Vinícius José Carvalho Reis

Ontogeny and phylogeny in Trichomycteridae (Teleostei, Siluriformes): patterns in the development of morphological complexes

Ontogenia e filogenia de Trichomycteridae (Teleostei, Siluriformes): padrões no desenvolvimento de complexos morphológicos

Ontogénie et phylogénie chez les Trichomycteridae (Teleostei: Siluriformes): modèles de développement de complexes morphologiques

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> Thesis submitted to the Graduate Programs of the Museu de Zoologia da Universidade de São Paulo and to the Museum National d'Histoire Naturelle in partial fulfillment of the requirements for the double degree of Doctor of Science (Systematics, Animal Taxonomy and Biodiversity) and in Systematic and Evolution respectively.
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Ontogeny and phylogeny in Trichomycteridae (Teleostei, Siluriformes): patterns in the development of morphological complexes

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General Abstract

This thesis offers the first large-scale study on the ontogeny of the musculoskeletal system in Trichomycteridae and its implications for understanding the phylogenetic relationships and evolution of the family. Trichomycteridae is a monophyletic group of neotropical catfish with exceptionally rich morphological diversity. This diversity is reflected in a wide range of habitats and trophic niches. The feeding habits of the group vary from invertivores to strict hematophagy, the latter a unique case in Actinopterygii. Using developmental series and juvenile specimens representing most trichomycterid lineages, detailed descriptions of the development of various musculoskeletal systems of the head, such as the mandibular complex, opercular apparatus, branchial skeleton, suspensorium, and neurocranium are presented. Such information, new for the most part, provides a solid framework for formulating and testing hypotheses of homology, some of which representing long-standing controversies in Siluriformes, such as the supraoccipital, parietal, pterotic, extrascapular, and posttemporal. Observations also permit direct mapping of transformation sequences and connections between highly divergent conditions in adult specimens, such as the mouth apparatus of juveniles and adults of Vandelliinae. Results obtained are incorporated into new morphological and total evidence phylogenetic analyses with broader taxonomic and data density than previously available, allowing a detailed understanding of the diversification history of Trichomycteridae. Those results are combined with developmental information to provide an ontogenetic framework for testing a new method for detecting heterochronies designed to map paedo- and peromorphic phenomena in the family. The most relevant phylogenetic results are that Microcambevinae probably result from long-branched attraction, and the identification of a new clade composed of *Stenolicmus ix* and *Ammoglanis pulex*, previously assigned to Sarcoglanidinae, and the removal of *Potamoglanis* from Tridentinae. The synergism of phylogenetic hypothesis with ontogeny reveals wide-evolutionary patterns, showing that Trichomycteridae is a mostly paedomorphic family, a ground plan upon which numerous internested peramorphic apomorphies have evolved. One major event of miniaturization occurred at the base of a large clade, here named the miniature clade. Within that clade, there are various events of further reduction in size. Surprisingly, within the miniature clade there is also an event of reverse size-increase, a phenomenon detected not only by phylogenetic structure but also by marks left in the structure and development of different anatomical complexes.

Résumé general

Cette thèse offre la première étude à grande échelle sur l'ontogénie du système musculosquelettique chez les Trichomycteridae et ses implications pour comprendre les relations phylogénétiques et l'évolution de la famille. Les Trichomycteridae sont un groupe monophylétique de poissons-chats néotropicaux présentant une diversité morphologique exceptionnellement riche. Cette diversité se reflète dans une large gamme d'habitats et de niches trophiques. Les habitudes alimentaires du groupe varient des invertivores à l'hématophagie stricte, ce dernier étant un cas unique chez les Actinopterygii. En utilisant des séries de développement et des spécimens juvéniles représentant la plupart des lignées de trichomycteridés, des descriptions détaillées du développement de différents systèmes musculosquelettiques de la tête, tels que le complexe mandibulaire, l'appareil operculaire, le squelette branchial, le suspensorium et le neurocrâne sont présentées. Ces informations, nouvelles pour la plupart, fournissent un cadre solide pour formuler et tester des hypothèses d'homologie, dont certaines sont l'objet de controverses de longue date chez les Siluriformes, telles que le supraoccipital, le pariétal, le ptérotique, l'extrascapulaire et le posttemporal. Les observations permettent également des correspondances directes des séquences de transformation et des connexions entre des conditions très divergentes chez les spécimens adultes, telles que l'appareil buccal des juvéniles et des adultes de Vandelliinae. Les résultats obtenus sont intégrés dans de nouvelles analyses phylogénétiques morphologiques mobilisant l'analyse simultanée de davantage de données concernant une plus grande densité taxonomique que précédemment disponibles, permettant une compréhension détaillée de l'histoire de la diversification des Trichomycteridae. Ces résultats sont combinés avec des informations développementales pour fournir un cadre ontogénétique permettant de tester une nouvelle méthode de détection des hétérochronies conçue pour détecter les phénomènes paedomorphes et peromorphes dans la famille. Les résultats phylogénétiques les plus pertinents concernent les Microcambevinae, qui résultent probablement d'une attraction de longues branches ; l'identification d'un nouveau clade composé de *Stenolicmus ix* et *Ammoglanis pulex*, précédemment assigné à Sarcoglanidinae, et l'exclusion de *Potamoglanis* de Tridentinae. La

synergie entre hypothèse phylogénétique et ontogénie permet une vision large de l'évolution de la famille, montrant que les Trichomycteridae sont une famille principalement paedomorphe, un plan de base sur lequel de nombreuses apomorphies péramorphes ont évolué de manière enchevêtrée. Un événement majeur de miniaturisation s'est produit à la base d'un grand clade, ici nommé le « clade miniature. » Au sein de ce clade, il y a eu divers événements de réduction supplémentaire de la taille. De manière surprenante, dans le clade miniature, il y a également eu un événement inverse d'augmentation de taille, un phénomène détecté non seulement par la structure phylogénétique mais aussi par les marques laissées dans la structure et le développement de différents complexes anatomiques.

Mots-clés : Trichomycteridae, Ontogénie, Phylogénie, Poisson-chat, Hétérochronie.

Resumo geral

Esta tese oferece o primeiro estudo em larga escala sobre a ontogenia do sistema musculoesquelético em Trichomycteridae e suas implicações para compreender as relações filogenéticas e a evolução da família. Trichomycteridae é um grupo monofilético de bagres neotropicais com uma diversidade morfológica excepcionalmente rica. Essa diversidade é refletida em uma ampla gama de habitats e nichos tróficos. Os hábitos alimentares do grupo variam de invertívoros a hematofagia estrita, sendo este último um caso único em Actinopterygii. Utilizando séries de desenvolvimento e espécimes juvenis que representam a maioria das linhagens da família, são apresentadas descrições detalhadas do desenvolvimento de vários sistemas musculoesqueléticos da cabeça, como o complexo mandibular, aparelho opercular, suspensório, arco hioide, arcos branquiais, e neurocrânio. Essas informações, em sua maioria novas, fornecem uma base sólida para formular e testar hipóteses de homologia, algumas das quais representando controvérsias de longa data em Siluriformes, como o supraoccipital, parietal, pterótico, extrascapular e posttemporal. As observações também permitem o mapeamento direto de sequências de transformação e conexões entre condições altamente divergentes em espécimes adultos, como o aparelho bucal de juvenis e adultos de Vandelliinae. Os resultados obtidos são incorporados em novas análises filogenéticas morfológicas e de evidências totais, com uma representação taxonômica mais ampla e densidade de dados maior do que antes disponível,

permitindo uma compreensão detalhada da história de diversificação de Trichomycteridae. Esses resultados são combinados com informações de desenvolvimento para fornecer um arcabouço ontogenético para testar um novo método de detecção de heterocronias projetado para mapear fenômenos de paedomorfia e peramorfia na família. Os resultados filogenéticos mais relevantes são que Microcambevinae provavelmente é resultado do fenômeno de atração de ramos longos, a identificação de um novo clado composto por *Stenolicmus ix* e *Ammoglanis pulex*, anteriormente atribuídos a Sarcoglanidinae, e a exclusão de *Potamoglanis* de Tridentinae. A sinergia da hipótese filogenética com a ontogenia revela padrões evolutivos amplos, mostrando que Trichomycteridae é uma família principalmente paedomórfica, um plano de base sobre o qual numerosas apomorfias peromórficas evoluíram. Um evento importante de miniaturização ocorreu na base de um grande clado, aqui chamado de clado miniatura. Dentro desse clado, existem vários eventos de redução adicional de tamanho. Surpreendentemente, dentro do clado miniatura também ocorre um evento de aumento reverso de tamanho, um fenômeno detectado não apenas pela estrutura filogenética, mas também pelas características deixadas na estrutura e desenvolvimento de diferentes complexos anatômicos.

Palavras-chaves : Trichomycteridae, Ontogenia, Phylogenia, Bagres, Heterocronia.

SUMMARY

GENERAL INTRODUCTION

Trichomycteridae is the second most diverse family of catfish widely distributed throughout the Neotropical region, occurring from Costa Rica to southern Argentina and Chile (de Pinna, 1998). Its species can be found in narrow streams at sea level to high altitude rivers and lakes on both sides of the Andes. The large morphological variation found in the family reflects an equally wide range of habits and ecologies (Baskin, 1973, Baskin *et al*., 1980; de Pinna, 1998; Arratia, 2008). A highly modified opercular apparatus is one of the most striking synapomorphy of Trichomycteridae. The interopercle is transformed into a compact structure that supports a platform carrying a set of odontodes in at least one stage of life on its representatives. Similarly, the opercle is modified into a compact bone structure commonly presenting odontodes in a well-delimited region. Many other synapomorphies, some unique in Siluriformes, also corroborate Trichomycteridae as a monophyletic group (de Pinna, 1998).

