Taxonomic revision of *Pimelodella* Eigenmann & Eigenmann, 1888 (Siluriformes: Heptapteridae): an integrative proposal to delimit species using a multidisciplinary strategy
Veronica Slobodian

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Revisão taxonômica de *Pimelodella* Eigenmann & Eigenmann, 1888 (Siluriformes: Heptapteridae): uma proposta integrativa para a delimitação de espécies com estratégias multidisciplinares

v.1

Original version

Thesis Presented to the Post-Graduate Program of the Museu de Zoologia da Universidade de São Paulo to obtain the degree of Doctor of Science in Systematics, Animal Taxonomy and Biodiversity

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São Paulo
2017
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Cataloging in Publication

Slobodian, Veronica

Taxonomic revision of Pimelodella Eigenmann & Eigenmann, 1888 (Siluriformes: Heptapteridae) : an integrative proposal to delimit species using a multidisciplinary strategy / Veronica Slobodian ; orientador Mário César Cardoso de Pinna. São Paulo, 2017.

2 v. (811 f.)

Tese de Doutorado – Programa de Pós-Graduação em Sistemática, Taxonomia e Biodiversidade, Museu de Zoologia, Universidade de São Paulo, 2017.
Abstract

Primary taxonomic research in neotropical ichthyology still suffers from limited integration between morphological and molecular tools, despite major recent advancements in both fields. Such tools, if used in an integrative manner, could help in solving long-standing taxonomic problems. The genus *Pimelodella* Eigenmann & Eigenmann, 1888 is a perfect case for an integrative and multidisciplinary approach in taxonomy. *Pimelodella* is a genus of the Heptapteridae broadly distributed throughout trans- and cis-Andean South America, and one of the main components of Neotropical Ichthyofauna. Nowadays is the most species-rich genus of the family, with 79 valid species. However, the validity and delimitation of those species is extremely problematic, due their broad geographic distribution, conserved morphology, and ancient and imprecise descriptions. *Pimelodella* is undoubtedly one of the most severe taxonomic bottlenecks in neotropical ichthyology. This project presents a taxonomic revision of *Pimelodella* using an integrative morphological-molecular approach. The traditional taxonomic revision covers the genus in its entirety, with all the components of this kind of study. All types were examined, and the number of valid species herein recognized was reduced to 55 species, for which full descriptions are presented. The molecular taxonomy was done for a circumscribed subset of the genus, with representation enough to understand the molecular divergences and compare them with the traditional taxonomy results, allowing an evaluation of the results of the revision.

Keywords: Integrative taxonomy. Neotropical Ichthyofauna. Comparative Anatomy. Species Trees.
Resumo

A pesquisa taxonômica primária ainda apresenta pouca integração entre as ferramentas morfológicas e moleculares para o estudo de peixes neotropicais, apesar de grandes avanços recentes em ambos os campos. Tais ferramentas, se usadas de maneira integrativa, poderiam solucionar grupos reconhecidos por representarem problemas taxonômicos renitentes. O gênero *Pimelodella* Eigenmann & Eigenmann, 1888 se enquadra como um ótimo caso para a aplicação de uma estratégia integrativa e multidisciplinar. *Pimelodella* é um gênero da família Heptapteridae, distribuído amplamente por drenagens sul-americanas trans- e cis-andinas e compreende um dos principais componentes da ictiofauna neotropical. Atualmente é reconhecido como o maior gênero da família, com 79 espécies válidas descritas. Entretanto, a validade e delimitação dessas espécies é problemática, devido à elevada diversidade do gênero, aliada à ampla distribuição, morfologia conservada e descrições antigas e imprecisas. Trata-se de um dos grandes gargalos taxonômicos na sistemática e taxonomia de peixes neotropicais. Este projeto apresenta uma revisão taxonômica de *Pimelodella* utilizando uma abordagem integrativa morfológica-molecular. A revisão taxonômica clássica cobre a integridade da diversidade do gênero, com todos os componentes deste tipo de estudo. Todos os tipos foram examinados, e o número de espécies válidas é aqui reduzido para 55 espécies, para as quais descrições completas são apresentadas. A parte molecular foi realizada em um subgroupo delimitado, com diversidade suficiente para que as estimativas de divergência molecular pudessem ser comparadas aos resultados da revisão morfológica, fornecendo um modelo de avaliação para o restante da revisão.

Palavras-chave: Taxonomia integrativa. Ictiofauna Neotropical. Anatomia Comparada. Árvores de espécies.
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Attachments list

Attachment 1. Original description of *Pimelodella humeralis*, in the article “A new species of *Pimelodella* (Siluriformes: Heptapteridae) from the Guiana Shield, Brazil” of Slobodian *et al.* (2017).

Attachment 2. R script to calculate ML trees and other results, to be used by ASTRAL in order to calculate the Species Tree.
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Introduction

The *Pimelodella* genus Eigenmann & Eigenmann, 1888

*Pimelodella* Eigenmann & Eigenmann 1888 is an important component of the freshwater fish fauna of the Neotropics. With 79 species currently considered as valid, *Pimelodella* is the most species-rich genus of Heptapteridae, a family comprising 211 species in 24 genera (Eschmeyer, Fricke & van der Laan, 2017). *Pimelodella* is distributed throughout cis- and trans-andean Neotropical drainages, from Panamá to Argentina (Eschmeyer, Fricke & van der Laan, 2017). Due to unsettled taxonomic and systematic problems, the genus represents one of the most difficult bottlenecks for understanding the diversity of Neotropical freshwater fishes.

