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ANIMAL SCIENCE

Assessing the role of taxonomic impediment in the knowledge on geographic distribution of Physidae (Gastropoda: Hygrophila) in South America, using an intensive-data approach

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Abstract: There is a marked disparity in the state of knowledge of Holartic x Neotropical species of the freshwater snail family Physidae; the incipiency of data on Neotropical physids reflecting the lower number of dedicated specialists. The gaps in the knowledge on Neotropical physids have led to historical uncertainty about species validity. Revisiting the species is essential to reduce taxonomic impediment and delineating their probable distribution is the first step to attain this purpose. We aimed at critically analyze occurrence records of South American physids, compiled through an intensive search in the literature, biodiversity and molecular databases. We present a provisional characterization of the distribution of this family in South America, considering the probable versus the poorly documented distribution of the species. The critical underrepresentation of South American physids in collections, molecular databases and literature reinforces the role of taxonomic impediment in delaying the advance of the knowledge on species diversity. Malacological collections represented the main source of records, evidencing the relevance of unpublished data associated to specimens to assess distributional information on neglected groups. As most of the species are represented by shells, the reassessment of species identity and distribution must be done, using molecular and anatomical criteria for species delimitation.

Key words: taxonomic impediment, freshwater gastropods, georeferencing tools, occurrence records, biodiversity databases.

INTRODUCTION

One of the main contributions of biodiversity research is providing the datasets necessary to identify and predict patterns of species distribution (Su 2018). However, collecting data for testing hypotheses on this subject may be challenging, as it is often necessary that the species occurrence records cover long periods of time and wide spatial scales (Graham et al. 2008, Boakes et al. 2010). These limitations, associated with the availability of a great volume of scientific data in biodiversity repositories, have made data-intensive science a popular new approach for studying biodiversity (Kelling et al. 2009, Wüest et al. 2020). Accordingly, malacological collections assemble a large number of specimens, covering a wide range of temporal and spatial scales and thus allowing the compilation of sets of occurrence data, that are representative both geographically and historically, to reconstruct species distribution (Boakes et al. 2010, Rawlings et al. 2011, Vinarski 2017).

The studies on freshwater snails distribution pattern have historically focused on the chemical, physical and biological factors determining species composition and abundance (Lodge et al. 1987), the ecological status of water bodies (Hoang & Tong 2015), the risk of parasitic diseases transmission (Pointier et al. 2009, Oloyede et al. 2016, Rumi et al. 2017, Rabone et al. 2019), the spatial distribution of endangered species (Collado & Fuentealba 2020), and the spread of invasive species (Fernandez et al. 2003, Kock & Wolmarans 2007). These studies are more often based on intensive malacological surveys and for this reason, they are spatially limited to a region of interest (Pointier et al. 2009, Oloyede et al. 2016). Studies based on field surveys to assess the distribution of freshwater snail species over broader spatial scales are scarce (e.g., Allan et al. 2017), due to inherent logistical and financial constraints. These challenges have stimulated the search for new approaches, as the use of occurrence data from malacological collections (Fernandez et al. 2003), bibliographic databases (Alonso et al. 2019), and the identification of environmental proxies of snail abundance (Wood et al. 2019).

Physidae is a family of freshwater gastropods with a current worldwide distribution that has been, at least partly, the result of intensive introductions and subsequent invasions (Taylor 2003, Albrecht et al. 2009). Most physid species have restricted distribution ranges (Taylor 2003) though some physids may occur in nonnative areas as introduced species (Martin 2001, Bousset et al. 2014, Ng et al. 2015, 2018, Collado et al. 2020). One species, in particular, ie.: *Physella acuta* (Draparnaud, 1805), have a remarkably wide distribution range, occurring in several countries, and at least four continents (Appleton & Dana 2005, Mahmoud et al. 2013). *Physella acuta* is recognized as a globally invasive species (Allan et al. 2017, Ebbs et al. 2018), its identity being often confirmed through anatomical (Paraense 2003, 2004, 2005) and molecular studies during malacological surveys (Ng et al 2015, Collado 2017, Lawton et al. 2018, Collado et al. 2020). Another species with an apparently wide distribution in Central and South America is *Stenophysa marmorata* (Guilding, 1828), type locality San Vincent Island (Great Antilles), which was introduced in Africa (Appleton 2003, Dana & Appleton 2007, Bony et al. 2008, Camara et al. 2012, Mansouri et al. 2013, Ibikounlé et al. 2014) and Europe (Mahmoud et al. 2013). Many authors reported the occurrence of this species in South America (Rumi et al. 2004, 2008, Paraense 2005), though its status as an invasive or native species in this continent is not clear (Appleton 2003, Taylor 2003).

The number of available studies on physid species from Central and South America is much lower, when compared to species with Holarctic distribution (Dillon & Wethington 2006, Wethington et al. 2009). Thus, there are many gaps in the knowledge on geographic distribution, molecular diversity, and anatomy of physids in tropical and subtropical regions in the Americas [for a revision, see Taylor (2003), Núñez (2011), Collado et al. (2020)]. The estimates of species number in Physidae varies according to different authors. Te (1978) argued that the total number of valid species is 40, while Taylor (2003) calculated them at 81. Pointier (2008) argued that the actual number of species in this family is 15 or 20, a number justified by synonymy, molecular data (Dillon & Wethington 2006, Wethington & Lydeard 2007, Wethington et al. 2009), and reproductive isolation (Wethington & Lydeard 2007).

The employment of molecular or even anatomical criteria for the identification of *S. marmorata* is uncommon and this species probably have been systematically confounded with other species in Brazil and Argentina (Taylor

2003, 2004). Despite of the great geographic dimension of Brazil, along with its vast water resources, including 12 hydrographic basins, and six different biomes, only four nominal species of physids are alleged to be native to this country, ie.: *Afrophysa brasiliensis* (Küster, 1844), *Physa papaveroi* Leme, 1966, *Physa rivalis* Potiez and Michaud, 1838, and *S. marmorata*. The distribution of these species in Brazil was never assessed before, and the more frequently reported species in published malacological surveys is *S. marmorata*. Similarly, many studies mentioned *S. marmorata* as a species of Argentinian freshwater malacofauna (Rumi et al. 2004, 2008, Gregoric et al. 2006). Nonetheless, this name may probably uncover a hidden diversity of physid species in both countries (Martin 2001, Paraense 2005).

Herein, using an intensive-data approach, geoprocessing tools, and several sources of occurrence records, we have mapped the distribution of native species of Physidae in South America. We discriminated the occurrence records for which species identity was confirmed, and occurrence records without confirmation of species identity. Accordingly, the generated maps allow to critically consider the confirmed and the probable distribution of the species. The analysis of the data associated to the specimens deposited in malacological collections, besides the analysis of molecular databases, allowed to provide insights on the role of taxonomic impediment on the state of knowledge of South American Physidae.

MATERIALS AND METHODS

Species occurrence data

We searched for occurrence records of *Stenophysa marmorata* (Guilding, 1828) and synonymies proposed by Taylor (2003), as well as other physid species mentioned for South America: *Afrophysa brasiliensis* (Küster, 1844), *Aplexa venezuelensis* (von Martens, 1859), *Mayabina carolita* (Jousseaume, 1887), *Mayabina spiculata* (Morelet, 1849), *Mexinauta peruvianus* (Gray, 1828), *Physa aspii* Holmberg, 1909, *Physa loosii* Holmberg, 1909, *Physella osculans* (Haldeman, 1841), *Physa papaveroi* Leme, 1966, *Physa rivalis* Potiez and Michaud, 1838 (non Maton and Rackett, 1807), *Physa rivalis minor* d'Orbigny, 1841, and *Physella venustula* (A. Gould, 1847). To determine currently accepted valid species and collate information about species' geographical ranges we consulted *MolluscaBase* (http://www.molluscabase.org) (MolluscaBase (2022) (Table I).

