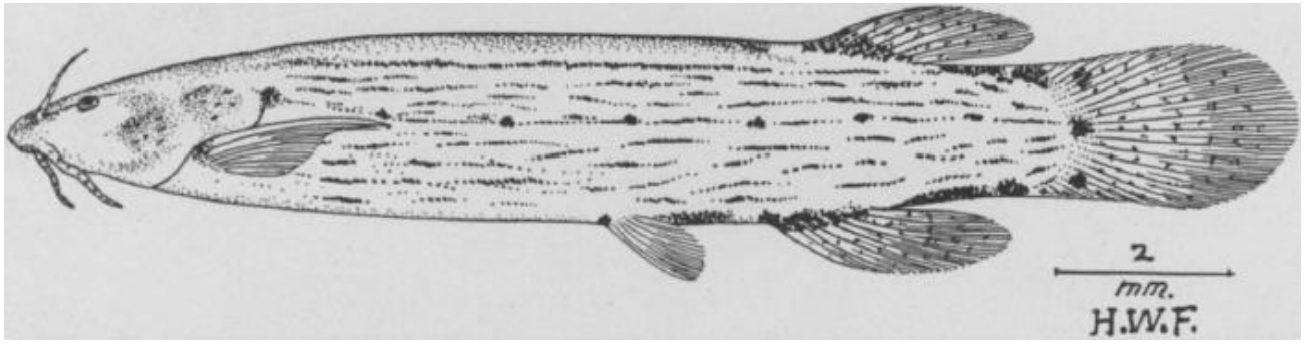
Universidade Federal do Rio de Janeiro

Instituto de Biologia

Programa de Pós-Graduação em Biodiversidade e Biologia Evolutiva

# Posicionamento filogenético com base em caracteres moleculares de bagres do grupo de espécies *Trichomycterus hasemani* (Siluriformes: Trichomycteridae)

Elisabeth Henschel de Lima Costa




Orientador: Prof. Dr. Wilson José Eduardo Moreira da Costa

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Dissertação de Mestrado apresentada ao Programa de Pós-graduação em Ciências Biológicas (Biodiversidade e Biologia Evolutiva), da Universidade Federal do Rio de Janeiro, como parte dos requisitos necessários à obtenção do título de Mestre em Ciências Biológicas (Biodiversidade e Biologia Evolutiva).

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Rio de Janeiro

Julho de 2017

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xii, 90f, 12il,

Orientador: Wilson José Eduardo Moreira da Costa

Dissertação - UFRJ / IB / Programa de Pós-graduação em Biodiversidade e Biologia Evolutiva, 2017.

Referências bibliográficas: f. 58-63

1. Trichomycteridae. 2. *Trichomycterus*. 3. Sistemática. 4. Genoma Mitocondrial. 5. Genoma Nuclear 5. Miniaturização. I. Costa, W.J.E.M. II. Universidade Federal do Rio de Janeiro, Instituto de Biologia, Programa de Pós-graduação em Biodiversidade e Biologia Evolutiva. III. Título.

A todas as mulheres cientistas: às que me antecederam,
às que são contemporâneas a mim e às que me sucederão.

**Agradecimentos**

Primeiramente gostaria de agradecer ao professor Wilson Costa, pela oportunidade, paciência e ensinamentos ao longo desses seis anos não só de orientação, mas também de amizade. Passamos por momentos difíceis ao longo desses dois anos e não me faltou apoio dele.

Em segundo lugar, agradeço às minhas três famílias: a do Rio de Janeiro, a de Rondônia e a de Niterói. Principalmente à minha mãe, padrasto e namorado que amorteceram grande parte desses dois anos que tiveram tudo para dar errado. Estresse, crises de ansiedade e choro, hospital, processos e uma cirurgia na reta final. Essas três pessoas foram meus pilares em todo meu progresso e recuperação. Minha mãe é alguém em quem me inspiro como mulher e profissional, sem a qual não saberia nem por onde começar várias etapas da minha vida. Também friso a importância da minha avó, sempre muito carinhosa e cautelosa comigo.

Agradeço também aos companheiros de laboratório. Zé Léo, meu coorientador e super amigo que tornou possível essa dissertação. Me passou todos os seus conhecimentos. Rolinha, meu companheiro de viagens. Sem ele, nenhum projeto que fiz ao longo desses seis anos seria possível. Axel, agradeço muito pela amizade, paciência em me escutar e ajudar ao longo de todo o processo. Também outra pessoa fundamental. Não posso me esquecer do Coveiro, que, apesar de longe, também me influenciou muito e me ajudou muito principalmente no começo da minha vida no laboratório. Anais, mulher forte e minha inspiração pessoal. Pedro Fasura, amigo das horas felizes e chopeladas e também sempre presente e disposto a dar um bom conselho e ajuda. Panda, muito companheiro e também muito paciente. Vilardinho, me ajudou muito nessa reta final quando eu estava em casa me recuperando da cirurgia. Bia também muito amiga. A Orlando e Gilvan agradeço o apoio no laboratório. No geral, agradeço muito pelo ambiente de amizade, companheirismo e cumplicidade que existe no Laboratório. Sei que isso é raro.

Não posso deixar de agradecer aos meus amigos da época de colégio: o grupo 95. Mais de dez anos juntos, muitas risadas, choros e brigas que contribuíram para o meu crescimento (ou não). Um grupo de amizades sólidas que sei que posso contar (e conto) a qualquer momento. Também agradeço a todos os meus amigos da faculdade, tanto colegas da época do ciclo básico da graduação quanto amigos feitos ao longo do bacharelado em Zoologia.

**Resumo**

A família Trichomycteridae engloba 297 espécies válidas de bagres que se distribuem desde a Costa Rica até a Patagônia, em ambos os lados dos Andes. Oito subfamílias são reconhecidas: Trichomycterinae, Vandelliinae, Stegophilinae, Tridentinae, Glanapteryginae, Sarcoglanidinae, Trichogeninae e Copionodontinae. A miniaturização é um fenômeno recorrente em Trichomycteridae, ocorrendo em todas as subfamílias exceto Copionodontinae e Trichogeninae. Trichomycterinae conta com o maior número de espécies miniaturizadas e os debates sobre o monofiletismo da subfamília tangem o posicionamento de algumas das suas seis miniaturas atualmente reconhecidas. O grupo de espécies *Trichomycterus hasemani* abrange quatro espécies miniaturizadas: *T. hasemani, T. johnsoni, T. anhanga* e *T. wapixana*. O posicionamento do grupo é amplamente discutido na literatura e postulou-se que essas espécies sejam mais relacionadas a Tridentinae que a Trichomycterinae. As hipóteses de relacionamento do grupo *T. hasemani* dentre os Trichomycteridae nunca foram testadas num paradigma filogenético. O objetivo da presente dissertação é fornecer o primeiro teste do monofiletismo e posicionamento do grupo *T. hasemani* por meio de uma análise filogenética baseada em caracteres moleculares. Fragmentos de dois genes mitocondriais e de três genes nucleares foram utilizados para o desenvolvimento de análises de Inferência Bayesiana e Máxima Verossimilhança. O monofiletismo do grupo *T. hasemani* foi corroborado e suas espécies foram posicionadas como uma linhagem da subfamília Tridentinae. Além das topologias apresentadas, diversos caracteres morfológicos corroboram o posicionamento do grupo *T. hasemani* como um novo gênero de Tridentinae. As sinapomorfias de Tridentinae são rediscutidas e duas linhagens distintas são recuperadas para a subfamília: uma com os quatro gêneros já reconhecidos e outra contendo o grupo *T. hasemani*.

Palavras-chave: Trichomycteridae, *Trichomycterus*, Sistemática, Genoma Mitocondrial, Genoma nuclear, Miniaturização.

**Abstract**

The family Trichomycteridae comprises 297 valid species distributed from Costa Rica to Patagonia and in both Andean sides. Eight subfamilies are currently recognized: Trichomycterinae, Vandelliinae, Stegophilinae, Tridentinae, Glanapteryginae, Sarcoglanidinae, Trichogeninae and Copionodontinae. Miniaturization is a widespread phenomenon in Trichomycteridae: it occurs in all subfamilies, except Copionondontinae and Trichogeninae. Trichomycterinae accounts for the highest number of miniaturized species among the family and the positioning of some miniaturized species are usually in the centre of discussions about its phyletic status. The *Trichomycterus hasemani* group comprises four miniaturized species: *T. hasemani, T. johnsoni, T. anhanga* and *T. wapixana*. Several authors discussed the positioning of the group within the Trichomycteridae and there is a general agreement that these species are more related to the Tridentinae than to the Trichomycterinae. Despite this consensus, the relationships of the group were never tested within a phylogenetic framework. The proposal of this work is to develop the first phylogenetic analysis focused on testing the positioning and monophyly of the *T. hasemani* group. Partial sequences of two mithocondrial genes and of three nuclear genes were sequenced and Bayesian Inference and Maximum Likelihood analyses were performed. The monophyly of the *T. hasemani* group was corroborated and it was positioned among the Tridentinae. The topologies herein presented and several morphological characters corroborate the group as a new Tridentinae genus. The sinapomorphies usually considered for Tridentinae are reviewed and two distinct lineages were recovered for the subfamily: one comprising the four Tridentinae genera and the other one comprising the *T. hasemani* group.

Keywords: Trichomycteridae, *Trichomycterus*, Systematics, Mithocondrial Genome, Nuclear Genome, Miniaturization.

**Sumário**

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## Lista de Abreviaturas e Siglas

an – antorbital

apal – autopalatino

CP – Comprimento Padrão

ep – epioccipital

ep+soc – epioccipital fusionado ao parietosupraoccipital

fr – frontal

gb – cápsula da bexiga natatória

hy – hiomandíbula

iop – interopérculo

max – maxila

met – mesetmoide

mtg – metapterigoide

op – opérculo

pop – pré-opérculo

pre – pré-maxilla

pt – pterótico

ptts – posttemporosupracleithrum

soc – parietosupraoccipital

sph – esfenóticos

v – primeira vértebra livre

## Introdução

*Contexto taxonômico*

A divisão Teleostei é o grupo mais diverso e rico em número de espécies de todos os vertebrados, sendo dominantes em ambientes tanto de água doce quanto de água salgada. Suas cerca de 30.000 espécies correspondem a 96% de todas as espécies de peixes existentes (Nelson *et al.*, 2016). Os teleósteos emergiram há cerca de 250-230 milhões de anos atrás, durante o Triássico Inferior ou Médio (Nelson *et al.*, 2016) e quatro grandes radiações originaram as linhagens atuais Elopomorpha, Osteoglossomorpha, Otocephala e Euteleostei. A subdivisão Otocephala caracteriza-se pela presença de uma conexão entre a bexiga natatória e o ouvido interno ("*otophysic connection"*) na maioria de seus membros, que se distribuem em duas superordens: Clupeomorpha (sardinhas e arenques) e Ostariophysi (Helfman et al., 2009).

A superordem Ostariophysi engloba cerca de 68% de todas as espécies de peixes de água doce, sendo dominante nesse ambiente tanto em número de espécies quanto de indivíduos (Helfman et al., 2009). O alto número de espécies reflete-se numa diversidade imensa de formas, como por exemplo carpas, bagres, peixes-faca, piranhas, tetras e poraquês. Os Ostariophysi se destacam pela produção de uma substância de alarme, um ferormônio quimicamente similar em todos os peixes da superordem. Essa substância, quando expelida no ambiente por células epiteliais danificadas, é detectada através do olfato e gera uma reação de escape nos indivíduos conspecíficos ou de espécies relacionadas (Nelson *et al.*, 2016). A superordem é dividida nas séries Anotophysi e Otophysi. Essa divisão se dá pela presença nos Otophysi do Aparelho de Weber, uma série de ossos modificados que conecta a bexiga natatória ao ouvido

interno. Quando ondas de som entram em contato com o corpo do peixe, a vibração da bexiga natatória é ampliada pelo Aparelho de Weber e conduzida ao ouvido interno (Helfman et al., 2009). Essa estrutura é ausente em Anotophysi, que compreende apenas a ordem Gonorynchiformes. Otophysi é composta pelas ordens Cypriniformes, Characiformes, Gymnotiformes e Siluriformes.

A ordem Siluriformes engloba 3737 espécies de peixes popularmente conhecidos como bagres ou cascudos (Eschmeyer & Fong, 2017). Esses peixes são encontrados em todos os continentes, porém a maior diversidade concentra-se nas Américas, com cerca de 2000 espécies (Nelson et al., 2016). Algumas das características que definem a ordem são a presença de nadadeira adiposa; a presença de um espinho nas nadadeiras peitorais e dorsal (em algumas famílias pode estar associado a glândulas de veneno); a presença de um pequeno espinho na frente do maior espinho na nadadeira dorsal formando um sistema de trava; a ausência de escamas (os indivíduos podem ter a pele nua ou recoberta por placas ósseas) e a presença de um a quatro pares de barbilhões na região oral (Helfman *et al.,* 2009). A ordem é primariamente de água doce, exceto pelas famílias Ariidae e Plotosidae, cujos membros são majoritariamente marinhos (Helfman et al.,2009). O registro fóssil de Siluriformes é amplo, sendo o mais antigo datado para o Cretáceo Superior (Nelson et al., 2016). Fósseis da ordem são conhecidos em todos os continentes, inclusive na Antártida sob a forma de fósseis datados do Oligoceno (Grande & Eastman, 1986).

A superfamília Loricarioidea localiza-se na região Neotropical e compreende seis famílias exclusivamente de água doce: Nematogenyidae, Trichomycteridae, Callichthyidae, Scoloplacidae, Astroblepidae e Loricariidae, totalizando 1538 espécies (Eschmeyer & Fong, 2017). Peyer (1922) foi o primeiro a reconhecer o grupo como

natural e se baseou principalmente na presença de odontódeos nesses peixes, que são dentes verdadeiros fora da cavidade oral (Ørvig, 1967) (Fig. 1). Cinquenta anos depois, Baskin (1973), em sua tese de doutorado, foi pioneiro ao analisar a superfamília sob o paradigma cladístico e concluiu que *Nematogenys* Girard, 1855 (único membro de Nematogenyidae) era a linhagem mais basal de Loricarioidea (Fig. 2A). Diversos estudos morfológicos corroboraram essa hipótese (Howes, 1983; Schaefer & Lauder, 1986; Schaefer, 1990), até que de Pinna (1992) propôs que Trichomycteridae e Nematogenyidae fossem grupos irmãos e que esse clado fosse, então, a linhagem mais basal da superfamília (Fig. 2B). Essa proposta foi corroborada por Diogo (2004), porém, Sullivan et al. (2006) ao realizarem uma análise molecular, não recuperaram o relacionamento de grupos irmãos entre Nemtaogenyidae e Trichomycteridae e não conseguiram estabelecer qual das duas famílias seria a linhagem mais basal de Loricarioidea (Fig. 2C).

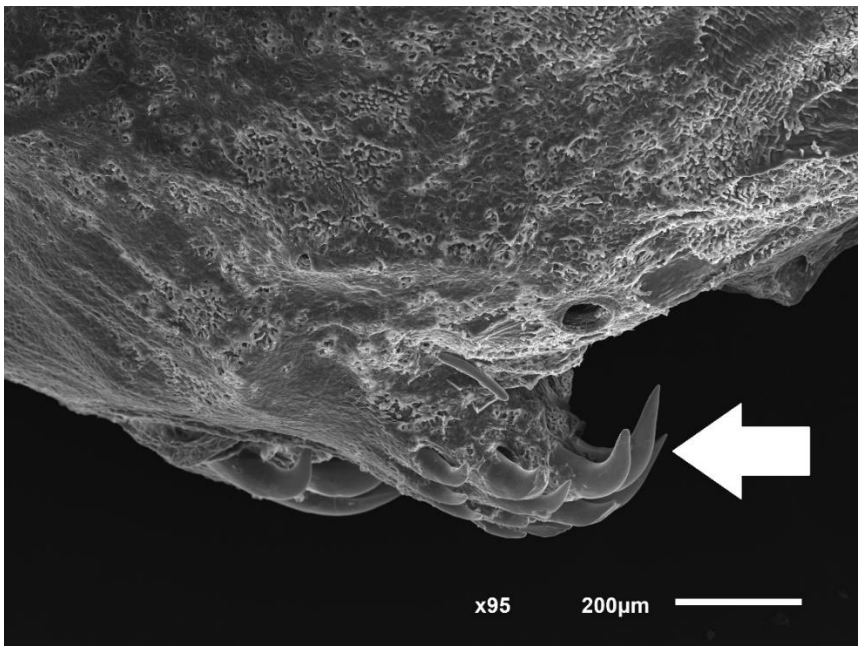


Figura 1. Microscopia de varredura indicando odontódeos na região do suspensório opercular em espécie de Trichomycteridae.

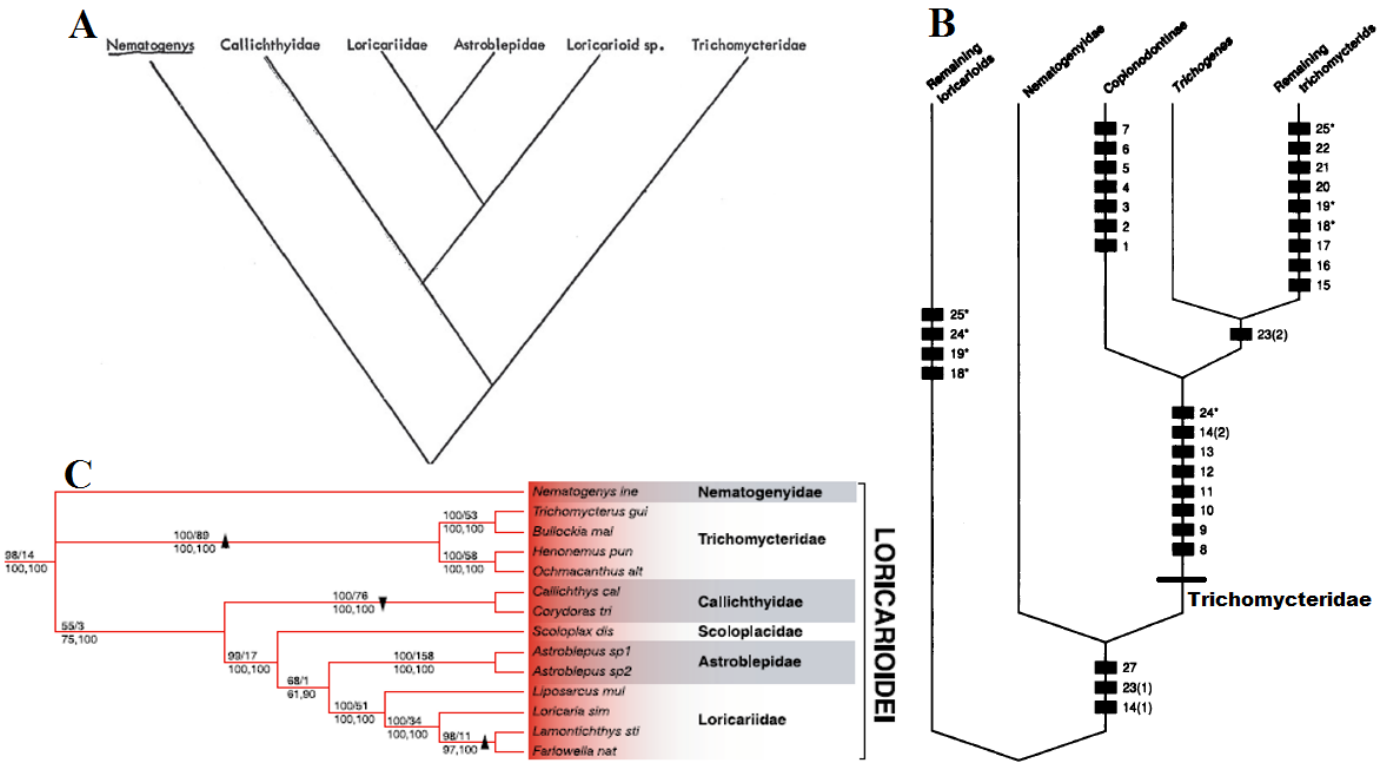


Figura 2. Propostas de relacionamento para Loricarioidea. A- Retirada de Baskin (1973); B- Modificada de de Pinna (1992); C- Retirada de Sullivan et al. (2006).

Trichomycteridae é a segunda família mais diversa de Loricarioidea e Siluriformes, abrangendo 297 espécies válidas (Eschmeyer & Fong, 2017). Esses bagres se distribuem da Costa Rica até a Patagônia e também se encontram em ambos os lados dos Andes (Baskin, 1973; de Pinna, 1998). Oito subfamílias têm sido reconhecidas para Trichomycteridae: Trichomycterinae Bleeker, 1858, Vandelliinae Bleeker, 1862, Stegophilinae Günther, 1864, Tridentinae Eigenmann, 1918, Glanapteryginae Myers, 1944, Sarcoglanidinae Myers & Weitzman, 1966, Trichogeninae Isbrücker, 1986 e Copionodontinae de Pinna, 1992. O monofiletismo da família é bem corroborado, sendo sustentado principalmente pela morfologia do suspensório mandibular: o interopérculo e o opérculo são modificados e interligados de forma a sustentarem séries de odontódeos

(Baskin, 1973; de Pinna 1992) (Fig. 3). O alto número de espécies da família reflete-se em uma ampla gama de formas, tamanhos e nichos ocupados por esses bagres, que são encontrados em diversos habitats, desde cachoeiras altamente oxigenadas a mais de 4000m de altura até águas estagnadas e menos oxigenadas próximas ao nível do mar (Schaefer et al., 2005; Aedriens et al.,2010).

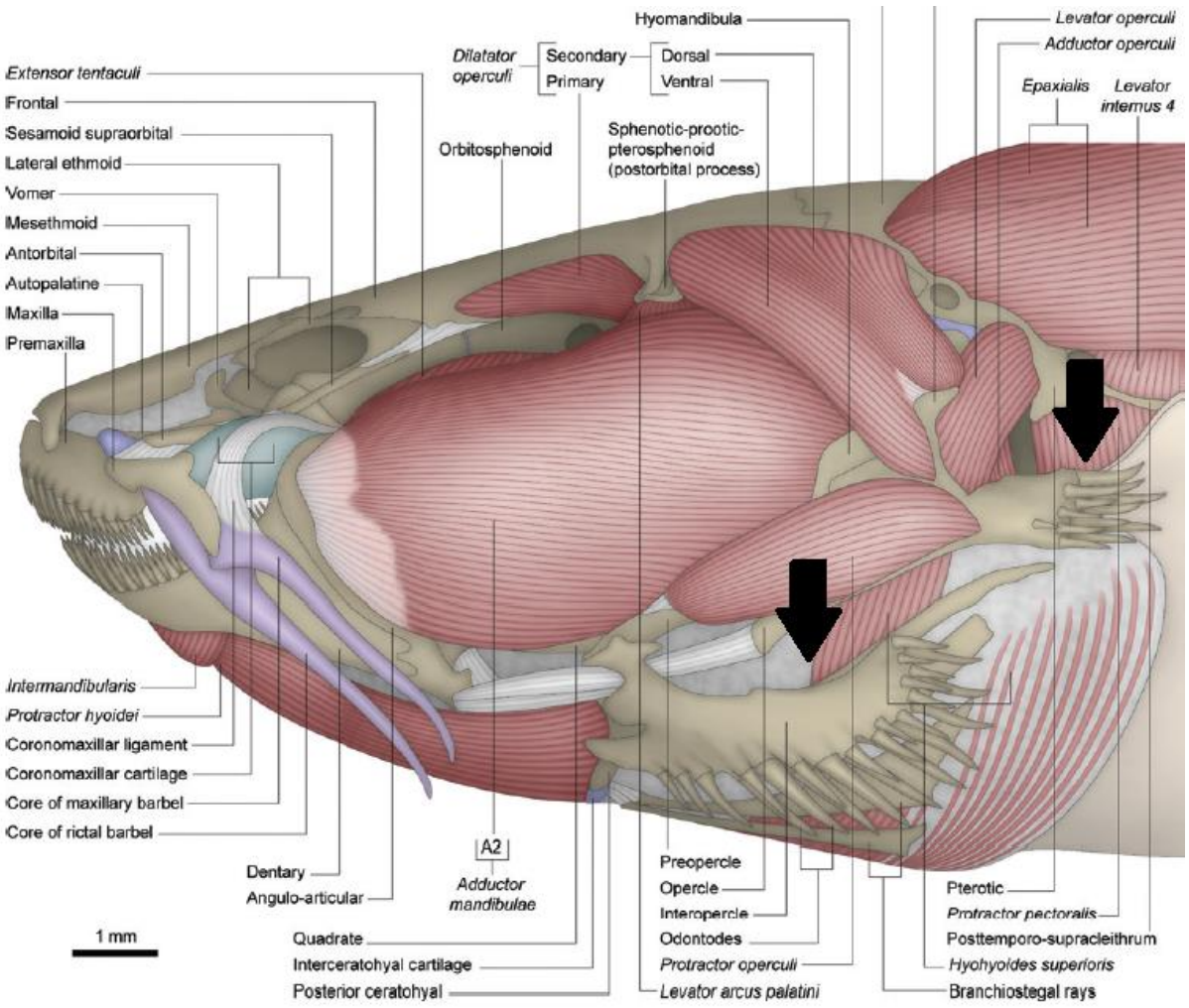


Figura 3. Vista lateral da cabeça de *Trichomycterus brasiliensis* Lütken, 1874. Setas pretas indicam o opérculo e interopérculo. Modificado de Datovo & Bockmann (2010).