*Pimelodella* was described in 1888 by Eigenmann & Eigenmann, to include *Pimelodus cristatus* Müller & Troschel, 1849 as type-species, *P. pectinifer* as a new species, plus several additional species previously included in *Pimelodus* (*P. brasiliensis* Steindachner, 1877, *P. buckleyi* Boulenger, 1887, *P. chagresi* Steindachner, 1876, *P. cristatus*, *P. elongatus* Günther, 1860, *P. gracilis* Vallenciennes, 1835, *P. hartii* Steindachner, 1877, *P. lateristrigus* Lichtenstein, 1823, *P. modestus* Günther, 1860, *P. vittata* Lütken, 1874 and *P. wesselii* Steindachner, 1877) The genus was diagnosed by: “head entirely covered in skin; occipital process narrow, of the same width throughout, meeting the dorsal plate; fontanel prolonged backward to the occipital process with a bridge across it behind the eye” (Eigenmann & Eigenmann, 1888: 131).

Carl Eigenmann (1917) revised *Pimelodella* and *Typhlobagrus*, the latter a monotypic genus proposed by Miranda Ribeiro (1907) for his new troglobitic species *T. kronei*. Eigenmann (1917) recognized 35 taxa in *Pimelodella* (34 species plus one subspecies) including 12 taxa (11 species plus one subspecies) then described as new. Eigenmann (1917) also provided a diagnosis of the genus based on several non-unique features: “nares remote; teeth villiform, in bands; gill-membranes free from the isthmus; dorsal short, with a feeble, pungent spine; anal short, with 11–15 rays; pectoral with a strong pungent spine variously armed with thorn-like teeth on its posterior (inner) edge; a long, adnate, adipose fin; caudal fin deeply forked, one or the other lobe frequently wider, or longer; well-developed maxillary barbels reaching to end of pectoral, or beyond the caudal; two pairs of mental barbels, sometimes in a; nearly straight line; a frontal and a parietal fontanel, the latter reaching to the base of the occipital process, which is narrow and reaches, or nearly reaches, the plate in front
of the dorsal; humeral process spine-like; roof of mouth without teeth; head covered with thin skin” (Eigenmann, 1917: p. 229).

Since Eigenmann’s (1917), *Typhlobagrus* has been synonymized with *Pimelodella*, and several other species have been newly described, removed from or transferred to *Pimelodella* (Ferraris, 2007), reaching a present total of 92 available names (Eschmeyer, Fricke & van der Laan, 2017) (Table 1). Several authors made substantial contributions to the taxonomy of the genus, e.g. Regan (1903, 1913), Miranda-Ribeiro (1907, 1911, 1914, 1918), Fowler (1914, 1915, 1940a, b, c, 1941a, b), Ahl (1925) and Dahl (1961, 1964). Revisionary work on other heptapterid genera resulted in the transfer, by default, of some species to *Pimelodella* without detailed studies on the systematics of the genus (Silfvergrip, 1996; Bockmann & Miquelarena, 2008), thus increasing its taxonomic complexity.

The diagnosis proposed by Eigenmann (1917) is insufficient to properly delimit *Pimelodella*, so that the genus has been redefined in subsequent contributions (Bockmann & Miquelarena, 2008; Slobodian, 2013; Slobodian & Bockmann, 2013). However, *Pimelodella* remains without a phylogenetic diagnosis, and its diversity remains poorly understood.

Despite a plethora of publications on *Pimelodella*, only few works after Eigenmann (1917) had an actual comparative scope: Mees’ (1974, 1986) focused on *Pimelodella* species in Surinam and French Guiana; Guazzelli’s (1997) investigated the taxonomy of eight *Pimelodella* species from Brazilian southern and southeastern coastal drainages; and Souza-Shibatta et al. (2013) measured the cytogenetic, morphologic and morphometric differences among *Pimelodella* in the Brazilian Pantanal (Mato Grosso do Sul and Mato Grosso States).

Today, *Pimelodella* is a genus rife with taxonomic problems of various sorts, large documented diversity, broadly distributed species, and outdated or inadequate descriptions. Taxonomic problems also stem from a highly conservative morphology and a lack of comprehensive studies on the numerous specimens vouchered in natural history collections. Many species of *Pimelodella* lack rigorous taxonomic study and, to some degree, those considered valid merely correspond to a list of unchallenged available names (Slobodian et al., 2017). Identification of *Pimelodella* species is expectedly troublesome, a fact blatantly demonstrated in collection material: the majority of material representing *Pimelodella* is undetermined, or wrongly identified at species level. In addition, phylogenetic work on the genus invariably stumble upon resilient taxonomic problems mentioned above, and therefore have limited applicability.
**General objectives and thesis approach**

The main purpose of this work is to mitigate the lack of knowledge on the taxonomy of *Pimelodella*. To that end, I present a thorough taxonomic revision encompassing all available names in *Pimelodella*, having as primary source of information external anatomy, morphometric, meristic and osteological data. Concomitantly, a molecular study was conducted for a sample of *Pimelodella* species, in order to discuss the molecular diversity and the explanatory power of molecular taxonomy in delimiting species of the genus, as seen through the results of the classical taxonomic results. With both morphological and molecular data, an integrative approach was conducted to characterize *Pimelodella* species on a biologically-broad basis, including also distributional and ecological data whenever available.

