

**BIOMPHALARIA PRONA (GASTROPODA: PLANORBIDAE):
A MORPHOLOGICAL AND BIOCHEMICAL STUDY**

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Two samples of Biomphalaria prona (Martens, 1873) from Lake Valencia (type locality) and seven from other Venezuelan localities were studied morphologically (shell and reproductive system) and biochemically (allozyme electrophoresis). In spite of marked differences in shell characters, all of them proved indistinguishable under the anatomic and biochemical criteria.

So far B. prona has been considered an endemic species, restricted to Lake Valencia. It is now demonstrated that the extralacustrine populations referred to Biomphalaria havanensis (Pfeiffer, 1839) by several authors correspond in shell characters to an extreme variant of B. prona from the Lake and really belong to the last-mentioned species. They may be regarded as the result of a process of directional selection favoring a shell phenotype other than those making up the modal class in the Lake.

Key words: Gastropoda Planorbidae – *Biomphalaria prona* – *Biomphalaria havanensis* – morphology – allozymes – Venezuela

This species was described by Martens (1873: 198-199, Pl. 2, Fig. 5) as *Planorbis pronus*:

Testa subinflata, solidula, striata, lineis spiralibus impressis nonnullis exarata, supra profunde umbilicata, infra mediocriter excavata; anfr. 3 1/2, rapide crescentes, rotundati, sutura profunda discreti, ultimo infra inflatus, ad excavationem basalem subangulatus, *prope aperturam valde descendens*; apertura diagonalis, subtriangularis, margine supero subhorizontali, leviter arcuato, margine infero stricto, recedente, columellari perpendiculari, subdilato; paries aperturalis callo albido tectus. Diam. maj. 10, min. 8, alt. 5, apert. alt. obliq. 5 1/2, diam. 4 Millim.

Valenciasee, zahlreich, früher von Otto, jetzt von Ernst dem Berliner Museum eingesandt,

leider nur in mehr oder weniger verbleichten Exemplaren. Wahrscheinlich auch schon von Appun gesammelt, da dieser S. 553 eines *Planorbis* erwähnt, den er nur in diesem See gefunden habe.

Owing to shell similarity with *Planorbis andecolus* Orbigny, 1835, for which Adams & Adams (1885) had erected the subgenus *Taphius*, Martens (1899), Germain (1921) and H. B. Baker (1930) placed it under that subgenus. On raising *Taphius* to generic rank, F. C. Baker (1945) listed *pronus* under it, and remarked: "The systematic position of the genus *Taphius* is greatly in doubt because its anatomy is unknown".

Examining *Planorbis andecolus*, Hubendick (1955a, b) found no anatomical support for separating *Taphius* from the South American genera *Australorbis* and *Tropicorbis*, and from the African *Biomphalaria* and *Afroplanorbis*. Paraense & Deslandes (1957) and Paraense (1958), dissecting topotypic specimens from

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Isla del Sol (Titicaca Island), in Lake Titicaca, agreed with Hubendick's conclusion.

H. B. Baker (1930) and Pilsbry (1934), on conchological grounds, referred *pronus* to the genus *Helisoma*. However, anatomical observation of specimens from Lake Valencia (type locality) by Paraense & Deslandes (1958b) showed that they conformed to *Taphius* and not to *Helisoma*.

Through Opinion 735, the International Commission on Zoological Nomenclature (1965) ruled that *Biomphalaria* was to be given precedence over *Taphius*.

BIOMPHALARIA PRONA FROM LAKE VALENCIA

So far *B. prona* has been referred, with a single exception (Chrosciechowski, 1973), exclusively to Lake Valencia (Martens, 1873; Clessin, 1886; Germain, 1921; Lutz, 1928; H. B. Baker, 1930; F. C. Baker, 1945; Paraense & Deslandes, 1958b; Hubendick, 1961). The taxonomic work of these authors, except Paraense & Deslandes (1958b), was only based on empty shells, which are extremely abundant on the shores, extending in some places far beyond the outer beach – the early reaches of the lake bottom. Scarcity of anatomical observations results from the tendency of earlier taxonomists to rely just on conchological characters. Some workers, however, seem to have had difficulty in finding live specimens (e. g. Hubendick, 1961). Lutz (1928) observed that they could be found on aquatic plants, chiefly *Potamogeton* and Characeae, which thrive near the margins. In Dec. 1956 the senior author only collected empty shells from the submerged bottom near the water's edge, but besides them there were some ones containing decomposing soft parts. Live specimens were found in large numbers attached to submerged plants, as noticed by Lutz (1928). It seems probable that they spend most of their lifetime in this situation, and that on dying they detach from the vegetation, are floated by decomposition gases and drifted shoreward by wind action.

Identification of *B. prona* has been based on peculiar shell characters pointed out in Martens' (1873) description: 3 1/2 whorls rapidly increasing in diameter, the outer one expanded and deflected leftward at the apertural region, right side deeply umbilicate. Its exclu-

siveness to Lake Valencia is a current belief which has been expressed even by authors familiar with Venezuelan malacology, e. g. Chrosciechowski (1968): "*B. prona* is so closely linked with Lake Valencia that could serve as its emblem. It is autochthonous to the area and is unknown outside the Lake". Lutz (1928) recognized *B. prona* in its small affluents.

