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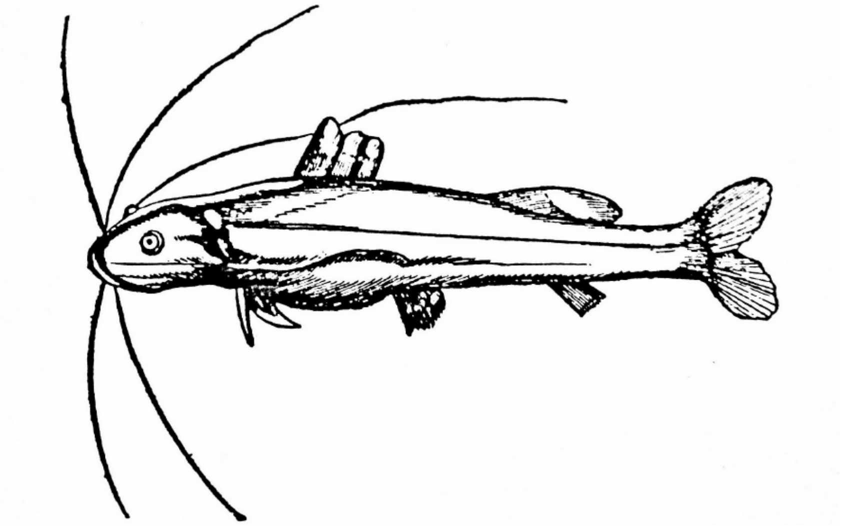
UNIVERSIDADE FEDERAL
DO RIO GRANDE DO SUL

PPGBAN
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL

INSTITUTO DE BIOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL

RAFAEL COSTA ANGRIZANI

DESVENDANDO RHAMDIA QUELEN Quoy & Gaimard, 1824



PORTOALEGRE
2017

RAFAEL COSTA ANGRIZANI

DESVENDANDO RHAMDIA QUELEN Quoy & Gaimard, 1824

Dissertação/Tese apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como requisito parcial à obtenção do título de Mestre/Doutor em Biologia Animal.

Área de concentração:

Orientador(a): Prof. Dr. Luiz Roberto Malabarba

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Aprovada em ____ de ____________ de _____.

BANCA EXAMINADORA

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À Gabriele e Aurora, meus amores e minha família.

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Resumo

As espécies de *Rhamdia* estão distribuídas por toda a região Neotropical. Muitas espécies foram descritas, adicionadas ou revalidadas após a descrição do gênero, resultando em mais de 100 nomes associados à *Rhamdia*. Independentemente do grande número de espécies, há apenas uma revisão taxonômica das espécies do gênero publicada. Esta revisão concluiu que *Rhamdia* é composta por apenas 11 espécies válidas entre mais de 100 nomes disponíveis. Atualmente, 27 espécies estão listadas para este gênero. A maior complexidade e diversidade não resolvida entre as espécies de *Rhamdia* estão associadas à *Rhamdia quelen,* que possui 47 espécies nominais sob sinonímia. *Rhamdia quelen* tem uma ampla distribuição geográfica, do México à Argentina, sendo reconhecida como um grande complexo de espécies. Para resolver os problemas que envolvem esse complexo, nessa pesquisa é proposta uma análise da diversidade genética de populações relacionadas à *R. quelen*. Portanto, foram utilizadas amostras de toda a distribuição da espécie e foram empregados quatro marcadores moleculares: os genes COI e CytB do mtDNA e os genes RAG2 e MyH6 do nDNA. Para essa análise, as relações filogenéticas foram inferidas por Inferência Bayesiana. Os resultados indicam que este gênero é um grupo monofilético bem suportado e os espécimes de *Rhamdia* são distribuídos em dois grandes clados: o clado denominado de Mesoamerican e o clado denominado de South-American. O clado Mesoamerican é formado por *R. guatemalensis* e *R. cinerascens* sendo *R. quelen* restrita à América do Sul. O clado *South-American* é dividido em três grupos principais, denominados de clado *Amazon*, clado *Upper-Amazon* e clado *Brazilian-Shield*. O clado *Brazilian-Shield* é composto por dois grupos principais, denominados de clado Continental e clado *Atlantic Coastal*, sendo o último dividido no clado *Atlantic Lowland* e no clado *Atlantic Highland*. As linhagens obtidas foram analisadas morfologicamente, de modo que puderam ser redescritas sete espécies da sinonímia de *Rhamdia quelen* e foram descritas cinco novas espécies, elevando a diversidade do gênero para inimagináveis trinta e sete espécies válidas.

Abstract

The species of *Rhamdia* are distributed throughout the Neotropical region. Several species have been described, transfered, synonymized or revalidated after the description of the genus, resulting in more than 100 nominal names associated with *Rhamdia*. Regardless the large number of species, there is only one taxonomic revision of the species of the genus published abou to 20 years ago. This revision concluded that *Rhamdia* contains only 11 valid species among more than 100 available names. Currently, 27 species are recognized for the genus. The largest complexity and unresolved diversity among *Rhamdia* species is associated to *Rhamdia quelen* that have 47 nominal species as junior synonyms. *Rhamdia quelen* has a wide geographic distribution, from Mexico to Argentina, and it has been recognized as a large species complex. In an attempt to resolve the issues related to this species complex, an analysis of the genetic diversity of populations related to the *R. quelen* is proposed in this research. Therefore, samples throughout the *R. quelen* distribution and four molecular markers were used: the genes COI and CytB of mtDNA and the genes RAG2 and MyH6 of nDNA. For this analysis, phylogenetic relationships were inferred by Bayesian Inference using a gene and a species tree approaches. The results indicate that this genus is a well-supported monophyletic group and the species of *Rhamdia* are distributed in two large clades: Mesoamerican clade and South-American clade. The Mesoamerican clade is formed by *R. guatemalensis* and *R. cinerascens* and the *R. quelen* would be restricted only to South America. The South American clade is divided into three main groups: the Amazon clade, the Upper-Amazon clade and the Brazilian-Shield clade. The Brazilian Shield clade is composed of two major groups, the Continental Clade and the Atlantic coastal clade, being the last one divided in the highland Atlantic coastal clade and the lowland Atlantic coastal clade. The lineages obtained were here morphologically analyzed, so that seven synonyms of *Rhamdia quelen* were revalidated and redescribed and five new species were described, bringing the diversity of the genus to thirty-seven species.

1. Introdução

1.1. A ordem Siluriformes e a família Heptapteridae

Os peixes da ordem Siluriformes são conhecidos popularmente como bagres e cascudos, são um grupo de peixes cosmopolitas podendo ser encontrados tanto em águas continentais como em ambientes marinhos. A ordem é reconhecida como o segundo grupo de peixes mais diverso: atualmente possui 38 famílias relacionadas e 3844 espécies válidas (Eschmeyer et al., 2017). A verdadeira diversidade do grupo é subestimada, visto que nos últimos 10 anos 666 espécies foram descritas (Eschmeyer et al., 2017) e estima-se que existam cerca de 1700 espécies não descritas para o grupo (Sabaj et al., 2004).

Entre as famílias da ordem, Heptapteridae chama a atenção por ser a sétima em número de espécies, com 212 espécies válidas distribuídas em 24 gêneros (Eschmeyer et al., 2017). É um grupo endêmico da região neotropical e suas espécies ocupam todos os ambientes de águas continentais, sendo componentes importantes das regiões de cabeceiras dos rios da América do sul e central (Bockmann, 1998). Os peixes que compõe a família costumam ser pequenos e de médio porte, dificilmente ultrapassando 200 mm de comprimento (Bockmann, 1998).

A situação taxonômica da família foi por muito tempo confusa e controversa, a história começa com o reconhecimento por Lundberg & McDade (1986) de um grupo monofilético dentro da família Pimelodidae. Esse grupo era formado por 13 gêneros: *Brachyglanis* Eigenmann, 1912, *Brachyrhamdia* Myers, 1927, *Cetopsorhamdia* Eigenmann & Fisher, 1916, *Goeldiella* Eigenmann & Norris, 1900, *Heptapterus* Bleeker, 1858, *Imparfinis* Eigenmann & Norris, 1900, *Myoglanis* Eigenmann, 1912, *Nannorhamdia* Regan, 1913, *Pariolius* Cope, 1872, *Pimelodella* Eigenmann & Eigenmann, 1888, *Rhamdella* Eigenmann & Eigenmann 1888, *Rhamdia* Bleeker 1858 e *Typhlobagrus* Miranda Ribeiro 1907. Posteriormente Lundberg et al. (1991) dividem a família Pimelodidae em três grandes clados, reconhecidos por ele como as subfamílias Pimelodinae (é família Pimelodidae propriamente dita), Pseudopimelodinae (futura família Pseudopimelodidae) e Rhamdiinae (futura família Heptapteridae). A subfamília Rhamdiinae de Lundberg et al. (1991) era composta por 26 gêneros: *Rhamdia* Bleeker 1858*,* *Pimelodella* Eigenmann & Eigenmann 1888*,* *Rhamdella*

Eigenmann & Eigenmann 1888*,* *Brachyrhamdia* Myers 1927*,* *Typhlobagrus* Miranda Ribeiro 1907*,* *Caecorhamdia* Norman 1926*,* *Caecorhamdella* Borodin 1927*,* *Goeldiella* Eigenmann & Norris 1900*,* *Cetopsorhamdia* Eigenmann & Fisher 1916*,* *Nannorhamdia* Regan 1913*,* *Horiomyzon* Stewart 1986*,* *Brachyglanis* Eigenmann 1912*,* *Myoglanis* Eigenmann 1912*,* *Leptorhamdia* Eigenmann 1912*,* *Acentronichthys* Eigenmann & Eigenmann 1889*,* *Chasmocranus* Eigenmann 1912*,* *Imparales* Schultz 1944*,* *Leptorhamdia* Eigenmann 1912*,* *Medemichthys* Dahl 1961*,* *Nemuroglanis* Eigenmann & Eigenmann 1889*,* *Pariolius* Cope 1872*,* *Phenacorhamdia* Dahl 1961*,* *Gladioglanis* Ferraris & Mago-Leccia 1989*,* *Phreatobius* Goeldi 1905 e *Rhamdiopsis* Haseman 1911. Então, Pinna (1991) apresenta uma reconstrução filogenética da ordem Siluriformes. Neste estudo, o autor reconhece o monofiletismo das três subfamílias reconhecias por Lundberg et al. (1991), elevando ao status de família estes três grupos e reconhecendo pela primeira vez a família Rhamdiidae (Heptapteridae). Silfvergrip (1996) atenta para a questão de prioridade de nomes, e troca o nome da família Rhamdiidae para Heptapteridae, como é reconhecida até hoje.

Bockmann (1998), em sua tese de doutorado, faz uma revisão completa da família Heptapteridae e uma abordagem filogenética baseada em caracteres morfológicos. Nesse estudo foram propostos 11 gêneros novos para a família, cujos nomes não estão disponíveis por não atenderemos critérios de publicação e disponibilidade do Código Internacional de Nomenclatura Zoológica. Além destes, são reconhecidos 23 gêneros válidos: *Acentronichthys* Eigenmann & Eigenmann, 1889; *Brachyglanis* Eigenmann, 1912; *Cetopsorhamdia* Eigenmann & Fisher, 1916; *Chasmocranus* Eigenmann, 1912; *Gladioglanis* Ferraris & Mago-Leccia, 1989; *Goeldiella* Eigenmann & Norris, 1900; *Heptapterus* Bleeker, 1858; *Horiomyzon* Stewart, 1986; *Imparfinis* Eigenmann & Norris, 1900; *Leptorhamdia* Eigenmann, 1918; *Mastiglanis* Bockmann, 1994; *Myoglanis* Eigenmann, 1912; *Nannoglanis* Boulenger, 1887; *Nemuroglanis* Eigenmann & Eigenmann, 1889; *Pariolius* Cope, 1872; *Phenacorhamdia* Dahl, 1961; *Phreatobius* Goeldi, 1905; *Pimelodella* Eigenmann & Eigenmann, 1888; *Rhamdella* Eigenmann & Eigenmann, 1888; *Rhamdia* Bleeker, 1858; *Rhamdioglanis* Ihering, 1907; *Rhamdiopsis* Haseman, 1911; e *Taunayia* Ribeiro, 1918.

1.2. O gênero *Rhamdia*

Dentro da família Heptapteridae o gênero *Rhamdia* chama muito atenção. Conhecidos no Brasil como jundiás, esses peixes apresentam uma relativa importância para a pesca esportiva e uma considerável importância econômica para sistemas de piscicultura. Esse grupo de peixes possui uma grande diversidade e uma longa, rica e conturbada história taxonômica.

Rhamdia foi descrita por Bleeker em 1858, e desde então mais de 100 nomes foram adicionados ou descritos para o gênero. *Rhamdia* foi criado para agrupar as seguintes espécies: *Heterobranchus sextentaculatus* Spix & Agassiz, 1829, *Pimelodu sgracilis* Valenciennes 1840, *Pimelodus hilarii* Valenciennes 1840, *Pimelodus pati* Valenciennes 1840, *Pimelodus pentlandii* Valenciennes 1840, *Pimelodus quelen* Quoy & Gaimard 1824, *Pimelodus sapo* Valenciennes 1840, *Pimelodus sebae* Cuvier, 1829 e *Pimelodus laukidi* Bleeker, 1858. A diagnose original do gênero era breve e muito superficial: Duas nadadeiras dorsais, a anterior raiada, a posterior adiposa; nadadeira anal de tamanho médio; sem dentes no vomer e no palato; seis barbilhões; membrana branchiostegal com 7-9 raios; espinho da nadadeira dorsal muito fino; escudo principal da cabeça evidente; narinas não tubulares ou com válvulas; nadadeira adiposa longa; nadadeira caudal bilobada.

O histórico do gênero é tão conturbado que até a espécie tipo foi alvo de muito debate. Alguns autores consideram *Pimelodus quelen* como a espécie tipo (Eigenmanm & Eigenmann, 1888, Eigenmann & Fisher, 1916; Eigenmann & Allen, 1942), outros reconhece a espécie *Pimelodus sebae* (Gill, 1861). Bleeker na descrição do gênero não designou um táxon para tal, que só foi escolhida em 1861 por Gill: a espécie *Pimelodus sebae*.

No mesmo ano em que Bleeker (1858) descrevia o gênero *Rhamdia*, Gill (1858) descrevia o gênero *Pimelenotus*, sinônimo de *Rhamdia*. A descrição de Gill (1858) era muito mais completa, passando por diversos aspectos morfológicos do grupo. Gill (1862), alguns anos mais tarde, reconhece que o trabalho de descrição do gênero *Rhamdia* de Bleeker foi publicado um mês antes. Dessa forma, o autor recomenda o uso o nome *Rhamdia*, tornando *Pimelenotus* um sinônimo.

De certa forma, *Rhamdia* demorou a ser aceito. Günther (1860, 1864, 1866, 1868) não reconhece o gênero. O autor descreve 16 espécies relacionadas à *Rhamdia,* todas descritas como *Pimelodus*. Outros autores, como Troschel (1865), Cope (1866, 1878), Steindachner (1876) e Boulenger (1887) seguem o mesmo que Günther, não reconhecendo o gênero em suas descrições de espécies relacionadas à *Rhamdia*. Apenas Gill (1870), durante esse período, reconhece o gênero como válido.

A situação relacionada à validade e reconhecimento do gênero *Rhamdia* foi solucionada por Eigenmann & Eigenmann (1888). Os autores descrevem cinco novas espécies, inserindo 25 espécies no gêneroeconsiderandoogênero *Rhamdella* como subgênero de *Rhamdia.* O grupo era composto pelas espécies: *Rhamdia breviceps*, *Rhamdia schomburgkii*, *Rhamdia bathyurus*, *Rhamdia obesa*, *Rhamdia sebae*, *Rhamdia foina*, *Rhamdia humilis*, *Rhamdia cinerascens*, *Rhamdia pentlandii*, *Rhamdia quelen*, *Rhamdia multiradiatus*, *Rhamdia sapo*, *Rhamdia hilarii*, *Rhamdia wagneri*, *Rhamdia longicauda,Rhamdia dorsalis*, *Rhamdia poeyi*, *Rhamdia tenella*, *Rhamdia microcephala*, *Rhamdia notata*, *Rhamdia eriarcha*, *Rhamdia exsudans*, *Rhamdia jenynsii*, *Rhamdia parryi* e *Rhamdia minuta*.

Algumas redescrições de *Rhamdia* foram feitas ao longo do tempo. Jordan & Evermann (1896) descrevem o gênero da seguinte forma: Bagre de água-doce sem dentes no vomer; nadadeira adiposa mais ou menos alongada; focinho bastante largo, não pronunciado; barbilhão afilado e levemente achatado, sem membranas nas bordas; cabeça não especialmente alargada; processo occipital pequeno ou insignificante; não alcançando a placa dorsal; a fontanela tem desenvolvimento favorável, curta nas espécies típicas, não continuada além dos olhos, exceto nos jovens, em que há geralmente duas pontes ósseas através da fontanela, a primeiro atrás dos olhos, a outra em frente ao occipital; as depressões por trás dessas pontes são persistentes, nos adultos a fontanela se torna obliterada. Eigenmann & Eigenmann (1890) reconhece os indivíduos de *Rhamdia* seguindo os seguintes caracteres: Os jovens dessas espécies geralmente tem a fontanela que se estende até a base do occipital. Processo com uma ponte atrás do olho e outro em Frente do osso occipital. A fontanela occipital às vezes permanece no adulto como um poço superficial a partir do qual os nervos da porção posterior da cabeça irradiam. Segundo Fowler (1906) *Rhamdia* é reconhecido pelas seguintes características: corpo alongado; focinho não muito pronunciado; boca terminal ou subterminal, mandíbulas com dentes viliformes em bandas, palato desdentado, narinas distantes umas das outras, sem barbilhões nasais, seis barbilhões, processo occipital que não se estende para a nadadeira dorsal. Nadadeira dorsal com espinho flexível e delgado com e 5-

8 raios ramificados; nadadeira adiposa longa; nadadeira anal curta ou de comprimento moderado; nadadeiras ventrais com seis raios. Eigenmann & Fisher (1917) redescrevem *Rhamdia* seguindo os seguintes caracteres: fontanela terminando no nível dos olhos; processo occipital que não atinge a placa dorsal; parte superior da cabeça fechada na pele, não granulada; cabeça mais longa do que ampla, focinho não pronunciado; barbilhão afilado ou plano. Fontanelas obsolescentes, occipital obsoleto; margem orbital livre. Hildebrand (1938) reconhece como principais caracteres diagnósticos do gênero: o espinho da nadadeira dorsal fraco e flexível; o processo occipital curto que não atinge a placa dorsal; a margem orbital livre; a nadadeira adiposa bastante longa ao longo do dorso. As descrições antigas do gênero eram muito genéricas e confusas, utilizando caracteres que ocorrem em outros grupos de siluriformes, pouco servindo para a diagnose correta de *Rhamdia*.

Mais recentemente, Silfvergrip (1996) apresenta a primeira revisão taxonômica para o gênero, nesse estudo o autor diagnostica *Rhamdia* da seguinte forma: *Rhamdia* é distinguível de outros Siluriformes por apresentar o conjunto dos seguintes caracteres: três pares de barbilhões, sem dentes no vômer; lábio com dobra dupla; o processo posterior da quarta parapófise expandiu-se distalmente com uma grande e várias pequenas dentações; processo supraoccipital livre de placa supraneural; borda da órbita livre; nadadeira adiposa com margem livre posterior; fontanela posterior fechada; processo pós-cleitro (umeral) bem desenvolvido. Além da diagnose adequada para o gênero, Silfvergrip também descreve a morfologia de *Rhamdia* com uma excelente precisão de detalhes. Bockmann (1998), em sua revisão da família Heptapteridae, realizou uma análise filogenética dos gêneros da família e diagnostica *Rhamdia* da seguinte forma: região posterior do crânio, sobre a região mediana da fontanela posterior ossificada e processo uncinado do hipobranquial 1 ausente. Diferentes das antigas descrições e diagnoses de *Rhamdia*, as diagnoses modernas são suficientes para a distinção e reconhecimento do gênero.

Ao longo da história de *Rhamdia*, diferentes autores descreveram 111 espécies nominais referentes ao gênero (Eschmeyer et al., 2017). Logo abaixo, será apresentado um breve histórico de cada um desses nomes, onde será apresentada a atual situação de cada táxon:

1.2.1. *Rhamdia quelen*:

A primeira espécie de *Rhamdia* propriamente descrita foi *Pimelodus quelen*, descrita por Quoy & Gaimard (1824). Como todas as descrições da época, ela é sucinta e muito vaga, sendo pouco informativa para a definição da espécie, o que contribuiu para Silfvergrip (1996) cometer o grande erro de sinonimizar mais de 40 espécies dentro de *R. quelen.*

O equívoco cometido por Silfvergrip (1996) começa com a confusão feita em relação à localidade tipo da espécie. Na descrição original é definido que *R. quelen* é originária do Brasil, porém a localidade certa foi sempre motivo de debates (Fowler, 1951; Burges, 1989; Mees, 1974; Silfvergrip, 1996). Valenciennes em 1840 aponta que *R. quelen* teria origem em Montevidéu, Uruguai. Entre 1821-1829, o Uruguai fazia parte do território Brasileiro (Fitzgibbon, 1954), motivo pelo qual tenha suscitado discussões quanto à origem desse táxon. O que nunca foi levado em consideração sobre a origem de *Rhamdia quelen* é a lista em anexo em Freycinet (1824). No final da publicação existe uma lista de todos os táxons descritos e a localidade de onde provém, ficando evidente que a localidade tipo de *R. quelen* é a baía do Rio de Janeiro, hoje conhecida como Baía de Guanabara. De acordo com essa lista é muito provável que *R. quelen* seja originária do rio Macacu, como as outras espécies descritas nessa publicação e provenientes de tributaries da baía de Guanabara.

Além da descrição original pobre e os problemas de identificação da localidade tipo, o holótipo de *R. quelen* se encontra perdido (Silfvergrip, 1996; Ferraris, 2007). Dessa forma, Silfvergrip (1996) designou um neótipo para espécie.

1.2.2. *Heterobranchus sextentaculatus*

Heterobranchus sextentaculatus Spix & Agassiz 1829 foi coletada "Brasiliae aequatorialis fluviis", em tradução livre: rios equatoriais do Brasil. A série tipo está destruída e Silfvergrip (1996) designou o exemplar NRM 16090 como neótipo de *R. quelen* e de *Heterobranchus sextentaculatus*. A espécie foi sinonimizada em *P. quelen* por Valenciennes (1840). Foi sinonimizada em *R. quelen* por Eigenmann & Eigenmann (1888) e mantida como sinônimo por Silfvergrip (1996). É muito difícil definir quem é essa espécie, a localidade tipo é indecifrável, os pesquisadores percorreram toda a América do Sul, e o tipo não existe.

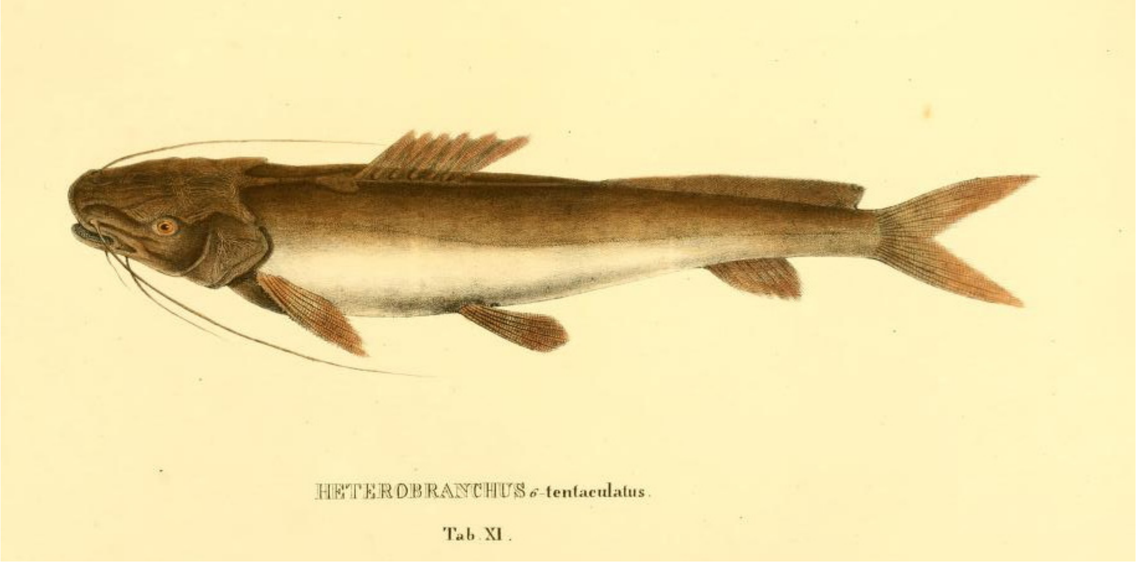

Figura 1: Ilustração original de *Heterobranchus sextentaculatus* por Spix (1829).

1.2.3. *Pimelodus sebae*

Pimelodus sebae foi mencionado pela primeira vez por Cuvier (1829) em uma nota de rodapé em alusão a ilustração de Seba (1759), naturalista que ilustrou em sua obra muitas espécies coletadas no Suriname. Portanto, o exemplar ilustrado por Seba deve ser considerado o holótipo dessa espécie (ICZN, 72.5.6. In the case of a nominal species-group taxon based on an illustration or description, or on a bibliographic reference to an illustration or description, the name-bearing type is the specimen or specimens illustrated or described, and not the illustration or description itself). Dessa forma, o Suriname é a localidade tipo para este táxon. Pouco tempo após o manuscrito de Cuvier (1829), Valenciennes (1840) redescreve formalmente *P. sebae,* usando espécimes do Suriname, da Guiana Inglesa, da Argentina, do Equador e do Rio de Janeiro (Brasil), transformando *P. sebae* em uma espécie com uma grande distribuição geográfica. *Pimelodus sebae* foi redescrito diversas vezes (Günther 1964; Steindachner 1879; Eigenmann & Eigenmann 1888; Miranda-Ribeiro 1907) e todos os estudos apresentaram problemas quanto à definição de sua distribuição geográfica. Foram Eigenmann & Eigenmann (1888) que inseriram *P. sebae* em *Rhamdia*.

Silfvergrip (1996) designou o espécime ilustrado por Seba como holótipo e o definiu como perdido. Silfvergrip (1996) sinonimizou *R. sebae* em *R. quelen*.

1.2.4. *Pimelodus hilarii*

Pimelodus hilarii foi descrito por Valenciennes (1840), esta espécie é originaria da bacia do rio São Francisco. Foi coletada por Saint Hilaire possivelmente no rio Pacuí (alto rio São Francisco) (Silfvergrip, 1996). Existem quatro síntipos dessa espécie depositados no Museu de História Natural de Paris (MNHN), três deles estão taxidermizados e são provenientes da bacia do rio São Francisco. O quarto está em álcool e é proveniente de Montevidéu (Uruguai), porém seu estado de conservação não permite ser examinado. Silfvergrip (1996) designou o espécime A9415, do rio São Francisco, como lectótipo para o táxon.

Essa espécie foi redescrita três vezes: por Günther (1864), Lütken (1875). Eigenmann & Eigenmann (1890), Evermann & Kendall (1907) e Miranda Ribeiro (1911). Lütken (1875) foi quem inseriu *R. hilarii* em *Rhamdia*. Silfvergrip (1996) sinonimiza essa espécie em *R. quelen,* porque de acordo com seus resultados as medidas, dados merísticos e outras características cabem na sua descrição da espécie.

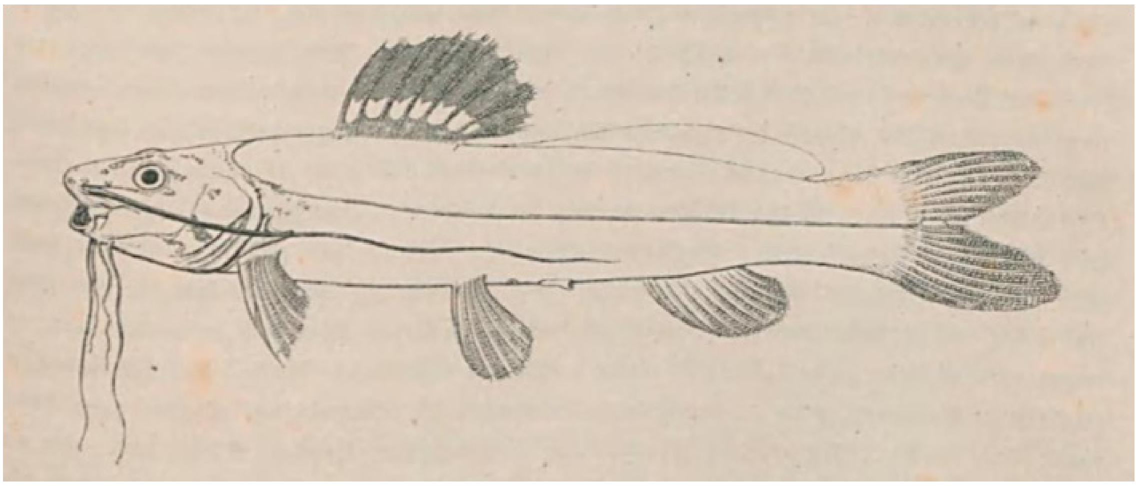

Figura 2: Ilustração da redescrição de *R. hilarii* por Lütken (1875).

1.2.5. *Pimelodus sapo*

Pimelodus sapo foi descrito por Valenciennes (1840) e coletado originalmente em Buenos Aires, Argentina, por D'Orbigny. O táxon possui um único espécime na série tipo, o holótipo MNHN 1576, depositado na coleção do Museu de História Natural de Paris (MNHN).

A espécie foi redescrita seis vezes: Kner (1858); Günther (1864), usando espécimes do rio da Prata; Steindachner (1868), usando espécimes de Montevidéu; Hensel (1870), usando espécimes do lago Guaíba; Steindachner (1876) de novo, usando espécimes do rio da Prata; Eigenmann & Eigenmann (1890), utilizando espécimes do Rio Grande do Sul e por Miranda Ribeiro (1911), que utilizou espécimes do lago Guaíba; e por Eigenmann & Fisher (1917). Foi inserida em *Rhamdia* por Bleeker (1858). Silfvergrip (1996) sinonimiza *R. sapo* em *R. quelen.*

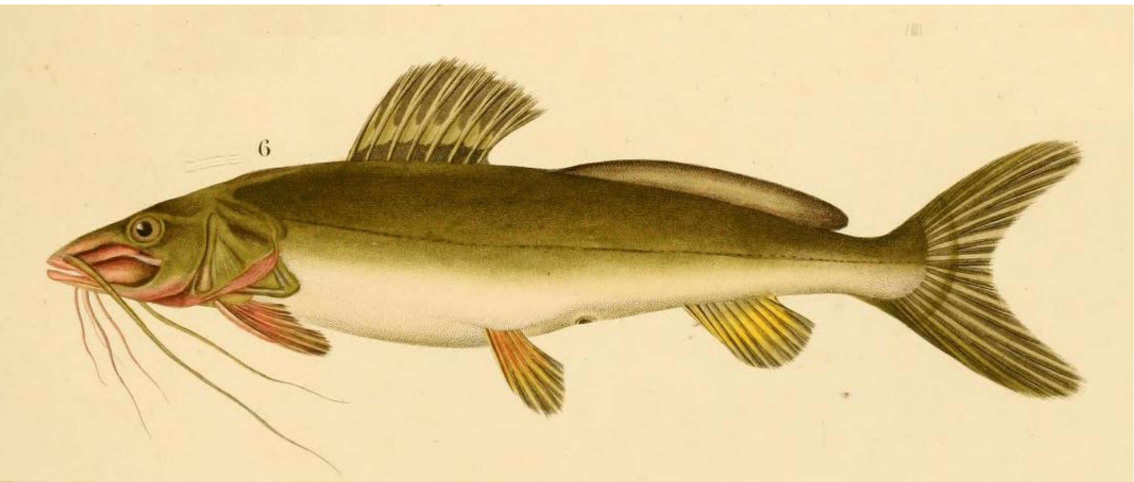

Figura 3: Ilustração de *Rhamdia sapo* retirado de Valenciennes (1840), ilustrado por Paul Louis Oudart.

1.2.6. *Pimelodus pentlandii*

Pimelodus pentlandii foi descrito por Valenciennes (1940) e coletado pelo Sr. Pentlandi no rio Apuriamac, tributário da porção alta do rio Ucayali. Os síntipos dessa espécie estão depositados no Museu de História Natural de Londres (BMNH). Silfvergrip (1996) escolheu o espécime BMNH 1862.11.15:11 como lectótipo.

Essa espécie foi redescrita por Günther (1864), Steindachner (1976), Steindachner (1882) e Eigenmann & Eigenmann (1888) que inseriram a espécie em *Rhamdia*. Diferindo muito de *R. quelen* por apresentar a cabeça e a nadadeira adiposa muito curta, essas características fizeram Silfvergrip (1996) cogitar em não sinonimizar esse táxon. Porém, a falta de mais espécimes para uma melhor análise, determinou com que essa espécie fosse sinonimizada em *R. quelen*.

1.2.7. *Pimelodus arekaima*

Pimelodus arekaima foi descrito por Jardine (1841), foi coletado no alto rio Essequibo. Não existe tipo conhecido, apenas a ilustração e descrição original. Günther (1864) sinonimiza a espécie em *Callophysus lateralis*. Eigenmann & Eigenmann (1888) sinonimizam este táxon em *Rhamdia multiradiatus* de acordo com a descrição original desconsiderando a ilustração, que de acordo com os autores não teria correspondência. Miranda Ribeiro (1911) considera a espécie válida como *Rhamdia arekaima*, também reconhecida por Burgess (1989). Considerada espécie *inquirenda* no gênero *Leiarius* (Pimelodidae) por Lundberg & Littmann (2003) e Ferraris (2007). Não faz parte do gênero *Rhamdia.*

1.2.8. *Pimelodus stegelichii*

Pimelodus stegelichii foi descrito por Müller &Troschel (1848) e é proveniente da Guiana. Existem quatro síntipos dessa espécie depositados no Museu de Zoologia de Berlim (ZMB), e um no Museu de Historia Natural de Londres (BMNH). Silfvergrip (1996) designou o lote ZMB 3043 como lectótipo dessa espécie.

Günther (1859) redescreveu a espécie usando um exemplar do Suriname e outro da região de Demerara, Guiana. Eigenmann & Eigenmann (1888) sinonimizaram a espécie em *R. sebae*. Silfvergrip (1996) sinonimiza essa espécie em *R. quelen*.

1.2.9. *Pimelodus sellonis*

Pimelodus sellonis foi descrito por Müller & Troschel (1849).De acordo com sua descrição é originário do Brasil, sem especificar a localidade mais precisamente. O holótipo dessa espécie está depositado no Museu de Zoologia de Berlim (ZBM), tombado com o número de lote ZBM 3041. Esse exemplar foi coletado por Friedrich Sellow, cuja campanha foi bem detalhada por Papavero (1971), porém é impossível determinar a localidade exata de coleta desse exemplar. Essa espécie foi sinonimizado em *R. quelen* por Eigenmann & Eigenmann (1888). De acordo com a última revisão de Silfvergrip (1996), esse táxon continua sendo sinônimo de *R. quelen.*

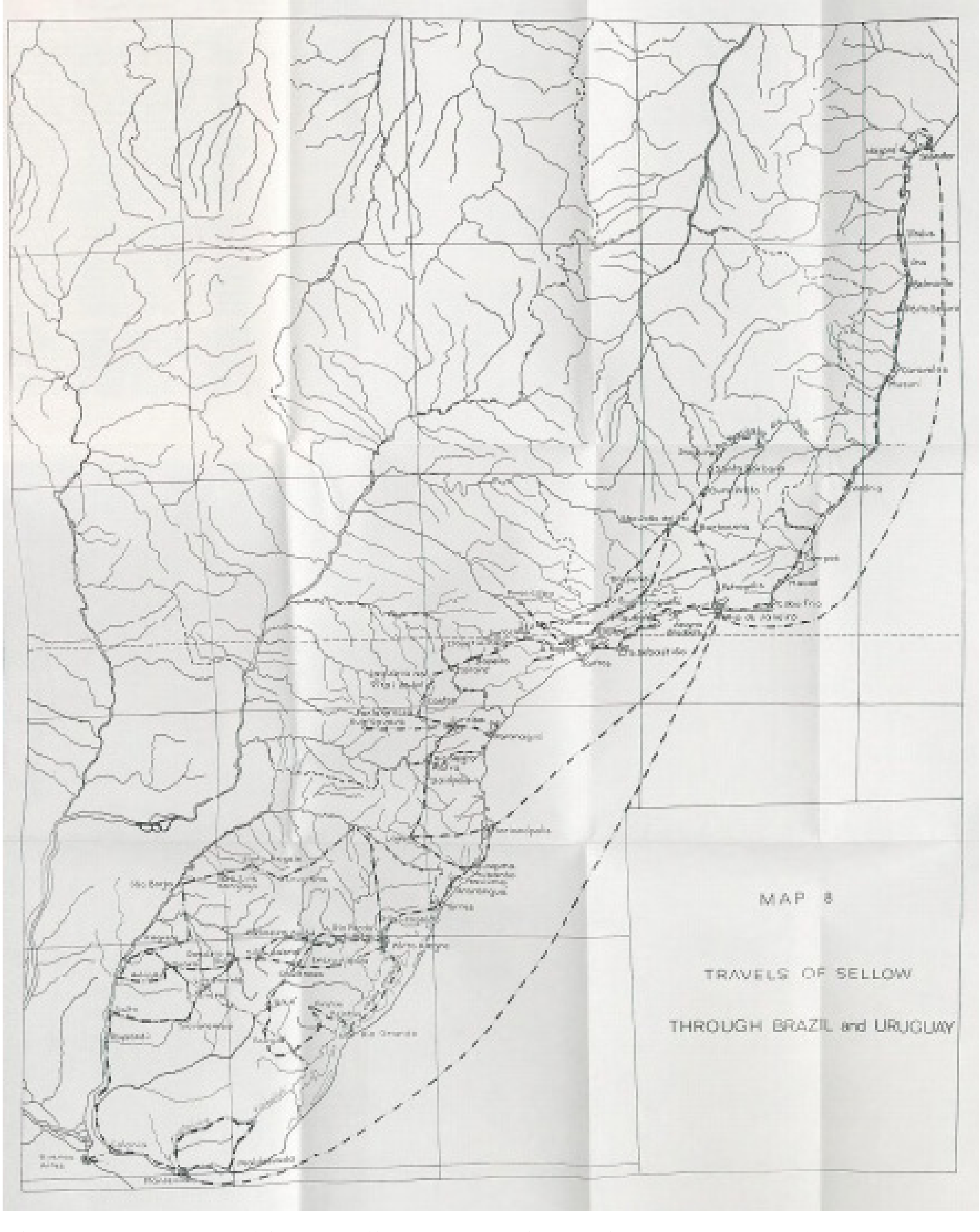

Figura 4: Rota percorrida por Sellow em1814 de acordo com Papavero (1971).

1.2.10. *Pimelodus deppei*

Pimelodus deppei foi descrito por Müller & Troschel (1849), foi coletado por Ferdinand Deppe. Na descrição original é definido como proveniente da “Sandwich-Inseln”, o problema é que essa ilha fica no Havaí, EUA. Essa espécie na verdade é proveniente do sul do México (Stresemann, 1954; Silfvergrip, 1996). Existem dois síntipos depositados no Museu de Zoologia de Berlim com os números de tombo ZMB 3046 e ZMB 3047. Silfvergrip (1996) designa o espécime ZMB 3046 como lectótipo. Essa espécie foi redescrita por Günther (1864). Silfvergrip (1996) sinonimiza *P. deppei* em *R. quelen* por apresentar serras nos dois lados do espinho da nadadeira peitoral.

1.2.11. *Pimelodus musculus*

Pimelodus musculus foi descrito por Müller & Troschel (1849) e a localidade tipo é a América (demasiadamente abrangente). O holótipo está depositado no Museu de Zoologia de Berlim identificado como ZMB 3048. Esta espécie foi sinonimizado por Günther (1864) em *Pimelodus muelleri* e posteriormente foi sinonimizada em *R. sebae* por Eigenmann & Eigenmann (1888). O espécime tipo está em péssimo estado de conservação, motivo pelo qual Silfvergrip (1996) sinonimizou esta espécie em *R. quelen,* mesmo reconhecendo que ela possuía características possíveis de ser sinonimizada em *R. muelleri.*

1.2.12. *Pimelodus foina*

Pimelodus foina foi descrito por Müller e Troschel (1849), coletado por Schomburgk na região de Takutu, Guiana. O holótipo ZBM 3039 está depositado no Museu de Zoologia de Berlim. Foi redescrita por Günther (1864), por Eigenmann & Eigenmann (1888), que também a inseriram em *Rhamdia,* e por Silfvergrip (1996). É considerada uma espécie válida, ocorrendo nas bacias dos rios Essequibo e Amazonas.

1.2.13. *Pimelodus breviceps*

Pimelodus breviceps foi descrito por Kner (1858), coletado na região de Marabitanos, Brasil. O holótipo NMW 45615 está depositado no museu de História Natural de Viena, Áustria. Gill (1858) redescreve esta espécie e a coloca em *Pseudopimelodus* Bleeker (1858). Foi redescrita por Günther (1864) como *Pimelodus breviceps*, sendo redescrita e inserida em

Rhamdia por Burgess (1989) e Eigenmann & Eigenmann (1888). Hoje está validada como *Pimelodella breviceps* (Kner 1858) (Bockmann & Guazzelli 2003, Ferraris 2007). Ocorre no alto rio Negro, bacia do rio Amazonas, Brasil.

1.2.14. *Pimelodus laticaudus*

Pimelodus laticaudus foi descrito por Kner (1858) e coletada no rio Jamapa, México. Os síntipos NMW 50554 foram depositados no museu de História Natural de Viena e estão perdidos. Foi redescrita por Günther (1864) como *P. laticaudus* e por Eigenmann & Eigenmann (1888) como *Rhamdella laticauda*, sendo alocada em *Rhamdia* por Miller (1984) e posteriormente redescrita como *R. laticauda* por Silfvergrip (1996). Recentemente foi realizado um estudo de sistemática e filogeografia de *Rhamdia* da América Central que incluí *R. laticauda* (Perdices et al., 2006). Hernandez et al. (2016) redescreve esse táxon que é considerado uma espécie válida. Ocorre em todas as bacias entre o México e o Panamá.

1.2.15. *Pimelenotus vilsoni*

Pimelenotus vilsoni foi descrita por Gill (1858) e coletada em Trinidad. O holótipo USNM 5927 está depositado na coleção científica do Smithsonian Museum. Foi sinonimizada em *Rhamdia sebae kneri* por Eigenmann & Eigenmann (1888). Inserido em *Pimelodus* por Regan (1906). Este táxon foi considerado como *Rhamdia vilsoni* por Fowler (1915) e por Burgess (1989). Foi sinonimizada em *Rhamdia quelen* por Silfvergrip (1996).

1.2.16. *Rhamdia laukidi*

Rhamdia laukidi foi descrita por Bleeker (1858) na mesma publicação em que é descrito o gênero *Rhamdia,* tendo como localidades tipo os rios Essequibo e Demerara. Os síntipos desse táxon nunca foram preservados, portanto, Silfvergrip (1996) designa o espécime ANSP 174652 (depositado na coleção da Academia de Ciências da Filadélfia, EUA) como neótipo, a descrição original apresenta caracteres claros, permitindo o reconhecimento da espécie. A espécie foi redescrita por Silfvergrip (1996). Atualmente é considerada uma espécie válida, ocorrendo nas bacias dos rios Amazonas, Essequibo e Orinoco.

1.2.17. *Pimelodus cinerascens*

Pimelodus cinerascens foi descrita por Günther (1860), tendo como localidade tipo a região de Esmeraldas, Equador. Os síntipos dessa espécie estão depositados no museu de História Natural de Londres (BMNH) e o lectótipo BMNH 1860.6.16.193 foi designado por Silfvergrip (1996). Foi redescrita por Günther (1864) e inserida em *Rhamdia* por Eigenmann & Eigenmann (1888). Foi sinonimizada em *R. wagneri* por Eigenmann & Eigenmann (1890) e em *R. quelen* por Silfvergrip (1996).

Perdices et al. (2002) realizou um estudo filogeográfico de *Rhamdia* da América Central e determinou que *R. cinerascens* é uma linhagem independente. Posteriormente Hernandez et al. (2015) redescrevem o táxon, tornando *R. cinerascens* uma espécie válida. Ocorre nos rios transandinos do Equador.

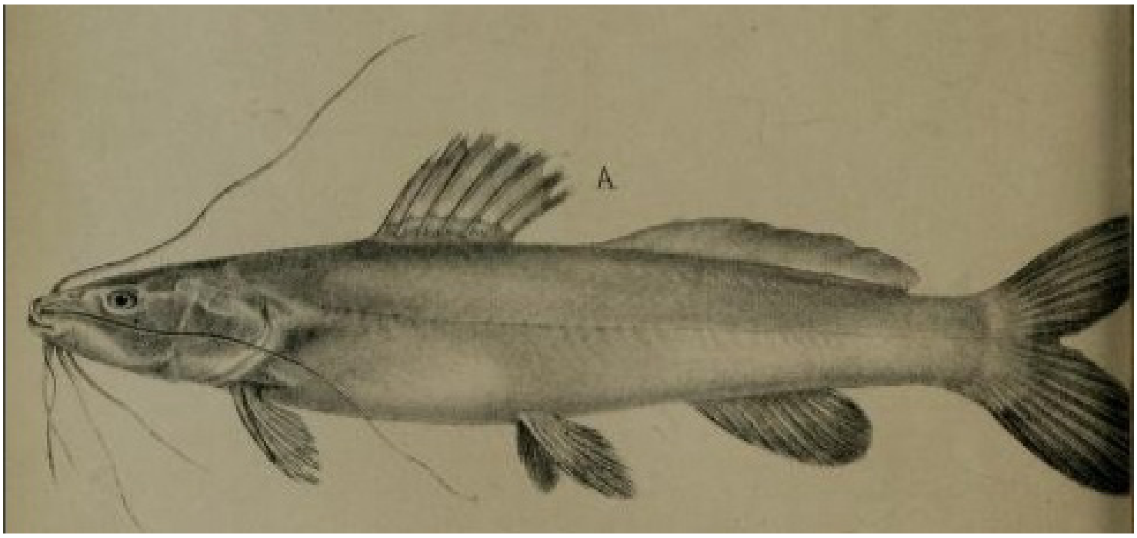

Figura 5: *Rhamdia cinerascens* ilustrada por G.H. Ford, publicado em Günther (1860).

1.2.18. *Pimelodus muelleri*

Pimelodus muelleri foi descrito por Günther (1864), tendo como localidade tipo o rio Capim, estado do Pará, Brasil. Os síntipos foram depositados no Museu Britânico de História Natural de Lonfres. Miranda Ribeiro (1911) considera um sinônimo de *R. sebae*. Silfvergrip (1996) designou o lectótipo BMNH 1849.11.8.101 e redescreveu a espécie como *Rhamdia muelleri.* Atualmente é uma espécie válida. O táxon ocorre nas bacias dos rios Amazonas, Essequibo e Orinoco.

1.2.19. *Pimelodus holomelas*

Pimelodus holomelas foi descrito por Günther (1864), coletado no rio Essequibo, Guiana. Os síntipos estão depositados no museu de História Natural de Londres. O lectótipo BMNH 1864.1.21.8 foi designado por Silfvergrip (1996).

Esta espécie foi sinonimizada em *R. sebae* por Miranda Ribeiro (1910). Günther (1864) considerava esta espécie relacionada à *R. muelleri*, porém conseguia diagnosticar as duas espécies pela nadadeira adiposa mais longa, barbilhão mais curto e cabeça mais longa em *P. holomelas*. Este táxon foi sinonimizado em *R. laukidi* por Silfvergrip (1996).

1.2.20. *Pimelodus guatemalensis*

Pimelodus guatemalensis foi descrito por Günther (1864) e coletado por Salvin no rio Huamuchal, Guatemala. Os síntipos foram depositados no Museu Britânico de Historia Natural de Londres, o lectótipo BMNH 1864.1.26.210 foi selecionado por Silfvergrip (1996). Esta espécie foi redescrita e inserida em *Rhamdia* por Jordan & Evermann (1896). Foi redescrita por Regan (1908), por Behre (1928) e por Hildebrand (1938), sendo considerada espécie válida por Hubbs (1936), Greenfield et al. (1982), Miller (1984), Bussing (1987), Burgess (1989) e Espinosa Pérez et al. (1993). Foi sinonimizada em *R. quelen* por Silfvergrip (1996), alegando que suas características morfológicas eram idênticas a *R. quelen*.

Após Silfvergrip (1996), *R. guatemalensis* foi mantida sinonímia de *R. quelen* por Bichuette & Trajano (2005) e considerada como espécie válida por Greenfield & Thomerson (1997), Weber & Wilkens (1998), Bussing (1998), Romero & Paulson (2001), Wilkens (2001), Perdices et al. (2002), Weber et al. (2003). Porém, Bockmann & Guazzelli (2003) mantém *R. guatemalensis* em *R. quelen*. Nelson et al. (2004), Miller (2006), Scharpf (2006), Matamoros et al. (2009), McMahan et al. (2013), Page et al. (2013), Angulo et al. (2013), não reconhecem *R. guatemalensis* como sinônimo de *R. quelen*, e sim como espécie válida. Então, Hernández et al. (2015), em um estudo genético e morfológico redescreve a espécie e a torna válida. Ocorre por toda a região transandina.

1.2.21. *Pimelodus wuchereri*

Pimelodus wuchereri foi descrito por Günther (1864), e coletado por Wucherer no estado da Bahia, Brasil. Os síntipos foram depositados no museu de História Natural de

Londres, e o lectótipo BMNH 1864.1.19.18 foi designado por Silfvergrip (1996). Esse táxon foi inserido em *Rhamdia* e sinonimizado em *R. quelen* por Eigenmann & Eigenmann (1888). Silfvergrip (1996) mantém a espécie como sinônimo de *R. quelen.*

1.2.22. *Pimelodus godmanni*

Pimelodus godmanni foi descrito por Günther (1864) utilizando uma série tipo de peixes coletados no México e nos rios San Geronimo e Motagua na Guatemala. Os síntipos foram depositados no Museu de Historia Natural de Londres. Silfvergrip (1996) designa o Lectótipo BMNH 1864.1.26.94. Foi redescrita e inserida em *Rhamdia* por Jordan & Evermann (1886). Foi redescrita e considerada válida por Regan (1908), por Behre (1928) e por Hildebrand (1938). Considerada sinônimo de *R. guatemalensis* por Espinosa Pérez et al. 1993. Foi sinonimizada em *R. quelen* por Silfvergrip (1996).

1.2.23. *Pimelodus micropterus*

Pimelodus micropterus foi descrita por Günther (1864), sendo coletada por Godman e Salvin no rio San Geronimo, Guatemala. O holótipo está depositado no Museu de Historia Natural de Londres identificado como BMNH 1864.1.26.92. Foi redescrita e inserida em *Rhamdia* por Jordan & Evermann (1886). Foi redescrita e considerada válida por Regan (1908), por Behre (1928) e por Hildebrand (1938). Silfvergrip (1996) questiona o estado de conservação do holótipo e não consegue inserir o exemplar em *R. laticauda*, *R. nicaraguense* ou *R. quelen*, considerando o táxon um sinônimo questionável de *R. quelen.*

1.2.24. *Pimelodus nicaraguensis*

Pimelodus nicaraguensis foi descrita por Günther (1864), coletado no lago Nicarágua, na Nicarágua. O holótipo está depositado no Museu de Historia Natural de Londres identificado como BMNH 1864.1.26.212. Foi redescrita e inserida em *Rhamdia* por Jordan & Evermann (1886). Foi redescrita e considerada válida por Regan (1908), por Behre (1928) e por Hildebrand (1938). É considerada válida por Bussing (1987) e Burgess (1989) e foi redescrita por Silfvergrip (1996). Ocorre nos rios da Costa Rica e Nicarágua.

1.2.25. *Pimelodus petenensis*

Pimelodus petenensis foi descrita por Günther (1864), coletado no lago Petén, na Guatemala. O holótipo está depositado no Museu de Historia Natural de Londres identificado como BMNH 1864.1.26.371. Foi redescrita e inserida em *Rhamdia* por Jordan &Evermann (1886). Foi redescrita e considerada válida por Regan (1908), por Behre (Carnegie Museum 1928) e por Hildebrand (1938). Considerada válida por Burgess (1989) e sinonimizada em *R. laticauda* por Silfvergrip (1996).

1.2.26. *Pimelodus hypselurus*

Pimelodus hypselurus foi descrita por Günther (1864) e coletada por M. Parzudaki no México. O holótipo está depositado no Museu de Historia Natural de Londres identificado como BMNH 1858.11.22.32. Foi redescrita e inserida em *Rhamdia* por Jordan & Evermann (1886). Foi redescrita e considerada válida por Meek (1904), por Regan (1908), por Behre (1928) e por Hildebrand (1938). É considerada válida por Burgess (1989). Foi sinonimizada em *R. laticauda* por Miller (1984) e posteriormente redescrita e mantida como sinônimo por Silfvergrip (1996).

1.2.27. *Pimelodus motaguensis*

Pimelodus motaguensis foi descrita por Günther (1864) e coletada por Salvin no rio Motagua, Guatemala. O holótipo está depositado no Museu de Historia Natural de Londres identificado como BMNH 1865.4.29.39. Foi redescrita e inserida em *Rhamdia* por Jordan & Evermann (1886). Foi redescrita e considerada válida por Regan (1908), por Behre (1928) e por Hildebrand (1938). É considerada válida por Burgess (1989). Foi sinonimizada em *R. laticauda* por Silfvergrip (1996).

1.2.28. *Pimelodus humilis*

Pimelodus humilis foi descrito por Günther (1864) e coletada na Venezuela. Os síntipos foram depositados no Museu de História Natural de Londres. O lectótipo BMNH 1965.2.19.1 foi designado por Silfvergrip (1996).

A espécie foi redescrita e inserida em *Rhamdia* por Eigenmann & Eigenmann (1890). É considerada válida por Burgess (1989). Foi redescrita e considerada válida por Silfvergrip

(1996). Ocorre nos rios costeiros da costa caribenha, aos redores de Caracas, Venezuela.

1.2.29. *Pimelodus salvini*

Pimelodus salvini foi descrita por Günther (1864) e coletada por Salvin no rio Geronimo, Guatemala. O holótipo está depositado no Museu de Historia Natural de Londres identificado como BMNH 1861.8.12.16. Foi redescrita e inserida em *Rhamdia* por Jordan & Evermann (1886). Foi redescrita e considerada válida por Regan (1908), por Behre (1928) e por Hildebrand (1938). Considerada válida por Burgess (1989). Foi sinonimizada em *R. laticauda* por Silfvergrip (1996).

1.2.30. *Pimelodus polycaulus*

Pimelodus polycaulus foi descrita por Günther (1864) e coletada por Salvin no rio Geronimo, Guatemala. O holótipo está depositado no Museu de Historia Natural de Londres identificado como BMNH 1864.1.26.93. Foi redescrita e inserida em *Rhamdia* por Jordan & Evermann (1886). Foi redescrita e considerada válida por Regan (1908), por Behre (1928) e por Hildebrand (1938). Considerada válida por Burgess (1989). Foi sinonimizada em *R. laticauda* por Silfvergrip (1996).

1.2.31. *Pimelodus baronismuelleri*

Pimelodus baronismuelleri foi descrita por Troschel (1865), coletada provavelmente nos rios da costa do Pacifico no México. Os síntipos dessa espécie estão perdidos. Silfvergrip sinonimiza este táxon em *R. quelen* porque na descrição original não possui nenhuma característica que a diferencie como uma espécie válida.

1.2.32. *Pimelodus brachypterus*

Pimelodusbrachypterus foi descrita por Cope (1867) e coletada em Orizaba, México. O holótipo está depositado na coleção da Academia de Ciências Naturais da Filadélfia identificado como ANSP 16471. Foi inserido em *Rhamdia* por Meek (1904). Esta espécie é considerada válida por Burgess (1989) e foi sinonimizada em *R. laticauda* por Silfvergrip (1996).

1.2.33. *Pimelodus managuensis*

Pimelodus managuensis foi descrita por Günther (1864) e coletada por Dow no lago Managua, Nicarágua. O holótipo está depositado no Museu de Historia Natural de Londres identificado como BMNH 1865.7.20.37. Foi redescrita por Günther (1868). Foi redescrita e inserida em *Rhamdia* por Jordan & Evermann (1886). Foi redescrita e considerada válida por Regan (1908), por Behre (Carnegie Museum 1928) e por Hildebrand (1938). Considerada válida por Burgess (1989). Foi sinonimizada em *R. nicaraguensis* por Silfvergrip (1996).

1.2.34. *Pimelodus wagneri*

Pimelodus wagneri foi descrita por Günther (1868), os exemplares foram coletados nos rios Chagres, Guajaquil e Neu-Granada, no Panamá. A série tipo foi coletada por Kner e Steindachner e identificados originalmente como *P. cinerascens.* Os síntipos foram depositados no Museu de História Natural de Viena, estão identificados como NMW 45618 e NMW 45619. *P. wagneri* foi redescrita e inserida em *Rhamdia* por Eigenmann & Eigenmann (1890). Foi redescrita e considerada válida por Meek (1904), por Regan (1908), por Behre (1928) e por Hildebrand (1938). É considerada válida por Burgess (1989). Foi sinonimizada em *R. quelen* por Silfvergrip (1996). Galvis et al. consideram *P. wagneri* como espécie válida, porém Bockmann e Guazzelli (2003) consideram este táxon sinônimo de *R. quelen.*

1.2.35. *Rhamdiacyanostigma*

Rhamdia cyanostigma foi descrita por Cope (1870) e foi coletada no rio Pebas, Peru. Os síntipos dessa espécie estão depositados na coleção da Academia de Ciências da Filadélfia identificadas como ANSP 8381-83. Foi inserida em *Pimelodella* por Ortega & Vari (1986), Burgess (1989) e Bockmann e Guazzelli (2003).

1.2.36. *Rhamdia dorsalis*

Rhamdia dorsalis foi descrita por Gill (1870) e foi coletada por Orton no rio Marañon (Peru) ou rio Napo (Equador), bacia Amazônica. O holótipo USNM 35334 está depositado no Museu Smithsonian. A espécie foi considerada válida por Ortega & Vari (1986) e Burgess (1989). O táxon foi sinonimizado em *R. quelen* por Silfvergrip (1996).

1.2.37. *Rhamdiamicrocephala*

Rhamdia microcephala Lütken (1874) e foi coletada no rio das Velhas, Brasil. Os síntipos NMW 45825 e ZMUC P29658-60 estão depositados no Museu de Historia Natural de Viena e no Museu de Zoologia da Universidade de Copenhague. Foi inserida em *Imparfinis* por Mees & Cala (1989). Foi redescrita por Miranda Ribeiro (1907). Considerada válida como *Imparfinis microcephalus* por Burgess (1989). Foi inserida em *Rhamdiopsis* por Britski (2001), considerada válida *Rhamdiopsis microcephala*por Bockmann & Guazzelli (2003), Ferraris (2007) e Bockmann & Castro (2010). Não faz parte do gênero *Rhamdia.*

1.2.38. *Rhamdia minuta*

Rhamdia minuta foi descrita por Lütken (1874) e coletada no rio das Velhas, estado de Minas Gerais, Brasil. Os síntipos ZMUC 325x, ZMUC 327x e ZMUC 328 estão depositados no Museu de Zoologia da Universidade de São Paulo. Foi redescrita por Eigenmann & Eigenmann (1890) e por Miranda Ribeiro (1911). Inserida em *Imparfinis* por Mees (1986) considerada válida como *Imparfinis minutus* por Burgess (1989), Casatti & Castro (1998), Le Bail et al. (2000), Britski (2001), Bockmann & Guazzelli (2003), Ferraris (2007), Ortega-Lara et al. (2011). Não faz parte do gênero *Rhamdia*

1.2.39. *Rhamdia bransfordii*

Rhamdia bransfordii foi descrita por Gill (1877) e coletada na região do Camp Marie Caretta, Panamá. O holótipo USNM 16674 se encontra depositado no museu do Smithsonian. Foi sinonimizada em *R. wagneri* por Eigenmann e Eigenmann (1890). Na última revisão do gênero, foi sinonimizada em *R. quelen* por Silfvergrip (1996).

1.2.40. *Pimelodus parahybae*

Pimelodus parahybae foi descrita por Steindachner (1877) e coletada no rio Paraíba do Sul, Brasil. Miranda Ribeiro (1911) inseriu a espécie em *Rhamdia.* O holótipo NMW 45852 está depositado no museu de Historia Natural de Viena. Silfvergrip (1996) sinonimizou este táxon em *R. quelen*.

1.2.41. *Pimelodus queleni cuprea*

Pimelodus queleni cuprea foi descrita por Steindachner (1877) e coletada no rio Paraíba do Sul, na cidade de Juiz de Fora, Brasil. Os síntipos estão depositados no Museu de História Natural de Viena, Silfvergrip designou o lectotype NMW 45789. A espécie foi sinonimizada em *R. quelen* por Eigenmann e Eigenmann (1890). Silfvergrip considera sinônimo de *R. quelen*.

1.2.42. *Pimelodus cuyabae*

Pimelodus cuyabae foi descrita por Steindachner (1877) e coletada em Cuiabá, Brasil. A série tipo foi depositada no Museu de História Natural de Viena e no Museu de zoologia de Munique. O lectótipo NMW 45919 foi selecionado por Silfvergrip (1996). O táxon foi sinonimizado em *R. quelen* por Eigenmann e Eigenmann (1890), Silfvergrip manteve *R. cuyabae* como sinônimo de *R. quelen.*

1.2.43. *Pimelodus knerii*

Pimelodus knerii foi descrito por Steindachner (1877) e coletado em Marabitanos, Brasil. A série tipo foi depositada no Museu de História Natural de Viena, o lote é composto por dois exemplares completamente diferentes um do outro. De acordo com a descrição original, Silfvergrip designa o lectótipo NMW 45790. Foi considerado sinônimo de *R. sebae* por Burgess (1989). Silfvergrip sinonimizou o táxon em *R. muelleri*.

1.2.44. *Pimelodus bathyurus*

Pimelodus bathyurus foi descrito por Cope (1878), coletado na região amazônica do Peru. A série tipo está depositada na coleção da Academia de Ciências Naturais da Filadélfia. Silfvergrip selecionou o lectótipo ANSP 21437. A espécie foi inserida em *Rhamdia* por Eigenmann & Eigenmann (1890). Foi considerada válida por Ortega & Vari (1986) e Burgess (1989). Silfvergrip (1996) sinonimiza *R. bathyurus* em *R. quelen* por não possuir exemplares suficientes para uma melhor análise.

1.2.45. *Pimelodus longicauda*

Pimelodus longicauda descrito por Boulenger (1887) e coletado no rio Canelos, Equador. Os síntipos BMNH 1880.12.8.100-104 estão depositados no Museu de História Natural de Londres. Foi inserido em *Rhamdia* por Eigenmann & Eigenmann (1890). Foi inserida em *Nannorhamdia* por Pearson (1937). Foi considerada como espécie válida *R. longicauda* por Ortega & Vari (1986) e Burgess (1989). O táxon foi inserido em *Imparfinis* e considerado como espécie válida *Imparfinis longicaudus* por Mees & Cala (1989).

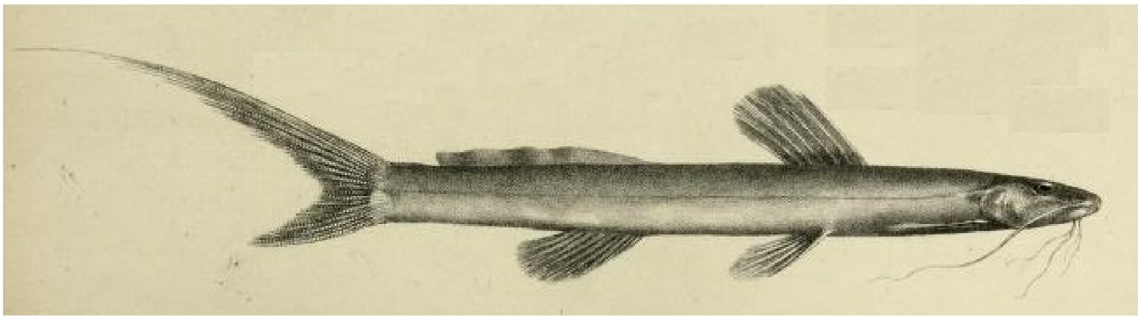

Figura 6: *Pimelodus longicauda*, retirado de Boulenger (1887), ilustrada Peter Smith.

1.2.46. *Rhamdia eriarcha*

Rhamdia eriarcha foi descrita por Eigenmann & Eigenmann (1888) no Rio Grande do Sul, Brasil. O holótipo MCZ 27272 está depositado no Museu de Zoologia Comparada da Universidade de Harvard. Considerada espécie válida como *Rhamdella eriarcha* por Malabarba (1989), Burgess (1989), Langeani (1990), Lucena & da Silva (1991), Miquelarena & Menni (1999), Bockmann & Guazzelli (2003), Ferraris (2007), Bockmann & Miquelarena (2008), Reis et al. (2014) e Bertaco et al. (2016). Ocorre na bacia do rio Jacuí. Não faz parte do gênero *Rhamdia.*

1.2.47. *Rhamdia obesa*

Rhamdia obesa foi descrita por Eigenmann e Eigenmann (1888) e coletado na cidade de Tefé, estado do Amazonas, Brasil. O holótipo MCZ 7518 está depositado no Museu de Zoologia Comparada de Harvard. Considerada espécie válida por Burgess (1989), foi sinonimizada em *R. muelleri* por Silfvergrip (1996).

1.2.48. *Rhamdia poeyi*

Rhamdia poeyi foi descrita por Eigenmann & Eigenmann (1888) e coletado por Honório no rio Tocantins, estado de Goiás, Brasil. O holótipo MCZ 8196 está depositado no Museu de Zoologia Comparada de Harvard, e encontra-se em um péssimo estado de conservação. É considera espécie válida por Burgess (1989), sendo redescrita por Silfvergrip (1996). Está espécie ocorre nos rios Mamoré (Bolívia), Napo (Equador) e Tocantins (Brasil).

1.2.49. *Rhamdia tenella*

Rhamdia tenella foi descrita por Eigenmann & Eigenmann (1888) e coletada no Lago Codajás, Amazonas, Brasil. O holótipo MCZ 7547 está depositado no Museu de Zoologia Comparada de Harvard. É considerada espécie válida por Burgess (1989). Foi sinonimizada em *R. laukidi* por Silfvergrip (1996).

1.2.50. *Rhamdia parryi*

Rhamdia parryi foi descrita por Eigenmann & Eigenmann (1888) e coletada no rio Zanaleneo, cidade de Chiapas, México. A série tipo está depositada no Museu de Zoologia Comparada de Harvard e o Lectotype: MCZ 27273 foi designado por Silfvergrip (1996). A espécie foi considerada válida por Miller (1984), Burgess (1989), Espinosa Pérez et al. (1993) e Weber e Wilkens (1998). O táxon foi sinonimizado em *R. laticauda* por Silfvergrip (1996). Atualmente é considerada espécie válida por Nelson et al. (2004), Miller (2006) e Page et al. (2013). Ocorre nos rios costeiros que deságuam no Oceano Pacifico do México e Guatemala.

1.2.51. *Rhamdella straminea*

Rhamdellastraminea foi descrita por Cope (1894) e coletada no estado do Rio Grande do Sul, Brasil. Os síntipos ANSP 21604 e 39835-36 estão depositados na coleção da Academia de Ciências Naturais da Filadélfia. Considerada válida por Burgess (1989). Foi sinonimizada em *Rhamdella eriarcha* por Malabarba (1989). Considerada como *Rhamdella eriarcha* por Langeani (1990), Bockmann & Guazzelli (2003) e Ferraris (2007). Bockmann & Miquelarena 2008 excluem este táxon de *Rhamdella* e consideram um táxon incerto de *Pimelodella* ou *Rhamdia*.

1.2.52. *Pimelodus parvus*

Pimelodus parvus foi descrito por Boulenger (1898) e coletado nos rios Santiago, Zamora e Bomboiza, Equador. Os síntipos estão depositados no Museu de Historia Natural de Londres e no Museu de Zoologia de Torino. Considerada espécie válida por Burgess (1989). Silfvergrip insere está espécie no gênero *Nannorhamdia sensu* Bussing 1970. Atualmente é considera uma espécie *Incertae sedis* em Heptapteridae por Bockmann & Guazzelli (2003) e Ferraris (2007).

1.2.53. *Rhamdia oaxacae*

Rhamdia oaxacae descrita por Meek (1902) e coletada no rio Quiotepec, Cuicatlán, Oaxaca, México. O holótipo FMNH 3716 está depositado no Museu de História Natural de Chicago. A espécie foi considerada sinônimo de *R. guatemalensis* Regan (1908). Foi considerada espécie válida por Burgess (1989). Novamente foi sinonimizada em *R. guatemalensis* por Espinosa Pérez et al. (1993). Mais recentemente, Silfvergrip (1996) sinonimizou*R. oaxacae* em *R. quelen*.

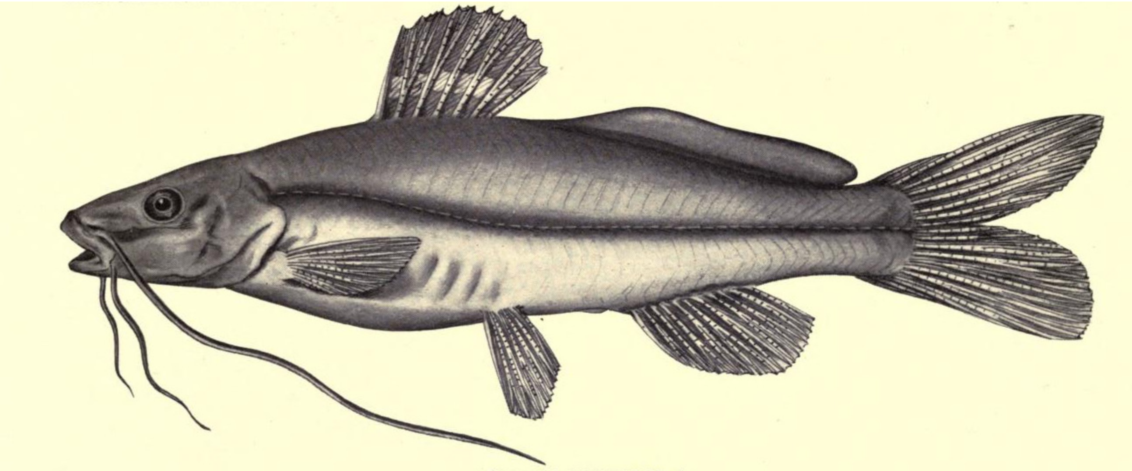

Figura 7: Ilustração de *R. oaxacae*, retirada de Meek (1902), ilustração de D.W. Douglas.

1.2.54. *Rhamdia depressa*

Rhamdia depressa foi descrita por Barbour & Cole (1906) e coletado em Ikil Cenote, próximo de Chichen-Itza, Yucatán, México. Os síntipos estão depositados no Museu de Zoologia Comparada de Harvard e no Museu de Zoologia da Universidade de Michigan.

Silfvergrip (1996) designou o lectótipo MCZ 29072. Regan (1908) sinonimiza o *R. depressa* em *R. boucardi*. Considerada espécie válida por Burgess (1989), foi sinonimizada em *R. quelen* por Silfvergrip (1996). Foi sinonimizada em *R. guatemalensis* por Scharpf (2006), porém é considerada sinônimo de *R. quelen* (Bockmann & Guazzelli 2003, Ferraris 2007).

1.2.55. *Rhamdia sacrificii*

Rhamdia sacrificii foi descrita por Barbour & Cole (1906) e foi coletada em Sacrificial Cenote, próximo a Chichen Itza, Yucatán, México. Os síntipos foram depositados no Museu de Zoologia Comparada de Havard. Silfvergrip (1996) designou o lectotype MCZ 29073. Esse táxon foi considerado sinônimo de *R. godmanni* por Regan (1906). Foi sinonimizada em *R. guatemalensis* por Burgess (1989) e por Espinosa Pérez et al. (1993). Foi sinonimizada em *R. laticauda* porSilfvergrip (1996).

1.2.56. *Rhamdia cabrerae*

Rhamdia cabrerae foi descrita por Meek (1906) coletada no lago Amatitlán, Guatemala. O holótipo FMNH 5500 foi depositado no Museu de Zoologia de Chicago. Considerado espécie válida por Burgess (1989). Foi sinonimizado em *R. laticauda* Silfvergrip (1996).

1.2.57. *Rhamdia gilli*

Rhamdia gilli Foi descrita por Starks (1906) e coletada no rio Eten, na costa do Pacifico, Peru. O holótipo USNM 53472 está depositado no Museu Smithsonian. Foi sinonimizada em *Pimelodellayuncensis* por Eigenmann (1917). Considerada espécie válida por Burgess (1989). Silfvergrip (1996) tenta associar está espécie ao gênero *Rhamdella*. O status desse táxon é incerto, necessitando uma revisão mais completa.

1.2.58. *Pimelodus boucardi*

Pimelodus boucardi foi descrito por Regan (1907) e coletado na península de Yucatán, México. O holotype BMNH 1880.7.13.33. está depositado no Museu de História Natural de Londres. Foi redescrita e inserida em *Rhamdia* por Regan (1908). Considerada espécie válida por Burgess (1989). Silfvergrip (1996) sinonimizou *R. boucardi* em *R. quelen*.

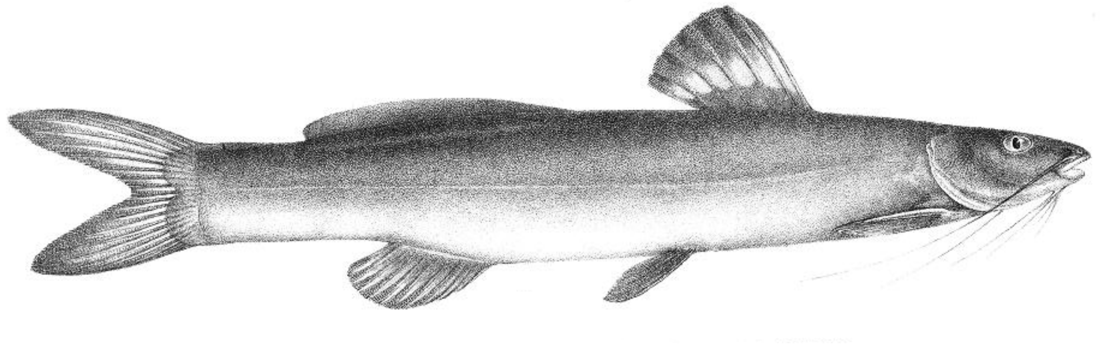

Figura 8. Ilustração de *R. boucardi* retirada de Regan (1908), ilustrada por J. Green.

1.2.59. *Pimelodus brachycephalus*

Pimelodus brachycephalus foi descrito por Regan (1907) e coletado no rio Nacasil, Guatemala. O holótipo BMNH 1875.6.9.5 está depositado no Museu de História Natural de Londres. Foi redescrita e inserida em *Rhamdia* por Regan (1908) e por Fowler (1936). Considerada espécie válida por Burgess (1989). Foi sinonimizada em *R. laticauda* por Silfvergrip (1996).

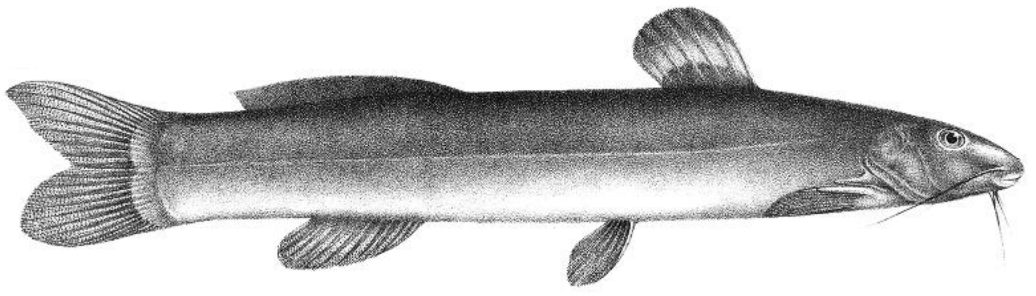

Figura 9. Ilustração de *R. brachycephalus* retirada de Regan (1908), ilustrada por J. Green.

1.2.60. *Pimelodus rogersi*

Pimelodus rogersi foi descrito por Regan (1907) e coletado por Rogers no rio Irazu, Costa Rica. Os síntipos foram depositados no Museu de História Natural de Londres, o lectótipo BMNH 1907.2.11.1 foi designado por Silfvergrip (1996). A espécie foi redescrita e inserida em *Rhamdia* por Regan (1908). Considerada espécie válida por Bussing (1987) e

Burgess (1989). Foi sinonimizada em *R. laticauda* por Silfvergrip (1996). Foi novamente considerada espécie válida por Bussing (1998), porém Bockmann & Guazzelli (2003) e Ferraris (2007) mantém *R. rogersi* em *R. laticauda.*

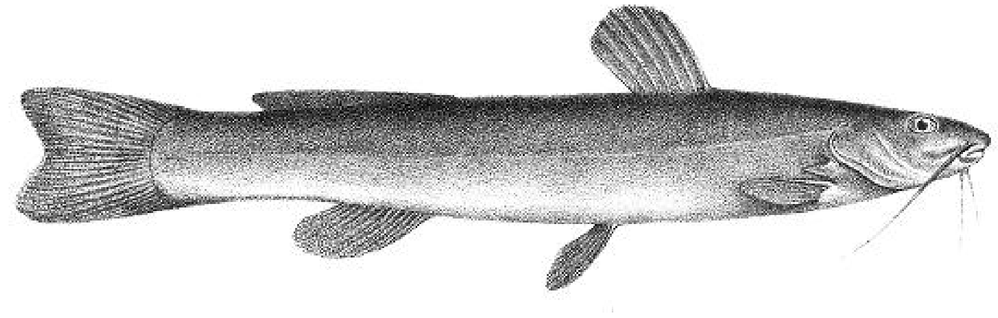

Figura 10. Ilustração de *R. rogersi* retirada de Regan (1908), ilustrada por J. Green.

1.2.61. *Rhamdia heteracantha*

Rhamdia heteracantha foi descrita por Regan (1907) e coletada por Underwood em Juan Viñas, Costa Rica. O holótipo BMNH 1907.6.28.32 está depositado no Museu de História Natural de Londres. Foi redescrita como *Rhamdia heteracantha* por Regan 1908. Silfvergrip (1996) sinonimizou *R. heteracantha* em *R. quelen*. Bussing (1998) sinonimiza em *R. guatemalensis,* porém Bockmann & Guazzelli (2003) e Ferraris (2007) mantém o táxon como sinônimo *R. quelen*

1.2.62. *Rhamdia underwoodi*

Rhamdia underwoodi foi descrita por Regan (1907) e coletada por Underwood em Juan Viñas, Costa Rica. Os síntipos foram depositados no Museu de História Natural de Londres, o lectótipo BMNH 1907.6.28.33 foi escolhido por Silfvergrip (1996). Foi redescrita como *Rhamdia underwoodi* por Regan (1908) e por Hildebrand (1938). Foi sinonimizada em *R. rogersi* por Bussing (1987). Silfvergrip (1997) sinonimiza *R. underwoodi* em *R. laticauda* Bussing (1998) volta a sinonimizar a espécie em *R. rogersi*, porém Bockmann & Guazzelli (2003) e Ferraris (2007) mantém esse táxon como sinônimo de *R. laticauda*

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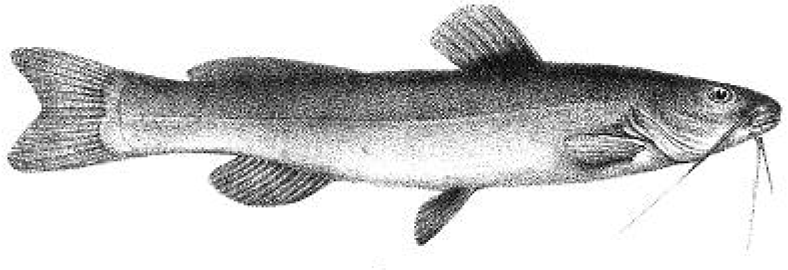

Figura 11: Ilustração de *R. underwoodi* retirada de Regan (1908), ilustrada por J. Green.

1.2.63. *Rhamdia barbata*

Rhamdia barbata foi descrito por Meek (1907) e coletada na lagoa San Francisco, Guatemala. O holótipo FMNH 5906 está depositado no Museu de Zoologia de Chicago. É considerada como espécie válida por Burgess (1989). Silfvergrip (1997) sinonimiza *R.barbata* em *R.quelen*. Bussing (1998) sinonimiza em *R. guatemalensis,* porém Bockmann & Guazzelli (2003) e Ferraris (2007) mantém esse táxon como sinônimo de *R. quelen.*

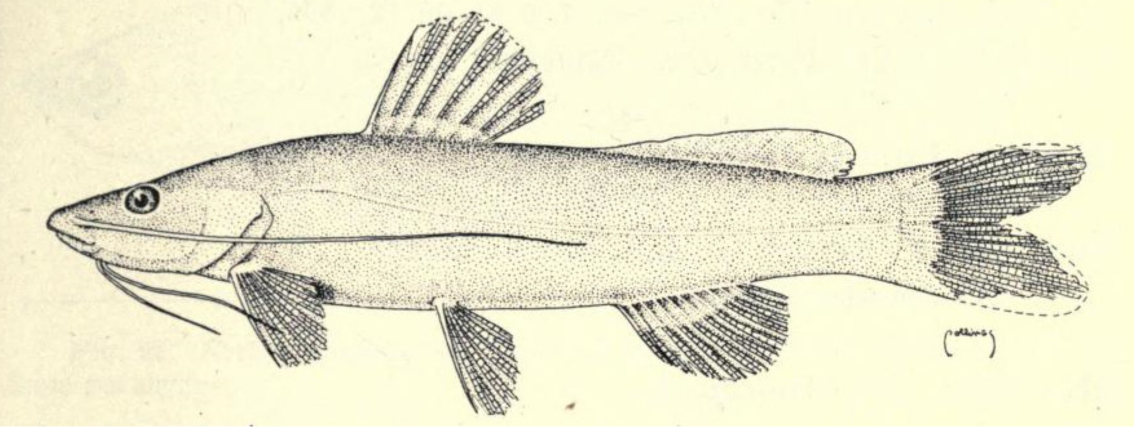

Figura 12. Ilustração de *R. barbata* retirada de Grey (1947).

1.2.64. *Rhamdia regani*

Rhamdia regani foi descrito por Meek (1907) e coletado em Turrialba, Costa Rica. O holotype FMNH 6019 foi depositado no Museu de Zoologia de Chicago. Essa espécie foi sinonimizada em *R. rogersi*. Por Meek (1914). Foi considerada válida como *R. regani* por Burgess (1989). Silfvergrip (1996) sinonimizou o táxon em *R. laticauda.*

1.2.65. *Rhamdia nasuta*

Rhamdia nasuta foi descrita por Meek (1909) e coletada em Buenos Aires de Térraba, Costa Rica. O holótipo FMNH 6480 foi depositado no museu de Zoologia de Chicago. A espécie é considerada válida por Burgess (1989). Silfvergrip (1996) sinonimiza esse táxon em *R. quelen.* Bussing (1998) sinonimiza em *R. guatemalensis,* porém Bockmann & Guazzelli (2003) e Ferraris (2007) mantém esse táxon como sinônimo de *R. quelen.*

1.2.66. *Rhamdia branneri*

Rhamdia branneri foi descrita por Haseman (1911) e coletado no rio Iguaçú, próximo a Serrinha, estado do Paraná, Brasil. O holótipo FMNH 54235 foi depositado no Museu de Zoologia de Chicago. Burgess (1989) considera a espécie válida. Silfvergrip (1996) sinonimiza o táxon em *R. quelen*. López et al. (2002) considera a espécie válida. Garavello & Shibatta 2016 redescrevem *R. branneri* que é considerada válida por Koerber et al. (2017) e é geneticamente confirmada como espécie válida por Ribolli et al. (2017).

1.2.67. *Rhamdia voulezi*

Rhamdia branner ivoulezi foi descrita por Haseman (1911) e coletado no rio Iguaçu em Porto União da Victória, estado do Paraná, Brasil. O holótipo FMNH 54238 foi depositado no Museu de Zoologia de Chicago. Burgess (1989) considera a espécie válida. Silfvergrip (1996) sinonimizou o táxon em *R. quelen*. López et al. (2002) considera a espécie válida. Garavello & Shibatta (2016) redescrevem *R. branneri* que é considerada válida por Koerber et al. (2017) e é geneticamente confirmada como espécie válida por Ribolli et al. (2017).

