortaleza dos Nogueiras, and São Pedro dos Crentes, at an altitude of approximately 650 m above sea level, and follows a long course, of 832.18 km, before discharging into São Marcos Bay, between the state capital, São Luís, and the town of Alcântara. The Mearim has a number of tributaries, the largest of which is the Pindaré River (Maranhão, 2016). The Pindaré basin covers an area of 40,400 km^2, and its principal river is 720 km long, from its origin in the Serra do Gurupi to its mouth in São Marcos Bay. The principal tributary of the Pindaré is the 270 km-long Zutiua River (Maranhão, 2002; Costa et al., 2011).

The hydrographic basin of the Turiaçu River covers an area of 14,149.87 km^2. The river originates on the slopes of the Serra do Tiracambu, and runs 442.01 km before discharging into Turiaçu Bay, between the municipalities of Turiaçu and Bacuri (Maranhão, 2016). The basin of the 126 km-long Pericumã River is part of the West Coast hydrological system, and covers an area of 10,800 km^2. The rivers of this system are typical of the Amazon region, with an ample estuarine sector lined with mangroves, which is under the constant influence of the local tides (Maranhão, 2002, 2016).

2.2. Sampling

The samples were collected from 11 points on the Mearim, Pindaré, Turiaçu, and Pericumã rivers. In the case of the Mearim River, in addition to its lower course, samples were also collected from the middle and upper stretches of the river, and its headwaters, at Corda, Grajaú, and Flores (Figure 1; Table 1). A total of 25 field trips, each lasting approximately three days, were conducted between May 2014 and February 2020, mostly on the Mearim River.

The collection of the biological samples was authorized by the Federal Institute for the Environment and Renewable Natural Resources (IBAMA) through the emission of ICMBio (Chico Mendes Institute for the Conservation of Biodiversity) licenses numbers 42119-1, 42119-2, 46367-1, 46367-2 and 64601-2.

2.3. Collection and identification of the specimens

The fish were captured using a number of different types of fishing gear, including cast nets, gillnets with a variety of mesh sizes (15–35 mm), and bottom paternoster lines, which were set transversally across the river. Samples of muscle tissue were extracted from all the specimens and placed in 1.5 mL microtubules containing 80% ethanol, which were stored at -20ºC for future molecular analyses. The specimens were first fixed in 10% formalin for a few days and then transferred to 70% alcohol for permanent storage (Malabarba and Reis, 1987). The specimens were

Table 1. Coordinates of the sampling points (municipalities) in the Mearim, Pindaré, Turiaçu, and Pericumã basins, in Maranhão, Brazil.

Site	River	Municipality	Coordinates
01	Mearim	Barra do Corda	05° 30' 10.50" S / 045° 15' 12.3" W
02	Corda		05° 50' 29.30" S / 045° 25' 35.7" W
03	Grajaú	Grajaú	05° 44' 08.41" S / 046° 09' 06.24" W
04	Flores	Joselândia	05° 05' 51.96" S / 044° 39' 00.82" W
05	Mearim	Pedreiras	04° 42' 35.60" S / 044° 34'33.60" W
06	Mearim	São Mateus do Maranhão	03° 52' 49.60" S / 044°36' 50.70" W
07	Mearim	Vitoria do Mearim	03° 27' 54.30" S / 044° 52' 11.40" W
08	Pindaré	Pindaré Mirim	03° 29' 28.00" S / 045° 08' 46.00" W
09	Pindaré	Penalva	03° 18' 9.95" S / 045° 11' 29.60" W
10	Turiaçu	Santa Helena	02° 15' 49.00" S / 045° 19' 24.00" W
11	Pericumã	Pinheiro	02° 31' 17.00" S / 045° 04' 57.00" W

identified using specialized references for each taxonomic group (Malabarba, 2004; Buitrago-Suárez and Burr, 2007; Piorski et al., 2008; Birindelli et al., 2011; Ottoni, 2011; Ribeiro et al., 2017; Guimarães et al., 2018; Saraiva et al., 2021; Oliveira et al., 2022), and were later confirmed by one of the authors of the present study (José Luís Olivan Birindelli), a specialist in fish taxonomy. The voucher material was deposited in the ichthyological collection of the Museum of Zoology at Londrina State University (MZUEL). The taxonomic classification, the valid scientific names of the species, authors, and the year when the taxon was described, together with data on the geographic distribution of the species were all based on the reviews of Fricke et al. (2023a, b).