A few among the specimens from Lake Valencia studied by Paraense & Deslandes (1958b) varied from Martens' description and figures, showing narrower shells with 5 whorls increasing less rapidly in diameter, the outer one less expanded and pointing forward (or slightly deflected leftward), and with the right side less steeply umbilicate.

BIOMPHALARIA PRONA OUTSIDE THE LAKE

A population of typical *B. prona* was found by Chrosciechowski (1973) in a dammed section of the Camatagua river, some 80 km southeast of Lake Valencia. In May, 1974, the senior author collected from a grassy marsh at Boca de Aroa, Falcón state, about 70 km northwest of the Lake, numerous specimens corresponding exclusively to the narrower variants in shell characters. Further collections, from Oct. 1986 on, by several of the coauthors revealed the presence of populations of those variants in several biotopes in the states of Carabobo, Cojedes, Guárico and Monagas.

MATERIAL AND METHODS

The present study deals with samples from nine localities, shown in Figs 1 and 2, and listed in Table I.

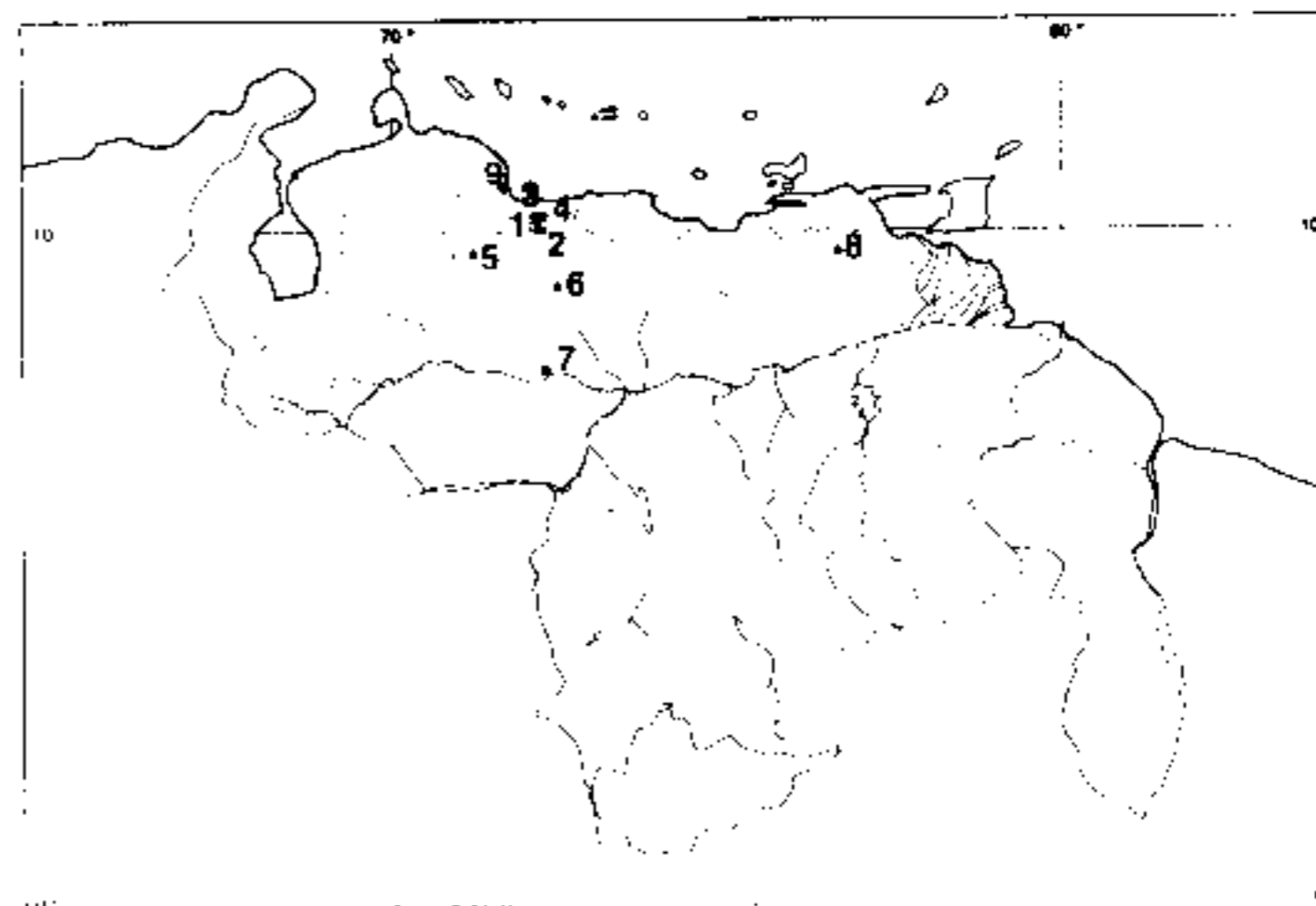


Fig. 1: map of Venezuela showing the nine sampling sites. For numerals see Table I.

