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"JÚLIO DE MESQUITA FILHO"
Câmpus de São José do Rio Preto

Douglas Lopes

**Taxonomy of Triportheidae Fowler (Teleostei: Ostariophysi:
Characiformes)**

São José do Rio Preto, SP
2024

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Tese apresentada como parte dos requisitos para obtenção do título de Doutor em Biologia Animal, junto ao Programa de Pós-Graduação em Biodiversidade, do Instituto de Biociências, Letras e Ciências Exatas da Universidade Estadual Paulista “Júlio de Mesquita Filho”, Câmpus de São José do Rio Preto.

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Comissão Examinadora

Prof. Dr. Fernando Rogério de Carvalho
UFMS – Universidade Federal de Mato Grosso do Sul
Orientador

Prof^ª. Dr^ª. Angela Maria Zanata
UFBA – Universidade Federal da Bahia

Prof. Dr. Fernando César Paiva Dagosta
UFGD – Universidade Federal da Grande Dourados

Prof. Dr. Vinícius de Araújo Bertaco
Museu de Ciências Naturais – Rio Grande do Sul

Prof. Dr. Francisco Langeani Neto
UNESP – São José do Rio Preto

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“[...] Mas eu, que nunca principio nem acabo,
Nasci do amor que há entre Deus e o diabo...”
José Régio (1926, p. 110)

RESUMO

Triporthidae é uma família de Characiformes (Teleostei: Ostariophysi) recentemente erigida para incluir *Agoniates*, *Clupeacharax*, *Engraulisoma*, *Lignobrycon* e *Triporthus*, gêneros que historicamente foram classificados em Characidae ou Gasteropelecidae. A proposta para Triporthidae foi feita com base em dados moleculares e outras hipóteses recentes têm, em grande parte, corroborado essa classificação, embora diferentes relações internas sejam propostas a cada nova hipótese. Essa variação nas relações internas é, em parte, influenciada pela má definição dos gêneros e espécies classificados na família, que, entre muitos impasses, têm diagnoses pouco detalhadas, a maioria das quais não são definidas por sinapomorfias e incluem espécies ainda não descritas, o que dificultam o conhecimento da real diversidade do grupo, bem como de suas sinapomorfias. Nesta tese, é realizado um estudo taxonômico com o objetivo de redefinir gêneros e espécies atualmente classificados como Triporthidae, com base em morfometria, merística e osteologia. Nossos resultados indicam que Triporthidae inclui 26 espécies válidas, cinco delas (distribuídas em três gêneros), novas para a ciência. Nossos resultados também atualizam os diagnósticos de todos os cinco gêneros examinados, redescrições de 21 espécies, sinonimização de dois nomes específicos e descrições de variações morfológicas e de coloração em função do dimorfismo sexual secundário e ontogenia. Uma chave para a identificação atualizada é apresentada para *Triporthus* e recomendações para uma melhor compreensão da diversidade de alguns gêneros são comentadas.

Palavras-chave: Merística. Monofiletismo. Morfometria. Osteologia. Revisão taxonômica.

ABSTRACT

Triporthidae is a family of Characiformes (Teleostei: Ostariophysi) recently erected to include *Agoniates*, *Clupeacharax*, *Engraulisoma*, *Lignobrycon* and *Triporthus*, genera that were historically classified in Characidae or Gasteropelecidae. The proposal for Triporthidae was made based on molecular data and other recent hypotheses have, for the most part, corroborated this classification, although different internal relationships are proposed with each new hypothesis. This variation in internal relationships is, in part, influenced by the poor definition of the genera and species classified in the family, which, among many impasses, have poorly detailed diagnoses, most of which are not defined by synapomorphies and include species that have not yet been described. In this thesis, a taxonomic study is conducted with the aim of redefine genera and species currently classified Triporthidae, based in morphometric, meristic and osteology. Our results indicates that Triporthidae includes 26 valid species, five of these (distributed in three genera), new to the science. Our results also updates in the diagnoses of all the five genera examined, redescrptions of 21 species, synonymization of two specific names and descriptions of morphological and coloration variations as a function of secondary sexual dimorphism and ontogeny. An updated identification key is presented for *Triporthus* and recommendations for a better understanding of the diversity of some genera are commented.

