

BIOMPHALARIA OBSTRUCTA (MORELET, 1849): A STUDY OF TOPOTYPIC SPECIMENS (MOLLUSCA: PULMONATA: PLANORBIDAE)

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A description of Biomphalaria obstructa (Morelet, 1849), based on specimens collected at its type locality – Isla del Carmen, state of Campeche, Mexico – is presented.

The shell is small, 13 mm in diameter, 3.5 mm in width and with 5.75 whorls in the largest specimen, thin, moderately lustrous and translucent, horn-colored. Whorls increasing regularly (neither slowly nor rapidly) in diameter, rounded on the periphery and right side, bluntly angular on the left. Suture well-marked, deeper on the left. Right side widely concave, with first whorl deeply situated and partly hidden by the next. Left side shallower than right one, largely flattened, with first whorl plainly visible. Aperture roundly heart-shaped, usually in the same plane as the body whorl but somewhat deflected to the left (less frequently to the right) in some specimens. Peristome sharp, seldom blunt; a distinct callus on the parietal wall. A number of young shells develop one set (seldom more) of apertural lamellae which tend to be resorbed as the shell grows.

Absence of renal ridge. Ovary with about 70 mostly unbranched diverticula. Seminal vesicle beset with well-developed knoblike to fingerlike diverticula. Vaginal pouch more or less developed. Spermatheca club-shaped when empty, egg-shaped when full, and with intermediate forms between those extremes. Spermathecal body usually somewhat longer than the duct. Prostate with 7 to 20 (mean 12.06 ± 2.51) usually short diverticula which give off plumpish branches spreading out in a fan shape and overlapping to some extent their immediate neighbors. Foremost prostatic diverticulum nearly always partially or completely inserted between the spermathecal body and the uterine wall. Penial sheath consistently narrower and shorter than the prepuce. Muscular coat of the penis consisting of an inner longitudinal and an outer circular layers. Ratios between organ lengths: caudal to cephalic parts of female duct = 0.55 to 1.37 (mean 0.85 ± 0.17); cephalic part of female duct to penial complex = 1.36 to 2.81 (mean 1.90 ± 0.33); penial sheath to prepuce = 0.42 to 0.96 (mean 0.67 ± 0.13).

Comparison with Morelet's type specimens of Planorbis orbiculus and P. retusus points to the identity of those nominal species with B. obstructa.

Key words: Mollusca – Planorbidae – *Biomphalaria obstructa* – *Planorbis orbiculus* – *Planorbis retusus* – Mexico – Taxonomy

Among the planorbids described by Morelet (1849) from Cuba, Belize and Mexico, three proceeded from Isla del Carmen, Mexico: *Planorbis orbiculus*, *P. retusus* and *P. obstructus*. Their descriptions read as follows (Morelet, 1849, p. 17, no figures):

37. *P. orbiculus*. – T. discoidea, planulata, fragilis, superne vel subtus paululum excavata, pallide fulva; anfr. 6, ultimo obtuse angulato; apertura obliqua, semilunaris; peristoma simplex, marginibus callo conspi-

cuo junctis. – Diam. 10. Altit. 3. – H. insulam Carmen et pagum Palizada Yucatecorum.

38. *P. retusus*. – T. orbicularis, superne irregulariter planulata, subtus plus minusve excavata; sub lente tenuissime decussata, pallide fulva; anfr. 4 plano-convexi; apertura oblique lunaris, marginibus subapproximatis, peristoma subincrassatum. – Diam. 7. Altit. $2\frac{1}{2}$. H. insulam Carmen.

39. *P. obstructus*. – T. discoidea, solidiuscula, superne planulata, perforata; subtus parum excavata, hyalina, albido-fulva; anfr. 4 semiteretes, ultimo ad peripheriam obtuse

angulato; apertura obliqua, obrotunda, intus lamellis 4 in ventre anfractus ultimi et dentibus duabus in pariete aperturali oppositis, una punctiforme, altera obliqua, compressa, profunde constricta; peristoma intus callo albicante marginatum. — Diam. 8. Altit. 2½. H. insulam Carmen.