Os membros de Vandelliinae representam 9 das menos de 20 espécies descritas de vertebrados exclusivamente hematófagos (Carvalho, 2003). Os peixes da subfamília Stegophilinae alimentam-se de muco e escamas de outros peixes e, junto com os Vandelliinae, são popularmente conhecidos como candirus (Gudger, 1930). Já os Glanapteryginae são bagres de corpo alongado e com adaptações para um estilo de vida fossorial e arenícola, como pigmentos, olhos e nadadeiras extremamente reduzidos ou ausentes (de Pinna & Zuanon, 2013). Os Sarcoglanidinae também vivem em íntima associação com o substrato arenoso e, além do tamanho diminuto, possuem o corpo completamente transparente (Myers & Weitzman, 1966; de Pinna, 1989). Em contraste com o hábito típico de se enterrar no substrato da maioria dos bagres (Baskin, 1973), os Trichogeninae exploram a coluna d'água, sendo geralmente encontrados a profundidade de meia água (de Pinna et al., 2010).

Um fenômeno recorrente em Trichomycteridae é a miniaturização, ocorrendo em todas as subfamílias exceto Trichogeninae e Copionodontinae. Espécies miniaturas foram definidas por Weitzman & Vari (1988) como as que não excedem 26 mm de comprimento padrão (medida entre a ponta do focinho e o final do pedúnculo caudal) e que geralmente atingem a maturidade sexual antes dos 20 mm de comprimento padrão. A miniaturização foi utilizada como um estado de caráter diagnóstico para a relação de grupos irmãos entre Glanapteryginae e Sarcoglanidinae (Costa & Bockmann, 1994) e proposta como um evento ocorrido na base de Tridentinae (de Pinna, 1989). Trichomycterinae é a subfamília com maior número de espécies miniaturizadas, sendo elas *Trichomycterus hasemani* (Eigenmann, 1914), *Trichomycterus santaeritae* (Eigenmann, 1918), *Trichomycterus johnsoni* (Fowler, 1932), *Trichomycterus anhanga*

Dutra, Wosiacki & de Pinna, 2012, *Trichomycterus wapixana* Henschel, 2016 e a recém descrita *Ituglanis compactus* Castro & Wosiacki, 2017.

Muito se discute sobre o monofiletismo de Trichomycterinae, apesar de nenhum trabalho publicado até o momento ter de fato apresentado uma análise filogenética abrangendo um número considerável de espécies da subfamília. Os debates sobre o status de Trichomycterinae tangem, em grande parte, o posicionamento de algumas de suas espécies miniaturizadas dentre os Trichomycteridae. A subfamília compreende 216 espécies válidas (Eschmeyer & Fong, 2017) distribuídas entre os gêneros *Eremophilus* Humboldt, 1805, *Trichomycterus* Valenciennes, 1832, *Hatcheria* Eigenmann, 1909, *Scleronema* Eigenmann, 1917, *Rhizosomichthys* Miles, 1943, *Bullockia* Arratia, Chang, Menu-Marque & Rojas, 1978, *Ituglanis* Costa & Bockmann, 1993 e *Silvinichthys* Arratia, 1998. Baskin (1973) inaugurou os estudos cladísticos para Trichomycteridae em sua tese de doutorado e testou o monofiletismo da família e das subfamílias existentes naquela época (todas exceto Trichogeninae e Copionodontinae). Das seis subfamílias testadas nesse trabalho, apenas Trichomycterinae não foi recuperada como monofilética (Fig. 4).

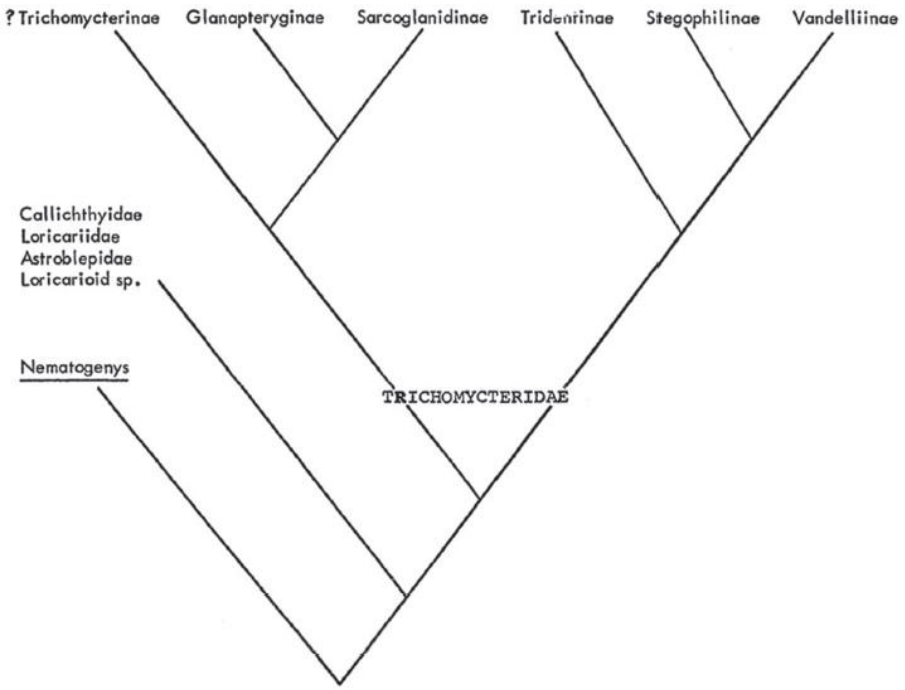


Figura 4. Proposta de relações filogenéticas entre as subfamílias de Trichomycteridae apresentada por Baskin (1973). A interrogação indica incerteza sobre o monofiletismo do grupo. Retirado de Baskin (1973).

Arratia et al. (1978) propuseram estados de caracteres diagnósticos para Trichomycterinae sem base em uma análise filogenética. Onze anos depois, de Pinna (1989) discutiu os caracteres propostos por Arratia et al. (1978) e concluiu que eram ou simplesiomorfias (i.e., sinapormofias para Trichomycteridae) ou caracteres de polarização incerta, explicitando que não haveriam evidências para o monofiletismo de Trichomycterinae. O autor também ressaltou a similaridade das fontanelas craniais dos neurocrânios de *T. hasemani, T. johnsoni* e Tridentinae, alegando que as duas espécies miniaturizadas seriam irmãs e mais relacionadas a Tridentinae que a Trichomycterinae (Fig. 5). Além disso, de Pinna (1989) propôs que *Scleronema, T. santaeritae* e *Trichomyterus boylei* (Nichols, 1956) seriam mais relacionadas a Sarcoglanidinae que a

Trichomycterinae. Segundo de Pinna (1989), *T. santaeritae* é conhecida apenas por seu holótipo, o que pode explicar a falta de menções a essa espécie em trabalhos posteriores. Apesar de ter desenvolvido essas suposições, de Pinna (1989) as fez sem base em uma análise filogenética e no próprio trabalho pontuou que essas hipóteses necessitavam de mais investigações. Arratia (1990) apresentou estados de caracteres exclusivos para Trichomycterinae (incluindo *Scleronema* e *T. boylei*) e todos os seus gêneros, exceto *Trichomycterus*. A autora se opôs à ideia de de Pinna (1989) de que *Scleronema* e *T. boylei* seriam mais relacionados a Sarcoglanidinae que a Trichomycterinae, alegando que esses táxons apresentam todas os estados de caracteres exclusivos por ela propostos para Trichomycterinae. Apesar de considerar Trichomycterinae como uma linhagem exclusiva, Arratia (1990) não analisou exemplares de *T. hasemani* ou *T. johnsoni* e se isentou de discutir o posicionamento dessas espécies.

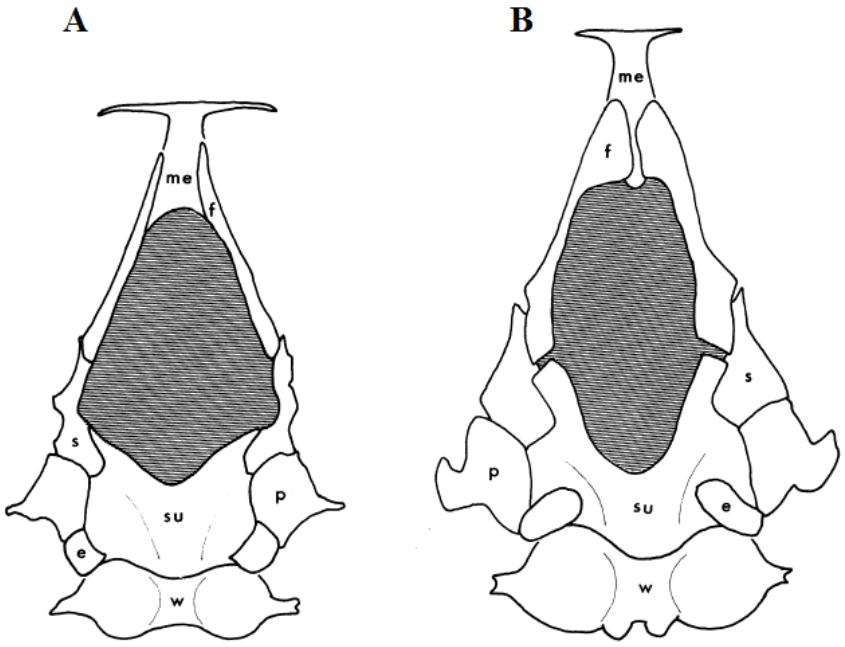


Figura 5. Vista dorsal dos neurocrânios de A- *Tridentopsis* sp. e B- *Trichomycterus hasemani*. A área hachurada representa a fontanela cranial. Modificado de de Pinna (1989).

Costa & Bockmann (1993) descreveram o gênero *Ituglanis* com base em nove espécies previamente alocadas em *Trichomycterus* e, apesar de não terem desenvolvido análise filogenética alguma, postularam que *Ituglanis* seria mais relacionado a outras subfamílias que a Trichomycterinae, adicionando então mais uma problemática à discussão do status de Trichomycterinae. Posteriormente, de Pinna (1998) publicou uma filogenia para Trichomycteridae baseada em informações compiladas da literatura disponível até aquele momento. A topologia por ele apresentada retrata Trichomycterinae como não-monofilética, com os gêneros *Scleronema* e *Ituglanis* posicionados no mesmo clado que Vandelliinae, Stegophilinae, Tridentinae, Glanapteryginae e Sarcoglanidinae (Fig. 6).

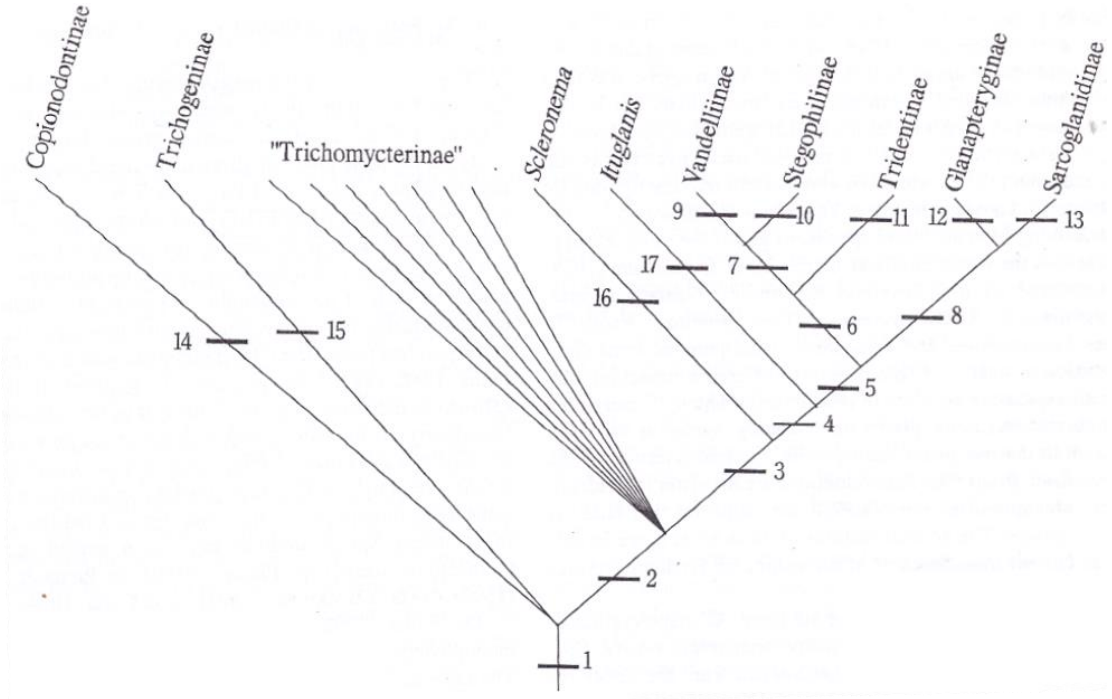


Figura 6. Proposta de relações filogenéticas entre as subfamílias de Trichomycteridae apresentada por de Pinna (1998). Retirado de de Pinna (1998).

Doze anos depois, Datovo & Bockmann (2010), numa análise filogenética de Trichomycteridae baseada em caracteres miológicos da cabeça, recuperaram o monofiletismo de Trichomycterinae contendo *Sclerонema* e *Ituglanis* (Fig. 7). Os autores fizeram observações em espécimes de *T. hasemani* e relataram que seus dados corroboraram a hipótese de de Pinna (1989), porém não incluíram formalmente *T. hasemani* em sua análise. Logo em seguida, DoNascimiento (2015) publicou uma análise filogenética baseada em caracteres morfológicos focada em Stegophilinae. Diversos Trichomycteridae foram utilizados como grupos externos e a topologia por ele apresentada retrata Trichomycterinae como não monofilética e a espécie *T. hasemani* posicionada num clado composto por Sarcoglanidinae, Glanapteryginae, Tridentinae, Vandelliinae e Stegophilinae, sendo grupo irmão das últimas três subfamílias (Fig. 8). É importante ressaltar que o autor não disponibilizou sua matriz de caracteres.

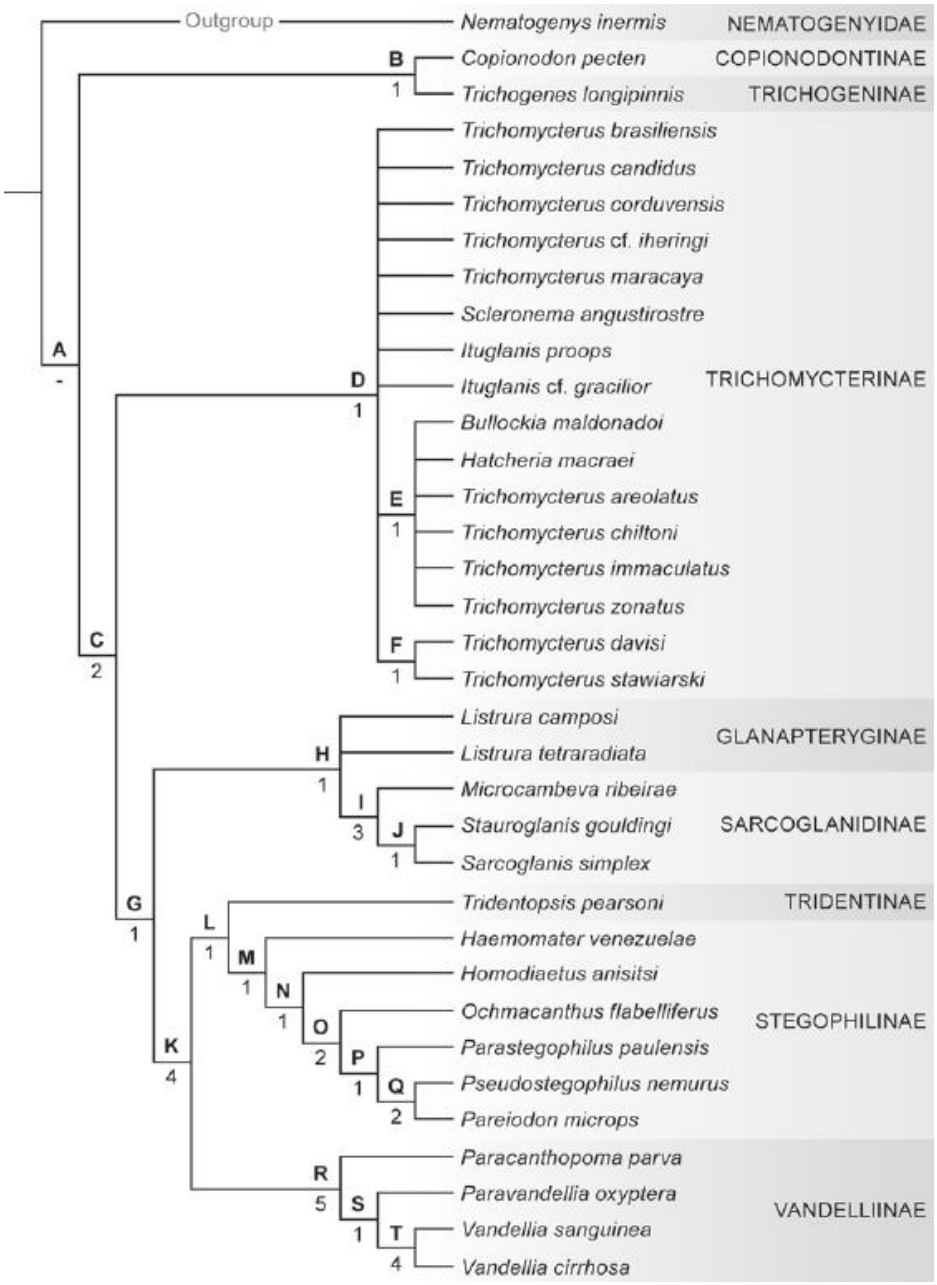


Figura 7. Proposta de relações filogenéticas entre as subfamílias de Trichomycteridae apresentada por Datovo & Bockmann (2010). Modificado de Datovo & Bockmann (2010).


Figura 8. Proposta de relações filogenéticas entre as subfamílias de Trichomycteridae apresentada por DoNascimiento (2015). Retirado de DoNascimiento (2015).

*Trichomycterus hasemani* e *T. johnsoni* hoje compõem parte do grupo *T. hasemani*, que também compreende as espécies *T. anhanga* (Fig. 9A) e *T. wapixana* (Fig. 9B). A distribuição geográfica dessas espécies contrasta com a típica distribuição de *Trichomycterus* por serem endêmicas de terras baixas na Amazônia e no Pantanal: *T. hasemani* é descrita para a bacia do rio Tapajós, Santarém, Pará; *T. anhanga* é descrita para a bacia do rio Madeira, Novo Aripuanã, Amazonas; *T. wapixana* é descrita para a bacia do rio Branco, Bonfim, Roraima e *T. johnsoni* é descrita para a bacia do rio Paraguai, Cáceres, Mato Grosso. O grupo foi nomeado por Dutra et al. (2012) com base na primeira hipótese de relacionamento entre *T. hasemani* e *T. johnsoni*, sugerida por de

Pinna (1989). Segundo os autores, o grupo é definido pela presença de uma ampla fontanela cranial delimitada pelo frontal e supraoccipital, pelo palatino medialmente curvado, pelo primeiro raio da nadadeira peitoral ser maior que os outros raios da mesma nadadeira, pela ausência da porção anterior do canal infraorbital do sistema laterosensorial e pela ausência ou presença de um raio branquiostegal no ceratohial posterior (Dutra et al., 2012). Todas as espécies do grupo são miniaturizadas e se encontram em habitats muito particulares, como folhiço, vegetação marginal e raízes de aguapés. Essa especificidade de habitats é típica de espécies miniaturizadas e se torna um obstáculo em coletas, uma vez que geralmente os esforços de amostragem não são voltados para esses microhabitats (Weitzman & Vari, 1988). Além disso, espécimes do grupo são difíceis de serem coletados mesmo quando o micro-habitat correto é amostrado, o que pode justificar a baixa incidência de populações numerosas de espécies do grupo depositadas em coleções científicas. O objetivo da presente dissertação é fornecer a primeira hipótese filogenética de posicionamento do grupo *T. hasemani*, além de ser o primeiro trabalho a testar formalmente seu monofiletismo. O uso de ferramentas moleculares para estudos sobre o grupo também é inédito e esse é o primeiro trabalho a amostrar quase todas as subfamílias de Trichomycteridae.


Figura 9. Espécies do grupo *T. hasemani*. A- *T. anhanga*, 10,0 mm CP. Retirado de Dutra et al. (2012). B- *T. wapixana*, 14,0 mm CP. Retirado de Henschel (2016).

*Diversidade da ictiofauna da Amazônia e Pantanal*

Considerando que o grupo alvo do presente estudo se distribui pela Amazônia e pelo Pantanal, é de fundamental importância discutir alguns aspectos relacionados a biodiversidade desses biomas.

A bacia amazônica é a maior da América do Sul, estendendo-se por uma área de 7.351.000 km², da qual cerca de 70% encontra-se no Brasil (Junk et al., 2007). A região conta com uma imensa diversidade de peixes, com cerca de 2500 espécies descritas e uma estimativa de mais de 1000 espécies ainda desconhecidas (Junk et al., 2007) – 45% dessas espécies de peixes são endêmicas da bacia amazônica (Reis et al., 2016). Em relação a composição de sua ictiofauna, cerca de 85% dos peixes da Amazônia pertencem à superordem Ostariophysi, sendo 39% pertencentes aos Siluriformes (Junk et al., 2007). Apesar de aparentemente homogênea, a floresta amazônica é um mosaico de ecossistemas, englobando desde a típica floresta úmida até savanas abertas, passando por ambientes de solo arenoso com vegetação escassa. Além disso, mesmo quando se trata de um único ecossistema, diversas variações ambientais locais são encontradas, principalmente devido ao regime de chuvas (Prance, 2013). A divisão básica dos ecossistemas amazônicos se dá entre áreas de terra firme e áreas alagadas sazonalmente. As regiões de terra firme se localizam acima do nível de alagamento. As áreas de alagamento sazonal são classificadas como várzeas (oriundas de alagamento por rios de "água branca") e igapós (alagamento por rios de "água preta"). As várzeas possuem o solo mais fértil que as regiões de terra firme, uma vez que sofrem com o depósito anual de matéria aluvial (por isso "água branca", com maior concentração de sedimentos), enquanto as regiões de igapós são mais pobres em sedimentos e a água é mais ácida (Junk et al., 2007; Prance, 2013). Estima-se que metade das espécies de peixes da

Amazônia ocorram em grandes rios e suas regiões de várzeas e igapós e o restante ocorra em pequenos tributários, que são áreas de alto endemismo devido ao isolamento geográfico (Junk et al., 2007).

Desde o final da década de 1960, a Amazônia sofre com um processo violento de ocupação e exploração, principalmente na sua porção brasileira. Construção de estradas, reservatórios e hidrelétricas, criação de gado e pastagens, mineração e o estabelecimento de agroindústrias são apenas alguns dos tipos de exploração na região (Garda et al., 2010). Em 2000, a população que habita a bacia amazônica atingiu 25 milhões de habitantes, concentrando-se principalmente em centros urbanos (Junk et al., 2007; Garda et al., 2010). 16% da floresta Amazônica já foi desmatada (INPE, 2006) e isso se reflete em uma drástica mudança nas redes de rios e planícies alagadas. Além disso, há uma forte dependência por parte da população local em relação ao uso de recursos pesqueiros (Junk et al., 2007). Considerando que grandes áreas da bacia amazônica, tanto ao norte quanto ao sul do rio Amazonas, são pouco amostradas e provavelmente acomodam um grande número de espécies ainda não descritas (Reis et al., 2016), a exploração da floresta amazônica além da sua capacidade de recuperação representa um risco de extinção de espécies ainda desconhecidas.