3. Results

A total of 2,859 specimens were collected from the rivers that drain the Baixada Maranhense, representing 100 fish species distributed in 79 genera, 34 families, and 11 orders (Table 2, Figure 2). These species occupy a variety of environments, ranging from exclusively freshwater habitats to estuaries. Overall, 81 species were collected from the Mearim River, 49 from the Pindaré, 34 from the Turiaçu, and 18 from the Pericumã River, of which, five – *Hoplerythrinus unitaeniatus* (Spix & Agassiz, 1829), *Hoplias malabaricus* (Bloch, 1794), *Crenicichla brasiliensis* (Bloch, 1792), *Trachelyopterus galeatus* (Linnaeus, 1766), and *Prochilodus lacustris* Steindachner, 1907 – were common to all four study rivers (Table 2).

The records of *Leporinus piau* Fowler, 1941 from the Mearim, Pindaré, and Pericumã rivers represent a new occurrence of the species in these basins. New occurrence records were also obtained for *Potamotrygon orbignyi* (Castelnau, 1855), *Pachypops fourcroi* (Lacepède, 1802), and *Peckoltia greedoi* Armbruster, Werneke & Tan, 2015, from the Mearim River, *Moenkhausia loweae* Géry, 1992 for the Pindaré, and *Serrasalmus spilopleura* Kner, 1858 for the Pericumã River (Table 2).

The distribution of the species by order and family were highly similar in the Pindaré and Mearim rivers (41 shared taxa), which were also the most diverse areas, whereas the Turiaçu and Pericumã basins were less diverse. A total of 34 species were exclusive to the Mearim River. Six exclusive taxa were recorded in the Pindaré and Turiaçu rivers, and two in the Pericumã (Table 2).

Considering the whole dataset, the most speciose orders was the Siluriformes, with 38 species (38% of the total), followed by the Characiformes, with 35 (35%), the Cichliformes, with eight (8%), and the Gymnotiformes, with seven species (7%). Together, these four orders account for 88% of the species recorded during the present study. By contrast, three orders, the Elopiformes, Mugiliformes and Synbranchiformes, were each represented by only a single taxon (Figure 3).

The families with the highest species richness were the Loricariidae, with 13 species (13% of the total), followed by the Characidae, with 10 (10%), the Auchenipteridae and Cichlidae, each with eight species (8%), and Serrasalmidae, with seven (7%) species (Figure 4). Four of the 100 taxa registered in the present study – *Colossoma macropomum* (Cuvier, 1816), *Megaleporinus macrocephalus* (Garavello & Britski, 1988), *Cichla* sp., and *Cichla kelberi* Kullander & Ferreira, 2006 – are not native.

4. Discussion

Castro and Dourado (2011) compiled an inventory of the fish fauna of the Baixada Maranhense, including the hydrographic basins of the Mearim, Pindaré, Turiaçu, and Pericumã rivers, based on published records, and identified a total of 109 species. However, more recent studies of these hydrographic systems have revealed an even greater diversity of fish (Guimarães et al., 2020a, c, 2021). One of the earliest ichthyological surveys conducted on the Pindaré and Turiaçu rivers listed only 36 species (Piorski et al., 2003), although the number of taxa recorded from the region has grown considerably in recent years as new studies have been conducted in specific sections or along the entire length of the rivers that contribute to the formation of the Baixada Maranhense wetland. The most recent studies of the Pindaré basin

Table 2. List of the fish species collected from the Pindaré (PIN), Mearim (MEA), Turiaçu (TU), and Pericumã (PER) rivers, in the state of Maranhão, Brazil.

