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A Guide for the Identification of the Snail Intermediate Hosts of SCHISTOSOMIASIS in the Americas

PAN AMERICAN HEALTH ORGANIZATION
Pan American Sanitary Bureau, Regional Office of the
WORLD HEALTH ORGANIZATION

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A Guide for the Identification of the Snail Intermediate Hosts of Schistosomiasis in the Americas

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525 Twenty-Third Street, N.W.
Washington, D.C. 20037, U.S.A.

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FOREWORD

This Guide was prepared by the Pan American Health Organization/World Health Organization Working Group for the Development of Guidance for Identification of American Planorbidae, which is composed of the following members:

Dr. Frederico S. Barbosa, Instituto de Higiene, Universidade Federal de Pernambuco, Caixa Postal 1626, Recife, Pernambuco, Brazil

Dr. Elmer G. Berry, Museum of Zoology, University of Michigan, Ann Arbor, Michigan

Dr. Harold W. Harry, Research Associate, Rice University, Houston, Texas, U.S.A.

Dr. Bengt Hubendick, Director, Naturhistoriska Museet, Göteborg, Sweden

Dr. Emile A. Malek, Associate Professor of Parasitology, Department of Tropical Medicine and Public Health, Tulane Medical School, New Orleans, Louisiana, U.S.A.

Dr. Wladimir Lobato Paraense, Centro Nacional de Pesquisas Malacológicas, Instituto Central de Biologia, Universidade de Brasília, Brasília, Brazil

Secretariat:

Dr. Earl C. Chamberlayne, Communicable Diseases Branch, Pan American Sanitary Bureau, Regional Office of the World Health Organization, Washington, D.C., U.S.A. (until April 1964)

Dr. Louis J. Olivier, Communicable Diseases Branch, Pan American Sanitary Bureau, Regional Office of the World Health Organization, Washington, D.C., U.S.A. (from April 1966)

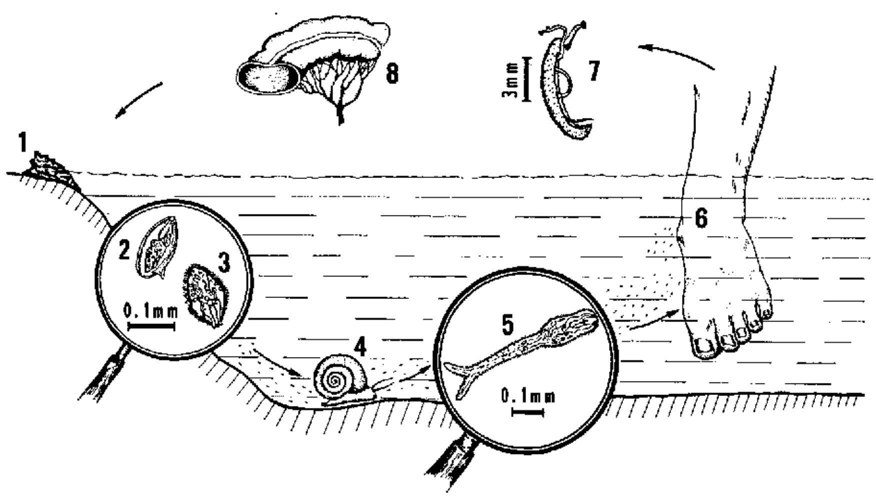
In addition to the members of the Group, a number of other specialists read the manuscript and made many useful suggestions. Their assistance is gratefully acknowledged.

The Guide represents an effort to summarize present knowledge of the taxonomy and identification of the snails in a practical form. The authors have reached agreement concerning the content of this book, but since such agreement inevitably requires compromises, it should not be assumed that all statements are necessarily endorsed by all the authors.

Life Cycle of *Schistosoma mansoni*

The eggs of *Schistosoma mansoni* leave the human host with the feces. If the feces (1) are deposited or washed into fresh water, the eggs (2) hatch and release a tiny, ciliated, free-swimming larva, known as miracidium (3). To survive, the latter must enter a snail within a few hours. If it encounters a suitable snail (4) it will penetrate the surface and enter the tissue, where it quickly loses its ciliated plates and becomes a large elongated sac, called a primary sporocyst. This sporocyst forms within it numerous, small, secondary sporocysts that eventually leave the primary sporocyst and move to the digestive gland of the snail. There they become very long, thin-walled sacs threaded into the snail's tissues. Each secondary sporocyst forms within its cavity numerous fork-tailed larvae, called cercariae (5). Some of these cercariae leave the sporocyst each day through a pore, migrate to the free surface of the snail, and escape into the water, usually around midday. Cercariae can be produced continuously by the sporocysts for weeks or even months. They swim actively, and if they come in contact with the human skin they can penetrate it with the aid of secretions from gland cells producing lytic enzymes (6). The worms enter the blood stream, travel to the heart, are pumped to the lungs, and then migrate to the branches of the hepatic portal vein in the liver. After the worms become adults they pair (7) and migrate to the mesenteric venules (8) of the portal system, where the females deposit large quantities of eggs. Some of the eggs pass through the wall of the intestine and are carried out of the body in the feces. Thus the life cycle of the worm is completed.

Fig. 1



INTRODUCTION

Medical malacology is the study of snails and other molluscs that serve as intermediate hosts of parasitic diseases of man and animals. According to present knowledge, almost all diseases known to be transmitted by snails are caused by parasitic worms of the class Trematoda, or flukes. Nearly all snails that harbor diseases of medical importance live in fresh water. In the Neotropics of the Western Hemisphere, the major disease of man caused by a trematode is Manson's schistosomiasis, or bilharziasis. This disease is not only gradually extending over a wider geographic area; it is also infecting a progressively larger number of people each year. Facioliasis, another trematode disease of the Neotropics, is gaining importance among cattle and other ruminants, and it is also of some importance in man. Paragonimiasis is still another snail-borne disease of the Neotropics that affects both animals and humans. Probably the most reasonable methods of control, or preferably prevention and eradication, of these diseases will be centered on control of the snails that are essential for the completion of the life cycles of the trematodes that cause them.

At present, control of the snail vectors of schistosomiasis is being accomplished by the use of molluscicides (chemicals that kill the snails) and to a lesser extent by introducing predators or competitors of the snails (biological control), or by weeding or draining the bodies of water containing the snail and other ecological or environmental approaches. Other efforts include fencing or posting of contaminated waters so that human access to them is limited and educating the public to avoid polluting the water or becoming infected with the disease. The details of these procedures have been extensively discussed in various publications of the World Health Organization. Suffice it to say that as of now they all have limitations, either because they are only temporarily effective or relatively expensive, or both.

Increased knowledge of the freshwater snails will do much to aid in improving present methods of control and in discovering new methods. The purpose of this Guide is to provide a background of existing knowledge on freshwater snails in the American Neotropics as it relates to trematode diseases of man and domestic animals. The Guide is directed mainly to public health workers who possess a reasonable knowledge of biology and to zoologists interested in medical malacology. It is intended primarily as an introduction to the subject, but it contains sufficient technical information so that it can be used for reference purposes. The incompleteness of existing knowledge must be recognized. Workers in the areas in which schistosomiasis is present can do much to improve current knowledge. Some of the more technical literature is listed in the bibliography for those who wish to pursue the subject in greater detail.

In most Neotropical areas the snails that are vectors of schistosomiasis are not present in every kind of freshwater environment. Accurate knowledge of the distribution and habitat selection of the snails is useful in control programs, for bodies of water without vector snails would, naturally, not require attention. There are usually several species of planorbid snails (the group that contains the intermediate hosts of *Schistosoma mansoni*) in any given area, though most of them can not serve as vectors of the fluke. It is essential to the conduct of efficient programs to know which snails can and which can not transmit the disease, particularly if they live in different kinds of freshwater habitats, as is frequently the case.

Unfortunately, owing to lack of sufficient external characteristics, it is often very difficult to distinguish closely related species of planorbid snails. Even the specialists have not reached universal agreement on differentiation of some of the planorbid species, but it is hoped that the confusion can be resolved by accumulating more data through the aid of many workers, whom this Guide may encourage. Problems in taxonomy are plainly stated as such in this manual, so that even beginning workers in medical malacology can recognize them and help to seek their solution. If they do not have the opportunity to pursue the problems intensively, at least they can watch for material to send to more experienced investigators who are able to undertake such work.

Many new and unexpected developments are likely to occur in the Neotropics that may be of interest to the medical malacologist. For instance, Rey (1959) claimed that a species of the freshwater amnicolid genus *Oncomelania* occurs in Mato Grosso, Brazil, in an area inhabited by immigrants from Japan and Okinawa. He stressed the possibility that another blood fluke, *S. japonicum*, might become established in the Americas. It has subsequently been observed that this snail has a wide distribution.

Another problem that might well be worthy of greater attention is cercarial dermatitis, or "swimmer's itch"—a disease of the skin caused by the cercariae of blood flukes that normally live in water fowl and certain mammals. These penetrate the skin of humans and cause an irritating rash, but the flukes do not reach maturity in man. This malady may be more extensive in the Neotropics than realized.

To assist in furthering investigation of problems such as these, the Schistosomiasis Snail Identification Center for the Americas was established in Belo Horizonte, Brazil, in 1963. The Center has the following specific functions:

- To receive and collect preserved and live material of snails of known or potential medical importance from interested workers and institutions.
- To store this material in such a way that it can be used for research at the Center or by other institutions or workers.
- To distribute information at reasonable intervals, and according to a gradually developed practical mailing list, on material available at the Center for use by interested workers and institutions.
- To distribute available snail and shell material on request from institutions and workers.
- To carry out identification of snails that are medically important, or suspected to be so, received by the Center from institutions, agencies, or workers.
- To carry out research on taxonomy, variability, ecology, population dynamics, and susceptibility of the snails concerned.
- To receive trainees and visiting research workers in such numbers as the facilities will permit.

Services of the Center can be obtained by writing to:

Schistosomiasis Snail Identification Center
for the Americas
Instituto Central de Biologia
Universidade de Brasilia
Brasília, Brazil

All activities related to medical malacology, whether in the area of research or control, depend on accurate identification of the snail species involved. The following Guide, based on current knowledge, is therefore presented as a practical tool.

1. NOTES ON THE ECOLOGY OF THE PLANORBID INTERMEDIATE HOSTS

Snail Ecology

The planorbid intermediate hosts have become adapted to a wide range of environmental conditions. They are found in freshwater bodies—large and small, flowing and standing; in waters with pH varying between 5.8 and 9.0; in tropical forest regions and in arid situations; at low or at high altitudes; and at water temperatures from 20° to 30°C.

Usually they inhabit the shallow waters—either still or only slightly flowing—of streams with moderate organic content, moderate light penetration, little turbidity, a muddy substratum rich in organic matter, submergent or emergent aquatic vegetation, and abundant microflora. They have been collected from rivers, lakes, marginal pools along streams, borrow-pits, marshes, flooded areas, irrigation canals, aqueducts, and water cress fields. They are not found in environments with high tidal fluctuations or in reaches of streams having a fall steeper than 20 meters per 1,000 meters of length, though protected pools or swampy areas alongside these steep streams often harbor them. They are generally not found in situations close to the sea, but in some areas fair-sized colonies have been discovered only about 200 meters upstream.

Often the snails are found in isolated freshwater environments quite independent of major drainage systems. This would indicate that the snails or their eggs are sometimes carried to these habitats passively by man and other animals.

Sometimes it is difficult to explain the absence of snails from habitats that are seemingly favorable. The combined effects of several factors rather than an extreme of any one factor may account for this phenomenon. It has become evident that aside from the known physical deterrents, such as stream gradient, the water quality in certain habitats may be largely responsible for their spotty distribution in otherwise suitable habitats. Studies on the copper content of natural waters indicate that this metal, and perhaps others, might be limiting agents in waters low in total dissolved solids. High concentrations of bicarbonate, carbonate, sulphate, chloride, magnesium, and calcium ions in natural fresh waters do not exclude these snail hosts. Lethal concentrations of these ions as determined by laboratory studies are not usually encountered in nature.

One of the notable characteristics of the planorbid intermediate hosts is their ability to withstand drought for long periods of time. It has been found that if desiccation takes place gradually in a habitat where the humidity in the immediate vicinity (microhabitat) of the snails is high, the level of subsoil water is high, and an adequate growth of weeds and accumulation of debris is present, a good proportion of them survive. Snails exhibit species and strain differences in their ability to survive during dry periods, and these are of significance from the standpoint of epidemiology and transmission of the disease. In certain areas, snail habitats are without water throughout the annual dry season, which may last from five to seven months. Some snails are able to survive the dry season by estivating in sheltered spots, under vegetation on mud, or in mud crevices. When the water returns, the survivors are able to repopulate the area within a short period, usually one to two months.

In certain permanent habitats where the water level fluctuates, snails may be stranded on the banks. Such snails can survive as long as they are on the wet mud and among vegetation. If the water recedes gradually, some of them are able to move down with the water. Rains also wash them into the water.

In many endemic areas of the Americas that have permanent habitats, the prevailing temperatures favor continuous reproduction of the snails throughout the year and thus the maintenance of large colonies.

Ecology Related to Transmission

The presence of a large colony of snails does not necessarily mean that transmission of the disease is taking place. On the other hand, a few infected snails may be capable of maintaining a high endemicity among humans. Snails exhibit species and strain variations in their susceptibility to infection with the schistosome. For example, *Biomphalaria straminea* (=*B. centimetralis*) in Brazil shows a much lower susceptibility to the infection than *B. glabrata,* yet it is responsible for high infection prevalence among the human population.

It is also to be noted that in some habitats where the snail occurs schistosomiasis is not regularly transmitted. This is the case, for instance, in the limestone area along the north coast of Puerto Rico. The absence of schistosomiasis in this area may perhaps be explained by the fact that, apart from occasional watering of livestock, these ponds are rarely used by the human population.

Under conditions in which the habitats dry up seasonally, it is to be expected that transmission of the disease is interrupted and is then normally resumed in the wet season about two months after the water returns to the snail habitats. Under permanent water conditions, transmission usually continues throughout the year.

During the dry season in northeastern Brazil, the young sporocysts of S. *mansoni* are able to survive in "dormancy" (diapause) while the snails (*B. glabrata*) are estivating on the soil.

2. BASIC MALACOLOGICAL CONCEPTS: MORPHOLOGY OF FRESHWATER SNAILS

The Shell

All freshwater snails secrete an external shell, which is composed of calcium carbonate. On its external surface is a thin cuticle of organic material. The natural color of the shell usually comes from the color of the cuticle and may vary from light tan to dark brown or even black. In some families—for example, Pilidae, Chilinidae, Neritidae, some of the Amnicolidae, and others—pigments are deposited in the calcareous shell. Often the shells are covered with extraneous deposits of diatoms, marl, or iron, and these must be removed to observe the natural color and texture of the shell. The texture of the shell may be smooth, polished, malleolate, beaded, or with spiral grooves or pits. Larger textural features—for example, grooves and spines—are called sculpture. The sculpture of the apex is often important for species determination, but it may be obliterated through erosion of the spire. Young shells are therefore more reliable for determining the apical sculpture.

The animal of freshwater snails is attached to the shell in one or only a few (Ancylidae, Neritidae) places by means of a strong columellar retractor muscle. The muscle runs from a layer of epithelial cells adjacent to the shell into the foot and head of the animal, where it branches out into many endings. By contracting this muscle, the snail can draw the head and foot completely inside the shell, thus escaping adversities in its environment. Some snails (the prosobranchs) have an operculum ("trap door") attached to the upper part of the foot. When they contract, the operculum just fits into the opening of the shell, thus providing even greater protection for these snails.

To understand the structure of a snail's shell, it is helpful to imagine a tube that gradually increases in diameter from the blind end (the embryonal, apical part of the shell) toward the open end (the aperture). The tube is usually coiled. The rate at which the tube increases in diameter and the position of the various turns of the coil with reference to each other are the two predominating variables that determine the general shape of the shell.

If the tube slowly increases in diameter and the coils are located mainly below each other, the shell will become turreted, as in *Thiara*. If the coils are located mainly outside each other (Fig. 2B), the shell will be flat—or discoidal or planispiral, as in *Biomphalaria*. If the tube increases rapidly in diameter and the coils are located outside and below each other, a shell with an appearance somewhere between these two extremes will result (Fig. 2A). If the tube is coiled very little and increases rapidly in diameter, the shell can be pyramidal or patelloid, as in the Ancylidae (Fig. 20).

The turning of the coil may be clockwise (dextral), in which case the shell aperture is directed to the right when it is facing the observer and the apex is held upwards (Fig. 2A). If it is counterclockwise (sinistral), the aperture is directed to the left when it is facing the observer and the apex is held upwards (Fig. 18). In discoidal shells the apical side may be hard to recognize. Planorbid shells are in fact sinistral. Some species have the spire secondarily pushed down through the peripheral whorls towards the originally umbilical side and are called pseudodextral (Fig. 3).

When a snail hatches from an egg mass, in the case of oviparous snails (Fig. 4A), or is born, in the case of ovoviviparous snails (Fig. 4B), it already has an apical whorl, and on rare occasions (some of the Thiaridae) even several. All subsequent growth of the shell is by addition of material at the edge of the aperture. Many species have each subsequent whorl spaced progressively farther from the axis, thus leaving a hole in the base, which is called the umbilicus (Fig. 5). The umbilicus varies in size in different species, according to how far from the axis each whorl is formed. If there is no opening in the base of the shell, the shell is called imperforate.

Freshwater snails increase the size of their shells throughout life, and it is often difficult to tell when examining a specimen of a species new to the observer whether it is of maximum size, since the shell maintains a relatively constant general shape regardless of the stage of growth. Such shells may be said to have indeterminate growth. A few freshwater snails of the Neotropics, among them certain populations of some species of the planorbids, have determinate growth—that is to say, they deflect the aperture when they have reached maximum size (Fig. 55).

It is important when examining a shell to determine the following data: whether it is operculate or nonoperculate; whether it is dextral or sinistral; and whether it is discoidal, conical, globose, turreted, or patelliform. The number of whorls should be determined, and it should be ascertained whether they are carinate, angular, or rounded, and whether the shell is perforate or imperforate. Guidance concerning these characters is given in Figures 5, 6, and 7. Figure 5 shows an ordinary gastropod shell, and Figure 6 shows a planorbid shell.

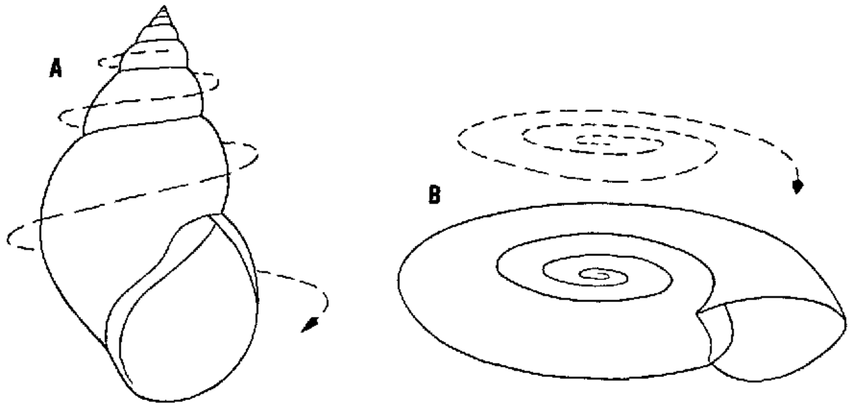


Fig. 2. Direction of growth in a gastropod shell (A, shell with a well-developed spire; B, discoidal shell)

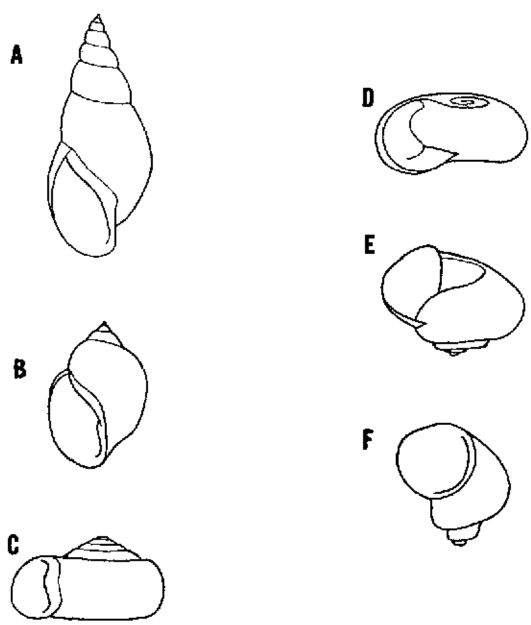


Fig. 3. Evolution of discoidal, or flat (D), and pseudodextral, or false right-turned (E-F), shell from the original spired (A, turreted; B, globose) and sinistral, or left-turned, form in the Planorbidae

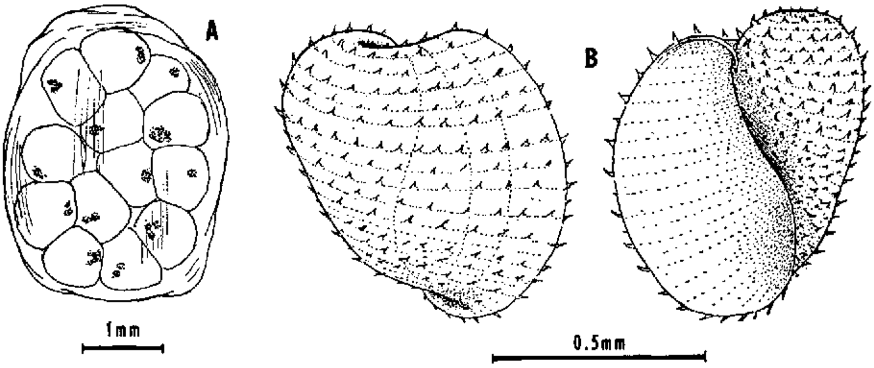


Fig. 4. Egg mass (A) and embryonic shells (B) of *Plesiophysa* from Brazil

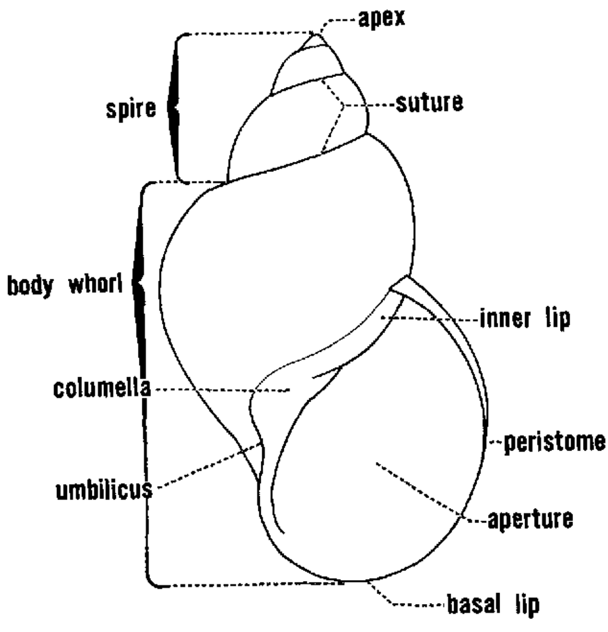


Fig. 5. Important features of a dextral, or right-turned, spired gastropod shell

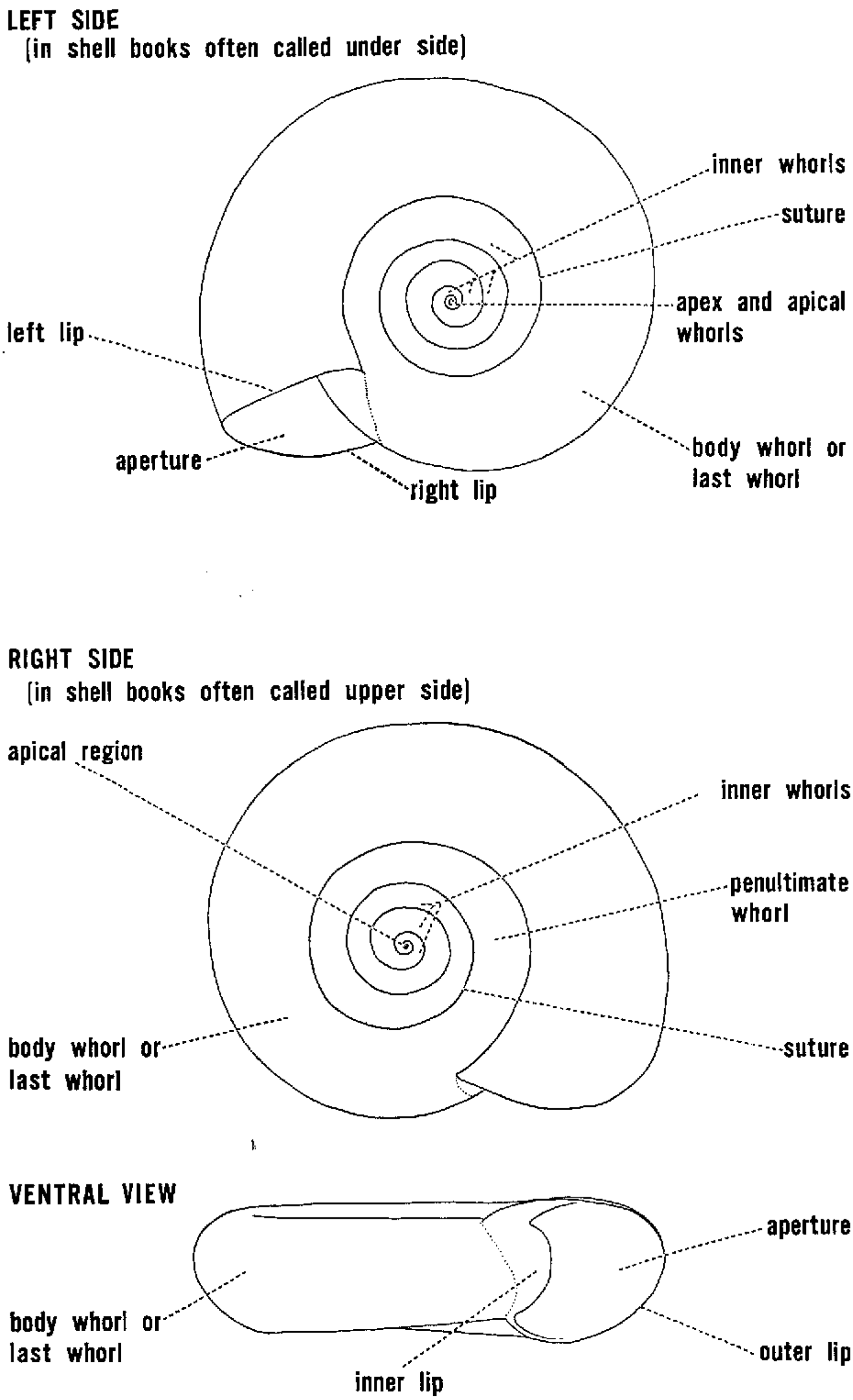


Fig. 6. Important characteristics of a discoidal or planispiral shell (*Biomphalaria*)

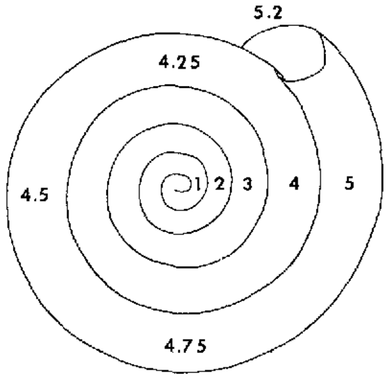


Fig. 7. Counting of whorls on a planorbid shell (left or right side is chosen according to convenience)

The Animal

It is possible to recognize several major parts of the snail besides the shell (Fig. 8). The part that fills the shell when the animal is extended and crawling is the visceral mass, and the part that extends beyond the aperture is the head and foot, or cephalopedal mass. There is no sharp boundary between them. The visceral mass fills all the whorls of the shell and normally conforms to the coiling and shape of the whorls. The cephalopedal mass is joined to the visceral mass by a constricted neck or body stalk.

The cephalopedal mass has a foot with a flat sole and a mouth in front, both of which are applied to the substrate when the snail crawls. On each side of the mouth is a labial palp, usually quadrate in form. In the Pilidae each is drawn out into a thin filament resembling a tentacle. Labial palps are absent in the Thiaridae. In many prosobranchs the front end of the head is distinctly separated from the foot and forms a proboscis.

On the dorsal (top) part of the head is a pair of appendages known as tentacles. There is also a pair of eyes, which may be in the head proper near the tentacles (Pulmonata), on the tentacles near their bases (some Prosobranchia), or on short stalks beside the tentacles (Pilidae).

The part of the body wall covering the visceral mass is called the mantle. The cavity inside the body is the hemocoel, and it is filled with body fluid, or blood. In most freshwater snails of the Neotropics the blood is colorless, though in some genera of the Planorbidae (but not *Drepanotrema*) it is red, owing to the presence of hemoglobin.

