

The Schistosome Vectors in the Americas

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With few exceptions, the nomenclature of planorbid molluscs has been a confusing subject. Consequently, whoever intends to investigate a group of those molluscs may first have to overcome a nomenclatural problem. Otherwise it would be impossible to recognize the species to be mentioned in this address. The present distribution of the three vectors is shown in Figs 1 and 2.

Biomphalaria glabrata

B. glabrata, the most important vector of *Schistosoma mansoni* in the Americas, had a doubtful birth certificate. It was originally described by Thomas Say (1818), based on a shell given to the Academy of Natural Sciences of Philadelphia by the French naturalist Felix Louis L'Herminier, who assured Say that he had collected it "near Charleston", in South Carolina, where he lived for some years. Several subsequent authors did not succeed in finding in South Carolina specimens answering to Say's description, and it is known today that the large planorbids occurring there belong to the genus *Helisoma*. Based on the fact that, before living in Charleston, L'Herminier had spent 20 years in the island of Guadeloupe, from where he had brought to Charleston an extensive collection of specimens, Pilsbry (1934) concluded: "It seems quite likely therefore that the type of *Planorbis glabratus* was one of the specimens L'Herminier brought from Guadeloupe, and which he subsequently thought (or Say inferred) that he had picked up around Charleston. ... I have no doubt that *P. glabratus* Say is identical with *P. guadaloupensis* Sowerby. The name is prior to Sowerby's". In the mentioned paper, Pilsbry proposed the new genus *Australorbis* for the species *glabratus*.

The occurrence of *B. glabrata* in the American continent was first recorded during the celebrated Spix-Martius expedition to Brazil from 1817 to 1820. Spix, responsible for the zoological part of the expedition, collected at Ilhéus and Almada, state of

Bahia, a batch of shells considered by him as a group of species, naming them *P. olivaceus*, *P. ferrugineus*, *P. nigricans*, *P. albescens* and *P. viridis*, evidently according to the color of the shells. Since until about a century ago the study of shelled molluscs was based almost exclusively on shell characters, it was convenient to collect empty shells during a long expedition. In a sample of field collected specimens the color may vary depending on environment and time. In natural environments the shell of living *B. glabrata* is usually olivaceous, and remains so for a variable time after death and decomposition of the animal (*P. olivaceus*). In regions of lateritic soil a rusty color may be imparted to shells (*P. ferrugineus*), which get darker in the course of time (*P. nigricans*). If the calcareous layer becomes perceptible through a worn periostracum the shell exhibits a whitish shade (*P. albescens*), which may become greenish by the action of green algae (*P. viridis*).

Spix traveled through the region of Ilhéus and Almada from December 13, 1818 to January 6, 1819, coinciding with Say's description of *P. glabratus* in 1818. He died in 1827, leaving midway the study of his specimens to be completed by JA Wagner (1827), who introduced substantial changes, maintaining the name *olivaceus* for the largest specimen and considering *ferrugineus* a smaller-shelled synonym. Moreover, he introduced a sixth specimen, not selected by Spix, naming it *P. lugubris* as senior synonym of the three remaining Spix's species. After describing such *P. lugubris* he states that it is found together with *P. olivaceus* and refers the reader to Fig. 1118 and the original description of the former in the 1786 edition of Martini-Chemnitz's *Conchylien-Cabinet* (rejected by the International Commission on Zoological Nomenclature). But Fig. 1118 of that work refers to a planorbid of the West Indies.

Besides Sowerby's *P. guadaloupensis* and Spix's *P. olivaceus*, *B. glabrata* was recorded throughout the West Indies and South America (Figs 1-2): Dominican Republic (Dunker 1853a, as *P. refulgens*); Puerto Rico (Shuttleworth 1854, as *P. guadaloupensis*); Surinam and French Guiana (Drouët 1859, as *P. xerampelinus*); Venezuela (Martens 1873,

as *P. guadelupensis* and *P. lugubris*); Martinique (Mazé 1874, as *P. guadelupensis*); Antigua (Sowerby 1877, as *P. antiguensis*); Vieques (Germain 1921, as *P. blauneri*); St. Martin (Jones 1923, as *P. antiguensis*); St. Kitts (Pilsbry 1934, as *A. glabratus christopherensis*); St. Lucia (FC Baker 1945, as *A. glabratus*); Curaçao (Kuyp 1949, as *A. glabratus lugubris*); Dominica (Smithsonian Institute Biological Survey 1964, cited by Prentice 1980); and Montserrat (Pointier 1975).

