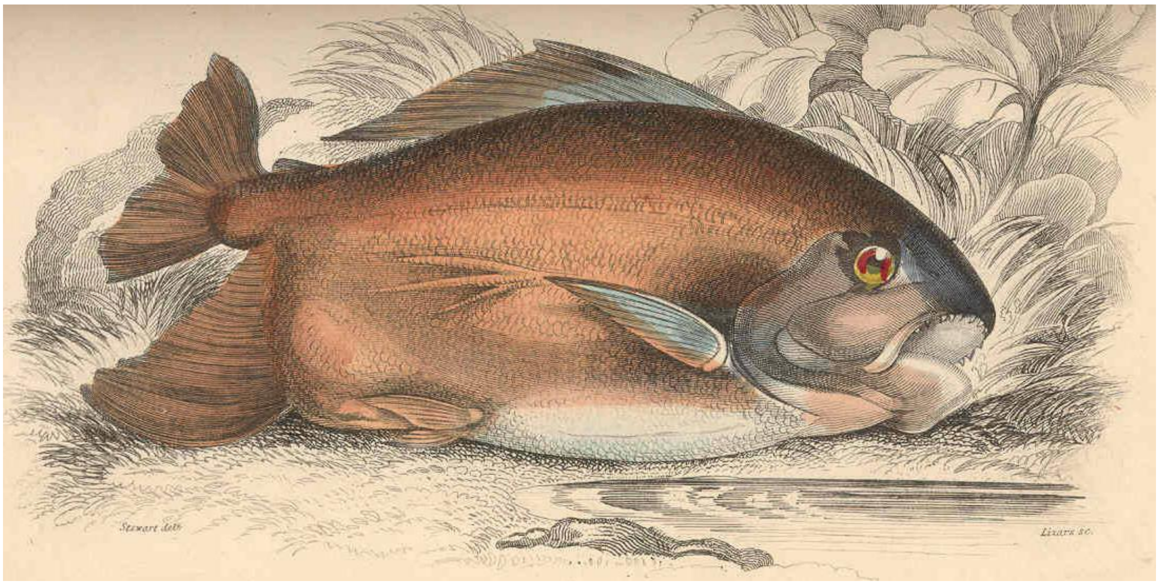
UNIVERSIDADE FEDERAL DO PARÁ
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA AQUÁTICA E PESCA
CIDADE UNIVERSITÁRIA JOSÉ DA SILVEIRA NETTO

Marcelo Costa Andrade



Diversidade do clado *Myleus* e ecologia trófica dos Serrasalmidae de corredeiras da região Amazônica (Ostariophysi: Characiformes)

Tese de Doutorado

Belém, 2017

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Diversity of Myleus clade and trophic ecology of the Serrasalmidae rapids-adapted from Amazon (Ostariophysi: Characiformes)

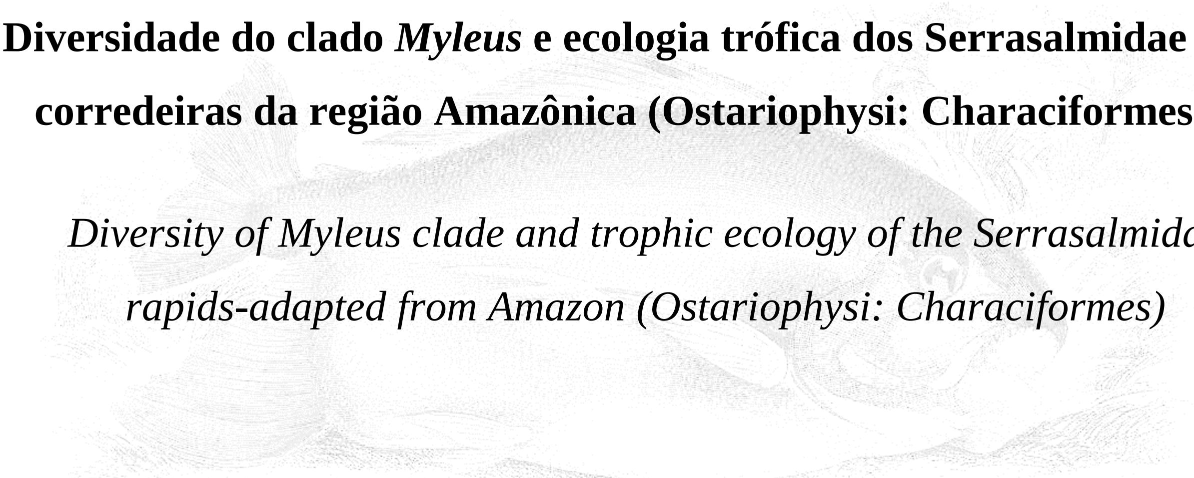

Ilustração da capa: fêmea de *Myleus pacu* (Jardine), *species inquirenda*, desenho original de Robert H. Schomburgk *In*: Jardine & Schomburgk (1841).

Ilustração da guarda-capa: macho de *Myleus pacu* (Jardine), *species inquirenda*, desenho original de Robert H. Schomburgk *In*: Jardine & Schomburgk (1841).

Tese de Doutorado apresentada ao Programa de Pós-Graduação em Ecologia Aquática e Pesca, Universidade Federal do Pará.
Área de concentração: Biodiversidade Aquática

Orientador: Dr. Tommaso Giarrizzo
Universidade Federal do Pará, Belém, Brasil

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Aquática e Pesca na área de concentração de Biodiversidade Aquática,
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Aviso

A presente tese integra parte dos requisitos necessários para a obtenção do título de Doutor em Ecologia Aquática e Pesca da área de Biodiversidade Aquática e, como tal, não deve ser vista como uma publicação no senso do Código Internacional de Nomenclatura Zoológica. Portanto, quaisquer informações inéditas, opiniões, hipóteses e conceitos novos apresentados aqui não estão disponíveis na literatura zoológica. Pessoas interessadas devem estar cientes de que cópias e referências públicas ao conteúdo deste documento devem ser feitas com prévia aprovação do autor.

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This thesis is submitted in partial fulfillment of the requirements for the degree of Ph.D. in Aquatic Ecology and Fishery of the knowledge area Aquatic Biodiversity and, as such is not intended as a publication in sense of the International Code of Zoological Nomenclature. Therefore, any new information, opinions, hypothesis and new concepts presented herein are not available in the zoological literature. Interested people should be aware that any copy or public reference to this document should only be done after previously author acceptance.

Dedico o presente estudo à Thuízy, pelo amor, resiliência e companheirismo ao logo desta jornada.

"Seja você quem for, seja qual for a posição social que você tenha na vida, a mais alta ou a mais baixa, tenha sempre como meta muita força, muita determinação e sempre faça tudo com muito amor e com muita fé em Deus, que um dia você chega lá. De alguma maneira você chega lá."

Ayrton Senna

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Resumo

Apesar do enorme potencial territorial e biológico, a Bacia Amazônica vem sendo seriamente ameaçada por atividades antrópicas. A utilização dos cursos hidrológicos para fins econômicos é cada vez mais expressiva sendo essa a principal causa geradora de perda de habitats Amazônicos, que por sua vez, gera declínio da biodiversidade em suas drenagens. Apesar da enorme importância da biodiversidade Amazônica, a conhecemos pouco até então, e menor ainda é a nossa compreensão sobre a interação entre as espécies e o seu ambiente natural. Nesse contexto, torna-se inadiável a aplicação de estudos com o propósito de reconhecer a diversidade dos organismos, bem como das relações desta com o ecossistema. Tendo em vista que os ambientes encachoeirados Amazônicos são uns dos mais ameaçados devido a ação antrópica, o presente estudo foi direcionado a um grupo altamente vulnerável, os peixes de corredeiras, e neste caso, focado nos peixes herbívoros da família Serrasalmidae. Baseando-se na taxonomia dos peixes serrasalmídeos, o estudo selecionou um grupo usualmente relacionado às corredeiras, o clado *Myleus*, pois suas espécies ou habitam este ambiente ao longo de toda a vida, ou o usam com frequência para forrageio. Em suma, a diversidade do grupo é composta por cinco gêneros e aproximadamente 30 espécies, no entanto, o seu histórico taxonômico mescla atribuições duvidosas de espécies e a evidente carência de conhecimento das necessidades ecológicas dessa biodiversidade. O estudo decorreu no reconhecimento dessa biodiversidade, bem como na produção de chaves de identificações para a devida delimitação taxonômica aos níveis genérico e especifico. Depois, três novas espécies foram descritas no estudo, assim como as relações filogenéticas entre as espécies de um gênero notadamente reofílico de corredeiras foram apresentadas. Além disso, levando em consideração três espécies sintópicas de serrasalmídeos de corredeira, o estudo avaliou a ecologia trófica desses peixes com base no comportamento alimentar, partilha de nicho e traços funcionais, bem como no fluxo de energia e a posição trófica das espécies ao longo da ontogenia. Partindo do princípio de que antes de se preservar é necessário conhecer a biodiversidade, o estudo é uma análise integrada que apresenta uma proposta de organização taxonômica de uma fauna de peixes exclusiva ou quase de corredeiras da região Amazônica, e ainda apresenta o nicho ecológico dessas espécies em seu ambiente natural.

Abstract

Despite the huge potential, both territorial and biological, the Amazon Basin has been severely threatened by anthropogenic disturbances. The exploitation of the watersheds for economic purposes is increasingly apparent and is the main cause of habitat loss in Amazonian region. Such changes generate biodiversity decline in its constituent drainages. Despite the great importance of Amazonian biodiversity, knowledge its diversity is meager, especially with regard to interactions among species and their natural environment. In this sense, the application of studies to recognize the diversity of organisms and their interactions with the ecosystem becomes imperative. Given that the Amazonian rapids are one of the environments most threatened by anthropogenic disturbances, the present study was directed to a highly vulnerable group, the rapids-adapted fish with a focus on the herbivorous fish of the Serrasalmidae family. Based on the serrasalmid taxonomy, the study selected a group typically associated with rapids, the *Myleus* clade. The *Myleus* clade species inhabit this environment throughout their life, or frequent the rapids to forage. The *Myleus* clade is composed of five genera and about 30 species. However, its taxonomic history is wrought with dubious assignment of species and a notable scarcity of information regarding the ecological requirements of this biodiversity. The study resulted in recognition of this biodiversity, as well as provided identification keys for purposes of proper taxonomic delimitation at generic and specific levels. Then, three new species were described in the study, as well as were presented the phylogenetic relationships within a genus of a remarkable rapids-adapted fish. In addition, considering three syntopic, rapids-adapted serrasalmids, the study evaluated the trophic ecology of these fish based on feeding behavior, niche partitioning and functional traits, as well as on the energy flow and trophic position of species along the ontogeny. Given that prior to preservation, it is necessary getting to know biodiversity better, the study is an integrative analysis that proposes a taxonomic reorganization for a rapids-exclusive group of fish from the Amazonian region, and presents the respective ecological niche of these species in their natural environment.

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Diretrizes

A presente Tese de Doutorado foi elaborada sob formato de compilação de artigos científicos, desenvolvidos sobre o tema "diversidade taxonômica e trófica dos peixes Serrasalmidae de corredeiras", submetidos a periódicos avaliados de acordo com o critério *Qualis*-CAPES na área de Biodiversidade. As diretrizes dos artigos seguem Resolução Nº 4.782, de 24 de fevereiro de 2016, a qual aprovou o Regimento do Programa de Pós-Graduação em Ecologia Aquática e Pesca da Universidade Federal do Pará PPGEAP/UFPA. A Tese foi estruturada baseando-se nas seguintes diretrizes do Regimento do PPGEAP em destaque:

> *CAPÍTULO VIII:*
>
> *"§ 2º O discente de Doutorado terá que comprovar ao Colegiado do Curso a publicação ou aceite de um artigo científico nos últimos dois anos a partir de sua matrícula (avaliado com critério Qualis-CAPES na área de Biodiversidade, cujo valor será aquele definido pelo Colegiado no ano vigente).*
>
> *§ 3º O discente de Doutorado deverá apresentar, também, até 30 (trinta) meses a partir de seu ingresso no Curso, um segundo artigo científico completo submetido ou escrito e formatado de forma a estar pronto para submissão a periódicos científicos, ou ainda, aceito ou publicado após o ingresso no Doutorado, desde que seja relacionado ao grande tema da Tese (avaliado com Qualis-CAPES na área de Biodiversidade, cujo valor será aquele definido pelo Colegiado no ano vigente). Nesse caso, o discente obrigatoriamente deverá ser o primeiro autor do artigo científico. Este artigo será avaliado por uma Comissão específica designada pelo Colegiado."*

Estrutura da Tese

Levando em consideração as diretrizes, a Tese segue a seguinte estrutura:

1. **Introdução geral**, onde o leitor irá encontrar uma breve apresentação sobre os peixes Serrasalmidae, incluindo o histórico taxonômico dos Serrasalmidae do clado *Myleus*, e também um apanhado sobre a diversidade trófica desses peixes;
2. **Objetivos da Tese**;
3. **Capítulo 1**, onde foram descritas duas espécies de Serrasalmidae de corredeira para as bacias do Xingu e Tocantins-Araguaia, que por décadas foram alvo de numerosos estudos, mas sob identidade taxonômica duvidosa; as descrições são acompanhadas ainda de observações sobre taxonomia, distribuição, ecologia e conservação das espécies frente a alterações antrópicas (artigo **publicado** em *Journal of Fish Biology* – 2016, Anexo 1);
4. **Capítulo 2**, seguindo a mesma ótica do capítulo anterior, foi descrito uma espécie de Serrasalmidae de corredeira do rio Itacaiúnas, Serra dos Carajás, uma das principais sub-bacias hidrográficas do Tocantins-Araguaia; o capítulo traz uma integração entre análises morfológicas e moleculares, e também notas sobre ecologia, distribuição e conservação (artigo **aceito para publicação** em *PloS ONE* – 2017);
5. **Capítulo 3**, onde foi apresentado a partilha de nicho entre os serrasalmídeos das corredeiras do baixo rio Xingu, baseado em análises de morfologia, dieta e de isótopos estáveis (artigo **submetido** à *Ecology of Freshwater Fish*);
6. **Considerações finais**;
7. **Apêndices**, chaves de identificação elaboradas para os peixes serrasalmídeos do clado *Myleus* e correlatos (Apêndices 1 e 2);
8. **Anexos**, referências a artigos relacionados a Tese publicados em decorrência de pesquisas desenvolvidas durante o Doutorado (Anexos 1-7).

Introdução geral

1.1. Introdução sobre os peixes herbívoros da família Serrasamidae

As espécies da família Serrasalmidae são peixes Characiformes Neotropicais composta pelos “pacus” e “piranhas”, conhecidos popularmente por seus representantes herbívoros e carnívoros, respectivamente (Andrade *et al*. 2015; Jégu 2003). No entanto, o comportamento alimentar na família é bastante diversificado, reconhecendo além dos herbívoros e carnívoros, representantes insetívoros (essencialmente quando juvenis), lepidófagos, frugívoros, e onívoros (Géry 1977; Goulding 1980; Jégu 2003; Jégu *et al*. 1989; Loubens & Panfili 1997).

Os Serrasalmidae têm distribuição cisandina, ocorrendo em todos os biótopos de água doce da região Neotropical, exceto em riachos muito estreitos e em áreas bentônicas de grande profundidade. Sua ocorrência fora da região é considerada resultado de introdução (Jégu 2003; Ota *et al*. 2013). Eles podem alcançar os mais variados tamanhos, desde as menores espécies com pouco mais de 13 cm comprimento padrão (e.g. *Acnodon normani* Gosline) até os considerados gigantes com aproximadamente 1 m de comprimento total [i.e. *Colossoma macropomum* (Cuvier)] (Jégu 2003). Atualmente, a família é composta por 93 espécies válidas (Eschmeyer *et al*. 2017), alocadas em 16 gêneros sendo um deles fóssil (Cione *et al*. 2009).

Os membros da família são facilmente reconhecidos morfologicamente por apresentarem corpo alto, comprimido lateralmente e, por apresentarem uma série de espinhos no abdômen formando uma serra ventral (Géry 1977), característica que nomeou a família. Filogeneticamente, “pacus” e “piranhas” formam grupos irmãos sendo sustentados, entre outros, pela presença do espinho pré-dorsal como sinapomorfia, e como grupo basal, a família consta dos Serrasalmidae sem tal espinho (*i.e.* gêneros *Colossoma*, *Piaractus* e *Mylossoma* Eigenmann & Kennedy) (Dahdul 2007; Jégu 2004). Dentre os Serrasalmidae herbívoros, os gêneros *Myleus* Müller & Troschel, *Mylesinus* Valenciennes, *Tometes* Valenciennes, *Ossubtus* Jégu (Jégu 2004), e juntamente com o gênero *Myloplus* Gill (Dahdul 2007), formam um clado monofilético filogenético. Porém, relações mal resolvidas com as espécies do gênero *Myloplus* persistem (Ortí *et al*. 2008). Assim, o então "clado *Myleus*" (termo cunhado originalmente por Ortí *et al*. 1996) é composto pelas espécies dos gêneros *Myleus*, *Mylesinus*, *Tometes Ossubtus*, e *Myloplus*, composto em sua maioria por espécies adaptadas nos ambientes encachoeirados dos tributários de Escudo (Andrade *et al*. 2013, 2016b).

1.2. Histórico taxonômico do clado *Myleus*

O histórico taxonômico das espécies do clado teve início com a descrição do gênero *Myleus* feita por Müller & Troschel (1844) para alocar as espécies *Myleus setiger* e *Myleus oligacanthus* que diferiam de *Myletes* Cuvier pela ausência do dente sinfiseano interno no dentário. Ambas, *Myleus setiger* e *Myleus oligacanthus*, foram descritas a partir de exemplares de drenagens costeias do escudo guianense. Mais tarde, Müller & Troschel (1845) redescreveram o gênero *Myleus* e adicionaram a ilustração da dentição de *Myleus setiger* sem o dente sinfiseano. Embora Valenciennes (1850) não ter examinado a espécie *Myleus setiger*, pois o único exemplar que havia sido cedido ao museu de Paris (MNHN) pelo museu de Leiden (RMHN) havia desaparecido na época, descreveu o gênero *Tometes* indicando ainda que as características morfológicas de *Tometes* assemelhavam-se as descritas para *Myleus* por Müller & Troschel (1844, 1845). No trabalho, Valenciennes (1850) descreveu as espécies de *Tometes*, *Tometes trilobatus*, *Tometes unilobatus* e *Tometes altipinnis*, e também a espécie *Mylesinus schomburgkii* (esta última foi descrita unicamente a partir da cabeça de um exemplar e de um desenho providenciado por Robert H. Schomburgk), as diferindo de *Myleus* pela presença do dente sinfiseano no dentário *versus* ausência em *Myleus*. Kner (1860), analisou exemplares de *Myleus setiger* emprestados por Johann Natterer ao museu de Viena (NMW), constatou a presença do dente sinfiseano na espécie, e ilustrou o mesmo em sua obra. Kner (1860) comentou que Müller & Troschel (1844, 1845) possivelmente não notaram o dente sinfiseano em *Myleus setiger*, pois o mesmo é tão pequeno que só pôde ser visto após a mucosa da boca do peixe ter sido dissecada. Kner (1860) considerou ainda não apropriada a separação a nível genérico feita por Valenciennes (1850) unicamente pela presença ou ausência do dente sinfiseano, Kner (1860) julgou essa característica relacionada ao dimorfismo sexual das espécies. Finalmente, Kner (1860) propôs que os gêneros *Myleus* e *Tometes* como sinonímia de *Myletes,* considerando ainda *Myleus setiger* e *Tometes trilobatus* como sinônimo juniores de *Myletes setiger* (Müller & Troschel).

Em estudo sobre os peixes heterognatos (= mandíbulas desiguais), Eigenmann (1903) propôs o gênero *Acnodon* para a espécie *Myleus oligacanthus* [= *Acnodon oligacanthus* (Müller & Troschel)] por apresentar, entre outras características, pré-maxila projetada anteriormente. Baseado nas características descritas por Kner (1860), Steindachner (1911) descreveu *Myleus gurupyensis* para a bacia do rio Gurupi, Brasil. Já Eigenmann (1912), em seu estudo sobre os peixes da Guiana (na época Guiana Britânica), trouxe respostas mais acuradas sobre o dimorfismo nos Serrasalmidae herbívoros, porém não confirmou que presença ou ausência do dente sinfiseano fosse uma característica dimórfica como sugerido por Kner (1860). Assim, Eigenmann (1912) redescreveu o gênero *Myleus* para aquelas espécies com serra ventral nítida nos juvenis que se torna menos evidente com a idade, seguindo a mesma observação feita para *Myletes pacu* Jardine, descrito por Jardine (1841) a partir dos desenhos de Robert H. Schomburgk (ilustrados na presente Tese na capa e guarda-capa). Portanto, Eigenmann (1912) considerou *Myletes pacu*, *Myletes setiger* e *Tometes trilobatus* como sinônimo juniores de *Myleus pacu* (Jardine).

Eigenmann (1915), descrevendo espécies de serrasalmídeos, fez referência à Humboldt de autoria para *Myleus pacu* para, possível erro tipográfico em alusão à *Myletes paco* descrito por Humboldt & Valenciennes (1821) [= sinônimo júnior de *Piaractus brachypomus* (Cuvier)], e apresentou duas figuras do osso pré-maxilar para a espécie (i.e. figura 12, pág. 269, e figura 13, pág. 270). A primeira figura mecionada apresenta *Myleus pacu* com dentes fortes, nitidamente molariformes e as duas séries de dentes separadas uma da outra (Fig. 1a). Já a segunda figura apresenta um exemplar com dentes delgados, incisiformes e as duas séries unidas uma a outra (Fig. 1b). Vale ressaltar que Jardine (1841), mesmo sem examinar material, pois o fez a descrição a partir de desenhos, julgou dentição molariforme para *Myletes pacu*, e que Eigenmann (1915) possivelmente tenha examinado *Myletes paco* (= *Piaractus brachypomus*), espécie com dentição estritamente molariforme.

Norman (1929), violando a regra da prioridade, sinonimizou *Myletes pacu* Jardine com *Myleus setiger* Müller & Troschel, que por sua vez foi revalidada. Além disso, sinonimizando as espécies *Myletes knerii* Steindachner, *Myletes* (*Tometes*) *micans* Lütken e *Tometes altipinnis*, Norman (1929) propôs as espécies como pertencentes ao gênero *Myleus*, i.e. *Myleus knerii* (Steindachner), *Myleus micans* (Lütken) e *Myleus altipinnis* (Valenciennes). *Myleus knerii* foi descrito a partir de um único exemplar coletado no rio Maroni (NMW 56394), Guiana Francesa, *Myleus micans* do rio das Velhas e *Myleus altipinnis* do rio Cipó. Provenientes da bacia do rio

São Francisco, essas duas últimas foram a primeira referência de espécies do grupo para uma bacia hidrográfica do escudo brasileiro.

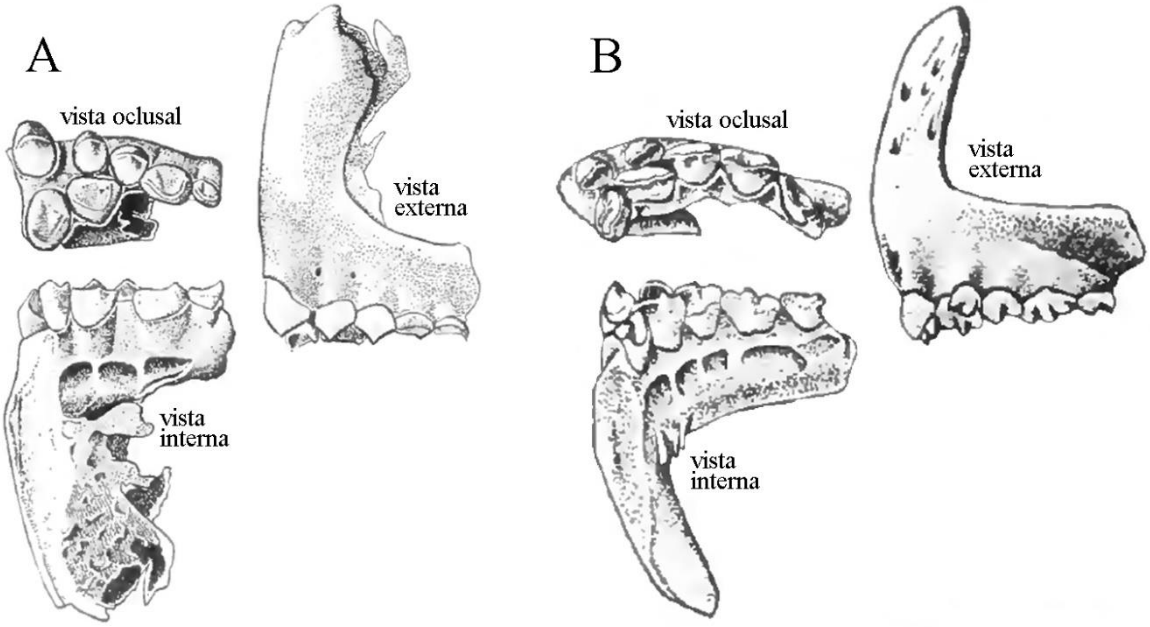

Figura 1. Vistas do osso pré-maxilar com dentição da espécie *Myleus pacu*. A) dentição molariforme, espécime com 255 mm CP; B) dentição incisiforme, espécime com 210 mm CP. Adaptada das figuras 12 e 13 de Eigenmann (1915), respectivamente.

Em estudo subsequente, Gosline (1951) concorda com a espécie descrita por Steindachner (1911) (i.e. *Myleus gurupyensis*), com as quatro espécies de *Myleus* propostas por Norman (1929) (i.e. *Myleus altipinnis*, *Myleus knerii*, *Myleus micans* e *Myleus setiger*), e revalida a espécie *Myleus pacu*. Gosline (1951) alocando ainda mais sete espécies de *Myletes* em *Myleus* [i.e. *Myloplus asterias* (Müller & Troschel), *Myletes latus* (Müller & Troschel), *Myleus rhomboidalis* (Cuvier), *Myleus rubripinnis* (Müller & Troschel), *Myleus schomburgkii* (Valenciennes), *Myleus tiete* (Eigenmann & Norris) e *Myleus torquatus* (Kner)], a espécie *Tomete maculatus* (erro tipográfico, *Tometes*) como *Myleus maculatus* (Amaral Campos), e também a espécie do gênero *Paramyloplus* (proposto por Norman (1929)) como *Myleus ternetzi* (Norman). Ao todo, Gosline (1951) atribuiu 14 espécies ao gênero *Myleus*. Gosline (1951) descreveu que *Myleus setiger* e *Myleus pacu* têm séries de dentes no prémaxilar sem espaçamento interno, mas as difere as duas espécies devido *Myleus setiger* apresentar série labial do pré-maxilar com todos os dentes em contato lateral formando uma linha contígua, enquanto *Myleus pacu* apresenta espaçamento lateral entre os dentes mais anteriores. Gosline (1951) reporta *Myleus setiger* e *Mylesinus schomburgkii* para a bacia do Tocantins-Araguaia, sendo esse o segundo relato de espécies do clado para o escudo brasileiro. No mesmo estudo, Gosline (1951) reportou a espécie *Utiaritichthys sennaebragai* Miranda Ribeiro para o rio Tocantins, relatando ainda que a mesma poderia ser atribuída ao gênero *Myleus* por apresentar serra pré-pélvica delgada composta por finos espinhos.

Posteriormente, Géry (1972) propôs quatro subgêneros para *Myleus* (*Myloplus* Gill, *Prosomyleus* Géry, *Paramyloplus*, e *Myleus* nominal). De acordo com o tipo de dentição proposto por Géry (1972) para *Myleus*, isto é, séries de dentes pré-maxilares juntas uma a outra e série labial formando linha contígua, unicamente *Myleus* (*Myleus*) *pacu* foi mantida. Para sinonimizar as espécies, Géry (1972) levou em consideração apenas Eigenmann (1912) e não Norman (1929) ou Gosline (1951), pois Eigenmann havia examinado exemplares tipos de várias espécies, Norman violou as regras de nomenclatura, e Gosline não foi convincente ao diferir *Myleus pacu* de *Myleus setiger*.

Machado-Allison (1983), apresentou a primeira hipótese filogética dos serrasalmídeos. Seguindo Gosline (1951), Machado-Allison (1983) utilizou definição para as espécies de *Myleus*, *Mylesinus* e *Utiaritichthys* sendo que a atribuição de *Utiaritichthys* em *Myleus* sugerida por Gosline (1951) foi parcialmente corroborada, pois Machado-Allison (1983) encontrou afinidade na relação filogenética das espécies de *Myleus*, *Mylesinus* e *Utiaritichthys* (Fig. 2).

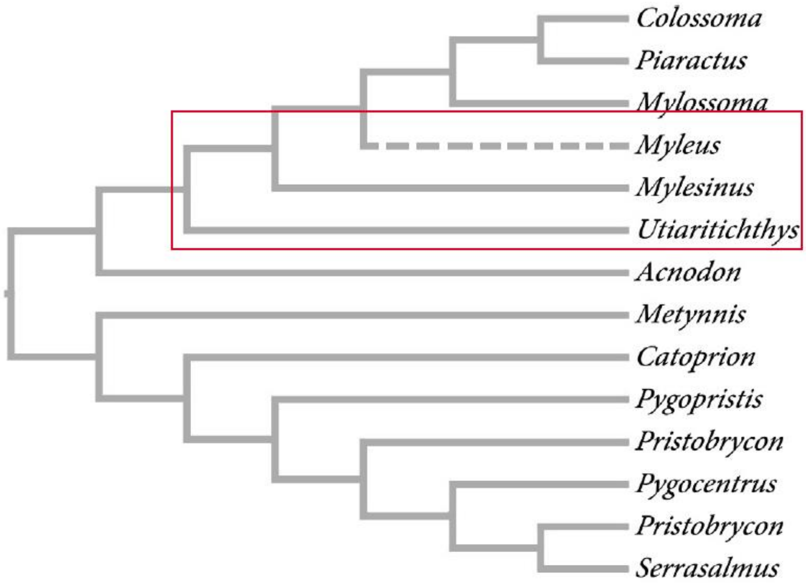

Figura 2. Hipótese de relação filogenética entre as espécies da família Serrasalmidae de acordo com Machado-Allison (1983). Retângulo delimitando as espécies de *Myleus*, *Mylesinus* e *Utiaritichthys*.

Jégu & Santos (1988) descrevem *Mylesinus paucisquamatus* Jégu & Santos para a bacia do Tocantins-Araguaia, espécie anteriormente atribuída por Gosline (1951) como *Mylesinus schomburgkii*. Apesar de já ter sido mencionada em Jégu & Santos (1988) na diagnose de *Mylesinus paucisquamatus*, Jégu *et al*. (1989) descreveram formalmente *Mylesinus paraschomburgkii* Jégu, Santos & Ferreira a partir de espécimes das bacias dos rios Uatumã (Amazonas) e Trombetas (Pará). Jégu *et al*. (1989) relataram ainda que *Mylesinus paraschomburgkii* possivelmente seja sinônimo júnior de *Mylesinus schomburgkii*, diagnosticando as duas espécies unicamente à diferenças nas proporções de subunidades da cabeça. É válido salientar que *Mylesinus schomburgkii* é conhecido apenas de um exemplar incompleto (apenas a cabeça MNHN A.9855) e do desenho da espécie retratado por Valenciennes (1850) (Fig. 3). Além disso, *Mylesinus paraschomburgkii* e *Mylesinus schomburgkii* ocorrem em drenagens do escudo guianense, porém *Mylesinus paraschomburgkii* ocorre em tributários da bacia amazônica (Brasil), enquanto *Mylesinus schomburgkii* tem provável ocorrência para o rio Essequibo (Guiana), rio costeiro do escudo que o drena rumo ao oceano Atlântico. Sendo assim, foram reconhecidas três espécies do gênero *Mylesinus*, i.e. *Mylesinus schomburgkii*, *Mylesinus paraschomburgkii* e *Mylesinus paucisquamatus*.

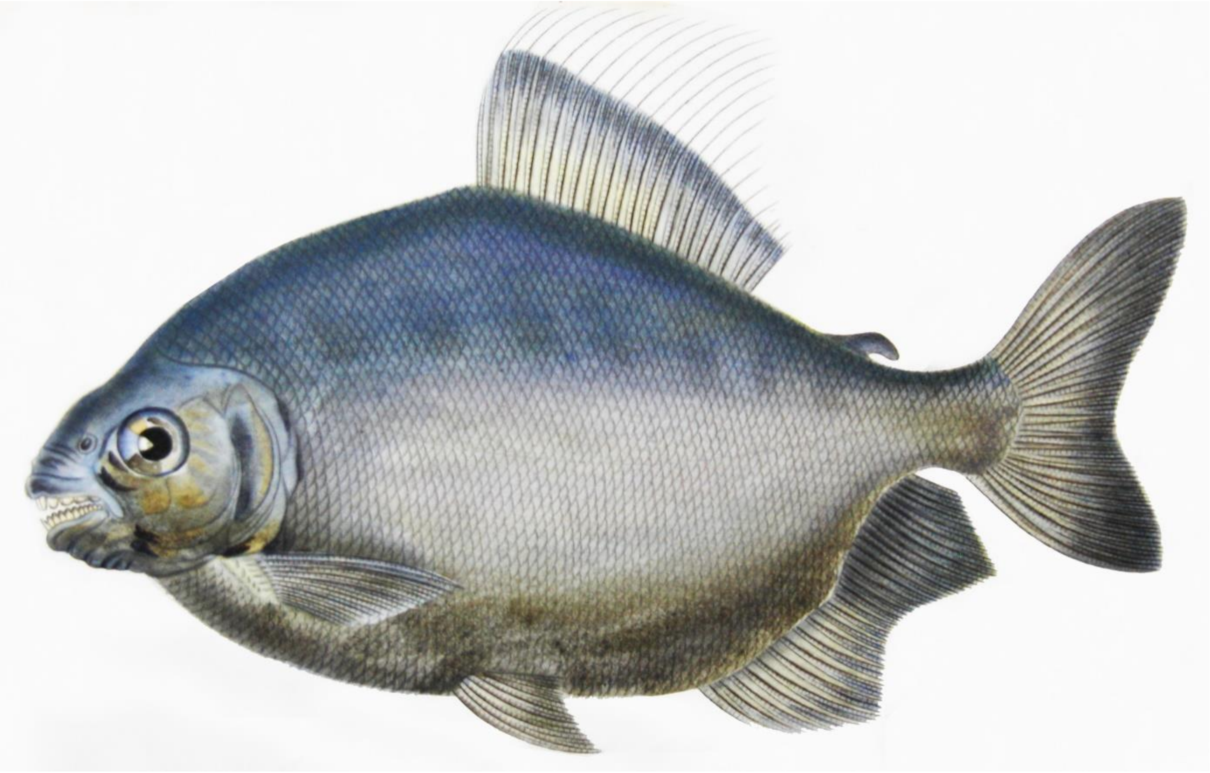

Figura 3. *Mylesinus schomburgkii* retratado em Valenciennes (1850).

Jégu (1992), examinando exemplares provenientes da Volta Grande do rio Xingu, descreveu o gênero *Ossubtus* para alocar a espécie monotípica *Ossubtus xinguense* Jégu. *Ossubtus* foi descrito com base em exemplares com boca estritamente inferior, ausência de espinhos pré-ventrais (característica típica dos serrasalmídeos), séries de dentes pré-maxilares juntas uma a outra, dentes incisiformes fracamente anexados às mandíbulas e mancha umeral conspícua nos juvenis. O gênero e a espécie foram redescritos (Anexo 2) com base no material-tipo e em material adicional por Andrade *et al*. (2016d), é considerada rara e endêmica da porção inferior da bacia do rio Xingu.

Ortí *et al*. (1996) apresentaram a primeira filogenia molecular dos Serrasalmidae, onde a partir das relações filogenéticas, cunhou o termo clado *Myleus*. Para o clado, Ortí *et al*. (1996) levaram em consideração as espécies *Mylesinus paraschomburgkii*, *Myleus* (*Myleus*) *pacu*, *Myleus* (*Myloplus*) *asterias*, *Myleus* (*Myloplus*) *rubripinnis*, *Myleus* (*Myloplus*) *tiete*, *Myleus* (*Prosomyleus*) *schomburgkii*, e um então provável "novo gênero" (i.e. N. gen. A). Note que Ortí *et al*. (1996) considera as espécies de *Myleus* de acordo com Géry (1972). Como resultado da filogenia suportada a partir de DNA mitocondrial, Ortí *et al*. (1996) apresentaram o clado *Myleus* como parafilético, relatando ainda maior relação entre as três espécies, *Myleus* (*Myleus*) *pacu*, *Mylesinus paraschomburgkii* e "N. gen. A", do que com as três espécies de *Myleus* (*Myloplus*) e também com *Myleus* (*Prosomyleus*) *schomburgkii* (Fig. 4). Ortí *et al*. (1996) constatou que o gênero *Myleus*, como sugerido por Géry (1972), resulta em um clado parafilético, e por consequência necessita de estudos à busca de uma melhor resolução.

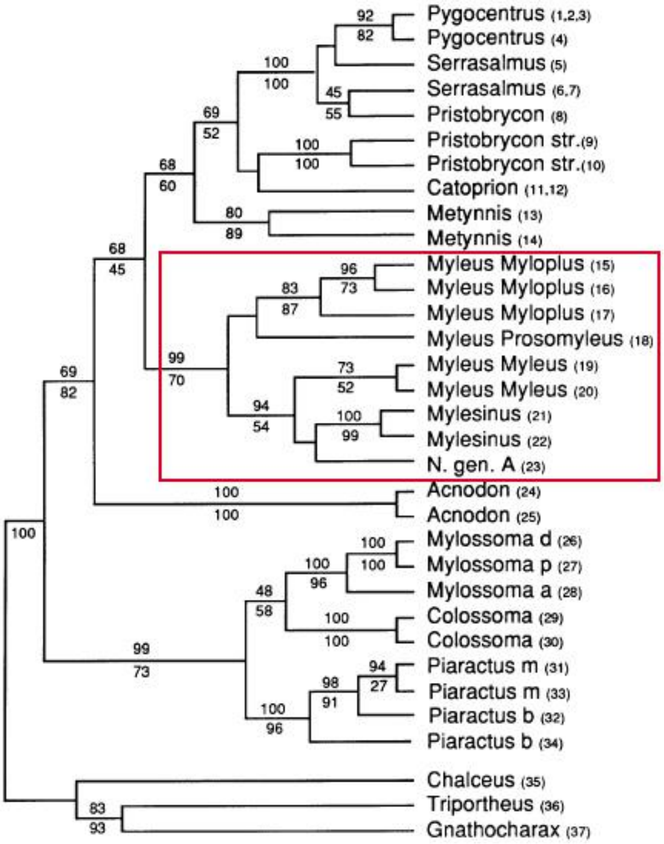

Figura 4. Hipótese de relação filogenética entre as espécies da família Serrasalmidae de acordo com (Ortí *et al*. 1996). Retângulo delimitando o clado parafilético *Myleus*.

Jégu & Santos (2002) reavaliam o status taxonômico do gênero *Myleus* a partir da análise da série-tipo da espécie, além de material adicional e ilustrações, e consideraram que

Myleus setiger e *Myleus pacu* como espécies distintas. Jardine (1841) apresentou ilustrações de dois *Myleus pacu*, um macho (ilustrado na guarda-capa da Tese) com cerca de 400 mm de comprimento total e uma fêmea (ilustrada na capa da tese) com cerca de 600 mm. Além disso, Jardine (1841) descreveu *Myleus pacu* com 43 raios totais na nadadeira anal. Jégu & Santos (2002) mencionam que o formato do corpo de *Myletes pacu* nas ilustrações de Jardine (1841) é muito alongado e o número de raios na nadadeira anal descrito pelo autor é muito elevado (43 *versus* 33-38 dos exemplares de *Myleus setiger* examinados). Além disso, Jégu & Santos (2002) não examinaram qualquer espécime com comprimento tão grande quanto o relatado por Jardine (1841) (*Myleus pacu* ~ 600 mm CT *versus Myleus setiger* ~ 300 mm CP). Jégu & Santos (2002) ao checar o material proveniente do rio Essequibo (mesmo material que Eigenmann (1912) utilizou para alocar *Myleus setiger* em sinonímia de *Myleus pacu*), constataram que esses espécimes eram mais relacionados à *Myleus* (*Myloplus*) do que com as espécies de *Myleus* (*Myleus*), isso porque a série labial de dentes pré-maxilares não era contígua, com um diastema frontal, e as duas séries serem afastadas uma da outra internamente (*versus* série labial do pré-maxilar sem diastema e duas séries pré-maxilares juntas uma da outra, sem afastamento interno em *Myleus setiger*). Portanto, *Myleus setiger* que estava em sinonímia de *Myleus pacu* desde Eigenmann (1912) foi revalidado. Além disso, os espécimes utilizados por Eigenmann (1912) (i.e. FMNH 59292 e FMNH 59298) têm dente sinfiseano reto e de mesma altura que a série principal do dentário (*versus* curvo posteriormente e de menor tamanho que a série principal em *Myleus setiger*). Jégu & Santos (2002) validaram também a espécie *Myleus knerii* que difere de *Myleus setiger* pelo maior número de raios ramificados na dorsal (24 *versus* 18-20, respectivamente). *Myleus pacu*, por sua vez, devido não existir espécimes-tipo para comprovação de sua validade, foi considerado *species inquirenda*.

Jégu *et al*. (2002), a partir da análise do material tipo de *Tometes*, revalidaram o gênero. Jégu *et al*. (2002) constataram que o espécime-tipo de *Tometes unilobatus* (MNHN A.8651), se trata na verdade de uma fêmea de *Tometes trilobatus*, e propõem *Tometes trilobatus* como espécie-tipo do gênero. No mesmo ano, Jégu *et al*. (2002b, 2002c) descreveram mais duas espécies para o gênero *Tometes*, i.e. *Tometes makue* Jégu, Santos & Belmont-Jégu e *Tometes lebaili* Jégu, Keith & Belmont-Jégu. As então três espécies válidas do gênero *Tometes* ocorrem nas drenagens do escudo guianense.

Jégu (2004) atestou a monofilia do clado formado pelas espécies dos gêneros *Myleus*, *Mylesinus*, *Tometes* e *Ossubtus* (Fig. 6) suportada por 12 sinapomorfias não exclusivas: 1) presença de pequena mancha umeral nos juvenis; 2) quando com boca fechada, série principal de dentes no dentário posicionada atrás das duas séries de dentes pré-maxilares; 3) séries de dentes pré-maxilares unidas uma à outra sem espaçamento interno; 4) processo lateral do pré-maxilar comprimido anteroposteriormente; 5) extremidade distal do pré-maxilar limitada ao nível do último dente pré-maxilar; 6) face interna do processo transversal do pré-maxilar formando um eixo que oferece suporte ao maxilar; 7) processo lateral do pré-maxilar com formato, em vista frontal, triangular à sub-retangular; 8) fossa olfativa ampla devido ao mesetmóide estreito; 9) mesetmóide alongado de formato quadrangular à retangular; 10) processo posterior mesetmóide com extremidade posterior oblíqua e articulada com o processo anterior do etmóide lateral; 11) redução do processo transversal do osso pós-temporal em um pequeno espinho; 12) segundo, terceiro e quarto dente da série labial do pré-maxilar com cúspide posterior inserida em um sulco formado na cúspide anterior do dente subsequente.

