MALACOLOGIA, 1976, 15(2): 241-287

MONOGRAPH ON *"LITHOGLYPHOPSIS" APERTA*, THE SNAIL HOST OF MEKONG RIVER SCHISTOSOMIASIS[1]

George M. Davis[2], Viroj Kitikoon[3], and Prasong Temcharoen[4]

ABSTRACT

We discuss the morphology, histology, ecology, distribution, systematics, and evolutionary relationships of *"Lithoglyphopsis" aperta* Temcharoen, the snail host of Mekong River *Schistosoma* sp., and part of a vast, complex, endemic hydrobiid fauna consisting of 11 genera and over 80 species.

"L." aperta is a member of the Hydrobiidae (as broadly outlined by Fretter & Graham, 1962), subfamily Triculinae (as defined by Davis, 1968b). *"L." aperta* cannot be assigned to *Lithoglyphopsis* because its shell and radula differ from those of the type-species, *L. modesta* (Gredler) from China, and because *L. modesta* is apparently more closely allied to other Mekong River genera in these traits. The female reproductive system of *"L." aperta* is similar to that of *Tricula burchi* Davis, a species from NW Thailand outside the Mekong River drainage. It is not possible to assign *aperta* to a named genus until the morphologies of numerous other hydrobiid taxa in the Mekong River are known.

"L." aperta is typically hydrobiid in grade of morphological organization, in the nervous, digestive, ctenidial and male reproductive systems. Differences from other hydrobiid taxa are in the female reproductive system and micromorphological features of the digestive tract. *"L." aperta* and species of *Tricula* from Thailand have a female reproductive system where sperm enter at the posterior end of the mantle cavity and travel to the bursa copulatrix via a spermathecal duct. These and related traits are the basis for the subfamily Triculinae. Hydrobiid taxa from Europe (Hydrobiinae s.s.) belong in a different phyletic line, where sperm enter the female reproductive system at the anterior end of the mantle cavity and travel via a ciliated groove in the pallial oviduct to the bursa copulatrix.

"L." aperta, as well as taxa of the Pomatiopsinae (e.g. *Oncomelania, Pomatiopsis*), differ from most known mesogastropods in lacking a hypobranchial gland. *"L." aperta*, other triculines, pomatiopsines and hydrobiines, as well as taxa studied in the Bithyniidae, Truncatellidae and Assimineidae differ from other mesogastropods, e.g. Viviparidae, Pleuroceridae, Littorinidae, etc., in that the salivary glands are dorsal to the nerve ring, i.e. do not pass through the nerve ring.

"L." aperta lives on solid substrata, particularly wood, shells and leaves in the Mekong River from Khemarat, Thailand, to the Cambodian border, 200 river miles downstream. The range probably extends another 100 river miles downstream to Kratie, Cambodia. It is an *"r"*-selected species by having a high density-independent mortality and using much of its resources for reproduction. The species is a colonizer in a river with severe annual floods. Females live less than 12 months; they apparently lay eggs in late January or February and die. In early March neither adults nor young can be collected. By mid or late March young suddenly flourish. The new generation does not mature until late May or June, after the beginning of the rainy season. The large bursa copulatrix, 63% the length of the pallial oviduct, is a unique feature of *aperta* and may help to maintain sperm during the peak flood months of August to November.

Three races of *"L." aperta* are described, differentiated by shell size, shape, sculpture, mantle pigment patterns, ecology, time of development, and minor aspects of anatomy. The beta race has been found only in the rapids of the Mun River; alpha and gamma races are extensively sympatric at Khemarat and Ban Dan in the Mekong River. The gamma race dominates at Khong Island. All 3 races can transmit the Mekong schistosome.