The work is divided in two chapters: The first reviews the taxonomy of *Pimelodella* with traditional morphological data, following a classical approach with descriptions and diagnoses of valid species, synonymies and a discussion on taxonomically-significant morphological characters.

The second chapter includes an essay on the molecular diversity of *Pimelodella* and the explanatory power of molecular characters to unravel the taxonomy of the genus using species trees methodology. This strategy is based on gathering information from several gene trees and then analyzing the divergence pattern of loci, time of divergence and probable events of coalescence (*cf.* Edwards *et al.*, 2007; Liu & Pearl, 2007; Carstens & Knowles, 2007; Liu *et al.*, 2008; Kubatko *et al.*, 2009). The results were compared with the obtained through a traditional concatenate analysis.

A final discussion offers an integrative approach to the taxonomy of *Pimelodella* using multidisciplinary strategies and data from both morphological and molecular results.
Chapter 1
Taxonomic revision of *Pimelodella*
Eigenmann & Eigenmann, 1888
Introduction

**Taxonomic history of the genus *Pimelodella***

*Pimelodella* was described in 1888 by Eigenmann & Eigenmann to include 11 species previously allocated in *Pimelodus* or *Pseudorhamdia* (*P. brasiliensis*, *P. buckleyi*, *P. chagresi*, *P. cristatus*, *P. elongatus*, *P. gracilis*, *P. harttii*, *P. lateristriga*, *P. modestus*, *P. vittata*, *P. wesseli*) plus a newly-described *P. pectinifer*. At the time of description, Eigenmann & Eigenmann (1888) also synonymized part of described *Pseudorhamdia* to *Pimelodella* (*Pseudorhamdia* original type is *P. maculatus*, not included among the *Pimelodella*, so *Pseudorhamdia* genus do not have priority over *Pimelodella*). The genus was proposed to accommodate *Pimelodus* species with a narrow supraoccipital process, reaching the anterior nuchal plate, and a completely opened posterior fontanel (Eigenmann & Eigenmann, 1888: 131). Eigenmann & Eigenmann (1888) implicitly arranged genera due to some sort of perceived similarity (Bockmann, 1998), and *Pimelodella* was listed immediately after the genus *Rhamdia* Bleeker (1858) (and *Rhamdella*, a subgenus), and in an appendix Eigenmann & Eigenmann (1888: 172) placed *Heptapterus* Bleeker (1858) and *Nannoglanis* Boulenger (1887) after *Rhamdella*.

In 1890, Eigenmann & Eigenmann redescribed species of *Pimelodella* in detail, also offering an identification key. In 1891, Eigenmann & Eigenmann produced a catalog, in which then 12 known species were listed. Between 1891 and 1910, the species *Pimelodus eigenmanni* Boulenger 1891, *Pimelodella yuncensis* Steindachner, 1902, *Pimelodus* (*Pimelodella*) *griseus* Regan, 1903, *Pimelodus* (*Pimelodella*) *taeniophorus* Regan, 1903 and *Pimelodella mucosa* Eigenmann & Ward, 1907 were described.

Another catalog was produced by Eigenmann (1910), where the new species cited above were indicated under or transferred to *Pimelodella*, along with *P. meeki* as a *nomen novum* for the unavailable *P. eigenmannii* Meek (1905), and the citation of the names *P. macturkii* (*sic*) and *P. megalops* as manuscripts in preparation, which were later formally described by Eigenmann (1912). Between 1912 and 1917, *Pimelodella eutaenia* Regan, 1913, *Pimelodella taenioptera* Miranda Ribeiro, 1913, *Pimelodella copei* Fowler, 1915 and *Pimelodella peruensis* Fowler, 1915 were described.

The last taxonomic revision of *Pimelodella* was then made by Eigenmann (1917) in which 12 new taxa were described (11 new species and 1 new subspecies), and *P. wesselli* was synonymized to *P. cristata*. In that work, a new diagnosis was proposed for the genus.
Eigenmann’s revision (1917) delimited the geographic distribution of *Pimelodella* to rivers from Panamá to Argentina, a range which remains correct today. Most of the species were described (or redescribed) and illustrated, and all known species had their pectoral-fin spines illustrated. A key is presented for the 35 taxa of *Pimelodella* and 1 *Typhlobagrus* (interpreted as an offshoot of *Pimelodella* at that time, later into *Pimelodella*). This is the most comprehensive work on *Pimelodella* taxonomy to date, and after that *Pimelodella* was treated just in part, either subsets of species or isolated descriptions.

Fowler (1940a, b, 1941a) described several *Pimelodella* species in many works on the fauna of specific regions or rivers. However, his works include little discussion on the differences among the species, but solely descriptions and, at most, comparisons with a few species from nearby localities. After Eigenmann, Fowler was the author who described most species of *Pimelodella*: *P. copei* and *P. peruense* (Fowler, 1915); *P. hartwelli* (Fowler, 1940a); *P. chaparae, P. cochabambae* (transferred to *Imparfinis* by Mees & Cala, 1989) and *P. howesi* (Fowler, 1940b); *P. dorsay, P. enochi, P. laurenti, P. paharybae* and *P. witmeri* (Fowler, 1941a); and also *Rhamdella leptosoma* (Fowler, 1914), *R. papariae, R. robinsoni* and *R. wolfi* (Fowler, 1941a), now in *Pimelodella*.