Jégu *et al*. (2004), a partir da análise do material tipo das então espécies *Myleus* (*Myloplus*) *asterias* e *Myleus* (*Myloplus*) *rubripinnis*, diferenciaram estas duas espécies da espécie-tipo de *Myleus* (i.e. *Myleus setiger*), entre outras características, por terem dentes molariformes e duas fileiras de dentes pré-maxilares com espaçamento interno *versus* incisiformes e duas fileiras de dentes pré-maxilares encostadas uma da outra. Jégu *et al*. (2004) afirmaram que as duas espécies não deveriam mais ser atribuídas a *Myleus*, propuseram então a revalidação do gênero *Myloplus* Gill com as duas espécies, *Myloplus asterias* (Müller & Troschel) espécie-tipo, e *Myloplus rubripinnis* (Müller & Troschel). Jégu *et al*. (2004) foi o estudo que revalidou o gênero *Myloplus*, mas um ano antes, Jégu *et al*. (2003), com base nos exemplares FMNH 59292 e FMNH 59298, que haviam sido atribuídos a *Myleus pacu* por Eigenmann (1912), mais material adicional das drenagens costeiras do escudo guianense, descreveram a espécie *Myloplus planquettei* Jégu, Keith & Le Bail.

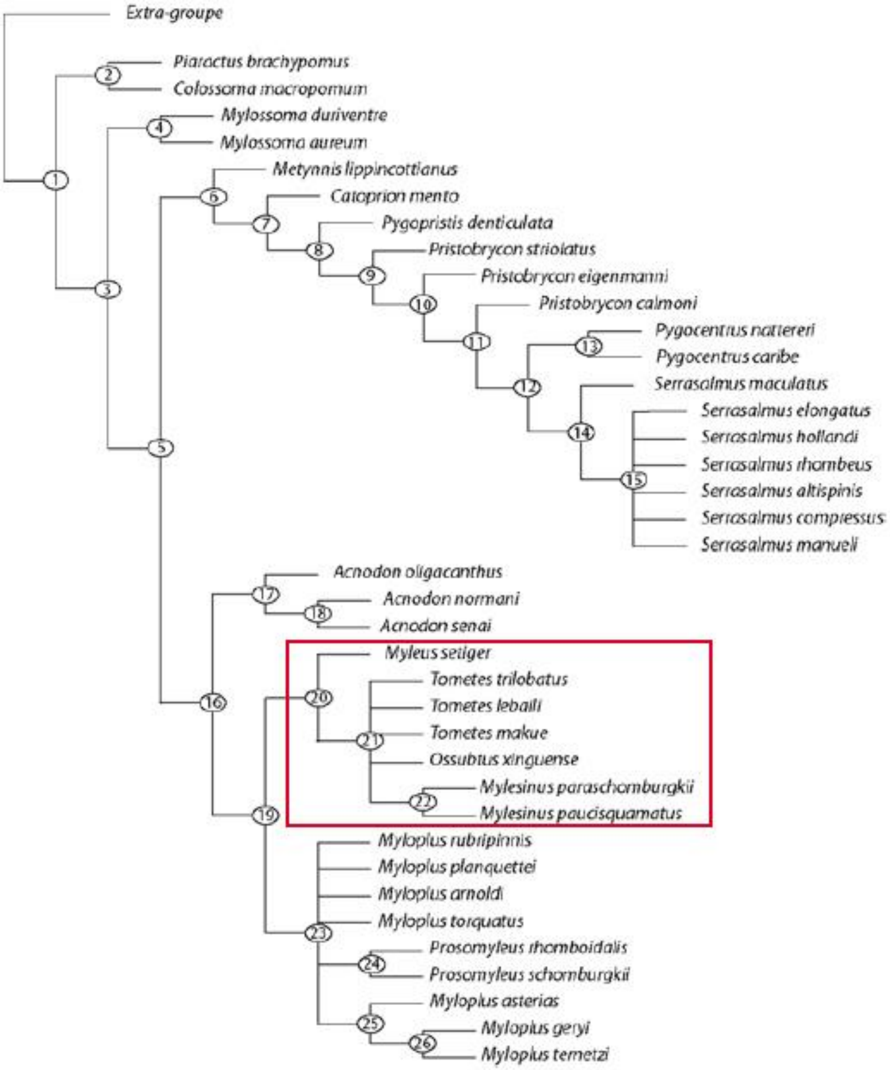

Figura 5. Hipótese de relação filogenética entre as espécies da família Serrasalmidae de acordo com Jégu *et al*. (2004). Retângulo delimitando o clado monofilético *Myleus*.

Dahdul (2007), utilizando dados morfológicos, assim como Jégu *et al*. (2004), corroborou a monofilia para o clado *Myleus*, que por sua vez foi composto pelos gêneros

Myleus, *Mylesinus*, *Tometes*, *Ossubtus* e adicionalmente pelo gênero *Myloplus*. Resultado este que foi de acordo com Ortí *et al*. (1996).

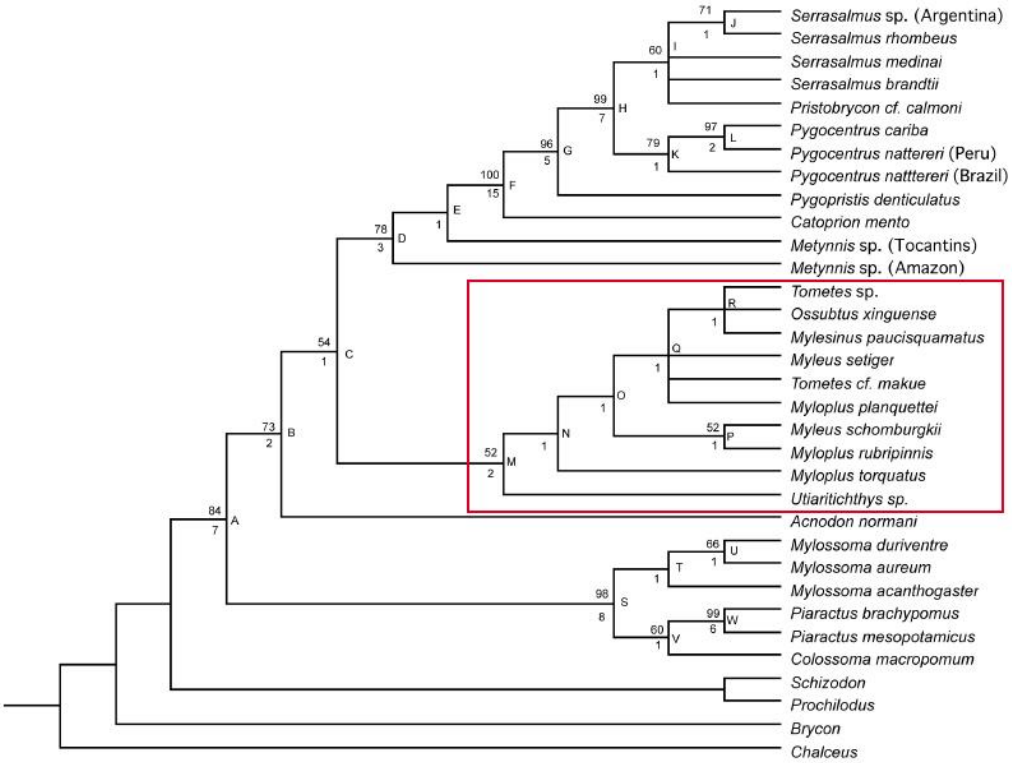

Figura 6. Hipótese de relação filogenética entre as espécies da família Serrasalmidae de acordo com Dahdul (2007). Retângulo delimitando o clado monofilético *Myleus*.

Ortí *et al*. (2008), utilizando a definição mais recente do gênero *Myleus* feita por Jégu & Santos (2002), prepararam uma nova filogenia molecular para a família e confirmaram a monofilia de Serrasalmidae. Ortí *et al*. (2008) apresentaram ainda três clados principais para os Serrasalmidae, o grupo “pacu” (formados pelas espécies dos gêneros *Colossoma*, *Mylossoma* e *Piaractus*), “piranha” (*Serrasalmus*, *Pygocentrus*, *Pygopristis*, *Pristobrycon*, *Catoprion* e *Metynnis*) e “*Myleus*” (*Myleus*, *Mylesinus*, *Tometes* e *Ossubtus*), corroborando a filogenia morfológica proposta por Jégu (2004). Ortí *et al*. (2008) afirmaram que o clado *Myleus* juntamente com as espécies do gênero *Myloplus* forma um grupo polifilético (Fig. 7), e que apenas as relações filogenéticas entre *Myleus setiger* e as espécies de *Mylesinus* e *Tometes* [este último atribuído como “N. gen. A” em Ortí *et al*. (1996)] foram bem suportadas.

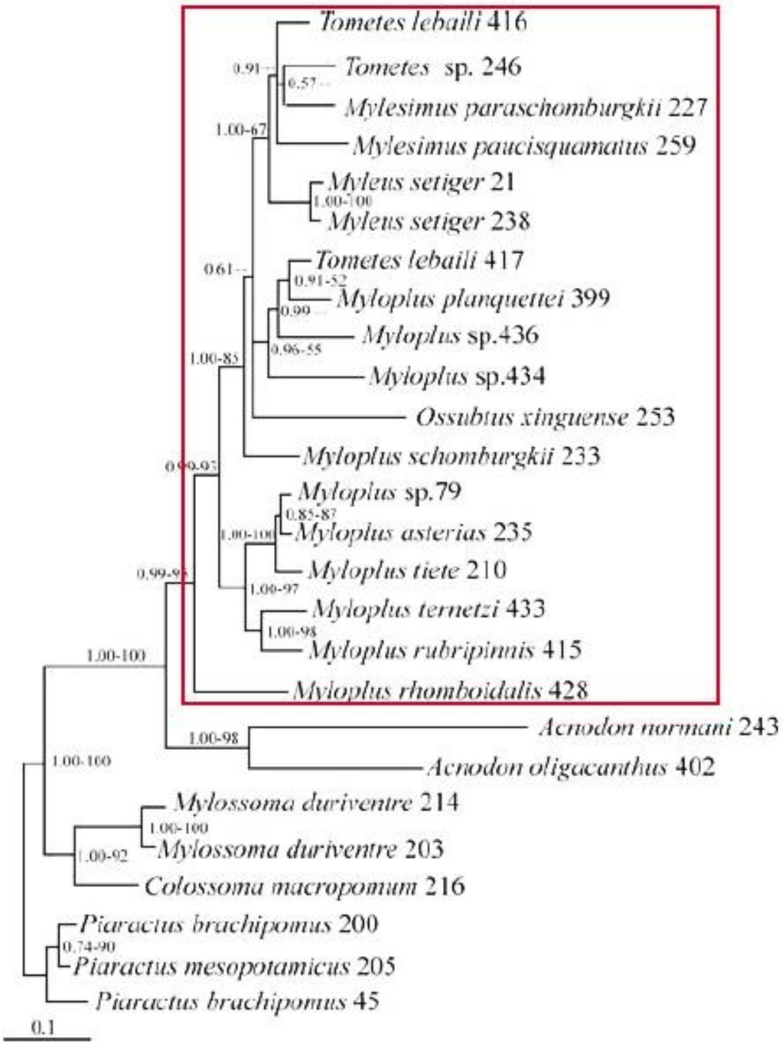

Figura 7. Hipótese de relação filogenética entre as espécies da família Serrasalmidae de acordo com Ortí *et al*. (2008). Retângulo delimitando o clado polifilético *Myleus*.

Andrade *et al*. (2013), baseado em material proveniente da bacia do rio Trombetas atribuído como espécie desconhecida de *Utiaritichthys*, descreveram *Tometes camunani* Andrade, Giarrizzo & Jégu que, assim como as três demais espécies do gênero *Tometes*, ocorre exclusivamente em drenagens do escudo guianense. A atribuição ao gênero *Utiaritichthys* deveu-se ao reporte feito por Gosline (1951) onde *Utiaritichthys sennaebragai* foi descrito como sendo similar à *Myleus* por apresentar serra pré-pélvica delgada, mas com dentição diferente de um *Myleus* usual.

Thompson *et al*. (2014) apresentou a mais recente hipótese filogenética dos Serrasalmidae. As relações filogenéticas para o clado *Myleus* (Fig. 8), em suma, corroboraram os resultados encontrados por Ortí *et al*. (2008), onde as espécies dos gêneros *Myleus*, *Mylesinus*, *Tometes*, *Ossubtus* e *Myloplus* formam um clado polifilético com baixa resolução. Thompson *et al*. (2014) encontraram ainda a espécie *Myloplus rhomboidalis* como o táxon mais basal dentre as espécies do clado *Myleus*.

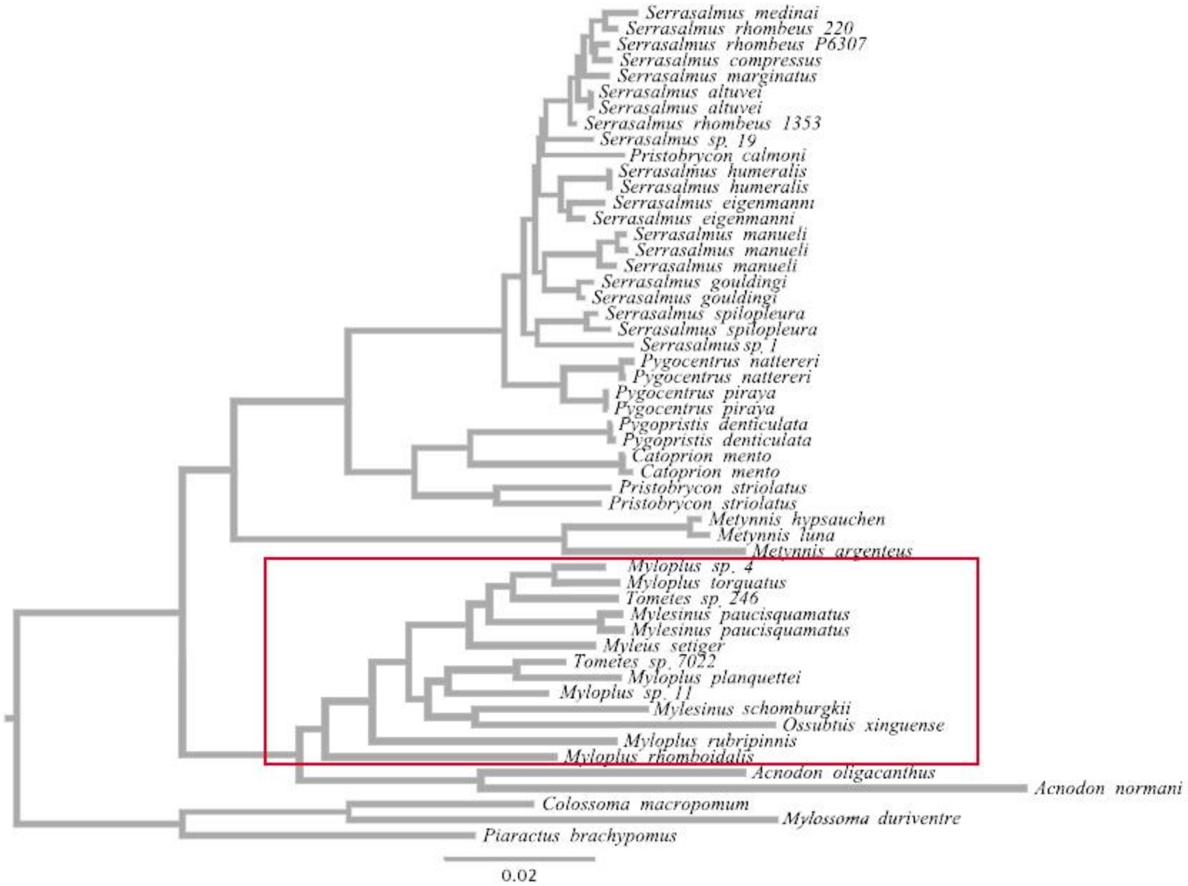

Figura 8. Hipótese de relação filogenética entre as espécies da família Serrasalmidae de acordo com Thompson *et al*. (2014). Retângulo delimitando o clado polifilético *Myleus*.

Andrade *et al*. (2016b) descreveram as duas espécies *Tometes ancylorhynchus* Andrade, Jégu & Giarrizzo e *Tometes kranponhah* Andrade, Jégu & Giarrizzo, a primeira ocorrendo nas drenagens das bacias dos rios Xingu e Tocantins-Araguaia, e a segunda endêmica da bacia do rio Xingu, sendo esse a primeira descrição do gênero *Tometes* para o escudo brasileiro. Vale ressaltrar que *Tometes ancylorhynchus* se trata na verdade da espécie que Gosline (1951) reportou como *Utiaritichthys sennaebragai* para a bacia do Tocantins-Araguaia, e *Tometes kranponhah* a espécie que Ortí *et al*. (2008) reportou como "N. gen. A" para a bacia do rio Xingu.

Andrade *et al*. (2016a), examinando material da bacia do rio Madeira atribuído a uma espécie desconhecida de *Tometes,* descreveram a partir desse material a espécie *Myloplus zorroi* Andrade, Jégu & Giarrizzo (Anexo 3). Tomando como base as características diagnósticas das espécies dos gêneros *Myleus* e *Mylopus*, propostas por Jégu & Santos (2002) e Jégu *et al*. (2004), respectivamente, Andrade *et al*. (2016a) propuseram ainda que oito espécies anteriormente atribuídas ao gênero *Myleus*[1] fossem alocadas em *Myloplus* [i.e. *Myloplus arnoldi** (Ahl), *Myloplus levis** (Eigenmann & McAtee), *Myloplus lobatus** (Valenciennes), *Myloplus rhomboidalis* (Cuvier), *Myloplus schomburgkii* (Jardine), *Myloplus ternetzi* (Norman), *Myloplus tiete* (Eigenmann & Norris) e *Myloplus torquatus* (Kner)]. Em estudo subsequente, utilizando a mesma definição, Andrade *et al*. (2016c) descrevem *Myloplus lucienae* Andrade, Ota, Bastos & Jégu (Anexo 4) para a bacia do rio Negro, totalizando 13 espécies atribuídas ao gênero *Myloplus* e, por consequência, cinco espécies atribuídas ao gênero *Myleus*, a constar *Myleus altipinnis*, *Myleus knerii*, *Myleus micans*, *Myleus setiger* e a *species inquirenda* conhecida unicamente pela descrição original e do desenho de Jardine (1841), *Myleus pacu*.

Assim, o clado *Myleus* constitui um grupo polifilético formado por 28 espécies distribuídas em cinco gêneros (*Myleus*, *Mylesinus*, *Tometes*, *Ossubtus* e *Myloplus*), sendo cinco espécies válidas alocadas no gênero *Myleus*, três espécies de *Mylesinus*, seis espécies de *Tometes*, o monotípico *Ossubtus*, e o mais especioso com 13 espécies de *Myloplus*. No entanto, diversidade e distribuição do clado *Myleus* continua mal compreendida, principalmente no que

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[1] Espécies atribuídas em estudos como checklist de espécies, por exemplo, Jégu (2003), três dessas espécies (indicadas com o uso de um asterisco) ainda sem estudo formal quanto o seu status taxonômico.

diz respeito a atribuição das espécies aos gêneros como atualmente conhecidos, em especial, a atribuição das espécies entre os gêneros *Myleus* e *Myloplus*. Chaves de identificação para os gêneros *Myleus*, *Mylesinus*, *Tometes*, *Ossubtus* e *Myloplus* (Apêndice 1) e suas respectivas espécies e com distribuição conhecida foi fornecida (Apêndice 2).

1.3. Ecologia trófica dos Serrasalmidae de corredeiras

Os peixes do clado *Myleus* são aqueles serrasalmídeos herbívoros particularmente relacionados aos ambientes encachoeirados, esses peixes são usualmente encontrados nas porções mais altas dos rios que drenam os escudos (Andrade *et al*. 2013). O termo 'serrasalmídeo de corredeira' é usualmente atribuído àquelas espécies dos gêneros que compõem o clado *Myleus* (*sensu* Jégu 2004), isso é, espécies de *Myleus*, *Tometes*, *Mylesinus* e *Ossubtus*. Além disso, as espécies do clado *Myleus* são caracterizadas por adaptações funcionais, como por exemplo, dentes incisiformes especializados no corte de folhas das macrófitas aquáticas que ocorrem nas corredeiras (Andrade *et al*. 2016d; Jégu & Santos 2002), e um longo intestino que os auxilia assimilar fontes vegetais, principal recurso alimentar destas espécies (Jégu *et al*. 1989, 2002a; b). Para tanto, a excelente sincronia entre os traços funcionais e a utilização dos recursos podem colaborar potencialmente numa maior eficiência no fluxo de energia entre as fontes e seus consumidores (Correa & Winemiller 2014).

Informações ecológicas para os serrasalmídeos não reofílicos são abundantes, como por exemplo, para os grandes frugívoros/omnívoros de interesse comercial (*e.g. Colossoma macropomum* e *Piaractus brachypomus*) e também para as carnívoras piranhas (*e.g. Serrasalmus* spp.), abundantes em reservatórios (Casatti *et al*. 2003; Correa *et al*. 2007; Correa & Winemiller 2014; Ferreira *et al*. 2014; Goulding 1980; Loubens & Panfili 1997, 2001; Oliveira *et al*. 2004). Por outro lado, estudos sobre ecologia trófica dos serrasalmídeos de corredeira são escassos, os mais detalhados se restringem aos realizados para a espécie *Mylesinus paraschomburgkii* (Jégu *et al*. 1989; Santos *et al*. 1997), e também pelo recente trabalho elaborado para *Mylesinus paucisquamatus* (Vitorino Júnior *et al*. 2016). Jégu *et al*. (1989) descreveram modificações morfológicas funcionais relacionadas com a mudança do comportamento alimentar entre os juvenis, com comportamento invertívoro, e os adultos estritamente herbívoros. Já Santos *et al*. (1997) analisaram de maneira minuciosa a alimentação desta mesma espécie entre quatro tributários da margem esquerda do rio Amazonas, apresentando a estrema importância da macrófita Podostomaceae na alimentação da espécie. Por exemplo, Vitorino Júnior *et al*. (2016), para o estudo sobre a espécie *Mylesinus paucisquamatus*, reuniram cerca de 80 indivíduos da espécie que haviam sido coletados ao longo de uma década. Indicando raridade, reofilia e especialização alimentar vinculado ao hábitat de corredeiras, Vitorino Júnior *et al*. (2016) apontaram ainda o agravamento da vulnerabilidade imposta a *Mylesinus paucisquamatus* frente a perda de hábitat provocada por ações antrópicas. Não é de se admirar que informações ecológicas sobre os serrasalmídeos de corredeiras sejam incipientes, esses peixes habitam um ambiente de onde coletas são dificultadas pela ação de águas rápidas.

Em ecologia trófica, destaca-se o conhecimento sobre as relações das espécies com o seu ambiente, normalmente bem compreendidas a partir de estudos sobre o fluxo de energia entre os organismos envolvidos (Newsome *et al*. 2007, 2010). Em organismos aquáticos, os peixes podem ser considerados como o último nível de uma série de transformações do carbono (= fluxo de energia) que têm início com a fixação do CO_2 pelas fontes autotróficas (Forsberg *et al*. 1993). O carbono presente nos peixes é resultado da assimilação do carbono dos produtores primários e da eficiência com a qual este é passado ao longo da cadeia alimentar nos consumidores (Fry 2006). Levando em consideração o método tradicional da análise da dieta, este pode mascarar ou estimar de maneira errônea o fluxo de energia em ecossistemas aquáticos

(Gu *et al*. 1996). Isso porque a ocorrência de determinado item alimentar no estômago do consumidor não reflete necessariamente sua importância como fonte de carbono para aquele indivíduo ou mesmo como fonte na cadeia alimentar (Forsberg *et al*. 1993), fornecendo apenas um esboço da dieta naquele momento específico, dificultando uma correta identificação das principais fontes alimentares para os consumidores (Pearson *et al*. 2003). Do mesmo modo, o processo diferenciado na digestão de cada item pode acarretar numa assimilação do carbono também diferenciada (Caswell & Reed 1976; Forsberg *et al*. 1993), dado que, geralmente, os itens alimentares identificáveis no estômago dos peixes são aqueles menos digeríveis na dieta (Todd *et al*. 1997). Já aqueles não identificáveis não são determinados como fazendo parte dela, dificultando uma acurada definição sobre dieta, posição trófica e partilha de nicho. No entanto, como alternativa para solucionar as limitações da metodologia tradicional, análises de isótopos estáveis de carbono ($\delta^{13}C$) e nitrogênio ($\delta^{15}N$) vêm sendo bem sucedidas na definição dos componentes alimentares assimilados por um longo período de tempo (Hesslein *et al*. 1993), se tornando assim um bom método na descrição das relações tróficas. Para tanto, estudos que integrem os métodos tradicionais e isótopos estáveis são robustos como descritores tróficos (Correa & Winemiller 2014). Tendo em vista que os serrasalmídeos de corredeira apresentam grande variabilidade alimentar durante o crescimento, e a utilização dos mesmos recursos nas corredeiras, o estudo foi parcialmente dedicado na caracterização da partilha de nicho trófico desses peixes com base em três espécies sintópicas num rio de águas claras da bacia Amazônica brasileira (*i.e.* rio Xingu) utilizando uma abordagem integrada associando o método tradicional da análise de conteúdos estomacais e a análise de isótopos estáveis.

A bacia do rio Xingu abrange os serrasalmídeos de corredeira *Myleus setiger*, *Ossubtus xinguense*, *Tometes ancylorhynchus* e *Tometes kranponhah*, que durante o período de seca partilham o ambiente de águas rápidas (Andrade *et al*. 2016b). O rio Xingu apresenta ainda inúmeras corredeiras durante esse período, estas por sua vez fornecem a esses Serrasalmidae extensas áreas recobertas por Podostomaceae (Philbrick *et al*. 2010), plantas aquáticas comumente associadas a uma abundante macrofauna composta por larvas de insetos (Horeau *et al*. 1998).

No estudo recente sobre a diversidade trófica dos peixes de corredeiras do rio Xingu, utilizando análises morfológicas e de nicho isotópico, Zuluaga-Gómez *et al*. (2016) caracterizaram os serrasalmídeos de corredeiras com amplo nicho trófico. No entanto, mesmo sendo direcionado aos peixes das corredeiras, Zuluaga-Gómez *et al*. (2016) agruparam serrasalmídeos de distintos níveis tróficos desde herbívoros fortemente reofílicos *Myleus setiger*, *Tometes kranponhah* e *Ossubtus xinguense*, os frugívoros *Myloplus arnoldi* e *Myloplus schomburgkii*, comumente capturados em remansos, e até uma espécie estritamente carnívora *Serrasalmus rhombeus*, encontrada atipicamente em corredeiras. Observando a diversidade utilizada, torna-se impreciso caracterizar os serrasalmídeos de corredeiras como tendo amplo nicho trófico. Assim, o presente estudo, que integra análises tróficas e morfológicas funcionais, permitirá elucidar as relações entre os serrasalmídeos de corredeira e qual a importância trófica deste ambiente para estas espécies.

Objetivos

Geral

- Descrever a diversidade taxonômica do clado *Myleus* e a ecologia trófica dos serrasalmídeos das corredeiras Amazônicas.

Específicos

- Ilustrar a diversidade dos peixes Serrasalmidae do clado *Myleus*;

- Descrever as espécies novas para a ciência daqueles gêneros do clado *Myleus*, levando em consideração o clado monofilético proposto por Jégu (2004) e Ortí *et al.* (2008), isto é, espécies dos gêneros *Myleus*, *Tometes*, *Mylesinus* e *Ossubtus*;

- Propor chaves de identificação aos níveis genérico e específico do clado polifilético *Myleus*, isto é, espécies dos gêneros mencionados no item anterior, adicionadas da diversidade do gênero *Myloplus*;

- Apresentar distribuição, e aspectos sobre ecologia e conservação das espécies novas;

- Caracterizar a ecologia trófica dos serrasalmídeos de corredeiras a partir da análise integrada entre dieta e isótopos estáveis;

- Descrever a partilha dos nichos alimentar e isotópico entre três serrasalmídeos de corredeira sintópicos;

- Discorrer sobre as características morfológicas funcionais que tornaram estas espécies especializadas ao ambiente de corredeiras.

Resultados

A investigação sobre a diversidade dos serrasalmídeos de corredeira, baseadas em dados morfológicos (ver metodologia no Capítulo 1), ilustraram clara distinção entre os cinco gêneros incialmente propostos para o clado polifilético *Myleus*, a constar de *Myleus*, *Tometes*, *Mylesinus*, *Ossubtus* e *Myloplus* (ver chave de identificação de gêneros no Apêndice 1). Chaves de espécies para os gêneros foram providenciadas (Apêndice 2).

As análises morfológicas revelaram ainda três novas espécies para o gênero *Tometes* aqui descritas (Capítulos 1 e 2), e aliadas com análises moleculares das espécies de *Tometes*, relações filogenéticas entre as espécies foram apresentadas (Capítulo 2).

A ecologia trófica estudada para o período de estiagem (quando os peixes ficam confinados às corredeiras) entre três espécies sintópicas de serrasalmídeos de corredeira, revelaram elevada sobreposição dos nichos alimentar e isotópico, variações ontogenéticas no comportamento alimentar e na posição trófica, e traços morfológicos funcionais especializados ao ambiente de corredeira (Capítulo 3).

Metodologia, resultados detalhados e material examinado seguem nos três capítulos escritos em formato de artigos científicos apresentados na Tese. Adicionalmente, material examinado para espécies do gênero *Myloplus* nos artigos publicados conforme Anexos 6-7.

Capítulo 1

Tometes kranponhah e *Tometes ancylorhynchus* (Characiformes: Serrasalmidae), dois novos serrasalmídeos fitófagos e as primeiras espécies de *Tometes* descritas para o escudo brasileiro[2]

Marcelo C. Andrade, Michel Jégu & Tommaso Giarrizzo

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[2] Capítulo elaborado em forma de manuscrito de acordo com o periódico "Journal of Fish Biology", Qualis CAPES 2016 para área de Biodiversidade B1. Situação atual: artigo aceito em 2015 e publicado em 2016 (Anexo 1).

"Without taxonomy to give shape to the bricks and systematics to tell us how to put them together, the house of biological science would be a meaningless jumble"

Sir Robert May
"Baron May of Oxford"
Cientista australiano conhecido
pela aplicação de técnicas
matemáticas em estudos de
biologia populacional

Tometes kranponhah and *Tometes ancylorhynchus* (Characiformes: Serrasalmidae), two new phytophagous serrasalmids, and the first *Tometes* species described from the Brazilian Shield

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Running headline: Two new *Tometes* species from Brazilian Shield

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ABSTRACT

Two new species of *Tometes* from the Brazilian Shield rapids are described. *Tometes kranponhah* is endemic to the Xingu River basin, whereas *Tometes ancylorhynchus* occurs both in the Xingu and the Tocantins–Araguaia river basins. The two species are sympatric in the Xingu drainages and have many similarities in morphology and colouration. Major diagnostic differences are the dark pigmentation on the opercle of *T. kranponhah* and its distinct snout shape and arrangement of premaxillary teeth. In addition, *T. kranponhah* is a large fish that is abundant in the Xingu River, whereas *T. ancylorhynchus* is a medium-sized fish for which there are few records.

Key words: *Myleus*; rheophilic fish; Xingu; Tocantins; new species; taxonomy.

INTRODUCTION

Neotropical Serrasalmidae fishes are generally easily recognized by their compressed, disc-shaped bodies, dorsal fin preceded by a strong predorsal spine, and midventral keel formed by a series of abdominal spines (Géry, 1972, 1977). However, individuals in the *Myleus* clade, an unusual group of serrasalmids, do not possess a marked midventral keel in the prepelvic area, because these spines are poorly developed or even absent (Andrade *et al.*, 2013). Other diagnostic morphological features of this group are the presence of incisiform teeth and no internal gap separating the two rows of premaxillary teeth (Jégu, 2004). The *Myleus* group forms a monophyletic assemblage of rheophilic fishes that are only found in the highlands of the Brazilian and Guiana Shields (Jégu, 2004; Ortí *et al.*, 2008).

The group consists of four genera: *Myleus* Müller & Troschel 1844, *Mylesinus* Valenciennes 1850, *Ossubtus* Jégu 1992, and *Tometes* Valenciennes 1850. The most widely distributed species is *Myleus setiger* Müller & Troschel 1844, which occurs in the Brazilian and Guiana Shields. There are two species of *Mylesinus*: *Mylesinus paraschomburgkii* Jégu, Santos & Ferreira 1989 occurs widely in drainages of the Guiana Shield, whereas *Mylesinus paucisquamatus* Jégu & Santos 1989 is found only in the Tocantins–Araguaia basin. The monotypic *Ossubtus xinguense* Jégu 1992 is endemic to the Xingu River basin and is threatened (Jégu, 2003; Jégu & Zuanon, 2005; Andrade *et al.*, 2013). Finally, the genus *Tometes* contains four species, all found in the rivers of the Guiana Shield: *Tometes camunani* Andrade, Giarrizzo & Jégu 2013 is distributed in the Trombetas River basin, *Tometes lebaili* Jégu, Keith & Belmont-Jégu 2002 is distributed along the coastal drainages of French Guiana and Suriname, *Tometes makue* Jégu, Santos

& Belmont-Jégu 2002 is found in the middle and upper Negro and Orinoco River basins, and *Tometes trilobatus* Valenciennes 1850 is restricted to the northeastern Guiana Shield rivers.

In this report, two novel *Tometes* species from the Brazilian Shield are described. Their presence in this area extends the known range of this genus to the left-bank tributaries of the lower Amazon basin. Samples analysed in this study consisted of upper Xingu River specimens from the inventories of Leopold III and J. P. Gosse in 1968 and Tocantins–Araguaia basin specimens reported by Gosline (1951) and Géry (1977) as *Utiaritichthys sennaebragai* Miranda Ribeiro 1937. The two new species are difficult to distinguish due to similar colouration patterns. However, our detailed analysis focussing on variation in dentition and osteological characters enabled the two species to be distinguished.

MATERIAL AND METHODS

Measurements and counts were taken on the left side of the specimens whenever possible, following the methods detailed in Jégu *et al*. (2002a) and Jégu *et al*. (2003). For each species, meristic data are presented as the range of counts, followed in parentheses by the value observed for the holotype. Standard length (L_S) is expressed in mm and body measurements are expressed as percentages of L_S, while subunits of the head are expressed as percentages of head length (L_H). Vertebral and supraneural counts were made from 14 radiographed specimens, four dry skeletons (skel.), and two cleared and stained (c&s) specimens, prepared according to the methods of Taylor and Van Dyke (1985). Osteological terminology follows

Weitzman (1962). Vertebral counts include the Weberian apparatus considered as four elements and the fused caudal centra (PU1+U1) as a single bone.

Institutional abbreviations are as follows: ANSP (Academy of Natural Sciences of Drexel University, Philadelphia); BMNH (Natural History Museum, London); CAS (California Academy of Sciences, San Francisco); GEA (Laboratório de Ictiologia do Grupo de Ecologia Aquática, Universidade Federal do Pará, Belém); IEPA (Instituto de Ensino Profissional da Amazônia, Macapá); INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus); IRSNB (Institut royal des Sciences naturelles de Belgique, Bruxelles); LIA (Laboratório de Ictiologia de Altamira, Universidade Federal do Pará, Altamira); MNHN (Muséum national d'Histoire naturelle, Paris); MPEG (Museu Paraense Emilio Goeldi, Belém); MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo); UFPA (Universidade Federal do Pará, Belém); ZMA [Zoologisch Museum Universiteit van Amsterdam; specimens now at RMNH (Rijksmuseum Museum van Natuurlijke Historie, Leiden)]; and ZUEC (Museu de Zoologia da Universidade Estadual de Campinas 'Adão José Cardoso', Campinas).

RESULTS

TOMETES KRANPONHAH N. SP. (Figs. 1–2, 5, 7–9; Table I)

N. gen. 1. – Jégu (1992): 283 [distribution of rheophilic serrasalmids].

N. gen. A. – Ortí *et al.* (1996): 174 [molecular phylogeny of piranhas].

Tometes sp. – Zuanon (1999): 17 [natural history of fish fauna of rapids]; Géry & Zarske (2004): 39 Fig. 17 [fishes from Iriri River syntopic with *Moenkhausia heikoi*]; Ortí *et al*. (2008): Supplementary Material [molecular phylogeny of the Serrasalmidae].

Tometes sp. Xingu – Camargo & Giarrizzo (2009): 218–219 [biological parameters of Xingu River].

Utiaritichthys sennaebragai – Goulding (1980): 111 [in part, ecology of fishes]; Pereira & Castro (2014): 401 [in key of species, reference to Xingu River].

Holotype

MPEG 31000 (132.3 mm L_S), Brazil, Pará, Altamira, Rio Xingu, Cachoeira do Espelho, 3°38′49.9″S 52°22′54.5″W, L.M. Sousa & A.P. Gonçalves, 4 August 2012.

Paratypes

All from Brazil, Rio Xingu basin. ANSP 193019 (two specimens, 153.8–345.0 mm L_S), Pará, Altamira, Rio Iriri, Cachoeira Grande do Iriri, ca. 15 km upstream from confluence with Rio Xingu. 3°50′37″S 52°44′02″W. M.H. Sabaj Pérez *et al.*, October 2012. ANSP 193062 (one specimen, 90.4 mm L_S), Pará, Altamira, Rio Xingu, Volta Grande, Cachoeira do Jericoá, ca. 55 km east-southeast of Altamira. 3°21′57.4″S 51°43′59.2″W. M.H. Sabaj Pérez *et al.*, October 2012. ANSP 194659 (one specimen, 250 mm L_S), Pará, Altamira, Rio Iriri, along left bank within and immediately below Cachoeira Grande do Iriri, ca. 15 km upstream from confluence with Rio Xingu. 3°50′34.62″S 52°44′10.74″W. M.H. Sabaj Pérez *et al.*, 9 September 2013. GEA 1961 (one specimen, 124.9 mm L_S) and MPEG 31002 (22 specimens, 74.6–202.1 mm L_S), Pará, Altamira, Rio Xingu, Pedral do Landi, 3°35′11.2″S 51°49′07.7″W, M.C. Andrade & M.A. Zuluága-Gómez, October 2012. INPA 46976 (one specimen, 105.1 mm L_S), Pará, Altamira, Rio Iriri, Estação Ecológica Terra do

Meio, 6°42′40.5″S 53°55′05.2″W. B.F. Morales *et al.*, 21 August 2012. INPA 11729 (one specimen c&s, 86.8 mm *L*S), Pará, Senador José Porfírio, Rio Xingu, Cachoeira Kaituká, 3°33′47″S 51°53′20″W, Eq. Ictiologia INPA, 12 October 1992. IRSNB 889 (six specimens, 72.2–83.2 mm *L*S), Mato Grosso, Rio Xingu, Cachoeira Von Martius, 10°02′56.5″S 52°58′03.3″W, Léopold III, S.M. & J.P. Gosse, 30 November 1964. LIA 2305 (one specimen, 88.5 mm *L*S), Pará, Altamira, Rio Xingu, Pedral do Landi, 3°35′11.2″S 51°49′07.7″W, M.C. Andrade & M.A. Zuluága-Gómez, 10 October 2012. MPEG 31001 (five specimens, 257.5–319.0 mm *L*S), Pará, Altamira, Rio Xingu, Pedral do Roboque Velho, nearby Ilha da Taboca, 3°22′04″S 51°59′59″W, M.C. Andrade, 27 July 2011. MPEG 31003 (three specimens, 304.6–350.0 mm *L*S), Pará, Altamira, Rio Bacajá, 3°39′45.5″S 51°33′19.8″W, M.C. Andrade, 11 January 2011. MPEG 31004 (one specimen, 234.9 mm *L*S), Pará, Altamira, Rio Bacajá, 3°45′27″S 51°34′58.5″W, M.C. Andrade, 25 October 2010. MPEG 31005 (one specimen, 111.7 mm *L*S), Pará, Belo Monte, Rio Xingu, 3°07′14.5″S 51°42′56.8″W, M.C. Andrade, 13 April 2012. MPEG 31006 (one specimen, 320.1 mm *L*S), Pará, Altamira, Rio Bacajá, 3°34′47″S 51°35′28.6″W, R.R.S. Oliveira, 26 November 2012. MZUSP 105645 (one specimen, 207.8 mm *L*S), Pará, Altamira, Rio Xingu, 3°14′49″S 51°41′40″W, M. Camargo-Zorro, 25 July 2001. MZUSP 105684 (one specimen, 260.1 mm *L*S), Pará, Altamira, Rio Xingu, Boa Esperança, 3°32′26.2″S 52°21′13.7″W, Eq. Ictiologia da UFPA, 11 November 2000. ZUEC 10024 (two specimens, 60.4–115.1 mm *L*S), Pará, Altamira, Rio Iriri, Cachoeira Grande, 3°50′36.9″S 52°44′00.6″W, L.M. Sousa, 2 July 2012.

