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Freshwater mussels from South America: state of the art of Unionida, specially Rhipidodontini

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Abstract: Unionida is the most diverse clade of freshwater bivalves. Among the groups occurring in South America, one with the highest number of species is Rhipidodontini (Hyriidae, Unionida, Paleoheterodonta, Bivalvia). However several issues remains on taxonomy and systematic of this group, leading to problems on species identification, description, as also as a limiting factor to other type of studies (e.g., ecology, conservation,...). In this paper is presented a synthesis of available knowledge about *Diplodon* Spix in Wagner, 1827 and *Rhipidodonta* Mörch, 1853 in South America, as a first step in order to a better understating of Rhipidodontini. The evaluation of different authors exposes the little agreement between them that resulted in a sort of divergent taxonomical opinions. Some comments on ecology, conservation and habitat preferences were made. This work can also encourage future research on taxonomy, systematic, ecology and conservation of freshwater mussels in South America.

Keywords: *Diplodon*, *Rhipidodonta*, *Hyriidae*, *Bivalvia*, *Freshwater bivalve*.

Bivalves de água doce da América do Sul: estado da arte de Unionida, especialmente Rhipidodontini

Resumo: Unionida é o clado mais diverso de bivalves de água doce. Entre os grupos que ocorrem na América do Sul, um dos com maior número de espécies é Rhipidodontini (Hyriidae, Unionida, Paleoheterodonta, Bivalvia). Porém, diversas questões taxonômicas e sistemáticas ainda incidem sob este grupo, levando a problemas de identificação de espécies, descrição, entre outros, como também tem atuado como limitador de outros tipos de estudos (e.g., ecologia, conservação,...). Neste trabalho é apresentada uma revisão do conhecimento acerca dos gêneros *Diplodon* Spix in Wagner, 1827 e *Rhipidodonta* Mörch, 1853 na América do Sul como um primeiro passo para a melhor compreensão de Rhipidodontini. Avaliando-se diferentes autores, se torna claro a pouca concordância entre eles, resultando em opiniões taxonômicas divergentes. São feitos também alguns comentários sobre ecologia, conservação e preferências ambientais. Este trabalho também deve encorajar futuros trabalhos sobre a taxonomia, sistemática, ecologia e conservação de bivalves de água na América do Sul.

Palavras-chave: *Diplodon*, *Rhipidodonta*, *Hyriidae*, *Bivalvia*, *Bivalve de água doce*.

Introduction

Mollusca is the second phylum in number of species, with estimates on the number of living species ranging up to 200,000 (Ponder & Lindberg 2008). Bivalvia constitutes one of the most representative groups of this phylum with more than 8,000 species living worldwide. Although most are marine species, about 1,300 live in freshwater in all continents, except Antarctica (Ruppert et al. 2005, Bogan 2008). Several lineages colonized freshwater ecosystems, especially the order Unionida (Paleoheterodonta), as well as some species of Arcida, Mytilida (Pteriomorpha), Venerida, Myida, and Anomalodesmata (Heterodonta), suggesting that bivalve invasions of freshwater environments occurred numerous times (Haag 2012). All living species of Unionida and

Sphaeriidae (Heterodonta: Venerida) live exclusively in freshwater (Mansur 2007, Giribet 2008). Freshwater mussels (Unionida) are one of the most endangered animal group due to continuous degradation of their ecosystems (Strayer et al. 2004, Amaral et al. 2008, Pereira et al. 2014). More recently Asian freshwater bivalves like *Limnoperna fortunei* (Dunker, 1857) (Mytilidae) and *Corbicula* spp. (Cyrenidae) that have been introduced to several distant countries and continents including South America caused severe ecological and economical loss (Darrigran & Damborenea 2006, Mansur et al. 2012, Boltovskoy & Correa 2015, Xu et al. 2015).

Bivalves inhabit the bottom substrate, and are important members of freshwater communities performing important ecosystem services (Vaughn 2017). Except for the environmental differences between marine

and freshwater organisms, the freshwater species are generally similar to marine ones; although they are less colorful, camouflaged among sand grains and stones (Mansur 2007). Freshwater bivalves can be found in almost all available microhabitats, occupying different niches: burrowers of soft sediments (majority of species), burrowers of compacted sediments (e.g., *Mycetopoda* d'Orbigny, 1835 and *Mycetopodella* Marshall, 1928), wedgers of soft rocks and laterite (e.g., *Bartlettia* Adams, 1867), attached by byssus (e.g., *Byssanodonta* d'Orbigny, 1846 and *Eupera* Bourguignat, 1854) and species cemented to hard substrate (e.g., *Acostaea* d'Orbigny, 1851 and *Etheria* Lamarck, 1807) (Mansur 2007, 2012, Haag 2012, Pereira et al. 2014).

Our main goal was to summarize the knowledge about Unionida (Bivalvia, Paleoheterodonta) in South America, especially regarding Rhipidodontini (Hyriidae).

1. Systematics of Unionida

The taxonomic instability of bivalves results, in part, from the large amount of available names (Bieler & Mikkelsen 2006), which change according to the different characters emphasized by each author. The systematic of Bivalvia was addressed by several authors (Thiele 1934, Newell 1965, Cox et al. 1969, Franc 1960, Schneider 2001, Giribet 2008) and the position of Paleoheterodonta remains quite stable. Paleoheterodonta is usually presented as a "halfway" between Pteriomorphia and Heterodonta (Schneider 2001, Giribet 2008). Bieler et al. (2014) presented a slightly different arrangement where Paleoheterodonta is sister group to Archiheterodonta, and this is sister to a clade composed by Anomalodesmata + Imparidentia, that embraces most bivalves previously in Heterodonta. Unionida is included in Paleoheterodonta and it is a group of usually large-sized mussels that have a peculiar life cycle with a parasitic stage and presents the most successful radiation in freshwaters by bivalves (Graf & Cummings 2006, Haag 2012).

The inner relationships of Unionida are not as clear as the position of Paleoheterodonta. Simpson (1914) proposed only two families in Unionoida (= Unionida): Unionidae and Mutelidae. Most bivalves that are currently recognized as Unionidae, Margaritiferidae and Hyriidae (Figure 1A-C) compose the first group; and the current representatives of Mycetopodidae and Iridinidae are part of the second group (Figure 1D-E). Therefore, Unionidae *sensu* Simpson (1914) encompasses the species with larvae of glochidium type, whereas Mutelidae *sensu* Simpson (1914), those with the lasidium type. Ortmann (1921) recognized three families within the superfamily Naiades: Margaritanidae (= Margaritiferidae), Unionidae and Mutelidae (= Hyriidae + Mycetopodidae + Iridinidae). Based on morphological characteristics of their soft parts, not only on their shells, Ortmann (1911, 1921) noted similarities between hyriids and mutelids, and removed hyriids from Unionidae, establishing them as a subfamily of Mutelidae.

Thiele (1934) classified all freshwater mussels as Unionacea, recognizing four families: Margaritanidae, Unionidae, Mutelidae, and Aetheriidae (Figure 1). That is the first classification scheme that posed an exclusive family for freshwater oysters (Aetheriidae = Etheriidae) (Figure 1F). Thiele (1934) used the same subfamilies of Mutelidae proposed by Ortmann (1921).

These first arrangements of Unionida follow biogeographical patterns: Boreal species grouped in Margaritiferidae (or Margaritanidae) and Unionidae; and Austral species in Mutelidae (= Hyriidae + Mycetopodidae) (Ortmann 1921, Thiele 1934). However, the separation is not clear cut, for example, Thiele (1934) left *Virgus* Simpson, 1900 and other austral insular species of Oceania in Unionidae.

Modell (1942) proposed four families (Mutelidae, Elliptionidae, Margaritiferidae, and Unionidae) with many subfamilies. Elliptionidae comprises the majority of species traditionally allocated in Unionidae. Modell (1942) also suggested a relationship between this group and Mutelidae, wherein all lasidium bearers were grouped together. Modell

(1942) as Simpson (1914), placed hyriids within Unionidae. According to Modell (1942), Mutelidae is a basal group that originates all other mussels.