Only about a century from its finding by Spix in Bahia was *B. glabrata* recorded in Brazil by F Baker (1913), as *P. guadelupensis*, from the lakes Extremoz and Papari, state of Rio Grande do Norte. Lutz (1918) studied specimens from the states of Sergipe (as *P. olivaceus*) and Maranhão (as *P. guadaloupensis*). Since 1916 he asserted that schistosomiasis did not occur from Rio de Janeiro southwards for want of a molluscan vector, so much that for his studies he resorted to feces of pupils



Fig. 1: present distribution of schistosome vectors in South America.



Fig. 2: present distribution of *Biomphalaria glabrata* and *B. straminea* in the Caribbean.

from northeastern states in the Naval School of Rio and to "*P. olivaceus*" from the state of Sergipe. In the last-mentioned paper he describes his procedure for concentration of schistosome eggs, now often referred to as the Hoffman-Pons-Janer's (1934) method, proposed 18 years later.

It can not be assured that Lutz was right in affirming that there was no schistosomiasis from Rio de Janeiro southwards. Probably there was no diagnosis. Nowadays it is known that there is *B. glabrata* transmitting *S. mansoni* in southern São Paulo and northern Paraná. In Lutz's collection there are four specimens labeled *P. confusus* (but certainly *B. glabrata*) collected on May 5th, 1919 in Jatahy (now Jataizinho, a town in northern Paraná) by Souza-Araujo (1919), during an extensive helminthologic survey, from Sept. 1918 to Aug. 1919, which did not reveal any case of schistosomiasis. It seems certain that spread of the disease to northern Paraná is relatively recent. Up to the end of last century that region was covered by primary forest, a condition unfavorable for colonization by *Biomphalaria*. About 1867 it began to be settled by emigrants from São Paulo and Minas Gerais, occupation being completed in the 1920's with high-scale coffee plantation. There followed new immigratory waves, now from northeastern states, the seat of the oldest foci of schistosomiasis. The association of three factors – devastation of the natural environment by intensive agricul-

tural exploitation, land occupation by immigrants of low socioeconomic status, and eutrophication of the bodies of water – would certainly stimulate proliferation of the preexistent molluscan vector. Fig. 3 shows the progression of *B. glabrata* in the state of Paraná toward the Paraguayan frontier; records of successive surveys show that schistosomiasis did not preexist in the spotted localities.

In Jan. 1997 a population of *B. glabrata* was found in Esteio, a locality of Rio Grande do Sul near Porto Alegre (Carvalho et al. 1998).

Biomphalaria tenagophila

This species was described by Orbigny (1835) as *P. tenagophilus*, based on specimens from the Argentine province of Corrientes. He found it again in Rio de Janeiro, calling it *P. ferrugineus* Spix, which as seen above is a synonym of *B. glabrata*. He stated further (Orbigny 1841) that he had collected it from marshes at São Cristóvão district, Rio de Janeiro city, "where it is very rare". I searched for this planorbis in São Cristóvão, finding specimens that agree with Orbigny's description, but are indistinguishable from *B. tenagophila* in anatomy and crossing tests (Paraense 1961b).

In 1856 Dunker described the species *P. bahiensis*, based on specimens collected in Bahia and Rio de Janeiro. As shown elsewhere (Paraense 1961a, b), Dunker was really dealing with two species: *B. glabrata* from Bahia and *B. tenagophila* from Rio de Janeiro.