Eigenmann & Allen (1942) presented the distribution of the *Pimelodella* species, their diagnosis and referred material; plus descriptions of *P. montana* Allen, 1942 in Eigenmann & Allen, 1942, and *P. peruana* Eigenmann & Myers in Eigenmann & Allen, 1942. Catalogs such as Gosline (1945) and Fowler (1951) included all species of *Pimelodella* described to the respective dates (Fowler, 1951 includes only Brazilian species). Also, *Caecorhamdella brasiliensis* Borodin (1927a) and *Typhlobagrus kronei* Miranda Ribeiro, 1907 were maintained under those genera (Gosline, 1945: 34; 43; Fowler, 1951: 518–519; 578–579).

Schultz (1944) was the first to synonymize *Brachyrhamdia* in *Pimelodella*, but without discussion. In the same work, *P. linami* and *P. chagresi odynea* were described from the Maracaibo, but without much resort to comparative material. Innes & Myers (1950) also suggested *Brachyrhamdia* as a junior-synonym of *Pimelodella*. Two other genera synonymized with *Pimelodella* were *Typhlobagrus* Miranda Ribeiro, 1907a (Pavan, 1946: 359) and *Caecorhamdella* Borodin, 1927a (Trajano & Britski, 1992: 83).

Dahl (1961) published the first comparison of *Pimelodella* species bearing filaments on dorsal fin, *P. griffini, P. linami* and *P. figueiroi*. Dahl (1961) proposes that the filamentous prolongation of the dorsal fin as absent in an adult females and immature specimens of *P. figueiroi*, suggesting the filament as a secondary sexual character of the adult male. He further suggested that the same might apply to other *Pimelodella* species. *Pimelodella boschmai* was
described by van der Stigchel (1964), but the only comparison made with other filamentous *Pimelodella* was with *P. griffini*.

Another important author in understanding the diversity of *Pimelodella*, Mees (1974, 1983, 1986), who offered general comparisons for *Pimelodella* identification. He objectioned to Fowler’s descriptions (1940b, 1941a), in which different species were described on the basis of differences on eye size. Mees’ own findings showed that character as related to sexual dimorphism in *P. cristata*. Mees (1974) also suggested that *Pimelodus altipinnis* was in fact a *Pimelodella*, following an earlier suggestion of Van der Stigchel, 1946; that *P. altipinnis* (Steindachner, 1874), *P. geryi* Hoedeman (1961) and *P. wesseli* (Steindachner, 1876) were junior-synonyms of *P. cristata*, and that *P. insignis* was a junior-synonym of *P. boschmai*. Mees (1974) also proposed *P. gracilis* (Valenciennes, 1835) as senior-synonym of *P. cristata* or, alternatively, that *P. gracilis* was confined to the Uruguay-Paraná-La Plata basins. Similar forms from Guianas, Orinoco and Suriman were, in that case, *P. cristata*, and similar forms from Amazon would be *P. steindachneri*. Discussions on the value of coloration patterns in species identification were made, with the observation that single species of *Pimelodella* from different rivers may differ to a limited degree (Mees, 1974).

In a work about the naked catfishes from French Guiana, Mees (1983) narrowed the type-locality of *P. lateristriga*, to the vicinity of the city of Rio de Janeiro, based on data about the travels of the collector, von Olfers. He also highlighted differences in vertebral counts and color pattern for material identified as *P. cristata*, Despite the recognized need for further study, he did not think those characteristics were sufficient to discriminate species (Mees, 1983).

The first time *Pimelodella* was studied under a cladistic perspective was in Howes (1983), in which it grouped the genus with *Rhamdia* and *Heptapterus* inside the Pimelodidae. However, the family Heptapteridae as currently composed, was first diagnosed (as a unnamed group) in Lundberg & McDade (1986). Therein, *Pimelodella* was also attributed to a monophyletic subgroup including also *Brachyrhamdia*, *Cetopshorhamdia*, *Goeldiella*, *Pimelodella*, *Pimelodus heteropleura*, *Rhamdella*, *Rhamdia*, *Typhlobagrus* and an unidentified *Nannorhamdia*, based on the synapomorphy “fifth transverse process smaller than fourth, but similarly expanded and notched” (Lundberg & McDade, 1986: 6).

Axelrod & Burgess in Axelrod (1987) expressed doubt whether *Brachyrhamdia* was be distinguishable from *Pimelodella*. Later, Burgess (1989) transferred *B. imitator*, *B. marthae* and *B. meesi* into *Pimelodella*, without further explanation about the move.
Silfvergrip (1996) provisionally transferred *Pimelodus bahianus* to *Pimelodella*, and made some comparisons of anatomic features of *Pimelodella* and *Rhamdia*, especially in characters of dorsal, pectoral and adipose fins, and on sexual dimorphism. Silfvergrip also suggested *Pimelodus breviceps* might be a *Pimelodella*

Guazzelli (1997), in her unpublished dissertation, made a taxonomic review of *Pimelodella* species from South and Southeastern coastal drainages of Brazil. In that work, seven described species were proposed as valid (*P. australis, P. brasiliensis, P. ignobilis, P. kronei, P. lateristriga, P. pappenheimi, and P. transitoria*), a new species was proposed for the rio Paraiba do Sul, and *P. harttii* and *P. pectinifera* were included as junior synonyms of *P. lateristriga*.

Bockmann (1998), in his unpublished thesis, made the most comprehensive study yet on generic relationships in Heptapteridae. *Brachyrhamdia, Caecorhamdella* and *Typhlobagrus* were included as junior-synonyms of *Pimelodella*. Bockmann (1998) included only 8 *Pimelodella* species in his analysis, 5 of which belonging to *Brachyrhamdia*.