ORDER/FAMILY/SPECIES	PIN	MEA	TUR	PER	VOUCHER
MYLIOBATIFORMES					
Potamotrygonidae					
Potamotrygon motoro (Müller & Henle, 1841)		X			MZUEL 15322, 15423
Potamotrygon orbignyi (Castelnau, 1855) (NR)		X			MZUEL 15321
ACANTHURIFORMES					
Sciaenidae					
Pachypops fourcroi (Lacepède, 1802) (NR)		X			MZUEL 10454, 15365
Plagioscion squamosissimus (Heckel, 1840)	X	X			MZUEL 17412, 15314
CARANGIFORMES					
Achiridae					
Achirus achirus (Linnaeus, 1758)		X			MZUEL 15325
Centropomidae					
Centropomus parallelus Poey, 1860		X			MZUEL 15339
CHARACIFORMES					
Acestrorhynchidae					
Acestrorhynchus lacustris (Lütken, 1875)	X	X	X		MZUEL 17366, 15329, 17416
Acestrorhynchus microlepis (Jardine, 1841)			X		MZUEL 17417
Anostomidae					
Leporinus friderici (Bloch, 1794)		X		X	MZUEL 10532, 15356, 17364
Leporinus piau Fowler, 1941 (NR)	X	X		X	MZUEL 17367, 10530, 17418
Megaleporinus macrocephalus (Garavello & Britski, 1988)*		X			MZUEL 15357
Schizodon dissimilis (Garman, 1890)	X	X			MZUEL 17368, 15388
Schizodon sp.			X		MZUEL 17419
Characidae					
Astyanax bimaculatus (Linnaeus, 1758)	X	X		X	MZUEL 17371, 15334, 17354
Charax awa Guimarães, Brito, Ferreira & Ottoni, 2018**			X		MZUEL 17459
Moenkhausia loweae Géry, 1992 (NR)	X				MZUEL 17372
Moenkhausia oligolepis (Günther 1864)		X			MZUEL 17466
Moenkhausia dichroura (Kner, 1858)		X			MZUEL 15364, 15363
Psellogrammus kennedyi (Eigenmann, 1903)		X			MZUEL 15377, 15378
Poptella compressa (Günther 1864)	X	X	X		MZUEL 17376, 15386, 15409, 17438
Roeboides margareteae Lucena, 2003**	X	X			MZUEL 17369, 15340
Roeboides sazimai Lucena, 2007**	X				MZUEL 17370
Tetragonopterus argenteus Cuvier, 1816			X		MZUEL 17420
Cynodontidae					
Cynodon gibbus (Spix & Agassiz, 1829)	X	X			MZUEL 17380, 15346
Curimatidae					
Curimata macrops Eigenmann & Eigenmann, 1889**	X	X			MZUEL 17378, 15345
Psectrogaster rhomboides Eigenmann & Eigenmann 1889	X	X	X		MZUEL 17379, 15376, 17429, 17430
Steindachnerina notonota (Miranda Ribeiro, 1937)		X		X	MZUEL 15391, 17362
Erythrinidae					
Hoplerythrinus unitaeniatus (Spix & Agassiz, 1829)	X	X	X	X	MZUEL 17381, 15353, 17427, 17352
Hoplias malabaricus (Bloch, 1794)	X	X	X	X	MZUEL 17382, 15323, 17426, 17351
Gasteropelecidae					
Gasteropelecus sternicla (Linnaeus, 1758)		X			MZUEL 17464
Hemiodontidae					
Hemiodus parnaguae Eigenmann & Henn, 1916**	X	X	X		MZUEL 17384, 15352, 17425
Iguanodectidae					
Bryconops sp.		X			MZUEL 15337
Prochilodontidae					
Prochilodus lacustris Steindachner, 1907**	X	X	X	X	MZUEL 17383, 15375, 17428, 17355

*Indicates introduced species; **Endemic to the Maranhão and Parnaíba hydrological units, *sensu* Hubert and Renno (2006); (NR)New Record.

Table 2. Continued...

