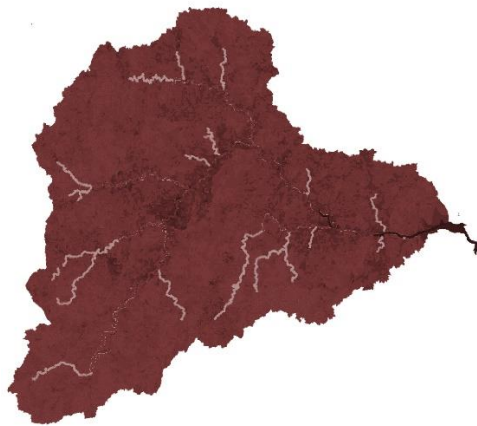


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Diversity of the genus *Trichomycterus* Valenciennes, 1832  
(Siluriforms, Trichomycteridae) in the Rio Doce basin: a  
systematic study integrating phenotypes, DNA and classical  
taxonomy



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Without memory, there is no culture. Without memory,  
there would be no civilization, no society, no future.

**Elie Wiesel**

## General Abstract

The diversity of the genus *Trichomycterus* Valenciennes 1832 in the Rio Doce basin is investigated using conventional and modern morphology and DNA analyses. The work is presented in two Chapters. Chapter One, entitled “Diversity of the genus *Trichomycterus* Valenciennes, 1832 (Siluriforms, Trichomycteridae) in the Rio Doce basin: a systematic study integrating phenotypes, DNA and classical taxonomy” integratively analyzes specimens of the genus from the entire Rio Doce drainage and adjacent basins, both from available world-wide collections and from active sampling efforts. A combination of phenotypic and DNA (COI barcoding analysis) provides evidence for the existence of 14 species in the basin, 10 of which are new: *T. alternatus* Eigenmann, 1917; *T. argos* Lezama *et al.*, 2012; *T. “astromycterus”* sp. nov.; *T. “barrocos”* sp. nov.; *T. “brucutu”* sp. nov.; *T. brunoi* Barbosa & Costa, 2010; *T. immaculatus* (Eigenmann & Eigenmann, 1889) *T. “illuvies”* sp. nov.; *T. “melanopygius”* sp. nov.; *T. “ipatinguensis”* sp. nov.; *T. “pussilipygius”* sp. nov.; *T. “sordislutum”* sp. nov.; *T. “vinnulus”* sp. nov.; and *T. “tantalus”* sp. nov. . In addition, a lectotype is designated for *T. immaculatus* and the species is considered as a senior synonym of *Trichomycterus pradensis* Sarmiento-Soares *et al.*, 2005. Although remarkable, such increase in species number of *Trichomycterus* in a single drainage matches similar recent increments in some other Southeastern Brazilian basins, such as the Paraíba do Sul and Iguaçu. The kind of differentiation among species herein recognized varies, with some of them being well-differentiated in morphology but not in barcoding data, and others showing the opposite phenomenon. The geographical distribution of each of the 14 species is plotted in the Rio Doce basin. The wide geographical distribution of some species (*T. alternatus* and *T. immaculatus*) is explained against data from geomorphological processes and comparative information on their biology. Chapter two, “The type specimens of *Trichomycterus alternatus*

(Eigenmann, 1917) and *T. zonatus* (Eigenmann, 1918), with elements for future revisionary work (Teleostei, Siluriformes, Trichomycteridae)” focuses on the complex taxonomy, nomenclature and type material status of *T. alternatus* and *T. zonatus*. The type series of the two species are analyzed in detail, both in morphology and locality data. Osteological information was obtained with conventional and a new technique of radiographic stereo-triplets. Our new data elucidates their species distinctiveness, diagnostic characteristics, type localities and show that *T. zonatus* does not occur in the Rio Doce basin.

Keywords: Integrative taxonomy; Neotropical catfish; barcoding; species delimitation; biogeographical dispersion.