The Mekong schistosome is not *S. japonicum* but a sibling species probably evolved from a common ancestor, and which diverged well over a million years ago. The hypothesis is presented that the triculine and pomatiopsine taxa had common ancestry several million years ago. The fossil record indicates that triculine taxa and *Oncomelania* of the Pomatiopsinae existed in Burma in the Pleistocene. Several million years ago snails of both lineages probably transmitted schistosomes with less specificity than occurring today. Precursors of present day *Oncomelania hupensis* evolved with greater genetic affinity for schistosome transmission than did precursors to modern triculine taxa. With extinction of *Oncomelania* in

[1]This research was supported in part by the Committee for Coordination of Investigations of the Lower Mekong Basin (Mekong Committee), with substantial help from the United States Agency for International Development through its Office of Regional Development in Bangkok. It was supported in part also by a U.S. National Institutes of Health Grant, No. IR22-A1, 11373-01 TMP.
[2]Academy of Natural Sciences of Philadelphia, Pennsylvania 19103, U.S.A.
[3]Faculty of Tropical Medicine, Mahidol University, Bangkok, Thailand.
[4]Faculty of Public Health, Mahidol University, Bangkok, Thailand.

the headwaters of the Mekong River during the Pleistocene, and with radiation of *O. hupensis* down the Yangtze River of China to Japan, Taiwan, the Philippines, and Sulawesi, the evolving snail-parasite interaction became highly specific, resulting in present day *S. japonicum* and the geographic subspecies of that parasite.

Triculine snails radiated in Burma, Thailand, Laos, and China. The present day Mekong schistosome appears to be a relict with limited distribution, transmitted by *"L." aperta* in a river, held in check by the vagaries of annual floods.

INTRODUCTION

Human schistosomiasis has been reported from the lower Mekong River in recent years (Barbier, 1966; Audebaud et al., 1968; Pathammavong, 1969; Sornmani et al., 1971; Iijima et al., 1971). The finding of this disease, which afflicts 200 million persons in the world, along the Mekong River evoked a strong reaction from those seeking to develop the water resources of the river.

Searches were made for the 1st intermediate host by the Faculty of Tropical Medicine of Mahidol University, Bangkok, and by World Health Organization teams (Iijima et al., 1971; Lo et al., 1971). Harinasuta et al. (1972) discovered that *"Lithoglyphopsis" aperta* Temcharoen (Hydrobiidae, Triculinae) from Khong Island, Laos (near the Cambodian border) could be experimentally infected. The life cycle was completed with cercariae shed from the snails and applied to mice, hamsters, and dogs (Sornmani et al., 1973). Subsequently, Kitikoon et al. (1973) found naturally infected *"L." aperta* in the Mekong River at Khong Island.

We have initiated intensive investigations of the biology of *"Lithoglyphopsis" aperta* because of its involvement with human schistosomes and because this species is part of a vast, endemic hydrobiid fauna that has previously been unstudied biologically and which has excited interest because of its intrinsic value in evolutionary studies. The quotation marks around *"Lithoglyphopsis"* indicate that *aperta* probably does not belong in the genus *Lithoglyphopsis.* This unresolved problem is taken up in the discussion section of the paper.

Eleven genera and over 80 species of Hydrobiidae, with an amazing variety of shell shapes and sculptural patterns, have been described from the Mekong River (Brandt & Temcharoen, 1971). These taxa represent the greatest assemblage of endemic hydrobiids within a single river or lake system known in the world. Aside from the original descriptions of shells and a few scanty notes on radulae, nothing is known of their biology. In the absence of anatomical data it is impossible to determine 1) variability within species, 2) limits of genera, and 3) relationships between Mekong River hydrobiids and extralimital hydrobiids.

One of us (Davis) has undertaken investigations of the Mekong River Hydrobiidae with several questions in mind. What is the temporal and spatial origin of the Mekong River hydrobiid fauna? How does this fauna relate to hydrobiids throughout the world? Are the Mekong River hydrobiids polyphyletic? What traits best serve to describe species, group species into genera, and assess lines of phylogeny? What are the relationships of vastly varying shell shapes and sculptural types to substrates, food, currents, seasonal fluctuations in the river, and temporal duration of the taxa in the Mekong drainage system? Is the capacity to transmit human schistosomes contained within a succinct lineage and can one establish a hypothesis to account for the molluscan host-parasite relationships seen in Asia today? Such a hypothesis would have to deal with the evolution of the host-parasite relationship leading both to the transmission of *Schistosoma japonicum* Katsurada in China by *Oncomelania hupensis* Gredler of the hydrobiid subfamily Pomatiopsinae, as well as the transmission of the Mekong schistosome by *"Lithoglyphopsis" aperta,* here classified in the hydrobiid subfamily Triculinae.