Parodiz & Bonetto (1963) proposed an arrangement in two superfamilies based mainly on the larval type, which was widely accepted by subsequent authors: Unionacea (Unionidae + Margaritiferidae + Hyriidae) with glochidium larva; and Mutelacea (Mutelidae + Mycetopodidae) with lasidium larva. Etheriidae is not included in the classification, as its larval stage was unknown at that time (Bogan & Roe 2008). The larval stage of *Acostaea rivolii* (Deshayes, 1827) (Etheriidae) was later identified as a lasidium (Arteaga-Sogamoso 1994, Bonetto, 1997). Kabat (1997) revised the names used in Unionida claiming that Etherioidea and Iridinidae should be used instead of Muteloidea and Mutelidae. The recent works accepted these suggestions (e.g., Graf & Cummings 2007).

In the beginning of the 21st century, there has been a reevaluation of systematic relationships based on phylogenetic methodologies, including molecular data in some of these analyses. The monophyly of Etheriidae was questioned by Bogan & Hoeh (2000) who considered *Acostea* and *Etheria* (traditionally included in Etheriidae) within Mycetopodidae and, *Pseudomulleria* Anthony, 1907, an Indian freshwater oyster, inside Unionidae. Bogan & Hoeh (2000) proposed multiple origins to cementation among freshwater bivalves, arguing the occurrence of the same process in the non-related Cyrenidae, *Posostrea anomioidea* Bogan & Bouchet, 1998. The analysis of Hoeh et al. (2001) is similar to Bogan & Hoeh (2000), suggesting that Hyriidae is a sister group to the remaining Unionida and considering Unionacea (*sensu* Parodiz & Bonetto, 1963) as a paraphyletic group. That scheme implies that the glochidium and the larvae incubation in the inner demibranch (endogenous) are plesiomorphic characteristics of Unionida.

Graf (2000) analyzed the relationships inside Etherioidea, with an emphasis on Hyriidae; suggesting that Hyriidae, Iridinidae and Etheriidae are monophyletic. Unionidae, once more had its monophyly questioned and *Grandidieria* Bourguignat, 1885, traditionally placed in Unionidae is considered a sister group of Etherioidea. Graf & Cummins (2006) suggested that Paleoheterodonta is monophyletic and divided Unionoida in two clades: Unionioidea (Unionidae + Margaritiferidae) and Etherioidea (Hyriidae + Etheriidae + Mycetopodidae + Iridinidae). Unlike other authors (e.g., Bogan & Hoeh, 2000; Hoeh et al. 2001), Graf & Cummings (2006) suggested the monophyly of Unionidae and Etheriidae, condition latter also supported by Whelan et al. (2011). In that scheme, Unionioidea is the

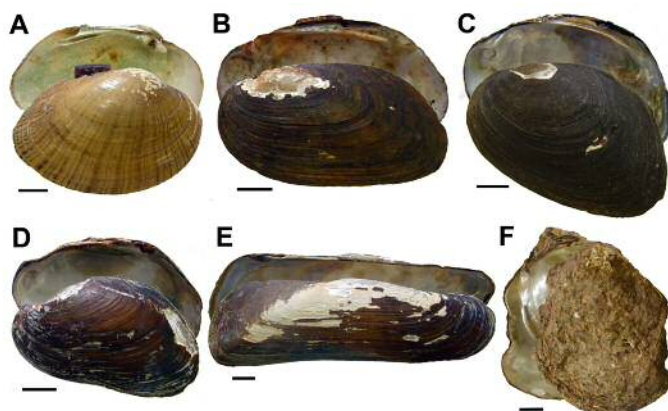


Figure 1. Members of Unionida. A – Unionidae, *Lampsilis fasciola* Rafinesque, 1820, MNRJ (Museu Nacional do Rio de Janeiro) 7468; B – Margaritiferidae, *Margaritifera* sp., MNRJ 32868; C – Etheriidae, *Echyridella menziesii* (Dieffenbach, 1843), MNRJ 4374; D – Iridinidae, *Aspatharia pfeifferiana* (Bernardi, 1860), MNRJ HSL 6328; E – Mycetopodidae, *Mycetopoda soleniformis* d'Orbigny, 1835, MNRJ 3841; F – Etheriidae, *Etheria elliptica* Lamarck, 1807, MNRJ HSL 6111. Scale bar = 1 cm.

basal group of Unionida, while Hyriidae is the basal group of Etherioidea. In certain aspects, this arrangement is a return to early schemes of systematic organization (e.g., Ortmann, 1921) with boreal species separated from the austral species. The exceptions are some austral species of Unionidae (Haas 1969, Graf & Cummings 2007).

Neveeskaja (2009) recognized two groups of living freshwater mussels: Unionoidea (Unionidae + Margaritiferidae) and Etherioidea (Mutelidae + Etheriidae), but did not list the genera within each group, so it is impossible to know precisely where Hyriidae and Mycetopodidae stand. As Mutelidae traditionally embrace the species of Iridinidae, Mycetopodidae and Hyriidae (Ortmann 1921, Thiele 1934, Graf 2000); we can suppose that Neveeskaja (2009) considered all the species of these families as belonging to Mutelidae.

A major point of disagreement between different authors is the position of Hyriidae, sometimes grouped with glochidium-bearing species, and sometimes grouped with the other Gondwanic species (Mycetopodidae and Etheriidae) (Bogan & Hoeh 2000, Graf 2000, Graf & Cummings 2006, Bogan 2008). Bieler et al. (2010) adopted an intermediate solution to the problem, dividing the living species of Unionida in three superfamilies (Table 1). In this classification, Hyrioidea (represented only by Hyriidae) occupy an intermediate position between the two other groups, Etherioidea and Unionoidea, reflecting the conflicting data from other authors concerning the position of Hyriidae (Bogan & Hoeh 2000, Hoeh et al. 2001, Graf & Cummins 2006, 2007). Graf et al. (2015) presented Hyriidae as sister to all other freshwater mussel families, in a position quite different from the previously one (Graf & Cummings 2006), however similar (regarding to Hyriidae position) to topology presented by Bogan & Hoeh (2000) and Hoeh et al. (2009).

2. Geographical distribution of South American mussels

Unionida occurs worldwide in different kinds of freshwater habitats except in Antarctica (Graf & Cummings 2006, Bogan 2008). Current estimates recognize approximately 900 species distributed among six families: Hyriidae, Mycetopodidae, Unionidae, Iridinidae and Etheriidae (Graf & Cummings 2006, 2007, Bieler et al. 2010).

Etheriidae is Gondwanic and comprises four species, occurring in Africa, *Etheria elliptica* Lamarck, 1807; India, *Pseudomulleria dalyi* (Smith, 1898) and South America, *Acostea rivoli* and *Bartlettia stefanensis* (Moricand, 1856) (Haas 1969, Graf & Cummings 2006, 2007). The monophyly of this family is disputed and there is no agreement as highlighted by different opinions available (Parodiz & Bonetto 1963, Bogan & Hoeh 2000, Bonetto 1997, Simone 2006, Hoeh et al. 2009, Mansur et al. 2012).

Mycetopodidae is Neotropical distributed all over South America east of the Andes and west of Central America all the way to Mexico (Graf & Cummings 2006, Bogan 2008). There are about 30 valid species of Mycetopodidae in 12 (Simone 2006) or 11 genera (Graf & Cummings 2007). Bonetto (1997) also includes *Acostaea* in Mycetopodidae, whereas other authors (Parodiz & Bonetto 1963, Graf 2000) believe that *Leila* Gray, 1840, usually placed in Mycetopodidae, belongs to Iridinidae. The origin of Mycetopodidae is in the Cretaceous (Cox et al. 1969).