## Resumo Geral

A diversidade do gênero *Trichomycterus* Valenciennes 1832 na bacia do Rio Doce é investigada utilizando métodos convencionais e modernos em análises morfológicas e moleculares. Os resultados desta dissertação são apresentados em dois capítulos. Capítulo um, intitulado “Diversity of the genus *Trichomycterus* Valenciennes, 1832 (Siluriforms, Trichomycteridae) in the Rio Doce basin: a systematic study integrating phenotypes, DNA and classical taxonomy” examinou espécimes pertencentes a este gênero encontrados no Rio Doce e em bacias adjacentes disponíveis em coleções nacionais e internacionais e coletados durante esta dissertação. O conjunto de dados obtidos através de análises morfológicas e moleculares (COI, DNA barcoding) revelou a existência de 14 espécies na bacia do Rio Doce, das quais 10 novas: *T. alternatus* Eigenmann, 1917; *T. argos* Lezama *et al.*, 2012; *T. “astromycterus”* sp. nov.; *T. “barrocos”* sp. nov.; *T. “brucutu”* sp. nov.; *T. brunoi* Barbosa & Costa, 2010; *T. immaculatus* (Eigenmann & Eigenmann, 1889)] *T. “illuvies”* sp. nov.; *T. “melanopygius”* sp. nov.; *T. “ipatinguensis”* sp. nov.; *T. “pussilipygius”* sp. nov.; *T. “sordislutum”* sp. nov.; *T. “vinnulus”* sp. nov.; and *T. “tantalus”* sp. nov. Além disso, é designado um lectótipo para *T. immaculatus*, espécie aqui proposta como sinônimo sênior de *Trichomycterus pradensis* Sarmiento-Soares *et al.*, 2005. O acentuado incremento em número de espécies de *Trichomycterus* para uma única bacia segue um padrão de crescimento em biodiversidade conhecida do gênero para outras drenagens do sudeste brasileiro a exemplo do rio Paraíba do Sul e Iguaçu. Os tipos de diferenciação detectada entre as espécies aqui tratadas variam, com algumas bem corroboradas morfológicamente, porém muito similares ou indiferenciáveis em análise de DNA *barcoding*, e outras apresentando o fenômeno oposto. As distribuições geográficas de cada uma das 14 espécies são mapeadas com base em todo o material examinado. A ampla distribuição geográfica de algumas espécies (*T.*

*alternatus* and *T. immaculatus*) é explicada através de processos geomorfológicos e informações comparativas sobre suas biólogias. O capítulo dois, “The type specimens of *Trichomycterus alternatus* (Eigenmann, 1917) and *T. zonatus* (Eigenmann, 1918), with elements for future revisionary work (Teleostei, Siluriformes, Trichomycteridae)” se concentra em esclarecer a complexa taxonomia, nomenclatura e o status do material tipo de *T. alternatus* e *T. zonatus*. As séries tipos das duas espécies foram minuciosamente analisadas tanto para morfologia como para suas respectivas localidades de proveniência. Informações osteológicas foram obtidas através de técnicas de radiografia convencionais e uma nova metodologia chamada *stereo triplets*. Os dados obtidos corroboram as respectivas espécies como distintas, e permitem uma avaliação precisa de seus respectivos caracteres diagnósticos e localidades tipo. Também se chegou à conclusão que *T. zonatus* não ocorre na bacia do Rio Doce.

Palavras-chaves: Taxonomia integrativa; bagres neotropicais; barcoding; delimitação de espécies; dispersão biogeográfica.



**Chapter 1-** Diversity of the genus *Trichomycterus* Valenciennes, 1832 (Siluriforms, Trichomycteridae) in the Rio Doce basin: a systematic study integrating phenotypes, DNA and classical taxonomy.

## Introduction

The Neotropical region comprises 5,000 freshwater fish species and is the richest ichthyofauna on the planet (Reis *et al.*, 2003). This diversity is due to the high heterogeneity of present and past environments in that region, which allied with geologic and ecological factors, caused lineage diversification and ensuing increased biodiversity. Vari & Malabarba (1998) estimate a total number of 8000 neotropical fish species, a figure larger than present records.