The data used in this assessment came from online biodiversity databases, ie.: Species Link (https://specieslink.net/), Sistema de Informação sobre a Biodiversidade Brasileira – SibBr (https://www.sibbr.gov.br/) and the Global Biodiversity Information Facility – GBIF (2022) (https://www.gbif.org/); malacological collections with online access, ie.: Natural History Museum, London (NHMUK), Museum of Comparative Zoology, Harvard University (MCZ) and Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"- Invertebrates National Collection (MACNIn); and from the literature after research in the bibliographic databases Web of Science (www.webofscience.com/), Scielo (scielo.org/), Biodiversity Heritage Library (www.biodiversitylibrary.org/), Periódicos CAPES (www.periodicos.capes.gov.br/), Google Scholar (scholar.google.com.br/), Scopus (www.scopus.com/) with no restriction of publication year.

The searching keywords were applied as follows: "*Physidae*" or "*Afrophysa brasiliensis*" or "*Physa brasiliensis*" or "*Aplecta carolita*" or "*Mayabina carolita*" or "*Aplecta gualbertoi*" or "*Aplexa marmorata*" or "*Physa marmorata*" or "*Stenophysa marmorata*" or "*Physa nodulosa*" or "*Physa osculans*" or "*Physa papaveroi*" or "*Aplexa*

Table I. **Nominal species recorded in South America type locality, original combination, current taxonomic status, and occurrence records by country.**

Species name	Original combination	Type locality	Taxonomic status (Mollusca Base)	Records by country
***Mayabina carolita* (Jousseaume, 1887)**	*Aplecta carolita* Jousseaume, 1887	San Nicolás, Cantón Mejía, Ecuador	Accepted	Equador, Peru, Colombia
***Mayabina spiculata* (Morelet, 1849)**	*Physa spiculata* Morelet, 1849	Campeche, México	Accepted	México, Equador
***Stenophysa marmorata* (Guilding, 1828)**	*Physa marmorata* Guilding, 1828	St. Vincent, Lesser Antilles	Accepted	West Indies, Puerto Rico, Greater Antilles, Lesser Antilles, western Caribbean, Costa Rica, Panamá, Venezuela, Brazil, Argentina
***Afrophysa brasiliensis* (Küster, 1844)**	*Physa brasiliensis* Küster, 1844	Brazil	Accepted	Brazil, Ghana, Nigeria, South África
***Physella venustula* (Gould, 1847)**	*Physa venustula* Gould, 1847	Lima	Accepted	Peru, Argentina
***Aplexa venezuelensis* (Martens, 1859)**	*Physa venezuelensis* Martens, 1859	Mérida, Venezuela	Accepted	Venezuela
***Physa aspii* Holmberg, 1909**	*Physa aspii* Holmberg, 1909	Laguna de los Murciélagos, Prov. Formosa, Argentina	*taxon inquerendum*	Argentina
***Physa loosii* Holmberg, 1909**	*Physa loosii* Holmberg, 1909	Ciénaga al pie del Cerro de Pie de Palo, Prov. San Juan, Argentina	*Nomem dubium*	Argentina
***Physa rivalis minor* d´Orbigny, 1837**	*Physa rivalis var. minor* d´Orbigny, 1837	Montevideo, Uruguay	*Nomem dubium*	Uruguay, Argentina
***Physa papaveroi* Leme, 1966**	*Physa papaveroi* Leme, 1966	Dom Pedro II Park, São Paulo, Brazil	*Nomem dubium*	Brazil
Physella porteri (Germain, 1913)	*Physa porteri* Germain, 1913	brackish waters of Prov. Antofagasta, Chile	Accepted	Chile
***Mexinauta peruvianus* (Gray, 1828)**	*Physa peruviana* Gray, 1828	Swamps between Lima and Peru	Accepted	Ecuador, Peru
***Physa rivalis* Sowerby, 1822**	*Limnea* (*Physa*) *rivalis* Sowerby, 1822	Guadaloupe	Unaccepted	Brazil, Uruguay, Argentina

peruviana” or “*Mexinauta peruvianus*” or “*Physa porteri*” or “*Aplexa rivalis*” or “*Physa rivalis*” or “*Physa rivalis minor*” or “*Mayabina spiculata*” or “*Physa sowerbiana*” or “*Aplexa venezuelensis*” or “*Physa venezuelensis*” or “*Physella venustula*” or “*Physa aspii*” or “*Physa loosii*” or “*Physa porteri*” or “*Physa nodulosa*”) AND “Brazil” or “South America”. We selected published papers and PhD thesis with description of specific localities and/or geographical coordinates. We used *GEOLocate* (https://www.geo-locate.org/) to obtain the geographical coordinates for each locality, when this information wasn’t available, and *Calculadora Geográfica* (http://www.dpi.inpe.br/calcula/) to convert the coordinates to decimal degrees. We also obtained additional records, unavailable online, ceded by the curators of the malacological collections of the Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP), Instituto Oswaldo Cruz (Fiocruz), and Instituto de Pesquisas da Amazonia (INPA). After these steps, the data was arranged by species and reviewed to eliminate duplicates.

To characterize the knowledge gaps on molecular phylogeny and taxonomy of South American physids compared to the Holartic species, we searched for molecular records of all Physidae representatives available in GenBank in November 2022, using the search term “*Physidae* and the “Taxonomy” tab available on the NCBI platform (https://www.ncbi.nlm.nih.gov). All deposits were downloaded in full GenBank format. Using Perl scripts, the deposits were parsed to extract information related to the molecular markers used, species representativeness and quality of available molecular sequences.

Distribution Maps

All the maps presented in this work were generated by the *free-software Q-GIS 3.16.10 Hannover* (http://www.qgis.org). Species distributions were plotted and overlapped with layers of geopolitical boundary areas of South America obtained from DIVA resources (http://www.diva-gis.org/gdata) and Natural Earth (naturalearthdata.com/downloads/), along with layers of the main basins of South America and water lines obtained from WWF HydroSHEDS (https://www.hydrosheds.org/page/hydrobasinsandhydrosheds.org/page/hydrorivers). The basin complexes included here are based on the Freshwater Ecoregion of the World (FEOW) (Abell et al. 2008) grouped by hydrologic and biogeographic units. All layers were clipped using QGis for the South America. For all spatial analyses, all vector layers were used under the World Geodetic System 1984 and EPSG 4326 as reference system. The maps were made from georeferenced occurrence records in South America.

RESULTS

Our occurrence dataset was composed of 851 georeferenced records of the 13 nominal species from all the researched sources: 49.58% of the total come from literature, 47.70% from biodiversity databases and 2.70% from specimens housed in malacological collections. The total number of documents and collection records with useful information for this study was 57 and 794, respectively. Part of the occurrence dataset obtained from malacological collections could not be georeferenced because the information on the specific localities was lacking (127 records), or the specimens were identified as genus only (514 records).

The recovered distribution of the South American physid species ranged from Venezuela (6.4238° N 66.5897° W) to Chile (35.6751° S 71.543° W). The nominal species with the highest number of occurrence records were *S.*

marmorata (732 records), followed by *P. rivalis minor* (43), *A. brasiliensis* (15), *P. venustula* (15), *P. rivalis* (18), *M. peruvianus* (9), *M. carolita* (7), *P. papaveroi* (5) besides *P. aspii* (2) and *P. loosii* (2) with equal number of records. The species *A. venezuelensis, M. spiculata*, and *P. porteri* had only one record (Table II). There was only one record available for *P. osculans*. However, because of the inconsistent information in this record regarding the location's accuracy, we decided to exclude it from the analysis.