Guazzelli (2003), in her unpublished thesis, proposed a phylogenetic hypothesis for species of *Pimelodella*, including 18 described and 17 undetermined or new species. Guazzelli (2003) maintained *Brachyrhamdia* as a junior-synonym of *Pimelodella*. The clade including *Pimelodella+Brachyrhamdia* in her analysis is corroborated by 7 synapomorphies, all of which homoplastic (Guazzelli, 2003).

Relationships among *Pimelodella* species in Guazzelli (2003) are massively unresolved, the only exception being a group formed by *P. cristata, P. witmeri* and 7 new species (clade 58, diagnosed by 4 homoplastic synapomorphies). Guazzelli (2003) also highlights the need of extensive revisionary work on *Pimelodella*, before its biodiversity is realistically known.

Bockmann & Guazzelli (2003) presented a checklist of Heptapteridae species, in which they transferred to *Pimelodella* the species *Nannorhamdia macrocephala, Pimelodus breviceps, Rhamdia eigenmanniorum, Pimelodus ophthalmicus, Pimelodus taeniophorus and Pimelodus wesseli*, erected *Pimelodella chagresi odynea* to full species and synonymized *P. insignis* to *P. boschmai*. However, no explicit reasons were presented for implementing those taxonomic changes. That work treated *Brachyrhamdia* as a valid genus, and *Typhlobagrus* and *Caecorhamdella* as junior-synonyms of *Pimelodella* (Bockmann & Guazzelli, 2003).

Leiva (2005), in his unpublished dissertation, made a taxonomic review of *Pimelodella* species from trans-Andean Colombian rivers. In that work, he indicated *P. chagresi, P eutaenia, P. grisea, P. modestus, P. odynea* and *P. reyesi* as valid species, describing three additional new species (Leiva, 2005).
Ferraris (2007) proposed *P. bahianus* and *P. rendahl* as species inquirenda in *Pimelodella*. That work also treated *Brachyrhamdia* as a valid genus, and *Typhlobagrus* and *Caecorhamdella* as junior-synonyms of *Pimelodella* (Ferraris, 2007).

Bockmann & Miquelarena (2008) suggested *Nannorhamdia macrocephala*, *Rhamdella leptosoma*, *R. papariae*, *R. robinsoni* and *R. wolfi* as probably members of *Pimelodella*, transferred *Rhamdella ignobilis* and *R. longipinnis* to *Pimelodella*, and suggested *Pimelodus exsudans*, *P. jenynsii* and *Rhamdella straminea* as members of *Pimelodella* or *Rhamdia*. That work suggested *Brachyrhamdia* as a valid genus, recovered as sister-group of *Pimelodella*, but did not proposed apomorphies for the latter clade.

*Nannorhamdia macrocephala* was suggested as a *Pimelodella* due to the presence of long maxillary barbels, inner caudal-fin rays that do not articulate directly on the hypural plates and with interradial membranes only along their basal halves, all synapomorphies of *Pimelodella* according to Bockmann (1998), and despite the supraoccipital process short, not reaching the prenuchal plate (Bockmann & Miquelarena, 2008).

*Rhamdella leptosoma* was suggested (Bockmann & Miquelarena, 2008) as a possible *Pimelodella* due to overall appearance and geographical distribution (since the *Rhamdella*, as defined in that work, was limited to southern South America), and despite the short supraoccipital process. *Rhamdella papariae*, *R. robinsoni* and *R. wolfi* were suggested as belonging to *Pimelodella* on the basis of information in original descriptions and associated illustrations (*e.g.* slender body, large eyes, well-developed supraoccipital process, long maxillary barbel, reaching anal-fin base, robust pectoral spine, dark stripe along lateral surface of the body, etc.) (Bockmann & Miquelarena, 2008). Type material of *Rhamdella ignobilis* and *R. longipinnis* was examined and supported their transfer to *Pimelodella* on the basis of long maxillary barbels and a sharp long supraoccipital process that contacts the predorsal plate (Bockmann & Miquelarena, 2008).

Bockmann & Miquelarena (2008) also suggested *Pimelodus exsudans* Jenyns, 1842 and *Pimelodus jenynsii* Günther, 1864 as *Pimelodella* or *Rhamdia* based on the descriptions of both species, and arguing that the characters suggested by Eigenmann & Eigenmann (1888, 1890) to place both in *Rhamdella* are not accurate enough to justify this transfer. Also, Bockmann & Guazzelli (2008) argued *Rhamdella* genus does not occur in Rio de Janeiro vicinities, the collection locality of *Pimelodus exsudans* and *P. jenynsii*. *Rhamdella straminea* was also suggested as a *Pimelodella* or *Rhamdia* due to the presence of long maxillary barbels reaching the middle of ventral fins, despite the long cranial fontanel (Bockmann & Miquelarena, 2008).
Slobodian (2013), in an unpublished dissertation, produced a phylogenetic analysis of *Brachyrhamdia*, including all its species plus 12 of *Pimelodella*. That work recovered *Brachyrhamdia* as an apical lineage inside a widely unresolved *Pimelodella*, with 14 apomorphic characters, 6 of which exclusive and unreversed (clade 19). The clade encompassing *Pimelodella*+*Brachyrhamdia* (clade 7) is diagnosed by numerous synapomorphies and can be considered as well-corroborated (Slobodian, 2013).