Additional material (not types)

All from Brazil, State of Pará, Rio Xingu basin. MPEG 31007 (three specimens, 173.6–192.0 mm *L*S), Pará, Altamira, Rio Xingu, Pedral do Roboque Velho, nearby Ilha da

Taboca, 3°22′04″S 51°59′59″W, M.C. Andrade, 27 July 2011. MPEG 31008 (two specimens, 83.4–86.9 mm L_S), Pará, Anapú, Rio Xingu, Cachoeira Tapaiúna, 3°08′40″S 51°40′19″W, M. Camargo-Zorro, 9 January 2001. MPEG 31009 (one specimen, 57.7 mm L_S), Pará, Vitória do Xingu, Rio Xingu, Cachoeira do Jericoá, 3°21′57.4″S 51°43′59.2″W, L.M. Sousa, July 2012. MPEG 31010 (two specimens, 45.8–67.7 mm L_S), Pará, Altamira, Rio Xingu, Pedral do Landi, 3°35′11.2″S 51°49′07.7″W, M.C. Andrade, July 2012. MPEG 31011 (one specimen, 153 mm L_S), Pará, Altamira, Rio Bacajá, 3°39′45.5″S 51°33′19.8″W, M.C. Andrade, 11 January 2011. GEA 1497 (one specimen, 120 mm L_S, skel.), Pará, Altamira, Rio Xingu, Pedral do Landi, 3°35′11.2″S 51°49′07.7″W, M.C. Andrade & M.A. Zuluága-Gómez, 10 October 2012. MPEG 31012 (one specimen, 215.3 mm L_S), Pará, Altamira, Rio Xingu, 2°40′46.4″S 52°00′01.9″W, L.M. Sousa, 4 July 2012. MPEG 31013 (one specimen, 190.6 mm L_S), Pará, Altamira, Rio Xingu, upstream of the confluence with Rio Bacajá, 3°34′51.7″S 51°51′03.6″ W, M.C. Andrade, 27 July 2011. GEA 1724 (one specimen, 370 mm L_S), Pará, Altamira, Rio Xingu, 3°18′04″S 51°41′10″W, A.P. Gonçalves, 17 January 2013. INPA 46977 (three specimens, 66.2–87.5 mm L_S), Pará, Altamira, Rio Iriri, Estação Ecológica Terra do Meio, 6°51′12.5″S 53°51′10.8″W. B.F. Morales *et al.*, 18 August 2012. INPA 46978 (one specimen, 314.2 mm L_S), Pará, Altamira, Rio Iriri, Estação Ecológica Terra do Meio, 6°41′51.4″S 53°55′33.6″W. B.F. Morales *et al.*, 20 August 2012. INPA 46979 (one specimen, 64.75 mm L_S), Pará, Altamira, Rio Iriri, Estação Ecológica Terra do Meio, 5°45′28.1″S 54°13′29.6″W. B.F. Morales *et al.*, 27 August 2012. INPA 46980 (one specimen, 70.2 mm L_S), Pará, Altamira, Rio Iriri, Estação Ecológica Terra do Meio, 5°28′39.3″S 54°21′24.1″W. B.F. Morales *et al.*, 30 August 2012. GEA 1939 (one specimen, 305 mm L_S, skel.), Pará, Altamira, Rio Xingu, Pedral do Roboque Velho, nearby Ilha da Taboca, 3°22′04″S 51°59′59″W, M.C. Andrade, 27 July 2011. GEA 1940 (head, 72 mm H_L, skel.), Pará, Altamira, Rio Bacajá, Prato do Índio, 3°33′21.3″S 51°40′31.4″W, M.C. Andrade, 29 October 2010. GEA 1954 (one specimen, 94.4 mm L_{S}), Pará, Altamira, Rio Xingu, Cachoeira do Espelho, 3°40′06.8″S 52°26′16.4″W, L.M. Sousa, 4 July 2012. GEA 1959 (one specimen, 59.9 mm L_{S}), Pará, Altamira, Rio Xingu, Volta Grande, rapids downstream of Cachoeira do Jericoá, 3°19′28.9″S 51°44′53.5″W, L.M. Sousa, 21 September 2012. LIA 59 (37 specimens, 57.3–92.2 mm L_{S}), Pará, Vitória do Xingu, Rio Xingu, Cachoeira do Jericoá, 3°21′57.4″S 51°43′59.2″W, A.P. Gonçalves *et al.*, 24 November 2012. MNHN 1998–1174 (not found in collection, three specimens, 90–110 mm L_{S}), Pará, Altamira, Rio Xingu, J. Zuanon & L. Rapp Py-Daniel, October 1990. MNHN 1998–1175 (not found in collection, eight specimens, 60–100 mm L_{S}), Pará, Senador José Porfírio, Rio Xingu, Cachoeira Kaituká, 3°33′47″S 51°53′20″W, J. Zuanon & L. Rapp Py-Daniel, 12 October 1992. MNHN 1998–1176 (not found in collection, three specimens, 76–143 mm L_{S}), Pará, Altamira, Rio Xingu, J. Zuanon & L. Rapp Py-Daniel, 29 September 1990. MNHN 1998–1177 (not found in collection, five specimens, 65–112 mm L_{S}), Pará, Senador José Porfírio, Rio Xingu, Cachoeira Kaituká, 3°33′47″S 51°53′20″W, J. Zuanon & L. Rapp Py-Daniel, 9 October 1990. MNHN 1998–1180 (not found in collection, six specimens, 80–225 mm L_{S}), Pará, Altamira, Rio Xingu, M. Jégu, 10 October 1992. MZUSP 94945 (one specimen, 322.4 mm L_{S}), Mato Grosso, Paranatinga, Rio Culuene, stretch between Cachoeira to Ribeirão Corgão, 13°49′00″S 53°15′00″W, A. Akama & J.L.O. Birindelli, 15 January 2006. MZUSP 110948 (one specimen, 267 mm L_{S}, skel.), Pará, Altamira, Rio Iriri, Cachoeira Grande, 3°50′37″S 52°44′02″W, O. Oyakawa, J.L.O. Birindelli, C. Moreira, A. Akama, L. Sousa & H. Varella, 16 November 2011. INPA 4088 (three specimens, 98.6–110.2 mm L_{S}), Pará, Senador José Porfírio, Rio Xingu, Cachoeira Kaituká, 3°33′47″S 51°53′20″W, J. Zuanon & L. Rapp Py-Daniel, 9 October 1990. INPA 4087 (two specimens, 116–120.7 mm L_{S}), Pará, Altamira, Rio Xingu, Ilha Babaquara, 3°12′43″S

52°12′12″W, J. Zuanon & L. Rapp Py-Daniel, 5 October 1990. INPA 31021 (four specimens, 71.2–122.8 mm L_S), Pará, Altamira, Rio Xingu, Cachoeira do Espelho, 3°39′05″S 52°22′43″W, H. López-Férnandez *et al.*, 24 August 2008. ROM ex-INPA 31021 (six specimens, 70–106 mm L_S), Pará, Altamira, Rio Xingu, Cachoeira do Espelho, 3°39′05″S 52°22′43″W, H. López-Férnandez *et al.*, 24 August 2008. INPA 31164 (two specimens, 32.1–115.8 mm L_S), Pará, Altamira, Rio Iriri, four hours downstream of confluence with Rio Novo, 4°14′14″S 53°24′34″ W, H. López-Férnandez *et al.*, 22 August 2008.

Diagnosis

Tometes kranponhah is distinguished from all congeners by the presence of a black, teardrop-shaped blotch on the opercle, more evident in adults (*versus* opercle without any pigment), and by lateral cusps on first and second labial premaxillary teeth of specimens larger than 70 mm L_S (*versus* lack of lateral cusps on those teeth). *Tometes kranponhah* is further distinguished from congeners, except *T. trilobatus*, by lateral contact between its first and second labial premaxillary teeth (*versus* lateral spacing between these teeth, more evident in adults). In addition, *T. kranponhah* is distinguished from *T. trilobatus*, *T. lebaili*, and *T. ancylorhynchus* by having 38–43 scale rows around the caudal peduncle (*versus* 27–34, 32–36, and 30–36 scale rows, respectively); from *T. camunani* and *T. ancylorhynchus* by having straight dorsal profile of the neurocranium (*versus* gentle concavity in the neurocranium at level of the epiphyseal bar in specimens larger than 60 mm L_S); from *T. trilobatus* by having 80–103 total perforated scales on the lateral line (*versus* 63–79) and 75–98 perforated scales on the lateral line until the hypural joint (*versus* 58–72); from *T.*

makue by possessing 25–39 total spines on the abdominal serrae (*versus* 10–23) and 10–23 simple prepelvic spines (*versus* none to nine); and from *T. lebaili* by having terminal mouth (*versus* upturned mouth).

Description

Morphometric data of *T. kranponhah* in Table I. Species medium-sized to large, compared with congeners; largest examined specimen 370 mm L_S. Body elongated, high, ovoid, and very compressed (Figs. 1–2). Greatest body depth at dorsal-fin origin. Dorsal profile of body slightly convex from snout tip to dorsal-fin origin. Dorsal-fin base straight to convex, interdorsal profile straight. Ventral head and body profile slightly convex. Anal-fin base slightly convex in juveniles and strongly convex in adults.

Table I. Morphometric data of *Tometes kranponhah* (Hol = holotype; n = number of observations; SD = standard deviation)

	Hol	n	Range	Mean ± SD
Standard length (mm)	132.3	96	51.5–370	119.9
	Percent of standard length			
Body depth	58.3	96	52.6–65.4	58.3 ± 2.5
Head length	24.5	96	21.1–28.3	26.0 ± 0.8
Distance snout to supraoccipital spine	29.7	96	25.2–33.4	30.2 ± 1.0
Predorsal length	56.4	96	53.8–60.1	56.6 ± 1.4
Dorsal-fin base length	27.3	96	25.8–33.3	28.6 ± 1.2
Interdorsal length	13.0	96	9.0–14.8	12.2 ± 0.9
Adipose-fin base length	5.9	96	2.3–6.2	5.1 ± 0.5

Caudal-peduncle depth	10.9	96	9.5–11.5	10.4 ± 0.4
Anal-fin base length	32.9	96	29.3–35.8	32.6 ± 1.3
Preanal length	75.5	96	68.9–78.3	75.0 ± 1.5
Prepelvic length	55.1	95	52.3–59.4	56.0 ± 1.4
Prepeitoral length	24.4	96	21.8–29.5	25.1 ± 1.6
Distance pelvic-fin origin to anal-fin origin	21.5	95	18.7–25.2	21.1 ± 1.3
Distance pectoral-fin origin to pelvic-fin origin	31.8	95	28.7–34.7	31.3 ± 1.5
Width of caudal peduncle	3.3	96	1.7–5.6	3.0 ± 0.9
Pectoral-fin length	22.0	96	19.9–25.2	22.4 ± 1.0
Pelvic-fin length	16.4	94	13.8–17.4	15.8 ± 0.7
1st anal-fin lobe length	27.7	93	17.6–42.9	29.7 ± 3.5
2nd anal-fin lobe length	-	10	13.2–23.6	17.8 ± 4.0
Dorsal-fin lobe length	36.4	94	21.6–60.5	34.0 ± 7.0
Distance dorsal-fin origin to anal-fin origin	62.4	96	57.2–69.9	61.5 ± 2.3
Distance dorsal-fin end to anal-fin origin	47.0	96	41.8–51.5	45.8 ± 1.9
Distance dorsal-fin end to anal-fin end	25.5	96	19.3–27.6	24.7 ± 1.2
	Percent of head length			
Snout length	34.7	96	27.6–40.4	33.2 ± 3.2
Interorbital width	43.1	96	35.6–50.4	41.2 ± 3.1
Width head	64.2	96	46.5–68.1	57.3 ± 3.1
Postorbital distance	26.5	96	25.5–33.0	29.3 ± 1.5
4th infraorbital width	13.4	96	10.8–18.4	14.1 ± 1.1
Eye vertical diameter	36.4	96	25.3–44.1	38.4 ± 4.7
Mouth length	22.2	96	10.2–27.9	19.4 ± 3.8
3rd infraorbital width	11.3	96	6.4–14.7	9.2 ± 1.2

Cheek gap width	11.1	96	7.5–15.0	11.1 ± 1.5
Mouth width	34.9	96	24.8–39.4	31.3 ± 3.4

Snout slightly elongated. Mouth terminal, upper jaw slightly larger than lower jaw. Incisiform premaxillary and dentary teeth. Two rows of premaxillary teeth joined antero-posteriorly (Fig. 3a), forming protruding arc in ventral view, evident in specimens larger than 200 mm L_S. Premaxilla with five incisiform teeth in labial row and two in lingual row (Figs. 3a, 4a). Labial premaxillary teeth appearing out of mouth (Fig. 5). Posterior cusp of first labial premaxillary tooth in contact with anterior edge of second tooth (Figs. 3a, 4a), only slightly spaced in specimens up to 70 mm L_S. In specimens larger than 70 mm L_S (Fig. 4a), first labial premaxillary tooth bicuspid, second to fifth labial premaxillary teeth tricuspid. Base narrower than edge in teeth of premaxillary labial row. Main cusp of jaw teeth with sharp edge in specimens up to 70 mm L_S and rounded to spatulate in specimens larger than 70 mm L_S. First to third labial premaxillary teeth with aligned crowns in ventral view (Fig. 3a), approximately same size and same width (Fig. 4a). Fourth and fifth labial premaxillary teeth shorter than first three, decreasing in size posteriorly, tricuspid (Fig. 4a), and with sigmoid crown in ventral view (Fig. 3a). Dentary with five to six (five) incisiform teeth decreasing in size posteriorly, first tooth tricuspid, second to last tooth bicuspid, posterior cusp externally overlapping anterior cusp of next tooth. Pair of symphyseal teeth on dentary. Maxilla edentulous.

Figure 1. *Tometes kranponhah*, new species from the Xingu River basin. Holotype, MPEG 31000, 132.3 mm standard length (L_S).

Scales cycloid, irregularly sized. Perforated lateral line scales from supracleithrum to hypural plate 75–98 (87), and total perforated lateral line scales 80–103 (92). Horizontal scale rows between dorsal-fin origin and lateral line 50–72 (53). Horizontal scale rows between lateral line and pelvic-fin insertion 49–73 (49). Circumpeduncular scales 38–43 (43). Abdomen rounded, lacking ventral keel. Ventral spines reduced, not forming evident serrae. Prepelvic serrae weakly inserted on abdomen. Prepelvic serrae with 10–23 spines (12). Simple postpelvic serrae with seven to 11 spines (10). Double postpelvic serrae with four to seven spines (6). Total serrae with 25–39 spines (28).

Figure 2. *Tometes kranponhah*, new species from the Xingu River basin. Paratypes, (♂) MPEG 31003, 350 mm standard length (L_S), male; (♀) GEA 1719, 306 mm L_S, female.

Dorsal-fin rays ii–iv, 19–22 (iii, 20). Dorsal-fin origin at midbody, preceded by strong, forward-directed spine. In specimens up to 150 mm L_S, distal margin of dorsal-fin falcate possessing anterior rays with strong positive allometry; in specimens larger than 150 mm L_S, allometry almost isometric (Fig. 6). Dorsal fin slightly falcate in specimens larger than 150 mm L_S (Fig. 7a). In specimens smaller than 150 mm L_S, anterior rays forming elongated filament (Fig. 7b), surpassing adipose-fin origin or base of caudal-fin rays when adpressed. Anal-fin rays iii–iv, 30–34 (iv, 32). Pectoral-fin rays i, 15–18 (i, 16). Pelvic-fin rays i, 7. Adipose fin present, base oblique and shorter than or approximately same length as orbital diameter. Caudal fin forked with similarly sized lobes. Caudal fin with lobes pointed in specimens up to 200 mm L_S and gently rounded in specimens larger than 200 mm L_S.

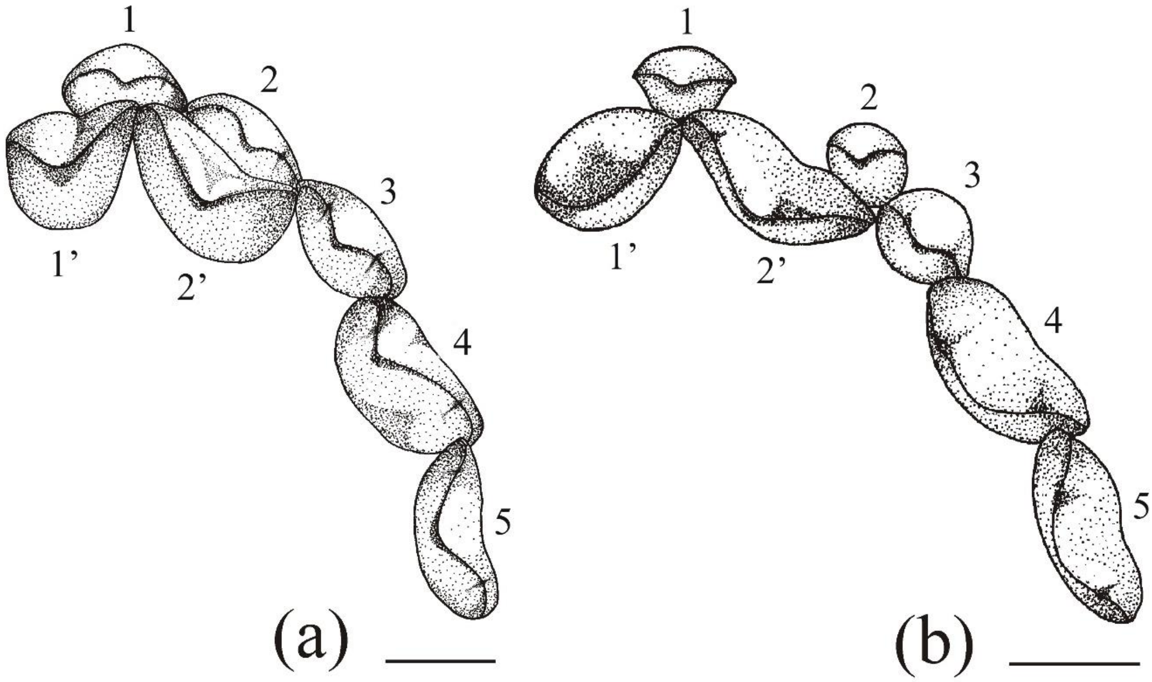

Figure 3. Ventral view of left premaxilla. (a) GEA 1497, *Tometes kranponhah*, 120 mm standard length (L_S), (b) GEA1714, *Tometes ancylorhynchus*, 126 mm L_S. 1–5: Labial row of premaxillary teeth; 1′–2′: Lingual row of premaxillary teeth. Scale bars: 1 mm.

Neurocranium triangular, with straight dorsal profile in lateral view. Mesethmoid trapezoid, elongated forward, with anterior process pointed and directed downward. Ascending premaxillary process slender, pointed, and oriented antero-posteriorly in relation to bone axis (Fig. 4a). Lateral premaxillary process trapezoid, with posterior margin acute to subrectangular, and dimple in ventral view where it fits anterodorsal portion of maxillary. Large olfactory fossae. Dentary elongated, slender, slightly arched, with four bony lamellae at symphysis. Ethmoidal wings elongated, positioned on anterior half of mesethmoid. Six to seven supraneurals. Forty to 41 total vertebrae. Ten to 11 predorsal vertebrae, and 15–16 postdorsal vertebrae. Two to 3 vertebrae between verticals through last dorsal-fin pterygiophore and first anal-fin pterygiophore. Gill rakers on first branchial arch 27–32; on epibranchial 12–14; on ceratobranchial 14–17; and at cartilage between ceratobranchial and epibranchial 1.

Colouration in alcohol

Overall ground colour silvery to tan, darker dorsally. Dorsal portion of head usually darker. Dark blotch in central portion of opercle, slightly pigmented in juveniles up to 100 mm L_S, and conspicuously teardrop-shaped in specimens larger than 100 mm L_S. Head of adults, mainly mature males, with darker pigmentation above opercle, on fifth and sixth infraorbitals (Fig. 5). Specimens up to 120 mm L_S with well-defined humeral spot over sixth to ninth perforated scale of lateral line (Fig. 8). Diffuse blotch sometimes covering humeral region, gently elongated vertically, composed of several scattered melanophores. Specimens up to 120 mm L_S with faint blotches on flanks, usually vertically elongated, but sometimes circular, more visible on ventral portion of flanks (Fig. 8). Adults, mainly mature males, with irregular dark blotches on flanks. Ventral portion of head pale. Juveniles and adult females with pale abdominal region, mature males with dimmed, dark abdominal region. Smaller specimens with hyaline pectoral and pelvic fins; anterior rays of dorsal and anal fins darker, and distal portion of posterior rays with dark edge; caudal fin with dark band at edge; hyaline adipose fin with few melanophores. Larger specimens have more subtle forms of these marks on fins: fins uniformly brown with distal portion slightly darker or sometimes hyaline, and adipose fin marks limited to thin dark band distally. Filamentous extensions on dorsal fin of mature males uniformly darkened.

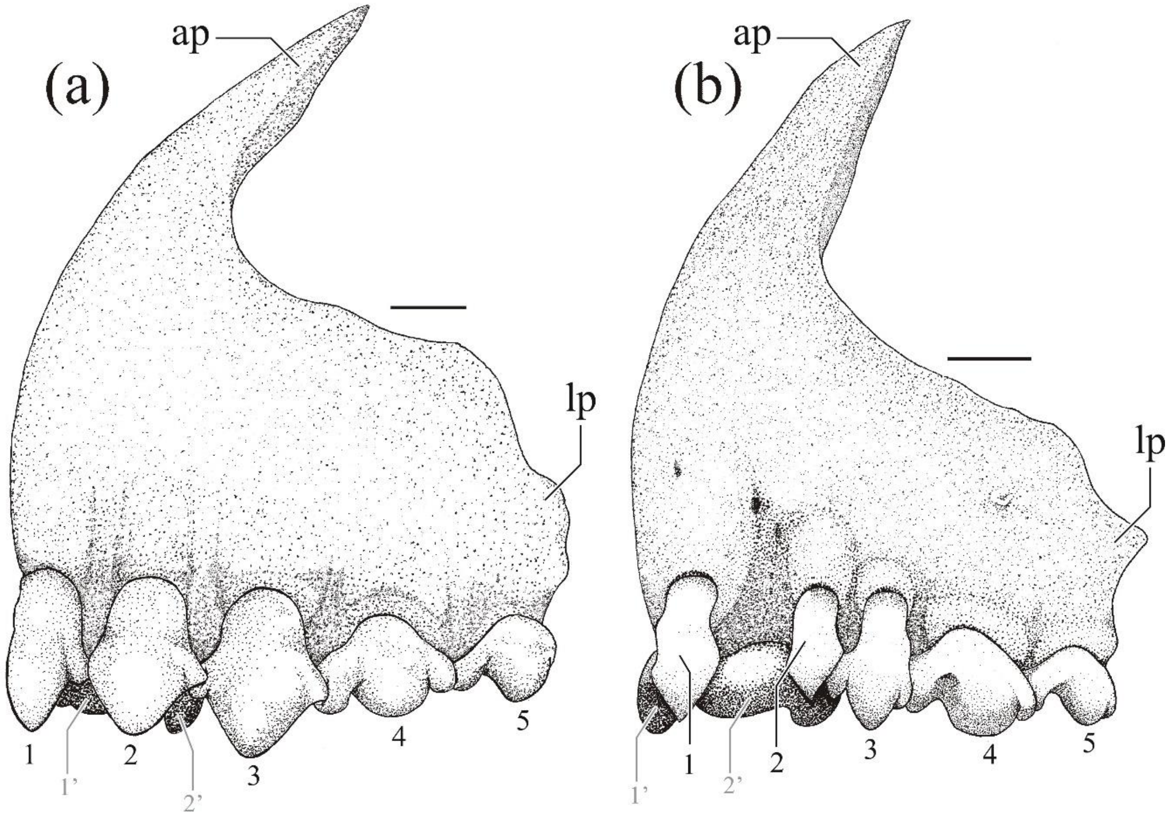

Figure 4. Lateral view of left premaxilla. (a) GEA 1497, *Tometes kranponhah*, 120 mm standard length (L_{S}), (b) GEA1714, *Tometes ancylorhynchus*, 126 mm L_{S}. 1–5: Labial row of premaxillary teeth; 1′–2′: Lingual row of premaxillary teeth; ap: Ascending process of premaxilla; lp: Lateral process of premaxilla. Horizontal scale bars: 1 mm.

Colouration in life

Overall colour silvery. Flanks reddish gray in adults during breeding period. Head darker dorsally, somewhat darker above opercle, fifth and sixth infraorbitals (Fig. 5). Blotch on opercle black to dark olive green in adults (Fig. 7a). Blotch on opercle of juveniles conspicuous, but somewhat dimmed (Fig. 7b). Irregular dark blotches on flanks of adults, mainly mature males. Ventral portion of body and head pale. Pectoral and pelvic fins uniformly light brown. Dorsal fin with anterior rays darker and posterior rays orange to red in juveniles but uniformly light brown in adults. Anterior rays of anal fin orange to red; distal portion of posterior rays of dorsal and anal fins darker. Juveniles with distal dark band on caudal fin, caudal fin uniformly orange to light brown in adults. Adipose fin with few melanophores and with thin distal black band. Filamentous extensions of dorsal fin of mature males darkened.

Figure 5. Head view of a *Tometes kranponhah* specimen. MPEG 31006, 320 mm standard length (L_S), male.

Sexual dimorphism

Adults of *Tometes kranponhah* exhibit secondary sexual dimorphic character in the form of irregularly shaped dark blotches scattered on flanks more evident in mature males. Mature males, 180 mm L_{S} and larger, have an additional lobe on the anal fin, formed by the extension of the middle rays and centered on 13th to 17th branched rays (Fig. 2). Three of 12 largest males examined (MPEG 31006, 320 mm L_{S}; MPEG 31003, 324 and 350 mm L_{S}) display stiff, laterally curved hooks on distal-most lepidotrichia of anal-fin rays (Fig. 9). Some males larger than 180 mm L_{S} present filament extensions on dorsal-fin rays (Fig. 2); in some cases, these filaments are very long and resemble hair (see *Etymology* section below). Abdominal region of males dimmed and dark (Fig. 2).

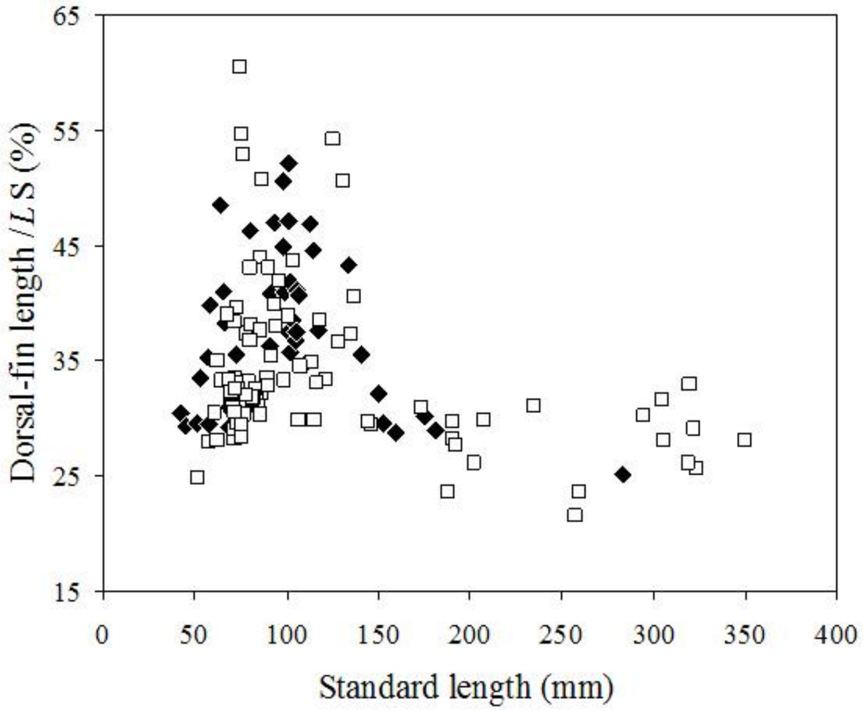

Figure 6. Variation in the length of the first rays of the dorsal fin expressed in percentage of standard length (L_{S}). Symbols: *Tometes kranponhah* (□); *Tometes ancylorhynchus* (♦).

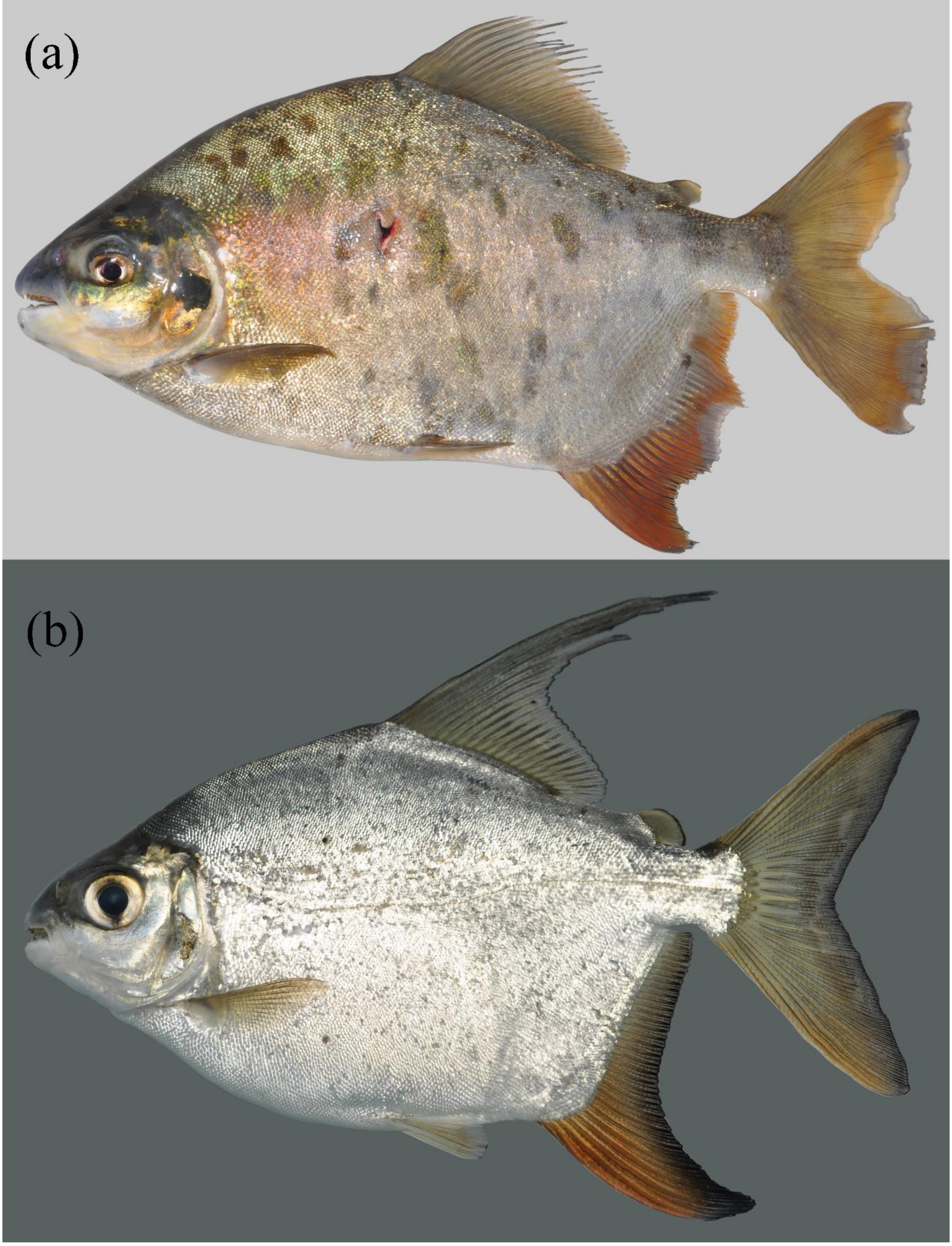

Figure 7. *Tometes kranponhah*, photographed alive. (a) ANSP 193019, 345 mm standard length (L_S), male; (b) ANSP 193062, 90.4 mm L_S, juvenile. (Photo by M.H. Sabaj Pérez).

Figure 8. Juvenile specimen of *Tometes kranponhah* from Rio Xingu basin, MPEG 31010, 46 mm standard length (L_S).

Figure 9. Hooks laterally curved on additional anal-fin lobe in mature *Tometes kranponhah* males. MPEG 31006, 320 mm standard length (L_S), male.

Distribution

Tometes kranponhah is known from rapids and waterfalls associated with rock outcrops, covered by aquatic macrophytes, of the Xingu River and its tributaries. The species is widely distributed in the Xingu River basin, and its presence is confirmed in a protected area, the Terra do Meio Conservation Unit (Iriri River, Pará State). The species also occurs in the main tributaries of the basin, including the Iriri and Bacajá Rivers in the Pará and Mato Grosso States, Brazilian Shield (Fig. 10).

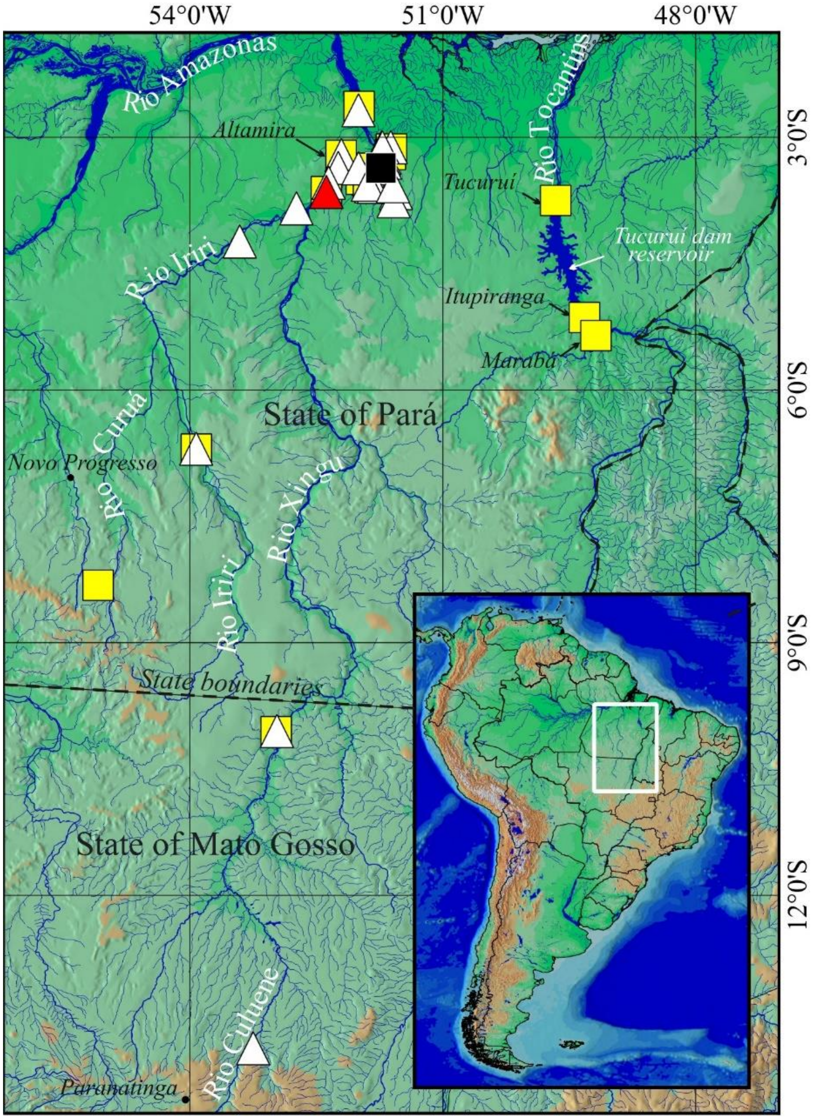

Figure 10. Distribution of *Tometes kranponhah* (triangles) and *Tometes ancylorhynchus* (squares). Type localities for *T. kranponhah* (▲) and *T. ancylorhynchus* (■).

Etymology

The species epithet was selected in honour of the indigenous Pytako tribe inhabiting the banks of the Xingu River basin, who know the fish as *kranponhah*. This word is an adjective from the Xikrin language that can be broken down into *kran* (= head, mountain, or deeply rounded head) and *ponhah* (= hair or hairy), also translated as ‘long haired’. This is in reference to the long filaments formed by the extensions of the dorsal-fin rays in mature males.

Remarks

Tometes kranponhah is a rheophilic serrasalmid, commonly occurring in areas of the Xingu River basin marked by the presence of Myrtaceae trees. It is typically found in the rapids among rocky outcrop zones covered by Podostemaceae (Fig. 11), its main food source. *Tometes kranponhah* is usually collected in midwater with other sympatric, rheophilic species, including *Leporellus vittatus* Valenciennes 1850, *Hypomasticus julii* Santos, Jégu & Lima 1996, and *Tometes ancylorhynchus*, a new species described below. Bottom-dwelling fishes in the rapids that may also be collected include *Baryancistrus xanthellus* Rapp Py-Daniel, Zuanon & Ribeiro de Oliveira 2011 and *Baryancistrus chrysolomus* Rapp Py-Daniel, Zuanon & Ribeiro de Oliveira 2011.

Figure 11. The Xingu River at Cachoeira do Jericoá (3°21′57.4″S 51°43′59.2″), Vitória do Xingu, State of Pará, Brazil (Photo by A.P. Gonçalves).

Juveniles (around 70 mm L_S) often form large mixed schools with *T. ancylorhynchus*. Less frequently, they form mixed schools with *Myleus setiger* Müller & Troschel 1844 and *Myleus arnoldi* (Ahl 1936), a behaviour that suggests they are using protective mimicry (M.C. Andrade pers. obs.). Fish larger than 100 mm L_S are often seen swimming in strong currents or resting after traversing vortex zones behind rocks, where they are easily caught with casting nets. The largest specimens (> 300 mm L_S) were captured mainly by fishermen using underwater harpoons (see Fig. 6a, harpoon wound in the flank) or fishing rods baited with araçá guava (fruit of a Fabaceae tree, typically found near rapids).

Despite its deep, flat body, the fish is able to remain close to macrophytes near the bank and feed without being carried away by the strong current. The shape of the body probably acts like a wing and keeps the fish anchored near the plants. This description recalls an earlier characterization by Zuanon (1999) of this species as a grazer that feeds on aquatic plants (such as Podostemaceae) while positioning its body laterally to the plants.

Although *Tometes kranponhah* occurs abundantly in artisanal fisheries, the fish is not eaten by the native people, mainly due to the rubbery texture of the cooked meat. Hence, this species is also called *'pacu-couro-duro',* or *'hard leathered pacu'* (N. Balão pers. comm.).

TOMETES ANCYLORHYNCHUS N. SP. (Figs. 12–14; Table II)

N. gen. 2. – Jégu (1992): 283 [distribution of rheophilic serrasalmids].

Tometes sp. – Agostinho *et al.* (2007): 126 [fishes recorded on migration ladders of Lajeado Hydroelectric dam]; Lucinda *et al.* (2007): 78 [checklist of Lajeado reservoir, TO]; Mérona *et al.* (2010): 115 [fishes affected by Tucuruí Hydroelectric dam]; Ferreira *et al.* (2011): 280 [fish inventory of the Parque Estadual do Cantão, TO, Araguaia River].

Utiaritichthys sennaebragai. – Miranda Ribeiro 1937. Gosline (1951): 60, plate 2 [record of the species at lower Tocantins-Araguaia basin]; Géry (1976): 51–52 [diagnosis and key of genera]; Géry (1977): 267, figure in lower portion of page [mentions specimens from the Tocantins and Araguaia Rivers]; Santos *et al.* (1984): 37 [checklist of fishes from Tucuruí Hydroelectric dam]; Begossi & Garavello (1990): 348 [species from Tocantins River collected between Imperatriz and Estreito, MA]; Lowe-McConnell (1991): 68 and 80, Fig. 7 [fishes from Araguaia]; Mérona *et al.*

(2001): 389 [species from Tucuruí Hydroelectric dam]; Jégu (2003): 192 [checklist, mentions right tributaries of middle and lower Amazon River]; Garavello *et al.* (2010): 584 [fishes most important for consumers in Estreito, MA, Tocantins River]; Pereira & Castro (2014): 401 [in key of species, reference to Xingu and Tocantins–Araguaia River basins].

Utiaritichthys sennae-bragi. – not Miranda Ribeiro. Nelson (1961): 605 [mention, swim bladder morphology].

Holotype

MPEG 31014 (150.4 mm L_{S}), Brazil, Pará, Vitória do Xingu, Rio Xingu, Cachoeira do Jericoá, 3°21′52.3″S 51°44′02.7″W, L.M. Sousa & A.P. Gonçalves, 1 July 2012.

Paratypes

All from Brazil, Rio Xingu basin. GEA 1949 (one specimen, 148.7 mm L_{S}), Pará, Altamira, Rio Iriri, rapids downstream of Cachoeira Grande, 3°49′10.6″S 52°39′34.5″W, L.M. Sousa, 17 October 2014. GEA 1952 (one specimen, 111.1 mm L_{S}), Pará, Altamira, Rio Xingu, Cachoeira do Espelho, 3°40′06.8″S 52°26′16.4″W, L.M. Sousa, 17 November 2012. INPA 11742 (one specimen, c&s, 86.8 mm L_{S}), Pará, Senador José Porfírio, Rio Xingu, Cachoeira Kaituká, 3°33′47″S 51°53′20″W, Eq. Ictiologia INPA, 12 October 1992. IRSNB 888 (six specimens, 56.9–72.5 mm L_{S}), Mato Grosso, Rio Xingu, Cachoeira Von Martius, 10°02′56.5″S 52°58′03.3″W, Léopold III, S.M. & J.P. Gosse, 30 November 1964. LIA 2306 (one specimen, 98.2 mm L_{S}), Pará, Altamira, Rio Xingu, Cachoeira Kaituká, 3°34′39.5″S 51°54′37.3″W, L.M. Sousa, 19 September 2012. MNHN 1999–1168 (two specimens, 101.9–174.8 mm L_{S}), Pará, Altamira, Rio Xingu, M. Jégu, 1999. MPEG 31015 (seven specimens, 91.2–152.5 mm L_{S}), Pará, Altamira, Rio Xingu, Pedral do Roboque

Velho, close to Ilha da Taboca, 3°22′05″S 51°59′59.3″W, M.C. Andrade, 27 July 2011. MPEG 31016 (one specimen, 159.7 mm *L*S), Pará, Altamira, Rio Xingu, Robojinho, Cachoeira do Porfírio, 3°29′48.9″S 51°57′58.7″W, M.C. Andrade, 27 July 2011. MPEG 31017 (one specimen, 79.9 mm *L*S), Pará, Anapú, Rio Xingu, Cachoeira Tapaiúna, 3°08′17.2″S 51°36′35.7″W, M. Camargo-Zorro, 9 January 2001. MZUSP 107404 (one specimen, 101.7 mm *L*S), Pará, Pontão, Belo Monte, property of Mr. Waldomiro & Mrs. Maria, 3°06′49″S 51°43′23″W, Eq. ECIX, 12 Jul 2010. ZUEC 10023 (one specimen, 118.7 mm *L*S), Pará, Altamira, Rio Xingu, 3°24′53.6″S 52°13′09′W, L.M. Sousa, 19 November 2012.