It has been increasingly obvious to current workers that traditional treatment of shells and radulae alone is insufficient to assess relationships within and between species, to define genera, or to gain insight into phylogeny. It has been adequately demonstrated that studies of complete male and female reproductive systems have yielded data giving insight into relationships in the Rissoacea (Johansson, 1939, 1956; Krull, 1935; Davis, 1968a, b). Characters of potential value for assessing systematic relationships may also be derived from the digestive system (Graham, 1939). The nervous, circulatory and excretory systems, however, are highly conservative in the Rissoacea and thus are of lesser value for lower

category systematics.

This paper is the first in a series dealing with the hydrobiids of the Mekong River. Anatomy and histology are used for comparisons with other taxa. Three races of *"Lithoglyphopsis" aperta* thus far found in the Mekong River are described. Anatomical data enable a further delineation of the subfamily Triculinae as defined by Davis (1968b), and a comparison with those other hydrobiids where anatomical data are available. Finally, *"Lithoglyphopsis" aperta* is compared with *Oncomelania hupensis,* the first intermediate host of *Schistosoma japonicum* in China, Japan, the Philippines and Sulawesi, on the basis of anatomy, distribution and evolution.

HISTORICAL REVIEW

After the first reports of human schistosomiasis in the lower Mekong River, several attempts were made to find the first intermediate host. It was taken for granted that the parasite was *Schistosoma japonicum* and thus, initially, the search was made for *Oncomelania.*

Results of such searches were summarized by Pathammavong (1969). *Wattebledia* (Bithyniidae) was found, but not *Oncomelania* (Hydrobiidae). *Wattebledia* is quite distantly related to *Oncomelania.* It is surprising that *Wattebledia* was so extensively collected and studied. The shell only vaguely resembles that of *Oncomelania* while the calcareous multispiral operculum clearly identifies *Wattebledia* as a bithyniid genus. Bithyniids are not naturally infected with mammalian or bird schistosomes (Malek, 1962; Ito, 1964). Efforts to infect *Bithynia tentaculata* with *Schistosoma haematobium* (Bilharz) Weinland, and *S. japonicum* failed (Stunkard, 1946).

In 1968, Brandt showed that hydrobiid snails were transmitting the Mekong schistosome and stated that *Hydrorissoia hospitalis* Brandt "was infected with miracidia from a human blood fluke in Laos. Specimens collected at Khong were found to be naturally infected with sporocysts of *Schistosoma."* In a later report (1970) Brandt stated that *Pachydrobia bavayi* Brandt "is now the first suspect among other species *(Manningiella, Hydrorissoia)* of being the first intermediate host of *Schistosoma japonicum. . . ."* This statement was based upon the observation that miracidia from eggs derived from a Laotian patient penetrated the snail.

Temcharoen (1971) noted that of all gastropods collected at Khong Island and exposed to miracidia of the Mekong *Schistosoma,* penetration was observed only with *Hydrorissoia hospitalis, Manningiella expansa* Brandt, *Pachydrobia bavayi,* and *Manningiella rolfbrandti* Temcharoen. But in all cases snails died before infections matured.

Penetration of a miracidium into a snail is no criterion for considering that species an intermediate host. Miracidia readily penetrate inappropriate snails (Chernin, 1968; Chernin & Perlstein, 1969) and even non-molluscan entities (Upatham, 1972; Upatham & Sturrock, 1973). Likewise, finding immature sporocysts is not sufficient evidence that a species is the first intermediate host for the Mekong schistosome. The reports (Brandt, 1968, 1970) were unworthy of publication because of insufficient data.

In 1968 and 1969, the World Health Organization sent a team consisting of a parasitologist and a malacologist to determine the extent of schistosomiasis in the Mekong Basin. Studies at Khong Island yielded *Schistosoma* sp. from dogs (Iijima et al., 1971). Lo et al. (1971) studied 10 species of operculate snails from Khong and found 26 types of larval trematodes including six furcocercous types. However, none of the latter resembled cercariae of human schistosomes. They suspected *Pachydrobia bavayi* to be the likely intermediate host for the Mekong schistosome.

The United States Agency for International Development granted the Smithsonian Institution funds in 1970 to undertake an analysis of water-borne disease problems in the Mekong River. A cooperative program was established with the Faculty of Tropical Medicine of Mahidol University, Bangkok.