The number of records per species in each hydrographic basin as well their distributions by country are described and illustrated in the Table II, Figures 1 and 2. In the case of *P. venezuelensis* those records correspond only to type material housed in malacological collections from South America. Of the 25 hydrographic basins in South America, we found occurrence records for 19 basins (Figs 1 and 2). The hydrographic systems Central Patagonia Highlands, Pampas Region and South America Colorado accounted for just one record each (Table II). Two or more species were recorded in the Amazon; Colombia-Ecuador Pacific Coast; La Plata; Magdalena; North Chile Pacific Coast; Orinoco; Peru Pacific Coast; Sao Francisco and Uruguay-Brazil South Atlantic Coast basins. The Uruguay-Brazil South Atlantic Coast basin was the hydrographic system with the highest number of records (451), followed by La Plata basin (171) (Table II).

Afrophysa brasiliensis, *M. carolita*, *M. peruvianus*, *P. rivalis*, *P. rivalis minor*, *S. marmorata, P. venustula,* and *P. loosii* were recorded in more than one basin, while the remaining species (ie.: *A. venezuelensis*, *M. spiculata*, *P. aspii*, *P. papaveroi,* and *P. porteri*) occurred in just one basin (Table II). According to the compiled occurrence records, *Stenophysa marmorata* showed the wider geographic distribution in South America, occurring in eight (ie.: Argentina, Brazil, Colombia, French Guiana, Guiana, Peru, Uruguay, and Venezuela) of the twelve South American countries, and 13 hydrological basins (i.e.: Amazon; Caribbean Coast; Colombia-Ecuador Pacific Coast; East Brazil South Atlantic Coast; La Plata; Magdalena; North Brazil South Atlantic Coast; Northeast South America South Atlantic Coast; Orinoco; São Francisco; Peru Pacifc Coast; Tocantins; Uruguay-Brazil South Atlantic Coast) (Supplementary Material - Fig. S1). Most of the records of this species were contained

Table II. **Number of records of physids by countries and Hydrological basins in South America.**

Species	Country (number of records)	Hydrological basins (number of records)
Afrophysa brasiliensis	Argentina (1)	Amazon (2)
	Brazil (13)	La Plata (7)
	Peru (1)	North Chile, Pacific Coast (1)
		Uruguay - Brazil, South Atlantic Coast (5)
Mayabina carolita	Peru (5)	Amazon (2)
	Colombia (1)	Colombia - Ecuador, Pacific Coast (1)
	Ecuador (1)	Magdalena (1)
		Peru, Pacific Coast (3)
Mexinauta peruvianus	Ecuador (1)	Amazon (4)
	Peru (8)	Colombia - Ecuador, Pacific Coast (1)
		Peru, Pacific Coast (4)

Table II. Continuation.

Physa rivalis	Argentina (1)	La Plata (9)
	Brazil (11)	Orinocco (2)
	Paraguay (1)	Sao Francisco (1)
	Peru (1)	Peru, Pacific Coast (1)
	Uruguay (3)	Uruguay - Brazil, South Atlantic Coast (5)
	Venezuela (1)	
Physa rivalis minor		Central Patagonia Highlands (1)
		La Plata (32)
	Brazil (2)	Mar Chiquita (3)
	Argentina (30)	North Argentina, South Atlantic Coast (3)
	Uruguay (11)	Pampas Region (1)
		Uruguay - Brazil, South Atlantic Coast (3)
Stenophysa marmorata		Amazon (18)
	Argentina (6)	Caribbean Coast (3)
	Brazil (707)	Colombia - Ecuador, Pacific Coast (1)
		East Brazil, South Atlantic Coast (19)
	Colombia (8)	La Plata (120)
	French Guiana (1)	Magdalena (1)
	Guiana (2)	North Brazil, South Atlantic Coast (40)
		Northeast South America, South Atlantic Coast (3)
	Peru (3)	Orinocco (2)
	Uruguay (1)	Peru, Pacific Coast
		Sao Francisco (32)
	Venezuela (4)	Tocantins (59)
		Uruguay - Brazil, South Atlantic Coast (432)
Physella venustula	Chile (8)	Colombia - Ecuador, Pacific Coast (1)
	Colombia (4)	Magdalena (2)
	Peru (1)	North Chile, Pacific Coast (8)
	Venezuela (1)	Orinocco (2)
		Peru, Pacific Coast (2)
Physa loosii	Argentina (2)	La Plata (1)
		South America, Colorado (1)
Physa aspii	Argentina (2)	La Plata (2)
Aplexa venezuelensis	Venezuela (1)	Orinocco (1)
Mayabina spiculata	Ecuador (1)	Colombia - Ecuador, Pacific Coast (1)
Physa papaveroi	Brazil (5)	Uruguay - Brazil, South Atlantic Coast (5)
Physella porteri	Chile (1)	North Chile, Pacific Coast (1)

in Brazil, including 19 of the 26 Brazilian states plus the Federal District. The species identity was confirmed by using traditional operational criteria (shell traits, anatomy of the soft parts or both criteria) for part of the occurrence records in most of the hydrological basins, except for the Occidental part of the North Brazil South Atlantic Coast, corresponding to Maranhão state. For the northern part of the East Brazil South Atlantic Coast species identity wasn't confirmed.

Afrophysa brasiliensis was recorded in three countries in (ie.: Brazil, Argentina, and Peru) and in four hydrological basins (ie.: Amazon, La Plata, North Chile Pacific Coast, and Uruguay-Brazil South Atlantic Coast). Most of the records were contained in Brazil, accounting for three states in the Southern and South regions (ie.: Rio de Janeiro, São Paulo, and Rio Grande do Sul), besides two records for Argentina and Peru, in the provinces of Misiones and Lima, respectively (Fig. S2). The occurrence records whose species identification was confirmed correspond to the probable native distribution area of this species in Southern Brazil, while the records for Amazonia and Peru seem to be outside its distribution range.

For *P. rivalis*, we found occurrence records in six countries (ie.: Argentina, Brazil, Paraguay, Peru, Uruguay, and Venezuela) and in five hydrological basins (ie.: La Plata; Orinoco; São Francisco; Peru Pacific Coast; and Uruguay-Brazil South Atlantic Coast) (Fig. S3). Despite of the one record for Peru is the only whose species identity was confirmed, we have found a concentration