There are around 80 species of Hyriidae, occurring throughout Oceania and South America, with only two or three species west of the Andes (Bonetto et al. 1986; Parada & Peredo, 2002; Graf & Cummings, 2007; Bogan, 2008). Hyriidae is monophyletic (Graf et al. 2015) and usually divided in two groups (sub-families), the Hyriinae, which comprises South American species, except by *Hyridella* Swainson, 1840 and some related Australian species; and *Velesunioninae*, that comprises most Australian species (Graf & Cummings, 2006, 2007; Bieler et al. 2010; Graf et al. 2015). Among Hyriidae seven genera are recognized to South America: *Prisodon*

Schumacher, 1817; *Paxyodon* Schumacher, 1817; *Callonaia* Simpson, 1900; *Castalia* Lamarck, 1819; *Castaliella* Simpson, 1900; *Diplodon* Spix in Wagner, 1827 and *Rhipidodonta* Mörch, 1893 (Simone, 2006); and, nine genera to Australia: *Hyridella*; *Cucumerunio* Iredale, 1934; *Echydella* McMichael & Hiscock, 1958; *Virgus*; *Velesunio* Iredale, 1934; *Alathyria* Iredale, 1934; *Lortilella* Iredale, 1934; *Microdonta* Tapparone Canefri, 1883; *Westralunio* Iredale, 1934 (Graf & Cummings, 2007). It is noteworthy that not all authors agree with the valid status of each of these genera. Simone (2006) considered *Triplodon* Spix in Wagner, 1827 as synonym, unlike Mansur & Pimpão (2008) who described a new species of this genus. The oldest Hyriidae record is from Triassic of New Zealand (Campbell et al. 2003) and from Jurassic of South America (Perea et al. 2009). Molecular clock indicated a Gondwanan origin of Hyriidae (Graf et al. 2015; Santos-Neto et al. 2016).

The Figures 2 to 4, based on the data available in Graf & Cummings (2007), allow a more detailed evaluation of the distribution of the South American species of Hyriidae, Etheriidae and Mycetopodidae. Graf & Cummings (2007) divides the Neotropical region in six areas: Mesoamerica (including Cuba), Transandean (including the basins of rivers Magdalena and Maracaibo), Amazonas-Orinoco (including the Guyanas), Atlantic coastal streams (including the São Francisco River basin), Paraná-Paraguay and Patagonia. The two main families (Hyriidae and Mycetopodidae) are widespread in the region; Mycetopodidae occurs in all regions and Hyriidae in five of them (Figure 2). Etheriidae are limited to three regions. In the regions of Atlantic coastal streams, Paraná-Paraguay and Patagonia prevails species of Hyriidae; in the others regions, there are

Table 1. Relationships of Paleoheterodonta, following Bieler et al. (2010), modified to include only the living taxa of Paleoheterodonta.

Paleoheterodonta	Trigoniida Unionida	Trigoniioidea Etherioidea	Trigoniidae Etheriidae Iridinidae Mycetopodidae Hyriidae Unionidae Margaritiferidae
		Hyrioidea Unionoidea	

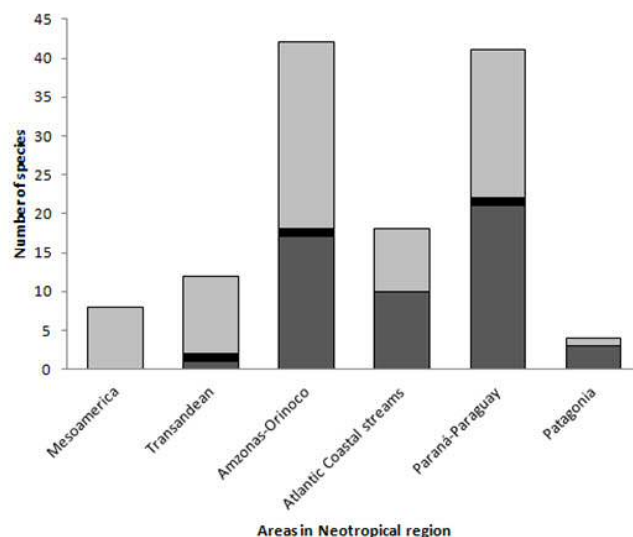


Figure 2. Number of species of Hyriidae and Mycetopodidae in different areas of Neotropical region. Based on the original data by Graf & Cummings (2007). Key: Dark gray – Hyriidae; Black – Etheriidae and Light gray – Mycetopodidae.

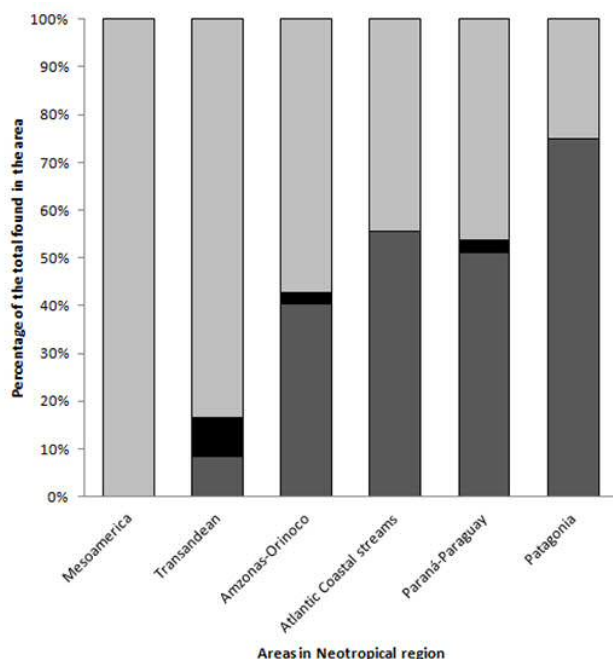


Figure 3. Representativeness of Hyriidae, Mycetopodidae and Etheriidae in the Neotropical region based on the original data by Graf & Cummings (2007). Key: Dark gray – Hyriidae; Black – Etheriidae and Light gray – Mycetopodidae.

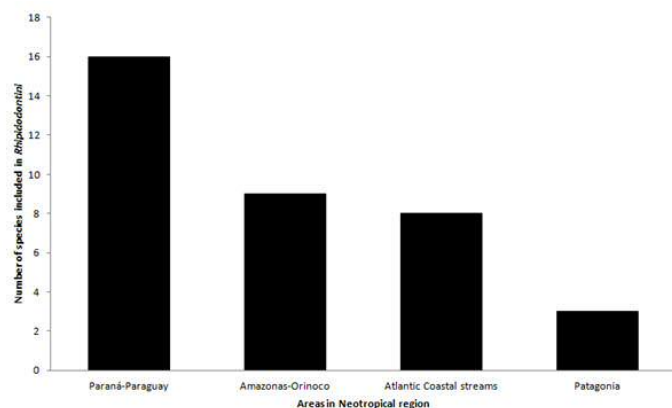


Figure 4. Number of species of Rhipidodontini (*Rhipidodonta* + *Diplodon*) in Neotropical region. The regions that are not presented don't have any Rhipidodontini species (i.e. Mesoamerica and Transandean). Based on the original data by Graf & Cummings (2007).

more Mycetopodidae species (Figure 2). The areas with the greatest total number of species are Amazonas-Orinoco (42 spp.) and Paraná-Paraguay (41 spp.), the first with the greatest number of Mycetopodidae (24 spp.) and the second with the greatest number of Hyriidae (21 spp.). Pereira et al. (2014) indicated the same areas as those of high diversity and pointed all region east of Andes (except by Northeast Brazil) as phylogenetically structured by Hyriidae and Mycetopodidae.

Comparing the representativeness of each family in different areas, we notice a trend towards a decrease in Mycetopodidae, along with an increase in Hyriidae (Figure 3), from North to South. The extremes are Mesoamerica, without Hyriidae species, and Patagonia where Hyriidae represents more than 70% of Unionida fauna. However, Patagonia is a poor

region in mussels richness and this high percentage amounts to only three species. Etheriidae is always a small fraction of total species.