Material for the study of these nominal species was gathered during three visits to Isla del Carmen. On November 26, 1956, I collected about 100 specimens from a drainage ditch related to a swampy area at the Tecolutla district of Ciudad del Carmen (Collection no. 247). A small number of specimens were dissected, but the remaining material dried up after accidental cracking of its container. Another collection was attempted on June 6, 1967 (Coll. no. 1628), but owing to prolonged drought only empty shells were found. Finally, on August 25, 1982, it was possible to collect about 700 specimens from marshes at Pirixal (Coll. no. 2763), Santa Rita (Coll. no. 2767) and the Airport (Coll. no. 2768); 120 of them were preserved for morphological study, and the remaining ones were brought alive to the laboratory in Rio de Janeiro, where they initiated a colony that is being kept until now.

MATERIALS AND METHODS

This study is based on the examination of the shells of all the collected snails, and of the soft parts of 100 specimens from Pirixal, 10 from Santa Rita, and 10 from the Airport.

The specimens to be dissected were allowed to relax overnight in aqueous solution of nembutal (0.05%). Then they were immersed for 40 sec in water heated at 70 °C, from which they were transferred to water at room temperature. The animals (under water) were drawn from the shell with a small forceps applied to the cephalopodal mass, and fixed in slightly modified Railliet-Henry's fluid (distilled water 930 ml, sodium chloride 6 g, formalin 50 ml, glacial acetic acid 20 ml).

In some specimens the body does not yield to traction; in such cases, to avoid rupture, the whole specimen (animal within the shell) is placed in the fixative.

Two specimens were embedded in paraffin, sectioned serially and stained with hematoxylin-eosin for microanatomic observation. The

radulae were separated from the buccal mass by digestion in a vial with 10% NaOH left overnight in the incubator at 56 °C. They were then rinsed in tap water and mounted in a drop of glycerin on a microscopic slide, with the dorsal (toothed) surface upwards as in the living animal. Measurements were made on camera lucida drawings.