The visceral organs, consisting of the digestive, excretory, circulatory, nervous, and reproductive systems, are located in the hemocoel. The

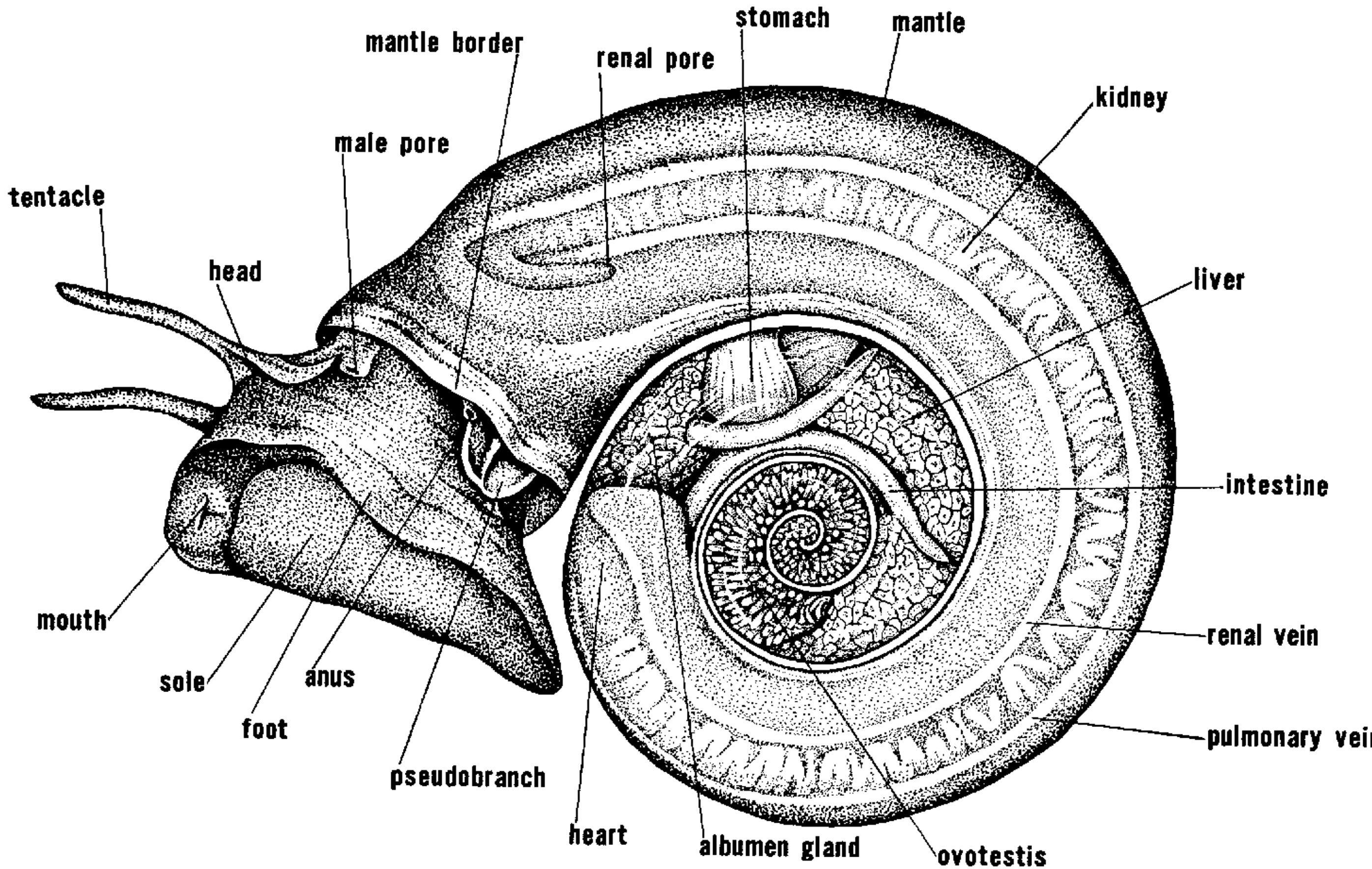


Fig. 8. A *Biomphalaria* with the shell removed and seen from the left, enlarged (after Demian)

respiratory system is constituted in part by the body wall, which is exposed to the external environment, and by special and varied modifications of the wall in different families.

The external structures of the cephalopedal mass and the pulmonary cavity of freshwater snails are not entirely symmetrical in their location. Thus, the reproductive opening or openings, the anus, and the pneumostome open only on one side of the midline and have no counterpart on the other. If these structures are on the right side of the cephalopedal mass, the animal is said to have dextral anatomy; if they are on the left, it has sinistral anatomy. Ordinarily, dextral shells contain dextral animals, and sinistral shells contain sinistral animals, but there are exceptions. Thus, *Acrorbis* and some varieties of *Biomphalaria andecola* (both Planorbidae) have sinistral animals in dextral shells (Fig. 3). Snails of the Planorbidae with disc-shaped shells have sinistral animals, but snails of the Pilidae and Amnicolidae, which also have disc-shaped shells (*Marisa,* in Fig. 12, and *Cochliopa,* respectively), have dextral animals.

When reference is made in the following descriptions to left- or right-hand position in the morphology of the snails, the positions are always in accordance with the left and right sides, as indicated in Figure 6.

The Organ Systems

Digestive System

The digestive system (Fig. 9) consists of a single tube that expands in various areas to form special organs. Several large glands (the salivary gland and the liver lobes) are attached to the tube. Immediately behind the mouth the digestive tube expands into a large sac, known as the buccal mass, the outer side of which is mostly covered with muscles.

The anterior end of the buccal mass (buccal atrium) is lined with a thin, acellular cuticle, and its anterior margin is thickened to form a jaw. The jaw may consist of many small platelets, or these platelets may be fused into one or more major pieces, which in turn have distinctive location, shape, and sculpture, depending on the family or genus.

At the posterior end of the buccal mass is the radula. This is a ribbon-shaped noncellular cuticle on which there are transverse rows of teeth. Each radular tooth has a basal plate attached to the radular membrane (the ribbon) and a free plate that is directed backward. The posterior margin of the free plate is sculptured into cusps and denticles. According to the position and shape of the teeth, e.g. the number of free denticles, a transverse row can be differentiated into a central tooth, lateral teeth, and marginal teeth.

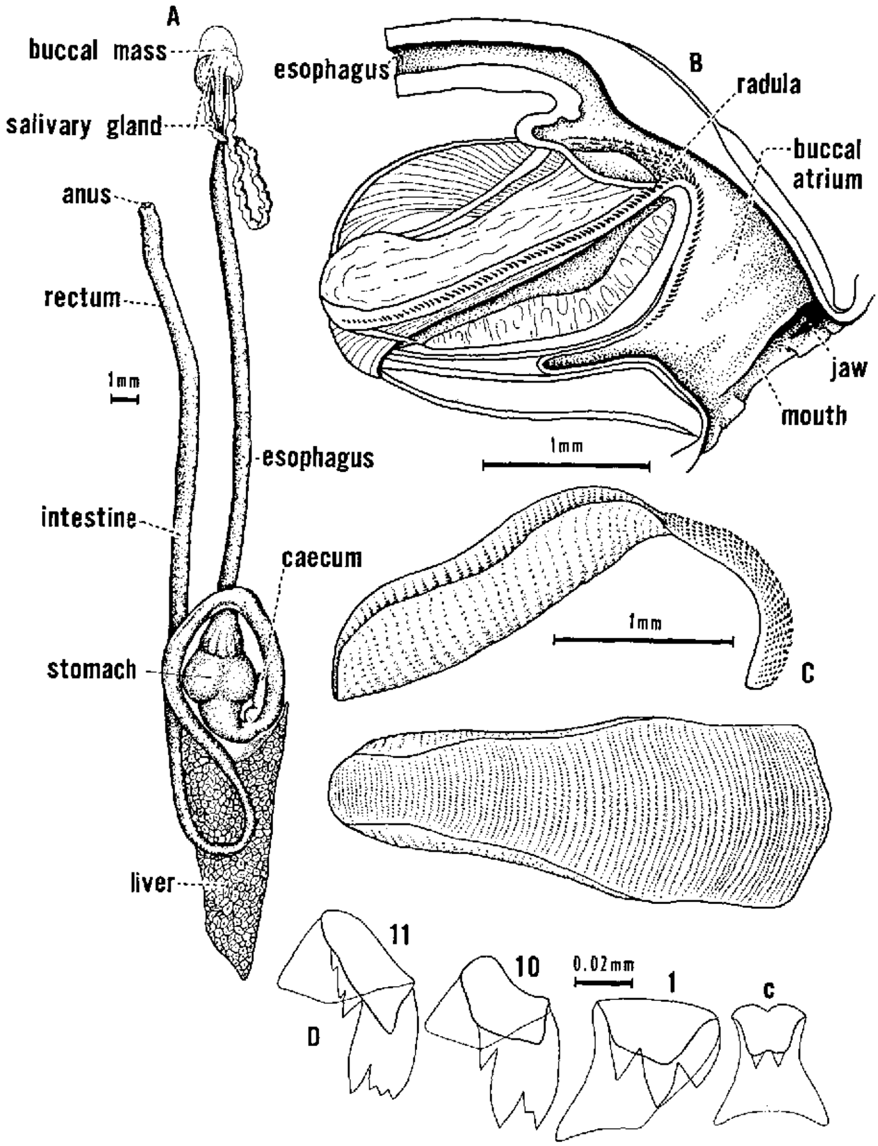


Fig. 9. Internal structures of *Biomphalaria*

A: The alimentary system dissected from a *Biomphalaria,* mainly dorsal view (after Demian)

B: Longitudinally sectioned buccal mass seen from the right (redrawn from Demian)

C: The radula seen from the right and from above

D: Selected teeth from the left half of a *Biomphalaria* radula

The esophagus emerges from the top of the buccal mass, and the duct of a salivary gland is attached to each side of its origin. The salivary glands may be branched to varying degrees, and they are often attached to each other and to the esophagus at their posterior end, which scarcely extends to the upper end of the cephalopedal hemocoel. The esophagus passes through this hemocoel and then expands in the apertural end of the upper visceral complex into a stomach.

In the freshwater pulmonates, the stomach is a spherical expansion of the digestive tract. Its anterior and posterior ends (the cardiac and pyloric parts, respectively) are membranous and separated by a muscular region between. The esophagus enters the cardiac end, and the intestine leaves the pyloric end. At the junction of the pyloric end and the intestine, the upper lobe of the liver enters the digestive tube proper, and opposite it is a small gastric caecum of unknown function. Whether it has a crystalline style is debatable. The intestine curves around the lower (apertural) end of the stomach, forming a lower loop, then swings apicad above the stomach, forming a much larger upper loop. It then passes to the roof of the mantle cavity and traverses that as the rectum. The anus opens near the pneumostome.

The stomach of most freshwater pulmonates, unlike prosobranchs, always contains sand grains.

Reproductive System

The reproductive system (Fig. 10) is one of the most important indicators for classifying freshwater snails, possibly because it is one of the most complex, stable, and diversified of all the organ systems. Even so, the function of many of the reproductive structures is still unknown.

The gonad is associated with the upper lobe of the liver and consists of many follicles, which drain into a sacculate gonadal atrium. In most prosobranchs, the sexes are separate. The gonad of the male is called the testis, that of the female the ovary. The pulmonates are hermaphroditic, and the gonad is called the ovotestis.

In the males of most prosobranchs (but not Thiaridae), the gonoduct, or vas deferens, leads to an external appendage called the penis, or verge. This structure is variously located in different families. Some female prosobranchs of the Thiaridae and Amnicolidae are ovoviviparous—that is, they retain the fertilized eggs inside the body until they hatch. Most prosobranchs, however, and all the freshwater pulmonates lay eggs and are therefore oviparous.

In the freshwater pulmonates the single hermaphroditic duct divides into separate male and female tubes in the region of the albumen gland. The female tube is differentiated into an oviduct, a uterus, a vagina, and a number of glands before it opens to the outside through the fe-

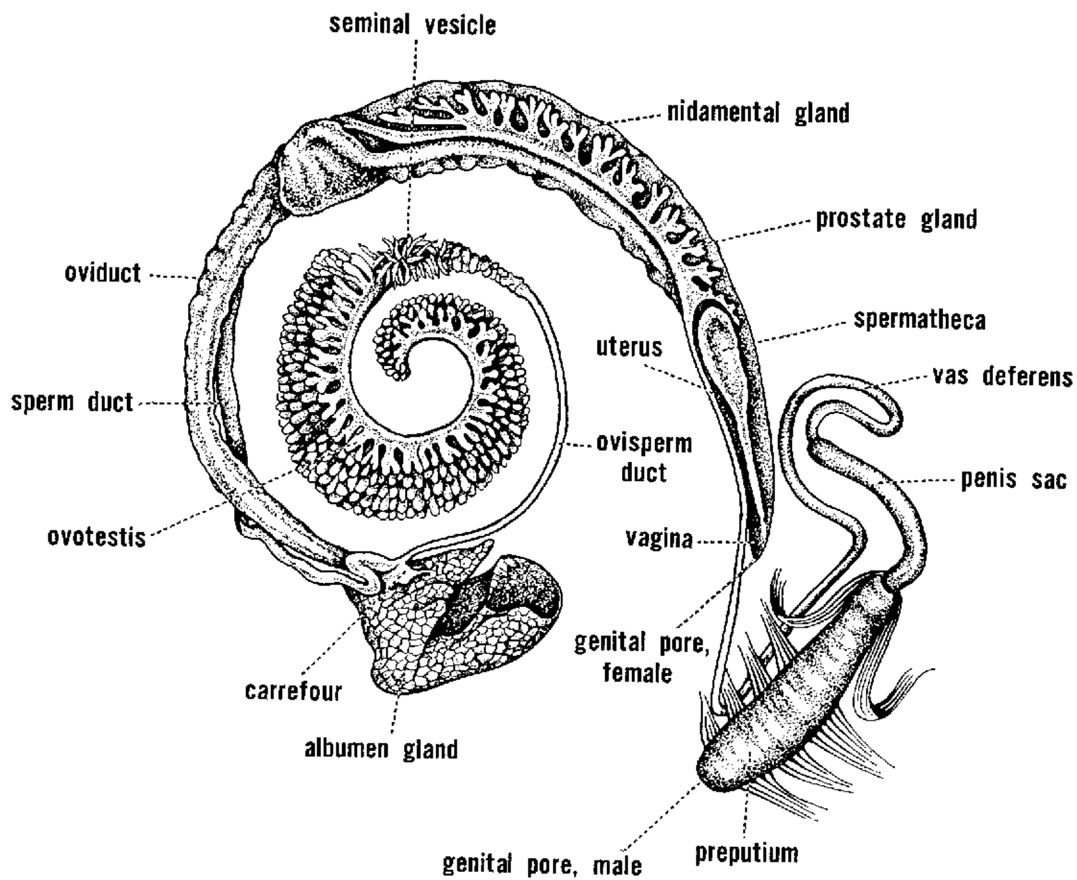


Fig. 10. The reproductive system dissected from a *Biomphalaria* (African) but kept in natural position, seen from the right (after Demian)

male genital pore. A spermathecal sac opens into the vagina generally through a duct. The simple or complex prostate gland opens into the vas deferens either directly or through a separate prostate duct. The upper portion of the male duct is called the sperm duct. The part below the prostate leading to the male copulatory organ is the vas deferens. The male copulatory organ is differentiated into a penis sac containing the penis, or verge, and the preputium, which opens at the male genital pore. The great diversity in the size, shape, and structure of the male organ is of systematic importance. In certain genera accessory structures are associated with the male copulatory organ—for example, flagella (Fig. 26) and preputial organs.

Nervous System

In freshwater snails the central nervous system is composed of several ganglia, or swollen masses of nerve cells, connected to each other by strands of nerve tissue called commissures and connectives. Nerves lead to various parts of the body from the ganglia. The ganglia and their joining strands are arranged to form two rings, the most important one encircling the frontal portion of the esophagus.

A small, spherical statocyst rests on each pedal ganglion. This contains particles that are displaced as the snail moves, giving it a sense of balance.

Excretory System

In its simplest form, the kidney of freshwater snails consists of a large, flattened sac, the wall of which is formed of a single layer of epithelial cells. The sac is situated in the roof of the mantle cavity, at its upper end, and it touches the pericardium.

In the pulmonates, the kidney (Figs. 8 and 38) is restricted to the roof of the pulmonary cavity and does not touch the hemocoel of the upper visceral complex. In larger species the epithelium of the wall is pushed inward to form lamellae, or kidney folds, which are variously formed and situated in different genera. Except in *Chilina*, there is a true ureter at the apertural end of the kidney. This is a narrow tube, usually without folds, that conducts the excretory products to a pore near the pneumostome. The shapes of the kidney and the ureter vary in different families or genera.

Circulatory System

The heart (Figs. 8 and 38) is located in the roof of the mantle (pulmonary) cavity near the apical end and generally on the side opposite the rectum. It is located inside an epithelial sac, called the pericardium.

The anterior portion, the auricle, pumps the blood into the posterior portion, the ventricle. Muscle fibers running obliquely across each chamber cause the heart chambers to contract alternately. A valve between the chambers and another at the entry into the auricle prevent the backward flow of blood.

At the point where the pericardium and kidney touch there is a small opening, the renopericardial passage, which connects the pericardial cavity with the cavity of the kidney.

Blood leaves the cephalopedal, isthmian, and upper visceral parts of the hemocoel by passing into the roof of the pulmonary cavity. There it seeps through the loosely packed connective tissue that fills all the space not occupied by the pericardium, kidney, and rectum. A few tubular channels, mere recessions in the connective tissue, carry most of the blood to the kidney, where it flows across the outer surface through another smaller set of channels. It then collects in a tubular sinus, the pulmonary vein, along the side of the kidney that is toward the heart. This prominent vessel carries the blood directly to the auricle.

The vessels of the pulmonary roof are veins, since they conduct the blood toward the heart. None is lined with an epithelium. As the blood passes through the roof of the mantle cavity it also exchanges carbon dioxide for oxygen, and thus the roof serves a respiratory function. Respiration is assisted by a gill in the prosobranchs, and by a pseudobranch in most of the Planorbidae, Ancylidae, and Chilinidae.

Blood flows from the heart into the aorta, the major artery. This vessel passes from the ventricle into the upper visceral complex, swings around the lower loop of the intestine, and forks out, sending one vessel into the upper visceral complex and the other through the isthmian hemocoel into the hemocoel of the cephalopedal mass. Each of these vessels branches many times, ending in spaces often termed "sinuses" in the connective tissue. In this way the blood bathes the various tissues and organs of the snail.

3. KEY TO THE GROUPS OF FRESHWATER SNAILS OF THE NEOTROPICS

In applying the following key to find the genus or family of a species, the investigator should always have a series of specimens. This will help assure that adult shells are being used. Immature shells are easily misidentified. It is best to work with living material, or at least with shells containing the animal preserved in alcohol, rather than with empty shells.

Determination Key to Families of Neotropical Freshwater Snails

Main Groups

With operculum; mantle opening directed more or less forward (operculate snails)	Prosobranchia
Without operculum; mantle opening directed more or less left or right side of the body (lung snails)	Pulmonata

Families of Prosobranchia

Spire reduced to a minute structure on the side of the body whorl, making the whole shell more or less subspherical (20 mm or less)	Neritidae (Fig. 11)
Shell large (20 mm or more) and more or less globose or thickly discoidal; spire not more than one third of shell height; labial palps drawn out into threads	Pilidae (Fig. 12) (syn. Ampullariidae)
Shell medium-sized and globose, similar to last family; no thread-like labial palps (known only in Cuba and North America)	(Fig. 13) Viviparidae
Shell small (less than 10 mm high), generally with well-developed spire	(Fig. 14) Amnicolidae (syn. Hydrobiidae)
Shell medium-sized (more than 10 mm high), with well-developed or,	

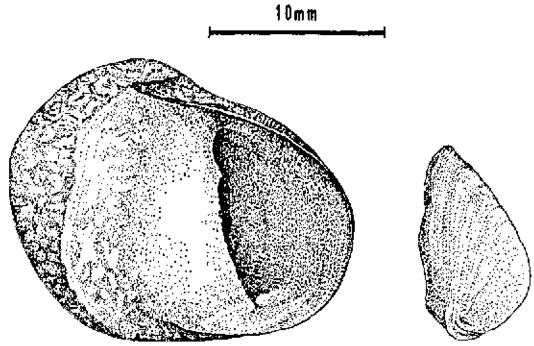


Fig. 11. Shell and operculum of *Neritina punctulata* Lamarck from a Puerto Rican rivér

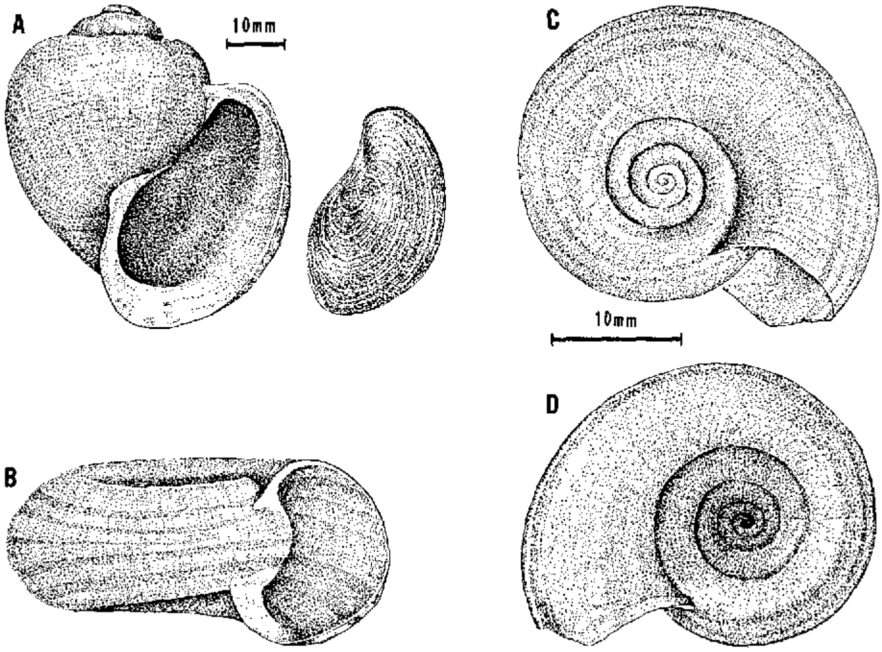


Fig. 12. A: Shell and operculum of *Ampullaria*
B: Shell of*Marisa cornuarietis* (L) from Trinidad, ventral view
C: Right side view of the same species
D: Left side view of the same species

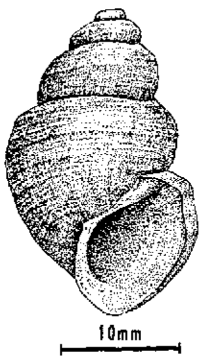


Fig. 13. Shell of *Lioplax pilsbryi* Walker from Florida—a representative of the Viviparidae

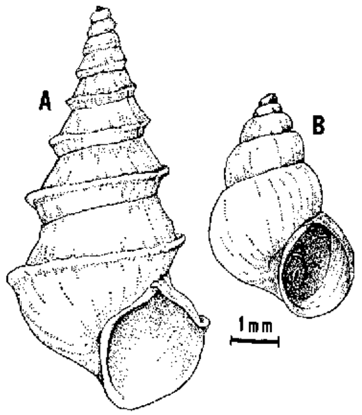


Fig. 14. A: Shell of *Littoridina andecola* (Orbigny) from Lake Titicaca, Peru
B: Shell, with operculum, of *Littoridina languiensis* Haas from Lake Langui, Peru

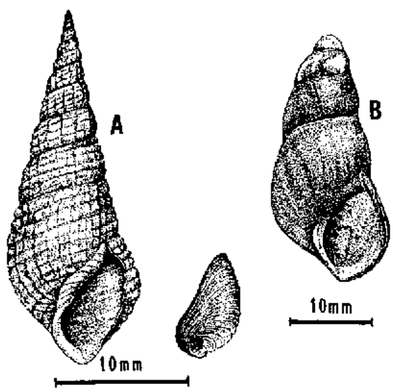


Fig. 15. A: Shell and operculum of *Tarebia granifera* (Lamarck), a melaniid snail introduced into Puerto Rico—a potential intermediate host of *Paragonimus westermani*
B: Shell of *Pachychilus laevissimus* Sowerby, a melaniid snail from Venezuela

generally, high spire	Thiaridae (Fig. 15) (syn. Melaniidae, in part)*

Families of Pulmonata

Shell dextral with distinct spire; columella without any sort of callosity; shell uniformly colored	(Fig. 16) Lymnaeidae
Shell dextral with distinct spire; columella with callus and with one or two folds (only in southern South America); shell often with brownish stripes or bands	Chilinidae (Fig. 17)
Shell sinistral with distinct spire; shell usually glossy; juvenile shell not hirsute; animal without pseudobranch; mantle border digitate or lobed	Physidae (Fig. 18)
Shell sinistral with distinct spire, textured, with raised, beaded spiral lines; juvenile shell hirsute; animal with pseudobranch; mantle border even	(Fig. 19) Plesiophysinae (subfamily of Planorbidae)
Shell discoidal (rarely spired and pseudodextral), e.g. *Drepanotrema* (*Acrorbis*) *petricola* and certain forms of *B. andecola*	Planorbidae (except Plesiophysinae)
Shell cap-shaped; spire reduced	Ancylidae (Fig. 20)

Diagnostic Characteristics of the Neotropical Genera of Planorbidae

Biomphalaria

Among the Planorbidae, there is only one genus, *Biomphalaria*,** that is important at present to the problem of schistosomiasis in the Neo-

* A few so-called pleurocerids (*Goniobasis, Pleurocera*) occur in the southern United States and agree with Thiaridae in the given diagnostic features.

** Opinion 735 of the International Commission on Zoological Nomenclature (*Bull Zool Nomencl* 22, Pt. 2: 94-99, May 1965) rules: "Under the plenary powers it is hereby ruled that the generic name *Biomphalaria* Preston, 1910 is to be given precedence over the generic names *Planorbina* Haldeman, 1842; *Taphius* H. & A. Adams, 1855; and *Armigerus* Clessin, 1884 by any zoologist who considers that any or all of these names apply to the same taxonomic genus."

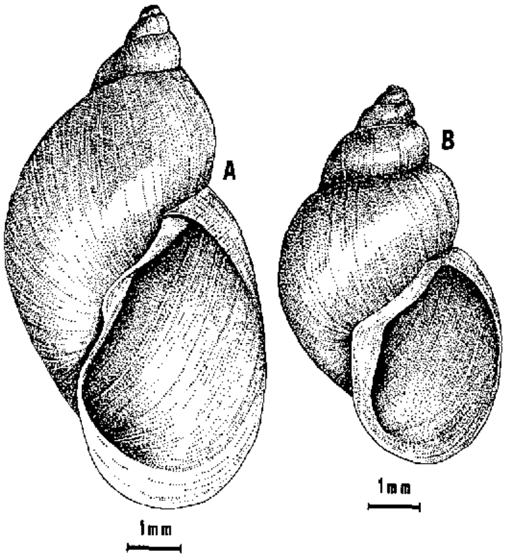
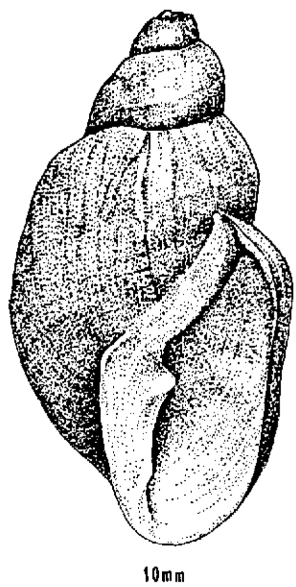


Fig. 16. A: Shell of *Lymnaea columella* Say from Puerto Rico
B: Shell of *Lymnaea cubensis* Pfeiffer from Puerto Rico

Fig. 17. Shell of *Chilina major* Sowerby from Chile



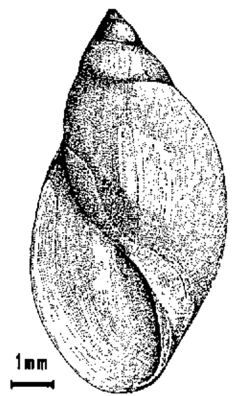


Fig. 18. Shell of *Physa marmorata* Guilding from Puerto Rico

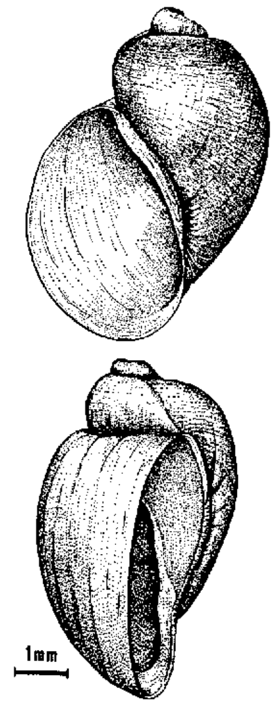


Fig. 19. Shell of the spired planorbid *Plesiophysa striata* (Orbigny) from Puerto Rico

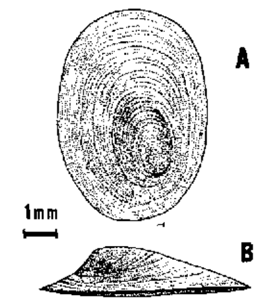


Fig. 20. Shell of *Gundlachia radiata* (Guilding), seen from above (A), and from the right (B)

tropics. A key and a detailed synopsis are therefore provided in later sections of this Guide.

The embryonic and the first few postembryonic whorls of the shell never have a sharply angled shoulder. The adult shell is nearly always discoidal, though some variants of *B. andecola* are pseudodextral with the spire slightly elevated. In a few species—for example, *B. tenagophila*—the shoulder is angled in the intermediate whorls and occasionally in the final whorl of larger specimens. In other species the shoulder is evenly rounded at all stages of growth. Some species never grow larger than 10 mm in diameter, with $4\frac{1}{2}$ whorls; others reach a maximum diameter of more than 30 mm and have about 6 whorls.

There is neither a preputial organ in the preputium nor a set of flagellar glands attached externally at the upper tip of the penis sac. The opening of the penis is terminal and the tip of the penis has no stylet.

The jaw is T-shaped, with the dorsal part composed of a single crescent-shaped piece. The central tooth of the radula has only two cusps, with no small accessory denticles on their shoulders.

The blood is red in all living specimens that have been observed.

The *Biomphalaria* genus ranges from the southern part of North America, through Middle America, to the southern part of South America.

Drepanotrema (Figs. 21-26)

Several species in this genus occur throughout the area in which *Biomphalaria* is found. They differ from *Biomphalaria* in their small shell size, which is generally less than 5 mm in diameter at 4 whorls (though a few species may grow about twice that size, with, of course, more whorls).

The jaw is composed of many minute platelets in both the lateral and dorsal parts. There are always glandular flagella at the tip of the penis sac. The penis has a terminal opening and no stylet on its tip. There is no penial gland in the preputium.

The blood is colorless in the species that have been studied.

The generic names *Drepanotrema, Acrorbis, Antillorbis,* and *Fossulorbis* have been used in the literature for species of this group.