ORDER/FAMILY/SPECIES	PIN	MEA	TUR	PER	VOUCHER
Serrasalmidae					
Colossoma macropomum (Cuvier, 1816)*		X			MZUEL 15316
Metynnis lippincottianus (Cope, 1870)	X		X	X	MZUEL 17375, 17424, 17363
Mylossoma duriventre (Cuvier, 1818)		X			MZUEL 15317
Pygocentrus nattereri Kner, 1858	X	X			MZUEL 17377, 15384
Serrasalmus eigenmanni Norman, 1929			X		MZUEL 17422
Serrasalmus rhombeus (Linnaeus, 1766)	X	X	X		MZUEL 17373, 15389, 17421
Serrasalmus spilopleura Kner, 1858 (NR)				X	MZUEL 17353
Triportheidae					
Triportheus signatus (Garman, 1890)	X	X	X		MZUEL 17374, 15397, 17423
CICHLIFORMES					
Cichlidae					
Aequidens tetramerus (Heckel, 1840)				X	MZUEL 17360
Cichla kelberi Kullander & Ferreira, 2006*	X				MZUEL 17408
Cichla sp.		X			-
Cichlasoma zarskei Ottoni, 2011**		X	X	X	MZUEL 15341, 17448, 17460
Crenicichla brasiliensis (Bloch, 1792)	X	X	X	X	MZUEL 17410, 15344, 17445, 17359
Crenicichla sp.			X		MZUEL 17446
Geophagus parnaibae Staeck & Schindler, 2006**	X	X	X		MZUEL 17409, 15349, 17447
Satanoperca sp.	X	X			MZUEL 17411, 15387
CLUPEIFORMES					
Engraulidae					
Lycengraulis batesii (Günther, 1868)		X			MZUEL 15361
Pterengraulis atherinoides (Linnaeus, 1766)	X	X			MZUEL 17414, 15381
Pristigasteridae					
Pellona castelnaeana Valenciennes, 1847		X			MZUEL 15320
ELOPIFORMES					
Megalopidae					
Megalops atlanticus Valenciennes, 1847		X	X		MZUEL 15362, 17451
GYMNOTIFORMES					
Apteronotidae					
Apteronotus albifrons (Linnaeus, 1766)		X			MZUEL 15332
Gymnotidae					
Electrophorus varii de Santana, Wosiacki, Crampton, Sabaj, Dillman, Mendes-Júnior & Castro, 2019		X			MZUEL 15347
Gymnotus carapo Linnaeus, 1758		X		X	MZUEL 15318, 17361
Rhamphichthyidae					
Rhamphichthys atlanticus Triques, 1999**	X	X			MZUEL 17413, 17453
Rhamphichthys pantherinus Castelnau, 1855			X		MZUEL 17449
Sternopygidae					
Eigenmannia sp.				X	MZUEL 17365
Sternopygus macrurus (Bloch & Schneider, 1801)	X	X		X	MZUEL 17415, 15392, 17450
MUGILIFORMES					
Mugilidae					
Mugil incilis Hancock, 1830		X			MZUEL 10453
SILURIFORMES					
Ariidae					
Sciades couma (Valenciennes, 1840)	X	X			MZUEL 17406, 15327
Aspredinidae					
Aspredo aspredo (Linnaeus, 1758)		X			MZUEL 15333

*Indicates introduced species; **Endemic to the Maranhão and Parnaíba hydrological units, *sensu* Hubert and Renno (2006); (NR)New Record.

Table 2. Continued...

ORDER/FAMILY/SPECIES	PIN	MEA	TUR	PER	VOUCHER
Auchenipteridae					
Ageneiosus dentatus Kner, 1858	X	X			MZUEL 17385, 15330
Ageneiosus ucayalensis Castelnau, 1855		X			MZUEL 17461
Ageneiosus inermis (Linnaeus, 1766)	X	X			MZUEL 17386, 15319
Ageneiosus vittatus Steindachner, 1908	X				MZUEL 17387
Auchenipterus menezesi Ferraris & Vari, 1999**	X	X	X		MZUEL 17388, 15336, 17431
Pseudauchenipterus nodosus (Bloch, 1794)		X			MZUEL 15380
Tatia sp.		X			MZUEL 15395
Trachelyopterus galeatus (Linnaeus, 1766)	X	X	X	X	MZUEL 17389, 15396, 17432, 17357
Callichthyidae					
Callichthys callichthys (Linnaeus 1758)	X	X		X	MZUEL 17393, 15338, 17358
Corydoras julii Steindachner, 1906		X			MZUEL 15342
Corydoras treitlii Steindachner 1906**		X			MZUEL 15343
Megalechis thoracata (Valenciennes 1840)	X				MZUEL 17392
Doradidae					
Hassar affinis (Steindachner, 1881)**	X	X	X		MZUEL 17390, 17454, 17433
Platydoras brachylecis Piorski, Garavello, Arce H. & Sabaj Pérez, 2008**	X	X	X		MZUEL 17391, 15374, 17434
Heptapteridae					
Pimelodella cristata (Müller, Troschel, 1849)		X			MZUEL 15368, 15370, 17462, 17463
Pimelodella parnahybae Fowler, 1941**	X		X		MZUEL 17399, 17400, 17443
Rhamdia quelen (Quoy & Gaimard, 1824)		X	X	X	MZUEL 15385, 17444, 17356
Loricariidae					
Ancistrus sp.		X			MZUEL 15331, 17467
Farlowella sp.		X			MZUEL 15348, 17469
Hemiodontichthys acipenserinus (Kner, 1853)		X			MZUEL 15351
Hypostomus krikati Oliveira, Guimarães, Brito & Ottoni, 2022**	X	X	X		MZUEL 17401, 15355, 17440
Hypoptopoma incognitum Aquino & Schaefer, 2010	X	X			MZUEL 17402, 15354
Loricariichthys derbyi Fowler, 1915	X	X	X		MZUEL 17403, 15360, 17442
Loricaria cataphracta Linnaeus, 1758	X	X			MZUEL 17404, 15358, 15359
Loricaria turi Saraiva, Abreu, Ottoni & Piorsk, 2021**			X		MZUEL 17441
Peckoltia greedoi Armbruster, Werneke & Tan, 2015** (NR)		X			MZUEL 17465,
Peckoltia sp.		X			MZUEL 15366, 15367
Pterygoplichthys parnaibae (Weber, 1991)**	X	X			MZUEL 17405, 15382
Pterygoplichthys sp.		X			MZUEL 15383
Sturisoma sp.		X			MZUEL 15393, 17468
Pimelodidae					
Brachyplatystoma vaillantii (Valenciennes, 1840)	X				MZUEL 17407
Hemisorubim platyrhynchos (Valenciennes, 1840)	X	X	X		MZUEL 17398, 15313, 17452, 17435
Pimelodus blochii Valenciennes, 1840	X	X	X		MZUEL 17394, 15371, 15372, 17437
Pimelodus ornatus Kner, 1858	X	X	X		MZUEL 17395, 15315, 17439
Pseudoplatystoma punctifer (Castelnau, 1855)	X	X	X		MZUEL 17397, 15326, 17436
Sorubim lima (Bloch & Schneider, 1801)	X	X			MZUEL 17396, 15390
SYNBRANCHIFORMES					
Synbranchidae					
Synbranchus marmoratus Bloch, 1795		X			MZUEL 15394