A bacia do Paraná-Paraguai representa a terceira bacia mais diversa da América do Sul, com 924 espécies de peixes e compreende a segunda maior área úmida do continente, o Pantanal. 50% dessas 924 espécies de peixes conhecidas para o Pantanal são endêmicas da região (Reis et al., 2016). Esse bioma corresponde a uma área de 140.000 km² no Brasil central, também se estendendo pela Bolívia e Paraguai (Pott & Pott, 2004) e é cercada a leste pelo Cerrado, a nordeste por uma área de transição entre Amazônia e Cerrado e a sudeste pelos chacos (Mittermeier et al., 1990). Além dos alagados

permanentes, o Pantanal se caracteriza pelas inundações no período de dezembro a junho e, durante a seca, grande parte de suas áreas antes alagadas são colonizadas por animais e plantas terrestres (Junk et al., 2006). Quando comparado à Amazônia, o Pantanal é relativamente pobre em números de espécies de peixes em áreas alagadas. Em relação a composição da ictiofauna, em sua grande maioria são encontrados Characiformes e Siluriformes (Britski et al., 1999).

Os biomas de zonas úmidas como o Pantanal estão entre os ecossistemas mais frágeis da Terra, uma vez que acumulam substâncias de áreas que os cercam e qualquer mudança na sazonalidade e volume das chuvas afeta drasticamente o volume das áreas alagadas (Junk et al., 2006). Distúrbios ecológicos no Pantanal em grande parte se dão pela criação de gado e a associação com queimadas para abertura de áreas de pasto, e acredita-se que a maior parte da vegetação local seja afetada por esses processos. Outros distúrbios também acontecem e geralmente têm consequências maiores sobre os sistemas de rios e alagados. O desmatamento em cabeceiras de rios e a consequente erosão e acúmulo de sedimentos, mineração, uso de pesticidas em áreas adjacentes com conexão fluvial (principalmente no cerrado), desvio de cursos de água para agricultura e pesca comercial durante a época de reprodução são exemplos de exploração excessiva do Pantanal (Mittermeier et al., 1990). Apesar da ictiofauna da região ser mais conhecida do que a da região amazônica, as listas de espécies geralmente são incompletas e não consideram histórias de vida das espécies e padrões de distribuição dentro do Pantanal, sendo necessário esforços de conservação para que esse conhecimento venha a ser disponibilizado em algum momento (Junk et al., 2006).

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**Multigene phylogeny supports the South American miniature catfish *Trichomycterus hasemani* group as a new genus of the Tridentinae (Siluriformes, Trichomycteridae)**

Elisabeth Henschel, José Leonardo O. Mattos, Axel M. Katz, Wilson J.E.M. Costa

Running title: *Trichomycterus hasemani* relationships

Henschel *et al.*

Henschel, E., Mattos, J.L.O, Katz, A.M. & Costa, W.J.E.M. (2017 Multigene phylogeny supports the South American miniature catfish *Trichomycterus hasemani group* as a new genus of the Tridentinae (Siluriformes: Trichomycteridae). *Zoologica Scripta*, 00, 000–000.

Trichomycteridae is a well-corroborated catfish family that comprises about 300 valid species distributed in eight subfamilies. The phyletic status of the Trichomycterinae is uncertain, with different hypothesis regarding the position of the miniaturized *Trichomycterus hasemani* group. This group comprises four valid species, and neither its monophyly nor its positioning among the Trichomycteridae were tested in a phylogenetic framework. Bayesian Inference and Maximum Likelihood analyses of a molecular dataset comprising the mithocondrial genes 12S and 16S and the nuclear genes H3, MYH6 and RAG2 (2983 bp) for 26 taxa highly supported the miniature catfish *Trichomycterus hasemani* group as monophyletic and sister to the Tridentinae, consequentely recognized as  a new genus of this subfamily. *Potamoglanis* gen. nov. is diagnosed by seven character states: an angle of 35–40° between the main longitudinal axis of the head and the main axis of the autopalatine; thin tubular shape of the second ceratobranchial; presence of 6 or 7 anal-fin rays; eyes dorsally placed on head; opercular and interopercular odontodes patches not juxtaposed; absence of a distal process on the hyomandibula and presence of a long process on the anterior region of the hyomandibula. *Potamoglanis* gen. nov is similar to the Tridentinae genera by the presence of a wide cranial fontanel; presence of a short ventral process in the opercular bone and by the origin of the dorsal fin placed in a vertical through the anal-fin origin.

## Introduction

Extending from South America to Tropical North America and the Antilles (Wallace, 1876), the Neotropical region comprises the most diverse vertebrate fauna among all the biogeographic realms (Albert & Reis, 2011). An estimate of 5160 species of freshwater fishes was made only for the South American Platform (Reis *et al.*, 2016). These fishes are distributed through a wide variety of habitats such as rivers, waterfalls, floodplains, temporary pools and lakes. In the light of this stunning diversity, the order Siluriformes is the most species rich fish group in the neotropics (Lundberg *et al.*, 2000). Siluriformes comprises about 3700 species distributed worldwide (Nelson *et al.*, 2016) divided into 12 superfamilies. The superfamily Loricarioidea accounts for the high number of catfish species in the Neotropical region: it comprises six families and 1538 exclusive freshwater valid species, including three of the most species-rich families within the whole order (Eschmeyer & Fong, 2017).

Trichomycteridae, the second most diverse family of Siluriformes and Loricarioidea, contains about 300 valid species (Eschmeyer & Fong, 2017) distributed from Costa Rica to Patagonia and in both Andean sides (Baskin 1973, de Pinna 1998). Eight subfamilies are currently recognized: Trichomycterinae (Bleeker, 1858), Vandelliinae (Bleeker, 1862), Stegophilinae (Günther, 1864), Tridentinae (Eigenmann, 1918), Glanapteryginae (Myers, 1944), Sarcoglanidinae (Myers & Weitzman, 1966), Trichogeninae (Isbrücker, 1986) and Copionodontinae (de Pinna, 1992). Its high number of species reflects on a spectacular range of shapes, sizes, colour patterns and niches. The Vandelliinae comprises nine of the less than 20 vertebrate hematophagous species (Carvalho, 2003) and feed on blood of other fishes gills (Kelley & Atz, 1964). According to Gudger (1930) and Baskin *et al.* (1980), the Stegophilinae are mucus and scale eaters and share with the Vandelliinae a simple tubular gut, typical of parasitic forms. Members of these two subfamilies are popularly known as *candirus* or *carneros* (Gudger, 1930). The Sarcoglanidinae are remarkable for its minute size, arenicolous habit and diaphanous body (Myers & Weitzman, 1966; Costa, 1994). The subfamily Glanapteryginae comprises odd elongate catfishes with several adaptations for a fossorial lifestyle such as eyes and fins extremely reduced or absent, loss of dark pigmentation of the body and increased number of vertebrae (Aedriens *et al.*, 2010; de Pinna & Zuanon, 2013). Both Sarcoglanidinae and Glanapteryginae are psammophilic. In contrast with the typical habit shared by most catfishes of burying themselves into

the substrate (Baskin, 1973), the Trichogeninae are mid-water swimmers, usually exploring the water column (de Pinna *et al.*, 2010). The Copionodontinae are mainly algivorous (Zanata & Primitivo, 2013) whereas most species of the Trichomycterinae are insectivorous (de Pinna, 1998). As clearly synthetized by Aedriens *et al.* (2010), the trichomycterids occupy a spectacular range of habitats, from water holes and stagnant waters to highly oxygenated waterfalls with strong currents. Despite all these specializations, a common phenomenon of the Trichomycteridae is miniaturization: it occurs in all subfamilies, except Trichogeninae and Copionodontinae (Toledo-Piza *et al.*, 2014). Miniaturized species were defined by Weitzman & Vari (1988) as not known to exceed 26 mm SL in nature or to reach sexual maturity under 20 mm SL. Miniatures also display several character states considered paedomorphic and typical of miniaturized taxa, such as reduction of the laterosensory canal system and in the number of fin rays and lower degree of development of skull bones (Weitzman & Vari, 1988). Trichomycterinae accounts for more miniaturized species than any other subfamily. Six miniatures are recognized for Trichomycterinae: *Trichomycterus hasemani* (Eigenmann, 1914), *T. santaeritae* (Eigenmnan, 1918), *T. johnsoni* (Fowler, 1932), *T. anhanga* Dutra, Wosiacki & de Pinna, 2012, *T. wapixana* Henschel, 2016 and the recently described *Ituglanis compactus* Castro & Wosiacki, 2017.

Some debate whether Trichomycterinae is monophyletic or not was frequent in the last 40 years, but no consensus was reached so far. The positioning of its miniaturized species usually are in the centre of these debates. Baskin's (1973) work was a landmark in developing the first cladistic analysis focused on the Trichomycteridae. Every subfamily he analysed at that time was recovered as monophyletic, except for Trichomycterinae. Arratia *et al.* (1978) proposed several exclusive character states for Trichomycterinae and, although not developing a cladistic analysis to test this hypothesis, considered Trichomycterinae as an independent lineage. de Pinna (1989) critically commented the character states proposed by Arratia *et al.* (1978) and concluded that they were either symplesiomorphies or characters of uncertain polarity. He also found a wide cranial fontanel shared by *T. hasemani*, *T. johnsoni* and the Tridentinae, interpreting this peculiar cranial morphology as evidence of relationships. In addition, de Pinna (1989) considered *Scleronema* Eigenmann, 1917, *T. boylei* (Nichols, 1956) and *T. santaeritae* to be more closely related to the Sarcoglanidinae than to other Trichomycterinae by the first two taxa having an enlarged maxilla and the

by the last taxon having a distinct morphology of teeth, eye and both nasal and maxillary barbels. Arratia (1990) published a morphological review of the Trichomycterinae, proposing unique character states to diagnose it, but she did not analyse *T. hasemani* or *T. johnsoni*. More recently, Datovo & Bockmann (2010), based on dorsolateral musculature of the head, recovered Trichomycterinae as a monophyletic group. The authors did not include *T. hasemani* or *T. johnsoni* in their analyses. Dutra *et al.* (2012) described *T. anhanga* and placed it along with *T. hasemani* and *T. johnsoni* in the *T. hasemani* group, which was diagnosed by the wide cranial fontanel among other morphological features, but the phylogenetic position in the family was not approached. DoNascimiento (2015) was the only one to include a species of the *T. hasemani* group within a phylogenetic framework, *T. hasemani*, which was recovered as the sister group of a clade comprising Tridentinae, Vandelliinae and Stegophilinae, but no taxonomic decisions were taken.

*Trichomycterus wapixana* was the fourth species placed in the *T. hasemani* group (Henschel, 2016). Species of the group are distributed through Amazon lowlands and Pantanal wetlands, occupying several particular habitats such as litter leaf, roots of aquatic plants, sandbanks and bordering vegetation of small streams (EH, pers. observ.). These habitats are typical of miniaturized fish species and usually sampling efforts are not guided to them (Weitzman & Vari, 1988). Attempts to collect specimens of the *T. hasemani* group are rare, which reflects on a scarcity of populations in collections. The main objectives of this work are to properly assign the phylogenetic position of the *T. hasemani* group within the Trichomycteridae and to test its monophyly, providing the first phylogenetic analysis that comprises most of the currently recognized species for the group and an undescribed species. It is also the first study using a molecular approach to include the Trichogeninae and a representative sample of Trichomycterinae and Tridentinae species.

## Material and Methods

### *Taxon sampling*

Field studies were conducted between 2012 and 2016 in order to obtain representatives of the *T. hasemani* group and seven of the eight currently recognized Trichomycteridae subfamilies. The collected specimens were euthanized by submerging them in a buffered solution of Ethyl 3-aminobenzoate methanesulfonate (MS-222) at a

concentration of 250mg/l, for a period of 10 min, following the guidelines of the Journal of the American Veterinary Medical Association (AVMA Guidelines) (Leary *et al.*, 2013) and European Commission DGXI consensus for fish euthanasia (Close *et al.*, 1996; Close *et al.*, 1997). Molecular data were obtained from specimens fixed and preserved in absolute ethanol. Specimens used for morphological comparisons were fixed in formalin for a period of 14 days and then transferred to 70% ethanol. All the collected material was deposited in the fish collection of Institute of Biology, Federal University of Rio de Janeiro (UFRJ). Out-group selection was directed to one taxa representing Loricarioidea (*Pareiorhina rudolphi* (Miranda-Ribeiro, 1911)) and to one taxa representing the most basal lineage of Trichomycteridae (*Trichogenes longipinnis* Britski & Ortega, 1983). Twenty-six species were used as terminals. A list of specimens and its respective GenBank accession numbers is provided in Table S1.

*DNA extraction, amplification and sequencing*

Total genomic DNA was extracted from muscle tissues using the DNeasy Blood & Tissue Kit (Qiagen), according to the manufacturer's protocol. The analyses included a set of partial sequences of three nuclear genes: histone (H3), recombination activating gene 2 (rag2) and myosin, heavy chain 6, cardiac muscle, alpha (MYH6) and partial sequences of two mitochondrial genes: 16S ribosomal RNA gene (16S) and 12S ribosomal RNA gene (12S). Amplification of the target DNA fragments was made through the Polymerase Chain Reaction (PCR) method, using the following primers: H3b-H and H3a-L (Colgan *et al.*, 1998); MYH6_F459 and MYH6_R1322 (Li *et al.*, 2007); MHRAG2-F1 and MHRAG2-R1 (Hardman & Page, 2003); 16SarL and 16SbrH (Palumbi *et al.*, 1991); 12S L1091 and 12S H1478 (Kocher *et al.*, 1989). Double stranded PCR amplifications were performed in 11µL reactions with reagents at the following concentrations: 5x Green GoTaq Reaction Buffer (Promega), 3.2 mM MgCl2, 1 µM of each primer, 75 ng of total genomic DNA, 0.2 mM of each dNTP and 1U of Taq polymerase. The thermocycling profile was: initial denaturation for 2 minutes at 94°C; 35 cycles of denaturation for 1 minute at 94°C, annealing for 1 minute–90 seconds at 41.3°C–62ºC and extension for 1 to 2 minutes at 72°C (depending on the size of the fragment); and terminal extension for 4 minutes at 72°C. Negative controls were used to check on contaminations. The PCR products were then purified using the Wizard SV Gel and PCR Clean-Up System (Promega). Sequencing reactions were made using the BigDye Terminator Cycle Sequencing Mix (Applied Biosystems) and

were realized 10 µl reactions containing 1 µlBigDye 2.5, 1.55 µl 5x sequencing buffer (Applied Biosystems), 2 µl of the amplified products (10–40ng) and 2 µl of primer with the following thermocycling profile: (1) 35 cycles of 10 seconds at 96°C, 5 seconds at 54°C and 4 minutes at 60°C. The nucleotides were sequenced on an ABI 3130 Genetic Analyzer.

*Phylogenetic analyses*

Sequences were aligned and edited in MEGA 7 software (Kumar *et al.*, 2015) using the ClustalW algorithm (Chenna *et al.*, 2003). Gaps were considered as informative characters. The best-fit evolutionary model selection was performed under the Akaike information criteria (AIC) in the software jModelTest 2 (Darriba *et al.*, 2012). For protein-coding sequences, the selection was determined to each codon position. When concatenating nuclear and mithocondrial genes, the datased was separated into 6 partitions according to the model found for each codon position of protein-coding genes. Bayesian Inference (BI) and Maximum Likelihood (ML) analyses were conducted using the softwares MrBayes 3.2 (Ronquist *et al.*, 2011) and Garli 2.0 (Zwickl, 2006), respectively. The BI analysis was conducted with the following parameters: two independent Markov chain Monte Carlo (MCMC) runs of two chains each for 2 million generations, with a tree sampling frequency of every 100 generations. The convergence of the MCMC chains and the proper burn-in value were assessed by evaluating the stationary phase of the chains using Tracer v. 1.5 (Rambaut *et al.*, 2013). The BI final consensus tree and its Bayesian posterior probabilities were generated with the remaining tree samples after removing the first 25% samples as burn-in. To test the support of the nodes in the ML analysis, 1000 bootstrap (Felsenstein, 1985) replicates were performed in the software Garli 2.0. Both analyses were shown rooted in *P. rudolphi*.

*Morphological comparisons*

Morphological comparisons were focused on the latero-sensory system and osteological features of cleared and stained specimens prepared according to Taylor & Van Dyke (1985). Terminology for the latero-sensory system follows Arratia & Huaquin (1995), osteological nomenclature follows Arratia (1998). The standard length (SL) measurement is according to Tchernavin (1944). A list of material analysed appears in Appendix S1. For the *T. hasemani* group, all described species and a new one under

description were included in the comparative analyses. For Trichomycteridae, all subfamilies were examined.

Results

*Phylogenetic analyses*

The final concatenated matrix comprised 2983 bp (396 bp from 12S, 504 from 16S, 327 from H3, 933 from RAG2 and 823 from MYH6). The best-fit evolutionary models found are shown in Table S2. The best log-likelihood score for the ML analysis was -10734.624444. Both analyses resulted in identical topologies (only the ML tree is presented in Figure S1).

The Trichomycterinae, excluding the *T. hasemani* group, is recovered as a monophyletic group. The *T. hasemani* group is consistently supported as monophyletic and positioned as sister group of a clade comprising *Miuroglanis* Eigenmann & Eigenmann, 1889, *Tridensimilis* Schultz, 1944 and *Tridens* Eigenmann & Eigemann, 1889, thus providing enough evidence to allocate it in a new genus within the Tridentinae (Fig. 1). A clade comprising the Glanapteryginae, Tridentinae (including the *T. hasemani* group), Sarcoglanidinae, Stegophilinae and Vandelliinae is recovered. The well-supported clade comprising the parasitic Stegophilinae and Vandelliinae (Baskin, 1973; de Pinna, 1998; Fernández & Schaefer, 2009; Datovo & Bockmann, 2010; DoNascimiento, 2015) is also well recovered.

*Taxonomic accounts*

*Potamoglanis*, gen.n.

*Etymology.* From the greek *potamo* (river; the gods of rivers in the Greek mythology) and *glanis* (catfish). Gender masculine.
*Type species. Pygidium hasemani* Eigenmann, 1914.

*Diagnosis. Potamoglanis* is distinguished from all other Trichomycteridae by an angle of 35–40° between the main longitudinal axis of the head and the main axis of the autopalatine (Fig. 2A-B) and by the unique thin tubular shape of the second hypobranchial (Fig. 3A). *Potamoglanis* is similar to other Tridentinae genera by the presence of a wide cranial fontanel (Fig. 4A-B); the presence of a short ventral process

in the opercular bone (Fig. 5A) and by the origin of the dorsal fin placed in a vertical through the anal-fin origin or just posterior to it. The new genus differs from other genera of Tridentinae by the presence of 6 or 7 anal-fin rays (vs. 15 or more); eyes dorsally placed on head, not ventrally visible (vs. laterally placed; ventrally visible); opercular and interopercular odontodes patches not juxtaposed, separated by more than the width of the interopercular patch (vs. odontodes patches juxtaposed, separated by less than the width of the interopercular patch); absence of a distal process on the hyomandibula (vs. presence) and the presence of a long process on the anterior region of the hyomandibula (vs. absence) (Fig. 5).

*Included species. Pygidium hasemani* Eigenmann, 1914; *Pygidium johnsoni* Fowler, 1932; *Trichomycterus anhanga* Dutra, Wosiacki & de Pinna, 2012; *Trichomycterus wapixana* Henschel, 2016.

*Distribution and habitat. P. hasemani, P. anhanga* and *P. wapixana* are found throughout the Amazon river basin, whereas *P. johnsoni* is endemic to Pantanal wetlands, Paraguay river basin. *Potamoglanis hasemani* is found in aquatic plants roots and *P. wapixana* inhabits marginal vegetation of small streams (EH, pers. observ.). *Potamoglanis anhanga* lives in places with mud and roots of aquatic plants of a small stream (mainly composed of sandbanks) (EH, pers. observ.). *Potamoglanis johnsoni* is endemic to the Pantanal and inhabits roots of aquatic plants (WJEMC and EH, pers. observ.).

*Remarks.* Several populations of small catfishes have been collected throughout the Amazon basin and identified as *P. hasemani* (EH pers. observ.), but this identification requires confirmation.

## Discussion

### *Phylogenetic positioning of Potamoglanis and monophyly of Tridentinae*

Our results corroborate *Potamoglanis* as the sister group of species traditionally placed in the Tridentinae. Tridentinae, until the present paper, comprised the genera *Miuroglanis, Tridensimilis, Tridentopsis* and *Tridens. Potamoglanis* is herein considered as the fifth Tridentinae genus.

Baskin (1973) enumerated eight synapomorphies for the Tridentinae: 1- cranial fontanel expanded; 2- maxillary bone very small; 3- eyes exposed ventrally; 4- opercular and

interopercular tooth patches juxtaposed; 5- opercular bone with a short ventral process; 6- origin of the dorsal fin just above or posterior to anal-fin origin; 7- hyomandibular with a distal process and 8- anal-fin rays 15 or more. When regarding *Potamoglanis* as a new Tridentinae genus, the characters 1, 5 and 6 are maintained as sinapormophies for the whole subfamily (see below). The other five character states are thus no longer considered as valid synapomorphies for the subfamily, but are useful to diagnose the clade comprising *Miuroglanis* Eigenmann & Eigenmann, 1889; *Tridens* Eigenmann & Eigenmann, 1889; *Tridentopsis* Myers, 1925 and *Tridensimilis* Schultz, 1944.

Baskin (1973) described the wide cranial fontanel of the Tridentinae as being anteriorly delimited by the posterior edge of the mesethmoid, laterally by the frontals and sphenotics and posteriorly by the parietosupraoccipital (Fig. 4A-C). de Pinna (1989) considered the presence of a similar structure in *P. hasemani* and *P. johnsoni* as evidence of relationship between these species and Tridentinae. An expanded cranial fontanel is also seen in *Paravandellia* Miranda-Ribeiro, 1912, but regarded as homoplastic (de Pinna, 1989) since it is the only Vandelliinae genus exhibiting this condition and this subfamily is a well-corroborated clade, phylogenetically distant of the Tridentinae. In other Trichomycteridae, this cranial fontanel is restricted to one or two openings in the frontals (Fig. 4E). Our results corroborate de Pinna's (1989) hypothesis that *Potamoglanis* is more closely related to the other Tridentinae genera and that *Paravandellia* is not closely related to them (Fig. 1).

The presence of a short ventral process in the opercular bone, described by Baskin (1973) being half as long as the width of the tooth patch are also observed in *Potamoglanis* (Fig. 5). Among other Trichomycteridae, this ventral process is usually as long as the width of the opercular tooth patch.

The origin of the dorsal fin above or just posterior to the anal-fin origin was first proposed by Eigenmann (1914) as a diagnostic character for Tridentinae. Later, Baskin (1973) recovered this character state as a valid synapomorphy for the subfamily. Since *Potamoglanis* also possess this unique positioning of both dorsal and anal fins, this character state is herein regarded as a synapomorphy for the Tridentinae.

The small size of the maxilla, described by Baskin (1973) to be less than one tenth the length of the entire neurocranium, is not seen in *P. anhanga.* All the remaining Tridentinae genera and *Potamoglanis* species have a laminar and small maxillary bone,

except *P. anhanga*, which has the maxilla approximately equal in size to the premaxilla (Fig. 2A). Despite being the smallest species among all the Trichomycteridae, *P. anhanga* possesses the proportionally largest maxilla within the Tridentinae. Thus, the small size of the maxilla can not be considered as a synapomorphy for the Tridentinae.

Costa & Bockmann (1994) delimited the TSVSG clade, comprising the Tridentinae, Sarcoglanidinae, Vandelliinae, Stegophilinae and Glanapteryginae. This hypothesis was based on four characters states: 1- reduced interopercular patch of odontodes, with 15 or fewer odontodes; 2- reduced number of pleural ribs (1 to 8); 3- metapterygoid reduced or absent and 4- tip of parasphenoid not reaching or reaching only the anterior portion of basioccipital. According to the present topologies, the TSVSG clade is recovered as well as the morphological diagnostic character states of the TSVSG clade are found in all species of *Potamoglanis.* The interopercular patch of odontodes is reduced, with six to 15 odontodes (Fig. 5A); *P. hasemani, P. johnsoni* and *P. wapixana* possess two pairs of pleural ribs and *P. anhanga*, one; the metapterygoid is extremely reduced in all species (Fig. 5A) and the parasphenoid does not reach the basioccipital.