Despite recovering *Brachyrhamdia* as an apical lineage inside *Pimelodella*, Slobodian (2013) suggested *Brachyrhamdia* should remain valid, because it is an easily recognizable and diagnosable clade, while *Pimelodella* is probably a paraphyletic group, whose species’ relationships can only be resolved in the scope of a more inclusive work.

*Pimelodella* remains without any published phylogenetic diagnosis and its monophyly is uncertain, but an assemblage composed of its species can be distinguished from other heptapterids, including *Brachyrhamdia*, by a unique character combination (Slobodian *et al.* 2017). *Pimelodella* nowadays includes 79 valid species, from a total of 92 available names, and is the most species-rich genus of Heptapteridae, a family composed of 211 species in 24 genera (Eschmeyer, Fricke & van der Laan, 2017). *Pimelodella* is distributed throughout cis- and trans-Andean Neotropical drainages from Panamá to Argentina (Eschmeyer, Fricke & van der Laan, 2017). The majority of species in the genus have never been subject to rigorous taxonomic study and those considered as valid often merely correspond to a selected list of available names (Slobodian *et al.*, 2017).

**Objectives**

The aim of this work is to present a thorough taxonomic revision of *Pimelodella*, encompassing all available names and using data from external anatomy, morphometrics, meristics, pigmentation and osteology data. It is subdivided into the following stages:
Chapter 2
Molecular taxonomy of *Pimelodella*
Eigenmann & Eigenmann, 1888
Introduction

Integrative taxonomic methods for species delimitation

Taxonomy is the science that pioneers the exploration of life on the planet, providing information subsidiary to ecology, conservation, and virtually all other studies related to living beings. However, taxonomy is not only a tool of technical support for the rest of biology, but a scientific field with its own struggles and objectives.

Although taxonomic studies have existed long before the advent of phylogenetic systematics, this paradigm provided a conceptual and philosophical framework that greatly benefited taxonomy: it brought testability to taxonomic delimitations, with the use of tools for the organization of organisms subjects according to their evolutionary relationships, and helped minimize authority influence in taxonomic decisions (Godfray & Knapp, 2004).

Besides phylogenetic systematics, advancement of several other methods and techniques in the past few decades allowed progress on species recognition and delimitation (Sites & Marshall, 2003; Camargo & Sites, 2013). Such advancements were particularly visible computational time and laboratory techniques (mainly molecular and cytogenetic data). However, such advances have normally been circumscribed to their particular area of expertise, with only partial incorporation into mainstream taxonomic research.

Integrative taxonomy brings an embracing approach, proposing that species delimitation should consider several sources of data (Padial et al., 2010), and that congruence and incongruence among results can be understood in light of each method’s characteristics. Sources of data comprehend morphology, molecular, cytogenetic, ecology, reproduction, behavior, geographical distribution, among others (Knowles & Carstens, 2007), and can increase the explanatory power of species hypotheses.

However, it is not uncommon that different sources diverge in their results about species boundaries. Such cases must be analyzed case by case (Schlick-Steiner et al., 2010). When different data disagree, reasons for such discordance should be analyzed (Schlick-Steiner et al., 2010; Carstens et al., 2013) according to possible evolutionary explanations.

Advances in methodologies and techniques for molecular data now allow faster extraction, sequencing and interpretation of results, resulting in substantial increase in their use in taxonomy and systematics (Camargo & Sites, 2013). The pursuit for a single genetic marker for exclusive species delimitation culminated in the initial success of the Barcode of Life project. Hebert et al. (2003a) proposed a portion of Cytochrome C Oxidase I (COI) as a global maker for biological identification, with initial success rates between 96–100% (Hebert
et al., 2003a; Barrett & Hebert, 2005). However, several well-established population genetics theories raised doubts about the limitations of such genetic data in delimiting species (Moritz & Cicero, 2004).

The limiting factors for DNA Barcode are several: species delimitation based on exclusivity criteria are usually incongruent with the delimitation through other sources of data (Sites & Marshall, 2004); DNA Barcode is usually not very effective for species recently diverged, without well-established geographical delimitation, and when dealing with a great amount of specimens per species. Posterior studies reported success rates have dropped to less than 70% of accuracy in species delimitation (Meyer & Paulay, 2005; Meier et al., 2008; Elias et al., 2007; Knowles & Carstens, 2007; Whitworth et al., 2007; Wiemens & Fiedler, 2007; Hollingsworth et al., 2009).

In the light of single loci limitations, the best approach to study molecular data in taxonomy includes the use of multiple loci, in order to avoid the “local optimum” given by a single gene tree (Edwards, 2009). Several studies argue that the increase in the number of loci analyzed results in increased accuracy in species delimitation (e.g. Dupuis et al., 2012), above all if the species have recently diverged (Knowles & Carstens, 2007).

When using molecular data for taxonomy, different loci often results in different gene trees, and the incongruences among those must be dealt in order to reconstruct a single species tree topology. Myriad processes can lead to incongruences between different gene trees, or even between a particular gene tree and the final species tree: horizontal transfer (including hybridization); gene duplication and extinction; and deep coalescence (Maddison, 1997). Among these, deep coalescence explanation argues ancestral polymorphisms can persist through speciation events, being most likely in large populations with short divergence periods, so that a particular gene tree may not be congruent with the species divergence sequence (Maddison, 1997; Knowles & Carstens, 2007).