*Indicates introduced species; **Endemic to the Maranhão and Parnaíba hydrological units, *sensu* Hubert and Renno (2006); (NR)New Record.

identified 101 (Guimarães et al., 2020a) and 102 species (Guimarães et al., 2021). Soares (2005) surveyed the lower Mearim River, and catalogued 60 fish species, whereas 15 years later, the total number of taxa recorded for this basin had reached 130 (Guimarães et al., 2020c). During this same period, Abreu et al. (2019) and Koerber et al. (2022) reviewed and compiled the data available on the fish fauna of the rivers of Maranhão, providing important insights into the diversity of these fish.

In a review of the principal studies of the fish fauna of all the coastal river systems of the state of Maranhão, Abreu et al. (2019) listed 160 species, of which, 112 were recorded in

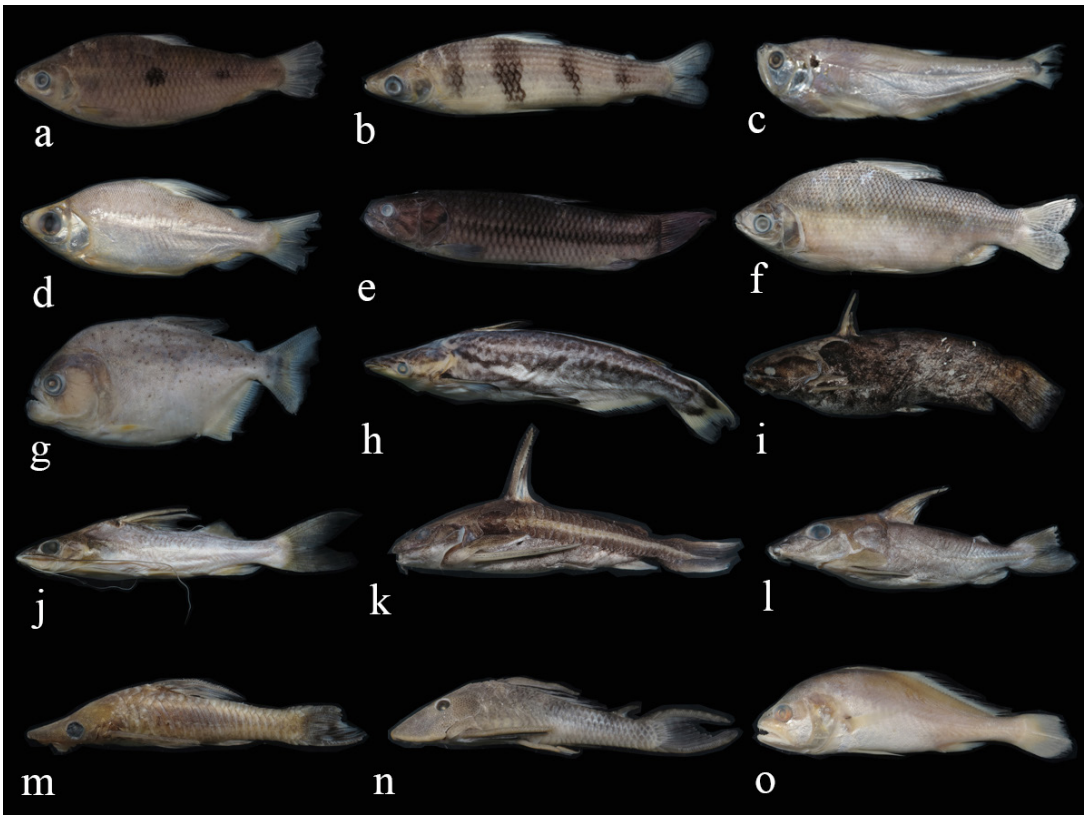

Figure 2. Some species collected in rivers of Baixada Maranhense, Northeastern Brazil. (a) *Leporinus piau*, MZUEL 17418, 141.75 mm SL; (b) *Schizodon dissimilis*, MZUEL 17368, 170.36 mm SL; (c) *Cynodon gibbus*, MZUEL 17380, 178.85 mm SL; (d) *Curimata macrops*, MZUEL 17378, 124.74 mm SL; (e) *Hoplerythrinus unitaeniatus*, MZUEL 17352, 171.39 mm SL; (f) *Prochilodus lacustris*, MZUEL 17355, 204.53 mm SL; (g) *Pygocentrus nattereri*, MZUEL 17377, 96.92 mm SL; (h) *Ageneiosus vittatus*, MZUEL 17387, 170.45 mm SL; (i) *Trachelyopterus galeatus*, MZUEL 17357, 122.05 mm SL; (j) *Pimelodus blochii*, MZUEL17394, 127.71 mm SL; (k) *Platydoras brachylecis*, MZUEL 17391, 131.86 mm SL; (l) *Hassar affinis*, MZUEL 17390, 119.03 mm SL; (m) *Hypoptopoma incognitum*, MZUEL 17402, 67.05 mm SL; (n) *Hypostomus krikati*, MZUEL 17440, 120.06 mm SL; (o) *Plagioscion squamosissimus*, MZUEL 17412, 157.52 mm SL.