1.2.68. *Rhamdia eigenmanniorum*

Rhamdia eigenmanniorum foi descrita por Miranda Ribeiro (1911) e coletada no rio Paraíba do Sul e rio Macacos, Brasil. Os síntipos MCZ 7438 e MCZ 7510 estão depositados no Museu de Zoologia Comparada da Universidade de Harvard. Foi sinonimizada em *Pimelodella eigenmanni* por Eigenmann (1917). Considerada espécie válida como *Pimelodella eigenmanniorum* (Miranda Ribeiro 1911) por Bockmann & Guazzelli (2003) e

Ferraris (2007). Ocorre no rio Paraíba do Sul e nos rios costeiros do estado do Rio de Janeiro, Brasil. Não faz parte do gênero *Rhamdia.*

1.2.69. *Rhamdia mounseyi*

Rhamdia mounseyi foi descrita por Regan (1913) e coletada por Mounsey no rio Ucayali, Peru. Os síntipos foram depositados no Museu de História Natural de Londres, o lectótipo BMNH 1913.7.30.13 foi escolhido por Silfvergrip (1996). Foi considerada válida por Ortega & Vari (1986), Burgess (1989). Foi sinonimizada em *R. quelen* por Silfvergrip (1996).

1.2.70. *Rhamdia holomelas rupununi*

Rhamdia holomelas rupununi foi descrita por Fowler (1914) como uma subespécie, foi coletada no rio Rupununi, Guiana. O holótipo ANSP 39339 foi depositado no museu da Academia de Ciências Naturais da Filadélfia. Foi sinonimizada em *R. foina* por Mees (1974) e mantida como sinonímia por Silfvergrip (1996).

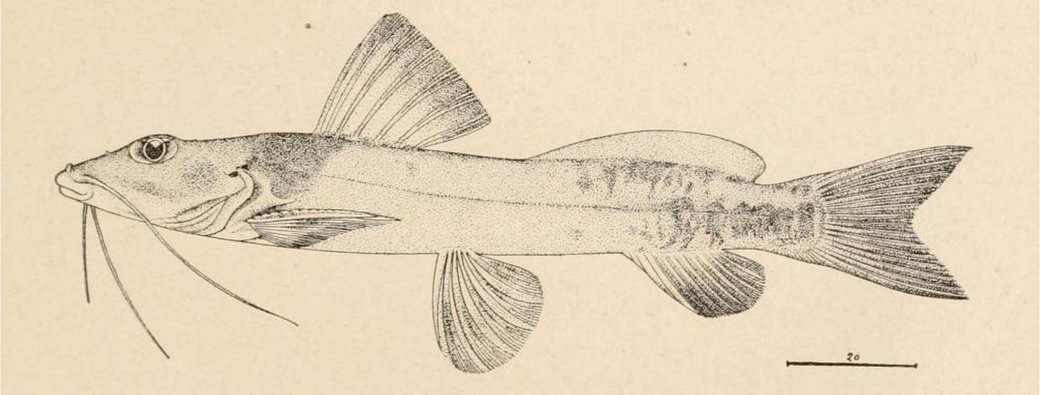

Fig. 11.—*Rhamdia holomelas rupununi* Fowler . (Type.)

Figura 13. Ilustração de *R. holomelas rupununi* retirada de Fowler (1914).

1.2.71. *Rhamdia riojae*

Rhamdia riojae foi descrita por Fowler (1914) e coletada em Rioja, próximo a Moyabamba e Baka Puerto, próximo rio Huallagua, Peru. O holótipo ANSP 21101 foi depositado no museu da Academia de Ciências Naturais da Filadélfia. Foi redescrita por Eigenmann & Allen (1942). A espécie é considerada válida por Ortega & Vari (1986) e Burgess (1989). Foi sinonimizada em *R. quelen* por Silfvergrip (1996).

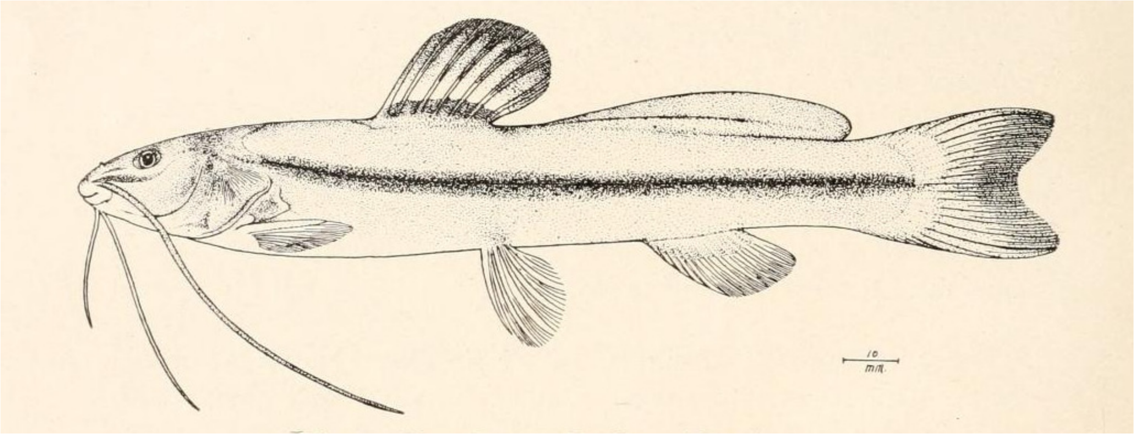

Figura 14. Ilustração de *Rhamdia riojae* retirada de Fowler (1914).

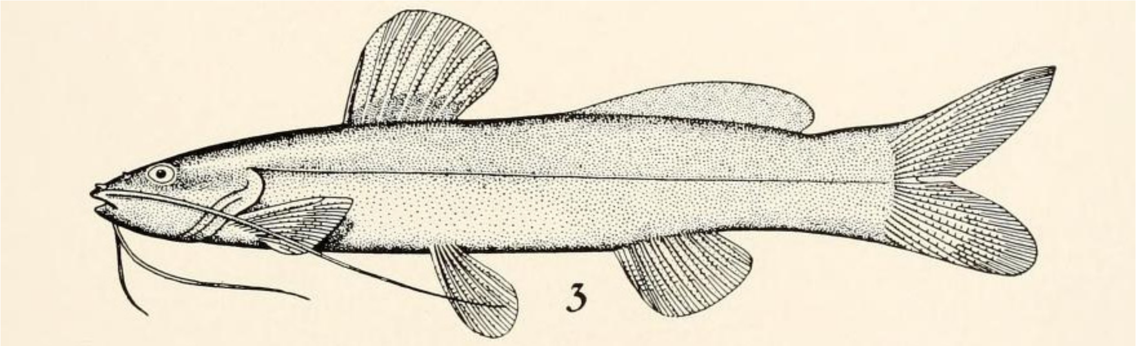

Figura 15: Ilustração de *Rhamdia riojae* retirada de Eigenmann & Allen (1942).

1.2.72. *Rhamdia ortoni*

Rhamdia ortoni foi descrita por Fowler (1914) e coletada por James Orton na Amazônia peruana. A descrição foi baseada em um único exemplar, o holótipo ANSP 21928 foi depositado no museu da Academia de Ciências Naturais da Filadélfia. Considerada como espécie válida por Ortega & Vari (1986) e Burgess (1989). Foi sinonimizada em *R. quelen* por Silfvergrip (1996).

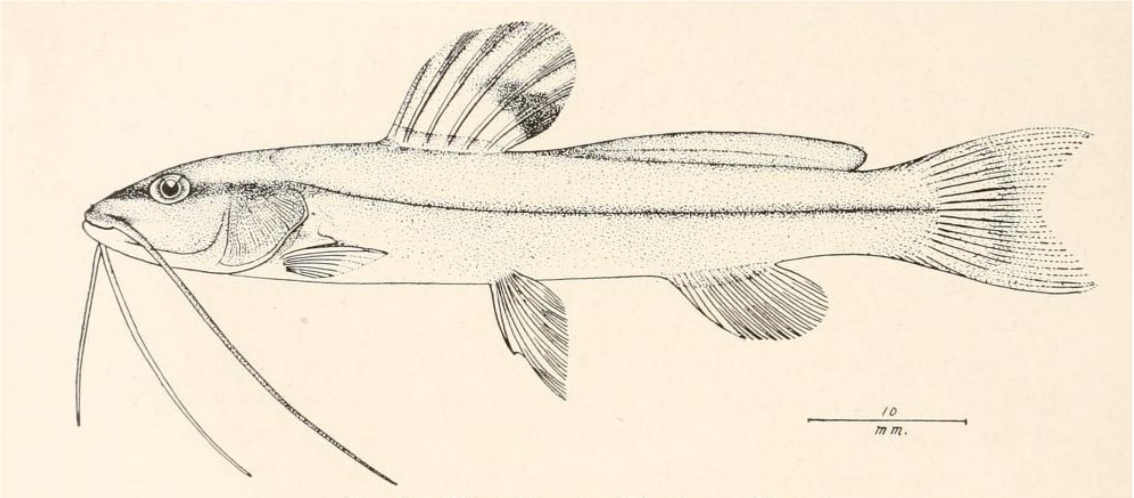

Figura 16: Ilustração de *R. ortoni* retirada de Fowler (1914).

1.2.73. *Rhamdia microps*

Rhamdia microps descrita por Eigenmann (Eigenmann & Fisher 1917) e coletada em Uruguaiana, estado do Rio Grande do Sul, Brasil. O holótipo FMNH 58285 está depositado no museu de Zoologia de Chicago. Considerada espécie válida por Burgess (1989), sinonimizada em *R. quelen* por Silfvergrip (1996).

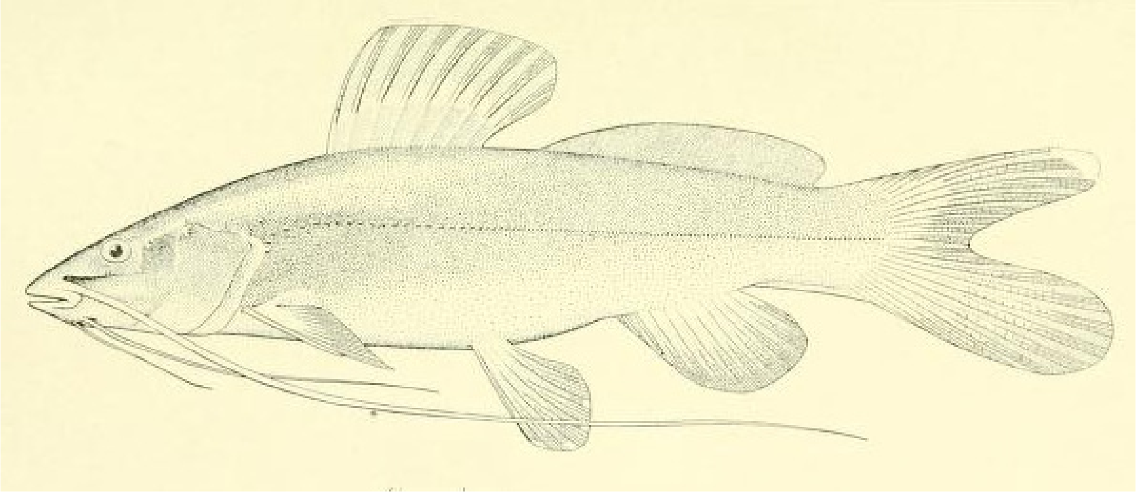

Figura 17: Ilustração de *R. microps* retirada de Ortega & Vari (1986).

1.2.74. *Rhamdia guairensis*

Rhamdia guairensis foi descrita por Eigenmann (1920) e coletada no rio Guaire, Caracas, Venezuela. Os síntipos foram depositados no museu da Universidade da Indiana e posteriormente transferidos para ao Museu da Academia de Ciências da Califórnia, Silfvergrip (1996) designou o Lectotype CAS 76655. Considerada espécie válida por Burgess (1989). Foi sinonimizada em *R. humilis* por Silfvergrip (1996).

1.2.75. *Rhamdia pubescens*

Rhamdia pubescens foi descrita por Miranda Ribeiro (1920) e coletada em Urucum, próximo a Corumbá, estado do Mato Grosso, Brasil. A série tipo foi depositada no Museu Nacional do Rio de Janeiro. O lectótipo MNRJ 925A foi designado por Silfvergrip (1996). Miranda Ribeiro (1920) associa esta espécie a *R. hilarii*. É considerada válida por Burgess (1989). Silfvergrip sinonimiza este táxon em *R. quelen*.

1.2.76. *Silurus rivularis*

Silurus rivularis foi descrito por Larrañaga (1923) e provavelmente foi coletado no país Uruguai. Não existe nenhum espécime depositado em coleção e a descrição não consegue definir a espécie. Devincenzi (1925) sinonimiza a espécie em *R. quelen*. Silfvergrip (1996), além de sinonimizar o táxon em *R. quelen*, designa para a espécie o neótipo NRM 16091, coletado rio Samiria, entre Caño Pastos e Hamburgo, Departamento de Loreto, Peru.

1.2.77. *Silurus novemradiatus*

Silurus novemradiatus foi descrito por Larrañaga (1923) e corresponde ao *Silurus rivularis*. Foi coletado no país Uruguai, não existe tipo preservado nem ilustração descrita. Considerada sinônimo *Rhamdia quelen* por Devincenzi (1925) e por Silfvergrip (1996).

1.2.78. *Rhamdia micayi*

Rhamdia micayi foi descrita por Eigenmann (1924) em Pearson (1924) e coletada no rio Popoi, rio Colorado, em Espia, na Bolívia. Os síntipos CAS 76656, 76657, 76658 estão depositados no museu. É considerada espécie válida por Burgess (1989). Silfvergrip (1996) considera este táxon sinônimo de *Rhamdia quelen.*

1.2.79. *Caecorhamdiaurichi*

Caecorhamdiaurichi foi descrito por Norman (1926) e coletada em um poço no interior da caverna Guacharo, Trinidad. Os síntipos foram depositados no Museu de Historia Natural de Londres. O Lectotype: BMNH 1926.7.28.1-2 foi selecionado por Silfvergrip (1996). Foi inserida no gênero *Rhamdia* por Mees (1974), que designou *C. urichi* como *Rhamdiaquelenurichi*. Silfvergrip (1996) sinonimiza a espécie em *R. quelen*, o autor não reconhece caracteres troglobóficos para o reconhecimento de espécies. Foi mantida em *R. quelen* por Romero & Paulson (2001). É considerada espécie válida por Bichuette & Trajano (2005) e Proudlove (2006), porém segue-se Bockmann & Guazzelli (2003) que mantiveram esse táxon em *R. quelen*.

1.2.80. *Rhamdiaalfaroi*

Rhamdiaalfaroi foi descrita por Fowler (1932) e coletada em Escobal, Costa Rica. O holótipo ANSP 53934 foi depositado na coleção da Academia de Ciências Naturais da Filadélfia. A espécie é considerada válida por Burgess (1989). Foi sinonimizada em *R. nicaraguensis* por Silfvergrip (1996) e mantida por Bussing (1998).

1.2.81. *Rhamdia guatemalensis muriei*

Rhamdia guatemalensis muriei foi descrita por Hubbs (1935) coletada em uma área alagada de Uaxactun, Petén, Guatemala. O holótipo UMMZ 97881 foi depositado no Museu de Zoologia da Universidade de Michigan. Sinonimizada em *R. guatemalensis* por Burgess (1989). A espécie foi sinonimizada em *R. quelen* por Silfvergrip (1996).

1.2.82. *Rhamdia amatitlanensis*

Rhamdia amatitlanensis foi descrita por Fowler (1936) e coletada por Schauensee em um arroio do lago Amatitlan, Guatemala. O holótipo ANSP 64136 está depositado na coleção da Academia de Ciências Naturais da Filadélfia. Espécie considerada válida por Burgess (1989). Foi sinonimizada em *R. laticauda* por Silfvergrip (1996).

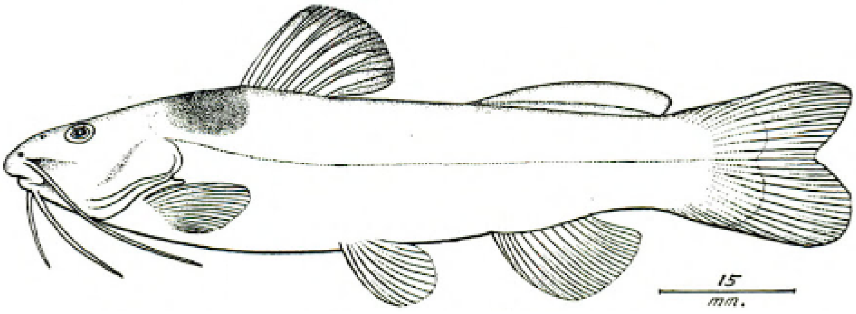

Figura 18: Ilustração de *Rhamdia amatitlanensis* retirada de Fowler (1936).

1.2.83. *Rhamdia guatemalensis decolor*

Rhamdia guatemalensis decolor foi descrita por Hubbs (1936) como subespécies de *R. guatemalensis* e coletada na caverna San Bulha, Motul, Yucatán, México. O holótipo UMMZ 102217 está depositado foi depositado no Museu de Zoologia da Universidade de Michigan. Sinonimizada em *R. guatemalensis* por Burgess (1989). Sinonimizada em *R. quelen* por Silfvergrip (1996). Foi novamente sinonimizada em *R. guatemalensis* por Romero & Paulson (2001) e Scharpf (2006). Porém, segue-se Bockmann & Guazzelli (2003) que mantiveram esse táxon em *R. quelen*.

1.2.84. *Rhamdia guatemalensis stygaea*

Rhamdia guatemalensis stygaea foi descrita por Hubbs (1936) como subespécies de *R. guatemalensis* e coletada na caverna San Isidro Cave, Salar Colony, near Merida, Yucatán, Mexico. O holótipo UMMZ 102218 está depositado foi depositado no Museu de Zoologia da Universidade de Michigan. Sinonimizada em *R. guatemalensis* por Burgess (1989). Sinonimizada em *R. quelen* por Silfvergrip (1996). Foi novamente sinonimizada em *R. guatemalensis* por Romero & Paulson (2001) e Scharpf (2006). Porém, segue-se Bockmann & Guazzelli (2003) que mantiveram esse táxon em *R. quelen*.

1.2.85. *Rhamdia saijaensis*

Rhamdia saijaensis foi descrita por Rendahl (1941) e coletado no rio Saija, Colômbia. O holótipo NRM 10675 está depositado no Museu de Historia Natural de Estocolmo. O táxon foi sinonimizado em *R. quelen* por Silfvergrip (1996). Hernandez et al. (2015) redescrevem a espécie, tornando-a válida.

1.2.86. *Rhamdella wolfi*

Rhamdella wolfi foi coletada por Fowler (1941) no rio Choró, estado do Ceará, Brasil. O holótipo ANSP 69388 está depositado na coleção da Academia de Ciências Naturais da Filadélfia. Inserida em *Rhamdia* por Burgess (1989). Considerada como *Rhamdiawolfi* por Bockmann & Guazzelli (2003) e Ferraris (2007). Inserida no gênero *Pimelodella* por Bockmann & Miquelarena (2008). Ocorre no rio Choró, Brasil. Não faz parte do gênero *Rhamdia.*

1.2.87. *Rhamdia duquei*

Rhamdia duquei foi descrita por Eigenmann & Pearson (em Eigenmann & Allen 1942) e coletada no rio Urubamba, Santa Ana, Peru. Os síntipos CAS-SU 57895, no mesmo lote está o holótipo, foram depositados no na coleção da Academia e Ciências da Califórnia. Espécie considerada válida por Ortega & Vari (1986) e Burgess (1989). Silfvergrip sinonimiza esse táxon em *R. quelen.*

1.2.88. *Rhamdia sebae martyi*

Rhamdia sebae martyi foi descrita por Güntert (1942) e coletada no riacho Canâwé, Departamento de Ita, Paraguai. O holótipo NMBA 5279 foi depositado no Museu de História Natural de Basel. Espécie considerada válida por Burgess (1989). Foi sinonimizada em *R. quelen* por Silfvergrip (1996).

1.2.89. *Nannorhamdia benedettii*

Nannorhamdia benedettii descrita por Fernández-Yépez& Martín Salazar (1952) e coletado em Quebrada Ojo de Agua, Baruta, Estado Miranda, Venezuela. O holótipo MHNLS 1672 está depositado no Museu de História Natural La Salle, Caracas. Sinonimizado em *Imparfinisbenedettii* por Mees & Cala (1989) e Burgess (1989). Foi sinonimizado em *R. humilis* por Silfvergrip (1996).

1.2.90. *Rhamdia lehmanni*

Rhamdia lehmanni foi descrito por Dahl (1961) e coletado no em um pequeno tributário do rio Guayabero, Colômbia. O holótipo está destruído, os parátipos ICNMHN 358 estão depositados no Museu de História Natural da Faculdade de Bogotá. Silfvergrip (1996) sinonimizou esta espécie em *R. quelen* sem analisar a série tipo apenas analisando a descrição original.

1.2.91. *Rhamdia luigiana*

Rhamdia luigiana foi descrito por Villa (1977) e coletado no lago Nicarágua, departamento de Granada, Nicarágua. O holótipo USNM 217535 está depositado no museu Smithsonian. Silfvergrip (1996) sinonimizou a espécie em *R. nicaraguensis*.

1.2.92. *Rhamdia laticauda typhla*

Rhamdia laticauda typhla foi descrito por Greenfield, Greenfield & Woods (1982), foi coletada em uma caverna na montanha Pine Ridge, em Las Cuevas, Belize. O holótipo FMNH 71605 está depositado no Museu de Campo de Chicago. É considerado uma subespécie de *R.laticauda*por Greenfield & Thomerson 1997, Weber & Wilkens 1998, Romero & Paulson 2001, Bichuette & Trajano 2005, Proudlove 2006. Silfvergrip (1996) sinonimizou o táxon em *R. laticauda.* Bockmann & Guazzelli (2003), Scharpf (2006) e Ferraris (2007) mantém o táxon sinonimizado em *R. laticauda.*

1.2.93. *Rhamdia reddelli*

Rhamdia reddelli foi descrita por Miller (1984) e coletada em Cueva del Nacimiento no rio San Antonio, em Acatlán, México. O holótipo UMMZ 211164 está depositado no Museu de Zoologia da Universidade de Michigan. Na revisão do gênero, Silfvergrip (1996) sinonimizou o táxon em *R.laticauda.* É considerado espécie válida por Espinosa Pérez et al. (1993), Romero & Paulson 2001, Wilkens 2001, Nelson et al. 2004, Proudlove 2006, Scharpf 2006, Ferraris 2007, Page et al. 2013. A espécie é considerada válida, ocorrendo nas cavernas da bacia do rio Papaloapan, México.

1.2.94. *Brachyrhamdia marthae*

Brachyrhamdia marthae foi descrita por Sands & Black (1985), existem dúvidas quanto a localidade tipo do táxon, que pode ser o Peru. O holótipo RMNH 29424 está depositado no Museu Nacional de História Natural de Leiden, Holanda. Inserida no gênero *Pimelodella* por Burgess (1989). Foi inserida em *Rhamdia* por Zarske (2003). Considerada como espécie válida *Brachyrhamdia marthae* por Bockmann & Guazzelli (2003), Ferraris (2007), Slobodian & Bockmann (2013), Sarmiento et al. (2014), Slobodian & Bockmann (2016). Ocorre nas drenagens dos rios Juruá, Mamoré e Madeira, no Brasil, Bolívia e Peru. Não faz parte do gênero *Rhamdia.*

1.2.95. *Rhamdia zongolicensis*

Rhamdia zongolicensis foi descrita por Wilkens (1993) na caverna de Ostoc, na Serra de Zongolica, no estado de Veracruz, México. O holótipo ZMH 8249 está depositado no Museu de Zoologia da Universidade de Hamburgo. Silfvergrip (1996) sinonimizou o táxon em *R. laticauda.* Foi mantida como sinônimo por Bockmann & Guazzelli (2003), Weber et al. (2003) e Ferraris (2007). Foi considerada sinônimo de *R. reddelli* por Miller (2006). É considerada espécie válida por Wilkens (1993), Weber & Wilkens (1998), Romero & Paulson (2001), Wilkens (2001), Nelson et al. (2004), Bichuette & Trajano (2005), Proudlove (2006), Page et al. (2013). Atualmente é considerada válida como *R. zongolicensis,* ocorrendo nas cavernas dos rios do estado de Veracruz, México.

1.2.96. *Rhamdia itacaiunas*

Rhamdia itacaiunas foi descrita por Silfvergrip (1996) durante a revisão sistemática do gênero*Rhamdia.* Foi coletada no Igarapé Repartimento na drenagem do rio Tocantins, estado do Amazonas, Brasil. O holótipo INPA 7985 está depositado na coleção do Instituo de Pesquisa da Amazônia. Ocorre no médio rio Tocantins, Brasil.

1.2.97. *Rhamdia jequitinhonha*

Rhamdia Jequitinhonha foi descrita por Silfvergrip (1996) e coletada no rio Araçuaí, Santa Rita, estado de Minas Gerais, Brasil. O holótipo MZUSP 38630 está depositado no Museu de Zoologia da Universidade de São Paulo. Espécie considerada válida por Bockmann & Guazzelli (2003), Ferraris (2007) e Garavello & Shibatta (2016). Ocorre na bacia do rio Jequitinhonha, Brasil.

1.2.98. *Rhamdiaxetequepeque*

Rhamdiaxetequepeque foi descrita por Silfvergrip (1996) e coletada no rio Jequetepeque, em Chilete, Peru. O holótipo ROM 70112 está depositado no Museu Real de Ontário. É considerada espécie válida por Bockmann & Guazzelli (2003) e Ferraris (2007). Ocorre no rio Jequetepeque, Peru.

1.2.99. *Rhamdiamacuspanensis*

Rhamdiamacuspanensis foi descrita por Weber & Wilkens (1998) e coletada nas grutas de Agua Blanca, no estado de Tabasco, México. O holótipo ZMH 8874 está depositado na coleção científica do Instituto Johann Heinrich von Thünen em Hamburgo. É considerada espécie válida por Romero & Paulson (2001), Weber et al. (2003), Nelson et al. (2004), Bichuette & Trajano (2005), Miller (2006), Proudlove (2006), Ferraris (2007), Page et al. (2013).

1.2.100. *Rhamdia laluchensis*

Rhamdia laluchensis foi descrita por Weber, Allegrucci & Sbordoni (2003) e foi coletada nas águas subterrâneas do sistema de La Lucha, município de Ocozocoautla, Chiapas, México. O holótipo ZMH 9373 está depositado na coleção cientifica do Instituto Johann Heinrich von Thünen em Hamburgo. A espécie é considerada válida por Bichuette & Trajano (2005), Proudlove (2006), Ferraris (2007) e Page et al. (2013). Ocorre nos rios subterrâneos de Chiapas, México.

1.2.101. *Rhamdia guasarensis*

*Rhamdia guasarensis*descrita porDo Nascimiento, Provenzano & Lundberg 2004, coletada em Surgencia del Tigre, Cerro Yolanda, bacia do rio Guasare, Serra do Perijá, Estado de Zulia, Venezuela. O holótipo MBUCV-V 29604 está depositado no Museu de Biologia, Universidade Central de Venezuela. Espécie considerada válida por Bichuette & Trajano (2005) e Ferraris (2007). É uma espécie troglobófica, ocorre na bacia do rio Guasare, Venezuela.

1.2.102. *Rhamdia enfurnada*

Rhamdia enfurnada foi descrita por Bichuette & Trajano (2005) coletada na Gruta do Enfurnado, bacia do rio São Francisco, Povoado de Descoberto, Município de Coribe, Serra do Ramalho, estado da Bahia, Brasil. O holótipo MZUSP 87776 está depositado Museu de Zoologia da Universidade de São Paulo.

1.2.103. Espécies de *Rhamdia* consideradas *incertae sedis:*

Existem táxons que foram relacionados ao gênero *Rhamdia* que devem ser considerados *incertae sedis.* Esses táxons não possuem informações suficientes que possam ser identificados como um membro do gênero. Esses nomes muitas vezes não possuem tipos conhecidos ou esses espécimes não estão em condições; alguns casos não apresentam localidade tipo definida e suas descrições ou ilustrações originais não possuem características suficientes para conectar o táxon em *Rhamdia.*

1.2.103.1 *Silurus erythropterus*

Silurus erythropterus foi descrito por Bloch (1794) e tem como localidade a América. Os síntipos ZMB 3048 e ZMB 8786 estão depositados no Museu de Zoologia de Berlim. DE acordo com a descrição e a ilustração original, este táxon não pode ser considerado Rhamdia. A ilustração original é um peixe vermelho com a nadadeira caudal lobada, com os lobos muito pontiagudos e com oito barbilhões, o que não ocorre em *Rhamdia*. Na descrição original é mencionado que as nadadeiras são vermelhas, o que não ocorre e nenhuma espécie de *Rhamdia* conhecida. A espécie é redescrita por Shaw (1804) e é chamado de pelo autor de Siluro de nadadeira vermelha; é indica como características marcantes as nadadeiras vermelhas e oito barbilhões, de acordo com o autor a espécie ocorre na América do Sul, Foi inserido em Pimelodus por Cuvier (1826). Sinonimizado em *Pimelodus catus* por Lacépède (1830). Sinonimizado em *Macronesaleppensis* (uma espécie asiática) por Günther (1864). De certa forma, *Silurus erythropterus* nunca foi relacionado à *Rhamdia*, Silfvergrip (1996) não trata desse táxon em sua revisão do gênero e Ferraris (2007) trata o táxon como sinônimo questionável de *Rhamdia quelen*.

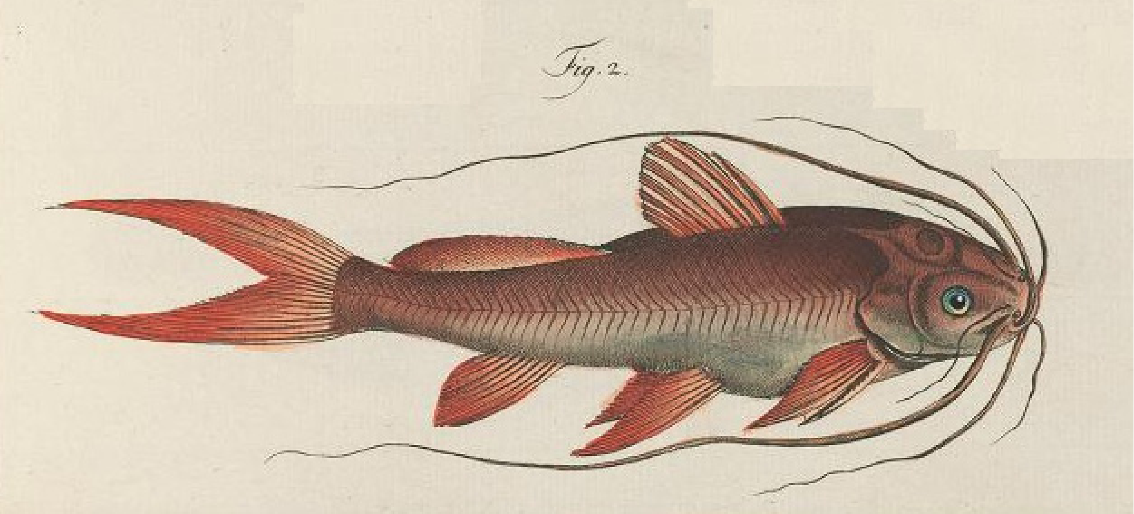

Figura 20: Ilustração original de *Silurus erythropterus.*

2.102.2. *Silurus quadrimaculatus*

Silurus quadrimaculatus foi descrito por Bloch (1794), tendo como localidade tipo a América. O holótipo ZMB 2944 está depositado no museu de Zoologia de Berlim e é considerado perdido. Foi inserido em *Pimelodus quadrimaculatus*por Burgess (1989). É considerado sinônimoquestionável de Rhamdia quelen por Silfvergrip (1996), Bockmann & Guazzelli (2003) e Ferraris (2007).

Como o holótipo está perdido e a localidade tipo é inexistente, as únicas informações que restam sobre o táxon são a descrição e a ilustração originais, e ambas chamam a atenção para quatro manchas na cabeça do peixe, característica que determina seu nome. Por estas características não podemos inserir o táxon em *Rhamdia*, muito menos como sinônimo de *R. quelen* como determinou Silfvergrip (1996). Dessa forma este táxon deve ser excluído do gênero *Rhamdia.*

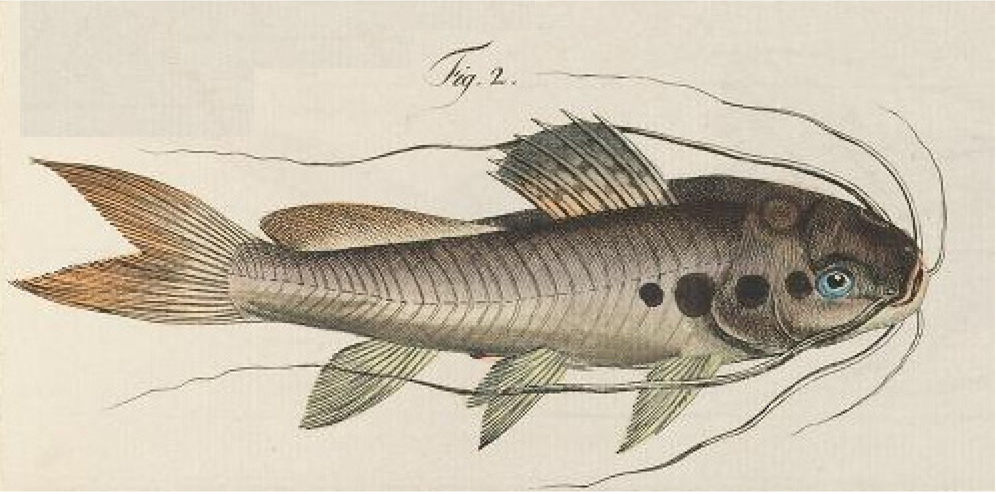

Figura 21: Ilustração original de *Silurus quadrimaculatus.*

1.2.102.3. *Pimelodus argentinus*

Pimelodus argentinus foi descrito por Humboldt (1821) e possivelmente foi coletado no rio Magdalena, Chilloa, Colômbia. Não existe tipo conhecido. Eigenmann & Eigenmann (1888) consideram este táxon como espécie duvidosa. É considerada espécie válida por Burgess (1989) e espécie duvidosa por Nico (2001). Possivelmente não é *Rhamdia*, na descrição original da espécie os espinhos das nadadeiras dorsal e peitoral não possuem serras, e até o momento, todas as espécies de *Rhamdia* possuem serras no espinho da nadadeira peitoral.

1.2.102.4. *Pimelodus velifer*

Pimelodus velifer foi descrita por Humboldt (1821) e coletada no rio Magdalena, Colômbia. Não possui espécime tipo. Considerada válida por Burgess (1989). Status considerada incertae por Nico (2001) e considerada espécie inquirenda na família Heptapteridae por Bockmann & Guazzelli (2003), Ferraris (2007).

1.2.102.5. *Pimelodus namdia*

Pimelodus namdia foi mencionado pela primeira vez por Cuvier (1829) em uma nota de rodapé em alusão a ilustração de Macgrivous (17). A localidade tipo do táxon nunca foi determinada. Silfvergrip (1996) não reconhece a ilustração como o holótipo da espécie e designa o neótipo NRM 16091 (o mesmo neótipo de *R. quelen*). Silfvergrip (1996) sinonimiza o táxon em *R. quelen*. Este táxon não possui localidade tipo, a descrição não é suficiente e o desenho, que deveria ser considerado o holótipo da espécie, deixa muitas dúvidas se o táxon possa ser uma *Rhamdia*.

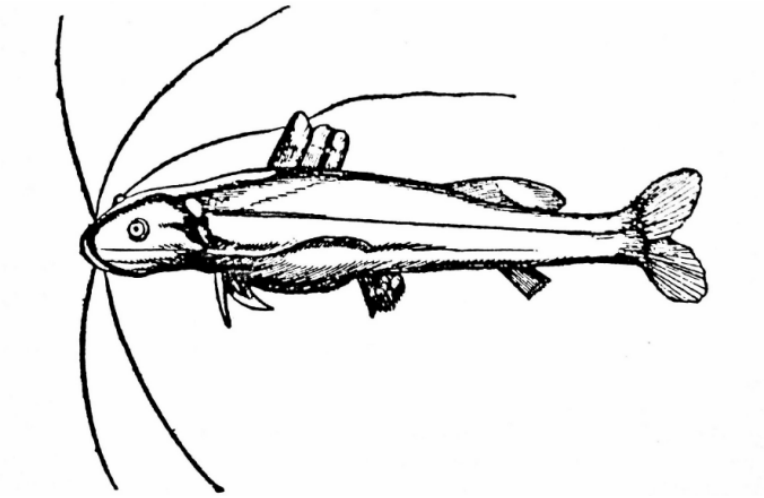

Figura 22: A "nhamdia" de Margravius (1648).

1.2.102.5. *Rhamdia javanica*

Rhamdia javanica descrita por Bleeker (1858) e coletada em Java. É considera espécie inquirenda em Siluriformes (Ferraris 2007, Kottelat 2013).

1.2.102.6. *Silurus sapipoca*

Silurus sapipoca foi descrita por Natterer (1858), não possui localidade tipo e nem tipo depositado. Eigenmann e Eigenmann (1888) sinonimizaram o táxon em *R. quelen*. Silfvergrip (1996) não menciona a espécie em sua revisão do gênero.

1.2.102.7. *Rhamdia schomburgkii*

Rhamdia schomburgkii Bleeker 1858, não possuí localidade tipo e nem mesmo, espécimes tipos preservados. Silvergrip (1996) não menciona a espécie em sua revisão. É considerada válida por Burgess (1989). Não tem como determinar se pode ser considerada *Rhamdia*.

1.3. Silfvergrip (1996) e a sua revisão do gênero *Rhamdia*

Silfvergrip foi o primeiro a apresentar uma longa e completa revisão do gênero *Rhamdia*. O autor analisa 2.050 espécimes ao longo de toda a distribuição do gênero, revisando todos os espécimes tipos possíveis e analisando todas as descrições originais. Suas análises foram realizadas utilizando a morfologia externa dos espécimes e alguns poucos caracteres osteológicos.

Esse estudo traz algumas importantes contribuições, como a diagnose mais acurada e uma completa descrição morfológica e osteológica do gênero. O autor ainda descreve um extensivo histórico das espécies relacionadas à *Rhamdia,* situando ao longo da história toda a complexidade do gênero. Como principal resultado, Silfvergrip transforma os 111 nomes relacionados à *Rhamdia* em apenas 11 espécies válidas: *Rhamdia foina* (Muller & Troschel) 1849; *Rhamdia humilis* (Günther) 1864; *Rhamdia itacaiunas* Silfvergrip 1996; *Rhamdia jequitinhonha* Silfvergrip 1996; *Rhamdia laticauda* (Kner) 1857; *Rhamdia laukidi* Bleeker 1858; *Rhamdia muelleri* Günther 1864; *Rhamdia nicaraguensis* (Günther) 1864; *Rhamdia poeyi* Eigenmann & Eigenmann, 1888; *Rhamdia quelen* (Quoy& Gaimard) 1794.

Toda essa extensa revisão é baseada em um conceito de espécie bem definido pelo autor, levando em consideração um conceito tipológico, onde é reconhecida uma determinada espécie por um conjunto único de estados de caracteres, levando em consideração sua variação intraespecífica. Nesta extensa revisão sãoidentificadasduas “superespécies”: *Rhamdialaticauda*, abrangendo 18 sinonímias e ocorrendo ao longo de toda a América Central; e a surpreendente *Rhamdia quelen*, abrigando 47 sinonímias e ocorrendo em toda a região neotropical.

Apesar do trabalho de Silfvergrip (1996) ser muito extenso e bem fundamentado, o autor comete muitos erros, começando pelas razoáveis descrições e diagnoses das espécies, sendo útil para alguns táxons e muito confusa para outros. Mas o grande erro do autor é referente à espécie *Rhamdia quelen* e suas sinonímias. A determinação dessa superespécie é envolta de muita controvérsia.

Foram analisadas cerca de 980 espécimes referente à *R. quelen* provenientes de quase toda a região neotropical, sendo encontradas extensas variações em todos os caracteres analisados. Porém, para Silfvergrip, toda variação encontrada está relacionada a diferenças populacionais influenciadas por fatores ambientais. O autor ainda reconhece que certos caracteres entre populações muito distantes geograficamente podem apresentar variação morfológica muito dispares. Porém, quando são analisadas populações ao longo dessa distribuição, o que se observa é uma gradação dessas características, descartando a possibilidade de separar as formas distantes.

Toda a análise referente à espécie *R. quelen* foi suportada pela estatística de componentes principais e em gráficos de regressão linear. Porém, é nítido e notório que os dados usados por Silfvergrip foram tratados de uma forma equivocada e/ou interpretados com um grande viés. O gráfico de componentes principal não foi mostrado ao longo do trabalho e os gráficos de regressão demostram essa total falta de critérios. Todos os 980 indivíduos de *R. quelen* são analisados no gráfico sem distinção de população, localidade, morfótipo ou qualquer outro tratamento. Dessa maneira, não é possível observar ou testar possíveis diferenças entre as populações analisadas.

Toda essa grande variação observada por Silfvergrip apareceu na diagnose do gênero, que foi descrita da seguinte maneira: *Rhamdia* é diagnosticada dos seus congêneres pelo conjunto dos seguintes caracteres: espinho da nadadeira peitoral com espinhos nos dois lados; lobos da nadadeira caudal iguais em tamanho ou o superior menor; membrana inter-radial E1/H1 menor que 2/3 do comprimento do raio E1/H1; com ou sem múltiplos poros na cabeça; abertura da aba da narina posterior aberta posteriormente; 5-16 rastros branquiais; 36-44 vértebras pós-weberianas; olhos de tamanho médio; com ou sem banda lateral; como ou sem manchas; com ou sem mancha escura sobre a nuca. Fica muito evidente que a diagnose de *R. quelen* é muito ambígua e abrangente, não servindo para o diagnóstico adequado da espécie. Ao longo do estudo de Silfvergrip fica nítido que *R. quelen* é composta por um complexo de diferentes formas negligenciado pelo autor.

Além dos gráficos pouco informativos e a diagnose inapropriada, o tratamento dado por Silfvergrip para os espécimes tipos e suas descrições originais é problemático. Em alguns casos, ele reconhece que os espécimes e suas descrições originais apresentam diferenças significativas, mas prefere sinonimizá-lascom *R. quelen,* considerando que não são diferenças estatisticamente significativas. Em outros casos, o autor simplesmente insere o táxon em *R. quelen* por simplesmente apresentar serras e ambos os lados do espinho da nadadeira peitoral. O autor chega a sinonimizar espécies alegando falta de espécimes para serem analisados. Ao ler algumas de suas justificativas, fica evidente que se o táxon não se enquadrava em uma de suas outras 10 espécies o autor sinonimizava o táxon em *R. quelen*, sem apresentar uma definição razoável para essa ação.

O maior problema das decisões taxonômicas de Silfvergrip foi adesignação do neótipo de *R. quelen*. O holótipo é dado como perdido, então, Silfvergrip (1996) designou como neótipoo exemplar NRM 16091 do rio Ucayali na Amazônia peruana. Na publicação original da descrição de *Rhamdiaquelen* de Quoy & Gaimard (1824)está bem definido que o tipo original foi coletado na bacia hidrográfica da baía do Rio de Janeiro (hoje conhecida como Baía de Guanabara).

A bacia amazônica é biogeograficamente distinta, isolada e distante da localidade tipo original: a bacia hidrográfica da baía de Guanabara, na costa atlântica brasileira. A escolha de um espécime da Amazônia peruana como neótipo foi um grave erro cometido por Silfvergrip (1996). Em sua tese ele descreve que os pesquisadores do período de 1800 poderiam confundir o Rio de Janeiro com Montevidéu, sendo assim, muito difícil definir a localidade tipo de *Rhamdia quelen*. Essa justificativa não procede, uma vez que na publicação original fica muito claro que a localidade tipo é a bacia hidrográfica da Baía de Guanabara, provavelmente no rio Macacu.

Mesmo que fosse possível confundir o Rio de Janeiro com Montevidéu, não se justifica a escolha de um neótipo da região amazônica peruana. O código internacional da nomenclatura zoológica não permite essa escolha: “ICZN Article 75.3. Qualifying conditions. A neotype is validly designated when there is an exceptional need and only when that need is stated expressly and when the designation is published with the following particulars: 75.3.6. evidence that the neotype came as nearly as practicable from the original type locality [Art. 76.1] and, where relevant, from the same geological horizon or host species as the original name-bearing type (see also Article 76.3 and Recommendation 76A.1)"; e na seção F "76.3. Type locality determined by the neotype. The place of origin of the neotype becomes the type locality of the nominal species-group taxon, despite any previously published statement of the type locality". Assim, é evidente que a designação do neótipo de *Rhamdia quelen*feita por Silfvergrip não é válida, sendo necessária a designação de um novo neótipo coletado na bacia hidrográfica da baía de Guanabara.

A pesquisa de Silfvergrip (1996) foi questionada por vários autores, uma vez que os dados utilizados foram baseados em estudos realizados com poucos espécimes e muitas lacunas na distribuição geográfica dos espécimes examinados, sendo também reconhecida a falta de caracteres robustos para o diagnóstico dessas espécies. Tendo em conta as deficiências na pesquisa de Silfvergrip (1996), muitos estudos foram realizados na tentativa de elucidar a situação taxonômica de algumas espécies de Rhamdia (Galvis et al 1997, Greenfield & Thomerson, 1998; Weber & Wilkins 1998; Romero & Paulson, 2001 Wilkens 2001; Lopez et al 2002; Perdices et al 2002; Weber et al 2003). Apesar desses esforços, o número de espécies válidas permaneceu incerto, com onze espécies válidas listadas por Bockmann & Guazelli (2003) e 17 espécies listadas por Ferraris (2007) e um grande número de espécies nominais sob seus sinônimos. As espécies válidas listadas por Ferraris (2007) incluem: *Rhamdia quelen* Quoy & Gaimard, 1824; *Rhamdia foina* Müller & Troschel, 1849; *Rhamdia laukidi* Bleeker, 1858; *Rhamdia laticauda* Kner, 1858; *Rhamdia humilis* Günther, 1864; *Rhamdia muelleri* Günther, 1864; *Rhamdia nicaraguensis* Günther, 1864; *Rhamdia parryi* Eigenmann & Eigenmann, 1888, *Rhamdia reddelli* Miller, 1984; *Rhamdia poeyi* Eigenmann & Eigenmann, 1888; *Rhamdia jequitinhonha* Silfvergrip, 1996; *Rhamdia xetequepeque* Silfvergrip, 1996; *Rhamdia itacaiunas* Silfvergrip, 1996; *Rhamdia macuspanensis* Weber & Wilkens, 1998; *Rhamdia laluchensis* Weber, Allegrucci & Sbordoni, 2003; *Rhamdia guasarensis*DoNascimiento, Provenzano & Lundberg, 2004; and *Rhamdia enfurnada* Bichuette & Trajano, 2005. Depois de 2007, duas novas espécies foram descritas: *Rhamdia gabrielae* Angrizani & Malabarba 2017 e *Rhamdia eurycephala* Angrizani & Malabarba 2017 e oito espécies foram revalidadas: *Rhamdia velifer* (Humboldt 1821); *Rhamdia schomburgkii* Bleeker 1858; *Rhamdia cinerascens* (Günther, 1860); *Rhamdia guatemalensis* (Günther, 1864); *Rhamdia parryi* Eigenmann & Eigenmann 1888; *Rhamdia branneri* Haseman, 1911; *Rhamdia voulezi* Haseman, 1911; *Rhamdia saijaensis* Rendahl, 1941; *Rhamdia reddelli* Miller 1984; *Rhamdia zongolicensis* Wilkens 1993, resultando em 27 espécies válidas reconhecidas atualmente para o gênero.

2. Objetivos

O objetivo principal dessa tese é revisar o complexo de espécies *Rhamdia quelen*. Para tanto, foram desenvolvidas as seguintes atividades:

- Estudo biogeográfico de populações de *R. quelen* ao longo da América do Sul através de sequências de DNA nuclear e mitocondrial,com inferências Bayesianas e datação dos grupos obtidos.
- Revisados dos tipos disponíveis das espécies nominais na sinonímia de *R. quelen*.
- Análise da morfologia externa, e quando possível, da interna de espécimes de *Rhamdia* coletados ao longo das principais drenagens da América do Sul.
- Descrição das espécies novas e redescrição das espécies revalidadas da sinonímia de *Rhamdia quelen*.

3. Material e métodos

3.1. Amostras

O estudo foi focado na resolução do complexo de espécies *R. quelen*. Foram utilizadas 238 amostras de tecidos refentes ao grupo, coletados ao longo de toda a distribuição do táxon. Foram utilizadas amostras de *R. laticauda* e *R. cinerascens* como representantes de *Rhamdia* transandinas. Como grupos externos foram usados amostras das espécies *Acentronichthys leptos*, *Rhamdioglanis frenatus, Imparfinis mishky, Taunaya bifasciata, Heptapterus mustelinus* e *Pimelodus maculatus*. A relação dos tecidos utilizados é encontrada na tabela 1.

Para as análises morfológicas, que incluí medidas e contagens, foram utilizadas xxx amostras. A relação desses espécimes é encontrada mais adiante, na descrição morfológica de cada espécie.

Tabela 1: Relação das amostras analisadas no estudo genético.

Species	N	Drainage	Sub-drainage	Lote
R. aff. *quelen*	1	Lagoa dos Patos	Rio dos Sinos	UFRGS 23328
R. aff. *quelen*	2	Lagoa dos Patos	Rio dos Sinos	UFRGS 19665
R. aff. *quelen*	2	Lagoa dos Patos	Rio dos Sinos	UFRGS 19375
R. aff. *quelen*	4	Lagoa dos Patos	Rio Caí	UFRGS 23327
R. aff. *quelen*	4	Lagoa dos Patos	Rio Caí	UFRGS 19663
R. aff. *quelen*	1	Lagoa dos Patos	Upper Rio Jaguarão	UFRGS 20046
R. aff. *quelen*	4	Lagoa dos Patos	Upper Rio Jaguarão	UFRGS 20047
R. aff. *quelen*	2	Lagoa dos Patos	Upper Rio Camaquã	UFRGS 19725
R. aff. *quelen*	2	Lagoa dos Patos	Lower Rio Camaquã	UFRGS 18424
R. aff. *quelen*	3	Lagoa dos Patos	Lower Rio Camaquã	UFRGS 18425
R. aff. *quelen*	2	Lagoa dos Patos	Upper Rio das Antas	MCP 48673
R. aff. *quelen*	2	Lagoa dos Patos	Upper Rio das Antas	MCP 48685
R. aff. *quelen*	1	Lagoa dos Patos	Upper Rio das Antas	MCP 48674
R. aff. *quelen*	1	Lagoa do Patos	Upper Rio Taquari	UFRGS 20059

R. aff. *quelen*	3	Lagoa do Patos	Upper Rio Taquari	UFRGS 20058
R. aff. *quelen*	2	Lagoa do Patos	Upper Rio Taquari	UFRGS 23166
R. aff. *quelen*	1	Lagoa do Patos	Upper Rio Taquari	UFRGS 22869
R. aff. *quelen*	1	Lagoa do Patos	Upper Rio Taquari	UFRGS 19535
R. aff. *quelen*	3	Lagoa dos Patos	Upper Rio Jacuí	UFRGS 18358
R. aff. *quelen*	2	Lagoa dos Patos	Upper Rio Jacuí	UFRGS 18359
R. aff. *quelen*	2	Lagoa dos Patos	Upper Rio Jacuí	UFRGS 18226
R. aff. *quelen*	3	Lagoa dos Patos	Upper Rio Jacuí	UFRGS 23530
R. aff. *quelen*	1	Lagoa dos Patos	Upper Rio Jacuí	UFRGS 23345
R. aff. *quelen*	3	Lagoa dos Patos	Upper Rio Jacuí	UFRGS 19369
R. aff. *quelen*	5	Tramandaí	Lagoa dos Quadros	UFRGS 17717
R. aff. *quelen*	5	Tramandaí	Lagoa Itapeva	UFRGS 19424
R. aff. *quelen*	5	Araranguá	Lower Rio Araranguá	UFRGS 21360
R. aff. *quelen*	3	Tubarão	Lower Rio Tubarão	UFRGS 21369
R. aff. *quelen*	2	Tubarão	Lower Rio Tubarão	UFRGS 21378
R. aff. *quelen*	1	Tijucas	Lower Rio Tijucas	UFRGS 18488
R. aff. *quelen*	1	Tijucas	Lower Rio Tijucas	UFRGS 21083
R. aff. *quelen*	1	Tijucas	Lower Rio Tijucas	UFRGS 21084
R. aff. *quelen*	1	Itapocú	Lower Rio Itapocu	UFRGS 21086
R. aff. *quelen*	2	Itapocú	Lower Rio Itapocu	LBP 20154
R. aff. *quelen*	2	Itajaí	Lower Rio Itajaí	UFRGS 21505
R. aff. *quelen*	2	Itajaí	Lower Rio Itajaí	UFRGS 21212
R. aff. *quelen*	2	Itajaí	Lower Rio Itajaí	UFRGS 21514
R. aff. *quelen*	6	Itajaí	Upper Rio Itajaí	UFRGS 19905
R. aff. *quelen*	2	Acarí	Rio Acarí	UFRGS 11934
R. aff. *quelen*	4	Acarí	Rio Acarí	UFRGS 21214
R. aff. *quelen*	1	Guaraqueçaba	Rio Serra negra	UFRGS 12459
R. aff. *quelen*	1	Ribeira	Lower Ribeira do Iguape	UFRGS 12399
R. aff. *quelen*	3	Ribeira	Lower Ribeira do Iguape	LBP 6843
R. aff. *quelen*	3	Ribeira	Lower Ribeira do Iguape	LBP 7496

R. aff. *quelen*	7	Ribeira	Lower Ribeira do Iguape	LBP 7395
R. aff. *quelen*	1	Ribeira	Lower Ribeira do Iguape	LBP 7432
R. aff. *quelen*	1	Ribeira	Lower Ribeira do Iguape	LBP 16840
R. aff. *quelen*	1	Ribeira	Lower Ribeira do Iguape	LBP 20201
R. aff. *quelen*	2	Itanhenhem	Lower Itanhenhem	UFRGS 18706
R. aff. *quelen*	1	Itanhenhem	Lower Itanhenhem	LBP 20214
R. aff. *quelen*	2	Picinguaba	Upper Rio Picinguaba	UFRGS 13691
R. aff. *quelen*	1	Mambucaba	Rio Pereque	LBP 7890
R. aff. *quelen*	3	Itagaré	Rio Itagaré	UFRGS 13652
R. aff. *quelen*	3	Itapanhau	Rio Itapanhau	LBP 14299
R. aff. *quelen*	1	Baía de Guanabara	Rio Macacu	MNRJ 46842
R. aff. *quelen*	2	Baía de Guanabara	Rio Macacu	MNRJ 43525
R. aff. *quelen*	2	Baía de Guanabara	Rio Suruí	MNRJ 41526
R. aff. *quelen*	1	Baía de Guanabara	Rio Paraíso	MNRJ 9763
R. aff. *quelen*	1	Baía de Guanabara	Rio Iguaçu	MNRJ 43148
R. aff. *quelen*	1	Paraíba do sul	Upper Paraíba do Sul	UFRGS
R. aff. *quelen*	2	Paraiba do sul	Medium Paraíba do Sul	LBP 8033
R. aff. *quelen*	1	Paraiba do sul	Medium Paraíba do Sul	LBP 10692
R. aff. *quelen*	1	Paraiba do sul	Medium Paraíba do Sul	LBP 2117
R. aff. *quelen*	1	Paraiba do sul	Medium Paraíba do Sul	LBP 16350
R. aff. *quelen*	2	Doce	Lower Rio Doce	UFRGS
R. aff. *quelen*	1	Doce	Lower Rio Doce	LBP 3449
R. aff. *quelen*	1	São Francisco	Upper São Francisco	LBP 6507
R. aff. *quelen*	1	São Francisco	Upper São Francisco	LBP 8951
R. aff. *quelen*	2	São Francisco	Upper São Francisco	LBP 17406
R. aff. *quelen*	2	São Francisco	Upper São Francisco	LBP 8965
R. aff. *quelen*	1	São Francisco	Upper São Francisco	LBP 16305
R. aff. *quelen*	1	São Francisco	Upper São Francisco	LBP 16317
R. aff. *quelen*	2	Paraná	Upper Rio Paraná	UFRGS 15354
R. aff. *quelen*	2	Paraná	Upper Rio Paraná	LBP 17403

R. aff. *quelen*	1	Uruguai	Upper Rio Uruguai	LBP 13042
R. aff. *quelen*	1	Uruguai	Upper Rio Uruguai	LBP 13068
R. aff. *quelen*	2	Uruguai	Medium Rio Uruguai	UFRGS 23532
R. aff. *quelen*	2	Uruguai	Medium Rio Uruguay	UFRGS 23533
R. aff. *quelen*	2	Uruguai	Medium Rio Uruguay	UFRGS 23531
R. aff. *quelen*	2	Uruguai	Medium Rio Uruguay	UFRGS 23534
R. aff. *quelen*	5	Uruguai	Medium Rio Uruguai	UFRGS 23529
R. aff. *quelen*	1	Uruguai	Rio Negro	UFRGS 14569
R. aff. *quelen*	2	Tapajós	Upper Rio Tapajos	LBP 20813
R. aff. *quelen*	1	Madeira	Upper Rio Madeira	LBP 12118
R. aff. *quelen*	1	Madeira	Upper Rio Madeira	LBP 10962
R. aff. *quelen*	1	Ucayali	Upper Ucayali	LBP 3296
R. gabrielae	5	Tramandai	Rio Maquiné	UFRGS 19093
R. gabrielae	15	Tramandai	Rio Maquiné	UFRGS 19094
R. gabrielae	10	Tramandai	Rio Três Forquilhas	UFRGS 18034
R. gabrielae	8	Mampituba	Upper Rio Mampituba	UFRGS 19902
R. gabrielae	10	Araranguá	Upper Rio Araranguá	UFRGS 19903
R. eurycephala	10	Tubarão	Upper Rio Tubarão	UFRGS 19904
R. guatemalensis	1	Belize	Rio Belize	LBP 19584
R. cineracens	2	Guayas	Rio Guayas	LBP 19332

3.2. Procedimentos moleculares

O DNA total foi extraído de tecidos conservados em álcool 96% seguindo o método de CTAB (Doyle & Doyle, 1987) modificado, de acordo com o seguinte protocolo:

- Macerar a amostra e colocá-la em um microtubo de 1,5 mL;
- Adicionar 500 µL da solução de CTAB, utilizar a capela;
- Adicionar 50 µL de β-mercapto-etanol, utilizar a capela;
- Adicionar 15 µL de Proteinase K (20 mg/ml);
- Incubar em banho Maria a 60° C por, pelo menos, uma hora ou até que o tecido esteja digerido, agitando (vórtex) a cada 15 min;
- Espere uns minutos para esfriar os tubos. Na capela, adicionar 500 µl de CIA (clorofórmio: álcool isoamílico) 24:1;
- Agitar os tubos manualmente por uns 3 min. (ficar virando eles, não sacudir);
- Centrifugar por 20 min. a 14.000 rpm;
- Com muito cuidado recolher a fase aquosa (fase superior - as fases não podem ser misturadas) e transferir para outro microtubo de 1,5 ml (cuidar para não encostar a ponteira na interface entre as fases. É melhor deixar sobrar volume do sobrenadante (fase superior) do que encostar na interface ou na segunda fase). Fazer na capela;
- Adicionar 2/3 do volume da fase aquosa recolhida de isopropanol absoluto gelado;
- Misture gentilmente até a solução ficar homogênea;
- Deixar precipitando no freezer de uma a duas horas (dependendo da quantidade de DNA vista na fase anterior);
- Centrifugar por 20 min. A 14.000 rpm e descartar o sobrenadante;
- Lavar 2x o pellet com 400 µl de etanol 70%, distribuindo o álcool pelas paredes do tubo para retirar impurezas;
- Colocar 200 µl de etanol absoluto gelado e em seguida descartar o álcool;
- Deixar o pellet secar colocando os tubos invertidos sobre um papel toalha por mais ou menos 20 min., ou aquecer em estufa (37° C);

- Quando o tubo estiver completamente seco, adicionar 50-150 µl de TE 1x (dependendo do tamanho do pellet) e 2 µl de RNAse (nós usamos 2 µl pois não temos pipeta para menos, o ideal seria 0,25 – 1,5 µl, mais econômico e funciona igual);
- Deixar em banho-maria a 37ºC por 1h e posteriormente, 24h em temperatura ambiente.

Os marcadores molecular utilizados nesse estudo foram o gene COI e o gene CitB, ambos do mtDNA e o gene MyH6 e Rag2, ambos do nDNA. Os fragmentos de DNA foram amplificados através da técnica de PCR (*Polymerase ChainReaction*) em reações de 20µl contendo 10–50 ng DNA, 0,2 µM de cada *primer*, 0,2 mM de dNTP, 1X de Tampão, 1,5 µM de $MgCl_2$ e 1U de Platinum Taq DNA polymerase (Invitrogen, São Paulo, SP, Brazil). Os primers utilizados se encontram na tabela 2 e as condições para amplificação dos fragmentos estão na tabela 3.

Tabela 2: Lista dos *primers* utilizados.

Marcador	Primer	Referencia
Coi	FishF2 _t1 5’TGTAAAACGACGGCCAGTCGACTAATCATAAAGATATCGGCAC3’ VF2_t1 5’TGTAAAACGACGGCCAGTCAACCAACCACAAAGACATTGGCAC3’ FishR2_t1 5’TGTAAAACGACGGCCAGTCAACCAACCACAAAGACATTGGCAC3’ FR1d_t1 5’CAGGAAACAGCTATGACACCTCAGGGTGTCCGAARAAYCARAA3’	Ivanova et al. 2000
CitB	GLUD-L 5´TGACTTGAARAACCAYCGTTG3´ CB3-H 5´GGCAAATAGGAARTATCATTC3´	Palumbi, 1991
MyH6 1º PCR	F459 5'CATMTTYTCCATCTCAGATAATGC3' R1325 5'ATTCTCACCACCATCCAGTTGAA3'	Li et al., 2007
MyH6 2º PCR	F507 5'GGAGAATCARTCKGTGCTCATCA3' R1322 5'CTCACCACCATCCAGTTGAACAT3'	Li et al., 2007
Rag2	MGF1 5´TGYTATCTCCCACCTCTGCGYTACC3´ MHR1 5´TCATCCTCCTCATCKTCCTCWTTGTA3´	Hardmann, 2004

Tabela 3: Condições de amplificação do *primer* utilizados.

	COI	CitB	1º MyH6	2º MyH6	Rag2
Desnaturação inicial	94º/10min	94º/5min	94º/3min	94º/5min	95º/2min
Nº de ciclos	35x	35x	30x	30x	30x
Desnaturação	94º/30seg	94º/30seg	94º/30seg	94º/30seg	95º/30seg
Anelamento	52º/40seg	48º/30seg	50º/45seg	62º/45seg	50º/30seg
Extensão	72º/1min	72º/1min	72º/1min30seg	72º/1min30seg	72º/1min30seg
Extensão final	72º/10min	72º/7min	72º/5min	72º/5min	72º/5min

Os produtos das reações de PCR foram analisados através de eletroforese em gel de agarose 1,5% corados com GelRed. Os produtos dos PCRs foram purificados com as enzimas ExoSap (GE healthcare). Os procedimentos de extração DNA, amplificação por PCR, eletroforese e purificação dos produtos de PCR foram realizados no Laboratório de Biologia Molecular do Programa de Pós-graduação em Biologia Animal da UFRGS.

Os fragmentos amplificados foram sequenciados pela empresa ACTGene (Porto Alegre). As sequências obtidas foram alinhadas no software ClustalW (Thompson et al., 1994) implementado no software MEGA 6 (Tamura et al., 2013).

3.2.1 Análise dos dados

A diversidade haplotípica, frequência nucleotídica, diversidade nucleotídica e a identificação dos haplótipos foram calculadas utilizando o programa DnaSP (Rozas et al. 2003). A rede de haplótipos foi realizada utilizando o programa Network 4.1.1.0 (www.fluxus-engineering.com/sharenet.htm) utilizando o algoritmo Mediam Joining. Os testes de neutralidade seletiva D de Tajima (Tajima, 1989) e *Fs* de Fu (Fu, 1997) foram realizados no programa ARLEQUIN 3.11 (Excoffier et al., 2005). Quando necessário, foi calculdado o indicie de fixação (Fst) par-a-par entre as populações (Wright 1978) e realizadas análises de variança molecular (AMOVA), ambos calculados no programa Arlequim 3.5 (Excoffier et al. 2005).

As relações filogeneticas entre as amostras analisadas foram inferidas através de inferência Bayesiana utilizando árvores de genes, gerado no programa MrBayes 3.2.2

(Ronquist *et al.*, 2012), e árvores de espécies, utilizando o programa BEAST 1.8.3 (Drummond & Rambaut, 2007). Os modelos evolutivos foram encontrados utilizando o programa Partition-Finder (Lanfear *et al.,* 2012) empregando *Bayesian Information Criterion* (BIC).

Um relógio molecular estrito foi aplicado para estimar o tempo de divergência entre as linhagens obtidas. Foi escolhido este relógio por se tratar de um complexo de espécie e espécies muito próximas filogenéticamente (Li & Drummond, 2012). Foi assumida uma taxa de evolução molecular de 0.001/site/milhões de anos para os marcadores do DNA mitocondrial (Bermingham *et al.,* 1997; Reeves & Bermingham, 2006; Ornelas-Garcia *et al.,* 2008). A taxa de evolução dos marcadores nucleares foi calibrada em função da taxa do DNA mitocndrial. As árvores de genes foram construidas com pelo menos 10 milhões de passos MCMC e as árvores de espécies foram obtidas com pelo menos 200 milhões de passos MCMC. Ambas as análises foram verificadas a cada 1000 passos; a eficiencia das cadeias foram observadas no programa TRACER 1.5 (Rambaut *et al*., 2014) usando 10% *burn-in*.

3.3. Procedimentos Morfológicos

As linhagens recuperadas nas análises genéticas tiveram sua morfologia externa analisada através de contagens e medidas, e quando possível, foram analisadas características osteológicas. Estas linhagens foram comparadas com os espécimes tipo existentes para os diferentes táxons do gênero, onde foi possível ser ligadas ou excluídas dos nomes disponíveis para o gênero *Rhamdia*.

Os dados merísticos, morfométricos e osteológicos tomados nos exemplares examinados baseiam-se nos trabalhos de Guedes (1980), Silfvergrip (1996) e Anza (2006). Os dados merísticos foram tomados com o auxílio de microscópio estereoscópico, quando necessário, e correspondem às contagens em geral:

- Raios ramificados da nadadeira anal;
- Raios da nadadeira dorsal;
- Raios da nadadeira peitoral;
- Raios da nadadeira pélvica;
- Raios ramificados do lobo superior da nadadeira caudal;

- Raios ramificados do lobo inferior da nadadeira caudal;
- Total de raios branquiostegais;
- Rastros do ramo inferior do primeiro arco branquial;
- Total de vértebras entre a vértebra Weberiana e o complexo ural.

Os dados morfométricos foram obtidos com paquímetro digital, medindo de ponto-a-ponto do lado esquerdo de cada exemplar, ao total foram levantadas xx medidas de cada espécime:

- Comprimento padrão - medido da ponta do focinho à inserção da nadadeira anal;
- Largura do corpo 1 - medida no ponto de maior largura do cleitro, posteriror à origem do espinho das nadadeiras peitorais;
- Largura do corpo 2 - Largura do corpo na origem das nadadeiras pélvicas;
- Altura do corpo - medida na origem do primeiro raio da nadadeira dorsal;
- Distância pré-dorsal - medida da ponta do focinho à origem do primeiro raio da nadadeira dorsal;
- Distância dorsal-caudal - medida da origem do último raio da nadadeira dorsal à inserção da nadeira caudal;
- Distância entre as nadadeiras dorsal e adiposa - medida da origem do último raio da nadadeira dorsal à origem da nadadeira adiposa;
- Distância pré-peitoral - medida da ponta do focinho à origem da nadadeira peitoral;
- Distância pré-ventral - medida da ponta do focinho à origem da nadadeira pélvica;
- Distância pré-anal - medida da ponta do focinho à origem do primeiro raio da nadadeira anal;
- Distância pélvica-anal - medida da origem da nadadeira pélvica à origem do primeiro raio da nadadeira anal;
- Comprimento do pedúnculo caudal - medido da origem do último raio da nadadeira anal à inserção da nadedeira caudal;
- Altura do pedúnculo caudal - altura do corpo na extremidade posterior da origem da nadadeira adiposa;

- Comprimento da nadadeira pélvica - medido da origem à extremidade do primeiro raio da nadadeira pélvica;
- Comprimento da base da nadadeira anal - medido da origem do primeiro raio à origem do último raio da nadadeira;
- Comprimento da nadadeira anal - medido da origem do primeiro raio à projeção, no corpo, da extremidade posterior da nadadeira;
- Comprimento da base da nadadeira dorsal - medido da origem do primeiro raio à origem do último raio da nadadeira;
- Altura da nadadeira dorsal - medida da origem da nadadeira à extremidade do primeiro raio mole;
- Comprimento do espinho da nadadeira dorsal - medido da origem à extremidade do espinho, considerando apenas a porção enrijecida do espinho;
- Comprimento do espinho da nadadeira peitoral - medido da origem à extremidade do espinho, considerando apenas a porção enrijecida do espinho;
- Comprimento da base da nadadeira adiposa - medido da origem anterior à origem posterior da nadadeira;
- Comprimento da cabeça - medido da ponta do focinho à margem posterior óssea do opérculo;
- Comprimento do focinho - medida da ponta do focinho ao centro das órbitas;
- Altura do focinho - medida vertical da altura da cabeça pelo centro das órbitas;
- Altura da cabeça - medida vertical da altura da cabeça na base do processo supra-occipital;
- Diâmetro da órbita - medido na maior horizontal entre as margens anterior e posterior da órbita;
- Distância interorbital - menor distância entre as órbitas;
- Largura da boca - medida de uma extremidade à outra, incluindo o sulco submandibular presente em cada uma das extremidades;
- Distância entre os barbilhões maxilares – medida entre as margens externas das bases dos barbilhões maxilares;

- Distância entre as narinas anteriores – medida entre as margens externas das narinas anteriores;
- Distância entre as narinas posteriores – medida entre as margens externas das narinas posteriores;
- Distância entre as narinas – medida entre a margem anterior da narina anterior e a margem posterior da narina posterior;
- Distância entre a narina posterior e olho – medida entre a margem anterior da narina posterior e a margem anterior da órbita.

As informações osteológicas foram tomadas a partir de exemplares diafanizados segundo a técnica de Taylor & Van Dyke (1985), que consiste basicamente de quatro etapas: clareamento e despigmentação, digestão de tecidos moles, coloração de cartilagens e coloração dos ossos. O clareamento e a despigmentação dos tecidos são realizados em solução de Peróxido de Hidrogênio (H_2O_2) e Hidróxido de Potássio (KOH). A digestão enzimática de tecidos moles é realizada em uma solução com tripsina. A coloração de cartilagens é feita em solução de azul de alcian e a coloração de ossos é feita em solução de vermelho de alizarina.

4. Capitulo 1

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Morphology and molecular data reveal the presence of two new species under *Rhamdia quelen* (Quoy & Gaimard, 1824) (Siluriformes: Heptapteridae) species complex

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Abstract

The eustatic movements triggered by glaciations during the Quaternary have shaped the landscape of Brazilian Atlantic Coast. Cyclic sea-level changes either isolated or connected freshwater fish populations, impacting their distribution and diversification. *Rhamdia quelen* has been widely recorded from the Brazilian Atlantic Coastal rivers, but it is also considered a species complex.A phylogeographic study carried out using three molecular markers of mtDNA and one of nDNA in the populations of *Rhamdia* from the hydrographic basins of Southern Atlantic Coast of Brazil recovered three evolutionarily distinct groups: one represented by the populations found in lowlands of all studied watersheds; the second group composed of populations found in the upper tributaries of the rio Araranguá, rio Mampituba and rio Tramandaí; and a third group found exclusively in the upper portions of rio Tubarão. The genetic divergences among these three lineages of *Rhamdia* is discussed according to sea level changes in the Quaternary. Two new species of *Rhamdia* are diagnosed and described based on morphological and molecular evidence.

Resumo

Os movimentos eustáticos, desencadeados pelas glaciações durante o Quaternário, moldaram a paisagem da costa atlântica brasileira. Essas mudanças cíclicas do nível do mar isolaram ou conectaram populações de peixes de água doce, impactando sua distribuição e diversificação. *Rhamdia quelen* tem sido amplamente registrada nos rios da costa atlântica brasileira, sendo considerada um complexo de espécies. Assim, foi realizado um estudo filogeográfico que utilizou três marcadores moleculares do mtDNA e um do nDNA em populações de *Rhamdia* das bacias hidrográficas do sul da costa atlântica brasileira. Foram encontrados três grupos evolutivamente distintos: um representado pelas populações encontradas nas terras baixas de todas as bacias hidrográficas estudadas; o segundo grupo composto por populações encontradas na porção alta dos rios Araranguá, Mampituba e Tramandaí; e um terceiro grupo, encontrado exclusivamente na porção alta do rio Tubarão. As divergências genéticas entre essas três linhagens de *Rhamdia* são relacionadas aos movimentos eustáticos do Quaternário. Esses três grupos foram analisados morfologicamente, resultando na diagnose e descrição de duas novas espécies de *Rhamdia*.

Key words: Atlantic coastal drainages**,** Integrative taxonomy, Neotropical fishes, Phylogeography, Sea level changes.

Running Title: Description of two new species of *Rhamdia*

Introduction

The landscape of the Southern Brazilian Atlantic coastal region is formed by many isolated hydrographic basins known as Coastal Drainages of Southeastern Brazil (CDSEB). These small drainages are separated from other continental drainages by the scarped mountainous region along the eastern face of Brazilian crystalline shield (Ribeiro, 2006). Since the separation of the Gondwana continent (~180 Ma), this region has been shaped by successive geological processes, starting with the megadome uplift, followed by active tectonic processes which resulted in block failures and headwaters capture, and more recently by erosive events (Ribeiro, 2006).

During the Pleistocene glacial period (~2.6 Ma), lower sea levels exposed continental shelves, permitting low-lying paleodrainages to join rivers that are now isolated (Weitzman, Menezes & Weitzman*,* 1988; Dias *et al.,* 2014; Thomaz *et al.,* 2015). Over the past 500 Ka, marine transgression events helped shape the Southern Brazil Atlantic coastal region by forming large sand barriers that impounded a large complex of lagoons (Villwock & Tomazelli, 1995; Tomazelli *et al.,* 2000). This complex geological history, combined with the isolation of small drainages and the existence of Atlantic Rainforest, makes this region a hotspot of biodiversity (Myers *et al.,* 2000), with one of the highest endemism rates for freshwater fishes in the Neotropics (Vari, 1988; Weitzman, *et al.,* 1988; Bizerril, 1994; Buckup, 2011).

Silfvergrip (1996) completed a thorough taxonomic revision of the genus *Rhamdia* synonymizing 47 nominal species into *Rhamdia quelen* (Quoy & Gaimard, 1824). This action established a broad geographic distribution for the species, from southern Mexico to central Argentina. The diagnosis of *R. quelen* proposed by Silfvergrip (1996), however, is too general to be useful and embraces several different morphotypes under a single name. Subsequent work proposed to revalidate some of the species in the synonymy of *R.quelen* (Greenfield & Thomerson, 1997; Galvis *et al.,* 1997; Bussing, 1998; Romero & Paulson, 2001; Wilkens, 2001; Lopez *et al.,* 2002, Perdices *et al.,* 2002; Weber*et al.,* 2003; Hernandez *et al.,* 2015; Garavello & Shibata, 2016). Nevertheless *R.quelen* remains a complex of several distinct species.

The genetic and morphological diversity of the *R. quelen* species complex is analyzed here for populationsfrom four contiguous drainages of the Southern Brazilian Atlantic coastal region (Fig. 1). These include three small isolated drainages (rio Araranguá, rio Mampituba and rio Tramandaí), which are recognized as one ecoregion for freshwater biodiversity called Tramandaí-Mampituba (unit 335 - Abell *et al.,* 2008), and the rio Tubarão, located just north of the rio Araranguá system and belonging to the Southwest Atlantic Rainforest ecoregion (unit 331 - Abell *et al.,* 2008). The Tramandaí-Mampituba ecoregion is recognized by the high endemism of fish species (Malabarba & Isaia, 1992; Reis & Schaefer, 1998). Rio Araranguá and rio Mampituba begin in the Serra Geral highlands and flow directly into the sea. The rio Tramandaí system, composed of two main tributaries (rio Maquiné and rio Três

Forquilhas), also begin in Serra Geral but empty into a coastal lagoon complex where the fish fauna is quite distinct from the rivers (Malabarba & Isaia, 1992; Malabarba *et al*., 2013; Hirschmann *et al.,* 2015).

Given diversity within the *R. quelen* species complex and differences in faunal composition among coastal drainages and within them (upland vs. lowland), we test the hypothesis that resident populations of *R. quelen* include different evolutionary entities separable by geography and habitat.

Material and methods

A total of 63 specimens of *Rhamdia* were used for genetic analyses. The tissue samples were taken from the fish collection of the Departamento de Zoologia, Universidade Federal do Rio Grande do Sul (UFGRS), and include specimens from rio Araranguá, rio Mampituba and rio Tramandaí drainages. The analysis further included specimens of *R.* aff. *quelen* from the Laguna dos Patos System located just south of Tramandaí River system and belonging to the Patos Lagoon ecoregion (unit 334; Abell *et al.,* 2008) for group delimitation and comparison. Tissue samples of species representing closely related genera such as *Rhamdella zelimai* Reis, Malabarba & Lucena, 2014and *Pimelodella australis* Eigenmann, 1917 were used as outgroups (Table 1).

Meristic and morphometric data were obtained from specimens deposited in the fish collections of the Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCP), Museu de Zoologia, Universidade de São Paulo, São Paulo (MZUSP) and Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre (UFRGS).

DNA extractions from tissues followed a modified CTAB protocol (Doyle & Doyle, 1987). PCR was used to amplify the mitochondrial genes Cytochrome Oxidase I (COI) (Ivanova *et al*., 2007) and Cytochrome B (CytB) (Palumbi *et al.,* 1991), the control region of mtDNA (Dloop) (Sivasundar*et al.,* 2001) and nuclear gene Myosin Heavy Chain 6 (MyH6) (Li *et al.,* 2007). PCRs were carried out in 20 µL reactions containing 10–50 ng DNA, 0.2 µM of each primer, 0.2 mM of each dNTP, 1X Buffer, 1.5 µM $MgCl_2$ and 1U Platinum Taq DNA polymerase (Invitrogen, São Paulo, SP, Brazil). PCR conditions followed recommendations reported for the respective primers. PCR products were checked by electrophoresis in agarose gel, purified using ExoSap (Exonuclease I and Shrimp Alkaline Phosphatase, GE Healthcare, Piscataway, NJ, USA) and sequenced in both directions by ACTGENE Ltda., Porto Alegre, Brazil.

Sequences were edited in BioEdit 7.1.3.0 (Hall, 1999) and aligned in CLUSTAL W (Thompson *et al.,* 1994). The haplotype diversity, nucleotide diversity and neutrality tests Fu's F (Fu, 1997) and Tajima's D (Tajima, 1989) were calculated on DNASP v.5 (Librado & Rozas, 2009). The haplotype network was constructed using Median-Joining method (Bandelt *et al.,* 1999) in NETWORK 4.1.0.8 (www.fluxus-engineering.com). Calculation of F-statistic (Φst) and analysis of molecular variance (AMOVA) were carried out in ARLEQUIN 3.5 (Excoffier *et al.,* 2005). Phylogenetic relationships were inferred by Bayesian Inference (BI) using a gene tree and carried out in MrBayes 3.2.2 (Ronquist *et al*., 2012), and a species tree carried out in BEAST 1.7.5 (Drummond & Rambaut, 2007). Partition-Finder program (Lanfear *et al.,* 2012) was used to find the best evolutionary model using Bayesian Information Criterion (BIC). A strict molecular clock was used to estimate the divergence time between lineages, which is used for analysis within species or among closely related species (Li & Drummond, 2012). For comparison, we used evolutionary rates proposed by Hirschmann *et al.* (2015) in a phylogeographic study of the same region, assuming an evolutionary rate 0.001/site/million years for mtDNA markers (Bermingham *et al.,* 1997; Reeves & Bermingham, 2006; Ornelas-Garcia *et al.,* 2008). The evolutionary rate of the nuclear marker was calibrated based on mtDNA rate. The gene trees were based on 10 million MCMC steps and the species tree was based on 100 million MCMC steps. Both trees were sampled every 1000 steps; chain efficiency was observed in TRACER 1.5 (Rambaut *et al*., 2014) with 10% burn-in. For genetic diversity analyses, populations were separated both by drainage and within drainage by habitat (i.e., *Rhamdia* from upstream portions on the Serra Geral formation were treated as a different population from those collected in downstream portions on the coastal plain.

Eight counts and 58 measurements (to 0.1 mm) were taken on the left side of 80 specimens of *Rhamdia* using a digital calliper and following Silfvergrip (1996) and Bichuette & Trajano (2005). Principal Component Analysis (PCA) was used to evaluate morphometric variation among individuals using the software PAST 2.17C (Hammer *et al*., 2001). The values for all characters were transformed to logarithms to equalize variances of allometric relationships (Bookstein *et al.*, 1985). Linear regression graphs of selected measurements were constructed using SIGMAPLOT 10.0 (Brannan *et al.,* 2002).

Comparative material. From Brazil. *Rhamdia* aff. *quelen*:MZUSP 14216, 6, state of Rio Grande do Sul, municipality of Maquiné, lagoa dos Quadros, 26 Oct 1978. MZUSP 25066, 1, state of Rio Grande do Sul, municipality of Maquiné, lagoa dos Quadros, 27 Jan 1977. UFRGS 1006, 1, state of Rio Grande do Sul, municipality of Tramandaí, lagoa Tramandaí, 29°57'59"S, 50°08'00"W, 7 Mai 1981. UFRGS 3688, 1, state of Rio Grande do Sul, municipality of Tramandaí, rio Tramandaí, 29°57'04"S, 50°6'52"W, 1 Sep 1984. UFRGS 3690, 1, state of Rio Grande do Sul, municipality of Tramandaí, rio Tramandaí, 29°57'04"S, 50°6'52"W, 1 Sep 1984. UFRGS 3694, 1, state of Rio Grande do Sul, Tramandaí, municipality of Tramandaí, rio Tramandaí, 29°57'04"S, 50°6'52"W, 01 Sep 1984. UFRGS 4108, 2, state of Rio Grande do Sul, municipality of Osório, Caieira lagoon, 29°52'21" S, 50°14'35"W, 20 Mai 1989. UFRGS 4111, 1, state of Rio Grande do Sul,municipality of Cidreira, brook by the roadside, 10 Jun 1989. UFRGS 7003, 1, state of Rio Grande do Sul, municipality of Maquiné, mouth of the Maquiné river, 29°43'04", 50°10'39"W, 10 Mar 2005. UFRGS 7004, 1, state of Rio Grande do Sul, municipality of Maquiné, mouth of the Maquiné river, 29°43'04", 50°10'39"W, 10 Mar 2005. UFRGS 7005, 1, state of Rio Grande do Sul, municipality of Três Forquilhas, Itapeva lagoon, 29°33'19"S, 50°00'40"W, 13 Mar 2005. UFRGS 7006, 1, state of Rio Grande do Sul, municipality of Três Forquilhas, Itapeva lagoon, 29°33'19"S, 50°00'40"W, 13 Mar 2005. UFRGS 7008, 1, state of Rio Grande do Sul, municipality of Três Forquilhas, Itapeva lagoon, 29°33'19"S, 50°00'40"W, 13 Mar 2005. UFRGS 17717, 4, state of Rio Grande do Sul, municipality of Capão da Canoa, lagoa dos Quadros, 29°39’58”S, 50°01’53”W, 03 Apr 2013. UFRGS 18425, 5, state of Rio Grande do Sul, municipality of Camaquã, arroio Sapata, rio Camaquã basin, 31°00’14”S, 52°05”58”W, 16 Jan 2014. UFRGS 19424, 8, state of Rio Grande do Sul, municipality of Tramandaí, lagoa dos Quadros, 29°36’14”S, 49°59’27”W. UFRGS 21360, state of Santa Catarina, municipality of Meleiro, sanga da Figueira, basin of rio Araranguá, 28°55’36”S, 49°33’25”W, 27 Jan 2016. UFRGS 22011, 3, state of Rio Grande do Sul, municipality of Maquiné, mouth of the Maquiné river, 29°42'25"S, 50°10'51"W, 10 Mar 2015. MCP 9964, 1, state of Rio Grande do

Sul, municipality of Maquiné, Quadros lagoon, 29°43'27"S, 50°08'57"W, 29 Jun 1984. *Rhamdia laukidi* Bleeker, 1858: MZUSP 81485, 3, state of Amazonas, municipality of Tiquié, igarapé Açaí tributary of rio Tiquié, 0°15'55"N, 69°58'16"W. MZUSP 85074, 3, state of Amazonas, municipality of Tiquié, rio Tiquié, 0°15'35"N, 70°02'42"W. *Rhamdia poeyi* Eigenmann & Eigenmann, 1888: MZUSP 024557, 4, state of Goiás, municipality of São Domingos, ribeirão Bezerra, rio Tocantins, 13°24'00"S, 46°19'00"W, 1974. *Rhamdia itacaiunas* Silfvergrip, 1996: MZUSP 34744, 2, state of Pará, municipality of Marabá, rio Itacaiunas, 05°22'00"S, 49°07'00"W, 14 Oct 1983. *Rhamdia enfurnada* Bichuette & Trajano, 2005: MZUSP 87776, Holotype, 1, state of Bahia, municipality of Coribe, Gruta do Enfurnado, rio São Francisco, 13º38'44"S, 44º12'05"W, 5 Sep 2003. *Rhamdia muelleri* (Günther, 1864):MZUSP 23034, 4, state of Pará, municipality of Belém, igarapé Paracuri, 01°26'60"S, 48°38'00"W, 01 Aug 1965. *Rhamdia jequitinhonha* Silfvergrip, 1996: MNRJ 22514, 1, state of Minas Gerais, municipality of Pedra Azul, 15^{o}54'50"S, 41^{o}23'31"W, 10 Jul 2001. From Peru: *Rhamdia quelen*, NRM 16091, 1, Department of Loreto, between Caño Pastos and Hamburgo, tributary to Río Samiria,12 Aug 1986.