Additional material (not types)

All from Brazil, State of Pará, Rio Xingu basin. MPEG 31018 (five specimens, 30–42.5 mm *L*S), Anapú, Rio Xingu, 3°17′56″S 51°40′55″W, L.M. Sousa, 9 July 2012. GEA 1192 (15 specimens, 91.4–117.9 mm *L*S), Altamira, Rio Xingu, Pedral do Caixão, nearby Ilha da Taboca, 3°22′12.4″S 51°59′53.7″W, M.C. Andrade, 27 July 2011. GEA 1714 (one specimen, skel., 126 mm *L*S), Vitória do Xingu, Rio Xingu, Cachoeira do Jericoá, 3°21′57.4″S 51°43′59.2″W, M.C. Andrade, 12 April 2012. GEA 1955 (two specimens, 156–158.5 mm *L*S), Pará, Altamira, Rio Xingu, rapids of Kaituká, 3°34′39.5″S 51°54′37.3″W, L.M. Sousa, 23 November 2012. GEA 1956 (one specimen, 41.9 mm *L*S), Pará, Altamira, Rio Xingu, rapids of Cachoeira do Espelho, 3°40′06.8″S 52°26′16.4″W, L.M. Sousa, 13 October 2013. GEA 1957 (one specimen, 41.9 mm *L*S), Pará, Altamira, Rio Xingu, rapids of Cachoeira do Espelho, 3°40′06.8″S 52°26′16.4″W, L.M. Sousa, 13 October 2013. GEA 1958 (one specimen, 60.5 mm *L*S), Pará, Altamira, Rio Xingu, rapids of Cachoeira do Jericoá, 3°19′28.9″S 51°44′53.5″W, L.M. Sousa, 21 September 2012. GEA 1960 (eight specimens, 37.2–44.5 mm *L*S), Pará, Altamira, Rio Xingu, rapids of

Kaituká, 3°34′39.5″S 51°54′37.3″W, L.M. Sousa, 7 July 2012. GEA 1962 (three specimens, 57.8–64.2 mm *L*S), Pará, Altamira, Rio Xingu, 3°24′53.6″S 52°13′09″W, L.M. Sousa, 16 September 2012. GEA 1969 (three specimens, 43–43.2 mm *L*S), Pará, Altamira, Rio Xingu, rapids of Kaituká, 3°34′39.5″S 51°54′37.3″W, L.M. Sousa, 7 July 2012. GEA 1970 (two specimens, 49.5–58.2 mm *L*S), Pará, Altamira, Rio Xingu, rapids of Kaituká, 3°34′39.5″S 51°54′37.3″W, L.M. Sousa, 22 October 2013. MPEG 31019 (four specimens, 39.4–47.8 mm *L*S), Altamira, Rio Xingu, 3°17′56″S 51°40′55″W, L.M. Sousa, 9 December 2012. LIA 1118 (four specimens, 42.4–57.8 mm *L*S), same locality of holotype. A.P. Gonçalves *et al.*, 24 November 2012. MNHN 1998–1169 (not found in collection, two specimens, 145–155 mm *L*S), Senador José Porfírio, Rio Xingu, Cachoeira Cotovelo, M. Jégu, 7 October 1992. MNHN 1998–1170 (not found in collection, six specimens, 30–45 mm *L*S), Senador José Porfírio, Rio Xingu, Paquiçamba Kaituká, 3°33′47″S 51°53′20″W, J. Zuanon & L. Rapp Py-Daniel, 9 October 1990. MNHN 1998–1171 (not found in collection, 14 specimens, 30–90 mm *L*S), Senador José Porfírio, Rio Xingu, Paquiçamba Kaituká, 3°33′47″S 51°53′20″W, M. Jégu, 12 October 1992. MNHN 1998–1172 (not found in collection, five specimens, 40–50 mm *L*S), Senador José Porfírio, Rio Xingu, Paquiçamba Kaituká, 3°33′47″S 51°53′20″W, M. Jégu, 13 October 1992. MNHN 1998–1173 (not found in collection, two specimens, 117–163 mm *L*S), Vitória do Xingu, Rio Xingu, Arroz Cru, J. Zuanon & L. Rapp Py-Daniel, October 1990. MNHN 1998–1263 (not found in collection, six specimens, 145–170 mm *L*S), Altamira, street market, 3°12′10″S 52°12′21″W, M. Jégu, 7 October 1992. MZUSP 36821 (two specimens, 63.8–283 mm *L*S), Altamira, Rio Xingu, Cachoeira do Espelho, 3°38′42.3″S 52°22′54.3″W, P.E. Vanzolini, 23 October 1986. MZUSP 97158 (two specimens, 20.2–81.4 mm *L*S), Novo Progresso, Rio Curuá, tributary of Rio Iriri, Vila de Castelo dos Sonhos, 8°19′07″S 55°05′23″W, J.L.O. Birindelli *et al.*, 22 October 2007. MZUSP 105652 (one specimen, 181.6 mm *L*S), Senador

José Porfírio, Rio Xingu, Paquiçamba Kaituká, 3°33′47″S 51°53′20″W, M. Camargo-Zorro, 5 November 2000. INPA 46974 (one specimen, 123.5 mm L_S), Altamira, Rio Xingu, ilha Babaquara, 3°12′43″S 52°12′12″W, J. Zuanon & L. Rapp Py-Daniel, 5 October 1990. INPA 46975 (one specimen, 89.9 mm L_S), Altamira, Rio Xingu, Ilha Babaquara, 3°12′43″S 52°12′12″W, J. Zuanon & L. Rapp Py-Daniel, 5 October 1990. INPA 46981 (five specimens, 53.1–81.6 mm L_S), Altarima, Rio Iriri, Estação Ecológica Terra do Meio, 5°45′28.1″S 54°13′29.6″W. B.F. Morales *et al.*, 27 August 2012.

Rio Tocantins–Araguaia basin. CAS 20222 (one specimen, 162 mm L_S) Marabá, Rio Tocantins, 5°18′59.4″S 49°06′01.9″W. C. Ternetz, 24 Apr 1924. INPA 2356 (one specimen, 187.8 mm L_S), Tucuruí, Rio Tocantins, upstream of Tucuruí Hydroelectric reservoir, 3°45′58″S 49°40′21″W. F. Martinho, 31 October 1987. INPA 3633 (15 specimens, 86.3–193.9 mm L_S), Itupiranga, Rio Tocantins, upstream of Tucuruí Hydroelectric reservoir, 3°45′58″S 49°40′21″W, Eq. Ictiologia INPA, 26 October 1980. INPA 3634 (three specimens, 169.1–208.5 mm L_S) Itupiranga, Rio Tocantins, upstream of Tucuruí Hydroelectric reservoir, 3°45′58″S 49°40′21″W, G.M. Santos, 26 December 1984. INPA 4485 (one specimen, 141.5 mm L_S), Tucuruí, Rio Tocantins, upstream of Tucuruí Hydroelectric reservoir, M. Jégu, September 1984. INPA 4505 (one specimen, 177 mm L_S), Tucuruí, Rio Tocantins, Tucuruí Hydroelectric reservoir. M. Jégu, 3 April 1985. INPA 43899 (three specimens, 114.8–158.1 mm L_S), Tucuruí, Rio Tocantins, 3°45′58″S 49°40′21″W. Eq. Ictiologia INPA, 2 May 1981.

Diagnosis

Tometes ancylorhynchus is distinguished from all congeners, except *T. camunani*, by the dorsal profile of the neurocranium possessing a slight concavity at the level of the epiphyseal bar, in specimens larger than 60 mm L_S (*versus* a straight dorsal profile). In specimens larger than 50 mm L_S, *T. ancylorhynchus* differs from *T. kranponhah* and *T. trilobatus* by having a gap between the first and the second labial premaxillary teeth that is the same width as the teeth base (*versus* first and second tooth maintaining lateral contact in specimens smaller than 70 mm L_S). *Tometes ancylorhynchus* is distinguished from *T. kranponhah* by the absence of lateral cusps of the first and second labial premaxillary teeth (*versus* presence of lateral cusps on first and second tooth in specimens larger than 70 mm L_S). *Tometes ancylorhynchus* is further distinguished from *T. kranponhah* and *T. camunani* by having 30–36 scale rows around the caudal peduncle (*versus* 38–43 and 37–42, respectively); from *T. makue* by possessing 24–35 total spines on abdominal serrae (*versus* 10–23), with 10–20 of these being simple prepelvic spines (*versus* none to nine); and from *T. lebaili* by having terminal mouth (*versus* upturned mouth).

Description

Morphometric data are presented in Table II. Relatively smaller than congeners; largest examined specimen 283 mm L_S. Body relatively short, high, ovoid and very compressed (Figs 12–14). Greatest body depth at dorsal-fin origin. Dorsal profile of body generally convex from snout tip to dorsal-fin origin, gently concave or straight at epiphyseal bar. Dorsal-fin base slightly convex and interdorsal space straight. Ventral profile generally convex from lower lip to vertical through central portion of orbit, gently concave at isthmus, and from central orbit to anal-fin origin convex. Anal-fin base slightly more convex in anterior portion.

Table II. Morphometric data of *Tometes ancylorhynchus* (Hol = holotype; n = number of observations; SD = standard deviation)

	Hol	n	Range	Mean ± SD
Standard length (mm)	150.4	46	30–283	94.2
	Percent of standard length			
Body depth	63.7	46	56.5–70.8	63.7 ± 2.8
Head length	23.2	46	21.5–27.7	24.8 ± 1.4
Distance snout to supraoccipital spine	30.0	46	27.4–35.2	31.2 ± 1.3
Predorsal length	58.9	46	54.7–64.1	59.4 ± 1.6
Dorsal-fin base length	27.6	46	25.7–35.0	27.8 ± 1.6
Interdorsal length	12.7	46	10.5–16.8	13.4 ± 1.2
Adipose-fin base length	6.4	46	4.6–7.6	6.1 ± 0.6
Caudal-peduncle depth	10.7	46	10.0–11.9	10.9 ± 0.4
Anal-fin base length	34.5	46	29.7–37.7	33.9 ± 1.7
Preanal length	76.1	46	71.5–79.4	76.9 ± 1.7
Prepelvic length	55.7	46	50.3–60.7	57.3 ± 1.9
Prepeitoral length	22.5	46	19.5–28.9	24.2 ± 1.8
Distance pelvic-fin origin to anal-fin origin	22.4	46	19.2–24.7	21.9 ± 1.4
Distance pectoral-fin origin to pelvic-fin origin	34.0	46	30.2–38.0	33.9 ± 1.6
Width of caudal peduncle	4.2	46	1.9–4.4	3.2 ± 0.6
Pectoral-fin length	21.1	46	19.4–24.0	21.7 ± 0.9
Pelvic-fin length	15.8	46	14.2–17.1	15.6 ± 0.6
1st anal-fin lobe length	31.4	44	15.8–36.2	29.2 ± 4.0

2nd anal-fin lobe length	-	4	10.3–16.3	12.6 ± 2.6
Dorsal-fin lobe length	32.2	43	25.0–52.1	37.7 ± 6.8
Distance dorsal-fin origin to anal-fin origin	66.2	46	59.7–70.3	66.5 ± 2.5
Distance dorsal-fin end to anal-fin origin	51.2	46	44.3–55.3	50.7 ± 2.6
Distance dorsal-fin end to anal-fin end	27.1	46	24.0–30.1	27.4 ± 1.3
	Percent of head length			
Snout length	29.2	46	26.6–36.3	30.3 ± 2.4
Interorbital width	46.9	46	36.0–50.5	42.6 ± 3.1
Width head	65.3	46	54.4–70.6	60.2 ± 3.6
Postorbital distance	28.5	46	25.4–33.6	28.4 ± 1.6
4th infraorbital width	12.4	46	10.8–15.9	13.7 ± 1.2
Eye vertical diameter	39.6	46	29.1–45.6	40.4 ± 3.3
Mouth length	10.4	46	10.4–22.4	16.2 ± 3.1
3rd infraorbital width	9.1	46	5.5–10.6	8.3 ± 1.3
Cheek gap width	9.3	46	9.2–15.6	11.9 ± 1.2
Mouth width	29.7	46	25.5–33.8	28.9 ± 2.1

Snout short and rounded following orbit curvature. Mouth terminal, jaws equally sized. Incisiform teeth on premaxilla and dentary. Labial premaxillary teeth discrete and not obviously jut out of mouth. Two rows of premaxillary teeth joined antero-posteriorly, forming slight arc in ventral view (Fig. 3b). Premaxilla with five incisiform teeth in labial row and two in lingual row (Figs. 3b, 4b). First labial premaxillary tooth separated from second by gap with same width as tooth base (Figs. 3b, 4b). First and second labial premaxillary teeth lanceolate, sharp edged, without lateral cusps, with base practically with same width as edge. Labial premaxillary teeth usually with sharp edge, moderately rounded crown of labial premaxillary teeth in larger specimens, due to wear caused by feeding. Third tooth tricuspid, more or less same size as first two. Fourth and fifth labial premaxillary teeth shorter than first three, decreasing in size posteriorly, tricuspid (Fig. 4b), with sigmoid crown in ventral view (Fig. 3b). Dentary with five to six (5) incisiform teeth. First tooth of dentary tricuspid, remaining teeth bicuspids, gently decreasing in size posteriorly, posterior cusp externally overlapping anterior cusp of next tooth. Pair of symphyseal teeth on dentary. Maxilla edentulous.

Scales cycloid, of regular size. Perforated lateral line scales from supracleithrum to hypural plate 63–87 (78), and total perforated lateral line scales 70–94 (85). Horizontal scale rows between dorsal-fin origin and lateral line 39–54 (46). Horizontal scale rows between lateral line and pelvic-fin insertion 33–54 (42). Circumpeduncular scales 30–36 (35). Abdomen rounded, lacking ventral keel. Ventral serrae reduced, tiny prepelvic spines sometimes hidden under skin. Ventral prepelvic serrae with 10–20 spines (12). Simple postpelvic serrae seven to 11 (8), double postpelvic serrae four to seven (5), and total spines 24–35 (25).

Dorsal-fin rays ii–iii, 18–22 (ii, 19). Dorsal-fin origin at midbody, preceded by strong, forward-directed spine. Distal margin of dorsal fin falcate. Anterior rays of dorsal fin very elongated, with strong allometry, specimens smaller than 130 mm L_S with positive allometry, whereas specimens larger than 130 mm L_S with negative allometry (Fig. 6). When adpressed, anterior rays reach to or surpass adipose fin origin. In specimens larger than 130 mm L_S, anterior rays of dorsal fin only slightly longer than posterior rays. Anal-fin rays iii–iv, 30–34 (iii, 32). Pectoral-fin rays i, 15–18 (i, 16). Pelvic-fin rays i, 7–8 (i, 7). Adipose fin present, oblique base, base approximately same length as orbital diameter. Caudal fin forked, lobes pointed and similarly sized.

Figure 12. *Tometes ancylorhynchus*, new species from the Xingu River and Tocantins basin. (♀) Holotype, MPEG 31014, 150.4 mm L_S, Xingu River, Cachoeira do Jericoá; (♂) Paratype, MPEG 31015, 152.5 mm L_S, Xingu River, Pedral do Reboque Velho.

Neurocranium triangular, with dorsal profile straight in specimens around 60 mm L_S or smaller, or with slight concavity at level of epiphyseal bar in largest specimens. Ascending premaxillary process slender, pointed, and oblique anteroposteriorly (Fig. 4b). Lateral premaxillary process trapezoid, with posterior margin subrectangular, with dimple where it fits anterodorsal portion of maxillary. Large olfactory fossae. Dentary elongated, slender, slightly arched, with four bony lamellae at symphysis. Mesethmoid elongated, pointed, with anterior process directed downward. Ethmoidal wings elongated, positioned on anterior half of mesethmoid. Six to seven supraneurals (7). Thirty-nine to 41 total vertebrae (40). Eleven predorsal vertebrae (11) and 14–15 postdorsal vertebrae (15). Two (2) vertebrae between verticals through last dorsal-fin pterygiophore and first anal-fin pterygiophore. Gill rakers on first branchial arch 26–28, on epibranchial 12–14, on ceratobranchial 13, and at cartilage between ceratobranchial and epibranchial 1.

Colouration in alcohol

Preserved colouration of *T. ancylorhynchus* similar to that described for preserved *T. kranponhah* specimens, except for: absence of marks on or above opercle, absence of marks on infraorbitals, and less evident blotches on flanks of mature males. Juveniles around 50 mm L_S with seven or eight vertical, irregular bands on flanks, and vertical bands of dorsum extending down to horizontal bands on middle flank (Fig. 13a–c). Faint humeral spot over fifth to eighth perforated scales of lateral line (Fig. 13a). Juvenile specimens around 30 mm L_S with six irregular blotches vertically elongated on dorsum and two blotches horizontally elongated. First blotch located on central portion of flank, positioned somewhat backward of flank, and second, smaller blotch located on caudal peduncle region (Fig. 13b).

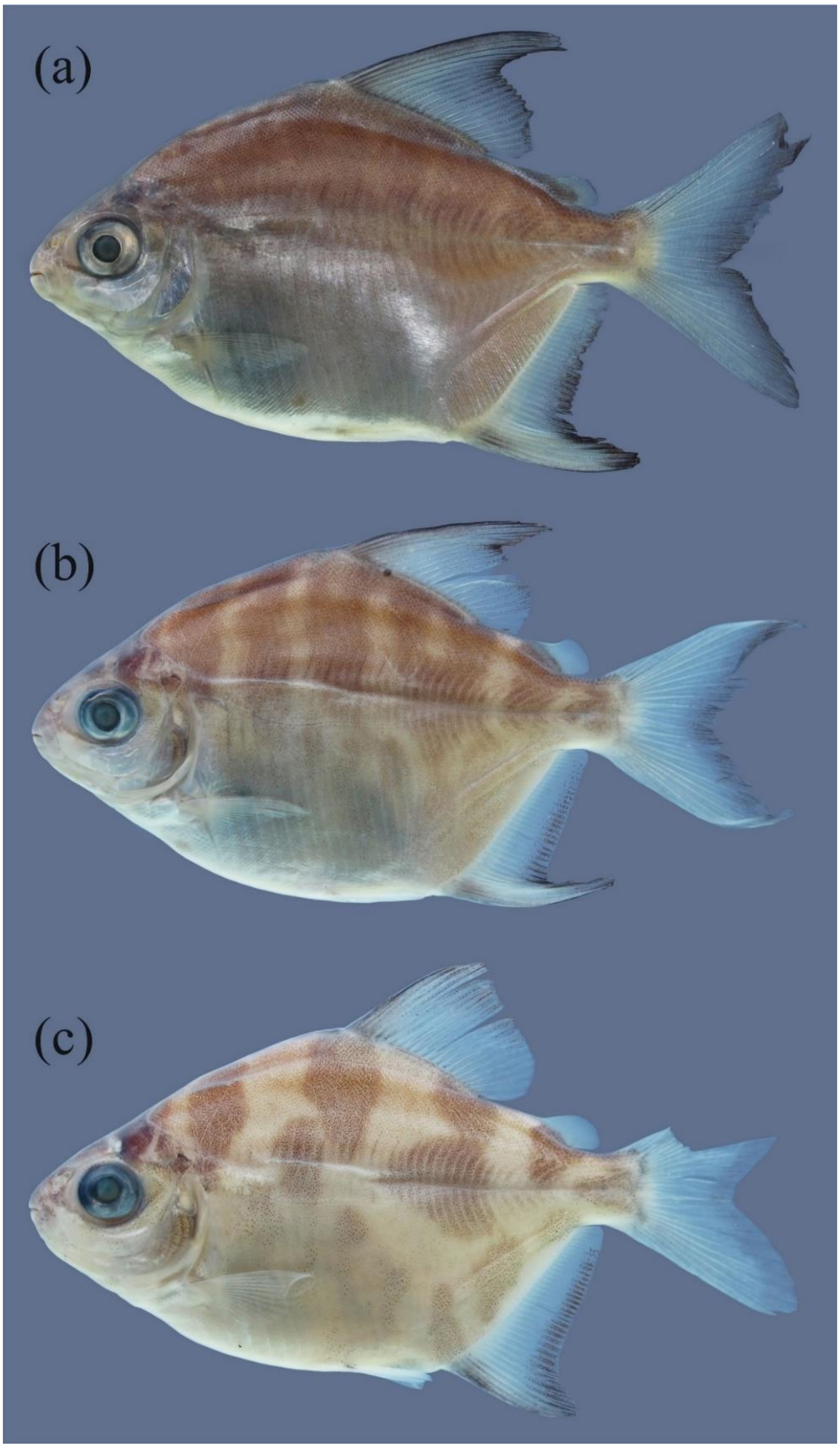

Figure 13. *Tometes ancylorhynchus* juveniles, specimens from the Xingu River. MPEG 31019, (a) 47.8 mm L_S, (b) 45.2 mm L_S, and (c) MPEG 31018, 30 mm L_S.

Colouration in life

Ground colouration clearly silver. Subtle rosy to red flank colouring in adults during breeding period (Fig. 14). Ventral portion of body and head pale. Pectoral and pelvic fins light brown. Dorsal and anal fins with anterior rays darker than posterior rays. Anal fin reddish orange. Caudal fin with dark distal band in juveniles, and orange to light brown distal band in adults. Adipose fin with few melanophores.

Figure 14. Living specimen of *Tometes ancylorhynchus* during the breeding period, MPEG 31016, 159.7 mm L_S, female.

Sexual dimorphism

The main secondary sexual character of *T. ancylorhynchus* is an additional lobe on the anal fin, similar to that of other serrasalmids of the *Myleus* group. Such lobe is formed by the extension of the 14th to 16th anal-fin rays in specimens larger than 140 mm L_S (Fig. 12). The four mature males examined did not possess dorsal-fin filaments or hooks on the anal fin.

Distribution

Tometes ancylorhynchus is known from the rapids and waterfalls of the Xingu and Tocantins–Araguaia River basins. The species is also recorded in the Terra do Meio Conservation Unit (Iriri River, State of Pará), where it occurs in the Xingu, Iriri, and Bacajá Rivers, in the States of Pará and Mato Grosso. These records of the Tocantins River include only one before it was dammed by the Tucuruí hydroelectric reservoir (CAS 20222), and five collected during the damming (lots INPA), Pará State, Brazil (Fig. 10).

Etymology

The species epithet, *ancylorhynchus*, is an appositive from the Greek *ancylo* (= curved), and *rhynchus* (= beak, snout, or rostrum), an allusion to the shape of the snout, which is relatively short and curved, resembling a curved parrot beak.

Remarks

Like *Tometes kranponhah, T. ancylorhynchus* is rheophilic and grazes on Podostemaceae. *Tometes ancylorhynchus* is usually collected syntopically with *T. kranponhah* in the Xingu River tributaries, although it is less common in collections than *T. kranponhah*. *Tometes ancylorhynchus* is commonly consumed, as its flesh is softer than the tough, rubbery meat of *T. kranponhah*, and is occasionally found in local fish markets (N. Balão pers. comm.).

DISCUSSION

The genus *Tometes* was resurrected by Jégu *et al.* (2002c), with the following diagnostic characters: thick incisiform teeth on the jaws; sigmoid edges on the fourth and fifth labial premaxillary teeth, which are shorter and broader than the remaining teeth; and poorly developed prepelvic serrae, formed by tiny prepelvic spines (*versus* slender incisiform teeth; aligned edges on the fourth and fifth labial premaxillary teeth, which are equal in height to the remaining teeth; and molariform with a well-marked prepelvic serrae formed by large thorns, which constitute an abdominal keel).

Before its revalidation, *Tometes* was synonymous with the genera *Myletes* Cuvier 1814 or *Myleus* for a century and a half, which resulted in several misidentifications. The first erroneous mention in the literature was made by Gosline (1951), who reported a specimen as *Utiaritichthys sennaebragai* in the Tocantins–Araguaia basin, even noting that it was very closely related to *Myleus* due to the poorly developed prepelvic spines. Although Gosline (1951) did not analyse or reference any type series of *U. sennaebragai*, a species that originates from the upper Tapajós basin, several other studies have documented the occurrence of *Utiaritichthys* in other drainages outside the Tapajós. Subsequently, however, a study that redescribed the types of *U. sennaebragai* (Jégu *et al*., 1992) did not recognise the specimens cited by Gosline (1951) and other authors (*e.g.* Géry, 1976, 1977, 1979; Machado-Allison, 1982, 1983; Santos *et al.*, 1984) as *U. sennaebragai*, or even as another species of *Utiaritichthys*. This conclusion was based on the presence of traits in these specimens that did not conform to diagnostic features in *U. sennaebragai*, among them incisiform teeth on the jaws, premaxillary teeth rows in complete contact internally, poorly developed prepelvic serrae, and deep body (> 50% of L_S, *versus U. sennaebragai* type features: molariform teeth, premaxillary teeth rows separated by internal gap, well-developed prepelvic serrae, and low body depth < 50% of L_S). Here, we reinforce the conclusion that the specimens mentioned by Gosline (1951: CAS 20222) and other authors as *U. sennaebragai* in the Tocantins–Araguaia basin are, in fact, the new species *T. ancylorhynchus*. In addition, reports of *Utiaritichthys* in the Xingu River basin may be either *T. ancylorhynchus* or *T. kranponhah*.

Prior to this report, valid species of *Tometes* were known to exist only in the Guiana Shield rivers (Andrade *et al.,* 2013), although some authors suggested a decade ago that undetermined *Tometes* species might be present in the Brazilian Shield drainages (*e.g.* the Xingu River: Géry & Zarske, 2004; the Tocantins River: Agostinho *et al.,* 2007). Part of the confusion may stem from the fact that *T. kranponhah* and *T. ancylorhynchus* occur syntoptically with other rheophilic serrasalmids that typically have similar colouration, such as *Mylesinus paucisquamatus* and *Myleus setiger*. Although this similarity causes difficulties in species identification, it appears to allow mixed-species schools to form that consist of at least four serrasalmid species (see Remarks regarding *T. kranponhah*). This behaviour may be associated with the strategy of protective mimicry, in which individuals gain increased protection from predators by congregating in large numbers (*e.g.* Pereira *et al.*, 2011).

Of the species in the *Myleus* group that are syntopic with the two new *Tometes* species, *Ossubtus xinguense* may be easily distinguished by its uncommon, clearly downturned mouth (*versus* a terminal or upturned mouth). However, more detailed analyses are required to distinguish *T. ancylorhynchus* and *T. kranponhah* from the other two syntopic species, *Mylesinus paucisquamatus* and *Myleus setiger*. First, *T. ancylorhynchus* may be distinguished from *Mylesinus paucisquamatus* by the arrangement and shape of the lingual premaxillary teeth, as well as the number of dentary teeth. *T. ancylorhynchus* and *T. kranponhah* always exhibit lateral contact between the first and second lingual premaxillary teeth (1′–2′), sigmoid edges on the fourth and fifth premaxillary labial teeth (Fig. 3), and five to six dentary teeth, moreover, *T. kranponhah* have 38–43 scale rows around the caudal peduncle (*versus Mylesinus paucisquamatus*: clear separation of the first and second lingual premaxillary teeth, aligned edges on the fourth and fifth labial teeth, seven to 10 dentary teeth, and 30–34 scale rows around the caudal peduncle). Both *T. ancylorhynchus* and *T. kranponhah* possess poorly developed prepelvic serrae typical of *Tometes,* in contrast with *Myleus setiger,* which exhibits reasonably well-developed prepelvic serrae that form a marked keel. The two new *Tometes* species may also be distinguished from *Myleus setiger* via their dentition. Both *T. ancylorhynchus* and *T. kranponhah* have a diastema larger than the tooth base, between the two first labial premaxillary teeth on both sides of the premaxilla (*versus Myleus setiger*: the two first teeth are either slightly touching or in full lateral contact, forming a unique labial row on both sides). Furthermore, *T. ancylorhynchus* possesses a lateral space between the first and second labial teeth, a trait not found in *Myleus setiger* and *T. kranponhah*, but shared with *T. camunani*, *T. lebaili*, and *T. makue*. While these two teeth exhibit lateral contact in *T. kranponhah* and *Myleus setiger* (as well as in *T. trilobatus*), and therefore cannot be used as a diagnostic feature for these species, only *T. kranponhah* displays lateral cusps on the first and second teeth (*versus T. trilobatus* and *Myleus setiger*: the first and second teeth are broad laterally, with round, spatulated edges, without lateral cusps).

The features described in this study are useful for the identification of adult specimens, but a few of them are less evident in juveniles. For example, the lateral contact between the first and second labial premaxillary teeth is found in smaller specimens (70 mm L_S or shorter) of both *Tometes* species described herein, although the lateral cusps do not appear in *T. kranponhah* until they are just above 70 mm L_S. However, juveniles of *T. kranponhah* have a faded blotch on the opercle that is not found in *T. ancylorhynchus* juveniles. Furthermore, *T. kranponhah* juveniles do not exhibit the irregular, vertically elongated blotches on their flanks that are observed in *T. ancylorhynchus* (Fig. 13), *T. lebaili* (see Fig. 2b, 2c *in* Jégu *et al*., 2002b), *T. makue* (see Fig. 2d *in* Jégu *et al*., 2002a), and *T. camunani* (see Fig. 3 *in* Andrade *et al.,* 2013). *Tometes kranponhah* and *T. ancylorhynchus* may be distinguished from each other at any size by the higher number of circumpeduncular scales of *T. kranponhah* (38–43 scale rows around the caudal peduncle, *versus* 30–36 circumpeduncular scale rows in *T. ancylorhynchus*).

According to the morphology-based phylogeny reported by Jégu (2004), the humeral spot of the juveniles on the fifth to 12th perforated scale of the lateral line is considered a synapomorphy of the *Myleus* clade (genera *Myleus, Tometes, Mylesinus*, and *Ossubtus*).The morphological analyses in this study have demonstrated that this feature varies with ontogeny and species. For example, juvenile *T. kranponhah* up to 120 mm L_S (Fig. 8) exhibit a well-defined humeral blotch that is somewhat shifted down, whereas some *T. ancylorhynchus* specimens display a small, faint humeral spot that can be inconspicuous (Fig. 13a–c). The same faint humeral spot may also be observed in juvenile *T. camunani* and *T. lebaili*. Therefore, given that the spot is non-exclusive to the *Myleus* clade (Jégu, 2004) and given our new findings on the character state of the humeral spot, this feature may not actually constitute a synapomorphy, and may instead be simply a derived character in some species of the *Myleus* group.

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COMPARATIVE MATERIAL EXAMINED

Mylesinus paraschomburgkii. All from Brazil, Pará, Rio Trombetas, downstream of the Cachoeira Vira Mundo. GEA 1182 (head, skel., 64.7 mm H_L). INPA 1226 (holotype, 250 mm L_S). INPA 1234 (three specimens, c&s, 45.8–97.8 mm L_S). MNHN 1987-1401 (three specimens, paratypes, 191.3–238.9 mm L_S); MNHN 1987-1402 (one specimen, paratype, 137.9 mm L_S); MNHN 1987-1403 (two specimens, paratypes, 283.9–303.9 mm L_S); MNHN 1987-1404 (three specimens, paratypes, 102.9–254.5 mm L_S); MNHN 1987-1405 (one specimen, paratype, 227.6 mm L_S). *Mylesinus paucisquamatus*. All from Brazil, Pará. GEA 836 (159.4 mm L_S), Parauapebas, Rio Itacaiúnas. INPA 1808 (holotype, 162 mm L_S), Tucuruí, Rio Tocantins, Jatobal. MNHN 1988-1705 (two specimens, paratypes, 131.7–137.9 mm L_S); MNHN 1988-1706 (four specimens, paratypes, 112.8–185.1 mm L_S); MNHN 1988-1707 (one specimen, paratype, 165.3 mm L_S), Tucuruí, Rio Tocantins, Jatobal. *Mylesinus schomburgkii*. MNHN A-9855 (head, 94.7 mm H_L), Guyana, Essequibo River. *Myleus setiger.* BMNH 1971.5.10.65 (one specimen, syntype, 182.9 mm L_S), British Guiana. GEA 1963 (one specimen, 176.3 mm L_S), Brazil, Pará, Altamira, Xingu Basin, Rio Bacajá. GEA 1964 (one specimen, 144.7 mm L_S), Brazil, Pará, Altamira, Rio Xingu, beach in front of Fortaleza community. GEA 1965 (one specimen, 109.1 mm L_S), Brazil, Pará, Altamira, Rio Xingu, Cachoeira do Espelho. GEA 1966 (one specimen, 84.6 mm L_S); GEA 1967 (two specimens, 61.2–68.3 mm L_S), Brazil, Pará, Altamira, Xingu Basin, Rio Bacajá. GEA 1971 (one specimen, skel., 137.5 mm L_S), Brazil, Rio Xingu. GEA 1972 (head, skel., 45 mm H_L), Brazil, Ourilândia do Norte, Itacaiúnas Basin, Rio Cateté. IEPA 2889 (one specimen, 111.9 mm L_S), Brazil, Amapá, Rio Araguari, UHE de Ferreira Gomes. MNHN A-8629 (one stuffed specimen, holotype of *Myletes divaricatus*, 186.7 mm L_S), Guyana, Essequibo River. MNHN A-9868 (one specimen, holotype of *Myletes doidyxodon* 137.9 mm L_S), Brazil, Amazon River. ZMA 106.947 (one specimen, 71.9 mm L_S), Suriname, Nickerie, Fallawatra river. ZMA 107.524 (two specimens, 22.8–66 mm L_S), Suriname, Nickerie, Stondansie fall in the Nickerie River. *Ossubtus xinguense*. All from Brazil, Pará, Altamira, Rio Xingu, Volta Grande. GEA 1973 (one specimen, 202.7 mm L_S). INPA 6535 (holotype, 170 mm L_S). MNHN 1992-0003 (one specimen, paratype, 39.7 mm L_S); MNHN 1992-0004 (two specimens, paratypes, 156.2–173 mm L_S); MNHN 1998-1168 (four specimens, 36.4–55.9 mm L_S). *Tometes camunani*. All from Brazil, Pará. MPEG 23447 (holotype, 224.3 mm L_S), Rio Erepecuru. MPEG 23439 (one specimen, paratype, 248 mm L_S); MPEG 23440 (one specimen, paratype, 384 mm L_S); MPEG 23441 (one specimen, paratype, 276 mm L_S); MPEG 23442 (one specimen, paratype, 98 mm L_S); MPEG 23443 (two specimens, paratypes, 247–293 mm L_S); MPEG 23444 (three specimens, paratypes, 291–329 mm L_S); MPEG 23445 (one specimen, paratype, 127 mm L_S); Rio Trombetas. MPEG 23446 (two specimens, paratypes, 212–235.4 mm L_S), Rio Erepecuru. MPEG 23449 (one specimen, skel., 91.8 mm SL); MPEG 23448 (one specimen, skel., 382 mm L_S), Rio Trombetas.INPA 2310 (one specimen, paratype, 167 mm L_S), Rio Cachorro. INPA 2311 (one specimen, paratype, 180 mm L_S), Rio Mapuera, Cachoeira Patauá. INPA 3639 (one specimen, paratype, 299 mm L_S); INPA 5173 (one specimen, paratype, 230 mm L_S); INPA 5176 (one specimen, paratype, 325 mm L_S), Rio Trombetas. MZUSP 15893 (five specimens, paratypes, 201–274 mm L_S), Rio Mapuera. ZUEC 7066 (one specimen, paratype, 236 mm L_S), Rio Erepecuru. ZUEC 7067 (one specimen, 291 mm L_S), Rio Trombetas. *Tometes lebaili*. IRSNB 19.294 (two specimens, 23.3–29.8 mm L_S), Suriname, Paloemeu River. IRSNB 19.295 (one specimen, 40.6 mm L_S), Suriname, Marowijne River. IRSNB 21.343 (one specimen, 400.5 mm L_S), Suriname, Marowijne, Paloemeu River, Papadronsoela. MNHN 2000-6038 (two specimens, paratypes, 128.5–146.1 mm L_S); MNHN 2000-6047 (one specimen, paratype, 91.4 mm L_S); MNHN 2001-1209 (one specimen, 89.4 mm L_S); MNHN 2001-1210 (one specimen, 93.6 mm L_S); MNHN 2001-

1212 (one specimen, paratype, 147.4 mm L_S); MNHN 2001-1213 (one specimen, 213.1 mm L_S); MNHN 2001-1213 (one specimen, paratype, 180.2 mm L_S); MNHN 2001-1215 (one specimen, paratype, 219.4 mm L_S); MNHN 2001-1231 (two specimens, paratype, 162.4–207.4 mm L_S); MNHN 2001-2384 (holotype, 106.7 mm L_S), French Guiana, Maroni River. *Tometes makue*. All from Brazil, Amazonas, São Gabriel da Cachoeira, Rio Negro. INPA 7344 (holotype, 240 mm L_S); INPA 3179 (one specimen, 125 mm L_S); INPA 4913 (one specimen, 370 mm L_S); INPA 4914 (two specimens 330–355 mm L_S); INPA 4915 (two specimens, 138–158 mm L_S); INPA 4916 (two specimens, 239–307 mm L_S); INPA 4917 (one specimen, 261 mm L_S); INPA 4920 (four specimens, 172–229 mm L_S); INPA 4924 (12 specimens, 53–78 mm L_S); MNHN 2001-2712 (three specimens, paratypes, 208.2–230.9 mm L_S). *Tometes trilobatus*. MNHN A-8649 (one stuffed specimen, syntype, 370 mm L_S); MNHN A-8650 (one stuffed specimen, syntype, 337.3 mm L_S); MNHN A-8651 (one stuffed specimen, holotype of *Tometes unilobatus*, 277 mm L_S), French Guiana, Cayenne. IRSNB 20.219 (two specimens, 64.1–64.6 mm L_S); IRSNB 20.688 (five specimens, 42.6–53.3 mm L_S), French Guiana, Camopi River. IEPA 3564 (one specimen, 85.5 mm L_S); IEPA 3568 (one specimen, 107.5 mm L_S); IEPA 3570 (one specimen, 89.8 mm L_S), Brazil, Amapá, Rio Araguari, UHE de Ferreira Gomes. INPA 19967 (one specimen, 116 mm L_S), Brazil, Amapá, Rio Araguari, Cachoeira Santa Rosa. IRSNB 20.688 (five specimens, 42.1–53.3 mm L_S), French Guiana, Oyapock River, Alicoto Falls. ZMA 107.687 (one specimen, 108.8 mm L_S), French Guiana and Brazil, Oyapock Basin, near of confluence with Crique Armontabo.

Capítulo 2

Uma nova espécie de *Tometes* Valenciennes 1850 (Characiformes: Serrasalmidae) da bacia do rio Tocantins-Araguaia com base na análise integrativa de dados moleculares e morfológicos[4]

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Izeni P. Farias & Tommaso Giarrizzo

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"Biodiversity is the greatest treasure we have... Its diminishment is to be prevented at all cost"

Thomas Eisner
"Father of chemical ecology"
Ecólogo e entomologista americano

A new species of *Tometes* Valenciennes 1850 (Characiformes: Serrasalmidae) from Tocantins-Araguaia River Basin based on integrative analysis of molecular and morphological data

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Abstract

A new large serrasalmid species of *Tometes* is described from the Tocantins-Araguaia River Basin. *Tometes* sp. ‘*siderocarajensis*’ is currently found in the rapids of the Itacaiúnas River Basin, and formerly inhabited the lower Tocantins River. The new species can be distinguished from all congeners, except from *T. ancylorhynchus*, by the presence of lateral space between 1st and 2nd premaxillary teeth, and by the absence of lateral cusps in these two teeth. However, *T.* sp. ‘*siderocarajensis*’ can be differentiated from syntopic congener *T. ancylorhynchus* by an entirely black with mottled red body in live specimens, densely pigmented pelvic fins with a high concentration of dark chromatophores, and the presence of 39 to 41 rows of circumpeduncular scales (*vs*. silvery body coloration with slightly reddish overtones on middle flank during breeding period in live specimens, hyaline to slightly pale coloration on distalmost region of pelvic fins, and 30 to 36 rows of circumpeduncular scales). Additionally, molecular sequence shows that *T.* sp. ‘*siderocarajensis*’ is reciprocally monophyletic, and diagnosable from all congeners by having two autapomorphic molecular characters in the mitochondrial gene COI. The phylogenetic reconstruction still show that *T.* sp. ‘*siderocarajensis*’ is close related to *T. trilobatus*. This is the first molecular study using an integrative taxonomic approach based on morphological and molecular sequence data for all described species of *Tometes*. These findings increase the number of formally described species of *Tometes* to seven. A key to the *Tometes* species is provided.

Introduction

Serrasalmidae is a Cis–Andean fish family that comprises more than 80 species, of which one is a fossil [1–3]. The serrasalmid species are easily recognized by having a very deep body (sometimes like a disk), often silvery in color, and scales modified into spines that generally form a ventral serrae [4–6]. The family is phylogenetically divided into three major clades, corroborated by both morphological and molecular studies: one composed by large herbivores of the genera *Colossoma*, *Piaractus*, and *Mylossoma*; another collectively referred as "*Myleus*" which is comprised mostly by herbivorous fishes from rapids; and a third composed of the famous 'piranhas' including the aquarium trade fishes 'silver dollars' of the genus *Metynnis* [3,7,8].

Myleus clade, *sensu* morphological phylogeny [7], is formed by the genera *Myleus*, *Mylesinus*, *Ossubtus*, *Tometes*, and, according to molecular phylogenies [8,9], some species of the genus *Myloplus*. With the exception of the latter genus, *Myleus* clade is comprised of strictly rheophilic species and is characterized by having incisiform teeth on the jaws, two premaxillary rows of teeth that maintain inner contact, and prepelvic serra composed of thin spines not forming an abdominal keel (absent in *Ossubtus xinguense*) [10,11]. The genus *Tometes* was taxonomically hidden for many years [12], and was hence mistaken with other serrasalmid genera, most notably *Utiaritichthys*, a genus that some authors consider rare and poorly-known (e.g. [13], [4,14], [15]). Recently, most of these assignments were reported as misidentifications of *Tometes* because both genera show diminute prepelvic spines. However, *Utiaritichthys* is strictly distinguished from *Tometes* by having molariform teeth with two premaxillary teeth rows interspaced by a gap *versus* incisiform teeth with two premaxillary teeth rows lacking inner gap [11]. *Tometes* contains six valid species distributed in South America along drainages of Brazilian and Guiana Shields [11].

During analyses of specimens from Mosaic of Conservation Units (MCU) of the Serra dos Carajás, Itacaiúnas River, a left-bank tributary of lower Tocantins River Basin, as well as some specimens collected in lower Tocantins River (prior to the flooding from the Tucuruí Hydroelectric reservoir) a new species of *Tometes* was discovered and described herein.

Material and methods

Ethics Statement

Statement from an ethics committee was not necessary, once the analysis did not involve endangered or protected species. Except from the specimens deposited under institutions, which tissues were extracted from specimens collected with appropriate permissions under authorizations numbers 11325-1 and 38263-1 issued by ICMBio (Chico Mendes Institute for Biodiversity Conservation), and also 045/2008-2011 issued by IBAMA (Brazilian Institute of Environment and Renewable Natural Resources).

Nomenclatural Acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: urn:lsid:zoobank.org:pub: 69CDF38A-05CD-4351-8791-91889B741DE2. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS.

Morphological analyses

Counts and measurements follow [16,17] and were taken whenever possible on left side of specimens. Counts are given in description as the range of counts followed by the value observed in holotype in parentheses. Standard length (SL) is expressed in millimeters; subunits of body are showed as percentage of SL, and the subunits of the head as percentage of head length (HL). Osteological description, vertebral and supraneurals analysis were obtained from two dry skeletons (labeled as "skel." in material examined). Osteological terminology follows [18] with modifications of [19]. Vertebral counts include the Weberian apparatus as four elements, and the compound caudal centrum (PU1+U1) is counted as one element. Institutional abbreviations are as follows: CAS (California Academy of Sciences, San Francisco); CTGA (Laboratório de Evolução e Genética Animal, Universidade Federal do Amazonas, Manaus); GEA (Laboratório de Ictiologia do Grupo de Ecologia Aquática, Universidade Federal do Pará, Belém); IEPA (Instituto de Ensino Profissional da Amazônia, Macapá); INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus); INRA (French National Institute for Agricultural Research, Paris); MNHN (Muséum national d'Histoire naturelle, Paris); MPEG (Museu Paraense Emilio Goeldi, Belém); MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo); TAMU (Texas Agricultural & Mechanical University, College Station); and ZUEC (Museu de Zoologia da Universidade Estadual de Campinas ‘Adão José Cardoso’, Campinas).

Molecular analyses

The molecular analyses were made using 28 specimens of the six valid *Tometes* plus the new species proposed herein, from six large tributaries of the Amazon Basin in Brazil: as Jari, Negro, Tapajós, Tocantins-Araguaia, Trombetas and Xingu river basins; and also from Maroni River, a costal drainage between French Guiana and Surinam. Tissues were preserved in 95% ethanol for DNA extraction and deposited at CTGA, with vouchers deposited at GEA, IEPA, INPA and MPEG. The sequences obtained in this study are deposited in GenBank under the following accession numbers KX868671 to KX868698.