Keywords: Meristics. Monophyly. Morphometry. Osteology. Taxonomic revision.

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LISTA DE ABREVIATURAS E SIGLAS

AO	antorbital
APL	autopalatine
BOC	basioccipital
CAV	caudal vertebrae
c&s	cleared and stained
Cle	cleithrum
Cor	coracoid
ECT	ectopterygoid
EPL	epipleural
EPN	epineural
EXO	exoccipital
FRO	frontal
HL	Head length
HYO	Hyomandibular
IO	Infraorbital
LET	lateral ethmoid
LLP	lateral line pore
MCO	mesocoracoid
MES	mesethmoid
MSC	mesocoracoid
MSP	mesopterygoid
MTP	metapterygoid
N	number

OSP	orbitosphenoid
PCV	pre-caudal vertebrae
PRA	proximal radial
PRO	prootic
PSC1	postcleithrum 1
PSP	parasphenoid
PTO	pterotic
PTS	pterosphenoid
QUA	quadrate
RSP	rinosphenoid
Sca	scapula
SD	Standard deviation
SL	Standard length
SO	Supraorbital
sp.	species (singular)
SPC	supracleithrum
SPH	sphenotic
spp.	species (plural)
SYM	sympletic
TRV	transitional vertebrae
WAP	Weber apparatus

LISTA DE SÍMBOLOS

<i>a</i>	intercept
<i>b</i>	slope
cm	centimeter
Km	kilometer
mm	milimeter
r²	Percent of influence
p	Significance value

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1. GENERAL INTRODUCTION

Triporthidae is a Neotropical taxon, elevated to the family level status in Oliveira *et al.* (2011) to housing the Triporthinae Fowler (*sensu* Buckup; Menezes and Ghazzi, 2007), Agoniatinae Bleeker (*sensu* Buckup; Menezes and Ghazzi, 2007), *Clupeacharax* Pearson and *Engraulisoma* Castro, based on a phylogenetic hypothesis using molecular data. These genera were historically classified in Characidae and Gasteropelecidae, and until this moment, the internal and external relationships were poorly known. After the proposition of Triporthidae, Mariguela *et al.* (2016) conducted a new phylogenetic approach, focused on testing the hypothesis presented in Oliveira *et al.* (2011) and providing a hypothesis for internal relationships and historical biogeography of the group. The results obtained in Mariguela *et al.* (2016) corroborated the hypothesis of Oliveira *et al.* (2011), including most of the internal topology, but highlighted the complexity of the group and the necessity of a new approach, including taxonomic revisions, to describe new species recognized in their dataset.

Other phylogenetic hypotheses corroborated in part the recognition of Triporthidae apart from Characidae, as historically classified. Betancur-R *et al.* (2018), using genomic data, corroborated the clade composed of the five genera grouped in Triporthidae by Oliveira *et al.* (2011), but with differences in internal relationships between the genera. Mirande (2018), using combined data from morphological and molecular characters, also corroborated the recognition of Triporthidae, but including only *Triporthus* Cope, *Lignobrycon* Eigenmann & Myers, *Agoniates* Müller & Troschell, and *Clupeacharax*. In this hypothesis, *Engraulisoma* was grouped as the sister-group of the remaining Gasteropelecidae and classified within this family. Mirande (2018) also mixed two names to refer to Triporthidae along his hypothesis. In part of the text, the name is referred to as Triporthidae and in other parts, as Agoniatidae. Despite the *consensus* hypothesis of recognition of Triporthidae, the inclusion of *Engraulisoma* in the family, as well as the internal relationships between the genera, are still contrasting. Additionally, most of the phylogenetic hypotheses mentioned did not focus on Triporthidae and included a limited number of taxa, from just one or a few localities, making it difficult to delimit the genera and species as monophyletic units, as well as investigating the synapomorphies of each genus and understanding the real diversity of species, based on a phylogenetic approach.