the rivers that form the Baixada Maranhense. A recent update of the fish fauna of the state of Maranhão, which included the drainages surveyed in the present study, listed 263 species, as well as identifying the principal knowledge gaps that require further investigation. This number of species does not refer specifically to the basins of the Baixada Maranhense, however, but to all the freshwater habitats found in Maranhão (Koerber et al., 2022). The inventory presented here, considering all the rivers evaluated, listed 100 taxa, of which six (*Potamotrygon orbignyi* (Castelnau, 1855), *Leporinus piau* Fowler, 1941, *Moenkhausia loweae* Géry, 1992, *Serrasalmus spilopleura* Kner, 1858, *Pachypops fourcroi* (Lacepède, 1802) and *Peckoltia greedoi* Armbruster, Werneke & Tan, 2015) are considered to be new records for one or more of the drainage basins surveyed here (Table 2), based on the existing data. This reinforces the need for further research into the diversity of the fish fauna of Maranhão, given that many more species are likely to have gone undocumented up to now.

It was not possible to identify 11 of the 96 native taxa recorded here to the species level (i.e., *Crenicichla* sp., *Satanoperca* sp., *Schizodon* sp., *Bryconops* sp., *Eigenmannia* sp., *Tatia* sp., *Ancistrus* sp., *Farlowella* sp., *Peckoltia* sp., *Pterygoplichthys* sp., and *Sturisoma* sp.). This may have been due to a combination of the limited morphological resolution of some groups and the overall paucity of data on the species that occur in the coastal rivers of the state of Maranhão, problems already reported in previous studies (Guimarães et al., 2018, 2020a; Brito et al., 2019; Vieira et al., 2023). In particular, it is possible that the state's fish fauna may even include species that have yet to be described formally. In this context, the adoption

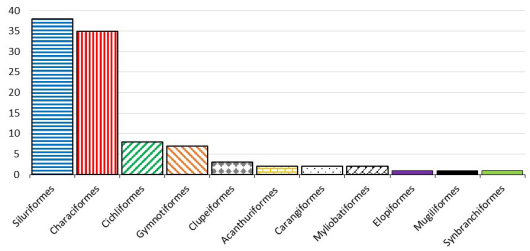

Figure 3. Number of species by order collected in the Mearim, Pindaré, Turiaçu and Pericumã rivers, Maranhão, Brazil.