Total DNA was isolated from approximately 50mg of tissue using standard phenol-chloroform extraction methods [20]. A fragment of approximately 750 bp of the mitochondrial control region was amplified using the primers LPROF (5' AACYCCCRCCCCTAACYCCCAAAG 3') and DLOsteri R1 (3' GTAAAACGACGGCCAGTCCTGGTTTH 5'). About 670 bp mitochondrial region of the cytochrome C oxidase subunit I (COI) was amplified using the M13-tailed primer cocktails FishF2_FishR2 and VF2_VR1d [21]. The 15 µl polymerase chain reaction (PCR) mix included 1.2 µL of 10 mM dNTPs (2.5 mM each DNTP), 1.5 µL 10X buffer (75mM Tris HCL, 50 mM KCL, 20 mM $(NH_4)_2SO_4$), 1.2 µL 25 mM $MgCl_2$, 1.5 µL of primer cocktails (2 pM each) for COI and 1.5 µL of each primer for DLoop, 0.5 µL of Taq DNA polymerase, 1 µL of template DNA and 6.6 µL ddH2O. PCR conditions were as follows: 94°C (30 sec), 35 cycles of 94°C (30 sec), 50°C (35 sec), 72°C (1:30 min), followed by 72°C (5 min).

Amplicons obtained were submitted for purification and the sequencing was performed in an automatic ABI 3500 sequencer (Applied Biosystems).

The forward and reverse COI and control region chromatograms were assembled into contigs using Geneious 7.0.6 [22] and edited manually. The alignment was then checked manually for insertions, deletions or stop codons for COI sequences using translated amino acids. Genetic distances (uncorrected *p*-distances, recommended [23]) were calculated using the Ape 3.5 package [24] in R version 3.3.2 [25], with the pairwise deletion option set to "true". We used a cutoff of 2.0% for genetic distance as a threshold value adopted for the COI-based identification systems [26] in most Neotropical freshwater fish fauna [27]. We further visualized the divergence of these taxa using a Neighbor Joining (NJ) tree, which is the standard method of phylogenetic inference in DNA barcoding studies [26]. To demonstrate that the new species is divergent and diagnosable from all other nominal species of *Tometes*, assuming the Phylogenetic Species Concept [28], we used the R package SPIDER [29] to extract diagnostic molecular characters in the COI and control region sequences. Additionally, we concatenated the two genes and analyze the phylogenetic relationships among the species using a maximum-likelihood (ML) in the Ape 3.5 package [24]; the nucleotide substitution model (GTR+G) was selected using Phangorn with the AICc criterion, and node support was evaluated using 1,000 bootstrap replicates. In the ML analysis we included *Myloplus schomburgkii* and *Myloplus rubripinnis* as outgroups. Sequence alignment is available at https://github.com/legalLab/datasets.

Results

***Tometes* sp. '*siderocarajensis*'**

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Tometes sp. Tocantins: –Andrade et al. [30]: page 4 in figure 2b (premaxillary in labial view, and comparative material utilized).

Fig 1A, Fig 1B, Fig 2A, Fig 2B, Fig 3, Fig 4A, Fig 4B

Holotype. MPEG 33922 (1, 338.0 mm SL), Brazil, Pará, Parauapebas, Serra dos Carajás, Itacaiúnas River, nearby Paulo Fontelles Road, Caldeirão, 5°52'38.2"S 50° 29'27.8"W, Tocantins-Araguaia River Basin, 7 Sep 2010, D. Bastos & A. Jesus.

Paratypes. All from Brazil, Pará, Tocantins-Araguaia River Basin. GEA 1990 (1 skel., 340.0 mm SL), 3 Jul 2010, M. Andrade & A. Jesus, and MPEG 33925 (1, 332.0 mm SL), Oct 2008, D. Bastos & A. Jesus; same locality of holotype. GEA 1936 (1, 176.3 mm SL), same locality of holotype, 4 Jul 2008, T. Giarrizzo & A. Jesus. GEA 1942 (1, 306.1 mm SL), Parauapebas, Serra dos Carajás, Itacaiúnas River, downstream igarapé Salobo, Vira Mundo, 5°50'32.2"S 50°26'39"W, 20 Mar 2010, M. Andrade & A. Jesus. GEA 1944 (1, 200.3 mm SL), Parauapebas, Serra dos Carajás, Itacaiúnas River, upstream igarapé Cinzento, 5°53'07.9"S 50°31'54.6"W, 2 Jul 2008, T. Giarrizzo & A. Jesus. GEA 1945 (1 skel., 280.0 mm SL, Serra dos Carajás, Itacaiúnas River, Casa PAE, ICMBio, 5°55'44.7"S 50°43'2.6"W, Jun 2011, D. Ribeiro. ZUEC 12598 (2, 328.0–352.0 mm SL), same data as GEA 1945. INPA 52481 (7, 84.9–278.0 mm SL), Tocantins River, Itupiranga, Nov 1980, M. Jégu. INPA 52811 (1, 277.3 mm SL), Parauapebas, Serra dos Carajás, Itacaiúnas River, downstream igarapé Salobo, Vira Mundo, 5°50'32.2"S 50°26'39"W, Jun 2011, M. Andrade & A. Jesus. MPEG 33923 (2, 281.3–335.9 mm SL), Parauapebas, Serra dos Carajás, Itacaiúnas River, downstream igarapé Salobo, Vira Mundo, 5°50'32.2"S 50°26'39"W, 17 Dec 2009, M. Andrade & A. Jesus. MPEG 33924 (1, 287.5 mm SL), Ourilândia do Norte, Serra Onça–Puma, Cateté River, 6°34'1.2"S 51°01'57.1"W, 6 Jun 2011, A. Jesus. MZUSP 117052 (11, 248.5–341.3 mm SL), Parauapebas, Serra dos Carajás, Itacaiúnas River, Caldeirão, Nov 1983, M. Goulding.

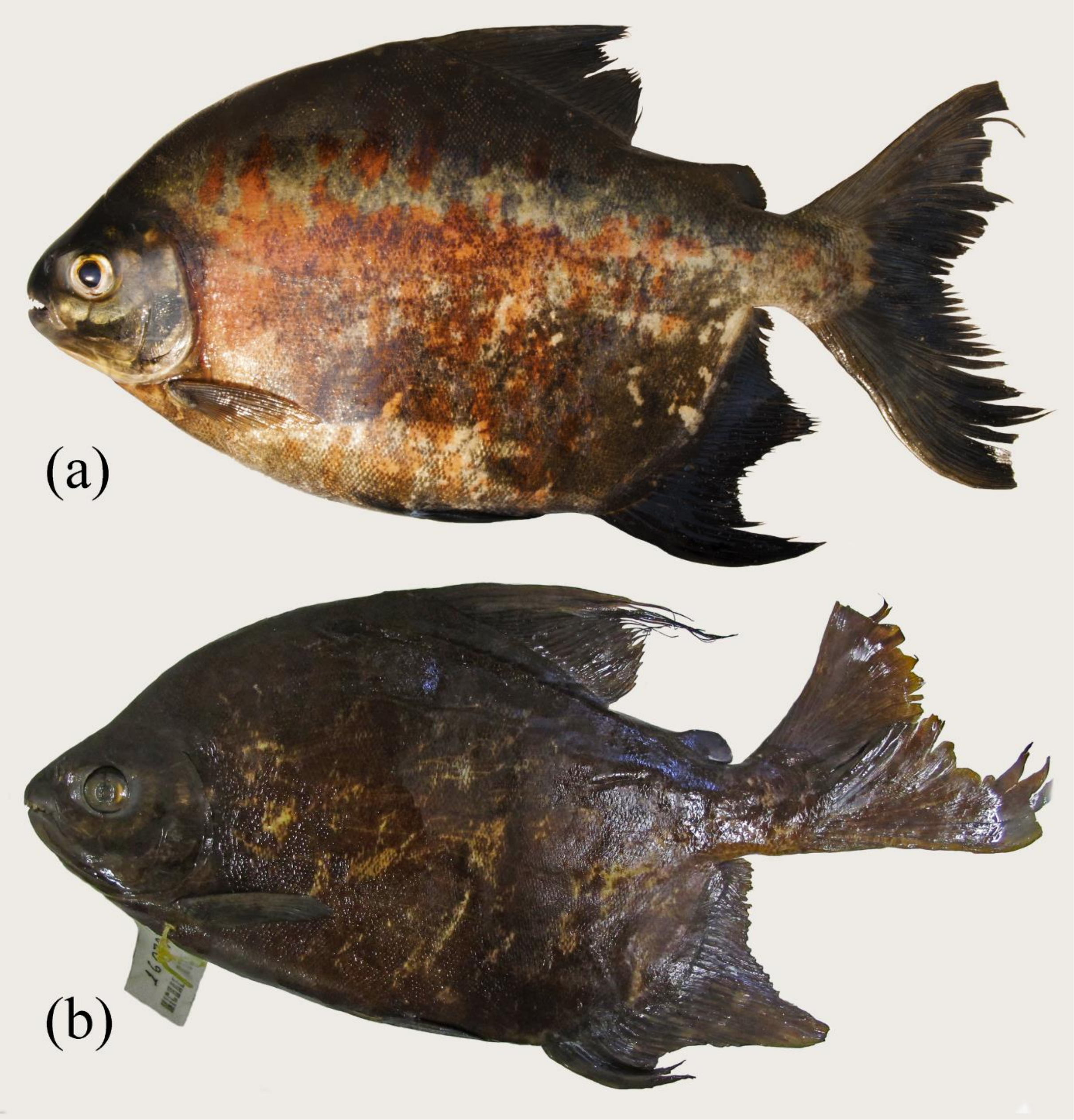

Figure 1. *Tometes* sp. '*siderocarajensis*' from Tocantins-Araguaia River Basin, (a) MPEG 33922, holotype photographed alive, male, 338.0 mm SL; (b) MZUSP 117052, paratype, preserved specimen, male, 341.3 mm SL.

Diagnosis.

Tometes sp. ‘*siderocarajensis*’ is distinguished from all congeners by dense pigmentation on the distalmost portion of the pelvic-fin rays or the entirety of the fin (Fig 2A, Fig 2B) [*vs.* pelvic fin hyaline or pale, or with few scattered dark chromatophores along distal portion of rays (Fig 2C, Fig 2E)]. Additionally, it is distinguished from all, except from *T. camunani* and *T. kranponhah*, by having more circumpeduncular scale rows (39–41 *vs.* 38 or less), and from *T. kranponhah* and *T. trilobatus* by having 1st and 2nd labial premaxillary teeth laterally spaced (Fig 3A) (*vs.* 1st and 2nd labial premaxillary teeth with lateral contact). The new species is further distinguished from *T. trilobatus* by having more perforated lateral line scales (74–84 *vs.* 58–72) and from *T. makue* by having more spines on ventral keel (11–17 prepelvic spines and 26–33 total spines *vs.* 0–9 and 10–23, respectively). Finally, *Tometes* sp. ‘*siderocarajensis*’ can be distinguished from *T. lebaili* by having a terminal to gently upturned mouth and invariably 5 dentary teeth (*vs.* a markedly upturned mouth and 6–7 dentary teeth).

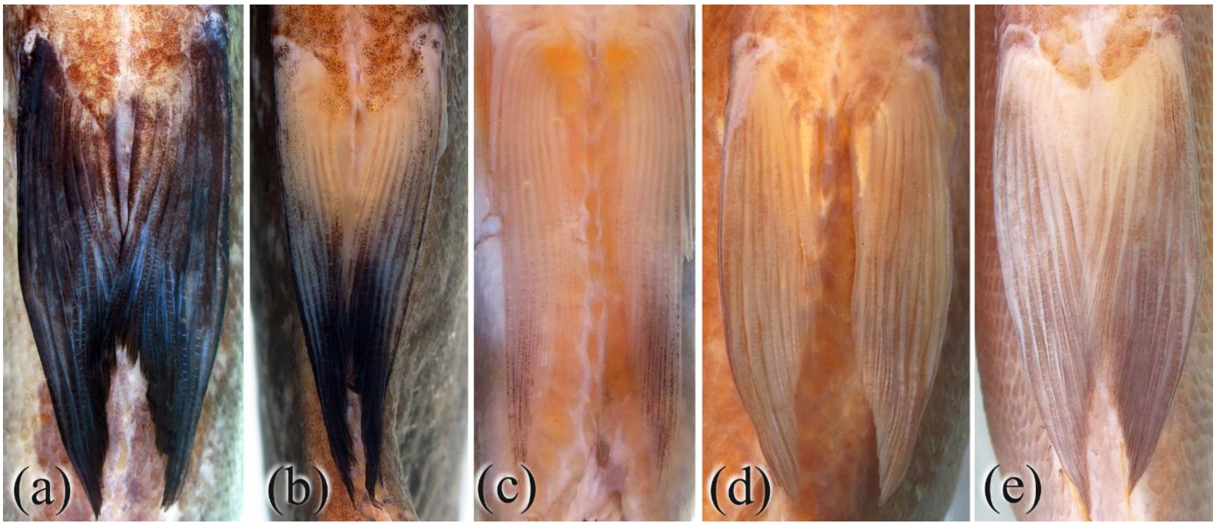

Figure 2. Ventral view of pelvic fins: *Tometes* sp. ‘*siderocarajensis*’ (a) MPEG 33925, paratype, male, 332.0 mm SL, and (b) GEA 1944, paratype, female, 200.3 mm SL. *Tometes ancylorhynchus*, (c) GEA 1955, female, 158.5 mm SL. *Tometes lebaili*, (d) MNHN 1993–3452, female, 251.0 mm SL. *Tometes trilobatus*, (e) MNHN 1998-0099, female, 248.0 mm SL.

Description.

Morphometric data presented in Table 1. Serrasalmid medium to large sized. Deep body, elongated to ovoid (Fig 1A, Fig 1B), laterally compressed. Greatest body depth at dorsal-fin origin. Snout tip slightly rounded. Dorsal profile of head straight to gently convex from vertical through nostrils to supraoccipital spine end. Dorsal-fin base straight to convex and interdorsal profile straight to gently concave. Ventral head and body profiles convex. Abdomen lacking ventral keel, thin prepelvic spines under skin. Prepelvic spines 11–17 (17). Postpelvic spines seven to 12 (8), and paired spines around anus five to eight (8). Total spines 26–33 (28). Anal-fin base straight to gently convex in females and strongly convex in males.

Table 1. Morphometric data for *Tometes* sp. '*siderocarajensis*'. Range of measurements includes the holotype (MPEG 33922). Hol, holotype; n, number of specimens; SD, standard deviation.

	Hol	n	Range	Mean±SD
Standard length	338.0	31	84.9–352.0	280.3
	Percentage of standard length			
Body depth	55.3	29	53.9–64.7	59.5±3.1
Head length	22.8	29	22.6–30.7	24.7±1.5
Distance from snout to supraoccipital spine	27.6	29	27.1–33.0	29.8±1.3
Predorsal length	53.7	29	53.3–59.6	57.5±1.6
Dorsal-fin base length	28.1	29	27.1–31.8	29.6±1.1
Interdorsal length	10.7	29	9.0–13.3	11.4±0.9
Adipose-fin base length	5.4	29	5.0–7.0	6.1±0.6
Caudal-peduncle depth	10.5	29	10.5–12.1	11.2±0.5
Caudal peduncle width	3.4	29	2.6–5.6	3.9±0.5
Prepectoral length	22.2	29	21.0–25.7	23.4±1.0
Pectoral-fin length	19.5	29	19.2–23.3	21.5±1.1
Pelvic-fin origin to anal-fin origin	19.6	29	18.8–24.2	21.7±1.5
Pectoral-fin origin to pelvic-fin origin	30.7	29	30.1–34.7	32.7±1.3

Prepelvic length	52.6	29	52.6–58.6	55.6±1.5
Pelvic-fin length	15.7	29	15.1–19.4	17.2±1.0
Preanal length	70.1	29	70.1–79.4	75.4±2.5
Anal-fin base length	29.3	29	29.3–34.2	31.6±1.3
Second anal-fin lobe length	15.2	12	13.1–22.4	18.2±3.5
Dorsal-fin lobe length	23.4	24	20.5–38.8	28.1±4.3
Dorsal-fin origin to anal-fin origin	59.0	29	58.8–70.1	63.8±3.1
Dorsal-fin end to anal-fin origin	43.2	29	42.0–52.3	47.1±2.4
Dorsal-fin end to anal-fin end	23.0	29	23.0–28.1	25.5±1.2
	Percentage of head length			
Snout length	35.5	29	27.5–39.8	34.6±3.3
Mouth length	27.1	29	16.2–28.8	23.2±2.6
Mouth width	38.0	29	30.8–41.1	36.8±2.7
Interorbital width	51.0	29	39.3–53.6	49.7±3.1
Head width	66.2	29	48.2–69.3	62.4±3.9
Third infraorbital width	12.5	29	8.5–14.7	11.3±1.2
Fourth infraorbital width	13.4	29	11.8–17.2	14.3±1.2
Eye vertical diameter	30.0	29	25.2–39.1	30.9±3.3
Postorbital distance	31.0	29	23.7–35.9	30.9±2.4

Mouth terminal to somewhat upturned, premaxillary slightly longer than dentary. Incisiform teeth. Premaxillary with five labial teeth and two lingual teeth (Fig 3A, Fig 3B). Labial premaxillary row abutting with lingual premaxillary row. First to 3rd teeth of labial premaxillary row high, without lateral cusps, and crows in ventral view with subtle curve; 4th and 5th teeth, smaller, tricuspids, and crows in ventral view forming sigmoid shape. First two teeth of labial premaxillary row laterally spaced. Dentary with five teeth on main row, fitted between the two rows of premaxillary teeth, and pair of symphyseal teeth. Dentary elongated, thin anteroposteriorly, gently arched with five bony lamellae at symphysis. Maxillary edentulous.

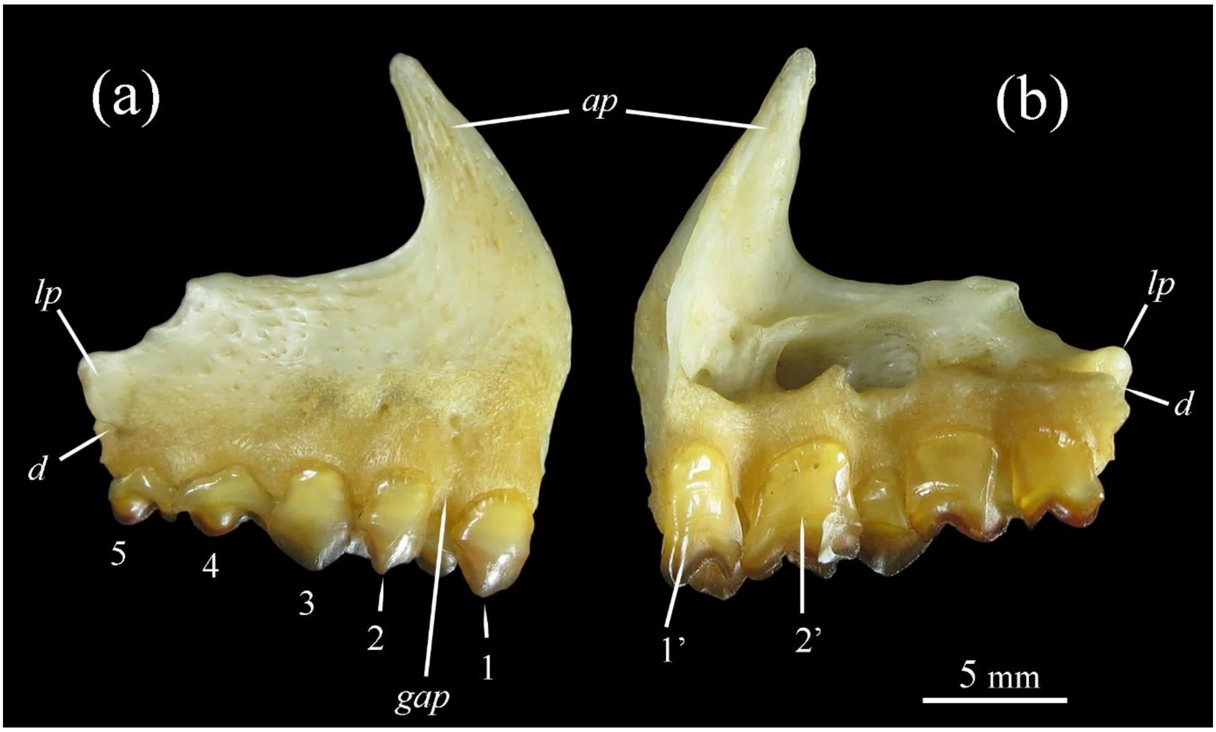

Figure 3. Premaxilla of the *Tometes* sp. ‘*siderocarajensis*’, GEA 1945, female, 280.0 mm SL, (a) lateral view, (b) internal view. 1–5: Labial premaxillary row; 1’–2’: Lingual premaxillary row; *ap*: Ascending process of premaxilla; *lp*: Lateral process of premaxilla; *d*: Dimple of articulation with anterodorsal portion of maxillary; gap: lateral space between 1 and 2.

Scales cycloid, irregular sized. Perforated lateral line scales from supracleithrum to hypural plate end 74–84 (80), and total perforated lateral line scales 79–90 (86). Horizontal scale rows between dorsal-fin origin and lateral line 45–53 (50). Horizontal scale rows between lateral line and pelvic-fin insertion 42–50 (46). Circumpeduncular scales rows 39–41 (40).

Dorsal fin preceded by forward directed spine. Dorsal-fin rays ii–iii (iii), 20–22 (21). Distal margin of dorsal fin falcate with filaments in some cases (see under sexual dimorphism). Anal-fin rays iii-iv (iii), 31–35 (34). Pectoral-fin rays i, 15–17 (16). Pelvic-fin rays invariably i, 7. Adipose fin present, with oblique base, distal margin gently straight, sub-rectangular shaped. Caudal fin forked with similarly-sized lobes, almost reaching body depth when vertically stretched. Five to six supraneurals. Forty-two total vertebrae. Nine predorsal vertebrae, and 16 postdorsal vertebrae. Two vertebrae between vertical through last dorsal fin pterygiophore and first anal-fin pterygiophore. First branchial arch with 28–29 gill rakers, 12–13 on upper branch; one at cartilage between ceratobranchial and epibranchial, and 14–16 on lower branch.

Neurocranium in lateral view as high as long, triangular, and with gently concavity at epiphyseal bar. Fontanells equally sized. Mesethmoid trapezoid, elongated forward with anterior process pointed and directed downward. Ethmoidal wings elongated forward, positioned on anterior half of mesethmoid. Wide olfactory fossae, and slender roof of mesethmoid.

Coloration in alcohol.

Ground color brown darkish with black and red blotches scattered on flanks (Fig 1A, Fig 1B, Fig 4A, Fig 4B). Some specimens can present pale coloration due to fading from alcohol and light (Fig 1B). Dorsal portion of head and flanks darker than lower portion. Portion of pelvic fins and first rays of anal fin densely blackened by presence of chromatophores (distalmost portion of pelvic-fin rays densely pigmented, or whole fin completely dark colored). Distal margin of caudal and dorsal fins conspicuously dark colored. Pectoral fins hyaline, and adipose fin with distal margin slightly darkened.

Coloration in life.

Overall color pattern brown with black and red blotches scattered on flanks. Dorsal profile of head, cheek gap, middle zone of opercle, and joint between operculum and subopercle with high concentration of dark chromatophores. Pectoral fins uniformly light brown, while adipose and caudal fins darker pigmented, and pelvic and anal fins densely blackened.

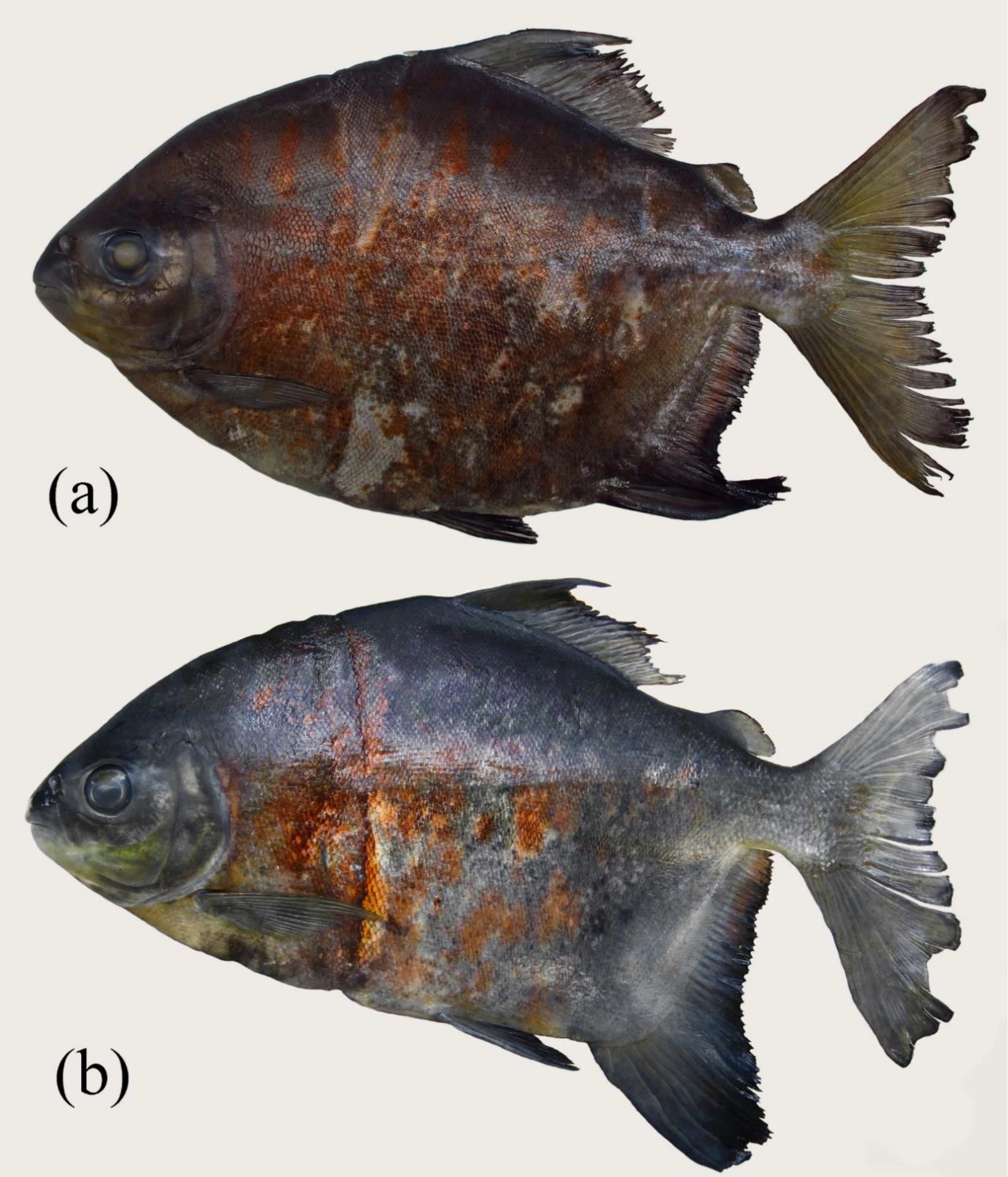

Figure 4. *Tometes* sp. '*siderocarajensis*', paratypes, (a) INPA 52811, female, 227.3 mm SL, (b) ZUEC 12598, female, 328.0 mm SL. Preserved specimens.

Sexual dimorphism.

Tometes sp. '*siderocarajensis*' displays secondary sexual features. The 17 mature males examined have an additional lobe formed by the middle branched anal-fin rays (Fig 1A, Fig 1B). Additional lobe centered on 14th–17th (16th) branched rays (Fig 1A, Fig 1B). The females do not have this additional lobe and show a falcate anal-fin distal margin (Fig 4A, Fig 4B). First lobes of dorsal- and anal-fin rays variable in length between sexes (females with dorsal fin ranging from 20.5–31.2 % SL ± 3.5; and anal fin 24.4–32.8 % SL ± 2.6; and males with dorsal fin ranging 23.2–30.1 % SL ± 2.5; and anal fin ranging 20.2–31.3 % SL ± 3.6). Four of the 17 males, measuring 280 mm SL or more [including the holotype], exhibit stiff hooks laterally curved on the distalmost lepidotrichia of the anal-fin rays, and six males, the largest measuring 300 mm SL, have dorsal fin with very thin elongations (Fig 1B), ranging 4.6–15.8 % SL.

Molecular Results.

The control region sequences length was approximately 730 bp, including 162 variable sites, of which 132 were parsimony informative. The COI sequence length was about 580 bp with no observed insertions, deletions or stop codons. Out of 103 variable sites, 83 were parsimony informative. All species had maximum intra-specific divergence values below 1.0%, except *T. makue* and *T. trilobatus*, each of which was represented by a single sample. The uncorrected *p*-distances divergence ranged from 0.0% to 0.9% (mean 0.2%) for intra-specific comparisons and from 1.6% to 9.1% (mean 5.8%) for congeneric comparisons. Using a cutoff of 2.0% for delimiting species, a pair of species (i.e. *T*. sp. '*siderocarajensis*' and *T. trilobatus*) showed interspecific values below this limit and could not be discriminated using this threshold alone.

The ND characters obtained for COI sequences is also used as a complementary analysis [31] to reinforce the utility of the DNA barcoding technique to identify species for those with low uncorrected *p*-distances divergence values (< 2.0%), such as *T.* sp. '*siderocarajensis*' and *T. trilobatus* (S1 Table), which showed two exclusive NDs each, in 83 informative sites. However, no exclusive NDs were observed for the control region sequences to differentiate this pair of species.

The neighbor-joining (NJ) topology showed that all species in this study are reciprocally monophyletic with high bootstrap values (Fig 5). The following valid *Tometes* species were readily distinguishable using the DNA barcoding approach: *T. makue* was recovered as sister group of *T. lebaili*. In turn, this clade was recovered as sister group of a more inclusive clade comprised of two other groups, the first of which includes *T. trilobatus* and *T.* sp. '*siderocarajensis*', and the second of which includes *T. camunani*, *T. ancylorhynchus*, and *T. kranponhah*. *Tometes makue* and *T. ancylorhynchus* presented the highest interspecific distances values (9.1%). Among congeners, *T. trilobatus* was more closely related to *T.* sp. '*siderocarajensis*' showing the lowest interspecific distance (1.6%).

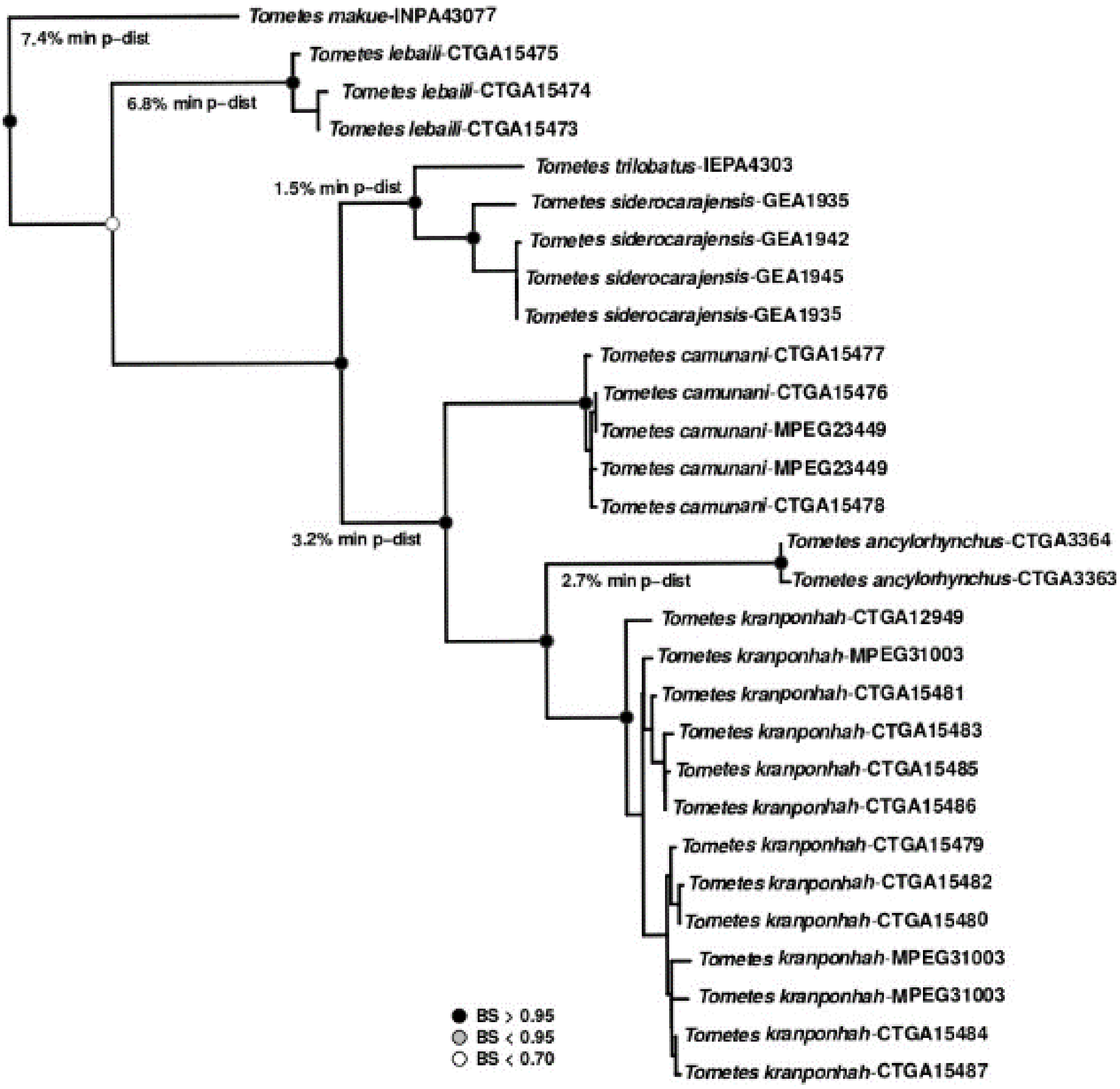

Figure 5. Neighbor-joining (NJ) tree of 28 mitochondrial cytochrome c oxidase subunit I gene sequences from seven *Tometes* species using uncorrected *p*-distance, showing the correct discrimination by distance genetic approach of the all species. Bootstrap values based on 1000 replicates are indicated at the branches.

Based on the concatenated sequences of the two genes, ML tree (Fig 6) shows that all *Tometes* species are monophyletic, pending confirmation of *T. trilobatus* and *T. makue* since only one specimen was available for analysis. Relationships among species are well supported except for the sister taxon relationship of *T. lebailli* and *T. makue*.

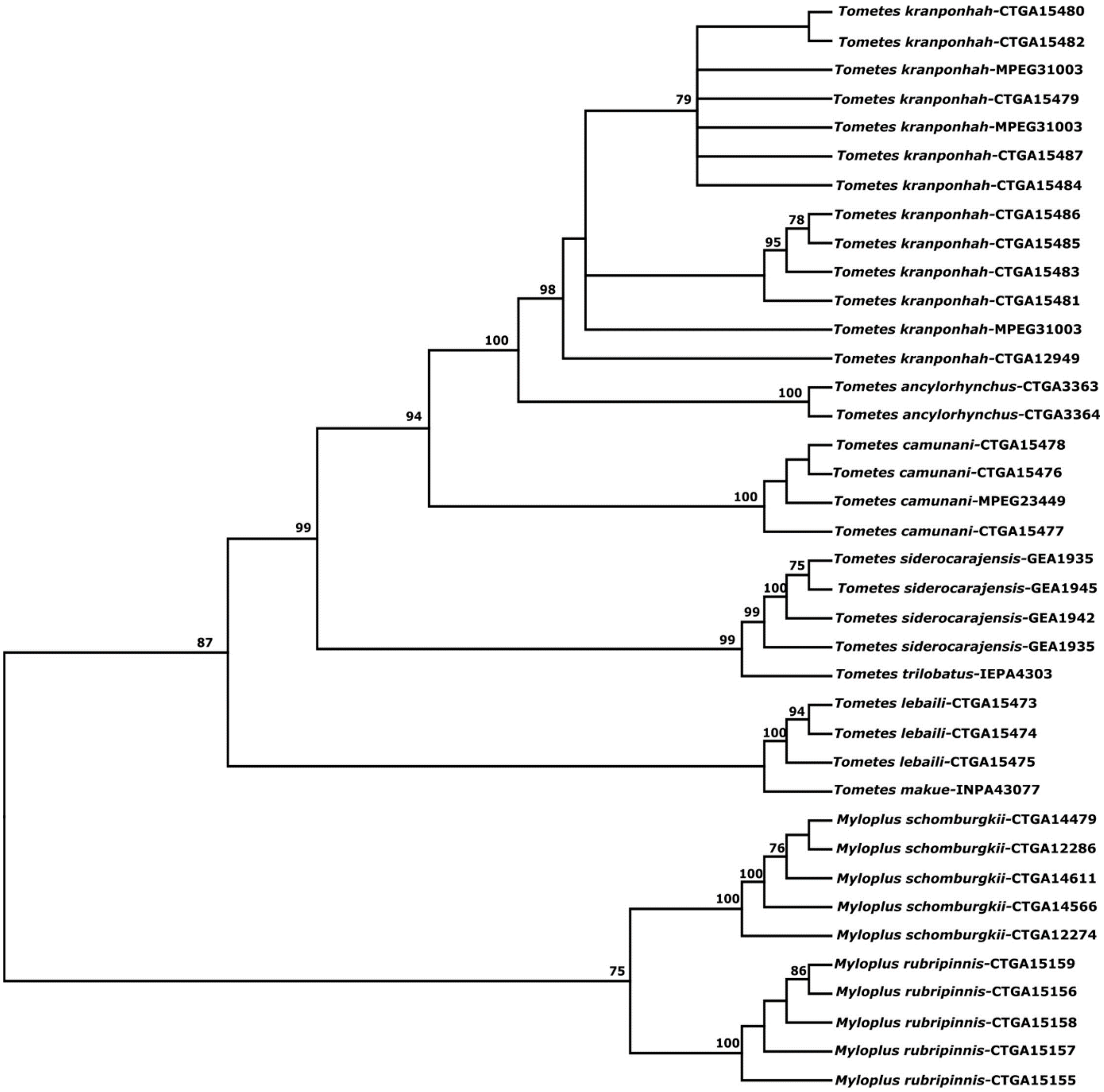

Figure 6. Maximum Likelihood tree inferred in RAxML using the concatenated data matrix of two mitochondrial genes (COI and Control Region), showing phylogenetic relationships within the genus *Tometes* genus. The numbers above branches are bootstrap probabilities > 50%. *Myloplus schomburgkii* and *Myloplus rubripinnis* were used as outgroups.

Etymology.

The epithet sp. '*siderocarajensis*' alludes to the locality 'Serra and Carajás', which is the largest high-grade iron deposit in the world. From the Greek–Latin *sidero* means 'iron', and *carajensis* in allusion to the type locality. A toponymic adjective.

Geographic distribution.

Tometes sp. ‘*siderocarajensis*’ is known to occur in the rapids of the Itacaiúnas River (Fig 7) and in its right-bank tributary, the Cateté River (average elevation of localities around 220 m a.s.l.), both located in the Mosaic of Conservation Units of Serra dos Carajás, Tocantins-Araguaia River Basin, State of Pará (Fig 8). In addition, *T.* sp. ‘*siderocarajensis*’ had its record confirmed in the Tocantins River based on specimens collected before the construction of the Tucuruí Hydroelectric Reservoir (INPA 52481), an area formerly known to contain many rapids but is currently flooded by the dam.

Figure 7. Itacaiúnas River, Pará State, at Mosaic of Conservation Units of Serra dos Carajás, type locality of *Tometes* sp. ‘*siderocarajensis*’.

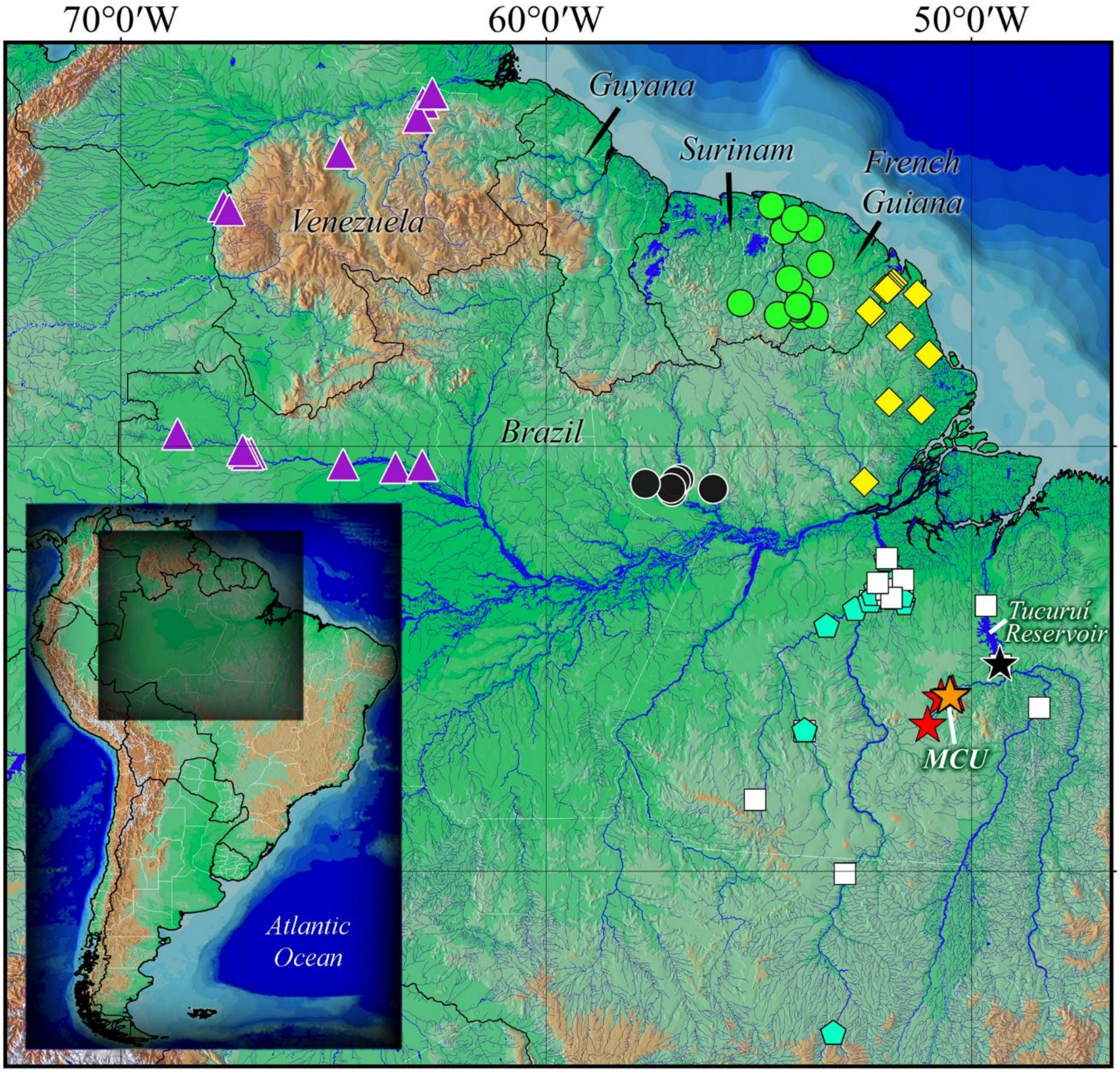

Figure 8. Distribution map of *Tometes* species. *Tometes ancylorhynchus* (white squares), *T. kranponhah* (blue pentagon), *T. makue* (purple triangle), *T. camunani* (black circle), *T. lebaili* (green circle), and *T. trilobatus* (yellow diamond). *Tometes* sp. ‘*siderocarajensis*’ (stars); orange star represents the type locality, black star the record before Tucuruí hydroelectric reservoir, and red stars the remaining localities. MCU: Mosaic of Conservation Units.