Trichomycteridae is one of the richest families of Siluriformes. According to de Pinna (1998), it is a monophyletic group with eight subfamilies, Copionodontinae, Glanapteryginae, Sarcoglanidinae, Stegophilinae, Trichogeninae, Trichomycterinae, Tridentinae and Vandellinae. Fishes from this family are characterized, among others particularities, by a highly modified opercular apparatus, adapted to locomotion in rocky environments and, in the case of parasite species (Stegophilinae and Vandellinae), used to attach into the host gill cavity (de Pinna, 1998; Adriaens *et al.*, 2010). Due to the ability to climb waterfalls in some family members, many species are found in high altitudes, resulting in pronounced endemism (Eigenmann, 1918; Santos, 2012).

Among Trichomycteridae subfamilies, Trichomycterinae has a very confusing systematics. Baskin (1973), de Pinna (1998) and Costa & Bockmann (1993) affirm that the subfamily is not a natural group. On the other hand, Arratia (1990) found four morphological characters that are candidates as putative synapomorphies for the group: (1) vomer with a large and unique posterior process; (2) Enarthrodial joint between the opercle and preopercle in adults; (3) pronounced notch in the posteromedial margin of the third ceratobranchial; and (4) anterior membranous process of basioccipital well developed, extending ventro-laterally to the parasphenoid and prootic. Wosiacki (2002), utilizing 61 Trichomycterinae species and 13 out-group species, corroborated the non-

monophyletic hypothesis for the group. Lastly, Datovo & Bockmann (2010) found a unique myological trait in trichomycterine taxa included in their study, the posterior portion of the levator internus 4 originating by the dorsal face of posttemporo-supracleitrum, and suggested this character as a possible synapomorphy for the subfamily.

Currently, there are eight genera in Trichomycterinae: *Bullockia*, *Eremophilus*, *Hatcheria*, *Ituglanis*, *Rhizosomichthys*, *Scleronema*, *Silvinichtys*, and *Trichomycterus* (de Pinna, 1998). Among those, *Trichomycterus* has the largest number of nominal species, 184 (Eschmeyer & Fong, 2018), and it is currently the most complex taxon in the family due to its geographical distribution, non-monophyletic status and confusing taxonomic history (de Pinna, 1989; 1998).

The genus *Trichomycterus* was described by Valenciennes in 1832, having as type species *T. nigricans* Valenciennes, 1832, from the State of Santa Catarina, Brazil. Since then, many species have been described, and today this genus is one of the most diverse from the neotropics. Many taxonomists throughout time have described species from this genus based mostly on external features, such as number of fin rays, body proportion, and pigmentation. However, starting with Tchernavin (1944) such characters have been gradually shown not to constitute reliable taxonomic proxies for species differentiation due to intraspecific and ontogenetic variation and allometric effects.

For most of the first half of the 20th century, there was no uniform taxonomic standard followed by the majority of ichthyologists. Descriptions of *Trichomycterus* species from that time are not uniform, resulting in difficulties comparing data among different species. As observed by Tchernavin (1944), to identify or compare species was sometimes impossible due to the lack of taxonomic uniformity. After his publication the awareness about the consequences on the lack of taxonomy standard and the use of intraspecific variable characters in genus lighted up the attention

of taxonomists, who started to more rigorously state taxonomy methodology and to avoid the use of unreliable characters (Baskin, 1973; de Pinna, 1992b; Costa, 1992; Barbosa, 2000; Bockmann & Sazima, 2004). Tchernavin (1944) was one of the first publications to describe and clearly explain the characters used to diagnose Trichomycterinae species and is in fact used as a standard to the present.

As mentioned above, *Trichomycterus* as a whole has a wide geographic range, and its species are found throughout South and part of Central America on both sides of the Andes (de Pinna, 1989). Many species of *Trichomycterus* have been described from the eastern coastal basins of Brazil. Among those, one of the largest is the Rio Doce.