An additional set of conspicuous apomorphic modifications are present in different subgroups of the family, some involving muscle and neomorphic ligaments without parallel in Siluriformes, and others related to fusion or absence of bones (Baskin, 1973; de Pinna, 1998; Datovo and Bockmann, 2010). Many of these specializations can be clearly associated with specific trophic niches, especially those related to semi-parasitic habits, lepidophagy and muciphagy (Stegophilinae and part of Tridentinae), hematophagy (Vandellinae) and scavengers (*Pareiodon micros* Kner, Stegophilinae). All these anatomical modifications were and continue to be the object of interest of systematists who seek to know the diversity and evolutionary history of the family, such as: Eigenmann and Eigenmann (1890), Eigenmann (1918), Peyer (1922), Berg (1940), Tchernavin (1944), Myers (1944), Myers and Weitzman (1966), Baskin (1973), Arratia (1990a, b), Arratia and Schultze (1990), Schmidt (1993), de Pinna (1992, 1998, 2016), Fernandez and Schaefer (2009), Adriaens *et al*. (2010), Datovo and Bockmann (2010), DoNascimiento (2015), Henschel *et al*. (2017), Costa *et al*. (2019), Ferrer and Malabarba (2020), Costa (2021a). Among those, Eigenmann (1918) stands out as the first to propose a phylogenetic hypothesis for the family, till then called Pygidiidae. However, due to the constant discoveries of additional data and new key-taxa in the family, the relationships among subgroups of Trichomycteridae have subsequently changed as noted in Myers (1944), Baskin (1973), de Pinna (1998), Datovo and Bockmann (2010), DoNascimiento (2015); Henschel *et al* (2017), Ochoa *et al* (2017, 2020), and

Costa *et al*. (2019). Notwithstanding, of all the morphological phylogenetic hypotheses proposed for Trichomycteridae, only that of Datovo and Bockman (2010) used quantitative analyzes to propose a hypothesis of relationship. Although Datovo and Bockman (2010) were limited to a restricted number of taxa representing the whole family, either limited to mythological characters to propose a new phylogenetic hypothesis for Trichomycteridae. Thus, a total evidence phylogenetic hypothesis that encompasses all genera of the family, using previously published morphological and molecular hypotheses, added by new data from this study, making use of ontogeny to test and / or substantiate hypotheses of homology and built on quantitative analysis, would be totally innovative and pioneering not only for Trichomycteridae, but for Loricarioidea.

Studies of development are great tools for revealing evolutionary patterns and processes in any organism. Studies integrating evolution and ontogeny (often associated with hypotheses of functional morphology) have been performed in several fish groups, supporting and/or testing hypotheses of homology and evolutionary tendencies for various morphological and behavioral traits (*e.g.* Loricarioidea - Schaefer and Lauder, 1986; Geerinckx *et al*., 2005; Geerinckx *et al*., 2007; Trichomycteridae – Arratia, 1990; Sparidae - Hernandez and Motta, 1997; Clariidae - Adriaens, 1998, Wyckmans *et al*., 2011; Cichlidae - Albertson *et al*., 2003, 2005, Santos-Santos *et al*., 2015; Cypriniformes - Bird *et al*. 2007; Cyprinodontiformes - Hernandez *et al*., 2009a; Ictaluridae - Hawkins, 2011; Kubicek *et al*., 2019; Kubicek, 2022). There is a consensus that ontogenetic studies are great tools for testing homologies, contributing to the development of phylogenetic hypotheses (Gould, 1977; Alberch, 1979; Fink, 1982; de Pinna and Grande, 2003; Grande and Young, 2004; Johnson and Britz, 2005; Laurin and Garmain, 2011; Bardin *et al*., 2017, Lecointre *et al*. 2020). The subject is actually one of the classic themes in biology, with more than 200 years discussing, returning to the historical quest for the relationship between ontogeny and phylogeny (Gould, 1977).

Although the evident importance of this subject, studies investigating ontogeny on Trichomycteridae are still incipient. Arratia (1990) and de Pinna *et al*. (2020) are the unique publications that attempted to use ontogenetic transformations in the family in a phylogenetic context. However, despite the relevance of both works, in Arratia's work, it was restricted to the Suspensorium complex with a modest comparative scope given the great diversity of the family,

while in de Pinna *et al*., it was restricted to the antorbital-lacrimal bone development in the considered basal subfamily Trichogeninae.

The situation described above makes evident the relevance of a broad study addressing the comparative ontogeny in Trichomycteridae and its implications on the understanding of its history of diversification. Ontogenetic data may refute or corroborate hypotheses of primary homology (e.g., Grande and Bemis, 1998; de Pinna and Grande, 2003; Grande, 2010; Carvalho *et al*., 2013; Mattox *et al*., 2014; Lecointre *et al*. 2020) and define the sequence of character state transformations (Nelson, 1978; Nelson and Platnick, 1981; Weston, 1988, 1994; de Pinna, 1994; Lecointre *et al*. 2020), two components of fundamental importance in evolutionary studies. The incorporation of data from life cycle studies, contrasting with just instantaneous morphological characters, gives a multidimensionality that greatly expands the relevance and meaning of phylogenetic analyses and consequent hypotheses of evolutionary transformation in association with phylogenetic diversification (Gould, 1977; Alberch, 1979).

Adriaens *et al*. (2010), Datovo and Bockmann (2010) and DoNascimiento (2015) attested that the musculoskeletal system of the skull in Trichomycteridae has undergone several modifications throughout the evolutionary history of the family, allowing the occupation of multiple niches: fossorial, psammophiles, carnivores, scavengers and the highly modified parasites. These contributions are still incipient, but they certainly allow us to foresee a vast universe still unexplored in the family. Vandelliinae is an extreme example in which profound musculoskeletal changes are evidently associated with strict hematophagy. At least some subfamily species, such as *Vandellia cirrhosa* Valenciennes in Cuvier and Valenciennes, apparently undergo a drastic process of metamorphosis, since juveniles of this species has a profoundly different morphology of the mouth in compare to adults (de Pinna, 1998; personal com.). Some morphological elements in adults of Vandelliinae are modified beyond any significant parallel to other groups. But the conditions in the juvenile specimens allow highly elucidative comparisons, with enormous relevance in understanding the profound morphological changes that the group has undergone throughout its history of diversification. Obviously, an ontogenetic study of Vandelliinae would provide key information for understanding the morphological changes associated with the emergence and diversification of parasitism in the family.

Beyond specific ontogenetic modifications, Trichomycteridae includes examples of peculiar developmental patterns. Some taxa, such as *I compactus* and *Potamoglanis* (*P. hasemani*, *P. johsoni*) include miniaturized species with fully ossified, although with some paedomorphic traits, and also the most paedomorphic species in the family with bone element reduction (*P. anhanga*). This suggests that very diverse developmental processes were involved in the miniaturization process of this clade, again providing a rich substrate for detailed ontogenetic studies as proposed here.

Much of the skull and related tissues are expressed by few pleiotropic genes (Albertson *et al*., 2005). Because of this, a specific genetic modification of a given character would lead to other cascading modifications (Albertson *et al*., 2003; 2005). A detailed mapping of ontogenetic transformations in Trichomycteridae, in combination with a robust phylogenetic hypothesis, would be a necessary framework for initiating future studies on possible pleiotropic associations and prospecting for ontogenetic cascade effects. In addition, the sequence and direction of ontogenetic transformations provide the only direct observation of character state transformations in phylogenetic reconstruction (Nelson, 1978; Nelson and Platnick, 1981; de Pinna, 1994), a controversial but widely relevant topic in comparative biology.

This study carried out a detailed study of the ontogeny of morphological complexes in Trichomycteridae, with emphasis on the skeleton, mapping the variations found in a detailed synthesis of the family ontogenetic transformations. This information was integrated into a phylogenetic kinship hypothesis that provided a fresh overview of family evolution.

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Chapter 1

Phylogeny of Trichomycteridae.

INTRODUCTION

Among the rich Neotropical catfish fauna, the family Trichomycteridae stands out as a particularly diversified clade. Popularly known as pencil catfishes or candirus, trichomycterids are the second most species-rich family within the Siluriformes, with 365 valid species (Fricke et al., 2023) found throughout the entire Neotropical region, from Costa Rica to Patagonia. Their diversity is manifest in all aspects, including habitats and trophic niches (de Pinna, 1998). They inhabit a wide range of environments, including narrow creeks, large Amazonian rivers, subterranean waters, leaf litter, lakes in the Andean range (up to 4500 meters above sea level), and even inshore Pacific islands (de Pinna and Wosiacki, 2003; Fernandez and Schaefer, 2005; Arratia and Menu-Marque, 1984; Rizzato et al., 2011). The family is currently composed of nine subfamilies: Copionodontinae, Trichogeninae, Trichomycterinae, Microcambevinae, Glanapteryginae, Sarcoglanidinae, Tridentinae, Stegophilinae, and Vandelliinae.