Several programs and methods intend to deal with deep coalescence problems, using Maximum Likelihood and Bayesian premises, like STEM (Kubatko et al., 2009), BEST (Liu & Pearl, 2007; Liu, 2008), BUCKy (Ané et al., 2007), and ASTRAL (Mirarab et al., 2014). The efficiency of those methods is estimated mainly by simulations and computational models, which estimate relative performances in finding the “true” species tree for a specific database (e.g. Degnan & Rosenberg, 2006; Knowles & Carstens, 2007; Heled & Drummond, 2010). Works on real groups are getting more common, and demonstrated to recover probable and well-supported species trees (e.g. Belfiore et al., 2008; Brumfield et al., 2008; Andrade et al., 2015; Streicher, et al., 2015).
In this chapter, the molecular taxonomy of *Pimelodella* species is studied by species tree and concatenated matrix methods. Results are interpreted against results from morphological delimitation and geographic distribution.

**Material and Methods**

**Taxon sampling**
Several species of *Pimelodella*, from most of its geographic range, were included, along with outgroup Heptapteridae taxa. The initial dataset comprises a total of 93 specimens belonging to *Pimelodella*, seven Heptapteridae genera, and one Pimelodidae (*Pimelodus*). Among Heptapteridae, representatives of *Brachyglanis, Imparfinis, Phenacorhamdia, Rhamdia* and *Rhamdioglanis* were included (10 specimens), besides several *Pimelodella*, that comprehends 83 specimens total. Samples of *Pimelodella* were initially identified to species level following results of Chapter 1, and found to represent 26 *Pimelodella* species, 18 already described and and 8 possibly new. The complete list of material examined is presented in Table 70.

The trees were rooted in *Pimelodus* sp.

**Molecular data collection**
Two mitochondrial (Cytochrome Oxidase C, subunit I and Cytochrome B) and two nuclear (exon-primed intron-crossing (EPIC) markers 39298e1 and 4274e20) were used as sources of data. Cytochrome Oxidase C, subunit I (COI) is one of the most used mitochondrial genes for phylogenetic analysis, as well as for species identification with DNA Barcoding (Hebert et al., 2003a). Despite its limitations (e.g. Moritz & Cicero, 2004), COI is a broadly used gene, with a differentiation rate sufficient to detect species differentiation (Hebert et al., 2003a).

Cytochrome B (CytB) is another mitochondrial gene that has been well studied (e.g. Irwin et al., 1991). Although more conservative than COI, CytB appears to evolve at approximately three times the rate found in 12S and 16S at lower genetic distances, and closer to twice the rate of these genes at higher genetic distances in some fishes (Sullivan et al., 2000).

The two nuclear genes are exon-primed intron-crossing (EPIC) markers, 39298e1 and 4274e20 (from Li et al., 2010). Introns have been successfully used in species-level studies (e.g. Li et al., 2010), and to sequence introns, the primers are designed on adjacent exon regions, and amplify across the intron (therefore, exon-primed intron-crossing). Because
Final conclusions
Integrative taxonomy delimitation
Final conclusions

Revisionary taxonomy is frequently dismissed as merely descriptive, which belies its strong intellectual content and hypothesis-driven nature (Wheeler, 2004). And even descriptive taxonomy is not just a tool to be used by the rest of biological studies, but the pioneering exploration of life on Earth, having several derivative functions as it lays the foundation for phylogenetic, ecology and conservational studies (Wilson, 2004), among several others. Without a previous well-done taxonomical study, the unfolding conclusions of other disciplines are weak, unstable and unreliable, at least, and might have cascade-like processes affecting hypotheses and ideas (Bortolus, 2008).

Taxonomic assessment of complex and hyperdiverse groups is not a trivial task for several reasons. The issues of species delimitation and even species conceptualization are long treated in the literature (e.g. Baum & Shaw, 1995; Mayden, 1997; de Pinna, 1999; Wheeler & Meier, 2000; de Queiroz, 2007; Camargo & Sites, 2013; Carstens et al., 2013), and are topics still far from being exterminated. Furthermore, working hypothesis on species limits become mired in light of the morphological variation distributed across many specimens and localities (Sabaj & Arce, 2017).

In order to work with practical taxonomy, one has to forego on an unified species concept which embraces both species conceptualization and delimitation at the same time (de Queiroz, 2007), since the practical mishaps are somewhat dependent on the specificities of the biological group in question. The species conceptualization used here in this thesis refer to species necessarily as separately evolving metapopulation lineages, view shared by all contemporary species concepts (de Queiroz, 2007). However, despite fulfilling the necessary properties for species conceptualization, the hypothesis of species as separately evolving metapopulation lineages is not sufficient to species delimitation.

The sufficient assumptions for species delimitation rely on operational criteria, and an unification of those throughout all biological studies is on the verge of impossible. Given species are natural kinds, they can be recognized by homeostatic property clusters (e.g. Boyd, 1999), and not by an immutable set of necessary and sufficient conditions. This view is adequate to the Realism accommodation thesis, which claims that the accommodation of inferential practices to relevant causal structures establishes the reliability and inducibility of the system in question (Boyd, 1999; 2002).

The before mentioned operational criteria is adequate to the taxonomic study here conducted, since in the light of more characters and evidence, the boundaries of a given
species can slightly change, but be recognizable nevertheless. The species here recognized have fuzzy boundaries (Kosco, 1993), and the epistemic access condition is based on what is predicated by the type under given conceptual resources. Therefore, in light of the morphological characters (measurements, counts, coloration pattern, etc.) presented by the type, other specimens are accommodated to the conceptual matrix outlined. Likewise, in the light of molecular data, the morphological characters used to delimit a particular species are revisited and questioned about their sufficiency.