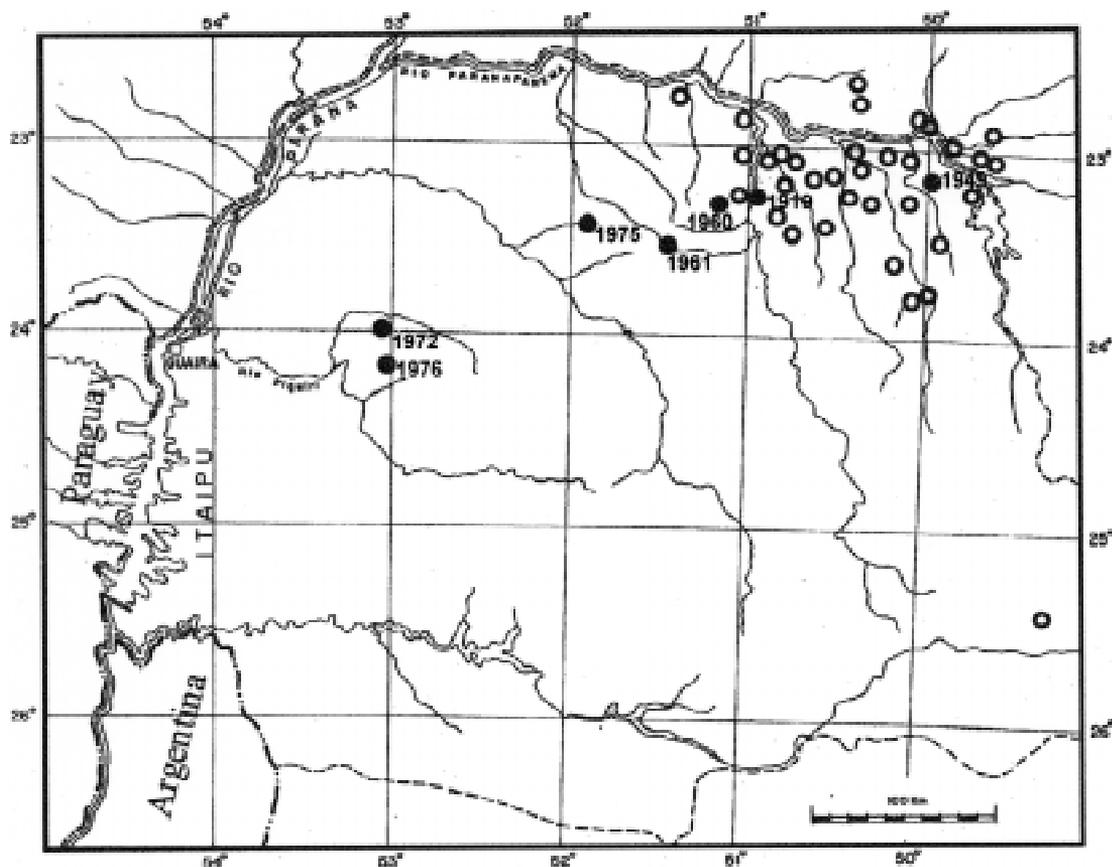


Fig. 3: distribution of *Biomphalaria glabrata* over the State of Paraná (Brazil), and chronology of westward expansion of schistosomiasis.

Lutz (1918) admitted that Spix's *P. nigricans* (from Bahia) was identical to the planorbis usually found by him in Rio de Janeiro. His opinion was reinforced by the fact that he had received specimens, considered typical by him, from the town of Caravelas, in Bahia. For some years several authors (including myself) adopted Lutz's nomenclature, treating as *nigricans* the *tenagophila* from Rio de Janeiro southwards. Only in 1960 did I notice that the snail from Caravelas is really *tenagophila*. In 1994 I collected it in Ibirapuã and Itamaraju, the latter, about 100 km north of Caravelas, being the northernmost limit of its distribution.

The above-mentioned planorbis from São Cristóvão was found by Lutz (1918) "in the same place as D'ORBIGNY", and named *P. confusus* by him. Lutz reasoned as follows: "The observations of D'ORBIGNY on the *Planorbis*, referred by him to *ferrugineus* SPIX, can not apply to *olivaceus* SPIX, as the dimensions would suggest. Not only is *olivaceus* never found in Rio (where *Schistosomum* is unknown) but the species still existing in São Christovão is our *confusus* (unable

to transmit the parasite). Its largest specimens, but rarely found in Manguinhos, are very like *olivaceus*, but do not exceed 25 mm". Realizing later that the name *confusus* had been given by Rochebrune (1882) to an Oriental planorbis, he changed it to *immunis* (Lutz 1923) for obvious reason. Now it is known that *P. immunis* is a synonym of *B. tenagophila* (see Paraense 1961b), which ceased being immune to transmit at least a race of the schistosome (Paraense & Corrêa 1963, 1981).