Helisoma (Fig. 27)

Throughout North America, Middle America, and South America (from Venezuela to Southwestern Peru) snails are found that closely resemble some species of *Biomphalaria* but in reality belong to the genus *Helisoma.* Their embryonic and early postembryonic whorls have an angled shoulder, and this angle may or may not continue

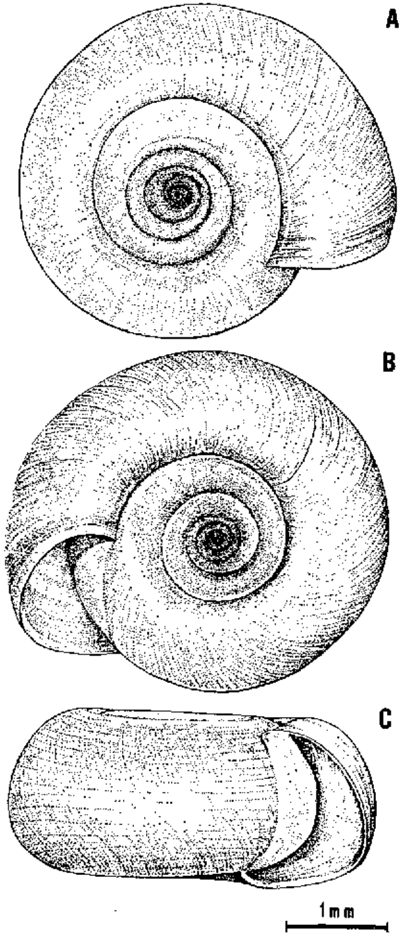


Fig. 21. Shell of *Drepanotrema anatinum* (Orbigny) from Puerto Rico (A, right side; B, left side; C, ventral view)

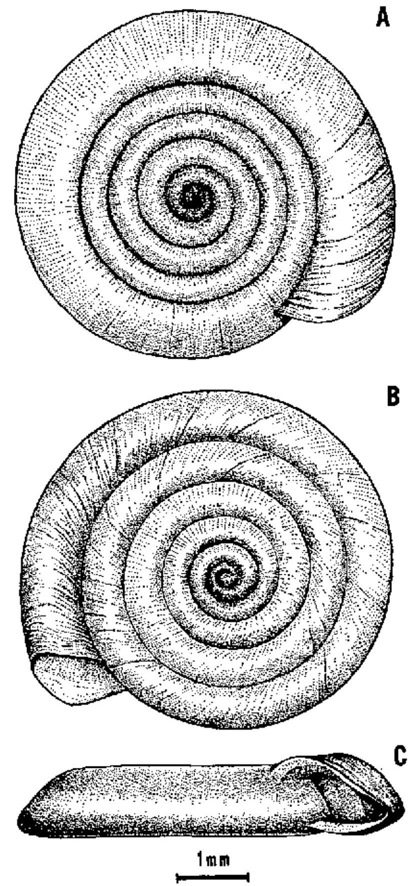


Fig. 22. Shell of *Drepanotrema cimex* (Moricand) from Puerto Rico (A, right side; B, left side; C, ventral view)

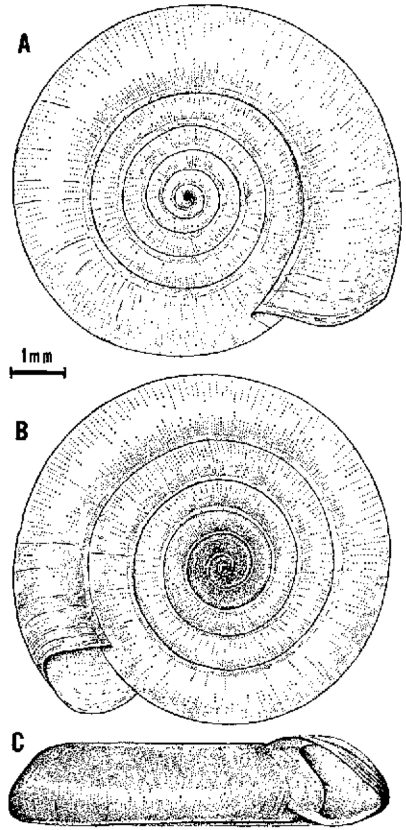


Fig. 23. Shell of *Drepanotrema lucidum* (Pfeiffer) from Puerto Rico (A, right side; B, left side; C, ventral view)

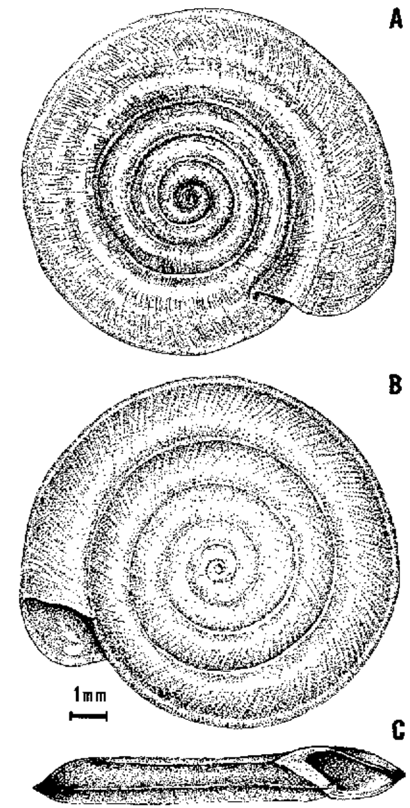


Fig. 24. Shell of *Drepanotrema kermatoides* (Orbigny) from Guadeloupe, W.I. (A, right side; B, left side; C, ventral view)

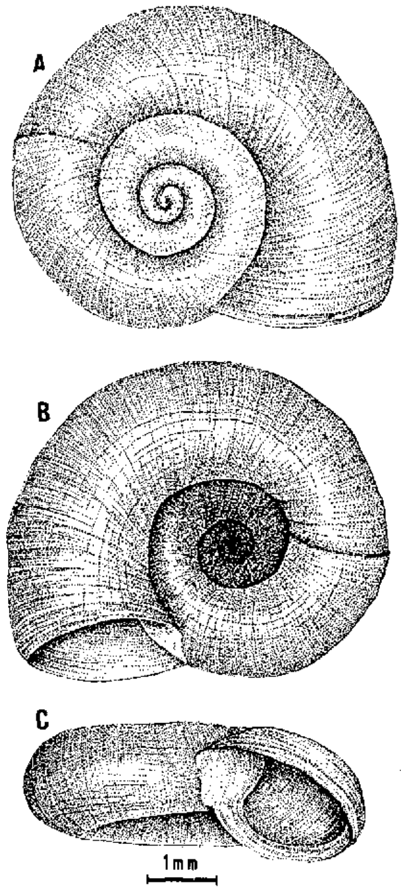


Fig. 25. Shell of *Drepanotrema (Antillorbis) aeruginosum* (Morelet) from Puerto Rico (A, right side; B, left side; C, ventral view)

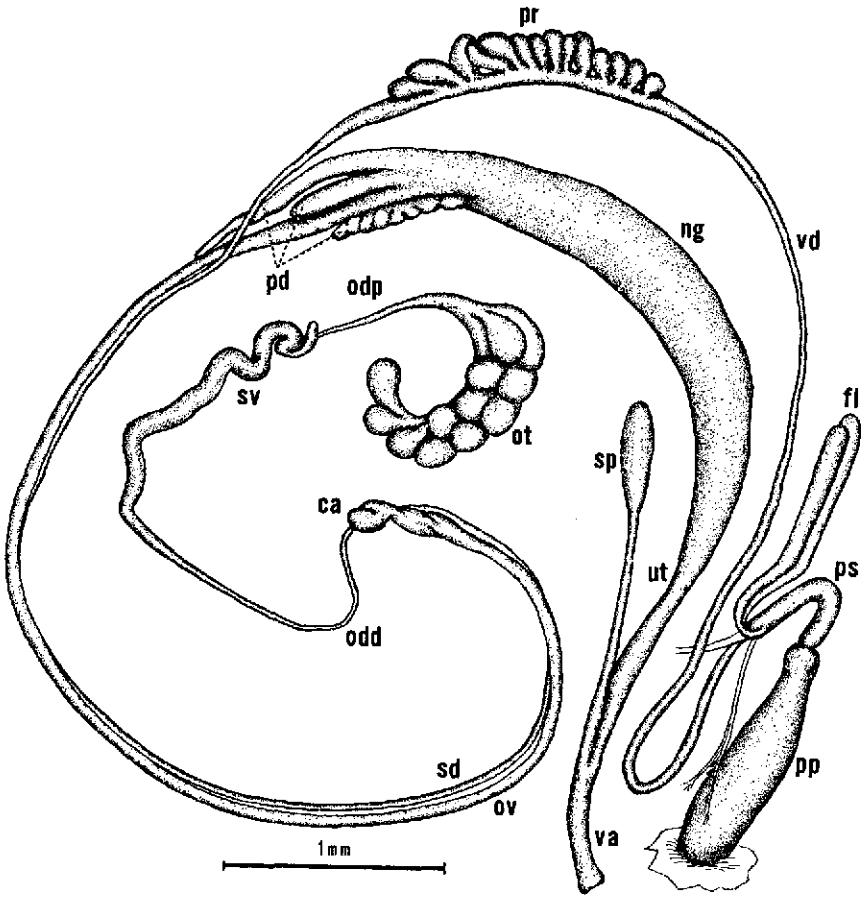


Fig. 26. Reproductive system of *Drepanotrema anatinum* (Orbigny) from Brazil. See p. 112 for key to abbreviations.

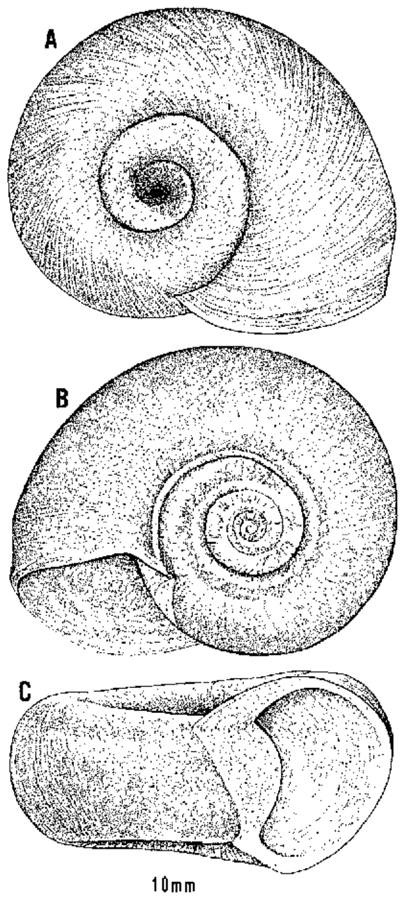


Fig. 27. Shell of *Helisoma foveale* (Menke) from an irrigation tank in southern Puerto Rico (A, right side; B, left side; C, ventral view)

throughout the next whorls. The shells are usually discoidal and may grow to 25 mm in diameter with about 5 whorls. There are some rare cases of populations in which the spire is elevated but sinistral or pseudodextral.

The jaw and central teeth of the radula are like those of *Biomphalaria*. There are no flagellar glands at the tip of the penis sac, but a large preputial organ is present with an external duct that connects with the penis sac. The tip of the penis has a stylet, and the seminal opening is lateral.

Plesiophysa (Fig. 19)

Some rare snails known from limited localities in Brazil and from a few locations in the Antilles are related to the planorbid genera cited above, though superficially they resemble species of the Physidae. The shell is sinistral with an elevated spire. It differs from *Physa* in that it has spiral lines of small beads or nodules and the shell of younger specimens is hirsute.

Species of Undetermined Genera

There are several rare and minute species in the Neotropics that have never been studied anatomically. The genera to which they belong therefore cannot be accurately designated. None of them in the adult stage is larger than 5 mm in diameter. They have been placed under the genera *Gyraulus, Promenetus, Menetus,* etc.

4. KEY TO NEOTROPICAL BIOMPHALARIA SPECIES*

1. Ventral surface of the renal tube with a pigmented longitudinal ridge (Fig. 38, **rer**), or a pigmented line in young specimens	*glabrata*
Ventral surface of the renal tube smooth and barely pigmented (Fig. 62, **ret**)	2
2. Vaginal wall with a pouch or swelling to the right of the spermathecal duct (Fig. 63, **vp**)	3
Vaginal wall without a pouch or swelling to the right of the spermathecal duct (Fig. 58, **va**)	13
3. Ovotestis diverticula over 200 (Fig. 63, **ot**)	*tenagophila*
Ovotestis diverticula under 150 (Fig. 50, **ot**)	4
4. Vaginal pouch scarcely extending beyond the level of the insertion of the spermathecal duct, the latter emptying outside and caudad to the pouch (Fig. 65, **vp**)	*trigyra*
Vaginal pouch normally extending well beyond the level of the insertion of the spermathecal duct, the latter emptying inside the pouch (Fig. 50, **vp**)	5
5. Maximum width of the distal half of the vas deferens about the same as that of the middle part of the penis sac (Fig. 29, **vd, ps**)	6
Maximum width of the distal half of the vas deferens distinctly narrower than the middle part of the penis sac (Fig. 54, **vd, ps**)	7
6. Clearly distinct and bulgy vaginal pouch (Fig. 29, **vp**)	*amazonica*
Poorly developed vaginal pouch, lacking in some specimens or coexisting with a little-developed corrugation to the left of the spermathecal duct (Fig. 46 A) [See 14]	*intermedia*
7. Lateral teeth of the radula with rectangular, bluntly pointed mesocone (Fig. 66 C)	8
Lateral teeth of the radula with dagger-like or triangular mesocone (Fig. 66 A, B, F)	9

* See list of abbreviations at the end of Guide.

8. Ovotestis diverticula under 30 (Fig. 31, **ot**) .... *andecola*
Ovotestis diverticula over 30 (Fig. 54, **ot**) .... *peregrina*

9. Vaginal pouch conspicuous (Fig. 54, **vp**); prostatic diverticula arborescent, with terminal branches bent to the right and left sides and clustering together into a compact cauliflower-like surface (Fig. 54, **pr**) .... *prona*
Vaginal pouch little to moderately developed (Fig. 41, **vp**); prostatic diverticula subdivided into branches with tips arranged more or less into a row (Fig. 41, **pr**) 10

10. Vaginal pouch slightly projecting but distinct (Fig. 41, **vp**) .... *havanensis*
Vaginal pouch extremely low, sometimes nearly indistinct (Fig. 48, **vp**) 11

11. Prostatic diverticula over 13 (Fig. 48, **pr**) .... *obstructa*
Prostatic diverticula under 13 (Fig. 35, **pr**) 12

12. Seminal vesicle with conspicuous diverticula (Fig. 35, **sv**); vagina with a median constriction (Fig. 35, **va**); vaginal pouch only vaguely indicated as a flattened elevation hardly delimited from the surrounding surface (Fig. 35, **vp**) .... *cousini*
Seminal vesicle with poorly developed diverticula (Fig. 52, **sv**); vagina cylindric (Fig. 52, **va**); vaginal pouch apparently lacking in some specimens [see 18]............. *philippiana*

13. Vaginal wall with corrugations to the left of the spermathecal duct (Fig. 60, **vc**) 14
Vaginal wall without corrugations to the left of the spermathecal duct (Fig. 58, **va**) 15

14. Vaginal wall strongly corrugated to the left of the spermathecal duct (Fig. 60, **vc**) .... *straminea*
Vaginal wall weakly corrugated (sometimes merely swollen) to the left of the spermathecal duct (Fig. 45, **vc**; Fig. 46 A); little to moderately developed vaginal pouch to the right coexisting with the corrugation in some specimens (Fig. 46 A) [see 6]............................... *intermedia*

15. Vaginal wall smooth (Fig. 58, **va**); ovotestis diverticula over 200 (Fig. 58, **ot**) .... *sericea*
Vaginal wall smooth (Fig. 43, **va**); ovotestis diverticula under 150 (Fig. 43, **ot**) 16

16. Very long penial complex and spermatheca (Fig. 56, **ps-pp, sp**); penis sac more than 4 times as long as the preputium (Fig. 56, **ps, pp**); spermatheca more than twice as long as the preputium (Fig. 56, **sp, pp**) .... *schrammi*

Comparatively short penial complex and spermatheca (Fig. 43, **ps-pp, sp**); penis sac clearly less than 4 times as long as the preputium (Fig. 43, **ps, pp**); spermatheca less than twice as long as the preputium (Fig. 43, **sp, pp**) 17

17. Seminal vesicle with conspicuous diverticula (Fig. 33, **sv**) .... *chilensis*

Seminal vesicle with poorly developed diverticula (Fig. 43, **sv**) 18

18. Prostatic diverticula usually 0-4, occasionally 5-6 (Fig. 52, **pr**); little-developed vaginal pouch in some specimens [see 12] .... *philippiana*

Prostatic diverticula usually over 6, exceptionally 4-5 (Fig. 43, **pr**) .... *helophila*

5. SYNOPSIS OF THE BIOMPHALARIA SPECIES

Animal species are not static entities; they are subject to genetic changes. The accumulation of these changes over time brings about animal evolution. If populations of one species in a certain geographic area are by some means isolated from the populations of the same species from another area, independent evolution in the two areas may result in a splitting of the species into two geographical races. Further independent evolution of the two races may transform the races into distinct species. Though as a rule true distinct species do not interbreed spontaneously in nature, specimens of different races of the same species do, and they produce fertile progeny. This difference between races of a single species and entirely distinct species is of course not always clear-cut; it develops gradually over the course of evolution. It is therefore difficult and sometimes even impossible to distinguish as races or distinct species forms that have recently evolved from a common ancestor. Even if they should rightly be regarded as species, hybridization might occasionally occur.

Forms that have obscure taxonomic status often occupy neighboring geographical areas and sometimes create hybrid populations where the areas meet. They may or may not be morphologically distinct. However, as a principle, the concept of species is biologically based. At present the investigators are not in position to judge whether some of the taxonomic units distinguished here correspond to true biological species. For example, the forms dealt with under the names *B. peregrina*, *B. chilensis*, *B. straminea*, *B. intermedia*, *B. obstructa*, and *B. havanensis* might well have a recent common origin.

Biomphalaria amazonica Paraense, 1966

The Shell (Fig. 28)

The shell reaches a maximum of about 8 mm in diameter and 2.5 mm in width, with about 5 whorls increasing moderately in diameter.

The whorls are rounded on both sides, except the body whorl, which is somewhat flattened in full-grown shells. The periphery is rounded. The aperture is egg-shaped, sometimes rounded, a little oblique, and more or less bent to the left in most full-grown specimens.

On the right side the body whorl is even with the penultimate whorl, and the inner whorls describe a funnel-shaped concavity; the apical whorl is deeply sunken. The left side is broadly and shallowly concave and shows the surface of the whorls more plainly than the right side.

The Soft Parts (Fig. 29)

The pigmentation of the normally exposed parts is grayish brown, with the mantle pigment distributed in dark patches, tending to coalesce on the roof and right side of the pulmonary cavity.

There are about 50 ovotestis diverticula, which are pear- or club-shaped and predominantly unbranched though sometimes bifurcate and exceptionally trifurcate. The seminal vesicle has conspicuous diverticula. The vagina is cylindric, with a bulging pouch to the right of the spermathecal duct. The spermatheca is usually club-shaped, with a duct less than half as long as the spermathecal body and not well delimited from the latter. The prostate has 8 to 12 diverticula, most of which are divided into two or three short branches, which may have small ovoid or elongate bud-like subdivisions. The distal half of the vas deferens is nearly as wide as the penis sheath, and the latter is about half as long as the preputium, which at the caudal end is only a little wider than the penis sheath and gradually expands to become about twice as wide at the cephalic end.

There is no renal ridge.

The lateral radular teeth have dagger-like or triangular cusps.

Geographical Distribution

The species is known only from Manaus (Amazonas) Brazil.

Ecological Features

It is found in slowly running waters that have abundant *Eichornia* and other aquatic and semiaquatic plants and pH 6.0 to 6.3.

Genetics

No data have been recorded.

Epidemiological Importance

The species does not seem to be susceptible to infection with *Schistosoma mansoni.*

Nomenclature

Type locality: Manaus (Amazonas) Brazil.

No synonyms have been recorded.

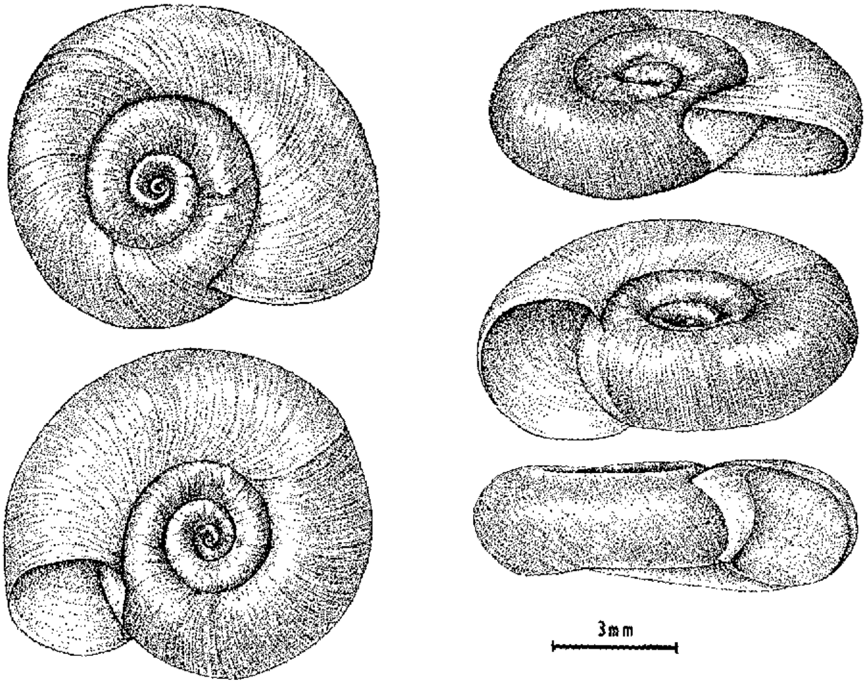


Fig. 28. Shell of *Biomphalaria amazonica* Paraense from Manaus, Brazil

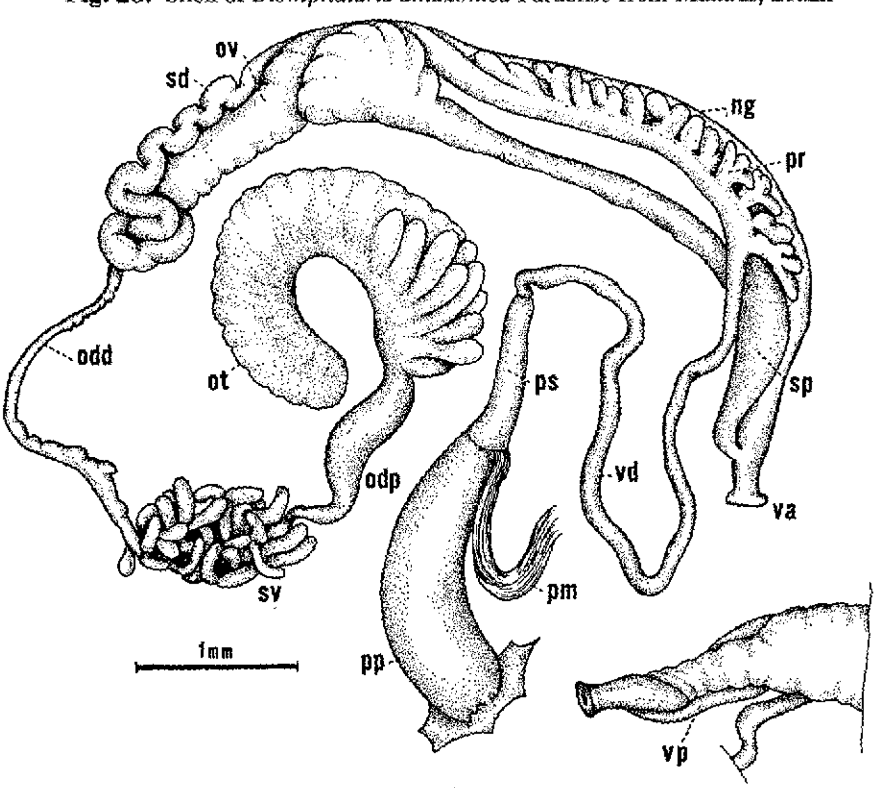


Fig. 29. Reproductive system of *Biomphalaria amazonica* Paraense from Manaus, Brazil (ovotestis not completely worked out). See p. 112 for key to abbreviations.

Biomphalaria andecola (Orbigny, 1935)

The Shell (Fig. 30)

The shell rarely exceeds a diameter of 21.9 or a width of 9.8 mm. Specimens 16 mm in diameter and 6 mm in height are regarded as large shells. Normal dimensions are about 6.2 and 3.3 mm, respectively. The number of whorls is 3 to 3½ at 6 to 10 mm in diameter, 4 at 16 mm, and 4½ at 20 mm.

The whorl increases rapidly in diameter and width. Occasionally its periphery is angular; but more often it is carinate, and sometimes even sharply so. The aperture is irregularly circular, with a tendency toward a pentagonal outline. It is sometimes extended, particularly toward the left.

The shape of the right side varies from convex to almost flat and even concave centrally. At one end of the range of shapes the shell has fairly smooth rounded whorls separated by a depressed suture and the central area is slightly concave. At the other extreme the shell is convex with a sharply angular area slightly concave, forming a low spire and a pseudodextral shell type. Intermediate forms combine the extremes into a complete series.

The left side is normally separated from the right by a carina or at least an angulation. Another angulation or carina surrounds the deep umbilicus. Between this angulation and the periphery of the shell there is often a third angulation that is not quite so sharp. On the left side the body whorl covers most of the preceding whorl. Only a minor part of the earlier whorl is visible in the bottom of the deep, steep-walled umbilicus.

The shell does not have any pronounced sculpture apart from fine growth lines. Its general color is yellowish to pale brown. The carinae, at least the peripheral one, when developed, may be paler.

The Soft Parts (Fig. 31)

The body consists almost entirely of the stout body whorl. The inner whorls taper rapidly and occupy a very small space. The pigmentation of the normally exposed parts varies from pale gray to deep black. The visceral mass is darkly pigmented in an irregular pattern. The pigmentation is particularly intense on the roof of the mantle cavity.

The ovotestis diverticula are mainly simple and occasionally bifurcate. The part of the reproductive system between the carrefour and the female pore is unusually stout. The vagina has a well-developed pouch. The spermatheca may be rounded, ovate, or pear-shaped. Its duct is generally thick and very short, but sometimes fairly slender and of about the same length as the spermatheca. The prostate has 6 to 12

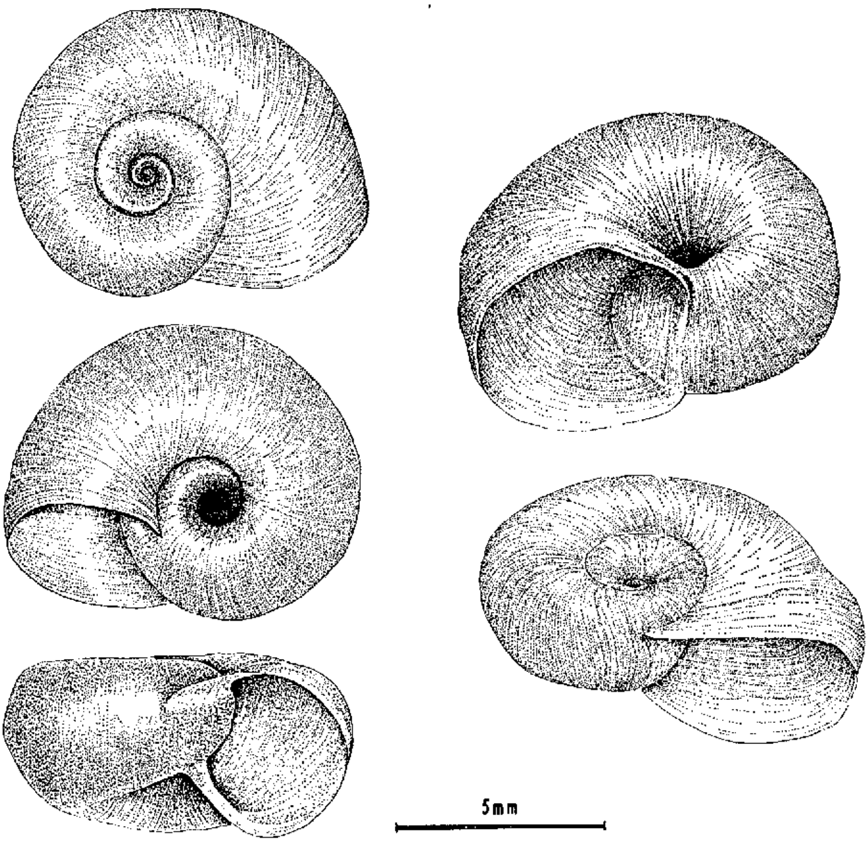


Fig. 30. Shell of *Biomphalaria andecola* (Orbigny) from Lake Titicaca, Bolivia

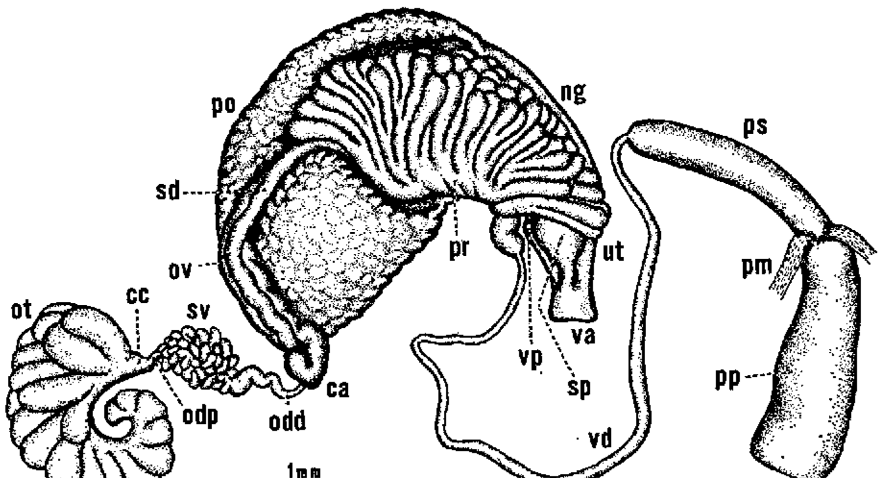


Fig. 31. Reproductive system of *Biomphalaria andecola* (Orbigny) from Lake Titicaca, Bolivia. See p. 112 for key to abbreviations.

long, slender, richly branched diverticula. Short, unbranched diverticula occur exceptionally. The diverticula branch from the sperm duct very near each other, causing the entire prostate to be very compact. The male copulatory organ is comparatively stout. The penis sac is slightly shorter than the preputium and, although thick, it is distinctly more slender than the latter. The main penial retractor muscle inserts on the innermost part of the preputium, where it merges into the penis sac.

The population of this species found in Ojos de Ascotán, near the Salar Ascotán in the Province of Antofagasta, Chile (described as *Taphius thermalus* by Biese in 1951) is generally characterized by a warty surface on the vaginal pouch. These warts correspond to depressions in the lumen of the organ caused by heavy infection with a flagellate parasite (*Cryptobia*) and lack taxonomic significance.

There is no renal ridge, but there is a rectal ridge continuing as a dorsal ridge, as in all the other species.

Geographical Distribution

This species is known from localities in the Andean highlands, such as Lake Titicaca and lagoons in the Titicaca basin (Bolivia and Peru), and from streams in the Province of Antofagasta, Chile.

Ecological Features

Unlike other species of the genus, *B. andecola* lives not only in shallow water but also in depths of up to at least 82 mm. In deeper waters it is purely discoidal, not pseudodextral, but still angulated. Apart from its remarkable tolerance to deep water, there are no recorded data about the ecology of this species.

Genetics

No data have been recorded.