The here presented species delimitations are the result of accommodation of morphological variation into a particular species conceptual description, in a manner the species can be recognized, despite the variation found. Most of the time, the morphological and molecular delimitations were congruent. When congruence was not achieved, initial identification was revisited in light of the new evidence.

So far, most of species recovered by molecular taxonomy were also recognized by the used morphological criteria. Some notable exceptions will be discussed furthermore.

*Pimelodella avanhandavae*, *P. gracilis* and *P. taeniophora* were not recognized as monophyletic entities (and, therefore, separately evolving metapopulation lineages) in molecular analyses. This topic deserves further investigation, since *Pimelodella avanhandavae* can be distinguished from the other two by 42–44 (rarely 41 or 45) total vertebrae, maxillary barbel reaching between origin and adpressed last fifth of anal fin, and pectoral fin spine morphology (Fig. 9). *Pimelodella gracilis* have 46 or more total vertebrae, maxillary barbel reaching between half anal-fin base and surpassing caudal-fin origin, and different pectoral fin spine morphology (Fig. 66). *Pimelodella taeniophora* have 40–42 total vertebrae, maxillary barbels as long as the ones of *P. gracilis*, but different pectoral-fin spine morphology (Fig. 194). It is noteworthy these three species have somewhat similar coloration patterns and, in the absence of x-rays, the identification of juvenile specimens (like were part of the specimens used in the molecular analyses) can be troublesome. Furthermore, pectoral-fin spine morphology can vary slightly ontogenetically (*e.g.* figures 56; 169), what makes the identification of juveniles of *Pimelodella* even more difficult. In the light of molecular results, x-rays of all *P. avanhandavae*, *P. gracilis* and *P. taeniophora* specimens must be taken, in order to re-investigate their identification.

Based on morphological characters, I proposed the synonym of *P. transitoria* to *P. kronei*, both described from Ribeira de Iguape basin. Other authors in the past have already suggested also that *P. transitoria* would be indistinguishable from *P. lateristriga* (Haseman, 1911; Eigenmann, 1917), and the molecular results here corroborate that conclusion.
However, the specimens of *P. lateristriga* included in the molecular analyses belong only to Ribeira de Iguape basin, meanwhile this species have a more broad distribution along several coastal basins in Southeastern and Northeastern Brazil. I believe the inclusion of *P. lateristriga* molecular material from other localities is necessary to properly tackle this problem, and I decide to maintain *P. kronei* as valid until then.

*Pimelodella mucosa* was recovered in molecular analyses as more closely related to other Heptapteridae genera than to other *Pimelodella*. Despite being recognizable as a *Pimelodella*, *P. mucosa* is notably different from other *Pimelodella* species. The inclusion of more *P. mucosa* molecular material is necessary, in order to investigate if this peculiar outcome is an artifact related to missing data, or if *P. mucosa* is indeed a extremely modified species, even belonging to a new genus. But in any way, this is an interesting outcome.

Considering all morphological diversity, I could observe some characters are more useful to species delimitation, and those were particularly treated under each species diagnosis. Despite small geographic variation in more broadly-distributed species, most *Pimelodella* have somewhat constant coloration patterns, what may serve as a first approach in order to identify those species with notable marks (like paired dorsal stripes, and dark marks on dorsal fin and body). The length of barbels is also useful to species delimitation, especially to those species that have notably short or notably long barbels. The length of adipose fin is also useful to species delimitation. Most of other measurements are somewhat constant among all *Pimelodella* species, but slightly differences and tendencies can give a grasp onto species identification, especially in the context of geographically restricted species. On the other hand, the absence of significant differences on morphometric, meristic and coloration data lead me to synonymize several species to a broadly-distributed *P. cristata*.

The number of total vertebrae and pectoral-fin spine morphology were also very useful characters used to species delimitation. However, acquisition of x-rays might be a hindrance to species identification using number of vertebrae as a character; and several *Pimelodella* species present severed pectoral spines (commonly entangled in fishing nets), what also makes the identification of collection material sometimes troublesome.

Regarding the geographic distribution, most of *Pimelodella* species are restricted to one or few hydrographic ecoregions, as can be observed on the maps presented in Figures 234–240, and detailed in each species’ section. Species with broader distributions usually do not have blatant diagnostic features (such as coloration marks, or particularly different pectoral-fin spine morphology), what makes their delimitation and identification even more
troublesome. Particularly for the case of broadly-distributed species, the inclusion of molecular data can bring light to recognition of separately evolving metapopulation lineages.

In sum, this thesis intended to discuss an integrative approach to species delimitation in *Pimelodella*, and so far the delimitations are mostly congruent across methods. The inferences drawn from species delimitation are, however, conservative, in order not to falsely delimit entities that do not represent actual evolutionary lineages (*vide* Carstens *et al.*, 2013). Also, species delimitation might change in the light of new evidence (both increase in sampling as well as different data sources), but this thesis can be considered a first approach in helping to solve the intricacies of species delimitation of a morphologically and species diverse group as *Pimelodella*. Based on the results and problems here presented, specific issues can be approached in the future, with a more intensive sampling of geographical restricted species, and inclusion of molecular data for a more inclusive dataset.
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