Results

A total of 2,468 bp were aligned for mtDNA sequences, 683 bp for COI gene, 832 bp for CytB gene and 951 bp for control region (Dloop). A total of 134 polymorphic sites were found, resulting in 34 haplotypes and haplotype diversity = 0.94. For MyH6 nuclear gene, 799 bp were obtained resulting in seven polymorphic sites, three haplotypes and haplotype diversity = 0.50.

The haplotype network for mtDNA data (Fig. 2) shows three consistent and genetically distinct groups. The Coastal Plain Group is composed of haplotypes present in coastal plain lagoons and in the lower parts of the studied drainages, including the neighbouring Laguna dos Patos System. The Maquiné-Mampituba Group is composed of haplotypes found in the upper portions of the rio Maquiné, rio Três Forquilhas, rio Mampituba and rio Araranguá drainages, located in the valleys of the Serra Geral formation. The Tubarão Group is composed of haplotypes found exclusively in the headwaters of rio Tubarão. The haplotype network generated with the nDNA data show similar results by recovering the same three groups (Fig. 2).

Tajima's D and Fu's Fs neutrality test were not statistically significant for most populations. However, Fu's Fs was negative and significant for the populations of Tramandaí system lagoons (-3.099) and lower rio Araranguá (-1.937) indicating a recent demographic expansion. The mismatch distribution analyses revealed unimodal curves for populations from Coastal Plain Group and Tubarão Group, indicating a demographic expansion (Fig. 3). The multimodal curve for Maquiné-Mampituba Group indicates a possible demographic balance.

The AMOVA test corroborates the haplotype network (Table 2) and shows a high genetic differentiation among the three groups (Fst 0.98). It also shows significant genetic structure among populations of Maquiné-Mampituba Group (Fst 0.39) and among populations of Coastal Plain Group (Fst 0.33). The Fst values among groups were high (Table 3) and support recognition of the three major groups as different species, as well as genetic structure within Maquiné-Mampituba Group populations and within Coastal Plain Group populations.

Bayesian Inference analysis yielded similar results. The genes trees (mitochondrial set and nuclear gene) support the same topology and are consistent with the haplotypes groups found in the network. The clades recovered in the mitochondrial gene three are monophyletic and well supported by high values of posterior probability (PP = 1) (Fig. 4).

The species tree also supports the same topology from previous analyses, defining the Coastal Plain Group as sister to the Maquiné-Mampituba + Tubarão groups. The tree is supported by high values of posterior probability (PP = 1). Strict molecular clock analysis estimated that the three *Rhamdia* groups diverged from *Rhamdella zelimai* ~11 Ma. The Coastal Plain Group diverged from other two groups in the Pleistocene period ~1.8 Ma. The Maquiné-Mampituba and Tubarão groups diverged in the Miocene period about ~240 Ka (Fig. 5).

Data from measurements and counts are in Table 4. The morphometric analysis corroborates the recognition of the three groups identified by molecular approaches. The only count that separates these groups is the number of branched dorsal-fin rays (seven in Coastal Plain Group*vs.* six in the two other groups). The most significant measurements for the diagnosis of these three groups are illustrated in linear regression graphs (Fig. 6) and include: maxillary-barbel length, distance between dorsal and adipose fins, pelvic-fin length, head height, orbit size and head width at eye level.

Principal components analysis (PCA) differentiate the three groups of *Rhamdia* (Fig. 7). PC1 accounted for 84.42% of the total variance, PC2 accounted for 7.72%, and PC3 accounted for 1.68%. Since PC1 largely reflects size variation, the plot of PC2 vs. PC3 is presented. Variables loading heavily on PC2 include: dorsal fin to adipose fin distance (0.78), maxillary barbel length (-0.32), pelvic-fin length (-0.22), and head width at eye level (0.12). Variables loading heavily on PC3 are: dorsal fin to adipose fin distance (0.45), maxillary barbel length (0.41), mental barbel length (0.31), orbital diameter external (0.25), and head width at eye level (-0.21).

The results provide enough evidence to recognize the three groups as separate species. The Coastal Plain Group will be treated provisionally as *R.* aff. *quelen* because it occurs outside of the focal region (e.g., Laguna dos Patos System) and likely represents a widely-distributed taxon. The Maquiné-Mampituba Group and the Tubarão Group are described as new species herein.

Rhamdia gabrielae sp. nov**.**
(Fig. 8; Table 4)

Rhamdia sp. Malabarba *et al.,* 2013:74 [diagnosis; photo; distribution records in the rio Tramandaí drainage].

Holotype. UFRGS 22010, 194 mm SL, Brazil, state of Rio Grande do Sul, municipality of Maquiné, arroio Pinheiro, tributary of rio Maquiné, 29^{o}39’43”S, 50^{o}15’55”W; F. G. Becker, 19 Jun 1999.

Paratypes (total = 65). All from Brazil:UFRGS 18033, 10 (1 c&s), 139.63–194.16 mm SL, state of Rio Grande do Sul, municipality of Maquiné, rio Maquiné, 29^{o}38’52”S, 50^{o}13’03”W; J. M. Santos, 30 Mai 13. UFRGS 19094, 8, 118.88–139.74 mm SL, state of Rio Grande do Sul, municipality of Maquiné, rio Maquiné, 29^{o}35’16”S, 50^{o}16’13”W; L. R. Malabarba, C. Hartmann, R. C. Angrizani, 7 Jul 2013. MCP 27312, 1 (c&s), 136 mm SL, state of Rio Grande do Sul, municipality of Maquiné Lajeado, arroio Lajeado tributary of rio Maquiné, 29°34'16"S, 50°16'51"W; F. Becker, F. Vilella, 23 Mar 2001. MCP 28113, 1 (c&s), 125 mm SL, state of Rio Grande do Sul, municipality of Maquiné, arroio Forqueta tributary of rio Três Forquilhas, 29°31'59"S, 50°14'00"W; F. Vilella, J. Anza, 13 Mar 2001. UFRGS 18008, 3, 141.53–145.67 mm SL, state of Rio Grande do Sul, municipality of Três Forquilhas, rio Três Forquilhas, 29°32’56”S, 50°04’13”W; J. Santos, 31 Mai 2013. UFRGS 18010, 14, 121.46–193.37 mm SL, state of Rio Grande do Sul, municipality of Três Forquilhas, rio Três Forquilhas, 29°32’56”S, 50°04’13”W; J. Santos, 31 Mai 2013. MZUSP 36464, 5, 108.5–220.04 mm SL, state of Santa Catarina, municipality of Morrinhos do Sul, rio Faxinalzinho tributary to rio Mampituba, E. Pereira, R. Reis, J. Pezzi, 20 Jul 1999. UFRGS 19902, 8, 102.22–137.05 mm SL, state of Santa Catarina, municipality of Mãe dos Homens, rio Mãe dos Homens, tributary to rio Mampituba, 29°13’02”S, 49°59’58”W, data. UFRGS 6194, 1, 260.50 mm SL, state of Santa Catarina, municipality of Treviso, rio Mãe Luiza tributary to rio Araranguá, 49°28’18”S, 28°27’58”W; C. Ricken, R. Vicente, 21 Oct 2002. UFRGS 19903, 14, 61.13–270.63 mm SL, state of Santa Catarina, municipality of Jordão, rio Jordão, tributary of Araranguá, 28°35’11”S, 49°31’24”W, R.C. Angrizani, L.R. Malabarba, M.C. Malabarba, 21 Feb 2015.

Diagnosis. *Rhamdia gabrielae* is diagnosed from sympatric populations of *R.* aff. *quelen* by the number of branched dorsal-fin rays (6 *vs.* 7–8); last ray of dorsal fin not reaching origin of adipose fin (*vs.* last ray reaching origin of adipose fin); posterior tip of anal fin not reaching vertical through posterior insertion of adipose fin base (*vs.* anal fin surpassing posterior insertion of adipose fin). *Rhamdia gabrielae* is diagnosed from the neotype of *R. quelensensu* Silfvergrip by shorter maxillary-barbel (46.6–69.9% SL *vs.* 97% SL); longer caudal-peduncle (17.1–21.4% SL *vs.* 14.62% SL); shorter pelvic-fin (10.6–14.6% SL *vs.* 15.62% SL); shallower dorsal-fin (11.2–16% SL *vs.* 18.41% SL), shorter dorsal-spine (5–10.6% SL *vs.* 15.42% SL) and shorter pectoral-fin spine (8.1–10.9% SL *vs.* 15.42% SL). *Rhamdia gabrielae* is diagnosed from *R. eurycephala* by head width across orbital line (63.00–73.85% HL *vs.* 75.18–89.58% HL). *Rhamdia gabrielae* is diagnosed from *R. laticauda*, *R. foina*, *R. poeyi* and *R. itacaiunas* by the upper lobe of caudal fin smaller than lower lobe (*vs.* lower lobe longer than the upper lobe); from *R. humilis* and *R. nicaraguensis* by having serrations on both sides of pectoral-fin spine (*vs.* only anterior serrations in *R. humilis* and only posterior serrations in

R. nicaraguensis); from *R. xetequepeque* and *R. muelleri* by smaller orbit (15–19% HL *vs.* 30.5–36.9 in *R. xetequepeque*, 21.7–37.8% in *R. muelleri*); from *R. xetequepeque* and *R. laukidi* by having 40–41 post-Weberian vertebrae (*vs.* 31–34 in *R. xetequepeque,* typically 43–46 in *R. laukidi*); from *R. jequitinhonha*by the head sensory pores simple (*vs.* head sensory pores multiple); from *R. muelleri* by shorter maxillary barbel (46.6–69.9% SL *vs.* 73.9–12.9% SL in *R. muelleri*); from *R. cinerascens*, *R. guatemalensis*, *R. saijaensis*, and *R. voulezi* by shorter dorsal-fin base (11.4–13.1% SL vs. more than 14.3%;); from *R.voulezi* by the last ray of dorsal fin not reaching anterior insertion of adipose fin (*vs.* last ray reaching origin of adipose fin); and from *R. reddelli*, *R. enfurnada*, *R. zongolicensis*, *R. macuspanensis* and *R. laluchensis* by the lack of morphological adaptations to troglobitic life.

Description. Measurements in Table 1. Body elongated; cross section of trunk roughly circular at dorsal-fin origin and along dorsal-fin base, gradually compressed posteriorly to caudal peduncle. Anterodorsal profile of body convex from supraoccipital to dorsal-fin base. Dorsal-fin base nearly straight, posteroventrally slanted, and gently convex from dorsal fin to base of caudal fin. Ventral body profile nearly straight from mouth to caudal-fin base. Body widest at pectoral girdle and deepest at dorsal-fin origin. Caudal peduncle longer than deep. Number of post-Weberian vertebrae 40(2) or 41(1).

Head depressed and flat dorsally. Dorsal head profile straight and rising slightly from snout tip to supraoccipital in lateral view. Head shape somewhat triangular in dorsal view. Snout rounded anteriorly in dorsal view, longer than deep. Transverse distance between posterior nares slightly smaller than that between anterior nares. Mouth wide, subterminal, transverse gape larger than interorbital distance; snout projecting slightly beyond lower jaw. Large, fleshy rictal fold at corners of mouth. Both upper and lower lips with several longitudinal plicae.

Barbels flattened in cross section, wide at their base and tapering towards distal tip. Maxillary barbel longest; length variable, maximallyexceeding origin of adipose fin; inserted above upper lip and posterolateral to anterior nares. Two pairs of mental barbels with bases aligned. Outer mental barbels surpassing origin of pectoral fin. Inner mental barbels shorter than outer mental barbels, maximally reaching origin of pectoral fin. Gular fold distinct and *V*-shaped. Branchiostegal rays 5(3).

Gill rakers thick and moderately long, with 8(1), 9(1) and 10 (1) rakers on first ceratobranchial, and 2(3), on first epibranchial. Eye large, slightly elliptical (longitudinally elongated); rim circumscribed by deep, continuous invagination that is distinctly more pronounced along lateral border. Eye positioned dorsolaterally, approximately at midpoint between tip of snout and corner of opercular membrane; interorbital space wide. Pupil rounded. Sensory channels of head simple.

Dorsal fin with two unbranched rays and six branched rays, distal margin convex and base length less than or equal to fin height. First unbranched dorsal-fin ray small and not externally visible, second unbranched ray stiffened proximally, segmented distally. Dorsal-fin origin anterior to midlength between pectoral and pelvic-fin origins; insertion of last branched ray just before or at pectoral-fin origin. Tip of last branched dorsal-fin ray not reaching anterior insertion of adipose fin. Adipose fin long; with ascendant curve in in lateral profile and posterior lobe conspicuously free from body. Adipose-fin origin at vertical through middle of depressed pelvic fin and posterior insertion at final third of caudal peduncle.

Pectoral fin within one unbranched and five branched rays; when adpressed, reaching approximately origin of third branched dorsal-fin ray. Unbranched ray of pectoral fin stiffened, straight and with strong serrations along distal anterior side and delicate serrations along proximal posterior side. Pelvic fin rounded, approximately same size of pectoral fin, having one unbranched ray and five branched rays, distal tipsurpassing genital papilla, never reaching anal-fin origin. Pelvic-fin origin nearly at middle of standard length, after insertion of last dorsal-fin ray. Anal fin rounded, with three unbranched rays anteriorly, followed by eight, nine or ten branched rays; when adpressed, never exceeds posterior insertion of adipose-fin. Length of anal-fin base equal to that of dorsal fin. Caudal fin deeply forked, lobes rounded; dorsal lobe smaller in depth and length; seven branched rays in dorsal lobe and nine branched rays in ventral lobe

Colour of preserved specimens. Body grayish, with or without irregular small brown spots. Head and fins grey without spots. Ventral portion of head and body white. Dorsal fin with dark band across middle length of rays. Maxillary barbels same colour as body.

Distribution and Habitat. Restricted to the upstream portions of hydrographic systems of rio

Maquiné, rio Três Forquilhas, rio Mampituba and rio Araranguá, Brazil. Found in rapid waters over rocky bottoms.

Etymology. In honour of Gabriele Volkmer, the wife of the first author of this paper.

Rhamdia eurycephala sp. nov.
(Fig. 9; Table 4)

Holotype. UFRGS 19908, 246.6 mm SL, Brazil, state of Santa Catarina, municipality of Anitápolis, rio do Povoamento, hydrographic basin of rio Tubarão, 27º51’36”S, 49º07’50”W; R. C. Angrizani, L. R. Malabarba, M. C. Malabarba, 21 Feb 2015.

Paratypes (Total = 58). All from Brazil, Santa Catarina State:MCP 17617, 23 (2 c&s), municipality of Anitápolis, creek tributary to rio Pinheiro, rio Tubarão,27°53'59"S, 49°06'59"W; W. Koch, 15 Jan 1995. UFRGS 19908, 16 (1 c&s), collected with holotype, municipality of Anitápolis, rio do Povoamento, hydrographic basin of rio Tubarão, 27º51’36”S 49º07’50”W, R.C. Angrizani, L.R. Malabarba, M.C. Malabarba, 21 Feb 2015. MZUSP 121730, 3, municipality of Anitápolis, rio do Povoamento, hydrographic basin of rio Tubarão, 27°51’50”S 49º07´54”W, R.C. Angrizani, L.R. Malabarba, M.C. Malabarba, 21 Feb 2015. UFRGS 19906, 16, municipality of Anitápolis, rio do Povoamento, hydrographic basin of rio Tubarão, 27°51’50”S 49º07´54”W, R.C. Angrizani, L.R. Malabarba, M.C. Malabarba, 21 Feb 2015.

Diagnose. *Rhamdia eurycephala* differs from all congeneric species by having the head width at eye level greater than the body width at pectoral-girdle.

Description. Measurements in Table 1. Body elongated; cross section of trunk roughly circular at dorsal-fin origin and along dorsal-fin base, gradually compressed posteriorly to caudal peduncle. Anterodorsal profile of body convex from supraoccipital to dorsal-fin base. Dorsal-fin base nearly straight, posteroventrally slanted, and scarcely convex from dorsal-fin to base of caudal fin. Ventral body profile nearly straight from mouth to caudal-fin base. Body widest at pectoral-girdle and deepest at dorsal-fin origin. Caudal peduncle longer than deep. Number of post-Weberian vertebrae 39(1) or 40(2).

Head depressed and flat dorsally; wider than pectoral girdle at eye level. Dorsal head profile straight and rising from snout tip to supraoccipital in lateral view. Snout broadly rounded in dorsal view, longer than deep. Head shape polygonal in dorsal view; cheek convex, especially in large specimens due to enlargement of adductor mandibulae muscle. Dorsal limit of adductor mandibulae muscle marked by deep longitudinal facial ridge extending from base of maxillary barbel to level of anterior border of eye. Transverse distance between posterior nares slightly smaller than that between anterior nares. Mouth wide, subterminal, larger than interorbital distance; snout projecting slightly beyond lower jaw. Gape transverse, with large, fleshy rictal fold at corners. Both upper and lower lips with several longitudinal plicae.

Barbels flattened, wide at their base and tapering towards distal tip. Maxillary barbel longest; length variable, maximally exceeding first rays of dorsal fin; inserted above upper lip and posterolateral to anterior nare. Two pairs of mental barbels with bases aligned. Outer mental barbels barely reaching origin of pectoral fin in smaller specimens, never reaching pectoral fin in larger specimens. Inner mental barbels shorter than outer mental barbels. Tip of adpressed inner mental barbel extending beyond posterior margin of branchiostegal membrane. Gular fold distinct and *V*-shaped. Branchiostegal rays 5(3). Gill rakers thick and moderately long, with 9(2), 8(1) rakers on first ceratobranchial, and 2(3), on first epibranchial. Eye large, slightly elliptical (longitudinally elongated); rim circumscribed by deep, continuous invagination that is distinctly more pronounced along lateral border. Eye positioned dorsally, approximately at midpoint between tip of snout and corner of opercular membrane; interorbital space widel. Pupil rounded. Sensory channels of the head simple.

Dorsal fin within two unbranched rays and six branched rays, distal margin convex and base length less than or equal to fin height. First unbranched dorsal-fin ray small and not externally visible, second unbranched ray stiffened proximally, segmented distally. Dorsal-fin origin anterior to midlength between pectoral and pelvic-fin origins; insertion of last branched ray just before or at pectoral-fin origin. Tip of last branched dorsal-fin ray not reaching anterior insertion of adipose fin. Adipose fin long; with ascendant curve in lateral profile and conspicuous posterior free lobe. Adipose-fin origin at vertical through middle of depressed pelvic fin and posterior insertion at final third of caudal peduncle.

Pectoral fin small with one unbranched and five branched rays; when adpressed, reaching approximately origin of third branched dorsal-fin ray. Unbranched ray of pectoral-fin stiffened, straight and with strong serrations along distal anterior side and basal posterior side. Pelvic fin rounded, small (9.8–12.5% SL) and approximately same size as pectoral fin, having one unbranched ray and five branched rays, distal tipsurpassing genital papilla, never reaching anal-fin origin. Pelvic-fin origin nearly at middle of standard length, after insertion of last dorsal-fin ray. Anal fin rounded, with three unbranched rays and seven, eight or nine branched rays; when adpressed, never exceeds posterior insertion of adipose fin. Length of anal-fin base equal to that of dorsal fin. Caudal fin deeply forked, lobes rounded; dorsal lobe slightly smaller in depth and length; seven branched rays in dorsal lobe and nine branched rays in ventral lobe.

Colour of preserved specimens. Body grayish with or without irregular small brown spots. Head and fins grey without spots. Ventral portion of body and head white. Dorsal fin with dark band across middle length of rays. Maxillary barbels same colour as body.

Distribution. Known from upstream portion of two tributaries to the Tubarão River Basin, in the state of Santa Catarina, Brazil.

Etymology. The name comes from the Greek *eury* meaning broad, wide, and *kephale* meaning head. A noun in apposition.

Discussion

Our study supports the recognition of three distinct species of *Rhamdia* in the Southern Atlantic Coast of Brazil. All three species fit within the diagnosis of *R. quelen sensu* Silfvergrip (1996) and specimens of two of them (*R. gabrielae*, MZUSP 36464, and *R.* aff. *quelen*, MCP 9964) are among his list of examined specimens for that species. Two species are recognized herein as new and diagnosed with consistent patterns of morphological divergence and geographical distribution supported by genetic differences among them and from the populations of *Rhamdia* from the Coastal Plain. The third species seems to have a larger distribution, occurring in the lower portion of most drainages of the study area. Consistent with literature reports (e.g. Malabarba *et al*., 2013; Bertaco *et al.,* 2016), it is provisionally named *Rhamdia* aff. *quelen* and expected to occur in similar habitats of other drainages. *Rhamdia* aff. *quelen* differs from the neotype of *R. quelen* proposed by Silfvergrip (1996), but its formal description requires the examination of material from a larger geographic area.

The genetic and morphological distinctiveness of three species of *Rhamdia* in a small geographic area supports the hypothesis that *R. quelen* sensu Silfvergrip is a complex of species, corroborating other studies (Perdices *et al*., 2002; Hernandez *et al*., 2015; Garavello & Shibatta, 2016). Perdices *et al.* (2002), using mtDNA data, concluded that the geographic distribution of *R. quelen* is restricted to South America and does not reach Central America. Those authors thereby proposed to revalidate two Central American species, *R. guatemalensis* and *R. cinerascens,* from the synonymy of *R. quelen*. Hernandez *et al.* (2015) investigated the complex of *R. quelen* in the trans-Andean region of Ecuador using morphological and mtDNA data. Their results recovered three species which had been synonymized by Silfvergrip (1996), *R. guatemalensis, R. cinerascens* and *R. saijaensis* and indicated that the geographic distribution of *R. quelen* is restricted to cis-Andean South America. In cis-Andean South America, Garavello & Shibatta (2016) used morphological and cytogenetic data on populations from the Iguaçu River to raise *R. voulezi* and *R. branneri* from the synonymy of *R. quelen*. All of those studies refute the wide geographic distribution of *R. quelen*. Many species in the long synonymy of *R. quelen* proposed by Silfvergrip (1996) should be re-evaluated.

Among Atlantic coast river drainages in southeastern Brazil, differences in species composition between lower and upper courses were described previously for the Tramandaí River system. Within this drainage, species found in the main rivers of the Serra Geral formation differ from those in coastal plain lagoons (Malabarba & Isaia, 1992; Malabarba *et al.,* 2013). *Rhamdiagabrielae* is found in the upper portions of an area recognized for its endemism of neotropical fishes (ecoregion Tramandaí-Mampituba; Abell *et al*., 2008; Hirschman *et al.,* 2014; Thomaz *et al*., 2015). *Rhamdiaeurycephala* is found exclusively in an upper tributary of the Tubarão River. In contrast, *Rhamdia* aff. *quelen* occurs widely in lakes and lower stretches of those rivers.

Villa (1977) recognized two distinct morphological groups within Central American *Rhamdia*: the highland group with narrow and shallow body, short maxillary barbels and short adipose fin (characteristics associated with rapid rivers); and the lowland group with wider and deeper body, long maxillary barbels and long adipose fin. The pattern described by Villa (1977) in Central America is similar to the one found herein. The two new species occur in highland areas with rapids and rocky bottoms and have a shallow body and shorter adipose fin and maxillary barbels. The third species is found in lowland portions of coastal basins in deep and calm waters, often in lagoons, and has a deeper body, long adipose fin and long maxillary barbels. This suggests that such adaptive morphological patterns are common to the genus. The deep divergence between the Brazilian upland and lowland lineages may reflect an early ecological divergence in the radiation of *Rhamdia.*

Phylogeographic approach

At least two events of lineage diversification for genus *Rhamdia* are inferred among southern CDSEB populations. *Rhamdia* aff. *quelen* diverged from *R.gabrielae* + *R.eurycephala* about 1.8 Ma. *Rhamdiagabrielae* and *R.eurycephala* diverged from each other about 240 Ka. Both splits occurred during the Pliocene, a period characterized by significant climatic changes due to successive glaciations. Sea levels fluctuated considerably during this period, influencing the configuration of rivers along the Brazilian coastal plain. The rivers were more connected during the glaciations stages and more isolated during interglacial stages (Weitzman *et al.,* 1988; Dias *et al.,* 2014).

Weitzman *et al.* (1988) proposed that the high endemism and diversification of fishes on the Brazilian coastal plain are related to successive marine cycles during the Quaternary. Recent studies show the importance of these events for the genetic diversity of neotropical fishes (Beheregaray*et al.,* 2002; Torres & Ribeiro, 2009; Pereira *et al.,* 2013; Thomaz *et al.,* 2015). Thomaz *et al.,* 2015 suggested that the configuration of divides between paleodrainages drive the genetic diversification of fishes on the Brazilian coastal plain. Indeed, our results show that Quaternary eustatic movements are important for speciation and endemism on the coastal plain. However, *R.gabrielae* and *R.eurycephala* may have occupied a single paleodrainage according to the last glacial maximum model proposed by Thomaz *et al.* (2015). Therefore, additional phenomena may be related to speciation within *Rhamdia*.

The reconstruction of past sea levels (Fig. 10) suggests that these drainages have been isolated only for a short period of time, whereas during most of the time these drainages had connections, as demonstrated by Thomaz et al. (2015). The first divergence (about 1.8 Ma) would be related to the colonization of new environments, since the species would occupy different habitats within the same hydrographic basin. The second divergence (about 240 Ka) probably was triggered by an interglacial period, causing coastal drainages isolation and prompting speciation of upland lineages (*R.gabrielae* and *R.eurycephala*) between isolated drainages.

The rivers of southern CDSEB have been isolated for at least 26–19 Ka, the age of the last glacial maximum (Thomaz *et al.,* 2015). Likewise *R. gabrielae*, two other fish species (*Bryconamericus lethostigmus* and *Diapoma itaimbe*) are endemic to the Tramandai-Mapituba ecoregion, and syntopic, inhabiting the upper portions of the same river drainages. The three species, however, show different patterns of population structure. Populations of *R.gabrielae* show little genetic differentiation (Fst = 0.34), while *Diapomaitaimbe* exhibits high genetic structure (Fst = 0.89; Hirschmann et al., 2015) and *Bryconamericus lethostigmus* show no genetic structure (Hischmann et al., 2017) among the same rivers. Hischmann et al. (2017) postulated that such phylogeographic differences could be explained by three different scenarios, or a combination of them: (1) Different mtDNA evolutionary rates between the species; (2) Different colonization times in these drainages; and (3) Gene flow among populations through paleaodrainages hampering population structure. Taking into account that *D. itaimbe* is present in the region for about 2 Ma and *B. lethostigmus* for about 0.34 Ma (Hischmann et al., 2016) and that the ancestor of *R. gabrielae* lineage may have arrived in this ecoregion around 1.8 Ma, the different colonization times may explain the lowest genetic differentiation of *Bryconamericus lethostigmus* only (Hischmann et al., 2016). Considering the lower genetic differentiation of *R.gabrielae* populations compared to *D. itaimbe*, but the similar time of colonization of these river drainages (2 Ma and 1.8 Ma, respectively), it can be assumed that *R. gabrielae* had a more intense gene flow among populations over time through palaeodrainages during the marine regressions than *D. itaimbe*.

Successive cycles of sea level can connect or isolate populations, promoting remarkable effects on population dynamics. Potentially, during marine transgressions, population size can be reduced, while during marine regression, the population size can be increased. According to our results of Neutrality and Mismatch distribution tests, two different patterns of demographic histories were found among species of *Rhamdia* in Tramandaí-Mampituba ecoregion. For *R.gabrielae*, our data indicate a demographic history of balanced populations, suggesting that this species has occupied a stable environment which was not affected by marine cycles. In contrast, populations of *R.* aff. *quelen* are expanding, suggesting that this species has occupied an unstable environment with successive marine cycles. A similar pattern was reported for the Brazilian coastal plain in Paraná state, wherein seven lowland species show strong signs of population growth related to marine cycles and four highland species presented stable populations (Tschá *et al.,* 2016).

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References

Abell, R, Thieme, M.L, Revenga, C, Bryer, M, Kottelat, M, Bogutskaya N, Coad, B, Mandrak, N, Balderas, S.C, Bussing, W, Stiassny, M.L.J, Skelton, P, Allen, G.R, Unmack, P, Naseka, A, Ng, R, Sindorf, N, Robertson, J, Armijo, E, Higgins, J.V, Heibel, T.J, Wikramanayake, E, Olson, D, López, H.L, Reis, R.E, Lundberg, J.G, Pérez, M.H.S, Petry, P. (2008). Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience*, 58, 403–414.

Bandelt, H.J, Forster, P, Röhl, A. (1999). Median-joining networks for inferring intraspecfic phylogenies. *Molecular Biology and Evolution*, 16, 37–48.

Beheregaray, L.B, Sunnucks, P, Briscoe, D.A. (2002). A rapid fish radiation associated with the last sea-level changes in southern Brazil: the silverside *Odontesthesperugiae* complex. *Proceedings of the Royal Society of London B: Biological Sciences,*269(1486), 65–73.

Bermingham, E, McCafferty, S.S, Martin, A.P. (1997). Fish biogeography and molecular clocks: perspectives from the Panamanian Isthmus. In: Kocher, T.D, Stepien, C.A, eds. *Molecular Systematics of Fishes*. San Diego, Academic Press, pp. 113–128.

Bertaco, V.A, Ferrer, J, Carvalho, F.R, Malabarba, L.R. (2016). Inventory of the freshwater fishes from a densely collected area in South America - a case study of the current knowledge of Neotropical fish diversity. *Zootaxa,*4138(3), 401–440.

Bichuette, M.E, Trajano, E. (2005). A new cave species of *Rhamdia* (Siluriformes: Heptapteridae) from Serra do Ramalho, northeastern Brazil, with notes on ecology and behavior. *NeotropicalIchthyology,*3(4), 587–595.

Bizerril, C.R.S.F. 1994. Análise taxonômica e biogeográfica da ictiofauna de água doce do leste brasileiro. *Acta Biologica Leopoldensia,* 16, 51–80.

Brannan, T, Althoff, B, Cabasa, F, Dixon, F, Jacobs, L.J, Nekorystnova, I, & Rubenstein, S. (2002). SigmaPlot. Exact graphics for exact science. *SPPS. INC.*

Buckup, P.A. (2011). The eastern Brazilian Shield. In: Albert JS, & Reis RE, eds. *Historical Biogeography of Neotropical Freshwater Fishes*. Berkeley, University of California Press, pp. 203–210.

Bussing, W.A. (1998). *Freshwater fishes of Costa Rica*. Editorial Universidad de Costa Rica, vol 4.

Dias, M.S, Oberdorff, T, Hugueny, B, Leprieur, F, Jezequel, C, Cornu, J.F, Brosse, S, Grenouillet, G. & Tedesco, P.A. (2014). Global imprint of historical connectivity on freshwater fish biodiversity. *Ecology Letters,* 17, 1130–1140.

Drummond, A.J, Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC evolutionary biology,*7(1), 214.

Excoffier, L, Laval, G. & Schneider, S. (2005). Arlequin 3.01: An integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online,* 1, 47–50.

Fu, Y.X. (1997). Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics*,147(2), 915–925.

Galvis, G, Mojica, J.I, Camargo, M. (1997). *Peces del Catatumbo*. Santafé de Bogotá, Asociación Cravo Norte, pp. 188.

Garavello, J.C, Shibatta, O.A. (2016). Reappraisal of *Rhamdiabranneri* Haseman, 1911 and *R. voulezi* Haseman, 1911 (Siluriformes: Heptapteridae) from the rio Iguaçu with notes on their morphometry and karyotype. *Neotropical Ichthyology,*14(1).

Greenfield, D.W, Thomerson, J.E. (1997). *Fishes of the continental waters of Belize.* Florida, University Press of Florida.

Hall, T.A. (1999). BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series,* 41, 95–98.

Hammer, Ø, Harper, D.A.T, Ryan, P.D. (2009). *PAST-Palaeontological Statistics, ver. 1.89.* Oslo, University of Oslo, pp. 1–31.

Hernández, C.L, Ortega-Lara, A, Sánchez-Garcés, G.C, & Alford, M.H. (2015). Genetic and morphometric evidence for the recognition of several recently synonymized species of trans-Andean Rhamdia (Pisces: Siluriformes: Heptapteridae). *Copeia*, *103*(3), 563-579.

Hirschmann, A, Malabarba, L.R, Thomaz, A.T. & Fagundes, N.J.R. (2015). Riverine habitat specificity constrains dispersion in a Neotropical fish (Characidae) along Southern Brazilian drainages. *ZoologicaScripta,*44(4), 374–382.

Hirschmann, A, Fagundes, N.J, & Malabarba, L.R. (2017). Ontogenetic changes in mouth morphology triggers conflicting hypotheses of relationships in characid fishes (Ostariophysi: Characiformes). *Neotropical Ichthyology*, *15*(1), e160073.

Ivanova, N.V, Zemlak, T.S, Hanner, R.H, Hebert, P.D. (2007). Universal primer cocktails for fish DNA barcoding. *Molecular Ecology Notes,*7(4), 544–548.

Lanfear, R, Calcott, B, Ho, S.Y.W. & Guindon, S. (2012). PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution,* 29, 1695–1701.

Li, C, Ortí, G, Zhang, G & Lu, G. (2007). A practical approach to phylogenomics: the phylogeny of ray-finned fish (Actinopterygii) as a case study. *BMC Evolutionary Biology,*7(1), 1.

Li, W.L.S. & Drummond, A.J. (2012). Model averaging and Bayes factor calculation of relaxed molecular clocks in Bayesian phylogenetics. *Molecular Biology and Evolution,* 29, 751–761.

Librado, P, Rozas, J. (2009). DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics,* 25, 1451–1452.

Lopez, H.L, Morgan, C.C. & Montenegro, M.J. (2002). Ichthyological ecoregions of Argentina. *ProBiota,* 1, 1–68.

Ornelas-García, C.P, Domínguez-Domínguez, O. & Doadrio, I. (2008). Evolutionary history of thefish genus *Astyanax* Baird & Girard (1854) (Actinopterygii, Characidae) in Mesoamerica reveals multiple morphological homoplasies. *BMC Evolutionary Biology,* 8, 340–357.

Malabarba, L.R. & Isaia, E.A. (1992). The fresh water fish fauna of the rio Tramandaí drainage, Rio Grande do Sul, Brazil, with a discussion of its historical origin. *Comunicações do Museu de Ciências e Tecnologia, PUCRS, Série Zoologia* 5, 197–223.

Malabarba, L.R, Neto, P.C, Bertaco, V.D.A, Carvalho, T.P, dos Santos, J.F. & Artioli, L.G.S. (2013). *Guia de identificação dos peixes da bacia do rio Tramandaí*. Porto Alegre, Via Sapiens.

Miller, K.G, Mountain, G.S, Wright, J.D. & Browning, J.V. (2011). A 180-million record of sea level and ice volume variations from continental margin and deep-sea isotopic records. *Oceanography,* 24, 40.

Myers, N, Mittermeier, R.A, Mittermeier, C.G, Fonseca, G.A.B, Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature,* 403, 853–858.

Palumbi, S, Martin, A, Romano, S, McMillan, W.O., Stice, L. & Grabowski, G. (1991). The simple fool's guide to PCR. Honolulu, University of Hawaii.

Perdices, A, Bermingham, E, Montilla, A. & Doadrio, I. 2002. Evolutionary history of the genus *Rhamdia* (Teleostei: Pimelodidae) in Central America. *Molecular Phylogenetics and Evolution,*25(1), 172–189.

Pereira, T.L, Santos, U, Schaefer, C.E, Souza, G.O, Paiva, S.R, Malabarba, L.R, Schmidt, E.E. & Dergam, J.A. (2013). Dispersal and vicariance of *Hoplias malabaricus* (Bloch, 1794) (Teleostei, Erythrinidae) populations of the Brazilian continental margin. *Journal of Biogeography,* 40, 905–914.

Reeves, R.G.U.Y. & Bermingham, E. (2006). Colonization, population expansion, and lineage turnover: phylogeography of Mesoamerican characiform fish. *Biological*

Journal of the Linnean Society, 88, 235–255.

Reis, R.E. & Schaefer, S.A. (1998). New cascudinhos from southern Brazil: systematics, endemism, and relationships (Siluriformes, Loricariidae, Hypoptopomatinae). *American Museum Novitates,* 3254, 1–25.

Ribeiro, A.C. (2006). Tectonic history and the biogeography of the freshwater fishes from the coastal drainages of eastern Brazil: an example of faunal evolution associated with a divergent continental margin. *Neotropical Ichthyology,* 4(2), 225–246.

Romero, A. & Paulson, K.M. (2001). It's a wonderful hypogean life: a guide to the troglomorphic fishes of the world. In: *The biology of hypogean fishes*. Springer Netherlands, 13–41.

Silfvergrip, A.M.C. (1996). *A systematic review of the Neotropical catfish genus* Rhamdia*(Teleostei, Pimelodidae)*. Stockholm, Swedish Museum of Natural History.

Sivasundar, A, Bermingham, E. & Orti, G. (2001). Population structure and biogeography of migratory freshwater fishes (*Prochilodus*: Characiformes) in major South American rivers. *Molecular Ecology,*10(2), 407–417.

Tajima, F. (1989). Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics,*123(3), 585–595.

Thomaz, A.T, Malabarba, L.R., Bonatto, S.L. & Knowles, L.L. (2015). Testing the effect of palaeodrainages versus habitat stability on genetic divergence in riverine systems: study of a Neotropical fish of the Brazilian coastal Atlantic Forest. *Journal of Biogeography*, 42(12): 2389–2401.

Thompson JD, Higgins DG, Gibson TJ. (1994). CLUSTAL W: improving the sensitivity of progressive multiple sequence" alignment through sequence weighting, position specific gap penalties and weight matrix choice. *Nucleic Acids Research,* 2, 4673–4680.

Tomazelli, L.J, Dillenburg, S.R, Villwock, J.A. (2000). Late Quaternary geological history of Rio Grande do Sul coastal plain, southern Brazil. *Revista Brasileira de Geociências,* 30, 474–476.

Torres, R.A, Ribeiro, J. (2009). The remarkable species complex *Mimagoniatesmicrolepis* (Characiformes: Glandulocaudinae) from the Southern Atlantic Rain forest (Brazil) as revealed by molecular systematic and population genetic analyses. *Hydrobiologia,* 617, 157–170.

Tschá, M.K, Baggio, R.A, Marteleto, F.M, Abilhoa, V, Bachmann, L. & Boeger, W.A. (2016). Sea level variations have influenced the demographic history of estuarine and freshwater fishes of the coastal plain of Paraná, Brazil. *Journal of Fish Biology,* 1–12

Vari, R.P. (1988). The Curimatidae, a lowland Neotropical fish family (Pisces: Characiformes): distribution, endemism, and phylogenetic biogeography. In: Vanzolini, P.E. & Heyer, W.R, eds. *Proceedings of a Workshop on Neotropical Distribution Patterns*. Rio de Janeiro, Academia Brasileira de Ciências, pp. 343–377.

Villa, J. (1977). A new species of pimelodid catfish of the genus *Rhamdia* from Nicaragua, Central Amercia. *Brenesia,* 2(13), 133–142.

Villwock, J.A. & Tomazelli, L.J. (1995). Geologia costeira do Rio Grande do Sul. *Notas Técnicas,* 8, 1–45.

Weber, A, Allegrucci, G. & Sbordoni, V. (2003). *Rhamdia laluchensis*, a new species of troglobitic catfish (Siluriformes: Pimelodidae) from Chiapas, Mexico. *Ichthyological Exploration of Freshwaters,*14(3), 273–280.

Weitzman, S.H, Menezes, N.A. & Weitzman, M.J. (1988). Phylogenetic biogeography of the Glandulocaudini (Teleostei: Characiformes, Characidae) with comments on the distributions of other freshwater fishes in eastern and southeastern Brazil. *Proceedings of a workshop on neotropical distribution patterns*. Rio de Janeiro, Academia Brasileira de Ciências, pp. 379–427.

Wilkens, H. (2001). Convergent adaptations to cave life in the *Rhamdia laticauda* catfish group (Pimelodidae, Teleostei). In: *The biology of hypogean fishes*. Springer Netherlands, pp. 251–261.

Figures

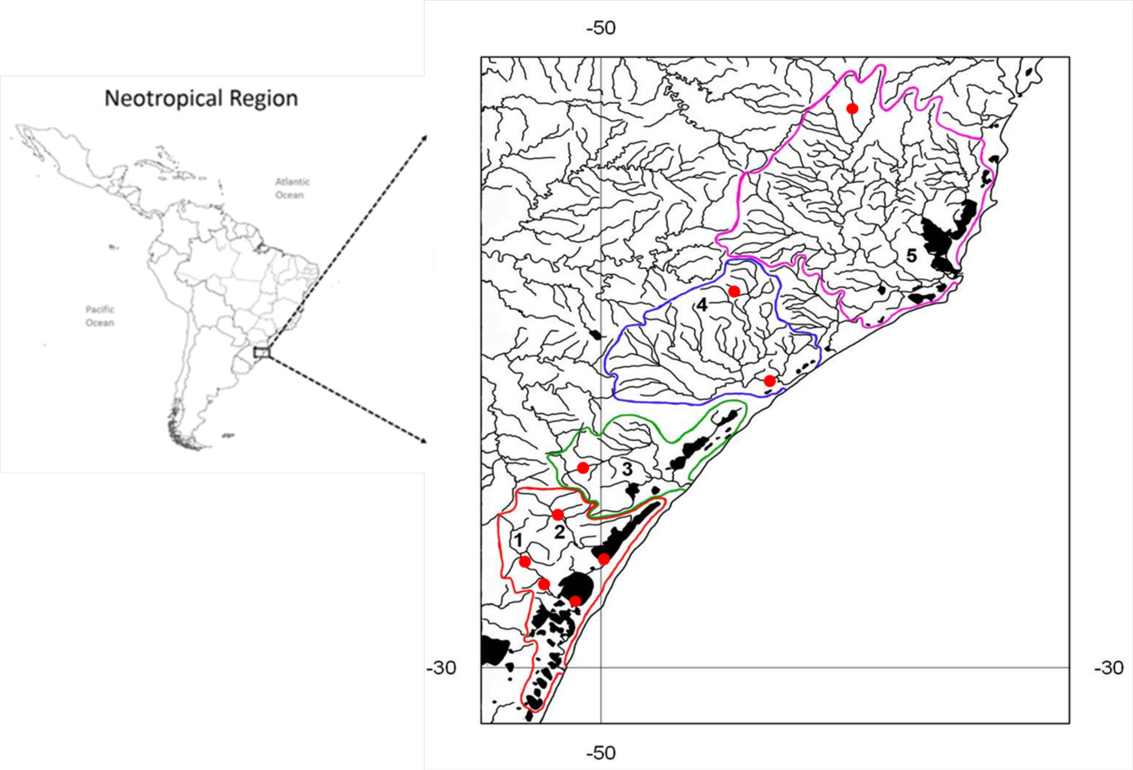

Figure 1. Study area: 1) rio Maquiné; 2) rio Três Forquilhas; 3) rio Mampituba; 4) rio Araranguá, and 5) rio Tubarão. The hydrographic basins are surrounded by coloured lines. Rivers 1–4 form part of the Tramandaí-Mampituba ecoregion. Red dots represent collection localities of *Rhamdia* specimens used in genetic analyses.

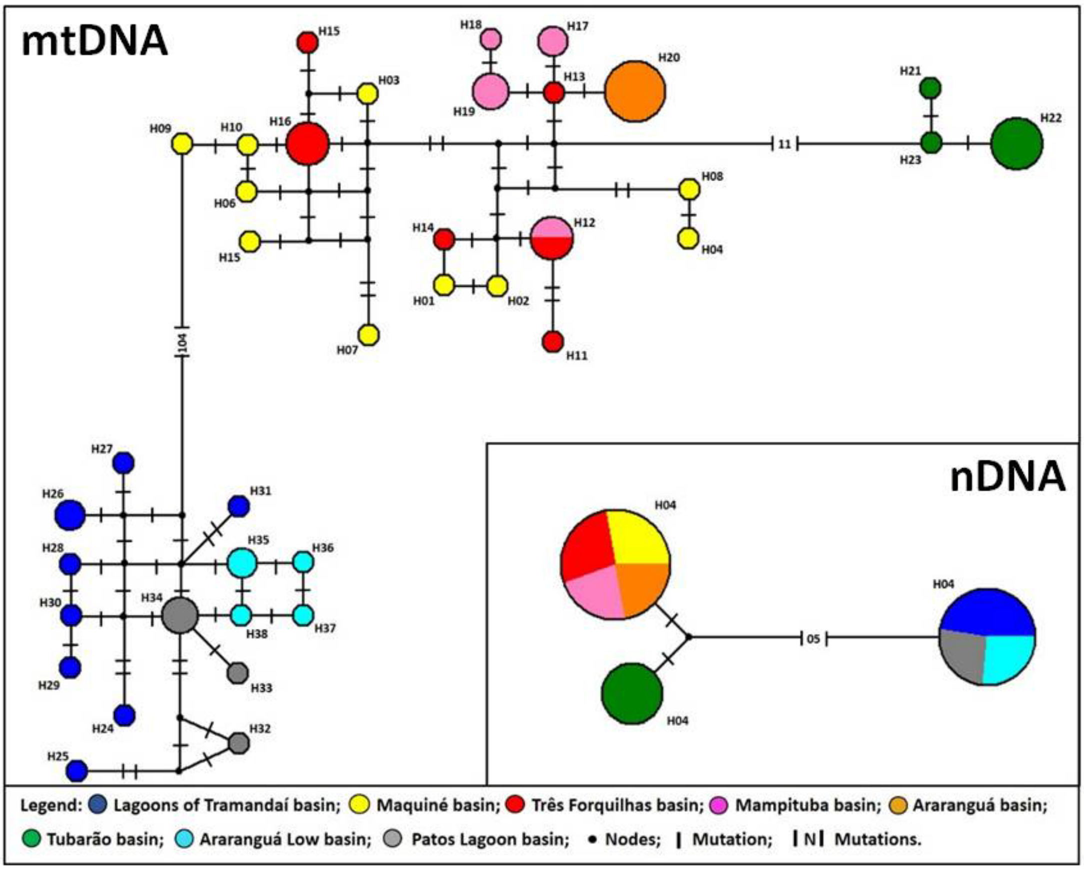

Figure 2. Haplotype network using Median-Joining for *Rhamdia* samples for mitochondrial data (mtDNA) and nuclear data (nDNA). Each circle represents a single haplotype and its size is proportional to its frequency. Different colours represent different populations. Coastal Plain Group (*Rhamdiaaff. quelen*) represented in blues and gray, Tubarão Group (*Rhamdia eurycephala*) represented in green, and Maquiné-Mampituba Group (*Rhamdia gabrielae*) represented in hot colours.

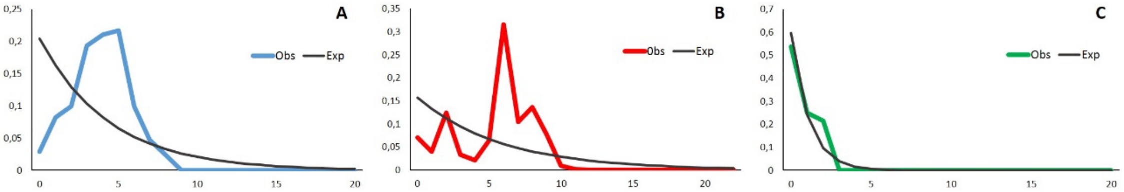

Figure 3. Mismatch distribution for: (A) Coastal Plain Group (*Rhamdiaaff. quelen*), (B) Maquiné-Mampituba Group(*Rhamdia gabrielae*), and (C) Tubarão Group (*Rhamdia eurycephala*). Coloured line is observed data and gray line is expected data.

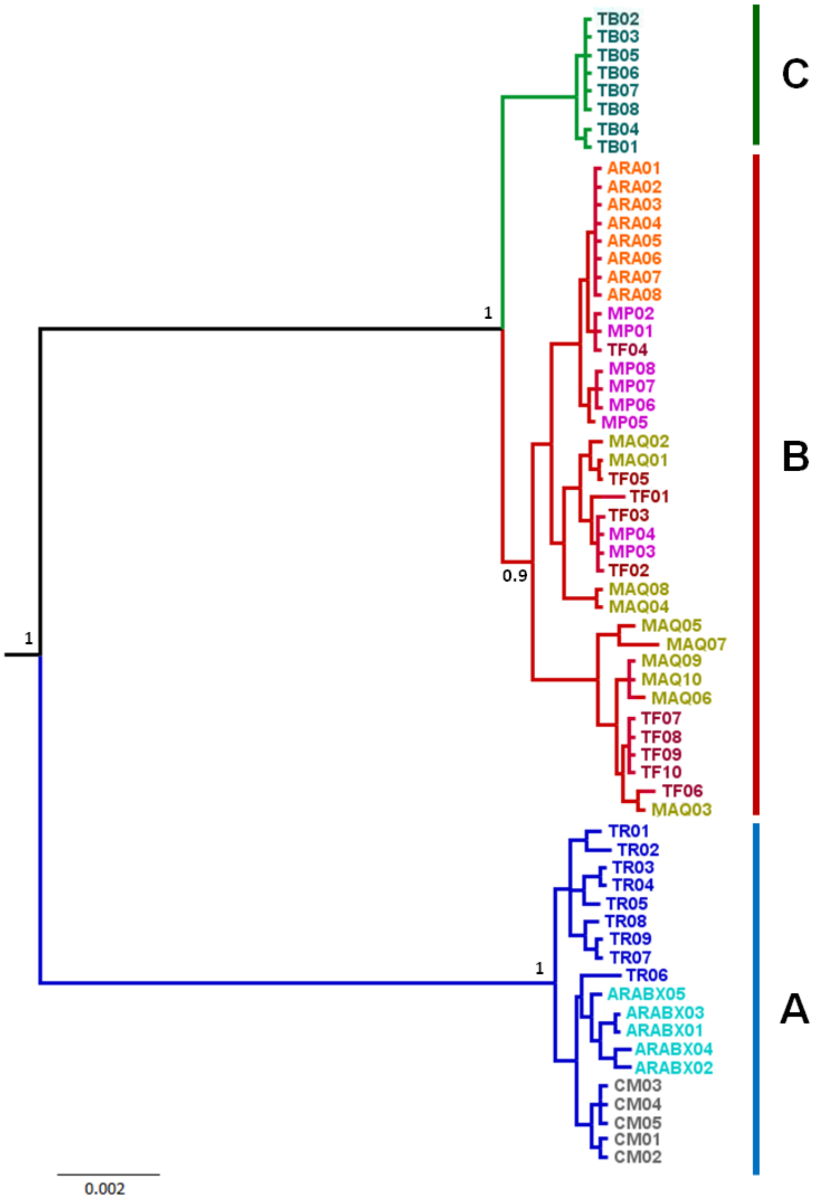

Figure 4. Gene tree for all DNA data set produced by Bayesian analysis in MrBayes. Values on nodes represent Bayesian posterior probabilities: (A)Coastal Plain Group (*Rhamdiaaff. quelen*), (B)Maquiné-Mampituba Group (*Rhamdia gabrielae*) and (C) Tubarão Group (*Rhamdia eurycephala*). TB (green) – rio Tubarão; ARA (Orange) – upper rio Araranguá; MP (pink) – rio Mampituba; TF (red) – rio Três Forquilhas; MAQ (yellow) – rio Maquiné; TR (dark blue) – Tramandaí lagoons; ARAB (light blue) – lower rio Araranguá; CM (grey) – laguna dos Patos

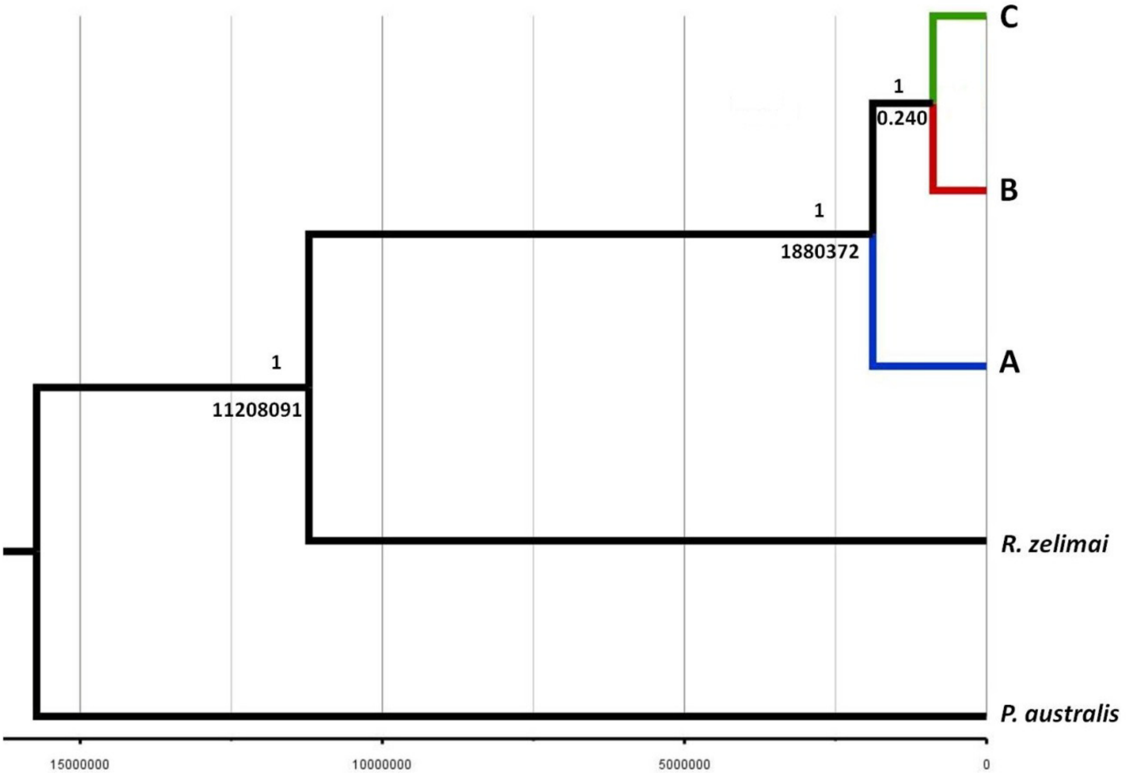

Figure 5. Species tree with strongest support according to Bayesian posterior probabilities produced in Beast. Numbers on the top represent posterior probabilities and number on the bottom of are the divergence dates of the respective node. The colourful branches indicate the groups recovered in previous analyses. (A)Coastal Plain Group, (B)Maquiné-Mampituba Group (*Rhamdia gabrielae*) and (C) Tubarão Group (*Rhamdia eurycephala*).

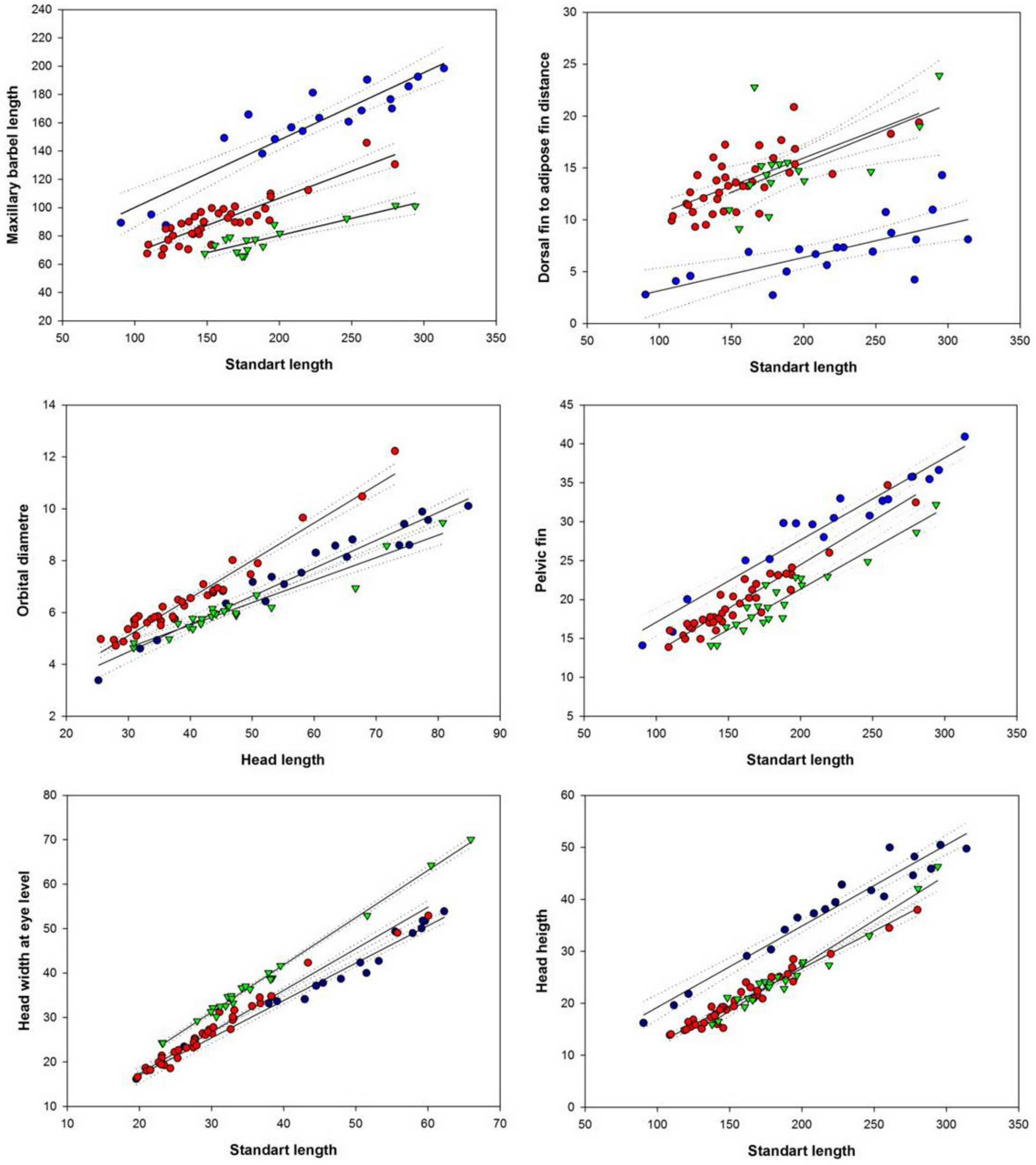

Figure 6. Linear regression plots of the main morphological measurements that diagnose the two new species of *Rhamdia* in southern CDSEB region. Blue circle: *Rhamdia* aff. *quelen*; red circle: *Rhamdia gabrielae*; green triangle: *Rhamdia eurycephala*. Dashed lines represent 95% confidence interval.

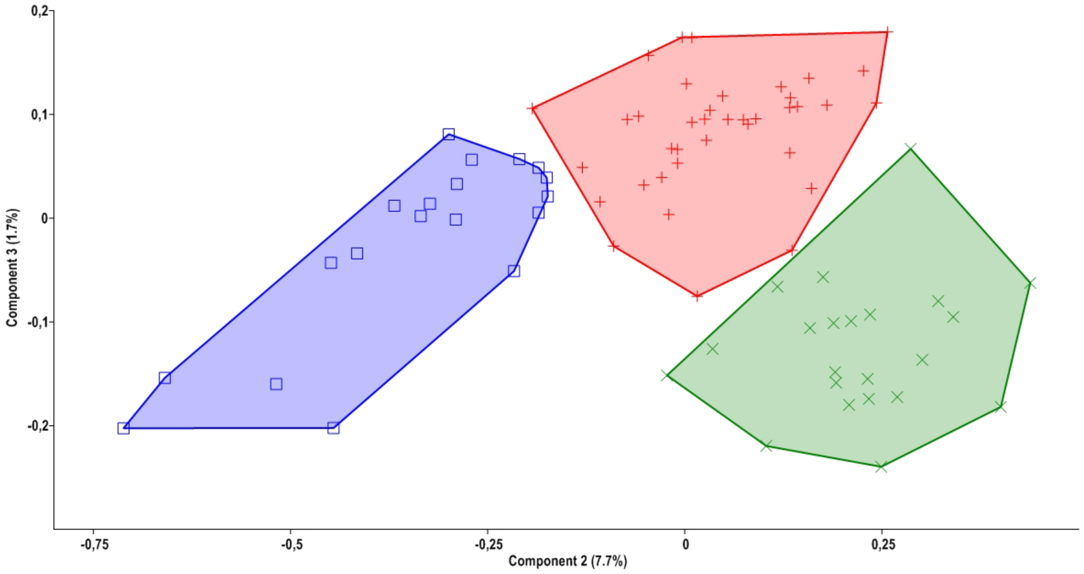

Figure 7. Scatter plot of combined samples of *Rhamdiagabrielae* (red), *Rhamdiaeurycephala* (green) and *Rhamdia* aff. *quelen* (blue) on the second and third principal component axis.

Figure 8. Holotype of *Rhamdiagabrielae* (UFRGS 20010), 194 mm SL. In dorsal, lateral, and ventral views.

Figure 9. *Rhamdia eurycephala* (UFRGS 19908), 246.6 mm SL. In dorsal, lateral, and ventral views.

[redacted]

Figure 10. Variation in sea level for the last 2 Ma shown according to Miller *et al*. (2011). The red lines represent the points of divergence between the lines of Rhamdia, A) First divergence and B) second divergence

Tables

Table 1. Species, drainage, voucher specimen and geographical coordinates of tissue samples used in the molecular analyses.

Species	N	Drainage	Voucher	Coordinates
Rhamdiagabrielae	5	Rio Maquiné	UFRGS 18093	S29°39’09”/W50°12’33”
Rhamdiagabrielae	5	Rio Maquiné	UFRGS 19094	S29°35’16”/W50°16’13”
Rhamdiagabrielae	10	Rio Três Forquilhas	UFRGS 18010	S29°32’56”/W50°04’13”
Rhamdiagabrielae	8	Rio Mampituba	UFRGS 19902	S29°13’02”/W49°59’58”
Rhamdiagabrielae	8	Upper rio Araranguá	UFRGS 19903	S28°35’11”/W49°31’24”
Rhamdiaeurycephala	8	Upper rio Tubarão	UFRGS 19904	S27°51’36”/W49°07’50”
Rhamdiaaff. quelen	5	Lower rio Araranguá	UFRGS 21360	S28°55’36”/W49°33’25”
Rhamdiaaff. quelen	5	Lagoa Itapeva	UFRGS 19424	S29°36’14”/W49°59’27”
Rhamdiaaff. quelen	4	Lagoa dos Quadros	UFRGS 17717	S29°39’58”/W50°01’53”
Rhamdia aff. quelen	5	Lagoa dos Patos	UFRGS 18425	S31°00’14”/W52°05”58”
Rhamdella zelimai	1	Rio Maquiné	UFRGS 19092	S29°35’16”/W50°16’13”
Pimelodella australis	1	Lagoa dos Quadros	UFRGS 19510	S29°39’58”/W50°01’53”

Table 2. Molecular variance (AMOVA) for mtDNA data among and within 1) all groups, 2) Coastal Plain Group populations, and 3) Maquiné-Mampituba Group populations.

	1. All groups		2. Coastal Plain Group		3. Maquiné-Mampituba Group	
Source of variation	d.f.	Percentage of variation	d.f.	Percentage of variation	d.f.	Percentage of variation
Among groups	2	92.31	-	-	-	-
Among populations	3	2.87	3	33.94	3	34.73
Within population	48	4.82	32	66.06	32	65.27
Fst	0.95182		0.33944		0.34735	

Table 3. Fst values among analysed populations of Maquiné-Mampituba Group (MAQ – rio Maquiné, TF – rio Três Forquilhas, MAM – rio Mampituba, ARA – Upper rio Araranguá), Tubarão Group (TUB – rio Tubarão), and Coastal plain Group (TRA - Lagoons of Tramandaí basin, LARA - Lower rio Araranguá and PATOS - Patos basin). Significant values in bold.

	MAQ	TF	MAM	ARA	TUB	TRA	LARA	PATOS
MAQ	-							
TF	0.02078	-						
MAM	**0.28350**	**0.27844**	**-**					
ARA	**0.51768**	**0.58250**	**0.45714**	-				
TUB	**0.71898**	**0.78250**	**0.84111**	**0.97365**	**-**			
TRA	**0.95122**	**0.95882**	**0.96420**	**0.97775**	**0.97471**	**-**		
LARA	**0.95716**	**0.96752**	**0.97654**	**0.99606**	**0.99208**	**0.36851**	**-**	
PATOS	**0.95578**	**0.96752**	**0.97654**	**0.99606**	**0.99070**	**0.24018**	**0.50000**	**-**

Table4. Morphometric data of the three species of *Rhamdia*.

	***Rhamdiagabrielae* (n=38)**			***Rhamdiaeurycephala* (n=20)**			***Rhamdia* aff. *quelen* (n=22)**	
	min-max	Mean±SD	Holotype	min-max	Mean±SD	Holotype	min-max	Mean±SD
Standard length (mm)	109.0-280.0	158.0	194.0	137.8-294.0	188.48	246.6	90.4-314.0	218.16
Percent of Standard Length								
Maxillary-barbel length	46.6-69.9	58.1±6.2	56.5	31.2-47.7	39..7±4.7	37.4	61.2-98.7	74.2±11.1
Pectoral-girdle width	17.5-21.5	19.0±0.9	18.3	16.4-22.4	19.0±1.5	20.0	19.7-23.4	21.0±0.8
Pelvic-girdle width	7.3-11.8	9.9±0.8	10.3	8.4-11.4	9.8±0.8	10.5	9.0-11.5	10.5±0.6
Body depth	15.1-20.9	17.1±1.1	17.1	14.7-19.1	16.8±1.4	17.3	20.1-22.9	21.3±0.8
Pre-dorsal distance	34.2-38.4	35.8±0.9	34.3	31.6-38.9	35.4±2.0	37.2	34.5-39.3	37.1±1.1
Dorsal-fin to caudal-fin distance	52.0-56.9	54.1±1.3	54.2	48.6-57.9	53.8±2.3	50.4	44.5-51.0	48.1±1.6
Dorsal-fin to adipose-fin distance	6.2-11.8	8.8±1.4	07.9	5.8-13.7	8.3±1.8	5.9	1.5-4.8	3.2±.8
Pre-pectoral distance	22.4-27.9	24.8±1.1	23.7	21.3-26.0	23.7±1.4	25.9	25.2-28.6	26.7±0.9
Pre-pelvic distance	46.5-53.6	49.6±1.8	49.4	45.9-51.7	49.0±1.6	50.2	46.7-54.7	51.3±1.9
Pre-anal distance	64.4-72.2	68.6±1.7	67.2	64.7-70.7	68.1±1.2	69.4	65.0-73.7	69.7±2.4
Pelvic-fin to anal-fin distance	18.2-21.6	20.0±0.9	18.8	18.3-21.3	19.6±0.83	19.15	16.4-22.0	19.4±1.3
Adipose-fin to caudal-fin distance	7.6-10.4	8.9±0.7	08.2	9.0-11.6	10.4±0.7	9.6	8.3-13.5	10.7±1.2
Caudal-peduncle length	17.1-21.4	19.3±1.1	20.7	17.3-21.0	19.6±1.1	17.3	17.1-21.0	19.1±1.0
Caudal-peduncle depth	9.4-12.1	10.7±0.5	12.8	9.4-10.6	10.1±0.4	10.0	9.2-11.2	10.2±0.4
Pelvic-fin length	10.6-14,6	12.6±0.8	13.1	09.4-11.5	10.6±0.6	10.0	12.2-16.5	13.8±1.3
Anal-fin base length	10.9-14.9	12.8±0.8	14.8	11.3-14.2	12.3±0.6	12.1	08.7-14.3	12.1±1.5
Anal-fin length	18.6-22.6	20.4±0.9	20.0	17.3-21.5	19.5±1.0	18.7	15.8-22.3	20.1±1.6
Dorsal-fin base length	11.4-13.1	13.3±0.7	12.8	12.4-14.1	13.2±0.4	12.4	13.9-19.0	17.0±1.1
Dorsal-fin height	11.2-16.0	13.5±1.0	13.0	11.6-16.0	13.2±1.1	12.3	11.6-17.1	14.7±1.4

Dorsal-fin spine length	5.0-10.6	7.0±1.1	6.1	5.7-7.8	6.8±0.6	5.8	7.0-9.7	8.6±0.9
Pectoral-fin spine length	8.1-10.9	9.9±0.8	9.0	6.6-9.7	8.4±0.8	7.6	11.2-14.3	12.8±0.8
Adipose-fin base length	31.7-39.4	36.1±1.9	37.2	32.6-39.0	35.4±1.5	36.5	32.0-34.7	33.5±0.9
Head length	22.7-27.1	25.0±1.0	23.3	23.1-27.5	25.4±1.1	27.0	25.6-28.7	27.3±1.0
Percent of Head Length								
Snout length	40.1-46.7	42.5±1.7	41.9	40.1-45.1	42.5±1.5	44.7	36.9-45.2	39.9±2.3
Snout height	33.4-41.0	37.4±1.9	37.7	33.6-44.2	38.7±2.9	35.8	34.0-45.7	40.3±3.2
Head height	43.1-61,9	52.1±3.6	53.3	49.5-58.7	53.6±2.7	49.4	58.4-68.5	63.7±3.1
Orbital diameter	15.0-19.0	16.2±1.0	17.4	10.4-14.7	13.1±1.1	10.4	11.4-14.7	13.1±0.9
Interorbital distance	28.1-37.0	32.5±2.2	32.5	29.0-38.4	33.1±2.3	35.7	34.0-42.2	37.7±2.0
Mouth length	44.1-56.4	49.1±3.1	50.22	47.9-54.7	50.9±1.9	50.9	43.2-52.1	47.4±2.6
Maxillary-barbels distance	34.0-42.3	37.9±2.1	37.4	27.8-41.4	37.6±3.2	38.1	34.2-40.2	37.3±1.6
Anterior nares distance	18.7-25.6	22.5±1.7	25.24	22.9-25.6	24.7±0.6	24.9	19.7-26.2	22.4±1.5
Anterior nares to posterior nares distance	14.3-17.9	16.0±0.9	15.65	13.3-16.0	14.6±0.8	14.4	11.4-16.0	13.9±1.4
Posterior nares to orbit distance	15.6-19.8	18.0±1.2	19.19	15.3-19.2	17.8±1.1	18.8	15.3-19.6	18.0±1.1
Posterior nares distance	15.8-19.9	17.8±1.1	18.26	18.0-20.5	19.2±0.8	19.3	18.5-24.1	20.6±1.4
External mental-barbels distance	31.7-41.6	36.5±2.9	39.5	37.7-44.7	41.1±1.9	37.6	33.3-40.0	36.6±1.9
Internal mental-barbels distance	13.4-22.7	17.6±2.2	22.08	16.4-23.2	19.6±1.7	18.8	15.4-20.4	17.6±1.4
Distance between mental-barbel	8.8-12.5	9.8±0.9	9.9	8.9-12.3	10.7±0.9	9.4	7.7-11.3	9.7±0.9
External mental-barbel length	81.0-122	100±10.8	102.0	54.4-93.1	77.3±11.7	54.4	87.2-114.9	101.0±8.3
Internal mental-barbel length	24.0-83.8	58.7±11.4	61.5	32.0-63.4	47.7±9.1	32.4	43.1-70.7	56.3±8.1
Head width at eye level	59.7-76.1	67.7±3.99	66.3	78.3-89.6	80.7±3.2	79.3	62.6-67.6	65.2±1.6

Capitulo 2

Artigo submetido para o periodico “PlosONE”

Biogeography of *Rhamdia quelen* (Siluriformes: Heptapteridae) species complex in South America

Running title: Biogeography of *Rhamdia*

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Abstract

The species of *Rhamdia* are distributed throughout the Neotropical region. Several species have been described, added, synonymized or revalidated after the description of the genus, resulting in more than 100 names associated to *Rhamdia*. Regardless the large number of species, there is only one revision of the species of the genus published. This revision is based on characters of external and internal morphology and concluded that *Rhamdia* contains only 11 valid species among more than 100 available names. Currently, 27 species are recognized for this genus. The largest complexity and unresolved diversity among *Rhamdia* species is associated to *Rhamdiaquelen* that have 47 nominal species under synonyms. *Rhamdiaquelen* has a wide geographic distribution, from Mexico to Argentina, and it has been recognized as a large species complex. In an attempt to resolve the issues surrounding this complex, a biogeographical approach of populations related to the *R. quelen* is proposed in this research. Therefore, samples throughout the *R. quelen* distribution and four molecular markers were used: the genes COI and CytB of mtDNA and the genes RAG2 and MyH6 of nDNA. For this analysis, a phylogenetic relationships were inferred by Bayesian Inference using a gene tree and a species tree. The results indicate that this genus is a well-supported monophyletic group and the specimens of *Rhamdia* are distributed in two large clades: Mesoamerican clade and South-American clade. The Mesoamerican clade is formed by *R. guatemalensis* and *R. cinerascens* and the *R. quelen* would be restricted only to South America. The South American clade is divided into three main groups: the Amazon clade, the Upper-Amazon clade and the Brazilian-Shield clade. The Brazilian Shield clade is composed of two major groups, the Continental Clade and the Atlantic coastal clade, being the last one divided in the highland Atlantic coastal clade and the lowland Atlantic coastal clade.

Key words: Bayesian analysis, Biogeography, Genetic diversity, Mitochondrial DNA, Neotropical fishes, Nuclear DNA, Species complex, Species tree, *Rhamdia*.

Introduction

The species of *Rhamdia* Bleeker, 1958 are distributed throughout the Neotropical region (Pinna 1998; Silfvergrip 1996) and, in Brazil, they are commonly known as jundiás. According to Bockmann (1998), this genus is diagnosed by the presence of an ossified posterior fontanelle and the absence of uncinate process of hypobranchial 1.

Several species have been described, added, synonymized or revalidated after the description of the genus, resulting in more than 100 names associated to *Rhamdia*. Regardless the large number of species, there is only one revision of the species of the genus published so far by Silfvergrip (1996). Based on characters of external and internal morphology, Silfvergrip concluded that *Rhamdia* contains only 11 valid species among more than 100 available names.

Silfvergrip (1996) research has been questioned by several authors, since the data used were based on studies carried out with few specimens and many gaps in the geographical distribution of examined specimens, being also recognized the lack of robust characters for the diagnosis of these species. Taking into account the shortcomings in Silfvergrip (1996) research, many studies have been carried out in an attempt to elucidate the taxonomic situation of some *Rhamdia* species (Galvis *et al* 1997; Greenfield & Thomerson 1998; Weber & Wilkins 1998; Romero & Paulson 2001; Wilkens 2001; Lopez *et al* 2002; Perdices *et al* 2002; Weber *et al* 2003). Despite these efforts, the number of valid species remained uncertain, with eleven valid species listed by Bockmann & Guazelli (2003) and 17 species listed by Ferraris (2007), and a large number of nominal species under their synonyms.

The valid species of *Rhamdia* listed by Ferraris (2007) include: *Rhamdiaquelen* Quoy & Gaimard ,1824; *Rhamdiafoina* Müller & Troschel, 1849; *Rhamdialaukidi* Bleeker, 1858; *Rhamdialaticauda* Kner, 1858; *Rhamdiahumilis* Günther, 1864; *Rhamdiamuelleri* Günther, 1864; *Rhamdianicaraguensis* Günther, 1864; *Rhamdia parryi* Eigenmann & Eigenmann, 1888, *Rhamdia reddelli* Miller, 1984; *Rhamdiapoeyi* Eigenmann & Eigenmann, 1888; *Rhamdiajequitinhonha* Silfvergrip, 1996; *Rhamdia xetequepeque* Silfvergrip, 1996; *Rhamdiaitacaiunas* Silfvergrip, 1996; *Rhamdia macuspanensis* Weber & Wilkens, 1998; *Rhamdia laluchensis* Weber, Allegrucci & Sbordoni, 2003; *Rhamdia guasarensis* DoNascimento, Provenzano & Lundberg, 2004; and *Rhamdia enfurnada* Bichuette & Trajano, 2005. After 2007, two new species have been described *Rhamdia gabrielae* Angrizani & Malabarba 2017 and *Rhamdia eurycephalae* Angrizani & Malabarba 2017 and eight species were revalidated [*Rhamdia velifer* (Humboldt 1821); *Rhamdia schomburgkii* Bleeker 1858*; Rhamdia cinerascens* (Günther, 1860); *Rhamdia guatemalensis* (Günther, 1864); *Rhamdia parryi* Eigenmann & Eigenmann 1888; *Rhamdia branneri* Haseman, 1911; *Rhamdia voulezi* Haseman, 1911; *Rhamdia saijaensis* Rendahl, 1941; *Rhamdia reddelli* Miller 1984; *Rhamdia zongolicensis* Wilkens 1993, thus resulting in 27 valid species for the genus (Eschmeyer *et al* 2017).

The largest complexity and unresolved diversity among *Rhamdia* species is associated to *Rhamdia quelen*, that deserves a special research effort to achieve a resolution. Silfvergrip (1996) placed 47 nominal species under the synonyms of *R. quelen*, and assigned a wide geographic distribution for this species, from Mexico to Argentina. Independent research reports, however, have refuted this hypothesis of a polymorphic species largely distributed, demonstrating that west Andean and east Andean populations of *Rhamdia* form distinct and sister clades, thus excluding *Rhamdia quelen* from North and Central Americas and west Andean drainages of South America (Perdices *et al* 2012; Hernandez *et al* 2015). Further research on smaller areas among Cis-Andean populations have also demonstrated that *Rhamdia quelen* as defined includes different and morphologically or molecular recognizable species or lineages (Garavello & Shibata 2016; Angrizani & Malabarba 2017; Ríos *et al* 2017).

In this paper, relationships among several populations related to the *Rhamdiaquelen* complex from the Brazilian shield were analyzed in a biogeographical approach. The Brazilian shield corresponds to an extensive block of uplands that extends from the limits of the Amazon plain to the Prata River estuary (Lundberg *et al* 1998). This area is drained For Parana-Paraguay systems, the São Francisco River and small drainages flowing into the Atlantic Ocean known as Coastal Drainages of the Brazilian Southeastern (CDSEB). The geological evolution of the high mountain chain in Brazilian shield, associated to the eustatics movements that shaped their eastern limits, provided an opportunity for vicariance, isolation and dispersion of fish species.

A genetic analysis of *Rhamdia* specimens from the rivers of Brazilian shield is proposed in this paper, based on analysis of mitochondrial and nuclear DNA markers. The recent description of two new species of *Rhamdia* from small geographical areas in CDSEB (Angrizani & Malabarba 2017) reinforces the need for in-depth studies regarding the *Rhamdia quelen* complex.

Material and methods

A total of 208 specimens of *Rhamdia* seven outgroup species of closely related genera (*Rhamdella zelimai* Reis, Malabarba & Lucena, 2014; *Pimelodella australis* Eigenmann, 1917; *Acentronichthys leptos* Eigenmann & Eigenmann, 1889; *Taunayia bifasciata* (Eigenmann & Norris, 1900); *Rhamdioglanis frenatus* Ihering, 1907; *Heptapterus mustelinus* (Valenciennes, 1835) and *Imparfinis mishky* Almirón, Casciotta, Bechara, Ruíz Díaz, Bruno, D'Ambrosio, Solimano & Soneira, 2007) and one representative of Pimelodidae (*Pimelodus maculatus* Lacepède, 1803) were used for genetic analysis. The tissue samples were taken from the fish collections of the Departamento de Zoologia, Universidade Federal do Rio

Grande do Sul (UFGRS); Museu Nacional, Rio de Janeiro (MNRJ); Museu de Zoologia da Universidade de São Paulo (MZUSP) and Universidade Paulista, Botucatu (LBP) (Table 1).

DNA extractions from tissues followed a modified CTAB protocol (Doyle & Doyle 1987). PCR was used to amplify the mitochondrial genes Cytochrome Oxidase I (COI) (Ivanova *et al* 2007) and Cytochrome B (CytB) (Palumbi *et al* 1991), nuclear genes Myosin Heavy Chain 6 (MyH6) (Li *et al* 2007) and RAG2 (Hardman 2004). PCRs were carried out in 20 μL reactions containing 10-50 ng DNA, 0.2 μM of each primer, 0.2 mM of each dNTP, 1X Buffer, 1.5 μM $MgCl_2$ and 1U Platinum Taq DNA polymerase (Invitrogen, São Paulo, SP, Brazil). PCR conditions followed paper reported for the respective primers. PCR products were checked by electrophoresis in agarose gel, purified using ExoSap (Exonuclease I and Shrimp Alkaline Phosphatase, GE Healthcare, Piscataway, NJ, USA) and sequenced in both directions by ACTGENE Ltda, Porto Alegre, Brazil. Sequences were aligned in CLUSTAL W (Thompson *et al* 1994) implemented in MEGA 6 (Tamura *et al* 2013).

Phylogenetic relationships were inferred by Bayesian Inference using a gene tree and carried out in MrBayes 3.2.2 (Ronquist *et al* 2012). PartitionFinder (Lanfear *et al* 2012) was used to select the model of nucleotide substitution most appropriate for the data. To estimate the posterior probabilities distribution in BI, two simultaneous Markov chain Monte Carlo (MCMC) analysis were run for 30.000,000 generations each. Topologies were sampled every 1,000 generations. The consensus tree was constructed after eliminating the first 10,000 trees.

The groups formed in the gene tree were tested as lineages in a species tree (Heled & Drummond 2010) carried out in BEAST 1.8.4 (Drummond & Rambaut 2007), as well as, the divergence times among phylogenetic relationships. Partition-Finder program (Lanfear *et al* 2012) was used to find the best evolutionary model using Bayesian Information Criterion (BIC). A strict molecular clock was used to estimate the divergence time between lineages, which is used for analysis of species or among closely related species (Li & Drummond 2012). Assuming an evolutionary rate 0.001/site/million years for mtDNA markers (Bermingham *et al* 1997; Reeves & Bermingham 2006; Ornelas-Garcia *et al* 2008) and the evolutionary rate of the nuclear marker was calibrated based on mtDNA rate. The speciation model used was the Yule Process. As a calibration point was used the rise of Andes Cordillera Oriental. This vicariant event isolated the Magdalena basin approximately 12 Ma ago (Albert *et al* 2006; Lundberg *et al* 1998). The calibration point was set using a normal distribution with a mean of 12 my and a standard deviation of 1 my. For the species tree 200.000,000 MCMC steps was used, sampled every 1,000 steps with 10% burn-in. Chain efficiency was observed in TRACER 1.5 (Rambaut *et al* 2014).

Results

A total of 3,217 bp were aligned for a set of DNA sequences, 683 bp for COI gene, 832 bp for CytB gene, 799 bp for MyH6 gene and 936 for RAG2. A total of 127 informative site were found for COI gene, 154 for CytB gene, 32 for MyH6 and 44 for RAG2. The beast evolutionary model for the mitochondrial genes was GTR+I+G and for the nuclear genes was HKY+I.

The phylogenetic tree allocated the 208 individuals of *Rhamdia* in 20 different groups (Fig.1, Fig.2, Fig.3, Fig.4). *Rhamdia* is a well-supported monophyletic group (Fig. 1). These groups have strong support (PP>0.9) and a consistent geographic distribution occurring in a single or in adjacent drainages (Fig. 5). All twenty groups recovered in the gene tree were confirmed as different lineages in the species tree (Fig 6), presenting high support (PP>0.95). They are distributed in two large clades: Mesoamerican clade and South-American clade. The Mesoamerican clade is formed by *R. guatemalensis* and *R. cinerascens*. The South American clade is divided into three main groups: the Amazon clade, the Upper-Amazon clade and the Brazilian-Shield clade. The Amazon clade is composed by the rio Madeira and the rio Tapajós lineages. The Upper-Amazon clade is formed by the Peruvian Amazon lineage. The Brazilian Shield clade is composed of two major groups, the Continental clade and the Atlantic coastal clade, being the last divided in the highland Atlantic coastal clade and the lowland Atlantic coastal clade (Fig. 5).