Epidemiological Importance

This species is not known to be an intermediate host of *S. mansoni*.

Nomenclature

Type locality: Isla del Sol, Lake Titicaca, Bolivia.

The following described forms are most probably conspecific: *Planorbis montanus* Orbigny, 1835; *P. titicacensis* Clessin, 1884; *P. heteropleurus* Pilsbry and Vanatta, 1896; *P. concentratus* Pilsbry, 1924;

and *Taphius thermalus* Biese, 1951. Pilsbry later put *P. heteropleurus* into a separate genus, *Platytaphius*.

Biomphalaria chilensis (Anton, 1839)

The Shell (Fig. 32)

Shells of average size measure 9 to 11 mm in diameter and about 3 mm in width. The largest specimen available measured 13 mm in diameter and 4 mm in width. Specimens with 4 to 4½ whorls measure 9 to 11 mm in diameter. The specimen measuring 13 mm in diameter had 5½ whorls. The whorls, which increase rapidly in diameter, are rounded and not carinate. The aperture is unarmed and irregularly circular, with a tendency in larger specimens to be more wide than long. In some instances the aperture is slightly deviated towards the left.

The right side is flattened along the periphery and slightly concave toward the center. The left side is more concave than the right side and deeply umbilicate. On both sides the whorls are smoothly rounded.

The Soft Parts (Fig. 33)

The body is elongate, as in most members of the family. The color is uniformly blackish.

The ovotestis consists of many club-shaped diverticula arranged in two or three rows. The diverticula, usually 20 to 27 in each row, are simple, unbranched, and seldom bifurcated. The seminal vesicle is very well developed and beset with many small-sized protuberances and a few large diverticula. A short duct links the seminal vesicle to the ovotestis. The spermatheca is elongate, sac-like, and attached to the vagina by the short spermathecal duct, which is always shorter than the spermatheca itself. The uterus enlarges gradually to join the nidamental gland, which is very swollen. The oviduct is very short. The vagina has no visible corrugation or pouch. The prostate is comparatively short and bears from 7 to 13 diverticula. The diverticula are usually branched at the tips, though never arborescent, and closely packed at their point of origin. The two or three last distal diverticula, especially the last one, are very elongate and lie over the sperm duct. The penial complex is elongate. The preputium is nearly equal in length to the penis sac. The latter is slightly larger in diameter than the vas deferens, which is long and somewhat irregular in diameter.

There is no renal ridge.

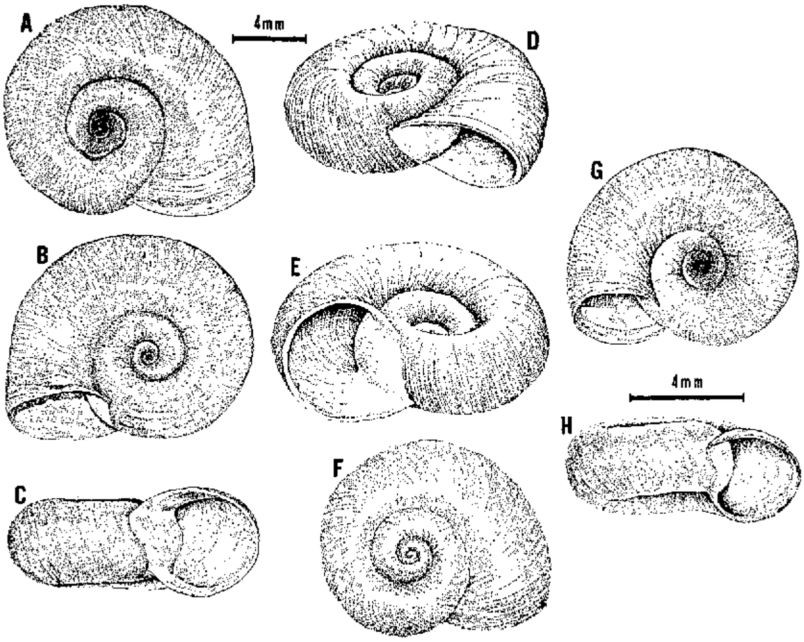


Fig. 32. Shell of *Biomphalaria chilensis* (Anton)
A-E: From Estero Lenga, Concepción, Chile
F-H: From Santiago, Chile

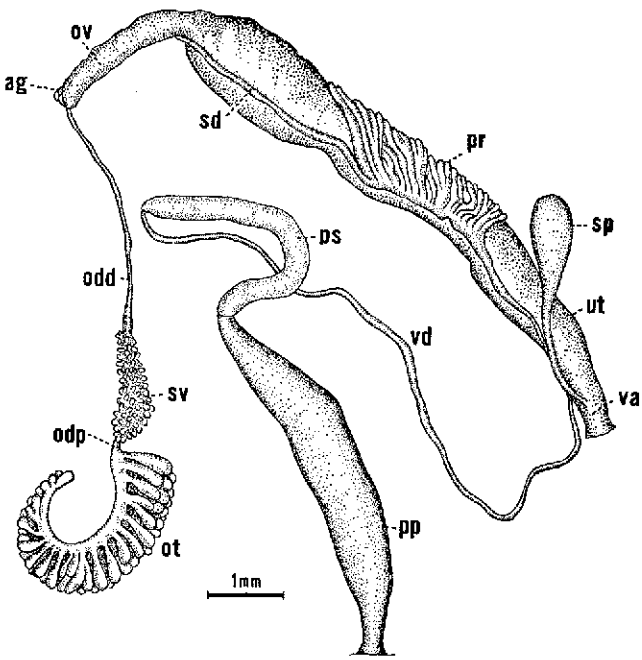


Fig. 33. Reproductive system of *Biomphalaria chilensis* (Anton). See p. 112 for key to abbreviations.

In the lateral radular teeth the middle cusp is truncated and not pointed, giving it a squarish appearance (Fig. 66E).

Geographical Distribution

The species is only known with certainty from Chile.

Ecological Features

No data have been recorded.

Genetics

B. chilensis is reproductively isolated from two Brazilian populations of *B. glabrata,* one from Recife (Pernambuco) and the other from Santa Luzia (Minas Gerais). It is also isolated from *B. tenagophila* from São Paulo, Brazil. In three out of six reciprocal crosses attempted between this species and *B. straminea* from Recife, fertile hybrids were obtained, although the number of viable eggs was small (Barbosa, Carneiro, and Barbosa, 1956).

Epidemiological Importance

This species is a potential host for a Brazilian strain of *S. mansoni.* Laboratory infection was obtained in 3 out of 44 snail specimens (Barbosa and Barbosa, 1958b).

Nomenclature

Type locality: Maypo, Chile.
Described by Anton in 1839 as *Planorbis chilensis.*

Biomphalaria cousini Paraense, 1966

The Shell (Fig. 34)

The shell grows to about 8 mm in diameter and 3 mm in width, with about 4½ whorls increasing moderately in diameter.

The whorls are rounded on both sides, with a somewhat sharper curvature on the left. The periphery is rounded. The aperture is egg-shaped, less frequently rounded, oblique, and bent to the left, sometimes exaggeratedly, in full-grown specimens.

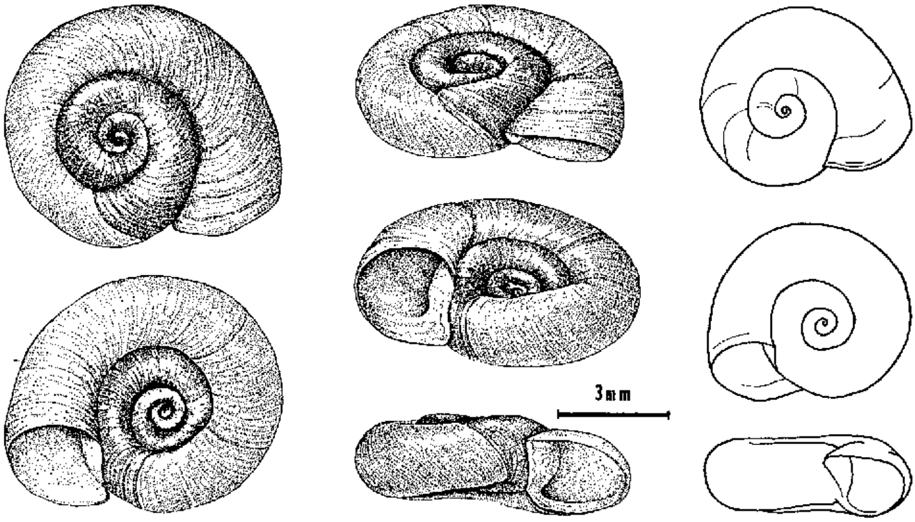


Fig. 34. Shell of *Biomphalaria cousini* Paraense from Santo Domingo de los Colorados, Ecuador.

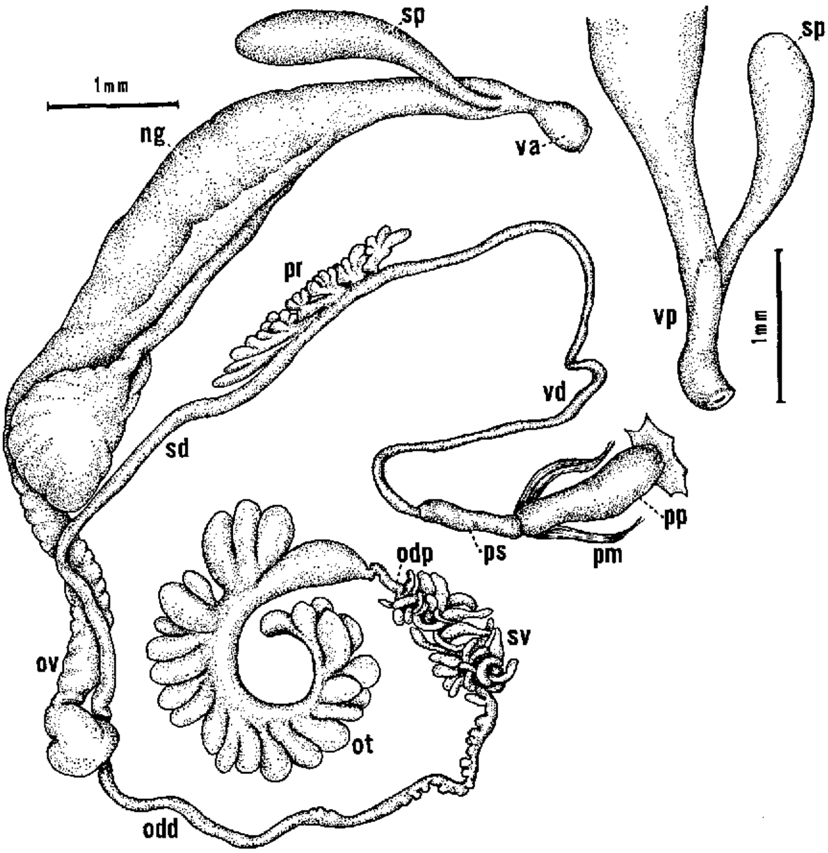


Fig. 35. Reproductive system of *Biomphalaria cousini* Paraense from Santo Domingo de los Colorados, Ecuador. See p. 112 for key to abbreviations.

The right side has a deeply sunken apical whorl and subsequent whorls surrounding a funnel-shaped concavity that broadens at the level of the penultimate whorl. The left side is broadly concave, showing the surface of the whorls more plainly than the right side.

There are no internal lamellae.

The Soft Parts (Fig. 35)

The pigmentation of the normally exposed parts is grayish brown. The mantle pigment is distributed in blackish patches.

There are up to about 30 ovotestis diverticula, arranged either in pairs or one after another. The diverticula are pear-shaped and predominantly unbranched, though sometimes they are bifurcate and occasionally trifurcate. The seminal vesicle has conspicuous diverticula. The distal portion of the vagina is swollen, and the vaginal pouch is located to the right of the spermathecal duct, only vaguely indicated as a flattened elevation and hardly delimited from the surrounding surface. The spermatheca is usually club-shaped, with a duct about half as long as the spermathecal body and frequently well delimited from the latter. The prostate has from 5 to 11 diverticula, most of which are divided into two or three comparatively long secondary branches, which may give tertiary elongate or bud-like subdivisions. The distal half of the vas deferens is distinctly narrower than the penis sac. The penis sac is about half as long and half as wide as the preputium, and the preputium is moderately widened toward the distal end.

There is no renal ridge.

The lateral radular teeth have dagger-like or triangular cusps.

Geographical Distribution

The species is known only from Santo Domingo de los Colorados (Pichincha) Ecuador.

Ecological Features

It has been found in a slowly running brook among aquatic grasses.

Genetics

No data have been recorded.

Epidemiological Importance

This species does not seem to be susceptible to infection with *S. mansoni.*

Nomenclature

Type locality: Santo Domingo de los Colorados (Pichincha) Ecuador.

No synonyms have been recorded.

Biomphalaria glabrata (Say, 1818)

The Shell (Figs. 36 and 37)

The shell may reach a maximum of about 40 mm in diameter, though usually it ranges between 15 and 30 mm, the ordinary size of adults varying with populations or geographic areas. The width is between 5 and 8 mm in most specimens at 20 mm diameter. The adult shell has about 5 to 6½ whorls, increasing slowly or sometimes more rapidly in diameter.

The whorls are normally rounded on the sides, though sometimes flattened, angular, or even carinate on the left and less frequently on the right. The suture ranges from shallow to deep between flattened and rounded or angular whorls, respectively.

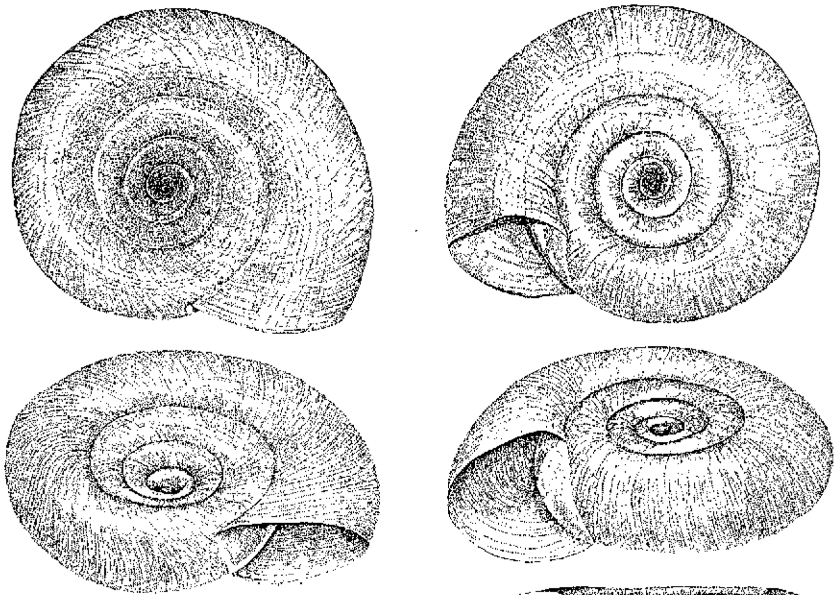
Each side varies from broadly and shallowly to deeply concave, generally in inverse proportion to the opposite side. The right side may be flat or even a little convex in individuals of some populations.

The periphery varies from rounded to bluntly angular and is frequently shifted to the right. The aperture may be narrow, egg-shaped, semicircular, rounded, or transverse; it is usually subangular on the lower left, directed forward or bent more or less leftward, and generally oblique to the right or to the left. The peristome is thin and continuous. Specimens of about 2 to 9 mm from habitats subject to seasonal drought may develop one or more sets of apertural lamellae (usually six per set), which later are wholly or partly resorbed. In some cases the whole set persists inside full-grown shells.

The Soft Parts (Figs. 38 and 39)

The pigmentation of the normally exposed parts ranges from pale gray to deep black.

There are usually over 200 ovotestis diverticula, which are predominantly trifurcate but may be divided into from two to five or more branches and in exceptional cases are even unbranched. The seminal vesicle has conspicuous diverticula. The vagina is cylindrical with a well-developed pouch to the right of the spermathecal duct. The spermatheca may be rounded, ovate, pear-shaped, or club-shaped, with a slender duct usually as long as the body. The prostate usually has



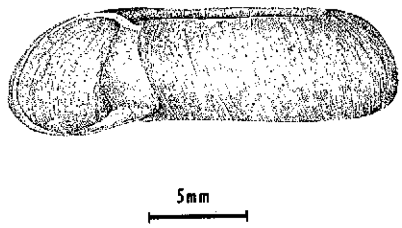


Fig. 36. Shell of *Biomphalaria glabrata* (Say) from Lake Estremoz, Rio Grande do Norte, Brazil

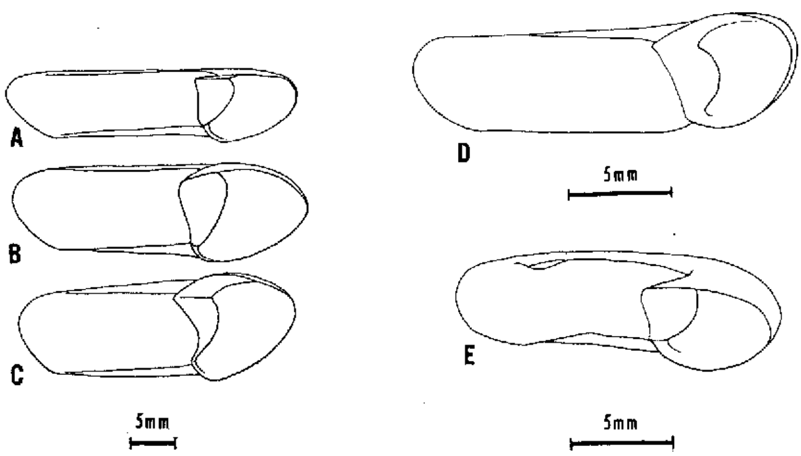


Fig. 37. Shell variation in *Biomphalaria glabrata* (Say)
A-C: Three specimens of the same population, from Salvador, Brazil
D: Specimen from Brasília, Brazil
E: Specimen from João Pessoa, Brazil

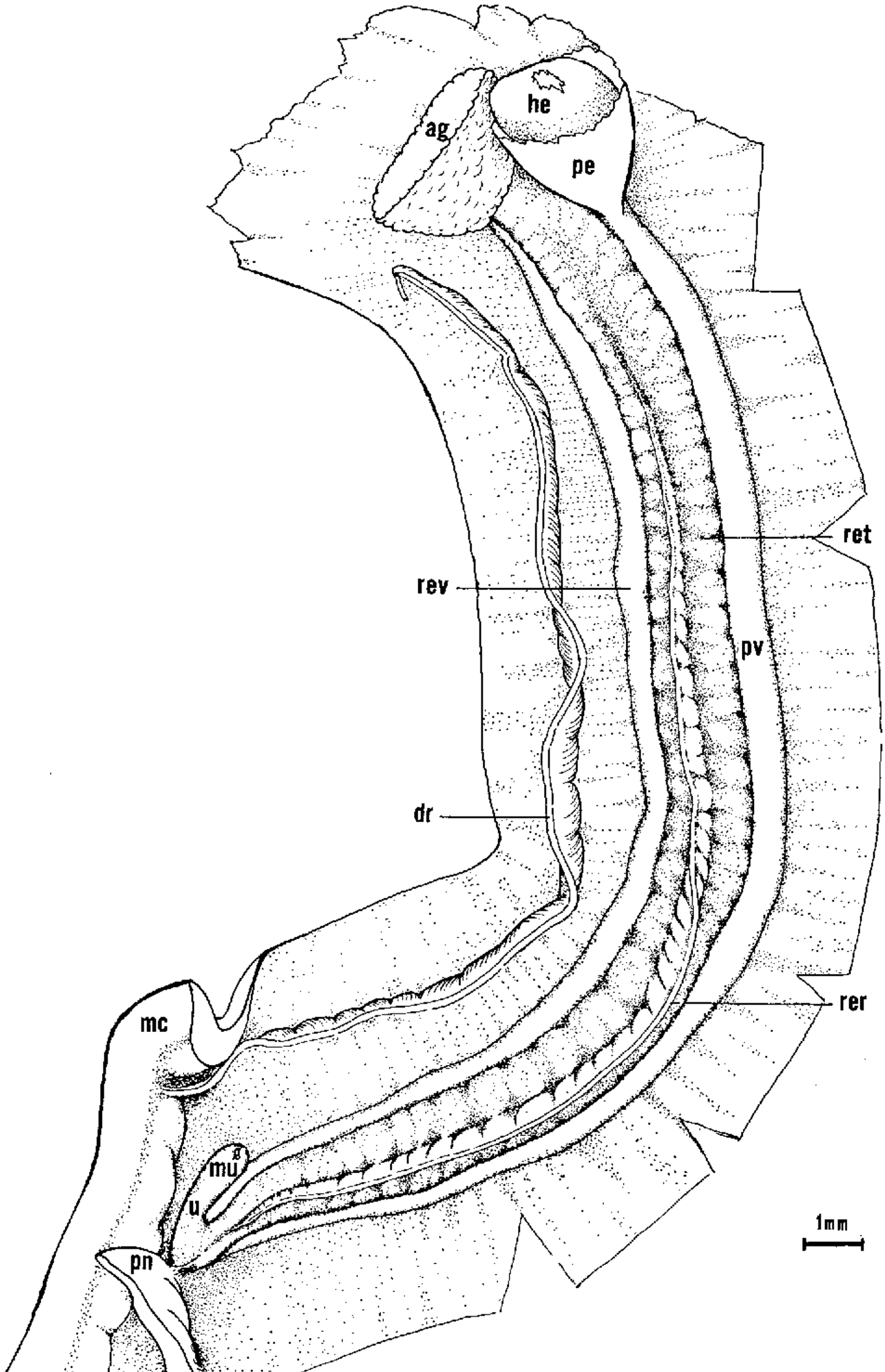


Fig. 38. Ceiling of mantle cavity of *Biomphalaria glabrata* (Say) from Brazil. See p. 112 for key to abbreviations.

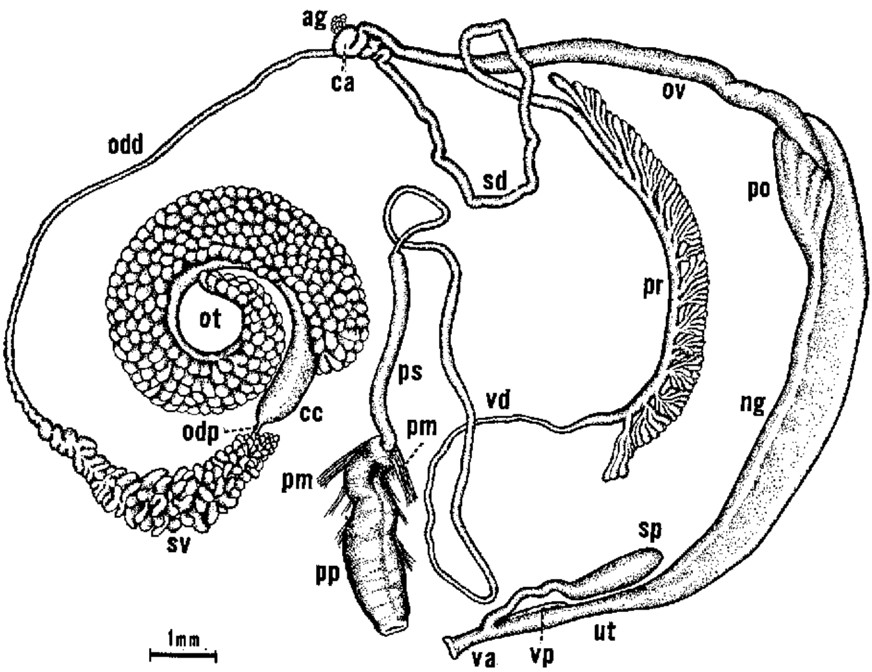


Fig. 39. Reproductive system of *Biomphalaria glabrata* (Say) from Brazil. See p. 112 for key to abbreviations.

15 to 30 long, slender, mainly arborescent, diverticula. The distal half of the vas deferens is nearly as wide as the penis sac. The penis sac is about as long as the preputium and distinctly narrower.

Young specimens up to about 10 mm in diameter show a longitudinal pigmented line on the membrane that covers the renal tube ventrally. As the snail grows, a longitudinal fold rises over that line and develops into a pigmented ridge. These renal characters alone are sufficient for separating this species from all the others in the genus.

The lateral radular teeth have dagger-like cusps (Fig. 66B).

Geographical Distribution

The species is found in many islands of the West Indies (Hispaniola, Puerto Rico, Vieques, St. Kitts, Antigua, St. Philip, Guadeloupe, Marie-Galante, Martinique, St. Lucia, Curaçāo), Venezuela, Surinam, French Guiana, and Brazil (between 20° N and 26° S).

Ecological Features

Its usual habitats are standing and slowly to swiftly flowing fresh waters—puddles, pools, marshes, permanent and temporary ponds, shallow areas of lakes, irrigation and drainage ditches, dams, quiet waters along banks of brooks, creeks, and small rivers. It adapts to wide ranges of water temperature and salinity, and to hydrogen ion concentrations between 5.8 and 9.0.

Genetics

Hybridization with the Egyptian *B. alexandrina* (Barbosa, Coelho, and Carneiro, 1956), as well as with Brazilian populations of *B. tenagophila* and *B. straminea* (Barbosa, 1960), has been successful.

Epidemiological Importance

This species is the most important intermediate host of *S. mansoni* in the Americas. Strain differences in susceptibility to the same Brazilian strain of *S. mansoni* have been demonstrated.

Nomenclature

Type locality: Guadeloupe Island (Pilsbry, by designation, 1934).

Type species of Pilsbry's genus *Australorbis* and senior synonym of the following described forms: *Planorbis guadaloupensis* Sowerby, 1822; *P. olivaceus* "Spix" Wagner, 1827; *P. ferrugineus* "Spix" Wagner, 1827; *P. lugubris* Wagner, 1827; *P. nigricans* "Spix" Wagner, 1827; *P.*

albescens "Spix" Wagner, 1827; *P. viridis* "Spix" Wagner, 1827; *P. lundii* Beck, 1837; *P. cumingianus* Dunker, 1848; *P. refulgens* Dunker, 1853; *P. becki* Dunker, 1856; *P. bahiensis* Dunker, 1856, *pro parte* (specimens from Bahia); *P. xerampelinus* Drouët, 1859; and *P. blauneri* "Shuttleworth" Germain, 1921.

Biomphalaria havanensis (Pfeiffer, 1839)

The Shell (Fig. 40)

The shell grows to about 13 mm in diameter and 3.5 mm in width, with about 5 whorls, increasing moderately in diameter, which are rounded or, more frequently, bluntly subangular, and separated by a deep suture.

The right side has a deeply sunken apical whorl and subsequent whorls describing an initially narrow concavity that broadens from the level of the third whorl outward. In certain populations this side may be flat to slightly concave. The left side is broadly and shallowly concave, sometimes flattened around the shallow central depression.

The periphery varies from rounded to broadly subangulate and is usually somewhat shifted to the right. The aperture may be egg-shaped, rounded, or slightly transverse; it may be deflected to the left in certain individuals or in a majority of adults of some populations; and it is usually oblique. The peristome is thin and continuous. In habitats subject to seasonal drought, young shells may develop a set of apertural lamellae (usually six), which later are wholly or partly resorbed.

The Soft Parts (Fig. 41)

The pigmentation of the normally exposed parts is grayish to deep black. The mantle pigment is distributed in dark patches, concentrated especially on the roof and right side of the pulmonary cavity.

There are usually over 60 ovotestis diverticula, arranged in transverse rows of two or three, predominantly unbranched, club-shaped, or pear-shaped, though sometimes bifurcate and occasionally trifurcate. The seminal vesicle has conspicuous diverticula. The vagina has a poorly developed pouch, usually well delimited from the surrounding surface, to the right of the spermathecal duct. The spermathecal sac is club-shaped to roundish, and the spermathecal duct is slender, usually well delimited from the sac, and half as long. The prostate, in most instances, has 9 to 18 short diverticula that split early into primary divisions and soon give rise to short tertiary and quaternary subdivisions.

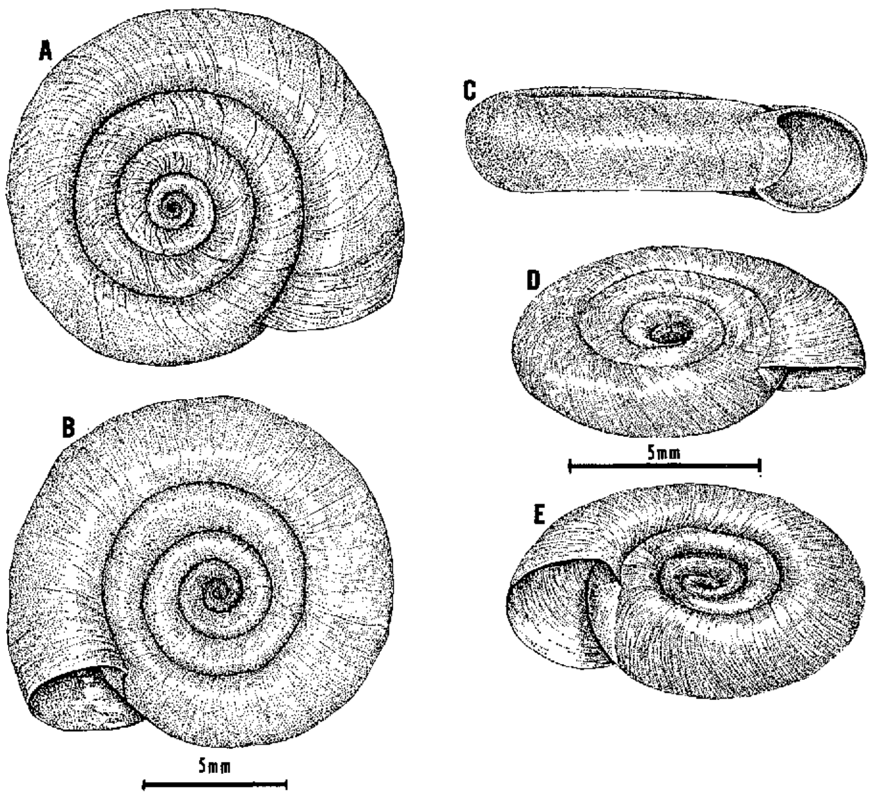


Fig. 40. Shell of *Biomphalaria havanensis* (Pfeiffer)
A-C: From Haiti
D-E: From Mexico (U.S. Nat. Museum 220012)

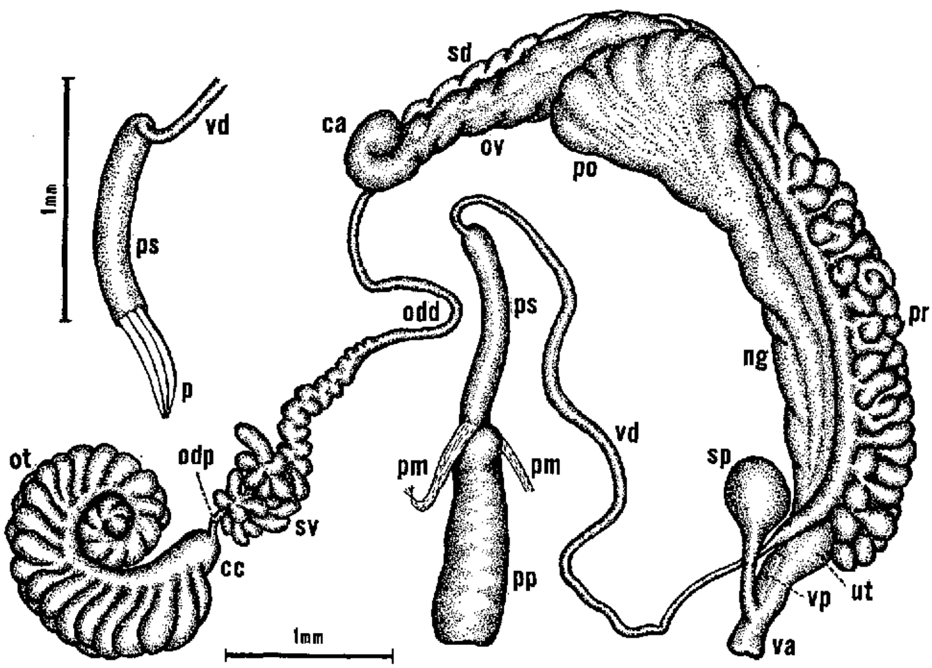


Fig. 41. Reproductive system of *Biomphalaria havanensis* (Pfeiffer) from Cuba. See p. 112 for key to abbreviations.