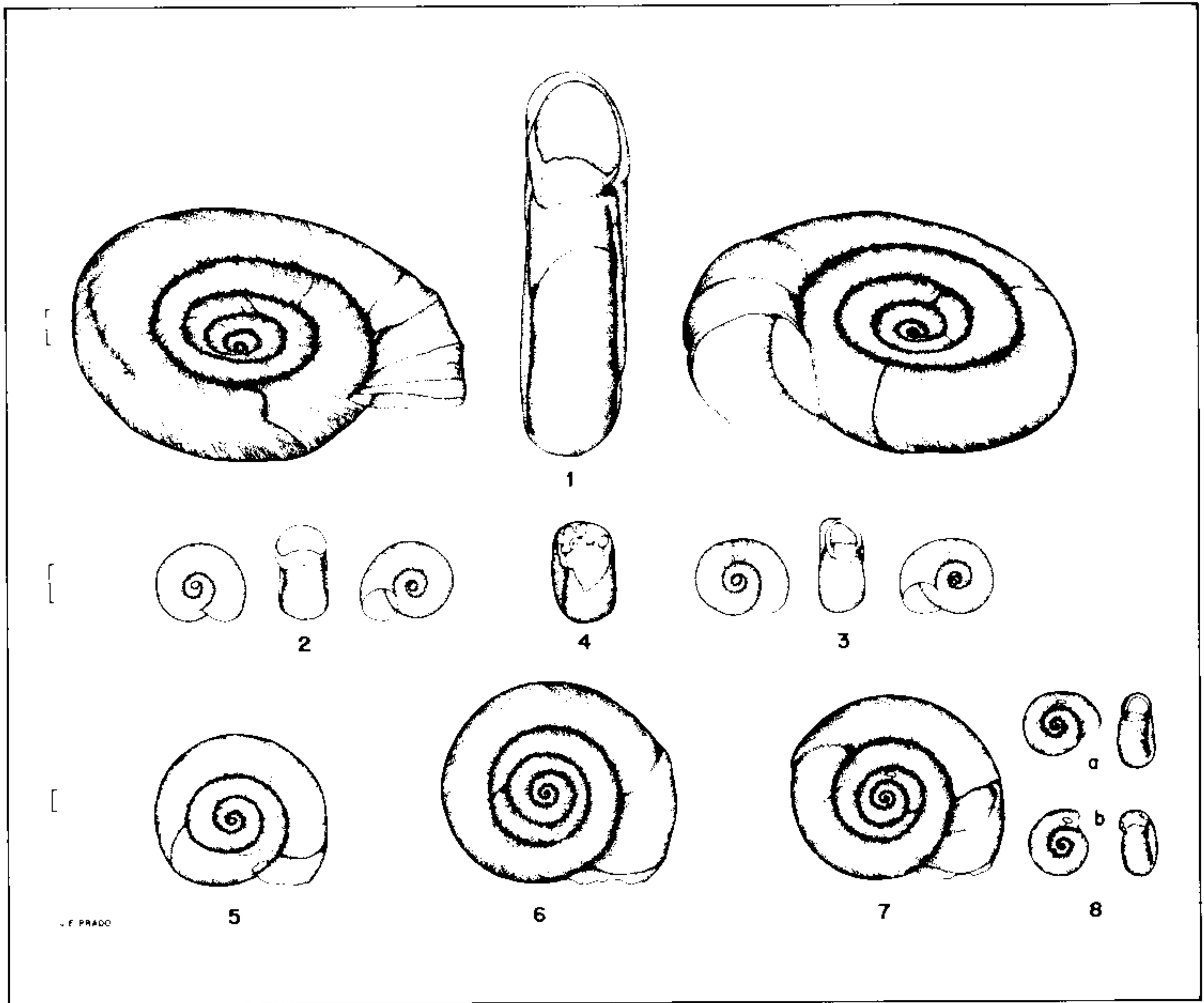
RESULTS

Shell — The shell is small, 13 mm in diameter, 3.5 mm in width at the aperture (2.5 mm at the beginning of the outer whorl) and with 5.75 whorls in the largest specimen (from Pirixal), thin, moderately lustrous and translucent, horn-colored. The whorls increase regularly (neither slowly nor rapidly) in diameter, are rounded on the periphery and right side, bluntly angular on the left. Surface with fine growth lines and almost imperceptible spiral lines. Suture well-marked, deeper on the left side. Right side widely concave, with the first whorl deeply situated and partly hidden by the next. Left side shallower than the right one, largely flattened, with the first whorl plainly visible. Aperture roundly heart-shaped, usually in the same plane as the body whorl but somewhat deflected to the left (less frequently to the right) in some specimens. Peristome sharp, seldom blunt; a distinct callus on the parietal wall. Fig. 1 shows a shell from Pirixal.

Most shells from Pirixal and Santa Rita, and a few from Tecolutla and the Airport, are extensively pitted by erosion of the periostracum; in many specimens coalescence of the pits leave wide areas of the outer calcareous layer unprotected.

A number of shells from each sample show a set of six apertural lamellae, as described by Morelet (1849) for *P. obstructus* (see above). Lamellae are present in 20 of the 98 shells from Tecolutla.

A single shell from Pirixal, 4 mm in diameter, had a well-developed set of lamellae in the apertural region. Owing to opacity of the shells caused by erosion, deeply situated lamellae could not be seen in the specimens from Pirixal and Santa Rita. Dissection of 99 shells from Pirixal, 6 to 13 mm in diameter, revealed the presence of lamellae, most of which undergoing resorption, in the inner whorls of 7 specimens; 2 of them had two sets and 1 had