Figure 4 presents the diversity of Rhipidodontini (*Rhipidodonta* + *Diplodon*). There are no representatives of Rhipidodontini in the Mesoamerica and Transandean regions. The unique species of Hyriidae pointed out by Graf & Cummings (2007) to Transandean region is *Castalia multisulcata* Hupé, 1857 that belongs to Castaliini. Rhipidodontini represents most species of Hyriidae in Neotropics resulting in similarities between figure 4 and 2. The difference between the Amazonas-Orinoco region and Atlantic coastal streams region, lower in Figure 2 than in Figure 4, are due to the occurrence of exclusive Amazonian Hyriidae genera like *Callonaia*, *Castaliella* and *Prisodon*. Graf & Cummings (2007) included these genera in other tribes (Hyriini or Castaliini).

3. Taxonomy and systematics of Rhipidodontini

The most important studies concerning the systematics of Rhipidodontini (Figure 5) are shown in Table 2 and Appendix I (see Supplementary material): Simpson (1914), Ortmann (1921), Morretes (1949), Parodiz (1968), Haas (1969), Simone (2006) and Graf & Cummings (2007). The following discussion focused on specific epithet, regardless of the genus or subgenus the author employed. For example, Haas (1969) used *Diplodon* (*Rhipidodonta*) *rhombea* Spix in Wagner, 1827, while Graf & Cummings (2007) used *Rhipidodonta rhombea*; regardless of genus designation, we regarded that both authors considered “*rhombeus*” as a valid species. *Diplodon* is traditionally divided in subgenera, mainly based on features of the shell, and the two most used are *Rhipidodonta* and *Diplodon s.s.*

Simpson (1914) and Thiele (1934) recognized three subgenera: *Diplodon s.s.*, *Rhipidodonta* (= *Cyclomya* Simpson, 1900) and *Bulloideus* Simpson, 1900 (see Table 2 and Appendix I). Ortmann (1921) and Morretes (1949) recognized two subgenera, *Diplodon* and *Rhipidodonta*. The species placed in *Bulloideus* were usually included in *Rhipidodonta* by the authors that did not use the first subgenera. Haas (1969) recognized four subgenera, adding *Schleschiella* Modell, 1950 to those mentioned previously. Ortmann (1921) was the first to notice differences in glochidium, however, he did not assign those variations to subgenera. The characteristics of glochidium were linked to subgenera by Bonetto (1961, 1965) and Parodiz & Bonetto (1963). Simone (2006) raised *Rhipidodonta* to genus status, an idea followed later by Graf & Cummings (2006, 2007), considering *Diplodon* to encompass the species with parasite glochidium, and *Rhipidodonta* those with non-parasite glochidium. These two genera (*Diplodon* and *Rhipidodonta*) were included in tribe Rhipidodontini (Graf & Cummings 2007), with all species previously arranged in subgenera by other authors (Table 2, Appendix I). Simone (2006) do not presented an explanation to support his decision, and probably for this reason some authors like Pereira et al (2014) don't followed his suggestions. It is clear that glochidium is a good diagnostic feature in Hyriidae (Parodiz & Bonetto 1963, Mansur 1999, Mansur & Silva 1999, Pimpão et al. 2012), but is also necessary to find other characteristics on the morphology of adult specimens as well as on molecular aspects to substantiate this division. It is also important to mention that in South America there are many under-sampled areas and undescribed glochidia of Rhipidodontini. We propose to adopted parsimoniously the suggestion of Simone (2006), using *Rhipidodonta* only to the species that the glochidium is described and without any doubts about identification.

Glochidium is known for 31 nominal species of *Diplodon* and for 17 nominal species of *Rhipidodonta*. In cases where the glochidium type is missing, the genus assignment is based only on adult shell morphology. That is the case of some species recognized in several works as *Diplodon rhombeus* (= *Rhipidodonta rhombea* after Simone 2006) (Figure 5G). There were also some cases of “change” of the glochidium type, after detailed revision; for example, glochidium type in *Diplodon suavidicus* (d'Orbigny, 1835) (Figure 5E) was firstly assigned as non-parasite (Simone 2006) and

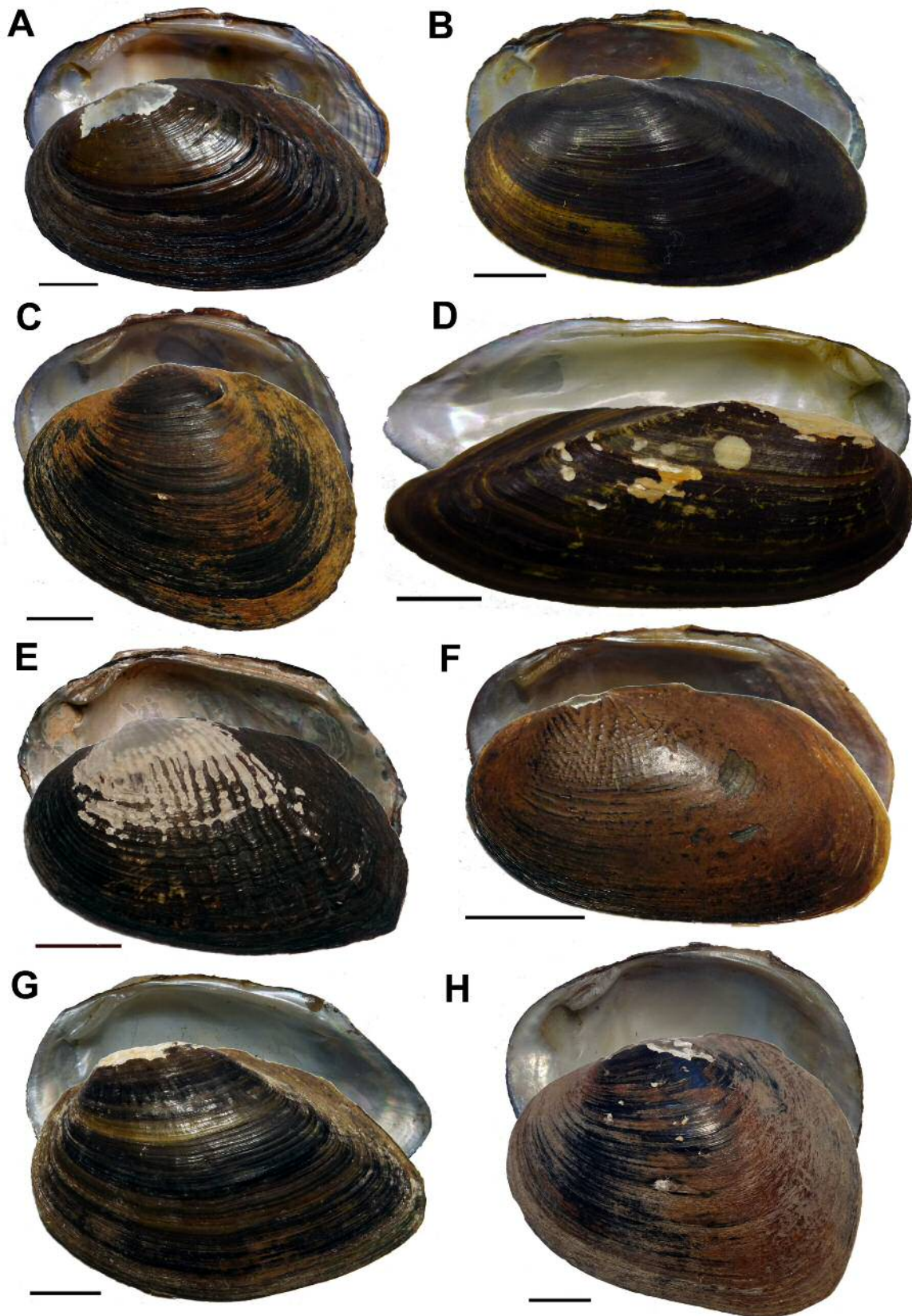


Figure 5. Members of Rhipidodontini. A- *Rhipidodonta charruana* (d'Orbigny, 1835), MHN (Museo Nacional de Historia Natural – Montivideo) 1210; B – *Diplodon chilensis* (Gray, 1828), LMD (Aquazoo Löbbecke Museum Düsseldorf) w/n (Lisikhe collection); C – *Diplodon fontainianus* (d'Orbigny, 1835), MHN 6285; D – *Diplodon parallelopipedon* (Lea, 1834), LMD w/n (Lisikhe collection); E – *Rhipidodonta hylaea* (d'Orbigny, 1835), ZMB (Museum für Naturkunde) w/n (Paetel collection); F – *Diplodon multistriatus* (Lea, 1831), MHN 3966; G – *Diplodon parodizi* Bonetto, 1962, MHN – Soc. Taguató 670; H – *Diplodon rhombeus* Spix in Wagner, 1827, SMF (Senckenberg Forschungsinstitut und Naturmuseum) 11248. Scale bar = 1 cm.

later as parasite (Pimpão et al. 2012). Pimpão et al. (2012) successfully used the glochidium to differentiate Amazonian species of Hyriidae, thus proving that glochidium can be powerful in species delimitation.