Copionodontinae and Trichogeninae, considered relictual taxa, are mid-water swimmers inhabiting the mid- to lower portion of the water column of creeks, with low associated fish diversity and never coexisting with other trichomycterid lineages (pers. obs.; de Pinna, 1992; Sazima, 2004; Primitivo-Oliveira, 2011). Trichomycterinae, the most species-rich subfamily, comprises nine genera and 265 valid species (Fricke et al., 2023). They usually dwell amongst pebbles at the substrate, with some species burying in sandy patches, such as *Scleronema* Eigenmann 1917 and *Trichomycterus astromycterus* Reis et al., 2019. Microcambevinae, the most recently established subfamily, consists of *Microcambeva* Costa and Bockmann 1994, and *Listrura* de Pinna 1988. Those genera were split from two distinct subfamilies where they were formerly included, respectively Sarcoglanidinae and Glanapteryginae. The three subfamilies are interstitial, living in leaf litter, sand, or buried in the substrate (Zuanon and Sazima, 2004; Schaefer et al., 2005; Zuanon et al., 2006; Costa et al., 2019; Costa and Katz, 2021). Microcambevinae inhabit the Atlantic Forest biome, while Sarcoglanidinae and Glanapteryginae are found in the Amazon.

Tridentinae is composed exclusively of miniature species, for the most part active in the water column (Roberts, 1972; Ferraris, 1991; Datovo and Bockmann, 2010). Their sister group, a clade composed of Stegophilinae and Vandelliinae, are commonly known as true candirus or carneros.

The diversity of habitats and feeding behaviors within Trichomycteridae is directly associated with a prominent synapomorphy of the family, a highly modified opercular-interopercular apparatus equipped with specialized odontodes (integumentary teeth) on both bones. This specialized complex assists members of the family in clinging and crawling through rocks and pebbles or anchoring themselves to their hosts (Stegophilinae and Vandelliinae).

One of the most interesting aspects of the diversity of Trichomycteridae is their wide array of feeding habits and trophic adaptations (Datovo and Bockmann, 2010). While a majority of species are generalist predators of aquatic or allochtonous invertebrates (Nico and de Pinna, 1996; de Pinna, 1998; Sazima, 2004), there are notable exceptions within the family. Copionodontinae, for example, are scrappers with spatulated teeth, and species in Stegophilinae feed on mucus and scales from host species (Baskin et al., 1980; Winemiller and Yan, 1989), with some species also scrapping flesh from open wounds in other fish (Luling, 1984). Vandelliinae include exclusively hematophagous species, a unique case in jawed fishes (de Pinna, 1992; de Pinna, 1998; Fernández and Schaefer, 2009; Kelley and Atz, 1964; Machado and Sazima, 1983). The specialized feeding habits of those two latter subfamilies are reflected in their highly modified mouth apparatus. They possess new specialized bones, such the median premaxilla, concomitantly with the loss of other bones, such as the vomer and parts of the branchial arches. Additionally, they have highly specialized teeth in the form of hooks or claws, called scalpelloid teeth, which are used to anchor themselves to their hosts.

In this chapter, we provide a brief overview and discussion of the history of systematic research on trichomycterids. We also offer results of a reanalysis of the relevant data available for elucidating its phylogenetic relationships and their implications to the classification of the family.

A brief review of the Systematics of the Trichomycteridae

Most of the history of the systematics of Trichomycteridae has taken place in the evolutionary era. Although a few taxa have been described before the widespread acceptance of Darwinian evolution, those have mostly been isolated descriptions with little in terms of affinities or groupings. Therefore, unravelling the diversity of Trichomycteridae has mostly been a pursuit to understanding their evolution. One consistent finding across studies employing both phylogenetic and pre-phylogenetic traditions on Trichomycteridae, is that the group, once

recognized, has never been refuted. The first time trichomycterids were nomenclaturally recognized as a family-level group was in Bleeker (1858), labeled as the Phalanx C Trichomycterini within the subfamily Silurichthyoidei of the family "Siluroidei", the latter identical to today Siluriformes. The same subfamily Silurichthyoidei included also Phalanxes Cetopsini, Trachelyopterini and Schilbeini. Shortly thereafter, Bleeker (1863) changed such arrangement, ranking trichomycterids as subfamily Trichomycteriformes and assigning it to family Siluroidei (then one of six families in Siluri) together with seven other subfamilies from around the world ("Ailiaeformes," "Astroblepiformes," "Bagriformes," "Malapteruriformes," "Siluriformes," "Sisoriformes," "Trachelyopteriformes"). Bleeker´s 1863 Trichomycteriformes was splited into three Stirps, Nematogenyini, Trichomycterini and Vandelliini. Curiously, the genera *Stegophilus* and *Pareiodon* were included in the Trichomycterini. Gill (1872) elevated Trichomycteridae to the rank of family in a format alied to today´s understanding, a classification that has remained unchanged to this day.

Starting with Eigenmann (1888), the name *Pygidium* Meyen, 1835 was resurrected and widely used in subsequent publications, including its family-level derivative, Pygidiidae. The situation was mostly reversed in Tchernavin (1944), who concluded that Eigenmann´s change was based on a misinterpretation of the history and status of the names concerned, and reinstated *Trichomycterus* and Trichomycteridae.

A group equivalent to today´s Trichomycteridae was not recognized in Eigenmann & Eigenmann (1889, 1890). Although the family Pygidiidae is included in the respective classification, it comprises the Cetopsinae as one of its three subfamilies, with the Trichomycterinae and Stegophilinae not united into an exclusive taxon. On the other hand, the authors recognize *Stegophilus* as closely related to *Vandellia*.

In 1918, Eigenmann conducted a comprehensive study of the taxonomy of Pygidiidae (= Trichomycteridae), in a revision which included all species then known and which is still the largest ever done with the family. Eigenmann recognized six subfamilies: Nematogenyinae, Pygidinae, Pareiodontinae, Tridentinae, Stegophilinae, and Vandelliinae (Fig. 1A). Cetopsidae was excluded from the family. A phylogenetic tree in the same publication, which includes all genera then known, places *Nematogenys* as the most basal branch in the family. In addition to the various subfamilies, the tree includes other groups which are still considered as valid today, such

as the one including Tridentinae, Stegophilinae and Vandelliinae. Within the latter, the two latter subfamilies are positioned as closest relatives, again a component still held true to this date. The only major subsequent modification on Eigenmann´s scheme (putting aside taxa then unknown) is the position of *Pareiodon* Kner 1855, then considered as the "sister group" to Tridentinae, Stegophilinae, and Vandelliinae but currently internested in Stegophilinae and no longer considered as a separate subfamily. The tree in Eigenmann 1918 is a remarkable achievement in its modernity. It represents exclusively relationships which today would be characterized as sister-group relationships, and no attempt is made to include actual ancestors at the nodes. Therefore, the tree can be easily read as a modern cladogram. In Eigenmann (1927), the genus *Nematogenys* was excluded from Trichomycteridae and placed in its own monotypic family Nematogenyidae, a move that was not followed by other authors for many years.

A general discussion on trichomycterid was presented in Myers (1944), centered around the establishment of a new subfamily, Glanapteryginae. The new taxon comprised species that still today rank as some of the most aberrant in the family and indeed among catfishes, such as *Pygidianops* and *Typhlobelus*, both highly specialized for an interstitial lifestyle. The Glanapteryginae was proposed as close to Phreatobiinae (= Phreatobiidae, today known not to be closely related to Trichomycteridae, Baskin, 1973; de Pinna, 1998). While some of the relationships in Myers (1944) mirror those in Eigenmann (1918), there are some important differences. Myers´ tree is a significant departure from the standards previously used by Eigenmann (1918). Such differences go beyond the mere definition of groups and are testimony to profound philosophical shifts in the theory of phylogenetic reconstruction which took place in the intervening period. Myers´ scheme includes instances of ancestor-descedant relatinships. For example, the Nematogenyinae is placed as ancestor to all other Trichomycteridae, the Pygidiinae (=Trichomycterinae) is ancestor to the group composed of Pareiodontinae, Tridentinae, Stegophilinae, and Vandelliinae, and the Auchenipteridae is a tentative ancestor of Trichomycteridae, Doradidae, and Cetopsidae. The attempt to recognize ancestor-descendant relationships (and its corollary, actual ancestors), along with the placement of supraspecific taxa as ancestors to other taxa, is a typical product of the state of systematics in those years, derived from so-called Modern Synthesis and sublimated in the evolutionary taxonomy tradition, or gradism (Hull, 1988). Eigenmann´s work precedes such changes and recognizes taxa based on directly character evidence and propinquity of descent, bypassing attempts to recognize actual

ancestors. This is a pattern broadly recognized in the history of systematics, where contributions preceding the modern synthesis (and sometimes even evolutionary theory) are closer to present-day (and in fact, Darwinian) understanding of phylogenetic relationships than those subsequently conducted under the influence of gradism (Nelson & Platnick, 1981).

Myers and Weitzman (1966) introduced the subfamily Sarcoglanidinae for two monotypic genera, *Sarcoglanis* and *Malacoglanis*. The subfamily was characterized by the absence of teeth in the upper jaw, the pectoral fin rays extending beyond the fin membrane, and the presence of an adipose organ above the pectoral fin. At that time, Sarcoglanidinae was considered to be close to Trichomycterinae (= Pygidiinae), specifically to *Scleronema*. The authors also reiterated the basal position of *Nematogenys* within Trichomycteridae and moved Phreatobiinae from Trichomycteridae to Pimelodidae. Although this paper is clearly pre-phylogenetic in its historical context and use of terminology, it nonetheless emphasizes comparative characters which later would be interpreted as synapomorphic. Myers & Weitzman express disagreement with some of the views expressed earlier by one of them (Myers, 1944), in particular regarding the placement of Auchenipteridae as ancestral to Trichomycteridae.