The Trichomycterinae, comprising the genera *Trichomycterus*, *Hatcheria* Eigenmann, 1909, *Scleronema* Eigenmann, 1917, *Bullockia* Arratia, Chang, Menu-Marque & Rojas, 1978 and *Ituglanis* Costa & Bockmann, 1993, was recovered as a monophyletic group by Datovo & Bockmann (2010). According to these authors, monophyly of Trichomycterinae is supported by the origin of the muscle *levator internus 4* attaching the ventral surface of the pterotic and both ventral and dorsal surfaces of the supracleithrum. In other Trichomycteridae, this muscle only inserts onto the ventral surface of the pterotic and/or ventral surface of the posttemporosupracleithrum (Datovo & Bockmann, 2010). Despite not including *P. hasemani* in their data matrix, Datovo & Bockmann (2010) mentioned that the condition of the *levator internus 4* in this species is similar to the non-Trichomycterinae trichomycterids. The hypothesis of Trichomycterinae monophyly supported by Datovo & Bockmann (2010) contrasted with previous studies, in which *Scleronema* and *Ituglanis* were considered more closely related to members of the TSVSG clade (de Pinna, 1989; 1998; Costa & Bockmann, 1993). Our molecular analysis highly supports the morphological study by Datovo & Bockmann (2010).

DoNascimiento (2015) provided a morphological phylogeny focusing on internal relationships of the Stegophilinae, but also including representatives of every

Trichomycteridae subfamily. This study was the first to assign a species of *Potamoglanis* in a phylogenetic framework. *Potamoglanis hasemani* was positioned within the TSVSG clade, as the sister group of the clade Tridentinae + Vandelliinae + Stegophilinae. Since the data matrix was not included in DoNascimiento's (2015) paper and it is not available elsewhere, their characters cannot be evaluated.

*Monophyly of Potamoglanis*

The synapomorphic character states herein proposed for *Potamoglanis* are: an angle of 35–40° between the main longitudinal axis of the head and the main axis of the autopalatine (Fig. 2A-B); the tubular thin shape of the second hypobranchial (Fig. 3A); the fewer number of anal fin rays (6 or 7); smaller eyes (not ventrally visible); interopercular and opercular patches of odontodes not juxtaposed; the presence of a long process on the anterior margin of the hyomanidbula and the absence of a distal process in the hyomandibula (Fig. 5A).

Costa & Bockmann (1994) proposed the presence of an anteriorly directed process on the hyomandibula as a synapomophy for a clade composed by Glanapteryginae + Sarcoglanidinae (Costa & Bockmann, 1994, Fig. 6). This process is also found in *Potamoglanis* species (Fig. 5A), which is herein treated as a distinct character from the posterodorsal process on the hyomandibula proposed by Baskin (1973) as a synapomoprhy for the Tridentinae (Fig. 5B). The posteriorly directed process present in Tridentinae is positioned in a different region of the hyomandibula and is thus treated as a synapomorphy for the clade comprising *Miuroglanis, Tridens* and *Tridensimilis*. The anterior process of the hyomandibula found in *Potalmoglanis* is unique among the Tridentinae.

Dutra *et al.* (2012) proposed the following character states to diagnose the *T. hasemani* group: 1- presence of a wide cranial fontanel; 2- a "medially-bent" autopalatine; 3- first pectoral fin-ray longer than other rays; 4- absence of the anterior portion of the infraorbital canal corresponding to pores i1 and i3; 5- presence of one or none branchiostegal rays in the posterior ceratohyal. The presence of an elongate first pectoral-fin as synapomoprhic ray is subjective and Dutra *et al.* (2012) proposed no measurement or proportion. A long first pectoral-fin ray is also present in *Tridentopsis pearsoni* Myers, 1925 (Baskin, 1973), making this character state invalid to diagnose *Potamoglanis*. The infraorbital canal could not be examined by us in other Tridentinae

genera, but Arratia & Huaquin (1995) reported the absence of pores i1 and i3 in *Tridentopsis pearsoni* Myers, 1925. Therefore, absence of the anterior portion of the intraorbital canal system cannot be considered as diagnostic for *Potamoglanis*. The presence of one or none branchiostegal rays in the posterior ceratohyal cannot be regarded as a valid character state to diagnose the *Potamoglanis* due to intrapopulational polymorphism: in some specimens four or more branchiostegal rays are found in the posterior ceratohyal (Fig. 6), whereas in others no branchiostegal rays is found in this region of the hyoid arch.

The "medially-bent" autopalatine is herein observed to constitute an angle of 35–40° between the main longitudinal axis of the head and the main axis of the autopalatine in species of *Potamoglanis* and considered to be an exclusive character state among trichomycterids (Fig. 2A-B). Furthermore, the posterior edge of the autopalatine in *P. hasemani*, *P. johnsoni* and *P. wapixana* is directed to the lateral ethmoid and frontals and in *P. anhanga*, it is extremely reduced, uniquely among trichomycterids. In the remaining Trichomycteridae the autopalatine is directed to the suspensorium (Fig. 2C).

The unique thin tubular shape of the second hypobranchial (Fig. 3A) is herein proposed as a diagnostic character state for *Potamoglanis*. Usually among Trichomycteridae, the second hypobranchial is triangular, with its posterior margin equal in size or longer than the lateral margins (Fig. 3B). In *Potamoglanis* the lateral facets are elongated when compared to the posterior margin, thus forming a tubular shape.

Acknowledgements

We are grateful to M.A. Barbosa for assistance during examination of morphological characters and to P. Bragança for help and encouraging field trips. Thanks are also due to F. Pereira-Rangel and P. Fasura for laboratorial assistance.

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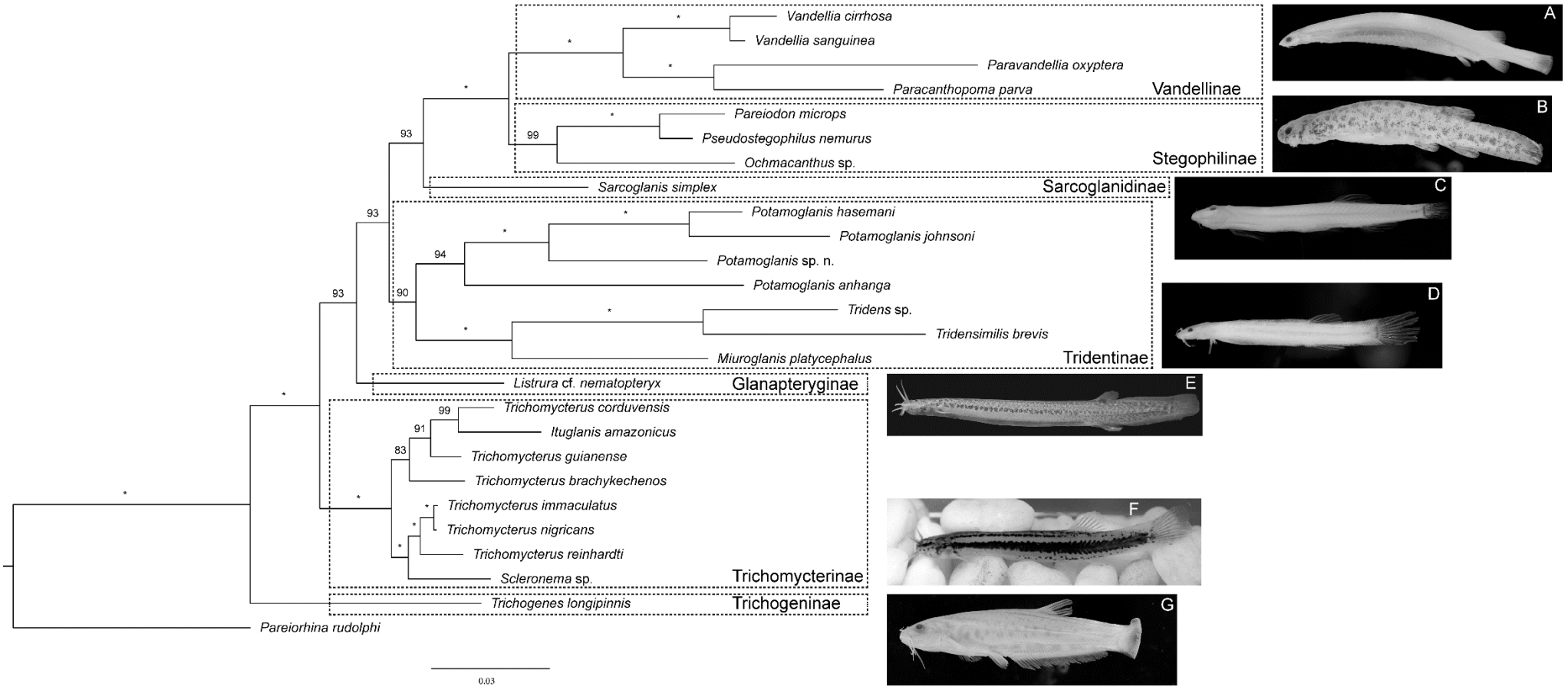



Fig. 1. Phylogenetic positioning of *Potamoglanis* among the Trichomycteridae, inferred by Bayesian Inference from the analysis of molecular data (2983 bp). An asterisk indicates maximum support value. - A. *Paracanthopoma parva* Giltay, 1935. - B. *Ochmacanthus reinhardtii* (Steindachner, 1882). - C. *Stauroglanis gouldingi* de Pinna, 1989. - D. *Potamoglanis anhanga.* - E. *Listrura camposi* Villa-Verde, Lazzarotto & Lima, 2012. - F. *Trichomycterus reinhardtii* (Eigenmann, 1917). – G. *Trichogenes longipinnis*.

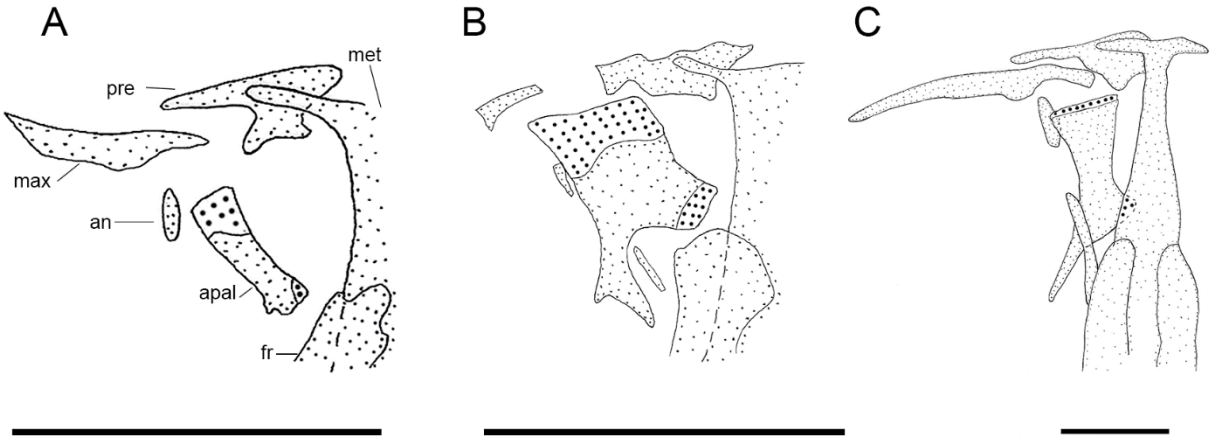



Fig. 2. A-C. Left autopalatine, dorsal view of: - A. *Potamoglanis anhanga,* UFRJ 11251, 10.0 mm SL. Scale bar = 0.5 mm. - B. *P. johnsoni,* UFRJ 11530, 13.0 mm SL. Scale bar = 1.0 mm. - C. *Microcambeva* sp., MZUSP 79953, 38.0 mm SL. Scale bars = 1.0 mm.

Abbreviations: an, antorbital; apal, autopalatine; fr, frontal; max, maxilla; met; mesethmoid; pre, premaxilla.

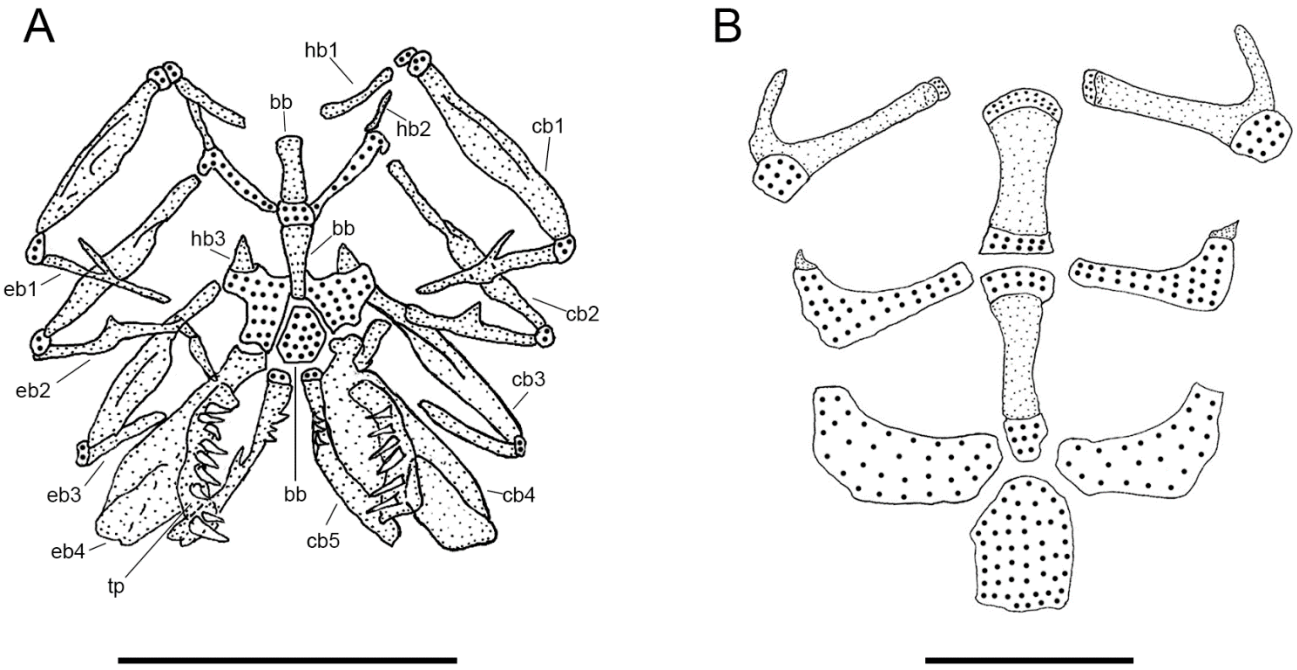



Fig. 3. A-B. Branchial arches, ventral view of: - A. *P. johnsoni,* UFRJ 11530, 13.0 mm SL. - B. *Trichogenes longipinnis,* UFRJ 0682, 51.7 mm SL. Scale bars = 1.0 mm.

Abbreviations: bb, basibranchials; cb1-5, ceratobranchial 1-5; eb1-4, epibranchial 1-4; hb1-3, hypobranchial 1-3; tp, tooth plate.

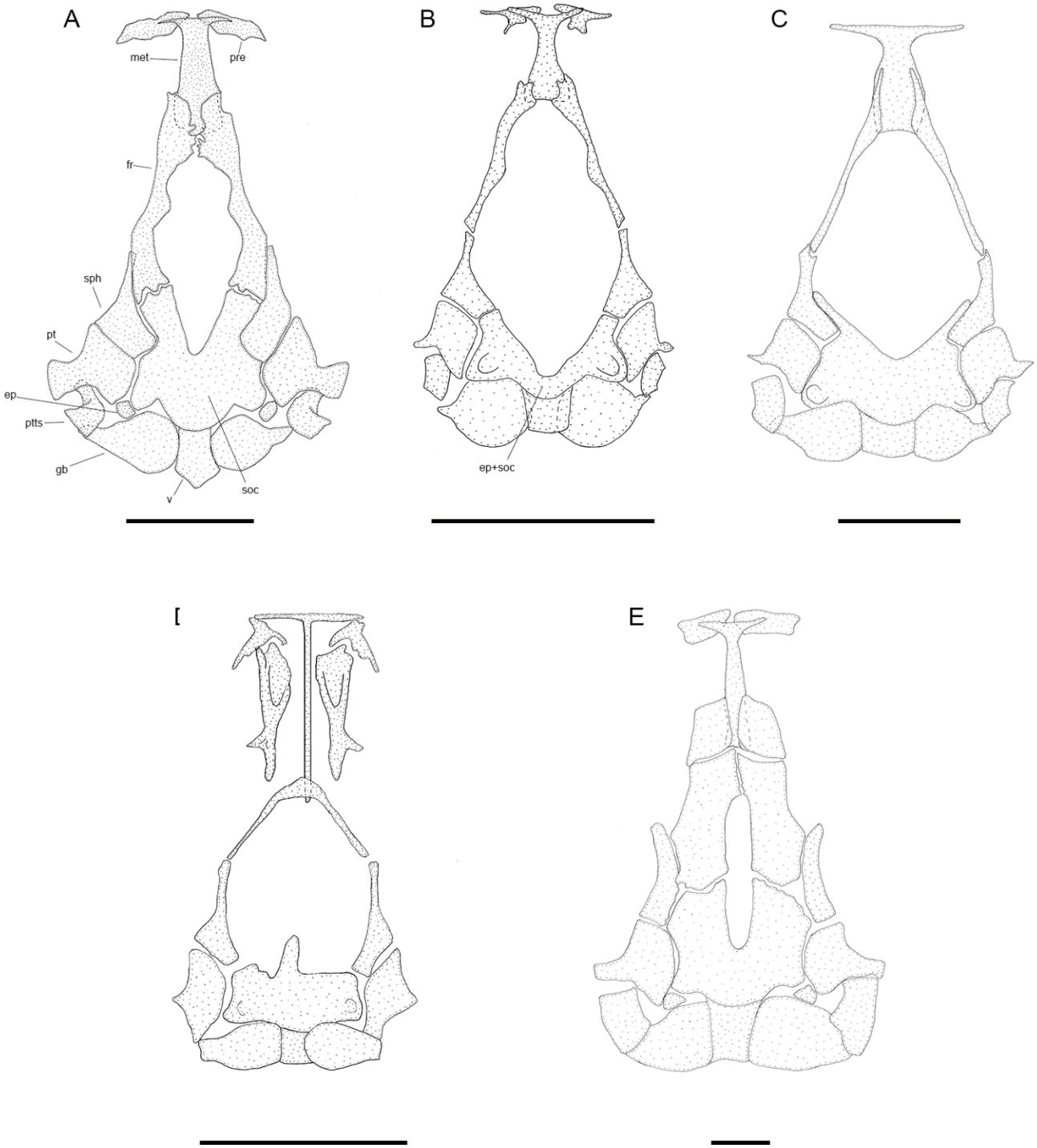



Fig. 4. A-E. Neurocranium, dorsal view of: - A. *Potamoglanis hasemani*, UFRJ 9653, 17.0 mm SL. - B. *P. anhanga*, UFRJ 11251, 10.0 mm SL. - C. *Tridentopsis* sp., UFRJ 1077, 18.0 mm SL. - D. *Paravandellia oxyptera*, UFRJ 1112, 13.0 mm SL. - E. *Trichomycterus reinhardti*, UFRJ 9995, 40.9 mm SL. Scale bars = 1.0 mm. Abbreviations: ep, epioccipital; ep+soc, epioccipital fused to parietosupraoccipital; fr, frontal; gb, gasbladder capsule; met, mesethmoid; pre, premaxilla; pt, pterotic; ptts, posttemporosupracleithrum; soc, parietosupraoccipital; sph, sphenotic; v, first free vertebra.

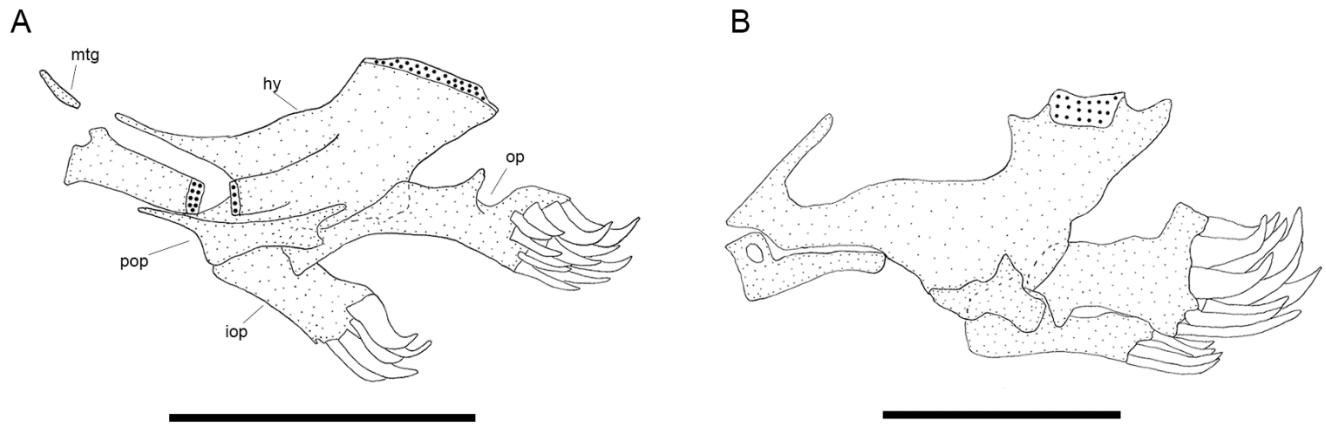



Fig. 5. A-B. Left suspensory, dorsal view of: - A. *Potamoglanis wapixana*, UFRJ 9369, 13.8 mm SL. - B. *Tridentopsis* sp., UFRJ 1077, 18.0 mm SL. Scale bars = 1.0 mm. Abbreviations: hy, hyomandibula; iop, interopercle; mtg, metapterygoid; op, opercle; pop, preopercle.

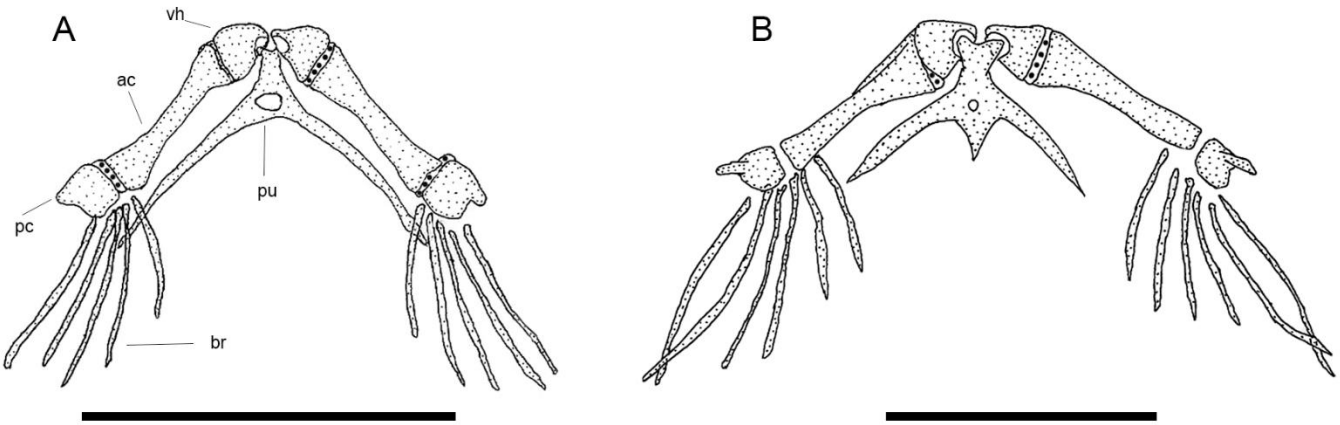



Fig. 6. A-B. Hyoid arch, ventral view of: - A. *Potamoglanis anhanga*, UFRJ 11251, 10.0 mm SL. - B. *P. johnsoni*, UFRJ 11530, 13.0 mm SL. Scale bars = 1.0 mm. Abbreviations: ac, anterior ceratohyal; br, branchiostegal rays; pc, posterior ceratohyal; pu, parurohyal; vh, hypohial.