TABLE I
Characteristics of the nine sampling sites

Name	State	Code	Type of site	pH	Conductivity ($\mu\text{S}/\text{cm}$)	No. snails
1 - Lago de Valencia Punta Palmita	Carabobo	PUP	Natural lake North	8.85	2020	27 ^a
2 - Lago de Valencia Yuma	Carabobo	YUM	Natural lake South	8.72	1990	35
3 - Agua Caliente	Carabobo	ACM	Small stream	7.16	500	33
4 - Mariara	Carabobo	MAR	Pond	7.50	1380	23
5 - Las Vegas	Cojedes	LAV	Rice field drains	-	-	22 ^a
6 - Corozo Pando	Guárico	RCP	Rice field drains	7.44	212	28 ^a
7 - San Fernando	Guárico	SAF	Small stream	-	-	27
8 - Guamo	Monagas	GUA	Artificial lake	-	-	7
9 - Boca de Aroa	Falcón		Grassy marsh	-	-	- ^a

a: reproductive system examined (N = 20).

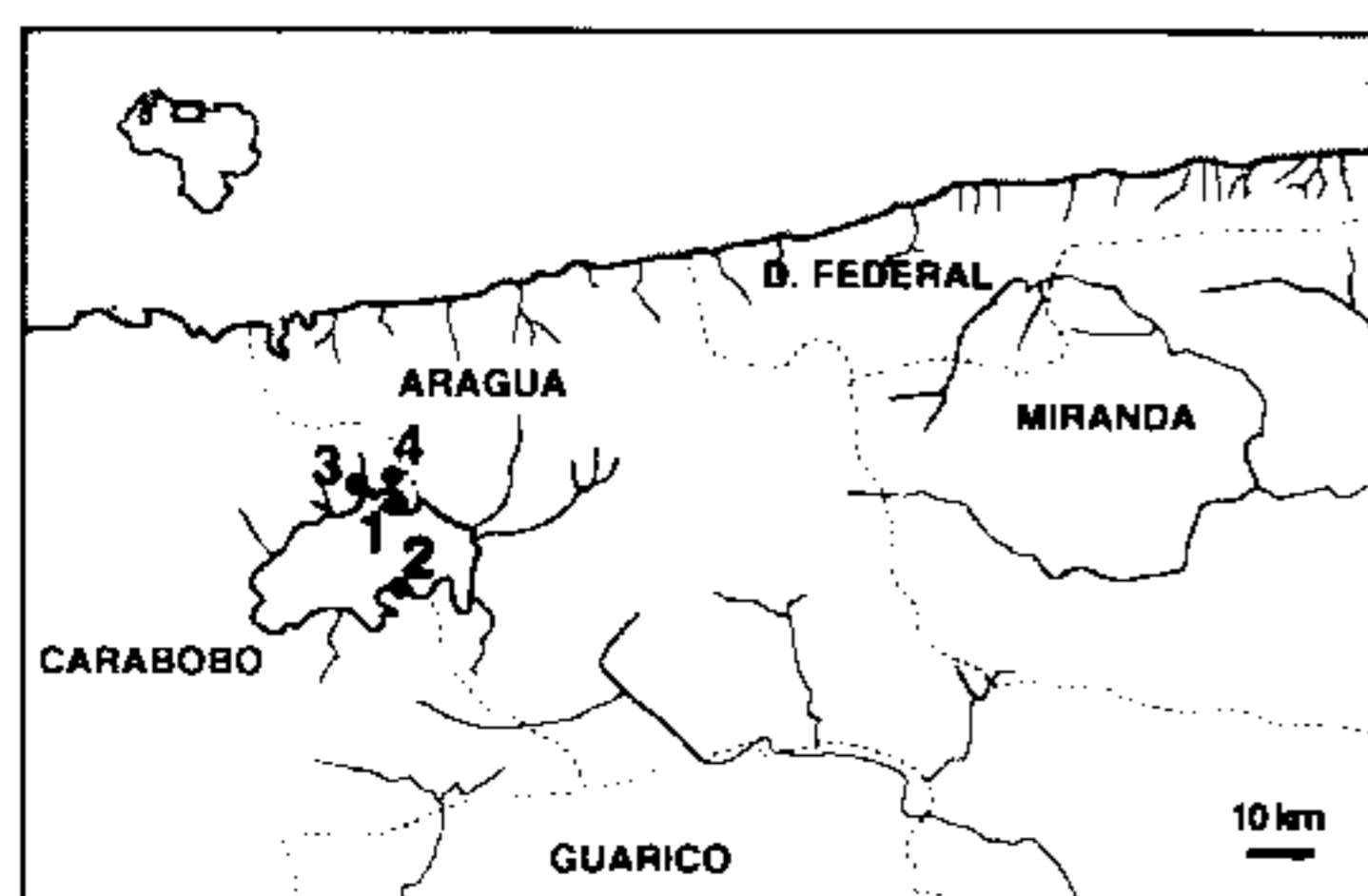


Fig. 2: endemic area of schistosomiasis in Venezuela (dotted) showing the four sampling sites in the Lake Valencia area. For numerals see Table I.

Anatomical observations and measurements were made in dissected snails from localities 1, 5, 6 and 9 (20 specimens of each). Five specimens from each of the other localities were also dissected for species identification.