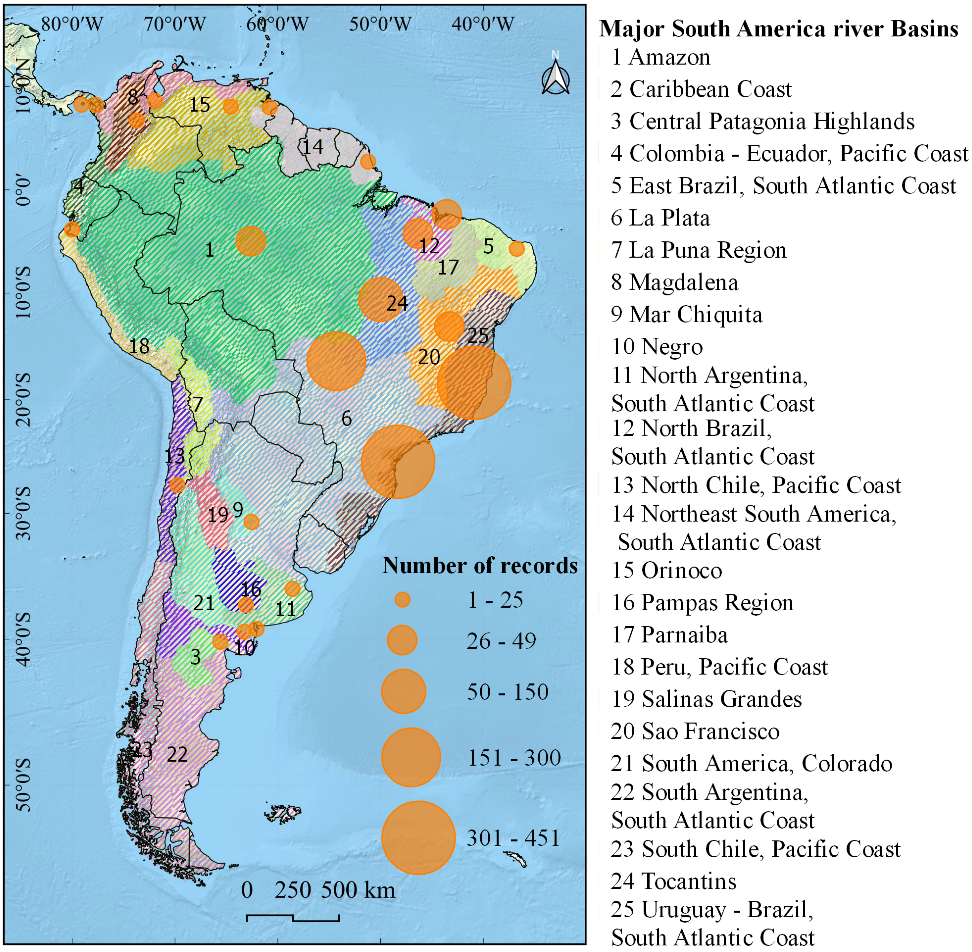

Figure 1. Number of records of physid species by hydrological basins in South America obtained from an intensive search in the literature, biodiversity databases and malacological collections.

of records for this species in an area including Southeastern-South Brazil, Paraguay, and Uruguay. The sole record for Venezuela and for Peru seems to be outside the probable range of this species. However, because the species identity for most occurrence records for *P. rivalis* is unresolved, the distribution range of this species remains unclear. Considering the subspecies *P. rivalis minor*, we found occurrence records for three countries (ie.: Brazil, Argentina, and Uruguay) and six hydrological basins (ie.: Central Patagonia Highlands; La Plata; Mar Chiquita; North-Argentina South Atlantic Coast; Pampas region; and Uruguay-Brazil South Atlantic Coast) (Fig. S4). Species identification for most of the occurrence records of this species was checked. However, the sole record for Brazil seems to be inconsistent with its main distribution in Argentina and Uruguay.

Mayabina carolita was recorded in three countries (ie.: Colombia, Ecuador, and Peru) and in four hydrological basins (ie.: Amazon; Colombia-Ecuador Pacific Coast; Magdalena; Peru Pacific Coast) (Fig. S5). Despite of species identity couldn't be checked for any occurrence record obtained for *M. carolita*, the recovered distribution seems to be consistent. Nonetheless, this species distribution still needs to be validated after confirmation of the species taxonomic identity.

We found occurrence records for *M. peruvianus* in Peru and Ecuador in three

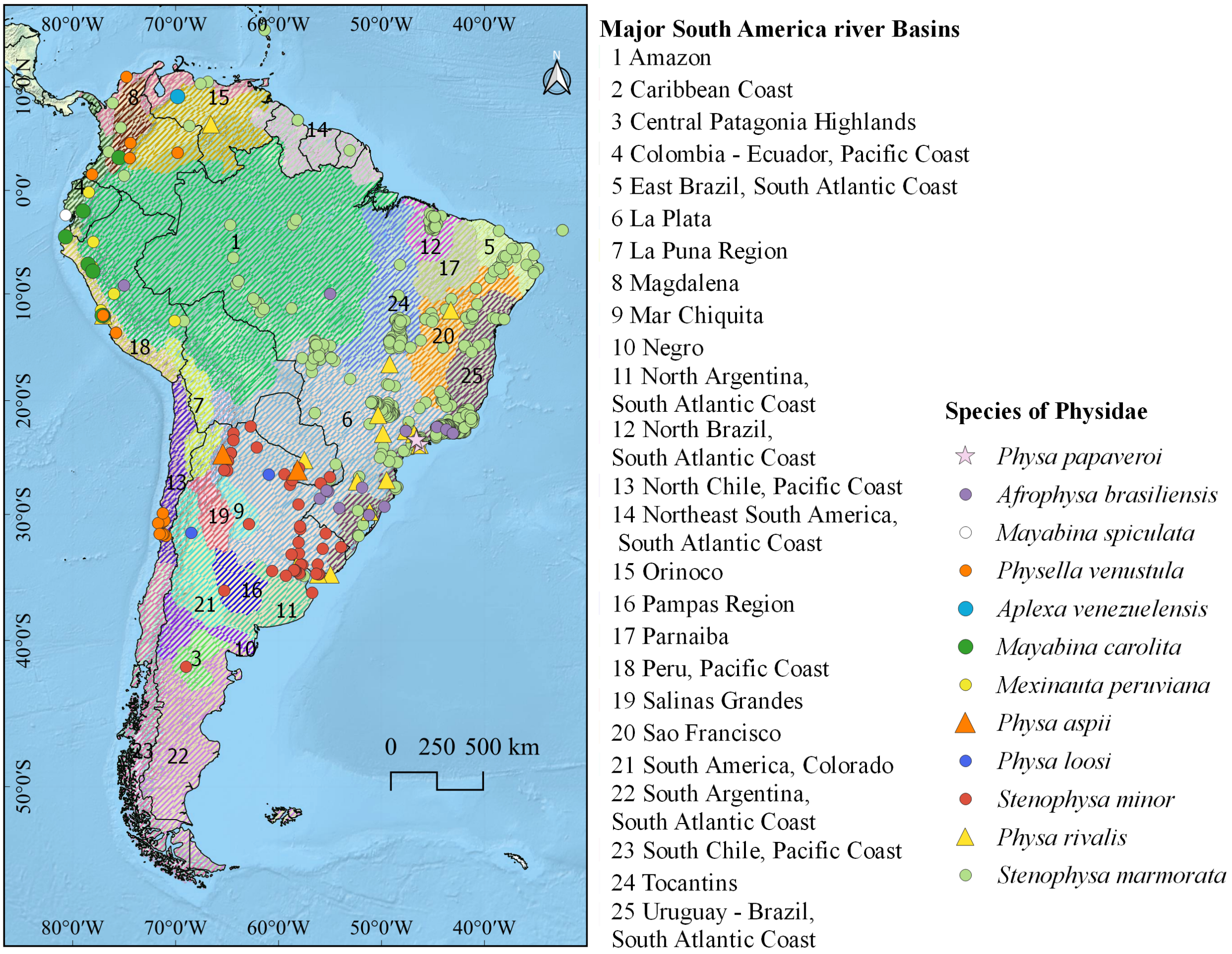

Figure 2. Distribution map of physid species recorded in hydrological basins of South America.

hydrological basins, including the Amazon, Peru Pacific Coast, and Colombia-Ecuador Pacific Coast (Fig. S6). The only records with confirmation of species identity were ascribed to Peru (Peru Pacific Coast basin). The recovered distribution for this species seems consistent, despite the need to confirm species identification associated to some of the records for Peru and all records for Ecuador.

Physella venustula was recorded in Chile, Colombia, and Peru, in five hydrological basins, including the Colombia-Ecuador Pacific Coast, Magdalena, North Chile Pacific Coast basin, Orinoco, and Peru Pacific Coast (Fig. S10).