From the genera classified in Triporthidae currently (*sensu* Oliveira *et al.*, 2011), only *Engraulisoma* was described in a phylogenetic systematic context (Castro, 1981), and this genus is the only one with more details of characters and a preliminary classification in its

description. *Agoniates* was the first genus currently classified in Triportheidae to be described, and its diagnosis is based mainly on teeth characteristics, body shape, and size of dorsal and anal fins (Müller; Troschell, 1845). The genus was described as monotypic, but a second species was described in Eigenmann (1914), with the presentation of more detailed characters. A third species was described in Géry (1963), but later synonymized in Zarske, Géry (1997). Despite the new descriptions and redescrptions, synapomorphies and relationship hypotheses for *Agoniates*, in a context with the remaining Triportheidae, need more comparative studies.

Chalcinus Valenciennes, 1850 was the second genus described, currently classified in Triportheidae. *Chalcinus* was described to include two new species and a previously described species, that was treated as *Chalceus* Cuvier. After the description, several other species were described in *Chalcinus* in the 19th century, from several South American river basins. Parallely, *Triporthesus* Cope, 1872 was described to include two new species: *T. albus* and *T. flavus* from the Peruvian Amazon. Cope (1872) also described in the same work *C. culter* and did not consider *Chalcinus* and *Triporthesus* as synonyms, as happened in Garman (1890). *Chalcinus* remained as a valid name until Myers (1940), who observed that *Chalcinus* is a preoccupied name in Hymenoptera (in Rafinesque, 1818), as an unjustified amendment of *Chalcis* Fabris. For this reason, *Triporthesus* was revalidated, to include the species previously housed in *Chalcinus*. *Triporthesus* is the most diverse genus in Triportheidae, with 17 valid species (Fricke *et al.*, 2024; Lopes; Carvalho, 2024), and is known as a genus with highly conservative morphology (Malabarba, 2004), with several unresolved questions in its taxonomy, including undescribed species (Mariguela *et al.*, 2016) and problems diagnosing the described species (Malabarba, 2004; Lopes; Carvalho, 2024).

The third genus described, currently classified in Triportheidae, is *Clupeacharax* Pearson, 1924. Pearson (1924) presented *Clupeacharax* as monotypic, characterized by an elongated and compressed body, keeled, with the origin of the anal fin anterior to the origin of the dorsal fin. Additional information about teeth and fins is also available in the original description. *Clupeacharax* was included in the phylogenetic hypothesis of Castro (1981), with comparisons to *Engraulisoma*, but without a complete osteological description, and all the presented conditions were in the sense of comparing these genera. *Clupeacharax anchoveoides* Pearson, 1924 was described from the rio Madeira basin and later its distribution was expanded to other river basins, including the rio Paraguay basin (Britski; Sillimon and Lopes, 1999) and the lower rio Paraná basin (López; Miquelarena and Menni, 2003). With a wide distribution and no comparisons of the populations of *C. anchoveoides* along its occurrence, *Clupeacharax* is a

genus that has never been reviewed and is poorly defined within the contemporary classification system.

The fourth genus described, currently classified in Triportheidae, was *Lignobrycon* Eigenmann & Myers, 1929. *Lignobrycon* was described to house a fossil species, previously described as †*Tetragonopterus ligniticus* Woodward, 1898. This species was characterized by the position of the origin of the anal and dorsal fins and vertebrae (Eigenmann; Myers, 1929). *Lignobrycon* was later considered a synonym of †*Eobrycon* (Schaeffer, 1947) and *Triportheus* (Travassos; Santos, 1955). *Moojenichthys* Miranda Ribeiro, 1956 was described to include a new living species, that was considered closely related to *Triportheus*. Considering this relationship, *Moojenichthys* was tested in Castro; Vari (1990) and considered valid, despite the recognition of a sister-group relationship with *Triportheus*. Malabarba (1998) compared †*T. ligniticus* with the living species of *Triportheus* and *Moojenichthys* and revalidated *Lignobrycon*, due to the great differences between †*L. ligniticus* and the living species of *Triportheus*. Malabarba (1998) also recognized that *Lignobrycon* and *Moojenichthys* can be considered synonyms and transferred *M. myersi* to *Lignobrycon*, which currently houses one fossil species and one living species.