One concept that appeared in several older works was that of a “group of species” (Simpson 1914, Ortmann 1921, Haas 1930, 1931a,b), abandoned in more recent works (Haas 1969, Simone 2006, Graf & Cummings 2007). A “group of species” includes several species that share some characteristics, usually the shell structure, and the most prominent species (according to the author) lend their name to the group. However, the characteristics of the different groups are not very clear, which led to some overlapping. A group of species does not hold taxonomic status and is used only as a way to organize the species by morphological similarity. All the authors that used “group of species” presented six groups; however, the choice of main species and the composition of each group was different (Table 3). The groups of *Diplodon granosus* (Bruguière, 1792) and *D. delodontus* (Lamarck, 1819) (= *D. lacteolus*) were mentioned by the three authors above (Simpson 1914, Ortmann 1921, Haas 1930, 1931a,b); however, the species included in each group were different according to each author. For example, Simpson (1914) allocated 27 species in the group of *D. granosus*, whereas Ortmann (1921) and Haas (1930, 1931a,b), proposed only one species with three subspecies. The concept of “group of species” was similar to the concept of “super-species” used by Parodiz (1968, 1973), but also not applied in subsequent works (e.g., Simone 2006, Graf & Cummings 2006).

Simpson (1914) presented the highest number of species (80), with seven new species and one new subspecies. Some species names were used only by Simpson (1914) like *Diplodon ampullaceus* (Lea, 1866), *Diplodon aplatus* (Reeve, 1865), *Diplodon effulgens* (Lea, 1856), *Diplodon modestus* (Küster, 1856), *Diplodon quadrans* (Lea, 1859) and *Diplodon rufofuscus* (Lea, 1859). Simpson (1914) also included some Australian species in *Diplodon* (subgenera: *Hyridella*, *Cucumaria* and *Laevirostris*), which were removed by subsequent authors (e.g., Ortmann 1921, Haas 1969). Simpson (1914) synonymized some species names and described the species based mainly on their shell, using few information about the soft

parts. *Diplodon dunkerianus* (Lea, 1856) and *D. martensi* (Ihering, 1893) were only presented by Simpson (1914) and Parodiz (1968), among the authors of Table 2. However, there are more recent references to *D. martensi* (Mansur 1970, Vaz et al. 1987, Mansur 1999, Pfeifer & Pitoni 2003) and *D. dunkerianus* (Amaral et al. 2008).

Ortmann (1921) presented a similar number of species compared to later works (Haas 1969, Graf & Cummings 2007); however, the species listed were different. Ortmann based on the Unionida soft-parts morphology, proposed the first phylogenetic relationships of the Unionida families and subfamilies, as well as one of the first schemes to classify the South American naiades, which is still partially accepted. He also brought a wealth of information on the shell comparative morphology and glochidia of Hyriidae, a tool needed to better understand the high degree of polymorphism at the specific level.

The tendency to describe several new species decreases after Ortmann (1921). However, Haas (1916, 1929, 1938, 1966) still described four new species in separate works. This change in point of view is probably due to a better comprehension of shell polymorphism. The study of the naiads starts to acquire its current shape in Haas (1969), when he upgraded and expanded the synonymic lists started by Simpson (1914) and Ortmann (1921). Several species validated by Haas (1969) remained with the same status in subsequent works. For example, out of the 27 species considered valid by Graf & Cummings (2007), 23 received the status of species or subspecies by Haas (1969).

There are 149 species names associated to *Diplodon* and *Rhipidodonta*, excluding fossil species and *nomen nudum* (Parodiz 1968, Bonetto & Tassara 1987), 109 (73.15%) were used in species or subspecies rank by at least one of the authors of Table 2 and Appendix I (Simpson 1914, Ortmann 1921, Morretes 1949, Parodiz 1968, Haas 1969, Simone 2006, Graf & Cummings 2007), leaving out 40 species names (26.85%) that were not used by any of them. Despite the high number of species names used (i.e. 109), most of them were used only by one or two authors, 28.86% and 18.80%, respectively (Figure 6, Appendix I).

Table 2. Number of species of Rhipidodontini considered valid by different authors. Noteworthy that for our purposes, a global scope work is almost equal to a South America scope because the recent fauna Rhipidodontini occurs only in South America. * - The author presents some Australian forms as *Diplodon* subgenera (*Hyridella* Swainson, 1840; *Cucumaria* Conrad, 1853; *Laevirostris* Simpson, 1900), that are not included in this table, in order to allow an equal comparison with other authors. ** - Considered doubtful by the author.

Reference	Genera or subgenera	Number of valid species	Geographic scope
Simpson (1914)	<i>Diplodon</i> (<i>Diplodon</i>); <i>Diplodon</i> (<i>Cyclomya</i>); <i>Diplodon</i> (<i>Bulloideus</i>)	80 species + 4 subspecies*	Global
Ortmann (1921)	<i>Diplodon</i> (<i>Diplodon</i>); <i>Diplodon</i> (<i>Cyclomya</i>)	28 species	South America
Morretes (1949)	<i>Diplodon</i> (<i>Diplodon</i>); <i>Diplodon</i> (<i>Rhipidodonta</i>)	36 species + 2 subspecies	Brazil
Haas (1969)	<i>Diplodon</i> (<i>Diplodon</i>); <i>Diplodon</i> (<i>Rhipidodonta</i>); <i>Diplodon</i> (<i>Schleschiella</i>); <i>Diplodon</i> (<i>Bulloideus</i>)	22 species + 13 subspecies	Global
Parodiz (1968)	<i>Diplodon</i> (<i>Diplodon</i>); <i>Diplodon</i> (<i>Rhipidodonta</i>)	32 species + 6 subspecies	South America
Simone (2006)	<i>Diplodon</i> ; <i>Rhipidodonta</i>	22 (14 spp. in <i>Diplodon</i> , 8 spp. in <i>Rhipidodonta</i>) + 2 spp. doubtful**	Brazil and nearby areas
Graf & Cummings (2007)	<i>Rhipidodonta</i> ; <i>Diplodon</i>	27 (19 spp. in <i>Diplodon</i> , 8 spp. in <i>Rhipidodonta</i>)	Global

Table 3. Groups of species of *Diplodon* Spix in Wagner, 1827 presented by different authors.