**Supporting information.**

Table S1. Terminal taxa for molecular phylogeny and respective GenBank accession numbers.

| | 12S | 16S | H3 | MYH6 | RAG2 |
|---|---|---|---|---|---|
| Trichomycteridae: Trichogeninae | | | | | |
| *Trichogenes longipinnis* | XXXX | XXXX | XXXX | XXXX | XXXX |
| | | | | | |
| Trichomycteridae: *Trichomycterinae* | | | | | |
| *Ituglanis amazonicus* | XXXX | XXXX | XXXX | XXXX | — |
| *Scleronema* sp. | XXXX | XXXX | XXXX | XXXX | XXXX |
| *Trichomycterus nigricans* | — | XXXX | — | XXXX | — |
| *Trichomycterus brachykechenos* | XXXX | XXXX | XXXX | XXXX | XXXX |
| *Trichomycterus reinhardti* | XXXX | XXXX | XXXX | XXXX | XXXX |
| *Trichomycterus immaculatus* | XXXX | XXXX | XXXX | XXXX | XXXX |
| *Trichomycterus cf. guianense* | FJ744608 | FJ744634 | FJ744683 | — | DQ492319.1 |
| *Trichomycterus corduvensis* | FJ744607 | FJ744632 | FJ744682 | — | — |
| | | | | | |
| Trichomycteridae: Glanapteryginae | | | | | |
| *Listrua cf. nematopteryx* | — | XXXX | XXXX | — | — |
| | | | | | |
| Trichomycteridae: Vandelliinae | | | | | |
| *Paracanthopoma parva* | XXXX | XXXX | XXXX | XXXX | — |
| *Paravandellia oxyptera* | XXXX | XXXX | XXXX | XXXX | — |
| *Vandellia sanguinea* | FJ744628 | FJ744651 | FJ744694 | — | — |
| *Vandellia cirrhosa* | FJ744629 | FJ744652 | FJ744695 | — | — |

| | | | | | |
|---|---|---|---|---|---|
| Trichomycteridae: Stegophilinae | | | | | |
| *Ochmacanthus* sp. | FJ744623 | FJ744646 | XXXX | — | — |
| *Pareiodon microps* | FJ744609 | FJ744635 | FJ744684 | — | — |
| *Pseudostegophilus nemurus* | FJ744613 | FJ744639 | FJ744685 | — | — |
| Trichomycteridae: Sarcoglanidinae | | | | | |
| *Sarcoglanis simplex* | FJ744630 | FJ744653 | FJ744696 | — | — |
| Trichomycteridae: Tridentinae | | | | | |
| *Miuroglanis platycephalus* | XXXX | XXXX | XXXX | — | XXXX |
| *Potamoglanis anhanga* | XXXX | XXXX | XXXX | XXXX | XXXX |
| *Potamoglanis hasemani* | XXXX | XXXX | XXXX | — | — |
| *Potamoglanis johnsoni* | — | — | XXXX | — | — |
| *Potamoglanis* sp.n. | XXXX | XXXX | XXXX | — | — |
| *Tridens* sp. | FJ744625 | FJ744648 | — | — | — |
| *Tridensimilis brevis* | — | XXXX | XXXX | XXXX | — |
| Loricariidae | | | | | |
| *Pareiorhina rudolphi* | — | XXXX | XXXX | XXXX | XXXX |

Table S2. Best-fit evolutionary models found for each mitochondrial gene and for each codon position of nuclear genes.

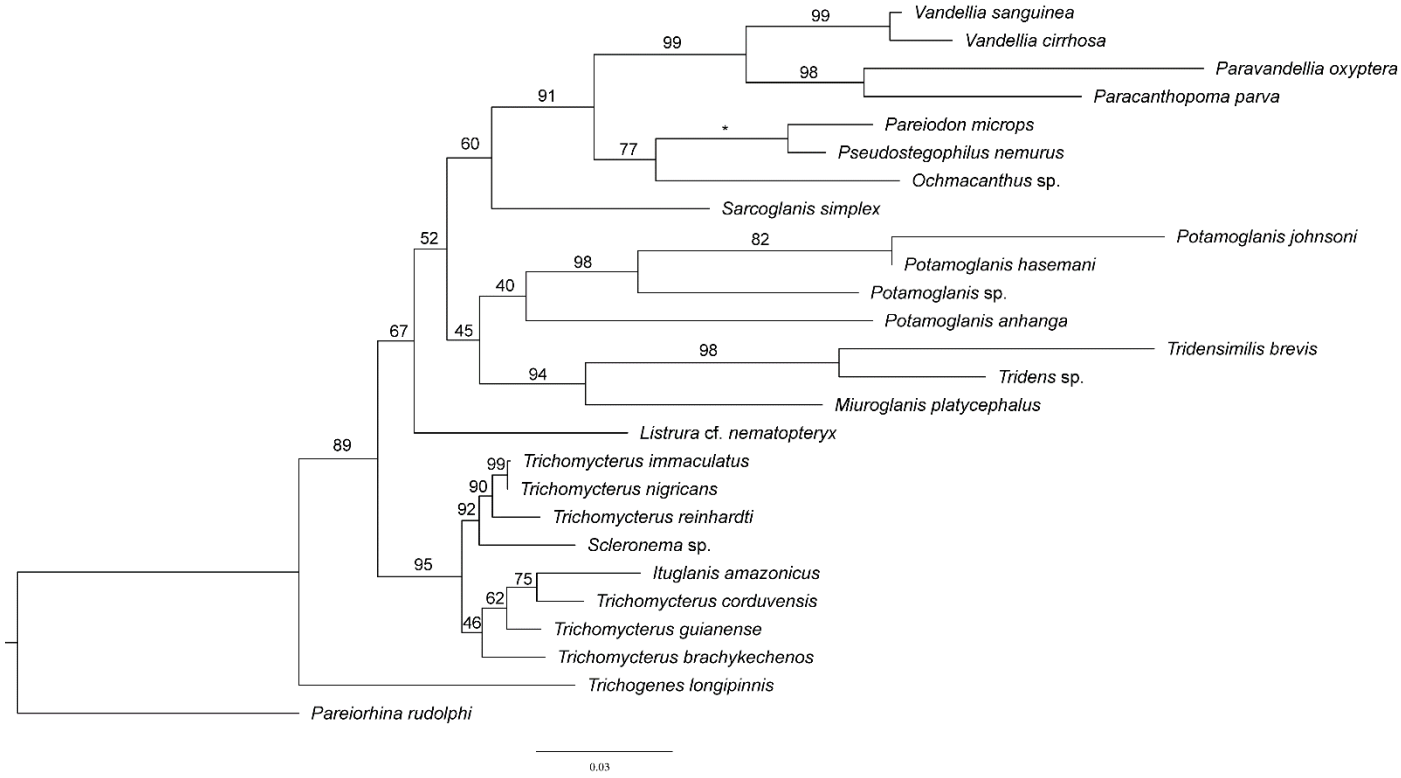
| Mitochondrial genes | | | |
|---|---|---|---|
| 16S | GTR+I+G | | |
| 12S | GTR+I+G | | |
| Nuclear genes | 1st codon position | 2nd codon position | 3rd codon position |
| H3 | GTR+I | HKY | GTR+G |
| RAG2 | HKY+I | HKY+I | GTR+I |
| MYH6 | GTR+I+G | GTR+I | SYM+G |

Appendix S1. List of material examined for the analysis of morphological characters.

Trichomycteridae: *Ammoglanis amapaensis* Mattos, Costa & Gama, 2008: UFRJ 6602, 2 (C&S), 15.7–16.2 mm SL; Brazil: Amapá: Serra do Navio. *Copionodon pecten* de Pinna, 1992: UFRJ 4171, 1, 52.2 mm S. *Copionodon* sp.: MZUSP 48962, 8, 30.9–58.6 mm SL; MZUSP 48962, 2 (C&S), 51.2–64.0 mm SL. *Ituglanis amazonicus* (Steindachner, 1882): USNM, 1 (C&S). *Homodiaetus passarellii* (Miranda-Ribeiro, 1994): UFRJ 7128, 9, 31.0–41.1 mm SL; Brazil: Rio de Janeiro: Magé. *Ituglanis paraguassuensis* Campos-Paiva & Costa, 2007: UFRJ 7282, 1 (C&S), 38.9 mm SL; Brazil: Bahia: Iassú; UFRJ 10709, 15, 25.7–43.6 mm SL; Brazil: Bahia: Utinga. *Listrura* sp.: UFRJ 9279, 37, 16.3–36.1 mm SL; UFRJ 9691, 3 (C&S), 23.3–37.4 mm SL; Brazil: Rio de Janeiro: Cachoeiras de Macacu. *Microcambeva barbata* Costa & Bockmann, 1994: UFRJ 0684, 2 (C&S), 21.6–23.8 mm SL; Brazil: Rio de Janeiro: Silva Jardim. *Microcambeva* sp.: MZUSP 79953, 1 (C&S), 38.0 mm SL. *Ochmacanthus batrachostomus* (Miranda-Ribeiro, 1912): UFRJ 8603, 3 (C&S), 21.4–27.0 mm SL; Brazil: Mato Grosso: Poconé. *Ochmacanthus reinhardtii* (Steindachner, 1882): UFRJ 11348, 10, 25.2–31.8 mm SL; UFRJ 11525, 4 (C&S), 28.1–29.3 mm SL; Brazil: Amazonas: Humaitá. *Paracanthopoma parva* Giltay, 1935: UFRJ 11366, 29, 15.0–22.6 mm SL; Brazil: Rondônia: Porto Velho; UFRJ 11523, 1, 14.7 mm SL; Brazil: Amazonas: Rio Preto da Eva. *Paracanthopoma* sp.: MZUSP 40585, 2 (C&S), 24.3–25.4 mm SL. *Parastegophilus paulensis* (Miranda-Ribeiro, 1918): UFRJ 1118, 1, 135.0 mm SL; Brazil: São Paulo: Botucatu. *Parastegophilus* sp.: MZUSP 40237, 1(C&S), 37.0 mm SL. *Paravandellia oxyptera* Miranda-Ribeiro, 1912: UFRJ 11111, 38, 9.6–16.3 mm SL; UFRJ 11112, 5 (C&S), 11.9–13.0 mm SL; Brazil: Mato Grosso: Rio Branco. *Pareiodon microps* Kner, 1855: UFRJ 1135, 2, 103.3–135.0 mm SL; Brazil: Amazonas: Tefé. *Plectrochilus machadoi* Miranda-Ribeiro, 1917: MZUSP 9594, 11, 31.1–63.5 mm SL; MZUSP 9594, 1 (C&S), 56.0 mm SL; Brazil: Amazonas: Manacapuru. *Potamoglanis anhanga* (Dutra, Wosiacki & de Pinna, 2012): MZUSP 108822, 2, 9.7–10.2 mm SL; MZUSP 108822, 1 (C&S), 10.0 mm SL; Brazil: Amazonas: Novo Aripuanã; UFRJ 11251, 13, 9.2–11.6 mm SL; UFRJ 11528, 5 (C&S), 9.7–10.0 mm SL; Brazil: Rondônia: Candeias do Jamari. *Potamoglanis hasemani* (Eigenmann, 1914): UFRJ 9645, 3, 15.7–17.8 mm SL; UFRJ 9653, 3 (C&S), 16.3–17.3 mm SL; Brazil: Pará: Santarém. *Potamoglanis johnsoni* (Fowler, 1932): UFRJ 3823, 17, 12.6–14.6 mm SL; UFRJ 11530, 5 (C&S), 12.9–13.6 mm SL; Brazil: Mato Grosso: Cáceres.

*Potamoglanis* sp.: UFRJ 9708, 4, 11.8–12.9 mm SL; UFRJ 9709, 20, 10.7–14.6 mm SL; UFRJ 10020, 4 (C&S), 11.6–12.2 mm SL; UFRJ 10127, 4 (C&S), 12.1-12.6 mm SL; Brazil: Pará. UFRJ 9710, 2 ex., 11.7–13.5 mm SL; UFRJ 9711, 3 ex., 12.9–11.2 mm SL; UFRJ 10714, 3 ex. (c&s), 11.4-12.2 mm SL; UFRJ 10918, 2 ex. (c&s), 11.0-11.4 mm SL; Brazil: Pará. *Potamoglanis wapixana* (Henschel, 2016): UFRJ 8946, 7, 12.5–14.5 mm SL; UFRJ 9006, 3, 13.5–13.8 mm SL; UFRJ 9369, 3 (C&S), 12.9–13.8 mm SL; Brazil: Roraima: Bonfim; UFRJ 8952, 3, 12.1–13.9 mm SL; UFRJ 9460, 1 (C&S), 12.8 mm SL; Brazil: Roraima: Cantá; UFRJ 8965, 1, 13.5 mm SL; UFRJ 9461, 1 (C&S), 13.3 mm SL; Brazil: Roraima: Caracaraí. *Pseudostegophilus* sp.: MZUSP 3042, 3 (C&S), 30.3–52.4 mm SL. *Pygidianops amphioxus* de Pinna & Kirovsky, 2011: UFRJ 11247, 6, 24.6–28.1 mm SL; UFRJ 11524, 3 (C&S), 26.2–30.3 mm SL; Brazil: Amazonas: Rio Preto da Eva. *Scleronema* sp.: UFRJ 10591, 14, 30.6–43.8 mm SL; UFRJ 10645, 1 (C&S), 43.3 mm SL; Brazil: Rio Grande do Sul. *Stauroglanis gouldingi* de Pinna, 1989: UFRJ 11261, 5, 20.1–22.2 mm SL; UFRJ 11521, 3 (C&S), 20.3–20.9 mm SL; Brazil: Amazonas: Rio Preto da Eva. *Trichogenes longipinnis* Britski & Ortega, 1973: UFRJ 0682, 2 (C&S), 45.5–51.7mm SL; Brazil: São Paulo: Picinguaba. *Trichomycterus brachykechenos* Ferrer & Malabarba, 2013: UFRJ 10586, 1 (C&S), 58.7 mm SL; Brazil: Rio Grande do Sul: Lajeado. *Trichomycterus immaculatus* (Eigenmann & Eigenmann, 1889): UFRJ 0557, 2 (C&S), 41.7–43.6 mm SL; Brazil: Minas Gerais: Ipatinga; UFRJ 7265, 1, 60.9 mm SL; Brazil: Rio de Janeiro: Teresópolis. *Trichomycterus nigricans* Valenciennes, 1832: UFRJ 10996, 1 (C&S), 74.3 mm SL; Brazil: Rio de Janeiro. *Trichomycterus reinhardti* (Eigenmann, 1917): UFRJ 9497, 12, 38.7–48.1 mm SL; UFRJ 9995, 2 (C&S), 37.0–40.9 mm SL; Brazil: Minas Gerais: Ouro Preto. *Tridensimilis brevis* (Eigenmann & Eigenmann, 1889): UFRJ 11257, 6, 15.4–20.4 mm SL; UFRJ 11520, 3 (C&S), 19.8–19.9 mm SL; Brazil: Acre: Xapuri. *Tridentopsis* sp.: UFRJ 4952, 3, 17.7–19.2 mm SL; UFRJ 1077, 2 (C&S), 16.9–18.0 mm SL; Brazil: Mato Grosso do Sul.

Figure S1. Phylogenetic positioning of *Potamoglanis* among the Trichomycteridae, inferred by Maximum Likelihood (2983 bp).



## Discussão

*Posicionamento do grupo T. hasemani e monofiletismo de Tridentinae*

O posicionamento do grupo *T. hasemani* recuperado nas topologias apresentadas corrobora a hipótese de de Pinna (1989): essas espécies miniaturizadas são mais relacionadas a Tridentinae do que a Trichomycterinae e representam uma linhagem distinta da qual estão formalmente alocados. Tridentinae, até o momento, engloba 4 gêneros: *Miuroglanis* Eigenmann & Eigenmann, 1889; *Tridens* Eigenmann & Eigenmann, 1889; *Tridentopsis* Myers, 1925 e *Tridensimilis* Schultz, 1944. No presente trabalho, o grupo *T. hasemani* é considerado o quinto gênero de Tridentinae.

Eigenmann (1918), ao desenvolver a descrição original de Tridentinae, cita como características diagnósticas para o grupo a presença de uma longa nadadeira anal, com 15 a 25 raios, origem da nadadeira anal alinhada com a origem da nadadeira dorsal, olhos grandes e lateralmente dispostos e nadadeira caudal arredondada. À época de Eigenmann, somente os gêneros *Miuroglanis* e *Tridens* eram conhecidos. Posteriormente, ao testar o monofiletismo de Tridentinae, Baskin (1973) considera os seguintes estados de caracteres como sinapomorfias para a subfamília: 1- fontanela cranial expandida; 2- osso maxilar pequeno; 3- olhos ventralmente expostos; 4- placas opercular e interopercular de odontódeos justapostas; 5- osso opercular com um curto processo ventral; 6- origem da nadadeira dorsal na mesma vertical ou posterior à origem da anal; 7- hiomandíbula com processo distal e 8- 15 ou mais raios na nadadeira anal. Ao se conceber o grupo *T. hasemani* como um gênero distinto de Tridentinae, os estados de caracteres 1, 5 e 6 permanecem como sinapomorfias para a subfamília, enquanto os restantes são considerados sinapomorfias para o clado composto por *Miuroglanis, Tridens, Tridensimilis* e *Tridentopsis.*

A presença de uma ampla fontanela cranial foi o estado de caráter considerado por de Pinna (1989) como a principal evidência de relacionamento entre o grupo *T. hasemani* e Tridentinae. Essa estrutura é delimitada anteriormente pela borda posterior do mesetmoide, lateralmente pelos frontais e esfenóticos e posteriormente pela margem anterior do parietosupraoccipital (Fig. 10A-C). Uma fontanela similar é encontrada no gênero de Vandelliinae *Paravandellia* Miranda-Ribeiro, 1912, (Fig. 10D) porém as topologias aqui apresentadas corroboram a ideia de de Pinna (1989) de que seriam estruturas homoplásticas. *Paravandellia* é o único gênero de Vandelliinae a apresentar essa fontanela cranial e essa subfamília é um clado bem corroborado e filogeneticamente distante de Tridentinae. O formato e amplitude dessa fontanela cranial varia dentro de Tridentinae, sendo o caso mais extremo de redução em *T. anhanga*, em que os frontais não chegam a se conectar com o mesetmoide. Estruturas mais ossificadas são encontradas em *T. hasemani* e *T. johnsoni*. O estado plesiomórfico em Trichomycteridae é uma fontanela cranial reduzida a dois orifícios separados por uma junção dos frontais, o mais anterior delimitado apenas pelos frontais e o mais posterior delimitados pelos frontais e parietosupraoccipital (Fig. 10E).

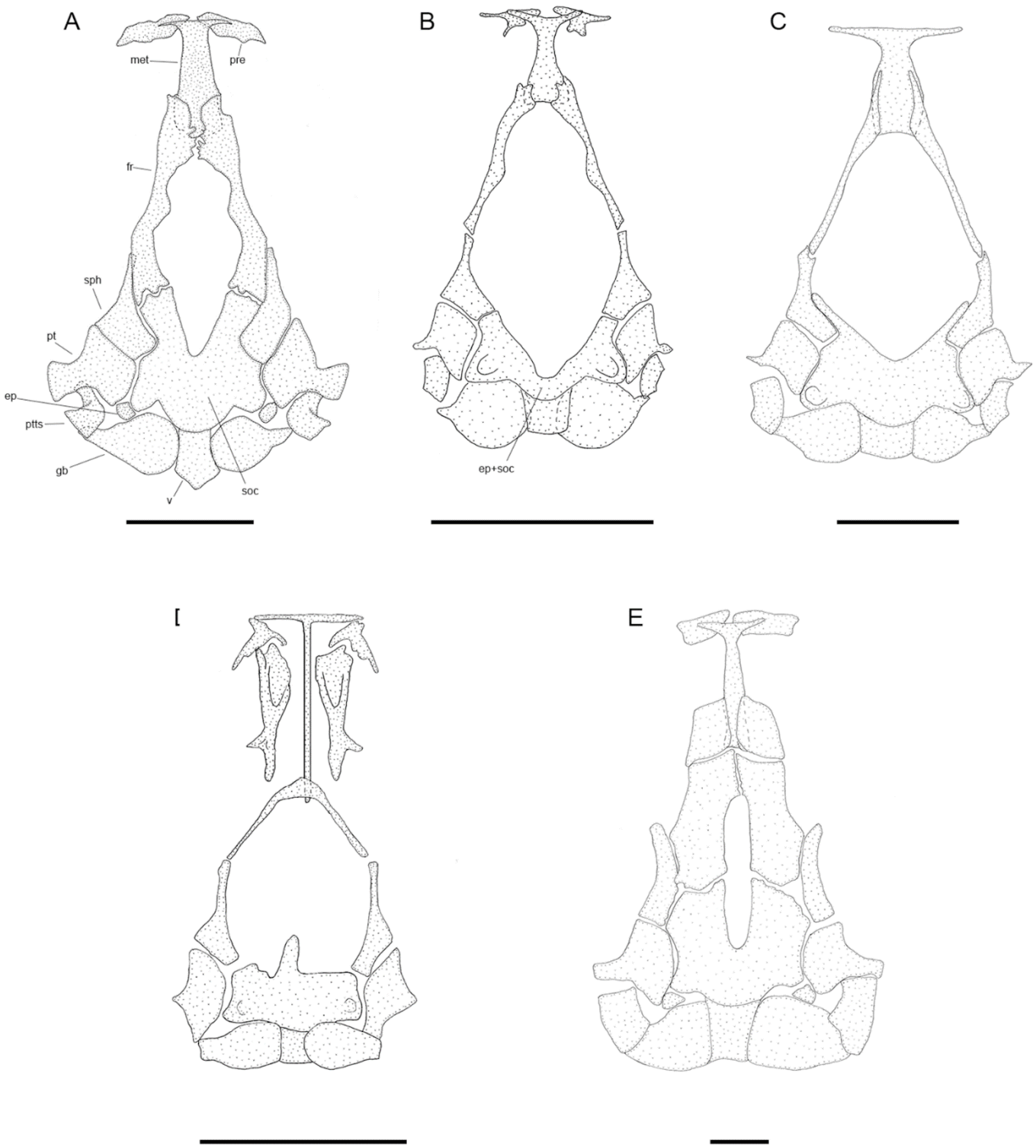



Figura 10. Vista dorsal do neurocrânio. Barra de escala = 1,0 mm. A. *Trichomycterus hasemani*, UFRJ 9653, 17,0 mm CP, × 5.0. B. *T. anhanga*, UFRJ 11251, 10,0 mm CP, × 5.0. - C. *Tridentopsis* sp., UFRJ 1077, 18,0 mm CP, × 4.0. - D. *Paravandellia oxyptera*, UFRJ 1112, 13,0 mm CP, × 5.0. - E. *Trichomycterus reinhardti*, UFRJ 9995, 40,9 mm CP, × 2.0.

O curto processo ventral no osso opercular é encontrado em todos os Tridentinae, inclusive no grupo *T. hasemani* (Fig. 11). Geralmente o osso opercular em Trichomycteridae apresenta um processo ventral que se iguala em comprimento à placa opercular de odontódeos (Baskin, 1973 Figs. 41-44, 46-40), enquanto em Tridentinae o processo se limita a metade do comprimento da placa opercular de odontódeos.

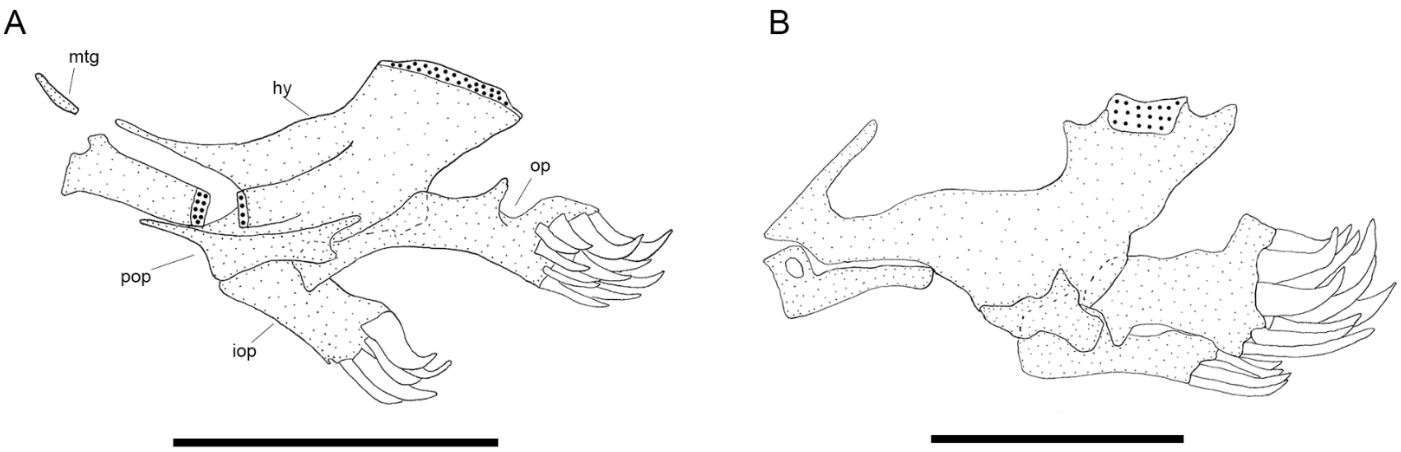



Figura 11. Vista dorsal do suspensório. Barra de escala = 1,0 mm. A. *Trichomycterus wapixana,* UFRJ 9369, 13,8 mm CP, × 5.0. B. *Tridentopsis* sp., UFRJ 1077, 18,0 mm CP, × 4.0.