The fifth genus described and currently classified in Triportheidae (in most phylogenetic hypotheses) was *Engraulisoma* Castro, 1981. This was the only genus described in the context of phylogenetic systematics, and Castro (1891) presented some hypothetical comparisons with other genera, such as *Bryconamericus* Eigenmann and *Clupeacharax*. Castro (1984) conducted an osteological study on *Engraulisoma* and provided a description and a hypothesis of its relationships. However, this work was not formally published, and there is no study that specifically describes and discusses the characters defining this genus and its relationships. Additionally, similarly to *Clupeacharax*, *Engraulisoma* is considered monotypic, and *E. taeniatum* Castro, 1981 was described from the rio Paraguay basin and later reported from the rio Amazonas basin (in Ortega; Vari, 1986), the río Orinoco basin (in Taphorn, 1992), the lower rio Paraná basin (Braga, 1998), and recently from the río Uruguay basin (Serra *et al.*, 2024).

Although many genera within Triportheidae are poorly defined and lack recognized autapomorphies, some authors have proposed hypotheses regarding their relationships in various contexts, relying primarily on osteological characters or external morphology, and poorly defined synapomorphies. Miranda Ribeiro (1956) considered *Moojenichthys* as closely related to *Clupeacharax* and *Triportheus*. Despite the characters and conditions that influenced this hypothesis not being clearly presented, it is probable that the elongated and compressed body, with a ventral keel formed by the expansion of coracoids, influenced this proposal. On

the other hand, Weitzman (1960) considered *Triporthus* related to *Brycon* Valenciennes and *Chalceus* Cuvier. Géry (1963) considered a relationship between *Agoniates*, *Clupeacharax*, and *Triporthus*, which was not corroborated in Castro (1984), who considered *Clupeacharax* as the sister-group of *Engraulisoma*, and the clade formed by these species not related to *Agoniates* or *Triporthus*. Castro; Vari (1990) hypothesized a sister-group relationship between *Triporthus* and *Moojenichthys* (= *Lignobrycon*), which was corroborated in Malabarba (1998).

Zanata (2000) corroborated a sister-group relationship between *Lignobrycon* and *Triporthus*, and a sister-group relationship between this clade and *Agoniates*. In contrast, Mirande (2009, 2010) considered *Triporthus* as the sister group of *Brycon* and stated these genera in Bryconinae, hypothesizing a relationship between *Agoniates* and the clade formed by *Acestrorhynchus* Eigenmann & Kennedy and *Rhaphiodon* Agassiz, and considered *Engraulisoma* and *Clupeacharax* as non-Characidae, transferring these genera to Gasteropelecidae. Dagosta; Datovo (2013) provided the most recent work to define and test the monophyly of groups currently classified in Triportheidae, corroborating the monophyly of Agoniatinae. Dagosta; Datovo (2013) presented six morphological characters that corroborate Agoniatinae as monophyletic and commented that at least ten character conditions presented in Mirande (2010) could be indicative of a close relationship between part of Triportheidae (*sensu* Oliveira *et al.*, 2011).

Based on the complex taxonomic and systematic history of the genera currently classified in Triportheidae, this work provides a review at the generic and specific level of all taxa recognized in the family. This review includes redescription of the genera and species, osteological descriptions, recognition of diagnostic characters at the species level, synapomorphies at the generic level, description of new species, synonymization of two names, identification keys, and updates on diagnosis, sexual and ontogenetic dimorphism knowledge, coloration patterns, and distribution.

8 CONCLUSIONS

The taxonomic revision conduct here reveals a great number of unknow information about the genera and species classified In Triportheidae. The revision conducted with *Triportheus* possibilited the recognition of 17 species, distributed in two morphological patterns, with high conservative morphology. All the previously recognized species were redescribed and new diagnosis, with addition of recognized characters are presented here. The type species of *T. albus* is considered here very similar to *T. brachipomus*, including overlapping distribution along the Amazon core (rios Amazonas, Tocantins/Araguaia basins, río Orinoco basin and coastal rivers from Guyanas and, for this reason, are considered synonyms. Using the principle of priority, the valid name is *T. brachipomus*. All the characters previously presented as diagnostic between the populations identified with these names were systematically reevaliated and not corroborated, due the overlaps. Our data suggests that the differences between populations along the wide distribution of *T. albus* are influenced by the isolation by distance, an evolutionary phenomenon that can promote the speciation along the geological time.