Author	Groups proposed
Simpson (1914)	<i>Diplodon lacteolus</i> , <i>D. granosus</i> , <i>D. burroughianus</i> , <i>D. pazi</i> , <i>D. parallelipipedon</i> , <i>D. quadrans</i>
Ortmann (1921)	<i>D. hylaeus</i> , <i>D. granosus</i> , <i>D. chilensis</i> , <i>D. charruanus</i> , <i>D. lacteolus</i> , <i>D. ellipticus</i>
Haas (1930, 1931a,b)	<i>D. chilensis</i> , <i>D. charruanus</i> , <i>D. hylaeus</i> , <i>D. parallelipipedon</i> , <i>D. delodontus</i> , <i>D. granosus</i>

Only four species (2.68%) are recognized as valid by all authors, namely: *Diplodon charruanus* (d'Orbigny, 1835), *Diplodon granosus*, *Diplodon hylaeus* and *Diplodon parallelipedon* (Lea, 1834) (Figure 5A,D,E). Besides these, all the authors cited the “set” *ellipticus* Spix in Wagner, 1827 + *wagnerianus* Simpson, 1900 that refers to the same biological species, though Haas (1969) used *ellipticus* as a subspecies of *Diplodon granosus*. This agreement between the authors could suggest that these species are easily recognizable. This is (probably) true to *Diplodon hylaeus* and *Diplodon parallelipedon*, which have peculiar shell characteristics. The others (*charruanus/granosus/ellipticus*) were among the first species described to South America and have priority but were involved in taxonomical problems.

Six names: *D. besckeanus* (Dunker, 1848), *D. burroughianus* (Lea, 1834), *D. suavidicus* (Lea, 1856), *Diplodon gratus* (Lea, 1860), *Diplodon patagonicus* (d'Orbigny, 1835) and *Diplodon fontainianus* (d'Orbigny, 1835) were used by six authors as species or subspecies, representing 4.03% of all names. *Diplodon lacteolus* is clearly a synonymy of *Diplodon delodontus* as already noted by Lea (1836) in the original description. The “set” *lacteolus* + *delodontus* was mentioned by all the authors except for Morretes (1949).

This evaluation illustrates the divergence among authors, a result of different characteristics employed for species differentiation. Even in the species recognized by most authors, there are considerable differences in descriptions and synonymic lists.

Despite the differences in the geographic scope of Simone (2006) and Graf & Cummings (2007), they agree completely about the eight species included in *Rhipidodonta*. The few differences between these authors comprised species included in *Diplodon s.s.* Five species in Graf & Cummings

(2007) were not included in Simone (2006), namely: *Diplodon chilensis* (Gray, 1828); *Diplodon flucki* Morrison, 1943; *Diplodon guaporensis* Bonetto & Tassara, 1987; *Diplodon losadae* Haas, 1966 and *Diplodon solidulus* (Philippi, 1869). Despite the differences, Simone (2006) and Graf & Cummings (2007) were the most similar works presented in Appendix I.

4. Identification of Rhipidodontini

Shell characteristics were considered since the first researches on Rhipidodontini (e.g., Simpson 1914). The study of anatomical features was introduced by Ortmann (1921) and recently some molecular studies were done (e.g., Graf & Cummings 2006, Santos-Neto 2016). However, none of these approaches have been exhausted.

The shell outline was used for a long time to differentiate the subgenera of *Diplodon*. For example, the rounded species were asserted to *Rhipidodonta* and the more elongated species to *Diplodon s.s.* This division based only on shell proven to be artificial and not agree with other aspects. Nowadays, the shell structures were still in use and were not described in detail for most species (Miyahira et al. 2013). The most important characteristics of the shell are the umbo position, umbonal sculpture and hinge details. The ultra-structure of the shell was poorly studied in Hyriidae (Bieler et al. 2014) and must to be improved.

Only after the studies of Ortmann (1921) and Parodiz & Bonetto (1963) that provide the basic information on the glochidium type (with or without hooks) it was possible to link larva to subgenera and later to genera. *Diplodon* has glochidium with hooks and an obligate stage as parasite of fishes (Mansur et al. 2012, Pimpão et al. 2012). The life cycle of *D. martensi* was described by Mansur (1999) and remains as the unique species to have the cycle described in Brazil. The glochidium of *Rhipidodonta* is hookless and the life cycle still poorly known. The glochidium develop at the marsupium and the mussel release a juvenile (Wächtler et al. 2001, Mansur & Silva 1999, Mansur et al. 2012, Pimpão et al. 2012). Unfortunately the glochidium type was not described to all species of Rhipidodontini (Table 4). According to Pimpão et al. (2012) the glochidium was useful not only to separate the genera but also to identify species based on morphometrics and a detailed description. In order to avoid unnecessary taxonomical fluctuations, it is recommended that species remains at *Diplodon* until information on glochidia were obtained.

Some details of internal morphology was described only to the following species, *Diplodon charruanus*, *D. pilsbryi* Marshall, 1928, *D. besckeanus*, *D. multistriatus* (Lea, 1831), *D. rhombeus fontainianus* and *D. rotundus gratus* (Hebling & Penteado 1974, Alvarenga & Ricci 1981, Mansur & Anflor 1982, Ricci et al. 1988, Avelar & Cunha 2009). Meyer et al. (2012, 2014) described the reproductive system of *D. expansus* (Küster, 1856) and *D. ellipticus* from a histological perspective. Considering the reduced knowledge about Rhipidodontini morphology it is difficult to elect good diagnostic features in soft parts. Until now some differences between species were found with success on the outline and morphology of branchiae, position of marsupium, labial palps and stomach.

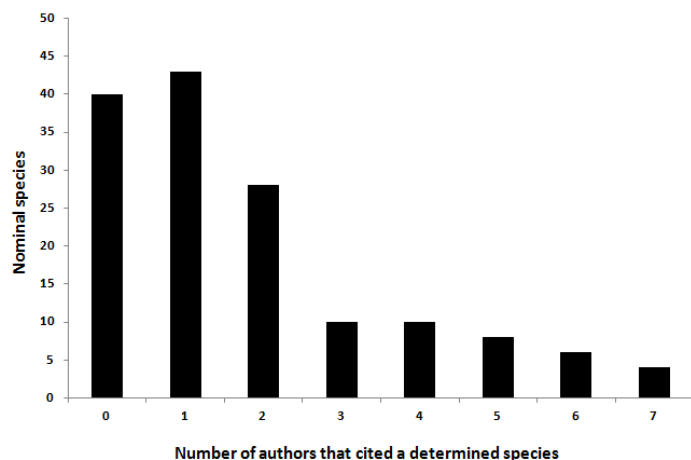


Figure 6. Number of times that a determined nominal species is cited by the evaluated authors (Table 3). See the Appendix I to base data.

Table 4. Nominal species of Rhipidodontini with glochidium type described in the literature. (Lea 1869, Ortmann 1921, Bonetto 1954, 1960, 1961, Bonetto & Ezcurra-de-Drago 1965, Alvarenga & Ricci 1979, Bonetto et al. 1986, Mansur & Campos-Velho 1990, Ricci et al. 1990, Martinez-Escabassiere & Royero 1995, Mansur & Silva 1999, Pimpão et al. 2012). We used *Diplodon* for all species to avoid new combinations without further studies

Glochidium with hooks (<i>Diplodon s.s.</i>)	Hookless glochidium (<i>Rhipidodonta</i>)
<i>D. atratus</i> , <i>D. berthae</i> , <i>D. besckeanus</i> , <i>D. decipiens</i> , <i>D. delodontus</i> , <i>D. ellipticus</i> var. <i>santanus</i> , <i>D. expansus</i> , <i>D. granosus</i> , <i>D. guaranianus</i> , <i>D. firmus</i> , <i>D. fontaineanus</i> , <i>D. frenzeli</i> , <i>D. hartwrighti</i> , <i>D. imitator</i> , <i>D. martensi</i> , <i>D. mogymirim</i> , <i>D. multistriatus</i> , <i>D. obsolescens</i> , <i>D. parallelipedon</i> , <i>D. parodizi</i> , <i>D. paulista</i> , <i>D. peculiares</i> , <i>D. piceus</i> , <i>D. rhuacoicus</i> , <i>D. rotundus</i> , <i>D. simillimus</i> , <i>D. solidulus</i> , <i>D. suavidicus</i> , <i>D. trivialis</i> , <i>D. vicarius</i> , <i>D. wagnerianus</i> e <i>D. yaguaronis</i>	<i>D. assuncionis</i> , <i>D. bulloides</i> , <i>D. burroughianus</i> , <i>D. charruanus</i> , <i>D. garbei</i> , <i>D. hasemani</i> , <i>D. hildae</i> , <i>D. hylaeus</i> , <i>D. iheringi</i> , <i>D. koseritzki</i> , <i>D. paranensis</i> , <i>D. peraeformis</i> , <i>D. rhuacoicus</i> , <i>D. subcuadratus</i> , <i>D. suppositus</i> e <i>D. variabilis</i>

Only four species of *Diplodon* were used in molecular approaches: *D. deceptus* Simpson, 1914, *D. suavidicus*, *D. demeraraensis* (Lea, 1859) and *D. chilensis* (Hoeh & Bogan 2000, Graf et al. 2015, Santos-Neto et al. 2016). All these molecular studies deals with wider questions, inner relations of Rhipidodontini were never investigated in detail.