The few records associated to the names *Physa papaveroi*, *P. loosii*, *P. aspii, Physella porteri, A. venezuelensis*, and *M. spiculata* may indicate that these species present more restricted distribution. *Physa papaveroi* was recorded only in Brazil, with five records in the Uruguay-Brazil South Atlantic Coast basin (Fig. S7); *A. venezuelensis* was recorded only in Venezuela, with one record in the Orinoco basin (Fig. S8); *P. porteri* was recorded only in Chile, with one record in the North Chile Pacific Coast basin (Fig. S8); *P. loosii* was recorded in Argentina, with one record in the La Plata basin and one record in the South America Colorado basin (Fig. S9); *P. aspii* was recorded only in Argentina, with two records in La Plata basin (Fig. S9); *M. spiculata* was recorded only in Ecuador, with one record in the Colombia-Ecuador Pacific Coast basin (Fig. S10). The species identification associated to all these records could not be confirmed.

The search for molecular database records recovered 3,757 sequences for Physidae. Only three complete mitochondrial genomes have been deposited, all of them belonging to the same species, *Physella acuta*. About 5% of the deposited sequences do not presented identification at specific level, being identified only at the family and subfamily levels. Among these unidentified sequences 14% corresponded to species from South America and 86% from other continents. Regarding the DNA sequences identified at the specific level, the deposits were predominantly ascribed to *Physella acuta* (59%), followed by *Physella ancillaria* (10%), *Physella gyrina* 6%), *Beringophysa jennessi* (7%), *Physella zionis* (3%), *Physa natricina* (2%), and *Aplexa elongata* (2%), *Stenophysa marmorata* (1%), *Physa fontinalis* (1%), *Physella johnsoni* (1%), *and Aplexa hypnorum* (1%). The remaining 24 species presented a single sequence each, together representing 7% of the available sequences. Regarding the molecular markers available for Physidae, 59 different markers were found, and the most representative in descending order were: Cytochrome oxidase subunit I (70%), 16S-rDNA (18%), 28S-rDNA (6%), NADH dehydrogenase subunit 4 (4%) and Cytochrome b oxidase (2%). The other molecular makers were associated to few sequences and presented low taxonomic representation. Considering all the valid species from South America, according to MolluscaBase, only two species (14%) were represented in molecular databases, ie.: *Stenophysa marmorata* (molecular markers: actin, 16S-rDNA and COI-mtDNA) and *Stenophysa minor* (5.8S r-DNA). *Stenophysa marmorata* presented 20 sequences (16 sequences deposited as *S. marmorata* and four sequences deposited as *Aplexa marmorata*), while *S. minor* presented only a single sequence.

The analysis of the data associated with specimens deposited in malacological collections showed that of the 13 species herein analyzed, only two, *S. marmorata* and *P. rivalis*, are represented in these collections by ethanol preserved specimens (Fig. 3). Considering all the species, most of the specimens are represented by shells only. For eight species out of the 13 species analyzed the sole source of occurrence records was malacological collections. Most of these records seems to be historical, the last collection date for most of the species remounting to several decades ago.

DISCUSSION

The distribution of the freshwater snail family Physidae is mainly Holartic, but this taxon also includes several species occurring in Central and South America (Taylor 2003, Wethington & Lydeard 2007). There is a marked disparity in the state of knowledge on North American x Central and South American species; the incipiency of data on Neotropical physids reflecting the lower number of research groups and specialists dedicated to their study, and consequently the scarcity of scientific publications, DNA sequences available in biodiversity databases, and specimens deposited in Malacological collections (Sartini et al. 2022). The many gaps in the knowledge on distribution, taxonomy, and morphology of South American physids have led to historical uncertainty about species validity (Taylor 2003, 2004, Núñez & Pelichotti 2003, Núñez 2011). Thus, revisiting species to provide basic knowledge on geographic distribution, as

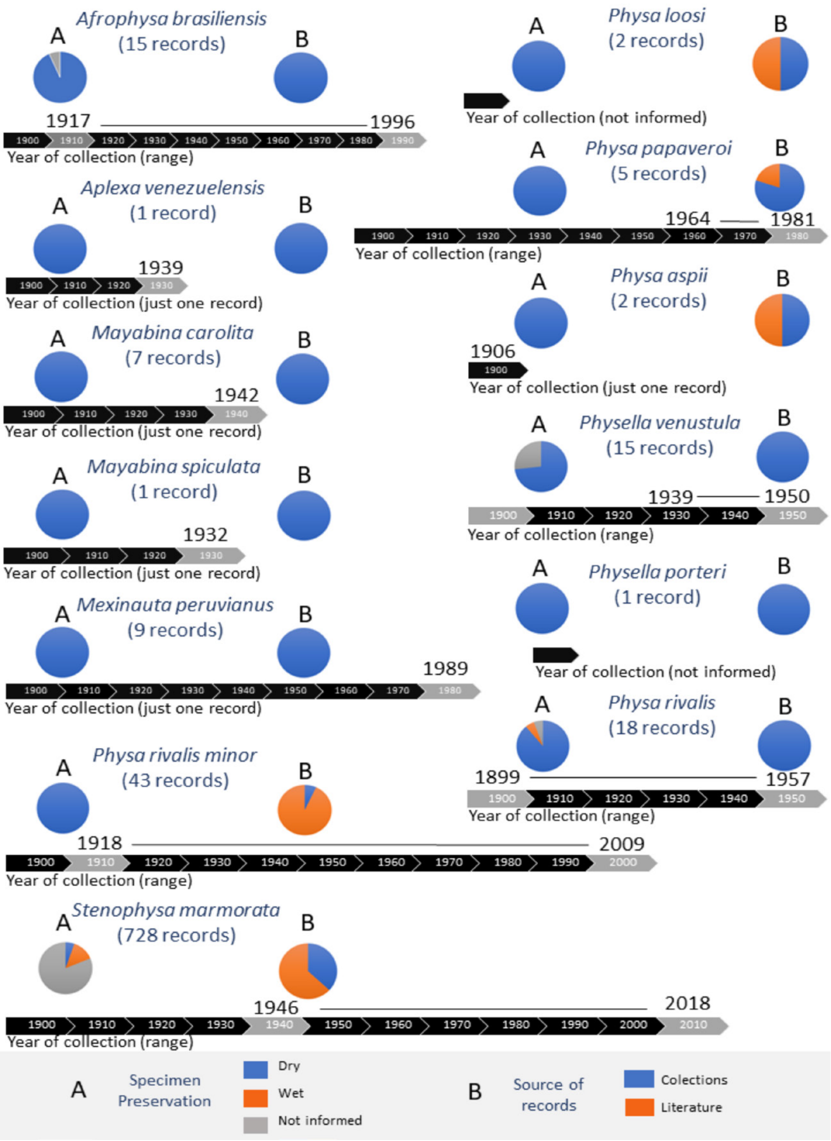

Figure 3. Relative contributions of literature and malacological collections as sources of occurrence records for South American physid species; via of preservation of the specimens from collections, and collection date range.

well as reliable operational criteria for species delimitation is essential to reduce taxonomic impediment. Delineating the probable distribution of Neotropical physid species is the first step to attain this purpose, allowing researchers to better decide how to direct efforts to specimens' collection and subsequent analysis.