Triportheus curtus, an emblematic species, rare and with disruptive distribution is considered synonym of *T. rotundatus* here. The syntypes of this species, collected in Ilha do Marajó, are easily recognized as *T. rotundatus* by the two three rows of dentary teeth and six scales above lateral line. The population named as '*T. curtus*' from the Western Amazon is recognized here as a new species, that is described. An undescribed species from the rio Xingu basin is also recognized and presented with its morphometric and meristhic data. From great part of the previously described species, new diagnostic information is presented, including characteristics of secondary sexual dimorphism and ontogenetic variation on form. Updates on coloration in alcohol and in life also was presented or updated to species that this feature is previously known. Updates on distribution are also presented, with distribution maps.

Clupeacharax is reviewed here to the first time, one century after the original description. The genus is redescribed and redefined, based on external diagnostic characters and osteological features, recognized here as synapomorphies to the genus. Two new species are recognized, *Clupeacharax* sp.n 'paraguay' from the Paraná-Paraguay river system and *Clupeacharax* sp.n 'tocantins-araguaia' from rios Tocantins/Araguaia basin and are presented in this work. *Clupeacharax anchoveoides* is redescribed, including an osteological description

and its distribution is delimited to the Western Amazon rivers, including rios Solimões, Purus, Madeira and their tributaries.

The revision of *Engraulisoma* also resulted in a redefinition of the genus, based on external and osteological characters. Synapomorphies previously described (but not published) to this genus were revisited and new synapomorphies were also recognized. A new species from the río Orinoco basin was recognized and is described in this work. Despite this, more individuals need to be examined and a new approach, including molecular tools are necessary, to clarify the real diversity of this widely distributed genus. *E. taeniatum* is redescribed, including an osteological description and its distribution is limited to the río de La Plata basin and rio Amazonas basin.

Agoniates and *Lignobrycon* are redescribed here, with addition of new characters to taxonomy and discussion of the characters previously proposed to these genera. The species in *Agoniates* are redescribed, with discussions about interspecific differences in measurements and counts and updates on coloration patterns knowledge. The distribution of the species is also updated and discussed. To *Lignobrycon*, redescription was focused on *L. myersi*, with comments about the synapomorphies of the genus and autapomorphies to this species. Secondary sexual dimorphism and ontogenetic variations in counts are recognized and described here.

The presented results highlighted that Triportheidae houses genera with complex taxonomy, influenced mainly by the conservative morphology. Part of the reviewed genera was examined to the first time after the original description and received the first definition based on synapomorphies. In specific level, redescription demonstrated that several characters never explored to Triportheidae species can be considered diagnostic. Taxonomic problems, as synonymies are also recognized and five new species, from three genera are described herein. Our results advance the knowledge of the taxonomy and the synapomorphies of Triportheidae and provide important information is generic and specific level, that can be used to propose a new morphological definition to the family. Additionally, the present results reduces the shortfalls of knowledge about biodiversity, by the robust definition of the recognized taxa.

REFERENCES

- BETANCUR-R, R.; ARCILA, D.; VARI, R. P.; HUGHES, L. C.; OLIVEIRA, C.; SABAJ, M. H.; ORTÍ, G. Phylogenomic incongruence, hypothesis testing and taxonomic sampling: the monophyly of characiform fishes. *Evolution*, 2018. Disponível em: <https://doi.org/10.1111/evo.13649>.
- BRAGA, L. Registro de *Engraulisoma taeniatum* Castro, en el Paraná medio, Argentina (Osteichthyes, Characidae). *Physis*, v. 56, n. 130, p. 29–30, 1998.
- BRITSKI, H. A.; SILIMON, K. Z.; LOPES, B. S. Peixes do Pantanal: Manual de identificação. 1. ed. Brasília, DF: Embrapa, 1999.
- BUCKUP, P. A.; MENEZES, N. A.; GHAZZI, M. S. Catálogo das espécies de peixes de água doce do Brasil. Rio de Janeiro: Museu Nacional, 2007.
- CASTRO, R. M. C. *Engraulisoma taeniatum*, um novo gênero e espécie de Characidae da bacia do rio Paraguai (Pisces, Ostariophysi). *Papéis Avulsos de Zoologia*, v. 34, n. 11, p. 135–139, 1981.
- CASTRO, R. M. C. Osteologia e relações filogenéticas de *Engraulisoma taeniatum* Castro, 1981 (Ostariophysi, Characiformes, Characidae). 1984. Dissertação (Mestrado em Zoologia) – Universidade de São Paulo, São Paulo, 166p.
- CASTRO, R. M. C.; VARI, R. P. *Moojenichthys* Miranda-Ribeiro (Pisces: Ostariophysi: Characidae), a phylogenetical reappraisal and redescription. *Proceedings of the Biological Society of Washington*, v. 103, n. 3, p. 525–542, 1990.
- COPE, E. D. On the fishes of the Ambyiacu River. *Proceedings of the Academy of Natural Sciences of Philadelphia*, v. 23, p. 250–294, 1872.
- CUVIER, G.; VALENCIENNES, A. *Histoire naturelle des poissons*. Paris: P. Bertrand, 1850. v. 22, 395p.