The Rio Doce basin spans the Brazilian States of Minas Gerais and Espírito Santo (Fig. 01). It has the one of the most diverse fish faunas in Eastern Brazilian drainages, including a significant proportion of endemics (Barros *et al.*, 2012; Dergam *et al.*, 2017; Sales *et al.*, 2018). However, the Rio Doce is at present severely degraded by anthropic impacts such as damming, sewage discharge, and the recent burst of Samarco SA ore tailing dam, and its biodiversity is critically endangered. There are currently six *Trichomycterus* species reported for in the Rio Doce: *T. alternatus* Eigenmann, 1917; *T. argos* Lezama, Triques & Santos, 2012; *T. auroguttatus* Costa, 1992; *T. brasiliensis* Lutken, 1874; 2010, *T. immaculatus* Eigenmann & Eigenmann, 1889; *T. pradensis* Sarmiento-Soares, 2005 (Sato *et al.*, 2004; Vieira, 2010; Lezama, 2012; Da Silva, 2013; Sales *et al.*, 2018). Of those, only *T. alternatus* and *T. argos* were originally described from that basin, with the former also reported widely from other eastern basins of Brazil. Those records, however, are highly questionable, because a thorough investigation into the applicability of those names have never been made to the Rio Doce *Trichomycterus* species and the underlying taxonomy is widely recognized as precarious. Examination of material available in museum

collections, done in association with this work, has revealed an unexpected diversity of *Trichomycterus* in the waters of the Rio Doce, with many forms that clearly do not fit currently known taxa. It has also shown that the applicability of available names is largely arbitrary and poorly supported by data. Resolution of this issue requires both a systematic investigation into the biological reality of the specific entities assignable to *Trichomycterus* in the Rio Doce and also a taxonomic investigation into the applicability of available taxon names.

Neotropical hyperdiverse fish taxa commonly have old and complex taxonomies and to diagnose species from those taxa is usually laborious and sometimes impossible (Wosiacki, 2002; Costa-Silva *et al.*, 2015; Sales *et al.*, 2018). From the middle of the 20<sup>th</sup> century until now the number of *Trichomycterus* species from Southeastern Brazil has more than tripled, from nine valid species to 33 (Eschmeyer & Fong, 2018). The abrupt increase in biodiversity of this taxon is a consequence of a new generation of Brazilians ichthyologists. Although the diversity of *Trichomycterus* is gradually being revealed and it is helping to create conservation strategies for the taxon, diagnosing of species of the genus has become a problem when allied with their high morphological plasticity (e.g color pattern and morphometry) as has been demonstrated in *Trichomycterus davisi* (Haseman 1911) and *T. brasiliensis* (Bockmann & Sazima, 2004; Barbosa & Costa, 2010; and Nascimento *et al.*, 2017).

Molecular analyses using mitochondrial DNA have often been employed alongside morphological data in order to diagnose taxonomic groups and their phylogenetic relationship in fish species (Avise *et al.*, 1998; Avise & Wlaker, 1999; Martin & Bermingham, 2000; Chiachio *et al.*, 2008; Cardoso & Montoya-Burgos, 2009; Carvalho *et al.*, 2015, Costa-Silva *et al.*, 2015, Sales *et al.*, 2018). DNA barcoding, in particular, has been applied to help discriminate species of Trichomycteridae in Southeastern Brazil, as a test of the efficiency of alpha taxonomy studies.

(Pereira *et al.*, 2010 and 2013; Ochoa *et al.*, 2017; Sales *et al.*, 2018). Those particular genes have been widely used in this sort of studies because of their advantages in species-level applications in comparison with nuclear genes, such as absence of introns, limited recombination and haploid mode of inheritance (Saccone *et al.*, 1999).

Of multiple mitochondrial markers, cytochrome oxidase sub-unity I (COI) has been the most used to diagnose species. That gene stands out because of its fast evolutionary rate (in comparison with other commonly used mitochondrial markers such as 16S and Cyt-b, and its low conspecific variation relative to its congeneric variation. (Hebert *et al.*, 2003). Since Hebert *et al.*, (2003) this gene has been used to diagnose all kinds of animal species from invertebrates to vertebrates, such as springtails (Hogg & Hebert, 2004a), butterflies (Hebert *et al.*, 2004a; Elias *et al.*, 2007), crustaceans (Costa *et al.*, 2007; Lefebure *et al.*, 2006), fish (Ward *et al.*, 2005; Hubert *et al.*, 2008; Valdez-Moreno *et al.*, 2009; Carvalho *et al.*, 2011; Rosso *et al.*, 2012), birds (Hebert *et al.*, 2004b; Yoo *et al.*, 2006) and mammals (Clare *et al.*, 2007). COI has also been used to other purposes such as identification of invasive species (Corin *et al.* 2007), wildlife forensics investigations (Pons, 2006; Dawnay *et al.*, 2007; Nelson *et al.*, 2007), diagnosis of cryptic communities (Pfenninger *et al.* 2007; Costa-Silva *et al.*, 2015), and fisheries strategies (Metcalf *et al.*, 2007).