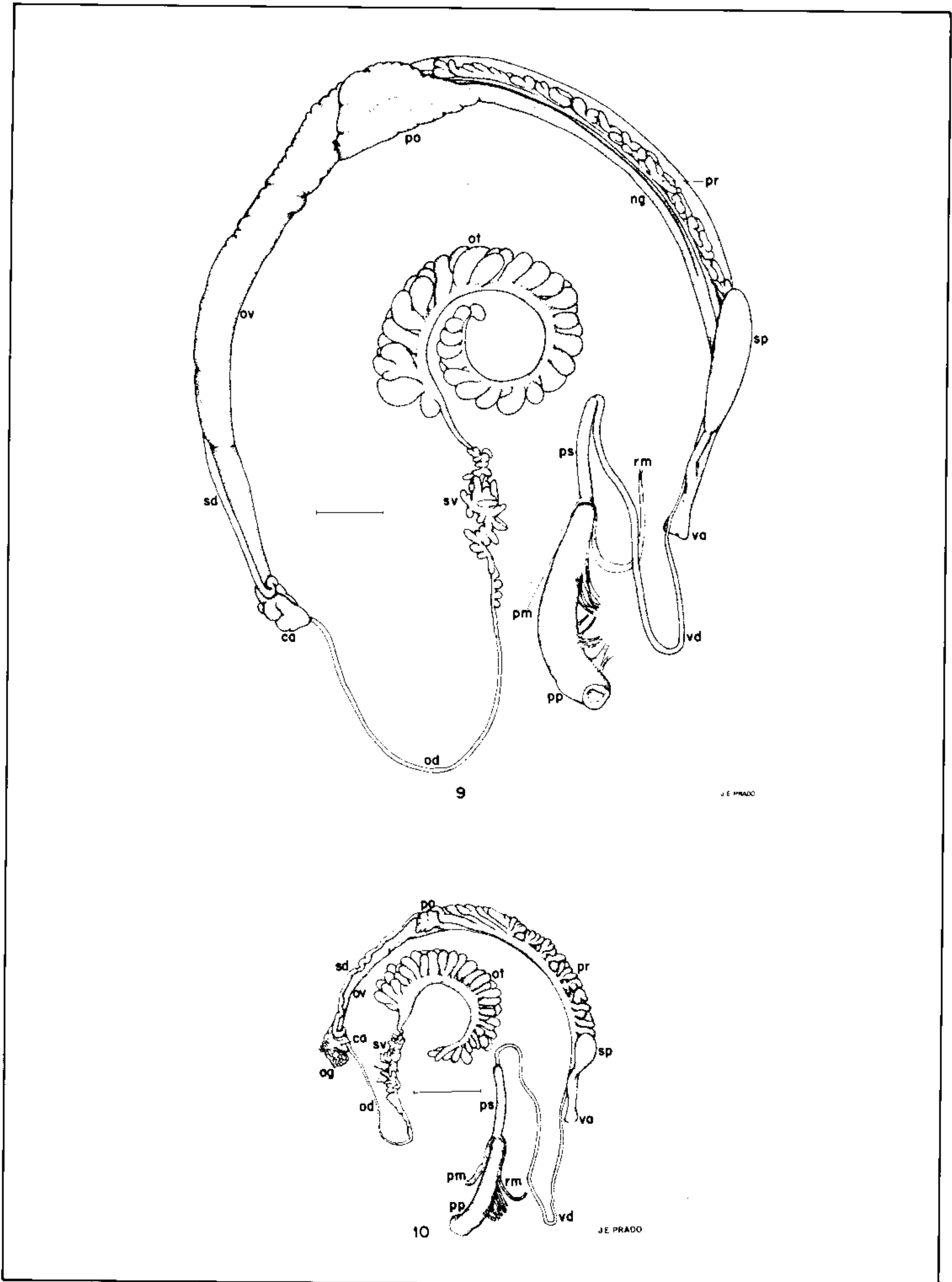
Biomphalaria obstructa from Isla del Carmen, Mexico – Fig. 1: adult shell. Fig. 2: young non-lamellate shell. Fig. 3: young lamellate shell. Fig. 4: young lamellate shell; fore portion of apertural region removed to show lamellae. Figs 5-7: shells with persisting lamellae formed in inner whorls at an earlier growth stage. Fig. 8: central portion of specimen shown in Fig. 7, corresponding to its growth stage upon lamellae formation (a), and after removal of fore portion of former apertural region to show partially resorbed lamellae (b). Bar = 1 mm.

three sets of lamellae. Thus 8% of the Pirixal sample were lamellate.