The Smithsonian-Mahidol team placed emphasis on collecting hydrobiid snails from the Mekong and challenging the various species with miracidia of the Mekong schistosome. Miracidia were hatched from eggs passed by dogs from Khong Island infected with the Mekong schistosome. Also, snails from populations of various hydrobiids were crushed and examined to detect infections. As a result of these experiments, *"Lithoglyphopsis" aperta* was found to be a suitable first intermediate host of the Mekong

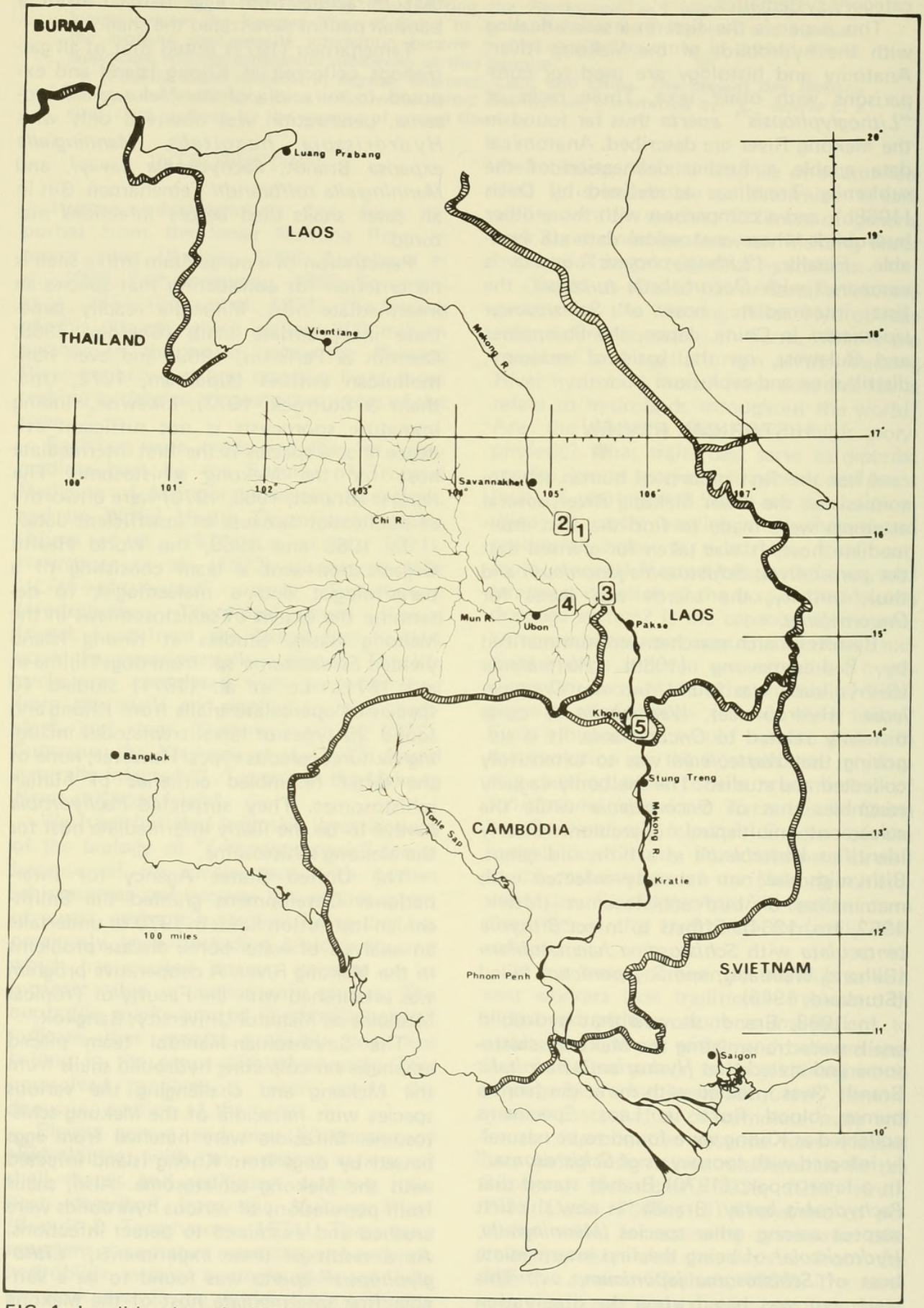


FIG. 1. Localities along the Mekong River where *"Lithoglyphopsis" aperta* has been collected. Alpha and gamma races have been collected together at localities 1 and 5. Beta race snails have thus far been found only at locality 4. Gamma race snails predominate at localities 2, 3 and 5.

schistosome (Harinasuta et al., 1972; Sornmani et al., 1973). Naturally infected snails were found at Khong Island near Ban Xieng Wang (Kitikoon et al., 1973).