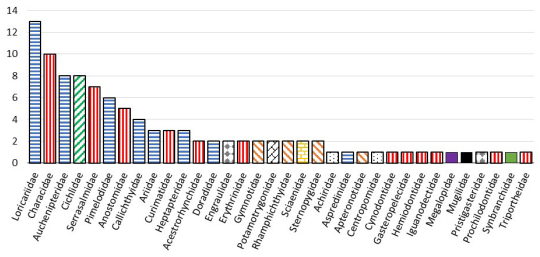

Figure 4. Number of species collected per family from the Mearim, Pindaré, Turiaçu and Pericumã rivers, Maranhão, Brazil. The families color-coded by their taxonomic order.

of an integrated approach that includes morphological and molecular data will be extremely valuable for the eventual delimitation and description of many of the taxa mentioned here. In fact, an integrated taxonomic approach was recently used to describe a number of new fish species from the hydrographic basins of the Brazilian state of Maranhão (Guimarães et al., 2019, 2020b; Aguiar et al., 2022).

Both *Colossoma macropomum* (Cuvier, 1816), which is amply distributed in the Amazon-Orinoco basin, and *Megaleporinus macrocephalus* (Garavello & Britski, 1988), which is found widely in the Paraguay River, were identified in the Mearim River. These non-native species have enormous potential for aquaculture, and haver been introduced into many Brazilian river basins (Godinho and Godinho, 2003; Barbosa and Soares, 2009; Barbosa et al., 2017; Almeida et al., 2021), including those surveyed in the present study, where they are raised on fish farms. While *Cichla* sp. and *Cichla kelberi* Kullander & Ferreira, 2006 are found primarily in the Araguaia-Tocantins basin, they are certainly not native to the Pindaré or Mearim rivers (Fricke et al., 2023a). It has been speculated that these species may have reached the river systems of Maranhão accidentally during the rainy season, when reservoirs and fish farming ponds overflow due to the excess precipitation, creating an effective link with local river channels, through which farmed fish may disperse. These artificial bodies of water are common within the study area, where they are used to raise fish. As they are efficient predators, peacock bass (*C. kelberi*) may have a profound impact on many of the populations of local fish species (Castro and Dourado, 2011). Brito et al. (2019) emphasize the importance of monitoring populations of introduced species, in order to better control their stocks, and thereby reduce the possible impacts on the diversity of the native fauna of aquatic ecosystems.

In contrast with the findings of Guimarães et al. (2020c), who recorded 130 species, the greatest species diversity was observed in the Mearim basin, possibly because it is one of the largest hydrographic systems in Maranhão, and has been sampled relatively extensively in comparison with the state's other drainages. Castro and Dourado (2011) observed a similar prominence of this environment (60 species), although a survey of the Munim River basin (Vieira et al., 2023) revealed a surprisingly high fish species richness (123 species) in comparison with the other major river basins of Maranhão state (Barros et al., 2011), which implies that the fish diversity of many of these drainages has been underestimated (Vieira et al., 2023).

The predominance of siluriforms and characiforms in the fish communities of the rivers of the Baixada Maranhense is consistent with the pattern observed in most other freshwater environments in the Neotropical region (Polaz et al., 2014; Ramos et al., 2014; Melo et al., 2016; Reis et al., 2016; Honorio and Martins, 2018; Guimarães et al., 2020a). In general terms, the composition of the fish fauna recorded in the present study is similar to that found in other hydrographic basins of the state of Maranhão (Barros et al., 2011; Ramos et al., 2014; Ribeiro et al., 2014; Matavelli et al., 2015; Guimarães et al., 2020a, 2021; Vieira et al., 2023). The most speciose families were the Loricariidae, Characidae, Auchenipteridae, Cichlidae, and Serrasalmidae. The Loricariidae and Characidae are particularly diverse, with an ample distribution in the Amazon basin (Reis et al., 2003). The high species richness recorded for these families is consistent with the pattern observed in other hydrographic basins (Volcan et al., 2012; Polaz et al., 2014; Silva et al., 2015a).