Studies on physid species in the Neotropics and particularly in Brazil, are mostly concerned to the invasive *P. acuta*, and the native *S. marmorata* (Coimbra-Junior & Santos 1986, Paraense 1986, Teles et al. 1991, 2002, Vaz et al. 1992, Souza et al. 1998, 2006, Thiengo et al. 1998, 2001, 2002a, 2002b, 2004, 2005, 2006, Carvalho et al. 2001, Fernandez et al. 2010, 2014, Maldonado et al. 2001, 2003, Medeiros et al. 2002, Queiroz et al. 2002, Callisto et al. 2005, Oliveira et al. 2007, Agudo-Padrón 2008, Ituarte et al. 2008, Moreno 2008, El-Kouba et al. 2009, Agudo-Padrón & Lenhard 2011, Barbosa 2011, León 2011, Núñez 2011, Mota et al. 2012, Pinto & Melo 2012, Souza & Melo 2012, Ohlweiler et al. 2013, Cantanhede et al. 2014, Pinto et al. 2014, Cortés-Guzmán & Linares 2016, Mattos 2017, Almeida et al. 2018, Maciel et al. 2018, Collado et al. 2020). Several nominal species were never revisited after their descriptions (Taylor 2003). Consequently, the operational criteria used to delimit these species remain largely based on shell morphology, impairing the estimation of species diversity and distribution, as the shells of South American physids, with few exceptions, are very similar (Fig. 4).

Herein, we have compiled and critically analyzed occurrence records of South American physids obtained through an intensive search in the literature, biodiversity databases, and malacological collections whose data is unavailable online. In some cases, we were

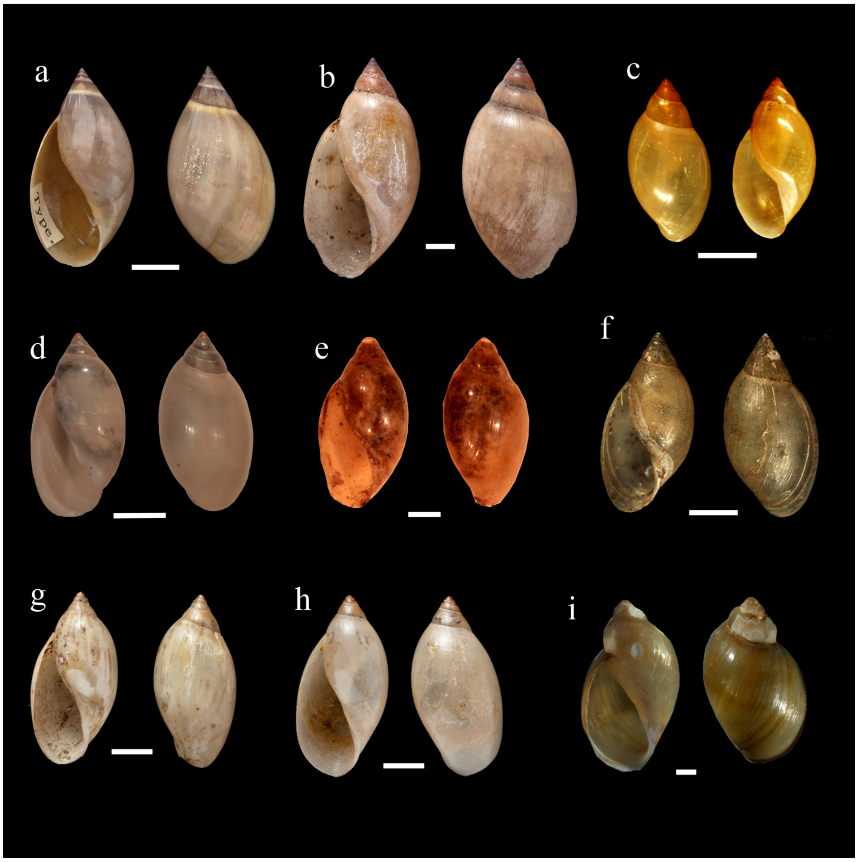

Figure 4. South American physids with Aplexini-like shells. **4a.** Syntypes of *Mexinauta peruvianus*. Scale bar: 3 mm. Source: NHMUK 1950.5.24.3-6. **4b.** Syntypes of *Physa sowerbyana* (=*Stenophysa marmorata*). Scale bar: 3mm. Source: NHMUK 1854.10.4.111-112; **4c.** Topotype of *Stenophysa marmorata*. Scale bar: 5 mm. Source: Laboratório de Referência Nacional em Malacologia Méd–ca - IOC–Fiocruz, Rio de Janeiro, Brasil. **4d.** Syntypes of *Physa loosii* . Scale bar: 2 mm. Source: MACN 1404; **4e.** Syntypes of *Physa aspii*. Scale bar: 2 mm. Source: MACN 1407; **4f.** *Mayabina carolita*; **4g.** Probably syntypes of *Physa rivalis major* (= *Mexinauta peruvianus*). Scale bar: 3 mm. Source: NHMUK 1854.12.4.259. **4h.** Possible syntypes of *Physa rivalis minor*. Scale bar: 3 mm. Resource: NHMUK 1854.12.4.256. **4i.** Paratype of *P. papaveroi*. Scale: 1 mm. Source: MZSP 16618.

able to validate species identification using shell morphological criteria currently accepted, because the images of these specimens were available in the databases, or they were ceded by the curators of malacological collections. Nonetheless, for most of the records herein compiled, we could not validate species labelling. Thus, we present a provisional characterization of the distribution of this family in South America, focusing on native species. We discriminated the occurrence records for which species identity was confirmed, and occurrence records without confirmation of species identity. Accordingly, the generated maps allow to critically consider the likely distributions of the species.

The number of occurrence records ascribed to *S. marmorata* (732) recovered herein was noticeably higher than the records ascribed to the remaining species (1 to 43), being associated to eight (ie.: Argentina, Brazil, Colombia, French Guiana, Guiana, Peru, Uruguay, and Venezuela) of the twelve South American countries, and 13 hydrological basins (i.e.: Amazon; Caribbean Coast; Colombia-Ecuador Pacific Coast; East Brazil South Atlantic Coast; La Plata; Magdalena; North Brazil South Atlantic Coast; Northeast South America South Atlantic Coast; Peru Pacific Coast; Orinoco; São Francisco; Tocantins; Uruguay-Brazil South Atlantic Coast). This apparent widespread distribution of *S. marmorata*, including several isolated hydrographic basins indicates the possibility of species misidentifications due to the similarities in shell shape, which is the main criteria available for the discrimination of South American physids. Even the occurrence records whose species identity was confirmed may cover a cryptic diversity as the traditional operational criteria for species delimitation in Physidae are often ineffective, the results of molecular studies showing both the overestimation of species numbers and the presence of cryptic species (Wethington & Lydeard 2007, Pip & Franck 2008, Albrecht et al. 2009, Wethington et al. 2009, Gates et al. 2013, Gustafson et al. 2014, Ng et al. 2015, Collado 2017, Ebbs et al. 2018, Collado et al. 2020, Sartini et al. 2022). Alternatively, this apparently wide distribution may also indicate the presence of a complex of cryptic species under the name *S. marmorata*. The use of phylogenetic tools for species delimitation has the potential to reduce taxonomic impediment, detect synonymies, and bring evidence of complex of cryptic species as observed for North American physids (Young et al. 2021, Sartini et al. 2022). Sartini et al. (2022) using coalescence-based methods for species delimitation have demonstrated the presence of taxonomic inflation and cryptic diversity in Holartic Physidae. This may be true for Neotropical physid species as well. However, there is virtually no published study aimed at investigating species limits and cryptic diversity in Central and South American Physids, and the critical underrepresentation in molecular databases confirms the significance of molecular and taxonomic impediment for our knowledge on Neotropical physids.

Despite our data compilation efforts, we found very few records for the nominal species *A. brasiliensis*, *A. venezuelensis*, *M. carolita*, *M. spiculata*, *M. peruvianus*, *P. papaveroi*, *P. rivalis*, *P. rivalis minor*, *P. aspii*, *P. loosii P. venustula*, and *P. porteri*. The scarcity or absence of records in malacological collections may indicate that these species have not been recollected over time. Alternatively, the lack of records may reflect a taxonomic impediment, due to the insufficiency of the operational criteria in delimiting species as well as the scarcity of freshwater malacology specialists dedicated to the study of South American physids (Lydeard et al. 2004, Lysne et al. 2008, Böhm et al. 2020).