In 1973, Baskin became the first to employ cladistic analysis to support the monophyly of Trichomycteridae (Fig. 1B), in a study which is the first to employ phylogenetics on any group of neotropical fishes (de Pinna, 2016). Baskin divided the family into two large monophyletic groups, with three subfamilies each: the Trichomycterinae-group (Trichomycterinae, Glanapteryginae, and Sarcoglanidinae) and the Vandelliinae-group (Tridentinae, Stegophilinae, and Vandelliinae). Five of the subfamilies were corroborated as monophyletic by the author, with only Trichomycterinae lacking putative synapomorphies. Still, the latter subfamily was not shown to be non-monophyletic, but simply lacked evidence of monophyly. Hypotheses of relationships are explicitly presented for all trichomycterid genera within each of the subfamilies. Baskin also discussed relationships among the broader group of loricarioid catfishes, and hypothesized *Nematogenys* as the sister group to all other loricarioid families. Under such new scheme, including the genus in Trichomycteridae would incur in a paraphyletic group. As a consequence, Baskin resurrected Eigenmann´s 1927 idea of a separate Nematogenyidae. The same study placed the genus *Pareiodon* within the Stegophilinae, as an aberrant member of the subfamily adapted to a trophic niche different (flesh- and carrion-feeding) from that of other

stegophilines. Such interesting hypothesis has been largely corroborated in subsequent studies. Finally, the author corroborated the exclusion of Phreatobius from the family.

Despite the monophyly of the Trichomycterinae-group, Baskin disagreed with Myers and Weitzman (1966) about the relationship of Sarcoglanidinae, proposing the latter subfamily as more closely related to Glanapteryginae than to Trichomycterinae. According to Baskin, Sarcoglanidinae and Glanapteryginae shared characteristics such as a reduced number of premaxillary teeth, the presence of a dorsal membrane, fewer than 8 anal rays, an opercular bone with a long posterior process, and reduced or absent opercular and interopercular odontodes which showed that they were sister groups.

The most drastic qualitative expansion of trichomycterid diversity came in the 1980s, when Britski and Ortega (1983) described *Trichogenes longipinnis*, a relictual and primitive trichomycterid. That single taxon displayed conditions and combinations of conditions until then only hypothetical. For example, *Trichogenes* was the first trichomycterid to have primitive states such as separate sphenotic, prootic, and pterosphenoid bones, and the only one to have a complete infraorbital latero-sensory canal branch as well as a Weberian complex separate from the back of the skull. Three years later, Isbrucker (1986) placed *Trichogenes* in its own subfamily, but without explicit justification for that decision. Shortly after that, de Pinna (1992) described another primitive trichomycterid group, Copionodontinae, which, together with Trichogeninae, exhibited plesiomorphic conditions unique within Trichomycteridae. Subsequent studies confirmed the basal position of the two subfamilies and their status as a separate clade sister to all other trichomycterids (de Pinna, 1998 – Fig. 1C; Datovo and Bockmann, 2010 – Fig. 1D; DoNascimiento, 2015 – Fig. 1E; Ochoa et al., 2017 – Fig. 1G, 2020 – Fig. 1I; Henschel et al., 2017 – 1F; Costa et al., 2019 –1H).

The Sarcoglanidinae was again revisited by de Pinna (1989) and Costa and Bockmann (1994), who reevaluated the synapomorphies for sarcoglanidines plus glanapterygines proposed by Baskin and put forward four others showing alternative groupings: the presence of a quadrate with a large, posteriorly directed dorsal process, a hyomandibula with a large anteriorly directed dorsal process, a reduced vomer, and miniaturization. Costa and Bockmann (1994) also concluded that the clade formed by Glanapteryginae and Sarcoglanidinae would form a more inclusive group with Tridentinae, Stegophilinae, and Vandelliinae, referred to as the TSVSG-

clade, i.e., all trichomycterids except Copionodontinae, Trichogeninae, and Trichomycterinae. The TSVSG-clade was defined by four synapomorphies: the reduction in the length of the interopercular patch of odontodes with 15 or fewer odontodes, a reduction in the number of pleural ribs (1-8), a reduced or absent metapterygoid bone, and a derived shape of the parasphenoid.

Relationship between Sarcoglanidinae and Glanapteryginae has been extensively debated, in what turned out to be the most contentious region of trichomycterid phylogenetics. Even the monophyly of those subfamilies is questionable (de Pinna, 1989a, b; de Pinna and Starnes, 1990; Costa and Bockmann, 1994; Datovo and Bockmann, 2010; DoNascimiento, 2015; Ochoa et al., 2017, 2020; Henschel et al., 2017; Costa et al., 2019; Costa and Katz, 2021). While all morphological phylogenetic hypotheses support the monophyly of both subfamilies, molecular studies disagree, particularly regarding their reciprocal monophyly (Ochoa et al., 2017, 2020; Henschel et al., 2017; Costa et al., 2019; Costa and Katz, 2021).

One of the fulcral points of that controversy is the positions of *Listrura* de Pinna, 1988, and *Microcambeva* Costa and Bockmann, 1994. The two genera are from the Atlantic Forest in Southeastern Brazil and were originally described in Glanapteryginae and Sarcoglanidinae, respectively, which are otherwise restricted to the Amazon region. Despite such geographical distance, *Listrura* and *Microcambeva* clearly fit within their original subfamilies on the basis of morphological data. But recent molecular studies using multiple loci and next-generation DNA have consistently separated the two genera from their respective subfamilies and placed them together in a well-supported clade (Costa et al., 2019; Ochoa et al., 2020 - Fig. 1H, I). Based on this molecular evidence, Costa et al. (2019) erected a new subfamily, Microcambevinae, to accommodate the two genera. The authors also found that the newly-erected subfamily belongs to the TSVSG-clade and is the sister group to all other subfamilies therein. These results were further supported by Ochoa et al. (2020) using next-generation DNA. With this, Costa et al. (2019) updated the former TSVSG-clade to the TSVSGM-clade, to include the Microcambevinae.

Although Microcambevinae is strongly supported by DNA sequences, it was never forecast in any previous morphological studies (de Pinna, 1989a; de Pinna and Starnes, 1990; Costa and Bockmann, 1994; Datovo and Bockmann, 2010; DoNascimiento, 2015). Costa et al.

(2019) and Costa and Katz (2021) newly proposed four synapomorphies for the new subfamily. They include a distinctive interopercular lateral process supporting thick ligaments, a protuberance on the posteromedial portion of the premaxilla dorsal surface, a lateral constriction on the anterior portion of the vomer, and the presence of a sinuous anterior margin of the osseous portion of the autopalatine. The previous synapomorphies used to unite *Listrura* in Glanapteryginae and *Microcambeva* in Sarcoglanidinae were then considered adaptative convergences for an interstitial lifestyle.

Taxonomically, the most challenging group within Trichomycteridae is the Trichomycterinae, particularly the genus *Trichomycterus*, with ~240 valid species. The subfamily comprises nine genera: Trichomycterus Valenciennes 1832, *Eremophilus* Humboldt 1805, *Hatcheria* Eigenmann 1909, *Scleronema* Eigenmann 1917, *Rhizosomichthys* Miles 1943, *Bullockia* Arratia et al. 1978, *Ituglanis* Costa and Bockmann 1993, *Silvinichthys* Arratia 1998, and *Cambeva* Katz et al. 2018. It is distributed throughout South and part of Central America, on both sides of the Andean range. Although Trichomycterinae includes the type species of the type genus of the family, evidence for its monophyly was only disclosed in Datovo and Bockmann (2010) (Fig. 1D). The authors found that the origin of the *levator internus* 4 from the dorsal face of the posttemporo-supracleithrum was unique to the examined Trichomycterinae genera. Their study, however, did not include the genera *Cambeva*, *Silvinichthys, Eremophilus*, and *Rhizosomichthys*, which still need examination for that particular character. The observations by Datovo and Bockmann exclude "*Trichomycterus*" *hasemani* and "*Trichomycterus*" *johnsoni* (both now in *Potamoglanis* Henschel et al., 2017) from Trichomycterinae. This agrees with de Pinna (1989a), who first suggested that *T. hasemani* and *T. johnsoni* did not belong to Trichomycterinae but were instead more closely related to other trichomycterid subgroups, possibly the Tridentinae. Later, Henschel et al. (2017) hypothesized that *Potamoglanis* formed a clade with Tridentinae (Fig. 1F). Despite the scarcity of morphological evidence, which continues to this day, monophyly of Trichomycterinae has been consistently supported in all subsequent molecular studies (Ochoa et al., 2017, 2020; Katz et al., 2018; Fernandez et al., 2021).

Trichomycterus, to this day, remains a problematic and non-natural group according to several studies (de Pinna, 1989a, 1998; Wosiacki, 2002; Ochoa et al., 2017, 2020; Katz et al.,

2018; Fernandez et al., 2021; Reis and de Pinna, 2022). Recent research has significantly impacted the classification of the genus, presenting new and sometimes unexpected scenarios. Ochoa et al. (2017) conducted the first multilocus phylogenetic analysis for Trichomycteridae (Fig. 1G). In the latter work *Trichomycterus* was divided into two clades. One clade was restricted to species occurring on the Atlantic coast of Brazil, while the other included the remaining species. Some species of the Atlantic coastal clade were more closely related to *Scleronema* than to other species in *Trichomycterus*. No morphological synapomorphies were found for those clades, leading the authors to designate them simply as lineages. Katz et al. (2018), reaching the same overall conclusion, described the genus *Cambeva* for the *Trichomycterus* species forming the sister group to *Scleronema*, thus rendering the remaining coastal Atlantic *Trichomycterus* a monophyletic group. The authors then restricted the genus *Trichomycterus* to those species, since the type species of the genus, *Trichomycterus nigricans* Valenciennes, 1832 is from that region (vicinity of Rio de Janeiro, Brazil). As a result, more than 135 *Trichomycterus* species not in the coastal Atlantic clade were left without a generic assignment. To further complicate matters, Fernandez et al. (2021) synonymized *Eremophilus* Humboldt 1805 with *Trichomycterus* Valenciennes, 1832. The intention was to move *E. mutisii* into *Trichomycterus*, as *Trichomycterus mutisii*. However, since *Eremophilus* has priority, the result would be the opposite, i.e., to move all species currently in *Trichomycterus* into *Eremophilus*, resulting in changed generic assignment of 195 species. This nomenclatural change was not followed and *Eremophilus* remains monotypic.