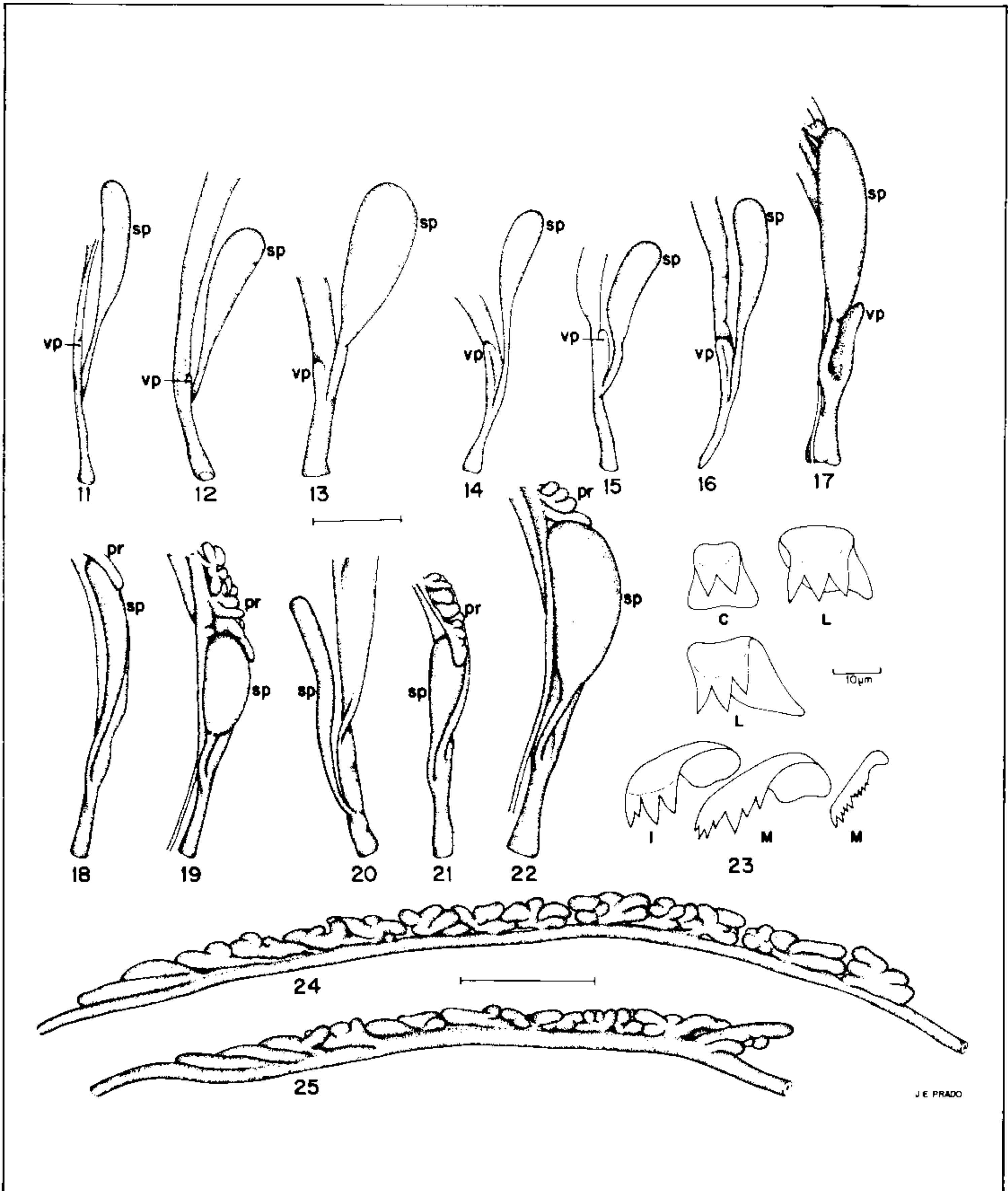
Up to about 3 mm in diameter the non-lamellate shell looks like the one shown in Fig. 2: its whorls increase regularly in breadth in geometric progression, thus describing an equiangular (logarithmic) spiral, and its aperture points forward. In a lamellate shell of the same size (Fig. 3) the inner whorls increase regularly, but the outer whorl gets narrower at the level of the lamellae, beyond which it resumes normal growth and deflects more or less markedly to the left. At this lamellate stage most specimens cease to grow; the sharp peristome becomes blunt and thick, so that when growth is resumed the shell aperture at the time of rest is indicated by a ridge or varix (growth ring).

With continuing growth, the lamellae are left at a more and more backward situation, as shown in Figs 5 to 7. Although the lamellae may persist in some adult specimens, they usually are gradually resorbed as the shell grows forward. Fig. 4 shows a set of newly formed lamellae in a young specimen, to be compared with Fig. 8, which shows a partially resorbed old set deeply situated in the specimen of Fig. 7 and disclosed by cutting out the shell portion in front of it.

Besides the growth rings associated with lamellae formation, a large number of shells had one or more ridges (Figs 1, 5, 6 and 7), corresponding in all probability to successive growth stops imposed by adverse climatic conditions such as periodic environmental drought.