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 Raillet-Henry's fluid (distilled water 930 ml, sodium chloride 6 g, formalin 50 ml, glacial acetic acid 20 ml).

The snails for biochemical investigation were collected from localities 1 through 8 and preserved in liquid nitrogen. Whole bodies of 7 to 35 specimens from each site were homog-

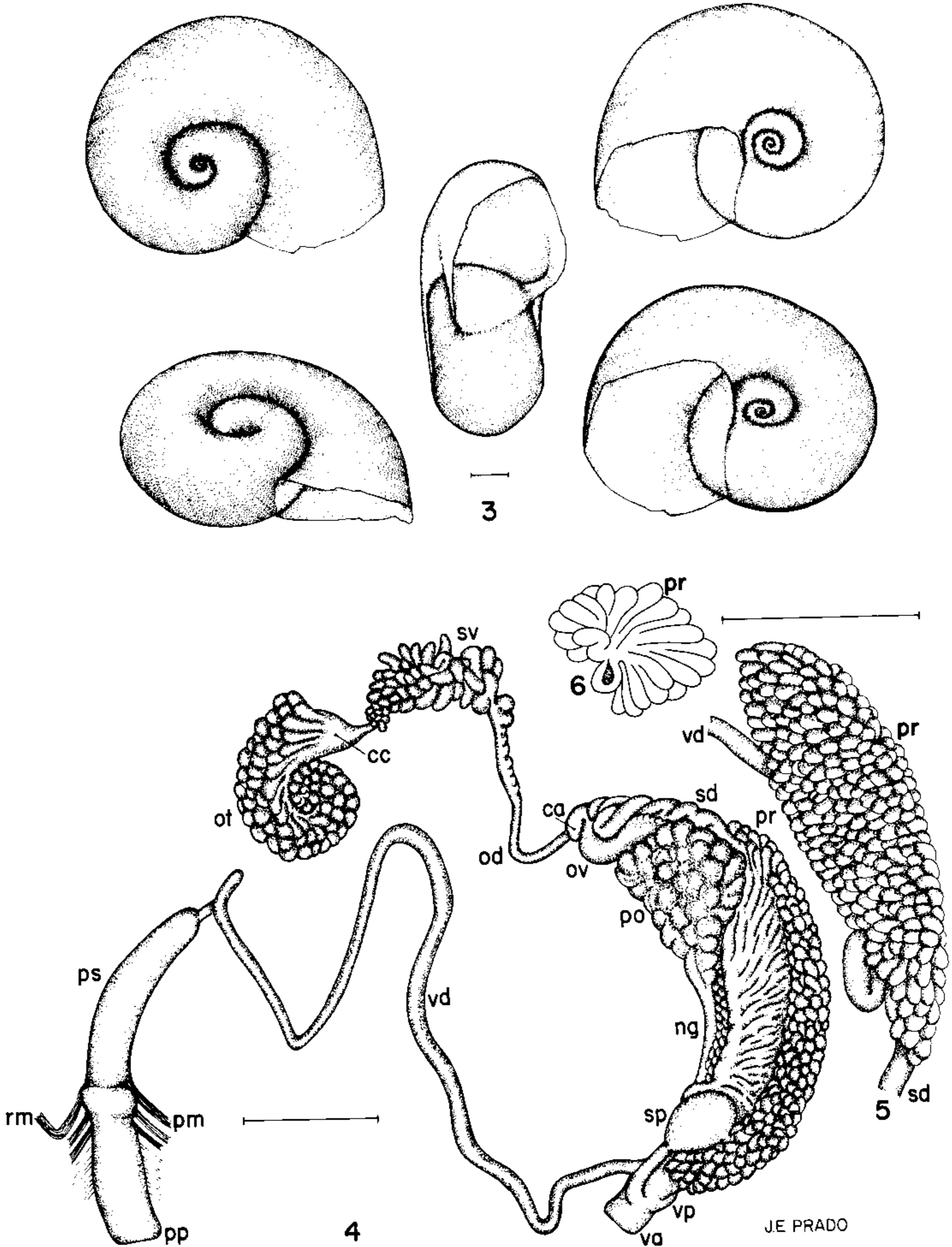
enized with an ultradurax in 100 to 200 ml of grinding buffer: tris, EDTA, NADP (Pasteur et al., 1987) and the supernatant was stored at -80 °C. Thirteen polymorphic loci were studied by electrophoresis on 12% horizontal starch gels.

Allozyme mobilities were designated relatively to those present in the reference strain GLA-TEM which were arbitrarily assigned a value of 100. GLA-TEM is for homozygous strain of the Brazilian *Biomphalaria glabrata* reared in the laboratory for 15 years by Dr M. Vianey-Liaud. The unbiased genetic distances (Nei, 1978) were computed from the allele frequency data and used to perform a cluster analysis by the unweighted pair group distance method (BIOSYS-1, Swofford & Selander, 1981).