Since we are dealing with adaptation of the schistosome to a previously refractory host, it would be worthwhile to remember the circumstances. In 1956, Corrêa et al. detected five autochthonous cases of schistosomiasis in Pindamonhangaba, a town on the Paraíba valley, a region of the state of São Paulo till then free from the disease. They examined 408 "*A. nigricans*" (= *B. tenagophila*) from local draining ditches, finding a single one infected with *S. mansoni*. Subsequent investigation showed that in the next six years *tenagophila*-transmitted schistosomiasis had spread to seven additional towns in the valley (To-

ledo 1959, Piza et al. 1959, Piza & Ramos 1960, Piza et al. 1960a, b, Corrêa et al. 1962).

Investigating the schistosome from the Paraíba valley (infective to *tenagophila*, as seen above) in comparison with the schistosome from Minas Gerais (infective to *glabrata*), we observed that the former was uninfective to *glabrata* and the latter was uninfective to *tenagophila* of the valley (Paraense & Corrêa 1963). Further investigation (Paraense & Corrêa 1978) showed that 15 out of 20 populations of *B. tenagophila* from the species range were susceptible to *S. mansoni* from the Paraíba valley (sample SJ, from São José dos Campos). Comparing the relatively lower infection rate of those populations to those observed in *B. glabrata* exposed to the BH schistosome (from Belo Horizonte, state of Minas Gerais), we concluded that it might be understood "in the context of an ongoing process of adaptation of the *tenagophila*-infecting schistosome by selection through successive passages by the snail host".

Finally, additional experiments (Paraense & Corrêa 1981) led to the conclusions that the SJ schistosome is less adapted to its vector snail than the BH parasite to its own; that they are interfertile, producing hybrids infective to BH and SJ snails at lower rates than in the sympatric combinations; and that they are to be considered biological races rather than mere strains. Now hybridization of the two races is surely taking place in nature as a result of human migration.

To prevent expansion of schistosomiasis from the Paraíba valley a special office was created that, in spite of adopting all the currently recommended strategy for snail control, did not accomplish that purpose. After many years of arduous effort it was noticed that new cases did not occur westwardly, notwithstanding the presence of the vector. Till then the consensus of the specialists was that *B. tenagophila* ranged westward from São Paulo to Paraguay through the state of Mato Grosso do Sul. Coincidentally I was then collecting snails in Mato Grosso do Sul, verifying that the so-called *tenagophila* was really a new species – *B. occidentalis* – reproductively isolated from *B. tenagophila* (Paraense 1981) and insusceptible to infection with the SJ race of *S. mansoni* (Paraense & Corrêa 1982). I extended the survey to the westernmost area of São Paulo, identifying *B. occidentalis* in five localities. A subsequent review of that area by the state agency for control of endemic diseases (Vaz et al. 1983) found *B. occidentalis* in a great majority of 252 biotopes, and *B. tenagophila* in a single one. Thus it was understood that the westward expansion of schistosomiasis in São Paulo was being stopped by nature and not by control measures (Fig. 4).

A planorbid of Santos, on the coast of São Paulo, gave rise to great nomenclatural confusion. Arantes (1923) identified the first two cases of autochthonous schistosomiasis in the city, also in the state. He sent specimens of the planorbid vector to Pirajá da Silva, who regarded it as probably *P. centimetralis* Lutz (now *B. straminea*). Moura (1945) and Pinto (1945) identified it as *A. glabratus*. According to Coutinho (1949a, b) there would be another unidentified species besides *A. glabratus*. Bequaert and Lucena (1951) considered it identical with the African *B. alexandrina pfeifferi* (Krauss), which they believed to have been introduced during the slave trade. Afterwards Lucena (1953), following Jaeckel's opinion, considered that snail identical with *A. camerunensis* Boettger from Cameroon. Such identification was firstly denied by Boettger himself, who assured that the snail was Wagner's *P. lugubris*, but agreed later (Lucena 1956) that it really was his *A. camerunensis*. Ruiz and Carvalho (1953) identified two species in Santos: *A. immunis* (Lutz) and *A. nigricans* (Spix), the former being much more frequent and the only one infected with *S. mansoni*. Examining samples from 10 populations of that planorbid (Paraense & Deslandes 1956) we proved them to belong to a single species, indistinguishable morphologically (shell and anatomy) and genetically (crossing experiments) from *A. nigricans* (now *B. tenagophila*).