Biomphalaria obstructa from Isla del Carmen, Mexico – Fig. 9: reproductive system; adult specimen, 11 mm diameter. ca = carrefour, ng = nidamental gland, od = distal segment of ovispermiduct, of = ovotestis, ov = oviduct, pm = protractor muscle of penial complex, po = pouch of oviduct, pp = prepuce, pr = prostate, ps = penial sheath, rm = retractor muscle of penial complex, sd = spermiduct, sp = spermatheca, sv = seminal vesicle, va = vagina, vd = vas deferens. Fig. 10: reproductive system; young specimen, 5 mm diameter. ag = fragment of albumen gland. Other abbreviations as in Fig. 9. Bar = 1 mm.



Biomphalaria obstructa from Isla del Carmen, Mexico – Figs 11-22: vaginal complex, showing variation in shape of spermatheca (sp) and of vaginal pouch (vp), and in position of foremost prostatic diverticula in relation to spermathecal body. Fig. 23: radular teeth. C = central, I = intermediate, L = lateral, M = marginal. Figs 24, 25: prostates. Bar = 1 mm (except Fig. 23).

Reproductive system – The following description of the reproductive system (Figs 9, 10) is based on 100 dissected specimens from Pirixal.

The ovotestis is composed of about 70 diverticula, most of which are unbranched.

A minutely dissected ovotestis had 63 diverticula, of which 45 were simple, 13 bifurcate, 4 trifurcate and 1 quadrifid. In another specimen with 75 diverticula, 48 were simple, 18 bifurcate, 7 trifurcate and 2 quadrifid. The ovispermiduct and the seminal vesicle show no special features; the latter is beset with well-developed

diverticula varying in shape from knoblike to fingerlike.

The oviduct, the pouch of the oviduct and the nidamental gland have no special characteristics. The ventral wall of the vagina (in contact with the columellar muscle) shows a more or less developed swelling, the vaginal pouch, sometimes little perceptible (Figs 11, 12); in this case it is made better visible by removing the covering membrane and connecting fibers which may disguise the underlying surface. The vaginal pouch is in contact with the spermathecal duct, which sometimes leaves its imprint on it (Figs 14, 16). The lower portion of the vagina (from the spermathecal opening to the vaginal outlet) frequently increases in width distally. The shape of the spermatheca varies with the amount of its contents. In the empty state it is club-shaped (Fig. 20), when filled it becomes approximately egg-shaped (Figs 19, 22), and between those extremes it shows all intermediate forms. The spermathecal body is usually somewhat longer than the duct, but in the empty or half-filled spermatheca the body frequently tapers into the duct so as to render the boundary between them imperceptible (Figs 18, 20). The caudal part of the female duct (from the carrefour to the middle of the pouch of the oviduct) is about as long as the cephalic part (from the middle of the pouch of the oviduct to the vaginal opening); the ratio between their lengths (caudal: cephalic) varies from 0.55 to 1.37 (mean 0.85 ± 0.17). The ratio between the lengths of the cephalic part and of the penial complex (penial sheath plus prepuce) varies from 1.36 to 2.81 (mean 1.90 ± 0.33).

The spermiduct runs parallel to the oviduct, and after traversing the dorsal groove of the pouch of the oviduct gives rise to the prostate, with a row of 7 to 20 (mean 12.06 ± 2.51) diverticula. The hindmost prostatic diverticulum is usually long and unbranched (Fig. 25), less frequently bifurcate (Fig. 24) or subdivided. The intermediate diverticula are shorter and give off small branches which spread out in a fan shape, each diverticulum overlapping to some extent its immediate neighbors. The foremost diverticulum varies in shape from knoblike (Fig. 19) to fingerlike (Figs 22, 25) or more or less branched (Figs 21, 24); it is nearly always inserted, partially (Fig. 22) or completely, between the spermathecal body