The issues surrounding *Trichomycterus* extend beyond systematic concerns, as the taxonomy of the genus is also complex, plagued by various problems such as neglected old names, inconsistent descriptive methods, and abundant synonymy (Eigenmann, 1918; Tchernavin, 1944; Baskin, 1973; de Pinna, 1989a; Wosiacki, 2002; Bockmann and Sazima, 2004; Barbosa, 2004; Reis and de Pinna, 2019; DoNascimiento and Prada-Pedreros, 2020; Costa and Katz, 2021; Costa, 2021; Fernandez et al., 2021). Tchernavin (1944) was the first to explicitly raise concerns about the growing taxonomic issues surrounding *Trichomycterus*. The author criticized the heterogeneous and insufficiently detailed taxonomic descriptions found in Eigenmann's works. Nearly 80 years have passed since Tchernavin's observations, and the diversity of the genus has increased from 97 to almost 200 valid species, yet his criticisms remain valid and prolific descriptions of new names continue.

The parasitic subfamilies have been mostly controversy-free regarding their monophyly and composition. On the other hand, they have received far less research attention than other clades. The Tridentinae has remained practically untouched for several decades, with only the occasional and well spaced-out description of new species. The Stegophilinae has been to object of a major contribution in the form of a PhD Thesis (Do Nascimiento, 2012), which resolved many taxonomic issues on the basis of a phylogenetic hypothesis including a massive amount of morphological data. The Vandelliinae, the most iconic of the candirus, has also been sparsely visited by researchers, and even descriptions of new species have been scant. Some efforts have been dedicated to vandelliines recently (Henschel et al., 2021; Dagosta & de Pinna, 2021; de Pinna & Dagosta, 2022), and there has been at least one revisionary work on *Paracanthopoma* (de Pinna & Dagosta, 2022) which greatly increased its number of included species and provided a redefinition of the genus and of its sister group, *Paravandellia*.

GENERAL METHODOLOGY

Specimens used in this study are both old and newly collected. The latter were obtained during fieldwork conducted by the author and concentrated in the time frame estimated from available collections and respective SL´s to be that when young specimens would be available. Access to the museum specimens was authorized by their respective curators. The care and use of experimental animals complied with animal welfare laws, guidelines and policies as approved by Conselho Nacional de Controle e Experimentação Animal (CONCEA, 2013) under a collecting permit from the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (SISBIO #61727). As recommended by the CONCEA (2013), specimens sampled in this study were euthanized by immersion in a solution of eugenol. Fishes were then fixed in 10% formalin for up to 1 week and subsequently transferred to 70% ethanol for permanent storage. Specimens collected directly for this study are deposited in the ichthyological collection of the Museum of Zoology of the University of São Paulo.

Morphological analyses

The anatomical nomenclature was based on the following works. Neurocranium: Arratia (1975); Kindred (1919); Daget (1965); Srinivasachar, 1957 a, b. Suspensorium: Arratia (1990a). Gill arches: Nelson (1969, with modifications by Carvalho *et al.*, 2013). Parurohyal: Arratia and Schultze (1990). Jaws: Nelson (1973), Adriaens *et al.* (2001). Latero-sensory canal system: Pastana *et al.* (2019). Weberian apparatus: Chardon (1968), Bridge and Haddon (1892). Pectoral girdle: Lundberg (1975). Odontodes and dermal plates: Ørvig, (1977), Bhatti, 1938. Caudal skeleton: Lundberg and Baskin (1969), Arratia (1976, 1983), Schultze and Arratia (1989); Monod (1968). Myology: Datovo and Bockmann (2010).

Anatomical preparations

Adult and sub-adult specimens were cleared by the methods of Taylor and van Dyke (1985), while larval and / or juvenile specimens by the method of Walker and Kimmel (2007). Dissection of specimens followed Weitzman's (1974). Anatomical illustrations were performed with the aid of a stereomicroscope equipped with self-assembly device and digital camera. In some cases, computerized microtomographic images were employed using MZUSP facilities (Phoenix v | tome | x M - General Electric Company). Images and plates were built and edited in Adobe Photoshop CS6.

Taxonomic classification

To this date, no phylogenetic analysis has used all or nearly all genera in Trichomycteridae. The present case is the closest to that, with at least one representative of each of the 44 genera of the family, except *Schultzichthys* and *Homodiaetus*. Because the monophyly of Trichomycteridae is well-corroborated enough to be considered beyond reasonable doubt, there was no need for extensive outgroup sampling, so that the analysis includes 50 trichomycterids plus four outgroups. The name Microcambevinae is used to refer to the set corresponding to *Listrura* plus *Microcambeva*, although that clade is not corroborated in the present study. Classification of Trichomycteridae follows Reis and de Pinna, 2023.

Institution Abbreviations

AMNH – American Museum of Natural History, New York; **FMNH –** Field Museum of Natural History, Chicago; **INPA –** Instituto Nacional de Pesquisa da Amazônia, Manaus; **MZUSP –** Museu de Zoologia da Universidade de São Paulo, São Paulo; **USNM –** National Museum of Natural History, Smithsonian Institutionm Washington, DC; **MCZ –** Museum of Comparative Zoology, Cambridge; **MCP –** Coleção de Peixes do Museu de Ciências e Tecnologia da PUCRS, Porto Alegre; **UFJF –** Universidade Federal de Juiz de Fora, Juiz de Fora; **INHS –** Illinois Natural History Survey, Champaign; **ZSM –** Zoologische Staatssammlung, München; **UMMZ –** University of Michigan Museum of Zoology, Ann Arbor.

List of taxa used in the cladistic and ontogenetic analyses

Diplomystidae: *Diplomyctes nahelbutaensis* – MZUSP 88526, 72.7 mm SL. *Diplomystes camposensis* – Universidad de Conception Uncat. DLa 201,1 cands, 70.4 mm SL; Universidad de Conception Uncat. Den 210, 1 cands, 21.2 mm SL. **Nematogenyidae:** *Nematogenys inermis* – MZUSP 107490, 4, 40.6 – 53 mm SL. MZUSP 107493, 1 cands, 65.8 mm SL; MZUSP 88522, 2 cands, 29.9 – 35.4 mm SL; MZUSP 12692, 1 cands, 163 mm SL. **Callichthyidae:** *Callichthys callichthys* – AMNH 97156, 3 cands, 64.2 – 67.33 mm SL; MZUSP 38378, 6, 25.3 – 46.8 mm SL. **Astroblepidae:** *Astroblepus chotae* – USNM 167674, 1 cands, 126 mm SL. *Astroblepus grixalvii* – USNM 167876, 3 cands, 43.9 – 66.8 mm SL. *Astroblepus* sp. – MZUSP 80088, 2, 14.9 – 15.7 mm SL. MZUSP 80087, 5, 24.7 – 33.3 mm SL. **Trichogeninae:** *Trichogenes beagle* – MZUSP 124888, 1, 38.4 mm SL. *Trichogenes claviger* – MZUSP 124882, 23, 21.4 – 49.9 mm SL, 2cands, 24.2 – 41.8 mm SL. *Trichogenes longipinnis* – MZUSP 94973, 1 cands, 69.5 mm SL; MZUSP 80933, 1 cands, 10 mm SL; MZUSP 126738, 16 cands, 11.6 – 22.5 mm SL; MZUSP 83456, 1, 11 mm SL, 1 cands 21.5 mm SL; MZUSP 126739, 3 cands, 10.7 – 12 mm SL; MZUSP 83454, 10.8 mm SL, 1 cands, 29 mm SL; MZUSP 48108, 3, 69.6 – 91.1 mm SL; MZUSP 83452, 3, 20.3 – 53.2 mm SL, 4 cands, 13.5–53.2 mm SL; MZUSP 83443, 1 cands, 10 mm SL; MZUSP 83441, 3 cands, 11.5 – 15.2 mm SL. **Copionodontinae:** *Copionodon orthiocarinatus* – MZUSP 100723, 5, 34.2 – 49.8 mm SL. *Copionodon pecten* – MZUSP 3278, 4