A surprising find of *B. tenagophila* was at the Valle de Condebamba (2,500 m above sea level), in the sierra Department of Cajamarca, Peru (Paraense et al. 1964). They were morphologically identical with the Brazilian *tenagophila* but reproductively isolated from three strains of the latter, including the SJ snail from the Paraíba valley. Exposed to the BH schistosome they showed an infection rate of 43.3%, with retarded development of the parasite, which did not reach the cercarial stage. Contrariwise, 72.7% became heavily infected with the SJ schistosome, cercarial shedding beginning 30 to 60 days after exposure to miracidia.

Besides Brazil, Argentina and Peru, *B. tenagophila* also occurs in Bolivia (Orbigny 1835), Paraguay (Paravicini 1894) and Uruguay (Marshall 1930, as *P. paysanduensis*). Its distribution is shown in Fig. 1. So far it was not found outside South America.

Biomphalaria straminea

This snail from Cuming's collection in the Natural History Museum, London, is labeled as proceeding from South America. It was described (not figured) by Dunker (1848) as *P. stramineus*. A subsequent description (Dunker 1850: 42-43), with figures of a specimen, is insufficient for a sure recognition; he says that his *P. stramineus* is very similar to the figure of *P.*

montanus Orbigny from lake Titicaca but does by no means adjust to Orbigny's description of that species. He also refers to another specimen of Cuming's collection, from Aconcagua, Chile, having doubts about considering it a variety of *P. stramineus* or a separate species. As to *P. montanus*, Pilsbry (1924) and Hubendick (1955) showed that it is a form of *P. andecolus* Orbigny, 1835, also from lake Titicaca, anatomically (Paraense & Deslandes 1957) quite different from what is now known as *B. straminea*. Concerning the specimen from Aconcagua, it is quite probably the snail from that province described by Biese (1951) as *Tropicorbis schmiererianus*. The likeness between

the shells of those nominal species hinders the solution of this problem.

Martens (1859), studying Venezuelan material from the coastal region of lake Maracaibo and the environs of Mérida, restricted the type locality of *P. stramineus* to Lagunilla. In reality there is a town called Lagunillas (not Lagunilla) in either region, and Martens did not clearly indicate the place of his "Lagunilla". About *P. stramineus* he only says (translation): "Lagunilla (see above Ampullaria) associated with leaves of water plants". By "Ampullaria" he means *A. eximia* Dunker and *A. punctulata* Reeve, both from "Laguna von



Fig. 4: present distribution of *Biomphalaria occidentalis* and *B. tenagophila*.

Lagunilla”, “of warm, little wavy, saline water”. Ending his description of *A. eximia*, Dunker (1853b) states that “according to information of Mr. consul Gruner, from Bremen, the locality of this snail is the province of Coro, on the lake of Maracaibo”. As a matter of fact, Coro is the capital of Falcón state, and lies about 250 km to the northeast of that lake.

In May 1974 I collected in the other Lagunillas, situated 30 km west of Mérida city, a snail described as *P. meridaensis* by Preston (1907). Its shell resembles that of what is now called *B. straminea*, but anatomically it is indistinguishable from *B. prona* (see Paraense 1992), described by Martens himself (1873) from lake Valencia, and whose shell is notably modified outside the lake (Paraense et al. 1992).

Summing up, almost certainly Martens’ Lagunilla is the Venezuelan village on lake Maracaibo, whose saline water, derived from the Caribbean sea through the gulf of Venezuela, communicates its salinity to the “Laguna von Lagunilla” mentioned by him. By the way, in northeastern Brazil *B. straminea* has been found thriving in saline waters, 1-2 g NaCl/liter (Lucena 1946).