Despite all its advantages, the use of COI in systematic studies has some caveats, such as the occasional inability to segregate otherwise well-diferenciated species and the possibility of mitochondrial introgression (Rubinoff *et al.*, 2006). However, such cases are the exception rather than the rule and affect only 5% to 10% of cases (Ward *et al.* 2005; Hubert *et al.* 2008; Valdez-Moreno *et al.* 2009; Pereira *et al.*, 2013). For all its net benefits, the Fish DNA Barcoding of Life Campaign was created as an international and cost-effective iniciative to gather all COI sequence

and associated taxonomic information in a database organized as a web-platform <http://www.fishbol.org/> (Ward *et al.*, 2009).

This chapter intends to study the diversity of the genus *Trichomycterus* in the Rio Doce using both COI data and phenotypic characteristics, including those traditionally employed in the taxonomy of the genus. We make a special effort to provide information on intraspecific and ontogenetic variation, as well as detailed assessments on geographical distribution. Results demonstrate that *Trichomycterus* in the Rio Doce was poorly understood on all aspects, including previously entirely unknown species, cryptic species, poorly-defined species and species described multiple times (junior synonyms). We also use our data on taxonomy and geographical distribution to offer insights on biogeography and offer possible explanations on why some species are so widespread while others are narrowly endemic.

## Conclusão

### *Can genetic divergence be used as a proxy for taxonomic differentiation?*

In sum, it is clear that barcoding and morphological data are largely congruent in our results. This is strong indication that the taxonomic decisions implemented here are supported by separate types of biological data and thus robust from an ontological perspective. Such reasoning implies that congruent conclusions from independent sources of evidence provide empirical support for lineage differentiation. Also, the degree of barcode differentiation cannot be translated into a single cutoff value. Initial proposals of barcoding taxonomy expected a rather uniform divergence rate as a general standard for specific differentiation (Hebert *et al.*, 2003; Ward *et al.*, 2009). Later research quickly demonstrated that those initial expectations were naive and that taxonomic differentiation reflective of specific distinctiveness varies widely among different groups of organisms (Pereira *et al.*, 2013; Costa-Silva *et al.*, 2015; Sales *et al.*, 2018) and even within closely related clades (Costa-Silva *et al.*, 2015; Carvalho *et al.*, 2015; Sales *et al.*, 2018). But beyond questions of congruence or incongruence, the most interesting situations are in fact those where the separate types of data mutually illuminate each other. Cases such as those of *T. "astromycterus"*, *T. "vinnulus"*, *T. "melanopygius"* and *T. "ipatinguensis"* on the one hand, and the population of *T. alternatus* from Rio Cubatão and the specimen from Rio Doce at Baguari, on the other, show that no single type of data can be taken as *prima facie* evidence of taxonomic differentiation. In the former two cases, COI differentiation alone would be utterly incapable to detect the existence of those two well-differentiated and readily diagnosable species. In the latter, morphological data have as yet failed to reflect pronounced barcoding distinctiveness most likely reflective of - yet unrecognized - taxonomic distinctiveness.



## *Diversity and distribution of Trichomycterus in the Rio Doce basin*

In sum, the scenario described above implies that *T. immaculatus* invaded the Paraíba do Sul from the Doce. This hypothesis can be tested by an investigation into the genetic variability of the species in the two basins. The colonization event necessarily implies a bottleneck effect which results in reduced genetic variability of the founding population (Nei *et al.*, 1975). Our hypothesis thus predicts that *T. immaculatus* in the Paraíba do Sul will have reduced genetic variability relative to its conspecifics in the Rio Doce. This can easily be tested with additional samples and analyses from throughout the distribution range of *T. immaculatus*. The same reasoning applies to similar conjectures about *T. alternatus* and *T. argos/T. brasiliensis* discussed above. The alternative hypothesis, naturally, is classical vicariance, where the ancestor of *T. immaculatus* was broadly distributed in both basins, perhaps by past hydrographic conjoining, and became isolated once the drainages separated.