RESULTS

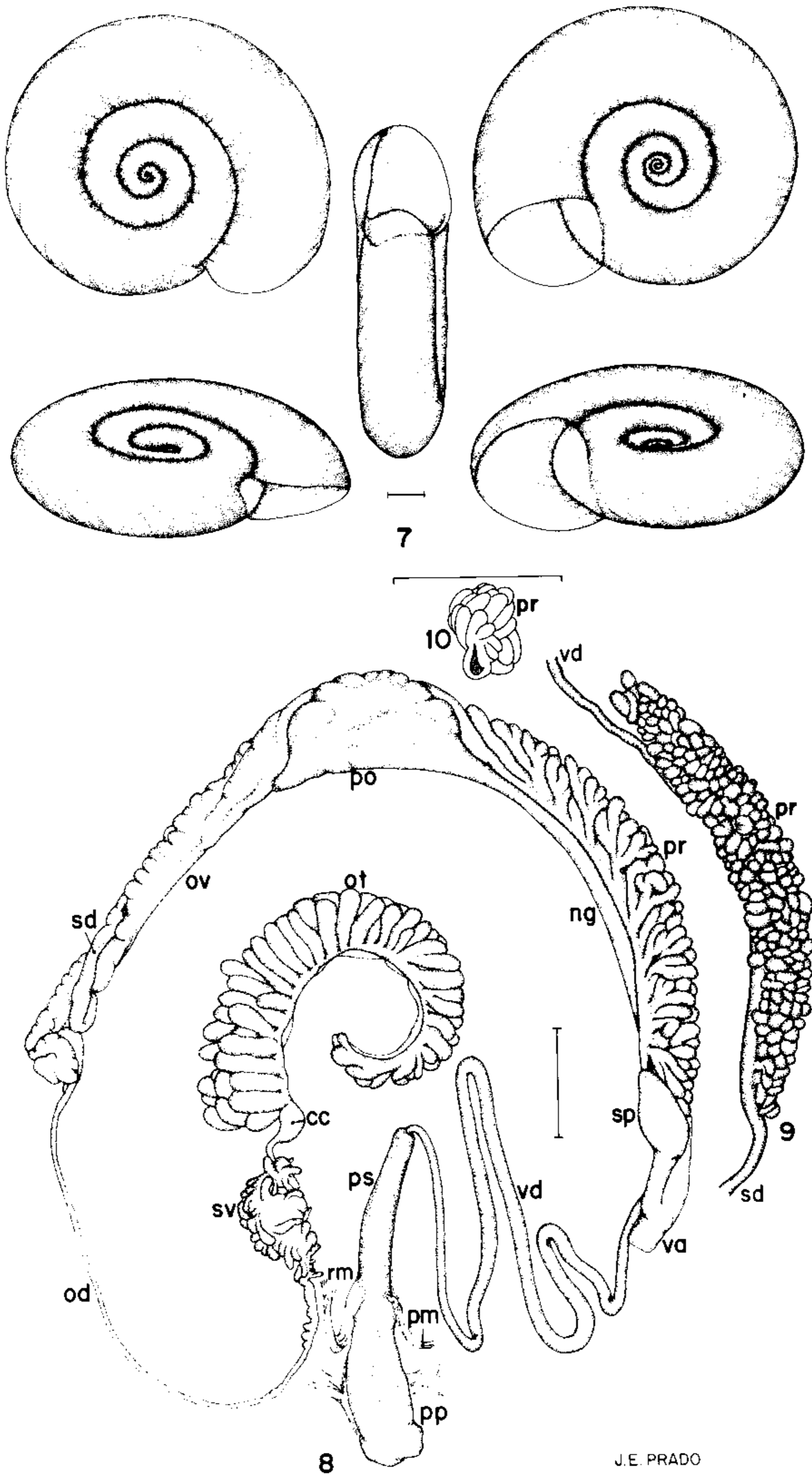
Shell - The shells from Lake Valencia (localities 1 and 2) agree with Martens' original description and figures, our largest specimen measuring 7.5 mm in diameter. A typical shell is shown in Fig. 3. The snails from the remaining eight localities have a narrower shell (Fig. 7) similar to the scarce extreme "variant" observed among those from the lake by Paraense & Deslandes (1958b) and shown in their Fig. 4, reaching 10 mm in the sample from Boca de Aroa.

Reproductive system - The ovotestis is composed of about 70 diverticula, most of which are unbranched. In three minutely dissected ovotestes the diverticula were distributed as follows: Punta Palmita: 50 simple, 12 bifur-



Biomphalaria prona from Lake Valencia, Venezuela – Fig. 3: shell. Fig. 4: reproductive system. ca = carrefour, cc = collecting canal of ovotestis, ng = nidamental gland, od = distal segment of ovispermiduct, ot = 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, vp = vaginal pouch. Fig 5: prostate, left side (disconnected from nidamental gland). Fig. 6: prostatic diverticulum, interproximal aspect. Bar – 1 mm.

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Biomphalaria prona from Las Vegas, Venezuela – Fig. 7: shell. Fig. 8: reproductive system. Fig. 9: prostate, left side (disconnected from nidamental gland). Fig. 10: prostatic diverticulum, interproximal aspect. Bar = 1 mm.