DAGOSTA, F. C. P.; DATOVO, A. Monophyly of the Agoniatinae (Characiformes: Characidae). *Zootaxa*, v. 3646, n. 3, p. 265–276, 2013. Disponível em: <http://dx.doi.org/10.11646/zootaxa.3646.3.5>.

EIGENMANN, C. H.; MYERS, G. S. The American Characidae. Pt V. *Memoirs of the Museum of Comparative Zoology*, v. 43, n. 5, p. 429–558, 1929.

EIGENMANN, C. H. Some results from studies of South American fishes. IV. New genera and species of South American fishes. (Contrib. Zool. Lab. Ind. Univ. No. 135). *Indiana University Studies*, v. 20, p. 44–48, 1914.

FRICKE, R.; ESCHMEYER, W.; FONG, D. (eds.). *Catalog of fishes: genera, species, references*. 2024. Disponível em: <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>. Acesso em: 22 set. 2024.

GARMAN, S. On the species of the genus *Chalcinus* in the Museum of Comparative Zoology at Cambridge, Mass., U.S.A. *Bulletin of the Essex Institute*, v. 22, n. 1–3, p. 1–7, 1890.

GÉRY, J. Essai sur les affinités phylogénétiques des *Agoniates* et l'origine des Characidae, à propos de la description d'une forme nouvelle de l'Amazone péruvienne: *Agoniates ladigesii*. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, v. 60, p. 265–284, 1963.

LOPES, D. A.; CARVALHO, F. R. Taxonomy of *Triporthus* (Ostariophysi: Triporthidae) from the rios Paraná-Paraguay basin, South America. *Neotropical Ichthyology*, v. 22, n. 4, e230121, 2024. Disponível em: <https://doi.org/10.1590/1982-0224-2023-0121>.

LÓPEZ, H. L.; MIQUELARENA, A. M.; MENNI, R. C. Lista comentada de los peces continentales de la Argentina. *ProBiota Série Técnica Didáctica*, v. 5, p. 1–87, 2003.

MALABARBA, M. C. S. L. Phylogeny of fossil Characiformes and paleobiogeography of the Tremembé Formation, São Paulo, Brazil. In: MALABARBA, L. R.; REIS, R. E.; VARI, R.