cands, 9.3 – 10.6 mm SL; MZUSP 42470, 2 cands, 12.5–13.2 mm SL; MZUSP 93283, 5 cands, 13.8 – 38.5 mm SL; MZUSP 93278, 2, 14.8 – 18.8 mm SL; MZUSP 93282, 5 cands, 34.2 – 53.5 mm SL. *Glaphyropoma spinosum* – MZUSP 99743, 1, 47.4 mm SL. **Trichomycterinae:** *Cambeva davisi* – MZUSP 79587, 1, 48.7 mm SL. *Cambeva zonata* – MZUSP 83139, 2 cands, 37.9–57.8 mm SL. *Eremophilus mutisii* – MZUSP 35406, 1, 79 mm SL; MZUSP 123510, 1, 126.8 mm SL. *Hatcheria macraei* –MDP2019051602, 1, 75.9 mm SL. *Ituglanis amazonicus* – MZUSP 86821, 1, 42.2 mm SL; MZUSP 89865, 2 cands, 11.5–13.2 mm SL; MZUSP 115765, 1 cands, 21.1–22.9 mm SL. *Rhizosomichthys totae* – MCZ 35744, 1, 120 mm SL. *Scleronema operculatum* – MCPandMAPA Uncat., 3 cands, 35.4–15.8 mm SL; MCP 23189, 1, 24.5 mm SL; MCP 231909, 4, 13.2 – 18.5 mm SL. *Silvinichthys mendonzensis* – MZUSP 75189, 1, 44.5 mm SL. *Trichomycterus alternatus* – MZUSP 109391, 1, 52.1 mm SL. *Trichomycterus astromycterus* – MZUSP 123760, 9 cands, 11 – 47.1 mm SL. *Trichomycterus areolatus* – MZUSP 88531, 2, 53.4 – 66.3 mm SL. *Trichomycterus boyley* – MZUSP 48103, 1, 39.6 mm SL. *Trichomycterus guianensis* – MZUSP109099, 1, 75.3 mm SL. *Trichomycterus immaculatus* – UFJF 941, 1, 84.5 mm SL. **Sarcoglanidinae:** *Microcambeva ribeirae* – MZUSP 65764, 6, 24.4 – 37.9 mm SL; MZUSP 68169, 3, 36.6 – 43.8 mm SL. *Amoglanis diaphanus* – MZUSP 86249, 9, 14.5 – 16 mm SL. *Malacoglanis gelatinosus* – FMNH 98520, 1, 19.9 mm SL. *Sarcoglanis simplex* – INPA 8165, 2 cands, 14.1 – 19.3 mm SL; INPA 36889, 1 cands, 11.4 mm SL. *Stauroglanis gouldingi* – MZUSP 79826, 2, 24.8 – 25.1 mm SL. *Stenolicmus ix* – ZSM 25343, 4, 15.5 – 19.5 mm SL. **Glanapteryginae:** *Listrura camposi* – MZUSP 95189, 2, 37.6 –39.8 mm SL; IBS 2013100814, 3, 36.8 – 46.6 mm SL. *Listrura tetraradiata* – MNRJ 19064, 2 cands, 35.8 – 38.7 mm SL; MZUSP 126770, 3 cands, 10.7 –11.8 mm SL; MZUSP 126771, 6 cands, 15.1 – 29.3 mm SL. *Glanapteryx anguilla* – MZUSP 36530, 2, 49 – ? mm SL; MZUSP Uncat., 1, 49.1 mm SL. *Typhlobelus guacamaya* – MZUSP 106846, 1, 24.8 mm SL. *Pygidianops amphioxus* – MZUSP 81769, 1, 16.9 mm SL; INPA 35502, 1 cands, 9.8 mm SL; PNXMZ 2003070402, 2 cands, 19 – 20 mm SL. **Tridentinae:** *Potamoglanis johnsoni* – MZUSP 104801, 1, 15.12 mm SL. *Potamoglanis hasemani* – MZUSP 93963, 1, 14.6 mm SL. *Potamoglanis anhaga* – MZUSP 108822, 1, 6.5 mm SL. *Tridensimilis* sp. – MCZ 02186, 1, 10.7 mm SL; MCZ 6320, 1, ? mm SL. *Tridens melanops* – INHS 40467, 1, 14.8 mm SL; USNM 301661, 1, 9.5 mm SL. *Miuroglanis amictus* – MZUSP 7449, 1, 13.7 mm SL. *Tridentopis* sp. – FMNH 99711, 10, 16.9 – 17.1 mm SL. **Stegophilinae:** *Ochmacanthus alternus* – MZUSP 30473, 3 cands, 37 – 41.1 mm SL.

Ochmacanthus batrachostoma – MZUSP 95012, 1 cands, 24 mm SL; ANSP 174744, 1 cands, 27.9 mm SL; NUP 2879, 1, 25 mm SL. *Ochmacanthus reinhardti* – UMMZ 204463, 1, 27.8 mm SL. *Ochmacanthus* sp. – FMNH 99611, 6, 13 – 34.4 mm SL, 2 cands, 13 – 13.8 mm SL; FMNH 99751, 6, 20.9 – 36.9 mm SL, 1 cands, 20.9 mm SL; MZUSP 24160, 1 cands, 20.3 mm SL. *Haemomaster venezuelae* – MZUSP 30375, 1, 58.7 mm SL. *Henonemus punctatus* – USNM 1074, 1, 49.6 mm SL. *Homodiaetus anisitsi* – USMN 297968, 1 cands, 18.5 mm SL; MCP 9987, 1 cands, 39 mm SL. *Pareiodon microps* – MZUSP 23522, 3, 52.6 – 53 mm SL. *Pseudostegophilus maculatus* –MZUSP 35736, 2, 43.9 – 48.7 mm SL. *Stegophilus insidiosus* – MZUSP 40048, 1, 37.2 mm SL. *Apomatocerus alleni* – MZUSP 26191, 1, 98.7 mm SL. *Acanthopoma annectens* – MZUSP 30420, 1, 37.5 mm SL. *Megalocentor echthrus* – MZUSP 30391, 1, 57.9 mm SL. **Vandelliinae:** *Paravandellia oxiptera* – MZUSP 95207, 2, 20.1 – 20.7 mm SL;. *Paravandellia phaneronema* – MCZ 35874, 1, 25.5 mm SL; *Paravandellia* sp. – MZUSP 56248, 1, 8.4 mm SL. *Prectrochilus machadoi* – MZUSP 57286, 1, 69.2 mm SL. *Paracanthopoma capeta* – MZUSP 29154, 14.5 mm SL; MZUSP 1000144, 6, 2(cands), 14.1–15.6 mm SL; *Paracanthopoma parva* – MZUSP 30400, 3, 27.9 – 29.1 mm SL. *Vandellia cirrhosa* – MZUSP 0436, 3, 59.3 – 123.1 mm SL. *Vandellia beccarii* – INPA 55291, 2 cands, 20 – 23.8 mm SL; MBUCV 3120, 1 cands, 21.4 mm SL; FMNH 97307, 1 cands, 23.5 mm SL; ANSP 162672, 5 cands, 37.6 – 49 mm SL; UF 81976, 1, 51.6 mm SL.

Comparative material

Diplomystidae: *Olivaichthys viedmensis* – MZUSP 44740, 71.5 mm SL. **Callichthyidae:** *Corydoras flaveolus* – MZUSP 47925, 1cands, 36.8 mm SL; MZUSP 110255, 25, 33.1 38.3 mm SL. **Cetopsidae:** *Denticetopsis* sp. – MZUSP 122350, 2, 37.2 – 46.8 mm SL. **Sisoridae:** *Conta conta* – UMMZ 208632, 42.42 –49.8 mm SL.

Data Analyses

Ontogenetic data

The relationships between ontogenetic transformations and hypotheses of phylogenetic relationships have been a subject of intense debate in evolutionary biology usually focused on techniques for coding characters states in accordance with their ontogenetic trajectories (Gould, 1977; Alberch *et al*., 1979; Fink, 1982; Mabee, 1993; Alberch and Blanco, 1996; Jeffery *et al*., 2005; Wiens, 2005; Germain and Laurin, 2009; Laurin and Germain, 2011; Wolfe and Hegna 2013; Bardin *et al*., 2017).

Morphological variation can be explained mostly by small alterations in timing and rates during development (Gould, 1977). Alberch and Alberch (1981) proposed that a systematic classification can be built on the basis of processes rather than outcomes. Thus, we intend to use the theoretical framework of Alberch *et al*., 1979 allied with different methods of coding ontogenetic stages and characters (Alberch *et al*., 1979; Fink, 1982; Mabee, 1993; Alberch and Blanco, 1996; Wiens, 2005; Germain and Laurin, 2009; Laurin and Germain, 2011; Wolfe and Hegna 2013; Bardin *et al*., 2017) in order to test the homology of transformation processes rather than only their outcome states.

Assuming that any stage of development has the potential to contain information on the phylogenetic directionality of transitions between character states (Pinna, 1994), ontogenetic dada was obtained by truncated series according to availability of comparative material. This is a realistically feasible approach as demonstrated by Johnson and Brothers (1993) and Mabee (1993). Data on directionality of ontogenetic transformations between character states was used to generate hypotheses about character polarity in phylogenetic analyses.

Heterochronic detection analysis

Heterochronic detection analysis was conducted following Lecointre *et al*. (2020) with modifications, as all ontogenetic series were obtained from wild environments. That method follows a few others such as Jeffery *et al*., (2005) which propose to understand the evolution of heterochrony using parsimony analysis. A total of 69 qualitative morphological (external and osteological) characters related to ontogeny were gathered from 64 operational taxonomic units (OTU) representing nine taxa in different developmental stages. Those characters were organized as an Excel matrix, starting with character 0 according to the default output of TNT v.1.5 for

Windows (Goloboff and Catalano, 2016). To assess the stage of development of each OTU, the percentage of its standard length was calculated relative to the largest SL recorded for its species. The maximum standard length information was obtained from the Check List of the Freshwater Fishes of South and Central America (2003) or by searching in collections. OTU' standard length and its respective percentage in Table 1. The same 69 characters were coded both as binary (absence and presence), as previously demonstrated by Lecointre *et al*. (2020), (Appendix 1) and as ordered multistate (Appendix 2), which was first applied in this study.

Parsimony analyses for the heterochronic detection were run in TNT v.1.5 for Windows (Goloboff and Catalano, 2016). Searches used the four new-technology algorithms (Goloboff, 1999; Nixon, 1999; Goloboff *et al*., 2008b), with parameters adjusted to moderate datasets in which ratchet and tree-drifting tend to be more effective (Goloboff, 2002): 20 iterations of ratchet, 20 cycles of treedrifting, five rounds of tree fusing and constrained (CSS) and random (RSS) sectorial searches. These parameters were used in driven searches set to reach 50 hits of the best score, with random seed equaling zero and collapsing of unsupported nodes (Goloboff *et al*., 2008b). All remaining search parameters followed program defaults. The root was placed at the earliest stage of development, here taken as 0%, when all character states are absent.