and the uterine wall. In some specimens the foremost diverticulum surrounds the periphery of the spermathecal body, and less frequently it overlaps the top of the latter (Fig. 21). The vas deferens, as usual with the Planorbidae, has a narrower descending and a wider ascending loop, the latter about half as wide as the penial sheath. The penial sheath, uniformly cylindrical in shape, is consistently narrower and shorter than the prepuce. The ratio between the lengths of the penial sheath and the prepuce varies from 0.42 to 0.96 (mean 0.67 ± 0.13). The penis, about as long as the penial sheath, tapers to a point where is the outlet of the penial canal. Histologically it shows a well-developed erectile tissue surrounding the penial canal and enveloped by a double muscular coat, of which the inner layer is longitudinal and the outer one circular, the whole invested by the outer epithelium. As in other *Biomphalaria* species, there are two main extrinsic muscles inserted into the cephalic end of the penial sheath, at its junction with the prepuce: a retractor arising from the columellar muscle and a protractor connected with the head wall. A variable number of smaller retractor and protractor muscles are attached to the preputial wall.

The above description of the reproductive system applies equally to lamellate and non-lamellate specimens. Fig. 10 shows the reproductive system of a lamellate specimen 5 mm in shell diameter.

Jaw and radula — The jaw and the radula do not differ from those of other biomphalarias. Five specimens from Pirixal, 10 mm in shell diameter, showed the following radular averages: formula 22-1-22; 118 horizontal rows of teeth; 8 laterals, 4 intermediates and 10 marginals (Fig. 23).

The specimens from Santa Rita and the Airport, as well as 8 specimens from Tecolutla examined before accidental drying up, did not differ in anatomic characters from those from Pirixal.

MORELET'S SPECIMENS

In May 1970 I examined the types of *Planorbis orbiculus*, *P. retusus* and *P. obstructus* at the British Museum (Natural History), represented by three shells of each nominal species.