Remarks.

Tometes sp. ‘*siderocarajensis*’ is typically found in rapids associated with rocky outcropping covered in aquatic macrophytes of the families Podostemaceae and Fabaceae, which act as a food source for these fish. The species is commonly caught by local, professional and amateur fishermen in the Itacaiúnas River. As bait, the fisherman use either leaves from

Podostemaceae wrapped around a hood with sewing line, or hooks with the fruits of Fabaceae (Andrade, *pers. comm.*). Fishermen report that this fish provides a "good fight", making it one of the most sought-after species for sport fishing in the region. Nevertheless, *T.* sp. '*siderocarajensis*' is easily caught using gillnets placed around rapids [notice the vertical mark caused by gillnets on each specimen (Fig 4A, Fig 4B)].

One large specimen (GEA 1990, 340.0 mm SL) was dissected and the gastrointestinal contents examined. The stomach was completely full of undigested items, and free of parasites or aquatic macroinvertebrates. Large pieces of Podostemaceae (leaves and flowers) represented the vast majority of stomach contents, but we also found three small Fabaceae fruits (two of these cut in half without being crushed, and a third entire) and a cricket (Orthoptera) around 45 mm total length and split in half. The uncoiled intestine is long, and measures approximately four times the SL of the fish. Intestinal contents were composed of leaves (majority), flowers and seeds (a small amount), and abundance of Nematode fauna (mainly *Rondonia rondoni* Travassos 1919). It's worth mentioning that the nematodes were only found in the last two thirds of the intestine, with a higher concentration in the second third.

The new species was only recorded in Tocantins-Araguaia drainages where it occurs syntopically with three other serrasalmid, rapids-adapted species, *Mylesinus paucisquamatus* Jégu and Santos 1988, *Myleus setiger* Müller and Troschel 1844, and *Tometes ancylorhynchus* Andrade, Jégu and Giarrizzo 2016. Whereas *M. setiger* and *T. ancylorhynchus* have soft and palatable meat, *T.* sp. '*siderocarajensis*', *T. kranponhah,* and *M. paucisquamatus* are locally referred as 'pacu–borracha' (literally translated as 'rubber pacu'), due to the rubbery texture of its flesh when cooked [11]. Notwithstanding, *T.* sp.

‘*siderocarajensis*’ is still consumed by fishermen of the Itacaiúnas River, due in part to its capacity to reach large sizes (~300 mm SL and up to 2 kg) relative to *M. paucisquamatus* (~ 200 mm SL and 400 g) and because it is an excellent food source that cannot be wasted. Furthermore, local human consumers dislike *M. paucisquamatus* because it tends to harbor higher abundances of endoparasitic fauna (Andrade, *pers. comm.*).

Discussion

Morphology.– *Tometes* sp. ‘*siderocarajensis*’ has a darker body coloration, relative to its congeners with silvery gray coloration and noticeably silver-reddish overtones during the breeding period. Among its congeners, only large and live individuals of *T. lebaili* exhibit body coloration as dark as live specimens of *T.* sp. ‘*siderocarajensis*’; however, figure 3 of [32] describes a large specimen of *T. lebaili* (~ 400 mm SL) presenting black coloration of pelvic fin with highlights of yellow. A similar coloration description for pelvic fins was noted in live specimens of *T. trilobatus* [12]: “*Toutes les nageoires sont noires, nettement plus foncées que le corps*” (all fins are black, evidently darker than the body color). However, *T.* sp. ‘*siderocarajensis*’ have distinctly dark pigmentation of pelvic fins in when compared to conspecifics (Fig 2A, Fig 2B). In addition, *T. trilobatus* and *T. lebaili* occur in left-bank tributaries of the Amazon Basin and in coastal drainages of the Guiana Shield, respectively (Fig 8), whereas *T.* sp. ‘*siderocarajensis*’ occurs exclusively in the Tocantins-Araguaia River Basin, within the Brazilian Shield drainage (Fig 8). *Tometes* sp. ‘*siderocarajensis*’ can be further distinguished from *T. trilobatus* and *T. lebaili* by having more circumpeduncular scale rows (39–41 *vs.* 27–34 and 32–36, respectively), and further yet from *T. trilobatus* by the distinctive arrangement of its 1st and 2nd labial premaxillary teeth (Fig 3A and Fig 9A, respectively), and the strikingly different morphology of the 4th and 5th labial premaxillary teeth (Fig 3A and Fig 9B, respectively).

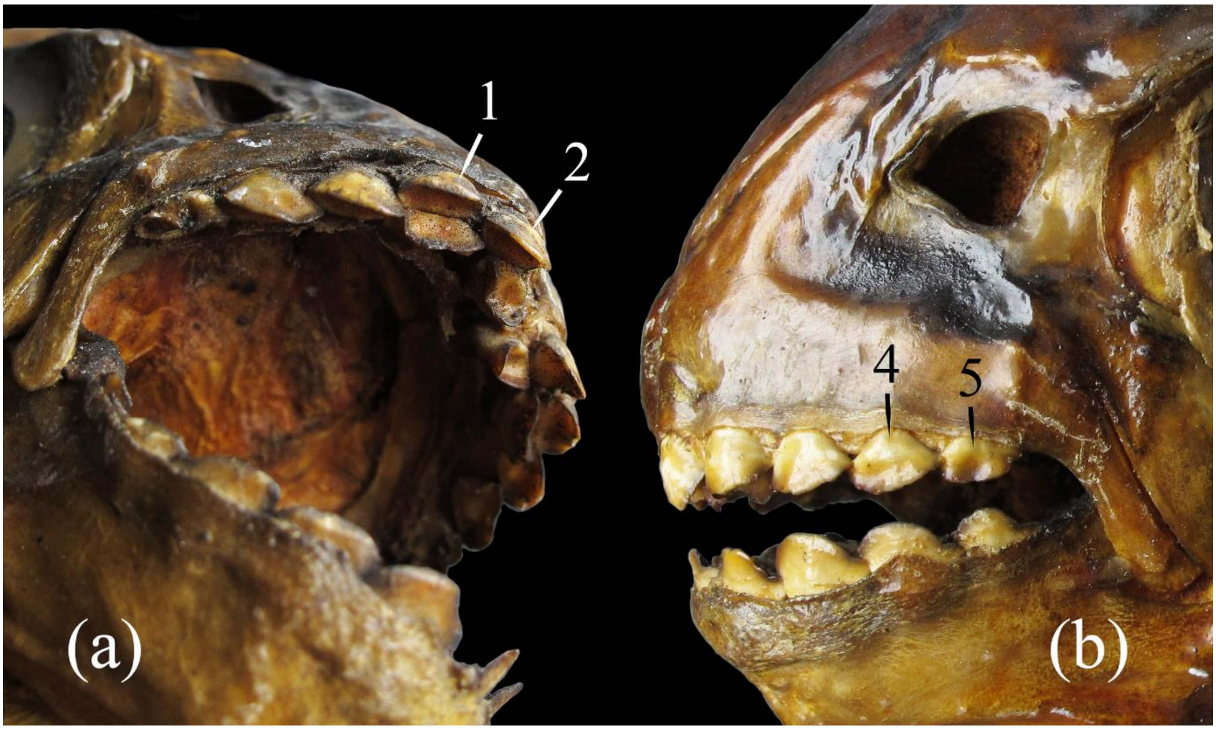

Figure 9. Teeth of *Tometes trilobatus*, (a) MNHN A.8650, lectotype, male, 337.3 mm SL, ventral view of premaxilla, (b) MNHN A.8649, paralectotype, female, 370.8 mm SL, lateral view. 1–2: first and second teeth of labial premaxillary row; 4–5: fourth and fifth teeth of lingual premaxillary row.

Besides the dark body coloration and densely pigmented with dark chromatophores pelvic fins, when compared to *T. ancylorhynchus*, which has distribution to Tocantins-Araguaia Basin, as well as *T.* sp. ‘*siderocarajensis*’ [formerly sympatric distribution, see under *Geographical distribution* and (Fig 8)], the new species can be differentiated by having more circumpeduncular scale rows (39–41 *vs.* 30–36, respectively). See more in key to *Tometes* species below.

In the charge, *Tometes* species were largely confused with *Utiaritichthys* species [e.g. *T. ancylorhynchus* from Xingu and Toncantins-Araguaia River basins, *T. camunani* from

Trombetas Basin and *T. kranponhah* from Xingu Basin (Fig 8)]. The paratypes of *T.* sp. ‘*siderocarajensis*’ cataloged under MZUSP 117052, collected by Michael Goulding in the early 1980s at Itacaiúnas River, were misidentified as *Utiaritichthys sennaebragai*. Although *U. sennaebragai* is recognized only to Tapajós River Basin and occurrences outside of this basin are considered to be misidentifications [11,33], species are still reported in other watersheds such as Xingu, Tocantins-Araguaia, Madeira, Orinoco, and others [34]. This was most likely influenced by [13], which diagnosed a serrasalmid specimen (catalog CAS 20222) with a poorly-developed abdominal serra as *U. sennaebragai*. This diagnosis was recently changed to *T. ancylorhynchus* by Andrade et al. [11]. It is noteworthy that this lot as well as INPA 52481 (*T.* sp. ‘*siderocarajensis*’), came from an area where the rapids of the Tocantins-Araguaia River Basin were formerly located, at the cities of Marabá and Itupiranga, respectively. However, most of this area is currently submersed by the Tucuruí reservoir (Fig 8). Due to the loss of rapid stretches and flooded areas on the lower Tocantins River, the possibility of finding rheophilic fish is remote.

Molecular analysis.– The isolated application of a single technique for description of a novel species (i.e. morphological or genetic analysis alone), has been criticized and contains several caveats, when a small number of individuals per species are used or only a small fraction of the global richness is considered [35]. The present study is the first to use DNA barcode methodology to assist in the description of a new species of Serrasalmidae. Despite the low number of samples per species, the DNA barcoding analysis of 28 specimens representing the entire *Tometes* genus was effective, and allowed for the correct discrimination of all analyzed species.

The mean of intra- and interspecific distances were 0.2% and 5.8%, respectively, and differed from studies of [27] and [36] for freshwater fishes in South America, which found averages of 1.3% and 6.8% and 2.3% and 19.3%, respectively. Thus, the mean interspecific distance found among *Tometes* species is low (5.8%) compared to the global average found in studies of freshwater fishes in North America and in the Neotropical region (6.8%). The average of the intraspecific distances was even lower than those found for fishes of the Neotropics and other regions [27,37–39]. This relatively low interspecific distance may reflect a recent divergence experienced by *Tometes* species. A similar result was obtained by [40] for freshwater stingrays in the Amazon Basin. However, the *Tometes* species are distinguished by their morphology. Except for *T. makue* and *T. lebaili,* all other *Tometes* species have low interspecific distances (mean 3.3%). Working with *Hypostomus* [41] and studying two serrasalmid genera representative of the piranhas [42] (i.e. *Serrasalmus* spp. and *Pygocentrus* spp.), proposed a hypothesis of radiation of these groups, which may have originated from 2 to 12 MYA. These authors also suggest that the low distance pattern can be found in other Neotropical fish groups, and is indicative of recent diversification. Because approximately 70% of the comparisons among *Tometes* species showed less divergence than 6% (S1 Table), our results were consistent with this pattern. So, *T. makue* from Negro River and *T. lebaili* from Maroni River were recovered as sister species, whereas *T. ancylorhynchus* from Araguaia was recovered as the close taxa close to *T. kranponhah* from Xingu (Fig 5). The interspecific molecular distance between *T. trilobatus* from Jari River (left-bank tributary of Amazon River Basin) and the *T.* sp. '*siderocarajensis*' from Itacaiúnas River (sub-basin of lower Tocantins-Araguaia River Basin) reveals the recent divergence between these taxa, and agrees with hypothesis of diversification of freshwater species [43]. *Tometes*, as well as the genera *Mylesinus*, *Ossubtus* and *Myleus* (*stricto sensu* [44]), are highly rheophilic serrasalmid fishes with high degrees of endemism since most of their representative species are restricted to a few or even a single river basin.

Although the divergence between *T. trilobatus* and *T.* sp. '*siderocarajensis*' is below the barcoding threshold (2%) for interspecific distinction, all species showed particular diagnostic nucleotides. *Tometes* sp. '*siderocarajensis*' had two diagnostic nucleotides in 83 informative sites for the COI gene, and the same was observed to *T. trilobatus*, which was distinguished by also having two diagnostic nucleotides distinctive from the new species. According to [45], using diagnostic nucleotides for comparisons of closely related species is more difficult, since the nucleotide composition is more similar. *Tometes* sp. '*siderocarajensis*' presented two nucleotide sequences as diagnostic sites for the COI gene, sites 594 (T/A) and 696 (A/G), and *T. trilobatus* presented the diagnostic sites 120 (A/G) and 180 (G/A), which corroborate with the proposal of a new serrasalmid taxa (S2 Table). Therefore, *Tometes* sp. '*siderocarajensis*' should be considered a distinct species within the *Tometes* genus due to both morphological and molecular characteristics that distinguish it from congeners. The data suggest that the new species is monophyletic, and clearly diagnosable from other species of *Tometes* by morphological and molecular autapomorphies. This leads us to conclude that *T.* sp. '*siderocarajensis*' is following a unique evolutionary trajectory under the phylogenetic species concept [28], and thus merits the status of a valid novel species.

Distribution pattern and conservation.– Despite the fact that other serrasalmids *M. paucisquamatus*, *M. setiger* and its congener *T. ancylorhynchus* occur in the same Tocantins-Araguaia River Basin, *T.* sp. '*siderocarajensis*' is the only *Tometes* species currently known to occur in Itacaiúnas sub-basin. The species *T. ancylorhynchus* (INPA 3134) and *T.* sp.

‘*siderocarajensis*’ (INPA 52481) were last documented to co-occur in the lower Tocatins River (Fig 8) in 1980, but have not been found there since this area was flooded by the hydroelectric dam. *Tometes ancylorhynchus*, which also occurs in the Xingu and Tocantins-Araguaia River basins [11], apparently does not occur in the sub-basin of the Itacaiúnas River. On the other hand, *M. paucisquamatus*, which is endemic of the Tocantins-Araguaia, is widespread throughout this basin, since it is found along with the two aforementioned species. Although possibility a result of habitat loss, *T.* sp. ‘*siderocarajensis*’ is supposedly endemic to the Itacaiúnas sub-basin, which is the main tributary of the Tocantins River that drains the Carajás mineral province [46]. Taking into account that the Tocantins-Araguaia Basin is strongly modified by hydroelectric dams, the Itacaiúnas sub-basin has been constantly degraded by the effects of mining, soybean-farming and cattle ranching [46], and that the distribution of *T.* sp. ‘*siderocarajensis*’ is restricted to the rapids of this sub-basin, we stress the importance of the Mosaic of Conservation Units of the Serra dos Carajás as a protected area for whole biodiversity of the Itacaiúnas sub-basin. We continue to recommend the protection of rapids of the Serra dos Carajás to ensure the presence of rheophilic species.

Key to species of *Tometes* Valenciennes 1850.

1. Mouth terminal to slight subinferior … 2

1’. Mouth clearly oblique upward turned … *T. lebaili* (Atlantic coastal drainages occurring in French Guiana rivers of Litany, Mana, Maroni, and Tampoc, as well as in Suriname rivers of Commewine, Oulemary, and Tapanahony)

2. First and second teeth of the premaxillary labial row with evident lateral contact … 3

2’. First and second teeth of the premaxillary labial row clearly laterally spaced … 4

3. Twenty-seven to 34 circumpeduncular scales, first and second premaxillary labial teeth lacking lateral cusps, no defined marks on opercle … *T. trilobatus* (Oiapoque River drainage between French Guiana and Brazil, and in the Northeastern Brazilian Rivers of Anotaié, Araguari, Cassiporé, Flexal, and Jari)

3’. Thirty-eight to 43 circumpeduncular scales, lateral cusps on first and second premaxillary labial teeth, tear-drop black blotch on opercle … *T. kranponhah* (Xingu River Basin, such as drainages of the Iriri, Xingu, Bacajá rivers)

4. Prepelvic spines counting from 11 to more … 5

4’. Prepelvic spines ranging from none to 9 … *T. makue* (Negro River Basin in Brazil, and Orinoco River Basin in Venezuela)

5. Circumpeduncular scale rows counting from 37 to more … 6

5’. Circumpeduncular scale rows ranging from 30 to 36 … *T. ancylorhynchus* (Tributaries of the Xingu River Basin and Tocantins-Araguaia River Basin, except Itacaiúnas River drainage)

6. Pelvic fins hyaline, ground body coloration predominantly silver, 10 to 11 predorsal vertebrae, and six to eight supraneurals … *T. camunani* (upper Trombetas River Basin)

6’. Pelvic fins black pigmented from the middle of fin to its tip or totally black pigmented, ground body coloration predominantly blackened, nine predorsal vertebrae, and five supraneurals … *T.* sp. ‘*siderocarajensis*’ (Rio Tocantins-Araguaia Basin at Itacaiúnas River and former occurrence in Tocantins River at area flooded by Tucuruí reservoir)

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Suporting information

S1 Table. Minimum *p*-distances between *Tometes* species. Molecular distances are based on the 580-bp fragment of mtDNA COI.

mtDNA COI	1	2	3	4	5	6
1. *T.* sp. ‘*siderocarajensis*’						
2. *T. trilobatus*	0.016					
3. *T. kranponhah*	0.027	0.034				
4. *T. camunani*	0.031	0.037	0.037			
5. *T. ancylorhynchus*	0.056	0.052	0.027	0.053		
6. *T. lebaili*	0.073	0.079	0.067	0.068	0.073	
7. *T. makue*	0.091	0.089	0.079	0.074	0.093	0.080

S2 Table. Species level diagnostic characters observed in the mtDNA COI gene of *Tometes* sp. ‘*siderocarajensis*’ and its congeners. First line indicates position of the character within the mtDNA COI gene.

	120	180	594	696
1. *Tometes* sp. ‘*siderocarajensis*’	G	A	T	A
2. *Tometes ancylorhynchus*	G	A	A	G
3. *Tometes kranponhah*	G	A	A	G
4. *Tometes camunani*	G	A	A	G
5. *Tometes lebaili*	G	A	A	G
6. *Tometes makue*	G	A	G	G
7. *Tometes trilobatus*	A	G	A	G

S1 Comparative material examined.

Mylesinus paucisquamatus: All from Brazil, Pará, GEA 836 (1, 159.4 mm SL), Parauapebas, rio Itacaiúnas. INPA 1808 (holotype, 162 mm SL), Tucuruí, rio Tocantins, Jatobal. MNHN 1988-1705 (2 paratypes, 131.7–137.9 mm SL); MNHN 1988-1706 (4 paratypes, 112.8–185.1 mm SL); MNHN 1988-1707 (1 paratype, 165.3 mm SL), Tucuruí, rio Tocantins, Jatobal. MZUSP 83996 (5, 38.3–102.1 mm SL), Novo Jardim, Lagoa bonita, marginal lake of rio Palmeiras.

Myleus setiger: BMNH 1971.5.10.65 (1 syntype, 182.9 mm SL), British Guiana. GEA 1963 (1, 176.3 mm SL), Brazil, Pará, Altamira, Xingu Basin, rio Bacajá. GEA 1971 (1 skel., 137.5 mm SL), Brazil, rio Xingu. GEA 1972 (1 head, skel., 45 mm HL), Brazil, Ourilândia do Norte, Itacaiúnas Basin, rio Cateté. MNHN A.8629 (1 stuffed specimen, holotype of *Myletes divaricatus*, 186.7 mm SL), Guyana, Essequibo River. MNHN A.9868 (, holotype of *Myletes doidyxodon* 137.9 mm SL), Brazil, Amazon River. MZUSP 40489 (1, 87.4 mm SL), Goiás, Flores de Goiás, rio Paranã (cachoeira), Fazenda Olho D'água.

Tometes ancylorhynchus: All from Brazil. CAS 20222 (1, 162 mm SL), Marabá, rio Tocantins. GEA 1714 (1 skel., 126 mm SL), Vitória do Xingu, rio Xingu, Cachoeira do Je0072icoá. GEA 1949 (1 paratype, 148.7 mm SL), Altamira, rio Iriri, rapids downstream of Cachoeira Grande. GEA 1955 (2, 156–158.5 mm SL), Altamira, rio Xingu, rapids of Kaituká. INPA 2356 (1, 187.8 mm SL), Tucuruí, rio Tocantins, upstream of Tucuruí Hydroelectric reservoir. INPA 3633 (15, 86.3–193.9 mm SL); INPA 3634 (3, 169.1–208.5 mm SL) Itupiranga, rio Tocantins, upstream of Tucuruí Hydreletric reservoir. INPA 4485 (1, 141.5 mm SL); INPA 4505 (1, 177.0 mm SL), Tucuruí, rio Tocantins, Tucuruí Hydroelectric reservoir; INPA 5134 (3, 124.1–162.4 mm SL), Itupiranga, rio Tocantins; INPA 52482 (6, 147.7–175.3 mm SL), Araguatins, rio Araguaia, Santa Isabel Hydroelectric reservoir. MNHN 1999–1168 (2 paratypes, 101.9–174.8 mm SL), rio Xingu. MPEG 31014 (holotype, 150.4 mm SL), Vitória do Xingu, rio Xingu, Cachoeira do Jericoá. MPEG 31015 (7 paratypes, 91.2–152.5 mm SL), Altamira, rio Xingu, Pedral do Roboque Velho. MPEG 31016 (1 paratype, 159.7 mm SL), Altamira, rio Xingu, Robojinho, Cachoeira do Porfírio. ZUEC 10023 (1 paratype, 118.7 mm SL), Altamira, rio Xingu.

Tometes camunani: All from Brazil, Pará, MPEG 23447 (holotype, 224.3 mm SL), rio Erepecuru. MPEG 23439 (1 paratype, 248.0 mm SL); MPEG 23440 (1 paratype, 384.0 mm SL); MPEG 23441 (1 paratype, 276.0 mm SL); MPEG 23443 (2 paratypes, 247.0–293.0 mm SL); MPEG 23444 (3 paratypes, 291.0–329.0 mm SL), rio Trombetas. MPEG 23448 (1 skel., 382.0 mm SL), rio Trombetas. INPA 3639 (1 paratype, 299.0 mm SL), rio Trombetas.

Tometes kranponhah: All from Brazil, Pará, Altamira, Xingu basin. ANSP 193019 (1 paratype, 153.8 mm SL); ANSP 193019 (1 paratype, 345.0 mm SL), rio Iriri, Cachoeira Grande do Iriri. ANSP 194659 (1 paratype, 250.0 mm SL), rio Iriri, below Cachoeira Grande do Iriri. GEA 1939 (1 skel., 305.0 mm SL), rio Xingu, Pedral do Roboque Velho. MPEG 31000 (holotype, 132.3 mm SL), rio Xingu, Cachoeira do Espelho. MPEG 31001 (5 paratypes, 257.5–319.0 mm SL), rio Xingu, Pedral do Roboque Velho. MPEG 31003 (3 paratypes, 304.6–350.0 mm SL); MPEG 31004 (1 paratype, 234.9 mm SL); MPEG 31006 (1 paratype, 320.1 mm SL), rio Bacajá. MZUSP 105645 (1 paratype, 207.8 mm SL), rio Xingu, Cnec. MZUSP 110948 (1 skel., 267.0 mm SL), rio Iriri, Cachoeira Grande.

Tometes lebaili: IRSNB 21.343 (1, 400.5 mm SL), Suriname, Marowijne, Paloemeu River, Papadronsoela. MNHN 1993-3452 (1, 251.0 mm SL), French Guyana, St. Laurent du Maroni, Maripasoula, Maroni River. MNHN 2000-6038 (2 paratypes, 128.5–146.1 mm SL); MNHN 2001-1212 (1 paratype, 147.4 mm SL); MNHN 2001-1213 (1, 213.1 mm SL); MNHN 2001-1215 (1 paratype, 219.4 mm SL); MNHN 2001-2384 (holotype, 106.7 mm SL), French Guiana, Maroni River.

Tometes makue: All from Brazil, Amazonas, São Gabriel da Cachoeira, rio Negro. INPA 7344 (holotype, 240.0 mm SL); INPA 3179 (1, 125.0 mm SL); INPA 4913 (1, 370.0 mm SL); INPA 4914 (2, 330.0–355.0 mm SL); INPA 4915 (2, 138.0–158.0 mm SL); INPA 4916 (2, 239.0–307.0 mm SL); INPA 4917 (1, 261.0 mm SL); INPA 4920 (4, 172.0–229.0 mm SL); MNHN 2001-2712 (3 paratypes, 208.2–230.9 mm SL). INPA 43077 (1, 57.2 mm SL).

Tometes trilobatus: MNHN A.8649 (1 stuffed specimen, Paralectotype, 370.0 mm SL); MNHN A.8650 (1 stuffed specimen, Lectotype, 337.3 mm SL); MNHN A.8651 (1 stuffed specimen, holotype of *Tometes unilobatus*, 277.0 mm SL), French Guiana, Cayenne. MNHN 1998-0099 (1, 248.0 mm SL), French Guyana, Cayenne, Saut Maripa, Oyapock river. IEPA 2853 (1, 277.9 mm SL), Brazil, Amapá, Rio Anotaié, Oiapoque. IEPA 3564 (1, 85.4 mm SL); IEPA 3568 (1, 107.5 mm SL); IEPA 3570 (1, 89.8 mm SL), Brazil, Amapá, rio Araguari, UHE de Ferreira Gomes. IEPA 3577 (1, 422.0 mm SL), Brazil, Amapá, Rio Cassiporé. IEPA 4303 (1, 263.1 mm SL), Brazil, Amapá, rio Jari, Laranjal do Jari. INPA 19967 (1, 116.0 mm SL), Brazil, Amapá, rio Araguari, Cachoeira Santa Rosa. ZMA 107.687 (1, 108.8 mm SL), French Guiana and Brazil, Oyapock Basin, near of confluence with Crique Armontabo.

Capítulo 3

Segregação de nicho trófico entre os peixes serrasalmídeos herbívoros das corredeiras do baixo rio Xingu, Brasil[5]

Marcelo C. Andrade, Daniel B. Fitzgerald, Kirk O. Winemiller,
Priscilla S. Barbosa & Tommaso Giarrizzo

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"If scientists know so little of raw biological diversity at the taxonomic level, we know even less of the life cycles, physiology, and niches of each species in turn"

Edward O. Wilson
"The father of Biodiversity"
Biólogo e entomologista americano

Trophic niche segregation among herbivorous serrasalmid fishes from rapids of the Lower Xingu River, Brazil

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Running headline: niche segregation in serrasalmids

Abstract

In the Amazon Basin, several species of herbivorous serrasalmid fishes inhabit rapids, but it is unknown if coexistence is associated with food resource partitioning. We investigated potential trophic niche segregation among juveniles and adults of three herbivorous serrasalmids, *Myleus setiger, Ossubtus xinguense* and *Tometes kranponhah,* that coexist in rapids of the Xingu River. Rapids were sampled during the low-water season, and 449 specimens were obtained for analysis of diet, stable isotope ratios of muscle tissue, and functional traits associated with feeding and habitat use. The three species overlapped in dietary and isotopic space, with adult *O. xinguense* being most divergent. Juvenile and adult *T. kranponhah* and juvenile *O. xinguense*, two groups with broad diets, had the lowest trophic positions, and adult *O. xinguense*, with a diet dominated by Podostemaceae, had the highest trophic position. Reduction of aquatic habitat during the low-water period increases fish densities within Xingu rapids. High trophic overlap during this period suggests that either food resources are not limiting, or niches are partitioned by other means. Differences in functional traits of the three serrasalmids could be associated with differential efficiencies of swimming and feeding within microhabitats that vary according to water velocity and other features.

Key words: dietary analysis, herbivory, niche overlap, niche partitioning, ontogenetic niche shift.

Introduction

Rapids and waterfalls are inhabited by aquatic species adapted to cope with high water velocities (Lujan & Conway 2015). Life in rapids requires special morphological, physiological, and behavioral adaptations to extreme environmental conditions, and rapids-adapted fishes worldwide possess convergent suits of phenotypes (Stewart & Roberts 1976; Lujan & Conway 2015). For example, fishes from widely divergent evolutionary lineages have reduced swimbladders that limit buoyancy and elongate bodies that reduce drag when resting on substrates in fast-flowing water (Stewart & Roberts 1976; Kullander 1988; Conway et al. 2012; Birindelli & Britski 2013; Lujan & Conway 2015). Many benthic fishes possess broad pectoral and pelvic fins that function like hydrofoils, as well as modified mouths capable of suctioning to hard substrates, which assist in holding position in fast water (Conway et al. 2012; Lujan & Conway 2015).

Harsh abiotic environmental conditions of rapids constitute physical barriers to longitudinal dispersal by other aquatic organisms (Junk & Soares 2001). Rheophilic species inhabiting isolated rapids complexes also can have limited dispersal among local populations when these are separated by long stretches of inhospitable habitat (Carvalho et al. 2007). This dispersal limitation may increase competition for food resources, as well as the importance of niche partitioning in facilitating coexistence of rheophilic fishes. Because many rapids-adapted fishes have limited dispersal and tend to be ecological specialists, they are particularly vulnerable to major environmental change, including anthropogenic disturbances such as flow alteration from hydroelectric dams (Vitorino Júnior et al. 2016).

In the Neotropics, many rapids-adapted fishes exploit autochthonous food resources, including crabs, snails, aquatic insect larvae, sponges and several kinds of aquatic plants (Horeau et al. 1998; Zuanon 1999; Moreira & Zuanon 2002; Pagezy & Jégu 2002; Zuanon & Sazima 2002). Anostomid and loricariid fishes inhabiting rapids of Neotropical rivers encompass diverse phenotypes (Zuluaga-Gómez et al. 2016), but most species within these families seem to have relatively narrow trophic niches reflecting herbivory or detritivory. The family Serrasalmidae is best known for the carnivorous piranhas (Jégu 2003; Chakrabarty & Fink 2011), but several species the family are herbivores, some of which inhabit rapids nearly exclusively. The family, as a whole, encompasses diverse feeding strategies, including carnivory, insectivory, omnivory, herbivory, frugivory, and lepidophagy (Goulding 1980; Sazima 1983; Sazima & Machado 1990; Leite & Jégu 1990; Loubens & Panfili 1997; 2001; Santos et al. 1997; Correa et al. 2007; 2014; 2016; Trindade & Juca-Chagas 2008; Correa & Winemiller 2014). Some serrasalmid species are habitat generalists, but others are restricted to specific habitat types. For example, the tambaqui (*Colossoma macropomum*) and pacu

(*Piaractus* spp.) inhabit lowland river and floodplain habitats where they feed on fruits and seeds (Goulding 1980; Jégu & Keith 1999). Species of the genera *Myleus, Mylesinus, Tometes*, *Ossubtus*, and certain species of *Myloplus* are habitat specialists restricted to rapids (Jégu et al. 1989; 2002a; 2003; Jégu & Santos 2002; Pagezy & Jégu 2002; Jégu & Zuanon 2005; Andrade et al. 2016a, b).

Here we compare the trophic ecology of three serrasalmids (*Myleus setiger*, *Tometes kranponhah* and *Ossubtus xinguense*) that coexist in rapids of the lower Xingu River, a major tributary of the lower Amazon River, Brazil. All three species have diets dominated by aquatic macrophytes (Jégu & Santos 2002; Jégu & Zuanon 2005; Andrade et al. 2015; 2016a). Both adults and juveniles are commonly found in fast-flowing waters of rapids, often in close association with rocks covered by aquatic macrophytes of the family Podostemaceae (Andrade et al. 2013). *Myleus setiger* is the most widely distributed of the three species, occurring in several major Amazon tributaries that drain the Guiana and Brazilian shields, whereas *T. kranponhah* and *O. xinguense* are endemic to the Xingu Basin (Andrade et al. 2016a). In addition, the three species have functional traits specialized for herbivory and feeding within rapids, such as incisiform teeth that effectively cut leaves, and deep, laterally flattened bodies that allow fish to swim efficiently in fast water (Meunier et al. 2004). All three of these species undergo ontogenetic transitions in the length of the gastrointestinal tract, with adults having relatively longer guts (Jégu et al. 1989; 2002a). This size allometry is assumed to be associated with a shift from generalist feeding to a diet dominated by epilithic macrophytes, including riverweeds (Podostemaceae) and bryophytes (mosses and liverworts).

Coexistence of these three rapids-adapted serrasalmids might be facilitated by differences in how they exploit microhabitats, food resources, or both. Here we evaluate patterns of trophic niche segregation and variation in functional morphology. We predict that ontogenetic diet shifts in all three species will show transitions from invertivory to herbivory with corresponding decrease in interspecific trophic niche overlap. We further predict that differences in morphological traits reflecting how these fishes acquire food differently according to the species and its stage of life showing lesser niche overlap in species or life stages with little morphological similarity.

Materials and Methods

Study site and sample collection

Specimens of three common rheophilic serrasalmid species were collected in the Xingu River and two of its major tributaries (Iriri and Bacajá rivers; Fig. 1). Collections were made along a 270-km stretch of river from *Cachoeira Grande* on the Iriri (3°51’10”S 52°43’40”W) to the downstream end of the *Volta Grande* (Big Bend) near *Belo Monte* (3°03’57”S 51°49’35”W). In addition, the Bacajá River was sampled from its confluence with the Xingu River (3°45’26”S 51°34’57”W) until 40-km upstream. Sampling was conducted during several dry seasons: June–July 2012, September–October 2013, October 2014 and October 2015. Fishes were captured from rapids using gillnets placed in relatively deep, slow-flowing areas, and castnets thrown in shallower, faster-flowing sections of rapids in or near macrophyte beds. *Myleus setiger* and *Tometes kranponhah* (hereafter ‘*Myleus*’ and ‘*Tometes*’, respectively) are relatively common and distributed throughout the Xingu Basin (Andrade et al. 2016a), whereas *Ossubtus xinguense* (hereafter ‘*Ossubtus*’) is less common and restricted to rapids of the Lower Xingu and *Volta Grande* region (Jégu & Zuanon 2005; Andrade et al. 2016c). Other serrasalmid species, such as *Serrasalmus* and *Myloplus* spp., are also found within the Xingu River Basin, but are not typically captured from rapids. To test whether species partition niches between different life stages, we first classified individuals as juveniles (<

100 mm standard length, SL) or adults (adults ≥ 100 mm SL) (Appendix 1) based on information in Jégu et al. (1989; 2002a, b) and Andrade et al. (2013; 2015; 2016a, b, c).

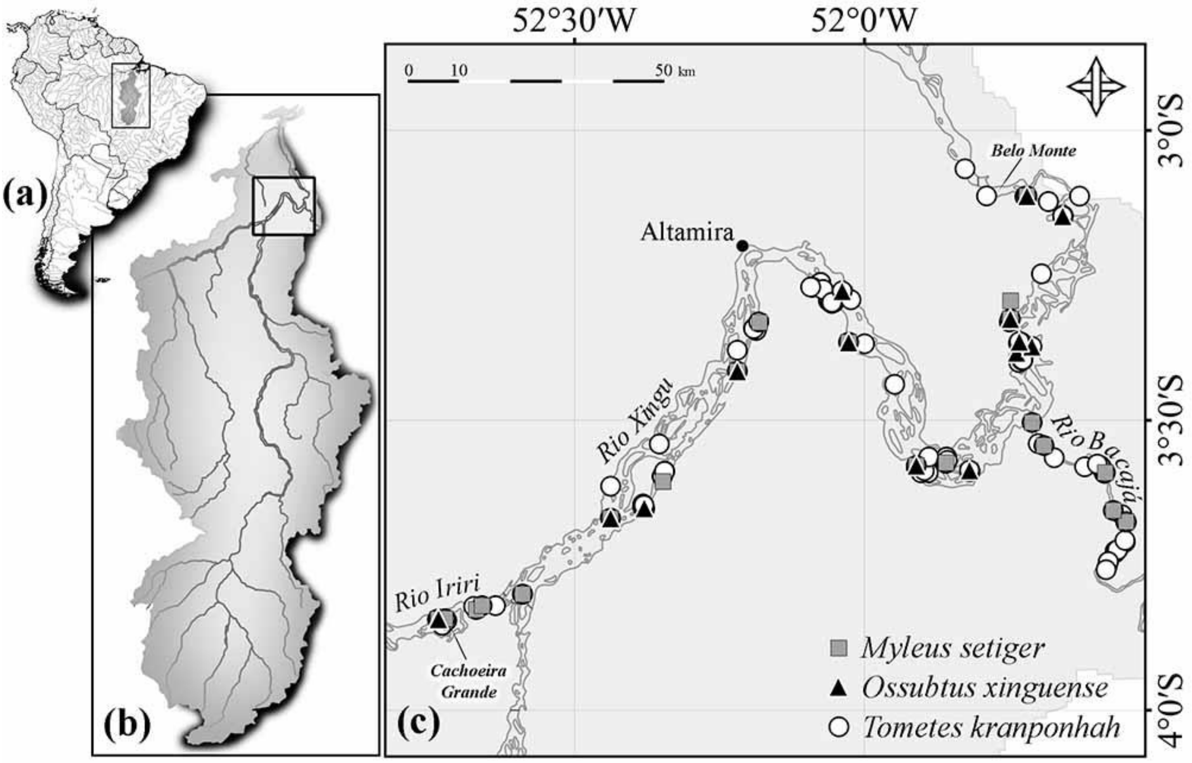

Fig. 1. Maps showing (a) location of Xingu Basin in South America, (b) the study reach in the lower Xingu River, and (c) collection locations for three serrasalmid species in the Iriri, Xingu and Bacajá rivers.

Morphological traits

Sixteen morphological features were measured according to methods in Gatz (1979) and Winemiller (1991): SL, body depth, body width, head depth, height of eye, head length, caudal-peduncle length, caudal-peduncle depth, caudal-peduncle width, pectoral-fin length, pectoral-fin width, eye diameter, mouth width, mouth orientation, gastrointestinal length, and swimbladder length (Appendix 2). We also measured the length of the nasal chamber of the skull, the space that houses the olfactory bulb, in the longitudinal dimension (Andrade et al. 2016c). Linear measures were made on preserved specimens using digital callipers (precision 0.1 mm). Morphological traits were selected based on their functional roles in habitat use and swimming ability or feeding behaviour (Appendix 2). For example, body size (indexed by SL) influences feeding ecology (Verwaijen et al. 2002; Montaña & Winemiller 2013), relative body depth influences lateral turning (Zuluaga-Gómez et al. 2016), and relative intestine length is associated with diet (Wagner et al. 2009).

Diet

Each specimen examined for dietary analysis was measured (SL mm) before dissection and removal of the stomach. Empty stomachs were recorded, but did not contribute to sample sizes reported for dietary analyses. Food items from stomachs were classified according to eight categories: 1- leaves and flowers of terrestrial plants; 2- seeds (mainly from riparian plants); 3- Podostemaceae (mainly leaves of this aquatic macrophyte); 4- periphyton (benthic algae and associated microfauna and biofilm); 5- detritus (particulate organic material); 6- sediments (mainly silt and sand); 7- fish fins and scales; and 8- aquatic macroinvertebrates (mainly Chironomidae and Simuliidae associated with aquatic plants). The wet weight of each prey category from each stomach was measured with a digital electronic balance and recorded the nearest 0.0001g.

Stable isotopes

For isotopic analysis, 2 g of muscle tissue was taken from the dorsal flank region of fish specimens using a clean scalpel. Most tissue samples were stored frozen, but a few were preserved in salt, which has been shown to have negligible influence on carbon and nitrogen isotope ratios of fish muscle tissue (Arrington & Winemiller 2002). Tissue samples were dried to constant weight in an air-circulating oven at 60°C, pulverized to a fine homogeneous powder, weighed and packed into tin capsules according to methods described in Zeug & Winemiller (2008). The samples were analyzed for carbon and nitrogen stable isotope ratios at the Center for Stable Isotopes, University of New Mexico, using a Costech ECS 4010 Elemental Analyzer coupled to a ThermoFisher Scientific Delta V Advantage mass spectrometer via a CONFLO IV interface. Isotope ratios are reported using the delta (δ) notation relative to carbon from Pee Dee Belemnite as the standard for carbon and atmospheric molecular nitrogen as a standard for nitrogen. Routine analysis of laboratory standards indicated measurement error was less than 0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$.

Data analysis

Morphological functional space

To describe ecomorphological trends and to ordinate species and ontogenetic stages, Principal Components Analysis (PCA) was performed on the correlation matrix calculated from log-transformed morphological data. PCA was performed using ‘factoextra’ package (Kassambara & Mundt 2016) in R version 3.2.3 (R Development Core Team 2016).

Trophic niche

The dietary importance of each food category for juvenile and adult size classes of each serrasalmid species was estimated using the alimentary index: $Ai = Fi \times Wi / \sum_{i=1}^{n}(Fi \times Wi)$, where Fi is the relative frequency of occurrence of prey category i and Wi is the relative biomass of prey category i (Kawakami & Vazzoler 1980). Dietary similarity was calculated as Bray-Curtis similarity based on Ai values; similarity of food category consumption was based on Whittaker’s index of association (Clarke & Gorley 2015). The level of specialization between ontogenetic stages was inferred using Levin’s measure of niche breadth (Krebs 1999): $B = 1/\sum p_j^2$, where p_j is the proportion of individuals found using resource j. Niche partitioning among species and between ontogenetic stages were assessed using Pianka’s niche overlap index: $O_{jk} = \sum_1^n p_{ij} p_{ik} / \sqrt{\sum_1^n p_{ij^2} \sum_1^n p_{ik^2}}$, which measures the niche overlap between species *j* and *k*, where p*ij* = proportion of the *i*th resource to the species *j*, p*ik* = proportion of *i*th resource to the species *k*, and *n* = number of resource categories (Pianka 1973). This metric ranges from zero (no overlap) to 1 (perfect overlap). The significance of niche overlap among groups (species and ontogenetic stages) was tested by comparison with a null model based on the RA3 algorithm of Gotelli & Ellison (2013) with 9999 Monte Carlo randomizations. The RA3 algorithm maintains the niche breadth of each group and randomizes entries in the resource matrix by assuming all resources are used equally by all groups. To reveal dietary patterns among life stages and species, we performed Principal Coordinate Analysis (PCoA) using Ai values; significance of between-group dietary variation was tested using Permutational Multivariate Analysis of Variance (PERMANOVA). Both PCoA and PERMANOVA were made with 9999 permutations based on a dissimilarity of Bray-Curtis matrix using the package ‘vegan’ 2.3-5 (Oksanen et al. 2016) in R.