Phylogenetic data

DNA sampling

Sequences of three mitochondrial genes (COI, Cytb, 16S) and two nuclear genes (MYH6, and RAG2) utilized in this study were obtained from GenBank, and the BOLD website, selected after evidence of correct identification either by direct examination of vouchers or other associated information allowing verification in published sources (Table 2).

Sequence analysis

Sequences from mitochondrial and nuclear genes were used in total evidence phylogenetic inference using Parsimony and Bayesian approaches. Alignments and sequence editing were performed in a non-commercial license of GENEIOUS 11.1.7 software to obtain a

consensus sequence. Alignments were generated using the MUSCLE algorithm (Edgar, 2004), under default parameters. The resulting matrix was visually inspected for any insertions and deletions. Gaps were removed in the matrix analyzed. Stop codons were checked using GENEIOUS.

Morphological and Total Evidence Parsimony Analyses

For the morphology-only parsimony analysis, a total of 287 morphological (external, osteological, myological, and behavioral) characters new and obtained from literature from 54 taxa (50 trichomycterids, and 4 outgroups) were gathered in a matrix in Excel, of which 10 are quantitative (meristic) and the remaining are qualitative (Appendix 3 and 4). Character numbering started from 0, following the default output of TNT v.1.5 for Windows (Goloboff and Catalano, 2016). Quantitative characters were treated as continuous in the parsimony analyses following Goloboff *et al*. (2006), thus avoiding the possible distortions produced by the discretization of meristic data (Farris, 1990; Goloboff *et al*., 2006). Before the incorporation of quantitative characters into the matrix, raw values in ranges of variation were rescaled from zero (lowest value) to one (highest value) in order to prevent unbalanced dominance of characters expressed in higher orders of magnitude (Koch *et al*., 2014). Quantitative characters include only counts (Char. 0 to 9). Spreadsheets containing raw and rescaled values used in quantitative characters are available in Appendix 3. Discrete multistate characters were treated as additive when clear morphoclinal transformational series could be identified from the observed character states (Nixon and Carpenter, 2011); this was the case for characters 11, 12, 13, 16, 31, 39, 57, 60, 68, 76, 78, 80, 86, 88, 91, 92, 107, 108, 114, 115, 120, 131, 142, 144, 154, 155, 159, 161, 163, 164, 166, 172, 184, 185, 187, 191, 198, 225, 258, 260, 277. Characters unique to a single taxon (autapomorphies) were included in the analysis. Phylogenetic interrelationships were inferred through equal and implied-weighting parsimony analyses (Goloboff, 1993). For the total evidence parsimony hypotheses, the morphological matrix above mentioned was combined with the molecular set (3206 bp) of 39 species (out- and ingroup) (Appendix 5) to form the concatenated dataset.

Parsimony analyses were run in TNT v.1.5 for Windows (Goloboff and Catalano, 2016). Searches used the four new-technology algorithms (Goloboff, 1999; Nixon, 1999; Goloboff *et*

al., 2008b), with parameters adjusted to moderate datasets in which ratchet and tree-drifting tend to be more effective (Goloboff, 2002): 20 iterations of ratchet, 20 cycles of treedrifting, five rounds of tree fusing and constrained (CSS) and random (RSS) sectorial searches. These parameters were used in driven searches set to reach 50 hits of the best score, with random seed equaling zero and collapsing of unsupported nodes (Goloboff *et al*., 2008b). All remaining search parameters followed program defaults. *Diplomystes camposensis*, considered the most basal Siluriformes, was used to root the trees after ontogenetic evidence which shown the species retaining several character states that are plesiomorphic relative to the conditions of the order, and thus to Trichomycteridae (Howes, 1983; Mo 1991; de Pinna, 1998; Diogo, 2004; Hardman, 2005; Diogo and Peng 2010).

Relative Bremer supports (Goloboff and Farris, 2001) were calculated in TNT v.1.5 by successively searching (via TBR) for suboptimal trees with ≤ 10 extra steps. In these calculations, ≤ 2000 unique suboptimal trees were retained for each tested extra step, thus totaling around19991 unique suboptimal trees with ≤ 10 extra steps. Consistency (CI) and retention indices (RI) for the reference tree were calculated in TNT v.1.5 with the script *wstats.run* (see Appendix 6 to 9 for index values). List of synapomorphy for each three was done by TNT v.1.5 which considered only the not ambiguous synapomorphies, thus those not influenced by deltran and acctran inferences (Appendix 12 to 15).

Total Evidence Bayesian tree

The Total Evidence Bayesian tree was inferred using MrBayes on XSEDE at the CIPRES science gateway. The concatenated data set, totalizing 3493 characters from 54 taxa, was partitioned according to the codon position for each gene, with morphological data placed in a separate partition. The substitution model of molecular for each partition was set to GTR+I+G to 16S, COI, MYH6; GTR+G to RAG2; HKY+I+G to Cytb, while the substitution model for the morphological partition was set to Mkv (Lewis, 2001) using ascertainment bias correction. The MCMC was run for 10 million generations saving every 1000 generations. The first 200 000 generations (20%) were discarded as burn-in, and remaining generations were used to summarize parameters and topologies. The analysis was rooted in *Diplomystes camposensis* after ontogenetic evidence which shows the species retaining several character states that are plesiomorphic relative

to the conditions of the order, and thus to Trichomycteridae (Howes, 1983; Mo 1991; de Pinna, 1998; Diogo, 2004; Hardman, 2005; Diogo and Peng 2010). Script with partitions and their respective models of nucleotide substitution appears in Appendix 10. Morphological matrix used with all characters discretized in Appendix 11.

CONCLUSION

Trichomycteridae stands out as one of the most evolutionarily cohesive units among catfish families in previous studies, displaying astonishing diversity and widespread distribution throughout the Neotropical region. This study reinforces the hypothesis of monophyly of Trichomycteridae through comprehensive analysis of morphological and molecular data. Within Trichomycteridae, six subfamilies—Copionodontinae, Trichogeninae, Glanapteryginae, Tridentinae, Stegophilinae, and Vandelliinae—are unequivocally demonstrated as monophyletic. Remaining subfamilies are dependent on either the kind of data or type of analysis, or both.

Although more recent hypotheses considered Trichomycterinae as monophyletic, the subfamily was found to be paraphyletic in the equal-weight morphological hypothesis. Conditions thought to be unique for the subfamily, such as the origin of the *levator internus* 4 muscle from the dorsal face of the posttemporo-supracleithrum, and the dorsal tip of the dentary branch of the coronoid process bending posteriorly over the dorsal tip of the anguloarticular and covering it, failed to warrant monophyly of the subfamily in the latter analysis. Surprisingly, *Potamoglanis* did not consistently group with Tridentinae, although it came out as the sister group of the parasite clade in the implied-weight morphological hypothesis. Consequently, the phylogenetic position of *Potamoglanis* remains uncertain, suggesting the possibility that it represents a new subfamily. The Tridentinae in its traditional composition, comprising *Tridentopsis, Miuroglanis, Tridens*, and *Tridensimilis*, is confirmed as monophyletic.

Microcambevinae was only recovered when molecular data were incorporated into the analysis. *Listrura* and *Microcambeva* returned to their respective former subfamilies, Glanapteryginae and Sarcoglanidinae, even when characters associated with fossorial behavior

are experimentally removed from the dataset. Further analysis suggests that Microcambevinae is probably a result of long-branch attraction effects.

Sarcoglanidinae is not demonstrably monophyletic, with *Ammoglanis pulex* and *Stenolicmus ix* consistently positioned outside of the subfamily. Those two species form a cohesive clade in all analyses, yet their exact phylogenetic position within the family remains unresolved. The parasite clade, consisting of Tridentinae, Stegophilinae, and Vandelliinae, is recovered in all analyses, with Tridentinae consistently appearing as the sister group of the other two subfamilies.

In sum, while Trichomycteridae is firmly established as a monophyletic family, its internal relationships retain some areas of persistent unresolution. The primary challenges at the subfamilial level lie mostly within Sarcoglanidinae and Glanapteryginae, with some areas of uncertainty also in Trichomycterinae.

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Chapter 2

Ontogeny of Trichomycteridae

INTRODUCTION

Ontogeny is one of the major areas of research into evolutionary patterns and processes. Studies integrating evolution and ontogeny (often associated with hypotheses of functional morphology) have been performed in several fish groups, supporting and/or testing hypotheses of homology and evolutionary tendencies for different morphological and behavioral traits (*e.g.* Loricarioidea - Schaefer and Lauder, 1986; Trichomycteridae – Arratia, 1990; Sparidae - Hernandez and Motta, 1997; Clariidae - Adriaens, 1998, Wyckmans *et al.*, 2011; Cichlidae - Albertson *et al.*, 2003, 2005, Santos-Santos *et al.*, 2015; Cypriniformes - Bird *et al.* 2007; Cyprinodontiformes - Hernandez *et al.*, 2009; Ictaluridae - Hawkins, 2011). There is consensus that ontogenetic studies are excellent tools for testing homologies, thus contributing to the development of phylogenetic hypotheses (Gould, 1977; Alberch *et al.*, 1979; Fink, 1982; de Pinna and Grande, 2003; Grande and Young, 2004; Johnson and Britz, 2005; Laurin and Garmain, 2010; Bardin *et al.*, 2017, Lecointre *et al.* 2020). The millennial subject is actually one of the classical themes in biology, from Aristotle to the present, often materialized in the historical quest for the relationship between ontogeny and phylogeny (Gould, 1977; Rieppel, 1988).