## *Taxonomic situation in Trichomycterus*

In sum, our experience with the *Trichomycterus* of the Rio Doce demonstrates that contingent factors in the history of the systematics of the genus have paved the way for standards which may be resulting in taxonomic inflation of the diversity of the genus in Southeastern Brazil. A concerted effort must be undertaken in order to attain uniformity of taxonomic practices in *Trichomycterus* descriptions on the basis of wide-ranging and objectively standardized sources of data. Attention to intraspecific and geographic variation is also tantamount in this process.

Although a hard-to-reach objective, this is a necessary precondition for significant progress in understanding the diversity and evolution of the genus and to forestall the creation of newborn synonyms. Once applied, the tempestuous cloud on this genus can finally start to dissipate.

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**Chapter 2.** – The type specimens of *Trichomycterus alternatus* (Eigenmann, 1917) and *Trichomycterus zonatus* (Eigenmann, 1918), with elements for future revisionary work (Teleostei, Siluriformes, Trichomycteridae).

## Abstract

Among the most pervasive elements in mid- to high-elevation coastal streams of Southeastern Brazil are the trichomycterid catfish species *Trichomycterus alternatus* Eigenmann, 1917 and *Trichomycterus zonatus* Eigenmann, 1918. Despite their abundance and ecological ubiquity, uncertainty still reigns in the applicability of their names. Examination of the type material of the two species reveals that part of the confusion stems from a mixing of species in the *T. zonatus* type-series. Such situation triggered a long-lasting chain of taxonomic misinterpretations and erroneous identification protocols and traditions. We disentangle this situation, providing detailed information on the holotypes and remaining type specimens of each species by classical and pioneering (Stereo Triplet) morphology analyses for data obtention. This will allow further taxonomic work to proceed on a firm nomenclatural basis. We also clarify and map the reported localities of the type material and offer comments into the validity of *T. alternatus* and *T. zonatus*, along with that of possibly related forms.

## Resumo

Dentre as espécies de peixes neotropicais mais bem distribuídas entre médias e elevadas altitudes para as regiões costeiras do sudeste brasileiro, duas espécies de bagres da família Trichomycteridae se destacam, *Trichomycterus alternatus* Eigenmann, 1917 e *Trichomycterus zonatus* Eigenmann, 1918. Apesar da abundância e presença em diversos ecossistemas, diversas incertezas ainda permeiam a taxonomia dessas duas espécies. O exame detalhado dos respectivos materiais tipos revelou que a complexidade taxonômica provem em parte da presença de uma segunda espécie no material tipo de *T. zonatus*. Este fato provavelmente resultou em uma longa cascata de interpretações taxonômicas equivocadas e protocolos de identificação errôneos. Esta questão é resolvida a partir de informações detalhadas sobre a morfologia interna e externa dos materiais tipos de *T. alternatus* e *T. zonatus*, utilizando análises morfológicas clássicas e pioneiras (Stereo Triplet) para a obtenção de dados. Com base nas informações prestadas, trabalhos futuros poderão prosseguir em bases nomenclaturais sólidas determinando a aplicabilidade dos nomes das respectivas espécies. Também são esclarecidas e mapeadas as localidades-tipo dessas espécies, com comentários a respeito da validade de *T. alternatus* e *T. zonatus*. Finalmente, as duas espécies, em suas concepções revisadas, são comparadas a formas já descritas para o sudeste brasileiro.