The Continental clade (CC) is composed of six lineages, distributed respectively along the upper rio São Francisco (CC1), upper rio Paraná (CC2), upper tributaries of laguna dos Patos (CC3), lower upper rio Uruguay (CC4), upper rio Itajaí (CC5) and lower rio Uruguay (CC6).

The Highland Atlantic Coastal clade (HA) is composed of four lineages, corresponding to *R. gabrielae* from the rio Maquiné, rio Três Forquilhas, rio Mampituba and rio Araranguá (HA3), *R. eurycephala* from the upper rio Tubarão (HA4), and two lineages in upper tributaries of the laguna dos Patos drainage, the upper rio Taquari (HA1) and upper rio Jacuí (HA2).

The Lowland Atlantic Coastal clade (LA) is composed of five lineages, respectively distributed in the rio Doce (LA1); rio Paraíba (LA2); rio Acarí and rio Itagaré (LA5); rio Araranguá, rio Tramandaí, laguna dos Patos, rio Quaraí, and rio Negro (LA4) and one with a large latitudinal distribution along Atlantic rivers from Rio de Janeiro to Santa Catarina states (LA3).

All groups and lineages presented here had high values of posterior probability (Fig. 5). The species tree also shows the ages of cladogenetic events associated to the diversification of *Rhamdia*.

Discussion

The monophyly of *Rhamdia* has been long considered doubtful (Bichuette & Trajano 2005; Bockmann 1998; Bockmann & Miquelarena 2008; Lundberg *et al* 1991; Silfvergrip 1996), however, the analysis carried out in this paper indicate that this genus is a well-supported monophyletic group (PP = 1), corroborating other studies (Perdices *et al* 2002.; Hernandez *et al* 2015).

The phylogenetic analyses generated in this study recovered 20 evolutionary lineages for the genus *Rhamdia*. Two of these lineages correspond to *R. cineracens* and *R. guatemalensis*, belonging to the Mesoamerican clade (Perdices *et al* 2002; Hernandez *et al* 2015). The other 18 lineages are part of the South American clade and are found in the eastern Andes region of South America, including several populations treated as *Rhamdia quelen sensu* Silfvergrip, thus corroborating the hypothesis that *R. quelen* is a large and unresolved species complex.

These 18 lineages show clear biogeographical patterns of distribution, being divided in three major clades: the Amazon clade, the Upper-Amazon clade and the Brazilian-Shield clade. Fourteen lineages, grouped in three major clades (CC, HA, LA), belong to the Brazilian-Shield clade, analyzed in deep here with more representative samples. Instead of a polymorphic species with a large distribution, we found evidence of the existence of multiple species, including the co-occurrence of two, three or even four lineages of *Rhamdia* in a single drainage (e.g. lineages LA4, CC5, HA1, HA2 co-occurring in the laguna dos Patos drainage; lineages CC4, CC3 and LA4 co-occurring in the rio Uruguay drainage; lineages CC6 and LA3 co-occurring in the rio Itajaí drainage; lineages LA3 and *R. eurycephala* (HA4) co-occurring in the rio Tubarão drainage; lineages LA4 and *R. gabrielae* (HA3) co-occurring in the rio Tramandaí and rio Araranguá drainages). The recent description of two of these lineages (HA3 and HA4) as two new species (*R. gabrielae* and *R. eurycephala*, respectively) with genetic, morphological and geographical patterns consistently defined (Angrizani & Malabarba 2017) may indicate that all the lineages recovered herein are different species. Actually there are only five species of *Rhamdia* considered as valid and in use in rivers draining the eastern and western portions of the Brazilian-Shield (*R. branneri, R. enfurnada, R. jequitinhonha, R, quelen,* and *R. voulezi*) contra 14 lineages defined herein, indicating several species to be described or removed from the synonym of other species of *Rhamdia*, especially *R. quelen*.

Biogeographical approach

The species diversification within the genus dates back to the Miocene epoch, when the first cladogenetic event observed for *Rhamdia* resulted in separation of two groups: a west-Andean group (Meso-American clade) and a east-Andean group (South-American clade). According to Perdices *et al* (2002), the separation of these two clades is dated in 8.8 mya and according to Hernadez *et al* (2015) is dated 10.5 mya. The dates proposed by these authors coincide with the occurrence of geological events that resulted in the rise of the Andes and the modification of the rivers Orinoco and Amazonas (Lundberg *et al* 1998). In this research, the dating of this geological event was used to calibrate the species tree, in which 10 mya was defined as the first separation inside the genus.

The second cladogenetic event within the genus is estimated at 7.7 mya. Corresponds to the divergence between Amazon and Upper-Amazon clades within the Amazon hydrographic basin. The origin of the genus apparently occurred in the Paleo-Amazon region, after that, the *Rhamdia* species expanded to Central America and to other regions of South America (Perdices *et al* 2002). The oldest speciation events for *Rhamdia* happened among the Amazonian clades (7.7 mya). This fact reinforces the hypothesis that the origin of *Rhamdia* is Amazonian, however, in-depth study with more specimens from the Amazonian and trans-

Andean regions must be performed to infer the origin of *Rhamdia* more accurately.

Brazilian-Shield clade

The third divergence found for *Rhamdia* corresponds to the separation between the Upper-Amazon and Brazilian-Shield clades and it is dated to ~3.5 mya. The rivers of the Upper Amazon region have a long history shared with the Paraguay-Paraná basin, where the headwater capture events and the formation of semipermeable barriers connected these basins until the appearance of the Michicola arc ~10 mya (Lundberg *et al* 1998). Genetic divergences among clades from the Amazon and Paraná-Paraguay basins are very well reported for several groups of Neotropical fish, with variable dates: 10.5 mya for *Hypostomus* (Montoya-Burgos 2003), 8 mya for *Serrasalmus* (Hubert *et al* 2007), 4.1-2.3 mya for *Prochilodus* (Sivasundar *et al* 2001), 2.2 mya for *Megaleporinus* (Ramirez *et al* 2017) and 3.5 mya for *Rhamdia* (our results). These studies demonstrate different timetables of river colonization from Brazilian crystalline shield, indicating that the connections between these basins are more complex than expected (Carvalho & Albert 2011). The results of this research indicate that *Rhamdia* lineages dispersed to rivers of the Brazilian Crystalline Shield through the historical connections between these river basins.

The first cladogenesis within the Brazilian-Shield clade occurred at ~2.7 mya when separating the Continental and Atlantic clades. The Continental clade lineages occur predominantly in the hydrographic systems of Prata River, the São Francisco River and the Patos Lagoon drainage; the lineages of Atlantic clade occur in the rivers draining to the Atlantic along the Brazilian coastal. Cladogenesis involving these regions are very well detailed for several neotropical fish groups (Weitzman *et al* 1988; Costa 2001; Ribeiro *et al* 2006, Menezes *et al* 2008; Torres & Ribeiro 2009; Carvalho *et al* 2013; Roxo *et al* 2012; Roxo *et al* 2014; Ramirez *et al* 2017). This cladogenesis corresponds to pattern B described by Ribeiro (2006), which corresponds to vicariant events associated with secondary rearrangements between interior and coastal drainages.

Continental clade

The first divergence within the Continental clade occurred in 1.4 mya, separating the CC4lineage as the sister group of the rest of the clade. The correct phylogenetic position of this lineage is controversial, in the concatenated gene tree analysis it appears as a sister group of the Continetal and Atlantic clades. In the species tree it appears within the Continental clade. The CC4 linage occurs in the lower Uruguay River, in the extreme south of Brazil, distant geographically from the headwaters of the Paraná/Paraguay basin. The lack of sampling in other localities of the La Plata River basin prevents a more precise delimitation of the geographical distribution of this lineage.

The second cladogenesis within the group occurred ~1 mya million years ago and separated the lineage CC6 of the others. Unlike the other lineages of the clade, this is the only one present in the region of the Brazilian coastal plain, occurring in the headwaters of the Itajaí river, in Santa Catarina State (Figure 1). This lineage dispersed to this region possibly through headwater capture events, which are very well reported and documented among coastal rivers and other adjacent basins (Ab'Saber 2003, Ribeiro 2006; Buckup 2011). Similar dispersal events are reported for other Neotropical fish groups in other coastal watersheds (Weitzman *et al* 1988, Costa 2001; Ribeiro *et al* 2006; Serra *et al* 2007; Carvalho *et al* 2013; Ramirez *et al* 2017).

The third cladogenesis of this group is dated in ~0.5 mya and correspond to the separation of the CC3 lineage. This lineage occurs in the basin of the middle and upper Uruguay River and it is in sympatry with the CC4 and LA4 lineages. The next divergence occurred at ~0.3 mya, separating the CC5 lineage. This lineage occurs in all rivers of the Patos Lagoon basin, except for the lower portions of these rivers. The last cladogenetic event of this group occurred between the CC1 and CC2 lineages, and it is dated to ~0.2 mya. The CC1 lineage is found to the São Francisco river basin and the CC2 lineage is related to the Rio Grande and Paranaíba river basins. Cladogenesis among lineages of the Upper Paraná river basins and rio São Francisco basin are well known for other fishes (Roxo *et al* 2014; Ramirez *et al* 2017), and dispersion through headwater capture events are likely the cause for these divergences.

The divergences among the lineages of this clade are recent. In order to solve the internal relationships of this clade the use of molecular markers with faster evolution rates is necessary, as well as a more complete sampling of the watersheds involved.

Atlantic clade

The Atlantic clade is composed of two groups: the Highland clade and the Lowland clade, that diverged ~2.4 mya probably in a sympatric speciation. The Highland clade is composed of four lineages that occur in southern Brazil in adjacent basins. The HA2 and the HA1 lineages occur in the upper portion of the Patos lagoon basin, *R. gabrielae* (HA3) occurs in the coastal rivers of the Maquiné-Mampituba ecoregion and the *R. eurycephala* (HA4) occurs in the upper portion of the Tubarão coastal river basin.The Highland lineages occur in upper portions of rivers, with environments of rapids and shallow waters differently from the Lowland group, which prefer lentic and deeper waters. Possibly, the differentiation event of the ancestor of this clade happened through colonization of new environments (Angrizani & Malabarba 2107).

The Lowland clade is composed of five lineages: LA5, LA4, LA3, LA2 and LA1. Within this clade, the LA5 lineage separated from the rest of the group in ~1.8 mya and it is the most external lineage. This lineage occurs in a very specific environment: rivers of dark water in regions close to the coast. Probably, the adaptation to this kind of environment originated the speciation process, like *Mimagoniates lateralis*, the unique species of the your genus with occurs in this environment (Weitzman *et al* 1988; Menni *et al* 1996)

The next divergence in this clade separated the LA4 lineage ~1.4 mya. This lineage presents a great geographical distribution, occurring in five different basins in southern America: low portions of the La Plata river basin, Patos Lagoon basin and the southern portion of the Brazilian coastal plain between the Tramandaí and Araranguá rivers. Along its geographic distribution, this lineage occurs in sympatry or in syntopy with other lineages.

The LA3 lineage had its divergence in ~1.1 mya spread along the Brazilian coastal plain, from the Tubarão river in the state of Santa Catarina, until the basin of Guanabara Bay, in Rio de Janeiro (Fig. 4). This lineage presents a large geographical distribution and occurs in a series of isolated hydrographic basins known as Coastal Drainages of Southeastern Brazil. The other two lineages of this group are more recent, diverging in ~0.6 mya. The LA2 group occurs in the Paraíba do Sul river basin and the LA1 lineage occurs in the basin of the Doce river.

According to the results of this research, the dispersion of *Rhamdia* lineages in the Brazilian coastal plain occurred from south to north. The oldest lineages of this clade, LA5 and LA4, occurs in southern of South America, and the most recent ones are found in the Paraíba do Sul and Doce River basins, norther to the lineage distribution of this clade. With the exception of the LA5 lineage that is present in a very specific environment, the first breaking site among the lineages of this clade was between the basins of the Araranguá river and the Tubarão river, respectively, between the LA4 and LA3 lineages. This break coincides with the boundaries between two recognized ecoregions for aquatic organisms (Abbel *et al* 2004). Besides being the breaking point between these two lineages of the Lowland clade, this break is also the separation point between the *R. gabrielae* (HA3) and *R. eurycephala* (HA4) lineages of the Highland clade. This pattern also takes place in other groups of neotropical fish (Thomaz *et al* 2015). The second break among the lineages of this clade happened norther to the first break, separating the LA3 lineages from the LA2 and LA1 lineages, also coinciding with the division into different ecoregions (Abbel *et al* 2004). This same pattern is also found for *Hoplias malabaricus* (Pereira *et al* 2013) and in the genus *Megaleporinus* (Ramirez *et al* 2017).

The Brazilian coastal plain is recognized for presenting high levels of fish endemism (Weitzman *et al* 1988). Diversification events and ichthyofauna speciation are well reported for this region (Beheregaray *et al* 2002; Torres & Ribeiro 2009; Roxo *et al* 2014; Pereira *et al* 2013, Hirschmann *et al* 2015; Thomaz *et al* 2015). These processes would be related to the successive eustatic movements that this region has undergone throughout the last 2.6 mya (Weitzman *et al* 1988, Albert & Reis 2011). During the glaciation stages occurred marine regressions and the coastal rivers were connected in paleodrainages, whereas, during the interglacial stages, the marine transgressions isolated these rivers (Weitzman *et al* 1988; Dias *et al* 2014). Thomaz *et al* (2015) suggested that the configurations and ruptures between different paleodrainages are a preponderant factor for the genetic diversification of fish in the Brazilian coastal plain. For *Rhamdia*, these eustatic processes were fundamental to the lineage patterns that we find today in the Brazilian coastal plain.

Taxonomic problems and conservation

The introduction of exotic species causes serious impacts on natural ecosystems, being considered by IUCN as the second largest cause of biodiversity loss in the world, only behind habitat destruction (Rodriguez 2001). Aquatic ecosystems are particularly vulnerable to this impact and events like this can modify the composition of natural communities (Figueredo & Giani 2005; Latine & Petrere 2007; Giacomini *et al* 2011). For instance, the introduction of *Cichlaocellaris* in Gatun Lake, Panama, promoted the disruption of the native community and led to the drastic reduction of native species (Zaret 1975). The introduction of *Latesniloticus* in Lake Victoria, Africa, caused the population decline and temporary disappearance of hundreds of endemic species of cichlids (Kitchell *et al* 1997). The introduced species of the genus *Cichla* and of *Pygocentrusnattereri* in the lagoons of the middle Rio Doce, Brazil, is responsible for the reduction of the diversity of the ichthyofauna (Latini & Petrere 2004).

Fish introductions are very common in Brazil (Lima Junior *et al* 2012; Pelicice *et al* 2014), resulting mainly of recreational fishing, stocking and fish farming (Agostinho *et al* 2005; Azevedo-Santos *et al* 2015). There are 109 species of invasive fishes in Brazil (MMA 2016) and the Amazonian fishes are among the species most introduced in other geographic basins (Lima Junior *et al* 2012; MMA 2016). The main invasive fishes in Brazilian waters are economically important, easily recognizable and have a well-defined taxonomy, and despite these facts they still cause many problems (Agostinho *et al* 2005; Lima Junior *et al* 2012; Pelicice *et al* 2014). But what could happen when a group of economically important fish with an unresolved taxonomy and underestimated diversity is largely used in fish farming originated from several wild stocks from geographically distant places? This is the case of *R. quelen*.

Rhamdia quelen is the 14th commercial freshwater fish in economic importance in Brazilian pisciculture (MPA 2012), and the first native fish of commercial importance in southern Brazil (Baldisserotto 2009). The production of this species in the year 2011 corresponded to 1747 tons of fish (MPA 2012). *Rhamdia quelen* has a great potential for fish farming due to its accelerated growth, resistance to cold, food efficiency, handling resistance and tasty meat (Meyer & Fracalossi 2004, Fracalossi *et al* 2004). Because it is a native species of easy production and present good profitability for fish farming, *R. quelen* is pointed out as a solution for the problems caused by invasive species from exotic fish production in Brazil (Baldisseroto 2009), and that is where the problem lies.

In this research, *R. quelen* was defined as a large complex group, since there are at least 18 potential species, including some of them living in sympatry or even in syntopy. The taxonomical indefinition of these species, concomitantly with the economic importance that this group has reached, turns this complex into potential invading fishes. Therefore, the taxonomic revision of the *R. quelen* complex group is fundamental, given its important role in commercial and ecological scenarios and also the importance of natural communities and endemic species conservation.

References

Abell, R., Thieme, M. L., Revenga, C., Bryer, M., Kottelat, M., Bogutskaya, N., ... & Stiassny, M. L. (2008). Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience*, *58*(5), 403-414.

Ab'Sáber, A. N. (2003). *Os domínios de natureza no Brasil: potencialidades paisagísticas* (Vol. 1). Ateliê Editorial.

Agostinho, A. A., Thomaz, S. M., & Gomes, L. C. (2005). Conservation of the biodiversity of Brazil's inland waters. *Conservation Biology*, *19*(3), 646-652.

Albert, J. S., & Reis, R. (Eds.). (2011). *Historical biogeography of Neotropical freshwater fishes*. Univ of California Press.

Azevedo-Santos, V. M., Pelicice, F. M., Lima-Junior, D. P., Magalhães, A. L. B., Orsi, M. L., Vitule, J. R. S., & Agostinho, A. A. (2015). How to avoid fish introductions in Brazil: education and information as alternatives. *Natureza & Conservação*, *13*(2), 123-132.

Albert, J. S., Lovejoy, N. R., & Crampton, W. G. (2006). Miocene tectonism and the separation of cis-and trans-Andean river basins: Evidence from Neotropical fishes. *Journal of South American Earth Sciences*, *21*(1), 14-27.

Angrizani RC, Malabarba, LR. 2017. Species delimitation of *Rhamdia* (Bleeker, 1858)(Siluriformes: Heptapteridae) using morphology and molecular data reveals the presence of two new species under *Rhamdia quelen* (Quoy & Gaimard, 1824) species complex. Zootaxa,

Baldisserotto, B. (2009). Freshwater fish culture in Rio Grande do Sul State: actual situation, problems and future perspectives. *Ciência Rural*, *39*(1), 291-299.

Bichuette, M. E., & Trajano, E. (2005). A new cave species of Rhamdia (Siluriformes: Heptapteridae) from Serra do Ramalho, northeastern Brazil, with notes on ecology and behavior. *Neotropical Ichthyology*, *3*(4), 587-595.

Beheregaray, L. B., Sunnucks, P., & Briscoe, D. A. (2002). A rapid fish radiation associated with the last sea-level changes in southern Brazil: the silverside Odontesthes perugiae complex. *Proceedings of the Royal Society of London B: Biological Sciences*, *269*(1486), 65-73.

Bermingham, E., McCafferty, S. S., & Martin, A. P. (1997). Fish biogeography and molecular clocks: perspectives from the Panamanian Isthmus. *Molecular systematics of fishes*.

Bockmann, F. A. (1998). *Análise filogenética da família Heptapteridae (Teleostei, Ostariophysi, Siluriformes) e redefinição de seus gêneros*(Doctoral dissertation).

Bockmann, F. A., & Guazzelli, G. M. (2003). Family Heptapteridae (Heptapterids). *Checklist of the freshwater fishes of South and Central America. Porto Alegre: Editora da Pontifícia Universidade Católica do Rio Grande do Sul-EDIPUCRS*, 406-431.

Bockmann, F. A., & Miquelarena, A. M. (2008). Anatomy and phylogenetic relationships of a new catfish species from northeastern Argentina with comments on the phylogenetic relationships of the genus Rhamdella Eigenmann and Eigenmann 1888 (Siluriformes, Heptapteridae). *Zootaxa*, *1780*, 1-54.

Buckup, P. A. (2011). The eastern Brazilian shield. *Historical Biogeography of Neotropical Freshwater Fishes. California: University of California Press, Berkeley*, 203-210.

Carvalho, P. H., Maia Queiroz Lima, S., Henrique Zawadzki, C., Oliveira, C., & de Pinna, M. (2016). Phylogeographic patterns in suckermouth catfish Hypostomus ancistroides (Loricariidae): dispersion, vicariance and species complexity across a Neotropical biogeographic region. *Mitochondrial DNA Part A*, *27*(5), 3590-3596.

Costa, W. J. E. M. (2001). The neotropical annual fish genus Cynolebias (Cyprinodontiformes: Rivulidae): phylogenetic relationships, taxonomic revision and biogeography. *Ichthyological Exploration of Freshwaters*, *12*(4), 333-383.

Dias, M. S., Oberdorff, T., Hugueny, B., Leprieur, F., Jézéquel, C., Cornu, J. F., ... & Tedesco, P. A. (2014). Global imprint of historical connectivity on freshwater fish biodiversity. *Ecology letters*, *17*(9), 1130-1140.

Doyle, J. J., & Doyle, J. L. (1987). CTAB DNA extraction in plants. *Phytochemical Bulletin*, *19*, 11-15.

Drummond, A. J., & Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC evolutionary biology*, *7*(1), 214.

Eschmeyer, W. N., Fricke, R. & Van der Laan, R. (eds). (2017). Catalog of fishes: genera, species, references. (http://researcharchive.Calacademy.org/research/ichthyology/catalog/fishcatmain.asp).

Ferraris, C. J. (2007). *Checklist of catfishes, recent and fossil (Osteichthyes: Siluriformes), and catalogue of siluriform primary types* (pp. 1-628). Auckland, New Zealand: Magnolia Press.

Figueredo, C. C., & Giani, A. (2005). Ecological interactions between Nile tilapia (Oreochromis niloticus, L.) and the phytoplanktonic community of the Furnas Reservoir (Brazil). *Freshwater Biology*, *50*(8), 1391-1403.

Fracalossi, D. M., Meyer, G., Santamaria, F. M., Weingartner, M., & Zaniboni Filho, E. (2004). Desempenho do jundiá, Rhamdia quelen, e do dourado, Salminus brasiliensis, em viveiros de terra na região sul do Brasil. *Acta Scientiarum. Animal Sciences*, *26*(3), 345-352.

Galvis, G., Mojica, J. I., & Camargo, M. (1997). *Peces del Catatumbo*. Asociación Cravo Norte.

Garavello, J. C., & Shibatta, O. A. (2016). Reappraisal of Rhamdia branneri Haseman, 1911 and R. voulezi Haseman, 1911 (Siluriformes: Heptapteridae) from the rio Iguaçu with notes on their morphometry and karyotype. *Neotropical Ichthyology*, *14*(1).

Giacomini, H. C., Lima Jr, D. P., Latini, A. O., & Espírito-Santo, H. M. V. (2011). Spatio-temporal segregation and size distribution of fish assemblages as related to non-native species occurrence in the middle rio Doce Valley, MG, Brazil. *Neotropical Ichthyology*, *9*(1), 135-146.

Greenfield, D. W., & Thomerson, J. E. (1997). Fishes of the continental waters of Belize.

Hardman, M. (2004). The phylogenetic relationships among Noturus catfishes (Siluriformes: Ictaluridae) as inferred from mitochondrial gene cytochrome b and nuclear recombination activating gene 2. *Molecular phylogenetics and evolution*, *30*(2), 395-408.

Heled, J., & Drummond, A. J. (2009). Bayesian inference of species trees from multilocus data. *Molecular biology and evolution*, *27*(3), 570-580.

Hernández, C. L., Ortega-Lara, A., Sánchez-Garcés, G. C., & Alford, M. H. (2015). Genetic and morphometric evidence for the recognition of several recently synonymized species of trans-Andean Rhamdia (Pisces: Siluriformes: Heptapteridae). *Copeia*, *103*(3), 563-579.

Hubert, N., Duponchelle, F., Nunez, Paugy, D., & Renno, J. F. (2007). Phylogeography of the piranha genera Serrasalmus and Pygocentrus: implications for the diversification of the Neotropical ichthyofauna. *Molecular Ecology*, *16*(10), 2115-2136.

Hirschmann, A., Malabarba, L. R., Thomaz, A. T., & Fagundes, N. J. R. (2015). Riverine habitat specificity constrains dispersion in a Neotropical fish (Characidae) along Southern Brazilian drainages. *Zoologica Scripta*, *44*(4), 374-382. .

Ivanova, N. V., Zemlak, T. S., Hanner, R. H., & Hebert, P. D. (2007). Universal primer cocktails for fish DNA barcoding. *Molecular Ecology Resources*, *7*(4), 544-548.

Kitchell, J. F., Schindler, D. E., Ogutu-Ohwayo, R., & Reinthal, P. N. (1997). The Nile perch in Lake Victoria: interactions between predation and fisheries. *Ecological Applications*, *7*(2), 653-664.

Lanfear, R., Calcott, B., Ho, S. Y., & Guindon, S. (2012). PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular biology and evolution*, *29*(6), 1695-1701.

Latini, A. O., & Petrere, M. (2004). Reduction of a native fish fauna by alien species: an example from Brazilian freshwater tropical lakes. *Fisheries management and Ecology*, *11*(2), 71-79.

Latini, A. O., & Petrere Jr, M. (2007). Which factors determine non-indigenous fish dispersal? A study of the red piranha in tropical Brazilian lakes. In: *Biological invaders in inland waters: Profiles, distribution, and threats* (pp. 415-422). Springer Netherlands.

Latini, A. O., Resende, D. C., Pombo, V. B., & Coradin, L. (Org.). (2016). *Espécies exóticas invasoras de águas continentais no Brasil. Série Biodiversidade, 39.*(791p).Brasília: MMA.

Li, W. L. S., & Drummond, A. J. (2011). Model averaging and Bayes factor calculation of relaxed molecular clocks in Bayesian phylogenetics. *Molecular biology and evolution*, *29*(2), 751-761.

Li, C., Ortí, G., Zhang, G., & Lu, G. (2007). A practical approach to phylogenomics: the phylogeny of ray-finned fish (Actinopterygii) as a case study. *BMC Evolutionary*

Biology, *7*(1), 44.

Lima Junior, D. P., Pelicice, F. M., Vitule, J. R. S., & Agostinho, A. A. (2012). Aquicultura, política e meio ambiente no Brasil: Novas propostas e velhos equívocos. *Natureza & Conservação*, 10(1):1-4.

Lopez, H. L., Morgan, C. C., & Montenegro, M. J. (2002). Ichthyological ecoregions of Argentina. *ProBiota,* 1, 1–68.

Lundberg, J. G., Marshall, L. G., Guerrero, J., Horton, B., Malabarba, M. C. S. L., & Wesselingh, F. (1998). The stage for Neotropical fish diversification: a history of tropical South American rivers. *Phylogeny and classification of Neotropical fishes*, *603*, 14-48.

Lundberg, J. G., Bornbusch, A. H., & Mago-Leccia, F. (1991). Gladioglanis conquistador n. sp. from Ecuador with diagnoses of the subfamilies Rhamdiinae Bleeker and Pseudopimelodinae n. subf.(Siluriformes: Pimelodidae). *Copeia*, 190-209.

Menni, R. C., Gómez, S. E., & Armengol, F. L. (1996). Subtle relationships: freshwater fishes and water chemistry in southern South America. *Hydrobiologia*, *328*(3), 173-197.

Meyer, G., & Fracalossi, D. M. (2004). Protein requirement of jundia fingerlings, Rhamdia quelen, at two dietary energy concentrations. *Aquaculture*, *240*(1), 331-343.

Montoya-Burgos, J. I. (2003). Historical biogeography of the catfish genus Hypostomus (Siluriformes: Loricariidae), with implications on the diversification of Neotropical ichthyofauna. *Molecular Ecology*, *12*(7), 1855-1867.

MPA Ministério da Pesca e Aquicultura. (2012). *Boletim Estatístico da Pesca e Aquicultura. Brasil 2008-2009*. (101p). Brasília, Ministério da Pesca e Aquicultura.

Miller, K. G., Mountain, G. S., Wright, J. D., & Browning, J. V. (2011). A 180-million-year record of sea level and ice volume variations from continental margin and deep-sea isotopic records. *Oceanography*, *24*(2), 40-53.

Ornelas-García, C. P., Domínguez-Domínguez, O., & Doadrio, I. (2008). Evolutionary history of the fish genus Astyanax Baird & Girard (1854)(Actinopterygii, Characidae) in Mesoamerica reveals multiple morphological homoplasies. *BMC evolutionary biology*, *8*(1), 340.

Palumbi, S. (1991). Simple fool's guide to PCR.

Pelicice, F. M., Vitule, J. R. S., Lima Junior, D. P., Orsi, M. L., & Agostinho, A. A. (2014). A serious new threat to Brazilian freshwater ecosystems: the naturalization of nonnative fish by decree. *Conservation Letters*, *7*(1), 55-60.

Perdices, A., Bermingham, E., Montilla, A., & Doadrio, I. (2002). Evolutionary history of the genus Rhamdia (Teleostei: Pimelodidae) in central America. *Molecular Phylogenetics and Evolution*, *25*(1), 172-189.

Pereira, T. L., Santos, U., Schaefer, C. E., Souza, G. O., Paiva, S. R., Malabarba, L. R., ... & Dergam, J. A. (2013). Dispersal and vicariance of Hoplias malabaricus (Bloch, 1794)(Teleostei, Erythrinidae) populations of the Brazilian continental margin. *Journal of Biogeography*, *40*(5), 905-914.

Pinna, M. C. C. (1998). Phylogenetic relationship of Neotropical Siluriformes (Teleostei, Ostariophisy): Historical overview and synthesis of hypotheses. In: L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. Lucena & C. A. S. Lucena (Eds), *Phylogeny and Classification of Neotropical fishes* (pp. 279-330). Porto Alegre, RS: Edipucrs.

Quoy, J. R. C., & Gaimard, J. P. (1824). Zoologie. Chaptre IX. In: L. de Freycinet (Ed.), *Voyage autour du monde.* Paris.

Rambaut, A., Suchard, M. A., Xie, D., & Drummond, A. J. (2015). Tracer v1. 6. 2014.

Ramirez, J. L., Birindelli, J. L., & Galetti, P. M. (2017). A new genus of Anostomidae (Ostariophysi: Characiformes): Diversity, phylogeny and biogeography based on cytogenetic, molecular and morphological data. *Molecular phylogenetics and evolution*, *107*, 308-323.

Reeves, R. G., & Bermingham, E. (2006). Colonization, population expansion, and lineage turnover: phylogeography of Mesoamerican characiform fish. *Biological Journal of the Linnean Society*, *88*(2), 235-255.

Ribeiro, A. C. (2006). Tectonic history and the biogeography of the freshwater fishes from the coastal drainages of eastern Brazil: an example of faunal evolution associated with a divergent continental margin. *Neotropical Ichthyology*, *4*(2), 225-246.

Ribeiro, A. C., Lima, F. C., Riccomini, C., & Menezes, N. A. (2006). Fishes of the Atlantic Rainforest of Boracéia: testimonies of the Quaternary fault reactivation within a Neoproterozoic tectonic province in Southeastern Brazil. *Ichthyological Exploration of Freshwaters*, *17*(2), 157.

Ride, W. (1999). *International code of zoological nomenclature*. International Trust for

Zoological Nomenclature.

Rodríguez, J. P. (2001). Exotic species introductions into South America: an underestimated threat?. *Biodiversity & Conservation*, *10*(11), 1983-1996.

Romero, A., & Paulson, K. M. (2001). It's a wonderful hypogean life: a guide to the troglomorphic fishes of the world. *Environmental Biology of Fishes*, *62*(1-3), 13-41.

Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D. L., Darling, A., Höhna, S., ... & Huelsenbeck, J. P. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic biology*, *61*(3), 539-542.

Roxo, F. F., Albert, J. S., Silva, G. S., Zawadzki, C. H., Foresti, F., & Oliveira, C. (2014). Molecular phylogeny and biogeographic history of the armored Neotropical catfish subfamilies Hypoptopomatinae, Neoplecostominae and Otothyrinae (Siluriformes: Loricariidae). *PLOS one*, *9*(8), e105564.

Roxo, F. F., Zawadzki, C. H., Alexandrou, M. A., Costa Silva, G. J., Chiachio, M. C., Foresti, F., & Oliveira, C. (2012). Evolutionary and biogeographic history of the subfamily Neoplecostominae (Siluriformes: Loricariidae). *Ecology and Evolution*, *2*(10), 2438-2449.

Serra, J. P., Carvalho, F. R. D., & Langeani, F. (2007). Ichthyofauna of the rio Itatinga in the Parque das Neblinas, Bertioga, São Paulo State: composition and biogeography. *Biota Neotropica*, *7*(1), 0-0.

Silfvergrip, A. M. (1996). *A systematic revision of the Neotropical catfish genus Rhamdia (Teleostei, Pimelodidae)*. Department of Zoology. University of Stockholm.

Sivasundar, A., Bermingham, E., & Orti, G. (2001). Population structure and biogeography of migratory freshwater fishes (Prochilodus: Characiformes) in major South American rivers. *Molecular Ecology*, *10*(2), 407-417.

Tamura, K., Stecher, G., Peterson, D., Filipski, A., & Kumar, S. (2013). MEGA6: molecular evolutionary genetics analysis version 6.0. *Molecular biology and evolution*, *30*(12), 2725-2729.

Thomaz, A. T., Malabarba, L. R., Bonatto, S. L., & Knowles, L. L. (2015). Testing the effect of palaeodrainages versus habitat stability on genetic divergence in riverine systems: study of a Neotropical fish of the Brazilian coastal Atlantic Forest. *Journal of biogeography*, *42*(12), 2389-2401.

Thompson, J. D., Higgins, D. G., & Gibson, T. J. (1994). CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic acids research*, *22*(22), 4673-4680.

Torres, R. A., & Ribeiro, J. (2009). The remarkable species complex Mimagoniates microlepis (Characiformes: Glandulocaudinae) from the Southern Atlantic Rain forest (Brazil) as revealed by molecular systematic and population genetic analyses. *Hydrobiologia*, *617*(1), 157-170.

Vari, R. P. (1988). The Curimatidae, a lowland neotropical fish family (Pisces: Characiformes): distribution, endemism, and phylogenetic biogeography. In: *Neotropical Distribution Patterns: Proceedings of a Workshop. Rio de Janeiro: Academia Brasileira de Ciencias.*

Villa, J. (1977). A new species of pimelodid catfish of the genus Rhamdia from Nicaragua, Central America. *Brenesia*.

Weber, A., & Wilkens, H. (1998). Rhamdia macuspanensis: a new species of troglobitic pimelodid catfish (Siluriformes; Pimelodidae) from a cave in Tabasco, Mexico. *Copeia*, 998-1004.

Weber, A., Allegrucci, G., & Sbordoni, V. (2003). Rhamdia laluchensis, a new species of troglobitic catfish (Siluriformes: Pimelodidae) from Chiapas, Mexico. *Ichthyological Exploration of Freshwaters*, *14*(3), 273-280.

Weitzman, S. H., Menezes, N. A., & Weitzman, M. J. (1988). Phylogenetic biogeography of the Glandulocaudini (Teleostei: Characiformes, Characidae) with comments on the distribution of other freshwater fishes in eastern and southeastern Brazil. In: *Proceedings of a workshop on Neotropical distribution patterns* (Vol. 379, p. 427). Rio de Janeiro: Academia Brasileira de Ciências.

Wilkens, H. (2001). Convergent adaptations to cave life in the Rhamdia laticauda catfish group (Pimelodidae, Teleostei). In *The biology of hypogean fishes* (pp. 251-261). Springer Netherlands.

Zaret, T. M. (1974). The Ecology, of Introductions: a Case-study from a Central American Lake. *Environmental Conservation*, *1*(4), 308-309.

Table 1: List of *Rhamdia* specimens showing: the code used, the name of the species, the

number of individuals, the corresponding drainage and sub-drainage, the catalog number of the voucher and the specimens country and the related clade.

Code	**Species**	**N**	**Drainage**	**Sub-drainage**	**Lote**	**Clade**
Sin01	*R.* aff *quelen*	1	Lagoa dos Patos	Rio dos Sinos	UFRGS 23328	LA4
Sin02-03	*R.* aff *quelen*	2	Lagoa dos Patos	Rio dos Sinos	UFRGS 19665	CC5
Sin04-05	*R.* aff *quelen*	2	Lagoa dos Patos	Rio dos Sinos	UFRGS 19375	CC5
Cai01-04	*R.* aff *quelen*	4	Lagoa dos Patos	Rio Caí	UFRGS 23327	LA4
Cai05-08	*R.* aff *quelen*	4	Lagoa dos Patos	Rio Caí	UFRGS 19663	CC5
Jag01	*R.* aff *quelen*	1	Lagoa dos Patos	Upper rio Jaguarão	UFRGS 20046	LA4
Jag02-05	*R.* aff *quelen*	4	Lagoa dos Patos	Upper rio Jaguarão	UFRGS 20047	CC5
CamU01-02	*R.* aff *quelen*	2	Lagoa dos Patos	Upper rio Camaquã	UGRGS 19725	CC5
CamL01-02	*R.* aff *quelen*	2	Lagoa dos Patos	Lower rio Camaquã	UFRGS 18424	LA4
CamL03-05	*R.* aff *quelen*	3	Lagoa dos Patos	Lower rio Camaquã	UFRGS 18425	LA4
Ant01-02	*R.* aff *quelen*	2	Lagoa dos Patos	Upper Rio das Antas	MCP 48673	CC5
Ant03-04	*R.* aff *quelen*	2	Lagoa dos Patos	Upper Rio das Antas	MCP 48685	CC5
Ant05	*R.* aff *quelen*	1	Lagoa dos Patos	Upper Rio das Antas	MCP 48674	CC5
TaqU01	*R.* aff *quelen*	1	Lagoa do Patos	Upper Rio Taquari	UFRGS 20059	LA4
TaqU02 -04	*R.* aff *quelen*	3	Lagoa do Patos	Upper Rio Taquari	UFRGS 20058	CC5
TaqU05-06	*R.* aff *quelen*	2	Lagoa do Patos	Upper Rio Taquari	UFRGS 23166	HA1
TaqU07	*R.* aff *quelen*	1	Lagoa do Patos	Upper Rio Taquari	UFRGS 22869	HA1
Taq08	*R.* aff *quelen*	1	Lagoa do Patos	Upper Rio Taquari	UFRGS 19535	CC5
JacU01-03	*R.* aff *quelen*	3	Lagoa dos Patos	Upper rio Jacuí	UFRGS 18358	CC5
JacU04-05	*R.* aff *quelen*	2	Lagoa dos Patos	Upper rio Jacuí	UFRGS 18359	HA2
JacU06-07	*R.* aff *quelen*	2	Lagoa dos Patos	Upper rio Jacuí	UFRGS 18226	CC5
JacU08-10	*R.* aff *quelen*	3	Lagoa dos Patos	Upper rio Jacuí	UFRGS 23530	HA2
JacU11	*R.* aff *quelen*	1	Lagoa dos Patos	Upper rio Jacuí	UFRGS 23345	LA4
JacU12-14	*R.* aff *quelen*	3	Lagoa dos Patos	Upper rio Jacuí	UFRGS 19369	CC5
Tra01-05	*R.* aff *quelen*	5	Tramandaí	Lagoa dos Quadros	UFRGS 17717	LA4
Tra06-10	*R.* aff *quelen*	5	Tramandaí	Lagoa Itapeva	UFRGS 19424	LA4
AraL01-05	*R.* aff *quelen*	5	Araranguá	Lower rio Araranguá	UFRGS 21360	LA4
TubL01-03	*R.* aff *quelen*	3	Tubarão	Lower rio Tubarão	UFRGS 21369	LA3
TubL04-05	*R.* aff *quelen*	2	Tubarão	Lower rio Tubarão	UFRGS 21378	LA3
Tij01	*R.* aff *quelen*	1	Tijucas	Lower rio Tijucas	UFRGS 18488	LA3
Tij02	*R.* aff *quelen*	1	Tijucas	Lower rio Tijucas	UFRGS 21083	LA3
Tij03	*R.* aff *quelen*	1	Tijucas	Lower rio Tijucas	UFRGS 21084	LA3
Itpc01	*R.* aff *quelen*	1	Itapocú	Lower rio Itapocu	UFRGS 21086	LA3
Itpc02-03	*R.* aff *quelen*	2	Itapocú	Lower rio Itapocu	LBP 20154	LA3
ItjL01-02	*R.* aff *quelen*	2	Itajaí	Lower rio Itajaí	UFRGS 21505	LA3
ItjL03-04	*R.* aff *quelen*	2	Itajaí	Lower rio Itajaí	UFRGS 21212	LA3
ItjL05-06	*R.* aff *quelen*	2	Itajaí	Lower rio Itajaí	UFRGS 21514	LA3

ItjU01-06	*R.* aff *quelen*	6	Itajaí	Upper rio Itajaí	UFRGS 19905	CC6
Sfs01-02	*R.* aff *quelen*	2	Acarí	Rio Acarí	UFRGS 11934	LA5
Sfs03-06	*R.* aff *quelen*	4	Acarí	Rio Acarí	UFRGS 21214	LA5
Grq01	*R.* aff *quelen*	1	Baía de Guaraqueçaba	Rio Serra negra	UFRGS 12459	LA3
Rib01	*R.* aff *quelen*	1	Ribeira	Lower Ribeira do Iguape	UFRGS 12399	LA3
Rib02-03	*R.* aff *quelen*	3	Ribeira	Lower Ribeira do Iguape	LBP 6843	LA3
Rib04-05	*R.* aff *quelen*	3	Ribeira	Lower Ribeira do Iguape	LBP 7496	LA3
Rib06-08	*R.* aff *quelen*	7	Ribeira	Lower Ribeira do Iguape	LBP 7395	LA3
Rib09	*R.* aff *quelen*	1	Ribeira	Lower Ribeira do Iguape	LBP 7432	LA3
Rib10	*R.* aff *quelen*	1	Ribeira	Lower Ribeira do Iguape	LBP 16840	LA3
Rib11	*R.* aff *quelen*	1	Ribeira	Lower Ribeira do Iguape	LBP 20201	LA3
Itan01-02	*R.* aff *quelen*	2	Itanhenhem	Lower Itanhenhem	UFRGS 18706	LA3
Itan03	*R.* aff *quelen*	1	Itanhenhem	Lower Itanhenhem	LBP 20214	LA3
Uba01-02	*R.* aff *quelen*	2	Picinguaba	Upper rio Picinguaba	UFRGS 13691	LA3
Uba03	*R.* aff *quelen*	1	Mambucaba	Rio Pereque	LBP 7890	LA3
Ber01	*R.* aff *quelen*	3	Itagaré	Rio Itagaré	UFRGS 13652	LA5
Ber02-03	*R.* aff *quelen*	3	Itapanhau	Rio Itapanhau	LBP 14299	LA5
Rj01	*R.* aff *quelen*	1	Baía de Guanabara	Rio Macacu	MNRJ 46842	LA3
Rj02-03	*R.* aff *quelen*	2	Baía de Guanabara	Rio Macacu	MNRJ 43525	LA3
Rj04-05	*R.* aff *quelen*	2	Baía de Guanabara	Rio Suruí	MNRJ 41526	LA3
Rj06	*R.* aff *quelen*	1	Baía de Guanabara	Rio Paraíso	MNRJ 9763	LA3
Rj07	*R.* aff *quelen*	1	Baía de Guanabara	Rio Iguaçu	MNRJ 43148	LA3
Pbs01	*R.* aff *quelen*	1	Paraíba do sul	Upper Paraíba do Sul	UFRGS	LA2
Pbs02-03	*R.* aff *quelen*	2	Paraiba do sul	Medium Paraíba do Sul	LBP 8033	LA2
Pbs04	*R.* aff *quelen*	1	Paraiba do sul	Medium Paraíba do Sul	LBP 10692	LA2
Pbs05	*R.* aff *quelen*	1	Paraiba do sul	Medium Paraíba do Sul	LBP 2117	LA2
Pbs06	*R.* aff *quelen*	1	Paraiba do sul	Medium Paraíba do Sul	LBP 16350	LA2
Dc01-02	*R.* aff *quelen*	2	Doce	Lower rio Doce	UFRGS	LA1
Dc03	*R.* aff *quelen*	1	Doce	Lower rio Doce	LBP 3449	LA1
Sf01	*R.* aff *quelen*	1	São Francisco	Upper São Francisco	LBP 6507	CC1
Sf02	*R.* aff *quelen*	1	São Francisco	Upper São Francisco	LBP 8951	CC1
Sf03-04	*R.* aff *quelen*	2	São Francisco	Upper São Francisco	LBP 17406	CC1
Sf05-06	*R.* aff *quelen*	2	São Francisco	Upper São Francisco	LBP 8965	CC1
Sf07	*R.* aff *quelen*	1	São Francisco	Upper São Francisco	LBP 16305	CC1
Sf08	*R.* aff *quelen*	1	São Francisco	Upper São Francisco	LBP 16317	CC1
Par01-02	*R.* aff *quelen*	2	Paraná	Upper rio Paraná	UFRGS 15354	CC2
Par03-04	*R.* aff *quelen*	2	Paraná	Upper rio Paraná	LBP 17403	CC2
UruU01	*R.* aff *quelen*	1	Uruguai	Upper rio Uruguai	LBP 13042	CC4
UruU02	*R.* aff *quelen*	1	Uruguai	Upper rio Uruguai	LBP 13068	CC4
UruM01-02	*R.* aff *quelen*	2	Uruguai	Medium rio Uruguai	UFRGS 23532	CC4
UruM03-04	*R.* aff *quelen*	2	Uruguai	Medium rio Uruguay	UFRGS 23533	CC4

UruM05-06	*R.* aff *quelen*	2	Uruguai	Medium rio Uruguay	UFRGS 23531	CC4
UruM07-08	*R.* aff *quelen*	2	Uruguai	Medium rio Uruguay	UFRGS 23534	CC4
UruL01-05	*R.* aff *quelen*	5	Uruguai	Medium rio Uruguai	UFRGS 23529	CC5
Uru01	*R.* aff *quelen*	1	Uruguai	Rio Negro	UFRGS 14569	LA4
Am01-02	*R.* aff *quelen*	2	Tapajós	Upper rio Tapajos	LBP 20813	Amazon
Am03	*R.* aff *quelen*	1	Madeira	Upper rio Madeira	LBP 12118	Amazon
Am04	*R.* aff *quelen*	1	Madeira	Upper rio Madeira	LBP 10962	Amazon
Per01	*R.* aff *quelen*	1	Ucayali	Upper Ucayali	LBP 3296	Upper Amazon
Maq01-05	*R. gabrielae*	5	Tramandai	Rio Maquiné	UFRGS 19093	HA3
Maq06-10	*R. gabrielae*	5	Tramandai	Rio Maquiné	UFRGS 19094	HA3
Tf01-10	*R. gabrielae*	5	Tramandai	Rio Três Forquilhas	UFRGS 18034	HA3
Mp01-08	*R. gabrielae*	5	Mampituba	Upper rio Mampituba	UFRGS 19902	HA3
Ara01-08	*R. gabrielae*	5	Araranguá	Upper rio Araranguá	UFRGS 19903	HA3
Tub01-08	*R. eurycephala*	5	Tubarão	Upper rio Tubarão	UFRGS 19904	HA4
Guat	*R. guatemalensis*	1	Belize	Rio Belize	LBP 19584	Mesoamerican
Ciner	*R. cineracens*	2	Guayas	Rio Guayas	LBP 19332	Mesoamerican

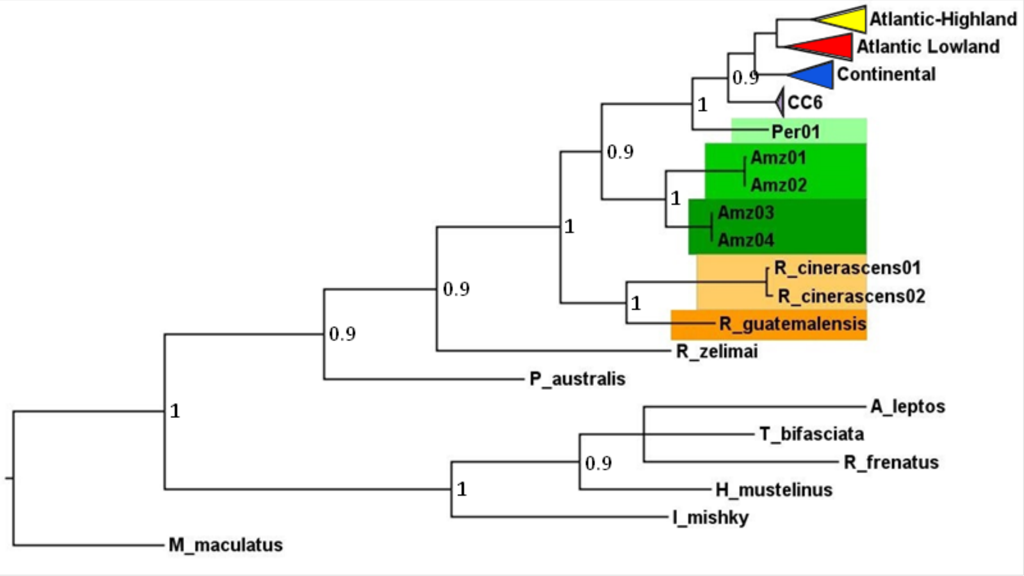

Figure 1: Phylogenetics gene tree produced by Bayesian analysis in MrBayes. Showing the relationship among *Rhamdia* and outgroup. Showing the interrelationship among specimens of the Upper-Amazon clade (light green highlights), Amazon clade (green highlights) and Mesoamerican clade (orange highlights). The others clades are colapsaded. Values in nodes are Bayesian posterior probabilities.

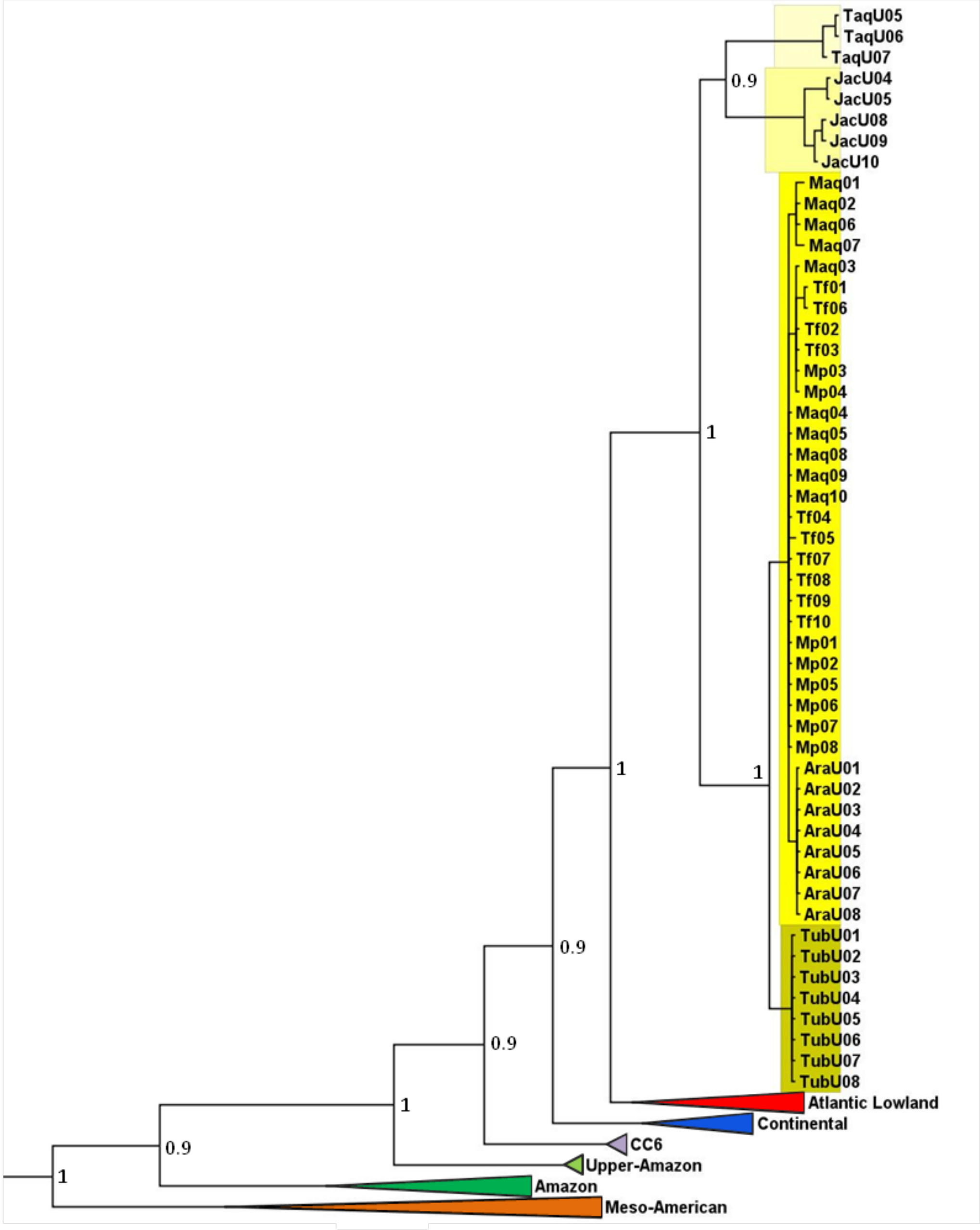

Figure 2: Phylogenetics gene tree produced by Bayesian analysis in MrBayes, showing the interrelationship among specimens of the Highland clade. Differes yellow highlights showing differs lineages inside clade. The others clades are colapsaded. Values in nodes are Bayesian posterior probabilities.

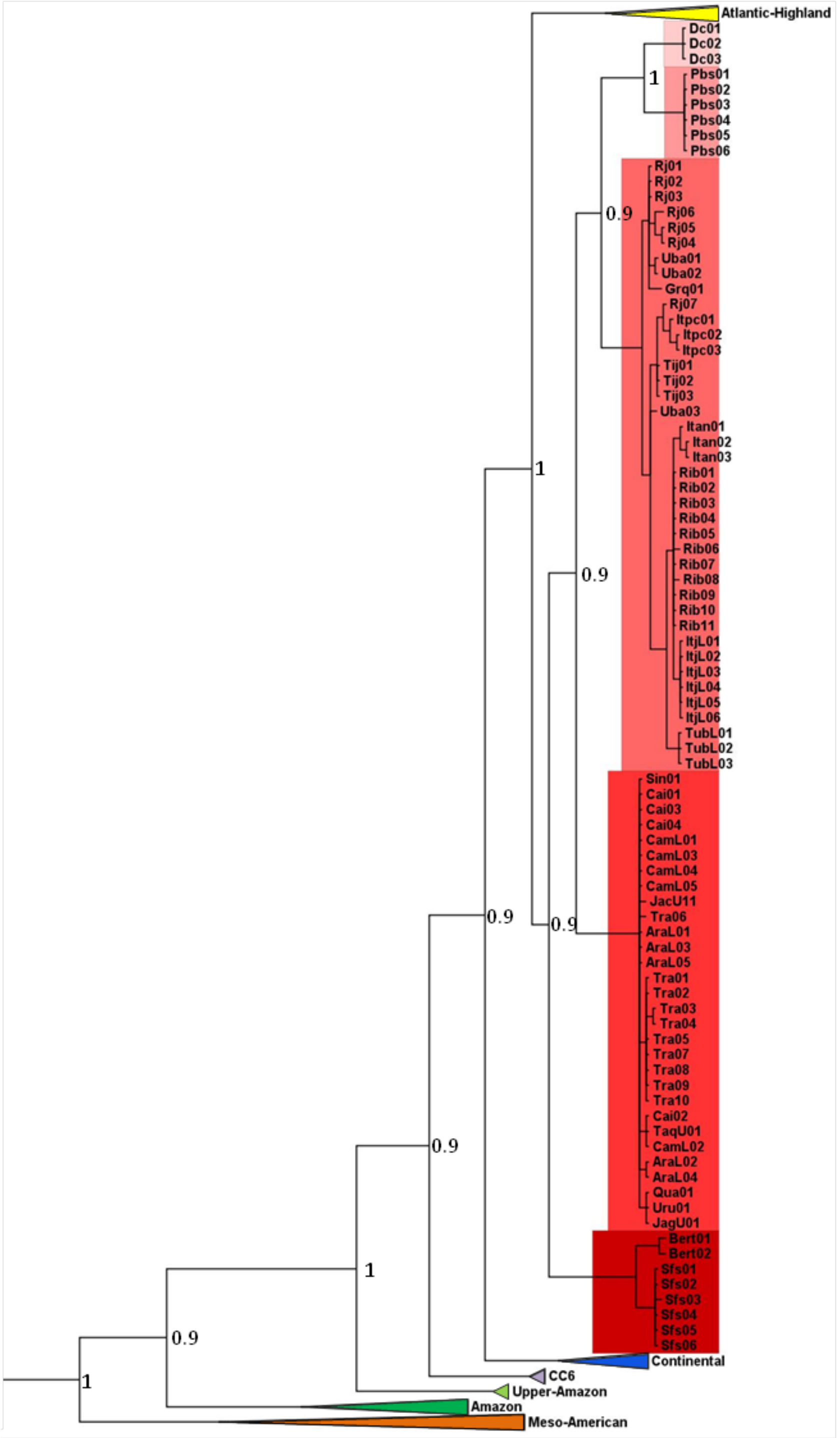

Figure 3: Phylogenetic gene tree produced by Bayesian analysis in MrBayes, showing the interrelationship among specimens of the Lowland clade. Differes red highlights show differs lineages inside clade. The others clades are colapsaded. Values on nodes are Bayesian posterior probalities.

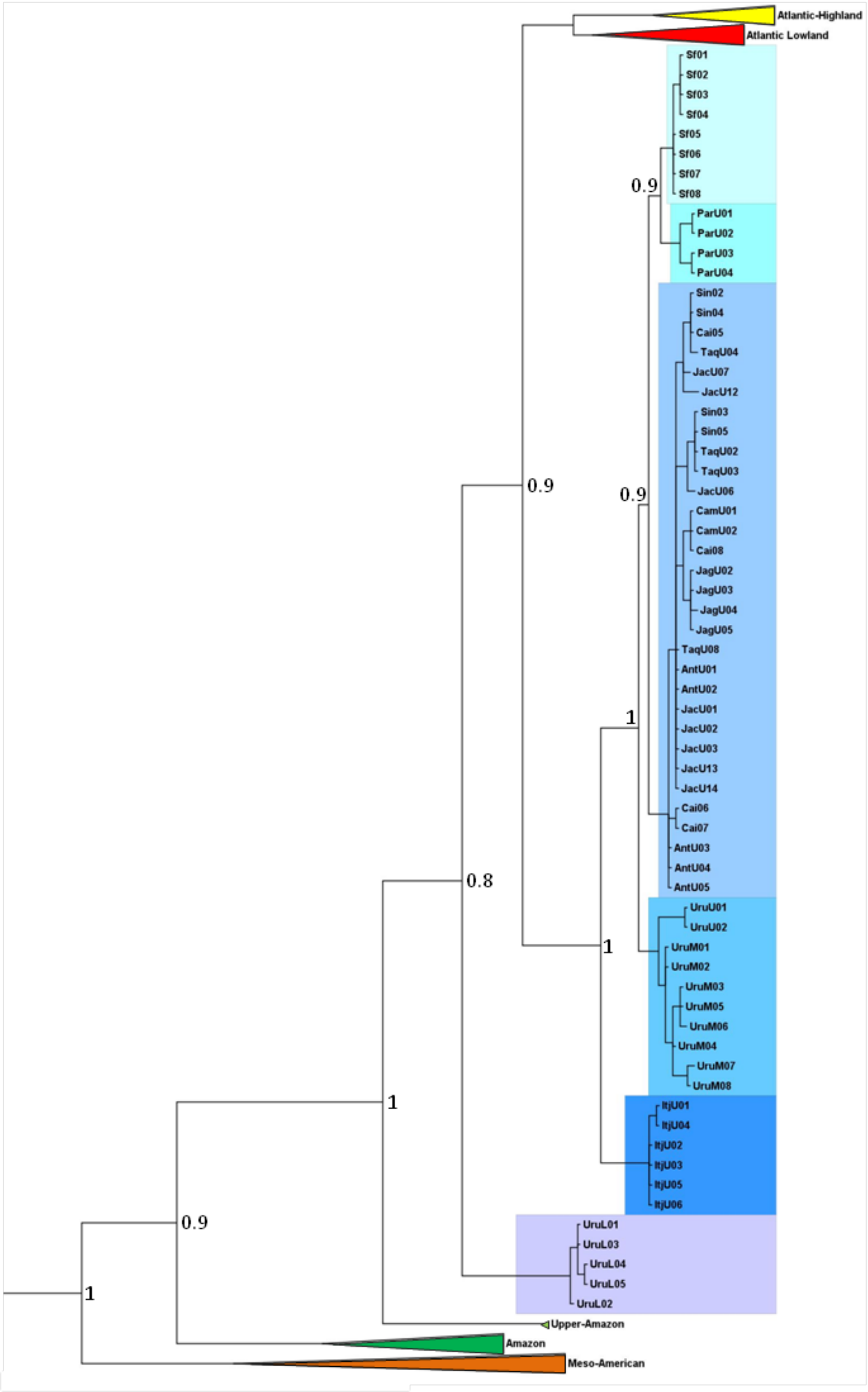

Figure 4: Phylogenetics gene tree produced by Bayesian analysis in MrBayes, showing the interrelationship among specimens of the Continental clade (Blue highlights) and CC6 lineage (Lilac highlights). The others clades are colapsaded. Values in nodes are Bayesian posterior probabilities.

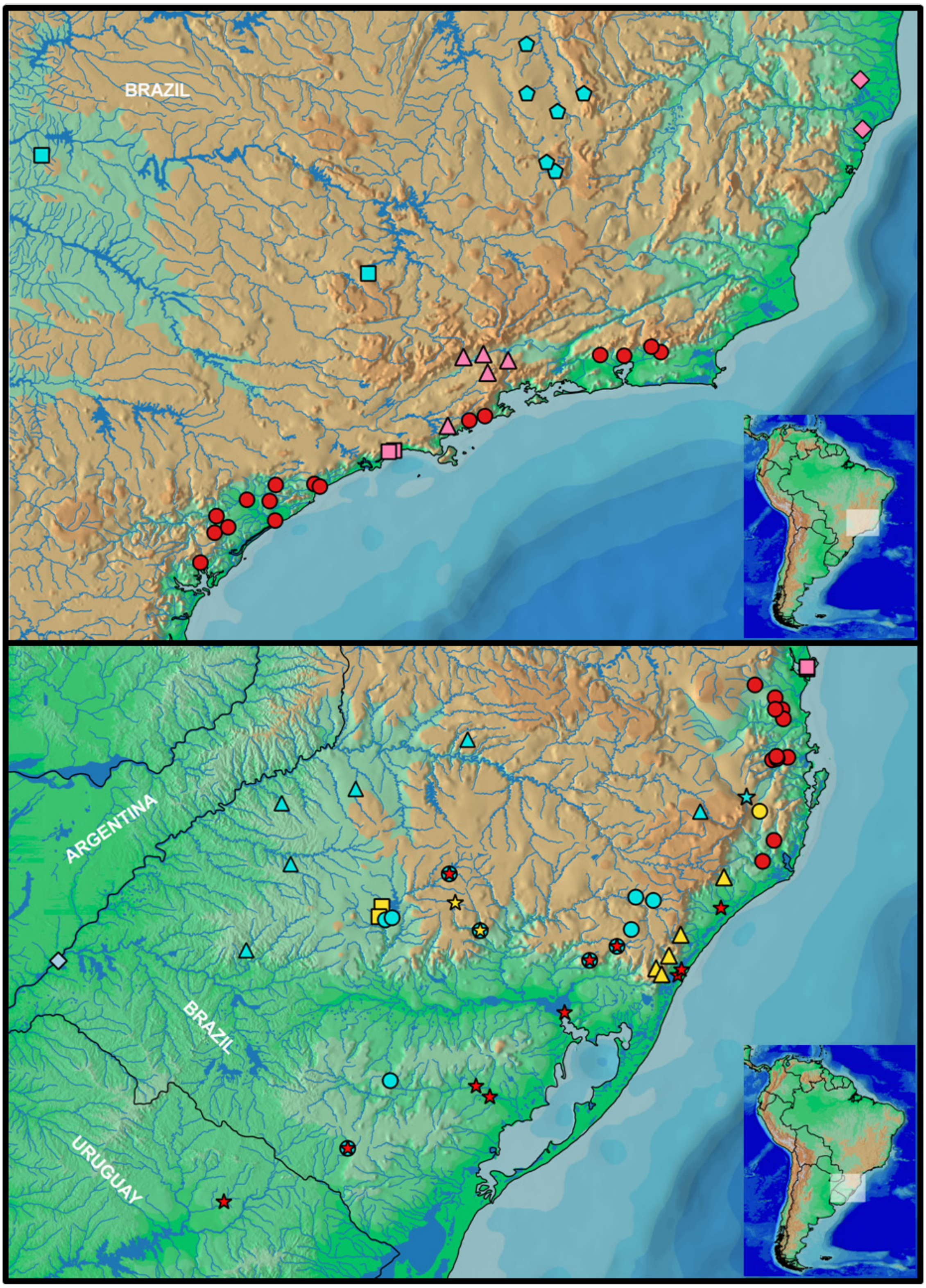

Figure 5: Distribution map of *Rhamdia* lineages. Blue pentagon is CC1 lineage. Blue square is CC1 lineage. Blue triangle is CC3. Blue circle is CC4 lineage. Blue star is CC5 lineage. Grey diamond is CC6 lineage. Pink diamond is LA1 lineage. Pink triangle is LA2 lineage. Red circle is LA3 lineage. Red star is LA4 lineage. Pink square is LA5 lineage. Yellow square is HA2 lineage. Yellow star is HA1 lineage. Yellow triangle is HA3 (*R. gabrielae*). Yellow circle is HA4 (*R. eurichephala*).

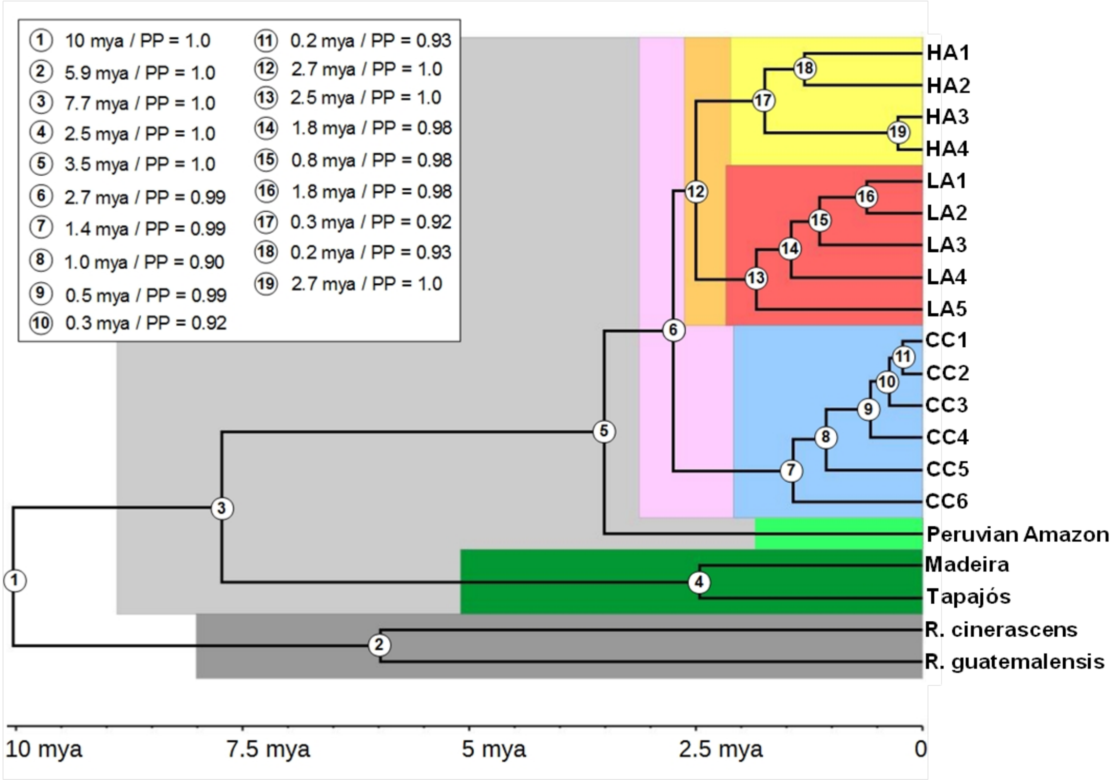

Figure 6: Specie tree produced by starbeast in Beast 1.8.4. In dark grey highlight is a Mesoamerican clade; in ligh grey highlight is a South America clade; in dark green highlight is Amazon clade; in light green highlight is Upper Amazon clade; in pink highlight Brazilian Shield clade; in blue highlight is the Continental clade; in orange highlight is Atlantic clade; in red highlight is the Lowland clade; in yellow highlight is Highland clade. The terminals are different lineages recovery for the bayesian analyses. In the nodes have a number. In nodes have numbers that represent the date and the highest probability value that can be viewed in the legend.

6. Capitulo 3

Artigo submetido para o periódico “Zootaxa”

Redescription of *Rhamdia quelen* and *Rhamdia sapo*(Siluriformes: Heptapteridae)

Running title: What a hell is *Rhamdia quelen*?

Introduction

Rhamdia species are distributed throughout freshwaters of the Neotropical region (Ferraris, 2007). This genus was proposed by Bleeker (1828) and since then over a hundred species have been referred to the group. In an attempt to organize the genus, Silfvergrip (1996) carried out a taxonomic revision in which the nominal species of the genus were assembled in only 11 valid taxa.

After Silfvergrip´s review, many species have been described or redescribed for the genus, that currently has 25 valid species: *Rhamdia quelen* Quoy & Gaimard, 1824; *R. foina* Müller & Troschel, 1849; *R. laukidi* Bleeker, 1858; *R. laticauda* Kner, 1858; *R. cinerascens* (Günther, 1860); *R. humilis* Günther, 1864; *R. muelleri* Günther, 1864; *R. nicaraguensis* Günther, 1864; *R. guatemalensis* (Günther, 1864); *R. parryi* Eigenmann & Eigenmann 1888; *R. poeyi* Eigenmann & Eigenmann, 1888; *R. branneri* Haseman, 1911; *R. voulezi* Haseman, 1911; *R. saijaensis* Rendahl, 1941; *R. reddelli* Miller 1984; *R. zongolicensis* Wilkens 1993; *R. jequitinhonha* Silfvergrip, 1996; *R. xetequepeque* Silfvergrip, 1996; *R. itacaiunas* Silfvergrip, 1996; *R. macuspanensis* Weber & Wilkens, 1998; *R. laluchensis* Weber, Allegrucci & Sbordoni, 2003; *R. guasarensis* DoNascimiento, Provenzano & Lundberg, 2004, and *R. enfurnada* Bichuette & Trajano, 2005, *R. gabrielae* Angrizani & Malabarba 2017 and *R. euricephalae* Angrizani & Malabarba 2017.

Among *Rhamdia* species that are considered valid, *R. quelen* deserves special attention. According to Silfvergrip's (1996) review, 47 nominal species are junior synonyms of *R. quelen*. As a result, this species has a wide geographic distribution, from Mexico to central Argentina. Silfvergrip also designated a neotype for *R. quelen* from the río Ucayali in the Peruvian Amazon, geographically distant from the original type locality located in a tributary of Guanabara Bay, Rio de Janeiro, Brazil (Quoy & Gaimard, 1824).

Many authors criticize and challenge Silfvergrip's proposal and indicate that *R. quelen* is a species complex, revalidating some species then considered synonyms (Perdices et al., 2002, Hernandez et al., 2015, Garavello and Shibatta, 2016) or describing new species related to this complex (Angrizani and Malabarba, 2017). Moreover, phylogeographic studies supports that *R. quelen* would be restricted to South America and that populations from Central America belong to different species (Perdices et al., 2002; Hernández et al., 2015; Angrizani and Malabarba, 2017).

Angrizani and Malabarba (2017) further found that *R. quelen* is made up of at least 18 different evolutionary lineages that would be arranged in five major clades: the Amazon, the Upper Amazon, the Continental, the Atlantic Lowland and the Atlantic Highland clades. They also rejected Silfvergrip´s proposal (1997) and indicated the need of taxonomic reviews to determine if these lineages constitute new species or species to be revalidated from the synonym of *R. quelen*.

The present study describes and diagnose morphologically two of the evolutionary lineages recognized by Angrizani and Malabarba (2017), related to the Atlantic lowland clade, including *R. quelen*, and *R. sapo*, which is revalidated from its synonym. In order to carry it out this taxonomic proposal, the neotype designation of Silfvergrip must be refuted and a new neotype is proposed, considering the rules of the International Code of Zoological Nomenclature. The identity of *R. branneri* Haseman, 1911 and *R. voulezi* Haseman, 1911 are reviewed and discussed.

Material and methods

Eight counts and 40 measurements (to 0.1 mm) were taken on the left side of 50 specimens of *R.quelen* and 50 specimens of *R. sapo*, using a digital caliper and following Angrizani and Malabarba (2017). A total of 91 DNA sequences from the COI gene, taken from GenBank and BOLD, were used to determine the geographic distribution of the species analyzed here and the correct position of *R. branneri* and *R. voulezi* (Table1). The alignments were carried out in Clustal W (Thompson et al., 1998) and a Neighbor-Joining tree was constructed using the MEGA 6 (Kumar et al., 2008).

Comparative material: Specimens of *Rhamdia quelen* species complex*:* From Peru: NRM 16091, Invalid Neotype for *Rhamdia quelen*designated bySilfvergrip (1996), 1, Department of

Loreto, between Caño Pastos and Hamburgo, tributary to río Samiria, S.O. Kullander, 12 Aug 1986. NRM 16104, 1, Peru, department of Ucayali, municipality of Pucallpa, canal to Paca Cocha, basin of rio Ucayali; 08°19'00"S, 74°34'00"W; S.O. Kullander & A. Hogeborn,16 Aug 1981. NRM 33542, 6, Peru, department of Loreto, rio Samiria, basin of rio Amazonas, S.O. Kullander, 12 Aug 1986. ANSP 143976, 1, Peru, department of Madre de Dios, municipality of Shintuya, basin of Madre de Dios; 12°40'52"S, 71°15'01"W; R. Horwitz, 20 Jun 1977. ANSP 143981, 1, Peru, department of Madre de Dios municipality of Atalaya rio Carbon, basin of Madre de Dios; 12°52'51"S, 71°21'29"O; Richard Horwitz,15 Jul 1977. ANSP 180728, Peru, 1, department of Apurimac, municipality of Santa Rosa, rio Antabamba, basin of Ucayali; 14°00'4"S, 73°11'0.62"W; M. Sabaj, L. Rapp Py-Daniel, L. de Souza, 05 Jul 2004. ANSP 180738, Peru department of Cuzco, municipality of Cuzco, rio Urubamba, basin of rio Ucayali Dr; 12°38'27"S, 72°53'41"W;: M. Sabaj, N. Salcedo, B. Rengifo, M. Arce, 20 Jul 2004. ANSP 191817, 2, Peru, department of Loreto, municipality of Iquitos, rio Nanay, basin of Amazonas; 03°49'51"S, 73°20'59"W; M. Sabaj, B. Sidlauskas, E. Correa Roldán & C. Sabaj. LBP 3296, 1, Peru, department of Pasco municipality of Pozuzo, rio Santa Cruz, basin of Ucayali; 10º02'20''S, 75º34'55''W; G. Koo, D. Preising, M. de Pinna, C. Oliveira, H. Ortega, E. Belapatiño, 12 Mar 2006. From Venezuela: ANSP 160239, 5, Venezuela, state of Bolivar, municipality of Puerto Ayacucho, Rio Parguaza, basin of Orinoco; 05°35'12"N, 67°39'08"W, B. Chernoff, W. Saul, C. Marrero, R. Royero. ANSP 139856, 1, Venezuela, state of Bolivar, municipality of Maripa, rio Mato, basin of Orinoco; 07°08'00"N, 65°10'00"W; J.E. Böhlke, W.G. Saul, L. Ferrer-Veliz. ANSP 137554, 1, Venezuela, state of Guárico, municipality of San Juan de los Morros, rio Paya, basin of rio Orinoco; 08°37'60"N, 67°19'60"W; N. R. Foster. ANSP 198574, 1, Venezuela, state of Monagas, municipality of Barrancas, stream of Guargua, basin of rio Orinocooleta; 08°39'48"N, 62°13'60"W; J.N. Baskin, H. Lopez, D. Stewart, L. Aguana. From Colombia: ANSP 177977, 1, Colombia, department of Meta, municipality of El Tigre, stream of Angosturas, basin of rio Meta; 03°58'00"N, 73°03'60"W; J.E. Böhlke, N. Foster, J. Thomerson. ANSP 137555, 1, Colombia, department of Meta, municipality of Villavicencio, rio Negro, tributary of rio Meta, basin of Orinoco; 04°08'14"N, 73°18'46"W; J.E. Böhlke, N. Foster, D. Smith. NRM 16100, 3, Colombia, department of Meta, municipality of Apiay, stream Union, tributary of río Meta, basin of Orinoco A.M.C. Silfvergrip, 6 Jan 1988. NRM 16000, 1, Colombia, department of

Meta, municipality of Apiay, stream of Quenane, rio Negro, tributary of rio Meta, basin of Orinoco basin; 04°00'33"N, 73°30'34"W; A.M.C. Silfvergrip, 13 Jan 1988. From Guiana: ANSP 179729, 1, Guiana, region Tukutu-Essequibo, municipality of Yapukarri, Two Puddle creek, tributary of rio Rupununi, basin of rio Essequibo; 03°45'11"N, 59°19'38"W; M. Sabaj, J. Armbruster, M. Thomas, D. Werneke, C. Allison, C. Chin, D. Arjoon. ANSP 179728, 6, Guyana, region of Potaro-Siparuni, municipality of Surumatra, tributary of rio Essequibo, basin of Essequibo; 04°08'58"N, 59°00'30"W; M. H. Sabaj, J. W. Armbruster, M. R. Thomas. From Paraguay: NRM 15874, 2, Paraguay, department of Presidente Hayes, municipality of Estancia Santa Maria, río Paraguay; 23°02'00"S, 59°12'00"O; S.O. Kullander, 1 Feb 1992. NRM 39585, 1, Paraguay, department of San Pedro, municipality of Puerto Milagro, La Paz stream, basin of rio Paraguay; 23°36'11"S, 57°26'36"W; G. Frisk, 6 Nov 1996. NRM 22888, 6, Paraguay, department of Paraguarí, municipality of La Rosada, Minas stream, tributary of Ybycui, basin of rio Paraguay; 26°05'38"S, 56°50'15"W; B. Delling, 11 Oct 1995. NRM 32904, 2, Paraguay, department of Ñeembucú, municipality of Humaita, swamp area, basin of rio Paraguay; 27°08'40"S, 58°32'20"W; E. Åhlander, 13 Sep 1995. From Brazil: UFRGS 19665, 3, Brazil, state of Rio Grande do Sul, municipality of Canela, rio Santa Maria, tributary of rio dos Sinos, basin of lagoa dos Patos; 29°20'47"S, 50°42'04"W; G Volkmer, 17 Oct 2015. UFRGS 19663, 4, Brazil, state of Rio Grande do Sul, municipality of Santa Maria do Herval, rio Cadeia, tributary of rio Caí, basin of Lagoa dos Patos; 29°30'03"S, 51°00'03"W; G. Volkmer, 17 Oct 2015. UFRGS 20047, 3, Brazil, state of Rio Grande do Sul, municipality of Candiota, arroio Candiota, tributary of rio Jaguarão, basin of Lagoa Mirim; ; R. Angrizani, 7 May 2015, MCP 48673, 6, Brazil, state of Rio Grande do Sul, municipality of Jaquirana, rio das Antas, basin of Lagoa dos Patos; 28°48'20"S, 50°29'38"W; J.P. Silva, 10 Mar 2015. UFRGS 20058, 3, Brazil, state of Rio Grande do Sul, municipality of Marau, rio Taquari, basin of laguna dos Patos ; 28^{o}21'01"S, 52^{o}12'57"O; G. Volkmer, 11 Nov 2014. UFRGS 23166 Brazil, state of Rio Grande do Sul, municipality of Soledade, little stream tributary of rio Taquari, basin of laguna dos Patos ; 28^{o}52'07"S, 52^{o}28'45"W; F. Becker, R. Dalla-Corte, 12 Nov 2013. UFRGS 18359, 2, Brazil, rio Grande do Sul, municipality of Salto do Jacuí, rio Lageado Pelado, tributary of rio Jacuí, basin of Lagoa dos Patos; 29°02'24"S, 53°17'31"W; A.P. Dufech & J.L. Santos, 31 Oct 2013. UFRGS 11934, 3, Brazil, state of Santa Catarina, municipality of São Francisco do Sul, tributary of rio Acari, basin of rio

Acari, 26°16'23"S, 48°36'34"W; L. Malabarba, R. Quevedo and V. Bertaco, 27 Jan 2007. LBP 8033, 1, Brazil, state of São Paulo, municipality of Piquete, Piquete stream, basin of Paraíba do Sul; 22°35'58"S, 45°09'38"W; C. Oliveira, M. Mehanna, L.H.G. Pereira and G.J.C. Silva 27 Mar 2009. LBP 10692, 1, Brazil, state of São Paulo, municipality of Lavrinhas, Rio Jacu, basin of rio Paraíba do Sul; 22°34'42"S, 44°53'22"W; J.A. Senhorini, 06 Oct 2010. UFRGS 18972, 2, Brazil, state of Espírito Santo, municipality of Aracruz, little stream, basin of rio Doce; 19°46'48"S, 40°09'55"W; P. Silva, U. Santos, A. Hirschmann, A. Thomaz & T. Carvalho, 13 Jan 2014. LBP 3449, 1, Brazil, state of Espírito Santo, municipality of Sooretama, Juparanã lagoon, basin of rio Doce, 19°09'51"S, 40°11'40"W; C. Oliveira, A.L. Alves, M.C. Chiachio, O.T. Oyakawa and M. Ghazzi, 01 Sep 2006. LBP 17406, LBP 8965, 2, Brazil, state of Minas Gerais, municipality of Curvelo, Amendoim stream, tributary of rio das Velhas, basin of rio São Francisco; 18°43'14"S, 44°20'47"W; C. Oliveira, F. Roxo, G. Silva and B. Melo, 01 Oct 2009. LBP 16305, 1, Brazil, state of Minas Gerais, municipality of Brumadinho, little stream, tributary of rio Paraopeba, basin of rio São Francisco; 20°11'40"S, 44°06'05"W; M. Mehanna, A. Ferreira, R. Devidé, R. Ramirez, 12 Jun 2012. UFRGS 15354, 2, Brazil, state of São Paulo, municpality of Guarani D'Oeste, Santa Rita stream, tributary of rio Grande, basin of rio Paraná; 20°06'13"S, 50°23'33"W; F. Carvalho, J. Neves & R. Neves, 17 Ago 2010. LBP 13042, 1, Brazil, state of Santa Catarina, municipality of rio Rufino, rio Rufino, basin of rio Uruguai; 27°51'45"S, 49°47'05"W; G.J.C. Silva, F. Roxo, J.H. Monteiro and R. Devidé, 27 Oct 2010. LBP 13068, 2, rio Ariranha, basin of rio Uruguai, 27°04'19"S, 52°20'36"W, Brazil, state of Santa Catarina, municipality of Xavantina, G. Silva, F. Roxo, J. Monteiro, R. Devidé, 28 Oct 2010. UFRGS 23532, 2, Brazil, state of Rio Grande do Sul, municipality of Erval Seco, rio Guarita, basin of rio Uruguai; 27°36'49"S, 53°34'28"W; G. Volkmer, 24 Nov 2014. UFRGS 23533, 2, Brazil state of Rio Grande do Sul, municipality of Santa Rosa, rio Santa Rosa, basin of rio Uruguai; 27°46'15"S, 54°23'14"W; G. Volkmer, 26 Nov 2011. UFRGS 23531, 2, Brazil, state of Rio Grande do Sul, municipality of Eugenio de Castro, rio Ijuizinho, tributary of rio Ijuí, basin of rio Uruguai; 28°26'33"S, 54°17'09"W; G. Volkmer, 28 Nov 2014. LBP 20813, 3, Brazil, state os Mato Grosso, municipality of Nova Mutum, rio Carandá, basin of rio Tapajós; 13°48'00"S, 55°57'51"W; G. Silva, C. Araya, N. Mateussi, B.F. Melo, 29 Oct 2015. LBP 12118, 1, Brazil, state of Rondônia, municipality of Porto Velho, rio Quinta, basin of rio Madeira; 09°03'40"S, 64°01'16"W, C. Oliveira, M.