Trichomycteridae is the second most species-rich neotropical catfish family, with 365 valid species (Frick *et al.* 2022). Its diversity is expressed not only in number of species but also in degree of divergence in many biological layers (de Pinna, 1998). Currently with nine subfamilies (Copionodontinae, Trichogeninae, Trichomycterinae, Microcambevinae, Sarcoglanidinae, Glanapteryginae, Tridentinae, Stegophilinae, and Vandelliinae), trichomycterids are widespread in the Neotropics from Costa Rica to Patagonia, from the sea level to 4500 masl in the Andean mountains (de Pinna and Wosiacki, 2003; Fernandez and Schaefer, 2005; Arratia and Menu-Marque, 1984; Rizzato *et al.*, 2011). This vast geographical distribution is related to one of the key synapomorphies of the family, a profoundly modified opercular-interopercular apparatus with a patch of odontodes on each bone (Eigenmann 1918; Myers, 1944; Baskin, 1973). This modified anatomical complex allows trichomycterids to live in fast waters hanging onto rocks, to climb waterfalls, or to attach to the host in case of parasitic forms (de Pinna, 1998). Habitats of the family also encompass a large array, such as mid-water (Copionodontinae and Trichogeninae), bottom dwelling (Trichomycterinae), or interstitial (Glanapteryginae, Sarcoglanidinae)(de Pinna, 1992; Zuanon and Sazima, 2004; Schaefer *et al.*, 2005; Zuanon *et al.*, 2006; Costa *et al.* 2019; Costa and

Katz, 2021). Those with interstitial life-style can be strictly psammophilous (Glanapteryginae and Sarcoglanidinae, some Microcambevinae), or live buried in other kinds of substrates, such as leaf litter, or mud (some Microcambevinae, Tridentinae, Stegophilinae and Vandelliinae) (Haseman, 1911; Devincenzi and Teague, 1942; Baskin *et al*., 1980; Winemiller and Yan, 1989; Datovo and Bockmann, 2010; Costa *et al*. 2019). The interstitial life-style has evolved convergently in various lineages, according to available phylogenies (Ochoa *et al*. 2017, 2020; Costa *et al*. 2019). Morphological adaptations for this kind of habitat are variable. While *Microcambeva* and Sarcoglanidinae are well-ossified with adaptations such as a large premaxilla, *Listrura* and Glanapteryginae are mostly paedomorphic with reductions and absence of fins and reduction of some bones (Baskin 1973; de Pinna, 1989; Costa *et al*. 2019).

Trichomycteridae is a small-size catfish family (~70 mm SL on average). Some representatives are smaller, thus considered as miniatures when not reaching beyond 26 mm SL (Weitzman and Vari, 1988). Such body-size miniaturization is usually related to some form of paedomorphosis, i.e. developmental truncation (Gould, 1977; Weitzman and Vari, 1988). Miniature trichomycterids have interesting particularities which indicate that their size-reduction processes are not homogeneous. For example, Sarcoglanidinae, Glanapteryginae and Tridentinae are composed mostly of miniature species, a majority of which have obviously paedomorphic features related to developmental truncation, such as weakly mineralized bones, lack of an ossified cranial roof, and reduction or loss of some organs and bones (de Pinna, 1989; Costa and Bockmann, 1994). On the other hand, *Potamoglanis* (Tridentinae) includes miniature species with full skeletal development and little evidence of developmental truncation (*P. hasemani*, *P. johnsoni*), except the unossified cranial roof, and at least one truly pedomorphic species with generalized skeletal reductions (*P. anhanga*). This suggests that distinct developmental processes were involved in the miniaturization process within that clade, which provides a rich substrate for detailed ontogenetic studies.

Feeding habits are remarkably diverse in Trichomycteridae, with different clades occupying a vastly different niches. The most common form is generalist predation of benthic or allochthonous animals. However, some lineages include species which are scrappers (Copionodontinae), carnivorous or scavengers (*Pareiodon*), mucus and scale eating (Stegophilinae), or hematophagous (Vandelliinae). The latter groups stands out as the only case of

strict hematophagy among bony fishes. They are also well-known for accidentally digging into the urethra of humans and other mammals that swim in their habitat (Gudger, 1930). Parasitism in Trichomycteridae involve deep musculoskeletal modifications (Adriaens *et al*., 2010; Datovo and Bockmann, 2010; and DoNascimiento, 2015). *Vandellia cirrhosa* Valenciennes in Cuvier and Valenciennes, the most common vampire species in the family, apparently pass through a dramatic process of metamorphosis, with juveniles having a generalist predator mouth morphology, profoundly different from that of adults (de Pinna, 1998; personal com.).

An understanding of the evolution of such morphological modifications associated with diverging trophic niches is still incipient. Much of the missing knowledge results from a lack of information on development. Arratia (1983) was the first to study the ontogeny of any anatomical complex in Trichomycteridae, the caudal skeleton in some members of Trichomycterinae. That study was followed by few others on the ontogeny of the urohyal (Arratia and Schultze, 1990), the suspensorium (Arratia, 1990), and the lacrimal-antorbital (de Pinna *et al*. 2020). Despite the relevance of such pioneering efforts, most of the diversity in the family remain entirely uncharted in the field of development.

Ontogenetic data are fundamental for evolutionary studies on several layers. They generate or refute hypotheses of primary homology (e.g., Grande and Bemis, 1998; de Pinna and Grande, 2003; Grande, 2010; Carvalho *et al*., 2013; Mattox *et al*., 2014; Lecointre *et al*. 2020), help to define sequences of character-state transformations (Nelson, 1978; Nelson and Platnick, 1981; Weston, 1988, 1994; de Pinna, 1994), and allow the mapping of heterochronic phenomena Lecointre *et al*. 2020. The incorporation of data from life cycles, in contrast to purely instantaneous morphologies, provides multidimensionality that greatly expands the relevance and meaning of phylogenetic analyses and consequent hypotheses of evolutionary transformation in association with cladistic diversification (Gould, 1977; Alberch *et al*., 1979).

A detailed mapping of ontogenetic transformations in Trichomycteridae, in combination with a robust phylogenetic hypothesis, is a necessary framework for initiating studies on evo-devo. The direction of ontogenetic transformations provides the only direct observation of character state transformations and temporality in phylogenetic reconstruction (Nelson, 1978; Nelson and Platnick, 1981; de Pinna, 1994), a controversial but deeply relevant topic in comparative biology. Thus, in this section I present a detailed study of the ontogeny of morphological complexes in

Trichomycteridae, with emphasis on the skeleton, mapping the variations discovered. This information was integrated into a phylogenetic hypothesis (Chapter 1) that provided a new view of the evolution of the family.

CONCLUSION

Trichomycteridae is one of the most morphologically diversified catfish families. Representatives of this family range from generalist to highly specialized niches, the most extreme one being blood feeding. Expectedly, their morphology displays equally remarkable variation, ranging from generalized catfishes to highly aberrant ones, living deeply buried into the substrate or strictly parasites feeding on blood of their hosts. Through ontogenetic data, this chapter aimed to understand the evolution of Trichomycteridae.

Conclusions drawn from this study shed light on various aspects, including the absence of the parietal bone in the order, and the fusion between the extrascapular and the pterotic bones in Siluriformes (although that bone is absent in the Trichomycteridae). The unique nature of the median premaxilla and the evolution of the dorsal-fin spine within the family are elucidated. Detailed observations of the development of trichomycterids also allow direct mapping of transformation sequences and the identification of connections between highly divergent conditions in adult specimens, such as the mouth apparatus of Vandelliinae and that in other members of the miniature clade.

An ontophylogenetic analysis, including developmental stages of Nematogenyidae and most trichomycterid lineages, including Trichogeninae, Copionodontinae, Trichomycterinae, Glanapteryginae, Stegophilinae, and Vandelliinae reveal that Copionodontinae and Trichogeninae as the most developmentally retarded, while Trichomycterinae, Stegophilinas, and Vandelliinae have accelerated development. Glanapteryginae is generally the most paedomorphic group within the family.

The integration of phylogenetic hypotheses from Chapter 1 with the ontogenetic data in this chapter unveiled broad evolutionary patterns in Trichomycteridae, showing an increasing

trend toward paedomorphism and subsequent miniaturization. Therefore, Trichomycteridae can be characterized as a predominantly paedomorphic family, providing a foundation upon which numerous nested peramorphic apomorphies have evolved. Additionally, these findings suggest the occurrence of two events of miniaturization within the family. The most notable one at the base of a large clade encompassing all trichomycterids except for Copionodontinae, Trichogeninae, and Trichomycterinae, named as the miniature clade. Within this clade, further size reduction events were observed. Surprisingly, the miniature clade also exhibited a phenomenon of reverse size-increase, evident not only through phylogenetic structure but also in the development of anatomical structures. Some of those are the absence of the epiphyseal bar in the chondrocranium, secondary growth of the supraoccipital bone, the anterior outgrowth of the hyomandibula, reduced size of the interopercle compared with the opercle, and the spear-like anterior outgrowth of the hyomandibula. This new category of miniature forms was thus coined "giant miniatures," as they descend from the miniature clade despite their large size. Those giant miniatures exhibit numerous paedomorphic conditions shared with their smaller miniature relatives.

The large morphological and species diversity in the miniature clade is associated with a miniaturization event which fits an adapted concept of key innovation. The innovation in this case is not a specific morphological trait, but rather a large-scale heterochronic event. Also, the resulting diversification is not reflected in differential number of species between sister groups (as is usual in the concept of key innovation) but rather in the differential range of morphological diversification.

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