The distal half of the vas deferens is distinctly narrower than the penis sac. The penis sac is usually half as long as the preputium and distinctly narrower, though it may be nearly equal in length.

There is no renal ridge.

The lateral radular teeth have dagger-like or triangular cusps (Fig. 66A).

Geographical Distribution

The species is found in the Antilles region, Mexico, Central America, and probably some areas of northern South America.

Ecological Features

It usually inhabits ponds, shallow areas of lakes, dams, quiet waters along the banks of brooks and creeks, and bottoms of shallow streams.

Genetics

No data have been recorded.

Epidemiological Importance

Susceptibility to laboratory infection with *S. mansoni* has been recorded by Richards (1963a) for specimens from Puerto Rico called by him *Tropicorbis riisei*. The colony, now extinct, from Baton Rouge, tentatively identified as *T. havanensis* by Berry (Cram, Jones, and Wright, 1945) was shown to be susceptible to infection with *S. mansoni*.

Nomenclature

Type locality: Havana, Cuba.

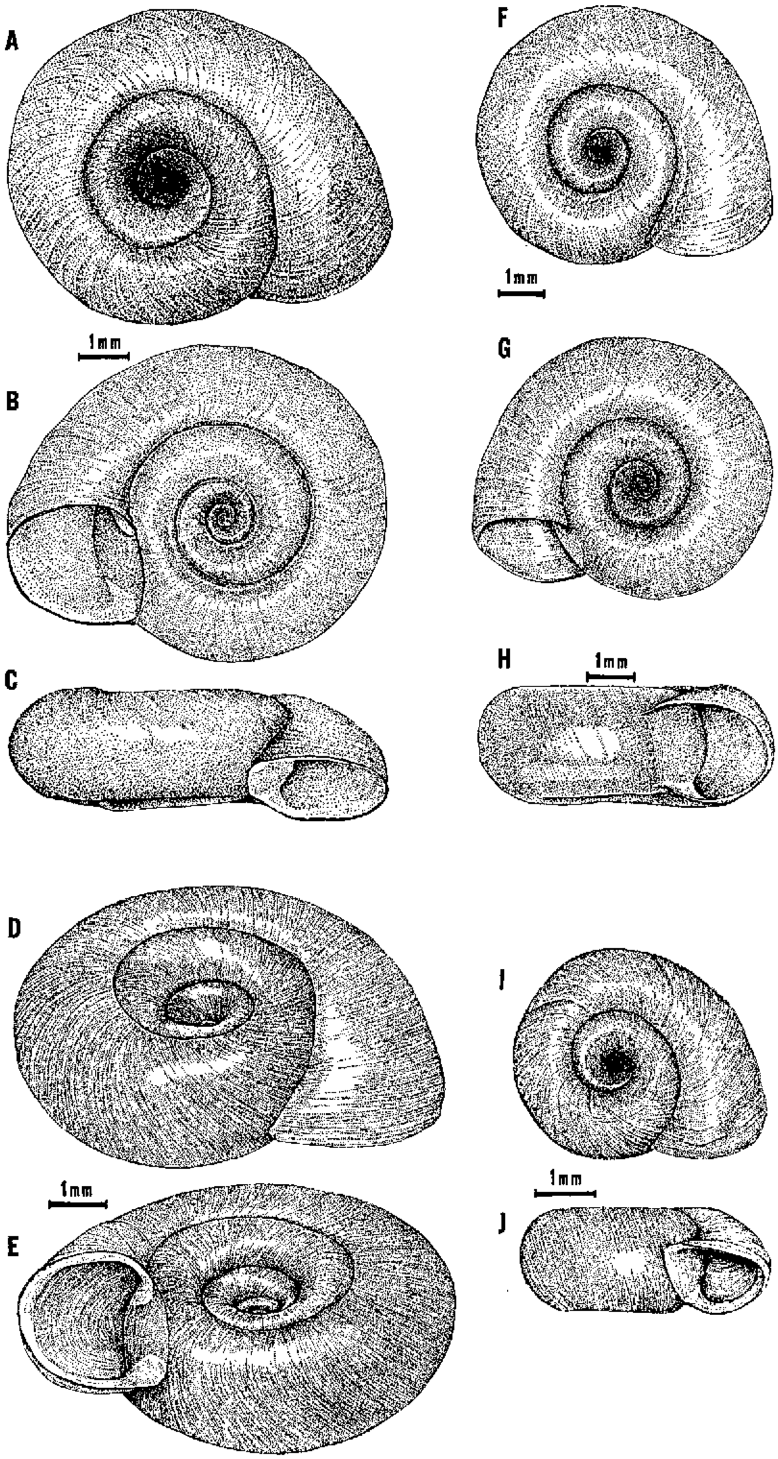
Among the synonyms are *Planorbis terverianus* Orbigny, 1841; *P. maya* Morelet, 1849; *P. orbiculus* Morelet, 1849; *P. retusus* Morelet, 1849; *P. liebmanni* Dunker, 1856; probably *P. riisei* "Dunker" Clessin, 1883; *P. obvolutus* Clessin, 1885; and probably *P. meridaensis* Preston, 1907.

Biomphalaria helophila (Orbigny, 1835)

The Shell (Fig. 42)

The shell reaches a maximum of about 7 mm in diameter and 2 mm in width. The adult shell has about 4 rapidly increasing whorls.

Fig. 42. Shells of *Biomphalaria helophila* (Orbigny)



A-E:
From Guadeloupe,
the West Indies

F-H:
From Pinar del
Río, Cuba

I-J:
From Cuba
(British Museum
N.H., London)

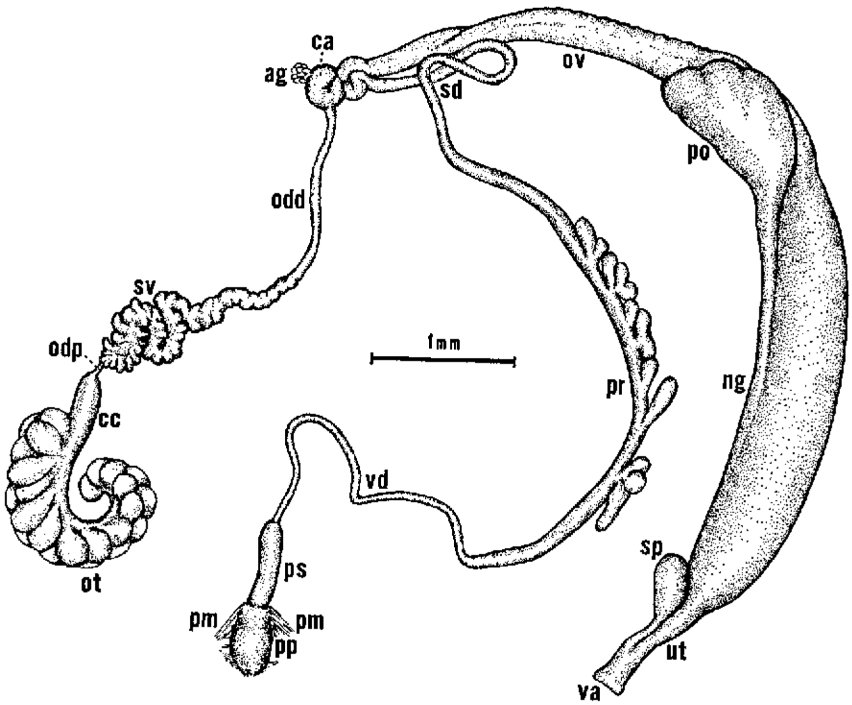


Fig. 43. Reproductive system of *Biomphalaria helophila* (Orbigny) from Peru. See p. 112 for key to abbreviations.

The whorls are rounded on the right and bluntly carinate on the left. The periphery is smooth. The aperture is directed forward in young specimens, but as the shell grows larger it gradually bends to the left. In older specimens a callous thickening of the lip may be found. Many shells develop a permanent set of apertural lamellae (usually six—two parietal and four palatal).

The right side is flattened and deeply umbilicate, with the inner whorls obscured at the bottom of the umbilicus. The left side is concave, with a vortex-shaped central depression, shallower than on the right side. At the bottom of this depression the inner whorl is plainly visible.

The Soft Parts (Fig. 43)

The pigmentation of the normally exposed parts ranges from pale to dark gray. The mantle pigment is distributed in dark patches, which are visible through the shell.

There are up to about 30 ovotestis diverticula, predominantly unbranched but occasionally bifurcate. The seminal vesicle has poorly developed parietal diverticula. The vagina is smooth-walled. The spermatheca may be rounded, ovate, pear-shaped, or club-shaped, and it has a slender duct, usually as long as the sac. The prostate, in most instances, has from 5 to 16 diverticula, which are mainly bifurcate or trifurcate. The penis sac ranges from the same length to about four times as long as the preputium, and it is only a little narrower. The penial complex is comparatively short—only a fourth to an eighth as long as the whole female duct.

There is no renal ridge.

The lateral radular teeth have dagger-like or triangular cusps.

Geographical Distribution

The species has been reported from Peru, Cuba, and Puerto Rico.

Ecological Features

It is found in shallow standing or slowly flowing waters and in environments subject to seasonal drought.

Genetics

No data have been recorded.

Epidemiological Importance

The species is susceptible to laboratory infection with *S. mansoni* (specimens from Puerto Rico, under the name *albicans*, in Richards, 1963a).

Nomenclature

Type locality: Callao, Peru.

Senior synonym of *Planorbis albicans* Pfeiffer, 1839. *B. helophila* is undoubtedly closely related to *B. schrammi*. The possibility that these are actually two different forms of one single species should not be excluded.

Biomphalaria intermedia (Paraense and Deslandes, 1962)

The Shell (Fig. 44)

The shell attains a maximum of about 12 mm in diameter and 3 mm in width. The full-grown shell has about 5 rather slowly increasing whorls.

The whorls are rounded on the right side and bluntly carinate on the left. In many specimens the outer whorl is flattened on the right at the apertural region and slightly deflected toward the left. The periphery is rounded. The aperture may be ovate or heart-shaped.

The right side is broadly concave and deeply umbilicate, showing all the whorls plainly. The left side is slightly concave and the whorls are plainly visible.

The Soft Parts (Figs. 45 and 46)

The pigmentation of the normally exposed parts ranges from pale to dark gray. The mantle pigment is distributed in dark patches.

The ovotestis diverticula are predominantly unbranched, though sometimes they are bifurcate and occasionally trifurcate. The seminal vesicle has conspicuous diverticula. The vagina is either smooth or has a swelling resembling a rudimentary pouch on the right of the spermatheca, and is swollen or weakly corrugated on the left. The spermatheca may be rounded, ovate, pear-shaped, or club-shaped, and it has a slender (occasionally stout) duct about as long as the spermathecal sac. The prostate, in most instances, has from 7 to 15 diverticula, mainly bifurcate or trifurcate. The penis sac is about as long as the preputium and much narrower.

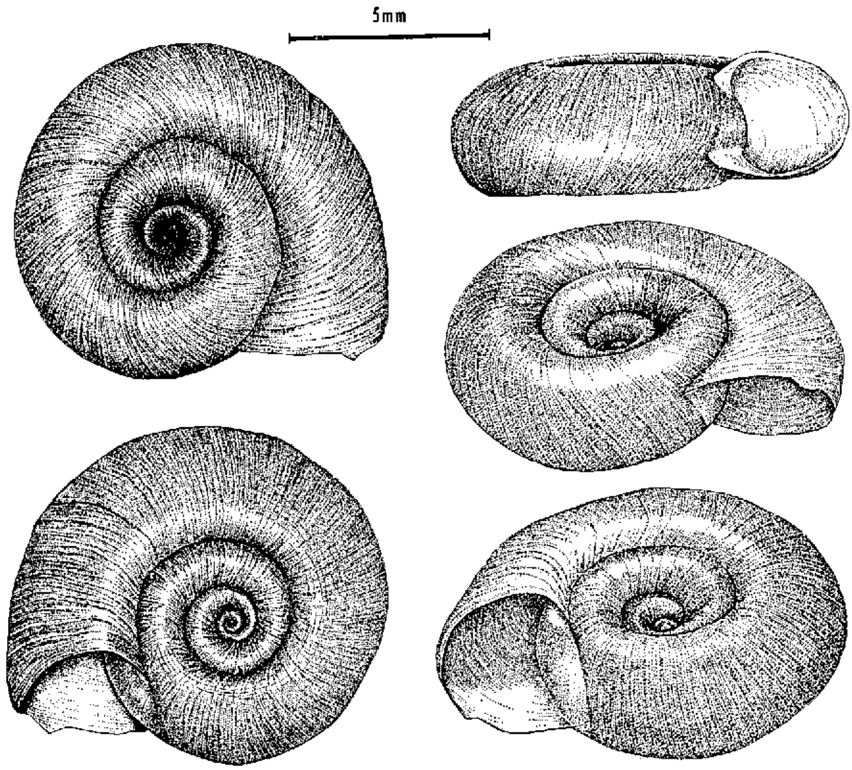


Fig. 44. Shells of *Biomphalaria intermedia* (Paraense and Deslandes) from São Paulo, Brazil (paratype)

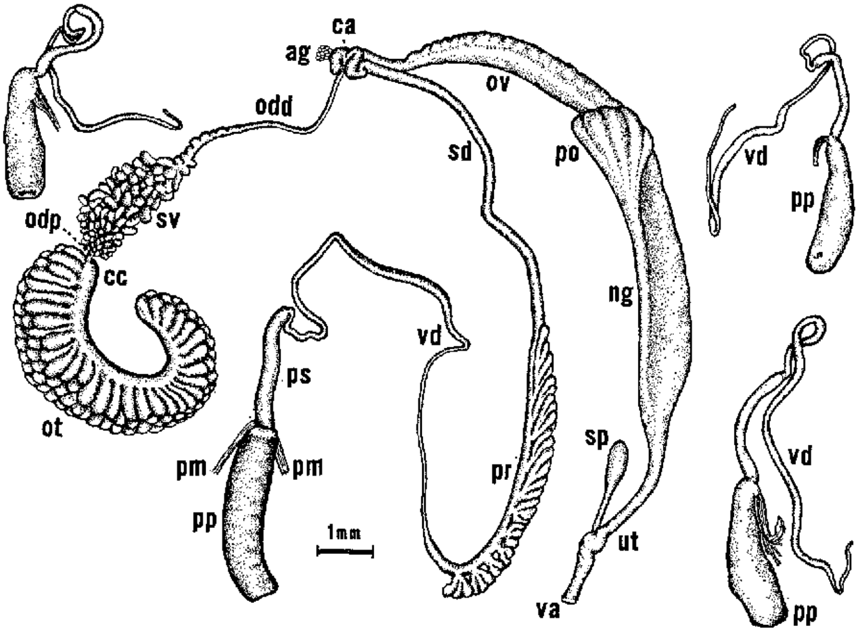


Fig. 45. Reproductive system of *Biomphalaria intermedia* (Paraense and Deslandes) from São Paulo, Brazil. See p. 112 for key to abbreviations.

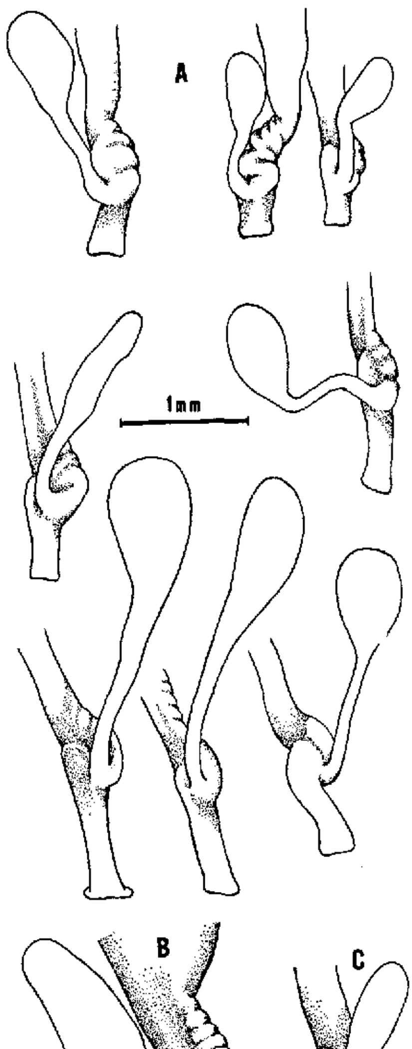


Fig. 46. Female copulatory organ
A: Variation within *Biomphalaria intermedia* (8 figs.)
B: *Biomphalaria straminea*
C: *Biomphalaria peregrina*

There is no renal ridge.
The lateral radular teeth have dagger-like or triangular cusps.

Geographical Distribution

The species is known from the highlands of São Paulo State in Brazil.

Ecological Features

Its usual habitats are slowly flowing waters in creeks, marshes, irrigation canals, and drainage ditches.

Genetics

Fertile offspring were produced by crosses between *B. intermedia* and *B. straminea* from Pernambuco, Brazil; *B. intermedia* can be reproductively isolated from *B. peregrina* and *B. tenagophila* (Paraense, unpublished).

Epidemiological Importance

This species is not susceptible to infection with *S. mansoni.*

Nomenclature

Type locality: Valparaiso (São Paulo State) Brazil.
No synonyms have been recorded.

Biomphalaria obstructa (Morelet, 1849)

The Shell (Fig. 47)

The shell grows to about 10 mm in diameter and 2 mm in width. The adult shell has 4½ to 5 slowly increasing whorls.

The periphery of the whorls is round; the sutures are pronounced. The aperture is heart-shaped, with distinct lamellae in the young snails. Many specimens show deflection of the aperture toward the left.

Both sides are slightly concave.

The Soft Parts (Fig. 48)

Black patches are present on both the right and left sides of the mantle.

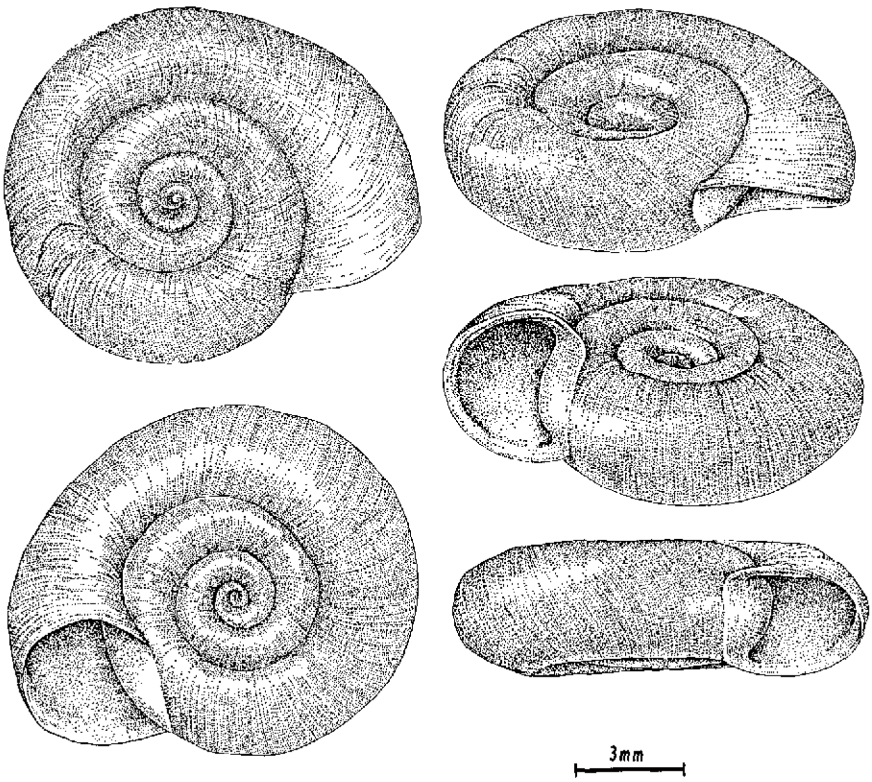


Fig. 47. Shell of *Biomphalaria obstructa* (Morelet) from Brownsville, Texas

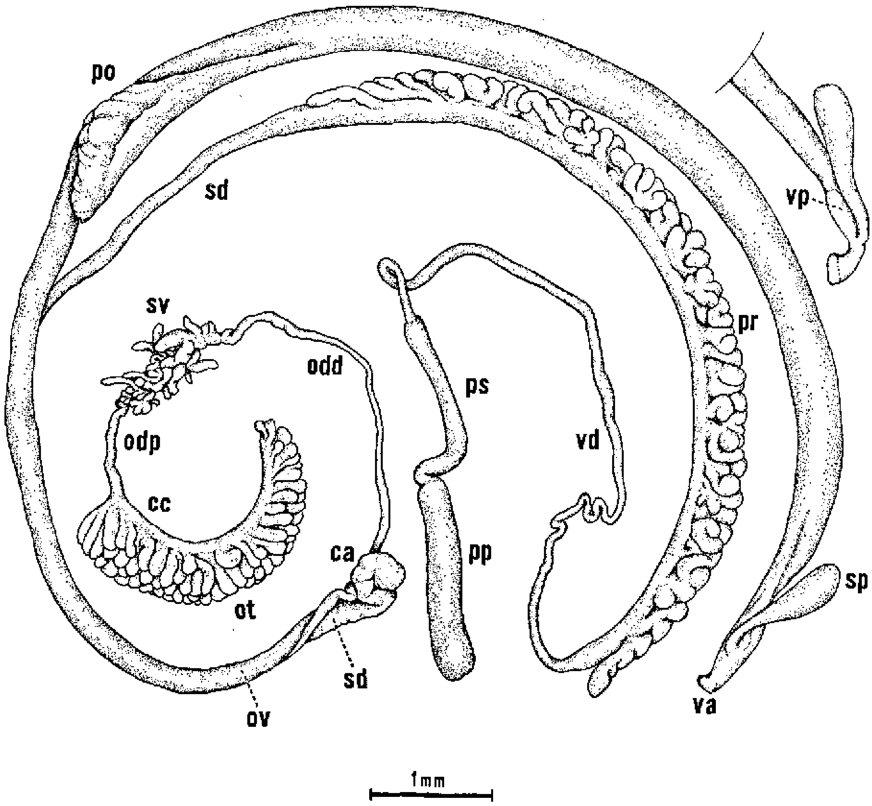


Fig. 48. Reproductive system of *Biomphalaria obstructa* (Morelet) from Louisiana. See p. 112 for key to abbreviations.

The ovotestis diverticula are predominantly unbranched. The seminal vesicle has poorly to well-developed parietal diverticula. The vagina is smooth, without corrugations, and has an extremely small pouch almost hidden in the surrounding tissue. The spermatheca is pear-shaped, with the duct slightly longer than the sac. The prostate has from 18 to 25 unbranched or branched diverticula, 2.7 to 4.3 mm in length in specimens about 7 mm in diameter. The penis sac is narrower and slightly shorter or equal to the preputium. The ratio of the female genital tract to the oviduct is 1:0.32; the ratio of the female genital tract to the penial complex is 1:0.44.

There is no renal ridge.

The lateral radular teeth have dagger-like or triangular cusps.

Geographical Distribution

This species is found in the southern part of the United States and in Mexico, Puerto Rico, and Cuba.

Ecological Features

It abounds in swamps, mud flats, borrow-pits, and reservoirs.

Genetics

No data have been recorded.

Epidemiological Importance

The species is not susceptible to infection with S. *mansoni*.

Nomenclature

Type locality: Carmen Island, Mexico.

No synonyms have been recorded.

Biomphalaria peregrina (Orbigny, 1835)

The Shell (Fig. 49)

The shell attains a maximum of about 16 mm in diameter and 4.5 mm in width. The full-grown shell has about 5 or 6 whorls, which usually increase slowly.

The whorls are rounded or somewhat flattened on the right and rounded or subangulate on the left. The periphery is smoothly rounded.

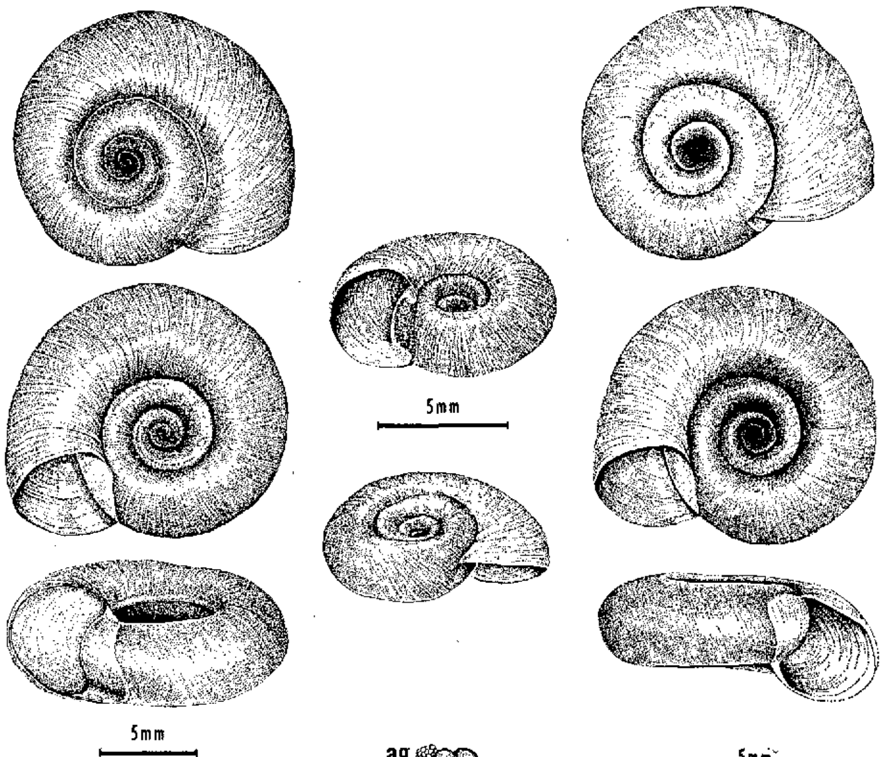


Fig. 49. Shell of *Biomphalaria peregrina* (Orbigny) from Curitiba, Brazil

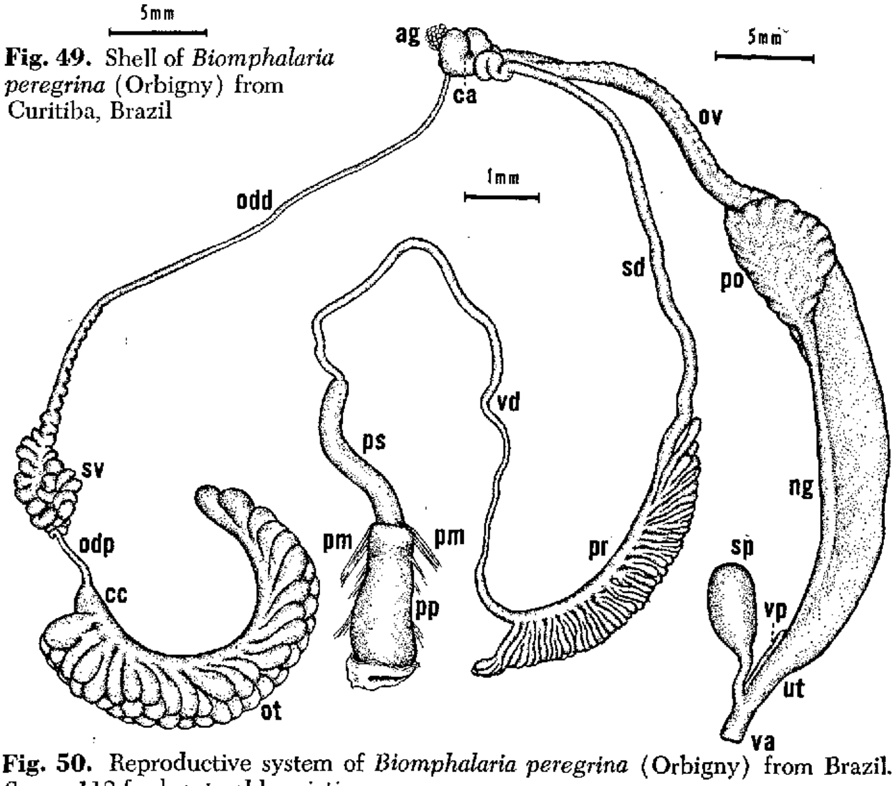


Fig. 50. Reproductive system of *Biomphalaria peregrina* (Orbigny) from Brazil. See p. 112 for key to abbreviations.

The aperture may be egg-shaped, rounded, or slightly transverse, and directed forward. In some populations, however, it is bent to the left in most full-grown specimens. In habitats subject to seasonal drought young shells may, on occasion, develop a set of apertural lamellae (usually six).

The right side ranges from flattened to broadly concave and deeply umbilicate. The left side is broadly concave, with a vortex-shaped central depression.