Eigenmann (1914), ao descrever *T. hasemani*, ressaltou o fato da nadadeira dorsal estar alinhada ou um pouco posteriormente posicionada em relação a origem da nadadeira anal. Fowler (1932) também notou essa condição na publicação que descreve *T. johnsoni*, postulando que essa espécie seria "aparentemente relacionada" a *T. hasemani* devido a esse posicionamento das nadadeiras dorsal e anal. Esse caráter foi posteriormente considerado por Eigenmann (1918) como diagnóstico para Tridentinae e recuperado por Baskin (1973) como uma das sinapomorfias para a subfamília. As espécies *T. anhanga*, *T. wapixana* e a nova espécie incluída nesse trabalho também apresentam a nadadeira dorsal alinhada ou posteriormente deslocada em relação à anal.

Considerando as topologias aqui apresentadas e o grupo *T. hasemani* como membro de Tridentinae, esse estado de caráter permanece considerado como uma sinapomorfia para a subfamília.

Baskin (1973) recuperou dois clados em Trichomycteridae: um com Trichomycterinae como grupo irmão de Glanapteryginae + Sarcoglanidinae e outro com Tridentinae como grupo irmão de Stegophilinae + Vandelliinae (Fig.4). Vinte anos depois, Costa & Bockmann (1994) propuseram o clado TSVSG, composto pelas subfamílias Tridentinae, Stegophilinae, Vandelliinae, Sarcoglanidinae e Glanapteryginae. Nessa configuração, Sarcoglanidinae e Glanapteryginae seriam grupos irmãos e Tridentinae seria grupo irmão de Stegophilinae + Vandelliinae. Os autores não desenvolveram uma filogenia para testar essas hipóteses, mas análises desenvolvidas posteriormente e a apresentada neste trabalho corroboram a existência do clado TSVSG (Datovo & Bockmann, 2010; DoNascimiento, 2015), apesar de diferirem nas propostas de relacionamentos internos do clado. Segundo Costa & Bockmann (1994), esse grupo se caracteriza pela placa interopercular de odontódeos ser reduzida em comprimento e sustentar 15 ou menos odontódeos; redução no número de costelas pleurais (1-8) e metapterigoide reduzido ou ausente. Atentando para o fato do grupo *T. hasemani* estar alocado em Tridentinae e apresentar todas essas características, quando se considera o clado TSVSG deve-se incluir o grupo *T. hasemani*.

DoNascimiento (2015) incluiu *T. hasemani* em sua análise filogenética. A espécie foi recuperada dentro do clado TSVSG, como grupo irmão de Tridentinae + Vandelliinae + Stegophilinae. Uma vez que o autor não disponibilizou sua matriz de caracteres e não explicitou quais estados de caracteres diagnosticam esse táxon, torna-se impossível discutir o posicionamento de *T. hasemani* nessa filogenia.

*Monofiletismo do grupo T. hasemani*

De acordo com as topologias aqui apresentadas, Tridentinae é composto por duas linhagens distintas: uma englobando o grupo *T. hasemani* e outra formada pelos gêneros já conhecidos *Miuroglanis, Tridens, Tridensimilis*. *Tridentopsis,* apesar de não incluído nessa análise, é considerado como integrante de Tridentinae e, mais especificamente, dessa segunda linhagem pois apresenta os estados de caracteres propostos por Baskin (1973) para esse posicionamento.

Os outros cinco estados de caracteres que Baskin (1973) utiliza para sustentar o monofiletismo de Tridentinae, quando se considera o grupo *T. hasemani* como integrante da subfamília, passam a ser lidos como diagnósticos para o clado composto por *Miuroglanis, Tridens, Tridensimilis* e *Tridentopsis*.

O tamanho diminuto do osso maxilar é visto em espécies desses 4 gêneros e também em *T. hasemani, T. johnsoni*, *T. wapixana* e na nova espécie do grupo. Porém, proporcionalmente, a condição em *T. anhanga* é bem distinta: o osso maxilar é aproximadamente do mesmo tamanho que a pré-maxila, enquanto nas outras espécies o maxilar corresponde a menos da metade da largura da pré-maxila (Fig. 12).

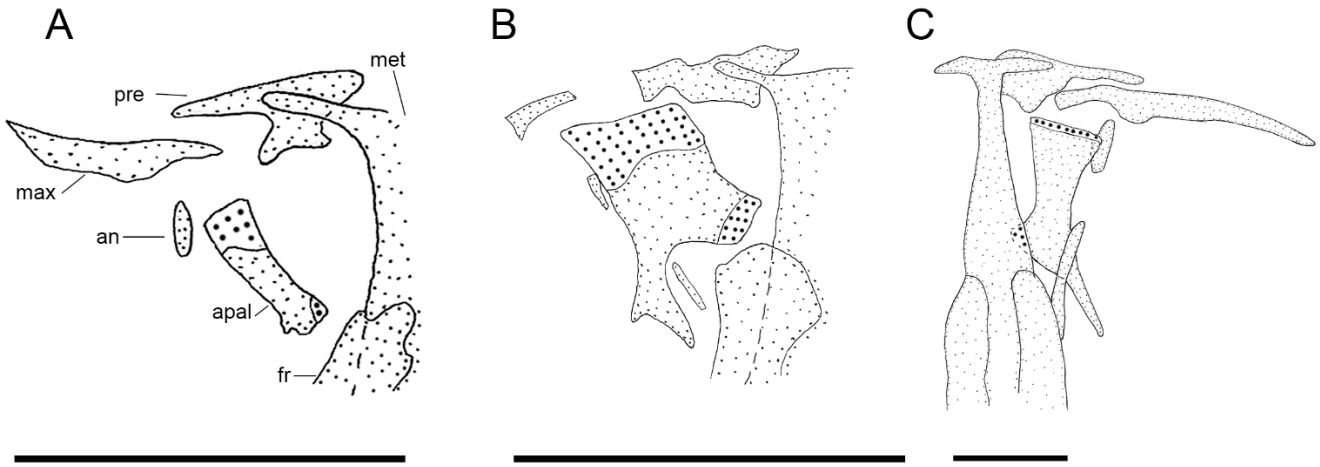



Figura 12. Vista dorsal do autopalatino. A. *Trichomycterus anhanga*, UFRJ 11251, 10,0 mm CP, × 5.0. Barra de escala = 0,5 mm. B. *T. johnsoni*, UFRJ 11530, 13,0 mm CP, × 5.0. Barra de escala = 1,0 mm. C. *Microcambeva* sp., MZUSP 79953, 38,0 mm SL, × 3.2. Barra de escala = 1,0 mm.

Os olhos em *Miuroglanis, Tridens, Tridensimilis* e *Tridentopsis* são lateralmente posicionados e visíveis em vista ventral. O mesmo não ocorre nas espécies do grupo *T. hasemani*, que possuem olhos menores e em posição dorsal na cabeça.

Um estado de caráter único em toda a família proposto por Baskin (1973) é a justaposição das placas opercular e interopercular de odontódeos, condição encontrada somente nos 4 gêneros já conhecidos de Tridentinae (Fig. 11B). Nesses gêneros, o espaço entre as placas de odontódeos corresponde a menos da metade da largura de qualquer uma das duas. O grupo *T. hasemani* apresenta a condição encontrada nos outros Trichomycteridae: a distância entre as placas opercular e interopercular correspondem a um comprimento maior do que a largura da placa interopercular (Fig.11A).

Outro estado de caráter exclusivo proposto por Baskin (1973) é a presença de um processo distal na borda medial da hiomandíbula, curvado e posteriormente direcionado.

O grupo *T. hasemani* também apresenta um processo na hiomandíbula, mas este se assemelha ao presente em Sarcoglanidinae e Glanapteryginae (Costa & Bockmann, 1993): a porção anterior do osso é modificada em um processo longo e não curvado, completamente diferente em forma e posicionamento do processo presente em *Miuroglanis, Tridens, Tridensimilis* e *Tridentopsis* (Fig. 11).

A grande quantidade de raios na nadadeira anal (15 a 22 raios) também diferencia os 4 gêneros de Tridentinae do grupo *T. hasemani*, que possui 6 ou 7 raios na nadadeira anal. O outro único caso similar de um grande número de raios nessa nadadeira ocorre em Trichogeninae, que possui 30 a 34 raios ramificados na nadadeira anal.

Por fim, Dutra et al. (2012) propuseram os seguintes estados de caracteres para o grupo: 1- presença de uma ampla fontanela cranial delimitada pelo frontal e supraoccipital; 2- autopalatino medialmente curvado; 3- primeiro raio da nadadeira peitoral maior que os outros; 4- ausência da porção anterior do canal infraorbital (poros i1 e i3) do sistema laterosensorial e 5- ausência ou presença de um raio branquiostegal no ceratohial posterior. O primeiro estado de caráter já foi discutido e considerado uma sinapomorfia para Tridentinae. A presença de um primeiro raio alongado na nadadeira peitoral é vaga, uma vez que, de acordo com Baskin (1973), *Tridentopsis pearsoni* também possui o primeiro raio da nadadeira peitoral alongado, assim como esta condição também está presente em Trichomycterinae e Sarcoglanidinae. A distribuição de poros do canal infraorbital não foi possível de ser verificada nos demais gêneros de Tridentinae, porém, segundo Arratia & Huaquin (1995), *T. pearsoni* não possui os poros i1 e i3, o que torna esse estado de caráter inválido para diagnosticar o grupo *T. hasemani* enquanto gênero de Tridentinae. A ausência ou presença de um raio branquiostegal no ceratohial posterior é variável dentro das populações de espécies do grupo *T. hasemani*. O único estado de caráter com potencial para diagnosticar as espécies do grupo *T. hasemani* é a

presença de um autopalatino medialmente curvado, que, nessa dissertação, propõe-se que as suas cartilagens anterior e posterior formem entre si um ângulo de 25-30º, o que é exclusivo em Trichomycteridae (Fig. 12).

Dessa forma, o presente estudo corrobora a hipótese de de Pinna (1989) de que o grupo *T. hasemani* é uma linhagem completamente distinta de Trichomycterinae e não só relacionada a Tridentinae como incluída nessa subfamília. Levando em conta as topologias aqui apresentadas e os estados de caracteres discutidos, conclui-se que o grupo *T. hasemani* deve ser alocado em um gênero distinto de *Trichomycterus*.

*Miniaturização*

*"The Tridentinae differ in having the anal fin much longer than the others. Nothing is known of their habits and they are so small (the largest known specimen is but 27 mm. long) that it is a wonder that any of them have arrived in the bottles of the naturalist."* Eigenmann (1914: 261).

A miniaturização é um fenômeno bem difundido entre os animais, ocorrendo tanto em invertebrados (e.g. anelídeos, moluscos, insetos e aracnídeos) quanto em vertebrados (e.g. peixes, anfíbios, répteis e mamíferos) (Hanken & Wake, 1993). O estudo de espécies miniaturizadas de peixes de água doce teve seu marco inicial com a publicação de Weitzman & Vari (1988), que definem como miniaturas os peixes que não excedem 26 mm de comprimento padrão na natureza.

A surpresa de Eigenmann (1918) ao constatar que peixes com o tamanho tão diminuto quanto dos Tridentinae tenham sido coletados, transportados e analisados não é sem fundamento. Apesar de nos últimos anos o ritmo de descrição e estudo de espécies miniaturizadas tenha aumentado consideravelmente (e.g. Buckup, 1993, Costa, 1998; Costa, 2011; Costa & Lazzarotto, 2014; Toledo-Piza et al., 2014; Costa et al., 2015;

Henschel, 2016; Mattox et al., 2016; Castro & Wosiacki, 2017), a falta de informação detalhada sobre esses peixes geralmente se dá pelo próprio tamanho pequeno. Os esforços de coleta normalmente não são voltados para o micro-habitat ocupado pelas miniaturas, além dos próprios equipamentos não possuírem, em grande parte, o refinamento necessário para coletar esses pequenos indivíduos. As miniaturas também costumam não serem percebidas em coleções de museus e universidades. No caso do gênero *Scoloplax* Bailey & Baskin, 1976, 110 anos se passaram entre a coleta dos espécimes na Expedição Thayer em 1866 até a descrição formal do gênero e da sua primeira espécie. O mesmo ocorreu com o gênero *Fluviphylax* Whitley, 1965: ele aloca espécies que também foram coletados na Expedição Thayer, mas que só foram descritas em 1996 (Costa, 1996).

Além da medida estabelecida por Weitzman & Vari (1988) para se considerar uma espécie de peixe como miniatura, os autores citam uma série de efeitos pedomórficos oriundos do processo: redução do sistema laterosensorial na cabeça e corpo, redução no número de raios das nadadeiras e escamas e redução da ossificação dos ossos da cabeça. Essas consequências da miniaturização são facilmente encontradas nas espécies do grupo *T. hasemani* e nas espécies miniaturizadas de Tridentinae (todas as espécies do gênero *Tridentopsis, Tridensimilis venezuelae* e *Miuroglanis platycephalus*). A presença da fontanela cranial expandida em *Paravandellia* também é oriunda da miniaturização. Além dos efeitos relacionados a redução e simplificação estrutural, muitas espécies miniaturizadas apresentam novidades morfológicas, como por exemplo a presença de um órgão copulatório derivado das nadadeiras pélvicas em miniaturas de Phallostetidae (Atheriniformes) (Roberts, 1971). Outro exemplo de novidades morfológicas em miniaturas é o caso do gênero miniaturizado de Cypriniformes *Paedocypris* Kottelat, Britz, Tan & Witte, 2006: ao mesmo tempo em que as espécies do gênero possuem

simplificações estruturais, os machos apresentam uma série de modificações relacionadas às cinturas pélvica e peitoral e principalmente à nadadeira pélvica, caracteres únicos entre os membros da ordem (Britz & Conway, 2009). Esses efeitos da miniaturização dificultam o acesso às características morfológicas, o que se torna um obstáculo no desenvolvimento de análises filogenéticas (gerando muitas homoplasias) e dificulta acessar a quantidade de vezes que a miniaturização ocorreu em determinado táxon (Hanken & Wake, 1993). No gênero de Characiformes *Nannostomus* Günther, 1872, o tamanho diminuto de três espécies miniaturizadas é provavelmente derivado, mas as tentativas de elucidar os relacionamentos entre os membros do gênero com base em dados morfológicos não foram bem-sucedidas. No gênero *Corydoras* Lacepède, 1803, um gênero muito rico em número de espécies, o relacionamento entre quatro espécies miniaturizadas permanece sem resolução, mas provavelmente trata-se de um único evento de miniaturização (Weitzman & Vari, 1988).

Oitenta anos se passaram entre a descrição de *T. johnsoni* e *T. anhanga*, a espécie mais distinta morfologicamente do grupo *T. hasemani*. Apesar desse grande intervalo de tempo, muitas populações de espécies do grupo estão disponíveis em diversas coleções do Brasil e hipóteses sobre o relacionamento e posicionamento dessas espécies foram desenvolvidas. A dificuldade em acessar e polarizar caracteres morfológicos pode ser o principal motivo pelo qual, até o momento, nenhuma análise filogenética foi desenvolvida para testar o monofiletismo e posicionamento do grupo *T. hasemani*. O uso de dados moleculares para desenvolver as filogenias aqui apresentadas se isenta dos efeitos da miniaturização, permitindo uma compreensão da distribuição dos caracteres morfológicos *a posteriori*.

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**Apêndice I**

VERTEBRATE ZOOLOGY

66 (2): 117–123
20.10.2016

SENCKENBERG



# A new catfish species of the *Trichomycterus hasemani* group (Siluriformes: Trichomycteridae), from the Branco river basin, northern Brazil

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Accepted 16.vii.2016.
Published online at www.senckenberg.de/vertebrate-zoology on 28.ix.2016.

## Abstract

*Trichomycterus wapixana* is described from the Branco river basin, Roraima State, northern Brazil. It belongs to the *T. hasemani* group, composed of *T. hasemani*, *T. johnsoni* and *T. anhanga* and defined by the presence of a single wide cranial fontanel delimited by the frontal and supraoccipital, absence of the pores i1 and i3, absence of branchiostegal rays on the posterior ceratohyal and the by the presence of a large and distally expanded process on the palatine. It differs from the other species of that assemblage by having a unique combination of character states, including number of vertebrae, relative position of anal fin, relative position of pelvic and dorsal fin, presence of pelvic fin and pelvic girdle, number of dorsal and ventral procurrent rays in the caudal fin, anal-fin rays, pectoral-fin rays, branchiostegal rays, pleural ribs, morphology of palatine, presence of parasphenoid and relative position of urogenital pore.

## Key words

*Trichomycterus hasemani* group, taxonomy, Trichomycteridae, miniaturization.

## Introduction

Trichomycteridae is a family of catfishes comprising 278 valid species (ESCHMEYER & FONG, 2014) distributed from Costa Rica to Patagonia, in both cis- and trans- Andean drainages (DE PINNA, 1998). Trichomycterinae is the only one of the eight recognized subfamilies which monophyly has not been supported in phylogenetic studies (BASKIN, 1973; DE PINNA 1989; COSTA & BOCKMANN, 1993). *Trichomycterus* VALENCIENNES is the most species-rich genus of the family, comprising over 140 species (FERNANDEZ & VARI, 2009; KATZ *et al.*, 2013). Its extensive geographical range, high number of described species and lack of synapomorphies make *Trichomycterus* a huge taxonomic problem within the Trichomycteridae (BARBOSA & COSTA, 2003). This condition is illustrated by the description of *Ituglanis* COSTA & BOCKMANN 1993, in which this new genus was described based on nine species that were previously placed in *Trichomycterus* (COSTA & BOCKMANN, 1993).

Despite ARRATIA (1990) and DATOVO & BOCKMANN (2010) tried to establish derived character states for the Trichomycterinae, these works did not include *Trichomycterus hasemani* (EIGENMANN, 1914) and *T. johnsoni* (FOWLER, 1932). According to de PINNA (1989), *T. hasemani* and *T. johnsoni* are each other closest relatives and *T. hasemani* is related to the Tridentinae due to their expanded cranial fontanel, considering all these taxa derived from a single miniaturization event. Recently, DUTRA *et al.* (2012) described *T. anhanga* DUTRA, WOSIACKI & DE PINNA 2012 as being closely related to *T. hasemani* and *T. johnsoni,* naming the "*T. hasemani* group" for this species assemblage. The "*T. hasemani* group" is monophyletic and possibly related to non-Trichomycterinae

taxa (DE PINNA, 1989, DUTRA *et al.,* 2012). The geographical distribution of this group contrasts with the distribution of other species placed in *Trichomycterus*, by occurring in lowlands of the Amazon rainforest and Pantanal, instead of being endemic to mountain river drainages of southeastern and southern Brazil (BARBOSA & COSTA, 2010), Andes (ARRATIA, 1998) and those draining the Guyana Shield (EIGENMANN, 1909; EIGENMANN, 1912; LASSO & PROVENZANO, 2002). The new species herein described was collected in the Branco river basin.

## Material and Methods

Measurements follow DUTRA *et al.* (2012) with the addition of pre-pelvic length (from the middle of the pelvic-fin base to the snout tip). Measurements are presented as percentages of standard length (SL), except for subunits of the head, which are presented as percentages of head length (HL). Counts, following BARBOSA & COSTA (2003), were made only in cleared and stained specimens (c&s) prepared following TAYLOR & VAN DYKE (1985). Scale bars = 1 mm. Nomenclature for the latero-sensory system is according to ARRATIA & HUAQUIN (1995). Specimens were euthanized submerging them in a buffered solution of Ethyl 3-aminobenzoate methanesulfonate (MS-222) at a concentration of 250mg/l, for a period of 10 min, following the guidelines of the Journal of the American Veterinary Medical Association (AVMA Guidelines), and European Commission DGXI consensus for fish euthanasia. Material is deposited in the ichthyological collection of the Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro (UFRJ), Field Museum of Natural History (FMNH) and in the Academy of Natural Sciences of Philadelphia (ANSP). The method for species delimitation follows the Population Aggregation Analysis (DAVIS & NIXON, 1992), in which one or more populations are recognized as a species by a unique combination of character states.

## *Trichomycterus wapixana* new species

Fig. 1a – b; Fig. 2

**Holotype**. UFRJ 10251,14.0 mm SL; Brazil: Estado de Roraima: Município de Bonfim: flooded areas in the Tacutu river drainage, tributary of the Branco river drainage, Amazonas river basin, 03° 24' 07"N 59°56'23"W, altitude about 110 m; collected by E. Henschel, F. P. Ottoni, P. Bragança; 10 September 2012.

**Paratypes**. UFRJ 8946, 7 ex., 12.5–14.5 mm SL; UFRJ 9006, 3 ex., 13.5–13.8 mm SL; UFRJ 9369, 3 ex. (c&s), 12.9–13.8 mm SL; all collected with holotype. UFRJ 8945, 3 ex., 13.9–15.5 mm SL; UFRJ 9004, 3 ex., 14.3–15.7 mm SL; UFRJ 9457, 1 ex. (c&s), 14.1 mm SL; Brazil: Estado de Roraima: Município de Bonfim: grove with buriti palms 65km after the bridge over Branco river, Branco river basin, 03° 09' 30" N 60° 14' 48", altitude about 120 m; same collectors as the holotype; 10 september 2012. UFRJ 8951, 3 ex., 13.3–13,5 mm SL; UFRJ 9455, 1 ex. (c&s), 13.3 mm SL; Brazil: Estado de Roraima: Município de Bonfim: igarapé 29km after the bridge over rio Branco, rio Branco basin, 02° 56' 14.0" N 60° 27'39.6" W, altitude 94 m; same collectors as the holotype; 10 september 2012. UFRJ 8952, 3 ex., 12.1–13.9 mm SL; UFRJ 9460, 1 ex. (c&s), 12.8 mm SL; Brazil: Estado de Roraima: Município de Cantá: Quitauaú river, Branco river basin, 02° 34' 02.0"N 60° 38' 08.4" W, altitude 82 m; same collectors as the holotype; 13 september 2012. UFRJ 8965, 1 ex., 13.5 mm SL; UFRJ 9461, 1 ex. (c&s), 13.3 mm SL; Brazil: Estado de Roraima: Município de Caracaraí: igarapé in rio Anauá drainage, rio Branco basin, 01° 27' 56.0" N 60° 47' 04.4" W, altitude 75 m; same collectors as the holotype; 18 september 2012. UFRJ 8950, 7 ex., 13.2–15.1 mm SL; UFRJ 9005, 4 ex., 13.3–13.9 mm SL; UFRJ 9370, 2 ex. (c&s), 13.4–4.9 mm SL; Brazil: Estado de Roraima: Município de Caracaraí: riacho in Anauá river drainage, Branco river basin, 01° 12' 06.0" N 60° 18' 38.6" W, altitude 97 m; same collectors as the holotype; 16 september 2012.

**Additional material (non-types)**. UFRJ 8957, 8 ex., 13.2–14.6 mm SL; UFRJ 9007, 5 ex., 12.9–13.8 mm SL; UFRJ 9462, 3 ex. (c&s), 14.3–15.0 mm SL; Brazil: Estado de Roraima: Município de Rorainópolis: igarapé in Jauaperi river drainage, Negro river basin, 00° 43' 54.7" N 60° 27' 27.4" W, altitude 82 m; collected by E. Henschel, F. P. Ottoni, P. Bragança; 14 september 2012.

**Comparative material.** *Trichomycterus hasemani*: FMNH 56424, holotype, 10.0 mm SL; Brazil: Estado do Pará: Santarém (only photographs and X-ray). UFRJ 9465, 3 ex., 15.7–17.8 mm SL; UFRJ 9653, 3 ex. (c&s), 16.7–17.3 mm SL; Brazil: Estado do Pará: Santarém: Lago do Maicá. *Trichomycterus johnsoni*: ANSP 53873, holotype, 16.0 mm SL; Brazil: Estado do Mato Grosso: Descalvados (only photographs). UFRJ 3823, 22 ex., 12.6–14.6 mm SL; UFRJ 9061, 1 ex. (c&s), 14.0 mm SL; UFRJ 9368, 4 ex. (c&s), 12.3–12.9 mm SL; Brazil: Estado do Mato Grosso: Cáceres: Paraguai river basin.