Taylor, M. Alexandroum and G.J.C. Silva, 26 Ago 2010. LBP 10962, 1, Brazil, state Rondônia, municipality Nova Mamoré, little stream, tributary of rio Madeira; 09°57'03"S, 65°17'44"W; C. Oliveira, M. Alexandrou, G. Silva, M. Taylor, 21 Oct 2010. UFRGS 23529, 5, Brazil, state of Rio Grande do Sul, municipality of Uruguaina, rio Uruguai; 29°30'20"S, 56°50'41"W; R. Malabarba, M. Malabarba, K. Bonato, R. Angrizani, 14 May 2015. *Pimelodus sebae:* sintypes: 2,MNHN A-9420, MNHN A-9421, Argentina; *Pimelodus hilarii:* Holotype MNHN a-9415, 1, Brazil, Rio São Francisco, G. Saint-Hilaire. *Pimelodus pentlandii:* Lectotype BMNH 1862.11.15:11, 1, Peru, rio Apuriamac. *Pimelodus wuchereri:* Lectotype BMNH 1864.1.19.18, 1, Brazil, Bahia. *Pimelodus godmanni:* Lectotype BMNH 1864.1.26.94, 1, Guatemala, Río San Geronimo, Godman & Salvin. *Pimelodus micropterus:* Holotype BMNH 1864.1.26.92, 1, Guatemala, Río San Geronimo, Salvin. *Pimelodus wagneri:* Holotype NMW 45618, Pacific and Atlantic rivers of Panama. *Rhamdia bransfordii:* Holotype USNM 16674, Panama, Camp Marie Caretta. *Pimelodus bathyurus:* Lectotype ANSP 21437, Peru, Peruvian Amazon, J. Orton, 1877. *Pimelodus parahybae:* Holotype NMW 45852, 1, Brazil, rio Parahyba. *Pimelodus quelen cuprea:* Holotype NMW 45887:1, 1, Brazil, municipality of Juiz de Fora, rio Parahyba. *Pimelodus cuyabae:* Lectotype NMW 45919:1, 1, Brazil, rio Paraguai, Cuyabá. *Pimelodus boucardi:* Holotype BMNH 1880.7.13.33, 1, Mexico, Est yucatan. *Rhamdia dorsalis:* Holotype USNM 35334, Ecuador, rio Maranon or Napo Rivers. *Rhamdia mounseyi:* Lectotype BMNH 1913.7.30:13, 1, Peru, River Ucayali. *Rhamdia riojae:* Holotype ANSP 21101, 1, Peru, munucipality of Rioja, rio Huallaga. J. Orton, 1873. *Rhamdia ortoni:* Holotype ANSP 21928, Peru, Peruvian Amazon. J. Orton. *Rhamdia gilli:*Holotype USNM 53472, Peru, Río Eten. *Caecorhmadia urichi:* BMNH 1926.7.28:1, Holotype, 1, Trinidad, Oropuche Cave. *Rhamdia heteracantha:* BMNH 1907.6.28.3, Holotype, 1, Costa Rica, Juan Viñas. *Rhamdia foina:* ANSP 189114, 1, Suriname, distric of Sipalawiniawa, municipality of Anapaike, Lawa river, basin of Marowijne river; 03°20'49.54"N, 54°03'41.35"W; M. Sabaj, P. Willink, J. Mol and K. Wan, 24 Apr 2007. ANSP 190948, 1, Venezuela, state of Amazonas, municipality of San Fernando de Atabapo, Cano Guapa Sucia at mouth, river Atabapo, basin of Orinoco; 04°01'00"N, 67°41'14"W; N.K. Lujan and M. Arce, 2013. ANSP 190951, 1, Venezuela, state of Amazonas, municipality of Santa Barbara, Ventuari river, basin of Orinoco river; 04°04'33"N, 66°53'16"W; N.K. Lujan, M. Arce, E.L. Richmond, M.B. Grant & T.E. Wesley, 2010.

Rhamdia laukidi: MZUSP 81485, 3, Brazil, state of Amazonas, municipality of Tiquié, igarapé Açaí tributary of rio Tiquié, 0°15'55"N, 69°58'16"W. MZUSP 85074, 3, state of Amazonas, municipality of Tiquié, rio Tiquié, 0°15'35"N, 70°02'42"W. ANSP 174652, Neotype, 1, Venezuela, state of Amazonas, municipality of Tama Tama, Casiquiare river, basin of Orinoco; 03°06'29.00"N, 65°49'56"W; B. Chernoff, J. Fernandez, O. Castillo. ANSP 162516, 2, Venezuela, state of Amazonas, municipality of Tama Tama, Casiquiare river, basin of Orinoco; 03°06'29.00"N, 65°49'56"W; B. Chernoff, J. Fernandez, O. Castillo. ANSP 134383, 2, Colombia, departament of Meta, municipality of La Siberia, Tributary of Cano La Raya, basin of rio Meta; 04°04'47"N, 73°06'39"W; J.E. Bohlke, W.G. Saul & L. Fuiman. *Rhamdia laticauda:* NRM 53310, 5, El Salvador, province of Santa Ana, Municipality ofMetapan, basin of Río Lempa, Kullander, SO & Ready, JS, 23 Feb 2006. NRM 53213, 6,El Slavador, provinceSan Miguel, municipality ofCarolina, Río Torola, basin of Río Lempa, Kullander, SO, 20 Feb 2006. NRM 31832, 3, Guatemala, province of Chiquimula, municipality ofChiquimula**,** Río Motagua, Fredriksson, C & Mähl, S, 11 Feb 1995. *Rhamdia cinerascens:* BMNH 1860.6.16:193, lectotype, 1, Ecuador, municipality of Guayaquil or Esmeraldas, Río Daule. ANSP 92426, 1, municipality of Guayaquil. Rio Guayas, 02°14'12"S, 79°52'04"W. *Rhamdia humillis:* BMNH 1965.2.19:1, Holotype, 1, Venezuela. *Rhamdia muelleri:* MZUSP 23034, 4, state of Pará, municipality of Belém, igarapé Paracuri, 01°26'60"S, 48°38'00"W, 01 Aug 1965.ANSP 166960, 1, Venezuela, state of Bolivar, municipality of Maripa, rio Urbana; 07°15'26.75"N, 64°59'00"W; J. E. Bohlke, W.G. Saul & E. Ferrer-Veliz. ANSP 149827, 1, Venezuela, state of Bolivar, municipality of Maripa, rio Urbana; 07°15'26.75"N, 64°59'00"W; J. E. Bohlke, W.G. Saul & E. Ferrer-Veliz. ANSP 162519, 1, Venezuela, state of Amazonas, municipality of Tama Tama, rio Orinoco; 03°03'58"N, 66°27'53"W; B. Chernoff, W. Saul, H. Lopez, J. Fernandez, O. Castillo, M.E. Antonio & J. Moreno. *Rhamdia nicaraguensis:* ANSP 163732, 2,Costa Rica, municipality of Heredia, brook of Rio Cuarto; 10°20'39"N, 84°13'08"W; P. Fromm, 1989. ANSP 124137, 1, Nicaragua, minicipality of Bethehem, Pis River, Basin of Wanx River; 14°09'14"N, 84°37'13"W; W. Huber, 1979. *Rhamdia guatemalensis:* BMNH 1864.1.26:210, Holotype 1, Guatemala, laguna Huamuchal, Salvin. NRM 53260, 15, El Salvador, Province Morazán, Municipality Yamabal, río Yamabal, basin of Río Grande de San Miguel, Kullander, SO, 21 Feb 2006. NRM 53387, 1, El Salvador, province San Miguel, municipality El Transito, Basin of Río Grande de San Miguel, Laguna Jocotal, Kullander, SO, 22 Feb 2006.NRM 53355, 3, El Salvador, province of Santa Ana, municipality Metapan, basin of Río Lempa, Lago Güija, Kullander, SO & Ready, JS, 23 Feb 2006. *Rhamdia poeyi:* MZUSP 024557, 4, state of Goiás, municipality of São Domingos, ribeirão Bezerra, rio Tocantins, 13°24'00"S, 46°19'00"W, 1974. *Rhamdia saijaensis:* NRM 10675, Holotype, 1, Colombia, south of Buenaventura, rio Saija, G. Gerring, 1939. NRM 15329, 3, Colombia, south of Buenaventura, rio Saija, G. Gerring, 1939. *Rhamdia jequitinhonha:* MNRJ 22514, 1, Brazil, state of Minas Gerais, municipality of Pedra Azul, 15°54'50"S, 41°23'31"W, 10 Jul 2001. *Rhamdia xetequepeque:* NRM 34053, 5, Peru, province of Cajamarca, municipality of Chilete, Río Jequetepeque, Holm, E, 11 Jul 1986. *Rhamdia itacaiunas:*MZUSP 34744, Paratype, 2, Brazil, state of Pará, municipality of Marabá, rio Itacaiunas, 05°22'00"S, 49°07'00"W, 14 Oct 1983. *Rhamdia gabrielae:* UFRGS 22010, 194 mm SL, Brazil, state of Rio Grande do Sul, municipality of Maquiné, arroio Pinheiro, tributary of rio Maquiné, 29°39'43"S, 50°15'55"W; F. G. Becker, 19 Jun 1999. UFRGS 18033, 10, state of Rio Grande do Sul, municipality of Maquiné, rio Maquiné, 29°38'52"S, 50°13'03"W; J. M. Santos, 30 Mai 2013. *Rhamdia euricephalae:*UFRGS 19908, Holotype, 1, Brazil, state of Santa Catarina, municipality of Anitápolis, rio do Povoamento, hydrographic basin of rio Tubarão, 27°51'36"S, 49°07'50"W; R. C. Angrizani, L. R. Malabarba, M. C. Malabarba, 21 Feb 2015. UFRGS 19906, 16, municipality of Anitápolis, rio do Povoamento, hydrographic basin of rio Tubarão, 27°51'50"S 49°07′54"W, R.C. Angrizani, L.R. Malabarba, M.C. Malabarba, 21 Feb 2015. *Rhamdia enfurnada:* MZUSP 87776, Holotype, 1, Brazil, state of Bahia, municipality of Coribe, gruta do Enfurnado, rio São Francisco, 13°38'44"S, 44°12'05"W, 5 Sep 2003.*Rhamdia guasarensis:* ANSP 179878*,* Venezuela, state of Zulia, municipality of Cerro Yolanda, basin of Rio Guasare; 10°52'26"N, 72°30'44"W; J. Lagarde, 2004.

Results

Rhamdia quelen Quoy & Gaimard, 1824

(Fig. 1)

Pimelodus namdia Cuvier 1829: 294, Le Règne Animal (Edition 2) v. 2.
Heterobranchus sextentaculatus Spix & Agassiz 1829:28, Pl. 11, Reise nach Griechenland und der Türkei; Brazil.
Pimelodus sellonis Müller & Troschel 1849:2, Horae Ichthyologicae No3; Brazil.
Rhamdia branneri Haseman, 1911: 377 pl. LXXV; Creek of rio Iguassú (current Iguaçu), near Serrinha, Paraná State, Brazil.

Neotype (by present designation – see discussion about invalid designation by Silfvergrip, 1996): MNRJ 13730**,** Brazil, state of Rio de Janeiro, municipality of Cachoeira de Macacu, tributary of Soarinho river, tributary of Macacu river, hidrographic basin of Guanabara bay, 22°38’6”S,42°43’6”W; P. A. Buckup and D. F. Moraes Jr, 21 Fev 1995.

Examined material: All from Brazil: MCP 11030, 2, 97.2-100.0 mm SL, state of Santa Catarina, municipality of Sanga de Areia stream, basin of Tubarão river; 28°28’00”S, 49°01’60”W; C. Lucena, L. Malabarba e L. Bergmann, 8 Dec 1986. UFRGS 21369, 2, 7.2-21.5 mm SL, state of Santa Catarina, municipality of São Martinho, Guabiroba river, basin of Tubarão river; 28°10'52"S, 48°58'25"W; R. Angrizani, J. Wingert, J. Ferrer and F. Kuhn, 26 Jan 2016. UFRGS 21378, 2, 15.2-19.5mm SL, state of Santa Catarina, municipality of Tubarão, Pouso river, basin of Tubarão river; 28°24'39"S, 49°05'56"W; R. Angrizani, J. Wingert, J. Ferrer and F. Kuhn26 Jan 2016. UFRGS 18488, 1, 9.6 mm SL, state of Santa Catarina, municipality of São João Batista, Tijucas river; 27°16'00"S, 48°49'15"W; A. Thomaz, A. Hirschmann, P. Silva, C. and T. Carvalho, 10 Dez 2013. UFRGS 21083, 1, 6.8 mm SL, state of Santa Catarina, municipality of Nova Trento, Nova Trento stream, basin of Tijucas river, 27°16'47"S, 48°56'20"W, T. Carvalho, F. Carvalho and A. Thomaz, 03 Sep 2015. UFRGS 21084, 1, 5.2 mm SL, state of Santa Catarina, municipality of Nova Trento, Mesquita river, 27°17'40"S, 48°58'27"W, T. Carvalho, F. Carvalho and A. Thomaz, 03 Sep 2015. UFRGS 21085, 1, 8.5 mm SL, state of Santa Catarina, municipality of Nova Trento, Santa Paulina stream, basin of Tijucas; 27°15'23"S, 48°56'45"W; T. Carvalho, F. Carvalho and A. Thomaz, 03 Sep 2015. MCP 16538, 18, 96.3-228.6 mm SL, state of Santa Catarina, municipality of Apiúna, São Luiz stream, basin of Itajaí river; 27°01’60”S, 49°23’00”W; C. Lucena, J. Pezzi, E. Vidal and A. Jardim, 15 Oct 1993. MCP 16560, 24, 119.4–210.5 mm SL. State of Santa Catarina, municipality of Gaspar, Canas stream, basin of Itajaí river; 26°57’00”S, 48°56’00”W; C. Lucena, J. Pezzi, E. Vidal e A. Jardim, 15 Oct 1993. MCP 25518, 3, 202.5–246.9 mm SL, state of Santa Catarina, municipality of Rio dos Cedros, Cedros river, basin of Itajaí river; 26°4 4’00”S, 49°16’60”W; B. Marteres, 17 Nov 1999.. UFRGS 21505, 7, 102-148.2 mm SL, state of Santa Catarina, municipality of Luiz Alves, Luiz Alves river, basin of Itajaí river; 26°44'18”S, 48°57'32"W, R. Angrizani and G. Volkmer, 02 Feb 2016. UFRGS 21514, 4, 89.2-140.5 mm SL, state of Santa Catarina, municipality of Ilhota braço, 26°50'38"S, 48°52'10"W, R. Angrizani and G. Volkmer, 02 Feb 2016. UFRGS 21512, 3, 85.1-144.2 mm SL, state of Santa Catarina, municipality of Luiz Alves, Luiz Alves river, basin of Itajaí river; 26°43'53"S, 48°52'32"W; R. Angrizani & G. Volkmer, 02 Feb 2016. UFRGS 21513, 4, 102.4-144.4 mm SL, state of Santa Catarina, municipality of rio Luiz Alves, Luiz Alves river; 26°44'26"S, 48°53'02"W; R. Angrizani and G. Volkmer, 02 Feb 2016. MCP 16584, 1, 164.0 mm SL, state of Santa Catarina, municipality of Águas Mornas, Teresópolis river, basin of Cubatão river; 27°45’00”S, 48°56’00”W; C. Lucena, J. Pezzi, E. Vidal e A. Jardim, 16 Oct 1993. MZUSP 36480, 9, 128.2-190.2 mm SL, state of Santa Catarina, municipality of Joinville, Lindo stream, basin of Cubatão river; 26°10’00”S, 48°54’00”W; L. Malabarba, R. Reis e C. Lucena, 19 Set 1985. MCP 28727, 4, 121.5-150.0 mm SL, state fo Santa Catarina, municipality of Florianópolis, basin of Ratones river; 27°30’40”S, 48°29’11”W; L. Malabarba, V. Bertaco e M. Azevedo, 25 Oct 2001. MCP 28758, 2, 149.3-151.2 mm SL, state of Santa Catarina, municipality of Garopaba, little stream, basin of Ribeirão lagoon; 27°57’15”S, 48°38’45”W; L. Malabarba, V. Bertaco e M. Azevedo, 26 Oct 2001. MCP 28762, 1, 230.0 mm SL; state of Santa Catarina, municipality of Garopaba, little stream, basin of Macacu lagoon; 28°00’39”S, 48°39’21”W; L. Malabarba, V. Bertaco e M. Azevedo, 26 Oct 2001. MCP 6895, 1, 196.2 mm SL, state of Santa Catarina, municipality Corupá, Itapocu river; 26°26’00”S, 49°15’00”W; C. Lucena, L. Malabarba e A.

Bergmann, 20 Nov 1985.. MZUSP 36465, 1, state of Santa Catarina, municipality of Corupá, Itapocu river; 26°25’00”S, 49°15’00”W; L. Malabarba, R. Reis and C. Lucena, 20 Sep 1985. UFRGS 21086, 1, 92.5 mm SL, state of Santa Catarina, municipality of Massaranduba, Massaramduba stream, basin of Itapocu river, 26°36'41"S, 48°57'39"W, T. Carvalho, F. Carvalho and A. Thomaz, 03 Sep 2015. LBP 20154, 2, 6.2-80.2 mm SL, state of Santa Catarina, municipality of Jaraguá do Sul, Cavalo stream, basin of Itapocu river; 26°28’12”S, 49°10’56”W; P. Camelier, G. Silva, R. Devidé, C. Souza, 17 Jun 2015**.** MHNCI 8065, 4, 91.5-140.7 mm SL, state of Paraná, municipality of Morretes, Caninana river, basin of Nhumdiaquara river; 25°28’37”S, 48°50’04”W; J. Andreguetto e B. Marterer, 24 Nov 1986. MHNCI 10663, 8, 91.5-239.0 mm SL, state of Paraná, municipality of Morretes, Caninana river, basin of Nhumdiaquara river; 25°28’37”S, 48°50’04”W;; M. Britto, 03 Mar 2004. MHNCI 1382, 1, 237.5 mm SL, state of Paraná, municipality of Antonina, Cachoeira river; 25°25'21.64"S, 48°44'7.40"W; V. Abilhoa and L. Bastos, 4 Fev 2000. MHNCI 1383, 1, 233.5 mm SL, state of Paraná, municipality of Antonina, Cachoeira river; 25°25'21.64"S, 48°44'7.40"W; V. Abilhoa and L. Bastos, 4 Fev 2000. MHNCI 1384, 1, 195.1 mm SL, state of Paraná, municipality of Antonina, Cachoeira river; 25°25'21.64"S, 48°44'7.40"W; V. Abilhoa and L. Bastos, 4 Fev 2000. MHNCI 1385, 1, 248.8 mm SL, state of Paraná, municipality of Antonina, Cachoeira river; 25°25'21.64"S, 48°44'7.40"W; V. Abilhoa and L. Bastos, 4 Fev 2000. MHNCI 1386, 1, 252.2 mm SL, state of Paraná, municipality of Antonina, Cachoeira river; 25°25'21.64"S, 48°44'7.40"W; V. Abilhoa and L. Bastos, 4 Fev 2000. MHNCI 1387, 1, 250.6 mm SL, state of Paraná, municipality of Antonina, Cachoeira river; 25°25'21.64"S, 48°44'7.40"W; V. Abilhoa and L. Bastos, 4 Fev 2000. MHNCI 6340, 3, 145.0-220.5 mm SL, state of Paraná, municipality of Antonina, Capivari river, basin of Cachoeira river; 25°25’43”S, 48°42’43”W; E. Grando and A. Cordeiro, 14 Fev 2004.

Bacia do rio Morato. MHNCI 7878, 4, 25-85 mm SL, state of Paraná, municipality of Guaraqueçaba, Velho river, basin of Morato river; 25°18’24”S, 48°19’44”W; W. Wosiacki and J. Matheus, 25 Jun 1994. UFRGS 12459, 1, 74.2 mm SL, state of Paraná, municipality of Guaraqueçaba, Serra Negra stream; 25°10’26”S, 48°25’13”W; V. Bertaco, F. Carvalho, Jerep and A. Thomaz, 22 Apr 2008. MCP 12178, 8, 100.8-222.3 mm SL, state of São Paulo, municipality of Juquiá, Juquiá river, basin of Ribeira do Iguape river; 24°19’00”S, 47°36’60”W; C. Lucena, L. Malabarba and A. Bergmann, 27 Jul 1988. MZUSP 22578, 2, 144.3-203.9 mm SL, state of São Paulo, municipality of Iporanga, Betari river, basin of Ribeira do Iguape river; 24°34’00”S, 48°40’00”W; expedição do Departamento de Zoologia. 10 Oct 1961. MZUSP 28413, 1, 132.8 mm SL, state of São Paulo, municipality of Iporanga, Ouro Grosso stream, basin of Ribeira do Iguape river; 24°35’00”S, 48°35’60”W; E. Trajano, 01 Jun 1983. MZUSP 35303, 10, 95.5-108.3 mm SL, state of São Paulo, municipality of Miracatu, Grande stream, basin of Ribeira do Iguape river; 24°16’60”S, 47°27’00”W; O. Oyakawa, 20 Jul 1985. MZUSP 36543, 5, 116.9-234.4 mm Sl, state of São Paulo, municipality of Juquiá, Fundo stream, basin of Ribeira do Iguape river; 24°20’00”S, 47°38’00”W; O. Oyakawa, L. Portugal and F. Langeani, 12 Dez 1985. MZUSP 37991, 3, 129.7-255.4 mm SL, state of São Paulo, municipality of Barra do Turvo, Pardo river, basin of Ribeira do Iguape river; 24°42’00”S, 48°34’60”W; O. Oyakawa, 22 Jul 1987. MZUSP 38600, 1, 126.5 mm SL; state of São Paulo, municipality of Juquiá, Poço Grande stream, base of Ribeira do Iguape river; 24°19’60”S, 47°37’60”W; O. Oyakawa, 29 Mar 1987. MZUSP 39997, 6, 134.9-189.3 mm SL, state of São Paulo, municipality of Barra do Turvo, Pardo river, basin of Ribeira do Iguape; 24°42’00”S, 48°34’60”W; O. Oyakawa. 02 Fev 1998. MZUSP 40104, 32, 99.0-163.5 mm SL, state of São Paulo, municipality of Miracatu, Ribeirão dos Morais stream, basin of Ribeirão do Iguape river; 24°16’60”S, 47°27’00”W; O. Oyakawa and J. Oyakawa, 03 Jan 1989. MZUSP 42093, 1, 284.4 mm SL, state of São Paulo, municpality of Iguape, marginal lagoon, basin of Ribeira do Iguape river; 24°19’00”S, 47°30’00”W; O. Oyakawa, 13 Oct 1985. MZUSP 42254, 1, 313.9 mm SL, state of São Paulo, municipality of Registro, Votupoca river, basin of Ribeira do Iguape; 24°30’00”S, 47°51’00”W; M. Damato and O. Oyakawa, 01 Mar 1990. MZUSP 42584, 12, 148.9-160.7 mm SL; state of São Paulo, municipality of Ribeira, Ribeira do Iguape river; 24°39’00”S, 49°00’00”W; O. Oyakawa, 01 Mar 1991. MZUSP 45183, 1, 174.2 mm SL, state of são Paulo, municipality of Eldorado, Batatal river, basin of Ribeira do Iguape river; 24°32’00”S, 48°07’00”W; M. Damato, 03 Jun 1993. MZUSP 53551, 1, 139.3 mm SL, state of São Paulo, municipality of Iporanga, Betari river, basin of Ribeira do Iguape river; 24°35’00”S, 48°37’00”W; O. Oyakawa, V. Garutti, M. Piza and C. Ragazo, 20 Mar 1998. MZUSP 55163, 1, 91.2 mm SL, state of São Paulo, municipality of Eldorado, Ribeira do Iguape river; 24°29’24”S, 48°03’14”W; O. Oyakawa, K. Mautari and F. Colbert, 27 Oct 1998. MZUSP 58455, 7, 87.5-140.7 mm SL, state of São Paulo, municipality of Iporanga, Monjolos stream, basin of Ribeira do Iguape river; 24°33’13”S, 48°40’40”W; P. Gerhard and R. Moraes, 15 Nov 1998. MZUSP 60192, 4, 87.5-108.9 mm SL; state of São Paulo, municipality of Barra do Turvo, Fria stream, basin of Ribeira do Iguape river; 24°44’19”S, 48°30’35”W; O. Oyakawa, A. Akama, J. Nolasco and V. Abilhoa, 21 Mar 2000. MZUSP 60231, 8, 88.5-140.7 mm SL, state of Paraná, municipality of Adrianópolis, Pardo river, basin of Ribeira do Iguape; 24°47’55”S, 48°33’05”W; O. Oyakawa, A. Akama, J. Nolasco and V. Abilhoa, 22 Mar 2000. MZUSP 61701, 1, 89.7 mm SL, state of São Paulo, municpality of Iporanga, Ouro Grosso stream, basin of Ribeira do Iguape river; 24°33´06”S, 48°40’32”W; O. Oyakawa, 09 May 2000. MZUSP 61735, 1, 119.1 mm SL, state os São Paulo, municipality of Iporanga, Batatal river, basin of Ribeira do Iguape river; 24°35’26”S, 48°16’23”W; O. Oyakawa, 12 May 2000. MZUSP 62352, 1, 88.8 mm SL, state of São Paulo, municipality of Iporanga, Iporanga river, basin of Ribeira do Iguape river; 24°29’51”S, 48°35’21”W; R. Moraes and J. Sturve, 20 Jan 2000. MZUSP 65713, 1, 125.0 mm SL, state of São Paulo, municpality of Sete Barras, Ipiranga river, basin of ribeira do Iguape river; 24°10’46”S, 47°51’27”W; O. Oyakawa, A. Akama and J. Nolasco, 28 Nov 2000. MZUSP 68287, 1, 98.2 mm SL; state of São Paulo, municipality of Cajati, Queimado river, basin of Ribeira do Iguape river; 24°48’02”S, 48°13’32”W; O. Oyakawa, A. Akama, J. Nolasco and P. Nasakumi, 09 Mar 2001. MZUSP 68288, 7, 98.9-128.9 mm SL, state of São Paulo, municipality of Cajati, Queimado river, basin of Ribeira do Iguape river; 24°48’02”S, 48°13’32”W; O. Oyakawa, A. Akama, J. Nolasco and P. Nasakumi, 09 Mar 2001. MZUSP 69392, 1, 126.8 mm SL, state of São Paulo, municipality of Sete Barras, Basban stream, basin of Ribeira do Iguape river; 24°12’19”S, 47°53’51”W; O. Oyakawa, A. Akama, J. Nolasco and M. de Pinna, 18 May 2001. MZUSP 70609, 4, 100.4-107.3 mm SL; state of São Paulo, municipality of Ribeira, Palmeiras stream, basin of Ribeira do Iguape river; 24°36’21”S, 49°04’58”W; O. Oyakawa, 09 Ago 2001. MZUSP 70611, 9, 100.4-265.0 mm SL; state of São Paulo, municipality of Itapirapuã Paulista, Criminosas river, basin of Ribeira do Iguape river; 24°34’16”S, 48°10’22”W; O. Oyakawa, 09 Ago 2001. MZUSP 72952, 4, 265.0-292.9 mm SL, state of São Paulo, municipality of Registro, Jacupiranga river, basin of Ribeira do Iguape river; 24°28'48"S, 47°50'24"W; M. Santos and M. Morato, 09 Jan 1995. MZUSP 72959, 1, 207.5 mm SL; state of São Paulo, municipality of Pariquera, Pariquera-Mirim river, basin of Ribeira do Iguape river; ;09 Ago 2001; M. Santos and M. Morato, 10 Jan 1995. MZUSP 72960, 1, 207.5 mm

SL; state of São Paulo, municipality of Iporanga, Pilões river; 24°42'36"S, 47°52'48"W; M. Santos and M. Morato, 19 Jan 1995. MZUSP 72961, 1, 283.3 mm SL; state of São Paulo, municipality of Iporanga, Iporanga river, basin of Ribeira do Iguape; 24°34'48"S, 48°35'24"W; M. Santos and M. Morato, 17 Jan 1995. MZUSP 78664, 5, 100.2-207.3 mm SL, state of São Paulo, municipality of Itairiri, Areado river, basin of Ribeira do Iguape river; 24^{o}15’01”S, 47^{o}09’35”W;, 13/09/2001. MZUSP 78666, 3, 88.6-98.7 mm SL, state of São Paulo, municipality of Pedro de Toledo, Taquari river, basin of Ribeira do Iguape river; 24^{o}11’51”S, 47^{o}17’22”W; O. Oyakawa, 14 Set 2001. MZUSP 79603, 7, 98.1-141.4 mm SL, state of Paraná, municipality of Cerro Azul, Bonito stream, basin of Ribeira do Iguape river; 24°49'24"S, 49°15'39"W; O. Oyakawa, J. Nolasco, V. Moreira and L. Bastos, 20 May 2002. MZUSP 79957, 1, 137.8 mm SL, state of São Paulo, municipality of Iguape, Espraiado river, basin of Ribeira do Iguape river; 24^{o}23’11”S, 47^{o},21’09”W; O. Oyakawa, J. Nolasco, V. Moreira and P. Nakasumi, 10 Oct 2002. MZUSP 79959, 2, 103.0-105.0 mm SL, state of São Paulo, municipality of Iguape, Espraiado river, basin of Ribeira do Iguape river; 24^{o}21’55”S, 47^{o}18’31”W; O. Oyakawa, J. Nolasco, V. Moreira and P. Nakasumi, 10 Oct 2002. MZUSP 79961, 1, 106.1 mm SL, state of São Paulo, municipality of Iguape, Espraiado river, basin of Ribeira do Iguape river; 24^{o}23’11”S, 47^{o}21’09”W; O. Oyakawa, J. Nolasco, V. Moreira and Nakasumi, 10 Oct 2002. MZUSP 81654, 8, 83.6-157.1 mm SL; state of São Paulo, municipality of Itaoca, Palmital river, basin of Ribeira do Iguape river; 24^{o}36’12”S, 48^{o}52’24”W; O. Oyakawa, 02 May 2003. MZUSP 82608, 1, 143.2 mm SL; state of São Paulo, municipality of Iporanga, Betari river, basin of Ribeira do Iguape river; 24°34'48"S, 48°35'24"W; S. Buck, P. Gerhard and J. Santos, 01 Jun 1996. MZUSP 83023, 1, state of São Paulo, municipality of Iguape, Momuna river, basin of Ribeira do Iguape river; 24^{o}42’57”S, 47^{o}41’27”W; O. Oyakawa, 28 May 2003. MZUSP 84377, 8, 92.6-97.2 mm SL, state of São Paulo, municipality of Sete Barras, Preto river, basin of Ribeira do Iguape river; 24^{o}11’33”S, 47^{o}53’25”W; O. Oyakawa, J. Birindelli and L. Sousa, 01 Apr 2004. MZUSP 84396, 4, 90.7-93.5 mm SL; state of São Paulo, minicipality of Sete Barras, Ipiranga river, basin of Ribeira do Iguape river; 24^{o}10’46”S, 47^{o}51’14”W; O. Oyakawa, J. Birindelli and L. Sousa, 01 Apr 2004. MHNCI 8997, 4, 168.9-208.6 mm SL; state of Paraná, municipality of Bocaiúva do Sul, Capivari river, basin of Ribeira do Iguape river; 24^{o}59’56”S, 48^{o}37’41”W; V. Abilhoa and L. Bastos, 22 Sep 2000. MHNCI 9853; 3, 166-204.6 mm SL; state of Paraná, municipality of Bocaiúva do Sul, Faxinal river, basin of Ribeira do Iguape river; 25°02’50”S, 48°36’19”W; V. Abilhoa and L. Bastos, 04 Ago 2000. UFRGS 12399, 1, 30.2 mm SL, state of São Paulo, municipality of Iguape, stream of Ribeira de Iguape river, 24°39’00”S, 47°29’17”W; V. Bertaco, F. Carvalho, F. Jerep and A. Thomaz, 23 Apr 2008. LBP 6843, 3, 22.3-205.7 mm SL, state of São Paulo, municipality of Miracatu, Fau river, basin of Ribeira do Iguape river; 24°12’44”S, 47°28’61”W; C. Oliveira, M. Alexandrou, J. Alves and J. Henriques, 02 Sep 2008. LBP 7496, 3, 105.6-135.1 mm SL, state of São Paulo, municipality of Registro, Ribeira do Iguape river; 24°23’29”S, 47°50’06”; C. Oliveira, O. Oyakawa, R. Devidé, F. Roxo, J. Henriques and P. Hollanda, 19 Nov 2008. LBP 7395, 7, 72.4 mm SL, state of São Paulo, municipality of Itapeúna, Jaguary river, basin of Ribeira de Iguape river; 24°35’41”S, 48°12’53”W,C.Oliveira, O. Oyakawa, R. Devidé, F. Roxo, J. Henriques and P. Hollanda, 17 Nov 2008. LBP 7432, 1, 42.4 mm SL, state of São Paulo, municipality of Jacupiranga Pindauba river, basin of Ribeira de Iguape river; 24°45’25”S, 48°04’07”W; C. Oliveira, O. Oyakawa, R. Devidé, F. Roxo, J. Henriques and P. Hollanda, 18 Nov 2008. LBP 16840, 1, 66.3 mm SL, state of São Paulo, municipality of Miracatu,,Fau river, basin of Ribeira de Iguape river, 24°12’26”S, 47°28’36”W; R. Devidé, 14 Ago 2012. LBP 20201, 1, 138.00 mm SL, state of São Paulo, municipality of Cajati, tributary of Ribeira de Iguape river; 24°48’05”S, 48°14’16”W, P. Camelier, G. Silva, R. Devidé and C. Souza, 20 Jul 2015. UFRGS 18706, 2, 60.2-82 mm SL, state of São Paulo, municipality of Peruíbe, Bananal river, basin of Itanhaém river, 24°11’45”S, 46°59’40”W; P. Silva, A. Hirschmann, A. Thomaz and T. Carvalho, 15 Dec 2013. LBP 20214, 1, 92.4 mm SL, state of São Paulo, municipality of Itanhaém, tributary of Itanhaém river; 24°13’39”S, 46°55’35”W; P. Camelier, G. Silva, R. Devidé, C. Souza, 20 Jul 2015. UFRGS 13691, 2, 78.2-81.3 mm SL, state of São Paulo, municipality of Ubatuba, Picinguaba river; 23°21’00”S, 44°52’12”W; V. Bertaco, J. Ferrer, G. Neves and A. Thomaz, 31 Jul 2008. LBP 7890, 1, 184.85 mm SL, state of São Paulo, municipality of Ubatuba, Indaiá river; 23°24’15”S, 45°03’50”W; C. Oliveira, 11 Dez 2008. MNRJ 46842, 3, 80.96-134.67 mm SL, state of Rio de Janeiro, municipality of Cachoeiras de Macacu, Jororo stream, basin of Baía de Guanabara; 22°33’15”S, 42°40’3”8W; P. Buckup, M. Britto, C. Moreira, 28 Apr 2016. MNRJ 43525, 3, state of Rio de Janeiro, municipality of Cachoeira de Macacu, Macacu river, basin of Guanabara bay; 22°29’12”S, 42°39’42”W; P. Buckup, D. Moraes Jr, G. Vergara, M. Gonzales, D. Peixoto and P. Cortes, 13 Nov 2014.

MNRJ 14962, 2, 159.30-161.75 mm de SL, state of Rio de Janeiro, municipality of Cachoeiras de Macacu, Macacu river, basin of Guanabara bay; 22°29'12"S, 42°39'43"W; G. Nunan, K. Grosser, W. Koch and D. Moraes, 9 Apr 1996. MNRJ 13746, 4, 94.36-118.73 mm SL, state of Rio de Janeiro, municipality of Cachoeiras de Macacu, Branco river, basin of Guanabara bay, 22°33'55"S, 42°37'43"W; P. Buckup and D. Moraes Jr, 21 Mar 1995. MNRJ 13730, 6, 115.27-150.66 mm SL, state of Rio de Janeiro, municipality of Cachoeiras de Macacu, Soarinho river, basin of Guanabara bay; 22°38'6"S,42°43'6"W; P. Buckup, D. Moraes Jr, 21 Mar 1995. MNRJ 47193, 1, 137.37 mm SL, state of Rio de Janeiro, municpality of Cachoeiras de Macacu, Branco river, basin of Guanabara bay; 22°33'37"S, 42°40'34"W; P. Buckup, M. Britto and C. Moreira, 28 Apr 2016. MNRJ 41526, 7, 112.63-183.80 mm SL, state of Rio de Janeiro, municipality of Mage, Surui river, basin of Guanabara bay; 22°36'2"S, 43°5'30"W; P. Buckup, C. Quijada, T. Parente and E.Neuhaus, 2 Oct 2013. MNRJ 43305, 3, 118.61-155.79 mm SL, state of Rio de Janeiro, municipality of Nova Iguacu, Tingua river, basin of Guanabara bay; 22°39'08"S, 43°24'06"W; M. Britto, D. Moraes Jr, K. Ferreira and V. Meza, 12 Ago 2014. MNRJ 41132, 1, 236.46 mm SL, state of Rio de Janeiro, municipality of Itaborai, Caceribu river, basin of Guanabara bay; 22°40'17"S, 42°53'13"W; A. Pacheco, 20 Oct 2011. MNRJ 43148, 1, 120 mm SL, state of Rio de Janeiro, municipality of Nova Iguaçu, basin of Guanabara bay, Tinguá river, basin of Guanabara bay; 22°35'25"S, 43°25'59"W; P. Buckup, D. Moraes Jr, C. Quijada and E. Neuhaus, 4 Jul 2014.

Diagnosis - *Rhamdia quelen* differ from *Rhamdia sapo* by anal fin not reaching vertical through posterior termination of adipose fin base (*vs.* posterior tip of anal fin surpassing posterior insertion of adipose fin). From the neotype of *R. quelen sensu* Silfvergrip by longer caudal-peduncle length (17.6-21.5% SL *vs.* 14.62% SL); and shorter dorsal-spine length (7.8-10.5 % SL *vs.* 15.42% SL). Differs from *Rhamdia gabrielae* by larger dorsal base length (13.8-17.1% SL *vs*. 11.4-13.1% SL). From *R. eurycephala* by the head width in orbit line (61.1-68.8 % HL *vs.* 75.18-89.58% HL). From *R. laticauda*, *R. foina*, *R. poeyi* and *R. itacaiunas* by the upper lobe of caudal fin smaller than lower lobe (*vs.* upper lobe longer than the lower lobe). From *R. humilis* and *R. nicaraguensis* by having serrations on both sides of pectoral fin spine (*vs.* serrations only the anterior side in *R. humilis* and serrations only posterior side in *R. nicaraguensis*). From *R. xetequepeque* and *R. muelleri* by the smaller orbits (13.2-17.8% HL *vs.* 30.5-36.9% in *R. xetequepeque*, 21.7-37.8% in *R. muelleri*). From *R. Jequitinhonha* by wider interorbital distance (34.8-39.6% HL vs. 24.2% HL). From *R. laukidi* and *R. cinerascens* by longer snout (38.8-44.1% HL *vs.* 29.0-36.9% HL in *R. laukidi* and 32.5-35.4% HL in *R. cinerascens*). From *R. guatemalensis* by absense of a dark lateral longitudinal conspicuous band (*vs.* presence of a dark lateral longitudinal conspicuous band). *R. saijaensis* by larger head length (24.0-26.7% SL *vs.* 20.9-23.4% SL). From *R. reddelli*, *R. enfurnada*, *R. zongolicensis*, *R. macuspanensis,R. laluchensis* and *R. guasarensis* by the lack of morphological adaptations to troglobitic life.

Description - Measurements in Table 1. Body elongated and deep; cross section of trunk roughly circular at dorsal-fin origin and along dorsal-fin base, gradually compressed posteriorly through caudal peduncle. Anterodorsal profile of body convex from supraoccipital to dorsal-fin base. Dorsal-fin base nearly straight, posteroventrally slanted, and gently convex from dorsal fin to base of adipose fin. Ventral body profile slightly curved from mouth to caudal-fin base. Body widest at pectoral girdle and deepest at dorsal-fin origin. Caudal peduncle longer than deep. Number of post-Weberian vertebrae 39-40.

Head deep. Dorsal head profile straight and posterodorsally very slanted from snout tip to supraoccipital in lateral view. Head shape somewhat trapezoidal in dorsal view. Snout slightly rounded anteriorly in dorsal view, so long than deep . Distance between posterior nares slightly smaller than that between anterior nares. Mouth wide, subterminal, gape larger than interorbital distance; snout projecting slightly beyond lower jaw. Gape transverse, with fleshy rictal fold at corners. Rictal fold large. Both upper and lower lips with several longitudinal plicae. Barbels flattened in cross section, wide at their bases and tapering towards distal tip. Maxillary barbel longest; length variable exceeding maximum origin of anal fin; inserted above upper lip and posterolateral to anterior nares. Two pairs of mental barbels. External mental barbels surpassing all insertion of pectoral fin. Inner mental barbels aligned to and shorter than external mental barbels, surpassing origin of pectoral fin. Gular fold distinct and V-shaped. Branchiostegal rays 6-7. Gill rakers thick and moderately long, with: 9-10 rakers on first ceratobranchial. Eye large, slightly elliptical (greatest length in longitudinal axis), with rim circumscribed with deep, continuous invagination, distinctly more pronounced at lateral border. Eye positioned dorsolaterally, centered approximately at midpoint between tip of snout and corner of opercular membrane, and widely separated by large interorbital space. Pupil rounded. Sensory channels of head simple.

Dorsal fin with 2 unbranched rays and 6 branched rays, distal margin convex; length of dorsal-fin base larger than fin height. First unbranched dorsal-fin ray small and not externally visible, second unbranched dorsal fin ray stiffened in proximal portion and segmented in distal portion. Dorsal-fin origin anterior to middle distance between pectoral and pelvic fin origins; insertion of last branched ray just at pelvic fin origin. Tip of last branched dorsal-fin ray at most reaching anterior insertion of adipose fin. Adipose fin long; within ascendant curve in lateral profile and posterior lobe conspicuously free from body. Adipose-fin origin at vertical through right after posterior insertion pelvic fin and posterior insertion at medium of caudal peduncle.

Pectoral fin within one unbranched and 7-9 branched rays; when adpressed reaching approximately origin of third branched ray of dorsal fin. Unbranched ray of pectoral fin stiffened, straight and with strong serrations on both sides and along the entire length. Pelvic fin rounded, approximately same size of pectoral fin, with one unbranched and 5 branched rays,surpassing genital papilla, never reaching anal-fin origin. Pelvic-fin origin nearly at body midlength, just at insertion of last dorsal-fin ray. Anal fin rounded, with 2-3 unbranched rays anteriorly, followed by 8-10 branched rays; when adpressed never exceeds posterior insertion of adipose fin. Anal-fin base smaller than dorsal-fin base length. Caudal fin deeply forked, lobes rounded; dorsal lobe smaller in height and length; 7 branched rays in dorsal lobe and 8-9 branched rays in ventral lobe.

Color pattern of preserved specimens - Body brown or gray with or without very small dark brown irregular spots. Head and fins brown or gray without spots. Ventral portion of body and head white. Maxillary barbels same color as body.

Distribution and Habitat -Occurs along the hydrographical basins of the Brazilian Atlantic coast, between the basin of the Guanabara Bay, Rio de Janeiro State, and the basin of the Tubarão River, Santa Catarina State. Occurring also in the hydrographic basin of the Iguaçu River, Paraná State (Fig3).

Rhamdia sapo Valenciennes, 1840

(Fig. 2, 3)

Synonymy:

Rhamdia branneri voulezi Haseman, 1911: 378, pl. LXXVI; Porto União da Vitória (current União da Vitória), rio Iguassu (current Iguaçu), Paraná State, Brazil;

Rhamdia microps Eigenmann & Fisher 1917: 394, pl. 38 [Annals of the Carnegie Museum v. 11 (nos 3/4) (art. 13); ref. 15089] Uruguayana, Brazil. Holotype: FMNH 58285

Silurusrivularis Larrañaga 1923:376, Escritos de Don Dámaso Antonio Larrañaga v. 2; Uruguai.

Holotype: MNHN 0000-1576, Buenos Aires, Argentina. Valenciennes 1835:Pl. 2 (figs. 6-8), Voyage dans l'Amérique méridionale.

Examined material: *Rhamdia quelen*: From Brazil: Basin of rio Tramandaí: MCP 10081, 1, 182.0 mm SL, state of Rio Grande do Sul, municipality of Maquiné, Maquiné river, basin of Tramandaí river; 29°44'0.00"S, 50°10'0.00"W; Fishers of EEPLQ, 17 Jul 1984. MCP 11222, 1, 119.4 mm SL, state of Rio Grande do Sul, municipality of Cidreira, Cidreira lagoon, basin of Tramandaí river; 30°13'00"S, 50°15'00"W; E. Pereira, P. Azevedo e L. Bergmann, 28 Mar 1987. MCP 18399, 1, 122.3 mm SL, state of Rio Grande do Sul, municipality of Capão da Canoa, Pinguela lagoon, basin of Tramandaí river; 29°50'00"S, 50°08'00"W ; J. Pezzi, W. Santos, V. Bertaco and A. Cardoso, 14 Dez 1995. MCP 9964, 1, 112.5 mm SL, state of Rio Grande do Sul, municipality of Maquiné, Quadros lagoon, basin of Tramandaí river; 29°44'00"S, 50°09'00"W; Fishers of EEPLQ, 29 Jun 1984. MZUSP 14216, 10, 122.3-182.0 mm SL, state of Rio Grande do Sul, municipality of Maquiné, Quadros lagoon, basin of Tramandaí; 29°43'00"S, 50°06'59"W; C. da Silva, 26 Oct 1978. MZUSP 25066, 2, 122.2-189.8 mm SL,, state of Rio Grande do Sul, municipality of Maquiné, Quadros lagoon, basin of Tramandaí; 29°43'00"S, 50°06'59"W; C. da Silva, 27 Jan 1977. UFRGS 1006, 1, 122.2 mm SL; state of Rio Grande do Sul, municipality of Tramandaí, Tramandaí lagoon, basin of Tramandaí; 29°56'57"S, 50°08'39"W; P. Buckup, 09 Dez 1981. UFRGS 4006, 2, state of Rio

Grande do Sul, municipality of Cidreira, Lessa lagoon, basin of Tramandaí; 29°50'00"S, 50°09'60"W; L. Malabarba, 07 May 1989. UFRGS 4108, 3, 91.0-189.8 mm SL; state of Rio Grande do Sul, municipality of Osório, Caieira lagoon, basin of Tramandaí; 29°58'39"S, 50°08'23"W; L. Malabarba, 20 May 1989. UFRGS 4111, 1, 112.6 mm SL, state of Rio Grande do Sul, municipality of Cidreira, Rancho Alto stream, basin of Tramandaí; 30°09'60"S 50°16'60"W; L. Malabarba, 10 Jun 1989. UFRGS 7003, 1, 180.0 mm SL, state of Rio Grande do Sul, municipality of Maquiné, Maquiné river, basin of Tramandaí; 29°43'50"S, 50°10'39"W; J. Anza, J. Giora, L. Malabarba and G. Neves, 10 Mar 2005. UFRGS 7004, 1, 287.6 mm SL, state of Rio Grande do Sul, municipality of Maquiné, Maquiné river, basin of Tramandaí river; 29°43'50"S, 50°10'39"W; J. Anza, J. Giora, L. Malabarba and G. Neves, 10 Mar 2005. UFRGS 7005, 1, 280.3 mm SL, state of Rio Grande do Sul, municipality of Três Forquilhas, Itapeva lagoon; 29°43'50"S, 50°10'39"W; J. Anza, J. Giora, L. Malabarba and G. Neves. 13 Mar 2005. UFRGS 7006, 1, 246.7 mm SL; state of Rio Grande do Sul, municipality of Três Forquilhas, Itapeva lagoon; 29°43'50"S, 50°10'39"W; J. Anza, J. Giora, L. Malabarba and G. Neves, 13 Mar 2005. UFRGS 7007, 1, 231.6 mm SL, state of Rio Grande do Sul, municipality of Três Forquilhas, Itapeva lagoon; 29°43'50"S, 50°10'39"W; J. Anza, J. Giora, L. Malabarba and G. Neves, 13 Mar 2005. UFRGS 7008, 1, 294.5 mm SL, state of Rio Grande do Sul, municipality of Três Forquilhas, Itapeva lagoon; 29°43'50"S, 50°10'39"W; J. Anza, J. Giora, L. Malabarba e G. Neves, 13 Mar 2005. UFRGS 19424, 8, 231.6-246.7 mm SL, state of Rio Grande do Sul, municipality of Tramandaí, Quadros lagoon, basin of Tramandaí basin; 29°36'14"S, 49°59'27"W; R. Angrizani, 01 May 2015. UFRGS 3688, 7, Brazil, state of Rio Grande do Sul, municipality of Tramandaí, rio Tramandaí; 29°56'01"S, 50°07'58"W; L. Silva, 10 Ago 1984. UFRGS 17717, 4, Brazil, state of Rio Grande do Sul, municipality of Capão da Canoa, stream tributary of Quadros lagoon, basin of Tramandaí; 29°39'58"S, 50°01'53"W; L. Malabarba, A. Hirschmann, K. Bonato, C. Hartmann, R. Angrizani, 03 Apr 2013.Basin of rio Araranguá: UFRGS 21360, 4, 166.5-188.9 mm SL, state of Santa Catarina, municipality of Meleiro, Figueira stream, tributary of Itoupava river, basin of Araranguá river; 28°55'36"S, 49°33'25"W; R. Angrizani, J. Wingert, J. Ferrer and F. Kuhn. Basin of rio Camaquã: UFRGS 18424, 4, -17.00-21.09 mm SL, state of Rio Grande do Sul, municipality of Cristal, Camaquã river, basin of Patos lagoon; 30°53'05"S, 52°15'03"W; R. Angrizani, J. Miranda and A. Langoni, 16 Jan 2014. UFRGS

18425, 5, 18.02-23.02 mm SL, state of Rio Grande do Sul, municipality of Cristal, Sapata stream, tributary of Camaquã river, 31°00'14" S, 52°05'58"W; R. Angrizani, J. Miranda and A. Langoni, 16 Jan 2014.Basin of lagoa Mirim: UFRGS 1121, 1, 275.00 mm SL, state of Rio Grande do Sul, municipality of Rio Grande, Nicola lagoon, basin of Mirim lagoon; 32°31'60"S, 52°32'00"W; C. Souto and L. Malabarba, 18 Dez 1980. UFRGS 1128, 1, 324.00 mm SL, state of Rio Grande do Sul, municipality of Rio Grande, basin of Mirim lagoon; 32°36'59"S, 52°34'00"W; P. Buckup, 07 Jul 1979. UFRGS 1120, 1, 278.00 mm SL, state of Rio Grande do Sul, municipality of Rio Grande, Nicola lagoon, basin of Mirim lagoon; 32°31'60"S, 52°32'00"W; C. Souto and L. Malabarba, 18 Dez 1980. UFRGS 1127, 1, 282.00 mm SL,, state of Rio Grande do Sul, municipality of Rio Grande, Taim stream; 32°29'00"S, 52°34'60"W; P.A.Buckup, 07 Jul 1979. UFRGS 1126, 1, 232.00 mm SL, state of Rio Grande do Sul, municipality of Rio Grande, Taim stream, basin of Mirim lagoon; 32°29'00"S, 52°34'60"W; P. Buckup, 7 Jul 1979. UFRGS 2774, 1, 53.91 mm SL, state of Rio Grande do Sul, municipality of Rio Grande, Mangueira lagoon, basin of Mirim lagoon; 32°49'60"S, 52°39'00"W; L. Malabarba, 13 Dez 1979.UFRGS 2766, 3, 33.13-30.84 mm SL, state of Rio Grande do Sul, municipality of Rio Grande, Nicola lagoom; 32°31'60"S, 52°32'00"W; L. Malabarba, 10 Dez 1979.UFRGS 2772, 1, 26.84 mm SL, state of Rio Grande do Sul, municipality of Rio Grande, Estiva stream, basin of Mirim lagoon; 32°31'60"S, 52°32'00"W; P. Buckup, L. Malabarba and C. Souto, 10 Dez 1979. Basin of rio Gravataí: UFRGS 6921, 2, 66.42-64.06 mm SL, state of Rio Grande do Sul, municipality of Gravataí, Gravataí river, basin of Patos lagoon, 29°56'39"S, 50°59'30"W; M. Azevedo, A. Dufech, J. Ferrer, D. Cognato, V. Lampert, F. Flores-Lopes, 10 Dez 2004. UFRGS 22336, 1, 38.00 mm SL, state of Rio Grande do Sul, municipality of Viamão, Gravataí river basin of Patos lagoon, 30°05’31”S, 50°54’33”W; T. Carvalho, 10 Oct 2016. UFRGS 4967, 11, 62.94-34.39 mm SL, state of Rio Grande do Sul, municipality of Porto Alegre Gravataí river, basin of Patos lagoon; -29.9636116028 -51.0116653442; L. Malabarba, M. Azavedo, J. Anza and T. Hasper. 08 Nov 2000. UFRGS 22367, 1, 75.71 mm SL, state of Rio Grande do Sul, municipality of Viamão, Pachecos pond, basin of Patos lagoon; 30°06’10”S, 50°50’56”W; T. Carvalho. 20 Sep 2016. UFRGS 13848, 5, 15.2-20.5 mm SL, state of Rio Grande do Sul, municipality of Viamão, Grande pond; 30°04'41"S, 50°50'55"W; G. Frainer, S. Leonardi and J. Giora, 21 Sep 2010. UFRGS 16385, 1, 88.51 mm SL, state of Rio Grande do Sul, municipality of Viamão, Pachecos pond, basin of Patos lagoon; 30°05'44"S, 50°50'59"W; C. Machado, F. Santos, J. Miranda and J. Wingert, 21 Out 2011. UFRGS 18215, 3, 6.32-120.48 mm SL; state of Rio Grande do Sul, municipality of Viamão, Pachecos pond, basin of Patos lagoon; 30°05'19"S, 50°53'28"W; A. Langoni, 29 Out 2013. Basin of lago Guaiba: UFRGS 14362, 1, 168.69 mm SL, arroio Calombos, "braço morto" próximo a ponte na BR-290, Estação Experimental Agronômica da UFRGS. 30°06'17"S, 51°41'40"W. Eldorado do Sul, Rio Grande do Sul, Brazil, T. Carvalho, 02 Feb 2011. UFRGS 3234, 1, 285 mm SL, state of Rio Grande do Sul, municipality of Barra do Ribeiro, Guaiba lake; 30°16'60"S, 51°16'60"W; R. Malabarba, 31 Agu 1983. UFRGS 8260, 1, 229.80 mm SL, state of Rio Grande do Sul, municipality of Porto Alegre, Guaíba lake, basin of Patos lagoon; 29°58'31"S, 51°15'53"W; A. Saccol-Pereira and P. Milani, 28 Set 2004. UFRGS 8253, 1, 228.00-154.07 mm SL, state of Rio Grande do Sul, municipality of Porto Alegre, Guaíba lake, basin of Patos lagoon; 30°01'26"S, 51°14'37"W; F. Juliano, 05 Jun 2004. UFRGS 7059, 2, 224.40-227.57 mm SL, state of Rio Grande do Sul, municipality of Porto Alegre, Guaíba lake, basin of Patos lagoon; 30°00'34"S, 51°14'40"W; A. Saccol-Pereira and P. Milani, 10 Out 2004. UFRGS 851, 1, 85.37 mm SL, state of Rio Grande do Sul, municipality of Porto Alegre, Guaíba lake, basin of Patos lagoon; 30°02'60"S, 51°20'59"W, L. Malabarba, 21 Apr 1980. UFRGS 6796, 6, 239.21-226.03 mm SL, state of Rio Grande do Sul, municipality of Porto Alegre, Guaíba lake, basin of Patos lagoon; 30°23'38"S, 51°05'10"W, R. Malabarba, 04 Apr 2004. UFRGS 1090, 1, 101.50 mm SL, state of Rio Grande do Sul, municipality of Porto Alegre, Guaíba lake, basin of Patos lagoon, 30°03'00"S, 51°20'59"W; L. Malabarba, 10 Mar 1981.UFRGS 6163, 1, 337.25 mm SL, state of Rio Grande do Sul, municipality of Porto Alegre, Guaíba lake, basin of Patos lagoon; 30°01'12"S, 51°14'53"W, J. Pezzi and V. Bertaco, 08 Jan 2002.UFRGS 2957, 1, 200.00 mm SL, state of Rio Grande do Sul, municipality of Porto Alegre, Guaíba lake, basin of Patos lagoon; 29°57'00"S, 51°16'60"W; L. Malabarba, 27 Oct 1983. UFRGS 6456, 1, 236.00 mm SL, state of Rio Grande do Sul, municipality of Porto Alegre, Guaíba lake, basin of Patos lagoon; 29°54'60"S, 51°16'19"W; J. Anza, 04 Sep 2003. UFRGS 2958, 1, 214.00 mm SL, state of Rio Grande do Sul, municipality of Porto Alegre, Guaíba lake, basin of Patos lagoon; 29°57'00"S, 51°16'60"W; L. Malabarba, 27 Oct 1983. UFRGS 151, 1, 299.00 mm SL, state of Rio Grande do Sul, municipality of Porto Alegre, Guaíba lake, basin of Patos lagoon; 30°02'60"S, 51°11'00"W; L. Malabarba, 10 Oct 1977. UFRGS 6165, 1, 263.00 mm SL, state of Rio Grande do Sul, municipality of Porto Alegre, Guaíba lake, basin of Patos lagoon; 30°21'19"S, 51°04'19"O, V. Bertaco and J. Pezzi, 10 Jan 2002. UFRGS 6451, 1, 292 mm SL, state of Rio Grande do Sul, municipality of Porto Alegre, Guaíba lake, basin of Patos lagoon; 29°54'60"S, 51°16'19"W; J. Anza, 04 Sep 2003.UFRGS 6453, 1, 245.00 mm SL, state of Rio Grande do Sul, municipality of Porto Alegre, Formoso stream, Guaíba lake, basin of Patos lagoon; 29°54'60"S, 51°16'19"W; J. Anza, 04 Sep 2003.UFRGS 6452, 1, 222.00 mm SL, state of Rio Grande do Sul, municipality of Porto Alegre, Canal do Formoso stream, Guaíba lake, basin of Patos lagoon; 29°54'60"S, 51°16'19"W; J. Anza, 04 Sep 2003.UFRGS 87, 1, 313.00 mm SL, state of Rio Grande do Sul, municipality of Guaíba, Guaíba lake, basin of Patos lagoon; 30°07'00"S, 51°19'60"W; E. Reisch, 15 Oct 1974. Basin of rio Caí: UFRGS 19663, 4, 160.8-200.2 mm SL, state of Rio Grande do Sul, municipality of Santa Maria do Herval, Cadeia river, tributary of Caí river, basin of Patos lagoon, 29°30'03"S, 51°00'03"W, G. Volkmer. 17 Oct 2014. UFRGS 19380, 1, 184.18 mm SL, state of Rio Grande do Sul, municipality of Canela, Santa Cruz river, tributary of Caí river, basin of Patos lagoon; 29°17'51"S 50°34'07"W; G. Volkmer, 16 Jan 2014. UFRGS 19381, 1, 278.17 mm SL, state of Rio Grande do Sul, municipality of Canela, Santa Cruz river, tributary of Caí river, basin of Patos lagoon; 29°18'45"S, 50°40'25"W; G. Volkmer, 16 Jan 2014. Basin of rio dos Sinos: UFRGS 19665, 3, 319.9-370.1 mm SL, state of Rio Grande do Sul, municipality of Canela, Santa Maria river, tributary of Sinos river, basin of Patos lagoon, 29°20'47"S, 50°42'04"W; G. Volkmer, . Basin of rio Jacuí: UFRGS 23345, 1, 260.5 mm SL, Brazil, state of Rio Grande do Sul, municipality of Tio Hugo, rio Jacuí , basin of lagoa dos Patos; 28°32'59"S, 52°32'41"W; G. Volkmer, xxxxxx. Basin of rio Jaguarão: UFRGS 20046, 1, 210.5 mm SL,Brazil, state of Rio Grande do Sul, municipality of Candiota, Candiota stream, tributary of rio Jaguarão, basin of lagoa dos Patos; 31°34'07"S, 53°39'43"W; R. Angrizani,.Basin of rio Quarai: UFRGS 23148, 2, 80.54- 61.02 mm SL, state of Rio Grande do Sul, municipality of Quaraí, Areal stream, tributary of rio Quaraí, basin of Uruguai river; 30°25'56"S, 56°18'44"W; L. Malabarba and R. Reis. 16 Dez 2014.Basin of rio Ibicuí: UFRGS 1571, 1, 131.05 mm SL, state of Rio Grande do Sul, municipality of Santana do Livramento, Ibicuí da Armada river, basin of Uruguai river; 30°46'60"S, 55°03'60"W; L. Malabarba and R. Reis. 21 Dez 1982.Basin of rio Negro: UFRGS 22134, 1, 113.21 mm SL, Igrejinha stream, trybutari of Rio Negro river, basin of Uruguai river; 31°25'54"S, 54°15'01"W; L. Malabrba, M. Malabarba, J.

Chuctaya, and J. Ferrer, .From Uruguay: Basin of rio Queguay: UFRGS 7966, 1, 184.18 mm SL, state of Paysandu, municipality of Paysandu, Queguay Chico river, basin of Uruguai river; 32°01'57"S, 57°19'30"W; V. Bertaco, F. Canteira, J. Ferrer and L. Malabarba, 10 Sep 2005. Basin of rio Tacuarembó: UFRGS 14569,1, 181.22 mm SL, state of Tacuarembó, municipality Tacuarembó, Caraguatá river, tributary of Tacuarembó river, basin of Uruguai river; 32°09'29"S, 55°01'27"W; L. Malabarba, V. Bertaco, P. Lehmann and F. Canteira,

Diagnosis - *Rhamdia sapo* differ from *Rhamdia quelen* by posterior tip of anal fin surpassing posterior insertion of adipose fin (*vs.* anal fin not reaching vertical through posterior termination of adipose fin base). From the neotype NRM 16091 of *R. quelensensu* Silfvergrip by longer caudal-peduncle length (17.1-21.4% SL *vs.* 14.62% SL); shorter pelvic-fin length (10.6-14.6% SL *vs.* 15.62% SL); shorter dorsal-spine length (7.0-9.7% SL *vs.* 15.42% SL). Differs from *Rhamdia gabrielae* and *R. eurycephala* by last ray of dorsal fin trespassing origin of adipose fin (*vs.* last ray of dorsal fin not reaching origin of adipose fin). From *R. laticauda*, *R. foina*, *R. poeyi* and *R. itacaiunas* by the upper lobe of caudal fin smaller than lower lobe (*vs.* lower lobe longer than the upper lobe). From *R. humilis* and *R. nicaraguensis* by having serrations on both sides of pectoral fin spine (*vs.* serrations only in anterior side in *R. humilis* and serrations only in posterior side in *R. nicaraguensis*). From *R. xetequepeque,R. muelleri, R. jequitinhonha* by smaller orbits (11.4-14.7% HL *vs.* 30.5-36.9 in *R. xetequepeque*, 21.7-37.8% in *R. muelleri,* 20.4% in *R. jequitinhonha*). From *R. laukidi* by smaller adipose fin base length (32.0-34.7% SL *vs.* 44.5-51.3% SL). From *R. guatemalensis* by absence of dark lateral longitudinal conspicuous band (*vs.* presence of dark lateral longitudinal conspicuous band). From *R. cinerascens* by shorter dorsal-fin spine length (7.0-9.7% SL *vs*. 11.4 13.8% SL). From *R. saijaensis* by shorter adipose-fin base length (32-34,7% SL *vs*. 36.0 45.7% SL). From *R. reddelli*, *R. enfurnada*, *R. zongolicensis*, *R. macuspanensis* and *R. laluchensis* by lack of morphological adaptations to troglobitic life.

Description - Measurements in Table 1. Body elongated and deep; cross section of trunk roughly circular at dorsal-fin origin and along dorsal-fin base, gradually compressed posteriorly through caudal peduncle. Anterodorsal profile of body convex from supraoccipital to dorsal-fin base. Dorsal-fin base nearly straight, posteroventrally slanted, and gently convex from dorsal fin to base of adipose fin. Ventral body profile slightly curved from mouth to caudal-fin base. Body widest at pectoral girdle and deepest at dorsal-fin origin. Caudal peduncle longer than deep. Number of post-Weberian vertebrae 39-42.

Head deep. Dorsal head profile rounded and posterodorsally very slanted from snout tip to supraoccipital in lateral view. Head shape somewhat rounded in dorsal view. Snout rounded anteriorly in dorsal view, so long than deep. Distance between posterior equal that between anterior nares. Mouth wide, subterminal, gape larger than interorbital distance; snout projecting slightly beyond lower jaw. Gape transverse, with fleshy rictal fold at corners. Rictal fold large. Upper and lower lips with several longitudinal plicae.

Barbels flattened in cross section, wide at their bases and tapering towards distal tip. Maxillary barbel longest; length variable reaching maximum insertion of caudal fin; inserted above upper lip and posterolateral to anterior nares. Two pairs of mental barbels. External mental barbels surpassing origin of pectoral fin. Inner mental barbels aligned to and shorter than external mental barbels, never reaching origin of pectoral fin. Gular fold distinct and V-shaped. Branchiostegal rays 5-7. Gill rakers thick and moderately long, with: 8-10 rakers on first ceratobranchial. Eye large, slightly elliptical (greatest length in longitudinal axis), with rim circumscribed with deep, continuous invagination, distinctly more pronounced at lateral border. Eye positioned dorsolaterally, centered approximately at midpoint between tip of snout and corner of opercular membrane, and widely separated by large interorbital space. Pupil rounded. Sensory channels of head multiples.

Dorsal fin with 2 unbranched and 6-8 branched rays, distal margin convex; dorsal-fin base length larger than fin height. First unbranched dorsa-fin ray small and not externally visible, second unbranched dorsal fin ray stiffened in proximal portion and segmented in distal portion. Dorsal-fin origin anterior to middle distance between pectoral- and pelvic-fin origins; insertion of last branched ray at pelvic fin origin. Tip of last branched dorsal-fin ray trespassing anterior insertion of adipose fin. Adipose fin long; within ascendant curve in lateral profile and posterior lobe conspicuously free from body. Adipose-fin origin at vertical through posterior insertion of pelvic fin and posterior insertion at final third of caudal peduncle.

Pectoral fin with one unbranched and 7-9 branched rays; when adpressed reaching approximately origin of second branched ray of dorsal fin. Unbranched ray of pectoral fin stiffened, straight, with strong serrations in distal anterior face and delicate serration in proximal posterior face. Pelvic fin rounded, approximately same size of pectoral fin, with one unbranched and 5 branched rays,surpassing genital papilla, never reaching anal-fin origin. Pelvic-fin origin nearly at body midlength, after insertion of last dorsal-fin ray. Anal fin rounded, with 2-4 unbranched rays anteriorly, followed by 7-10 branched rays; when adpressed reaches or exceeds posterior insertion of adipose fin. Anal-fin base equal to dorsal-fin base length. Caudal fin deeply forked, lobes rounded; dorsal lobe smaller in height and length; 7-8 branched rays in dorsal lobe and 9-11 branched rays in ventral lobe.

Color pattern of preserved specimens - Body gray or brown with or without very small dark irregular spots. Head and fins gray or brown without spots. Ventral portion of body and head white. Maxillary barbels same color as body. Adipose fin is the same patterns of the body.

Distribution and Habitat – Occurs in hydrographical basins of Laguna dos Patos, Tramandaí systems, Manpituba systems and Araranguá systems, south of hidrographyc system of Prata river and Iguaçu river (Fig.3).

Neighbourn-Joining tree

The NJ trees generated recover the same topology found in Angrizani & Malabarba (2017) (Fig 4 and 5). This analysis was implemented using the COI gene sequences obtained for Angrizani & Malabarba (20017) and for in the genetic description of *R. voulezi* and *R. branneri* (Zamboni et al., 2017). In order to compare the similarity of these two species with *R. sapo* and *R. quelen*. The results described here, indicate that *R.voulezi* is genetically similar to *R. quelen* and *R. branneri* is genetically similar to *R. sapo*.In this way, its propose the synonimization of *R. braneri* in *R. quelen* and *R. voulezi* in *R. sapo*. Another interesting resouts is the genetic confirmation of the occurrence of *R. sapo* in the province of Buenos Aires, Argentina.

Discusion

The Neotype of *Rhamdia quelen.*

The holotype of *R. quelen* is lost (Ferraris 2007), and, in order to define the nominal taxon objectively, Silfvergrip (1996) designated a Neotype to the species from Peru, Department of Loreto, in a tributary to rio Samiria, Ucaiali River drainage, Amazon basin (NRM 16091). The type locality of *Rhamdia quelen*, however, was referred (page 701) by Quoy & Gaimard (1824) to "the la baie de Rio de Janeiro" and further mentioned at the end of the description (p. 229) as "Il provident du Brésil". The Neotype designation made by Silfvergrip (1996) is invalid because it does not attend all qualifying conditions (ICZN 2000: art. 75.3), in particular the evidence that the neotype came as nearly as practicable from the original type locality (art. 75.3.6). The fish fauna from the

Peruvian Amazon is distinct, isolated and geographically distant from the original type locality: the watershed of the Guanabara Bay, in the Brazilian Atlantic coast. In addition the populations of *R. quelen* from coastal Atlantic rivers draining to Guanabara Bay are phylogenetically distant from *Rhamdia* populations from the Ucayali river (Angrizani & Malabarba 2017), and the morphological data presented here demonstrates that they are different species.

Thus, it is evident that the neotype of *R. quelen sensu* Silfvergrip (1996) should be disregarded and a new one designated. Therefore, in this article a new neotype is designated for *Rhamdia quelen*, this time coming from the original locality of the description of the species: MNRJ 16091 collected in the Macacu river, tributary of the Guanabara Bay basin in Rio de Janeiro, Brazil. The designation of an Amazonian neotype made by Silfvergrip (1996) is invalid (ICZN 2000: art. 75.4), and has no priority over the Neotype designated in this paper.

Identity and synonyms of *Rhamdia quelen*

The original description of *R. quelen* is old and somewhat vague, having no useful characters for species recognition. In the first review of this genus, Silfvergrip (1996) synonymized 47 species within *R. quelen* and redescribed the species with the following diagnosis: pectoral fin spine with serrae on both sides; caudal fin lobes subequal, or with either lobe slightly longer; E1/H1 interradial membrane less than 2/3 of E1/H1 ray lengths; with or without multiple sensory pores on the head; posterior nostril velum open posterolaterally; maxillary barbels at least % of HL and % of SL mm Sk; gill-rakers from 5-16; post-Weberian vertebrae 36-44; eyes medium size; with or without lateral stripe; with or without dark saddle-like marking across nape.

The diagnosis presented by Silfvergrip is generalist and useless for the characterization and recognition of *R. quelen* and closely related species. The author justifies his choices due to the great variability and lack of patterns of the morphological and meristic characters used. Thus, these characters could not diagnose the different species included in *R. quelen*. Silfvergrip recognizes that some geographically distant populations have morphological characteristics that suggest their differentiation, but also stated that, when populations are added along the geographic distribution in the analysis, a graduation of these characteristics is observed, refusing the possibility of the existence of other species. This is not corroborated in our data, since there is morphological differentiation among groups corroborated by phylogeographic analysis, as demonstrated by Angrizani & Malabarba (2017) and in the diagnoses of *Rhamdia quelen* and *R. sapo* in this paper.

Phylogeographic and biogeographic studies show that *R. quelen* occurs only in South America (Perdices et al., 2002, Hernandez et al., 2015, Angrizani & Malabarba, 2017). Although we cannot advance decisions on the validity of the following nominal species described from Central America, they are not junior synonyms of *R. quelen*: *Pimelodus deppei* Müller & Troschel 1849, *Pimelodus cinerascens* 1860, *Pimelodus guatemalensis* Günther 1864, *Pimelodus godmanni* Günther 1864, *Pimelodus micropterus* Günther 1864, *Pimelodus baronis* Troschel 1865, *Pimelodus wagneri* Günther 1868, *Rhamdia bransfordii* Gill 1876, *Rhamdia oaxacae* Meek 1902, *Rhamdia depressa* Barbour & Cole 1906, *Pimelodus boucardi* Regan 1907, *Rhamdia heteracantha* Regan 1907, *Rhamdia barbata* Meek 1907, *Rhamdia nasuta* Meek 1909, *Caecorhamdia urichi* Norman 1926, *Rhamdia guatemalensis muriei* Hubbs 1935, *Rhamdia guatemalensis decolor* Hubbs 1936, *Rhamdia guatemalensis stygaea* Hubbs 1936, *Rhamdia saijaensis* Rendahl 1941, all indicated for Central America. Some of these synonymies have already been re-evaluated and raised to the status of valid species: *Rhamdia guatemalensis*, *Rhamdia cinerascens* e *Rhamdia saijaensis*

(Hernandez et al., 2015).

According to Angrizani & Malabarba (2017) the lineages of the *R. quelen* species complex are arranged in three great clades: the Upper-Amazon, the Amazon and the Brazilian-shield. The real *R. quelen* is inserted in the Brazilian-shield clade, thus, the following amazonian synonymys can be excluded from *R. quelen*: *Pimelodus pentlandii* Valenciennes 1840, *Pimelodus stegelichii* Müller & Troschel 1848, *Pimelodus bathyurus* Cope 1878, *Rhamdia gilli* Starks 1906, *Rhamdia mounseyi* Regan 1913, *Rhamdia riojae* Fowler 1915, *Rhamdia ortoni* Fowler 1915, *Rhamdia duquei* Eigenmann & Pearson 1942, *Rhamdia lehmanni* Dahl 1961. Moreover, it is important to mention that all types analyzed of these nominal species can be easily diagnosed from *R. quelen*.

The *R. quelen* belongs to the Brazilian clade shield, which is composed of 14 independent lineages. Taking into account the geographical distribution of these lineages, and analyzing morphologically the types of the nominal species considered as junior synonyms from the Brazilian shield rivers, we can exclude from *R. quelen* synonym the following names: *Pimelodus sebae* Cuvier 1829, *Pimelodus hilarii* Valenciennes 1840, *Pimelodus sapo* Valenciennes 1840, *Pimelodus sellonis* Müller & Troschel 1849, *Pimelodus wuchereri* Günher1864, *Pimelodus parahybae* Steindachner 1876, *Pimelodus queleni cuprea* Steindachner 1876, *Pimelodus cuyabae* Steindachner 1876, *Rhamdia branneri* Haseman 1911, *Rhamdia branneri voulezi* Haseman 1911, *Rhamdia microps* Eigenmann 1917 and *Rhamdia pubescens* Miranda Ribeiro 1920.

The following taxa continue to be synonyms of *R. quelen*: *Pimelodus namdia* Cuvier 1829, synonymized by Silfvergrip (1996), this species has neither original description nor preserved type; *Pimelodus sellonis* Müller & Troschel 1849, synonymized in this paper after analysis of the holotype ZMB 3041; *Heterobranchussextentaculatus* Agassiz 1829, synonymized by Valenciennes (Cuvier & Valenciennes, 1840), without preserved type and with useless original description, the type locality is Brazil; and *Rhamdia branneri* Haseman 1911, synonymized through genetic analysis generated in the present study.

The current geographic distribution of *R. quelen* is along the Brazilian coastal plain, from the basin of Guanabara Bay, in the state of Rio de Janeiro, to the basin of Tubarão River, in the state of Santa Catarina (Fig. 6). This species can still be found in the Iguaçu river basin, as showed when the DNA sequences of the COI geneof *Rhamdia* found in BOLD and

Genebank were analyzed (Fig X). In addition to the characteristics used in the diagnosis, the species can also be recognized by the following additional characters: Dorsal fin has 6 branched rays;tip of last branched dorsal-fin ray reaching or not the anterior insertion of adipose fin; the head measures 23.4-26.7% SL, with a straight dorsal profile; the snout is longer than deep; the maxillary barbels are very long, at the minimum exceeding the origin of pelvic fin and at the maximum exceeding the origin of the anal fin; the external mental barbels are very long, exceeding the posterior insertion of the pectoral fin; the internal mental barbells are long, exceeding the origin of the pectoral fin; the eyes are large measuring 13.3-17.8% SL; the sensory channels are simple; spines of the pectoral fin measure 10.6-14.0% SL, have saws on both sides along their entire length; the anal fin never reaches the posterior insertion of the adipose fin. The upper lobe of the caudal fin is smaller than the lower lobe.

The identity of *Rhamdia sapo*

Rhamdia sapo was originally described by Valenciennes in 1840, collected in Buenos Aires, Argentina. The original description of this species is very old and not detailed, so that it is not useful for its current diagnosis and recognition. Silfvergrip synonymized this species in *R. quelen* based on the lack of details in the original description. The author stated that when a large number of specimens related to this species is analyzed, a great intra and interpopulation variation is observed.

In the analysis performed in the present research, using many Silfvergrip characters, a well-established morphological pattern for *R. sapo* was found, with good diagnostic characters and a consistent distribution pattern. In addition to, *R. sapo* is genetically considered an independent evolutionary lineage (Angrizani and Malabarba, 2017).

The *R. sapo* holotype is found in the Natural History Museum of Paris and it is registered with the MNHN 1576 identifier. This holotype presents appropriated condition to be analyzed (Fig. 3). The specimen was examined in February 2017, allowing its redescription and linkage to the HA4 lineage of the Angrizani and Malabarba (2017) research. *Rhamdia sapo* has a large distribution area, occurring in the south of the River Plate basin (including the Iguaçu river and the Uruguay river) and in the basins of the Patos Lagoon, the Tramandaí river and the Araranguá river.

In addition to the characteristics used in the diagnosis, *R. sapo* can be recognized by the following additional characters: Dorsal fin having 6-8 branched rays;tip of last branched dorsal-fin ray trespassing anterior insertion of adipose fin; the head measures 25.6-28.7% SL, with a convex dorsal profile; the snout is longer than deep; the maxillary barbels are very long, at the minimum exceeding the origin of anal fin and at the maximum reach the origin of the caudal fin; the external mental barbels are long, exceeding the insertion of the pectoral fin; the internal mental barbells are long, never reach the origin of the pectoral fin; The eyes are large measuring 11.4-14.7% HL; the sensory channels are simple; spines of the pectoral fin measure 11.2-14.3% SL, have serrae on both sides, on the anterior side the serrae are strong and are arranged in the distal three thirds, on the posterior side the serrae are delicate and are arranged along the whole length; the anal fin exceed the posterior insertion of the adipose fin. The upper lobe of the caudal fin is smaller than the lower lobe.

The two redescribed species present consistent patterns of geographic distribution, genetic and morphological differences that allowed them to be diagnosed from other species of this genus. The original descriptions of these species are very old and not detailed so that they are not useful for their diagnosis. They belong to the same clade and the time of divergence between them is ~ 1.8 mya (Angrizani and Malabarba, 2017). The origin of these taxa occurred in the Brazilian coastal plain and the divergence between them was provided by the eustatic movements of the Pleistocene (Angrizani and Malabarba 2017).

Table 1: Morphometric data of the *Rhamdia quelen* and *Rhamdia sapo*.

	***Rhamdia quelen* (n=50)**			***Rhamdia sapo* (n=50)**		
	min-max	Mean±SD	Neotype	min-max	Mean±SD	Holotype
Standard length (mm)	93.71-247.8	157.06	150,66	90.4-314.0	218.16	341.98
Percent of Standard Length						
Maxillary-barbel length	61.0-85.1	71.8±7.2	76.5	61.2-98.7	74.2±11.1	44,4
Pectoral-girdle width	17.8-21.5	19.4±0.7	19.6	19.7-23.4	21.0±0.8	17.9
Pelvic-girdle width	8.7-10.6	9.6±0.4	9.2	9.0-11.5	10.5±0.6	9,4
Body depth	16.6-20.8	18.4±1.2	18.4	20.1-22.9	21.3±0.8	14.7
Pre-dorsal distance	33.1-37.2	35.3±1.1	34.5	34.5-39.3	37.1±1.1	35.7
Dorsal-fin to caudal-fin distance	50.2-54.2	52.1±1.1	50.9	44.5-51.0	48.1±1.6	50.8
Dorsal-fin to adipose-fin distance	3.0-7.5	4.5±1.2	3.0	1.5-4.8	3.2±.8	4.8
Pre-pectoral distance	22.2-25.9	24.0±0.9	23.5	25.2-28.6	26.7±0.9	24.0
Pre-pelvic distance	45.8-50.8	48.6±1.4	47.2	46.7-54.7	51.3±1.9	54.4

Pre-anal distance	66.3-70.1	68.3±0.9	68.7	65.0-73.7	69.7±2.4	75.8
Pelvic-fin to anal-fin distance	18.2-22.6	20.4±1.1	21.5	16.4-22.0	19.4±1.3	20.4
Adipose-fin to caudal-fin distance	9.1-11.3	10.1±0.6	9.7	8.3-13.5	10.7±1.2	11.3
Caudal-peduncle length	17.2-22.1	19.5±1.2	19.1	17.1-21.0	19.1±1.0	18.4
Caudal-peduncle depth	8.3-10.5	9.8±0.5	10.2	9.2-11.2	10.2±0.4	8.7
Pelvic-fin length	11.1-15.5	13.2±1.0	12.3	12.2-16.5	13.8±1.3	12.1
Anal-fin base length	10.8-14.4	12.7±1.0	13.4	08.7-14.3	12.1±1.5	11.9
Anal-fin length	18.1-22.8	20.7±1.1	21.5	15.8-22.3	20.1±1.6	20.4
Dorsal-fin base length	13.8-17.1	15.5±0.7	16.4	13.9-19.0	17.0±1.1	16.6
Dorsal-fin height	11.6-16.9	14.5±1.4	15.2	11.6-17.1	14.7±1.4	13.3
Dorsal-fin spine length	7.8-10.5	9.1±0.7	9.3	7.0-9.7	8.6±0.9	7.9
Pectoral-fin spine length	10.6-14.0	12.4±0.9	12.4	11.2-14.3	12.8±0.8	12.3
Adipose-fin base length	34.9-41.4	38.0±1.9	37.7	32.0-34.7	33.5±0.9	33.7
Head length	23.4-26.7	25.2±0.9	24.8	25.6-28.7	27.3±1.0	26.1
Percent of Head Length						
Snout length	38.8-44.1	41.1±0.9	40.2	36.9-45.2	39.9±2.3	38.1
Snout height	34.6-41.0	38.6±1.4	39.3	34.0-45.7	40.3±3.2	37.1
Head height	53.5-63.4	58.2±2.5	58.4	58.4-68.5	63.7±3.1	53.4
Orbital diameter	13.3-17.8	15.2±1.4	14.3	11.4-14.7	13.1±0.9	11.4
Interorbital distance	34.8-39.6	36.9±1.2	37.0	34.0-42.2	37.7±2.0	36.2
Mouth length	43.6-49.3	46.6±1.7	47.6	43.2-52.1	47.4±2.6	44.9
Maxillary-barbels distance	34.4-40.0	37.9±1.3	37.1	34.2-40.2	37.3±1.6	35.6
Anterior nares distance	20.0-26.7	23.1±1.5	20.8	19.7-26.2	22.4±1.5	23.0
Anterior nares to posterior nares distance	12.2-15.8	14.1±0.9	14.1	11.4-16.0	13.9±1.4	13.5
Posterior nares to orbit distance	15.7-20.8	18.2±1.3	17.1	15.3-19.6	18.0±1.1	19.4
Posterior nares distance	17.1-22.0	20.2±1.4	20.9	18.5-24.1	20.6±1.4	18.6
External mental-barbels distance	35.1-39.9	37.5±1.4	36.6	33.3-40.0	36.6±1.9	33.7
Internal mental-barbels distance	15.1-19.6	17.3±1.0	15.9	15.4-20.4	17.6±1.4	17.1
Distance between mental-barbel	8.2-11.1	10.1±0.6	10.1	7.7-11.3	9.7±0.9	7.9
External mental-barbel length	90.1-129.9	109.2±11.7	129.8	87.2-114.9	101.0±8.3	88.0
Internal mental-barbel length	48.8-74.2	63.5±6.9	60.4	43.1-70.7	56.3±8.1	46.2
Head width at eye level	61.1-68.8	65.6±2.1	62.6	62.6-67.6	65.2±1.6	62.6

Figure 1. Neotype of *Rhamdia quelen* (MNRJ xxxx), xxxx mm SL. In lateral, dorsal and ventral views.

Figure 2.*Rhamdia sapo* (UFRGS xxxxx), xxxx mm SL. In lateral, dorsal and ventral views.

Figure 3. Holotype of *Rhamdia sapo* (), 246.6 mm SL. In lateral view.