LOCALITIES, DISTRIBUTION, AND HABITATS

Localities

Snails collected for this study came from the 5 localities shown on Fig. 1. Collections were, for the most part, made in March and April, 1973. One collection was made in June. The sites were selected because they were accessible by road (many parts of the Mekong River are accessible only by boat), and because they were known to be suitable localities for numerous triculine species (Brandt, 1968, 1970; Temcharoen, 1971).

A. Thailand, Ubon Ratchathani Province
   1. 2.5-3.0 miles below Khemarat Town, Ban Khee Lek (= Ban Khi Lek); 16°2'30"N, 105°17'30"E. Mekong River.
   2. Several miles above Khemarat. Mekong River.
   3. Ban Dan Village, small islands at mouth of the Mun River, 15° 19'15"N, 105°30'45"E. Mekong River.
   4. Amphoe Pibun Mangsahan, large island E. of Pibun Mangsahan (= Ban Sai Mun); 15°14'45"N, 105°17'30"E. Mun River.

B. Laos, Sithandone Province
   5. Khong Island; 14°7'30"N, 105° 51'45"E. Mekong River.

Type-locality

The type-locality of *"Lithoglyphopsis" aperta* Temcharoen (1971) is Ban Na on Khong Island, Laos (Fig. 2, site 4). Temcharoen (1971) gave the distribution as being between Cham Passak (3/4 the distance between Khong Island and Pakse (Fig. 1) and Sompamit Falls near Khone, Laos, at the Cambodian border).

The holotype and paratypes by original designation are in the collections of the Senckenberg Institute, Frankfurt-am-Main, Germany. One of us (Davis) has studied the types. The holotype conforms to the alpha race snails discussed in this paper. Part of the paratype series (SMRL 16282) is housed in the Academy of Natural Sciences of Philadelphia (ANSP 320061). Some of these paratypes are badly worn. Temcharoen (1971) collected only shells.

Distribution (Fig. 1)

Temcharoen's and our collections show that *"L." aperta* is distributed in the Mekong River from a point several miles upstream from Khemarat to the Cambodian border, i.e. Sompamit Falls near Khone. This is a distance of 154 direct miles, 200 river miles. We suspect the species lives as far S as Kratie, Cambodia, because schistosomiasis has been reported from this river town and because the hydrobiid fauna extends at least to Kratie. If this is eventually verified, the species is distributed over 300 river miles.

Habitats and Life Cycle

Rainy and dry seasons are pronounced in the Mekong Basin. Heavy rains usually begin about early June. The river rapidly rises 40 to 60 ft and becomes a raging torrent. With the cessation of rains in November to December, it falls again most markedly in late November. Lowest water levels occur in April.

Young *"L." aperta* are found in mid to late March. Snails having 3.0-3.5 whorls and a shell 1.3 mm long have been found on 22 March 1973 near Khemarat. By late April the majority of the snails have 4.0-4.5 whorls and a length of 2.8 mm. Full maturity occurs from late May probably to late June, coinciding with the beginning of the rainy season.

At locality 1, Ban Khee Lek, rock outcroppings and islands cause the river to narrow. Gamma race snails were found on 14 April 1973, massed on sticks and rocks at 0.5-1.5 m depth in moderate to swift current near the Thailand shore side of islands at Ban Khee Lek. Later, on 5 June, the water had risen and the current was swifter. Alpha race snails were found underneath the rocks at about 1.5-2.0 m. Only 1 gamma race snail was found in this collection.

A pure population of gamma race snails was collected upstream from Khemarat on 5 June (locality 2). Snails were under rocks in about 2 m of water. They could only be collected by diving for rocks. The snails were only half-grown.