**Diagnosis**. *T. wapixana* is distinguished from all other species of the *T. hasemani* group by the presence of 34 to 36 vertebrae (vs. 32 in *T. hasemani* and *T. johnsoni,* 29 to 32 in *T. anhanga*); the origin of the anal fin in a vertical through the base of the 20th, 21st or 22nd vertebra (vs. 18th in *T. hasemani*, 17th in *T. johnsoni* and 16th in *T. anhanga*). It is distinguished from *T. hasemani* and *T. johnsoni* by having the origin of the pelvic fin in a vertical between the base of 15th and 17th vertebrae (vs. 14th in *T. hasemani* and 13th in *T. johnsoni*)and by the presence of a dark spot on the middle of the lower lip (vs. absence). *Trichomycterus wapixana* differs from *T. anhanga* by the presence of pelvic fins and girdle (vs. absence); the presence of 10 to 11 dorsal procurrent rays in the caudal fin (vs. 6 to 8); the presence of 9 to 12 ventral procurrent rays in the caudal fin (vs. 6 to 7); the presence of seven (ii +5 or iii + 4) anal fin rays (vs. ii + 4); the presence of five (i + 4 or ii + 3) pectoral fin rays (vs. i + 2); the origin of the dorsal fin at vertical through the base of the 20th, 21st or 22nd vertebra (vs. 16th or 17th); the presence of six branchiostegal rays (vs. four or five); the presence of two pairs of pleural ribs on first two vertebrae posterior to Weberian Complex (vs. single pair); the presence of a series of dark brown spots in the lateral midline of the body (vs. absence); the broad palatine (Fig. 4) (vs. narrow, comma-shaped palatine) (DUTRA *et al.,* 2012; fig. 2a) and by the presence of the parasphenoid (vs. absence). It differs further from *T. johnsoni* by the origin of the urogenital pore in

**Table 1.** Morphometric data of *Trichomycterus wapixana*.

| | H | Range | Mean | Standard deviation |
|---|---|---|---|---|
| Standard length (mm) | 14.0 | 12.1–15.5 | 13.6 | — |
| Percentage of standard length | | | | |
| Total length | 120.0 | 117.9–124.8 | 121.9 | 1.6 |
| Body depth | 17.1 | 14.8–18.5 | 16.7 | 1.0 |
| Peduncle length | 9.3 | 8.7–14.31 | 10.4 | 1.0 |
| Predorsal length | 69.3 | 65.2–74.4 | 71.6 | 1.7 |
| Preanal length | 69.3 | 65.9–76.0 | 71.4 | 2.0 |
| Prepelvic length | 57.1 | 54.5–62.6 | 59.1 | 1.9 |
| Dorsal fin base length | 7.9 | 6.2–12.6 | 8.9 | 1.3 |
| Anal fin base length | 10.0 | 6.2–10.1 | 8.2 | 1.1 |
| Head length | 13.6 | 13.5–18.1 | 15.5 | 1.3 |
| | | | | |
| **Percentage of head length** | | | | |
| Head width | 126.3 | 88.5–127.8 | 108.2 | 9.2 |
| Head depth | 78.9 | 53.8–70.0 | 62.8 | 4.6 |
| Interorbital | 31.6 | 25.0–36.0 | 29.3 | 3.0 |
| Snout length | 52.6 | 33.3–52.6 | 41.1 | 5.0 |
| Nasal barbel length | 63.2 | 35.0–68.4 | 52.0 | 8.2 |
| Maxillary barbel length | 100.0 | 63.2–119.0 | 85.5 | 12.0 |
| Rictal barbel length | 78.9 | 47.4–90.5 | 69.4 | 10.5 |
| Mouth width | 42.1 | 15.8–44.4 | 36.0 | 5.2 |
| Eye diameter | 15.8 | 9.5–16.7 | 13.2 | 2.0 |


**Fig. 1.** *Trichomycterus wapixana*: UFRJ 10251, 14.0 mm SL (holotype): Tacutu river drainage. (A) lateral view; and (B) dorsal view. Photos by: Axel Katz.

a vertical between the base of the 17th and 19th vertebrae (vs. 15th).

**Description**. Morphometric data for holotype and paratypes given in Table I. Body elongate, subcylindrical on anterior portion, gradually compressed until caudal peduncle. Dorsal profile slightly convex between snout and pectoral-fin origin, straight from that point to caudal peduncle. Ventral profile straight between tip of the snout and insertion of the pectoral fin, gently convex from that point to pelvic-fin origin and straight to end of caudal peduncle. Greatest body depth in vertical immediately in front of pelvic-fin origin. Dorsal and anal fins approximately triangular. Dorsal-fin origin in vertical through base of 20th, 21st or 22nd vertebra. Anal-fin origin in vertical through base of 20th, 21st or 22nd vertebra. Pelvic-fin origin in vertical through base of 15th, 16th or 17th vertebra. Pectoral fin about triangular. First pectoral-fin ray terminating in long filament, about 30–40% pectoral-fin length. Pelvic fin not covering urogenital pore, bases separated by interspace; insertion in vertical through base of 15th, 16th or 17th vertebra. Caudal fin truncate. Dorsal-fin

**Fig. 2**. Live specimen of *Trichomycterus wapixana*: UFRJ 8957; about 13.2 mm SL. Photo by: Pedro Bragança.

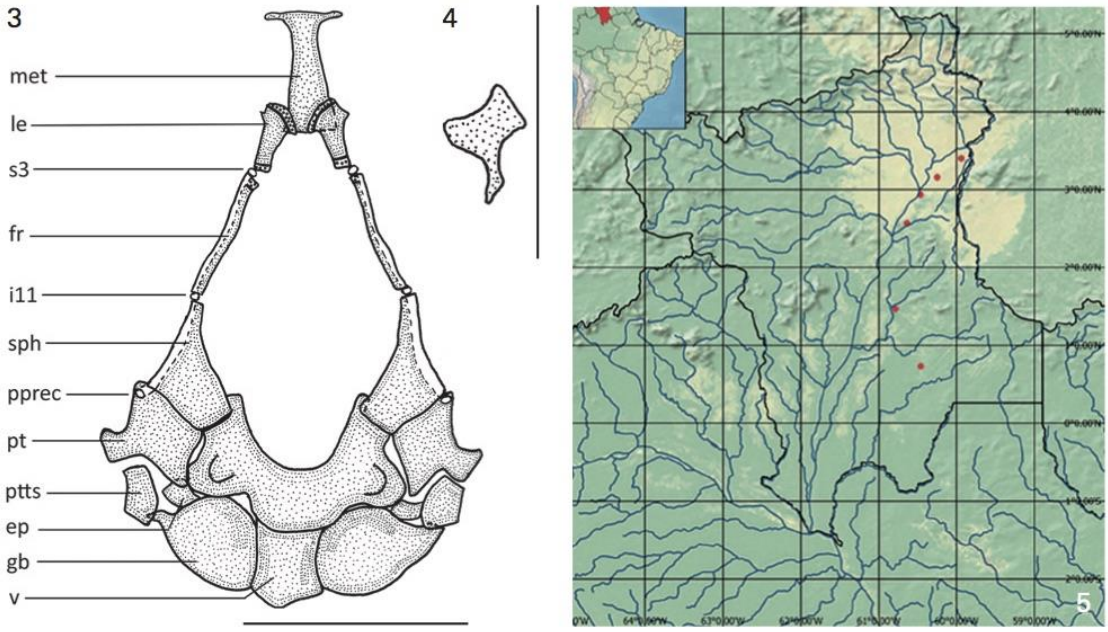


**Fig. 3.** Dorsal view of neurocranium of *Trichomycterus wapixana*: UFRJ 9461, 13.3 mm SL (paratype). ep = epiotic; fr = frontal; gb = gasbladder capsule; i11 = infraorbital 11 pore; le = lateral ethmoid; met = mesethmoid; pprec = preopercular pore; pt = pterotic; ptts = posttemporosupracleithrum; s3 = supraorbital 3 pore; sph = sphenotic; v = first vertebra. Scale bar = 1.0 mm.

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**Fig. 4.** Palatine of *Trichomycterus wapixana*: UFRJ 9461 (paratype). Scale bar = 1.0 mm.

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**Fig. 5.** Distribution of *Trichomycterus wapixana*.

rays 7–8 (iii + 4, ii + 5 or iiii + 4, iii + 5) ; anal-fin rays 7 (iii + 4, ii +5); pectoral-fin rays 5 (ii + 3, i + 4); pelvic-fin rays 4 (ii + 2); caudal-fin principal rays 12 (ii + 8 + ii, i + 9 + ii), dorsal procurrent rays 10 to 11, ventral procurrent rays 9 to 12. Total vertebrae 34 to 36; pleural ribs on first two vertebrae posterior to Weberian Complex.

Head trapezoidal in dorsal view. Mouth subterminal. Teeth conical. Tip of nasal barbel reaching posterior tip of interopercular patch of odontodes. Tip of maxillary barbel reaching middle of interopercular patch of odontodes. Tip of rictal barbel reaching posterior tip of interopercular patch of odontodes. Six branchiostegal rays. Odontodes conical. Interopercular odontodes 6 to 11, opercular odontodes 9 to 14. Lateral line with two pores, LL1 and LL2. Cephalic portion of latero-sensory canal system restricted to s3, i11 and a praeopercular pore, S4.

Colouration in preserved specimens (Fig. 1a and b). Ground colour cream. Head with dark brown spot extending from anterior surface of eye to anterior margin of upper lip. Dorsal region of neurocranium with light brown spot. Dark brown spot on basis of opercular patch of odontodes and on basis of interopercular patch of odontodes. Ventral surface of head with small dark spots on upper lip and dark spot on lower lip. Nasal, maxillary and rictal barbels with small dark spots concentrated at basis.

Dorsal and lateral surfaces of body with chromatophores distributed between head and caudal peduncle. Ventral surface of body with chromatophores concentrated on head and between pelvic and anal fins. Lateral surface with series of dark brown spots.

Dorsal and anal fin hyaline with dark brown blotch on basis of rays. Caudal fin with small dark brown cromatophores. Caudal fin with light brown bar on basis of rays and with small dark brown spot on middle of basis of rays. Pectoral fin hyaline with small dark spot on basis of filament. Pelvic fin hyaline with dark small spot on basis of fin.

**Etymology**. The wapixana is a native tribe from the Serra da Lua region in western Roraima state, northern Brazil. These natives have occupied this region for, at least, three centuries. The villages of Cantá and Bonfim, where *Trichomicterus wapixana* was mainly collected, are situated in this area. The Wapixana tribe was oppressed by other native tribes and by colonisers, fact that contributed for a huge cultural loss.

**Distribution**. Known from the Branco and Negro river drainages, Amazonas river basin (Fig. 5).

## Discussion

The "*Trichomycterus hasemani* group" has been considered as an *incertae sedis* group among trichomycterids. The first approach concerning the relationships between *T. hasemani* and *T. johnsoni* was made by de Pinna (1989), where these species were proposed to constitute a clade more related to the Tridentinae than to the Trichomycterinae. This hypothesis was based on the presence of an expanded cranial fontanel delimited by the frontal and supraoccipital in the two taxa. Later, de Pinna (1998), in a cladogram with information combined from several authors, listed the following synapomorphies to support the clade comprising the Vandelliinae, Stegophilinae and Tridentinae: 1 – absence of lacrimal; 2 – lateral opening of Weberian capsule at the end of a neck like constriction; 3 – jaw teeth S-shaped; 4 – mesethmoid cornu with ventral process. The *T. hasemani* group shares with this clade only the second condition, which makes the hypothesis of sister group relationships between the *T. hasemani* group and the Tridentinae doubtful.

Dutra *et al.* (2012) established the following character states to diagnose the *T. hasemani* group: 1 – a wide fontanel that occupies most of the skull roof and is delimited by the frontal and supraoccipital (Fig. 3); 2 – absence of the anterior portion of the infraorbital canal (pores i1 and i3); 3 – first pectoral-fin ray much longer than other rays; 4 – absence of branchiostegal rays on the posterior ceratohyal; and 5 – a large posterior process of the palatine, partly forked and expanded distally (Fig. 4). The species herein described shares all these five character states with *T. hasemani* and *T. johnsoni*. However, the palatine condition (Fig. 4) is quite different from the other species of the group in *T. anhanga*, since the partly forked posterior process of the palatine is entirely absent in this species (Dutra *et al.*, 2012; fig. 2a).

Costa & Bockmann (1994) stated that a sister-group relationship between Sarcoglanidinae and Glanapteryginae would be supported by the reduced dorsal portion of the quadrate, the presence of a large anteriorly directed process in the hyomandibula, vomer rudimentary and miniaturization. *Trichomycterus wapixana*, *T. hasemani* and *T. johnsoni* share with these two subfamilies the last three character states. These authors also established a clade comprising Sarcoglanidinae, Glanapteryginae, Tridentinae, Vandelliinae and Stegophilinae, the so-called TSVSG clade, on the basis of an interopercular patch of odontodes reduced in length and with 15 or fewer odontodes, a reduction in number of the pleural ribs (1–8), a short posterior portion of the parasphenoid, its tip not reaching the basioccipital or extending only to its anterior part, and metapterygoid reduced or absent. *Trichomycterus wapixana*, *T. hasemani* and *T. johnsoni* also have all these character states. Since these character states are unique within the Trichomycteridae, they indicate that possibly the *T. hasemani* group is closely related to the TSVSG clade. However, the position of the group within the family cannot be exactly established, which depends on an inclusive phylogenetic analysis, which is beyond the scope of this study. These species thus remain allocated in *Trichomycterus* until a proper phylogenetic analysis is developed.

Other miniature Amazonian species-groups also have a problematic taxonomy. In the case of the *Scoloplax* Bailey & Baskin, 1976, 110 years have passed since the specimens collection in Thayer Expedition in 1866 and the formal description of the genus. This genus was originally described as a member of the Loricariidae, being placed in a new monotypic family (Scoloplacidae) by Isbrücker (1980). According to Schaefer *et al.* (1989) the small size of these catfishes was the main problem to describe them, along with other factors such as lack of collecting effort, absence of any distinctive anatomy and their cryptic habitat. These authors also stated that the reductive characters derived from the miniaturization process represent synapomorphies at some phylogenetic level in *Scoloplax*. The same occurred with species of the genus *Fluviphylax* Whitley, 1965: specimens were collected in Thayer Expedition but remained undescribed until 1955 (Myers, 1955). Previously, Garman (1895) improperly identified these fishes as undetermined species of *Rivulus* Poey, 1860 (Costa & Le Bail, 1999). These authors also stated that the miniaturization in *Fluviphylax* is parsimoniously interpreted as a single event. Weitzman & Vari (1988) published a study focusing on the miniaturization in the several groups of the Neotropical region and the consequences of this process to the phylogeny of those taxa. In the characiform genus *Nannostomus* Günther, 1872, the small size of three miniaturized species is probably derived, but attempts to eluci-

date the relationships within the genus were not feasible, and in the catfish genus *Corydoras* LACEPÈDE, 1803, a very specious genus, the relationships within four miniaturized species are unresolved, but possibly involving a single miniaturization event (WEITZMAN & VARI, 1988). The species herein described belongs to a miniaturized group, but the relationships within the *T. hasemani* group cannot be established since its phylogenetic relationships are still unknown.

## Acknowledgements

Special thanks to W. Costa for reading and correcting the manuscript and for supervising me since 2011. P. Bragança and F. Ottoni assisted me daily and were always very helpful. A. Katz helped me with the photographs and gave me assistance when necessary. Thanks are also due to M. Barbosa, J. Mattos, P. Amorim, F. Rangel-Pereira, R. Rizzieri, O. Simões and G. Silva for general assistance.

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## Apêndice II

# *Trichomycterus bragancai* (Siluriformes: Trichomycteridae): a new miniaturized catfish of the *T. hasemani* group from the Acará river drainage, Northern Brazilian Amazon

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**Abstract.**

*Trichomycterus bragancai* is described from the rio Acará basin, Pará, northern Brazil. It is the fifth species described to the assemblage formed by *T. hasemani, T. johnsoni, T. anhanga* and *T. wapixana,* the *T. hasemani* group, which is mainly characterized by the presence of a wide skull roof. The new species is diagnosed by an exclusive combination of character states including number of vertebrae and ribs; relative position of urogenital pore, anal, dorsal and pelvic-fin; shape of supraoccipital, frontal and palatine; number of pectoral, pelvic, anal and dorsal-fin rays; number of interopercular and opercular odontodes; number of teeth in dentary and pre-maxilla; number of dorsal and ventral procurrent rays and presence of pores in the cephalic system.

**Keywords:** Trichomycterinae, catfish, taxonomy, miniaturization

**Introduction.**

The catfish family Trichomycteridae is a well corroborated monophyletic group of freshwater fishes, currently including about 290 valid species allocated in eight subfamilies: Copionodontinae, Trichogeninae, Trichomycterinae, Glanapteryginae, Sarcoglanidinae, Tridentinae, Stegophilinae and Vandelliinae (Baskin 1973, de Pinna 1998, de Pinna & Wosiacki 2003, Eschmeyer & Fong 2017). They are distributed in river basins since southern Central America to South America, between Costa Rica and Patagonia, in both Andean sides (Baskin 1973, de Pinna 1998, de Pinna & Wosiacki 2003, Barbosa & Costa 2010). Among its eight recognized subfamilies, only Trichomycterinae has not been considered to be monophyletic (Baskin 1973, Costa & Bockmann 1994, Dutra et al. 2012).

In addition to its numerical diversity, Trichomycteridae is also remarkable for its ability to explore distinct habitats (de Pinna 2008, Barbosa & Costa 2010). Most members of the

family live in sandy or gravel bottoms between rocks, in fast flowing, cold and highly oxygenated headwaters (Barbosa & Costa 2010, Barbosa 2013). Species of *Trichomycterus* Valenciennes, 1832 are able to climb waterfalls against strong currents, using their specialized opercular and interopercular patch of odontodes (de Pinna 1998, Barbosa & Costa 2010), whereas species of the Trichogeninae are nektonic and explore the water column (de Pinna et al. 2010), and most members of all other subfamilies are usually found at the river bottom, in interstitial spaces of loose sand and leaf litter (Costa 1994, Costa & Bockmann 1994, Nico & de Pinna 1996, Zuanon et al. 2006, DoNascimiento 2015). Furthermore, some trichomycterids of the Trichomycterinae genera *Ituglanis* Costa & Bockmann, 1993 and *Trichomycterus* inhabit caves.

The trophic diversity is also noteworthy in the family. Most of its members prey on small aquatic invertebrates (such as numerous insect larvae usually present in the environment) (VER DE PINNA 1998), whereas algivory has been reported for the Copionodontinae (Zanata & Primitivo 2013). Members of the Stegophilinae and Vandelliinae, popularly known as "candirus", are lepidophagous and hematophagous, respectively (Machado & Sazima 1983; Winemiller & Yan 1989; Zuanon & Sazima 2004).

The *Trichomycerus hasemani* group is a poorly known assemblage of four miniaturized species. One species, *T. johnsoni* (Fowler 1939, is endemic to the Pantanal wetlands. The remaining three species, *T. hasemani* (Eigenmann 1918), *T. wapixana* Henschel 2016 and *T. anhanga* Dutra, Wosiacki & de Pinna 2012, are found in the Amazon rainforest (Dutra et al. 2012; Henschel, 2016), which comprises the most extensive river basin of the world. This biome occupyies a total area of about 6 million km², extending from its headwaters in the Peruvian Andes to its mouth in the Atlantic Ocean (Roberts 1972). This basin is also notable for the high diversity of fishes, also standing out for the high frequency of miniaturized fishes (Weitzman & Vari 1988). The high frequency of miniaturized fishes

in this biome may be related to achieving food resources not available to the larger species. Moreover, the reduced size would be very important to prevent the attack of predatory fishes (Roberts 1972).

All species of the *T. hasemani* group are considered miniatures according to the criterion defined by Weitzman & Vari (1988): miniaturized species are not known to exceed 26mm SL in nature. They are diagnosed by the presence of a wide cranial fontanel delimited by frontal and supraoccipital, a "medially bent" palatine, the first pectoral-fin ray longer than the others, the absence of the anterior portion of the infraorbital canal (pores i1 and i3) and the absence or presence of one branchiostegal ray in the posterior ceratohyal (Dutra et al. 2012). A new species belonging to the *T. hasemani* group collected during a recent expedition to the eastern Amazon in Brazil, in a tributary of the Acará river, Amazonas river basin, is herein described.

**Material and Methods.**

Measurements follow Dutra et al. (2012) with the addition of pre-pelvic length (from the middle of the pelvic-fin base to the snout tip). Measurements are presented as percentages of standard length (SL), except for subunits of the head, which are presented as percentages of head length (HL). Clearing and staining procedures were made according to Taylor & van Dyke (1985). Counts follow Barbosa & Costa (2003). Nomenclature for the latero-sensory system follows Arratia & Huaquin (1995). Collected specimens were euthanized with a buffered solution of ethyl-3-amino-benzoat-methansulfonat (MS-222) at a concentration of 250 mg/l, for a period of 10 minutes. These specimens were fixed in formalin for two weeks and then transferred to ethyl alcohol 70%. A scanning electron microscope was used to take photographs of the head of one specimen of each species. The photographed specimens were transferred from alcohol 70% to alcohol 100% for a week and coated with a thin layer of gold. Analyzed material is deposited in the

ichthyological collection of the Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro (UFRJ). Comparative material is deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP), Fundação Universidade Federal de Rondônia (UNIR), Field Museum of Natural History (FMNH) and in the Academy of Natural Sciences of Philadelphia (ANSP). The Population Aggregation Analysis - PAA (Davis & Nixon 1992) was used as the method of species delimitation, in which a species is based on a non-overlapping combination of character states.

**Results**

*Trichomycterus bragancai* Henschel & Barbosa, sp. nov.

(Fig. 1 A-C; Table 1)

**Holotype.** UFRJ 11065, 13.9 mm SL; Brazil: Estado do Pará: Município de Tomé-Açu: stream at the road PA-256, 41 km of the city centre; tributary of the Rio Acará drainage, Baía do Guajará, lower Rio Amazon basin 02° 30’ 23”S 48°27’34”W, altitude about 35 m; collected by E. Henschel & P. Bragança; 6 March 2013.

**Paratypes.** UFRJ 9708, 4 ex., 11.8–12.9 mm SL; UFRJ 9709, 20 ex., 10.7–14.6 mm SL; UFRJ 10020, 4 ex. (c&s), 11.6–12.2 mm SL; UFRJ 10127, 4 ex. (c&s), 12.1-12.6 mm SL; UFRJ 10311, 3 ex. (c&s), 11.7-12.2 mm SL; UFRJ 10715, 5 ex. (c&s), 12.0-14.6 mm SL; CICCAA 00318, 7 ex., 11.0–12.6 mm SL; all collected with holotype. UFRJ 9710, 2 ex., 11.7–13.5 mm SL; UFRJ 9711, 3 ex., 12.9–11.2 mm SL; UFRJ 10714, 3 ex. (c&s), 11.4-12.2 mm SL; UFRJ 10918, 2 ex. (c&s), 11.0-11.4 mm SL; Brazil: Estado do Pará; Município de Tomé-Açu: stream at the road PA-256, 15 km of the city centre; tributary of the Rio Acará drainage, Baía do Guajará, lower Rio Amazon basin 02° 29’ 50” S 48° 20’ 57” W, altitude about 50 m; same collectors as the holotype; 6 March 2013.

**Diagnosis.** *Trichomycterus bragancai* differs from all its congeners except *T. hasemani*, *T. johnsoni*, *T. anhanga* and *T. wapixana* by the presence of an expanded cranial fontanel delimited by the frontal and supraoccipital (vs. cranial fontanel restricted to one or more openings along the skull) (Fig. 2). It is distinguished from *T. hasemani*, *T. johnsoni* and *T. wapixana* by the presence of five (iii + 2 or ii + 3) pelvic-fin rays (vs. ii + 2). *Trichomycterus bragancai* also differs from *T. hasemani*, *T. johnsoni* and *T. anhanga* by the presence of 34 vertebrae (vs. 32 in *T. hasemani* and *T. johnsoni*, 29–32 in *T. anhanga*); by having the origin of the anal fin in a vertical between centrum of 20$^{th}$–22$^{nd}$ vertebrae (vs. 18$^{th}$ in *T. hasemani*, 17$^{th}$ in *T. johnsoni* and 16$^{th}$ in *T. anhanga*) and by the presence of the S6 pore (vs. absence) (Figs. 3-5). It differs from *T. johnsoni* and *T. wapixana* by the origin of the urogenital pore in a vertical between centrum of 16$^{th}$–18$^{th}$ vertebrae (vs. 15$^{th}$ in *T. johnsoni*, 20$^{th}$–22$^{nd}$ in *T. wapixana*). It is distinguished from *T. anhanga* and *T. wapixana* by the presence of 12–13 dorsal procurrent rays (vs. 6–8 in *T. anhanga*, 9–11 in *T. wapixana*). *Trichomycterus bragancai* is distinguished from *T. hasemani* and *T. johnsoni* by posessing an U-shaped posterior region of the cranial fontanel (vs. V-shaped) (Fig. 2) and by the absence of the anterior inner outgrowth of frontal (vs. presence). It is distinguished from *T. hasemani* and *T. anhanga* by the presence of the L3 pore of the main lateral line (vs. absence). It differs from *T. johnsoni* by having the origin of the pelvic fin in a vertical between centrum of 14$^{th}$ and16$^{th}$ vertebrae (vs. 13$^{th}$). *Trichomycterus bragancai* differs from *T. anhanga* by the presence of pelvic fins and girdle (vs. absence); 11–13 ventral procurrent rays in the caudal fin (vs. 6–7); 8 (iii + 5 or iv + 4) dorsal-fin rays (vs. iii + 3 or v + 2); 7 (ii +5 or iii + 4) anal-fin rays (vs. ii + 4); 5 (ii + 3) pectoral-fin rays (vs. i + 2); 8–11 interopercular odontodes (vs. 5–7); 6 branchiostegal rays (vs. 4–5); 2 pairs of pleural ribs on first 2 vertebrae posterior to Weberian Complex (vs. single pair); palatine broad (vs. narrow, comma-shaped);

parasphenoid present (vs. absent); by the presence of the i11 pore (vs. absence); s3 pore present (vs. absent); preopercular canal pore present (vs. absent) and numerous premaxillary and dentary teeth (vs. 2 premaxillary and dentary teeth). It is distinguished from *T. wapixana* by the origin of the dorsal fin at vertical through centrum of 17$^{th}$–19$^{th}$ vertebrae (vs. 20$^{th}$–22$^{nd}$).