Analyzing all these information, it is clear that several gaps remain in available knowledge about Rhipidodontini. More data are necessary to provide better species identification and consequently the genera differentiation. Nowadays, the unique secure attribute to separate *Diplodon* and *Rhipidodonta* is the glochidium type. All these data will be necessary to discover the internal relationships of Rhipidodontini.

5. Ecological preferences of Rhipidodontini

The species can occur in lentic or lotic habitats, from small streams to big rivers and lakes; however, they are not common in strong currents. They tolerate a wide granulometric range, but prefer fine sediments, usually rich in organic matter. Some species can occur between or below pebbles, or even in rock cracks. They usually start appearing at a depth of 30 cm. They are sometimes found associated to roots of aquatic plants (Avelar & Cunha 2009). They prefer the final sections of the river, due to the highest amount of nutrients, and are rare or absent in headwaters (Pereira et al. 2011, Miyahira et al. 2017). They can share space with other native freshwater mussels, as is commonly seen in southern Brazil, northern Argentina and Uruguay, apparently without harm to the species (Mansur & Pereira 2006, Pereira et al. 2011, 2014, Mansur et al. 2012). The species of Rhipidodontini are sensitive to environmental changes and suffer with domestic and industrial sewage discharge, the main cause of decrease in populations of freshwater mussels (Strayer et al. 2004; Miyahira et al. 2012; Mansur et al. 2012; Pereira et al. 2014).

6. Threats and the conservation of Unionida

Freshwater mussels are among the most endangered species (Strayer et al. 2004, Bogan 2008, Santos et al. 2009, Miyahira et al. 2012). The main cause of this threat is the habitat change. At the basin of the Paraná River, one of the richest areas in Brazil regarding freshwater mussels, there is a series of 70 reservoirs, turning a long-term survival difficult for mussels (Santos et al. 2009, Mansur et al. 2012, Pereira et al. 2014). The change of lotic to lentic habitats caused by the dams profoundly changes the physical and chemical conditions, affecting not only the mussels but also the host fishes (in the case of parasitic life cycle of *Diplodon*). This situation creates relictual populations of mussels, alive but fated to die, because they cannot reproduce or disperse without fish host. The long life achieved by these mussels allows them to have a long survival, but without any hope (Philipp & Abele, 2009). This situation created an extinction debt that already stated to be paid in North American fauna with several recent extinctions (Haag 2012).

Freshwater mussels were exploited by the mother of pearl button industry for a long time, mainly in North America (Neves 1999, Haag 2012), but also in South America (Beasley 2001, Matos 2007, Clavijo 2017). That exploitation caused the decline of several mussel populations in the USA, especially in the first half of the twenty century (Strayer et al. 2004, Haag 2012). Although usually considered a threat from the olden days, populations of *Paxyodon*, *Triplodon* and *Castalia* in the Brazilian Amazon are still exploited by the button industry (Beasley 2001, Matos 2007).

Recently, one of the major threats to the native bivalves is the introduction of invasive species (Haag 2012, Mansur et al. 2012). Among the most harmful species that were introduced to Brazil are *Limnoperna fortunei*, *Corbicula fluminea* (Müller, 1774), *Corbicula fluminalis* (Müller, 1774) and *Corbicula largillierii* (Philippi, 1844). *Limnoperna fortunei* (golden mussel)

has caused the worst damages to native mussels populations, as they grow over any hard substrate, including the shell of native mussels, preventing them to open their valves, causing death by suffocation and starvation (Mansur et al. 2004a, Darrigran & Damborenea 2006, Mansur et al. 2012). Besides the ecological problems, the introduced species can cause several economic losses to industries and energy plants; clogging pipes, filters and other structures (Mansur et al. 2004a,b, Darrigran & Damborenea 2006, Mansur 2007, Darrigran et al. 2007). The damages caused by these bivalves were recently reviewed by Boltovskoy & Correa (2015).

In the 2008 edition of the Brazilian Red Book of Threatened Species, 26 out of the 29 listed molluscs are freshwater mussels, including ten species of *Diplodon* (Amaral et al. 2008). However, a recent re-evaluation of the list (Santos et al. 2015), which strictly used the criteria of IUCN listed only two species as threatened, 11 as Data Deficient and 9 as Near Threatened. It is clear that the environmental conditions in Brazil not improved in these few years. This is actually an evidence of the lack of data and the risk of extinction must be re-evaluated considering the Brazilian reality. The threat to freshwater mussels is a global phenomenon. In North America, there are 73 species critically endangered and 37 probably extinct (Neves 1999, Strayer et al. 2004, Haag 2012).

Knowledge on freshwater mussels of Brazil is not sufficient, with several important data to species extinction evaluation risk missing, such as information about population dynamics and reproductive cycle. This prevents the inclusion of species in IUCN risk categories, unless if distribution evidence is used, the better data that we have. However, even the information about distribution has problems. Many times the distribution of freshwater mussels is assigned to a hydrographic basin as a whole (e.g., Simone 2006, Mansur et al. 2012); however, the situation in the “real world” is quite different, as the distribution of the species is not homogeneous and depends on several environmental factors (Haag 2012, Mansur et al. 2012). The mussels assemblages are patchily distributed and the movements in adult mussels are restricted (Pereira et al. 2011, Haag 2012, Vaughn 2017, Miyahira et al. 2017). Thus, the distribution of a mussel can never consider the basin as the whole for evaluation of extinction risks. Pereira et al. 2011 evaluated six sites along a gradient at a stream in the state of Rio Grande do Sul (Brazil); *Anodontites trapesialis* (Lamarck, 1819) and *Anodontites lucidus* (d'Orbigny, 1835) were found in one site; *A. patagonicus* (Lamarck, 1919) in two; and *Diplodon pilsbryi* in three. Similar situation is found by Miyahira et al. (2017) in a river at state of Rio de Janeiro (Brazil); *A. trapesialis* and *D. ellipticus* where found respectively in two and three sites out of ten surveyed. Another problem about distribution information is the use of old data obtained in literature and museums records (e.g., Mansur & Pereira 2006, Simone 2006, Miyahira et al. 2013). Thus, the distribution presented in most works is closest to the original, but also includes several places where species do not occur anymore, leading to a wrong evaluation of the risk of extinction.

Moreover, complete morphological information is absent as detailed above and this not affect only the taxonomy, but also conservation. For example, *Diplodon pfeifferi* (Dunker, 1848) is a species recorded only at the state of Rio de Janeiro and listed in 2008 edition of the Brazilian Red Book (Amaral et al. 2008) but some authors include this species in the synonym of *D. granosus* (Simpson 1914, Haas 1969, Simone 2006), a species not listed as threatened. It is clear that the correct identification of these two species is not only a problem of taxonomy.

It is necessary to improve the evaluation of risk to our mussels, some recommendations are done: 1) detail the distribution of the species relating, when possible, to environmental factors; 2) separate the old (or museum) records from current records; 3) collect in sub-sampled areas; 4) improve our knowledge on morphology and genetics to solve the taxonomical questions; 5) study the population dynamics of the species and 6) study the species reproduction cycle.