The Soft Parts (Figs. 50 and 46)

The pigmentation of the normally exposed parts ranges from pale gray to a brownish color. There may be up to 100 ovotestis diverticula, which are predominantly unbranched, though sometimes they are bifurcate or trifurcate. The seminal vesicle has conspicuous diverticula. The vagina has a well-developed pouch to the right of the spermathecal duct. The spermatheca may be rounded, ovate, pear-shaped, or club-shaped, and its duct, either slender or comparatively stout, is usually as long as the spermathecal sac. The prostate, in most instances, has from 8 to 21 diverticula, mainly branched or arborescent. The distal half of the vas deferens is narrower than the penis sac, and the latter is about as long as the preputium but distinctly narrower.

There is no renal ridge.

Geographical Distribution

The species has been recorded from Ecuador, Bolivia (Barbosa, unpublished), Chile, Brazil, Paraguay, Uruguay, and Argentina—west of the Andes from about the Equator to 42°S, and east of the Andes from about 15° to 41°S. In eastern Brazil it is roughly limited by 45°W and 15°S.

Ecological Features

Its usual habitats are standing and slowly flowing fresh water—marshes, ponds, shallow areas of lakes, irrigation and drainage ditches, dams, and slowly running creeks.

Genetics

The form from Ecuador, called "*Tropicorbis philippianus*" by Barbosa, Barbosa, and Carneiro (1958a), hybridizes with *B. straminea* and *B. tenagophila* from Brazil.

Epidemiological Importance

Records of susceptibility of this species to laboratory infection with S. *mansoni* are given by Barbosa, Barbosa, and Rodríguez (1958) for specimens from Ecuador (*Tropicorbis philippianus*), by Richards (1963a) for specimens from Puerto Rico ("*T. riisei*"), and by Paraense and Correa (unpublished) for specimens from Lapa (Paraná), Brazil and from Quito and Lake San Pablo, Ecuador.

Nomenclature

Type locality: Patagonia, Argentina.

Among the synonyms are *Planorbis fuscus* Dunker, 1848; *P. jacobeanus* "Valenciennes" Hupe, 1854; *P. pedrinus* Miller, 1879; *P. canonicus* Cousin, 1887; *P. levistriatus* Preston, 1912; *Tropicorbis schmiererianus* Biese, 1951; *T. montanus* Biese, 1951; *Taphius costatus* Biese, 1951; *Australorbis inflexus* Paraense and Deslandes, 1956 and *Tropicorbis philippianus* (Dunker) of Barbosa, Barbosa, and Rodríguez (1958).

Biomphalaria philippiana (Dunker, 1848)

The Shell (Fig. 51)

The shell reaches a maximum of about 11 mm in diameter and 3 mm in width. The adult shell has about 5 rather slowly increasing whorls.

The whorls are flattened on the right and subangulate on the left. The periphery is broadly subangulate. The aperture is heart-shaped.

The right side is flat, with plainly visible whorls, separated by a shallow suture, and a moderately deep umbilical region. The left side is broadly concave or vortex-shaped, with plainly visible whorls and a deep suture.

There are fine growth lines, which in some specimens are paralleled by simple rib-like transverse thickenings. The shell color ranges from light yellow to deep brown, depending on the degree of impregnation with environmental material.

The Soft Parts (Fig. 52)

The pigmentation of the normally exposed parts ranges from pale to dark gray. The mantle pigment is distributed in dark patches, visible through the shell.

There are up to about 30 ovotestis diverticula, predominantly unbranched but occasionally bifurcate. The seminal vesicle has poorly

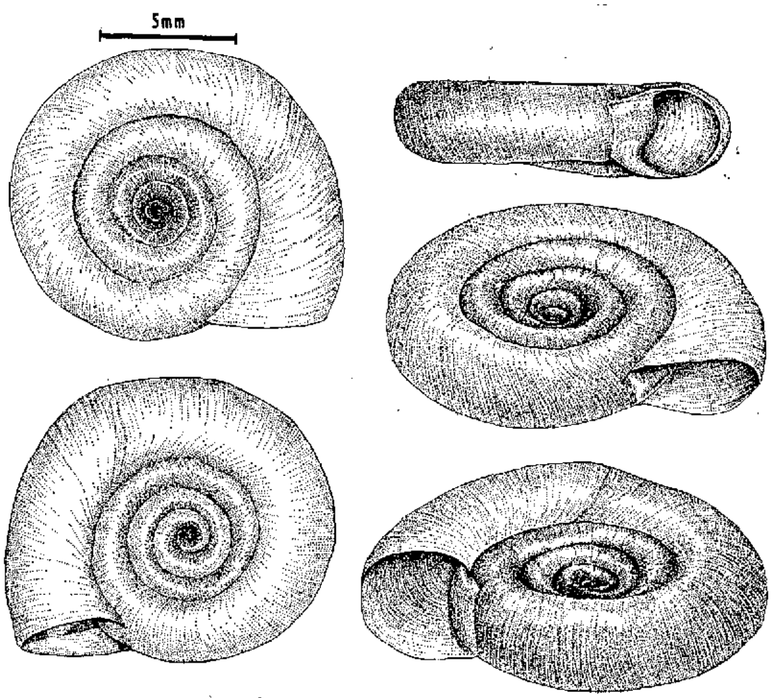


Fig. 51. Shell of *Biomphalaria philippiana* (Dunker) from Cochabamba, Bolivia (Coll. H. Cuming; British Mus. N.H.)

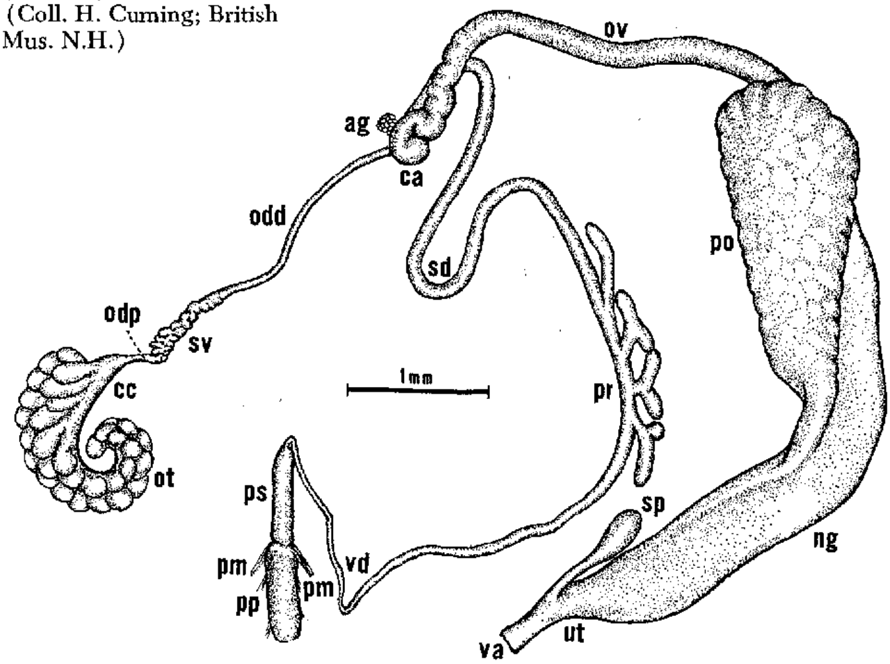


Fig. 52. Reproductive system of *Biomphalaria philippiana* (Dunker) from Brazil. See p. 112 for key to abbreviations.

developed parietal diverticula. The vagina is usually smooth-walled, but in some specimens it shows a more or less distinct pouch to the right of the spermathecal duct. The spermatheca may be rounded, ovate, pear-shaped, or club-shaped, with a slender duct usually as long as the sac. The prostate, in most instances, has up to 6 well-interspaced diverticula, which are mainly bifurcate or unbranched. The penis sac is about as long as the preputium and a little narrower. The penial complex is comparatively very short, having a ratio of from 1:2.5 to 1:7 with respect to the length of the female duct.

There is no renal ridge.

The lateral radular teeth have the same shape as in *B. helophila.*

Geographical Distribution

The species is known from Bolivia and southern Brazil.

Ecological Features

Until now it has been found only in slow-flowing creeks.

Genetics

No data have been recorded.

Epidemiological Importance

The species is not known to be able to serve as an intermediate host of *S. mansoni.*

Nomenclature

Type locality: Cochabamba, Bolivia.

The form from Ecuador called *Tropicorbis philippianus* (Dunker) by Barbosa, Barbosa, and Carneiro (1958a) belongs to *B. peregrina.*

Biomphalaria prona (Martens, 1873)

The Shell (Fig. 53)

The normal size of a full-grown shell with 3½ to 4 whorls is 7 to 8 mm in diameter and 3.2 to 3.5 mm in width. When the maximum diameter is 8 mm, the width may be about 6 mm. Martens gives the maximum diameter as 10 mm and the width as 5 mm. The aperture

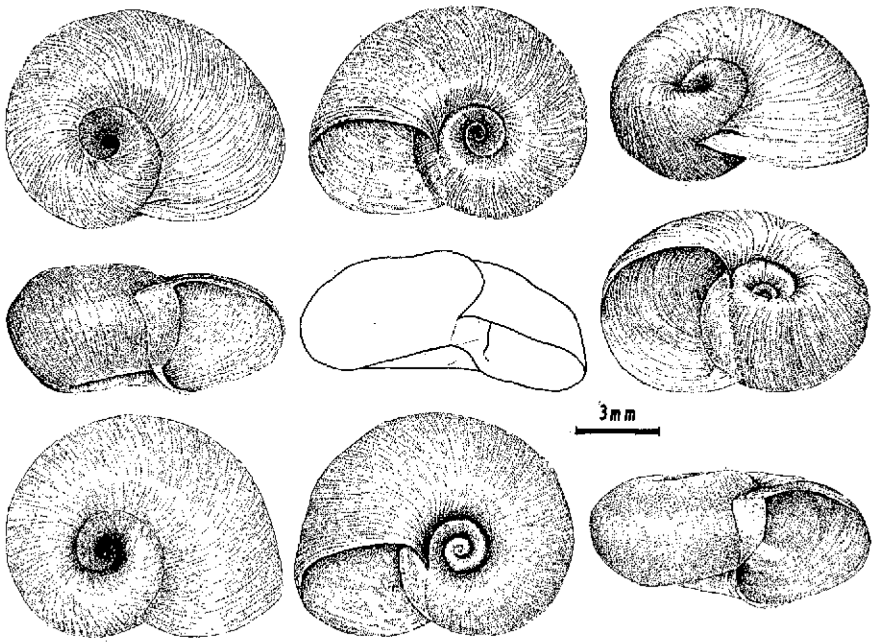


Fig. 53. Shell of *Biomphalaria prona* (Martens) from Lake Valencia, Venezuela

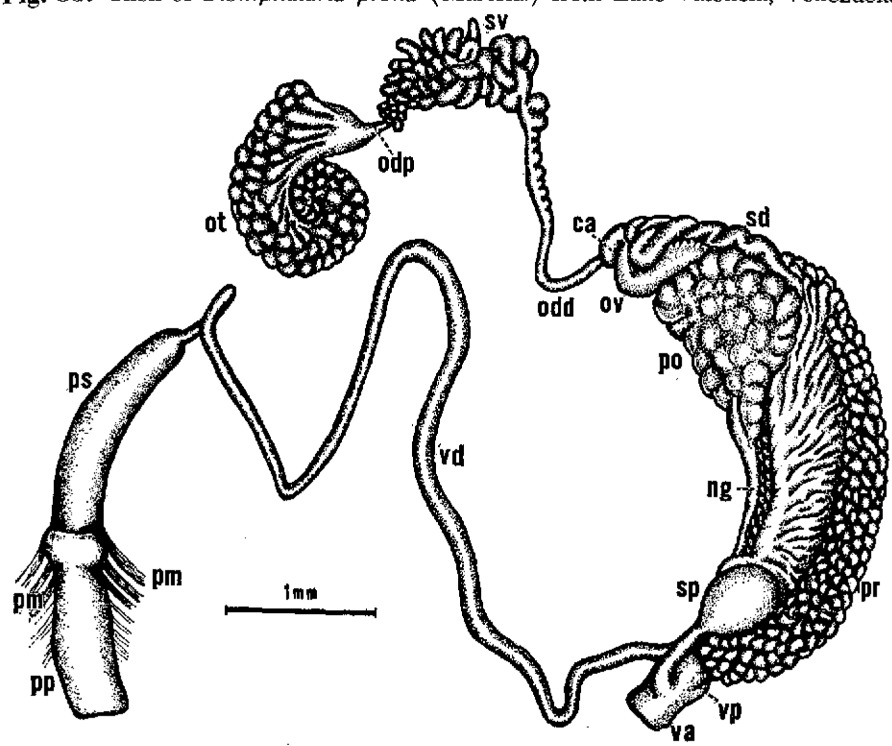


Fig. 54. Reproductive system of *Biomphalaria prona* (Martens) from Lake Valencia, Venezuela. See p. 112 for key to abbreviations.

widens rapidly during the growth of the adult shell, which changes the proportion between the diameter and maximum height.

The whorl increases rapidly in width, particularly in radial direction. The rapid widening of the last portion of the body whorl makes the full-grown shell elliptical rather than round. The width increases more toward the left. The cross-section of the whorl is roundish. The aperture is semiellipsoid with a moderate incut by the penultimate whorl. Sometimes it is expanded and irregularly triangular, the longest dimension being parallel with the diameter of the shell. Occasionally the last portion of the last whorl is declined toward the left, giving the shell a somewhat pseudodextral appearance. The right lip extends far beyond the left lip, making the aperture strongly oblique.

The right side is completely dominated by the last whorl. The umbilicus is fairly deep but very narrow. The inner whorls are rounded; the last portion of the last whorl is expanded and somewhat flattened. This last portion is sometimes more or less depressed in relation to the preceding whorls.

On the left side, the body whorl also dominates the other whorls and surrounds the depressed central area to form a rather wide and comparatively shallow umbilicus. The whorls are rounded and separated by a somewhat impressed suture. The last portion of the body whorl is slightly flattened and often more or less widened toward the left, causing the aperture to be wider. Sometimes the body whorl is subcarinated on the left side.

Apart from weak growth lines and extremely faint spiral lines on the right side, there is no shell sculpture. The shell ranges from brown to a yellowish color. Sometimes there is a paler band along the periphery.

The Soft Parts (Fig. 54)

In the soft body the last whorl predominates, the inner whorls occupying only a very small space. The pigmentation is widely variable. The distal parts, such as the head, foot, and mantle border, are more or less evenly pale to dark gray. The mantle may have dark spots of pigmentation, but it is often uniformly dark in color.

The ovotestis diverticula are club-shaped and nearly always simple, though occasionally they are bifurcate. The vagina has a smooth lateral pouch just above the junction with the spermathecal duct. The spermatheca is round or pear-shaped and its duct does not exceed the length of the spermatheca itself. The abundantly branched prostate diverticula, which spread on all sides and cluster into an almost cauliflower-like structure, are a particularly characteristic feature of the species. In the male copulatory organ the penis sac and preputium are of about the same length, the former being only slightly more slender than the latter.

There is no renal ridge.
The lateral radular teeth have dagger-like cusps.

Geographical Distribution

The species has been found with certainty only in Lake Valencia in Venezuela.

Ecological Features

It is known to live in shallow water attached to submerged vegetation. No further information about the ecology of this species is available.

Genetics

No data have been recorded.

Epidemiological Importance

The status of this species as an intermediate host for S. *mansoni* is not known.

Nomenclature

Type locality: Lake Valencia, Venezuela.
No synonyms have been recorded.

Biomphalaria schrammi (Crosse, 1864)

The Shell (Fig. 55)

The shell grows to about 7 mm in diameter and 1.5 to 2 mm in height. The adult shell has 4 to 5 rather rapidly increasing whorls.

The whorls are rounded on both sides. The periphery is smooth. The aperture is directed forward in young specimens, but as the shell grows larger it gradually bends to the left and develops a permanent set of lamellae (usually six–two parietal and four palatal). In older specimens a callous thickening of the lip may be found.

The right side is flattened and umbilicate, with the inner whorls obscured at the bottom of the umbilicus. The left side is concave, with a vortex-shaped central depression at the bottom of which the inner whorls are plainly visible.

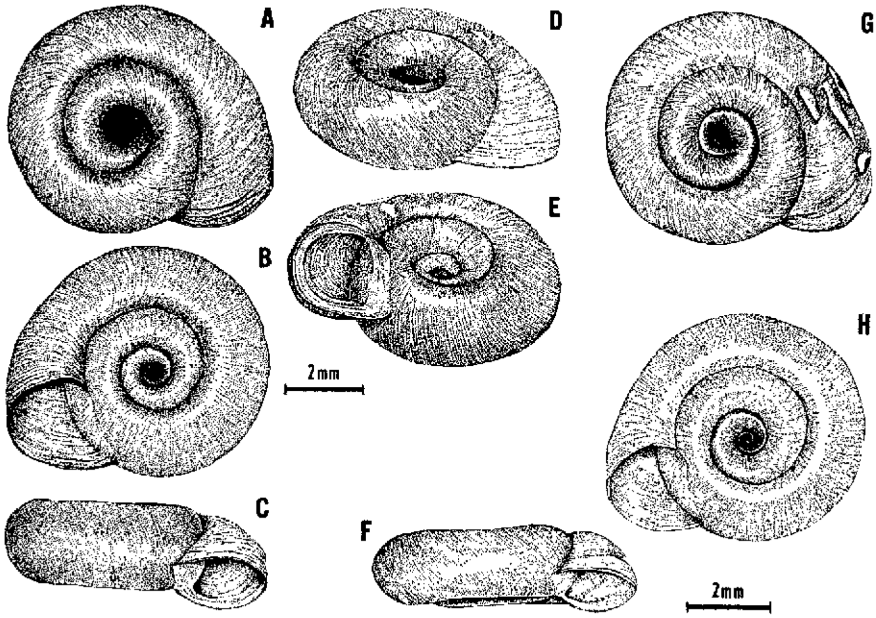


Fig. 55. Shell of *Biomphalaria schrammi* (Crosse)
A-E: From Pernambuco, Brazil
F-H: From Rio de Janeiro, Brazil

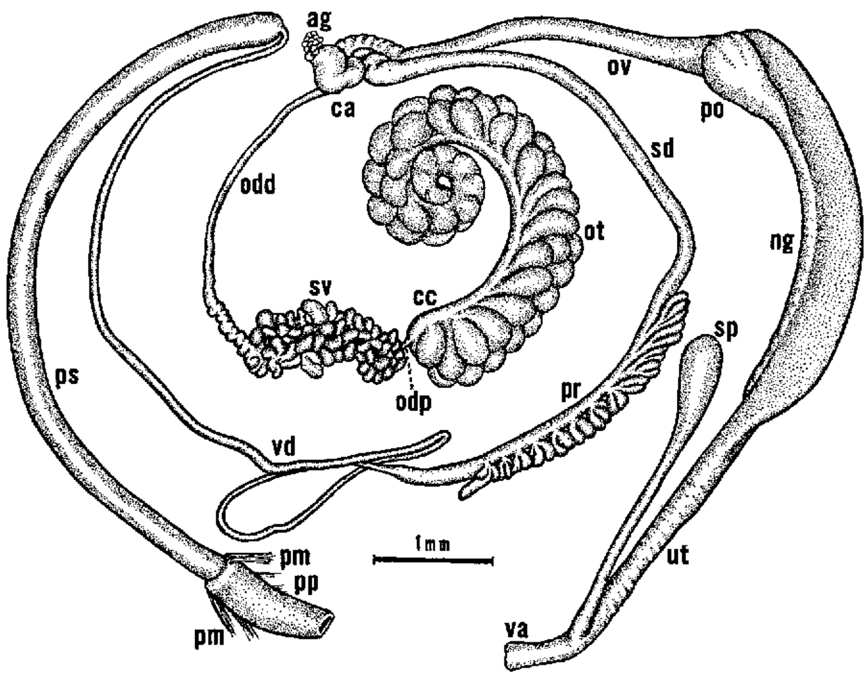


Fig. 56. Reproductive system of *Biomphalaria schrammi* (Crosse) from Brazil. See p. 112 for key to abbreviations.

The Soft Parts (Fig. 56)

The pigmentation of the normally exposed parts ranges from pale to dark gray. The mantle pigment is distributed in dark patches visible through the shell.

There are about 50 (though the number varies widely) ovotestis diverticula, predominantly unbranched and occasionally bifurcate. The seminal vesicle has poorly to well-developed parietal diverticula. The vagina is smooth-walled and unusually long. The spermatheca is as long as the vagina and is club-shaped, with the body tapering into a long slender duct. The prostate, in most instances, has from 8 to 17 diverticula, mainly bifurcate, trifurcate, or arborescent. The penis sac is from 4.5 to 7 times as long as the preputium and about the same width. The penial complex is comparatively very long—about half the length of the whole female duct.

There is no renal ridge.

The lateral radular teeth have dagger-like or triangular cusps (Fig. 66F).

Geographical Distribution

The species is known from Guadeloupe Island, French Guiana, and Brazil, reaching to about 24°S.

Ecological Features

It has been found in shallow standing and slowly running waters and appears to be adapted to environments subject to seasonal drought.

Genetics

No data have been recorded.

Epidemiological Importance

The species is not susceptible to infection with S. *mansoni.*

Nomenclature

Type locality: Guadeloupe Island.

Known synonyms are *Planorbis janeirensis* Clessin, 1884; *Segmentina paparyensis* Baker, 1914; *P.* (*Taphius*) *incertus* Lutz, 1918 (mislabeled by Lutz *P. incertulus* in Paraense and Deslandes, 1956); *P.* (*T.*) *nigrilabris* Lutz, 1918.

Biomphalaria sericea (Dunker, 1848)

The Shell (Fig. 57)

The medium-sized shells measure from 13 to 16 mm in diameter and are about 4.5 mm in width. The whorls increase rapidly in size and their number ranges from 3½ to 4½ for specimens of the above dimensions. The largest shell available measured 20 mm in diameter and 6 mm in width and had 5½ whorls.

The aperture is irregularly circular with a tendency toward a pentagonal outline. In a few instances the aperture is slightly bent toward the left. There are no apertural lamellae.

The right side varies from slightly convex to almost flat on the periphery to concave in the center. A very faint carina parallels the suture line in most specimens. A few specimens, however, are noticeably carinate on this side. The left side is deeply umbilicate and the carina is very conspicuous. Typical shells are very high and exhibit a distinctly marked double carination.

The surface of the shell is smooth with only a fine oblique striation of growth lines. The shell is uniformly light brown in color and has a horny texture.

The Soft Parts (Fig. 58)

The body is elongate, as in most of the other species of the family. The mantle is darkly pigmented in an irregular pattern.

The ovotestis is a large gland composed of multiple club-shaped diverticula, most of which are bifurcate or trifurcate. In cross-section the gland is seen to be composed of four to five diverticula extending in a fan-like manner from the hermaphrodite duct. The seminal vesicle is studded with small protrusions. The spermatheca is long and pear-shaped and is attached to the vagina by a long narrow duct. The uterus enlarges gradually to meet the nidamental gland. The vagina is relatively long and smooth without a visible corrugation or pouch. The prostate is relatively long and consists of about 12 diverticula, which are attached to the sperm duct. The two or three foremost diverticula are unbranched or only poorly branched; the others, especially those about midway along the prostate, are intensively branched. The primary branches arise from a single stem and each branch divides two or three times, producing an arborescent appearance. The penis sac is thin and always shorter than the preputium. The ratio of the preputium to the penis sac is 6:9.

There is no renal ridge.

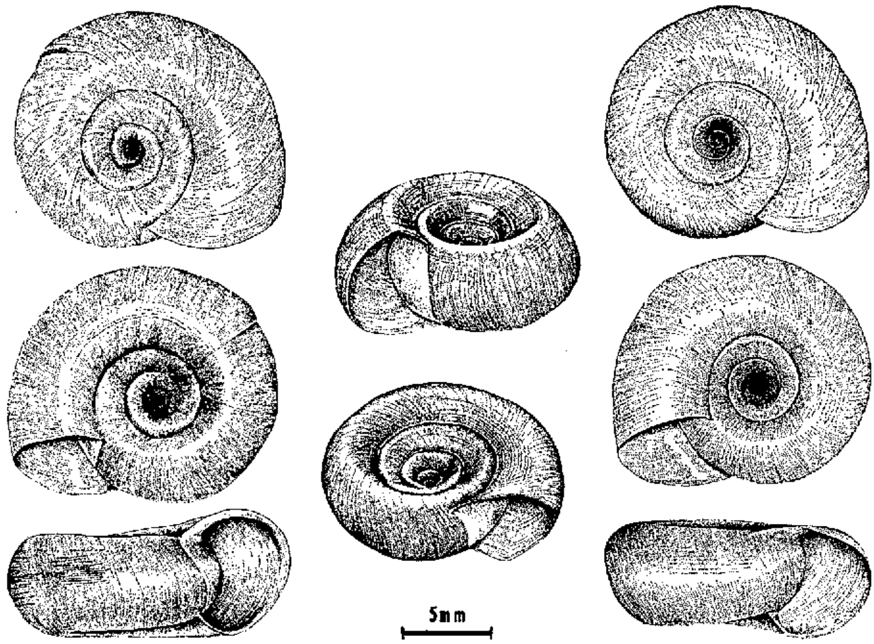


Fig. 57. Shell of *Biomphalaria sericea* (Dunker) (Paratype in British Museum N.H., London)

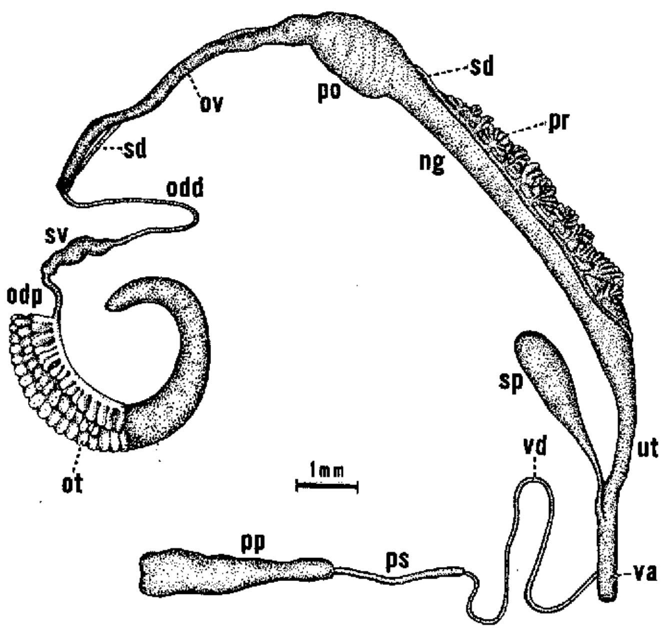


Fig. 58. Reproductive system of *Biomphalaria sericea* (Dunker) from Ecuador. See p. 112 for key to abbreviations.

Geographical Distribution

The species is known with certainty only from Los Ríos and Guayas, Ecuador.

Ecological Features

No data have been recorded.

Genetics

This species can be reproductively isolated from *B. tenagophila* from São Paulo, Brazil, and from *B. glabrata* from Recife, Brazil (Barbosa, Barbosa, and Carneiro, 1963).

Epidemiological Importance

The species can be considered a potential host for a Brazilian strain of *S. mansoni*. Laboratory infection was obtained in 14 out of 40 snail specimens (Barbosa, Barbosa, and Carneiro, 1963).

Nomenclature

For his species *sericea* Dunker gave no locality data. Cousin (1887) carefully described *Planorbis clevei* from Ecuador and subsequently in a handwritten note added that this species was from "Guayaquil, Ecuador. Yaguachi. Mapasinga." Probably Cousin's form is identical with the one here called *B. sericea*. However, since Barbosa, Barbosa, and Carneiro (1963) designated Los Ríos, Ecuador, which is near Guayaquil, as the type locality of *sericea*, this name is tied to the form in question in that area.

Biomphalaria straminea (Dunker, 1848)

The Shell (Fig. 59)

The shell attains a maximum size of about 15 mm in diameter and 2.5 to 3.5 mm in height. The full-grown shell has 4 to 5 whorls, usually increasing slowly.

The whorls are rounded on the right side and rounded or subangulate on the left side. The periphery is smooth. The aperture may be egg-shaped or heart-shaped. In most full-grown specimens of some populations it is bent to the left.

The right side ranges from flat to broadly concave and deeply umbilicate. The left side is more deeply concave than the right.

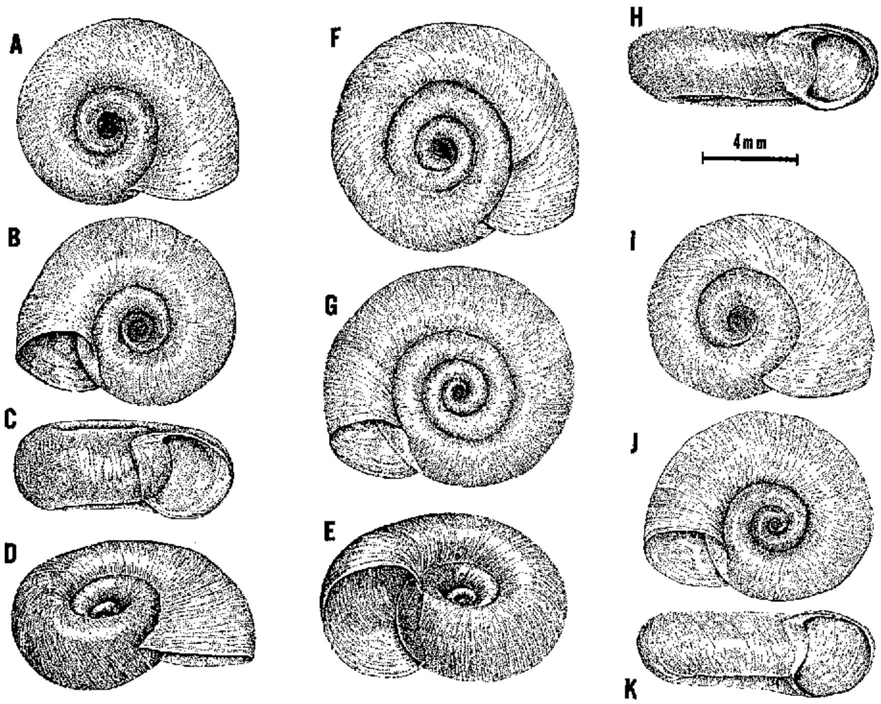


Fig. 59. Shell of *Biomphalaria straminea* (Dunker)
A-E: From Pernambuco, Brazil
F-H: From Georgetown, Guyana
I-K: From Carabobo, Venezuela

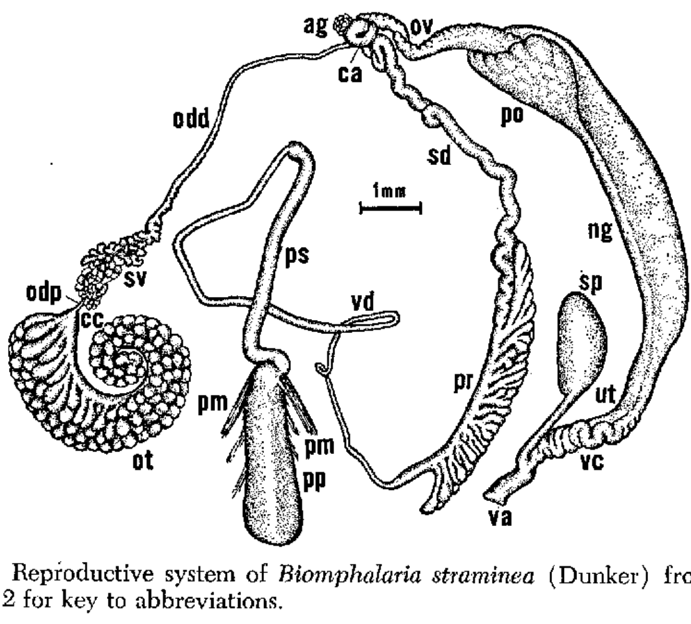


Fig. 60. Reproductive system of *Biomphalaria straminea* (Dunker) from Brazil. See p. 112 for key to abbreviations.