Isotopic niche

Prior to numerical analysis, muscle tissue samples with lipid concentrations higher than 5% (indicated by C:N ≥ 3.5 for aquatic animals) were corrected using the normalization algorithm proposed by Post et al. (2007): $\Delta\delta^{13}C_{corrected} = \Delta\delta^{13}C_{uncorrected} - 3.32 + 0.99 \times C{:}N$, where $\Delta\delta^{13}C_{uncorrected}$ is the ratio of heavy to light isotopes of C, and $C{:}N$ is the ratio of carbon to nitrogen content of the material. In order to merge samples from different field surveys and preservation methods (frozen *vs.* salt), differences in isotopic ratios were tested using the Kruskal-Wallis test (KW) for each species and ontogenetic stage. Partitioning of isotopic space among species and between ontogenetic stages was evaluated using the package Stable Isotope Bayesian Ellipses in R (SIBER) version 2.0.2, which estimates isotopic spaces and their overlap for groups having different numbers of samples (Jackson &

Britton 2014). The isotopic space occupied by each ontogenetic stage of each species was estimated using sample-size-corrected standard ellipse areas (SEA_C ‰^{2}) (Jackson et al. 2011). This analysis assumes that relationships based on isotopic space reflect trophic niche relationships (Layman et al. 2007).

Trophic positions were estimated using the method proposed by Vanderklift & Ponsard (2003). Trophic position is calculated as $TP = [(\delta^{15}N_{fish} - \delta^{15}N_{snail}) / 2.54] + 2$, where $\delta^{15}N_{fish}$ was the average $\delta^{15}N$ for a particular life stage and species, $\delta^{15}N_{snail}$ was the average $\delta^{15}N$ of a common primary consumer, 2.54 is the average enrichment in $\delta^{15}N$ per trophic level, and 2 correspond to the trophic level of the primary consumer. For the primary consumer, we used the soft tissues of *Doryssa starksi*, a freshwater snail common in the rapids.

Results

Morphological traits

PCA showed that the six species/ontogenetic stages occupied separate regions of morphological trait space (PERMANOVA, *Pseudo-F* = 190.2; $P < 0.001$). Juvenile and adult *Ossubtus* showed the greatest separation from other groups (Fig. 2). The first two principal components together modelled 57.6% of total morphological variation among two ontogenetic stages and three species (Table 1). PC1 (37.6% of variance) identified a gradient contrasting fishes with relatively deep bodies, narrow caudal peduncles, small eyes, wide and subterminal mouths, small olfactory chambers and long gastrointestinal tracts versus fishes with the opposite suite of attributes. PC1 therefore involved both habitat-use and trophic associated traits, and separated adult *Ossubtus* from remaining groups, especially juvenile and adult *Myleus* that both have long gastrointestinal tracts and wide mouths. PC2 (20.0% of variance) identified a different gradient contrasting fishes with shallower bodies, greater pectoral fin aspect ratio, supraterminal mouth orientation, smaller body size, and longer head versus fishes with the opposite combination of traits (Table 1). PC2 separated juvenile *Ossubtus*, a group with a relatively high aspect ratio of the pectoral fin and a longer head, from the remaining serrasalmids (Fig. 2).

Table 1. Principal components (PC) scores derived from 14 functional morphological traits of three serrasalmild rapids-adapted. Scores with higher significance highlighted in bold.

	PC1	**PC2**
Eigenvalue	5.3	2.8
% of variance	37.6	20.0
Morphological traits		
Habitat use		
RBD- relative body depth	0.29	**-0.34**
CPL- relative caudal-peduncle length	0.21	0.10
WCP- relative width of caudal peduncle	**-0.36**	-0.25
APC- aspect ratio of pectoral fin	-0.03	**0.47**
EPO- relative position of the eyes	-0.23	0.04
SWB- relative swimbladder length	0.00	-0.17
MOR- mouth orientation	**-0.31**	**0.33**
Trophic strategy		
SL- standard length	-0.20	**-0.46**
HL- relative head length	0.14	**0.40**
HH- relative head height	-0.11	0.14
SIE- relative eye size	**-0.33**	-0.03
WMO- relative width of the mouth	**0.33**	-0.03
GIT- relative gastrointestinal tract length	**0.34**	0.00
OFO- relative olfactory fossae opening	**-0.37**	0.21

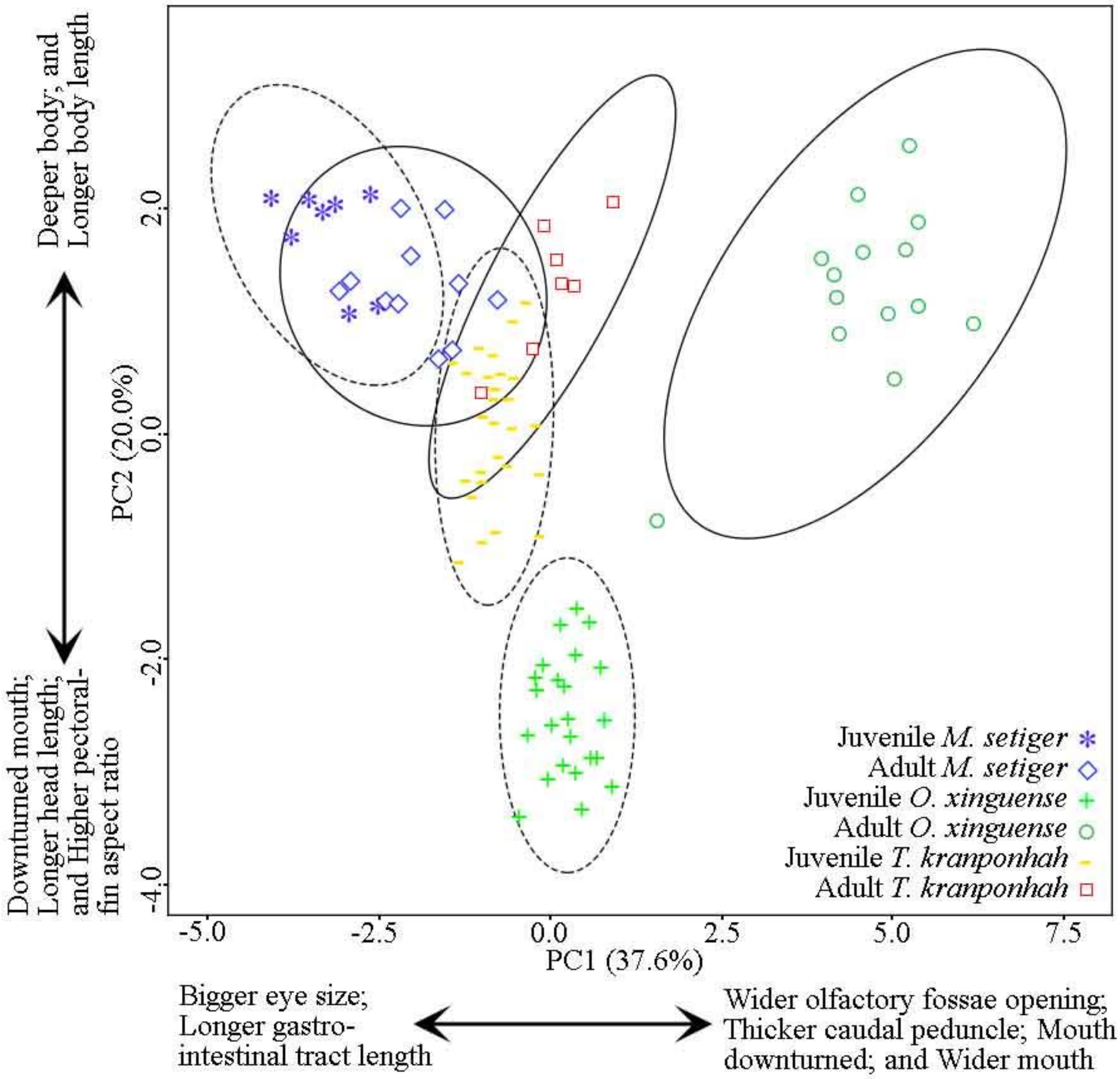

Fig. 2. Plot of principal components analysis, axis 1 and 2 derived from analysis of 14 ecomorphological traits of juvenile and adult *Myleus setiger*, *Ossubtus xinguense*, and *Tometes kranponhah*. Ellipses represent 95% confidence intervals of juveniles (dashed line) and adults (solid line).

Diet

The first two PCoA axes explained 66.7% of the total variance in diet (Fig. 3A). High scores on PCo1 were associated with consumption of terrestrial plants, aquatic macroinvertebrates, periphyton, sediments, and seeds. High scores on PCo2 were associated with greater consumption of Podostemaceae, fins and scales (Table 2). The PCoA revealed two groups, one corresponding to adult *Ossubtus*, and another formed by juveniles and adults of the remaining two species, including juvenile *Ossubtus* (Fig. 3A). Juvenile *Ossubtus* overlapped with adults of *Myleus* and *Tometes,* whereas juveniles of *Myleus* and *Tometes* were different and had a larger area of dispersion along axis 2, with *Myleus* having relatively low scores and *Tometes* having higher scores (Fig. 3A). The PERMANOVA analysis confirmed the presence of dietary differentiation among the three species when both stages were combined (*Pseudo-F* = 35.09; $P < 0.001$), between the two ontogenetic stages within species (*Pseudo-F* = 13.21; $P < 0.001$), and among the six combinations of species and ontogenetic-stages (*Pseudo-F* = 14.69; $P < 0.001$).

Table 2. Principal coordinates (PCo) scores derived from eight prey items consumed by the three serrasalmild rapids-adapted on dry season. Scores with higher significance highlighted in bold. All with significance $P < 0.001$.

	PCo1	PCo2	r^2
Allochthonous plants	**-0.93**	0.37	0.22
Aquatic macroinvertebrates	**-0.90**	-0.44	0.25
Detritus	-0.70	-0.71	0.15
Periphyton	**-0.97**	-0.25	0.10
Podostemaceae	-0.38	**-0.93**	0.12
Fins and scales	-0.36	**-0.93**	0.10
Sediments	**-0.96**	-0.29	0.18
Seeds	**-0.85**	-0.53	0.33

Comparisons of alimentary importance indices of the eight prey items using Whittaker's index revealed that adult *Ossubtus* were most differentiated from the other groups by feeding more on Podostemaceae and less on the remaining food categories, which dominated diets of the other two species. Juvenile *Ossubtus* fed mostly on periphyton, but nonetheless grouped with juvenile *Tometes* that fed mostly on allochthonous plant material. Juvenile and adult *Myleus* grouped together because they consumed mostly Podostemaceae, fins, and scales.

The largest ontogenetic shift in diet breath was observed for *Ossubtus*. Diet breadth of this species declined with body size (juveniles' $B = 6.57$; adults' $B = 1.79$). *Myleus* and *Tometes* had less variable diet breadth, with *Myleus* displaying lower values for juveniles ($B = 4.09$) than adults ($B = 4.85$) and *Tometes* displaying greater values for juveniles ($B = 5.96$) than adults ($B = 4.22$).

Dietary overlap between groups was variable, ranging from 0.23 (between juvenile *Myleus* and adult *Ossubtus*) to 0.96 (between juvenile and adult *Myleus*). Dietary overlap between juveniles and adults of each species was high. *Myleus* and *Ossubtus* had low interspecific dietary overlap for both juveniles ($O_{ij} = 0.49$) and adults ($O_{ij} = 0.29$), while dietary overlap between *Ossubtus* and *Tometes* was high for juveniles ($O_{ij} = 0.82$) and adults ($O_{ij} = 0.93$). Based on comparison with null model estimates, observed pairwise dietary niche overlap among all serrasalmid species and ontogenetic stages was significantly higher than expected at random [observed mean value (0.63) > simulated value (0.55); $P < 0.05$].

Isotopic patterns

Stable isotope signatures of the multiple samples from different surveys were not significantly different for juvenile and adult *Myleus* (carbon: $H = 0.98$, $df = 2$, $P = 0.61$; nitrogen: $H = 1.80$, $df = 2$, $P = 0.41$), juvenile and adult *Tometes* (carbon: $H = 5.42$, $df = 4$, $P = 0.25$; nitrogen: $H = 4.78$, $df = 4$, $P = 0.31$), and adult *Ossubtus* (carbon: $H = 5.97$, $df = 4$, $P = 0.20$; nitrogen: $H = 7.59$, $df = 4$, $P = 0.11$). Juvenile *Ossubtus*, in contrast, showed significant differences for carbon ($H = 5.40$, $df = 1$, $P < 0.05$) between samples from surveys from 2013 September (salted samples) and 2015 October (frozen samples). This difference for carbon probably was associated with seasonal variation in isotopic ratios of food sources more than preservation method. For Nitrogen isotopic ratios did not differ significantly among juveniles *Ossubtus* captured during different periods ($H = 1.67$, $df = 1$, $P = 0.20$).

The three serrsalmid species had $\delta^{13}C$ ranging from -36.2‰ to -19.4‰; and $\delta^{15}N$ ranging from 8.8‰ to 12.7‰ (Fig. 3B). Carbon signatures had large overlap among species. $\delta^{13}C$ of *Tometes* ranged from -36.2‰ to -21.4‰, *Ossubtus* ranged from -32.9‰ to -19.4‰; and *Myleus* ranged from -33.7‰ to -27.1‰. In contrast, $\delta^{15}N$ was more differentiated among species and ontogenetic stages. For example, adult *Ossubtus* had $\delta^{15}N$ ranging from 9.6‰ to 12.7‰, and juvenile *Tometes* $\delta^{15}N$ values, ranging from 8.8‰ to 10.4‰ (Fig. 3B). $\delta^{15}N$ values of juveniles and adults of *Myleus* and *Tometes* varied little. In contrast, the range of $\delta^{15}N$ values for *Ossubtus* differed considerably between juveniles (9.3–9.9‰) and adults (9.6–12.7‰).

Isotopic overlap between juvenile and adult *Tometes* was total, with juveniles occupying a broader isotopic space (SEA_C = 5.14 ‰^{2}) than adults (SEA_C = 1.96 ‰^{2}). *Myleus* occupied a relatively small isotopic space for both juveniles (SEA_C = 1.83 ‰^{2}) and adults (SEA_C = 2.52 ‰^{2}), with relatively low overlap between ontogenetic stages (24.6%). Juvenile and adult *Ossubtus* had no isotopic overlap. Juvenile *Ossubtus* occupied a smaller isotopic space than adults (SEA_C; 2.55 ‰^{2} versus 4.91 ‰^{2}, respectively; Fig. 3B). The highest interspecific isotopic overlap was between juvenile *Ossubtus* and juvenile *Tometes* (9.9%), while the lowest interspecific overlap was between juvenile *Tometes* and adult *Myleus* (0.5%). Adult *Ossubtus* did not overlap with any group (Fig. 3B). Based on $\delta^{15}N$ values, and assuming all else being equal with regard to isotopic signatures of basal resource of food chains supporting these consumers trophic positions ranged from 2.88 for adult *Tometes* to 3.54 for adult *Ossubtus*. Juvenile and adult *Tometes* (TP = 2.91 and 2.88, respectively) and juvenile *Ossubtus* (TP = 2.94) had the lowest trophic positions. *Myleus* had an intermediate position with juvenile TP = 3.15 and adult TP = 3.24, and adult *Ossubtus* had the highest trophic level with TP = 3.54 (Fig. 3B).

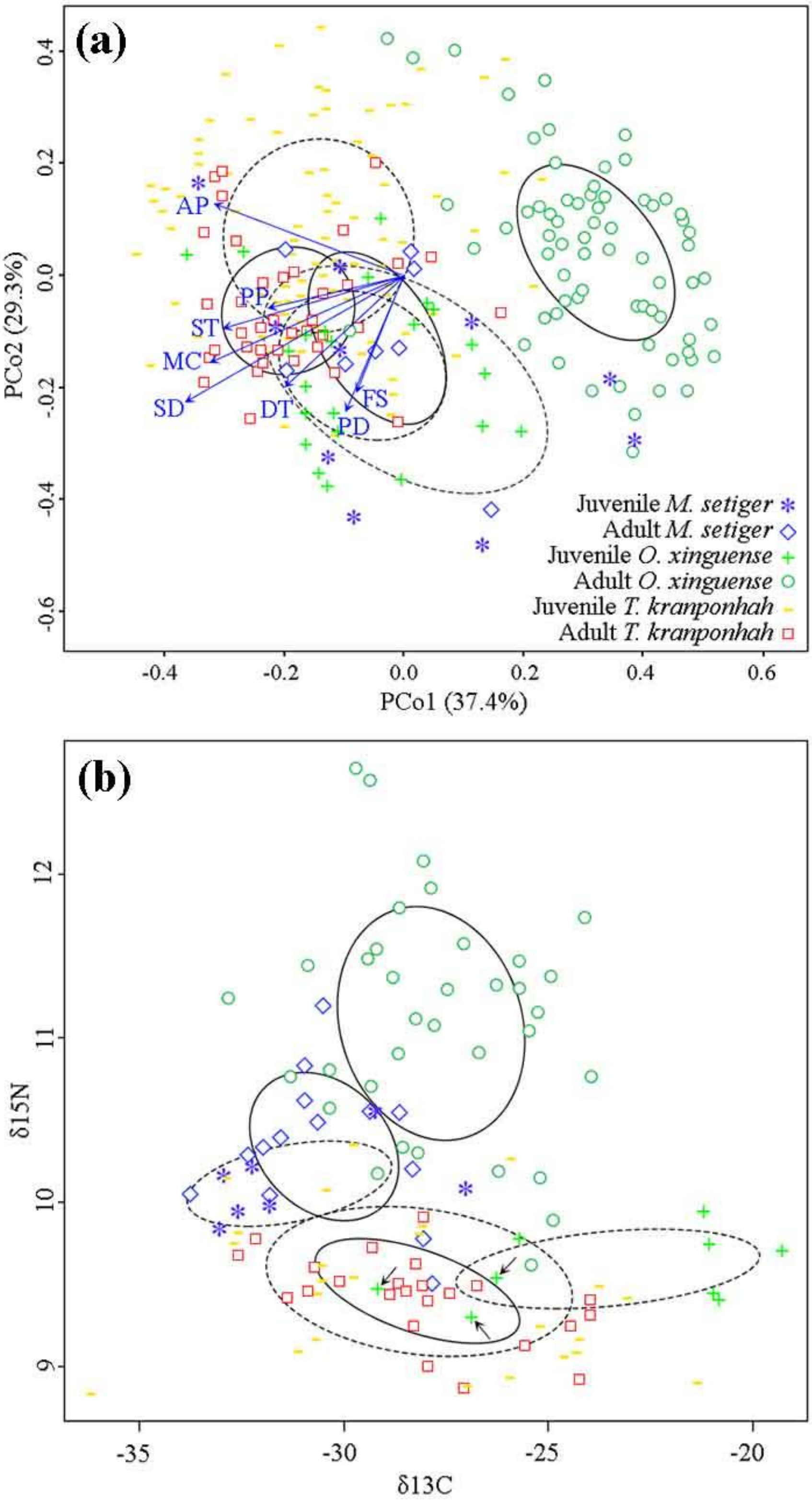

Fig. 3. Dietary and isotopic niche of the three rapids-dwelling serrasalmid, (a) principal coordinate analysis, axis 1 and 2 derived from analysis of diet composition, AP allochthonous plants, DT detritus, FS fins and scales, MC macroinvertebrates, PD Podostemaceae, PP Periphyton, SD seeds, ST sediments; (b) standard ellipse areas, axis 1 and 2 estimated by analysis of Stable Isotope Bayesian Ellipses in R (Jackson *et al.* 2011), and small arrows indicate the three samples of juvenile *O. xinguense* from September 2013 preserved in salt. Ellipses represent 95% confidence intervals of juveniles (dashed line) and adults (solid line).

Discussion

The three herbivorous serrasalmids that coexist in rapids of the Xingu River were separated along gradients of morphological traits associated with feeding and swimming performance. Varying degrees of morphological differentiation were observed between juvenile and adult size classes of each species. Morphological and trophic differentiation was greatest between *Ossubtus* and other two species, and *Ossubtus* also revealed greatest ontogenetic differentiation, which may partially reflect differences in microhabitat use. *Ossubtus* seems to be more closely confined to rapids habitats than *Myleus* or *Tometes* (Andrade et al. 2016c). Both juvenile and adult size classes of *Ossubtus* possess a subinferior mouth, as opposed to the terminal mouth position of *Myleus* and *Tometes*, as well as a more shallow (stream-lined) body that should reduce drag in fast-flowing water. Juvenile *Ossubtus* have higher values for the aspect ratio of the pectoral fin and lower values of body depth when compared with adults, suggesting that juveniles are particularly well-adapted to inhabit fast-flowing water (Andrade et al. 2016c). The relatively narrow caudal peduncle of juvenile *Ossubtus* may further increase their swimming efficiency in fast water. *Myleus* and *Tometes* have relatively greater body depths and narrower caudal peduncles, which are less efficient for swimming in fast currents, but greatly enhance maneuverability. This body shape would be advantageous in rapids complexes with areas of slower water velocities where foraging can involve lateral movements without displacement from hydraulic resistance.

Other interspecific morphological differences appear to be associated with foraging behavior and efficiency. *Ossubtus* has a relatively wider mouth than the other two species, which suggests it can obtain more material per bite. The smaller eyes and larger olfactory chamber of *Ossubtus* suggest that vision may be less important than olfaction when searching for food. In teleost fishes, a larger olfactory chamber often is associated with a greater number of olfactory folds that enhance the sense of smell (Bardach 1972). *Ossubtus* has a shorter relative gut length than *Myleus* and *Tometes*, and is therefore assumed to be more omnivorous (Wagner et al. 2009). Among frugivorous serrasalmid fishes of the western Amazon, those with relatively shorter guts had higher trophic positions (Correa & Winemiller 2014). Similarly, *Ossubtus* occupy a higher trophic position than the other two herbivorous serrasalmids, and still than juvenile *Ossubtus*, which was also reflected in the relatively higher δ^{15}N of adult *Ossubtus*.

There were some discrepancies between dietary and isotopic data. Dietary overlap between ontogenetic stages was high for both *Myleus* and *Tometes*. *Ossubtus*, in contrast, had low dietary overlap between juveniles and adults, and the isotopic space occupied by juveniles also was different than the space occupied by adults. For *Myleus* and *Tometes*, the isotopic spaces of juveniles and adults overlapped extensively. If we assume that δ^{15}N reflects vertical trophic position, *Tometes* and juvenile *Ossubtus* occupied the lowest positions. This inference contrasts with our dietary analysis that indicated *Tometes* and juvenile *Ossubtus* consumed the largest fractions of macroinvertebrates and therefore should occupy higher trophic position. Based on δ^{15}N, *Myleus* occupied an intermediate trophic position and adult *Ossubtus* occupied the highest position among these species. Based on our dietary analysis, adult *Ossubtus* consumed mostly aquatic macrophytes, and therefore should occupy a very low trophic position. The lack of congruence between trophic position inferred from δ^{15}N of consumer tissue or analysis of gut contents probably is due to spatial and temporal variation in δ^{15}N of aquatic macrophytes influenced by hydraulic conditions affecting isotopic fractionation associated with physical and physiological processes at cell-water boundary. Assuming that, the incongruence between methods promptly confirm that the trophic positions of juvenile and adult *Ossubtus* don’t reflect food resource feed that moment of capture, but from an earlier period.

Despite the lack of congruence between dietary and isotopic findings, both datasets revealed clear separation between *Ossubtus* and the other two serrasalmids, especially with regard to adult size classes. All three species feed nearly exclusively within rapids habitats, but not all food resources are autochthonous in origin, and terrestrial plant material and terrestrial arthropods can drift through these habitats. *Myleus* and *Tometes* displayed large overlap in diet, but showed relative partitioning in their isotopic niche spaces. Both species are trophic generalists compared to *Ossubtus,* which is reflected in similar morphological traits, and consequently similar diet and isotopic space suggesting greater niche conservatism. This result is congruent with trophic niche dimension trend to be analogous in organisms with greater morphological similarity (Winemiller et al. 2015). *Ossubtus* diet breadth was greater for juveniles than adults, but the isotopic niche space occupied by juveniles was smaller than that occupied by adults. Again, the isotopic ratios of adults probably reflect large spatial and temporal variation of isotopic ratios of the aquatic macrophytes on which they feed. In contrast, dietary and isotopic patterns were congruent for *Myleus* and *Tometes*, with adults and juveniles having slight differences between diets and isotopic spaces. Adults of *Myleus* and *Tometes* feed heavily on Podostemaceae, but do not appear to specialize on this resource to the same degree as *Ossubtus*. Juvenile *Ossubtus* consumed mostly periphyton and aquatic macroinvertebrates, and adults feed almost exclusively on Podostemaceae while somehow avoiding aquatic invertebrates associated with the plants (Fig. 4).

Our findings suggest that resource partitioning is not a major mechanism for coexistence of herbivorous serrasalmid fishes inhabiting rapids habitat during the annual low-water period in the lower Xingu River. Future research should examine how seasonal variation might impact trophic niche relationships of these species. Shallow rapids habitats are less available during the annual flood pulse, and these fishes might exploit different resources or move into different habitats during that period (Fitzgerald et al. 2016). Although high dietary overlap between *Myleus* and *Tometes* suggests these species did not partition available food resources, there could be niche partitioning along a different niche dimension, such as microhabitats use along gradients of structural complexity within the rapids (Fitzgerald et al. 2016).

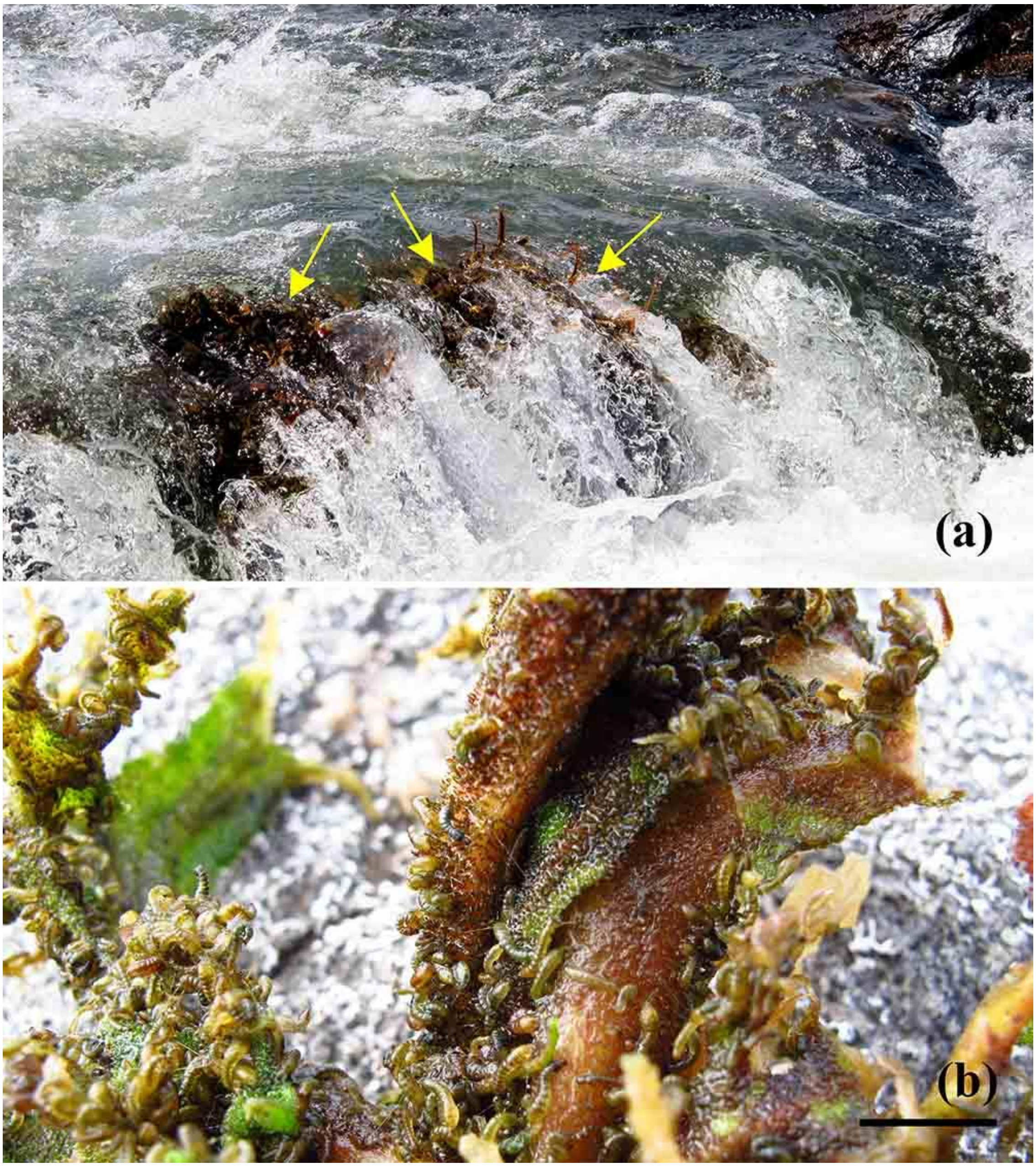

Fig. 4. Rapids at Xingu River (a) arrows indicate parts of Podostemaceae crop up over rocks, (b) part of a Podostemaceae newly water withdrawal showing abundant macroinvertebrate larvae associated. Scale bar = 10 mm.

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Appendix 1. Number of individuals from multiple sites of the Xingu River basin analysed for each method in this study, and classified according to the ontogeny pre-established into juveniles (J) and adults (A).

	Ontogeny	Ecomorphology	Diet	Stable Isotopes	Mean ± SD of SL (mm)
Myleus setiger	J	8	10	7	90.0 ± 7.0
	A	11	9	14	130.4 ± 25.5
Ossubtus xinguense	J	23	23	9	58.4 ± 11.6
	A	14	70	36	176.5 ± 22.0
Tometes kranponhah	J	28	86	26	74.6 ± 14.1
	A	7	41	27	145.5 ± 47.9
Total		91	239	119	

Appendix 2. Morphological traits with their respective formula and ecological explanation. Traits are subdivided into those mainly related to habitat use or trophic ecology.

Morphological trait	Formula	Explanation
Habitat use		
Relative depth of body	$RBD = \frac{Body\ depth}{SL}$	Inversely proportional to the water velocity and directly proportional to the ability to make manoeuvres.
Relative length of caudal peduncle	$CPL = \frac{\text{length of caudal peduncle}}{SL}$	Directly related to the swimming ability.
Relative width of caudal peduncle	$WCP = \frac{width\ of\ caudal\ peduncle}{SL}$	Inversely proportional to the amplitude of the swimming movements, trend to be higher in swimmers less active.
Aspect ratio of pectoral fin	$ARP = \frac{width\ of\ pectoral\ fin}{length\ of\ pectoral\ fin}$	Directly related swimming ability and with benthic habits, function to brake, maintain the position, accelerating the braking.
Eye position	$EPO = \frac{height\ of\ centre\ eye}{head\ length}$	Directly related to the water column position preference.
Relative length of swimbladder	$SWB = \frac{\text{swimbladder length}}{SL}$	Inversely related to the deeper on the water column.
Mouth orientation	*MOR = coded as: 1 to upturned; 2 to terminal; and 3 to inferior*	Indicates in which position the fish acquire food.
Trophic strategy		
Standard length	*SL = measure of standard length*	Directly proportional to the ability to acquire bigger preys.
Relative length of head	$HL = \frac{length\ of\ head}{SL}$	Directly proportional to the ability to acquire bigger preys.
Relative height of head	$HH = \frac{height\ of\ head}{head\ length}$	Directly proportional to the ability to acquire bigger preys.
Relative size of eye	$SIE = \frac{eye\ diameter}{head\ length}$	Directly related to the importance of the vision on feeding.

Relative width of mouth	$WMO = \frac{width\ of\ mouth}{head\ length}$	Directly proportional prey size or amount of prey per bite.
Relative length of gastrointestinal tract	$GIT = \frac{\text{gastrointestinal length}}{SL}$	Directly related to herbivory.
Relative opening of olfactory fossae	$OFO = \frac{\text{width of olfactory fossae}}{head\ length}$	Assumed here as directly related to find food using the sense of smell.

Considerações finais

A presente Tese exibiu a importância de uma abordagem integrada entre distintas áreas de conhecimento, sendo esta demonstrada aqui na evidência da biodiversidade taxonômica e trófica de um grupo de peixes Neotropicais bastante estudado, mas ainda com indiscutíveis lacunas de conhecimento. As análises com o uso de taxonomia tradicional, sejam elas a partir de características externas ou internas, proporcionaram a delimitação morfológica dos cinco gêneros de Serrasalmidae estudados (*Myleus*, *Mylesinus*, *Tometes*, *Ossubtus* e *Myloplus*), bem como a atribuição das suas respectivas espécies, e o atual conhecimento sobre sua distribuição geográfica. A Tese apresentou ainda três novas espécies do gênero *Tometes* e as relações filogenéticas, a partir de sistemática molecular, entre as sete espécies de *Tometes* conhecidas desde então. Complementarmente, a Tese apresentou as relações ecológicas de três notáveis serrasalmídeos de corredeira (*Myleus setiger*, *Ossubtus xinguense* e *Tometes kranponhah*) a partir de análises de variação de nicho, dos traços funcionais e do fluxo de energia ao longo do seu crescimento, apresentando também a importância das corredeiras para estas espécies, ambiente este incessantemente prejudicado pela ação antrópica. Evidentemente, o emprego de uma abordagem que combine taxonomia e ecologia trófica aplica-se a quaisquer organismos. Portanto, destaca-se a extrema relevância no investimento em abordagens integradas para a compreensão da biodiversidade Neotropical como um todo. Principalmente devido aos planos de progresso econômico adotado pelos países em desenvolvimento, tais como o Brasil, que priorizam acima de tudo a prosperidade da nação, e em muitos casos, mediante degradação do meio ambiente, extinguindo os bens e serviços proporcionados pela natureza para a humanidade.

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Apêndices

Apêndice 1

Chave de identificação de gêneros do clado polifilético *Myleus* (*Myleus* nominal, *Tometes*, *Mylesinus*, *Ossubtus* e *Myloplus*).

1. Dentes molariformes, espessos antero-posteriormente, com duas séries de dentes pré-maxilares ligeiramente afastadas ou mesmo claramente afastadas uma da outra formando um espaço interno .... ***Myloplus***

1’. Dentes incisiformes, delgados antero-posteriormente, com duas séries de dentes pré-maxilares claramente apoiadas uma na outra sem espaço entre si **2**

2. Boca evidentemente inferior ou oblígua orientada ventralmente .... ***Ossubtus*** (espécie monotípica ***Ossubtus xinguense*** endêmica de poucas corredeiras nas porções inferiores dos rios Iriri e Xingu, escudo brasileiro, bacia do rio Xingu, Brasil)

2’. Boca terminal ou claramente orientada dorsalmente **3**

3. Dois dentes mais anteriores da série labial do pré-maxilar apoiados lateralmente um no outro ou ligeiramente afastados com espaço muito menor que largura lateral da base do dente, e serra pré-pélvica formando uma quilha com espinhos relativamente robustos, primeiro espinho alcançando a porção mediana entre as verticais que ultrapassam as origens das nadadeiras pélvica e a peitoral; ou quando os dois dentes anteriores afastados lateralmente, na mesma largura lateral da base do dente, com o primeiro espinho da serra pré-pélvica alcançando ou quase a vertical que cruza a origem da nadadeira peitoral .... ***Myleus*** (5 espécies sendo uma delas, ***Myleus pacu***, considerada *species inquirenda* com provável distribuição para a bacia do rio Essequibo, drenagem costeira do escudo guianense, Guiana)

3’. Dois dentes mais anteriores da série labial do pré-maxilar sempre afastados lateralmente, espaçamento lateral entre os dentes maior que a base lateral dos dentes anteriores, e serra pré-pélvica formada por espinhos muito finos, bastante delgados, nunca formando quilha **4**

4. Dentes incisiformes no pré-maxilar e dentário muito delgados antero-posteriormente, fragilmente anexados no pré-maxilar sendo facilmente removidos; todos os dentes do pré-maxilar, em vista lateral, com o mesmo formato e tamanho e, em vista ventral, com a borda das coroas perfeitamente alinhadas .... ***Mylesinus***

4’. Dentes incisiformes no pré-maxilar e dentário relativamente espessos antero-posteriormente, fortemente anexados no pré-maxilar não facilmente removidos; dentes do pré-maxilar, em vista lateral, decrescendo de tamanho posteriormente, claramente com formatos diferentes e, em vista ventral, com a borda das corodas formando uma sinuosidade, nunca alinhadas .... ***Tometes***

Apêndice 2

Chaves de identificação das espécies dos gêneros *Myleus*, *Tometes*, *Mylesinus* e *Myloplus*[6]

Chave de identificação das espécies de *Myleus* Müller & Troschel

1. Dois dentes mais anteriores da série labial do pré-maxilar apoiados lateralmente um no outro formando uma linha contígua entre as séries dos dois lados do pré-maxilar; primeiro espinho da serra pré-pélvica alcançando apenas a porção mediana entre as origens da nadadeira pélvica e a peitoral **2**

1’. Dois dentes mais anteriores da série labial do pré-maxilar afastados lateralmente um do outro não formando uma linha contígua entre as séries dos dois lados do pré-maxilar; primeiro espinho da serra pré-pélvica alcançando ou quase a origem da nadadeira peitoral **3**

2. Nadadeira dorsal com 18 a 20 raios ramificados .... ***Myleus setiger***
(Espécie amplamente distribuída nas drenagens de escudo, ocorre nas bacias do Orinoco, Amazonas, nos tributários da margem esquerda do rio Amazonas, tais como rios Madeira, Tapajós, Xingu, Tocantins; nos tributários da margem direita, tais como rio Negro, Uatumã, Trombetas, Paru, Jari; e também nas drenagens costeiras do estado brasileiro do Amapá e na Guiana Francesa, exceto rio Maroni)

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[6] Nota: o gênero *Ossubtus* é monotípico com a espécie *Ossubtus xinguense* endêmica das corredeiras na porção baixa dos rios Iriri e Xingu, Bacia do rio Xingu, Brasil. Ver chave de identificação de gênero.

2’. Nadadeira dorsal com 23 a 24 raios ramificados .... ***Myleus knerii***

(Espécie da bacia do rio Maroni, Guiana Francesa)

3. Focinho afilado lembrando o bico de uma ave com o bico curvado; corpo arredondado e alto, altura do corpo contida entre 60% e 80% no comprimento padrão .... ***Myleus micans***

(Espécie endêmica da bacia do rio São Francisco, Brasil)

3’. Focinho abaulado; corpo alongado, altura do corpo contida entre 45% e 50% no comprimento padrão .... ***Myleus altipinnis***

(Endêmica da bacia do rio São Francisco, Brasil)

Chave de identificação das espécies de *Tometes* Valenciennes

1. Boca terminal a ligeiramente sub-inferior **2**

1’. Boca claramente obliqua orientada dorsalmente .... ***Tometes lebaili***

(Ocorrência da espécie restrita a drenagens costeiras do oceano Atlântico nos rios da Guiana Francesa, tais como rios Litany, Mana, Maroni e Tampoc; nos rios do Suriname, tais como rios Commewine, Oulemary e Tapanahony)

2. Primeiro e segundo dente da série labial do pré-maxilar em evidente contato lateral **3**

2’. Primeiro e segundo dente da série labial do pré-maxilar claramente espaçados lateralmente **4**

3. Vinte e sete a 34 séries de escamas circumpedunculares, ausência de cúspides laterais no primeiro e segundo dente labial do pré-maxilar; opérculo sem marcas definidas ....

.... ***Tometes trilobatus***

(Drenagens do rio Oiapoque entre a Guiana Francesa e Brasil, e em rios do estado brasileiro do Amapá, tais como rios Anotaié, Araguari, Cassiporé, Flexal e Jari)

3’. Trinta e oito a 43 séries de escamas circumpedunculares, presença de cúspides laterais no primeiro e segundo dente labial do pré-maxilar; opérculo com uma macha preta em formato de lágrima .... ***Tometes kranponhah***

(Tributários da bacia do rio Xingu, tais como os rios Iriri, Xingu e Bacajá)

4. Serra pré-pélvica com 11 espinhos ou mais **5**

4’. Serra pré-pélvica com nenhum a 9 espinhos .... ***Tometes makue***

(Bacia do rio Negro, Brasil, e Bacia do rio Orinoco, Venezuela)

5. Séries de escamas circumpedunculares variando de 37 a mais **6**

5’. Séries de escamas circumpedunculares variando de 30 a 36 .... ***Tometes ancylorhynchus***

(Tributários das Bacias dos rios Xingu e Tocantins-Araguaia, exceto drenagem do rio Itacaiúnas)

6. Nadadeiras pélvicas hialinas, coloração do corpo predominantemente prateada, 10 a 11 vértebras pré-dorsais, e seis a oito supraneurais .... ***Tometes camunani***

(Tributários superiores da Bacia do rio Trombetas)

6’. Nadadeiras pélvicas pigmentada de preto desde a porção mediana da nadadeira até sua extremidade, ou completamente pigmentada de preto, coloração do corpo predominantemente enegrecida, nove vértebras pré-dorsais, e cinco supraneurais .... ***Tometes* sp. ‘*siderocarajensis*’**

(Bacia do rio Tocantins-Araguaia na rio Itacaiúnas e anterior ocorrência no rio Tocantins nas antigas corredeiras da área atualmente inundada pelo reservatório da Usina Hidrelétrica de Tucuruí)

Chave de identificação das espécies de *Mylesinus* Valenciennes

1. Ausência do dente sinfiseano no dentário **2**

1'. Presença do dente sinfiseano no dentário .... ***Mylesinus paucisquamatus*** (Distribuído nas corredeiras da Bacia do Tocantins-Araguaia, incluindo sub-bacia do rio Itacaiúnas)

2. Focinho curto variando entre 31 e38% do comprimento da cabeça; olho relativamente grande variando entre 30 e 34% do comprimento da cabeça .... ***Mylesinus paraschomburgkii*** (Tributários da margem esquerda do rio Amazonas, tais como rios Uatumã, Trombetas, Paru, Jarí, e também em drenagens costeiras do estado brasileiro do Amapá, nos rios Flexal e Araguari)

2'. Focinho longo, 41% do comprimento da cabeça; olho relativamente pequeno com 28% do comprimento da cabeça .... ***Mylesinus schomburgkii*** (provável ocorrência na Bacia do rio Essequibo)

Chave de identificação das espécies de *Myloplus* Gill.