7. Summary of studies on Brazilian freshwater mussels

The first studies on South American Unionida fauna occurred during the time of great expeditions; several naturalists/collectors came to or received material from South America. One of the byproducts of this activity was that most part of South American type specimens are currently kept in European museums. Ironically, few species of naiads were described by South American researchers, some exceptions are Bonetto (1962), Bonetto & Tassara (1987) and Mansur & Pimpão (2008). In this phase, the descriptions were based mainly on the shells and, the species nowadays recognized as *Diplodon* or *Rhipidodonta*, were placed in the genus *Unio* Retzius, 1788 and commonly any variation of the shell was described as a new species, resulting in a large number of species names.

To this descriptive phase, a new phase in the study of South American freshwater mussels followed, that encompassed the organization and analysis of these names, with the aim to determine what really correspond to a biological species. Ihering (1893), a Deutsch zoologist established in Brazil, made the first attempt to organize some Brazilian species, and an improved work was published later (Ihering, 1910). He also published a series of studies about Brazilian mussels (e.g., Ihering, 1890, 1891), including some specimens from little studied states of Brazil, like Goiás (Ihering, 1904). Morretes (1949) is the first catalogue about freshwater mussels of Brazil made by a Brazilian researcher. Marshall (1917, 1922, 1923, 1926, 1927) described a series of South American species and proposed two new genera, *Diplodontites* Marshall, 1922 and *Mycetopodella*, both still in use (Simone 2006, Graf & Cummings 2007). Ortmann received a large amount of specimens from South America with soft parts that allowed him to describe new species and produced the above mentioned catalogue (Ortmann, 1921). Haas (1930, 1931a,b) published a catalog about South American species in a series of fully illustrated works. Haas (1969) is a landmark in the study of freshwater bivalves not only in South America but also in the world, and remains as the most “modern” global catalog of Unionida species with synonymic lists. At the same time Cox et al. (1969) presents a scheme including fossil groups.

The formation of South American freshwater mussel researches finally starts in the 1950's. Argentino A. Bonetto from the 1950's onwards published a series of papers concerning the mussel fauna of South America. From his extensive bibliography we can mention some of his studies about Rhipidodontini: dealing with diversity and anatomy (Bonetto 1954, 1962, 1964, 1965, 1967, Bonetto & Mansur 1970), larval stages (Bonetto 1961, 1965, Bonetto & Ezcurra 1965), museum collection revision (Bonetto 1973) and factors that affect mussel distribution (Bonetto et al. 1962, Bonetto & Di Persia 1975). The author also described two new species of *Diplodon* (Bonetto 1962, Bonetto & Tassara 1987) and one subgenus (Bonetto et al. 1986).

Amongst the most important papers published by Juan J. Parodiz about mussels are the compendium of available names for *Diplodon* (Parodiz 1968) and a study about the hybridization of *Diplodon delodontus* (Parodiz 1973). However, his masterpiece was the catalog about continental fossil molluscs (Parodiz 1969). Parodiz & Bonetto (1963) suggested a systematic arrangement of Unionida families based on larval type (see details above).

In Brazil, the studies of freshwater mussels intensified during the 1960's. Zanardini (1965) published a note about the occurrence and distribution of *Diplodon* and *Anodontites* Bruguière, 1792 in the state of Paraná. A greater increase in knowledge about freshwater mussel fauna began with the works of Mansur (1970) that presented the catalog of Hyriidae and Mycetopodidae of the state of Rio Grande do Sul. She published works dealing with specimens from southern Brazil (Mansur 1972, 1973, Mansur & Anflor 1982, Mansur & Pereira 2006) as well as from the Amazon River basin (Mansur & Valer 1992, Mansur & Pimpão 2008, Pimpão & Mansur 2009) and Pantanal (Serrano et al. 1998, Callil & Mansur 2005, 2007). There are also two technical works, one identifying Southern and Southeastern genera of mussels (Mansur et al. 1987) and another on

how to obtain and identify glochidia (Mansur & Campos-Velho 1991). Recently, her studies are mainly concerned with non-native bivalves (Mansur et al. 2012). The morphological aspects of Mycetopodidae were also studied in southern South America (Veitenheimer-Mendes 1973a,b, Veitenheimer-Mendes & Mansur 1978a,b, 1979).

Other researchers also studied freshwater mussels in Brazil. At the state of Rio de Janeiro, L.C. Alvarenga and C.N. Ricci studied the soft parts and glochidium of *Diplodon multistriatus* (Ricci et al. 1988, 1990), as well as the morphology of soft parts, glochidium and shell variation of *Diplodon besckeanus* (Alvarenga & Ricci 1977a,b, 1981). In the field of functional anatomy, there are the works of Wagner Avelar (Avelar & Santos 1992, Avelar 1993, Avelar & Cunha 2009) and Nilton Hebling (Hebling & Penteado 1974, Hebling 1976) concerning Hyriidae and Mycetopodidae species. Simone (1994, 1997) described the morphology of two species of *Anodontites*. Simone (2006) published an illustrated catalogue of molluscs species of Brazil (details above).

There are few studies on ecology, population dynamics and reproduction in Brazil. As the taxonomic and systematic issues have not been properly handled for most species, this often becomes an obstacle for ecological approaches. Henry & Simão (1985) analyzed the distribution of a population of *Diplodon delodontus expansus* (Küster, 1856) in the state of São Paulo. Beasley (2001) presents strategies for managing hyriids from the Amazon River basin. Meyer et al. (2010) evaluated the population structure and sexual proportion in a population of *Diplodon expansus*. Beasley et al. (2005) presented the reproductive cycle of *Paxyodon syrmatophorus* (Meuschen, 1781), while Avelar & Mendonça (1998) presented the gametogenesis of *Diplodon rotundus gratus*. Tomazelli et al. (2003) suggested the potential use of *A. trapesialis* as biological sentinel and the life cycle of this species were investigated by Callil & Mansur (2007) and Callil et al. (2012). Lopes et al. (2011) identified the parasite interaction in *Diplodon suavidicus* parasited by *Hysterothylacium* sp. (Nematoda). Recently the first phylogenetic approach of Hyriidae in Brazil was presented by Santos-Neto et al. (2016).

Important faunal surveys about freshwater mussels exist in other South American countries: French Guyana (Drouet 1859, Massemin et al. 2010), Suriname (Verhout 1914), Venezuela (Baker 1930, Lasso et al. 2009, Cummings & Mayer 2011), Peru (Ramírez et al. 2003), Paraguay (Quintana 1982), Argentina (Rumi et al. 2008), Uruguay (Corsi 1901, Olazarri 1966, Scarabino & Mansur 2007, Clavijo 2009) and Chile (Parada & Peredo 2002).

8. Conclusions

The large number of works concerning freshwater mussels in South America can give a false idea that the knowledge about these species is deep, but most of works are discreet and deal with one or two species. Comparative approaches of all kinds (morphological, ecological or molecular) are virtually absent. Even basic information is missing, as many species have not been studied beyond the original description. There have been some recent advances in Unionida systematic and the scheme with six or five families looks well established. However, the relationships inside the groups (e.g., families, genera) are poorly known and Rhipidodontini is not an exception. More data were needed to a better comprehension of the species and try to definitively solve questions like the status of *Rhipidodonta*. It is also an important step in order to reveal the real diversity of this group. The absence of good taxonomic and systematic information has been a limiting factor for biological and ecological studies, preventing appropriated extinction risk evaluation. The interactions of native with the invasive species need to be better understood, considering that the dispersion of the latter is notorious and harmful for native species. Integrating all this information is essential to development of appropriate conservation strategies for freshwater mussels in South America.

Supplementary material

The following online material is available for this article:

Appendix 1 – Taxonomical arrangement of principal revisions of Rhipidodontini. E – species; SE – subspecies; NA – not used by the author as species or subspecies.

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Conflicts of interest

The authors declare to have no conflict of interest.

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