The Soft Parts (Figs. 60 and 46)

The pigmentation of the normally exposed parts ranges from gray to a brownish color. The mantle pigment is distributed in dark patches.

The ovotestis diverticula are predominantly unbranched, though sometimes bifurcate and occasionally trifurcate. The seminal vesicle has conspicuous diverticula. The vagina has transverse folds on the right of the spermatheca, giving the former a corrugate appearance. The spermatheca may be rounded, ovate, pear-shaped, or club-shaped, and it has a slender duct usually as long as the spermathecal sac. The prostate, in most instances, has from 10 to 20 diverticula, mainly branched or arborescent. The center portion of the penis has three muscular layers, the middle one circular and the others longitudinal. (All other species so far recognized have a circular outer layer and a longitudinal inner layer). The penis sac is distinctly narrower than the preputium, and from one to three times as long.

There is no renal ridge.

The lateral radular teeth have dagger-like or triangular cusps.

Geographical Distribution

The species is known from Venezuela, the Guianas, and Brazil, reaching to about 20°S.

Ecological Features

Its usual habitats are standing and slowly flowing fresh waters—marshes, ponds, shallow areas of lakes, irrigation and drainage ditches, dams, and creeks. It is well adapted to habitats that undergo seasonal drought.

Genetics

Hybridization between *B. straminea* from Pernambuco, Brazil, and *B. glabrata* from Pernambuco, *B. peregrina* (called *Tropicorbis philippianus* in the paper) from Ecuador, and *B. chilensis* from Chile, with the production of fertile offspring in some instances, was recorded by Barbosa, Carneiro, and Barbosa (1956); Barbosa, Barbosa, and Carneiro (1958a); and Barbosa (1960). Similar results were obtained by Paraense (unpublished) between *B. straminea* from Pernambuco and *B. intermedia* from São Paulo, Brazil.

Epidemiological Importance

This species is a most important intermediate host of *S. mansoni*, chiefly in northeastern Brazil, where in extensive areas it is the only vector.

Nomenclature

Type locality: "South America" (Dunker, 1848), restricted to Venezuela and Ceará, Brazil, by Martens (1873).

Synonyms are *Planorbis kuhnianus* Dunker, 1883 and *P. centimetralis* Lutz, 1918. It was dealt with under *Taphius peregrinus* (Orbigny) by Hubendick (1961).

Biomphalaria tenagophila (Orbigny, 1835)

The Shell (Fig. 61)

The shell may reach about 35 mm in diameter, but it usually ranges from 15 to 25 mm. The height is widely variable—from 5 to 8 mm in most specimens at 20 mm in diameter. The adult shell has 5 to 7 slowly or sometimes more rapidly increasing whorls.

The whorls are laterally carinate, chiefly on the left. In thinner specimens the carination is attenuated and may even be obliterated on the left side, making them extremely difficult to distinguish from *B. glabrata* by shell characters. The periphery is smooth. The aperture is deltoid in high shells and somewhat egg-shaped in lower ones.

Shell sides vary from somewhat flat to deeply concave.

In addition to fine growth lines, parallel rib-like transverse thickenings may also occur in some specimens. The shell color ranges from yellow to black, depending on the degree of impregnation with environmental material.

The Soft Parts (Figs. 62 and 63)

The pigmentation of the normally exposed parts varies from pale gray to deep black.

The ovotestis diverticula are predominantly trifurcate, but they may be divided into as many as five or more branches or, exceptionally, they may be unbranched. The seminal vesicle has conspicuous diverticula. The vagina has a well-developed pouch to the right of the spermathecal duct. The spermatheca may be rounded, ovate, pear-shaped, or club-shaped, and it has a slender duct usually as long as the body. The prostate, in most instances, has 8 to 30 long, slender diverticula, mainly arborescent. The distal half of the vas deferens is nearly

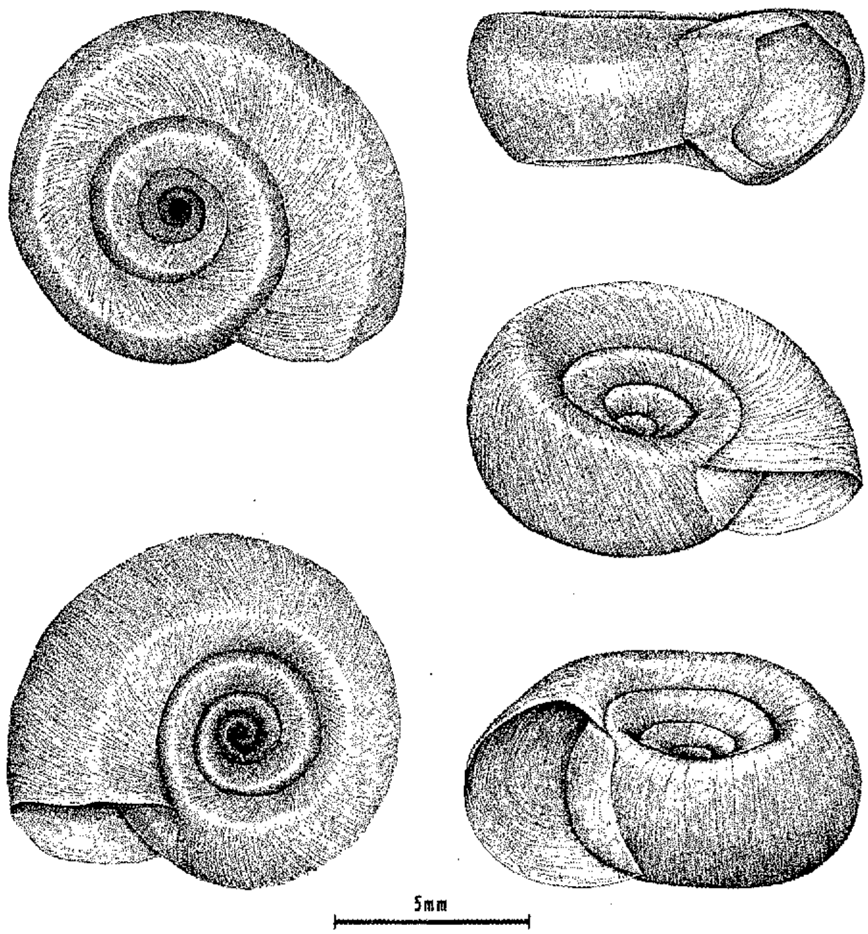


Fig. 61. Shell of *Biomphalaria tenagophila* (Orbigny) from Santa Fe, Argentina

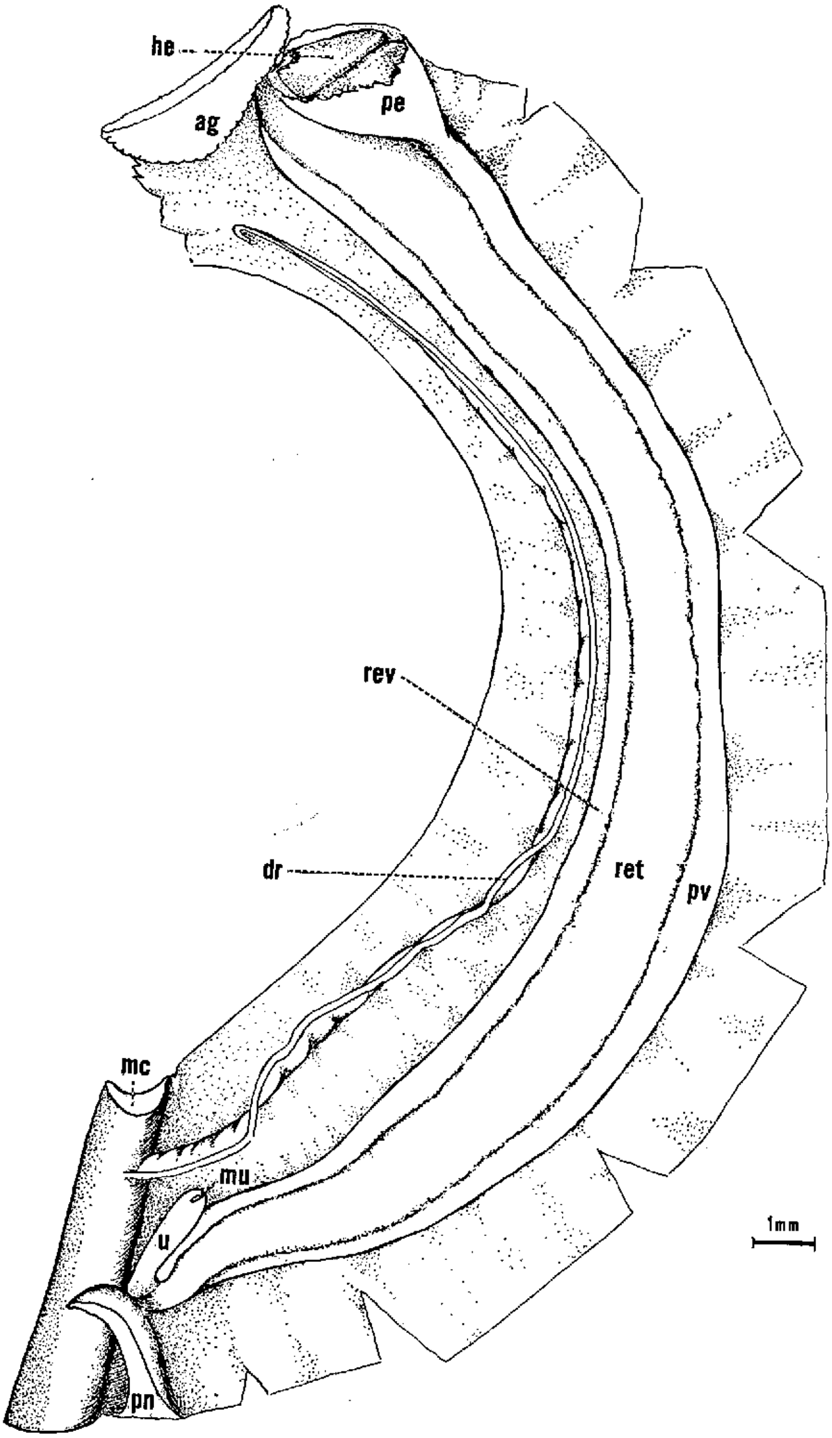


Fig. 62. Ceiling of mantle cavity of *Biomphalaria tenagophila* (Orbigny) from Brazil. See p. 112 for key to abbreviations.

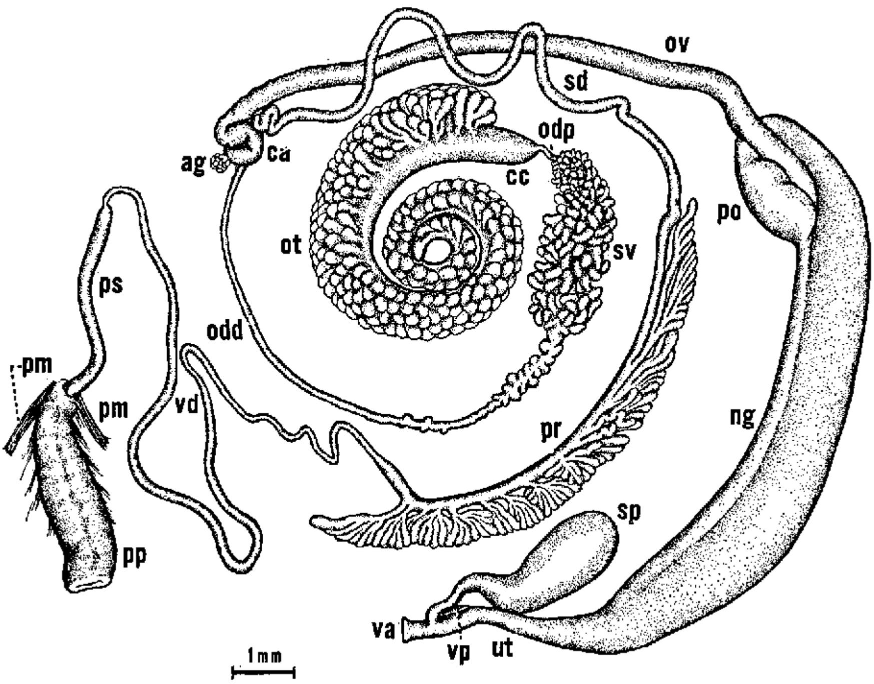


Fig. 63. Reproductive system of *Biomphalaria tenagophila* (Orbigny) from Brazil. See p. 112 for key to abbreviations.

as wide as the penis sac. The penis sac is about as long as the preputium and distinctly narrower.

There is no renal ridge.*

The lateral radular teeth have dagger-like cusps.

Geographical Distribution

The species is found in Argentina, Paraguay, Uruguay, and Brazil from about 15° southward; in Bolivia (Santa Cruz and Chiquitos); and in Peru (Cajamarca).

Ecological Features

Its usual habitats are standing and slowly flowing fresh waters—puddles, marshes, ponds, shallow areas of lakes, irrigation and drainage ditches, pools, dams, quiet waters along banks of brooks, creeks, and small rivers.

Genetics

Hybridization with *B. glabrata* has been recorded by Barbosa (1960).

Epidemiological Importance

This species is an intermediate host of *S. mansoni* in Brazil. It is of increasing importance because it acts as a highly susceptible intermediate host for the strain of that parasite occurring in the Paraíba River Valley in the state of São Paulo. Populations of *B. tenagophila* from areas outside the Paraíba Valley have usually proved to be susceptible to the strain of *S. mansoni* from the Paraíba Valley.

Nomenclature

Type locality: Corrientes, Argentina.

Senior synonym of the following described forms: *Planorbis bahiensis* Dunker, 1856; *pro parte* (specimens from Rio de Janeiro); *P. biangulatus* Sowerby, 1878; *P. immunis* Lutz, 1923 (new name for *P. confusus* Lutz, 1918); *P. paysanduensis* Marshall, 1930; *Australorbis amphiglyptus* Pilsbry, 1951; *A. nigricans* (Lutz) in Paraense and Deslandes (1955a and 1955e) and others.

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* Barbosa (1964), however, recorded in the State of Rio de Janeiro, Brazil, a few specimens of *B. tenagophila* whose renal tube showed a ridge identical with that known to be typical of *B. glabrata*.

Biomphalaria trigyra (Philippi, 1869)

The Shell (Fig. 64)

The shell grows to about 14 mm in diameter and 4.5 mm in width, with about 5½ whorls increasing slowly to moderately in diameter. The whorls are rounded on both sides and separated by a deep suture.

The right side has a deeply sunken central whorl and subsequent whorls describing a narrow funnel-shaped concavity that broadens at the level of the penultimate whorl. In some populations of larger specimens this side is broadly and shallowly concave around the narrow central depression. The left side ranges from broadly and moderately concave to flattened around the more depressed central whorls.

The periphery is rounded and not infrequently shifted to the right. The aperture is roundish to slightly transverse, sometimes a little deflected to the left, frequently oblique to the right. The peristome is thin and continuous.

There are no internal lamellae.

The Soft Parts (Fig. 65)

The pigmentation of the normally exposed parts varies from grayish brown to dark gray. The mantle pigment is distributed in grayish patches, tending to concentrate on the roof and right side of the pulmonary cavity.

There are usually about 100 ovotestis diverticula, arranged in transverse rows of three or four, predominantly unbranched and banana-shaped, though sometimes bifurcate and occasionally trifurcate. The seminal vesicle has conspicuous diverticula. The vagina is unusually short, with a small pouch to the right of the spermathecal duct. The caudal limit of this pouch scarcely extends beyond the level of the insertion of the spermathecal duct. The spermatheca may be club-shaped or egg-shaped, with the spermathecal sac usually tapering into a long duct. In contrast to the other species, in which the spermathecal duct empties directly into the cavity of the vaginal pouch, in this case the duct opens into the distal end of the uterus above the pouch. The prostate usually has from 5 to 10 diverticula, which are widely spaced in the larger specimens. The diverticula split early into primary divisions, which soon give rise to short tertiary and quaternary subdivisions. The foremost and the two or three caudal diverticula send out longer primary branches, and the intermediate ones overlap each other in a net-like arrangement. The distal half of the vas deferens is distinctly narrower than the penis sac. The penis sac is a little longer or up to about twice as long as the preputium and somewhat narrower.

There is no renal ridge.

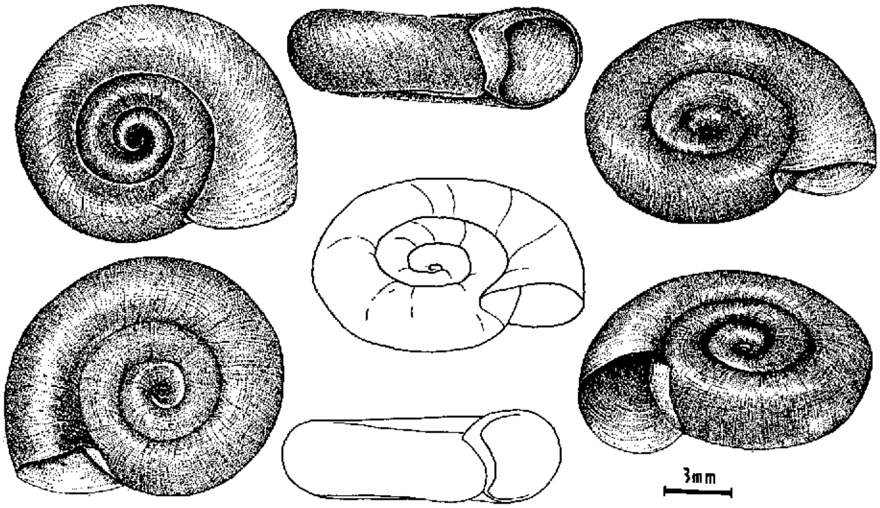

Fig. 64. Shell of *Biomphalaria trigyra* (Philippi) from Santa Lucía, Ecuador

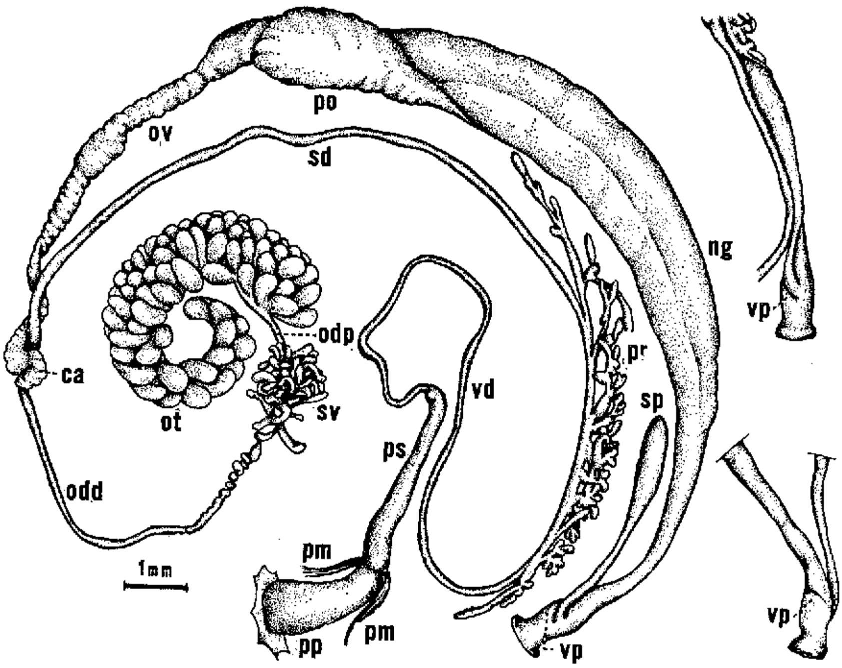

Fig. 65. Reproductive system of *Biomphalaria trigyra* (Philippi) from Santa Lucía, Ecuador. See p. 112 for key to abbreviations.

The lateral radular teeth have dagger-like or triangular cusps.

Geographical Distribution

The species is known in the coastal areas of northern Peru and in the southern half of Ecuador.

Ecological Features

It is found along banks and on the muddy bottom of slowly running brooks and creeks, in rice fields, and in pools and permanent ponds, chiefly among vegetation.

Genetics

No data have been recorded.

Epidemiological Importance

The species is not susceptible to experimental infection with *S. mansoni* (Paraense and Correa, unpublished).

Nomenclature

Type locality: Pimentel, Peru.
No synonyms have been recorded.

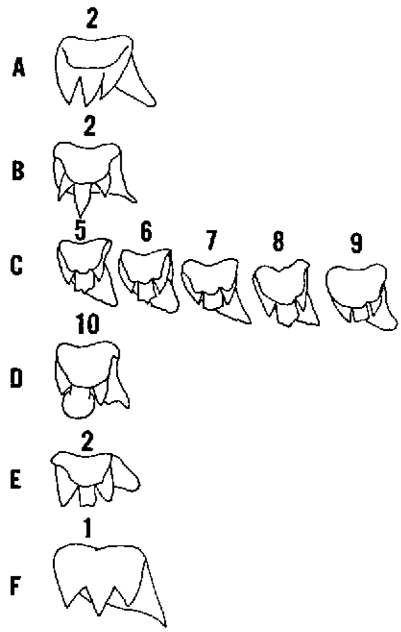

Fig. 66. Lateral teeth from the radula (varying magnifications)
A: *Biomphalaria havanensis* from Cuba
B: *Biomphalaria glabrata* from Brazil
C: *Biomphalaria peregrina* from Uruguay
D: *Biomphalaria peregrina* from Uruguay (abnormal)
E: *Biomphalaria chilensis* from Chile
F: *Biomphalaria schrammi* from Guadeloupe, W.I.
The numbers indicate the longitudinal row counted from the median row.

Appendix I

COLLECTION, PRESERVATION, AND STORAGE OF SNAILS

Equipment

The following equipment should be made available for the collector to take to the field: a number of jars with screen mesh caps in lieu of the ordinary lids, a number of cardboard boxes with perforated tops, specimen bottles, paper labels, a field notebook, hip wading boots, a thermometer, forceps, pH measuring paper or instruments, a scoop net (Fig. 67), insect repellent, and bottles of 70% alcohol.

Molluscan Survey

In endemic areas, all bodies of water should be regarded as possible sites of transmission of schistosomiasis. Thus, it is not advisable to touch the water, the vegetation, or the snails with any part of the body. Wading boots are useful. It is usually inconvenient to wear rubber gloves, because they tear easily and cause perspiration. Long forceps exerting only slight pressure are ideal for collecting the snails from the scoop or directly from the vegetation in the water. It is a good practice to rub the hands and arms with 70% alcohol when collecting, especially if they accidentally get wet. Brisk drying with a cloth is also effective.

An area to be surveyed for its snail fauna should first be mapped. The map should show all hydrographic details, including man-made and natural bodies of water, main and tributary water courses, seepages, side pools, and borrow-pits. The area should be studied periodically to determine the wet and dry seasons, flood periods, and temperature fluctuation. These factors will affect the population density of the snails. Often a habitat that at first does not appear to harbor any snail vectors will prove to contain them on subsequent examination.

The snail collection from each locality must be properly labeled and kept separate. Pencil should be used for labeling, and the label should preferably be placed inside the container with the snails. However, in time the snails may eat the paper and therefore an additional label on the outside is desirable.

The snails should be brought back to the laboratory in moist vegetation rather than in water. They should be kept cool and out of direct

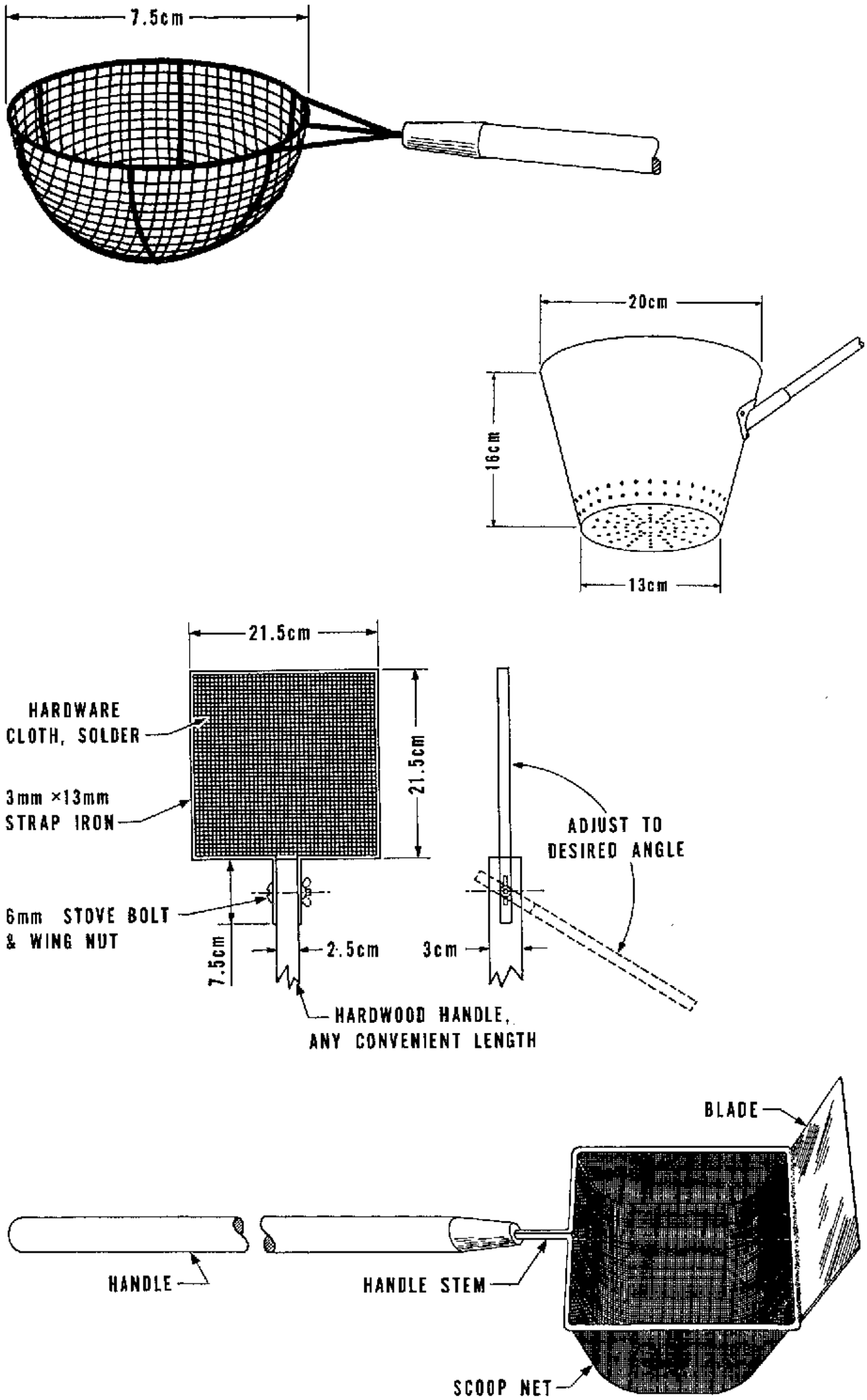

Fig. 67. Four types of dippers for snail collecting

sunlight in any available containers, such as jars, cloth sacks, cardboard boxes, or plastic bags.

In certain studies a qualitative account of the snails occurring in the area is adequate. In others, however, it is necessary to make a quantitative study of the snail population as well. There is no uniform method, applicable to all areas, that can be used for such studies. The nature of the habitat and the objective of the study will determine the sampling method to be selected. The various methods have been thoroughly described by the World Health Organization in its Monograph Series no. 50 (1965).

Field Record Sheet

A number of blank field record sheets should be prepared in advance. These may be printed, mimeographed, typed, or even written in longhand. It is most important that such a record be kept and that the collector have comparable data from each body of water. He should fill in as many of the blanks as possible while at the collecting station, though some parts may be completed in the laboratory. The sheet should include space for the following information:

Date
Collector
Locality
Type of environment
Size of habitat
Kind of substrate
Kind of margin
Character of the water
Aquatic vegetation
Aquatic animals (other than snails)
Shore vegetation
Miscellaneous data
Species of snails

- The **date** should include the day, month, and year. This is very important for determining seasonal variation in the environment.
- The name of the **collector** or collectors visiting the station on that particular date should be given.
- **Locality** should include the name of the body of water, the closest village or town, and the state or other political unit in which the water body is located. This information should be provided in such a way that the collection site can be found on a standard map by

someone who has not visited the area, and it should be as specific as possible.

- Note should be made as to whether the **environment** is a stream (any flowing water, regardless of size—this is technically called a lotic environment) or a lentic body of water (any nonflowing body of water, such as a pond, puddle, or lake, regardless of size). The terms applied to flowing and nonflowing bodies of water by laymen are inexact and mean different things to different people. Note should also be made as to whether the environment is temporary or permanent; whether the level of the water fluctuates greatly or not, and what might cause the fluctuation; and whether the water body is natural or artificial.

- In giving the **size of habitat,** the width, if it is a stream, or the width and length and general shape, if it is a static body of water, should be stated. An estimation of the average depth should also be given, and the surface dimensions may have to be estimated as well. Samples of various bottom materials might be collected for analysis.

- The description of **substrate** should note whether it is mud, sand, gravel, loose stone, or firm bedrock. If several kinds of substrate materials are present, all the major kinds should be listed, with an estimate of their relative amounts.

- Information about the **margin** should indicate whether the shore is regular or indented, whether the water is deep or shallow along the margin, and whether the substrate is bare or has aquatic vegetation covering it.