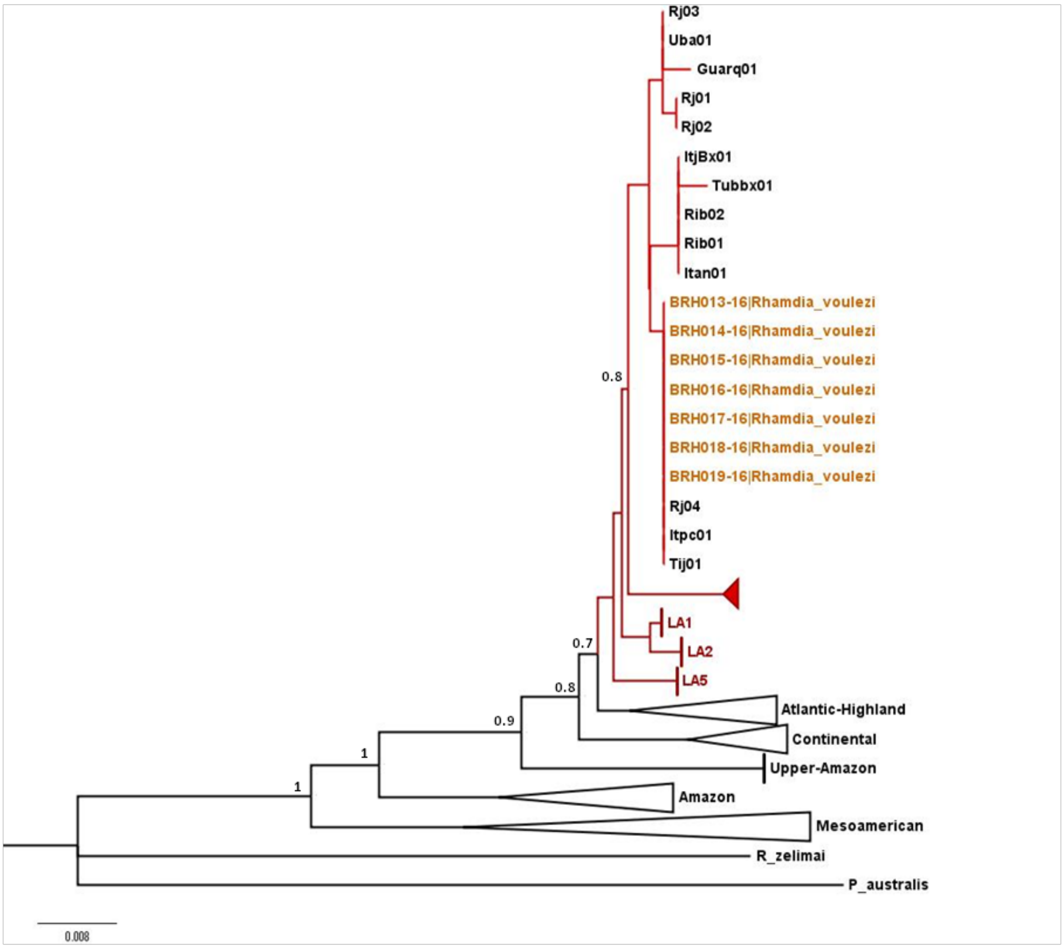

Figure 4. Two Neighbor-Joining (NJ) tree of *Rhamdia* specimens obtained using the COI gene sequences. Numbers above branches are bootstrap. A NJ tree showing interrelationship inside *R. sapo*. The clade and lineages names are the same used for Angrizani and Malabarba 2017. *Rhamdiavoulezi* is highlighthing. Upper-Amazon clade is the *Rhamdiaquelensensu* Silfvergrip (1996).

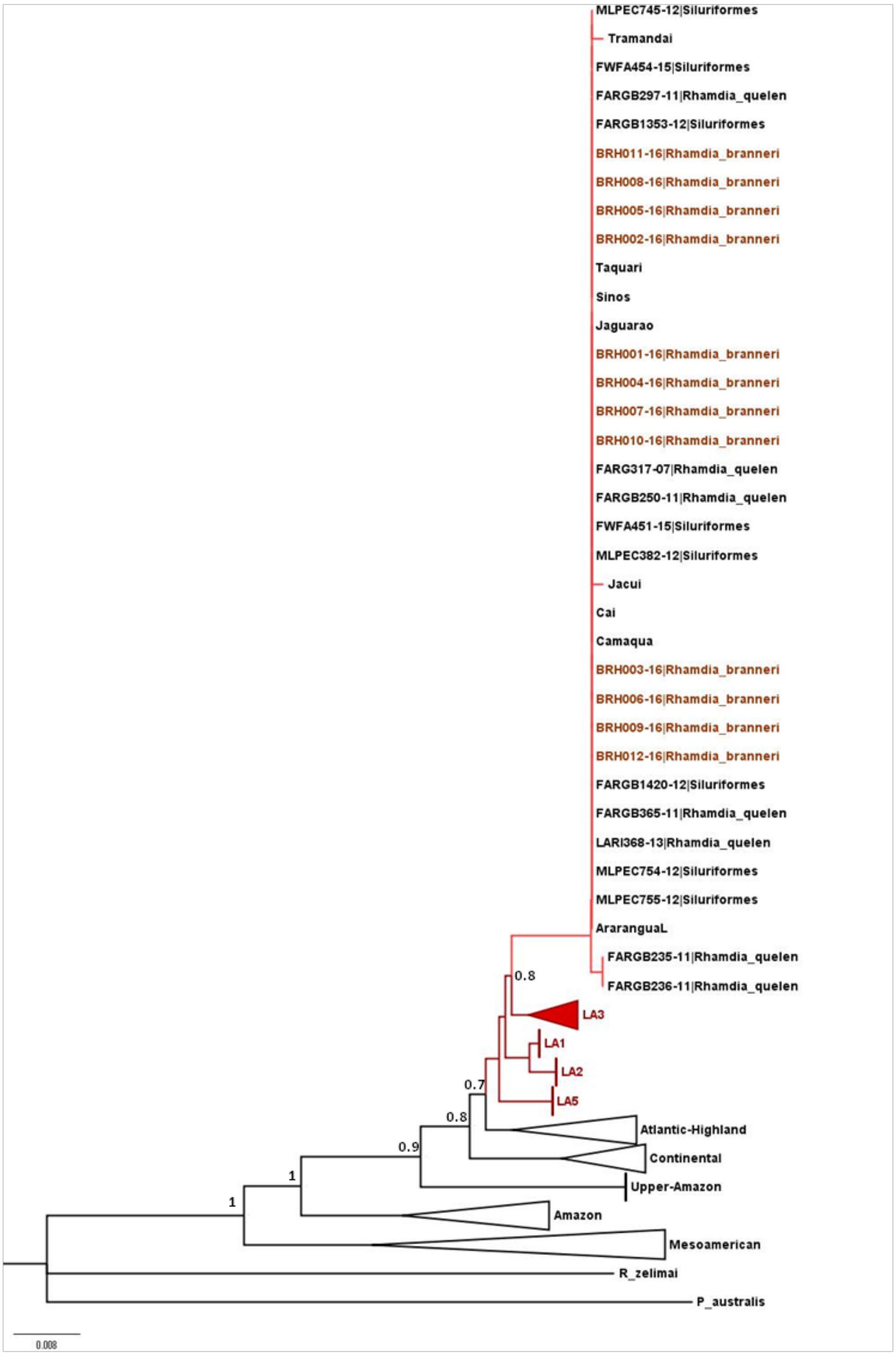

Figure 5. Two Neighbor-Joining (NJ) tree of *Rhamdia* specimens obtained using the COI gene sequences. Numbers above branches are bootstrap. A NJ tree showing interrelationship inside *R. quelen*. The clade and lineages names are the same used for Angrizani and Malabarba 2017. Rhamdia branneri is highlighthing. Upper-Amazon clade is the Rhamdia quelen sensu Silfvergrip (1996).

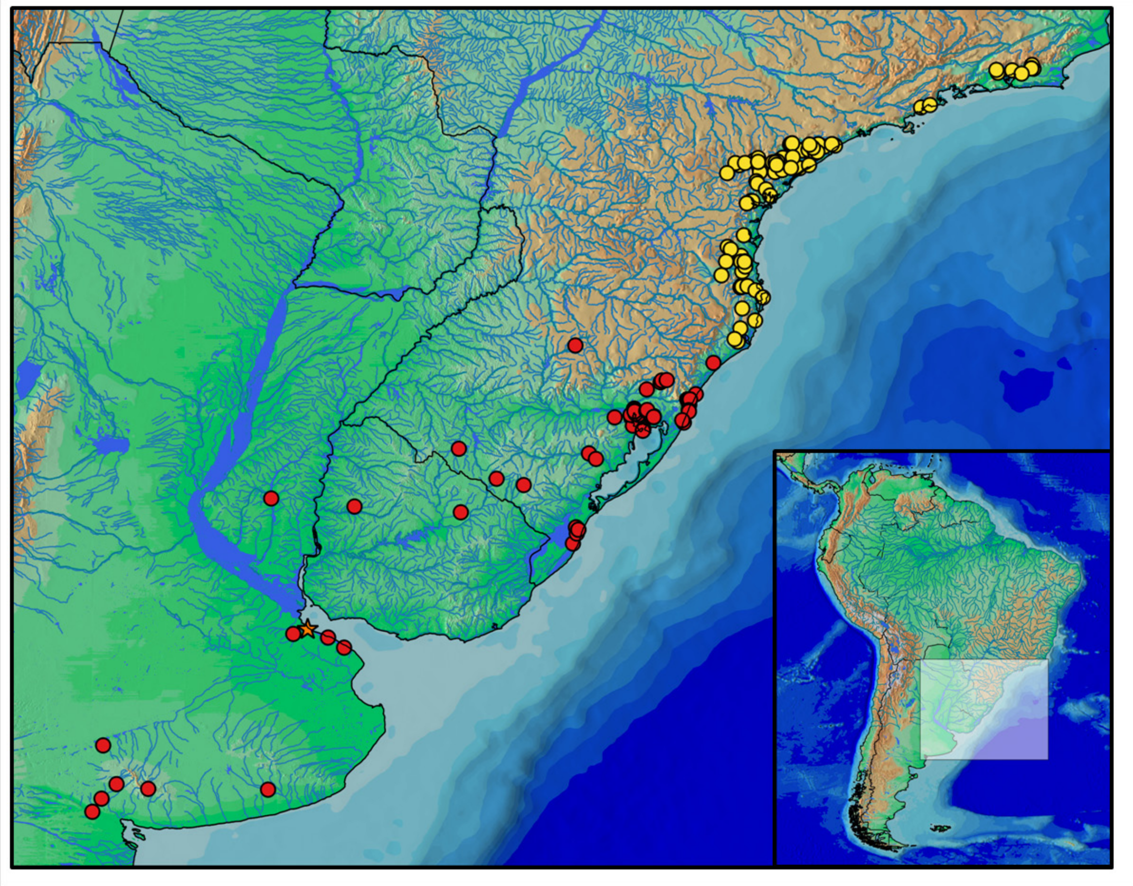

Figure 6. Distribution map of *Rhamdia quelen* (yelow circles) and *Rhamdia sapo* (red circles). Orange star is locality of *R. quelen* Neotype MNRJ xxxxx
and pink star is locaty of *R. sapo* Holotype.

References

Abell R, Thieme ML, Revenga C, Bryer M, Kottelat M, Bogutskaya N, Coad B, Mandrak N, Balderas SC, Bussing W, Stiassny MLJ, Skelton P, Allen GR, Unmack P, Naseka A, Ng R, Sindorf N, Robertson J, Armijo E, Higgins JV, Heibel TJ, Wikramanayake E, Olson D, López HL, Reis RE, Lundberg JG, Pérez MHS, Petry P. 2008. Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience*, 58, 403–414.

Angrizani RC, Malabarba, LR. 2017. Species delimitation of *Rhamdia* (Bleeker, 1858)(Siluriformes: Heptapteridae) using morphology and molecular data reveals the presence of two new species under *Rhamdia quelen* (Quoy & Gaimard, 1824) species complex. Zootaxa,

Bichuette ME, Trajano E. 2005. A new cave species of *Rhamdia* (Siluriformes: Heptapteridae) from Serra do Ramalho, northeastern Brazil, with notes on ecology and behavior. *NeotropicalIchthyology,*3(4), 587–595.

Ferraris CJ. 2007. *Checklist of catfishes, recent and fossil (Osteichthyes: Siluriformes), and catalogue of siluriform primary types* (pp. 1-628). Auckland, New Zealand: Magnolia Press.

Garavello, J.C, Shibatta, O.A. (2016). Reappraisal of *Rhamdiabranneri* Haseman, 1911 and *R. voulezi* Haseman, 1911 (Siluriformes: Heptapteridae) from the rio Iguaçu with notes on their morphometry and karyotype. *Neotropical Ichthyology,*14(1).

Hernández CL, Ortega-Lara A, Sánchez-Garcés GC, Alford MC. 2016. Genetic and Morphometric Evidence for the Recognition of Several Recently Synonymized Species of Trans-Andean *Rhamdia* (Pisces: Siluriformes: Heptapteridae*). Copeia,* 103(3), 563–579.

Perdices, A, Bermingham, E, Montilla, A. & Doadrio, I. 2002. Evolutionary history of the genus *Rhamdia* (Teleostei: Pimelodidae) in Central America. *Molecular Phylogenetics and Evolution,*25(1), 172–189.

Quoy JRC, Gaimard JP. 1824. Zoologie. Chaptre IX. In: Freycinet, L. de. (ed.) see Freycinet.

Silfvergrip AMC. 1996. *A systematic review of the Neotropical catfish genus Rhamdia (Teleostei, Pimelodidae).* Stockholm, Swedish Museum of Natural History.

Villa J. 1977. A new species of pimelodid catfish of the genus *Rhamdia* from Nicaragua, Central Amercia. *Brenesia,* 2(13), 133–142.

Weber A & Wilkens H. 1998. Rhamdia macuspanensis: a new species of troglobitic pimelodid catfish (Siluriformes; Pimelodidae) from a cave in Tabasco, Mexico. *Copeia*, 998-1004.

Weber A, Allegrucci G, Sbordoni V. 2003. *Rhamdia laluchensis*, a new species of troglobitic catfish (Siluriformes: Pimelodidae) from Chiapas, Mexico. *Ichthyological Exploration of Freshwaters*14(3): 273-280.

7. Capitulo 4

Artigo que deverá ser submetido para o periodico "Neotropical Ichthyology"

Review of *Rhamdia quelen* synonyms and redescription of seven revalidated species from South America (Siluriformes: Heptapteridae)

Abstract

The recent redescription, diagnosis and correction of the type locality of *Rhamdia quelen* allowed a review of 17 junior synonyms, originally described from South America. Through the morphological analysis of the type specimens and additional material from several museums, it is possible to diagnose seven valid species, that are redescribed herein: *Rhamdia pentlandii* and *Rhamdia dorsalis*, from western Amazon (Peru); *Rhamdia lehmanii*, from rio Orinoco drainage in Colombia and Venezuela; *Rhamdia stegelechii*, from the rio Essequibo and rio Demerara, Guiana; *R.hillarii*, from the rio São Francisco, Brazil; *R. parahybae*, from the rio Paraíba do Sul, Brazil and *Rhamdia pubecens* from lower Paraná, Paraguay and Uruguay drainages, Brazil, Argentina and Paraguay.

Introduction

Species of the genus *Rhamdia* are popularly known as “jundiás” and occur throughout the Neotropical region. The genus was described by Bleeker in 1858, and since its proposal more than 100 species have been described or added to the group. *Rhamdia* is diagnosed by the presence of the ossified posterior fontanelle and the absence of the uncinate proces hs in the first ypobranchial (Bockmann 1998).

Silfvergrip (1996) conducted the first review of the genus, recognizing eleven valid species among more than 100 species described and putatively include in the genus: *R. quelen* Quoy & Gaimard, 1824; *R. foina* Müller & Troschel, 1849; *R. laukidi* Bleeker, 1858; *R.laticauda* Kner, 1858; *R. humilis* Günther, 1864; *R. muelleri* Günther, 1864; *R. nicaraguensis* Günther, 1864; *R. poeyi* Eigenmann & Eigenmann, 1888; *R. jequitinhonha* Silfvergrip, 1996; *R. xetequepeque* Silfvergrip, 1996; *R. itacaiunas* Silfvergrip, 1996.

Among these, *R. quelen* is the most noticeable in possessing 47 junior synonyms (Silfvergrip 1996), recently the neotype designation was questioned by Angrizani & malabarba (2017) and invalid designation of a neotype from the río Ucayali in the Peruvian

Amazon, geographically distant from the original type locality in a tributary of Guanabara Bay, Rio de Janeiro, Brazil (Angrizani & Malabarba, 2017). Therefore, , *R. quelen* a species complex occurring from southern Mexico to central Argentina (Pedices et al., 2007; Herandez et al. 2015; Garavello & Shibata 2016; Angrizani & Malabarba 2017).

Some recent phylogeographic studies have demonstrated that populations of *Rhamdia* from Mexico and Central America form distinct lineages from South American representatives of the genus, including *R. quelen* (Perdices et al. 2007; Hernandez et al. (2015). The South America representatives of *R. quelen* complex, in turn, are distributed into 18 different lineages that may constitute distinct species (Angrizani & Malabarba 2017). With the redescription and morphological diagnosis of *Rhamdia quelen* (Angrizani & Malabarba submitted), it is now possible to review the validity of some of the nominal species of the genus previously considered junior synonyms of *Rhamdia quelen.* The genus presently contains 24 valid species. We herein revalidate and describe *R. pentlandii* (Valenciennes, 1840); *R. dorsalis* Gill, 1870; *R. lehmanni* Dahl, 1961; *R. stegelichii* (Müller & Troschel, 1849);*R. hilarii* (Cuvier & Valenciennes, 1840), *R. parahybae* (Steindachner, 1887); and *R. sebae* (Cuvier, 1829).

Material and methods

Institutional acronyms follow Sabaj Pérez (2014). A total of 340 specimens were examined: 13 of *R. pentlandii*, 18 of *R. dorsalis,* 37 of *R. sebae*, 30 of *R. lehmanii,* 56 of *R. cuyabae,* 11 of *R. hillarii,* 37 of *R. parahybae* and 138 of other species of *Rhamdia* as comparative material. Examined specimens include the type specimens of *R. bathyurus*, *R. cuyabae*, *R. dorsalis*, *R. duquei*, *R. hilarii*, *R. lehmanni*, *R. mounseyi*, *R. ortoni*, *R. parahybae*, *R. pentlandii*, *R. pubescens*, *R. queleni cuprea*, *R. riojae*, *R. sebae marty*, *R. sebae*, *R. stegelichii*, and *R. wuchereri*. Counts and measurements follow Angrizani & Malabarba (2017).

Comparative material – *Rhamdia quelen*: All from Brazil: MCP 11030, 2, state of Santa Catarina, municipality of, Sanga de Areia stream, basin of Tubarão river; 28°28’00”S, 49°01’60”W; C. Lucena, L. Malabarba e L. Bergmann, 8 Dec 1986. UFRGS 21369, 2, state of Santa Catarina, municipality of São Martinho, Guabiroba river, basin of Tubarão river; 28^{o}10'52"S, 48^{o}58'25"W; R. Angrizani, J. Wingert, J. Ferrer and F. Kuhn, 26 Jan 2016. UFRGS 18488, 1, state of Santa Catarina, municipality of São João Batista, Tijucas river; 27^{o}16'00"S, 48^{o}49'15"W; A. Thomaz, A. Hirschmann, P. Silva, C. and T. Carvalho, 10 Dez 2013. UFRGS 21083, 1, state of Santa Catarina, municipality of Nova Trento, Nova Trento stream, basin of Tijucas river, 27°16'47"S, 48°56'20"W, T. Carvalho, F. Carvalho and A. Thomaz, 03 Sep 2015. UFRGS 21505, 7, state of Santa Catarina, municipality of Luiz Alves, Luiz Alves river, basin of Itajaí river; 26°44'18”S, 48°57'32"W, R. Angrizani and G. Volkmer, 02 Feb 2016. MZUSP 36480, 9, state of Santa Catarina, municipality of Joinville, Lindo stream, basin of Cubatão river; 26^{o}10’00”S, 48^{o}54’00”W; L. Malabarba, R. Reis e C. Lucena, 19 Set 1985. MCP 6895, 1, state of Santa Catarina, municipality Corupá, Itapocu river; 26^{o}26’00”S, 49^{o}15’00”W; C. Lucena, L. Malabarba e A. Bergmann, 20 Nov 1985. UFRGS 21086, 1, state of Santa Catarina, municipality of Massaranduba, Massaramduba stream, basin of Itapocu river, 26°36'41"S, 48°57'39"W, T. Carvalho, F. Carvalho and A. Thomaz, 03 Sep 2015. MHNCI 8065, 4, state of Paraná, municipality of Morretes, Caninana river, basin of Nhumdiaquara river; 25^{o}28’37”S, 48^{o}50’04”W; J. Andreguetto e B. Marterer, 24 Nov 1986. MHNCI 7878, 4, state of Paraná, municipality of Guaraqueçaba, Velho river, basin of Morato river; 25^{o}18’24”S, 48^{o}19’44”W; W. Wosiacki and J. Matheus, 25 Jun 1994. MZUSP 22578, 2, state of São Paulo, municipality of Iporanga, Betari river, basin of Ribeira do Iguape river; 24^{o}34’00”S, 48^{o}40’00”W; expedição do Departamento de Zoologia. 10 Oct 1961. MZUSP 36543, 5, state of São Paulo, municipality of Juquiá, Fundo stream, basin of Ribeira do Iguape river; 24^{o}20’00”S, 47^{o}38’00”W; O. Oyakawa, L. Portugal and F. Langeani, 12 Dez 1985. MZUSP 42584, 12, state of São Paulo, municipality of Ribeira, Ribeira do Iguape river; 24^{o}39’00”S, 49^{o}00’00”W; O. Oyakawa, 01 Mar 1991. UFRGS 18706, 2, state of São Paulo, municipality of Peruíbe, Bananal river, basin of Itanhaém river, 24°11’45”S, 46°59’40”W; P. Silva, A. Hirschmann, A. Thomaz and T. Carvalho, 15 Dec 2013. MNRJ 46842, 3, state of Rio de Janeiro, municipality of Cachoeiras de Macacu, Jororo stream, basin of Baía de Guanabara; 22^{o}33’15”S, 42^{o}40’3”8W; P. Buckup, M. Britto, C. Moreira, 28 Apr 2016. MNRJ 43525, 3, state of Rio de Janeiro, municipality of Cachoeira de Macacu, Macacu river, basin of Guanabara bay; 22^{o}29’12”S, 42^{o}39’42”W; P. Buckup, D. Moraes Jr, G. Vergara, M. Gonzales, D. Peixoto and P. Cortes, 13 Nov 2014. MNRJ 43148, 1, state of Rio de Janeiro, municipality of Nova Iguaçu, basin of Guanabara bay, Tinguá river, basin of Guanabara bay; 22°35’25”S, 43°25’59”W; P. Buckup, D. Moraes Jr, C. Quijada and E. Neuhaus, 4 Jul 2014. *Rhamdia sapo*: From Brazil: UFRGS 17717, 4, Brazil, state of Rio Grande do Sul, municipality of Capão da Canoa, stream tributary of Quadros lagoon, basin of Tramandaí; 29°39'58"S, 50°01'53"W; L. Malabarba, A. Hirschmann, K. Bonato, C. Hartmann, R. Angrizani, 03 Apr 2013. Basin of rio Araranguá: UFRGS 21360, 4, state of Santa Catarina, municipality of Meleiro, Figueira stream, tributary of Itoupava river, basin of Araranguá river; 28°55'36"S, 49°33'25"W; R. Angrizani, J. Wingert, J. Ferrer and F. Kuhn. UFRGS 18424, 4, state of Rio Grande do Sul, municipality of Cristal, Camaquã river, basin of Patos lagoon; 30°53'05"S, 52°15'03"W; R. Angrizani, J. Miranda and A. Langoni, 16 Jan 2014. UFRGS 2766, 3, state of Rio Grande do Sul, municipalit of Rio Grande, Nicola lagoom; 32°31'60"S, 52°32'00"W; L. Malabarba, 10 Dez 1979. UFRGS 6921, 2, state of Rio Grande do Sul, municipality of Gravataí, Gravataí river, basin of Patos lagoon, 29°56'39"S, 50°59'30"W; M. Azevedo, A. Dufech, J. Ferrer, D. Cognato, V. Lampert, F. Flores-Lopes, 10 Dez 2004. UFRGS 13848, 5, state of Rio Grande do Sul, municipality of Viamão, Grande pond; 30°04'41"S, 50°50'55"W; G. Frainer, S. Leonardi and J. Giora, 21 Sep 2010. UFRGS 7059, 2, state of Rio Grande do Sul, municipality of Porto Alegre, Guaíba lake, basin of Patos lagoon; 30°00'34"S, 51°14'40"W; A. Saccol-Pereira and P. Milani, 10 Out 2004. UFRGS 6796, 6, state of Rio Grande do Sul, municipality of Porto Alegre, Guaíba lake, basin of Patos lagoon; 30°23'38"S, 51°05'10"W, R. Malabarba, 04 Apr 2004. UFRGS 19663, 4, state of Rio Grande do Sul, municipality of Santa Maria do Herval, Cadeia river, tributary of Caí river, basin of Patos lagoon, 29°30'03"S, 51°00'03"W, G. Volkmer. 17 Oct 2014. UFRGS 20046, 1, Brazil, state of Rio Grande do Sul, municipality of Candiota, Candiota stream, tributary of rio Jaguarão, basin of lagoa dos Patos; 31°34'07"S, 53°39'43"W; R. Angrizani, 02 Fev 2015. UFRGS 23148, 2, state of Rio Grande do Sul, municipality of Quaraí, Areal stream, tributary of rio Quaraí, basin of Uruguai river; 30°25'56"S, 56°18'44"W; L. Malabarba and R. Reis. 16 Dez 2014. Basin of rio Ibicuí: UFRGS 1571, 1, state of Rio Grande do Sul, municipality of Santana do Livramento, Ibicuí da Armada river, basin of Uruguai river; 30°46'60"S, 55°03'60"W; L. Malabarba and R. Reis. 21 Dez 1982. From Uruguay: UFRGS 7966, 1, state of Paysandu, municipality of Paysandu, Queguay Chico river, basin of Uruguai river; 32°01'57"S, 57°19'30"W; V. Bertaco, F. Canteira, J. Ferrer and L. Malabarba, 10 Sep 2005.

Basin of rio Tacuarembó: UFRGS 14569,1, state of Tacuarembó, municipality Tacuarembó, Caraguatá river, tributary of Tacuarembó river, basin of Uruguai river; 32°09'29"S, 55°01'27"W; L. Malabarba, V. Bertaco, P. Lehmann and F. Canteira. Rhamdia euricephala: Holotype**:**UFRGS 19908, 1, Brazil, state of Santa Catarina, municipality of Anitápolis, rio do Povoamento, hydrographic basin of rio Tubarão, 27º51’36”S, 49º07’50”W; R. C. Angrizani, L. R. Malabarba, M. C. Malabarba, 21 Feb 2015. UFRGS 19908, 16 (1 c&s), collected with holotype, municipality of Anitápolis, rio do Povoamento, hydrographic basin of rio Tubarão, 27º51’36”S 49º07’50”W, R.C. Angrizani, L.R. Malabarba, M.C. Malabarba, 21 Feb 2015. *Rhamdia gabrielae:* Holotype: UFRGS 22010, Brazil, state of Rio Grande do Sul, municipality of Maquiné, arroio Pinheiro, tributary of rio Maquiné, 29^{o}39’43”S, 50^{o}15’55”W; F. G. Becker, 19 Jun 1999. UFRGS 18033, 10 (1 c&s), state of Rio Grande do Sul, municipality of Maquiné, rio Maquiné, 29^{o}38’52”S, 50^{o}13’03”W; J. M. Santos, 30 Mai 2013**.** *Pimelodus godmanni:* Lectotype BMNH 1864.1.26.94, 1, Guatemala, Río San Geronimo, Godman & Salvin. *Pimelodus micropterus:* Holotype BMNH 1864.1.26.92, 1, Guatemala, Río San Geronimo, Salvin. *Pimelodus wagneri:* Holotype NMW 45618, Pacific and Atlantic rivers of Panama. *Rhamdia bransfordii:* Holotype USNM 16674, Panama, Camp Marie Caretta. *Pimelodus boucardi:* Holotype BMNH 1880.7.13.33, 1, Mexico, Est yucatan. *Rhamdia gilli:*Holotype USNM 53472, Peru, Río Eten. *Caecorhmadia urichi:* BMNH 1926.7.28:1, Holotype, 1, Trinidad, Oropuche Cave. *Rhamdia heteracantha:* BMNH 1907.6.28.3, Holotype, 1, Costa Rica, Juan Viñas. *Rhamdia foina:* ANSP 189114, 1, Suriname, distric of Sipalawiniawa, municipality of Anapaike, Lawa river, basin of Marowijne river; 03°20'49.54"N, 54°03'41.35"W; M. Sabaj, P. Willink, J. Mol and K. Wan, 24 Apr 2007. ANSP 190948, 1, Venezuela, state of Amazonas, municipality of San Fernando de Atabapo, Cano Guapa Sucia at mouth, river Atabapo, basin of Orinoco; 04°01'00"N, 67°41'14"W; N.K. Lujan and M. Arce, 2013. ANSP 190951, 1, Venezuela, state of Amazonas, municipality of Santa Barbara, Ventuari river, basin of Orinoco river; 04°04'33"N, 66°53'16"W; N.K. Lujan, M. Arce, E.L. Richmond, M.B. Grant & T.E. Wesley, 2010. *Rhamdia laukidi:* MZUSP 81485, 3, Brazil, state of Amazonas, municipality of Tiquié, igarapé Açaí tributary of rio Tiquié, 0°15'55"N, 69°58'16"W. MZUSP 85074, 3, state of Amazonas, municipality of Tiquié, rio Tiquié, 0°15'35"N, 70°02'42"W. ANSP 174652, Neotype, 1, Venezuela, state of Amazonas, municipality of Tama Tama, Casiquiare river, basin of Orinoco; 03°06'29.00"N, 65°49'56"W; B. Chernoff, J. Fernandez, O. Castillo. ANSP 162516, 2, Venezuela, state of Amazonas, municipality of Tama Tama, Casiquiare river, basin of Orinoco; 03°06'29.00"N, 65°49'56"W; B. Chernoff, J. Fernandez, O. Castillo. ANSP 134383, 2, Colombia, departament of Meta, municipality of La Siberia, Tributary of Cano La Raya, basin of rio Meta; 04°04'47"N, 73°06'39"W; J.E. Bohlke, W.G. Saul & L. Fuiman. *Rhamdia laticauda:* NRM 53310, 5, El Salvador, province of Santa Ana, Municipality ofMetapan, basin of Río Lempa, Kullander, SO & Ready, JS, 23 Feb 2006. NRM 53213, 6,El Slavador, provinceSan Miguel, municipality ofCarolina, Río Torola, basin of Río Lempa, Kullander, SO, 20 Feb 2006. NRM 31832, 3, Guatemala, province of Chiquimula, municipality ofChiquimula**,** Río Motagua, Fredriksson, C & Mähl, S, 11 Feb 1995. *Rhamdia cinerascens:* BMNH 1860.6.16:193, lectotype, 1, Ecuador, municipality of Guayaquil or Esmeraldas, Río Daule. ANSP 92426, 1, municipality of Guayaquil. Rio Guayas, 02°14'12"S, 79°52'04"W. *Rhamdia humillis:* BMNH 1965.2.19:1, Holotype, 1, Venezuela. *Rhamdia muelleri:* MZUSP 23034, 4, state of Pará, municipality of Belém, igarapé Paracuri, 01°26'60"S, 48°38'00"W, 01 Aug 1965.ANSP 166960, 1, Venezuela, state of Bolivar, municipality of Maripa, rio Urbana; 07°15'26.75"N, 64°59'00"W; J. E. Bohlke, W.G. Saul & E. Ferrer-Veliz. ANSP 149827, 1, Venezuela, state of Bolivar, municipality of Maripa, rio Urbana; 07°15'26.75"N, 64°59'00"W; J. E. Bohlke, W.G. Saul & E. Ferrer-Veliz. ANSP 162519, 1, Venezuela, state of Amazonas, municipality of Tama Tama, rio Orinoco; 03°03'58"N, 66°27'53"W; B. Chernoff, W. Saul, H. Lopez, J. Fernandez, O. Castillo, M.E. Antonio & J. Moreno. *Rhamdia nicaraguensis:* ANSP 163732, 2,Costa Rica, municipality of Heredia, brook of Rio Cuarto*;* 10°20'39"N, 84°13'08"W*;* P. Fromm, 1989. ANSP 124137, 1, Nicaragua, minicipality of Bethehem, Pis River, Basin of Wanx River; 14°09'14"N, 84°37'13"W; W. Huber, 1979. *Rhamdia guatemalensis:* BMNH 1864.1.26:210, Holotype 1, Guatemala, laguna Huamuchal, Salvin. NRM 53260, 15, El Salvador, Province Morazán, Municipality Yamabal, río Yamabal, basin of Río Grande de San Miguel, Kullander, SO, 21 Feb 2006. NRM 53387, 1, El Salvador, province San Miguel, municipality El Transito, Basin of Río Grande de San Miguel, Laguna Jocotal, Kullander, SO, 22 Feb 2006.NRM 53355, 3, El Salvador, province of Santa Ana, municipality Metapan, basin of Río Lempa, Lago Güija, Kullander, SO & Ready, JS, 23 Feb 2006. *Rhamdia poeyi:* MZUSP 024557, 4, state of Goiás, municipality of São Domingos, ribeirão Bezerra, rio Tocantins, 13°24'00"S, 46°19'00"W,

1974. *Rhamdia saijaensis:* NRM 10675, Holotype, 1, Colombia, south of Buenaventura, rio Saija, G. Gerring, 1939. NRM 15329, 3, Colombia, south of Buenaventura, rio Saija, G. Gerring, 1939. *Rhamdia jequitinhonha:* MNRJ 22514, 1, Brazil, state of Minas Gerais, municipality of Pedra Azul, 15°54'50"S, 41°23'31"W, 10 Jul 2001. *Rhamdia xetequepeque:* NRM 34053, 5, Peru, province of Cajamarca, municipality of Chilete, Río Jequetepeque, Holm, E, 11 Jul 1986. *Rhamdia itacaiunas:*MZUSP 34744, Paratype, 2, Brazil, state of Pará, municipality of Marabá, rio Itacaiunas, 05°22'00"S, 49°07'00"W, 14 Oct 1983. *Rhamdia gabrielae:* UFRGS 22010, 194 mm SL, Brazil, state of Rio Grande do Sul, municipality of Maquiné, arroio Pinheiro, tributary of rio Maquiné, 29°39'43"S, 50°15'55"W; F. G. Becker, 19 Jun 1999. UFRGS 18033, 10, state of Rio Grande do Sul, municipality of Maquiné, rio Maquiné, 29°38'52"S, 50°13'03"W; J. M. Santos, 30 Mai 2013. *Rhamdia euricephalae:*UFRGS 19908, Holotype, 1, Brazil, state of Santa Catarina, municipality of Anitápolis, rio do Povoamento, hydrographic basin of rio Tubarão, 27°51'36"S, 49°07'50"W; R. C. Angrizani, L. R. Malabarba, M. C. Malabarba, 21 Feb 2015. UFRGS 19906, 16, municipality of Anitápolis, rio do Povoamento, hydrographic basin of rio Tubarão, 27°51'50"S 49°07´54"W, R.C. Angrizani, L.R. Malabarba, M.C. Malabarba, 21 Feb 2015. *Rhamdia enfurnada:* MZUSP 87776, Holotype, 1, Brazil, state of Bahia, municipality of Coribe, gruta do Enfurnado, rio São Francisco, 13°38'44"S, 44°12'05"W, 5 Sep 2003. *Rhamdia guasarensis:* ANSP 179878, Venezuela, state of Zulia, municipality of Cerro Yolanda, basin of Rio Guasare; 10°52'26"N, 72°30'44"W; J. Lagarde, 2004.

Results

Rhamdia pentlandii (Valenciennes, 1840)

(Fig. 1, 2)

*Pimeloduspentlandii*Valenciennes, 1840 [in Cuvier & Valenciennes, 1840:183, Pl. 435; type locality: Río Apurímac, Peru].
Rhamdia duquei Eigenmann & Pearson, 1942 [in Eigenmann & Allen 1942:93; Type locality: Rio Urubamba, Santa Ana, Peru].

Lectotype: BMNH 1862.11.15:11, 1, 220 mm SL, Peru, rio Apurimac.

Examined material: All from Peru: ANSP 143976, 1, 59.58 mm SL, Peru, region of Madre de Dios, municipality of Shintuya, rio Madre de Dios; 12°39'60"S, 71°16'60"W; Richard Horwitz, 20 Jun 1977. ANSP 180790, 3, xx mm SL, Peru, region of Cuzco, municipality of Quellounoco, rio Urubamba , basin of rio Ucayali; 12°33'29"S, 72°29'53"W ; M. Sabaj, M. Arce, L. de Souza, L. Sousa, 19 Jul 2004. ANSP 180738, 1, 103.23 mm SL, Peru, region of Cuzco, municipality of Kiteni, Materiato stream, tributary of rio Urubamba, basin of rio Ucayali; 12°38'34"S, 72°53'19"W; M. Sabaj, N. Salcedo, B. Rengifo, M. Arce, 20 Jul 2004. ANSP 143981, 1, 113.23 mm SL, Peru, region of Madre de Dios, municipality of Atalaya, rio Carbon, basin of rio Madre de Dios; 12°52'60"S, 71°19'60"W; Richard Horwitz, 15 Jul 1977. ANSP 180639, 1, 185.21 m SL, Peru, region of Apurimac, municipality of Chincheros, rio Pampas, tributary of rio Apurimac, basin of Ucayali; 13°30'43"S, 73°48'54"W; M. Sabaj, N. Salcedo, L. Rapp Py-Daniel, 11 Jul 2004. ANSP 180728, 1, xx mm SL, Peru, region of Apurimac, municipality of Colcabamba, rio Antabamba, tributary of rio Pachachaca, basin of rio Ucayali; 14°00'44"S, 73°11'08"W; M. Sabaj, L. Rapp Py-Daniel, L. de Souza, 05 Jul 2004. ANSP 139061, 3, Peru, region of Huánuco, municipality of Tingo María, rio Rondos, tributary of rio Monzón, basin of Ucayali; 09°15'37"S, 76°13'57"W; P. Allard. CAS-SU 57895, 1, Holotype of *R. duquei,* Rio Urubamba, Santa Ana, Peru.

Diagnosis - *Rhamdia pentlandii* differs from *R. quelen, R. sapo, R. hillarii, R. sebae, R. dorsalis, R. lehmanni, R. steiglichii, R. foina, R. laukidi, R. cinerascens, R. humilis, R. muelleri, R. nicaraguensis, R. guatemalensis, R. poeyi, R. saijaensis, R. jequitinhonha, R. xetequepeque, R. gabrielae, R. euricephala,* by shorter adipose-fin base length (22.8-26.1% SL *vs.* 34.9-41.4% SL in *R. quelen,* 32.0-34.7% SL in *R. sapo,* 29.7-38.7% SL in *R. hillarii,* 37.4-42.3% SL in *R. sebae,* 31.6-38.3% SL in *R. dorsalis,* 36.0-40.9% SL in *R. lehmanni,* 39.1-46.6% SL in *R. steiglichii,* 27.9-33.2% SL in *R. foina,* 44.5-51.3% SL in *R. laukidi,* 30.3-33.3% SL in *R. cinerascens,* 27.6-33.5% SL in *R. humilis,* 42.4-55.3% SL in *R. muelleri,* 39.8-44.1% SL in *R. nicaraguensis,* 35.9-43.2% SL in *R. guatemalensis,* 27.0-35.6% SL in *R. poeyi,* 36.0-45.7% SL in *R. saijaensis,* 34.7% SL in *R. jequitinhonha,* 32.8-37.2% SL in *R. xetequepeque,* 31.7-39.4% SL in *R. gabrielae* and 32.9-39.0% SL in *R. euricephala*). Differs from *R. laticauda* and *R. itacaiunas* by the upper lobe of caudal fin smaller than lower lobe (*vs.* lower lobe longer than the upper lobe). Differs from *R. reddelli*, *R. enfurnada*, *R. zongolicensis*, *R. macuspanensis, R. guasarensis* and *R. laluchensis* by the lack of morphological adaptations to troglobitic life.

Description - Measurements in Table 1. Body elongated and deep; cross section of trunk roughly circular at dorsal-fin origin and along dorsal-fin base, gradually compressed posteriorly through caudal peduncle. Anterodorsal profile of body convex from supraoccipital to dorsal-fin base. Dorsal-fin base nearly straight, posteroventrally slanted, and gently convex from dorsal fin to base of adipose fin. Ventral body profile slightly curved from mouth to caudal-fin base. Body widest at pectoral girdle and deepest at dorsal-fin origin. Caudal peduncle longer than deep.

Head deep and short. Dorsal head profile straight and posterodorsally slanted from snout tip to supraoccipital in lateral view. Head shape straigth in dorsal view. Snout rounded anteriorly in dorsal view, so long as deep. Distance between posterior nares slightly smaller than that between anterior nares. Mouth wide, subterminal, gape larger than interorbital distance; snout projecting slightly beyond lower jaw. Gape transverse, with fleshy rictal fold at corners. Rictal fold large. Both upper and lower lips with several longitudinal plicae.

Barbels flattened in cross section, wide at their bases and tapering towards distal tip. Maxillary barbel longest; length variable reaching maximum insertion of pelvic fin; inserted above upper lip and posterolateral to anterior nares. Two pairs of mental barbels. Two pairs of mental barbels with bases aligned. Outer mental barbels surpassing origin of pectoral fin. Inner mental barbels shorter than outer mental barbels, maximally not reaching origin of pectoral fin. Gular fold distinct and V-shaped. Branchiostegal rays 6. Gill rakers thick and moderately long, with: 6 rakers on first ceratobranchial. Eye large, slightly elliptical (greatest length in longitudinal axis), with rim circumscribed with deep, continuous invagination, distinctly more pronounced at lateral border. Eye positioned laterally, centered approximately in first third between tip of snout and corner of opercular membrane, and widely separated by large interorbital space. Pupil rounded. Sensory channels of head simple.

Dorsal fin with 2 unbranched rays and 6 branched rays, distal margin convex and base length less to fin height. First unbranched dorsa-fin ray small and not externally visible, second unbranched dorsal fin ray stiffened in proximal portion and segmented in distal portion. Dorsal-fin origin anterior to middle distance between pectoral and pelvic fin origins; insertion of last branched ray just at pelvic fin origin. Tip of last branched dorsal-fin ray not reaching anterior insertion of adipose fin. Adipose fin short; within ascendant curve in lateral profile and posterior lobe conspicuously free from body. Adipose-fin origin at vertical through at middle distance between posterior insertion of pelvic fin and anterior insertion of anal fin, and posterior insertion at middle of caudal peduncle.

Pectoral fin within one unbranched and 7-8 branched rays; when adpressed reaching approximately origin of first branched ray of dorsal fin. Unbranched ray of pectoral fin stiffened, slightly curved and with strong serrations in anterior side and delicate serration in posterior side. Pelvic fin rounded, approximately same size of pectoral fin, within one unbranched ray and 5 branched rays, surpassing genital papilla, never reaching anal-fin origin. Pelvic-fin origin nearly at body midlength, before insertion of last dorsal-fin ray. Anal fin rounded, with 1-2 unbranched rays anteriorly, followed by 7-8 branched rays, when adpressed in max reach posterior insertion of adipose fin. Anal-fin base length shorter to dorsal-fin base length. Caudal fin deeply forked, lobes rounded; dorsal lobe smaller in height and length; 7-8 branched rays in dorsal lobe and 8-9 branched rays in ventral lobe.

Color pattern of preserved specimens - Body gray or brown without spots. Head and fins gray or brown without spots. Subtle dark lateral band. Ventral portion of body and head white. Maxillary barbels and mental barbels same color as body. Adipose fin is the same patterns of the body.

Distribution and Habitat - Occurs in upper portions of the rio Ucayali and rio Madre de Dios drainages, Peru (Figure 5).

Table 1: Morphometric data of the *R. pentlandii*.

Rhamdia pentlandii **(n= 13)**			
	min-max	Mean±SD	Holotype
Standard length (mm)	103.2-241.1	170.2	221.0
Percent of Standard Length			
Maxillary-barbel length	39.6-56.1	49.4±7.40	39.5
Pectoral-girdle width	17.6-18.8	18.2±0.48	17.6
Pelvic-girdle width	7.6-8.8	8.3±0.53	7.6
Body depth	15.1-17.5	16.5±0.99	15.1
Pre-dorsal distance	33.9-36.9	34.8±1.09	33.9
Dorsal-fin to caudal-fin distance	51.7-55.1	53.0±1.35	52.6
Dorsal-fin to adipose-fin distance	12.3-15.4	13.7±1.21	12.3
Pre-pectoral distance	22.1-25.2	23.2±1.19	23.4
Pre-pelvic distance	47.7-51.6	50.5±1.53	49.6
Pre-anal distance	64.3-69.8	67.0±2.94	64.3
Pelvic-fin to anal-fin distance	20.3-22.7	21.8±0.94	20.3
Adipose-fin to caudal-fin distance	17.9-19.7	18.9±0.73	18.7
Caudal-peduncle length	11.3-13.5	12.9±0.85	12.3
Caudal-peduncle depth	6.8-9.6	8.3±0.98	7.3
Pelvic-fin length	14.4-15.4	14.9±0.44	14.4
Anal-fin base length	10.8-12.5	11.4±0.71	10.8
Anal-fin length	18.2-22.3	19.8±1.63	18.2
Dorsal-fin base length	12.2-14.2	13.3±0.82	12.2
Dorsal-fin height	13.1-17.4	14.8±1.36	14.0

Dorsal-fin spine length	6.8-9.8	8.3±1.19	8.4
Pectoral-fin spine length	9.0-9.7	9.4±0.27	9.0
Adipose-fin base length	22.8-26.1	24.4±1.51	23.2
Head length	23.4-25.5	24.2±0.95	23.4
Percent of Head Length			
Snout length	33.7-35.6	34.6±0.85	35.6
Snout height	40.4-46.3	43.4±2.43	40.4
Head height	28.2-30.1	29.4±0.91	28.2
Orbital diameter	12.3-14.9	13.3±1.03	12.3
Interorbital distance	27.5-30.7	29.3±1.43	27.5
Mouth length	39.4-45.6	43.6±2.07	45.6
Maxillary-barbels distance	32.3-33.6	32.9±0.56	33.6
Anterior nares distance	18.4-21.6	20.3±1.40	21.6
Anterior nares to posterior nares distance	10.6-16.0	12.8±2.14	10.6
Posterior nares to orbit distance	15.7-17.0	16.5±0.50	17.0
Posterior nares distance	14.8-19.1	16.9±1.95	16.6
External mental-barbels distance	28.0-34.5	32.5±2.20	32.1
Internal mental-barbels distance	12.2-16.8	14.5±1.75	14.2
Distance between mental-barbel	7.1-9.2	7.8±0.81	7.2
External mental-barbel length	79.2-93.9	86.7±5.21	93.9
Internal mental-barbel length	47.6-65.2	55.4±6.49	52.2
Head width at eye level	51.8-53.0	52.3±0.58	53.0

Rhamdia dorsalis Gill, 1870

(Figs. 3, 4)

Rhamdia dorsalis Gill, 1870:94 [Type-locality: Río Marañon or Río Napo, Amazon system, Peru or Ecuador].
Rhamdia riojae Fowler 1915:209, Fig. 2 [Type locality: Rioja, near Moyabamba and Baka Puerto, on or near the lower course of Río Huallagua, Peru].
Rhamdia ortoni Fowler 1915:211, Fig. 3 [Type locality: Peruvian Amazon].
Rhamdia mounseyi Regan 1913:282 [Type locality: Río Ucayali, Peru].
Pimelodus bathyurus Cope 1878:674 [Type locality: Peruvian Amazon].

Holotype: USNM 35334, 1, 171.7 mm SL, Peru or Ecuador, Rio Maranhão or Rio Napo, Amazon basin system.

Examined material: NRM 16103, 1, 98.3 mm SL, Peru, Departament of Ucayali, municipality of Yarinacocha, stream of Paca Cocha, basin of rio Ucayali, S. Kullander, 21 Aug 1981. NRM 16104, 1, 90.6 mm SL, Peru, Departament of Ucayali, municipality of Pucallpa, canal to Paca Cocha, basin of rio Ucayali; 08°19'00"S, 74°34'00"W; S. Kullander and A. Hogeborn, 16 Aug 1981. NRM 16085, 2, Peru, Department of Loreto between Hamburgo and Santa Elena, tributary to río Samiria, basin of rio Ucayali, S. Kullander, 12 Aug 1986. NRM 16091, 1, 99.8 mm SL, Peru, Department of Loreto, between Caño Pastos and Hamburgo, tributary to río Samiria, S. Kullander, 12 Aug 1986. NRM 33542, 6, 90.6-151.5 mm SL, Peru, departament of Loreto, río Samiria, basin of rio Amazonas, S. Kullander, 12 Aug 1986. ANSP 191817, 2, Peru, departament of Loreto, municipality of Iquitos, rio Nanay, basin of Amazonas; 03°49'51"S, 73°20'59"W; M. Sabaj, B. Sidlauskas, E. Correa Roldán & C. Sabaj. ANSP 21101, 1, Holotype of *Rhamdiariojae*, 158 mm SL, Peru, departament of san Martin, municipality of Rioja, rio Huallaga, tributary of rio Mayo, basin of Ucayali; 06°03'25"S, 77°09'06"W; J. Orton, 1873. ANSP 21928, 1, Holotype of *Rhamdiaortoni*, 60 mm SL, Peru, Peruvian Amazon, J. Orton, 1873. BMNH 1913.7.30.13, 1, Lectotype of *Rhamdiamounseyi*, 115.3 mm SL, Peru, rio Ucayali, Amazon basin system. BMNH 1913.7.30.14-19, 6, 81.5-100.7 mm SL, Peru, rio Ucayali, Amazon basin system.

Diagnosis - *Rhamdia dorsalis* differs from *R. quelen*, *R. sapo*, *R. cuyabae*, *R. cinerascens*, *R.*

guatemalensis and *R. saijaensis* by shorter inter-orbital distance (32.0-33.2% HL *vs*. 34.8-39.6% HL in *R. quelen*, 34.0-42.2% HL in *R. sapo*, 33.2-42.5% HL in *R. sebae*, 35.8-41.9% HL in *R. cinerascens*, 35.3-40.6% HL in *R. guatemalensis* and 34.0-40.3% in *R. saijaensis*) and differs from *R. hillarii, R. laukidi* and *R. pentlandii* by longer inter-orbital distance (32.0-33.2% HL *vs*. 25.6-30.6% HL in *R. hillarii,* 25.1-28.9% HL in *R. laukidi* and27.5-30.7% HL in *R. pentlandii*). Differs from *R. foina*, *R poeyi* and *R. itacaiunas* by superior lobe of caudal fin smaller than inferior lobe (*vs*. superior lobe of caudal fin larger than inferior lobe). Differs from *R. laticauda*, *R. humilis*, *R. nicaraguensis* by serrae in both sides of pectoral fin spine (*vs*. serrae in one side of pectoral fin spine). Differs from *R. lehmanii, R. sebae* and *R. xequetepeque* by longer head length (24.3-27.6% SL *vs*. 18.6-23.4% SL in *R. lehmanii,* 20.2-23.7% in *R. sebae* and 20.7-23.7% SL in *R. xequetepeque*). Differs from *R. jequitinhonha*, *R. gabrielae* and *R. eurichephala* by longer maxillary barbel (83.0-98.5% SL *vs*. 39.2% SL in *R. jequitinhonha*, 46.6-69.9% SL in *R. gabrielae* and 31.2-47.7% in *R. eurichephala*)*R. reddelli*, *R. enfurnada*, *R. zongolicensis*, *R. macuspanensis* and *R. laluchensis* by the lack of morphological adaptations to troglobitic life.

Description - Measurements in Table 2. Body elongated; cross section of trunk roughly circular at dorsal-fin origin and along dorsal-fin base, gradually compressed posteriorly through caudal peduncle. Anterodorsal profile of body convex from supraoccipital to dorsal-fin base. Dorsal-fin base nearly straight, posteroventrally slanted, and gently convex from dorsal fin to base of adipose fin. Ventral body profile slightly curved from mouth to caudal-fin base. Body widest at pectoral girdle and deepest at dorsal-fin origin. Caudal peduncle so longest as deep. Number of post-Weberian vertebrae 40.

Head deep and relative long. Dorsal head profile straight and posterodorsally slanted from snout tip to supraoccipital in lateral view. Lateral head shape straight in dorsal view. Snout rounded anteriorly in dorsal view, so longest as deep. Distance between posterior nares shorter than distance between anterior nares. Mouth wide, subterminal, gape larger than interorbital distance; snout projecting slightly beyond lower jaw. Gape transverse, with fleshy rictal fold at corners. Rictal fold large. Both upper and lower lips with several longitudinal plicae.

Barbels flattened in cross section, wide at their bases and tapering towards distal tip.

Maxillary barbel longest; length variable reaching maximum posterior insertion of caudal fin; inserted above upper lip and posterolateral to anterior nares. Two pairs of mental barbels. External mental barbels longest; surpassing origin of pectoral fin. Inner mental barbels longest, aligned to and shorter than external mental barbels, surpassing origin of pectoral fin. Gular fold distinct and V-shaped. Branchiostegal rays 5-6. Gill rakers thick and moderately long, with: 6 rakers on first ceratobranchial. Eye large, slightly elliptical (greatest length in longitudinal axis), with rim circumscribed with deep, continuous invagination, distinctly more pronounced at lateral border. Eye positioned dorsolaterally, centered approximately in first third between tip of snout and corner of opercular membrane, and widely separated by large interorbital space. Pupil rounded. Sensory channels of head simple.

Dorsal fin with 2 unbranched rays and 6 branched rays, distal margin convex and base length less than fin height. First unbranched dorsa-fin ray small and not externally visible, second unbranched dorsal fin ray stiffened in proximal portion and segmented in distal portion. Dorsal-fin origin anterior to middle distance between pectoral and pelvic fin origins; insertion of last branched ray after pelvic fin origin. Tip of last branched dorsal-fin ray trespassing anterior insertion of adipose fin. Adipose fin long; within ascendant curve in lateral profile and posterior lobe conspicuously free from body. Adipose-fin origin at vertical through after posterior insertion pelvic-fin, and posterior insertion at middle of caudal peduncle.

Pectoral fin within one unbranched and 8 branched rays; when adpressed reaching approximately origin of second branched ray of dorsal fin. Unbranched ray of pectoral fin stiffened, slightly curved and with delicate serrations in distal third anterior side and delicate and spaced serrations in all posterior side. Pelvic fin rounded, approximately same size of pectoral fin, within one unbranched ray and 5 branched rays, surpassing genital papilla, never reaching anal-fin origin. Pelvic-fin origin nearly at body midlength, before insertion of last dorsal-fin ray. Anal fin rounded, with 2 unbranched rays anteriorly, followed by 8 branched rays, when adpressed never reach posterior insertion of adipose fin. Anal-fin base length shorter to dorsal-fin base length. Caudal fin deeply forked, dorsal lobe pointed and smaller in height and length; 7 branched rays in dorsal lobe and 8 branched rays in ventral lobe.

Color pattern of preserved specimens - Body gray or brown without spots. Head and fins gray or brown without spots. Ventral portion of body and head white. Maxillary barbels and mental barbels same color as body. Adipose fin is the same patterns of the body. Conspicuous humeral; thin dark lateral line.

Distribution and Habitat - Occurs in Peru in rio Ucayali, rio Maranhão and rio Napo, tributaries of the Amazon basin.

Table 2: Morphometric data of the *Rhamdia dorsalis*.

Rhamdia dorsalis **(n = 18)**			
	min-max	Mean±SD	Holotype
Standard length (mm)	90.6-187.4	133.7	171.7
Percent of Standard Length			
Maxillary-barbel length	83.0-98.5	91.6±5.40	83.0
Pectoral-girdle width	19.9-22.0	20.9±0.77	20.0
Pelvic-girdle width	8.8-10.6	9.8±051	9.5
Body depth	15.4-18.7	17.1±1.01	15.6
Pre-dorsal distance	32.7-36.9	34.6±1.51	36.8
Dorsal-fin to caudal-fin distance	48.6-52.8	50.3±1.49	49.6
Dorsal-fin to adipose-fin distance	3.4-7.4	5.1±1.44	7.4
Pre-pectoral distance	22.3-27.2	24.7±1.77	27.1
Pre-pelvic distance	45.5-51.3	48.8±1.70	51.3
Pre-anal distance	66.2-71.2	68.7±1.58	71.2
Pelvic-fin to anal-fin distance	21.0-24.8	22.3±1.35	21.7
Adipose-fin to caudal-fin distance	8.0-10.8	9.5±1.09	10.7
Caudal-peduncle length	14.2-22.5	19.2±2.76	14.2
Caudal-peduncle depth	8.6-11.1	10.0±0.78	8.6
Pelvic-fin length	11.9-14.9	13.4±1.05	12.7
Anal-fin base length	12.1-13.5	12.8±0.53	12.1
Anal-fin length	18.9-21.0	20.0±0.85	-

Dorsal-fin base length	13.8-17.7	16.1±1.35	15.3
Dorsal-fin height	14.2-18.0	16.5±1.39	14.2
Dorsal-fin spine length	8.4-11.7	10.3±1.20	8.4
Pectoral-fin spine length	9.9-15.6	14.4±1.90	9.8
Adipose-fin base length	31.6-38.3	36.4±2.30	31.5
Head length	24.3-27.6	26.1±1.25	26.7
Percent of Head Length			
Snout length	36.5-40.6	38.9±2.11	36.5
Snout height	57.6-59.0	58.1±0.79	57.6
Head height	37.8-39.4	38.4±0.88	38.0
Orbital diameter	12.8-15.4	14.5±1.46	12.7
Interorbital distance	32.0-33.2	32.7±0.63	32.0
Mouth length	44.8-50.8	48.1±3.05	44.7
Maxillary-barbels distance	35.0-40.1	37.9±2.62	34.9
Anterior nares distance	22.4-22.6	22.5±0.14	22.6
Anterior nares to posterior nares distance	12.0-14.9	13.4±1.44	13.4
Posterior nares to orbit distance	19.1-20.0	19.6±0.44	19.1
Posterior nares distance	16.7-18.9	18.0±1.17	18.4
External mental-barbels distance	33.1-37.4	35.1±2.17	33.0
Internal mental-barbels distance	16.0-19.4	17.3±1.79	15.9
Distance between mental-barbel	8.9-11.1	10.2±0.89	8.9
External mental-barbel length	98.3-109.5	104.3±5.66	98.2
Internal mental-barbel length	82.7-84.8	83.7±1.07	83.4
Head width at eye level	61.1-68.8	66.2±2.73	61.0

***Rhamdia sebae* (Cuvier 1829)**

(Figs. 6, 7)

Pimelodus sebae Cuvier, 1829:294 [Type locality: Right bank tributary to River Samiria between Caño Pastos and Hamburgo, Depto Loreto, Peru].
Pimelodus stegelichii Muller & Troschel 1848:628 [Type locality: Suriname].

Holotype - Illustration of Seba (1759), III, xxxix, 5'.

Examined material – From Guiana:ANSP 179729, 1, 85.0 mm SL, Guiana, region Tukutu-Essequibo, municipality of Yapukarri, Two Puddle creek, tributary of rio Rupununi, basin of rio Essequibo; 03°45'11"N, 59°19'38"W; M. Sabaj, J. Armbruster, M. Thomas, D. Werneke, C. Allison, C. Chin, D. Arjoon. ANSP 179728, 6, 124.9-84.5 mm SL, Guyana, region of Potaro-Siparuni, municipality of Surumatra, tributary of rio Essequibo, basin of Essequibo; 04°08'58"N, 59°00'30"W; M. H. Sabaj, J. W. Armbruster, M. R. Thomas. ANSP 167910, 4, 109.2-90.2 mm SL, Venezuela, state of Bolivar, municpality of El Miamo, Rio Macaruma, tributary of Yuruari/Cuyuni, basin of Essequibo; ; S. Schaefer, W. Saul, F. Provenzano. ANSP 167909, 4, 167.4-92.0 mm SL, Venezuela, state of Bolivar, municpality of Tumeremo, Curumito stream, tributary of rio Botanamo, basin of rio Cuyuni; 07°19'60"N, 61°19'60"W; S. Schaefer, W. Saul and F. Provenzano. ANSP 177233, 2, 143.5-62.6 mm SL, Guyana, region of Potaro-Siparuni, Tumble Down Creek, basin of Essequibo; 04°48'39"N, 58°51'11"W; G. Watkins. ANSP 177232, 4, 156.3-77.2 mm SL, Guyana, region of Potaro-Siparuni, Red Hill Creek, basin of rio Essequibo; 04°44'14"N, 58°59'17"W; G. Watkins. ANSP 175780, 11, 175.1-76.6 mm SL, Guyana, region of Potaro-Siparuni, Blackwater creek, basin of Essequibo; 04°43'58"N, 58°51'18"W; W. Saul, G. Watkins and N. Liley. ANSP 175780, 4, 131.2-123.8 mm SL, Guyana, region of Potaro-Siparuni, Blackwater creek, basin of Essequibo; 04°43'58"N, 58°51'18"W; W. Saul, G. Watkins and N. Liley. From Suriname: ANSP 8365, 2, xx-xx mm SL, Suriname, C. Hering, 1830. ZMB 3043, 1, 18.6 mm SL, Lectotype of *Pimelodus stegelichii*,Guyana. BMNH 1857.6.13.146, 1, 214.8 mm SL, Paralectotypes of *Pimelodus stegelichii*,Guyana, region of Demerara.

Diagnosis - *Rhamdia sebae* differs from *R. quelen*, *R. sapo*, *R. cuyabae*, *R. hillarii*, *R. pentlandii*, *R. parahybae*, *R. laukidi*, *R. cinerascens*, *R. saijaensis*, *R. jequitinhonha*, *R. xequetepeque*, *R. gabrielae* and *R. eurichephala* by pointed superior lobe of caudal fin (*vs*. rounded superior lobe of caudal fin). Differs from *R. foina*, *R poeyi* and *R. itacaiunas* by superior lobe of caudal fin smaller than inferior lobe (*vs*. superior lobe of caudal fin larger than inferior lobe). Differs from *R. laticauda*, *R. humilis*, *R. nicaraguensis* by serrae in both sides of pectoral fin spine (*vs*. serrae in one side of pectoral fin spine). Differs from *R. dorsalis* and *R. lehmanii* by longer adipose fin base length (40.2.1-46.6% SL *vs*. 31.6-38.3% SL in *R. dorsalis* and 36.0-39.8% SL in *R. lehmanii*). Differs from*R. reddelli*, *R. enfurnada*, *R. zongolicensis*, *R. macuspanensis* and *R. laluchensis* by the lack of morphological adaptations to troglobitic life.

Description - Measurements in Table 3. Body elongated; cross section of trunk roughly circular at dorsal-fin origin and along dorsal-fin base, gradually compressed posteriorly through caudal peduncle. Anterodorsal profile of body convex from supraoccipital to dorsal-fin base. Dorsal-fin base nearly straight, posteroventrally slanted, and gently convex from dorsal fin to base of adipose fin. Ventral body profile slightly curved from mouth to caudal-fin base. Body widest at pectoral girdle and deepest at dorsal-fin origin. Caudal peduncle longer than deep.

Head depressed. Dorsal head profile straight and posterodorsally slanted from snout tip to supraoccipital in lateral view. Head shape curve in dorsal view. Snout rounded anteriorly and slightly pointed in dorsal view, longest than deep. Distance between posterior nares longer than that between anterior nares. Mouth wide, subterminal, gape larger than interorbital distance; snout projecting slightly beyond lower jaw. Gape transverse, with fleshy rictal fold at corners. Rictal fold large. Both upper and lower lips with several longitudinal plicae.

Barbels flattened in cross section, wide at their bases and tapering towards distal tip. Maxillary barbel longest; length variable surpassing posterior insertion of anal fin; inserted above upper lip and posterolateral to anterior nares. Two pairs of mental barbels. External mental barbels surpassing origin of pectoral fin. Inner mental barbels aligned to and shorter than external mental barbels, surpassing origin of pectoral fin. Gular fold distinct and V-shaped. Branchiostegal rays 7. Gill rakers thick and moderately long, with: 6 rakers on first ceratobranchial. Eye large, slightly elliptical (greatest length in longitudinal axis), with rim circumscribed with deep, continuous invagination, distinctly more pronounced at lateral border. Eye positioned dorsolaterally, centered approximately in middle distance between tip of snout and corner of opercular membrane, and widely separated by large interorbital space. Pupil rounded. Sensory channels of head simple.

Dorsal fin with 2 unbranched rays and 6 branched rays, distal margin convex and base length less to fin height. First unbranched dorsa-fin ray small and not externally visible, second unbranched dorsal fin ray stiffened in proximal portion and segmented in distal portion. Dorsal-fin origin in middle distance between pectoral and pelvic fin origins; insertion of last branched ray after pelvic fin origin. Tip of last branched dorsal-fin ray trespassing anterior insertion of adipose fin. Adipose fin long; within ascendant curve in lateral profile and posterior lobe conspicuously free from body. Adipose-fin origin at vertical through after posterior insertion pelvic fin, and posterior insertion at middle of caudal peduncle.

Pectoral fin triangular in ventral view, within one unbranched and 8 branched rays; when adpressed reaching approximately origin of second branched ray of dorsal fin. Unbranched ray of pectoral fin stiffened, slightly curved and with delicate serrations in two distal third of anterior side and delicate serration in al posterior side. Pelvic fin rounded, approximately same size of pectoral fin, within one unbranched ray and 5 branched rays, surpassing genital papilla, never reaching anal-fin origin. Pelvic-fin origin before at body midlength, before insertion of last dorsal-fin ray. Anal fin rounded, with 2-3 unbranched rays anteriorly, followed by 7-8 branched rays, when adpressed never reach posterior insertion of adipose fin. Anal-fin base length shorter to dorsal-fin base length. Caudal fin deeply forked, ventral lobe rounded; dorsal lobe pointed, smaller in height and length; 7 branched rays in dorsal lobe and 9 branched rays in ventral lobe.

Color pattern of preserved specimens - Body gray or brown with or without very small dark irregular spots. Head and fins gray or brown without spots. Ventral portion of body and head white. Maxillary barbels and mental barbels same color as body. Adipose fin is the same patterns of the body.

Distribution and Habitat - Occurs in the rio Essequibo and rio Demerara drainages in Guyana. In also found in small drainages of Suriname (Fig. 10).

Table 3: Morphometric data of the *R. sebae.*

	Rhamdia sebae **(n= 37)**	
	min-max	Mean±SD
Standard length (mm)	97,23-175,15	130,05
Percent of Standard Length		
Maxillary-barbel length	71.4-93.4	83.7±6.19
Pectoral-girdle width	16.2-20.4	18.2±1.29
Pelvic-girdle width	8.2-10.2	9.4±0.54
Body depth	14.2-17.9	16.0±1.13
Pre-dorsal distance	30.5-34.7	33.0±1.12
Dorsal-fin to caudal-fin distance	50.3-56.4	53.5±1.72
Dorsal-fin to adipose-fin distance	1.8-7.0	4.1±1.76
Pre-pectoral distance	19.8-24.7	21.4±1.48
Pre-pelvic distance	44.0-48.0	46.5±1.20
Pre-anal distance	64.4-70.5	66.9±1.89
Pelvic-fin to anal-fin distance	22.1-28.8	25.6±2.56
Adipose-fin to caudal-fin distance	198-22.7	21.3±0.86
Caudal-peduncle length	8.1-10.4	9.1±0.65
Caudal-peduncle depth	8.9-11.2	10.0±0.75
Pelvic-fin length	13.1-16.4	14.2±1.03
Anal-fin base length	11.2-14.6	12.8±1.08
Anal-fin length	19.4-22.8	21.1±1.17
Dorsal-fin base length	14.1-17.8	15.5±1.34
Dorsal-fin height	15.6-19.3	17.1±1.08
Dorsal-fin spine length	6.7-10.6	9.0±1.16
Pectoral-fin spine length	12.1-14.5	13.0±0.76
Adipose-fin base length	40.2.1-46.6	43.0±2.09

Head length	20.2-23.7	22.1±1.07
Percent of Head Length		
Snout length	38.2-44.9	41.3±2.38
Snout height	36.9-41.5	39.8±1.66
Head height	55.3-62.0	58.8±2.40
Orbital diameter	16.1-19.6	17.7±1.03
Interorbital distance	27.5-33.0	29.8±1.73
Mouth length	42.7-50.2	47.2±2.41
Maxillary-barbels distance	36.1-40.8	38.5±1.24
Anterior nares distance	20.9-25.1	23.0±1.46
Anterior nares to posterior nares distance	13.7-17.3	15.7±1.21
Posterior nares to orbit distance	18.3-20.0	19.2±0.59
Posterior nares distance	15.3-19.2	17.2±1.10
External mental-barbels distance	349-41.3	38.0±1.70
Internal mental-barbels distance	15.7-19.1	17.4±1.11
Distance between mental-barbel	7.7-11.6	9.5±1.19
External mental-barbel length	123.1-172.3	146.3±15.08
Internal mental-barbel length	66.9-95.9	84.9±8.38
Head width at eye level	70.9-75.5	73.1±1.64

Rhamdia lehmanni Dahl 1961

(Figs 8, 9)

Rhamdia lehmanni Dahl, 1961:487 [Type-locality: Brook tributary to Río Guayabero, Colombia].

Paratype: ICNMHN 358, brook tributary to rio Guayabero, Colombia.

Examined Material: From Venezuela: ANSP 177978, 1, 125.2 mm SL, Venezuela, state of Amazonas, municipality of Morganito, rio Sipapo basin of rio Orinoco; 05°03'60"N, 67°45'60"W; B. Chernoff, W. Saul, R. Royero, O. Brull. ANSP 165308, 1, 112.3 mm SL, Venezuela, state of Apure, municipality of El Yagua, rio Arauca, basin of Orinoco; 07°30'00"N, 68°19'60"W; S. Schaefer, W.G. Saul, F. Provenzano & O. Castillo. ANSP 139529, 1, 165.6 mm SL,Venezuela, state of Bolivar, municipality of Barranca, stream of Cuchivero, tributary of rio Mato, basin of rio Orinoco; 07°00'00"N, 65°15'00"W; J. E. Bohlke. ANSP 141578, 5, 112.6-84.2 mm SL, Venezuela, state of Bolivar, municipality of Las Trincheras, Isolated lagoon, rio Caura, basin of Orinoco; 06°57'00"N, 64°49'60"W; J.E. Bohlke, W.G. Saul. ANSP 166827, 1, 157.7 mm SL, Venezuela, state of Anzoategui, municipality of Soledad, Tineo lagoon, basin of rio Orinoco; 08°11'25"N, 63°28'20"W; M. Rodriguez, S. Richardson, 16 May 1987. ANSP 139499, 1, 213.4 mm SL, Venezuela, state of Bolivar, municipality of Bejuquero, stream of Chuapo, tributary of rio Caura, basin of Orinoco; 07°07'00"N, 65°00'00"W; J.E. Bohlke, W.G. Saul & E. Ferrer-Veliz. ANSP 160239, 5, 86.7-61.85 mm SL, Venezuela, state of Bolivar, municipality of Puerto Ayacucho, Rio Parguaza, basin of Orinoco; 05°35'12"N, 67°39'08"W, B. Chernoff, W. Saul, C. Marrero, R. Royero. ANSP 139856, 1, 116.9 mm SL,Venezuela, state of Bolivar, municipality of Maripa, rio Mato, basin of Orinoco; 07°08'00"N, 65°10'00"W; J.E. Bohlke, W. Saul, L. Ferrer-Veliz. ANSP 137554, 1, 116.5 mm SL, Venezuela, state of Guarico, municipality of San Juan de los Morros, rio Paya, basin of rio Orinoco; 08°37'60"N, 67°19'60"W; N. R. Foster. ANSP 198574, 1, 139.1 mm SL, Venezuela, state of Monagas, municipality of Barrancas, stream of Guargua, basin of rio Orinocooleta; 08°39'48"N, 62°13'60"W; J.N. Baskin, H. Lopez, D.

Stewart, L. Aguana. From Colombia: ANSP 177977, 1, 171.1 mm SL, Colombia, departament of Meta, municipality of El Tigre, stream of Angosturas, basin of rio Meta; 03°58'00"N, 73°03'60"W; J.E. Bohlke, N. Foster, J. Thomerson. ANSP 137555, 1, 111.6 mm SL, Colombia, departament of Meta, municipality of Villavicencio, rio Negro, tributary of rio Meta, basin of Orinoco; 04°08'14"N, 73°18'46"W; J. Bohlke, N. Foster, D. Smith. NRM 16100, 3, Colombia, department of Meta, municipality of Apiay, stream Union, tributary of rio Meta, basin of Orinoco A. Silfvergrip, 6 Jan 1988. NRM 16000, 1, 152.2 mm SL, Colombia, department of Meta, municipality of Apiay, stream of Quenane, rio Negro, tributary of rio Meta, basin of Orinoco basin; 04°00'33"N, 73°30'34"W; A. Silfvergrip, 13 Jan 1988. NRM 16092, 4, xx mm SL, Colombia, department of Meta, municipality of Villavicencio, rio Ocoa, tributary of Río Meta, basin of rio Orinoco; 04°04'33"N, 73°22'31"W; A. Silfvergrip, 04 Jan 1988. NRM 16094, 1, xxx mm SL, Colombia, department of Meta, municipality of Rincón de Pompeya, rio Negro, tributary of rio Meta, basin of rio Orinoco; 04°02'02"N, 73°22'20"W; A. Silfvergrip, 21 Dec 1987. NRM 16099, Colombia, department of Meta, municipality of La Balsa, Río Negro, tributary of rio Meta, basin of Orinoco; 04°09'36"N, 73°28'16"W; A. Silfvergrip, 11 Jan 1988.

Diagnosis -*Rhamdia lehmanni* differs from *R. quelen*, *R. sapo*, *R. cuyabae*, *R. hillarii*, *R. pentlandii*, *R. parahybae*, *R. laukidi*, *R. cinerascens*, *R. saijaensis*, *R. jequitinhonha*, *R. xequetepeque*, *R. gabrielae* and *R. eurichephala* by pointed superior lobe of caudal fin (*vs.* rounded superior lobe of caudal fin). Differs from *R. foina*, *R poeyi* and *R. itacaiunas* by superior lobe of caudal fin smaller than inferior lobe (*vs.* superior lobe of caudal fin larger than inferior lobe). Differs from *R. laticauda*, *R. humilis*, *R. nicaraguensis* by serrae in both sides of pectoral fin spine (*vs.* serrae in one side of pectoral fin spine). Differs from *R. dorsalis* and *R. sebae* by longer adipose fin base length (40.2.1-46.6% SL *vs*. 31.6-38.3% SL in *R. dorsalis* and 36.0-39.8% SL in *R. sebae*). Differs from *R. reddelli*, *R. enfurnada*, *R. zongolicensis*, *R. guasarensis*, *R. macuspanensis* and *R. laluchensis* by the lack of morphological adaptations to troglobitic life.

Description - Measurements in Table 4. Body elongated; cross section of trunk roughly circular at dorsal-fin origin and along dorsal-fin base, gradually compressed posteriorly through caudal peduncle. Anterodorsal profile of body convex from supraoccipital to dorsal-fin base. Dorsal-fin base nearly straight, posteroventrally slanted, and gently convex from dorsal fin to base of adipose fin. Ventral body profile slightly curved from mouth to caudal-fin base. Body widest at pectoral girdle and deepest at dorsal-fin origin. Caudal peduncle longer than deep.

Head depressed. Dorsal head profile slightly rounded and posterodorsally slanted from snout tip to supraoccipital in lateral view. Head shape slightly rounded in dorsal view. Snout rounded anteriorly in dorsal view, longest than deep. Distance between posterior nares longer than that between anterior nares. Mouth wide, subterminal, gape larger than interorbital distance; snout projecting slightly beyond lower jaw. Gape transverse, with fleshy rictal fold at corners. Rictal fold large. Both upper and lower lips with several longitudinal plicae.

Barbels flattened in cross section, wide at their bases and tapering towards distal tip. Maxillary barbel longest; length variable surpassing insertion of anal fin; inserted above upper lip and posterolateral to anterior nares. Two pairs of long mental barbels. External mental barbels reaching point of pectoral fin. Inner mental barbels aligned to and shorter than external mental barbels, surpassing origin of pectoral fin. Gular fold distinct and V-shaped. Branchiostegal rays 6-7. Gill rakers thick and moderately long, with: 6 rakers on first ceratobranchial. Eye large, slightly elliptical (greatest length in longitudinal axis), with rim circumscribed with deep, continuous invagination, distinctly more pronounced at lateral border. Eye positioned dorsolaterally, centered approximately in middle distance between tip of snout and corner of opercular membrane, and widely separated by large interorbital space. Pupil rounded. Sensory channels of head simple.

Dorsal fin with 2 unbranched rays and 6 branched rays, distal margin convex and base length less to fin height. First unbranched dorsa-fin ray small and not externally visible, second unbranched dorsal fin ray stiffened in proximal portion and segmented in distal portion. Dorsal-fin origin anterior to middle distance between pectoral and pelvic fin origins; insertion of last branched ray after pelvic fin origin. Tip of last branched dorsal-fin ray trespassing anterior insertion of adipose fin. Adipose fin long; within ascendant curve in lateral profile and posterior lobe conspicuously free from body. Adipose-fin origin at vertical through after posterior insertion pelvic fin, and posterior insertion at approximately middle of caudal peduncle.

Pectoral fin triangular, within one unbranched and 8 branched rays; when adpressed reaching approximately origin of first branched ray of dorsal fin. Unbranched ray of pectoral fin stiffened, slightly curved and with strongh serrations in distal two third of anterior side and delicate serration in proximal two third of posterior side. Pelvic fin rounded, approximately same size of pectoral fin, within one unbranched ray and 5 branched rays, surpassing genital papilla, never reaching anal-fin origin. Pelvic-fin origin nearly at body midlength, before insertion of last dorsal-fin ray. Anal fin rounded, with 3 unbranched rays anteriorly, followed by 7 branched rays, when adpressed never reach posterior insertion of adipose fin. Anal-fin base length shorter to dorsal-fin base length. Caudal fin deeply forked, ventral lobe rounded; dorsal lobe pointed smaller in height and length; 7 branched rays in dorsal lobe and 8-9 branched rays in ventral lobe.

Color pattern of preserved specimens - Body gray or brown with or without very small dark irregular spots. Head and fins gray or brown without spots. Ventral portion of body and head white. Maxillary barbels and mental barbels same color as body. Adipose fin is the same patterns of the body.

Distribution and Habitat - Occurs in the Orinoco drainage (Fig. 10)

Table 4: Morphometric data of the *R. lehmanii*.

Rhamdia lehmanii **(n=30)**		
	min-max	Mean±SD
Standard length (mm)		
Percent of Standard Length		
Maxillary-barbel length	73.4-92.6	80.3±7.39
Pectoral-girdle width	17.1-20.2	19.3±1.31
Pelvic-girdle width	9.0-11.8	10.8±1.02
Body depth	14.0-19.6	16.9±2.12
Pre-dorsal distance	31.8-35.9	33.5±1.57
Dorsal-fin to caudal-fin distance	49.4-53.7	51.1±1.59

Dorsal-fin to adipose-fin distance	2.6-4.9	3.4±0.58
Pre-pectoral distance	21.7-27.8	24.0±2.21
Pre-pelvic distance	45.0-49.4	47.2±1.79
Pre-anal distance	67.3-72.1	70.5±1.69
Pelvic-fin to anal-fin distance	22.9-26.9	24.4±1.03
Adipose-fin to caudal-fin distance	8.0-10.1	9.1±0.80
Caudal-peduncle length	17.1-20.9	19.7±1.41
Caudal-peduncle depth	8.7-11.1	10.1±0.55
Pelvic-fin length	11.6-16.7	13.7±1.04
Anal-fin base length	10.9-13.6	11.8±0.48
Anal-fin length	19.7-22.8	20.8±1.06
Dorsal-fin base length	13.2-18.0	15.6±1.42
Dorsal-fin height	15.5-20.3	17.1±1.73
Dorsal-fin spine length	9.6-12.0	10.7±0.94
Pectoral-fin spine length	11.0-15.3	13.6±1.49
Adipose-fin base length	36.0-40.9	39.2±1.44
Head length	21.4-26.5	23.6±2.06
Percent of Head Length		
Snout length	37.3-41.4	39.6±1.34
Snout height	33.2-37.9	36.3±1.90
Head height	58.0-65.9	62.1±3.38
Orbital diameter	14.9-18.2	16.9±1.09
Interorbital distance	32.0-36.4	33.9±1.61
Mouth length	46.9-53.4	49.5±2.16
Maxillary-barbels distance	37.6-39.9	38.7±0.76
Anterior nares distance	20.9-23.7	22.1±0.98
Anterior nares to posterior nares distance	13.4-16.4	14.8±1.09
Posterior nares to orbit distance	19.0-23.0	20.6±1.44
Posterior nares distance	15.9-17.9	16.8±0.80
External mental-barbels distance	37.0-42.0	40.4±1.85

Internal mental-barbels distance	16.4-19.6	17.6±1.32
Distance between mental-barbel	8.4-11.5	10.1±1.25
External mental-barbel length	118.2-151.5	138.0±11.86
Internal mental-barbel length	68.7-97.8	82.2±10.15
Head width at eye level	71.6-77.1	74.8±2.01

***Rhamdia cuyabae* (Steindachner, 1887)**

(Figs. 11, 12)

Pimelodus (Rhamdia) cuyabae Steindachner, 1877:633 [Cuyaba (Cuiabá), Brazil].

Holotype - NMW 45919:1, Cuiabá, Brazil.

Examined material - From Paraguay: NRM 39585, 1, mm SL, Paraguay, department of Concepción, municipality of Concepción, La Paz stream, basin of rio Paraguay; 23°37'00"S, 57°23'45"W; G. Frisk, 6 Nov 1996. NRM 33189, 1, mm SL, Paraguay, department of Paraguarí, municipality of , Minas stream, basin of rio Paraguay; 26°04'45"S, 56°51'00"W; B. Delling, 12 Oct 1995. NRM 15874, 2, mm SL, Paraguay, department of Presidente Hayes, municipality of Estancia Santa Maria, swamp area, basin of rio Paraguay; 23°02'00"S, 59°12'00"W; S. Kullander, 1 Feb 1992. NRM 16780, 2, mm SL, Paraguay, department of Presidente Hayes, municipality of Puerto Yabapobo, rio Siete Puntas, basin of rio Paraguay; 23°36'11"S, 57°26'36"W; C. Olrog. NRM 22888, 6, mm SL, Paraguay, department of Paraguarí, municipality of Ybycuí, Minas stream, basin of rio Paraguay; 26°05'38"S, 56°50'15"W; B. Delling, 11 Oct 1995. NRM 25893, 1, mm SL, Paraguay, department of Presidente Hayes, municipality of Los Pastos, rio Pilcomayo, basin of rio Paraguay; 24°44'33"S, 58°44'33"W; S. Kullander, 30 May 1994. NRM 32904, 2, mm SL, Paraguay, department of Ñeembucú, municipality of Humaitá, swamp area, basin of rio Paraguay; 27°08'40"S, 58°32'20"W; E. Åhlander, 13 Sep 1995. NRM 31454, 4, mm SL, Paraguay, department of Presidente Hayes, swamp area, basin of rio Paraguay; 24°48'33"S, 57°46'56"W; S. Kullander, 16 Oct 1994. NRM 15473, 1, mm SL, Paraguay, department of Presidente Hayes, municipality of Purto Yabapobo, rio Siete Puntas, basin of rio Paraguay; 23°38'56"S, 57°26'07"W; C. Olrog, 5 Dec 1946. NRM 31414, 1, mm SL, Paraguay, department of, municipality of Roque Gonzales, Lago Ypoá, basin of rio Paraguay; 25°56'44"S, 57°27'05"W; S. Kullander, 7 Oct 1994. NRM 27606, 1, mm SL, Paraguay, department of Presidente Hayes, municipality of General Bruguez, rio Pilcomayo, basin of rio Paraguay; 24°43'39"S, 58°49'09"W; S. Kullander, 30 Jun 1994. From Argentine: MLP 3311, 5, 192.2-110.5 mm SL, Argentine, Province de Missiones, municipality os San José; 27°46'05"S, 55°47'52"W; Pindapoy stream, basin of rio Paraná. MLP 8804, 5, 114.1-90.8 mm SL, Argentine, Province of Formosa, municipaltity of Formosa, basin of rio Paraguai; 25°29'26"S, 57°49'32"W. MLP 8875, 1, 141.1 mm SL, Argentine, Province of Formosa, municipality of Col El Gato, swamp in basin of rio Paraguai; 26°11'05"S, 58°56'46"W. MLP 6957, 12, 166.3-148.8 mm SL, Argentine, Province of Santa Fé, municipality of Santa Fé, rio Paraná; 31°25'38"S, 60°30'15"W. MLP 8819, 1, 107.7 mm SL, Argentine, Province of Formosa, municipality of Clorinda, basin of rio Paraguai; 26°26'33"S, 58°24'02"W. MACN 8249, 2, 213.9-78.9 mm SL, Argentine, Province of Corrientes, municipality of Bella Vista; 28°31'12"S 58°58'30"W. MACN 7086, 1, 157.8 mm SL, Argentine, province of Corrientes, municipality of Corrientes, isla Cabral, rio Paraná; 27°35'16"S, 58°50'23"W. From Brazil: UFRGS Brazil, state of Rio Grande do Sul, municipality of Uruguaiana, rio Uruguai, basin of rio da Prata; 29°30'20"S, 56°50'41"W; L. Mabarba, M. Malabarba, K. Bonato, J. Chuktaya and R. Angrizani.