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TABLE II

Some quantitative characters of *Biomphalaria prona* from four Venezuelan localities
(N = 20 per locality)

Locality	Ratios between organ lengths									
	Prostatic diverticula		PFD/DFD		DFD/PC		PS/PP			
	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD
Lake Valencia										
Punta Palmita	7-12	9.80 1.85	0.30-0.49	0.38 0.05	0.95-1.40	1.18 0.13	0.60-1.35	1.11 0.17		
Las Vegas	8-13	10.15 1.39	0.45-0.77	0.60 0.09	1.87-2.89	2.30 0.34	0.73-1.33	1.02 0.17		
Corozo Pando	8-13	10.70 1.69	0.56-0.75	0.62 0.05	1.37-2.52	2.10 0.30	0.71-1.30	0.99 0.13		
Boca de Aroa	8-13	11.15 1.60	0.44-0.87	0.60 0.11	2.46-4.90	3.19 0.54	0.92-1.22	1.03 0.08		

PFD = Proximal female duct (from carrefour to middle of pouch of oviduct).

DFD = Distal female duct (from middle of pouch of oviduct to female gonopore).

PS = Penial sheath.

PP = Prepuce.

PC = Penial complex (penial sheath + prepuce).

cate, 1 trifurcate; Las Vegas: 48 simple, 18 bifurcate, 3 trifurcate, 1 quadrifid; Corozo Pando: 62 simple, 7 bifurcate, 1 trifurcate.

The wide-shelled forms of the lake (Fig. 4) have a crooking oviduct ending into a bulky pouch, a compact nidamental gland, a highly sinuous spermiduct, and multifurcate prostatic diverticula packed tightly together and spreading on all sides, many of them inflecting ventralward (Fig. 6) to show their tips under the prostatic duct. In this way those organs conform to the inner dimensions of a paucispiral shell with spacious body whorl. The abundant terminal ramifications of the prostatic diverticula give the organ a cauliflower-like appearance (Fig. 5).

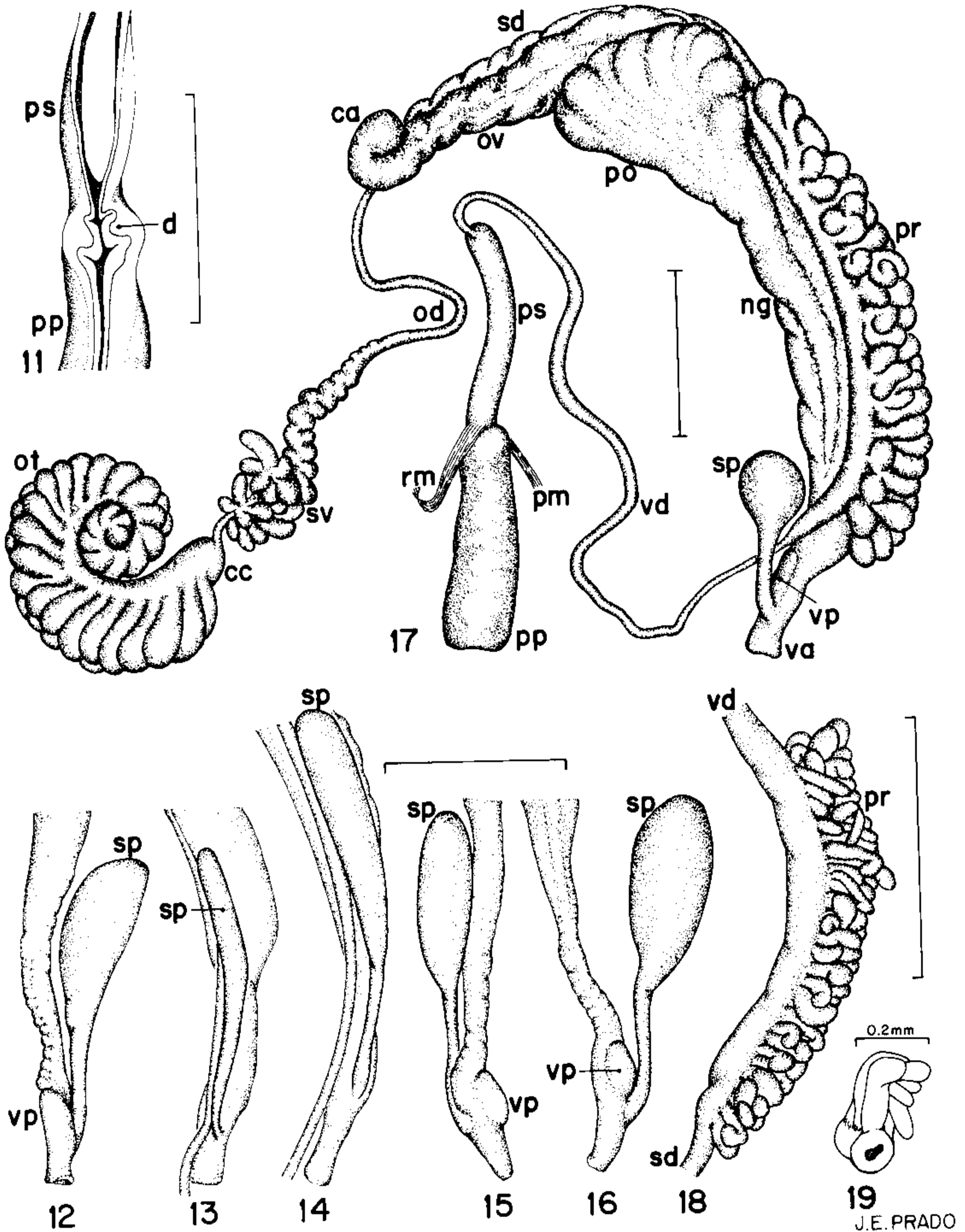
As to the extralacustrine forms, whose body must adapt to a longer and bilaterally flattened space, they show a comparatively straight oviduct with a moderately expanded pouch, a slenderer nidamental gland, a little flexuous spermiduct and a less intricate prostate (Figs 8, 9, 10).