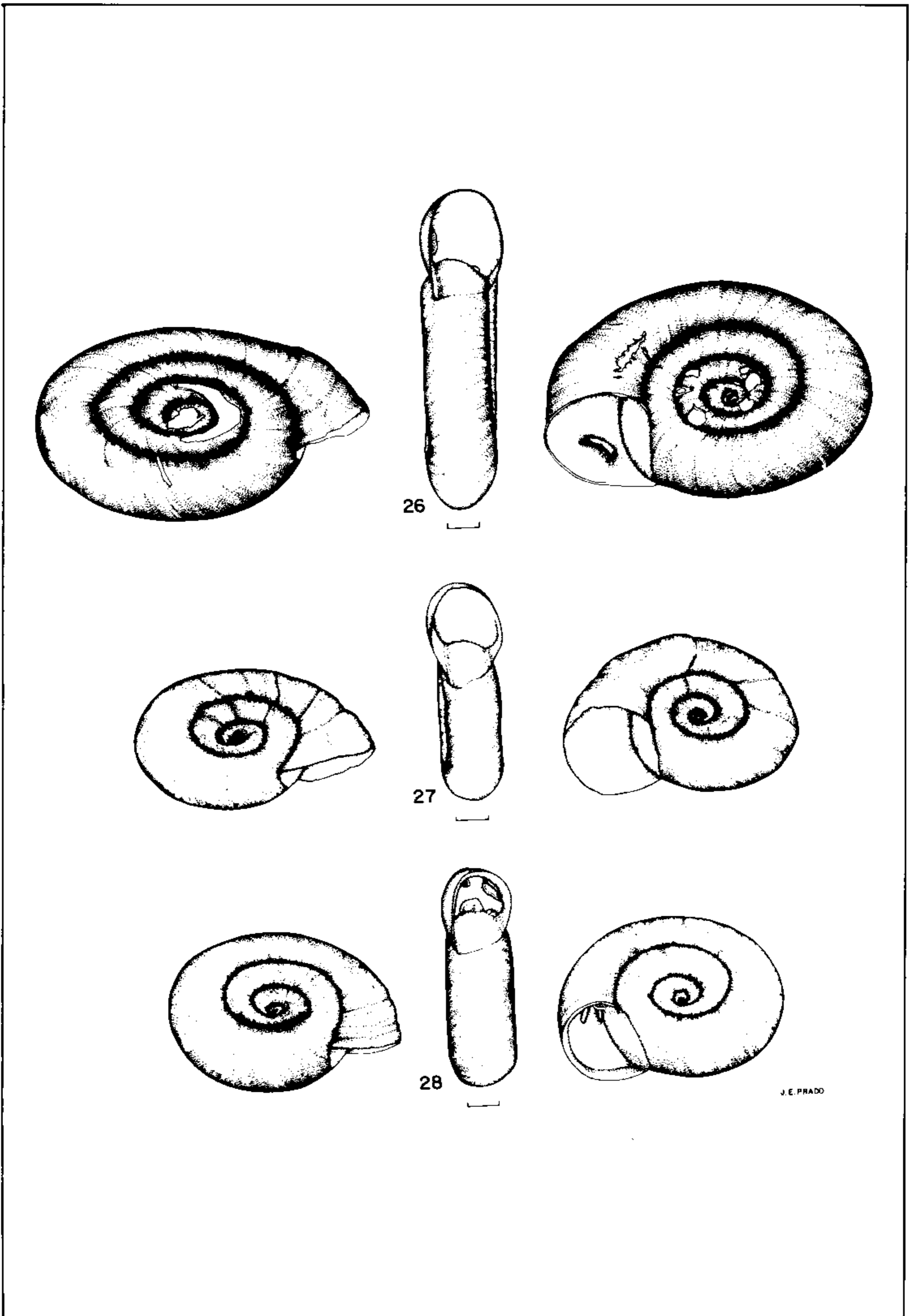


Fig. 26: type specimen of *Planorbis orbiculus* Morelet. Fig. 27: type specimen of *Planorbis retusus* Morelet. Fig. 28: type specimen of *Planorbis obstructus* Morelet. Bar = 1 mm.

The specimen of *P. orbiculus* shown in Fig. 26 has a slightly leftward deflected aperture, inside of which there are two concretions resembling partially resorbed lamellae. It seems, however, that they are no true lamellae, for the palatal one stands obliquely, not parallel to the whorl axis as usual; pseudolamellae like those were described in *Biomphalaria schrammi* (= *Australorbis janeirensis*, junior synonym) by Paraense & Deslandes (1956). Morelet's description of *P. orbiculus* certainly refers to one of the other two specimens, since no mention is made of the pseudolamellae.

The specimen of *P. retusus* shown in Fig. 27 should be the one described by Morelet, since it has 7 mm × 2.5 mm and 4 whorls. However, no mention is made of several growth rings and the apertural dilatation in front of the foremost ring. The other two shells are smaller, 6.5 mm in diameter, and also have growth rings.

Of the three shells of *P. obstructus*, the largest is depicted in Fig. 28.

P. orbiculus (Fig. 26) represents a full-grown form, and *P. retusus* (Fig. 27) and *P. obstructus* (Fig. 28) correspond to non-lamellate and lamellate mid-grown forms of a single species. The proportional narrowness of *P. orbiculus* is comparable to that of our specimen of Fig. 1; it results from the fact that in a given planispiral-shelled specimen the ratio diameter: width increases as the shell grows.

Among our specimens from Isla del Carmen there are individuals agreeing in shell characteristics to one or other of Morelet's nominal species. Lamellate and non-lamellate specimens are anatomically alike, and lamellate specimens appear in the progeny of both lamellate and non-lamellate ones, as in the following examples:

1. Of 100 F₁s from 4 non-lamellate specimens, 2 died early, 60 were non-lamellate and 38 developed lamellae;
2. Of 382 F₁s from 4 lamellate specimens, 4 died early, 321 were non-lamellate and 57 developed lamellae.

As the species name *obstructus* has been more widely used by subsequent authors than *orbiculus* and *retusus*, the samples studied in this paper are treated as *Biomphalaria obstructa*.

REMARKS

The present description of topotypic *B. obstructa* is intended for subsequent comparison with other nominal species considered or not as synonymous by the authors, and as a basis for subsequent observations on its geographic range. A review of the literature shows that this species has been referred to by numerous authors, identified nearly always by exclusively shell characters, which alone are insufficient to separate it from several other species of Neotropical planorbids. The papers by Malek (1969) and Naranjo-García (1983) are exceptions to that rule.

Among the anatomic characters considered in the above description, the ratio between the lengths of the penial sheath and the prepuce (ps:pp) deserves particular mention. It was consistently below 1, indicating that in all specimens the penial sheath was shorter than the prepuce. In specimens killed without previous narcotization the strongly muscular prepuce usually shows some degree of contraction with a resulting increase of the mean ps:pp ratio. Thus a perfect relaxation is essential for a full performance of that character, as well as of other length measurements.

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