Diagnosis - *Rhamdia cuyabae* differs from fall congeners by snout length shorter of than snout deep (vs. snout length longer of than snout deep in all others *Rhamdia*).

Description - Measurements in Table 5. Body elongated; cross section of trunk roughly circular at dorsal-fin origin and along dorsal-fin base, gradually compressed posteriorly through caudal peduncle. Anterodorsal profile of body convex from supraoccipital to dorsal-fin base. Dorsal-fin base nearly straight, posteroventrally slanted, and gently convex from dorsal fin to base of adipose fin. Ventral body profile slightly curved from mouth to caudal-fin base. Body widest at pectoral girdle and deepest at dorsal-fin origin. Caudal peduncle longer than deep. Number of post-Weberian vertebrae 39.

Head deep. Dorsal head profile rounded and posterodorsally slanted from snout tip to supraoccipital in lateral view. Head shape rounded in dorsal view. Snout rounded anteriorly in dorsal view, shorter than deep. Distance between posterior nares longer than that between anterior nares. Mouth wide, subterminal, gape larger than interorbital distance; snout projecting slightly beyond lower jaw. Gape transverse, with fleshy rictal fold at corners. Rictal fold large. Both upper and lower lips with several longitudinal plicae.

Barbels flattened in cross section, wide at their bases and tapering towards distal tip. Maxillary barbel longest; length variable reaching maximum insertion of anal fin; inserted above upper lip and posterolateral to anterior nares. Two pairs of mental barbels. External mental barbels reaching origin of pectoral fin. Inner mental barbels aligned to and shorter than external mental barbels, surpassing origin of pectoral fin. Gular fold distinct and V-shaped. Branchiostegal rays 5-6. Gill rakers thick and moderately long, with: 6-8 rakers on first ceratobranchial. Eye large, slightly elliptical (greatest length in longitudinal axis), with rim circumscribed with deep, continuous invagination, distinctly more pronounced at lateral border. Eye positioned dorsolaterally, centered approximately in first third between tip of snout and corner of opercular membrane, and widely separated by large interorbital space. Pupil rounded. Sensory channels of head simple.

Dorsal fin with 2 unbranched rays and 6-7 branched rays, distal margin convex and base length more to fin height. First unbranched dorsa-fin ray small and not externally visible, second unbranched dorsal fin ray stiffened in proximal portion and segmented in distal portion. Dorsal-fin origin anterior to middle distance between pectoral and pelvic fin origins; insertion of last branched ray after pelvic fin origin. Tip of last branched dorsal-fin ray trespassing anterior insertion of adipose fin. Adipose fin long; within ascendant curve in lateral profile and posterior lobe conspicuously free from body. Adipose-fin origin at vertical through after posterior insertion pelvic fin, and posterior insertion at middle of caudal peduncle.

Pectoral fin within one unbranched and 7-10 branched rays; when adpressed reaching approximately origin of first branched ray of dorsal fin. Unbranched ray of pectoral fin stiffened, slightly curved and with strongh serrations in two third of distal anterior side and delicate serration in all posterior side. Pelvic fin rounded, approximately same size of pectoral fin, within one unbranched ray and 5 branched rays, surpassing genital papilla, never reaching anal-fin origin. Pelvic-fin origin nearly at body midlength, before insertion of last dorsal-fin ray. Anal fin rounded, with 2-4 unbranched rays anteriorly, followed by 7-10 branched rays, when adpressed never reach posterior insertion of adipose fin. Anal-fin base length shorter to dorsal-fin base length. Caudal fin deeply forked, lobes rounded; dorsal lobe smaller in height and length; 6-8 branched rays in dorsal lobe and 7-10 branched rays in ventral lobe.

Color pattern of preserved specimens - Body gray or brown with or without very small dark irregular spots. Head and fins gray or brown without spots. Ventral portion of body and head white. Maxillary barbels and mental barbels same color as body. Adipose fin is the same patterns of the body.

Distribution and Habitat - Occurs in the rio da Prata system, in Brazil, Argentina and Paraguay (Fig. 13).

Table 5: Morphometric data of the *R. cuyabae.*

	Rhamdiacuyabae **(n=56)**		
	min-max	Mean±SD	Type
Standard length (mm)	90.8-342.1	166.9	342.1
Percent of Standard Length			
Maxillary-barbel length	44.4-83.7	67.71±1.69	-
Pectoral-girdle width	20.4-23.7	21.7±1.04	20.5
Pelvic-girdle width	10.0-12.3	10.9±0.72	11.3
Body depth	18.1-22.4	20.3±1.36	18.7
Pre-dorsal distance	32.2-37.1	34.8±1.62	32.2
Dorsal-fin to caudal-fin distance	49.5-56.0	51.4±1.48	55.9
Dorsal-fin to adipose-fin distance	1.9-5.8	3.5±1.32	5.8
Pre-pectoral distance	23.1-26.5	24.8±0.91	23.8
Pre-pelvic distance	48.6-53.4	50.7±1.55	46.6
Pre-anal distance	66.2-70.3	68.9±1.14	70.3

Pelvic-fin to anal-fin distance	18.5-23.6	20.3±1.51	23.6
Adipose-fin to caudal-fin distance	8.7-11.3	10.3±0.95	8.7
Caudal-peduncle length	17.7-22.0	19.8±1.17	18.8
Caudal-peduncle depth	11.5-13.7	12.4±0.71	11.5
Pelvic-fin length	13.2-16.6	14.4±1.01	13.2
Anal-fin base length	11.8-14.4	12.9±0.91	11.8
Anal-fin length	20.1-23.9	22.0±1.19	20.1
Dorsal-fin base length	14.6-17.5	16.4±0.97	16.7
Dorsal-fin height	14.5-18.1	16.2±1.22	-
Dorsal-fin spine length	9.7-12.0	10.6±0.69	10.1
Pectoral-fin spine length	12.3-14.9	13.7±0.76	12.9
Adipose-fin base length	37.4-42.3	39.3±1.48	41.2
Head length	23.8-26.9	25.5±0.90	23.8
Percent of Head Length			
Snout length	34.5-43.3	37.4±2.04	43.2
Snout height	39.9-49.0	44.6±2.47	49.0
Head height	65.3-74.0	69.3±3.35	65.7
Orbital diameter	13.4-17.2	15.4±1.12	14.5
Interorbital distance	33.2-42.5	37.9±3.22	33.2
Mouth length	42.2-54.7	49.5±3.42	42.2
Maxillary-barbels distance	34.7-40.8	37.9±1.79	38.4
Anterior nares distance	20.9-26.5	23.5±1.66	20.9
Anterior nares to posterior nares distance	12.3-15.9	14.2±0.93	14.3
Posterior nares to orbit distance	14.9-20.9	17.9±1.98	19.3
Posterior nares distance	16.9-23.1	19.7±2.14	23.1
External mental-barbels distance	38.3-43.4	40.5±1.64	42.3
Internal mental-barbels distance	15.5-19.7	17.7±1.27	19.7
Distance between mental-barbel	9.3-13.0	11.2±1.07	10.2
External mental-barbel length	116.3-166.8	141.5±14.57	116.3
Internal mental-barbel length	43.6-100.5	82.0±18.18	64.1
Head width at eye level	64.3-75.5	72.4±3.52	74.1

Rhamdia hilarii (Valenciennes 1840)

(Figs. 14, 15)

Pimelodus hilarii Valenciennes, 1840 [in Cuvier & Valenciennes 1840:180; type locality: Rio São Francisco, Brazil].
Pimelodus wuchereri Günther, 1864:123 [type locality: Bahia, Brazil].

Lectotype:MNHN A-9415, Brazil, state of Minas Gerais, rio São Francisco.

Examined material: All from Brazil: LBP 11831, 1, 130.0 mm SL, Brazil, state of Minas Gerais, municipality of São Roque de Minas, Maria da Prata stream, basin of rio São Francisco; 20°15'50"S, 46°20'57"W; M. Mehanna and J. Senhorini, 17 May 2011. LBP 16317, 1, 99.4 mm SL, Brazil, state of Minas Gerais, municipality of Moeda, stream in basin of rio São Francisco; 20°18'25"S, 43°59'38"W; M. Mehanna, A. Ferreira, R. Devidé and R. Ramirez, 13 Jun 2012. LBP 6515, 1, 112.7 mm SL, Brazil, state of Minas Gerais, municipality of Santana do Riacho, rio Cipó, basin of rio São Francisco; 19°20'22"S, 43°38'16"W; R. Teixeira, G. Silva, A. Ferreira and J. Henriques, 18 Jun 2008. LBP 8965, 2, 113.1-90.2 mm SL, Brasil, state of Minas Gerais, municipality of Curvelo, Amendoim stream, tributary of Rio das Velhas, basin of rio São Francisco; 18°43'14'S, 44°20'47"W; C. Oliveira, F. Roxo, G. Silva and B. Melo, 01 Oct 2009. LBP 6507, 1, Brazil, state of Minas Gerais, municipality of Santana do Riacho, rio Cipó, basin of rio São Francisco; 19°20'22"S, 43°38'16"W; R. Teixeira, G. Silva, A. Ferreira and J. Henriques, 18 Jun 2008. LBP 8951, 2, Brazil, state of Minas Gerais, municipality of Curvelo, Amendoim stream, tributary of rio das Velhas, basin of rio São Francisco; 18°43'14'S, 44°20'47"W; C. Oliveira, F. Roxo, G. Silva and B. Melo, 01 Oct 2009. LBP 17406, 3, Brazil, state of Minas Gerais, municipality of Pedro Leopoldo, stream in basin of rio São Francisco; 19°33'44"S, 43°57'56"W; R. Devide, G. Silva and V. Sene, 22 Feb 2013. LBP 16305, 1, Brazil, state of Minas Gerais, municipality of Brumadinho, stream in basin of rio São Francisco; 20°11'40"S, 44°06'05"W; M. Mehanna, A. Ferreira, R. Devidé and R. Ramirez, 12 Jun 2012. BMNH 1864.1.19.18, 1, 147.5 mm SL, Lectotype of *Rhamdia wuchereri,* Bahia, Brazil.

Diagnosis - *Rhamdia hilarii* differs from *R. sapo*, *R. cuyabae*, *R. sebae,R. dorsalis*, *R. lehmanii R. cuyabae, R. laukidi, R. muelleri* and *R. guatemalensis* by last unbrached ray of dorsal fin not reaching anterior insertion of adipose fin (vs. last unbrached ray trespassing anterior insertion of adipose fin). Differs from *R. foina*, *R poeyi, R. itacaiunas, R. parryi* and *R. xequetepeque* by superior lobe of caudal fin smaller than inferior lobe (*vs*. superior lobe of caudal fin larger than inferior lobe). Differs from *R. laticauda*, *R. humilis*, *R. nicaraguensis* by serrae in both sides of pectoral fin spine (*vs*. serrae in one side of pectoral fin spine). Differs from *R. quelen*, *R. parahybae,R. gabrielae*, *R. eurichephala* by sensory channels multiple (vs. sensory channels simple). Differs from *R. cinerascens* and *R. saijaensis* by insertion of adipose fin not equidistant between the dorsal and caudal fins (*vs*. insertion of the adipose fin equidistant between the dorsal and caudal fins).Differs from *R. jequitinhonha*, by longer maxillary barbel (45.1-64.4% SL *vs*. 39.2% SL). Differes from *R. reddelli*, *R. enfurnada*, *R. zongolicensis*, *R. macuspanensis* and *R. laluchensis* by the lack of morphological adaptations to troglobitic life.

Description - Measurements in Table 6. Body elongated; cross section of trunk roughly circular at dorsal-fin origin and along dorsal-fin base, gradually compressed posteriorly through caudal peduncle. Anterodorsal profile of body convex from supraoccipital to dorsal-fin base. Dorsal-fin base nearly straight, posteroventrally slanted, and gently convex from dorsal fin to base of adipose fin. Ventral body profile slightly curved from mouth to caudal-fin base. Body widest at pectoral girdle and deepest at dorsal-fin origin. Caudal peduncle longer than deep.

Dorsal head profile rounded and posterodorsally slanted from snout tip to supraoccipital in lateral view. Head shape rounded in dorsal view. Snout rounded anteriorly in dorsal view, longer than deep. Distance between posterior nares longer than that between anterior nares. Mouth wide, subterminal, gape larger than interorbital distance; snout projecting slightly beyond lower jaw. Gape transverse, with fleshy rictal fold at corners. Rictal fold large. Both upper and lower lips with several longitudinal plicae.

Barbels flattened in cross section, wide at their bases and tapering towards distal tip. Maxillary barbel longest; length variable reaching maximum insertion of pelvic fin; inserted above upper lip and posterolateral to anterior nares. Two pairs of mental barbels. External mental barbels surpassing origin of pectoral fin. Inner mental barbels aligned to and shorter than external mental barbels, reaching origin of pectoral fin. Gular fold distinct and V-shaped. Branchiostegal rays 5-6. Gill rakers thick and moderately long, with: 6-8 rakers on first ceratobranchial. Eye large, slightly elliptical (greatest length in longitudinal axis), with rim circumscribed with deep, continuous invagination, distinctly more pronounced at lateral border. Eye positioned dorsolaterally, centered approximately in first third between tip of snout and corner of opercular membrane, and widely separated by large interorbital space. Pupil rounded. Sensory channels of head multiple.

Dorsal fin with 2 unbranched rays and 7-8 branched rays, distal margin convex and base length more to fin height. First unbranched dorsa-fin ray small and not externally visible, second unbranched dorsal fin ray stiffened in proximal portion and segmented in distal portion. Dorsal-fin origin anterior to middle distance between pectoral and pelvic fin origins; insertion of last branched ray before pelvic fin origin. Tip of last branched dorsal-fin ray not reaching anterior insertion of adipose fin. Adipose fin long; within ascendant curve in lateral profile and posterior lobe conspicuously free from body. Adipose-fin origin at vertical through after posterior insertion pelvic fin, and posterior insertion at last third of caudal peduncle.

Pectoral fin within one unbranched and 7-8 branched rays; when adpressed reaching approximately origin of first branched ray of dorsal fin. Unbranched ray of pectoral fin stiffened, slightly curved and with strong serrations in half of distal anterior side and delicate serration in proximal posterior side. Pelvic fin rounded, approximately same size of pectoral fin, within one unbranched ray and 5 branched rays, surpassing genital papilla, never reaching anal-fin origin. Pelvic-fin origin nearly at body midlength, after insertion of last dorsal-fin ray. Anal fin rounded, with 2 unbranched rays anteriorly, followed by 7 branched rays, when adpressed never reach posterior insertion of adipose fin. Anal-fin base length shorter to dorsal-fin base length and approximately the same size as pelvic fin length. Caudal fin deeply forked, lobes rounded; dorsal lobe smaller in height and length; 7 branched rays in dorsal lobe and 8-9 branched rays in ventral lobe.

Color pattern of preserved specimens - Body brown or gray with or without very small dark brown irregular spots. With or without difuse humeral spot. Head and fins brown or gray without spots. Ventral portion of body and head white. Maxillary barbels same color as body.

Distribution and Habitat -Occurs in the rio São Francisco drainage, northeastern of Brazil (Fig. 16).

Table 6: Morphometric data of the *R. hilarii.*

Rhamdiahilarii

(N=11)

	min-max	Mean±SD	Holotype
Standard length (mm)	99.4-262.4	156.8	192.8
Percent of Standard Length			
Maxillary-barbel length	45.1-64.4	56.3±7.09	45.1
Pectoral-girdle width	16.7-20.0	18.5±1.34	19.9
Pelvic-girdle width	7.6-9.4	8.5±0.59	8.5
Body depth	14.4-17.5	16.3±1.04	16.9
Pre-dorsal distance	32.2-37.5	34.9±1.66	37.5
Dorsal-fin to caudal-fin distance	45.0-51.7	49.2±2.16	45.0
Dorsal-fin to adipose-fin distance	5.4-12.0	7.9±2.25	9.2
Pre-pectoral distance	21.5-26.8	24.4±1.70	26.7
Pre-pelvic distance	46.4-59.3	49.8±4.31	59.2
Pre-anal distance	65.3-74.9	70.1±3.04	74.9
Pelvic-fin to anal-fin distance	17.4-45.8	25.1±9.41	20.4
Adipose-fin to caudal-fin distance	7.4-11.7	9.3±1.41	7.8
Caudal-peduncle length	16.8-20.4	19.2±1.31	18.0
Caudal-peduncle depth	8.7-10.9	9.5±0.74	10.8
Pelvic-fin length	10.3-13.2	12.2±1.14	12.0
Anal-fin base length	10.1-13.1	12.0±0.99	13.0
Anal-fin length	16.6-20.5	18.9±1.64	16.6
Dorsal-fin base length	15.7-18.8	16.9±1.35	18.8
Dorsal-fin height	14.0-15.4	14.7±0.61	-
Dorsal-fin spine length	7.4-8.7	8.1±0.54	-

Pectoral-fin spine length	9.4-11.3	10.3±0.73	9.5
Adipose-fin base length	29.7-38.7	33.8±3.19	31.4
Head length	23,8-24,9	24.4±0.45	24.8
Percent of Head Length			
Snout length	38.5-44.4	40.6±2.14	42.3
Snout height	35.4-44.2	39.7±3.68	44.2
Head height	52.7-67.4	59.6±5.79	60.2
Orbital diameter	12.1-17.5	15.1±1.98	14.8
Interorbital distance	25.6-30.6	27.7±2.49	30.1
Mouth length	36.2-44.0	40.6±2.32	41.2
Maxillary-barbels distance	32.1-39.7	37.3±2.30	34.7
Anterior nares distance	19.1-24.1	21.9±1.34	20.7
Anterior nares to posterior nares distance	14.4-24.1	20.4±3.03	15.6
Posterior nares to orbit distance	13.7-18.6	16.3±1.81	17.9
Posterior nares distance	38.8-45.8	17.7±1.28	17.1
External mental-barbels distance	32.7-36.5	35.0±1.19	35.5
Internal mental-barbels distance	14.7-21.4	18.1±3.00	19.6
Distance between mental-barbel	6.5-10.5	9.4±1.30	7.0
External mental-barbel length	93.2-103.1	97.6±4.74	-
Internal mental-barbel length	57.5-69.2	62.2±5.45	-
Head width at eye level	54.4-62.3	57.7±3.18	55.7

Rhamdia parahybae Steindachner, 1876

(Figs. 17, 18)

Pimelodus (Rhamdia) parahybae Steindachner, 1877:615 [Rio Parahyba, southeastern Brazil].
Pimelodus queleni cuprea Steindachner 1877:623 [type locality: Rio Parahyba at Juiz de Fora. Brazil].

Lectotype -NMW 45852, rio Paraíba do Sul, southeastern Brazil.

Examined material – All grom Brazil: MNRJ 43769, 2, 140.1-86.7 mm SL, Brazil, state of Rio de Janeiro, municipality of Rio Claro, Passa Quatro river, tributary of rio Piraí. Basin of rio Paraiba do Sul; 22°49’04”S, 44°11’12”W; P. Buckup, D. Moraes Jr. and V. de Brito, 02 Jul 2015. MNRJ 25961, 2, 155.4- 55.4 mm SL, Brazil, state of Rio de Janeiro, municipality of Quatis, stream tributary of rio Paraíba do Sul; 22°24’59”S, 44°16’31”W; P. Buckup, J. Gomes and A. Aranda, 27 Oct 2003. MNRJ 46794, 5, 125.0-112.4 mm SL, Brazil, state of Rio de Janeiro, municipality of Rio Claro, rio Piraí, basin of rio Paraíba do Sul; 22°51’17”S, 44°11’55”W; E. Neuhaus 14 Apr 2016. MNRJ 46660, 4, 128.2-63.0 mm SL, Brazil, state of Rio de Janeiro, municipality of Rio Claro; 22°52’42”S, 44°13’37”W; P. Buckup, D. Moraes, V. Brito, E. Neuhaus and I. Santos, 12Apr 2016. MNRJ 17899, 2, 265.5-235.4 mm SL, Brazil, state of Rio de Janeiro, municipality of Resende; 22°31'24.75"S, 44°33'3.21"W; Dam of Funil, rio Paraíba do Sul, W. Bandeira, 10 Jun 1982. MNRJ 12366, 2, 161.9-79.9 mm SL, Brazil, state of Rio de Janeiro, municipality of Rio Claro; Passa Vinte stream, basin of rio Paraíba do Sul; 22°47’30”S, 44°03’00”W; D. Moraes Jr., J. Gomes and M. Menezes, 07 Jul 1991. MNRJ 12385, 6, 192.2-124.5 mm SL, Brazil, state of Minas Gerais, municipality of Além Paraíba, rio Paraíba do Sul; 21°53'04"S, 42°41'42"W; M. Moraes Jr. And D. Halboth, 22 Sep 1989. MNRJ 12370, 2, mm SL, Brazil, state of Rio de Janeiro, municipality of Rio Claro, rio Balsámo, basin of rio Paraíba do Sul; 22°50’30”S, 43°57’30”W; D. Moraes Jr., J. Gomes, M. Menezes, 27 Jun 1991. LBM 6312, 3, 119.1-83.7

mm SL, Brazil, state of São Paulo, municipality of Areias, Rio Santana, basin of rio Paraíba do Sul; 22°38'12.4"S, 44°36"56.4"W; R. Devidé, L. Pereira and G. Silva, 02 Apr 2008. LBM 6294, 2, 211.0-145.4 mm SL, Brazil, state of São Paulo, municipality of Areias, rio Itagaçaba, basin of rio Paraíba do Sul; 22°39'26"S, 44°45'49"W; R. Devidé, L. Pereira and G. Silva, 01 Apr 2008. LBM 1035, 2, 162.4-131.8 mm SL, Brazil, state of São Paulo, municipality of Taubaté, rio Paraíba do Sul; 23º06'07"S, 45º31'03"W. NMW 45789, Lectotype of *Pimelodus queleni cuprea*, 1, mm SL, Brazil, state of Minas Gerais, municipality of Juiz de Fora. NMW 45790, Paralectotype of *Pimelodus queleni cuprea*, 1, mm SL, Brazil, state of Minas Gerais, municipality of Juiz de Fora Rio Parahyba.

Diagnosis – Differs from all congeners by distance between the posterior naris equal distance between the anterior naris (*vs*. distance between posterior naris longer than that between anterior naris for all others *Rhamdia*).

Description - Measurements in Table 7. Body elongated and deep; cross section of trunk roughly circular at dorsal-fin origin and along dorsal-fin base, gradually compressed posteriorly through caudal peduncle. Anterodorsal profile of body convex from supraoccipital to dorsal-fin base. Dorsal-fin base nearly straight, posteroventrally slanted, and gently convex from dorsal fin to base of adipose fin. Ventral body profile slightly curved from mouth to caudal-fin base. Body widest at pectoral girdle and deepest at dorsal-fin origin. Caudal peduncle longer than deep. Number of post-Weberian vertebrae 40.

Head deep. Dorsal head profile straight and posterodorsally slanted from snout tip to supraoccipital in lateral view. Head shape somewhat trapezoidal in dorsal view. Snout slightly rounded anteriorly in dorsal view, so long as deep. Distance between the posterior naris equal distance between the anterior naris. Mouth wide, subterminal, gape larger than interorbital distance; snout projecting slightly beyond lower jaw. Gape transverse, with fleshy rictal fold at corners. Rictal fold large. Both upper and lower lips with several longitudinal plicae.

Barbels flattened in cross section, wide at their bases and tapering towards distal tip. Maxillary barbel longest; length variable reach maximum origin of anal fin; inserted above upper lip and posterolateral to anterior nares. Two pairs of mental barbels. External mental barbels surpassing all insertion of pectoral fin. Inner mental barbels aligned to and shorter than external mental barbels, reach origin of pectoral fin. Gular fold distinct and V-shaped. Branchiostegal rays 5-7. Gill rakers thick and moderately long, with: 8 rakers on first ceratobranchial. Eye large, slightly elliptical (greatest length in longitudinal axis), with rim circumscribed with deep, continuous invagination, distinctly more pronounced at lateral border. Eye positioned dorsolaterally, centered approximately at midpoint between tip of snout and corner of opercular membrane, and widely separated by large interorbital space. Pupil rounded. Sensory channels of head simple.

Dorsal fin with 2 unbranched rays and 6 branched rays, distal margin convex and base length more to fin height. First unbranched dorsal-fin ray small and not externally visible, second unbranched dorsal fin ray stiffened in proximal portion and segmented in distal portion. Dorsal-fin origin anterior to middle distance between pectoral and pelvic fin origins; insertion of last branched ray just at pelvic fin origin. Tip of last branched dorsal-fin ray at most reaching anterior insertion of adipose fin. Adipose fin long; within ascendant curve in in lateral profile and posterior lobe conspicuously free from body. Adipose-fin origin at vertical through right after posterior insertion pelvic fin and posterior insertion at medium of caudal peduncle.

Pectoral fin within one unbranched and 8 branched rays; when adpressed reaching approximately origin of third branched ray of dorsal fin. Unbranched ray of pectoral fin stiffened, slightly curved and with strong serrations in all anterior side and delicate serration in proximal two third of posterior side. Pelvic fin rounded, approximately same size of pectoral fin, within one unbranched ray and 5 branched rays,surpassing genital papilla, never reaching anal-fin origin. Pelvic-fin origin nearly at body midlength, just at insertion of last dorsal-fin ray. Anal fin rounded, with 2-3 unbranched rays anteriorly, followed by 7-8 branched rays, when adpressed never exceeds posterior insertion of adipose fin. Anal-fin base smaller to dorsal-fin base length. Caudal fin deeply forked, lobes rounded; dorsal lobe smaller in height and length; 7 branched rays in dorsal lobe and 8 branched rays in ventral lobe.

Color pattern of preserved specimens - Body brown or gray with or without very small dark brown irregular spots. With or without difuse humeral spot. Head and fins brown or gray without spots. Ventral portion of body and head white. Maxillary barbels same color as body.

Distribution and Habitat – Occours in rio Paraíba do Sul drainage, southerneastern Brazil (Fig. 19).

Table 7: Morphometric data of the *Rhamdia parahybae.*

Rhamdia parahybae **(n= 37)**			
	min-max	Mean±SD	Holotype
Standard length (mm)	83.77-252.42	149,05	201,51
Percent of Standard Length			
Maxillary-barbel length	47.2-82.3	66.0±11.74	78.1
Pectoral-girdle width	18.1-20.8	19.1±0.87	18.5
Pelvic-girdle width	7.9-10.8	9.0±0.75	8.9
Body depth	16.3-22.3	18.5±1.79	18.1
Pre-dorsal distance	33.2-37.3	35.1±1.36	33.1
Dorsal-fin to caudal-fin distance	48.2-54.0	51.6±1.70	52.4
Dorsal-fin to adipose-fin distance	2.7-8.9	6.0±1.69	2.6
Pre-pectoral distance	22.4-25.8	24.0±1.00	22.8
Pre-pelvic distance	46.0-51.3	48.5±1.26	48.3
Pre-anal distance	67.0-71.4	69.2±1.31	69.1
Pelvic-fin to anal-fin distance	18.9-23.7	21.1±1.32	21.8
Adipose-fin to caudal-fin distance	8.1-11.0	9.9±0.83	9.6
Caudal-peduncle length	16.8-21.1	19.6±1.18	19.4
Caudal-peduncle depth	8.8-12.0	10.0±0.86	11.1
Pelvic-fin length	11.4-14.6	13.0±0.97	14.4
Anal-fin base length	11.1-13.0	12.0±0.56	11.6
Anal-fin length	18.8-21.8	20.3±0.88	19.2
Dorsal-fin base length	13.2-17.1	15.3±1.05	17.1
Dorsal-fin height	11.6-16.7	14.5±1.50	16.5
Dorsal-fin spine length	7.5-9.9	8.6±0.68	8.6
Pectoral-fin spine length	9.3-13.7	11.7±1.33	12.2
Adipose-fin base length	31.5-40.0	36.2±2.30	39.9
Head length	23.1-27.3	24.8±0.92	24.0

Percent of Head Length			
Snout length	36.4-41.1	38.8±1.34	39,2
Snout height	34.1-42.6	38.3±2.18	34,0
Head height	52.3-60.1	56.8±2.62	60,1
Orbital diameter	12.8-16.4	14.5±1.23	13,1
Interorbital distance	30.2-37.5	33.6±1.93	34,3
Mouth length	40.2-46.0	42.8±1.84	40.2
Maxillary-barbels distance	33.6-38.9	36.4±1.87	33,5
Anterior nares distance	17.0-22.3	20.5±1.35	21,1
Anterior nares to posterior nares distance	11.1-16.4	13.3±1.50	12,4
Posterior nares to orbit distance	13.1-19.5	16.4±1.58	19,5
Posterior nares distance	17.0-23.2	20.5±1.49	20,2
External mental-barbels distance	30.5-42.5	36.2±2.71	30.5
Internal mental-barbels distance	13.1-18.1	16.2±1.37	13,0
Distance between mental-barbel	8.0-11.4	9.6±1.14	8,6
External mental-barbel length	80.8-125.7	103.6±12.41	105,3
Internal mental-barbel length	45.5-76.8	63.8±9.74	59,0
Head width at eye level	58.5-69.2	63.5±3.24	58,4

Discussion

After the first review for the genus *Rhamdia*, the taxonomic situation of the "super-species"*R. quelen sensu* Silfvergrip (1996) was a subject of much debate. Perdices et al. (2006) carried out the first phylogeographic study for the genus, defining that *R. quelen* sensu Silfvergrip (1996) is a large species complex. The authors indicate that *R. quelen* would only be present in South America, and that Central American synonymies should be elevated to species status. Hernandez et al. (2015) carried out a similar study and redescribed the species *R. cinerascens*, *R. guatemalensis* and *R. saijaensis* for Central America. The authors also state that *R. quelen* would only be present in South America.

Angrizani and Malabarba (2017) conducted a biogeographic study of South American populations of *Rhamdia*, all related to the *R. quelen* complex. The authors found 18 independent lineages with well defined and consistent geographical distributions. These lineages are arranged in four major clades: the Amazon, the Upper-Amazon, the Continental, the Atlantic Lowland and the Atlantic Highland.

Subsequently, the same authors redescribed the species *R. quelen*, which is considered the key to taxonomic resolutions within the genus (Angrizani and Malabarba, 2017). They presented a new diagnosis for *R. quelen*, defining the present geographic distribution of the species (the watersheds of the coastal plain of Brazil, between the states of Rio de Janeiro and Santa Catarina) and indicating a neotype from the correct type locality: Guanabara Bay in the State of Rio de Janeiro, Brazil. *Rhamdia quelen* is the LA3 lineage belonging to the Atlantic lowland clade (Angrizani and Malabarba 2017). According to the authors, of the 47 synonyms included in *R. quelen* by Silfvergrip (1996), only four are actually synonyms: *Pimelodus namdia* Cuvier, 1829, *Heterobranchus sextentaculatus* Spix & Agassiz, 1829, *Pimelodus sellonis* Müller & Troschel, 1849 and *Rhamdia branneri* Haseman, 1911.

The redescription of *R. quelen* and the biogeographic study for the genus paved the way for the taxonomic revision of the synonyms related to the *R. quelen* complex. The first redescription was carried out for the *R. sapo* species, which occurs in the lower portions of the Prata river, the Jacuí river and the Tramandaí-Mampituba ecoregion in southern Brazil (Angrizani and Malabarba, 2017). *Rhamdia sapo* is the LA2 line belonging to the Atlantic lowland clade (Angrizani and Malabarba, 2017). The taxa *R. microps*, *Silurus ribularis*, *Silurus 9-radiatus* and *R. branneri* are synonyms of *R. sapo* (Angrizani and Malababrba, 2017).

In this paper the following taxa are reviewed: *R. sebae, R. pentlandii, R. dorsalis, R. bathyurus, R. mounseyi, R. riojae, R. ortoni, R. duquei, R. lehmanni, R. stegelichii, R. hilarii, R. wuchereri, R. parahybae, R. queleni cuprea, R. cuyabae, R. pubescens, R sebae marty*, all names related to the *R. quelensensu* Silfvergrip complex (1996) distributed in South America.

Rhamdia pentlandii was described by Valenciennes (1940) as *Pimelodus pentlandii*, having as a type locality the Apuríamac river, tributary of the high portion of the Ucayali river in the Andean region of Peru. The specimens of this species are deposited in the London Natural History Museum (BMNH) and Silfvergrip (1996) chose the specimen BMNH

1862.11.15: 11 as a lectotype. This species was redescribed by Günther (1864) and inserted in *Rhamdia* by Eigenmann & Eigenmann (1888). Silfvergrip (1996) considered the possible validity of the species because the head and the adipose fin were very short. However, due to the lack of additional specimens he chose for the synonym with *R. quelen*. The results presented here allow the diagnosis of this taxon, which occurs in the Apuriamac, Urubamba and Madre de Díos rivers, in the Andean region of Peru. The species has *R. duquei* as a junior synonym. *Rhamdia pentlandi* is the Peruvian-Amazon lineage of the Upper-Amazon clade described by Angrizani & Malabarba (2017). The main characters for the species recognition are: the short head (23.4-25.5% CP) with straight dorsal and lateral profiles; the short adipose fin (22.8-26.1% CP); maxillary barbells reaching up to insertion of the pelvic fin (39.6-56.1% CP); the spine of the pectoral fin with strong saws on the anterior face and delicate saws on the back face; the upper lobe of the caudal fin rounded and shorter than the lower lobe.

Rhamdiadorsalis foi descrita por Gill (1870) e coletada por Orton (1868) em uma expedição ao longo das regiões andina e amazônica. O holótipo USNM 35334 está depositado no Smithsonian Museum. Na descrição original nunca foi definida a localidade tipo da espécie, que pode ter sido coletada nos rios Marañon ou Napo (Gill, 1870; Silfvergrip, 1996). De acordo com Orton (1868) a expedição iniciou descendo o rio Napo em direção a Pebas (Peru), alcançando o rio Maranõn e seguindo pelo rio Amazonas em direção ao Pará. Há um pequeno equívoco na descrição dessa rota, o rio Napo não desaguá no rio Maranõn, e sim, direto no rio Amazonas. Portanto, Orton nunca passou pelo rio Maranõn durante sua expedição, que pode ser descartado como localidade tipo de *R. dorsalis*. Ao analisar os espécimes da região amazônica peruana, percebe-se que são compatíveis com o holótipo de *R. dorsalis*, indicando que a localidade tipo da espécie deva ser algum rio do alto amazonas. Dessa forma, é muito conveniente definir o baixo rio Napo como localidade tipo de *R. dorsalis*.

Silfvergrip (1996) sinonimizou *R. dorsalis* porque o holótipo se enquadraria em sua diagnose de *R. quelen*. O espécime de *R. dorsalis* identificado por NRM 16090, depositado no museu de História Natural de Estocolmo, foi designado por Silfvergrip (1996) como neótipo de *R. quelen*, sendo esse, com certeza, o maior equívoco do autor. Essa espécie não foi analisada no estudo biogeográfico de Angrizani e Malabarba (2017). Porém, as características morfológicas dessa espécie são únicas e suficientes para sua caracterização, podendo ser facilmente diagnóstica pelos seguintes caracteres: cabeça curta (24.3-27.6% CP) com perfil dorsal e lateral retos; espaço interorbital relativamente curto (12.8-15.4% CP); espinho da nadadeira dorsal com serras delicadas no primeiro terço superior da face anterior e serras delicadas e espaçadas em toda a face posterior; nadadeira caudal com lobo superior pontiagudo e menor que o lobo inferior. Sua distribuição é na região Amazônica do Peru, nos rios Maranõn, Napo e Ucayali.

Rhamdia sebae was first mentioned by Cuvier (1829), as *Pimelodus sebae*, in a footnote alluding to the illustration of Seba (1759), a naturalist who illustrated in his work many species collected in Suriname. According to the International Code of Zoological Nomenclature (Art. 73.1.4), Seba´s illustration can and should be considered the holotype of this species, in such a way the correct type locality of this species is Suriname. Shortly after Cuvier (1829), Valenciennes (1840) formally redescribe *R. sebae*, using specimens from Suriname, British Guiana, Argentina, Ecuador and Rio de Janeiro (Brazil), making *R. sebae* a species with a large geographic distribution. In analyzing the specimens of the redescription of Valenciennes (1840) it is noted that there are specimens morphologically different from each other, and none of the specimens have the morphological characters of Suriname specimens. *Rhamdia sebae* was redescribed several times (Günther 1964, Steindachner 1879, Eigenmann & Eigenmann 1889, Miranda-Ribeiro 1907) and all studies presented problems regarding the definition of its geographical distribution. It was Eigenmann & Eigenmann (1889) who inserted *R. sebae* in *Rhamdia*.

Populations of *R. sebae* were not analyzed in the biogeographic study of Angrizani and Malabarba (2017). However, the analyzes of the specimens collected in Suriname enabled the diagnosis and morphological characterization of this taxon. Because it is an illustration, it was very difficult to analyze the holotype of the species. However, some features become evident when looking at the type: the head with straight lateral and dorsal profiles, dorsal fin presenting six rays and located very close to the insertion of the adipose fin, which in turn is very long; but what draws most attention in the drawing is the upper lobe of the caudal fin being pointed, a very striking feature of this species.

Rhamdia sebae is a senior synonym of *Pimelodus stegelichii*, described by Müller and Troschel (1848). This taxon was described based on four syntypes from Guyana and Suriname, being very important for the redescription and diagnosis of *R. sebae*. The species occurs in the Essequibo and Demerara river basins in Guyana, also occurring in Suriname. It has as diagnostic characters: head with straight dorsal profile and slightly curved lateral profile (20.2-23.7% CP); long barbells exceeding reaching up to anal fin insertion; dorsal fin with six branched rays, with height greater than the length of the base of the fin; the last branched radius of the dorsal fin exceeds the insertion of the adipose fin; very long adipose fin (40.2.1-46.6% CP); pectoral fin spine slightly curved, with delicate serrations on the initial two-thirds of the anterior face of the spine and with delicate serrations across the posterior face of the spine; upper lobe of the caudal fin with a pointed shape and smaller than the lower lobe that is rounded.

Rhamdia lehmanni was described by Dahl (1961) and collected in a small tributary of the Guayabero River, Colombia. The holotype is destroyed (Silfvergrip, 1996) and the ICNMHN 358 paratypes are deposited in the Museum of Natural History of the Faculty of Bogota. Silfvergrip (1996) synonimized this species to *R. quelen* without analyzing the type series, based only in the original description. This species was also not analyzed in the biogeographic study of Angrizani and Malabarba (2017), being here redescribed based on morphological characters that allow its diagnosis: the relatively short head (18.6-23.4% CP) with slightly concave dorsal and lateral profiles; the sensory pores of the head are simple; long maxillary barbels (73.4-92.6% CP) reaching anal-fin insertion; very long external mental barbell, almost reaching the insertion of the pelvic fin; dorsal fin with six branched rays, with height greater than the length of the base of the fin; last branched radius of the dorsal fin exceeds the insertion of the adipose fin; upper lobe of the caudal fin is pointed and smaller than the lower lobe that is rounded. *Rhamdia lehmanni* occurs in the Orinoco River basin, both in Colombia and Venezuela.

Rhamdia hilarii was described by Valenciennes (1840) in the genus *Pimelodus*. The species was first collected by Saint Hilaire in the São Francisco River basin, possibly on the Pacuí River (upper São Francisco River) (Silfvergrip, 1996). There are four syntypes of this species, all deposited in the Museum of Natural History of Paris, three of them are taxidermized and come from the basin of the São Francisco River. The fourth specimen is preserved in alcohol and comes from Montevideo (Uruguay), but is in bad state of preservation. Silfvergrip (1996) designated MNHN specimen A-9415 as a lectotype for the taxon. This species was redescribed by Günther (1864), Lutken (1875) and Eigenmann and

Eigenmann (1907) who inserted it in *Rhamdia*. Silfvergrip (1996) synonimized this species to *R. quelen*. *Rhamdia wucherrei* from Bahia is herein considered a junior synonym of *R. hilarii* for presenting the same morphological characteristics.

Rhamdia hilarii belongs to the Continental clade in the study of Angrizani & Malabarba (2017), being identified as the CC4 lineage. This species is present in the basin of the São Francisco River, and can be recognized by the following characters: short head (23.8-24.9% CP) with slightly concave dorsal and lateral profile; the sensory pores of the head are multiple; at least seven branched rays in the dorsal fin, the last radius of the dorsal fin does not exceed the insertion of the adipose fin; pectoral fin spine is short (9.4-11.3% CP); the anal fin does not extend beyond the posterior insertion of the adipose fin; upper lobe of the caudal fin is rounded and smaller than the lower lobe.

Rhamdia cuyabae was described by Steindachner (1877) as *Pimelodus cuyabae*. It was collected in Cuiabá, state of Mato Grosso, Brazil. The type series was deposited at the Vienna Natural History Museum and the lectotype NMW 45919 was selected by Silfvergrip (1996). The taxon was inserted into the genus *Rhamdia* and synonymized in *R. quelen* by Eigenmann and Eigenmann (1888). Silfvegrip (1996) maintained *R. cuyabae* as a synonym for *R. quelen*. In the biogeographic study of Angrizani & Malabarba (2017) this taxon is the lineage CC1 and is inserted in the Continental clade. The species *R. pubescens* and *R. sebae* marty are here synonimized in *R. cuyabae* after the morphological analysis of their type specimens.

Rhamdia cuyabae is easily diagnosed from the species of the genus because it has the following characters: head short (23.8-26.9% CP) and high (65.3-74.0% CC), with very concave dorsal and lateral profiles; the snout is deeper than longer; six branched rays of the dorsal fin, the last ray of the dorsal fin exceeds the insertion of the adipose fin; the maxillary barbels are long (44.4-83.7% CP), reaching at most the insertion of the anal fin; the pectoral fin spines have strongh serrations in two third of distal anterior side and delicate serration in all posterior side the upper lobe of the caudal fin is rounded and smaller than the lower lobe. This species occurs along the La Plata River basin.

Rhamdia parahybae was described by Steindachner (1877) and collected in the Paraíba do Sul river, Brazil. The holotype NMW 45852 is deposited in the Museum of Natural History of Vienna. The taxon was synonymized in *R. quelen* because the characteristics of its holotype fit the diagnosis of *R. quelen sensu* Silfvergrip (1996). In fact, these two species are very similar morphologically, after all they are sister species (Angrizani & Malabarba, 2017). *Rhamdia parahybae* belongs to the Atlantic Lowland clade identified in the study of Angrizani & Malabarba (2017) as the LA4 lineage. Despite the similarities with *R. quelen*, *R. parahybae* is easily diagnosed of all other species of *Rhamdia* because it has the same distance between both anterior and posterior nostrils. The *Pimelodus queleni cuprea* was described by Steindachner (1877) in the same study and collected in the Paraíba do Sul river. The species was described as a subspecies of *R. quelen*. However, the syntypes of this taxon present the characteristics of *R. parahybae*, being here synonymized in this species.

After this extensive taxonomic review, it can be defined that the 27 South American synonyms of the *R. quelen* sensu Silfvergrip (1996) complex can be distributed in nine valid species (R. *quelen, R. sebae, R. sapo, R. hilarii, R. pentlandii, R. dorsalis, R. lehmanni, R. cuyabae, R. parahybae*). The results obtained here demonstrate that *Rhamdia* is much more diverse than previously thought. Besides the species revalidated herein for the genus, there are four lineages of *Rhamdia* defined in the study of Angrizani and Malabarba (2017) that are still being morphologically analyzed, and that can raise the alpha diversity of the genus to 35 species.

References

Angrizani R.C, Malabarba, L.R. 2017. Species delimitation of *Rhamdia* (Bleeker, 1858)(Siluriformes: Heptapteridae) using morphology and molecular data reveals the presence of two new species under *Rhamdia quelen* (Quoy & Gaimard, 1824) species complex. *Zootaxa*,

Angrizani, R.C, Malabarba, L.R. 2017. What a hell is the real *Rhamdiaquelen* (Siluriformes: Heptapteridae)?. *Zootaxa*.

Cuvier, G. 1829. *Le Règne Animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*. Edition 2. v. 2: i-xv + 1-406 pp.

Dahl, G. 1961. Nematognathous fishes collected during the Macarena Expedition 1959. Part II: Pimelodidae, Callophysidae. *Novedades Colombianas* v. 1(6): 483-514.

Eigenmann, C.H, Eigenmann, R.S. 1888. Preliminary notes on South American Nematognathi. I. *Proceedings of the California Academy of Sciences* (1): 119-172.

Garavello, J.C, Shibatta, O.A. 2016. Reappraisal of *Rhamdiabranneri* Haseman, 1911 and *R. voulezi* Haseman, 1911 (Siluriformes: Heptapteridae) from the rio Iguaçu with notes on their morphometry and karyotype. *Neotropical Ichthyology,*14(1).

Gill, T.N. 1870. On some new species of fishes obtained by Prof. Orton from the Maranon, or Upper Amazon, and Napo Rivers. *Proceedings of the Academy of Natural Sciences of Philadelphia* v. 22: 92-96.

Günther, A. 1864. *Catalogue of the fishes in the British Museum. Catalogue of the Physostomi, containing the families Siluridae, Characinidae, Haplochitonidae, Sternoptychidae, Scopelidae, Stomiatidae in the collection of the British Museum*. British Museum, London v. 5: i-xxii, 1-455 pp.

Hernández, C.L, Ortega-Lara, A, Sánchez-Garcés, G.C, Alford, M.C. 2016. Genetic and Morphometric Evidence for the Recognition of Several Recently Synonymized Species of Trans-Andean *Rhamdia* (Pisces: Siluriformes: Heptapteridae*). Copeia,* 103(3), 563–579.

Lütken, C.F. 1875. *Velhas-Flodens Fiske. Et Bidrag til Brasiliens Ichthyologi; efter Professor J. Reinhardts Indsamlinger og Optegnelser. Det. Kongelige Danske visenskabernes selskabs skrifter. Naturvidenskabelig og mathematisk afdeling*. 5te Raekk [Ser. 5]. v. 12 (2): 121-253 + 2 unnum. + I-XXI, Pls. 1-5.

Müller, J. and Troschel F.H. 1848. In: Schomburgk, R. 1848. *Reisen in Britisch-Guiana in den Jahren 1840-1844 : nebst einer Fauna und Flora Guiana's nach Vorlagen von Johannes Müller, Ehrenberg, Erichson, Klotzsch, Troschel, Cabanis und Andern*. Leipzig. 1-429 pp.

Miranda Ribeiro, A. 1907. Fauna Braziliense. Peixes. II. Desmobranchios. *Arquivos do Museu Nacional de Rio de Janeiro* (14): 132-217.

Perdices, A, Bermingham, E, Montilla, A. & Doadrio, I. 2002. Evolutionary history of the genus *Rhamdia* (Teleostei: Pimelodidae) in Central America. *Molecular Phylogenetics and Evolution,*25(1), 172–189.

Quoy, J.R.C. and Gaimard, J.P. 1824. Description des Poissons. Chapter IX. In: Freycinet, L., 1824. *Voyage autour du Monde, entrepis par ordre du roi, sous le ministere et conformemént aux instructons de S. Exc. M. le Vicomte du Bouchage, secrétaire d'état au département de la marine, exécuté sur les corvettes de L.M. L'Uranie et "La*

Physicienne, pendant les années 1817, 1818, 1819 et 182. Paris. Pp. 192-401.

Silfvergrip AMC. 1996. *A systematic review of the Neotropical catfish genus Rhamdia (Teleostei, Pimelodidae)*. Stockholm, Swedish Museum of Natural History.

Seba, A. 1759. *Locupletissimi rerum naturalium thesauri accurata descriptio et iconibus artificiosissimis expressio per universam physices historiam*. H. K. Arksteus, Amstelaedami. v. 3: i-xxi, 1-212, Pls. 1-116.

Steindachner, F. 1877. *Die Süsswasserfische des südöstlichen Brasilien (III). Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche* Classe v. 74: 559-694.

Steindachner, F. 1879. *Zur Fisch-Fauna des Magdalenen-Stromes. Denkschriften der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche* Classe. v. 39: 19-78

Valenciennes, A. 1840. In : Cuvier, G. and Valenciennes, A. 1840. *Histoire naturelle des poissons. Tome quinzième. Suite du livre dix-septième. Siluroïdes*. Strasbourg v. 15: i-xxxi + 1-540 p

Figures:

Figure 1: Lectotype of *R. pentlandii*, BMNH 1862.11.15:11, 221 mm CP, Peru, rio Apuriamac. Lateral, dorsal and ventral views. Photo by Mark Allen.

Figure 2: Specimen of *R*. *pentlandii*, ANSP 180790 (88.2 mm SL), Peru, region of Cuzco, municipality of Quellounoco, rio Urubamba, basin of rio Ucayali. Lateral view.

Figure 3: Holotype of *R. dorsalis*, USNM 35334, 171.7 mm SL. Dorsal Lateral, and ventral views.

Figure 4: Specimen of *R. dorsalis*, ANSP 191817 (186.5 mm SL), in lateral view.

Figure 5: Distribution map of *Rhamdia* species in Peru. White circles are the distribution points of *R. dorsalis*; white star is the approximate location of the holotype of *R. dosralis*; pink circles represent the distribution points of *R. pentlandii* and the pink star is the approximate location of the holotype of *R. pentlandii*.

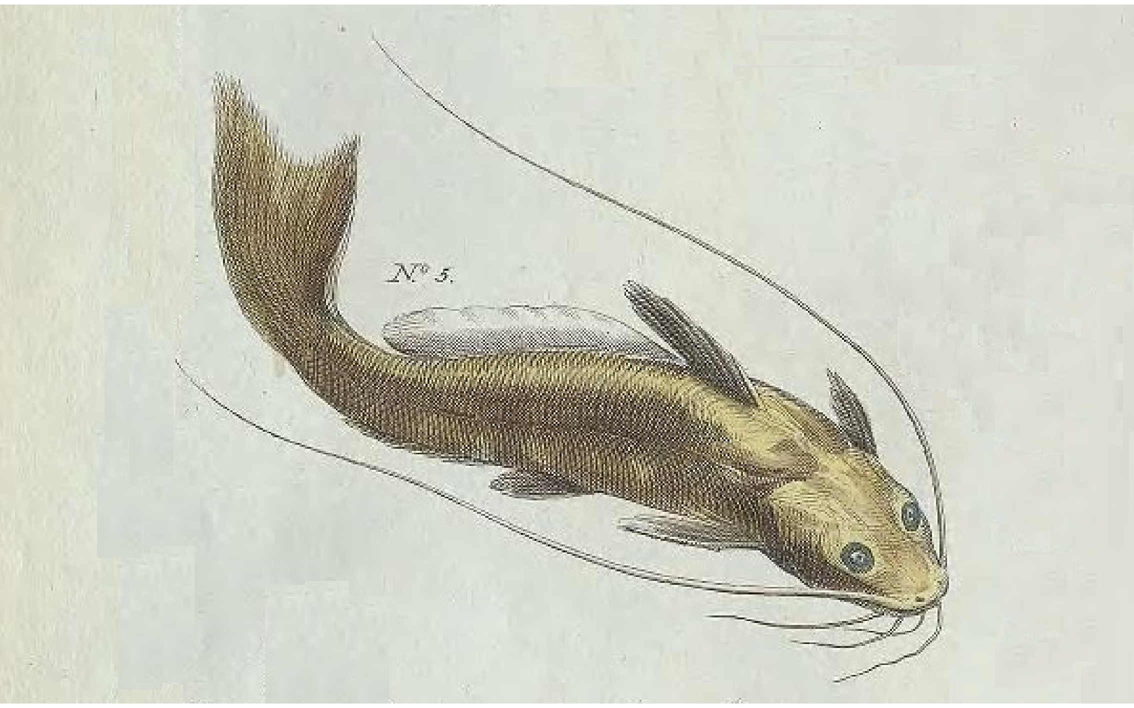

Figure 6: Holotype of *Rhamdia sebae*, illustration by Seba (1759), III, xxxix, N^{o}5.

Figure 7: Specimen of *Rhamdia sebae*, ANSP 177233 (143.4 mm CP), in lateral view.

Figura 8: Paratype of *R. lehmanii* (80.5 mm CP), in lateral, dorsal and ventral view. Photographed by Mark Allen.

Figure 9: Specimen of *Rhamdia lehmanii*, ANSP 39180 (139 mm CP), in lateral view.

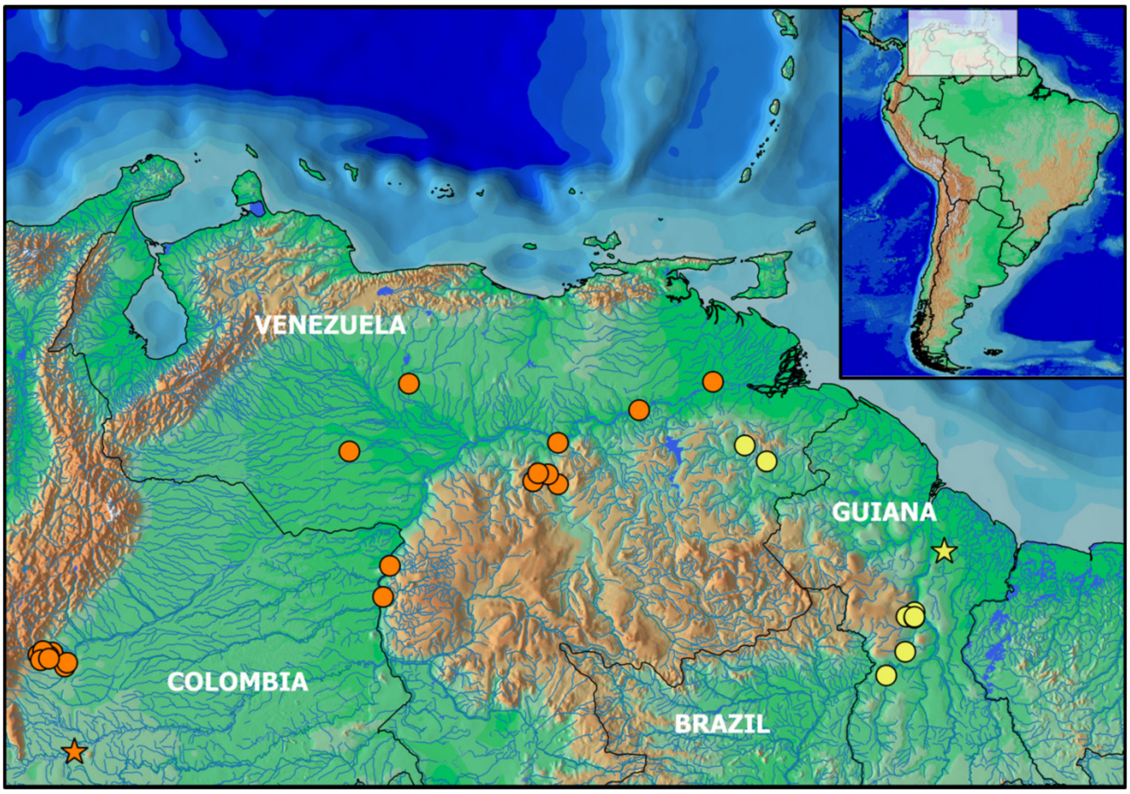

Figure 10: Distribution map of *R. lehmanii and R. sebae*. Orange circles are the distribution points of *R. lehmanii*; orange star is the approximate location of the paratype of *R. lehmanii*; yellow circles represent the distribution points of *R. sebae* and the yellow star is the approximate location of the holotype of *R. sebae*.

Figure 11: Holotype of *R.cuyabae,* NMW 45919 (342.1 mm SL), in lateral view.

Figura 12: Specimen of *R. cuyabae*, UFRGS (185 mm CP), in lateral view.

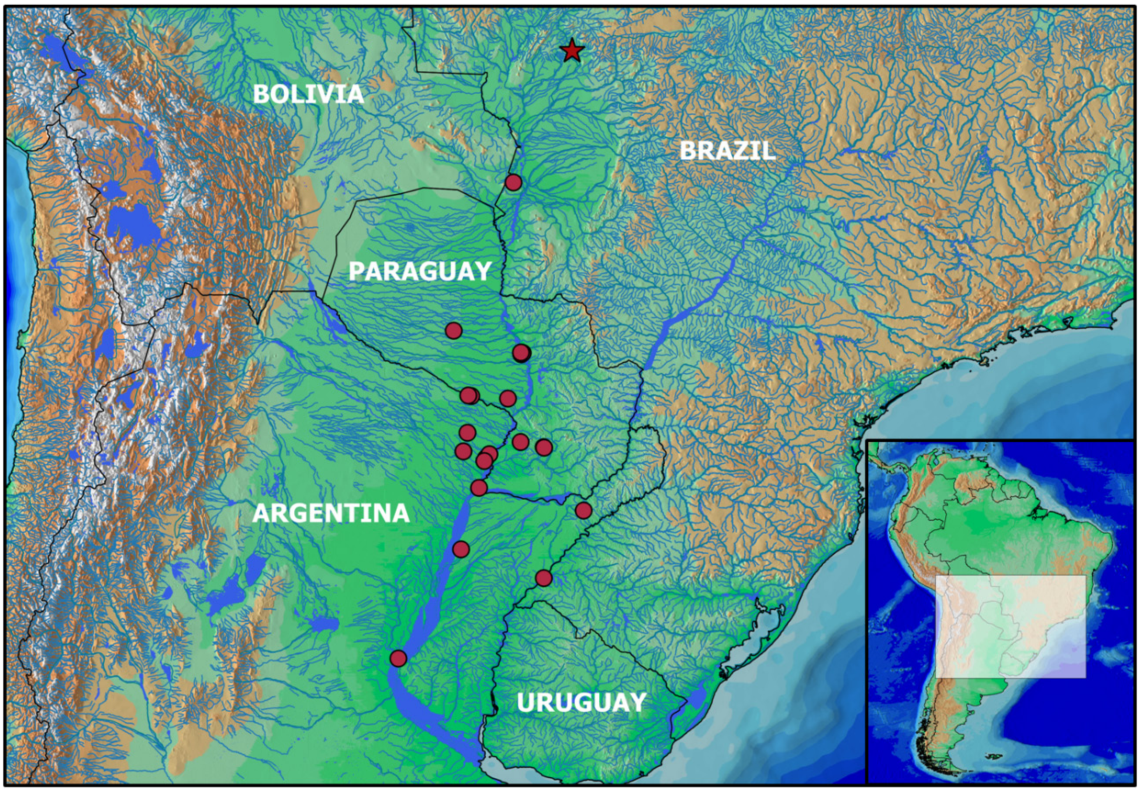

Figura 13: Distribution map of the *Rhamdiacuyabae* along the drainage of the rio da Prata. Red circles are the distribution points of the species and the red star is the approximate location of the holotype.

Figura 14: Holotype of *R. hilarii,* MNHN A-9415 (192.8 mm SL), in lateral view.

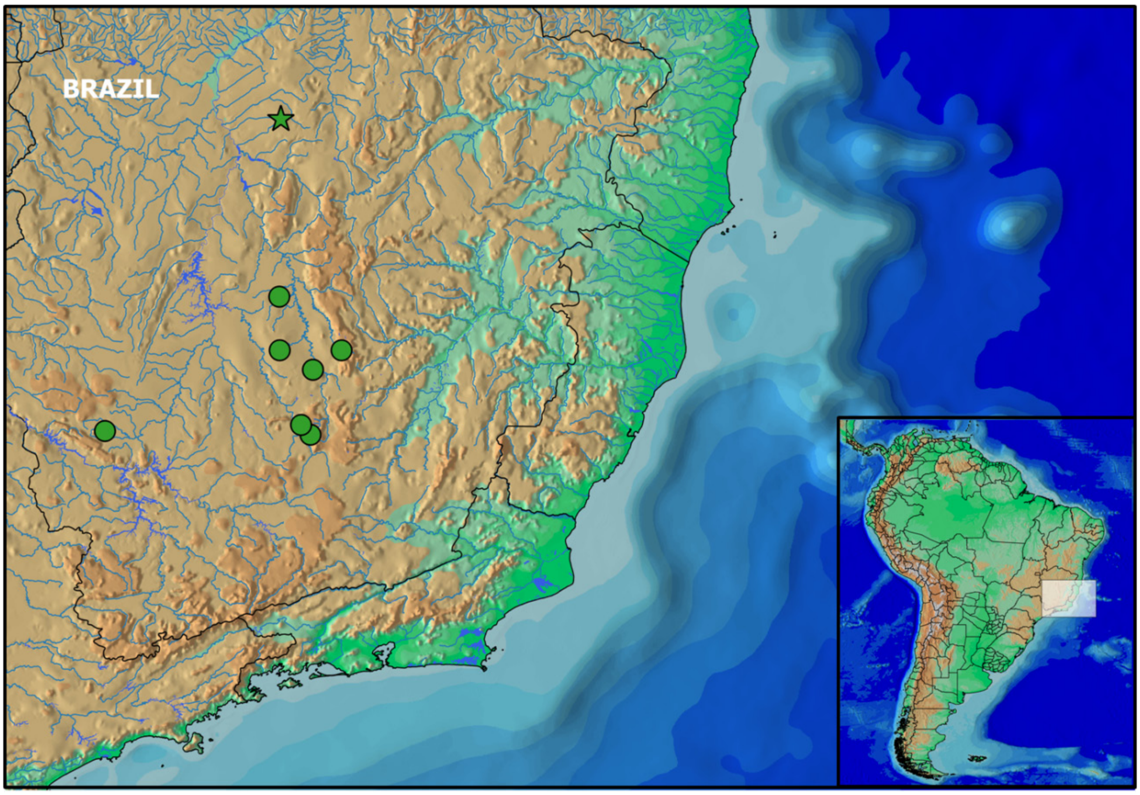

Figura 16: Distribution map of the *Rhamdiahilarii* along the drainage of the rio São Francisco. Green circles are the distribution points of the species and the green star is the approximate location of the species.

Figure 11: Holotype of *R. parahybae,* NMW 45852 (201.5 mm SL), in lateral view.

Figure 18: Specimen of *R. parahybae*, MNRJ 12382 (180 mm SL), lateral view.

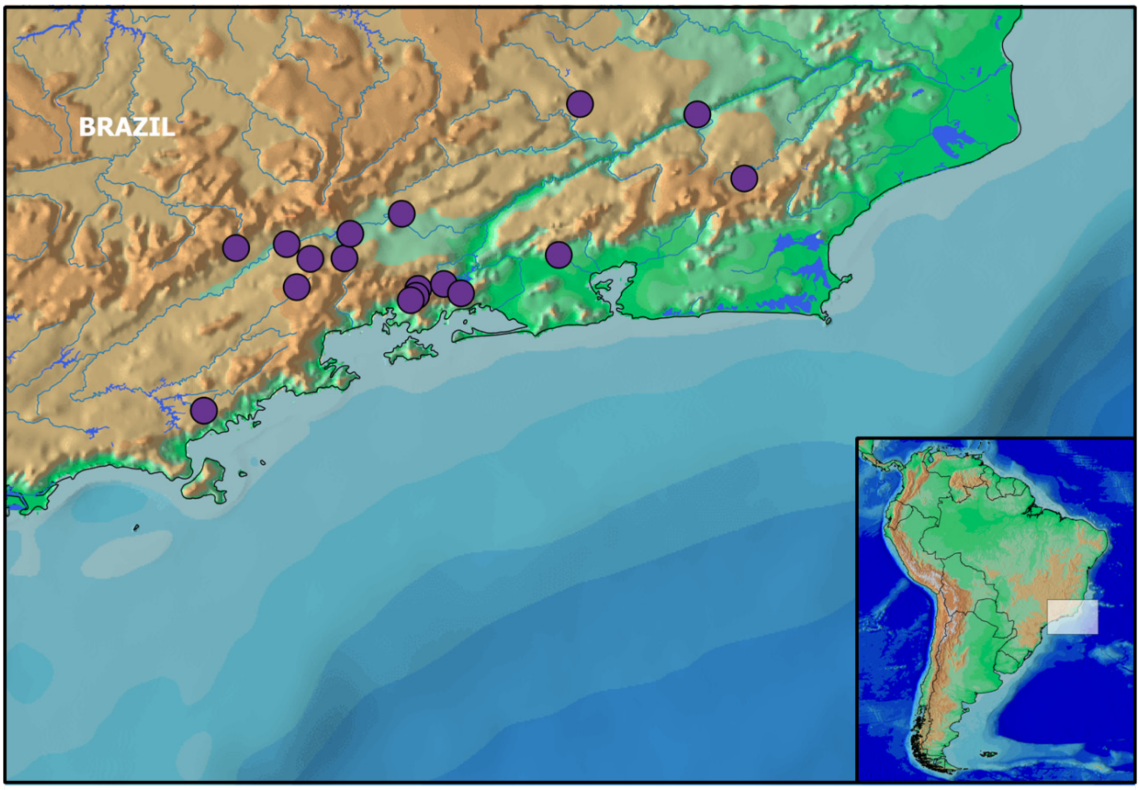

Figure 19: Distribution map of the *Rhamdia parahybae* along the drainage of the rio Paraíba do Sul. Purple circles are the distribution points of the species.

8. Capitulo 5

Artigo desenvolvido para ser publicado no periódico “Zootaxa”.

Description of five new species of *Rhamdia* from Southern Brazil

Abstract

The recent review of *Rhamdia quelen*, with the redescription of this species and others removed from its synonym allowed the recognition of several undescribed taxa. Five new species are described herein from South Brazil: *Rhamdia* sp.1, from the head waters of rio Jacuí; *Rhamdia* sp2, from tributaries of the laguna dos Patos; *Rhamdia* sp3, from medium and upper rio Uruguay; *Rhamdia* sp4, from the headwaters of rio Itajaí and *Rhamdia* sp5, São Francisco do Sul island and streams of Bertioga municipality.

Introduction

Species of the genus *Rhamdia* are distributed throughout the Neotropical region. The redescription of *Rhamdia quelen*, along with the redefinition of its type locality, allowed the revalidation and redescription of eight of its junior synonyms, as well the recognition of new species to be described (Angrizani & Malabarba, 2017a,b,c). After these recent reviews of the *Rhamdia quelen* species complex, there are currently 30 valid species recognized for the genus.

Angrizani & Malabarba (2017) further recognized 18 lineages of *Rhamdia*, whose specimens were analyzed on its morphology. Five of these lineages are morphologically distinct and cannot be associated to any available names, being herein described as new species.

Material and methods

Counts and measurements follows Angrizani & Malabarba (2017). Specimens measured include 20 specimens of *Rhamdia* sp1, 58 specimens of *Rhamdia* sp2, 20 specimens of *Rhamdia* sp3, 9 specimens of *Rhamdia* sp4, and specimens of *Rhamdia* sp5.

Rhamdia sp1

(Fig. 1)

Holotype: UFRGS 23350, 1, 163.2 mm SL, Brazil, state of Rio Grande do Sul, municipality of Fortaleza dos Valos, stream Lageado Paraíso, tributary of rio Jacuí, basin of Laguna dos Patos; 28°54'30"S, 53°17'10"W; J. Ferrer, R. Angrizani, L. Donin, J. Chuctaya, 30 Jul 2015.

Examined material: All from Brazil, state of Rio Grande do Sul:UFRGS 18359, 2, xx-xx mm SL, Brazil, state of Rio Grande do Sul, municipality of Salto do Jacuí, rio Lageado Pelado, tributary of rio Jacuí; 29°02'24"S, 53°17'31"W; A. Dufech and J. Santos, 31 Oct 2013. UFRGS 23530, 4, collected with Holotype, 145.3-118.5 mm SL, Brazil, state of Rio Grande do Sul, municipality of Fortaleza dos Valos, stream Lageado Paraíso, tributary of rio Jacuí, basin of Laguna dos Patos; 28°54'30"S, 53°17'10"W; J. Ferrer, R. Angrizani, L. Donin, J. Chuctaya, 30 Jul 2015. UFRGS XXXX, 3, 134.1-104.0 mm SL, Brazil, state of Rio Grande do Sul, municipality of Espumoso, rio Morcego, tributary of Jacuí, basin of Laguna dos Patos; 28°53'55"S, 52°49'05"W; K. Bonato, 19 Jun 2012. UFRGS xxxxx, 4, 128.1-107.0 mm SL, Brazil, state of Rio Grande do Sul, municipality of Espumoso, rio Morcego, tributary of Jacuí, basin of Laguna dos Patos; 28°53'55"S, 52°49'05"W; K. Bonato, 20 Apr 2013. UFRGS xxxxx, 1, 127.4 m SL, Brazil, state of Rio Grande do Sul, municipality of Mormaço, rio Quatí, tributary of Jacuí, basin of Laguna dos Patos; 28°38'31"S, 52°37'07"W; K. Bonato, 23 Feb 2013. UFRGS xxxxx, 2, 118-110.4 mm SL, Brazil, state of Rio Grande do Sul, municipality of Espumoso, rio Jacuizinho, tributary of rio Jacuí; 28°58'02"S, 52°47'20"W; K. Bonato, A. Hirschmann, C. Hartmann, 02 Ago 2012. UFRGS xxxxx, 1, 99.4 mm SL, Brazil, state of Rio Grande do Sul, municipality of Espumoso, rio dos Caixões, tributary of rio Jacuí, basin of Laguna dos Patos; 29°01'54"S, 52°49'25"W; K. Bonato, 19 Dec 2012. UFRGS 19264, 1, Brazil, state of Rio Grande do Sul, municipality of Tapera, riacho da Paz, tributary of Jacuí, basin of Laguna dos Patos; 28°42'57"S, 52°50'41"W; K. Bonato, N. Bertier and & A. Hirschmann, 19 Oct 2012.

Diagnosis - *Rhamdia sp.1* differs from *R. sapo*, *R. sebae,R. dorsalis*, *R. lehmanii R. cuyabae, R. laukidi, R. muelleri* and *R. guatemalensis* by last unbranched ray not reaching anterior insertion of adipose fin (*vs*. last unbranched ray trespassing anterior insertion of adipose fin). Differs from *R. foina*, *R poeyi, R. itacaiunas, R. parryi* and *R. xequetepeque* by superior lobe of caudal fin smaller than inferior lobe (*vs.* superior lobe of caudal fin larger than inferior lobe). Differs from *R. laticauda*, *R. humilis*, *R. nicaraguensis* by serrae in both sides of pectoral fin spine (*vs*. serrae in one side of pectoral fin spine). Differs from *R. quelen* and *R. parahybae,* by smaller interorbital distance (24.0-29.8% HL *vs.* 34.8-39.6% HL in *R. quelen* and 32.7-37.5% HL in *R. parahybae*). Differs from *R. gabrielae* by shorter Maxillary-barbels distance (7.6-8.0% SL *vs*. 9.0-11.0% SL in *R. gabrielae*). *R. eurichephala.* Differs from *R. cinerascens* and *R. saijaensis* by insertion of adipose fin not equidistant between the dorsal and caudal fins (vs. insertion of the adipose fin equidistant between the dorsal and caudal fins).Differs from *R. jequitinhonha*, by longer maxillary barbel (45.1-64.4% SL *vs*. 39.2% SL). Differs from*R. reddelli*, *R. enfurnada*, *R. zongolicensis*, *R. macuspanensis* and *R. laluchensis* by the lack of morphological adaptations to troglobitic life.

Description - Measurements in Table 1. Body elongated; cross section of trunk roughly circular at dorsal-fin origin and along dorsal-fin base, gradually compressed posteriorly to caudal peduncle. Anterodorsal profile of body convex from supraoccipital to dorsal-fin base. Dorsal-fin base nearly straight, posteroventrally slanted, and gently convex from dorsal fin to base of caudal fin. Ventral body profile nearly straight from mouth to caudal-fin base. Body widest at pectoral girdle and deepest at dorsal-fin origin. Caudal peduncle longer than deep. Number of post-Weberian vertebrae 39.

Head depressed. Dorsal head profile slightly rounded and posterodorsally slightly slanted from snout tip to supraoccipital in lateral view. Head shape somewhat conical in dorsal view. Lateral head profile flat. Snout rounded anteriorly in dorsal view, longer than deep. Transverse distance between posterior nares slightly smaller than that between anterior nares. Mouth wide, subterminal, transverse gape larger than interorbital distance; snout projecting slightly beyond lower jaw. Large, fleshy rictal fold at corners of mouth. Both upper and lower lips with several longitudinal plicae.

Barbels flattened in cross section, wide at their base and tapering towards distal tip. Maxillary barbel longest; length variable, maximally exceeding insertion of pelvic fin, never reach insertion of anal fin; inserted above upper lip and posterolateral to anterior nares. Two pairs of mental barbels with bases aligned. Outer mental barbels surpassing origin of pectoral fin. Inner mental barbels shorter than outer mental barbels, never reaching origin of pectoral fin. Gular fold distinct and V-shaped. Branchiostegal rays. Gill rakers thick and moderately long, with 8-9 rakers on first ceratobranchial. Eye large, slightly elliptical (longitudinally elongated); rim circumscribed by deep, continuous invagination that is distinctly more pronounced along lateral border. Eye positioned dorsolaterally, approximately at midpoint between tip of snout and corner of opercular membrane; interorbital space wide. Pupil rounded. Sensory channels of head simple and point shaped.

Dorsal fin with two unbranched rays and six branched rays, distal margin convex and base length less than to fin height. First unbranched dorsal-fin ray small and not externally visible, second unbranched ray stiffened proximally, segmented distally. Dorsal-fin origin at midlength between pectoral and pelvic-fin origins; insertion of last branched ray just before or at pelvic-fin origin. Tip of last branched dorsal-fin ray not reaching anterior insertion of adipose fin. Adipose fin long; with ascendant curve in in lateral profile and posterior lobe conspicuously free from body. Adipose-fin origin at vertical through middle of depressed pelvic fin and posterior insertion at final third of caudal peduncle.

Pectoral fin within one unbranched and five branched rays; when adpressed, reaching approximately origin of third branched dorsal-fin ray. Unbranched ray of pectoral fin stiffened, slight curved and with strong serrations along distal anterior side and delicate serrations along proximal posterior side. Pelvic fin rounded, approximately same size of pectoral fin, having one unbranched ray and five branched rays, distal tip surpassing genital papilla, never reaching anal-fin origin. Pelvic-fin origin nearly at middle of standard length, just after insertion of last dorsal-fin ray. Anal fin rounded, with three unbranched rays anteriorly, followed by eight, nine or ten branched rays; when adpressed, never exceeds posterior insertion of adipose-fin. Length of anal-fin base equal to that of dorsal fin. Caudal fin deeply forked, lobes rounded; dorsal lobe smaller in depth and length; 7 branched rays in dorsal lobe and 9 branched rays in ventral lobe.

Color pattern of preserved specimens - Body brown or gray with very small dark brown irregular spots in dorso of body. Head and fins brown or gray without spots. Ventral portion of body and head white. Maxillary barbels same color as body.

Distribution and Habitat –Occursin small streams of upper rio Jacuí drainage, tributary of Laguna dos Patos, state of Rio Grande do Sul, Brazil, (Figure 2).

Table 1: Morphometric data of the *Rhamdia* sp1.

	Rhamdia* sp*1 **(n=20)**		
	min-max	Mean±SD	Holotype
Standard length (mm)	118.55-200.3	151.53	163.24
Percent of Standard Length			
Maxillary-barbel length	36.9-59.2	48.2±10.39	36.9
Pectoral-girdle width	18.2-19.1	18.6±0.34	19.1
Pelvic-girdle width	8.4-9.8	9.3±0.52	9.5
Body depth	14.8-16.7	15.8±0.72	14.8
Pre-dorsal distance	33.6-35.7	34.2±0.86	33.6
Dorsal-fin to caudal-fin distance	51.3-54.5	52.7±1.47	54.5
Dorsal-fin to adipose-fin distance	6.3-9.1	7.5±1.06	7.3
Pre-pectoral distance	22.9-24.9	23.9±0.81	23.4
Pre-pelvic distance	46.8-48.7	47.9±0.77	47.3
Pre-anal distance	64.8-69.2	67.6±1.67	69.1
Pelvic-fin to anal-fin distance		0.0±0.00	0.0
Adipose-fin to caudal-fin distance	8.9-9.7	9.2±0.34	9.4
Caudal-peduncle length	18.0-21.5	19.3±1.41	18.5
Caudal-peduncle depth	9.5-11.2	10.2±0.63	11.1
Pelvic-fin length	11.6-13.8	12.5±0.81	12.0
Anal-fin base length	11.4-14.1	12.7±1.09	13.0
Anal-fin length	19.4-22.7	20.6±1.38	19.7
Dorsal-fin base length	13.3-14.3	13.8±0.44	13.4
Dorsal-fin height	14.4-16.4	15.2±0.74	14.4
Dorsal-fin spine length	8.1-9.6	8.9±0.71	8.3
Pectoral-fin spine length	8.9-12.9	10.5±1.49	10.2
Adipose-fin base length	33.7-38.1	36.0±1.79	38.1
Head length	22.8-24.1	33.0±5.66	23.1
Snout length	12.0-14.3	13.5±0.91	13.5
Head height	9.1-9.8	9.5±0.31	9.6
Orbital diameter	3.8-4.3	4.0±0.19	3.9
Interorbital distance	15.1-16.3	15.6±0.46	15.6

Maxillary-barbels distance	7.6-8.0	7.8+0.15	8.0
Percent of Head Length			
Snout length	39.0-41.8	40.6±1.10	41.4
Snout height	35.3-36.2	35.9±0.38	35.6
Head height	50.3-61.0	57.5±4.13	58.6
Orbital diameter	15.7-18.0	16.9±0.93	17.1
Interorbital distance	24.0-29.8	27.4±2.43	29.7
Mouth length	37.9-45.5	42.0±2.91	45.5
Maxillary-barbels distance	32.4-34.5	33.3±0.96	34.5
Anterior nares distance	20.3-22.1	21.1±0.76	22.0
Anterior nares to posterior nares distance	15.7-17.0	16.1±0.56	15.8
Posterior nares to orbit distance	17.3-19.9	18.8±1.02	17.3
Posterior nares distance	16.6-17.6	17.1±0.36	17.5
External mental-barbels distance	33.8-38.2	35.6±1.82	38.1
Internal mental-barbels distance	13.4-18.5	16.9±2.05	18.3
Distance between mental-barbel	7.9-10.0	9.0±0.78	9.3
External mental-barbel length	82.0-110.0	97.3±10.97	81.9
Internal mental-barbel length	39.0-63.3	55.7±10.11	40.7
Head width at eye level	64.8-69.6	66.6±2.07	67.5

Rhamdia sp2

(Fig. 3)

Holotype: UFRGS 24200, 1, 221.7 mm SL, Brazil, state of Rio Grande do Sul, municipality of Ipê, rio Ituim, tributary of rio das Antas, basin of Laguna dos Patos; 28°37'09"S, 51°21'13"W; J. Anza, and G. Frainer.

Examined material: All from Brazil, state of Rio Grande do Sul: UFRGS 850, 2, 151-74 mm SL, Brazil, state of Rio Grande do Sul, municipality of São Francisco de Paula, rio Tainhas, tributary of rio das Antas, basin of Laguna dos Patos; 29°15'00"S, 50°19'60"W, L. Malabarba, 17 Apr 1981. UFRGS 5811, 1, 254 mm SL, Brazil, state of Rio Grande do Sul, municipality of Carazinho, rio Jacuí-Mirim, tributary of rio Jacuí, basin of Laguna dos Patos; 28°15'39"S, 53°07'22"W, J. Anza and F. Vilela F, 16 Apr 2003.UFRGS 5812, 1, 222 mm SL, Brazil, state of Rio Grande do Sul, municipality of Carazinho, rio Jacuí-Mirim, tributary of rio Jacuí, basin of Laguna dos Patos; 28°15'19"S, 53°07'18"W; J. Anza and F. Vilela, 16 Apr 2003.UFRGS 5817, 1, 280 mm SL, Brazil, state of Rio Grande do Sul, municipality of Carazinho, rio Jacuí-Mirim, tributary of rio Jacuí, basin of Laguna dos Patos; 28°15'45"S, 53°07'25"W; J. Anza and F. Vilela, 16 Apr 2003.UFRGS 6463, 10, 175-124 mm SL, Brazil, state of Rio Grande do Sul, municipality of Vila Flores, rio da Prata, tributary of rio das Antas, basin of Laguna dos Patos; 28°56'01"S, 51°28'01"W, J. Anza and F. Vilella, 28 Nov 2003.UFRGS 9032, 1, 135 mm SL, Brazil, state of Rio Grande do Sul, municipality of Dois Lajeados, rio Carreiro, tributary of rio Taquari, basin of Laguna dos Patos; 28°56'23"S, 51°46'47"W; J. Ferrer and C. Machado, 02 Oct 2006.UFRGS 9075, 3, 282-234 mm SL, Brazil, state of Rio Grande do Sul, municipality of Nova Prata, rio Saltinho, tributary of rio das Antas, basin of Laguna dos Patos; 28°35'30"S, 51°23'56"W, R. Hirano, 15 Mar 2007.UFRGS 10096, 11, 255-75 mm SL, Brazil, state of Rio Grande do Sul, municipality of Dois Lajeados, rio Carreiro, tributary of Taquari, basin of Laguna dos Patos; 28°57'47"S, 51°45'43"W; J. Ferrer, J. Wingert, J. Giora and G. Neves, 30 May 2007.UFRGS 10439, 1, 236 mm SL, Brazil, state of Rio Grande do Sul, rio da Prata, municipality of Vila Flores, tributary of rio das Antas, basin of Laguna dos Patos; 28°51'11"S, 51°27'40"W; J. Ferrer and G. Frainer, 11 Sep 2008.UFRGS 13090, 1, 213 mm SL, Brazil, state of Rio Grande do Sul, municipality of Ipê, rio Ituim, Tributary of rio das Antas, basin of Laguna dos Patos; 28°37'09"S, 51°21'13"W; J. Anza, and G. Frainer, 25 Apr

2010. UFRGS 17703, 1, 179 mm SL, Brazil, state of Rio Grande do Sul, municipality of Bom Jesus, rio das Antas, basin of Laguna dos Patos; 28°47'55"S, 50°25'48"W; J. Ferrer and J. Wingert, 20 Apr 2013.UFRGS 16764, 4, 144-75 mm SL, Brazil, state of Rio Grande do Sul, municipality of Serafina Corrêa, little stream in rio Guaporé, tributary of rio das Antas, basin of Laguna dos Patos; 28°45'16"S, 51°59'13"W; L. Fries, C. Vogel, G. Rosa and L. Marongon, 14 May 2010.UFRGS 16810, 1, 265 mm SL, Brazil, state of Rio Grande do Sul, municipality of Guaporé, rio Guaporé, tributary of rio das Antas, basin of Laguna dos Patos; 28°45'31"S, 52°04'40"W; L. Fries, C. Vogel, G. Rosa and L. Marongon, 21 May 2010.UFRGS 18323, 1, 185 mm SL, Brazil, state of Rio Grande do Sul, municipality of Dois Lajeados, rio Carreiro, Tributary of rio Taquari, basin of Laguna dos Patos; 28°56'34"S, 51°46'05"W; J. Ferrer and J. Winger, 04 Dec 2013.UFRGS 19664, 1, 212 mm SL, Brazil, state of Rio Grande do Sul, municipality of São Francisco de Paula, rio Santa Cruz, tributary of rio Caí, basin of Laguna dos Patos; 29°17'24"S, 50°44'26"W; G. Volkmer, 17 Oct 2014.UFRGS 22121, 2, 178-116 mm SL, Brazil, state of Rio Grande do Sul, municipality of Santana da Boa Vista, stream of Neves, tributary of rio Camaquã, basin of Laguna dos Patos; 30°51'45"S, 53°13'27"W; L. Malabarba, C. Malabarba, J. Chuctaya and J. Ferrer, 16 Mar 2016.UFRGS 19665, 2, 208.1-202.3 mm SL, Brazil, state of Rio Grande do Sul, municipality of Canela, rio Santa Maria, tributary of rio dos Sinos, basin of Laguna dos Patos; 29°20'47"S, 50°42'04"W; G. Volkmer.UFRGS 19663, 4, 255.2-185.2 mm SL, Brazil, state of Rio Grande do Sul, municipality of Santa Maria do Herval, rio Cadeia, tributary of rio Caí, basin of Laguna dos Patos; 29°30'03"S, 51°00'03"W; G. Volkmer.UFRGS 20047, 3, 189.2-122.4 mm SL, Brazil, state of Rio Grande do Sul, municipality of Candiota, arroio Candiota, tributary of rio Jaguarão, basin of Lagoa Mirimcandi; ; R. Angrizani, 7 May 2015. UFRGS 20058, 2, 222-210 mm SL, Brazil Rio Grande do Sul, Passo Fundo, rio Capinguí, basin of rio Taquari, basin of Laguna dos Patos; 28°21'02"S, 52°13'01"W; G. Volkmer, 20 Nov 2014.UFRGS 18226, 2, 222-202mm SL, Brazil, state of Rio Grande do Sul, municipality of Salto do Jacuí, rio Jacuí, basin of Laguna dos Patos; 29°04'31"S, 53°12'21"W; G. Volkmer, 30 Oct 2013.UFRGS 19369, 2, 256.1-246.2 mm SL, Brazil, state of Rio Grande do Sul, municipality of Tio Hugo, rio Jacuí, basin of Laguna dos Patos; 28°32'59"S, 52°32'41"W; G. Volkmer, 20 Dec 2013.