The number of prostatic diverticula ranged from 7 to 13 in the dissected specimens.

The remaining reproductive organs are similar in both forms. The vagina is short, with a variably developed but well defined swelling (vaginal pouch) on the ventral wall

(Figs 12, 15, 16). The spermatheca varies in shape with the amount of its contents, from club-shaped (Figs 13, 14) to syringe-shaped (Fig. 4, sp), with intermediate forms (Figs 12, 15, 16). The middle portion of the vas deferens is wider than usual in comparison with other species of *Biomphalaria*. The penial sheath is stout, uniformly cylindrical, somewhat narrower than the prepuce (as wide as the latter in some specimens) and a little longer in most instances (Table II). The preputial diaphragm is well-developed, giving the proximal end of the prepuce a bulbous appearance in many specimens (Fig. 11, d).

Biochemical data – The studied populations were characterized both by a low intrapopulation polymorphism and by differentiation among populations as claimed by Mulvey & Vrijenhoek (1982) and Mulvey et al. (1988) for *B. glabrata*. The UGPMA analysis clustered all morphological *prona* species together and distinct from the external species *glabrata*, GLA-TEM (Fig. 20). Within the *prona* species two clusters were apparent, but the genetic distances were too low (0.2) to assert that they form distinct species. Mulvey et al. (1988) have found genetic distances around 0.5 between *B. glabrata* from different West Indian islands and *B. havanensis* from the Dominican Republic. The genetic distances between *B. prona* populations themselves lay between 0.1 and 0.2 (Table III).



Biomphalaria prona – Fig. 11: longisection to show diaphragm (d) between penial sheath and prepuce. Figs 12-16: variation of vaginal pouch and spermatheca. *Biomphalaria havanensis* from Havana, Cuba – Fig. 17: reproductive system (after Paraense & Deslandes, 1958a). Fig. 18: prostate, left side. Fig. 19: interproximal aspect of prostatic diverticulum. Lettering as in Fig. 4. Bar = 1 mm (except Fig. 19).

TABLE III

Matrix of genetic similarity and/or distance coefficients
 Below diagonal: Nei (1978) unbiased genetic identity
 Above diagonal: Nei (1978) unbiased genetic distance

Population	1	2	3	4	5	6	7	8	9
1 GLA TEM	*****	1.015	.762	.939	.950	.793	.719	.823	.679
2 PRO ACM	.363	*****	.294	.049	.296	.178	.145	.309	.157
3 PRO GUA	.467	.745	*****	.259	.454	.257	.250	.328	.223
4 PRO LAV	.391	.952	.772	*****	.262	.206	.155	.335	.172
5 PRO MAR	.387	.743	.635	.770	*****	.200	.214	.100	.177
6 PRO PUP	.452	.837	.774	.814	.818	*****	.170	.102	.014
7 PRO RCP	.487	.865	.779	.857	.808	.844	*****	.234	.114
8 PRO SAF	.439	.734	.720	.715	.905	.903	.791	*****	.089
9 PRO YUM	.507	.855	.800	.842	.838	.986	.892	.914	*****