- In describing the **character of the water,** if it is flowing, note should be made of whether the current is swift or slow; if it is static, of whether the surface is quiet or has waves. Note should also be made of whether the water is turbid (with mud, suspended clay, or algae) or clear. The color is important, too. Brown water is rich in natural organic materials and green water is rich in unicellular plants and algae. Evidence of human pollution should be recorded. Excessive pollution from sewage, abattoir waste, garbage, cone mill effluent, and other sources causes the appearance of special organisms in unusual abundance. These the worker may learn to recognize as indicative of organic pollution.

- If **aquatic vegetation** is present the investigator should state whether it is varied or uniform in nature, how abundant the major kinds of aquatic plants are, and whether they are submerged with floating leaves (water lilies, hyacinths, water lettuce) or emergent (extending well above the surface of the water, such as many species of sedges and various broad-leafed aquatic plants).

- All kinds of **aquatic animals other than snails** should be described, with some indication of their abundance, as in the case of aquatic vegetation. They may be indicated by their common names, but the description should be as specific as possible.
- With regard to **shore vegetation,** the investigator should note whether the margin has grass, shrubs, trees, cacti, or other plants, and to what extent it is shaded during the day.
- **Miscellaneous data** should include any other information of interest not mentioned elsewhere on the sheet, such as evidence of human use (bathing, washing, fishing) or use by domestic animals.
- Information on the **species of snails** may be completed in the laboratory after the proper identification is made. Data should include notes on the abundance of each species, including eggs or juveniles, and, if possible, indication of whether the snails were infected with S. *mansoni* or other species of trematodes.

Preservation of the Soft Parts

Snails preserved for anatomical studies of the soft parts may be prepared in several ways: (1) direct preservation, (2) relaxation followed by fixation and preservation, (3) freezing, (4) fixation and preservation in alcohol-glycerin, and (5) heating.

- Direct preservation

Snails collected for studies on the microstructure of the animal and larval trematodes may be fixed directly in hot Bouin's fluid (picric acid, formalin, and glacial acetic acid), AFA (alcohol, formalin, and acetic acid), or Carnoy's fluid (absolute alcohol, chloroform, and glacial acetic acid).

- Relaxation followed by fixation and preservation

A few crystals of menthol (other anesthetics such as chloretone, nembutal, or chloral hydrate can also be used) are added to the water covering the snails in a small bottle. Two or three drops of a saturated solution of menthol in 95% alcohol may be used instead. The specimens should be kept cool and undisturbed while being narcotized. After several hours (6 to 48, depending on the number and size of the snails and the volume of water used), the snails should be extended. At that time, to be sure the specimens are insensitive to strong stimuli, one or two snails should be carefully tested in the killing fluid before the entire lot is transferred. It is well to leave them in the menthol for an hour after they become insensitive to the stimuli. If they are left too long, however, the tissue will deteriorate, making the specimens useless for micromorphological studies. When the snails are fully relaxed, the water should be replaced with 5% formalin. After a day or so, they can be transferred to 70% alcohol. Each lot of specimens must be accompanied by a label showing the date and locality of collection and the name of the collector.

- Freezing

If a refrigerator is available, this is the best method for extracting the animals from their shells. Living snails are simply immersed in water and placed in the ordinary freezing compartment of the refrigerator for one night. Next morning, when the ice is allowed to melt, almost all the snails should be dead and well extended. They may be gently pulled from the shell with the help of forceps. (Knight, 1953)

Freezing can also be used after relaxation. The snails are left for several hours in water containing menthol crystals. After they become well extended, they are frozen in the manner described above. Next morning, the animals can easily be pulled from their shells. (Barbosa, Carneiro, and Barbosa, 1960)

- Fixation and preservation in alcohol-glycerin

Carneiro has developed an effective method for the fixation and preservation of freshwater snails in alcohol-glycerin (Barbosa, Carneiro, and Barbosa, 1960). The snails, after relaxation in mentholated water, are dropped into a solution of 9 parts 70% alcohol and 1 part glycerin, in which they may remain for an indefinite time. After 24 hours, the animals can be removed from their shells with forceps in the usual way. Large snails required a longer time in the solution. This method is particularly useful when many specimens are to be preserved in a small space.

- Heating

Each specimen is gently held with forceps and immersed in a beaker of water that has been heated to 68° to 70°C. It is very important that the temperature be within the range stated. The snail is held in the water for 30 to 60 seconds, depending on its size. If the immersion is done carefully, the cephalopedal mass will not retract too far inside the shell's aperture and the snail is killed and fixed by the heat. It is then removed from the water, the foot is grasped with fine-pointed forceps, and the animal is pulled gently from the shell. The operator can usually feel the breaking of the connection between the animal and its shell. This is the most critical part of the procedure. With experience and care, the whole animal may be extracted, leaving both the shell and the soft parts in excellent condition.

Storage

The snails should be stored in a tightly capped container so that evaporation does not occur. It is advisable to add a small amount of glycerin (one ml per 10 ml of preserving fluid) to prevent destruction of the material in the event the container should accidentally dry out completely. Screw-capped or snap-capped containers are suitable. The tops should be made of glass, hard rubber, or plastic. Metal tops should be avoided, since they may rust through, particularly if formalin has been used at any stage. All preserved material must be carefully labeled to show the date and locality of collection and the name of the collector. Unlabeled material is worthless from a scientific standpoint. Several vials of preserved soft parts, each one properly labeled and stoppered with cotton, may be placed in an inverted position in a large screw-capped or snap-capped jar and stored. This saves space and requires less care. Collections of soft parts preserved in fluid should be examined frequently to be sure the caps are tightly sealed and to replace any fluid lost by evaporation. Screw-capped containers may be sealed with adhesive tape to help diminish evaporation.

Appendix II

LABORATORY REARING OF SNAILS

General

A wide variety of types and forms of vessels can be used for rearing snails in the laboratory. If glass aquaria are not available, various other containers can be used—for example, enamel-coated or plastic pans or refrigerator vegetable trays. Well washed sand and gravel can be placed on the bottom of the aquarium to support rooted aquatic vegetation. Plants help in two ways: they provide oxygen, and they afford a suitable surface on which beneficial algae accumulate and on which the snails can crawl and deposit their eggs. Plastic film may be used for collecting the eggs.

If floating aquatic vegetation is used, then no sand or gravel is needed. Compressed air can be introduced into the aquaria for aeration and for operation of certain types of filters that can be obtained from aquarium and pet supply stores. The filters contain charcoal and glass wool for filtering the water and can be placed either inside or outside the aquarium.

The snails should only be placed in aquaria in which the water is known to be suitable. Spring, river, or pond water are usually ideal. When tap water is used it should first be dechlorinated by storing it in large bottles for about a week, by passing it through a special dechlorinating apparatus, or by passing it through sand and charcoal. The suitability of aquaria for snails is sometimes improved by allowing them to stand from a few days to several weeks. Overcrowding of the snails should be avoided, and the water must be changed from time to time.

Lettuce, either fresh or boiled, is a good source of food. Powdered dried lettuce is excellent for young snails. Certain dry leaves from trees also provide food, but they should first be soaked for 2 to 10 days to get rid of their acid content. It should be noted, however, that leaves of certain plants are toxic for snails—*Eucalyptus,* for example—and cannot be used. Maple and mango leaves are eaten readily by snails and are not toxic.

Hybridization

Hermaphroditic planorbid snails can both self- and cross-fertilize. Since total albinism (no pigmented eye spots) is a recessive character due to a single genetic factor, it can be used in crossing tests to serve as a genetic marker.

Thriving colonies of albino snails should be well isolated from other snails. Contamination through the use of common equipment should be avoided. Only laboratory-reared snails should be used in hybridization tests, and they should be kept isolated from the time they are very young, i.e. before attaining sexual maturity, to avoid cross-fertilization.

The partners, which should be sexually mature and of approximately the same diameter, are placed together in a small container for at least 15 days. Then the albino specimen is separated from its partner and the egg masses produced during the next 30 days are removed and observed. The presence of pigment in the eyes of the young snails, visible after the fourth day of embryonic development, obviously indicates cross-fertilization. Mendelian segregation of the pigmentation character can be observed in the F_2 generation. These results are obtained when the albino snail acts as the female and the pigmented one as the male.

Artificial Insemination

It is possible to inseminate planorbid snails by introducing the male products of one snail into the female opening of another snail. Since albinism is serving here as a genetic marker, it is recommended that albino specimens be used as females so that the results of the operation can be observed in the first generation. Obviously, pigmented offspring will result from cross-fertilization. Large snails make the operation much easier.

To perform this operation, snails having about half of the last whorl previously cut away are anesthetized by immersion for about 5 hours in water containing menthol crystals. The anesthetized snail is placed under a stereoscopic microscope and held left side up with forceps. The operator, using the microscope, introduces material from the seminal vesicles of a pigmented snail containing active spermatozoa into the female opening of the anesthetized albino specimen. This injection is done after the animal has been gently extended with forceps by a second operator. The mantle collar is pushed back to expose the female opening, and the male extract is introduced by means of a very thin pipette fitted with a rubber bulb. After the operation, the inseminated snail is transferred to clean water for recovery. The success of the operation will depend on proper anesthesia and the skill of the operator.

Appendix III

TECHNIQUES FOR STUDYING MORPHOLOGY

General

Study of the behavior and external characters of living snails is always useful to supplement observations on preserved material. Many of the natural pigments that can be studied in living material are destroyed by preservatives. Also, live material is usually much more pliable. The brittleness of preserved material can frequently be reduced by transferring the snail to glycerine for one or more hours, depending on the size of the specimen.

The use of stains often helps in overcoming the difficulties of working with pigmentless, complex anatomical material, such as parts of the snail body. For live snails neutral red or methylene blue are useful. A small crystal or a few drops of an alcoholic solution may be added to the fluid of the dissecting dish, but it is usually advisable to remove the particular structure to a separate dish for staining.

A careful description and drawings should be made of all parts observed. These notes and drawings should be dated, and the source of the material and a tentative identification of it should be placed on each page. This will help sharpen the investigator's ability to observe significant details. As more material is studied, the worker will continually find new characters that had not been previously noticed or had seemed unimportant.

To examine the snail under a stereoscopic microscope, it should be placed in a small glass dish and covered with water of 0.6% saline, if it is to be examined alive, or 70% alcohol, if it has been preserved. The shell is removed by gently crushing it or by applying heating or freezing techniques. In the case of preserved material, the animal may be gently pulled from the shell if the snail was relaxed before preservation. If the animal is very contracted, the shell may be gently crushed.

The inexperienced worker may find it easier to dissect larger snails in a Petri dish, the bottom of which has been filled with paraffin or beeswax, so that the specimen may be pinned out as dissection proceeds. The most useful tools for snail dissection are fine watchmaker's forceps.

Procedure for Snail Examination and Dissection

The nature and distribution of pigments in the roof of the mantle cavity and the upper visceral complex should be observed first. Effort should be made to identify as many structures as possible through the mantle before proceeding further. Drawings are very helpful at this stage. As dissection proceeds, the investigator should review the anatomical data in Chapter 3 and carefully study any available anatomical literature relevant to the material at hand.

Next the mantle cavity should be opened. This procedure can be facilitated by pinning the foot to the wax in the Petri dish with insect pins. A line is cut with small scissors from the mantle edge to the upper (apical) end of the cavity. The incision should begin at the pneumostome. A lateral incision is made to open the cavity completely. The right and left of the pulmonary cavity roof can then be turned aside and fastened with thin pins to the wax of the dish.

The upper visceral complex is opened by using the scissors to cut through the thin mantle membrane from the upper end of the mantle (or pulmonary) cavity to the apex of the whorls. This may also be done by using insect pins with blunted, hooked ends instead of scissors. The organs of this complex are embedded in each other and need to be carefully separated.

Next the hemocoel below the mantle (pulmonary) cavity is opened by cutting an incision through the floor of the cavity parallel to the cut in the roof. The incision should begin at the upper end of the cavity and continue forward along the body stalk, approximately at the midline, to the front of the head. Lateral cuts in the sides of the cephalopedal mass may be necessary. The flaps may be pinned back to facilitate observation. At this stage it is possible to remove the digestive system, the reproductive system, and the central nervous system intact so that they can be studied in greater detail.

The procedure just described is one of several possible approaches. In Figures 68 and 69 two other ways are indicated. Each worker has to find the one that suits him best. Successful dissection can only be accomplished after considerable practice.

Preparation of the Radula and Jaw

The buccal mass should be dissected out and placed overnight in a 10% solution of NaOH. Hypochlorite bleaches will digest the tissue from the radula and jaw and in an even shorter time. The radula and jaw are then teased apart with dissecting needles and the freed radular ribbon is washed. By means of a fine brush, the ribbon is transferred to a slide in a drop of water of glycerine and flattened out with the teeth directed

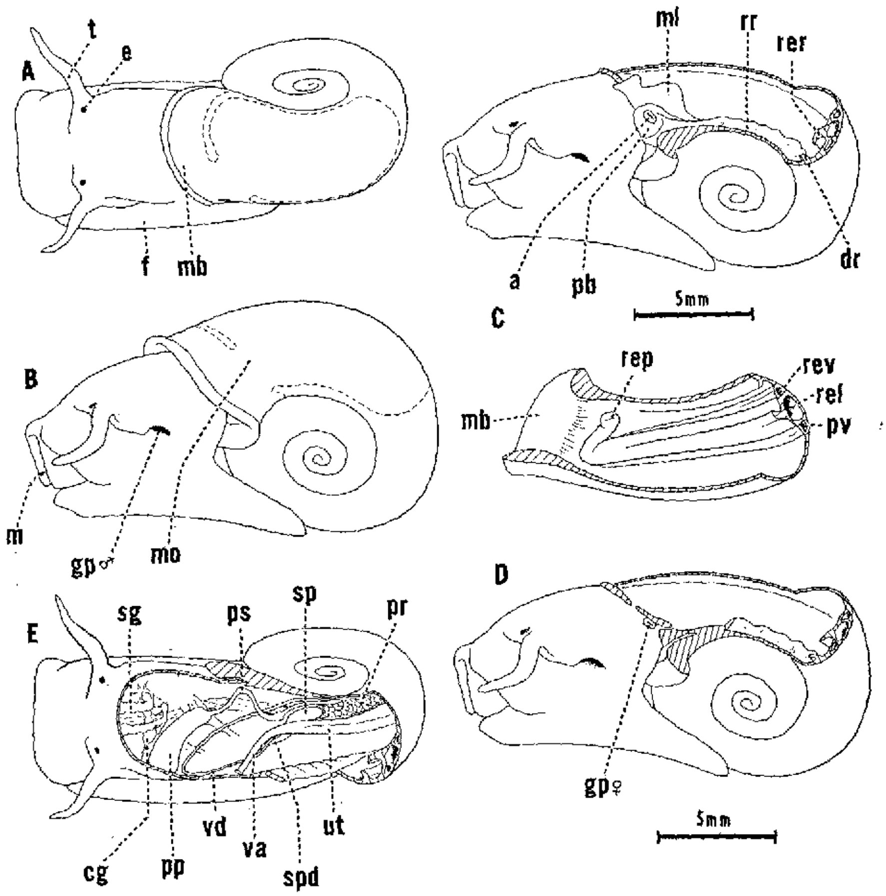

Fig. 68. One way of beginning dissection of a preserved and brittle animal. See p. 112 for key to abbreviations.

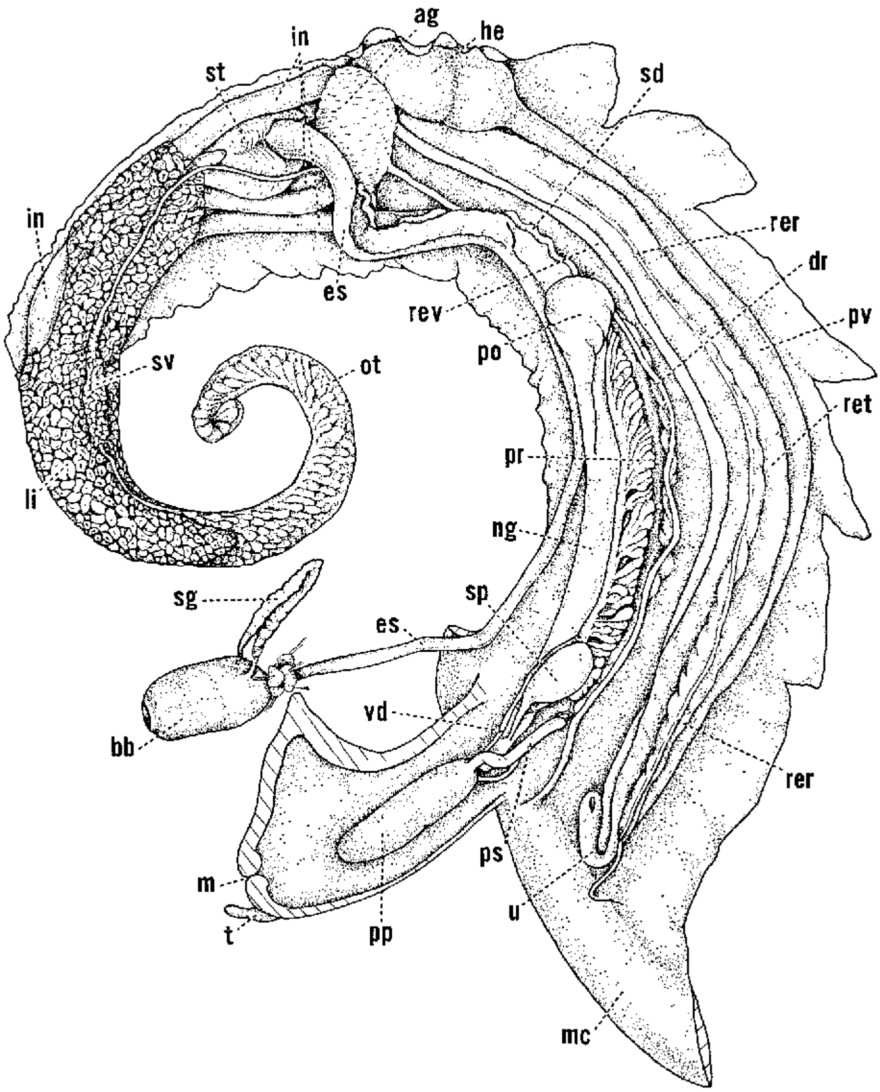

Fig. 69. Fresh material of planorbids can be dissected by simply cutting or tearing apart the various structures from each other. The diagram shows in a simplified way *Biomphalaria glabrata* after such a procedure. See p. 112 for key to abbreviations.

upwards. The ribbon is then rinsed with one or two washings of 70% alcohol and mounted by normal microscopical technique.

It is sometimes advisable to stain the radular ribbon in an aqueous solution of potassium permanganate, orange G, or one of the hematoxylin stains before transferring it to the glycerine drop on the slide.

Appendix IV

INFECTION OF SNAILS IN THE LABORATORY

Stools of infected persons, or feces, liver, and intestines of laboratory animals may be used as sources of miracidia for the experimental infection of snails in the laboratory.

Procedure with Stools

Stools should be chosen from patients who are known to have active infections and are passing a large number of eggs.

The stool is mixed in normal saline solution by means of an applicator stick or a tongue depressor. It is then passed through gauze and left to sediment for about 20 minutes. After this time, the supernatant is decanted and fresh saline is added to the sediment. Leaving the sediment, the supernatant is decanted once more. The eggs of the schistosomes are in the sediment and should hatch and release miracidia upon resuspension of the sediment in fresh water. The actively swimming miracidia can be seen readily under low magnification and can be picked up with a small pipette from shallow dishes. Since the miracidia are positively phototactic, they can be concentrated by placing the egg suspension in a vessel that has been darkened in one section with black paper or paint. If a flask is used, a small part at the top can be left uncovered, or it can be fitted with a small tube at the top or side into which the miracidia can swim and from which they can be taken with a pipette.

In order to expose the snails, 5 or 10 miracidia are placed along with a single snail in small individual dishes or vials. Cruder methods may also be used. For instance, many snails can be exposed in the same dish simply by introducing a large number of miracidia.

Note should be made of the conditions of exposure: temperature, pH of the water, and vigor of the miracidia. Only active miracidia, collected within an hour after hatching, should be used. The optimum temperature for exposing the snails is 27° to 28°C.

After selecting the snails to be exposed, it is advisable to rinse them in clean water before they are brought together with the miracidia so as to get rid of any contaminating particles on the shell and any microorganisms in the water.

Care should be taken to observe whether the snails are infested with *Chaetogaster.* These are small annelid ectoparasites that eat miracidia, and susceptible snails infested with *Chaetogaster* may not become infected.

Procedure with Tissues

When laboratory animals, such as white mice, are used as the source of miracidia, their livers or intestines are washed in saline and either ground in a homogenizer (blender) for 15 seconds to 2 minutes or ground with clean, fine sand and normal saline in a mortar.

The material from the homogenizer or mortar is then washed at least once with saline to separate the eggs from the major part of the debris, allowed to sediment, and then delivered into fresh water in which the eggs should hatch and release their miracidia.

Appendix V

SHIPMENT OF SNAILS

Snails may be shipped to distant places if a few precautions are followed. Since aquatic snails die rather rapidly in the presence of excessive amounts of carbon dioxide, care should be taken to allow plenty of air in the enclosed package for each specimen. They should not be sent in water, but rather in a moist, loosely packed material that will not decompose or become consolidated and suffocate the specimens. Care should also be taken to protect the shipment against excessive cold or heat, since both will kill the snails. Successful shipment has been accomplished by placing healthy specimens in a plastic bag with loosely packed moist material, e.g. twigs, small pieces of sedge, cattail stalks, or the like. The bag containing the specimens is placed in a regular mailing tube, wooden box, or cardboard carton. Shipment should be made as quickly as possible, and instructions to keep the package from becoming exposed to excessive heat or cold and to expedite prompt delivery should be written on the outside of the package.

Snails with fully developed schistosome infection do not withstand stress as well as uninfected snails. Moreover, even if the infected snails survive shipment the parasites may be lost because the snails have been out of water. If infected snails must be shipped, it is best to do so when the infection is 5 to 10 days old, since the early developing stages, unlike the later stages, are not damaged when the snails are kept out of water.

Brazil and most of the European countries have no quarantine regulations governing the importation of snails. The United States, however, does have specific regulations. Snails of possible significance to agriculture are the concern of the Division of Plant Inspection, Agriculture Research Service, U.S. Department of Agriculture, Federal Center Building, Hyattsville, Maryland, whereas snails that may be of significance to public health are the concern of the Foreign Quarantine Section, Communicable Diseases Center, Public Health Service, Atlanta, Georgia. Request should be made to these institutions for permission to import quarantinable material.

GLOSSARY

Animal	The soft parts of the snail. When the snail is actively crawling, a head-foot organ, or cephalopedal mass, extends outside the shell and a visceral mass fills it inside.
Aperture	The opening of the shell through which the animal protrudes and retracts its head-foot complex (Figs. 5 and 6).
Apex	The tip of the shell, or the center of a discoidal shell (Figs. 5 and 6).
Apicad	In the direction of the apex.
Beaded	Having raised tubercles on the surface on the shell.
Buccal Atrium	Interior of the anterior end of the buccal mass. Its anterior surface is the jaw (Fig. 9).
Buccal Mass	A muscular bulb-like structure at the anterior end of the digestive tube containing a radular ribbon. The esophagus begins at the posterior end of this mass (Fig. 9).
Callus	A calcareous deposit, sometimes thick, at the base of the columella near the shell aperture.
Carinate	Keeled or ridged (Figs. 14 and 61).
Carrefour	An outgrowth of the oviduct at the bifurcation of the hermaphroditic duct in pulmonates, believed to be a fertilization sac (Fig. 10).
Caecum	A blind pouch.
Cephalopedal Mass	See Animal.
Columella	The internal axial column formed by the axial portions of the coiled whorl (Fig. 5).
Columellar Muscle	A strong retractor muscle by which the animal is indirectly attached to the shell in one or a few places.

COMMISSURES AND CONNECTIVES	Strands of nerve tissues connecting the nerve ganglia to each other.
CONTAMINATION	Contact with material (eggs and young snails) from other snail colonies.
CORNEOUS	Horn-like, as the operculum of some shells.
COSTATE	With rib-like ridges (Fig. 15A).
CRYSTALLINE STYLE	A gelatinous rod-like structure containing digestive ferments.
DENTATE	Possessing teeth on the parietal wall at the aperture.
DEXTRAL	Shell coiling clockwise so that the aperture is to the right when facing the observer with the apex pointing upwards (Fig. 16).
DIAPAUSE	A rest period (a dormant period), such as is exhibited by sporocysts of S. *mansoni* during drought periods in estivating snails.
ECOLOGY	The science that deals with the mutual relationships between organisms and their environment. These complex interactions bring about the evolution of each community of organisms along with its habitat into a highly organized system, the ecosystem—a superindividual integrated structure which is considered the basic unit of ecology.
EDENTATE	Shell without teeth at its aperture.
FLAGELLUM	A sac-like structure extending from the upper part of male organ (Fig. 26).
GLOBOSE	Spherical.
GONODUCT	The female or the male genital tract leading from the gonad to the genital pore, often differentiated into several specialized parts.
GILL	Everted respiratory organ—in prosobranchs located in the mantle cavity and called the ctenidium, in pulmonates outside the cavity and called a pseudobranch.
HEMOCOEL	The cavity inside the body of a snail. Though not lined with epithelium, it is filled with blood and contains the various organ systems.

Hermaphroditic Duct — In pulmonate snails, the duct arising from the ovotestis that collects both sperm and ova and transports these products to the oviduct and the sperm duct (Fig. 10).

Holotype — One particular specimen used as a basis for describing a new species.

Imperforate — Shell with the umbilicus either closed or entirely absent (Fig. 15B).

Isthmian Hemocoel — The part of the hemocoel extending between the visceral mass and the cephalopedal mass.

Labial Palp — A quadrate fleshy structure on each side of the mouth opening. In the Pilidae it is drawn out to form a filament.

Lamellate — Possessing lamellae (with reference to an aperture).

Liver — A compound tubular gland, also called "digestive gland" or hepatopancreas, opening into the digestive tube at the junction of the pylorus of the stomach and the intestine (Fig. 9).

Malleolate — Having small, ill-defined circular or polygonal depressions on the surface of the shell.

Mantle — The part of the body wall covering the visceral mass (Fig. 8).

Mantle Cavity — The cavity constituted by a fold of the mantle, lined with the epithelium of the body wall. In pulmonates it is divided into an upper pulmonary cavity and a lower hypopeplar cavity.

Mantle Collar — A thick muscular collar—the apical or proximal edge of the mantle at the neck of the snail and the aperture of the shell.

Nuclear Whorls — Initial, generally top, whorls of the spire. This is the embryonic shell, or protoconch, that the snail possesses when it hatches (Fig. 4B).

Operculum — A "trap door" attached to the foot of some snails, which permits the animal to close the aperture when it withdraws inside the shell (Figs. 11, 12A and 15A).

Operculate	Having an operculum.
Oviparous	Producing eggs that hatch after leaving the body of the snail.
Ovoviviparous	Producing eggs that hatch inside the body of the snail.
Palatal	Pertaining to the outer lip of the shell aperture.
Paratype	Any one of several specimens other than the holotype used in describing a new species.
Parietal	Pertaining to the inner wall of the aperture —the part of the body wall opposite the outer lip.
Patelliform	Cap-like, limpet-shaped, as, for example, in members of the Ancylidae (Fig. 20).
Penial Complex	In pulmonates, the terminal portion of the male genital tract, consisting of a penis sac that receives the vas deferens and embraces a penis, a preputium that opens to the outside at the male genital opening, a number of penial muscles attached to the preputium, and sometimes accessory structures (Fig. 10).
Perforate	Shell with the umbilicus open (usually a small opening).
Pneumostome	External opening of the pulmonary, or mantle, cavity.
Preputial Organ	A large, generally glandular, structure inside the preputium of some planorbids that acts as a hold-fast organ to produce leverage during copulation.
Proboscis	The anterior end of the head—in the prosobranchs distinctly separated from the rest of the head-foot organ.
Pseudodextral	Shell seemingly dextral, but anatomy of snail corresponding to sinistral organization (Fig. 3).
Radula	A ribbon-shaped noncellular cuticle on which rows of teeth are arranged (Fig. 9).

Renopericardial Canal	The passage between the pericardial cavity and the distal portion of kidney.
Reproductive Isolation	A condition in which interbreeding between two or more populations is prevented by intrinsic factors. Two populations reproductively isolated will not breed.
Sculpture	Topographic shell surface design (Fig. 14).
Sinistral	Shell coiling counterclockwise so that the aperture lies on the left when facing the observer with the apex pointing upwards (Fig. 18).
Spermatheca	Sac and duct opening into the vagina (Fig. 10).
Spire	The part of the shell between the last whorl and the apex (Fig. 5).
Stylet	A chitinized process at the tip of the penis present in some genera.
Suture	The line of junction between whorls (Figs. 5 and 6).
Taxonomy	The science of identifying, naming, and systematically arranging living organisms.
Turreted	Tower-like (Fig. 15).
Type Locality	The place where the holotype was found.
Umbilicus	An axial space between the whorls opening at the end opposite the spire. If the umbilicus is regarded as an unequivocal morphological concept within the *Gastropoda,* it is located on the right side of the planorbid shell. However, in Planorbidae there is often a functional umbilicus on the left side. In this Guide the term umbilicus is used in either sense (Figs. 5, 21, and 30).

ABBREVIATIONS USED IN THE FIGURES AND KEY

a	anus
ag	albumen gland
ca	carrefour
bb	buccal bulb
cc	collecting canal
cg	brain
dr	dorsolateral ridge
e	eye
es	esophagus
f	foot
fl	flagellum
gp ♂	genital pore male
gp ♀	genital pore female
he	heart
in	intestine
li	liver
m	mouth
mb	mantle border
mc	mantle collar
ml	mantle lobe
mo	mantle opening
mu	meatus of ureter
ng	nidamental gland
odd	distal part of ovisperm duct
odp	proximal part of ovisperm duct
ot	ovotestis
ov	oviduct
p	penis
pb	pseudobranch
pd	processes from oviduct
pc	pericardium
pm	preputial muscle
pn	pneumostome
po	pouch of oviduct
pp	preputium
pr	prostate gland
ps	penis sac
pt	prostate tubule
pv	pulmonary vein
rel	renal lumen
rep	excretory pore
rer	renal ridge
ret	renal tube
rev	renal vessels
rr	rectal ridge
sd	sperm duct
sg	salivary gland
sp	spermathecal sac
spd	spermathecal duct
st	stomach
sv	seminal vesicle
t	tentacle
u	ureter
ut	uterus
va	vagina
vc	vaginal corrugations
vd	vas deferens
vp	vaginal pouch

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