- P.; LUCENA, C. A. S.; LUCENA, Z. M. S. (eds.). Phylogeny and classification of neotropical fishes. Porto Alegre: Edipucrs, 1998. p. 69–84.
- MALABARBA, M. C. S. L. Revision of Neotropical genus *Triportheus* Cope, 1872 (Characiformes: Characidae). *Neotropical Ichthyology*, v. 2, n. 4, p. 167–204, 2004. Disponível em: <https://doi.org/10.1590/S1679-62252004000400001>.
- MARIGUELA, T. C.; ROXO, F. F.; FORESTI, F.; OLIVEIRA, C. Phylogeny and biogeography of Triporthidae (Teleostei: Characiformes) based on molecular data. *Molecular Phylogenetics and Evolution*, v. 96, p. 130–139, 2016.
- MIRANDA-RIBEIRO, P. On a new genus and species of South American fishes. *Proceedings of the 14th International Congress of Zoology*, v. 16, p. 546–547, 1956.
- MIRANDE, J. M. Morphology, molecules and the phylogeny of Characidae (Teleostei, Characiformes). *Cladistics*, p. 1–19, 2018.
- MIRANDE, J. M. Phylogeny of the family Characidae (Teleostei: Characiformes): from characters to taxonomy. *Neotropical Ichthyology*, v. 8, n. 3, p. 385–568, 2010. Disponível em: <https://doi.org/10.1590/S1679-62252010000300001>.
- MIRANDE, J. M. Weighted parsimony phylogeny of the family Characidae (Teleostei: Characiformes). *Cladistics*, v. 25, p. 574–613, 2009.
- MÜLLER, J.; TROSCHER, F. H. *Horae Ichthyologicae. Beschreibung und Abbildung neuer Fische. Die Familie der Characinen.* Viet & Comp., Berlin. Heft 1–2, p. 1–40, 1844.
- MYERS, G. S. Suppression of *Acaropsis* and *Chalcinus*, two preoccupied generic names of South American fresh-water fishes. *Stanford Ichthyological Bulletin*, v. 1, n. 5, p. 170, 1940.
- OLIVEIRA, C.; AVELINO, G. S.; ABE, K. T.; MARIGUELA, T. C.; BENINE, R. C.; ORTÍ, G.; VARI, R. P.; CASTRO, R. M. C. Phylogenetic relationships within the speciose family Characidae (Teleostei: Ostariophysi: Characiformes) based on multilocus analysis and extensive ingroup sampling. *BMC Evolutionary Biology*, v. 11, n. 1, p. 275, 2011.

ORTEGA, H.; VARI, R. P. Annotated checklist of the freshwater fishes of Peru. *Smithsonian Contributions to Zoology*, v. 437, p. 1–25, 1984.

PEARSON, N. E. The fishes of the eastern slope of the Andes. I. The fishes of the rio Beni basin, Bolivia, collected by the Mulford Expedition. *Indiana University Studies*, p. 3–83, 1924.

RAFINESQUE, C. S. *Analyse de la nature, ou tableau de l'univers et des corps organisés*. Palerme, 224p., 1818.

SCHAEFFER, B. Cretaceous and Tertiary Actinopterygian fishes from Brazil. *Bulletin of the American Museum of Natural History*, v. 89, n. 1, p. 1–49, 1947.

SERRA, W. S.; SCARABINO, F.; GARCÍA, M.; SANGUINETTI, G. First record of *Engraulisoma taeniatum* Castro, 1981 (Characiformes, Triportheidae) for Uruguay and the Uruguay river basin. *Azara: Historia Natural*, v. 14, n. 2, p. 35–42, 2024.

TAPHORN, D. C. The characiform fishes of the Apure River drainage, Venezuela. *Biollania Edición Especial*, n. 4. *Monografía Científica Museu de Ciências Naturais, UNELLEZ*, v. 537, 1992.

TRAVASSOS, H.; SANTOS, R. S. Caracídeos fósseis da bacia do Paraíba. *Anais da Academia Brasileira de Ciências*, v. 27, n. 3, p. 297–322, 1955.

WEITZMAN, S. H. The phylogenetic relationships of *Triportheus*, a genus of South American characid fishes. *Stanford Ichthyological Bulletin*, v. 7, p. 239–244, 1960.

WOODWARD, A. S. Considerações sobre alguns peixes Terciários dos schistos de Taubaté, Estado de São Paulo, Brasil. *Revista do Museu Paulista, São Paulo*, v. 3, p. 63–70, 1898.

ZANATA, A. M. Estudo das relações filogenéticas do gênero *Brycon* Muller & Troschel, 1844 (Characidae; Characiformes). 2000. Tese (Doutorado) – Universidade de São Paulo, 358p.

ZARSKE, A.; GÉRY, J. Rediscovery of *Agoniates halecinus* Müller & Troschell, 1845, with a supplementary description of *Agoniates anchovia* Eigenmann, 1914, and a definition of the genus (Teleostei: Ostariophysi: Characiformes: Characidae). *Zoologische Abhandlungen. Staatliches Museum für Tierkunde in Dresden*, v. 49, p. 173–184, 1997.