## Introduction

*Trichomycterus alternatus* and *T. zonatus* are two of the most abundant catfish species in coastal freshwaters of Southeastern Brazil (Triques & Vono, 2004; Sato *et al.*, 2004; Vieira, 2010; Da Silva *et al.*, 2013; Sales *et al.*, 2018). They occur in cool, fast flowing, clear water streams and rivers, on rocky, sandy and mixed substrates, from just above sea level to over 1000 m altitude (de Pinna, 1998). Forms related to those taxa are nearly always present in biological inventories, ecological studies, faunistic surveys and freshwater samples in suitable habitats in that region (Sato *et al.*, 2004; Vieira, 2010; Da Silva, 2013; Sales *et al.*, 2018). Despite that, the two species remain poorly defined taxonomically and their identification is still confusing. As a consequence, their exact geographical range is yet uncharted and their degree of intraspecific variation remains undetermined. Numerous new species have been, and continue to be proposed for forms which are obviously related to *T. alternatus* and *T. zonatus* (e.g. *T. auroguttatus* Costa, 1992; *T. caudofasciatus* Alencar & Costa, 2004; *T. florensis* (Miranda Ribeiro 1943); *T. gasparinii* Barbosa, 2013; *T. longibarbatus* Costa, 1992; *T. mimosensis* Barbosa, 2013; *T. pantherinus* Alencar & Costa, 2004; *T. travassosi* (Miranda Ribeiro 1949)). Their validity depends on critical information about the delimitation and applicability of those two names, which have priority over most other species names assignable to *Trichomycterus* in Southeastern Brazil.

It is clear that information about the type material of *T. alternatus* and *T. zonatus* is critical for progress on that issue. Curiously, however, data from the types have rarely been considered in taxonomic publications discussing issues related to those species, even though they are in relatively good preservation condition and readily available for study. Most subsequent authors have simply relied on information provided in original publications by C. Eigenmann (e.g. Costa, 1992; Alencar & Costa, 2004; Barbosa, 2013). That information is quite limited when compared



to current descriptive standards and fail to provide comparative data critically needed today for taxonomic decisions. Besides, the type series of the two species reveals a number of problems related to localities, non-conspecificity between paratypes and holotypes, and inaccuracies in published data. Our aim in this paper is to disentangle that situation and to provide a clear picture of the situation of the type material, along with detailed morphological information on existing type specimens. We also refine and map the reported localities of the type material, offer data on recently-collected topotypes, and discuss the validity of *T. alternatus* and *T. zonatus*, along with that of possibly related forms.

We believe that accurate information on the relevant type material of *T. alternatus* and *T. zonatus* is tantamount for further research on the biological entities concerned and will allow upcoming contributions to proceed on a sound nomenclatural basis. This is necessary for increasing knowledge on the biodiversity of *Trichomycterus* in the Southeastern Brazilian region and ultimately to help untangling the broad-scale taxonomic maze of the genus.

## Conclusion

The summation of all the differences above leave little doubt that the type material of *T. alternatus* and *T. zonatus* represent different species. Their distinguishing characteristics equal or surpass, in kind and degree, those normally seen between different species of *Trichomycterus* (Triques & Vono, 2003; Bockmann & Sazima, 2004; Wosiacki & de Pinna, 2008). This is a straightforward conclusion in face of the data provided above. However, it differs considerably from conceptions widespread in the literature about the identity of *T. zonatus* (Lima, 2008), which apply the name indiscriminately to many *T. alternatus*-like forms of *Trichomycterus* in the coastal basins in the region between the Rio Doce and Ribeira de Iguape. In reality, *T. zonatus* is a rather rare species in collections and for this study we located a single lot additional to the type series (MZUSP83139). Therefore, *T. zonatus* is a species in reality not present in most of the geographical range where it has been allegedly reported, such as the Rio Paraíba do Sul, Rio Doce and all smaller coastal basins in the intervening region (Lima, 2008; de Oliveira, 2011). While its absence in the northern Southeastern Brazilian basins is likely, the southern range of *T. zonatus* is still undetermined.

The case of *T. alternatus* and *T. zonatus* is very specific considering the great diversity of *Trichomycterus* species in Southeastern Brazilian drainages. Nonetheless, we believe that the lessons to be learned from them are general and bring to surface widespread problems and vices which plague the taxonomy of the genus as a whole. Such traditions include the description of species without consideration for geographical, intraspecific and ontogenetic variation, and the lack of attention to information on type specimens of older yet obscure names which may have priority. We believe that detailed study will reveal similar situations with species of other species

groups of *Trichomycterus* in southeastern Brazil, such as *T. immaculatus* (Eigenmann, 1889), *T. brasiliensis* Lütken 1874.

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