It can be affirmed, however, that Cuming had never been to Venezuela. His shell collecting in the Americas was restricted to the Pacific coast, from the island of Chiló in Chile to Conchagua, in Honduras (see Dance 1986: 114).

Martens (1873) refers to specimens of *Planorbis stramineus* in the Museum of Berlin: from Lagunilla, collected by Engel; from Caracas, by Ernst; and from the Brazilian state of Ceará, by Zietz. Lutz (1928) considered *P. stramineus* a snail found by him near Maracay, asserting that it coincided with the species so determined by Martens. Of those localities the only one where *B. straminea* (as now defined) surely occurs is Ceará, where it is widespread. Since its presence in the other localities has not been confirmed, the name *straminea* is currently applied to the planorbid morphologically identical with the form occurring in Ceará.

The next record of *B. straminea* is F Baker’s (1913), who collected it in lake Papari (Brazilian state of Rio Grande do Norte) and Ceará, referring to it as follows: “There are about half a dozen very similar forms of *Planorbis* described from South America, not figured or imperfectly figured, quite possibly reducible to one or two species. *Planorbis stramineus* Dunker seems to be the first of these to be described”. Moreover, he records the occurrence of *B. peregrina* (Orbigny, 1835) in the coastal region of Ceará, which has never been confirmed: its northern limit is 15°S (Paraense 1966), whereas the southern limit of Ceará is 8°S.

Baker’s doubts mentioned above were also felt by Lutz (1918): “In the State of Pernambuco ... the

largest species of *Planorbis* are unknown, but a smaller one is widely spread, as well in rivers as in ponds. Trying to determine it, I found considerable difficulty. It looks somewhat like *peregrinus* D’ORB. of which F. BAKER mentions a specimen from Ceará which may belong to our species; the true *peregrinus*, however, which I obtained in Montevideo, is larger and differs by the form of the last whorl. BAKER also mentions *stramineus* DUNKER as a species of Ceará, but its size and form do not agree, if the drawing of REEVE-SOWERBY be correct. Without denying that this species may have been collected before, I do not think that it has been well defined, which obliges me to give it a name. I call it *centimetralis* to indicate the size which, in this case, helps very much to recognize it”. (In the semiarid region of Brazilian Northeast I found specimens measuring 15 mm).

As mentioned above, Lutz (1928) identified as *P. stramineus* a planorbid collected by him near Maracay. Since he had erected the species *centimetralis* ten years before, differentiating it from *straminea*, a doubt remains about the true identity of those Venezuelan specimens. Such confusion about *B. straminea* and many species of planorbids and other molluscs results from the fact of their descriptions having been based exclusively on shell characters.

Still regarding Venezuela, in December 1956 (Paraense 1963) I collected *B. straminea* in San Joaquín, state of Carabobo (some specimens shedding cercariae of *S. mansoni*), from a creek at Hacienda Cura, where members of a family were infected with the parasite. Malek (1969) mentions its presence in Guatire and Guaraymito, states of Miranda and Aragua, respectively.

B. straminea is also present in Uruguay (Olazarri 1984), Argentina (Paraense 1970) and Paraguay (Paraense 1970).

Outside South America (Figs 1, 2) *B. straminea* has been recorded in Martinique (Paraense 1970), Grenada (Richards 1973), Costa Rica (Paraense et al. 1981), Dominican Republic (Sodeman Jr et al. 1985), Dominica (Noblet & Damian 1991) and Guadeloupe (Pointier et al. 1993).

In the Neotropical region there is a planorbid – *B. kuhniiana* (Clessin, 1883) – very similar to *B. straminea*, which so far has proved refractory to infection with *S. mansoni*. Originally described from Suriname, I collected it in Paramaribo and in localities on the Tocantins river basin, northern Brazil (Paraense 1988), and also in Panama (Paraense 1999), where it was named *P. isthmicus* by Pilsbry (1920). Samples labeled “*B. straminea*” from Venezuela and Colombia have been received for identification in this laboratory.

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