**Description.** Morphometric data for holotype and paratypes given in Table I. Body elongate, subcylindrical on anterior portion, gradually compressed until caudal peduncle. Dorsal profile slightly convex between snout and pectoral-fin origin, straight from that point to caudal peduncle. Ventral profile straight between tip of snout and insertion of pectoral fin, gently convex from that point to pelvic-fin origin and straight to end of caudal peduncle. Greatest body depth in vertical between origin of pelvic and pectoral fins. Dorsal, anal, pelvic and pectoral fins about triangular. Pelvic fin not covering urogenital pore. Dorsal-fin origin in vertical through centrum of 17$^{th}$–19$^{th}$ vertebra. Anal-fin origin in vertical through centrum of 20$^{th}$–22$^{nd}$ vertebra. Pelvic-fin origin in vertical through centrum of 14$^{th}$–16$^{th}$ vertebrae. Urogenital pore in vertical through centrum of 16$^{th}$-18$^{th}$ vertebrae. Caudal fin truncate. Dorsal-fin rays 8 (iv + 4 or iii + 5); anal-fin rays 7 (iii + 4 or ii +5); pectoral-fin rays 5 (ii + 3); pelvic-fin rays 5 (iii + 2); caudal-fin principal rays 12 (ii + 8 + ii, i + 9 + ii), dorsal procurrent rays 11–13, ventral procurrent rays 11–13. Total vertebrae 34; pleural ribs on first two vertebrae posterior to Weberian Complex.

Head trapezoidal in dorsal view. Mouth subterminal. Maxillary and dentary teeth conical. Tip of nasal barbel reaching posterior tip of interopercular patch of odontodes. Tip of maxillary barbel reaching pectoral-fin basis. Tip of rictal barbel reaching posterior extremity of interopercular patch of odontodes. Six branchiostegal rays. Odontodes conical. Interopercular odontodes 9–14, opercular odontodes 11–14. Lateral line with

three pores, L1, L2 and L3. Cephalic portion of latero-sensory canal system with four pores, preopercular, i11, s6 and s3.

**Colouration in preserved specimens.** Body colour cream. Dorsal region of head with light brown triangular blotch extending from basis of opercular patch of odontodes to basis of pectoral fin. Nasal, maxillary and rictal barbels with small brown spots concentrated at basis. Dorsal surface of body with brown spots agglutinated in interrupted lines. Dark brown blotch on bases of opercular patch of odontodes and on bases of interopercular patch of odontodes. Ventral surface of head and body cream with few small brown spots. Lateral surface of body with series of dark brown blotches.

Dorsal and lateral surfaces of body with chromatophores distributed between head and caudal peduncle. Ventral surface of body with chromatophores concentrated on head and between pelvic and anal fins.

Dorsal and anal fin hyaline with brown spots on bases of rays. Caudal hyaline fin with small dark brown spots. Pectoral fin hyaline with small brown spot on bases of fin filament. Pelvic fin hyaline.

**Distribution.** Rio Acará drainage, Baía do Guajará, lower Rio Amazon basin, Estado do Pará, northern Brazil (Fig. 7).

**Ecological notes.** *Trichomycterus bragancai* was found living interstitially in a microhabitat composed of gravel and sand, in shallow streams about 4m width and 50 cm deep. The gut of cleared and stained individuals contained Tanytarsini (Diptera: Chironomidae) larvae.

**Etymology.** Named after Pedro Henrique Negreiros de Bragança, Brazilian ichthyologist who first invited the first author in 2012 to collect in the Amazon rainforest, and since then has been together with her in every field trip.

**Discussion.**

*Trichomycterus bragancai* is here assigned to the *T. hasemani* group due to the presence of all the five character states proposed by Dutra et al. (2012) to diagnose the group: 1- presence of branchiostegal rays on the posterior ceratohyal; 2- posterior process of the palatine distally expanded and partly forked (Fig. 2); 3- absence of the anterior portion of the infraorbital canal (Fig. 3-5); 4- nine or less branched caudal-fin rays; 5- first pectoral fin ray longer than the others.

Weitzman & Vari (1988) stated the arbitrary measure of 26 mm SL as a maximum size to consider several species of freshwater fishes as miniatures. The species of the *T. hasemani* group fit this criterion, but these authors also enunciate other paedomorphic morphological features that can be used to consider them as miniatures: 1- reduction of laterosensory canal system; 2- reductions in the number of fin rays and 3- low degree of development of skull bones. The reduced laterosensory canal system is one of the character states to define the *T. hasemani* group, since the infraorbital canal is restricted to only one pore (i11) in *T. hasemani*¸ *T. johnsoni, T. wapixana* and *T. bragancai* (Fig. 3-5). The supraorbital series is usually restricted to one pore (*T. hasemani*, *T. johnsoni* and *T. wapixana*), although *T. bragancai* has two supraorbital pores. *Trichomycterus anhanga* has the entire cephalic portion of the laterosensory canal system absent. Considering the reduction in the number of fin rays, in *T. anhanga* the most extreme case in the *T. hasemani* group is seen: this species lacks pelvic girdle and fins, dorsal and ventral procurrent rays and is also the one with less pectoral fin rays within the group. *Trichomycterus bragancai* possesses five pelvic-fin rays and is the species of the *T. hasemani* group with more pelvic-fin rays. A reduction in the ossification degree of skull bones in the *T. hasemani* group is mainly characterized by the presence of a wide skull roof (Fig. 2), but in *T. anhanga* this reduction goes further: this species lacks the

parasphenoid and has less premaxillary and dentary teeth and interopercular odontodes when compared to *T. hasemani*, *T. johnsoni* and *T. wapixana. T. johnsoni* possess the bones delimiting the fontanel are more ossified when compared to *T. anhanga*, *T. wapixana* and *T. bragancai*. In the last three species, the frontals do not reach the supraoccipital, while in *T. hasemani* and in *T. johnsoni* these bones attach to the supraoccipital.

According to Hanken & Wake (1993), reduction and structural simplification is the most widespread effect of miniaturization among several taxa, and these consequences can be found not only in the *T. hasemani* group but in other teleostean fishes. The loss of all or most parts of the laterosensory canal system is also seen in the miniaturized cyprinodontid genera *Cromeria* Boulenger 1901 and *Grasseichthys* Géry 1964, in which the lateral line canal system of the head is absent and they also lack the supraopercle (Britz & Moritz 2007). The three species of the characid genus *Priocharax* Weitzman & Vari 1987 lost the laterosensory canal system of the head and body. The miniaturized genera *Paedocypris* Kottelat, Britz, Tan & Witte 2006, *Sundadanio* Kottelat & Witte 1999 and *Danionella* Roberts 1986 lacks vomer, ectopterygoid, posttemporal and postcleithrum (Britz & Conway, 2009). According to Dutra et al. (2012), the aforementioned character states diagnostic for the *T. hasemani* group are mainly based on reductions, probably due to miniaturization.

**Comparative material.** Listed in Henschel (2016). *Trichomycterus hasemani*: UFRO 15209, 1 ex., 13.0 mm SL; Brazil: Estado de Rondônia: Candeias do Jamari. UFRO 21102, 1 ex., 16.0 mm SL; Brazil: Estado de Rondônia: Guajará Mirim. *Trichomycterus anhanga:* MZUSP 108822, 2+1 c&s, 9.7–10.2 mm SL; Brazil; Estado do Amazonas: Novo Aripuanã. *Tridens* sp.: UFRO 9618, 1 ex., 17.2 mm SL: Brazil: Estado de Rondônia: Porto Velho. *Miuroglanis platycephalus*: UFRO 12446, 5 ex., 13.6–14.1 mm

SL: Brazil: Estado de Rondônia: Porto Velho. *Tridentopsis pearsoni:* MZUSP 109849, 30 ex., 16.8–20.7 mm SL; Brazil: Estado do Acre: Xapuri. *Tridensimilis* sp.: MZUSP 23449, 1 ex., 16.9 mm SL; Brazil: Estado do Amazonas: Ati-Paranã.

**Acknowledgements**

Special thanks to Wilson Costa for critical reading, corrections and suggestions on the manuscript, to Pedro Henrique Bragança who was present and helped during the collection of the specimens and to Axel Katz for the photographs. We are especially grateful to Marcelo Salles and Inácio Domingos da Silva Neto (Laboratório de Imagens e Microscopia Ótica e de Varredura - UFRJ) who made the procedures with the scanning electron microscope possible. Thanks are also due to Alessio Datovo (MZUSP), Mario de Pinna (MZUSP), Carolina Doria (UFRO) and Mahmoud Mehanna (UFRO) for assistance before and while visiting these collections. We thank Jorge Luiz Nessimian (Laboratório de Entomologia – UFRJ) for promptly identifying the Tanytarsini specimens. This study was supported by FAPERJ (Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro). All procedures realized in order to the development of this paper agree with the brazilian laws.

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**Table 1**. Morphometric data of *Trichomycterus bragancai* (UFRJ 9709; UFRJ 9710).

| | H | Range | Mean | Standard deviation |
|---|---|---|---|---|
| Standard length (mm) | 13.9 | 11.8–14.4 | 13.0 | - |
| Percentage of standard length | | | | |
| Total length | 119.4 | 97.2–124.4 | 117.3 | 6.9 |
| Body depth | 12.9 | 11.8–17.4 | 15.2 | 1.6 |
| Peduncle length | 10.8 | 7.6–13.4 | 11.4 | 1.6 |
| Predorsal length | 66.2 | 57.6–79.3 | 69.6 | 4.9 |
| Preanal length | 69.1 | 56.9–78.5 | 70.5 | 5.1 |
| Prepelvic length | 54.0 | 45.1–58.7 | 54.3 | 3.3 |
| Dorsal fin base length | 8.6 | 4.2–9.4 | 7.7 | 1.5 |
| Anal fin base length | 7.2 | 5.6–9.0 | 7.5 | 0.9 |
| Head length | 14.4 | 12.5–16.5 | 14.9 | 1.2 |
| Percentage of head length | | | | |
| Head width | 110.0 | 95.5–133.3 | 113.1 | 8.4 |

| | | | | |
|---|---|---|---|---|
| Head depth | 60.0 | 50.0-100.0 | 69.3 | 11.7 |
| Interorbital | 40.0 | 31.8–47.4 | 41.0 | 4.9 |
| Snout length | 40.0 | 35.0–47.4 | 41.8 | 4.2 |
| Nasal barbel length | 75.0 | 45.0–80.0 | 60.5 | 11.6 |
| Maxillary barbel length | 75.0 | 52.6–110.0 | 77.3 | 15.5 |
| Rictal barbel length | 90.0 | 52.6–120.0 | 78.9 | 20.3 |
| Mouth width | 40.0 | 36.4–47.4 | 41.9 | 3.3 |
| Eye diameter | 15.0 | 13.3–15.8 | 14.7 | 0.8 |


**Figure 1.** *Trichomycterus bragancai*: UFRJ 11065, 13.9 mm SL (holotype): Acará river basin. (A) lateral view; (B) dorsal view; (C) ventral view. Photos by: Axel Katz.

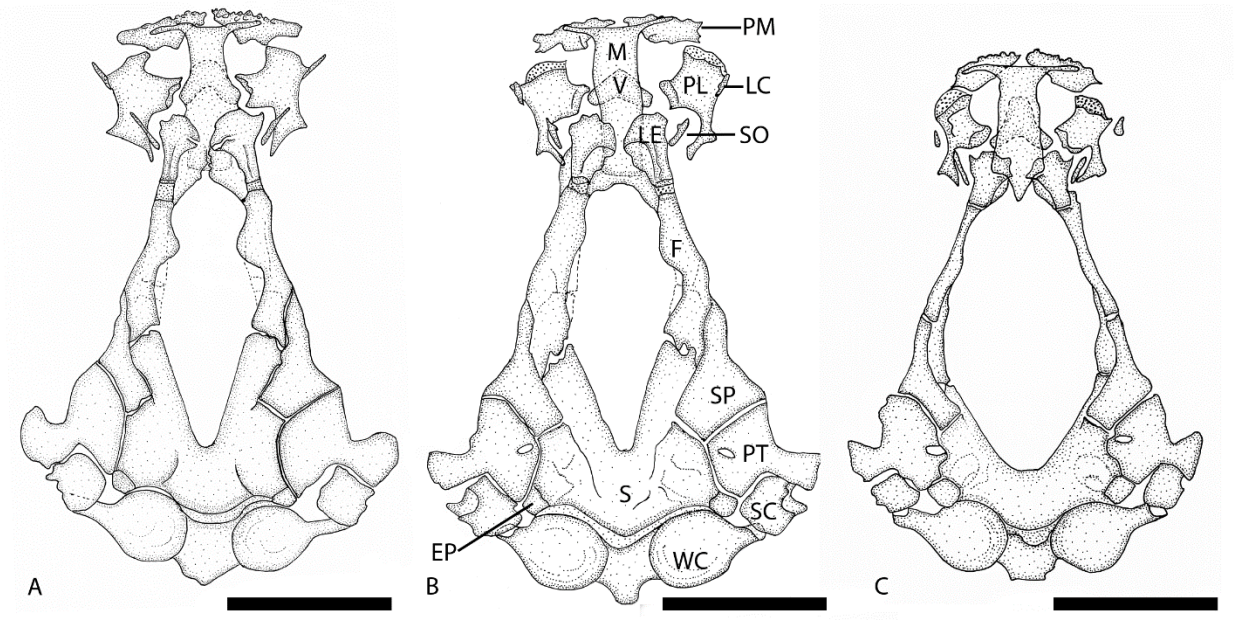


**Figure 2.** Dorsal view of neurocranium. (A) *Trichomycterus hasemani*, UFRJ 9653, 17.3 mm SL, (B) *Trichomycterus johnsoni*, UFRJ 9368, 14.0 mm SL, and (C) *Trichomycterus bragancai*, UFRJ 10020, paratype, 12.2 mm SL, dorsal view. Abbreviations: EP, epiotic; F, frontal; LC, lacrimal, LE, lateral etmoid; M, metapterygoid; PL, autopalatine; PM, premaxilla; PT, pterotic; S, supraoccipital; SC, supracleitrum, WC Weberian capsule. Larger stippling indicates cartilage. Scale bar = 1.0 mm.

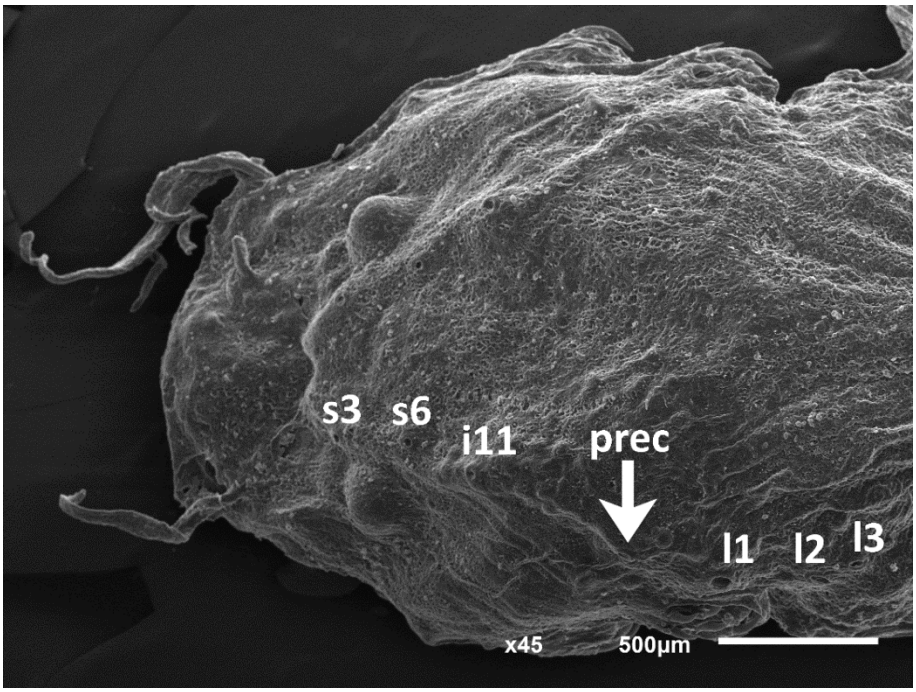


**Figure 3.** Dorsal view of head of *Trichomycterus bragancai*. UFRJ 9709, 11.7 mm SL (paratype). Abbreviations: s3-supraorbital 3; s6-supraorbital 6; i11-infraorbital 11; prec-preopercular pore; l1, l2 and l3-lateral line 1, 2 and 3.

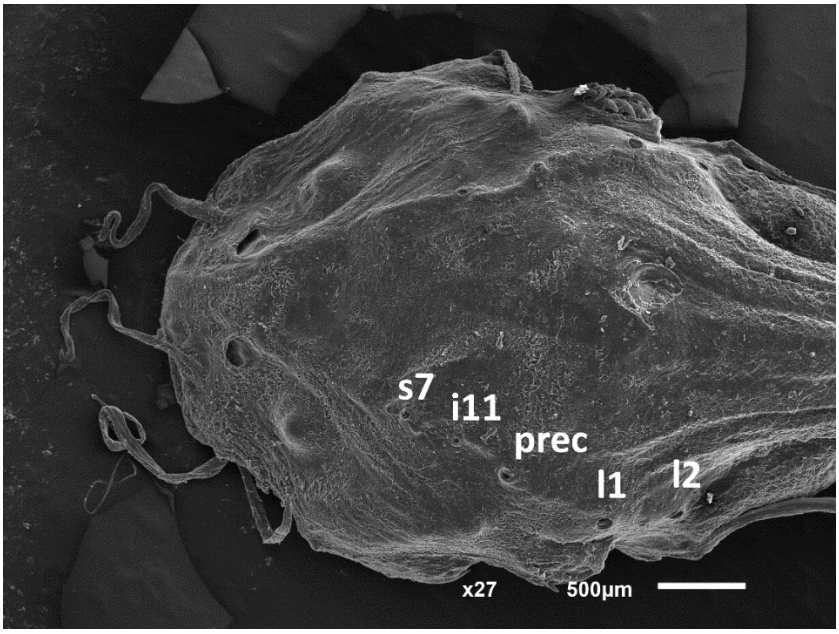


**Figure 4.** Dorsal view of head of *Trichomycterus hasemani*. UFRJ 9645, 17.4 mm SL. Abbreviations: s7-supraorbital 7; i11-infraorbital 11; prec-preopercular pore; l1 and l2-lateral line 1 and 2.

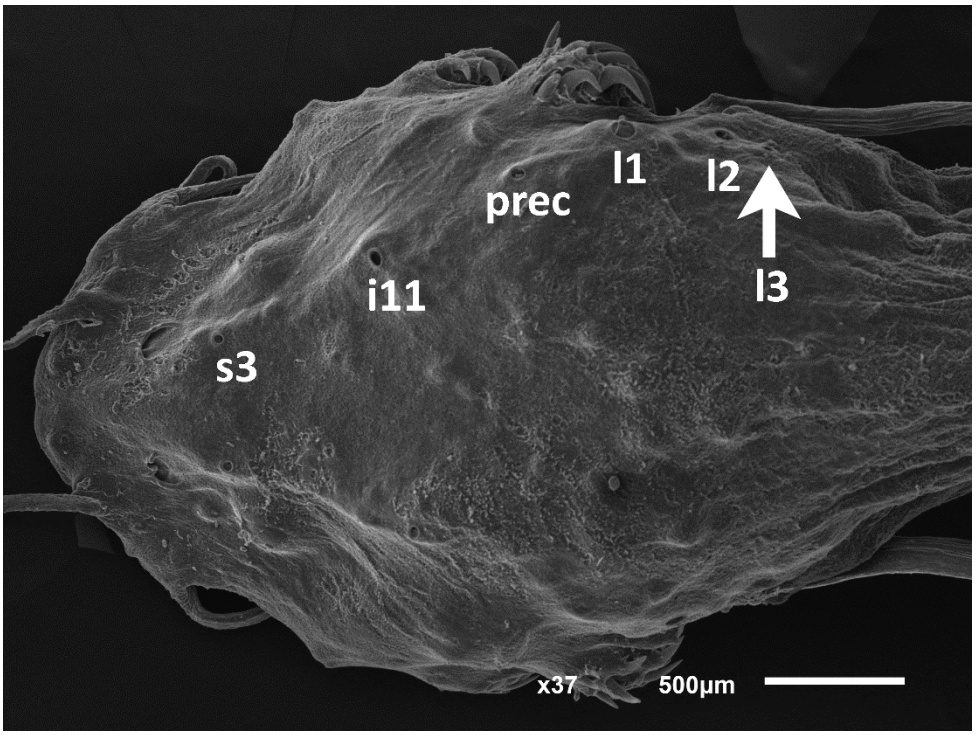


**Figure 5.** Dorsal view of head of *Trichomycterus johnsoni*. UFRJ 3823, 14.4 mm SL. Abbreviations: s3-supraorbital 3; i11-infraorbital 11; prec-preopercular pore; l1, l2 and l3-lateral line 1, 2 and 3.

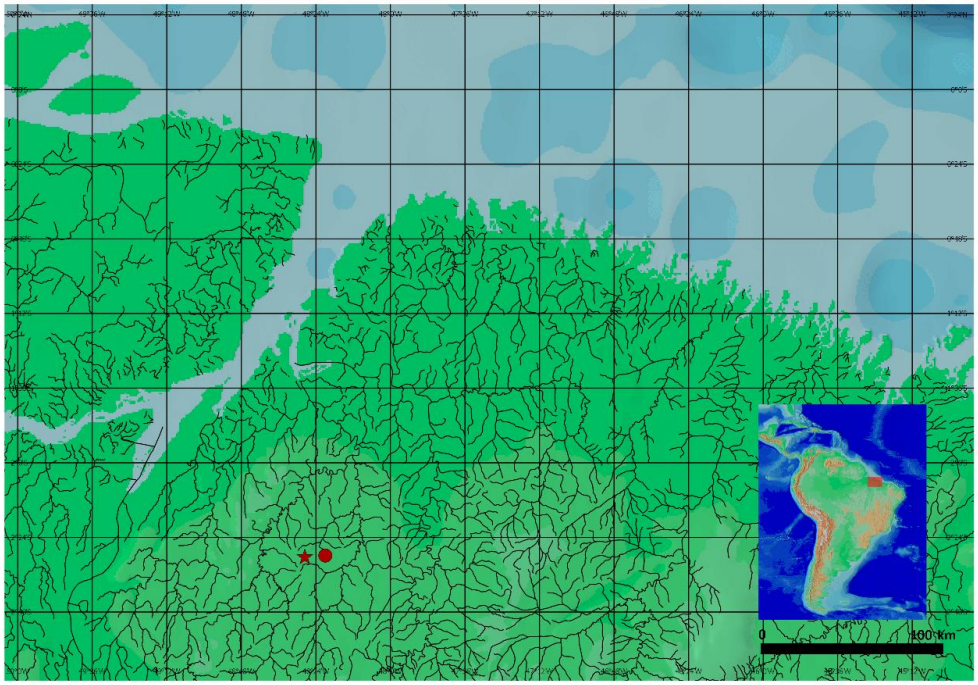


**Figure 7.** Geographic distribution of *Trichomycterus bragancai*, in the Acará river basin, northern Brazil. Symbols represent more than one collecting site. Star = holotype; circle = paratypes.