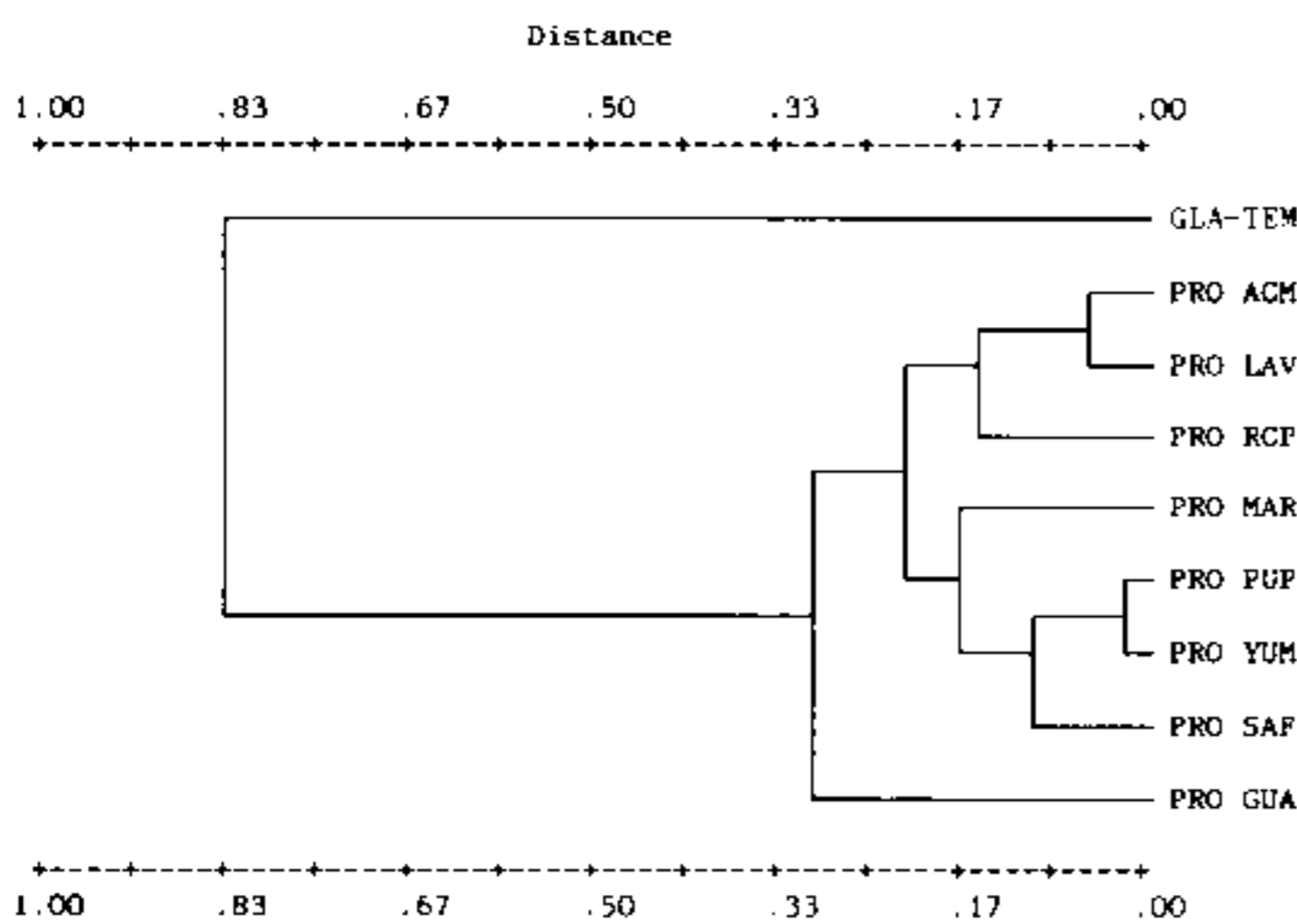


Fig. 20: UPGMA phenogram of eight populations of *Biomphalaria prona* from Venezuela using Nei's distance coefficient. For names and localization of populations see Table I and Figs 1-2. GLA-TEM: laboratory strain of *Biomphalaria glabrata* used as external group.

DISCUSSION

The above results show that under the conchological point of view *B. prona* is a polymorphic species. The fact that the various conchological morphs are anatomically similar indicates the taxonomic superiority of the anatomic over the shell characters, as previously emphasized by Paraense (1961) and corroborated in the present instance by the biochemical analysis.

The existence outside Lake Valencia of populations corresponding to the comparatively narrow-shelled variant depicted on Fig. 4 of Paraense & Deslandes' (1958b) description may be viewed as an instance of directional selection for that extreme phenotype.

The narrower variant has a shell similar to that of *B. havanensis*, having been represented

as such by Hubendick (1961) in his monograph on Venezuelan planorbids. His Figs 58 and 59, however, show a prostate and a penial complex conforming to those of *B. prona* rather than *B. havanensis*. Moreover, he notes that the middle portion of the vas deferens is "considerably thicker than the proximal and distal portions", considering that feature "the most important characteristic distinguishing *T. havanensis* from other Venezuelan species". On the other hand, he recognizes, obviously based on Paraense & Deslandes' (1958b) description, that "this characteristic is also present in *T. pronus* from Lago di Valencia".

Hubendick's view was followed by subsequent workers in Venezuela (e. g. Chroszczowski, 1969). In a previous arrangement of the samples recorded in Table III, the snails from PRO-ACM (Agua Caliente canal), PRO-LAV (Las Vegas rice-field drains) and PRO-RCP (Corozo Pando rice-field drains), and those from PRO-MAR (Mariara pond) and PRO-SAF (San Fernando stream), were referred to *havanensis*, the last two samples having been gathered to two populations which are typical *prona* from Lake Valencia (PRO-PUP and PRO-YUM). PRO-GUA population constituted a distinct cluster but only seven snails could be analyzed.

All the biochemical evidence fits well with the morphological data, supporting the conclusion that only one species, *B. prona*, must be considered in this group.

Comparison between Figs 4-6, 8-10 and 17 (this latter after Paraense & Deslandes, 1958a), 18, 19 will show the main characters separating *B. havanensis* from *B. prona*. In the former

the middle portion of the vas deferens is proportionally narrower, the limit between the penial sheath and the prepuce is marked by a deeper constriction, and the prostatic diverticula are less ramified and only slightly bent leftward (compare Fig. 19 with Figs 6 and 10).

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