Diagnosis - *Rhamdia sp2* differs from *R. sapo*, *R. cuyabae*, *R. sebae*,*R. dorsalis*, *R. lehmanii, R. laukidi, R. muelleri* and *R. guatemalensis* by last unbranched ray not reaching anterior insertion of adipose fin (vs. last unbranched ray trespassing anterior insertion of adipose fin).

Differs from *R. foina*, *R poeyi,R. itacaiunas, R. parryi* and *R. xequetepeque* by superior lobe of caudal fin smaller than inferior lobe (*vs*. superior lobe of caudal fin larger than inferior lobe). Differs from *R. laticauda*, *R. humilis*, *R. nicaraguensis* by serrae in both sides of pectoral fin spine (*vs*. serrae in one side of pectoral fin spine). Differs from *R. quelen*, *R. parahybae,R. gabrielae*, *R. eurycephala, Rhamdia sp1* by sensory channels multiple (vs. sensory channels simple). Differs from *R. hilarii* and *Rhamdiasp3* (Uruguai) by long head length (26.2-28.8 vs. 23.8-24.9% SL in *R. hilarii* and 23.0-25.1% in *Rhamdiasp3*). Differs from *R. cinerascens* and *R. saijaensis* by insertion of adipose fin not equidistant between the dorsal and caudal fins (vs. insertion of the adipose fin equidistant between the dorsal and caudal fins).Differs from *R. jequitinhonha*, by longer maxillary barbel (45.1-64.4% SL *vs*. 39.2% SL). Differs from*R. reddelli*, *R. enfurnada*, *R. zongolicensis*, *R. macuspanensis* and *R. laluchensis* by the lack of morphological adaptations to troglobitic life.

Description - Measurements in Table 2. Body elongated; cross section of trunk roughly circular at dorsal-fin origin and along dorsal-fin base, gradually compressed posteriorly through caudal peduncle. Anterodorsal profile of body convex from supraoccipital to dorsal-fin base. Dorsal-fin base nearly straight, posteroventrally slanted, and gently convex from dorsal fin to base of adipose fin. Ventral body profile slightly curved from mouth to caudal-fin base. Body widest at pectoral girdle and deepest at dorsal-fin origin. Caudal peduncle longer than deep. Number of post-Weberian vertebrae 40.

Head depressed and long. Dorsal head profile flat and posterodorsally slightly slanted from snout tip to supraoccipital in lateral view. Lateral head profile flat. Head shape trapezoidal in dorsal view. Snout slightly rounded anteriorly in dorsal view, longer than deep. Transverse distance between posterior nares smaller than that between anterior nares. Mouth wide, subterminal, gape larger than interorbital distance; snout projecting slightly beyond lower jaw. Gape transverse, with fleshy rictal fold at corners. Rictal fold large. Both upper and lower lips with several longitudinal plicae.

Barbels flattened in cross section, wide at their bases and tapering towards distal tip. Maxillary barbel longest; length variable trespassing maximum insertion of pelvic fin; inserted above upper lip and posterolateral to anterior nares. Two pairs of mental barbels. External mental barbels reaching origin of pectoral fin. Inner mental barbels aligned to and shorter than external mental barbels, not reaching origin of pectoral fin. Gular fold distinct and V-shaped. Branchiostegal rays 6-7. Gill rakers thick and moderately long, with: 9 rakers on first ceratobranchial. Eye large, slightly elliptical (greatest length in longitudinal axis), with rim circumscribed with deep, continuous invagination, distinctly more pronounced at lateral border. Eye positioned dorsally, centered approximately in midlength between tip of snout and corner of opercular membrane, and widely separated by large interorbital space. Pupil rounded. Sensory channels of head multiple in dendritic form.

Dorsal fin with 2 unbranched rays and 7-8 branched rays, distal margin convex and base length more to fin height. First unbranched dorsa-fin ray small and not externally visible, second unbranched dorsal fin ray stiffened in proximal portion and segmented in distal portion. Dorsal-fin origin anterior to middle distance between pectoral and pelvic fin origins; insertion of last branched ray before pelvic fin origin. Tip of last branched dorsal-fin ray not reaching anterior insertion of adipose fin. Adipose fin long; within ascendant curve in lateral profile and posterior lobe conspicuously free from body. Adipose-fin origin at vertical through after posterior insertion pelvic fin, and posterior insertion at final third of caudal peduncle.

Pectoral fin within one unbranched and 7-8 branched rays; when adpressed reaching approximately origin of second branched ray of dorsal fin. Unbranched ray of pectoral fin stiffened, slightly curved and with strong serrations in two third of distal anterior side and delicate serration in two third of proximal posterior side. Pelvic fin rounded, slightly smaller of pectoral fin, within one unbranched ray and 5 branched rays, surpassing genital papilla, never reaching anal-fin origin. Pelvic-fin origin nearly at body midlength, after insertion of last dorsal-fin ray. Anal fin rounded, 2 unbranched rays anteriorly, followed by 7-9 branched rays, when adpressed never reach posterior insertion of adipose fin. Anal-fin base length shorter to dorsal-fin base length and approximately the same size as pelvic fin length. Caudal fin deeply forked, lobes rounded; dorsal lobe smaller in height and length; 7 branched rays in dorsal lobe and 8-9 branched rays in ventral lobe.

Color pattern of preserved specimens - Body brown or gray with or without very small dark brown irregular spots. With or without diffuse humeral spot. Head and fins brown or gray without spots. Ventral portion of body and head white. Maxillary barbels same color as body.

Distribution and Habitat – Occurs in basins of rio Jacuí, rio Taquari, rio dos Sinos, rio Caí, rio Camaquã, rio Jaguarão. All rivers are tributary of Laguna dos Patos, state of Rio Grande do Sul, Brazil (figure 4).

Table 2: Morphometric data of the *Rhamdia* sp2.

***Rhamdia* sp2** **(n=58)**			
	min-max	Mean±SD	Holotype
Standard length (mm)	74.2-282.0	178.14	221.74
Percent of Standard Length			
Maxillary-barbel length	36.0-81.7	59,9±15,09	50.5
Pectoral-girdle width	17.8-20.9	19,7±0,80	18.9
Pelvic-girdle width	9.3-11.2	10,1±0,49	9.7
Body depth	16.0-20.6	18,2±1,22	16.9
Pre-dorsal distance	33.9-39.2	37,2±1,42	36.5
Dorsal-fin to caudal-fin distance	45.3-51.1	48,9±1,62	47.4
Dorsal-fin to adipose-fin distance	5.8-10.1	7,3±0,96	8.0
Pre-pectoral distance	22.2-28.5	25,5±1,70	24.9
Pre-pelvic distance	49.6-54.3	51,8±1,54	51.5
Pre-anal distance	66.6-73.1	69,7±1,62	68.8
Pelvic-fin to anal-fin distance	17.8-21.4	19,4±1,12	19.8
Adipose-fin to caudal-fin distance	8.3-11.3	9,5±0,73	10.0
Caudal-peduncle length	16.4-20.7	18,6±1,01	20.0
Caudal-peduncle depth	8.6-10.5	9,7±0,62	9.0
Pelvic-fin length	10.7-15.7	13,4±1,50	12.1
Anal-fin base length	10.8-14.0	12,3±0,85	12.8
Anal-fin length	17.3-21.8	19,7±1,44	18.3
Dorsal-fin base length	13.5-17.6	15,7±1,07	14.9
Dorsal-fin height	11.1-16.9	14,1±1,93	13.5
Dorsal-fin spine length	6.1-8.4	7,3±0,73	6.9
Pectoral-fin spine length	7.8-11.4	9,9±1,08	9.8
Adipose-fin base length	28.4-37.4	32,7±2,20	30.0
Head length	26.2-28.8	27,3±0,82	26.3
Percent of Head Length			
Snout length	38.0-43.7	40.7±1.40	40.5
Snout height	30.8-37.9	33.6±2.27	32.6
Head height	45.9-55.6	49.5±2.54	48.1

Orbital diameter	12.3-19.5	14.3±1.46	13.4
Interorbital distance	18.0-36.0	30.0±3.79	21.9
Mouth length	18.7-44.7	40.4±5.43	41.2
Maxillary-barbels distance	33.1-38.9	35.5±1.55	34.3
Anterior nares distance	20.0-23.4	21.6±1.15	19.6
Anterior nares to posterior nares distance	13.1-15.9	14.3±0.82	13.7
Posterior nares to orbit distance	16.8-19.8	18.0±1.28	14.4
Posterior nares distance	16.7-19.8	17.8±0.94	16.0
External mental-barbels distance	30.8-36.4	33.2±1.73	35.1
Internal mental-barbels distance	14.3-18.3	16.4±1.11	17.2
Distance between mental-barbel	7.1-9.9	8.5±0.91	9.7
External mental-barbel length	58.7-110.7	88.2±17.43	85.0
Internal mental-barbel length	39.0-70.8	53.4±7.70	46.7
Head width at eye level	59.2-69.7	63.5±2.79	63.1

***Rhamdia* sp3**

(Fig. 5)

Holotype:

Examined material: All from Brazil**:** UFRGS 7523, 1, 299.2 mm SL, Brazil, state of Santa Catarina, municipality of Arabutã, rio Jacutinha, basin of rio Uruguai; ; J. Scalcon, 21 Ago 2004. UFRGS 11743, 2, 136.1-205.2 mm SL, Brazil, state of Rio Grande do Sul, municipality of Dom Pedrito arroio Taquarembó stream, basin of rio Uruguai; ; J. Giora and J. Wingert, 19 Oct 2009. UFRGS 15758, 1, 130.5 mm SL, Brazil, state of Rio Grande do Sul, municipality of Três Passos, rio Turvo, basin of rio Uruguai; 27°29'32"S, 53°49'44"W; J. Anza and J. Ferrer, 28 Oct 2011. UFRGS 4135, 2, 85.4-112.8 mm SL, Brazil, state of Rio Grande do Sul, municipality of Tenente Portela, Parizinho stream, basin of rio Uruguai; ; L.Bernardini and G. Bond 08 Ago 1986. UFRGS 22684, 2, 85.2-109.8 mm SL, Brazil, state of Rio Grande do Sul, municipality of Maximiliano de Almeida, rio Uruguai; 27°31'05"S, 51°49'53"W, T. Carvalho, D. Faustino, V. Vargas and J. Chuctaya, 27 Feb 2017. UFRGS 1699, 1, 209.5 mm SL, Brazil, state of Rio Grande do Sul, municipality of Ronda Alta, rio Passo Fundo, basin of rio Uruguai; ; C. da Silva, 14 May 1982. UFRGS 23175, 7, 105.7-196.2 mm SL, Brazil, state of Rio Grande do Sul, municipality of Nova Esperança do Sul, Calça Bota stream, basin of Ibicuí, 29°23'13"S, 54°46'43"W; C. Hartmann, T. Guimarães, R. Dala Corte, M. Camana, 26 Mar 2014. UFRGS 23533, 2, 276-268 mm SL, Brazil, state of Rio Grande do Sul, municipality of Santa Rosa, rio Santa Rosa; 27°46'15"S, 54°23'14"W; G. Volkmer, 26 Nov 2014. UFRGS, 19376, 1, 289.2 mm SL, Brazil, state of Rio Grande do Sul, municipality of Erval Seco, rio Guarita, basin of rio Uruguai; 27°36'49"S, 53°34'28"W, G. Volkmer, 08 Jan 2014. UFRGS 23532, 2, 267-225 mm SL, Brazil, state of Rio Grande do Sul, municipality of Erval Seco, rio Guarita, basin of rio Uruguai; 27°36'49"S, 53°34'28"W, G. Volkmer, 24 Nov 2014. UFRGS 23531, 2, 290-189 mm SL, Brazil, state of Rio Grande do Sul, municipality of Eugênio de Castro, rio Ijuizinho, basin of rio Uruguai; 28°26'38"S, 54°17'19"W; G. Volkmer, 28 Nov 2014. UFRGS, 11680, 1, 204 mm SL, Brazil, state of Rio Grande do Sul, municipality of Quevedo, rio Toropi, tributary of rio Ibicuí, basin of rio Uruguai; ; A. Hirschmann, 11 Jun 2009. UFRGS 6020, 3, 220-219 mm SL, Brazil, state of Rio Grande do Sul, municipality of Panambi, rio Palmeira, tributary of rio Ijuí, basin of rio Uruguai; ; J. Anza and J. Pezzi 02 Nov

2002. UFRGS 7526, 1, 143.9 mm SL, Brazil, state of Rio Grande do Sul, municipality of Concórdia, rio Jacutinga, basin of rio Uruguai; ; J. Scalcon, 30 Oct 2004. UFRGS XXXX, 4, 300,135 mm SL, Brazil, state of rio Grande do Sul, municipality of Panambi, rio ; basin of rio Uruguai;; L. Pezzi and R. Angrizani,

Diagnosis - *Rhamdia* sp3 differs from *R. sapo*, *R. cuyabae*, *R. sebae,R. dorsalis*, *R. lehmanii, R. laukidi, R. muelleri* and *R. guatemalensis* by last unbranched ray not reaching anterior insertion of adipose fin (vs. last unbranched ray trespassing anterior insertion of adipose fin). Differs from *R. foina*, *R poeyi,R. itacaiunas, R. parryi* and *R. xequetepeque* by superior lobe of caudal fin smaller than inferior lobe (*vs.* superior lobe of caudal fin larger than inferior lobe). Differs from *R. laticauda*, *R. humilis*, *R. nicaraguensis* by serrae in both sides of pectoral fin spine (*vs*. serrae in one side of pectoral fin spine). Differs from *R. quelen*, *R. parahybae,R. gabrielae*, *R. eurycephala, Rhamdia* sp1*, Rhamdia* sp4 *Rhamdia* sp5by sensory channels multiple (vs. sensory channels simple). Differs from *Rhamdia* sp2 by shorter head length (23.0-25.1% SL vs. 26-28.8% SL in *Rhamdiasp2*). Differs from *R. hilarii* by longer orbital distance (31.0-37.8% HL vs. 25.6-27.6% HL in *R. hilarii*). Differs from *R. cinerascens* and *R. saijaensis* by insertion of adipose fin not equidistant between the dorsal and caudal fins (vs. insertion of the adipose fin equidistant between the dorsal and caudal fins).Differs from *R. jequitinhonha*, by longer maxillary barbel (45.1-64.4% SL *vs*. 39.2% SL). Differs from*R. reddelli*, *R. enfurnada*, *R. zongolicensis*, *R. macuspanensis* and *R. laluchensis* by the lack of morphological adaptations to troglobitic life.

Description - Measurements in Table 3. Body elongated; cross section of trunk roughly circular at dorsal-fin origin and along dorsal-fin base, gradually compressed posteriorly through caudal peduncle. Anterodorsal profile of body convex from supraoccipital to dorsal-fin base. Dorsal-fin base nearly straight, posteroventrally slanted, and gently convex from dorsal fin to base of adipose fin. Ventral body profile slightly curved from mouth to caudal-fin base. Body widest at pectoral girdle and deepest at dorsal-fin origin. Caudal peduncle longer than deep. Number of post-Weberian vertebrae 40.

Head depressed. Dorsal head profile slightly rounded and posterodorsally slightly slanted from snout tip to supraoccipital in lateral view. Lateral head profile rounded. Snout rounded anteriorly in dorsal view, longer than deep. Transverse distance between posterior nares smaller than that between anterior nares. Mouth wide, subterminal, gape larger than interorbital distance; snout projecting slightly beyond lower jaw. Gape transverse, with fleshy rictal fold at corners. Rictal fold large. Both upper and lower lips with several longitudinal plicae.

Barbels flattened in cross section, wide at their bases and tapering towards distal tip. Maxillary barbel longest; length variable trespassing maximum insertion of pelvic fin; inserted above upper lip and posterolateral to anterior nares. Two pairs of mental barbels. External mental barbels reaching origin of pectoral fin. Inner mental barbels aligned to and shorter than external mental barbels, not reaching origin of pectoral fin. Gular fold distinct and V-shaped. Branchiostegal rays 6. Gill rakers thick and moderately long, with: 10-11 rakers on first ceratobranchial. Eye large, slightly elliptical (greatest length in longitudinal axis), with rim circumscribed with deep, continuous invagination, distinctly more pronounced at lateral border. Eye positioned dorsolaterally, centered approximately in first third between tip of snout and corner of opercular membrane, and widely separated by large interorbital space. Pupil rounded. Sensory channels of head multiple and dendritic form.

Dorsal fin with 2 unbranched rays and 7-8 branched rays, distal margin convex and base length more to fin height. First unbranched dorsa-fin ray small and not externally visible, second unbranched dorsal fin ray stiffened in proximal portion and segmented in distal portion. Dorsal-fin origin anterior to middle distance between pectoral and pelvic fin origins; insertion of last branched ray before pelvic fin origin. Tip of last branched dorsal-fin ray not reaching anterior insertion of adipose fin. Adipose fin long; within ascendant curve in lateral profile and posterior lobe conspicuously free from body. Adipose-fin origin at vertical through after posterior insertion pelvic fin, and posterior insertion at middle of caudal peduncle.

Pectoral fin within one unbranched and 7-9 branched rays; when adpressed reaching approximately origin of first branched ray of dorsal fin. Unbranched ray of pectoral fin stiffened, straight and with strong serrations in all anterior side and delicate serration in all posterior side. Pelvic fin rounded, approximately same size of pectoral fin, within one unbranched ray and 5 branched rays, surpassing genital papilla, never reaching anal-fin origin. Pelvic-fin origin nearly at body midlength, after insertion of last dorsal-fin ray. Anal fin rounded, with 2 unbranched rays anteriorly, followed by 8-9 branched rays, when adpressed never reach posterior insertion of adipose fin. Anal-fin base length shorter to dorsal-fin base length and approximately the same size as pelvic fin length. Caudal fin deeply forked, lobes rounded; dorsal lobe smaller in height and length; 7 branched rays in dorsal lobe and 8-9 branched rays in ventral lobe.

Color pattern of preserved specimens - Body brown or gray with or without very small dark brown irregular spots. With or without diffuse humeral spot. Head and fins brown or gray without spots. Ventral portion of body and head white. Maxillary barbels same color as body..

Distribution and Habitat – Occurs in medium and high basin of rio Uruguai, Brazil.

Table 3: Morphometric data of the *Rhamdia* sp3.

***Rhamdia* sp3 (n=20)**			
	min-max	Mean±SD	Holotype
Standard length (mm)	108.7-274.0	184,18	274
Percent of Standard Length			
Maxillary-barbel length	56.6-85.1	63.0±9.35	56.7
Pectoral-girdle width	18.2-23.0	19.6±1.47	23.0
Pelvic-girdle width	9.5-12.8	10.5±0.99	12.7
Body depth	16.7-20.3	18.2±1.32	20.2
Pre-dorsal distance	31.9-37.7	34.7±1.68	35.5
Dorsal-fin to caudal-fin distance	46.4-53.8	49.9±2.38	46.3
Dorsal-fin to adipose-fin distance	5.7-8.7	7.0±1.03	8.6
Pre-pectoral distance	23.0-25.8	23.8±0.89	25.8
Pre-pelvic distance	47.9-53.5	50.3±1.98	53.5
Pre-anal distance	67.1-73.0	68.6±2.02	67.0
Pelvic-fin to anal-fin distance	17.9-21.5	20.0±1.22	21.5
Adipose-fin to caudal-fin distance	7.4-20.6	9.1±1.07	7.3
Caudal-peduncle length	9.6-20.6	19.4±0.75	18.5
Caudal-peduncle depth	9.3-11.2	10.2±0.65	11.2
Pelvic-fin length	11.4-13.7	12.5±0.78	12.5
Anal-fin base length	11.3-13.1	12.1±0.64	11.6
Anal-fin length	18.7-21.6	20.1±0.93	19.7
Dorsal-fin base length	14.7-17.5	16.5±0.89	16.7
Dorsal-fin height	11.4-16.5	13.7±1.64	13.2

Dorsal-fin spine length	6.4-8.9	7.6±0.93	7.4
Pectoral-fin spine length	7.9-11.8	10.0±1.30	10.8
Adipose-fin base length	31.2-36.7	34.2±1.75	32.4
Head length	23.0-25.1	24.6±1.00	25.0
Percent of Head Length			
Snout length	37.8-42.4	39.8±1.49	38.7
Snout height	34.4-37.8	35.9±1.07	36.9
Head height	41.3-58.8	51.8±5.05	41.3
Orbital diameter	17.5-22.4	192±2.02	18.0
Interorbital distance	31.0-37.8	33.3±2.60	37.7
Mouth length	39.7-45.2	43.6±1.78	43.4
Maxillary-barbels distance	33.8-38.5	36.3±1.39	36.6
Anterior nares distance	19.0-23.0	20.8±1.31	21.0
Anterior nares to posterior nares distance	13.1-15.6	14.6±0.73	13.1
Posterior nares to orbit distance	15.8-19.4	17.3±1.42	17.8
Posterior nares distance	17.7-21.2	18.9±1.28	17.8
External mental-barbels distance	35.1-37.9	36.1±0.95	35.7
Internal mental-barbels distance	15.1-19.3	17.7±1.29	18.0
Distance between mental-barbel	9.2-10.6	9.6±0.49	9.1
External mental-barbel length	82.7-107.3	92.5±9.81	82.6
Internal mental-barbel length	47.1-65.8	58.8±6.77	47.0
Head width at eye level	63.7-73.9	70.3±4.17	273.3

***Rhamdia* sp4**

(Fig. 6)

Holotype: UFRGS 19905, 1, 254.3 mm SL, Brazil, state of Santa Catarina, municipality of Alfredo Wagner, rio Adaga, basin of rio Itajaí; 27°42'24"S, 49°16'31"W; L. Malabarba, M. Malabarba and R. Angrizani, 22 Feb 2015.

Examined material: All from Brazil, state of Santa Catarina: UFRGS 19905, 7, Brazil, state of Santa Catarina, municipality of Alfredo Wagner, rio Adaga, basin of rio Itajaí; 27°42'24"S, 49°16'31"W; L. Malabarba, M. Malabarba and R. Angrizani, 22 Feb 2015. UFRGS, 19907, 1, Brazil, state of Santa Catarina, municipality of Alfredo Wagner, rio Adaga, basin of rio Itajaí; 27°11'33"S, 49°18'20"W; L. Malabarba, M. Malabarba and R. Angrizani, 22 Feb 2015. UFRGS 22946, 1, xx mm SL, Brazil, state of Rio Grande do Sul, municipality of Petrolândia, little stream, basin of rio Itajaí; 27°33'05"S, 49°42'21"W; J. Ferrer, L. Donin, N. Pio and T. Carvalho, 28 May 2015.

Diagnosis - *Rhamdia* sp4 differs from *R. sapo*, *R. cuyabae*, *R. sebae,R. dorsalis*, *R. lehmanii, R. laukidi, R. muelleri* and *R. guatemalensis* by last unbranched ray not reaching anterior insertion of adipose fin (vs. last unbranched ray trespassing anterior insertion of adipose fin). Differs from *R. foina*, *R poeyi,R. itacaiunas, R. parryi* and *R. xequetepeque* by superior lobe of caudal fin smaller than inferior lobe (*vs.* superior lobe of caudal fin larger than inferior lobe). Differs from *R. laticauda*, *R. humilis*, *R. nicaraguensis* by serrae in both sides of pectoral fin spine (*vs*. serrae in one side of pectoral fin spine). Differs from *R. quelen, R. parahybae, R. gabrielae, R. eurycephala, Rhamdia* sp3 and *Rhamdia* sp5by shorter interorbital distance (17.3-18.8% HL vs. 34.8-39.6% HL in *R. quelen*, 32.7-37.5% HL in *R. parahybae,* 28.1-37.0% HL in *R. gabrielae*, 29.0-38.4% HL in *R. eurycephala,* 31.0-37.8% HL in *Rhamdia* sp3and30.6-34.6% in *Rhamdia* sp5). Differs from *Rhamdia* sp2 by shorter orbital diameter (17.3-18.8% HL vs. 12.3-16.6% HL in *Rhamdia* sp2). Differs from *R. hilarii* and *Rhamdia* sp1by longer head length (25.6-27.0% HL vs. 23.8-24.9% SL in *R. hilarii,* 22.8-24.1% SLin *Rhamdia* sp1). Differs from *R. cinerascens* and *R. saijaensis* by insertion of adipose fin not equidistant between the dorsal and caudal fins (vs. insertion of the adipose fin equidistant between the dorsal and caudal fins).Differs from *R. jequitinhonha*, by longer maxillary barbel (45.1-64.4% SL *vs*. 39.2% SL). Differs from*R. reddelli*, *R. enfurnada*, *R. zongolicensis*, *R. macuspanensis* and *R. laluchensis* by the lack of morphological adaptations to troglobitic life.

Description - Measurements in Table 4. Body elongated; cross section of trunk roughly circular at dorsal-fin origin and along dorsal-fin base, gradually compressed posteriorly through caudal peduncle. Anterodorsal profile of body convex from supraoccipital to dorsal-fin base. Dorsal-fin base nearly straight, posteroventrally slanted, and gently convex from dorsal fin to base of adipose fin. Ventral body profile slightly curved from mouth to caudal-fin base. Body widest at pectoral girdle and deepest at dorsal-fin origin. Caudal peduncle longer than deep.

Head depressed and long. Dorsal head profile strait and posterodorsally slightly slanted from snout tip to supraoccipital in lateral view. Lateral head profile rounded. Snout rounded anteriorly in dorsal view, longer than deep. Transverse distance between posterior nares smaller than that between anterior nares. Mouth wide, subterminal, gape larger than interorbital distance; snout projecting slightly beyond lower jaw. Gape transverse, with fleshy rictal fold at corners. Rictal fold large. Both upper and lower lips with several longitudinal plicae.

Barbels flattened in cross section, wide at their bases and tapering towards distal tip. Maxillary barbel longest; length variable trespassing maximum insertion of pelvic fin; inserted above upper lip and posterolateral to anterior nares. Two pairs of mental barbels. External mental barbels not reaching origin of pectoral fin. Inner mental barbels aligned to and shorter than external mental barbels, not reaching origin of pectoral fin. Gular fold distinct and V-shaped. Branchiostegal rays 6-7. Gill rakers thick and moderately long, with: 9 rakers on first ceratobranchial. Eye large, slightly elliptical (greatest length in longitudinal axis), with rim circumscribed with deep, continuous invagination, distinctly more pronounced at lateral border. Eye positioned dorsally, centered approximately in middle distance between tip of snout and corner of opercular membrane, and widely separated by large interorbital space. Pupil rounded. Sensory channels of head simple and tubular form.

Dorsal fin with 2 unbranched rays and 7-8 branched rays, distal margin convex and base length more to fin height. First unbranched dorsa-fin ray small and not externally visible, second unbranched dorsal fin ray stiffened in proximal portion and segmented in distal portion. Dorsal-fin origin anterior to middle distance between pectoral and pelvic fin origins;

insertion of last branched ray before pelvic fin origin. Tip of last branched dorsal-fin ray not reaching anterior insertion of adipose fin. Adipose fin long; within ascendant curve in lateral profile and posterior lobe conspicuously free from body. Adipose-fin origin at vertical through after posterior insertion pelvic fin, and posterior insertion at middle of caudal peduncle.

Pectoral fin within one unbranched and 7-8 branched rays; when adpressed reaching approximately origin of dorsal fin. Unbranched ray of pectoral fin stiffened, slightly curved and with strong serrations in all anterior side and strong serration in all posterior side. Pelvic fin rounded, approximately same size of pectoral fin, within one unbranched ray and 5 branched rays, surpassing genital papilla, never reaching anal-fin origin. Pelvic-fin origin nearly at body midlength, after insertion of last dorsal-fin ray. Anal fin rounded, with 2 unbranched rays anteriorly, followed by 8 branched rays, when adpressed never reach posterior insertion of adipose fin. Anal-fin base length shorter to dorsal-fin base length and approximately the same size as pelvic fin length. Caudal fin deeply forked, lobes rounded; dorsal lobe smaller in height and length; 7 branched rays in dorsal lobe and 8-9 branched rays in ventral lobe.

Color pattern of preserved specimens - Body brown or gray with or without very small dark brown irregular spots. With or without diffuse humeral spot. Head and fins brown or gray without spots. Ventral portion of body and head white. Maxillary barbels same color as body.

Distribution and Habitat – Occurs in small rivers in upper basin of rio Itajaí, in state of Santa Catarina, Brazil (figure 2).

Table 4: Morphometric data of the *Rhamdia* sp4.

	***Rhamdia* sp4** **(n=9)**		
	min-max	Mean±SD	Holotype
Standard length (mm)	99.7-254.3	130.1	254.3
Percent of Standard Length			
Maxillary-barbel length	30.4-63.0	54.9±10.49	30.4
Pectoral-girdle width	17.9-20.8	19.3±1.00	19.2

Pelvic-girdle width	8.2-9.9	8.9±0.51	9.9
Body depth	14.3-17.3	15.9±1.06	16.6
Pre-dorsal distance	36.3-39.5	37.4±1.08	36.6
Dorsal-fin to caudal-fin distance	46.5-53.4	50.7±2.21	49.2
Dorsal-fin to adipose-fin distance	6.5-11.0	9.0±1.61	10.9
Pre-pectoral distance	23.7-25.6	24.6±0.77	24.0
Pre-pelvic distance	48.2-52.3	50.2±1.56	48.2
Pre-anal distance	66.9-73.5	69.4±2.57	67.6
Pelvic-fin to anal-fin distance	17.7-23.2	20.1±1.81	20.0
Adipose-fin to caudal-fin distance	17.8-19.3	18.5±0.54	18.5
Caudal-peduncle length	8.9-10.4	9.7±0.44	8.9
Caudal-peduncle depth	8.5-10.7	9.2±0.73	9.4
Pelvic-fin length	10.3-13.4	12.4±0.99	10.3
Anal-fin base length	10.5-12.7	11.6±0.92	12.5
Anal-fin length	17.9-20.4	18.8±0.80	18.9
Dorsal-fin base length	14.2-15.6	15.0±0.49	15.0
Dorsal-fin height	11.4-16.3	13.9±1.54	11.4
Dorsal-fin spine length	5.9-9.6	8.0±1.05	5.9
Pectoral-fin spine length	8.9-12.4	10.5±1.19	9.0
Adipose-fin base length	29.1-34.5	31.7±2.09	29.5
Head length	25.6-27.0	26.0±0.47	25.6
Percent of Head Length			
Snout length	35.5-40.4	37.9±1.69	39.3
Snout height	31.1-36.1	33.6±1.97	35.3
Head height	48.1-52.4	49.7±1.46	49.3
Orbital diameter	17.3-18.8	18.1±0.53	17.4
Interorbital distance	24.4-29.9	26.4±1.96	29.9
Mouth length	38.1-45.8	40.8±2.57	45.7
Maxillary-barbels distance	34.0-38.1	35.6±1.54	38.1
Anterior nares distance	20.0-24.1	21.9±1.64	23.6
Anterior nares to posterior nares distance	11.7-15.9	13.6±1.54	14.4
Posterior nares to orbit distance	13.4-18.2	15.2±1.49	18.2
Posterior nares distance	16.5-20.0	18.1±1.21	19.2

External mental-barbels distance	31.5-38.9	33.5±2.55	38.8
Internal mental-barbels distance	12.9-19.4	15.1±1.91	19.3
Distance between mental-barbel	7.4-9.8	8.6±0.86	8.6
External mental-barbel length	45.8-93.6	75.9±14.58	45.8
Internal mental-barbel length	39.4-54.6	48.2±4.67	39.4
Head width at eye level	58.0-67.4	61.1±3.07	67.3

Rhamdia sp5

(figure 7)

Holotype:

Diagnoses: *Rhamdia sp5* differs from *R. sapo*, *R. hilarii, R. cuyabae*, *R. sebae, R. dorsalis*, *R. lehmanii, R. laukidi, R. muelleri, R. saijaensis, R. guatemalensis, R. quelen, R. parahybae, R. Jequitinhonha, R. gabrielae, Rhamdia sp1, Rhamdia sp2, Rhamdia sp3, Rhamdia sp4* by smaller orbital diameter (10.1-12.6% HL vs. 13.3-17.8% HL in *R. quelen,* 11.4-14.7% HL in *R. sapo*, *R. hilarii,* 13.4-17.2% HL in *R. cuyabae*, 16.1-19.6% HL in *R. sebae,* 12.8-15.4% HL in *R. dorsalis*, 14.9-18.2% HL in *R. lehmanii,* 13.2-15.5% in *R. laukidi,* 21.7-37.8% HL in *R. muelleri,* 13.0-18.2% inHL *R. saijaensis,* 13.2-23.2% HL in *R. guatemalensis,* 12.8-16.0% HL in *R. parahybae,* 20.4% HL in *R. jequitinhonha,* 15.0-19.0% HL in *R. gabrielae,* 15.7-18.0 HL *Rhamdia* sp1*,* 12.3-19.5% HLin *Rhamdia* sp2*,* 17.5-22.4% HL *Rhamdia* sp3*,* 17.3-18.8% HL in *Rhamdia* sp4). Differs from *R. foina*, *R poeyi, R. itacaiunas, R. parryi* and *R. xequetepeque* by superior lobe of caudal fin smaller than inferior lobe (*vs.* superior lobe of caudal fin larger than inferior lobe). Differs from *R. eurycephala* by smaller head width at eye level (66.6-74.1% HL vs. 78.3-89.6% HL). Differs from *R. cinerascens* and by insertion of adipose fin not equidistant between the dorsal fin and caudal fin (vs. insertion of the adipose fin equidistant between the dorsal fin and caudal fin). Differs from *R. reddelli*, *R. enfurnada*, *R. zongolicensis*, *R. macuspanensis* and *R. laluchensis* by the lack of morphological adaptations to troglobitic life.

Description - Measurements in Table 5. Body elongated; cross section of trunk roughly circular at dorsal-fin origin and along dorsal-fin base, gradually compressed posteriorly to caudal peduncle. Anterodorsal profile of body convex from supraoccipital to dorsal-fin base. Dorsal-fin base nearly straight, posteroventrally slanted, and gently convex from dorsal fin to base of caudal fin. Ventral body profile nearly straight from mouth to caudal-fin base. Body widest at pectoral girdle and deepest at dorsal-fin origin. Caudal peduncle longer than deep.

Dorsal head profile slightly rounded and posterodorsally slanted from snout tip to supraoccipital in lateral view. Lateral head profile slightly rounded. Snout rounded anteriorly in dorsal view, longer than deep. Transverse distance between posterior nares slightly smaller than that between anterior nares. Mouth wide, subterminal, transverse gape larger than interorbital distance; snout projecting slightly beyond lower jaw. Large, fleshy rictal fold at corners of mouth. Both upper and lower lips with several longitudinal plicae.

Barbels flattened in cross section, wide at their bases and tapering towards distal tip. Maxillary barbel longest; length variable reaching maximum insertion of anal fin; inserted above upper lip and posterolateral to anterior nares. Two pairs of mental barbels. External mental barbels trespassing origin of pectoral fin. Inner mental barbels aligned to and shorter than external mental barbels, trespassing origin of pectoral fin. Gular fold distinct and V-shaped. Branchiostegal rays 5-6. Gill rakers thick and moderately short, with: 5 rakers on first ceratobranchial. Eye small, slightly elliptical (greatest length in longitudinal axis), with rim circumscribed with deep, continuous invagination, distinctly more pronounced at lateral border. Eye positioned dorsolaterally, approximately before midlength between tip of tip of snout and corner of opercular membrane, and widely separated by large interorbital space. Pupil rounded. Sensory channels of head simple and circular form.

Dorsal fin with two unbranched rays and six branched rays, distal margin convex and base length approximately equal than to fin height. First unbranched dorsal-fin ray small and not externally visible, second unbranched ray stiffened proximally, segmented distally. Dorsal-fin origin at midlength between pectoral and pelvic-fin origins; insertion of last branched ray just before or at pelvic-fin origin. Tip of last branched dorsal-fin ray not reaching anterior insertion of adipose fin. Adipose fin long; with ascendant curve in in lateral profile and posterior lobe conspicuously free from body. Adipose-fin origin at vertical through middle of depressed pelvic fin and posterior insertion at middle of caudal peduncle.

Pectoral fin within one unbranched and 7-8 branched rays; when adpressed, reaching approximately origin of second branched dorsal-fin ray. Unbranched ray of pectoral fin stiffened, straight and with strong serrations along distal anterior side and delicate serrations along proximal posterior side. Pelvic fin rounded, approximately same size of pectoral fin, having one unbranched ray and five branched rays, distal tip surpassing genital papilla, never reaching anal-fin origin. Pelvic-fin origin nearly at middle of standard length, just after insertion of last dorsal-fin ray. Anal fin rounded, with 2-3 unbranched rays anteriorly, followed by 8-9 branched rays; when adpressed, never exceeds posterior insertion of adipose-fin. Length of anal-fin base approximately equal to that of dorsal fin. Caudal fin deeply forked, lobes rounded; dorsal lobe smaller in depth and length; 7 branched rays in dorsal lobe and 8-9 branched rays in ventral lobe.

Color pattern of preserved specimens - Body brown or gray with very small dark brown irregular spots. With or without diffuse humeral spot. Head and fins brown or gray without spots. Ventral portion of body and head white. Maxillary barbels same color as body.

Distribution and Habitat – Occurs in basin of rio Acarí, in São Francisco island in state of Santa Catarina and in little stream in Bertioga, sate of São Paulo (Figure 2).

Table 5: Morphometric data of the *Rhamdia* sp5.

***Rhamdia* sp5** **(n=11)**			
	min-max	Mean±SD	Holotype
Standard length (mm)	132.1-217.46	160.62	217.4
Percent of Standard Length			
Maxillary-barbel length	48.4-62.6	57.2±4.36	62.5
Pectoral-girdle width	16.5-19.8	18.7±0.94	18.7
Pelvic-girdle width	7.8-9.3	8.5±0.49	9.0
Body depth	16.2-19.7	17.8±1.19	18.4
Pre-dorsal distance	32.4-35.0	30.7±0.85	33.6
Dorsal-fin to caudal-fin distance	50.5-58.8	53.9±2.57	54.2
Dorsal-fin to adipose-fin distance	4.6-7.8	6.2±1.06	7.8
Pre-pectoral distance	21.8-25.4	23.4±1.09	21.8
Pre-pelvic distance	47.0-50.4	48.7±1.23	48.6
Pre-anal distance	63.9-68.0	66.1±1.38	67.8
Pelvic-fin to anal-fin distance	17.4-21.8	19.1±1.44	21.8
Adipose-fin to caudal-fin distance	9.7-12.2	10.6±0.73	10.6
Caudal-peduncle length	18.0-21.2	19.4±0.94	21.2
Caudal-peduncle depth	8.2-10.3	9.1±0.58	9.2
Pelvic-fin length	11.2-14.4	12.6±1.12	14.3
Anal-fin base length	13.0-16.3	14.7±0.98	13.0
Anal-fin length	21.0-24.0	22.2±1.13	21.5
Dorsal-fin base length	12.9-15.3	13.9±0.75	13.4
Dorsal-fin height	12.5-14.6	13.4±0.78	14.0

Dorsal-fin spine length	6.2-7.6	6.8±0.45	6.9
Pectoral-fin spine length	8.7-10.6	9.4±0.61	8.9
Adipose-fin base length	35.9-40.8	38.1±1.76	35.8
Head length	22.8-25.6	23.9±0.77	22.7
Percent of Head Length			
Snout length	37.2-39.6	38.8±0.80	38.0
Snout height	31.6-36.8	34.4±1.57	35.8
Head height	55.8-61.4	58.0±1.92	57.2
Orbital diameter	10.1-12.6	11.1±0.67	11.3
Interorbital distance	30.6-34.6	32.9±1.24	34.3
Mouth length	43.6-53.2	49.3±2.89	48.4
Maxillary-barbels distance	36.2-39.9	38.8±1.12	39.4
Anterior nares distance	22.5-25.9	24.2±1.22	22.9
Anterior nares to posterior nares distance	12.2-14.2	13.2±0.70	12.6
Posterior nares to orbit distance	13.0-16.3	15.0±1.02	16.0
Posterior nares distance	19.1-22.3	20.4±0.95	20.2
External mental-barbels distance	41.8-44.6	43.1±1.06	43.4
Internal mental-barbels distance	22.5-25.2	23.5±0.79	22.5
Distance between mental-barbel	9.2-12.5	10.5±1.07	10.7
External mental-barbel length	100.2-119.3	108.5±6.83	117.5
Internal mental-barbel length	62.7-85.1	71.2±7.71	85.1
Head width at eye level	66.6-74.1	70.2±2.39	74.1

Discussion

The redescription of *R. quelen* was the key to carry out a correct taxonomic revision within the genus. All the 17 South American synonyms of *R. quelen* were revisited, being possible to allocate these nominal taxa in the following valid species: *R. quelen, R. sebae, R. sapo, R. hilarii, R. pentlandii, R. dorsalis, R. lehmanni, R. cuyabae* and *R. parahybae*.

These nine taxa correspond to nine of the 18 lineages supported by molecular data in the study of Angrizani & Malabarba (2017), and thus nine lineages remained unnamed since they cannot be related to any name available for *Rhamdia*. In the present study, specimens related to five of these lineages were morphologically analyzed, and it was possible to diagnose and describe five of them as new species for the genus.

Rhamdia sp1 corresponds to HA1 lineage present in the Atlantic-Highland clade. This species occurs in small streams in the upper portion of the Jacuí river drainage. This species can be recognized by: short head (22.8-24.1% CP) and low depth head (50.3-61.0 CC), with a dorsal profile rounded, straight laterally, with simple sensory pores; six branched rays in the dorsal fin, with the last branched ray not exceeding the insertion of the adipose fin; pectoral spine with strong saws in the two thirds distal length of the anterior face and with delicate saws in the proximal two thirds length of the posterior face; upper lobe of the caudal fin shorter than the inferior lobe.

Rhamdia sp2 corresponds to lineage CC3, present in the Continental clade. This species occurs in the rivers of the Patos lagoon drainage, being recognized by the following characteristics: long head (26-28.8% CP) and low depth head (45.9-55.6% CC), with dorsal and lateral profiles straight, with sensory pores multiple and dendritic; seven or eight branched rays in the dorsal fin, with the last branched ray not exceeding the insertion of the adipose fin; pectoral spine with strong saws in the two thirds distal length of the anterior face and delicate serrations in the proximal two thirds length of the posterior face; upper lobe of the caudal fin shorter than lower lobe.

Rhamdia sp3 corresponds to CC4 lineage, present in the Continental clade. This species occurs along the middle and upper portions of Uruguay River drainage, in the states of Rio Grande do Sul and Santa Catarina, Brazil. Rhamdia sp3 can be recognized by: short head (23.0-25.1% CP) and low depth head (41.3-58.8% CC), with sensorial pores multiple and dendritic; seven to nine branched rays in the dorsal fin, with the last branched ray not exceeding the insertion of the adipose fin; spine of the pectoral straight with strong saws throughout the anterior face and delicate serrations throughout the posterior face; upper lobe of the caudal fin shorter than the lower lobe.

Rhamdia sp4 corresponds to CC5 lineage, present in the Continental clade. This species occurs in small streams in the upper portion of the Itajaí River drainage, in the state of Santa Catarina, Brazil. This species can be recognized by: short head (25.6-27.0% CP) and low depth head (48.1-52.4% CC), with dorsal head profile straight and lateral head profile rounded, with sensorial pores simple and tubular; seven branched rays in the dorsal fin, with the last branched ray not exceeding the insertion of the adipose fin; pectoral-fin spine with strong serrations in all anterior side and delicate serration in all posterior side; upper lobe of the caudal fin shorter than the lower lobe.

Rhamdia sp5 corresponds to lineage LA5, present in Atlantic-Lowland clade. This species occurs in small coastal rivers of the island of São Francisco do Sul (Santa Catarina state) and in the region of the municipality of Bertioga (state of São Paulo). These rivers have dark water and are located in regions of strong marine influence. This species can be recognized by: short head (22.8-25.6% CP) and high depth head (55.8-61.4% CC), with dorsal and lateral profiles slightly rounded, with simple sensorial pores; six branched rays in the dorsal fin, with the last branched ray not exceeding the insertion of the adipose fin; pectoral spine with strong serrations along distal anterior side and delicate serrations along proximal posterior side; upper lobe of the caudal fin shorter than lower lobe.

Even though one hundred nominal species seems to be an exaggerated number of species for *Rhamdia*, and in fact several of these are synonyms or belong to other genera, the diversity of the genus has largely been underestimated in the last two decades. The five species described herein, along with those described or revalidated by Angrizani & Malabarba (2017a,b,c) raise this number to 35 species, an increase of more than three times in the number of species recognized in the last review of the genus (Silfvergrip, 1996).

References

Angrizani, R.A, Malabarba, L.R (2017). Biogeography of *Rhamdia quelen* (Siluriformes: Heptapteridae) species complex in South America.

Angrizani, R.A, Malabarba, L.R (2017). Redescription of *Rhamdia quelen* and *Rhamdia sapo* (Siluriformes: Heptapteridae).

Angrizani, R.A, Malabarba, L.R (2017).Review of *Rhamdia quelen* synonyms and redescription of seven revalidated species from South America (Siluriformes: Heptapteridae).

Bichuette, M.E, Trajano, E. (2005). A new cave species of *Rhamdia* (Siluriformes: Heptapteridae) from Serra do Ramalho, northeastern Brazil, with notes on ecology and behavior. *NeotropicalIchthyology,*3(4), 587–595.

Bussing, W.A. (1998). *Freshwater fishes of Costa Rica*. Editorial Universidad de Costa Rica, vol 4.

Galvis, G, Mojica, J.I, Camargo, M. (1997). *Peces del Catatumbo*. Santafé de Bogotá, Asociación Cravo Norte, pp. 188.

Garavello, J.C, Shibatta, O.A. (2016). Reappraisal of *Rhamdiabranneri* Haseman, 1911 and *R. voulezi* Haseman, 1911 (Siluriformes: Heptapteridae) from the rio Iguaçu with notes on their morphometry and karyotype. *Neotropical Ichthyology,*14(1).

Greenfield, D.W, Thomerson, J.E. (1997). *Fishes of the continental waters of Belize.* Florida, University Press of Florida.

Hernández, C.L, Ortega-Lara, A, Sánchez-Garcés, G.C, & Alford, M.H. (2015). Genetic and morphometric evidence for the recognition of several recently synonymized species of trans-Andean Rhamdia (Pisces: Siluriformes: Heptapteridae). *Copeia*, *103*(3), 563-579.

Lopez, H.L, Morgan, C.C. & Montenegro, M.J. (2002). Ichthyological ecoregions of Argentina. *ProBiota,* 1, 1–68.

Perdices, A, Bermingham, E, Montilla, A. & Doadrio, I. 2002. Evolutionary history of the genus *Rhamdia* (Teleostei: Pimelodidae) in Central America. *Molecular Phylogenetics and Evolution,*25(1), 172–189.

Romero, A. & Paulson, K.M. (2001). It's a wonderful hypogean life: a guide to the troglomorphic fishes of the world. In: *The biology of hypogean fishes*. Springer

Netherlands, 13–41.

Silfvergrip, A.M.C. (1996). *A systematic review of the Neotropical catfish genus* Rhamdia*(Teleostei, Pimelodidae)*. Stockholm, Swedish Museum of Natural History.

Weber, A, Allegrucci, G. & Sbordoni, V. (2003). *Rhamdia laluchensis*, a new species of troglobitic catfish (Siluriformes: Pimelodidae) from Chiapas, Mexico. *Ichthyological Exploration of Freshwaters,*14(3), 273–280.

Figura 1: Holotype of *Rhamdia* sp1, UFRGS 23350 (163.2 mm SL), in lateral view.

Figure 2: Distribution map of *Rhamdia* sp1, *Rhamdia* sp4, and *Rhamdia* sp5 in state of Santa Catarina and Rio Grande do Sul, Brazil. Pink circule represent distribution points of *Rhamdia* sp1 and pink star represent type locality of *Rhamdia* sp1. White circules are distribution point of *Rhamdia* sp4 and white star are type locality of *Rhamdia* sp4. Orange star represent the type locality of *Rhamdia* sp5.

Figura 3: Holotype of Rhamdia sp2. UFRGS (), in lateral view.

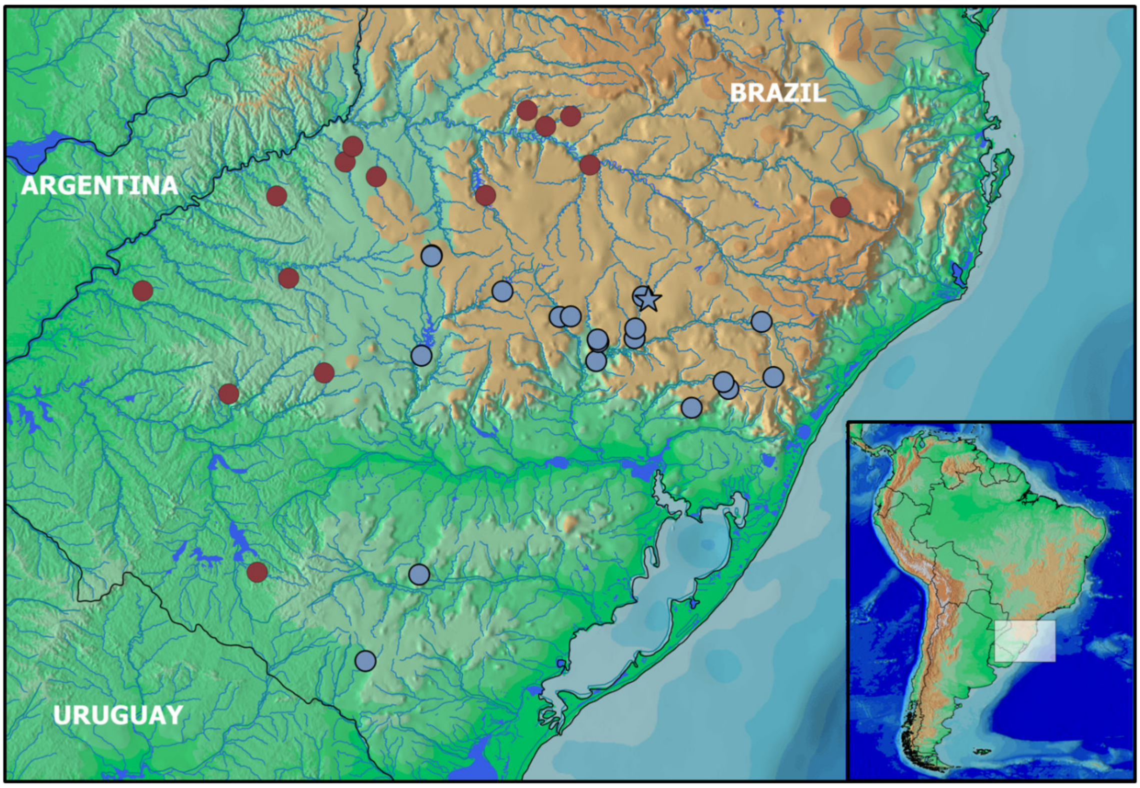

Figure 4: Distribution map of *Rhamdia* sp2, in drainage of laguna dos Patos, and *Rhamdia* sp3 in drainage of rio Uruguai. Grey circules are the distribution points of *Rhamdia* sp2 and grey star are the type locality of *Rhamdia* sp2. Crimson circules are distribution points of *Rhamdia* sp3 and crimson star are the type locality of *Rhamdia* sp3.

Figura 5: Holotype of Rhamdia sp3. UFRGS (274 mm), in lateral view.

Figura 6: Holotype of *Rhamdia* sp4, UFRGS 19905 (254.3 mm SL), in lateral view.

Figura 7: Holotype of *Rhamdia* sp5, UFRGS (217.4 mm SL), in lateral view.

9. Considerações finais

É demonstrado que *Rhamdia* é um grupo monofilético composto por dois grandes clados: um Cis-Andino e outro Trans-Andino.Neste estudo são discutidas as relações evolutivas dentro do complexo de espécies *Rhamdia quelen*, demonstrando que o complexo ocorre apenas na América do sul e é composto por pelo menos 18 diferentes linhagens evolutivas, que estão dispostas em três grandes clados.

Através de análises morfológicas integradas com os resultados genéticos foi possível delimitar corretamente a espécie*R. quelen*, indicando sua distribuição geográfica e localidade tipo, indicando-se um novo neótipo. Dessa forma foram revistos todos os sinônimos junioresde *R. quelen* que ocorrem na América do Sul, possibilitando revalidar 8 espécies antes sinonimizadas e descrever 5 novas espécies.Após esse estudo, *Rhamdia* voltou a ser um grupo diverso, com pelo menos 35 epsecies válidas.

A taxonomia integrativa, que foi utilizada nesse estudo, demontrou ser uma abordagem muito útil para delimitação de espécies em grupo com taxonomias complicadas e com caracteres morfologicos muito próximos, comoé o caso de *Rhamdia*.

Referencias

Angulo, A., Garita-Alvarado, C. A., Bussing, W. A., & López, M. I. (2013). Annotated checklist of the freshwater fishes of continental and insular Costa Rica: additions and nomenclatural revisions. *Check List*, *9*(5), 987-1019.

Anza, J. A. (2006). Revisão das espécies do gênero Rhamdia (siluriformes: heptapteridae) de drenagens costeiras do sul e sudeste do Brasil, um exemplo de diversidade subestimada do gênero.

Barbour, T., & Cole, L. J. (1906). Vertebrata from Yucatan, Reptilia, Amphibia, and Pisces.

Behre, E. H. (1928). A list of the fresh water fishes of western Panama between long. 81 45 and 83 15 W. *Ann. Carnegie Mus*, *18*(2), 305-328.

Bermingham, E, McCafferty, S.S, Martin, A.P. (1997). Fish biogeography and molecular clocks: perspectives from the Panamanian Isthmus. In: Kocher, T.D, Stepien, C.A, eds. *Molecular Systematics of Fishes*. San Diego, Academic Press, pp. 113–128.

Bertaco, V.A, Ferrer, J, Carvalho, F.R, Malabarba, L.R. (2016). Inventory of the freshwater fishes from a densely collected area in South America - a case study of the current knowledge of Neotropical fish diversity. *Zootaxa,*4138(3), 401–440.

Bleeker, P. (1858). De visschen van den Indischen Archipel beschreven en toegelicht. Deel I. Siluri. Acta Societatis Regiae Scientiarum Indo-Neêrlandicae v. 4 (art. 2): i-xii + 1-370. [Date of publication from Kottelat 2011:79 [ref. 31413] Also published as book: *Ichthyologiae Archipelagi Indici Prodromus. Vol 1. Siluri*. Batavia on 23 Sept. 1858.

Bloch, M. E. (1794). *Naturgeschichte der ausländischen Fische*. Berlin. v. 8: i-iv + 1-174, Pls. 361-396.

Bichuette, M.E, Trajano, E. (2005). A new cave species of *Rhamdia* (Siluriformes: Heptapteridae) from Serra do Ramalho, northeastern Brazil, with notes on ecology and behavior. *NeotropicalIchthyology,*3(4), 587–595.

Bockmann, F. A. (1998). *Análise filogenética da família Heptapteridae (Teleostei, Ostariophysi, Siluriformes) e redefinição de seus gêneros*(Doctoral dissertation).

Bockmann, F. A., Guazzelli, G. M. (2003). In: Reis, R. E., Kullander, S. O., & Ferraris, Jr, C. J. 2003. *Check list of the freshwater fishes of South and Central America*.Edipucrs.

Bockmann, F. A., & Castro, R. (2010). The blind catfish from the caves of Chapada Diamantina, Bahia, Brazil (Siluriformes: Heptapteridae): description, anatomy, phylogenetic relationships, natural history, and biogeography. *Neotropical Ichthyology*, *8*(4), 673-706.

Bockmann, F. A., & Miquelarena, A. M. (2008). Anatomy and phylogenetic relationships of a new catfish species from northeastern Argentina with comments on the phylogenetic relationships of the genus Rhamdella Eigenmann and Eigenmann 1888 (Siluriformes, Heptapteridae). *Zootaxa*, *1780*, 1-54.

Bussing, W.A. (1998). *Freshwater fishes of Costa Rica*. Editorial Universidad de Costa Rica, vol 4.

Britski, H. A. (2001). Sobre a obra Velhas-Flodens Fiske [Peixes do Rio das Velhas. In: Alves, C. B. M., & Pompeu, P. S. 2001. *Peixes do Rio das Velhas: passado e presente (CBM Alves & PS Pompeu, eds.). SEGRAC, Belo Horizonte*, 15-22.

Burgess, W. (1989). *An atlas of freshwater and marine catfishes: a preliminary survey of the Siluriformes*. tfh publications.

Bussing, W. A. (1987). *Peces de las aguas continentales de Costa Rica*. Editorial Universidad de Costa Rica.

Casatti, L., & Castro, R. M. C. (1998). A fish community of the São Francisco River headwaters riffles, southeastern Brazil. *Ichthyological exploration of freshwaters*, *9*, 229-242.

Cépède, L. (1830). *Les âges de la nature et histoire de l'espèce humaine* (Vol. 1). FG Levrault.

Cope, E. D. (1867). Supplement on some new species of American and African fishes. *Transactions of the American Philosophical Society*, *13*, 400-407.

Cuvier, G. (1829). *Le Règne Animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*. Edition 2. v. 2: i-xv + 1-406.

Dahl, G. 1961. Nematognathous fishes collected during the Macarena Expedition 1959. Part II: Pimelodidae, Callophysidae. *Novedades Colombianas* v. 1(6): 483-514.

Devincenzi, G. J. (1925). El primer ensayo sobre Ictyiología del Uruguay. La clase "Peces" de la zoología de don Dámaso A. Larrañaga. In: *Anales del Museo Nacional de Historia Natural de Montevideo (Ser. 2)*(Vol. 6, pp. 295-323).

DoNascimiento, C., Provenzano, F., & Lundberg, J. G. (2004). *Rhamdiaguasarensis* (Siluriformes: Heptapteridae), a new species of cave catfish from the Sierra de Perijá, northwestern Venezuela. *Proceedings of the Biological Society of Washington*, *117*(4), 564-574.

Doyle, J. J., & Doyle, J. L. (1987). CTAB DNA extraction in plants. *Phytochemical Bulletin*, *19*, 11-15.

Drummond, A.J, Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC evolutionary biology,*7(1), 214.

Eigenmann, C. H. (1917). *Pimelodella* and *Typhlobagrus*. Memoirs of the Carnegie Museum v. 7 (no. 4): 229-258, Pls. 29-35.

Eigenmann, C. H. (1920). The fishes of Lake Valencia, Caracas, and of the Rio Tuy at El Concejo, Venezuela. (Contrib. Zool. Lab. Ind. Univ. No. 170). *Indiana University Studies v. 7* (no. 44): 1-13, Pls. 1-3.

Eigenmann, C. H. (1920) In: Pearson, N. E. 1924. The fishes of the eastern slope of the Andes. I. The fishes of the Rio Beni basin, Bolivia, collected by the Mulford expedition. *Indiana University Studies v. 11* (no. 64): 1-83, Pls. 1-12.

Eigenmann, C.H, Eigenmann, R.S. (1888). Preliminary notes on South American Nematognathi. I. *Proceedings of the California Academy of Sciences* (1): 119-172.

Eigenmann, C. H. & Eigenmann. R. S. (1890). A revision of the South American Nematognathi or cat-fishes. Occasional Papers California Academy of Sciences No. 1: 1-508.

Eigenmann, C. H., & Fisher, H. G. (1917). *On Some Species of Rhamdia: A Genus of South American Siluridae, in the Carnegie Museum*. Carnegie Museum.

Eigenmann, C. H., & Allen, W. R. (1942). *Fishes of Western South America: 1. The Intercordilleran and Amazonian Lowlands of Peru. 2. The High Pampas of Peru, Bolivia and Northern Chile; With a Revision of the Peruvian Gymnotidae and of the Genus Orestias*. University of Kentucky.

Eschmeyer, W. N. and R. Fricke, and R. van der Laan (eds). CATALOG OF FISHES: GENERA, SPECIES, REFERENCES.(http://researcharchive.calacademy.org /research/ichthyology/catalog/fishcatmain.asp). Electronic version accessed dd mmm 2017.

Evermann, B. W. & and Kendall, W. C. (1907) Notes on a Collection of Fishes from Argentina, South America, with descriptions of Three New Species. *Proceedings of the United States National Museum* No. 1482.

Excoffier, L, Laval, G. & Schneider, S. (2005). Arlequin 3.01: An integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online,* 1, 47–50.

Fernández-Yepez, A., & Martín Salazar, F. (1952). Notas sobre la fauna ictiológica de la region Baruta-El Hatillo. *Memoria, Sociedad de Ciencias Naturales La Salle*, *12*, 31-45.

Ferraris CJ. 2007. *Checklist of catfishes, recent and fossil (Osteichthyes: Siluriformes), and catalogue of siluriform primary types* (pp. 1-628). Auckland, New Zealand: Magnolia Press.

Fitzgibbon, R. H. (1954). Uruguay Portrait Of A Democracy.

Fowler, H. W. (1906). Further knowledge of some heterognathous fishes. Part I. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 293-351.

Fowler, H. W. (1914). Fishes from the Rupununi River, British Guiana. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 229-284.

Fowler, H. W. (1915). The fishes of Trinidad, Grenada, and St. Lucia, British West Indies. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 520-546.

Fowler, H. W. (1932). Notes on fresh water fishes from Central America. *Proceedings of the Academy of Natural Sciences of Philadelphia*, *84*, 379-385.

Fowler, H. W. (1935). Fresh-water fishes obtained in Guatemala by Mr. Rodolphe Meyer de Schauensee in 1935. *Proceedings of the Academy of Natural Sciences of Philadelphia*, *87*, 515-531.

Fowler, H. W. (1941). A collection of fresh-water fishes obtained in eastern Brazil by Dr. Rodolpho von Ihering. *Proceedings of the Academy of Natural Sciences of Philadelphia*, *93*, 123-336.

Fu, Y.X. (1997). Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics*,147(2), 915–925.

Galvis, G, Mojica, J.I, Camargo, M. (1997). *Peces del Catatumbo*. Santafé de Bogotá, Asociación Cravo Norte, pp. 188.

Garavello, J.C, Shibatta, O.A. (2016). Reappraisal of *Rhamdiabranneri* Haseman, 1911 and *R. voulezi* Haseman, 1911 (Siluriformes: Heptapteridae) from the rio Iguaçu with notes on their morphometry and karyotype. *Neotropical Ichthyology,*14(1).

Greenfield, D.W, Thomerson, J.E. (1997). *Fishes of the continental waters of Belize.* Florida, University Press of Florida.

Gill, T. N. (1858). Synopsis of the fresh water fishes of the western portion of the island of Trinidad, *W. I. Annals of the Lyceum of Natural History of New York v. 6* (nos 10-13, art. 38): 363-430.

Gill, T.N. 1870. On some new species of fishes obtained by Prof. Orton from the Maranon, or Upper Amazon, and Napo Rivers. *Proceedings of the Academy of Natural Sciences of Philadelphia* v. 22: 92-96.

Gill, T. (1876). Notes on Fishes from the Isthmus of Panama, Collected by Dr. JF Bransford, USN. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 335-339.

Greenfield, D. W., Greenfield, T. A., & Woods, R. L. (1982). new subspecies of cave-dwelling pimelodid catfish, Rhamdia laticauda typhla from Belize, Central America. *Brenesia*.

Guedes, D. S. (1980). Contribuição ao estudo da sistemática e alimentação de jundiás (Rhamdia spp) na região central do Rio Grande do Sul (Pisces, Pimelodidae). *Santa Maria–RS*.

Günther, A. (1859). *Catalogue of the fishes in the British Museum. Catalogue of the acanthopterygian fishes in the collection of the British Museum. Gasterosteidae, Berycidae, Percidae, Aphredoderidae, Pristipomatidae, Mullidae, Sparidae.* v. 1: i-xxxi + 1-524.

Günther, A. (1860). Catalogue of the fishes in the British Museum. Catalogue of the acanthopterygian fishes in the collection of the British Museum. Squamipinnes, Cirrhitidae, Triglidae, Trachinidae, Sciaenidae, Polynemidae, Sphyraenidae, Trichiuridae, Scombridae, Carangidae, Xiphiidae. *British Mus., London. v. 2*: i-xxi + 1-548.

Günther, A. 1864. *Catalogue of the fishes in the British Museum. Catalogue of the Physostomi, containing the families Siluridae, Characinidae, Haplochitonidae, Sternoptychidae, Scopelidae, Stomiatidae in the collection of the British Museum.* British Museum, London v. 5: i-xxii, 1-455 pp.

Günther, A. (1868). XIV. An account of the Fishes of the States of Central America, based on collections made by Capt. JM Dow, F. Godman, Esq., and O. Salvin, Esq. *Journal of Zoology*, *6*(7), 377-494.

Güntert, H. (1942). *Beschreibung einiger zum Teil noch unbekannter s ̈damerikanischer*

Siluren aus dem Naturhistorichen Museum in Basel.

Hardman, M. (2004). The phylogenetic relationships among Noturus catfishes (Siluriformes: Ictaluridae) as inferred from mitochondrial gene cytochrome b and nuclear recombination activating gene 2. *Molecular phylogenetics and evolution*, *30*(2), 395-408.

Haseman, J. D. (1911). Some new species of fishes from the Rio Iguassú. *Ann. Carnegie Mus.*, *7*, 374-387.

Hensel, R. (1870). Beiträge zur Kenntniss der Wirbelthiere Südbrasiliens. (Fortsetzung). *Archiv für Naturgeschichte* v. 36 (no. 1): 50-91.

Hernández, C.L, Ortega-Lara, A, Sánchez-Garcés, G.C, & Alford, M.H. (2015). Genetic and morphometric evidence for the recognition of several recently synonymized species of trans-Andean Rhamdia (Pisces: Siluriformes: Heptapteridae). *Copeia*, *103*(3), 563-579.

Hildebrand, S. F. (1938). *A new catalogue of the fresh-water fishes of Panama*. Field Museum of Natural History.

Hubbs, C. L. (1935). Fresh-water fishes collected in British Honduras and Guatemala.

Hubbs, C. L. (1936). *Fishes of the Yucatan peninsula*. Carnegie Institution of Washington.

Humboldt, A. (1821).*Recherches sur les poissons fluviatiles de l'Amérique Équinoxiale*.

Jardine, W. (1841). In: Schomburgk, R. H. 1841. The Natural history of fishes of Guiana. Part. 1. The Naturalist's Library, Ichthyology, 3.

Jordan, D. S. & Evermann, B. W. (1896). The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Part I. *Bulletin of the United States National Museum No. 47:* i-lx + 1-1240.

Ivanova, N.V, Zemlak, T.S, Hanner, R.H, Hebert, P.D. (2007). Universal primer cocktails for fish DNA barcoding. *Molecular Ecology Notes,*7(4), 544–548.

Kner, R. (1858). Ichthyologische Beiträge. II. Abtheilung. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. *Mathematisch-Naturwissenschaftliche Classe v. 26* (s. 373): 373-448, Pls. 1-9.

Koerber, S., Litz, T. O., & Mirande, J. M. (2017). CLOFFAR-update 3-supplement to Checklist of the Freshwater Fishes of Argentina. *Ichthyological Contributions of PecesCriollos*, *47*, 1-9.

Kottelat, M. (2013). The fishes of the inland waters of southeast Asia: a catalogue and core bibliography of the fishes known to occur in freshwaters, mangroves and estuaries. *Raffles Bulletin of Zoology*.

Lanfear, R, Calcott, B, Ho, S.Y.W. & Guindon, S. (2012). PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution,* 29, 1695–1701.

Langeani, F. (1990). Revisão do gênero Neoplecostomus, com a descrição de quatro espécies novas do sudeste brasileiro (Ostariophysi, Siluriformes, Loricariidae). *Comunicações do Museu de Ciências e Tecnologia da PUCRS, série Zoologia*, *3*, 3-31.

Larrañaga, D. A. (1923). Escritos de Don Dámaso Antonio Larrañaga. *Los Publica el Instituto Histórico y Geográphico del Uruguay*. Edición Nacional. v. 2: 1-512.

Le Bail, P. Y, Keith, P & Planquette, P. (2000) *Atlas des poissons d'eau douce de Guyane*. Tome 2 - fascicule II. Siluriformes. 1-307.

Li, C, Ortí, G, Zhang, G & Lu, G. (2007). A practical approach to phylogenomics: the phylogeny of ray-finned fish (Actinopterygii) as a case study. *BMC Evolutionary Biology,*7(1), 1.

Li, W.L.S. & Drummond, A.J. (2012). Model averaging and Bayes factor calculation of relaxed molecular clocks in Bayesian phylogenetics. *Molecular Biology and Evolution,* 29, 751–761.

Librado, P, Rozas, J. (2009). DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics,* 25, 1451–1452.

Lopez, H.L, Morgan, C.C. & Montenegro, M.J. (2002). Ichthyological ecoregions of Argentina. *ProBiota,* 1, 1–68.

Lundberg, J. G., Bornbusch, A. H., & Mago-Leccia, F. (1991). Gladioglanis conquistador n. sp. from Ecuador with diagnoses of the subfamilies Rhamdiinae Bleeker and Pseudopimelodinae n. subf.(Siluriformes: Pimelodidae). *Copeia*, 190-209.

Lundberg, J. G., & McDade, L. (1986). A redescription of the rare Venezuelan catfish Brachyrhamdia imitator Myers (Siluriformes: Pimelodidae) with phylogenetic evidence for a large intrafamilial lineage. *Academy of Natural Sciences, Philadelphia*, *463*, 1-24.

Lundberg, J. G., Littmann, M. W., Reis, R. E., Kullander, S. O., & Ferraris Jr, C. J. (2003). Check list of the freshwater fishes of South and Central America. *Check list of the freshwater fishes of South and Central America*.

Lucena, C. D., & da Silva, J. P. (1991). Descrição de uma nova espécie do gênero Rhamdella Eigenmann & Eigenmann, 1888 (Siluriformes: Pimelodidae) para o médio rio Uruguai, sul do Brasil. *Comunicações do Museu de Ciências da PUCRS, SérieZoologia*, *4*, 28-47.

Lütken, C. F. (1874). Siluridae novae Brasiliae centralis a clarissimo J. Reinhardt in provincia Minas-geraës circa oppidulum Lagoa Santa, praecipue in flumine Rio das Velhas et affluentibus collectae, secundum characteres essentiales breviter descriptae. *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger og dets Medlemmers Arbeider (Kjøbenhavn) 1874* (no. 1): 29-36.

Lütken, C.F. (1875). *Velhas-Flodens Fiske. Et Bidrag til Brasiliens Ichthyologi; efter Professor J. Reinhardts Indsamlinger og Optegnelser. Det. Kongelige Danske visenskabernes selskabs skrifter. Naturvidenskabelig og mathematisk afdeling*. 5te Raekk [Ser. 5]. v. 12 (2): 121-253 + 2 unnum. + I-XXI, Pls. 1-5.

Malabarba, L. R. (1989). Histórico sistemático e lista comentada das espécies de peixes de água doce do sistema da laguna dos Patos, Rio Grande do Sul, Brasil. *Comunicações do Museu de Ciências e Tecnologia da PUCRS, série zoologia*, *2*(8), 107-179.

Matamoros, W. A., Schaefer, J. F., & Kreiser, B. R. (2009). Annotated checklist of the freshwater fishes of continental and insular Honduras. *Zootaxa*, *2307*, 1-38.

Mcmahan, C. D., Matamoros, W. A., CALDERÓN, F. S. Á., HENRÍQUEZ, W. Y., Recinos, H. M., Chakrabarty, P., ... & Herrera, N. (2013). Checklist of the inland fishes of El Salvador. *Zootaxa*, *3608*(6), 440-456.

Meek, S. E. (1902). *A contribution to the ichthyology of Mexico*(Vol. 3, No. 6). Field Columbian Museum.

Meek, S. E. (1904). *The fresh-water fishes of Mexico north of the Isthmus of Tehuantepec*(Vol. 5). Field Columbian Museum.

Mees, G. F. (1974). *The Auchenipteridae and Pimelodidae of Suriname (Pisces, Nematognathi)*. Brill.

Mees, G. F. (1986). Records of Auchenipteridae and Pimelodidae from French-Guiana (Picves, Nematognathi). *Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen Series C-Biological and Medical Sciences*, *89*(3), 311-325.

Mees, G. F., & Cala, P. (1989). 2 New species of *Imparfinis*from Northern South-America (PISCES, NEMATOGNATHI, PIMELODIDAE). *Porceedings of the Koninklijke*

Nederlandse Akademie Van Wetenschappen Series C-Biological and Medical Sciences, *92*(3), 379-394.

Miquelarena, A. M., & Menni, R. C. (1999). *Rhamdella aymarae*, a new species from the Itiyuro River, northern Argentina (Siluriformes: Pimelodidae). I*chthyol. Explor. Freshwaters*, *10*(3), 201-210.

Miller, R. R. (1984). *Rhamdiareddelli*, new species, the first blind pimelodid catfish from Middle America, with a key to the Mexican species. *San Diego Society of Natural History*.

Miranda Ribeiro, A. 1907. Fauna Braziliense. Peixes. II. Desmobranchios. *Arquivos do Museu Nacional de Rio de Janeiro* (14): 132-217.

Miranda Ribeiro, A. D. (1911). Fauna brasiliense. Peixes. Tomo IV (A)[Eleutherobranchios Aspirophoros]. Arquivos do Museu Nacional do Rio de Janeiro, 16(4), 1-504.

Miranda-Ribeiro, A. D. (1920). Os brachycephalideos do Museu Paulista. *Revista do Museu Paulista*, 12, 306-318.

Müller, J. and Troschel F.H. 1848. In: Schomburgk, R. 1848. *Reisen in Britisch-Guiana in den Jahren 1840-1844: nebst einer Fauna und Flora Guiana's nach Vorlagen von Johannes Müller, Ehrenberg, Erichson, Klotzsch, Troschel, Cabanis und Andern*. Leipzig. 1-429 pp.

Müller, J. and F. H. Troschel (1849). Reisen in Britisch-Guiana in den Jahren 1840-44. *Im Auftrag Sr. Mäjestat des Königs von Preussen ausgeführt von Richard Schomburgk. v. 3*. Berlin.

Nelson, J. S., E. J. Crossman, H. Espinosa Pérez, L. T. Findley, C. R. Gilbert, R. N. Lea and J. D. Williams (2004). Common and scientific names of fishes from the United States, Canada, and Mexico. Sixth Edition. *American Fisheries Society, Special Publication 29*. Bethesda, Maryland. Sixth Ed.: 1-386

Nico, L. G. (2001). Alexander von Humboldt (1769-1859): contributions to knowledge of new world fishes.

Norman, J. R. (1926). XLI.—A new blind catfish from Trinidad, with a list of the blind cave-fishes. *Journal of Natural History*, *18*(106), 324-331.

Ortega, H. & Vari, R. P. (1986). Annotated checklist of the freshwater fishes of Peru.

Ortega-Lara, A., Milani, N., DoNascimiento, C., Villa-Navarro, F., & Maldonado-Ocampo, J. A. (2011). Two new trans-Andean species of Imparfinis Eigenmann & Norris, 1900

(Siluriformes: Heptapteridae) from Colombia. *Neotropical Ichthyology*, *9*(4), 777-793.

Palumbi, S, Martin, A, Romano, S, McMillan, W.O., Stice, L. & Grabowski, G. (1991). The simple fool's guide to PCR. Honolulu, University of Hawaii.

Page, L. M., H. Espinosa-Pérez, L. D. Findley, C. R. Gilbert, R. N. Lea, N. E. Mandrak, R. L. Mayden and J. S. Nelson (2013). Common and scientific names of fishes from the United States, Canada, and Mexico. Seventh Edition. *American Fisheries Society, Special Publication 34*. I + xii + 1-384.

Papavero, N. (1971). Essays on the history of neotropical dipterology: with special reference to collectors (1750-1905) (Vol. 1). Museu de Zoologia, Universidade de São Paulo.

Pearson, N. E. (1924). *The Fishes of the Eastern Slope of the Andes: The Fishes of the Rio Beni Basin, Bolivia, Collected by the Mulford Expedition. I.* Indiana University.

Perdices, A, Bermingham, E, Montilla, A. & Doadrio, I. 2002. Evolutionary history of the genus *Rhamdia* (Teleostei: Pimelodidae) in Central America. *Molecular Phylogenetics and Evolution,*25(1), 172–189.

Pérez, H. E., Dillanes, M. T. G., & Mata, P. F. (1993). *Los peces dulceacuícolas mexicanos* (Vol. 3). Instituto de Biología, Universidad Nacional Autónoma de México.

Proudlove, G. S. (2006). *Subterranean fishes of the world: an account of the subterranean (hypogean) fishes described up to 2003 with a bibliography 1541-2004*. International Society for Subterranean Biology.

Quoy, J.R.C. and Gaimard, J.P. 1824. Description des Poissons. Chapter IX. In: Freycinet, L., 1824. *Voyage autour du Monde, entrepis par ordre du roi, sous le ministere et conformemént aux instructons de S. Exc. M. le Vicomte du Bouchage, secrétaire d'état au département de la marine, exécuté sur les corvettes de L.M. L'Uranie et "La Physicienne, pendant les années 1817, 1818, 1819 et 182*. Paris. Pp. 192-401.

Rambaut, A., Suchard, M. A., Xie, D., & Drummond, A. J. (2015). Tracer v1. 6. 2014.

Reeves, R. G., & Bermingham, E. (2006). Colonization, population expansion, and lineage turnover: phylogeography of Mesoamerican characiform fish. *Biological Journal of the Linnean Society*, *88*(2), 235-255.

Reis, R. E., Malabarba, L. R., & de Lucena, C. A. (2014). A new species of Rhamdella Eigenmann & Eigenmann, 1888 (Siluriformes: Heptapteridae) from the coastal basins of Southern Brazil. *Arquivos de Zoologia (São Paulo)*, *45*(esp), 41-50.

Regan, C. (1906). On the Freshwater Fishes of the Island of Trinidad, based on the collection, notes, and sketches made by Mr. Lechmere Guppy. *Journal of Zoology*, *76*(1-2), 378 -393.

Regan, C. T. (1907). XXX.—Descriptions of six new freshwater fishes from Mexico and Central America. *Journal of Natural History*, *19*(111), 258-260.

Regan, C. T. (1907). *Biologia Centrali-Americana. Pisces*. London. Part 215: 33-160, Pls. 5-20.

Regan, C. T. (1908). LX.—A collection of freshwater fishes made by Mr. CF underwood in Costa Rica. *Journal of Natural History*, *2*(11), 455-464.

Regan, C. T. (1913). XXXIV.—Fishes from the River Ucayali, Peru, collected by Mr. Mounsey. *Journal of Natural History*, *12*(69), 281-283.

Rendahl, H. (1941). *Fische aus dem pazifischen Abflussgebiet Kolumbiens*. Almqvist & Wiksell.

Ribolli, J., Scaranto, B. M., Shibatta, O. A., Bombardelli, R. A., & Zaniboni-Filho, E. (2017). DNA barcoding confirms the occurrence of Rhamdia branneri and Rhamdia voulezi (Siluriformes: Heptapteridae) in the Iguaçu River Basin. *Neotropical Ichthyology*, *15*(1).

Romero, A. & Paulson, K.M. (2001). It’s a wonderful hypogean life: a guide to the troglomorphic fishes of the world. In: *The biology of hypogean fishes*. Springer Netherlands, 13–41.

Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D. L., Darling, A., Höhna, S., ... & Huelsenbeck, J. P. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic biology*, *61*(3), 539-542.

Rozas, J., Sánchez-DelBarrio, J. C., Messeguer, X., & Rozas, R. (2003). DnaSP, DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics*, *19*(18), 2496-2497.

Sarmiento, J., Bigorne, R., Carvajal-Vallejos, F., Maldonado, M., Leciack, E., Oberdorff, T., ... & Tedesco, P. (2014). *Peces de Bolivia= Bolivian fishes*.

Sands, D. D., & Black, B. K. (1985). Two new species of Brachyrhamdia, Myers, 1927, from Brazil and Peru, together with a redefinition of the genus. *Catfishes of the World*, *3*, 58.

Scharpf, C. (2005). Annotated checklist of North American freshwater fishes, including subspecies and undescribed forms. *Part I: Petromyzontidae through Cyprinidae. Am. Curr*, *31*(4), 1-44.

Seba, A. 1759. *Locupletissimi rerum naturalium thesauri accurata descriptio et iconibus* *artificiosissimis expressio per universam physices historiam*. H. K. Arksteus, Amstelaedami. v. 3: i-xxi, 1-212, Pls. 1-116.

Shaw, G. (1826). *General zoology, or Systematic natural history*. Kearsley.

Slobodian, V., & Bockmann, F. A. (2013). A new Brachyrhamdia (Siluriformes: Heptapteridae) from Rio Japurá basin, Brazil, with comments on its phylogenetic affinities, biogeography and mimicry in the genus. *Zootaxa*, *3717*(1), 1-22.

Slobodian, V., & Bockmann, F. A. (2016). First reliable records of distribution of Brachyrhamdia meesi Sands & Black, 1985 (Siluriformes: Heptapteridae). *Ichthyologival Exploration of Freshwaters*, *27*(4), 355-360.

Spix, J. B. & Agassiz, L. (1829). Selecta genera et species piscium quos in itinere per Brasiliam annis MDCCCXVII-MDCCCXX jussu et auspiciis Maximiliani Josephi I colleget et pingendso curavit Dr J. B. de Spix Monachii. Part 1: i-xvi + i-ii + 1-82, Pls. 1-48; Part 2: 83-138, Pls. 49-101.

Starks, E. C. (1906). On a Collection of fishes made by PO Simons in Ecuador and Peru.

Steindachner, F. 1877. *Die Süsswasserfische des südöstlichen Brasilien (III). Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche* Classe v. 74: 559-694.

Steindachner, F. 1879. *Zur Fisch-Fauna des Magdalenen-Stromes. Denkschriften der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche* Classe. v. 39: 19-78

Steindachner, F. (1882). Ichthyologische Beiträge (XII). Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe v. 86 (1. Abth.): 61-82, Pls. 1-5.

Stresemann, E. (1954). Ferdinand Deppe's travels in Mexico, 1824-1829. *The Condor*, *56*(2), 86-92.

Silfvergrip, A.M.C. (1996). *A systematic review of the Neotropical catfish genus Rhamdia(Teleostei, Pimelodidae)*. Stockholm, Swedish Museum of Natural History.

Tajima, F. (1989). Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics,*123(3), 585–595.

Thompson JD, Higgins DG, Gibson TJ. (1994). CLUSTAL W: improving the sensitivity of progressive multiple sequence" alignment through sequence weighting, position specific gap penalties and weight matrix choice. *Nucleic Acids Research,* 2, 4673–4680.

Troschel, F. H. (1865) In: von Muller, J. W. (1864). *Reisen in den Vereinigten Staaten, Canada und Merico*.

Valenciennes, A. (1840). In : Cuvier, G. and Valenciennes, A. 1840. *Histoire naturelle des poissons. Tome quinzième. Suite du livre dix-septième. Siluroïdes*. Strasbourg v. 15: i-xxxi + 1-540 pp.

Villa, J. (1977). A new species of pimelodid catfish of the genus *Rhamdia* from Nicaragua, Central Amercia. *Brenesia,* 2(13), 133–142.

Villwock, J.A. & Tomazelli, L.J. (1995). Geologia costeira do Rio Grande do Sul. *Notas Técnicas,* 8, 1–45.

Weber, A, Allegrucci, G. & Sbordoni, V. (2003). *Rhamdia laluchensis*, a new species of troglobitic catfish (Siluriformes: Pimelodidae) from Chiapas, Mexico. *Ichthyological Exploration of Freshwaters,*14(3), 273–280.

Weber, A., & Wilkens, H. (1998). Rhamdia macuspanensis: a new species of troglobitic pimelodid catfish (Siluriformes; Pimelodidae) from a cave in Tabasco, Mexico. *Copeia*, 998-1004.

Wilkens, H. (1993). A new species of Rhamdia (Pisces: Pimelodidae) from a cave in the Sierra de Zongolica (Veracruz, México).

Wilkens, H. (2001). Convergent adaptations to cave life in the *Rhamdia laticauda* catfish group (Pimelodidae, Teleostei). In: *The biology of hypogean fishes*. Springer Netherlands, pp. 251–261.

Wright, S. (1978). Variability within and among populations. *Evolution and the Genetics of Populations*.

Zarske, A. (2003). Wiederbeschreibung von Rhamdia marthae (Sands & Black, 1985)(Teleostei, Siluriformes, Pimelodidae). *Zoologische Abhandlungen, Staatliches Museum für Tierkunde in Dresden*, *53*, 47-55.