1. Dentes molariformes, dentes pré-maxilares levemente a evidentemente espessos antero-posteriormente, duas séries de dentes pré-maxilares levemente afastadas uma da outra, formando um sutil arco entre os dois lados da pré-maxila **2**

1’. Dentes molariformes, dentes pré-maxilares claramente espessos antero-posteriormente de base arredondada, duas séries pré-maxilares bastante afastadas uma da outra formando um arranjo que lembra a letra “A” maiúscula **5**

2. Serra pré-pélvica com espinho mais anterior alcançando apenas a porção mediana do ventre entre as verticais que ultrapassam as origens das nadadeiras pélvica e a peitoral **3**

2’. Serra pré-pélvica com espinho mais anterior alcançando ou quase a origem da nadadeira peitoral **7**

3. Trinta a 35 séries de escamas entre a origem da nadadeira dorsal e a linha lateral, e 27 a 31 séries de escamas entre a linha lateral e a origem da nadadeira pélvica ..... ***Myloplus lucienae*** (Amplamente distribuída em tributários da Bacia do rio Negro, Brasil)

3’. Trinta e seis a 46 séries de escamas entre a origem da nadadeira dorsal e a linha lateral, e 32 a 42 séries de escamas entre a linha lateral e a origem da nadadeira pélvica **4**

4. Serra pré-pélvica variando entre 20 e 31 espinhos .... ***Myloplus planquettei*** (Drenagens costeiras do escudo guianense desde a bacia do rio Oiapoque no Amapá até a bacia do rio Essequibo na Guiana)

4’. Serra pré-pélvica variando entre 13 e 19 espinhos .... ***Myloplus zorroi*** (Tributários do rio Madeira, tais como rios Aripuanã e Roosevelt)

5. Barra vertical preta na porção mediana dos flancos .... ***Myloplus schomburgkii***

(Espécie amplamente distribuída nos tributários dos rios Amazonas e Orinoco)

5’. Flancos predominantemente prateados sem marca como descrito no item anterior **6**

6. Presença de uma mancha preta na porção antero-posterior da nadadeira dorsal, lábio inferior espesso, pronunciado anteriormente .... ***Myloplus rhomboidalis***

(Espécie amplamente distribuída nos tributários dos rios Amazonas e Orinoco, e também nas drenagens costeiras do Brasil, Guiana Francesa, Suriname, Guiana e Venezuela)

6’. Ausência de mancha na nadadeira dorsal, lábio inferior delgado, não pronunciado anteriormente .... ***Myloplus lobatus***

(Espécie distribuída nos tributários dos rios Amazonas e Orinoco entre o Brasil e Venezuela)

7. Ausência do par de dentes sinfiseanos cônicos no dentário, dois dentes mais anteriores da série principal do dentário com uma extensão interna cobrindo a sínfise .... ***Myloplus ternetzi***

(Espécie distribuída nos tributários dos costeiros do escudo guianense entre a Guiana Francesa e o estado brasileiro do Amapá, incluindo a Bacia do rio Jari no Brasil)

7’. Presença do par de dentes sinfiseanos cônicos no dentário, dois dentes mais anteriores da série principal do dentário nunca com uma extensão interna cobrindo a sínfise **8**

8. Esqueleto axial com 35 a 37 vértebras totais **9**

8’. Esqueleto axial com 40 a 42 vértebras totais **10**

9. Primeiro espinho da nadadeira dorsal densamente pigmentado de preto e porção distal da nadadeira caudal com banda preta vertical nítida; nadadeira dorsal com raios ramificados variando entre 19 e 22 .... ***Myloplus arnoldi***

(Espécie distribuída na Bacia Amazônica, em tributários da margem esquerda do rio Amazonas, como por exemplo, rios Trombetas, Jari, e também margem direita, como rios Xingu e Tapajós, incluindo ainda a Bacia do Tocantins-Araguaia e drenagens costeiras do escudo guianense no estado brasileiro do Amapá)

9’. Primeiro espinho da nadadeira dorsal não pigmentado e nenhuma marca evidente na nadadeira caudal, nadadeiras com coloração uniforme; nadadeira dorsal com raios ramificados variando entre 23 e 24 .... ***Myloplus torquatus***

(Espécie aparentemente endêmica da bacia do rio Branco, tributário de águas brancas da margem direita do rio Negro, estado do Amazonas, Brasil)

10. Corpo evidentemente arredondado, pedúnculo caudal curto, tão alongado quanto alto, fontanelas alongadas antero-posteriormente, fontanela anterior sempre de mesmo tamanho que a fontanela posterior, fontanela anterior com largura em cerca da metade do comprimento da fontanela **11**

10’. Corpo alongado, pedúnculo caudal alongado, evidentemente mais longo do que alto, fontanelas de formatos diverso do mencionado no item anterior **12**

11. Raios ramificados na nadadeira anal variando de 36 a 40; espinhos na serra pré-pélvica variando entre 21 e 28 .... ***Myloplus rubripinnis***

(Espécie amplamente distribuída na Bacia Amazônica e Orinoco, ocorrendo no Brasil, Bolívia, Peru, Colômbia, Venezuela, Guiana, Suriname e Guiana Francesa)

11’. Raios ramificados na nadadeira anal variando de 33 a 36; espinhos na serra pré-pélvica variando entre 31 e 34 .... ***Myloplus levis***

(Espécie distribuída na Bacia do Paraguay-Paraná entre o Brasil e o Paraguai)

12. Fontanelas anterior com formato arredondado e fontanela posterior muito reduzida com formato triangular; fontanela anterior levemente mais alongada que larga, largura similar ao comprimento .... ***Myloplus asterias***
(Espécie amplamente distribuída na Bacia Amazônica e Orinoco, ocorrendo no Brasil, Bolívia, Peru, Colômbia, Venezuela, Guiana, Suriname e Guiana Francesa)

12’. Fontanelas estreitas e alongadas antero-posteriormente; fontanela anterior muito mais alongada que larga, largura menor que a metade do comprimento da fontanela .... ***Myloplus tiete***
(Espécie distribuída na Bacia do Paraguay-Paraná entre o Brasil, Bolívia e o Paraguai)

Anexos

Anexo 1

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Tometes kranponhah and *Tometes ancylorhynchus* (Characiformes: Serrasalmidae), two new phytophagous serrasalmids, and the first *Tometes* species described from the Brazilian Shield

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Two new species of *Tometes* from the Brazilian Shield rapids are described. *Tometes kranponhah* is endemic to the Xingu River basin, whereas *Tometes ancylorhynchus* occurs both in the Xingu and the Tocantins–Araguaia River basins. The two species are sympatric in the Xingu drainages and have many similarities in morphology and colouration. Major diagnostic differences are the dark pigmentation on the opercle of *T. kranponhah* and its distinct snout shape and arrangement of premaxillary teeth. In addition, *T. kranponhah* is a large fish that is abundant in the Xingu River, whereas *T. ancylorhynchus* is a medium-sized fish for which there are few records.

Key words: *Myleus*; new species; rheophilic fishes; taxonomy; Tocantins; Xingu.

Anexo 2

PLOS | ONE

RESEARCH ARTICLE

Redescription and Geographical Distribution of the Endangered Fish *Ossubtus xinguense* Jégu 1992 (Characiformes, Serrasalmidae) with Comments on Conservation of the Rheophilic Fauna of the Xingu River

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Abstract

The monotypic species *Ossubtus xinguense* was originally described based on scarce material putatively divided into juveniles and adults. *Ossubtus xinguense* has a restricted distribution and was previously known only from a few rapids downstream of the city of Altamira, in the Volta Grande stretch of the Middle Xingu River. Until recently, the species was rare in museums because its habitat (large rapids) is difficult to sample. Large-scale collecting efforts targeting rapids throughout the Xingu River basin have yielded an abundance of new material. Based on an analysis of the type series and freshly preserved specimens, we redescribe *O. xinguense* and provide detailed osteological descriptions along with comments about its relationships within Serrasalmidae. Furthermore, we expand the geographical distribution of the species and discuss its conservation status.

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Introduction

The monotypic genus *Ossubtus* was established by Jégu [1] to include new species *O. xinguense*. The original description was based on 15 specimens from rapids in the Xingu River near Altamira city. At that time, the species was thought to be rare in nature and restricted to the vicinity of the type locality [2]. *Ossubtus xinguense* is endemic to the Xingu basin and inhabits rapids with rock outcrops covered by macrophytes of the family Podostemaceae [1], [2]. Those habitats are severely threatened by the recent completion of major construction on the Belo Monte

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RESEARCH ARTICLE

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Anexo 3

A new large species of *Myloplus* (Characiformes, Serrasalmidae) from the Rio Madeira basin, Brazil

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Abstract

Myloplus zorroi **sp. n.** is described from the Rio Madeira Basin in Amazonia. The new species had been treated as an undescribed *Tometes* species because of the absence of a marked abdominal keel and few small spines forming its prepelvic serrae, features commonly found in the species of the *Myleus* clade of the Serrasalmidae (species of genera *Myleus*, *Mylesinus, Ossubtus* and *Tometes*) and also in species of *Utiaritichthys*. *Myloplus zorroi* **sp. n.** shares the following characters with its congeners and *Utiaritichthys*: molariform teeth (versus incisiform teeth in *Myleus* clade members); a labial row of premaxillary teeth separated from lingual row by an internal gap (versus absence of internal gap between premaxillary teeth rows); and an ascending process of premaxilla wide from its base to the tip (versus ascending process tapering from its base to the tip). Like other *Myloplus* species, *M. zorroi* **sp. n.** differs from *Utiariticthys* by having a deeper body, approximately 60% of standard length (versus usually less than 50% of standard length). Considering all the morphological evidence, including the presence of 13–19 low spines forming the prepelvic serrae in *M. zorroi* **sp. n.** versus more than 20 high spines forming a marked prepelvic keel in other species of *Mylopus,* the new species is here assigned to *Myloplus*. Comparisons of the new species with nominal species of *Myloplus*, representatives of the *Myleus* clade, and other related taxa are provided.

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Anexo 4

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A new large *Myloplus* Gill 1896 from rio Negro basin, Brazilian Amazon (Characiformes: Serrasalmidae)

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Abstract

Myloplus lucienae, new species, is described from the blackwater tributaries of the rio Negro basin. It is one of the few *Myloplus* species typically found in rapid areas of the Guiana Shield. It is diagnosed from congeners by the combination of an elongated body, small prepelvic spines that reach anteriorly just to the middle of the abdomen between verticals through pectoral- and pelvic-fin origin, and large scales on flanks resulting in smaller scale counts.

Key words: Neotropical fishes, *Myleus*, taxonomy, Alfred Russell Wallace, Ostariophysi

Introduction

The genus *Myloplus* Gill consists of medium to large-sized Serrasalmidae with molariform teeth specialized to crush fruits and seeds (Jégu, 2003; Ota *et al.*, 2013). *Myloplus* species are primarily found in areas of South America containing slow-flowing rivers, ranging across the Amazon, Orinoco and coastal drainages of Guiana Shield and into the La Plata and rio São Francisco basins (Andrade *et al.*, 2016a; Jégu, 2003; Jégu *et al.*, 2003; Jégu & Ingenito, 2007). Currently, *Myloplus* comprises 12 species – most of which were previously assigned to the genus *Myleus* Müller & Troschel (Andrade *et al.*, 2016a). This makes *Myloplus* one of the most speciose genera of the Serrasalmidae, outnumbered only by *Serrasalmus* Lacepède and *Metynnis* Cope containing 26 and 15 species, respectively (Eschmeyer *et al.*, 2016).

However, the genus does not consist a monophyletic assemblage, and its taxonomic limits are still unclear according to most recent phylogenies (i.e. Ortí *et al.*, 1996, 2008; Thompson *et al.*, 2014). In addition, much confusion persists at the generic level mainly involving its distinction of the genus *Myleus*. Jégu *et al.* (2004) compared *Myloplus asterias* (Müller & Troschel), the type-species of *Myloplus*, and *Myleus setiger* (Müller & Troschel), the type-species of *Myleus*, ultimately leading to the resurrection of *Myloplus* as a distinct genus.

According to Jégu *et al.* (2004), *Myloplus* is diagnosed from *Myleus* by having a massif neurocranium (vs. slender), narrow olfactory fossa (vs. wide), molariform teeth (vs. incisiform), two rows of premaxillary teeth spaced by an internal gap (vs. abutting rows), pair of large symphyseal teeth (vs. tiny), wide ascending premaxillary process strongly attached to the mesethmoid (vs. tapering to the top and weakly attached), well-developed lateral premaxillary process that is two to three times longer than the last tooth basis (vs. shorter, and not exceeding the size of the last tooth basis), and well-developed prepelvic spines that form a marked keel (vs. not forming a keel). Based on this definition, we herein describe a new species from the rio Negro basin assigning it to the genus *Myloplus*.

Anexo 5

Length-weight relationships and condition factor of the eaglebeak pacu *Ossubtus xinguense* Jégu, 1992 (Characiformes, Serrasalmidae), an endangered species from Rio Xingu rapids, northern Brazil

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Abstract

This study reports on the length-weight relationships and condition factor for the endangered rheophilic fish *Ossubtus xinguense* Jégu from Rio Xingu rapids. This species is threatened by construction of the third largest hydroelectric in the world, the Belo Monte dam close to the city of Altamira, northern Brazil. Specimens were collected in the dry season between July 2012 and September 2012. Male specimens have body length larger than females, atypical in serrasalmid fishes, and different length-weight relationships were found between adult and juvenile specimens. This study presents the first biological characteristics for *O. xinguense*.

Keywords: conservation, hydroelectric impacts, growth stanzas, rheophilic fish, endemic species.

Relações peso-comprimento e fator de condição do pacu-capivara *Ossubtus xinguense* Jégu, 1992 (Characiformes, Serrasalmidae), uma espécie ameaçada de extinção das corredeiras do Rio Xingu, norte do Brasil

Resumo

Este estudo relata as relações peso–comprimento e fator de condição para o peixe reofílico ameaçado de extinção *Ossubtus xinguense* Jégu. Esta espécie, endêmica das corredeiras do Rio Xingu, é ameaçada pela construção da terceira maior hidrelétrica do mundo, denominada Belo Monte localizada às proximidades da cidade de Altamira, norte do Brasil. Os espécimes foram coletados na estação seca do rio, entre julho e setembro de 2012. Espécimes machos apresentaram tamanho corporal maior que fêmeas, condição atípica entre os peixes serrasalmídeos, e diferentes relações peso–comprimento foram encontradas entre espécimes juvenis e adultos. Este estudo apresenta as primeiras características biológicas para *O. xinguense*.

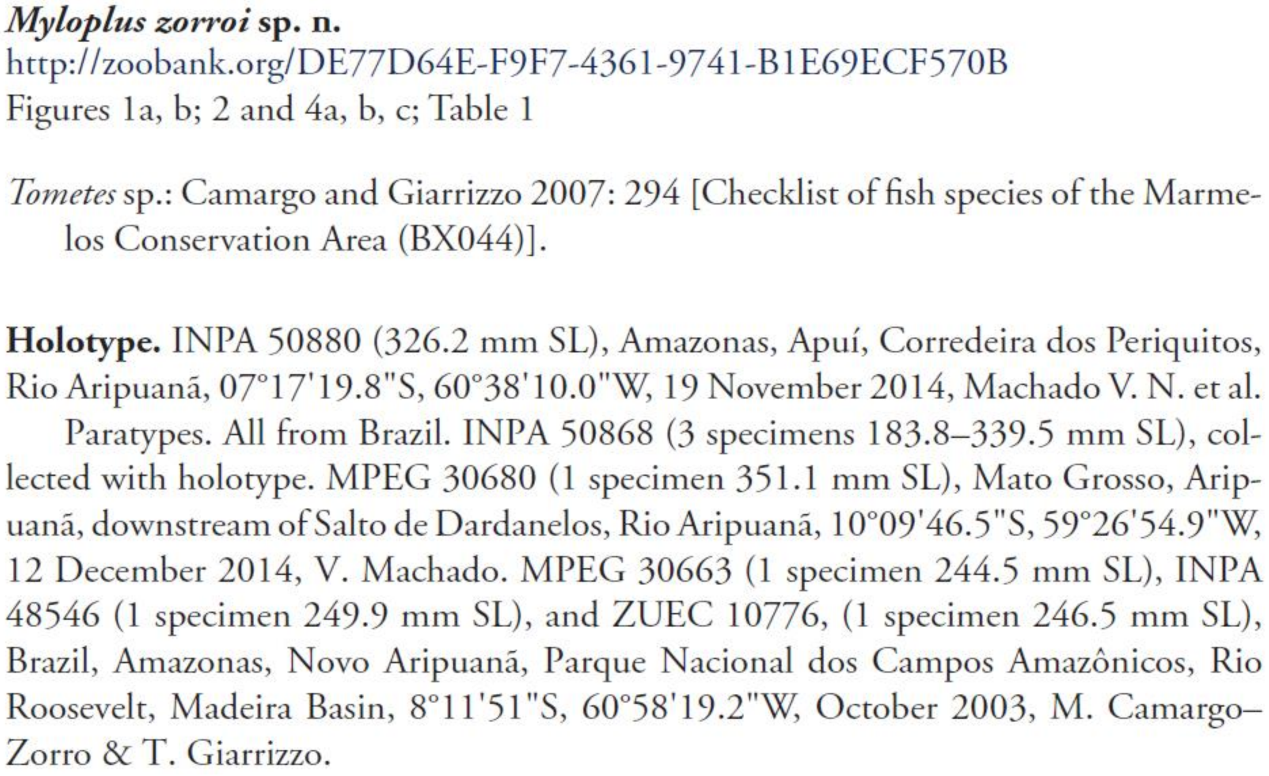
Palavras-chave: conservação, impactos por hidrelétricas, estrofes de crescimento, peixe reofílico, espécie endêmica.

1. Introduction

The Neotropical fish *Ossubtus xinguense* Jégu is a member of the Serrasalmidae family, which includes the famous piranhas (Jégu, 2003). *Ossubtus xinguense*, known as ‘eaglebeak pacu’ in the ornamental fish trade or as ‘pacu-capivara’ by local communities, is one of the rheophilic, endemic and rare fish from Rio Xingu. Due to its distribution restricted to rapids downstream of Altamira city, this species is seriously threatened by construction of the Belo Monte hydroelectric dam (Jégu and Zuanon, 2005).

The length-weight relationships (LWRs) and the condition factor (K) of fish are an important tool for assessing the conservation status of a fish population. The LWR are used to estimate the weight corresponding to a given length, convert growth in length equations to growth in weight, and allow life history and morphological comparison between different fish species and/or populations (Froese, 2006; Giarrizzo et al., 2006; Joyeux et al., 2009). Furthermore, the condition factor in fish serves as an indicator of the physiological state of the fish in relation to its welfare (Le Cren, 1951). Most Serrasalmidae fish display distinct allometries in its morphological features throughout the ontogeny, in general, with highest growth

Anexo 6



Myloplus zorroi **sp. n.**
http://zoobank.org/DE77D64E-F9F7-4361-9741-B1E69ECF570B
Figures 1a, b; 2 and 4a, b, c; Table 1

Tometes sp.: Camargo and Giarrizzo 2007: 294 [Checklist of fish species of the Marmelos Conservation Area (BX044)].

Holotype. INPA 50880 (326.2 mm SL), Amazonas, Apuí, Corredeira dos Periquitos, Rio Aripuanã, 07°17'19.8"S, 60°38'10.0"W, 19 November 2014, Machado V. N. et al.

Paratypes. All from Brazil. INPA 50868 (3 specimens 183.8–339.5 mm SL), collected with holotype. MPEG 30680 (1 specimen 351.1 mm SL), Mato Grosso, Aripuanã, downstream of Salto de Dardanelos, Rio Aripuanã, 10°09'46.5"S, 59°26'54.9"W, 12 December 2014, V. Machado. MPEG 30663 (1 specimen 244.5 mm SL), INPA 48546 (1 specimen 249.9 mm SL), and ZUEC 10776, (1 specimen 246.5 mm SL), Brazil, Amazonas, Novo Aripuanã, Parque Nacional dos Campos Amazônicos, Rio Roosevelt, Madeira Basin, 8°11'51"S, 60°58'19.2"W, October 2003, M. Camargo–Zorro & T. Giarrizzo.

Anexo 6 (continuação)

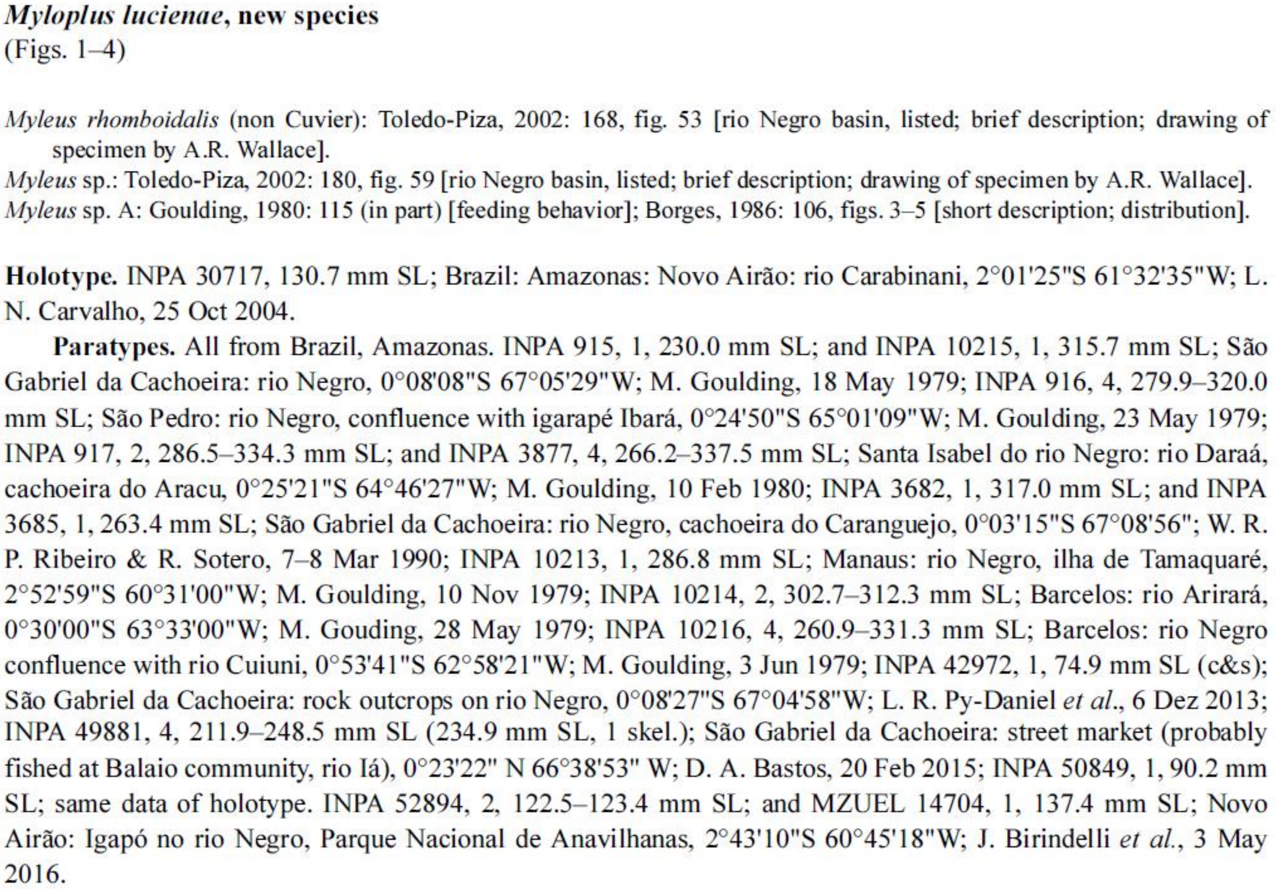
Comparative material

Myloplus arnoldi: IRSNB 21.253, 1 specimen, 147.7 mm SL, Rio Xingu, Cachoeira Von Martius, Mato Grosso, Brazil. MNHN 1998-1162, 2 specimens, 147.6–154.5 mm SL, Altamira market, Brazil. *Myloplus torquatus*: NMW 56449, 1 specimen, Paralectotype, 133 mm SL, Rio Branco, Marabitanos, Brazil. NMW 56450, Lectotype, 122 mm SL, Rio Branco, Brazil. *Myloplus ternetzi*: BMNH 1926.3.2.531-532, 2 specimens, Syntypes, 157.1–163.2 mm SL, Approuague River, Maparú Rapids, French Guiana. IEPA 3548, 5 specimens, 131.7–168.2 mm SL, Amapá, Brazil. IEPA 3560, 5 specimens, 98.4–117.5 mm SL, Flota do Amapá, Rio Araguari, Amapá, Brazil. IEPA 3586, 3 specimens, 18.1–29.9 mm SL, Oiapoque, Rio Anoitaí, Amapá, Brazil. RMNH 26467, Holotype of *Myleus* (*Paramyloplus*) *ternetzi goslinei*, 178.3 mm SL; and RMNH 33828, 6 specimens, Paratypes of *Myleus* (*Paramyloplus*) *ternetzi goslinei*, 67.1–142.6 mm SL, Brokopondo, Suriname River, Suriname. *Myloplus lobatus*: BMNH 1849.11.8.32-33, 2 specimens, Syntypes, 143.6–152.6 mm SL; and BMNH 97.11.26.8, 1 specimen, 124.2 mm SL, Rio Capim, Pará, Brazil. GEA 1988, 1 specimen, 166.7 mm SL, Parque Nacional dos Campos Amazônicos, Rio Roosevelt, Madeira Basin, Brazil. MNHN 0000-5244, 1 specimen, 188.2 mm SL, Rio Amazonas, Brazil. *Myloplus rhomboidalis*: BMNH 1926.10.27.174-6, 3 specimens, 54.4–78.8 mm SL. Rio Amazonas, Monte Alegre, Brazil. GEA 1500, 1 dry skeleton, 280 mm SL, Altamira market, Xingu Basin, Brazil. GEA 1501, 1 specimen, 230.1 mm SL, Parque Nacional dos Campos Amazônicos, Rio Roosevelt, Madeira Basin, Brazil. IRSNB 20.221, 4 specimens, 66.9–95.6 mm SL, Camopi River, Polydor, French Guiana. IRSNB 20.222, 5 specimens, 68–87.9 mm SL, Oyapock River, French Guiana. MNHN 4423, 1 specimen, 150.1 mm SL, Rio Amazonas, Brazil. MNHN A-9739, 1 specimen, 128 mm SL, Essequibo River, Guyana. MNHN A-9862, 2 specimens, 138.5–140.2 mm SL, Maná River, French Guiana. *Myloplus schomburgkii*: GEA 1974, 1 dry skeleton, 135 mm SL, Rio Xingu, Brazil. GEA 1987, 1 specimen, 224 mm SL, Parque Nacional dos Campos Amazônicos, Rio Roosevelt, Madeira Basin, Brazil. *Myloplus asterias*: BMNH 1864.1.21.33, 1 specimen, 135.9 mm SL, Essequibo River, Guyana. BMNH 1900.4.2.5, 1 specimen, 237.1 mm SL, Pará State, Rio Acará, Brazil. BMNH 1971.5.10.63, 1 specimen, 182.5 mm SL; and BMNH 1971.5.10:61-62, 2 specimens, Paralectotypes, 115.3–122.8 mm SL, Essequibo River, Guyana. BMNH 1972.7.5:91-93, 3 specimens, 117.9–135.4 mm SL, Rupununi River, Wichabai, Guyana. BMNH 1982.9.24:105-107, 3 specimens, 135.5–177.1 mm SL; and BMNH 1982.9.24:83, 1 specimen, 148.6 mm SL, Xingu Basin, Brazil. GEA 1989, 1 specimen, 198.1 mm SL, Parque Nacional dos

Anexo 6 (continuação)

Campos Amazônicos, Rio Roosevelt, Madeira Basin, Brazil. IEPA 2869, 1 specimen, 146.5 mm SL; and IEPA 2875, 1 specimen, 147.3 mm SL; and IEPA 2890, 1 specimen, 153.9 mm SL, Amapá, Brazil. MNHN 1998-0256, 4 specimens, 144.1–152.6 mm SL, Rio Amapari and Rio Araguari, Amapá, Brazil. *Myloplus planquettei*: IEPA 3544, 6 specimens, 136.4–167.5 mm SL; and IEPA 3545, 1 specimen, 108 mm SL, Rio Jari, Amapá, Brazil. MNHN 1997-0729, 1 specimen, Paratype, 66.7 mm SL, Maná River, Saut Valentin, French Guiana. MNHN 1997-0730, Holotype, 112.8 mm SL, Maroni River, Twenke, French Guiana. MNHN 2001-1224, 1 specimen, Paratype, 139.3 mm SL, Maná River, Kawatop, Litany, French Guiana. *Myloplus rubripinnis*: BMNH 1971.5.10.64, 1 specimen, Syntype, 76.5 mm SL, Essequibo River, Guyana. GEA 1301, 1 dry skeleton, 278 mm SL, Rio Bacajá, Brazil. IRSNB 19.298, 1 specimen, 43.9 mm SL, Distrikt Marowijne, Tapanahoni River, Paloemeu Vliegveld, Suriname. IRSNB 20.223, 3 specimens, 43.7–53.1 mm SL, Camopi River, Polydor, French Guiana. IRSNB 20.224, 2 specimens, 97.3–97.6 mm SL, Oyapock River downstream Crique Adjoumba, French Guiana. MNHN 2000-0148 (ex A-9870), 3 specimens, 176.6–224.4 mm SL, Cayenne, French Guiana. MNHN A-8632, 1 stuffed specimen, 248.3 mm SL, Cayenne, French Guiana. MNHN A-9870, 1 specimen, 285.4 mm SL, Cayenne, French Guiana. MNHN A-9895, 1 specimen, 237.2 mm SL, Colombia. RMNH 33703, 1 specimen, 177 mm SL; and RMNH 33704, 1 specimen, 183.9 mm SL, Mamadam, Surinam River, above Brokopondo, Surinam. ZMA 105-565, 2 specimens, 168.7–190.6 mm SL, Saramaca River Basin, Suriname. *Utiaritichthys longidorsalis*: INPA 3638, holotype, 198.4 mm SL, Mato Grosso, Aripuanã, Rio Aripuanã. *Utiaritichthys sennaebragai*: MZUSP 100015, 3 specimens, 28.4–72.0 mm SL, Mato Grosso, Rio Juruena downstream of bridge at BR-364. GEA 1994, 1 specimen, 245.0 mm SL, Mato Grosso, São Domingos, Rio Guaporé.

Anexo 7



***Myloplus lucienae*, new species**
(Figs. 1–4)

Myleus rhomboidalis (non Cuvier): Toledo-Piza, 2002: 168, fig. 53 [rio Negro basin, listed; brief description; drawing of specimen by A.R. Wallace].
Myleus sp.: Toledo-Piza, 2002: 180, fig. 59 [rio Negro basin, listed; brief description; drawing of specimen by A.R. Wallace].
Myleus sp. A: Goulding, 1980: 115 (in part) [feeding behavior]; Borges, 1986: 106, figs. 3–5 [short description; distribution].

Holotype. INPA 30717, 130.7 mm SL; Brazil: Amazonas: Novo Airão: rio Carabinani, 2°01'25"S 61°32'35"W; L. N. Carvalho, 25 Oct 2004.

Paratypes. All from Brazil, Amazonas. INPA 915, 1, 230.0 mm SL; and INPA 10215, 1, 315.7 mm SL; São Gabriel da Cachoeira: rio Negro, 0°08'08"S 67°05'29"W; M. Goulding, 18 May 1979; INPA 916, 4, 279.9–320.0 mm SL; São Pedro: rio Negro, confluence with igarapé Ibará, 0°24'50"S 65°01'09"W; M. Goulding, 23 May 1979; INPA 917, 2, 286.5–334.3 mm SL; and INPA 3877, 4, 266.2–337.5 mm SL; Santa Isabel do rio Negro: rio Daraá, cachoeira do Aracu, 0°25'21"S 64°46'27"W; M. Goulding, 10 Feb 1980; INPA 3682, 1, 317.0 mm SL; and INPA 3685, 1, 263.4 mm SL; São Gabriel da Cachoeira: rio Negro, cachoeira do Caranguejo, 0°03'15"S 67°08'56"; W. R. P. Ribeiro & R. Sotero, 7–8 Mar 1990; INPA 10213, 1, 286.8 mm SL; Manaus: rio Negro, ilha de Tamaquaré, 2°52'59"S 60°31'00"W; M. Goulding, 10 Nov 1979; INPA 10214, 2, 302.7–312.3 mm SL; Barcelos: rio Arirará, 0°30'00"S 63°33'00"W; M. Gouding, 28 May 1979; INPA 10216, 4, 260.9–331.3 mm SL; Barcelos: rio Negro confluence with rio Cuiuni, 0°53'41"S 62°58'21"W; M. Goulding, 3 Jun 1979; INPA 42972, 1, 74.9 mm SL (c&s); São Gabriel da Cachoeira: rock outcrops on rio Negro, 0°08'27"S 67°04'58"W; L. R. Py-Daniel *et al*., 6 Dez 2013; INPA 49881, 4, 211.9–248.5 mm SL (234.9 mm SL, 1 skel.); São Gabriel da Cachoeira: street market (probably fished at Balaio community, rio Iá), 0°23'22" N 66°38'53" W; D. A. Bastos, 20 Feb 2015; INPA 50849, 1, 90.2 mm SL; same data of holotype. INPA 52894, 2, 122.5–123.4 mm SL; and MZUEL 14704, 1, 137.4 mm SL; Novo Airão: Igapó no rio Negro, Parque Nacional de Anavilhanas, 2°43'10"S 60°45'18"W; J. Birindelli *et al*., 3 May 2016.

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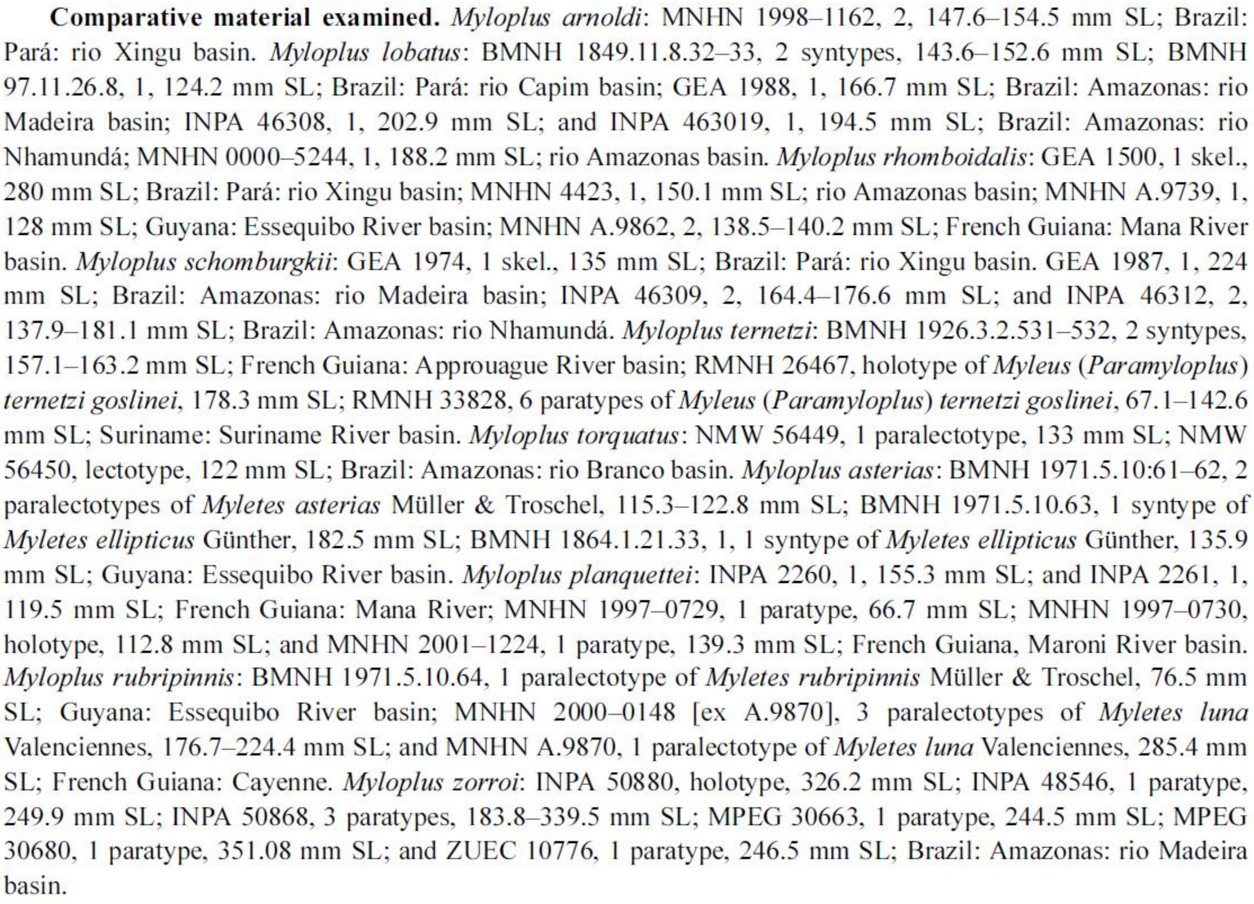
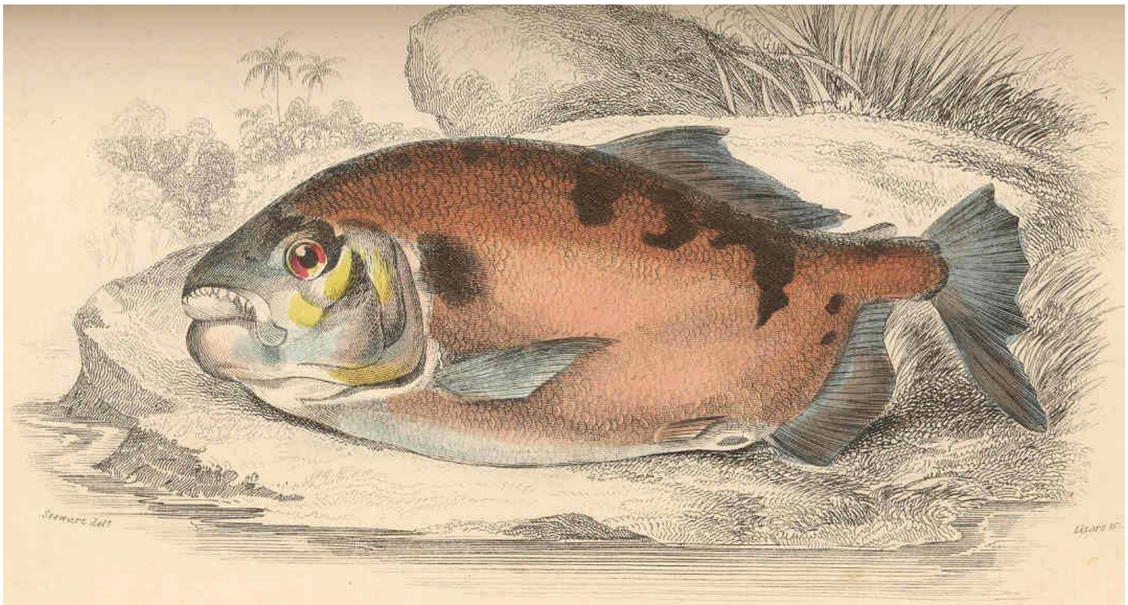


Comparative material examined. *Myloplus arnoldi*: MNHN 1998–1162, 2, 147.6–154.5 mm SL; Brazil: Pará: rio Xingu basin. *Myloplus lobatus*: BMNH 1849.11.8.32–33, 2 syntypes, 143.6–152.6 mm SL; BMNH 97.11.26.8, 1, 124.2 mm SL; Brazil: Pará: rio Capim basin; GEA 1988, 1, 166.7 mm SL; Brazil: Amazonas: rio Madeira basin; INPA 46308, 1, 202.9 mm SL; and INPA 463019, 1, 194.5 mm SL; Brazil: Amazonas: rio Nhamundá; MNHN 0000–5244, 1, 188.2 mm SL; rio Amazonas basin. *Myloplus rhomboidalis*: GEA 1500, 1 skel., 280 mm SL; Brazil: Pará: rio Xingu basin; MNHN 4423, 1, 150.1 mm SL; rio Amazonas basin; MNHN A.9739, 1, 128 mm SL; Guyana: Essequibo River basin; MNHN A.9862, 2, 138.5–140.2 mm SL; French Guiana: Mana River basin. *Myloplus schomburgkii*: GEA 1974, 1 skel., 135 mm SL; Brazil: Pará: rio Xingu basin. GEA 1987, 1, 224 mm SL; Brazil: Amazonas: rio Madeira basin; INPA 46309, 2, 164.4–176.6 mm SL; and INPA 46312, 2, 137.9–181.1 mm SL; Brazil: Amazonas: rio Nhamundá. *Myloplus ternetzi*: BMNH 1926.3.2.531–532, 2 syntypes, 157.1–163.2 mm SL; French Guiana: Approuague River basin; RMNH 26467, holotype of *Myleus* (*Paramyloplus*) *ternetzi goslinei*, 178.3 mm SL; RMNH 33828, 6 paratypes of *Myleus* (*Paramyloplus*) *ternetzi goslinei*, 67.1–142.6 mm SL; Suriname: Suriname River basin. *Myloplus torquatus*: NMW 56449, 1 paralectotype, 133 mm SL; NMW 56450, lectotype, 122 mm SL; Brazil: Amazonas: rio Branco basin. *Myloplus asterias*: BMNH 1971.5.10:61–62, 2 paralectotypes of *Myletes asterias* Müller & Troschel, 115.3–122.8 mm SL; BMNH 1971.5.10.63, 1 syntype of *Myletes ellipticus* Günther, 182.5 mm SL; BMNH 1864.1.21.33, 1, 1 syntype of *Myletes ellipticus* Günther, 135.9 mm SL; Guyana: Essequibo River basin. *Myloplus planquettei*: INPA 2260, 1, 155.3 mm SL; and INPA 2261, 1, 119.5 mm SL; French Guiana: Mana River; MNHN 1997–0729, 1 paratype, 66.7 mm SL; MNHN 1997–0730, holotype, 112.8 mm SL; and MNHN 2001–1224, 1 paratype, 139.3 mm SL; French Guiana, Maroni River basin. *Myloplus rubripinnis*: BMNH 1971.5.10.64, 1 paralectotype of *Myletes rubripinnis* Müller & Troschel, 76.5 mm SL; Guyana: Essequibo River basin; MNHN 2000–0148 [ex A.9870], 3 paralectotypes of *Myletes luna* Valenciennes, 176.7–224.4 mm SL; and MNHN A.9870, 1 paralectotype of *Myletes luna* Valenciennes, 285.4 mm SL; French Guiana: Cayenne. *Myloplus zorroi*: INPA 50880, holotype, 326.2 mm SL; INPA 48546, 1 paratype, 249.9 mm SL; INPA 50868, 3 paratypes, 183.8–339.5 mm SL; MPEG 30663, 1 paratype, 244.5 mm SL; MPEG 30680, 1 paratype, 351.08 mm SL; and ZUEC 10776, 1 paratype, 246.5 mm SL; Brazil: Amazonas: rio Madeira basin.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