Herein, the compiled records of physid species in Brazil from both malacological collections and literature accounted for the presence of two species described from this country, that is *A. brasiliensis*, *P. papaveroi,* and two species considered to be *indigenous to* South America, alleged to be synonyms, ie.: *P. rivalis* and *S. marmorata*, besides the Holartic invasive *P. acuta* (Santos et al. 2016). It is not clear if the native distribution area of *S. marmorata* also includes localities in southern parts of South America. Clench (1930) argued that this species seemed to be widespread, occurring in several localities of the Lesser Antilles and the Northeastern part of South America, including the Brazilian states of Pará and Ceará. This distribution pattern observed by Clench (1930) agrees with the opinion of Taylor (2003), according to which the distribution of *S. marmorata* does not extend southwards in South America. In Brazil, the records ascribed to *Stenophysa marmorata* correspond to 19 of the 26 states plus the Federal District. The other native species were associated with a smaller number of records; these results, however, may be due to a taxonomic impediment. *Afrophysa brasiliensis* may have been systematically confounded with *S. marmorata* and it is possible that *P. papaveroi* specimens has been ascribed to the invasive species *P. acuta* (Leme, 1966). *Physa papaveroi* was described based on shell morphology, radula and the anatomy of the soft parts (ovotestis and penial complex). Due to the similarities with *P. acuta P. papaveroi* is presently considered *nomen dubium* (MolluscaBase 2022) although its taxonomic status can only be solved with the employment of molecular tools.

All the 364 records of physids in Brazil, obtained from the literature (malacological surveys and species lists, published between 1986 and 2018) corresponded to *S. marmorata*. Great part of the studies does not inform the criteria used for species identification (Coimbra Júnior and Santos 1986, Vaz et al. 1992, Carvalho et al. 2001, Medeiros et al. 2002, Maldonado et al. 2003, Giovanelli et al. 2005, Oliveira et al. 2007, Agudo-Padrón 2008, Moreno 2008, Núñez 2010, 2011, Agudo-Padrón & Lenhard 2011, Pinto & Melo 2012, Fernandez et al. 2014). Considering the recovered studies in which the operational criteria for species delimitation are described, the identification of *S. marmorata* was based on the anatomy of the soft parts (Souza et al. 1998, Thiengo et al. 1998, 2001, 2002a, 2002b, 2004, 2006, Queiroz et al. 2002, Teles et al. 2002, El-Kouba et al. 2009), or the combination of anatomy and shell morphology (Souza et al. 2006, Barbosa 2011, León 2011, Mota et al. 2012, Souza & Melo 2012, Ohlweiler et al. 2013, Cantanhede et al. 2014). Nonetheless, only the microanatomy of the penial complex may reveal diagnostic characteristics to distinguish between *S. marmorata* and *A. brasiliensis* (Taylor 2003). Besides, the anatomy of the other species occurring in Brazil is still unknown. Thus, physid species identification in Brazil may have been impaired by the insufficiency of the operational criteria traditionally employed, even in the favorable scenario where the anatomy of the soft parts and the shell morphology are combined. As a result, species identity has been largely attributed to the supposedly widespread *S. marmorata*, probably obscuring the presence of morphologically cryptic species with more restricted distributions.

According to Taylor (2003) and Pointier (2008) *S. marmorata* is also virtually widespread in Central America and the Caribbean, where it was previously recorded in 11 countries [ie.: Antigua and Barbuda, Barbados, Dominica, Guadeloupe, Jamaica, Martinique, Montserrat (overseas British territory), Saint Kitts and Nevis, Saint Lucia, Trinidad and Tobago, and United States Virgin Islands]. Such a wide distribution may also be due to the widespread use of the name *S. marmorata* as discussed above.

The compiled records of physid species in Peru accounted for the presence of four native species from South America, i.e.: *M. peruvianus*, *M. carolita*, *S. marmorata*, and *P. rivalis*. *Mexinauta peruvianus* (=*Physa peruviana* Gray, 1828) was described for Peru, "inhabiting swamps between Lima and Callao" (Gray 1828). It is possible that *M. peruvianus* presents a restricted distribution area and may also be endangered or extinct, as evidenced by the significant environmental alteration in the area corresponding to the type locality of this species and the scarcity of records in databases despite some research efforts (Paraense 2003, Taylor 2003). Larrea et al. (1990) found this species in a few collecting sites in the Lima Department and Paraense (2003) found only *P. acuta* specimens during three searches at the type locality of *M. peruvianus*. This former author had access to three specimens from another locality (Balneario Las Delicias, Trujillo), which he ascribed to *M. peruvianus* with doubt. Contrarily to our finds for Brazil, there was only one record of *S. marmorata* in Peru, in a document from the grey literature. The low number of species occurrence records, most of them retrieved from collection databases, as well as the recovery of just one scientific paper with two specific localities (Larrea et al. 1990), evidences the scarcity of studies on physids in this country.

We found few records of physid species for Colombia and Ecuador. For Colombia we retrieved a similar number of records from the literature and collection databases. The only species recorded were *M. carolita*, *P. venustula*, and *S. marmorata*. For Ecuador, we obtained records for the species *M. carolita*, *M. spiculata*, and *M. peruvianus* only from collection databases. *Mayabina spiculata* was described from Guatemala, and lately recorded in new localities in Guatemala and Mexico (Fischer & Crosse 1870-1878, Martens 1890-1901, Baker 1922). Clench (1930) considered *Physa rivalis* Potiez & Michaud, 1838 (non Maton and Rackett, 1807) as a synonym of *M. peruvianus* arguing that the images of the shell of both species given by Gray (1828) and Potiez and Michaud (1838) were "practically the same". Both nominal species are valid according to the MolluscaBase (2022). In our opinion the taxonomic status of *P. rivalis* and the majority of the South American physid species only can be solved through the integration of anatomical and molecular approaches.

For Argentina, great part of the occurrence records was found in grey literature. Records of the native species *P. aspii* and *P. loosii* were very scarce. Fernández (1981) mentioned new localities for *P. aspii* in the Northwestern Argentina (in Salta province), without specifying locality and *P. loosii* for Chaco province, information repeated by subsequent authors (Núñez & Pelichotti 2003, Rumi et al. 2008). The taxonomic status of both species is uncertain (Taylor 2003). In MolluscaBase (2022) *P. aspii* is considered as *taxon inquirendum* and *P. loosii nomen dubium*, while Taylor (2003) considered both species as *incertae sedis*. There is a hypothesis according to which *P. loosii* and *P. aspii* are varieties of *M. peruvianus*, thought the absence of preserved type specimens and the imprecision of the type locality impairs the comparative anatomical study of these species, both described only based on shell morphology (Fernández 1981, Núñez 2011). Other species recorded for this country were *A. brasiliensis*, *P. rivalis*, *P. rivalis minor*, and *S. marmorata*. Nonetheless, Taylor (2003, 2004) argued that the distribution of *S. marmorata* do not includes the Argentinian territory and thus the specimens ascribed to *S. marmorata* from Argentina may belong to another species.