Considering all the 85 native taxa identified here to the specific level, 10 (*Lycengraulis batesii* (Günther, 1868), *Pterengraulis atherinoides* (Linnaeus, 1766), *Pellona castelnaeana* Valenciennes, 1847, *Megalops atlanticus* Valenciennes, 1847, *Mugil incilis* Hancock, 1830, *Centropomus parallelus* Poey, 1860, *Achirus achirus* (Linnaeus, 1758), *Sciades couma* (Valenciennes, 1840), *Aspredo aspredo* (Linnaeus, 1758), and *Pseudauchenipterus nodosus* (Bloch, 1794) are commonly found in brackish water environments or estuaries. Given this, they were excluded from the biogeographical considerations. Of the remaining 75 species, 18 – *Cichlasoma zarskei* Ottoni, 2011, *Geophagus parnaibae* Staeck & Schindler, 2006, *Charax awa* Guimarães, Brito, Ferreira & Ottoni, 2018, *Roeboides margareteae* Lucena, 2003, *Roeboides sazimai* Lucena, 2007, *Curimata macrops* Eigenmann & Eigenmann, 1889, *Hemiodus parnaguae* Eigenmann & Henn, 1916, *Prochilodus lacustris* Steindachner, 1907, *Rhamphichthys atlanticus* Triques, 1999, *Auchenipterus menezesi* Ferraris & Vari, 1999, *Hassar affinis* (Steindachner, 1881), *Platydoras brachylecis* Piorski, Garavello, Arce H. & Sabaj Pérez, 2008, *Corydoras treitlii* Steindachner 1906, *Pimelodella parnahybae* Fowler, 1941, *Hypostomus krikati* Oliveira, Guimarães, Brito & Ottoni, 2022, *Loricaria turi* Saraiva, Abreu, Ottoni & Piorsk, 2021, *Pterygoplichthys parnaibae* (Weber, 1991) and *Peckoltia greedoi* Armbruster, Werneke & Tan, 2015 – are known only from the river systems of Maranhão state and the Parnaíba basin. Seven species – *Crenicichla brasiliensis* (Bloch, 1792), *Leporinus piau* Fowler, 1941, *Schizodon dissimilis* (Garman, 1890), *Psectrogaster rhomboides* Eigenmann & Eigenmann 1889, *Triportheus signatus* (Garman, 1890), *Steindachnerina notonota* (Miranda Ribeiro, 1937) and *Loricariichthys derbyi* Fowler, 1915 – are also known from other drainages in northeastern Brazil. Most of the remaining 50 taxa are known to occur in the Amazon basin (in some cases ranging as far as the Orinoco River and coastal basins in Surinam and the Guyanas), and some others are even more widely distributed, occurring throughout much of South America (Fricke et al., 2023a; Froese and Pauly, 2023). The influence

of the Amazonian fish fauna on the Maranhão drainages, as well as the endemism identified in relation to Maranhão and the Parnaíba hydrological units, *sensu* Hubert and Renno (2006), are consistent with the findings of a number of previous studies (Barros et al., 2011; Guimarães et al., 2020a; Oliveira et al., 2020; Vieira et al., 2023).

The modern distribution patterns of the fish fauna of Maranhão and the neighboring drainages are a result of the combination of the present-day ecological landscapes with past geological events (Abreu et al., 2019, 2020). In particular, Abreu et al. (2019) concluded that the diversity and biogeography of the basins that drain the coastal plain of Maranhão have been influenced fundamentally by eustatic Quaternary changes in sea level. Given the region's geological characteristics, for example, possible marine incursions (transgressions) and regression events occurring at some time between the Miocene and Holocene may have resulted in the formation of links between the tributaries of the different basins (Abreu et al., 2020). Current advances in the understanding of geographic distributions and the presentation of new phylogenetic hypotheses would permit large-scale biogeographic analyses that would support a better understanding of spatial patterns and the processes that have determined the present-day biological arrangements (Dagosta and dePinna, 2018).

The results of the present study provide an important complement to the still limited data on the fish fauna of the Mearim, Pindaré, Turiaçu, and Pericumã basins. The study represents a major advance in the understanding of the fish diversity of the Brazilian state of Maranhão, providing important insights for the development of future conservation measures. Even so, further research and continuous monitoring will be necessary to better define the taxonomic, morphological, ecological, and biogeographic characteristics of the fish fauna that inhabits these aquatic ecosystems.

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