We found occurrence records for *P. porteri* and *P. venustula* in Chile. *Physella venustula* was originally described for Peru (Gould

1847) and it is considered a valid species according to MolluscaBase (2022). Taylor (2003), however, examined specimens from Peru and concluded that the shell of *P. venustula* are not distinguishable from the widespread *Haitia mexicana* (Philippi in Küster, 1841), now accepted as synonym of *P. acuta* (MolluscaBase 2022). Herein, we have considered the status of valid species for *P. venustula*, as the shell is not a good operational criterion for distinguishing physid species. The exact number of valid physid species in Chile is controversial. The species recorded for this country were *Physa chilensis* Clessin 1886, *Physa porteri* Germain, 1913, *Physa nodulosa* Biese, 1949, considered as native, besides *Physa rivalis* Sowerby, 1874 (Valdovinos 2006). Among these species, *P. chilensis* (type locality: "Chile") is considered *incertae sedis* by Taylor (2003) and *nomem dubium* by MolluscaBase (2022) and *Physa nodulosa* (type locality: Coquimbo province, Chile) is considered as a synonym of *P. venustula* (Taylor 2003, MolluscaBase 2022). The possibility that *Physa porteri* (type locality: Antofagasta province, Chile) is a synonym of *P. venustula* was also considered by Taylor (2003). Recently, morphological and molecular studies on physid populations in Chile, reinforced the doubts on the validity of *P. chilensis* and *P. nodulosa,* as specimens collected in the type localities and environs were identified as *P. acuta* (Collado 2017, Collado et al. 2020). For Venezuela we have found occurrence records for *A. venezuelensis, P. rivalis, P. venustula,* and *S. marmorata*. Taylor (2003) mentioned the occurrence of two native species of Physidae for this country, *Stenophysa simoni* (Jousseaume, 1889) (*Aplexa simoni*, original combination) (type locality: Caracas, Venezuela) and *A. venezuelensis*, both described based on shell traits. According to Taylor (2003), *S. simoni* may be, in fact, *S. marmorata*. For Uruguay, we found records of *P. rivalis*, *P. rivalis minor* and *S. marmorata.*

Some taxonomic mistakes concerning Neotropical physids have led to errors in species attribution, fomented by the insufficiency of the operational criteria for species delimitation and resulting in a historical uncertainty about nominal species validity (Núñez 2010). The nominal species *P. rivalis* is a good example of ambiguity generated by taxonomic impediment. Sowerby (1822) presented the first record of *P. rivalis* Maton and Rackett, 1807 in the Neotropical region (ie.: Guadalupe). After that, some authors attributed the authorship of *P. rivalis* from the Neotropics to Sowerby. When d'Orbigny (1835) mentioned *Physa rivalis* Sowerby, 1822 for South America (Uruguay, Chile, Argentina and Peru), starting from there a great controversy about the identity of physids present in these countries. Sowerby's species name was preoccupied by *Bulla rivalis* Turton, 1807 (= *Physa rivalis*) and *Physa rivalis* Maton and Rackett, 1807. Clench (1930) argued that *P. rivalis* Sowerby (*non* Turton *nec* Maton and Rackett) was in fact *S. marmorata*. d'Orbigny described two varieties of *P. rivalis* (*major* and *minor*) for South America, ascribing the variety major to *P. peruviana* Gray, 1828 from Peru. Later, d'Orbigny (1841) described *Physa sowerbyana* based on material from Cuba and considered *P. rivalis* Sowerby and *P. peruviana* Gray a synonym of *P. sowerbyana*. Parodiz (1956) took up the controversy over *Physa rivalis* and related species and proposed that the occurrence of *P. rivalis major* Gray was restricted to Peru, while *P. rivalis minor*, to Northern Brazil. Nowadays, *P. sowerbyana* is considered synonym of *S. marmorata* (MolluscaBase 2022), *Physa rivalis* (Maton and Rackett, 1807) is considered synonym of *P. acuta* (Taylor 2003, MolluscaBase 2022), and *P. rivalis* Potiez and Michaud, 1838 is considered *incertae sedis* (Taylor 2003). It is worth of note that all these taxonomic acts were based only on the examination of shell morphology, which is poorly informative in physid species with Aplexinae-like shells (Fig. 4). Thus, the status of these nominal species can only be clarified after anatomical and molecular data is available.

Afrophysa brasiliensis, on the other hand, is a good example of the need to apply new operational criteria for species delimitation in Neotropical physids. This species was described based on the shell morphology. The holotype, deposited in the Senckenberg Museum in Frankfurt, Germany, was destroyed during the Second World War. The type locality is contained in South Brazil (Küster 1844, Taylor 2003). Taylor (2003) obtained specimens from South Brazil (Porto Alegre, Rio Grande do Sul state), which he identified as *A. brasiliensis*, and compared the microanatomy and shell morphology of *A. brasiliensis* and *S. marmorata*. The shell of both species cannot be distinguished. Nonetheless, the anatomical analysis performed by Taylor (2003) revealed that the genus *Afrophysa* can be discriminated from *Physa* and *Stenophysa* by the characteristics of the penial sheath and the position of the penial canal.

Herein, we recorded *S. marmorata* in 13 hydrological basins geographically isolated; this pattern of distribution may be attributed to some mechanisms of dispersion or, alternatively, to species misidentifications. Widespread distributions of freshwater snail species have been mostly attributed to introduction by human activities (Hayes et al. 2008) and zoochorism by waterbirds (van Leeuwen & van der Velde 2012). The transportation of snails by migratory birds may occur by endo- or ectozoochorism (van Leeuwen & Van der Velde 2012, van Leeuwen et al. 2012, Flock et al. 2018), which was previously observed for *Physa* snails attached to the feathers of the Whitefaced Glossy Ibis in Utah, USA (Roscoe, 1955). Nonetheless, the extension of the occurrence records of *S. marmorata* in South America, including several isolated hydrological basins; also the apparent co-occurrence of specimens ascribed to *S. marmorata* and other physid species in the same hydrological basin observed in the present study (ie.: Amazon, Colombia-Ecuador Pacific Coast, La Plata, Magdalena, Orinoco, Peru Pacific Coast, São Francisco, Uruguay-Brazil South Atlantic Coast) indicates the possibility of species misidentifications and the need to reassess South American physids distribution using other operational criteria than shell morphology, and molecular approaches.

In the present study, of the 13 species analyzed, only two are represented in malacological collections by ethanol preserved specimens. This result shows that taxonomic identification of these lots was based mostly on shell traits. Considering that South American physids may have very similar shells, species misidentifications may be frequent; the absence of ethanol preserved specimens in malacological collections hindering the accomplishment of anatomical and molecular studies. For eight species herein analyzed, the sole source of occurrence records that we found was malacological collections. This result highlights the importance of the material deposited in museums, considering the scarcity of published studies on South American physids in one hand, also showing, on the other hand, that specimens from collections should be revisited using other operational criteria than the shell, so the taxonomic attribution may be reliable. Unfortunately, as the majority of the physid species are represented by dry specimens in malacological collections, and most of these records seems to be historical, remounting to several decades ago, recollection and reassessment of species identity and distributions must be done. The probable distributions of South American physids provided herein, may help freshwater malacologists in this task.

CONCLUSIONS

1) The apparent widespread distribution of *S. marmorata* in South America, allied to the fact that the main trait available for the discrimination of South American Physid species, the shell morphology, is proven to be ineffective as operational criteria for species delimitation in Physidae, evidences the possibility of species misidentifications and cryptic diversity under this name.
2) The critical underrepresentation of South American physid species in malacological collections, molecular databases and scientific literature evidences the role of the taxonomic impediment as an obstacle to the advance of our knowledge on species diversity, distribution range, and conservation status.
3) Malacological collections represented the main source of occurrence records for most species herein analyzed, evidencing the relevance of unpublished data associated to specimens housed in collections to assess distributional information on neglected taxonomic groups. Nonetheless, specimens from malacological collections must be revisited using molecular and anatomical criteria for species delimitation. Besides, as most of the species in these collections are represented by shells, recollection and reassessment of species identity and distribution must be done.

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SUPPLEMENTARY MATERIAL

Figures S1-S10.

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