The channel running between the 2 principal islands at locality 3 was about 1 m

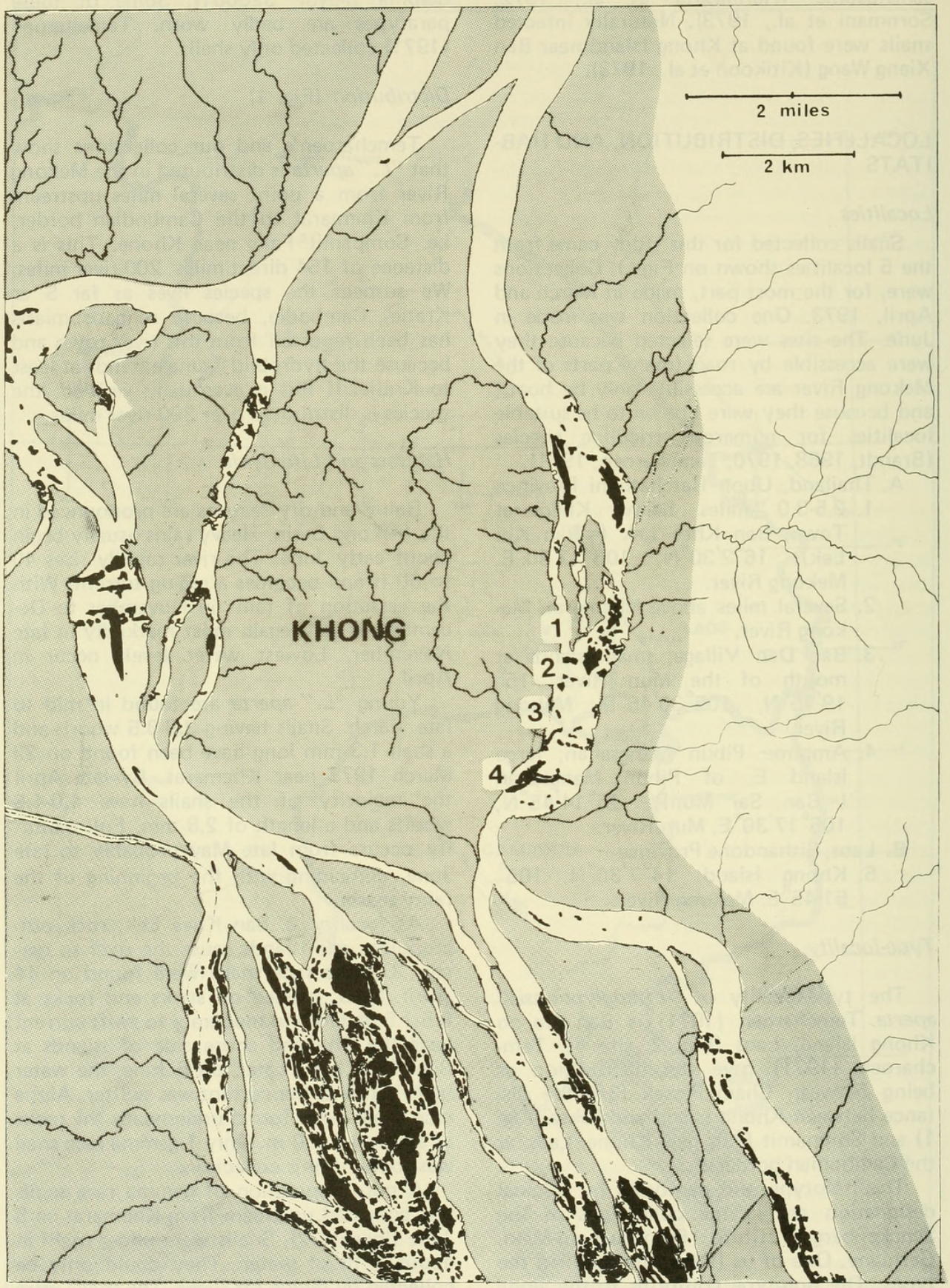


FIG. 2. Khong Island with 4 collection sites frequently visited for *"Lithoglyphopsis" aperta* and other hydrobiids. 1. Laotian Army camp; 2. infection site at a section of Muong Khong (Khong Town) called Ban Xieng Wang; 3. Government Hospital and Thomas Dooley House; 4. Ban Na, the type-locality. Note the thousands of small islands (in black) at the southern end of Khong Island through which the river percolates during the dry season.

deep at low water. There was little current. Collections on 18 April 1973, yielded thousands of half-grown gamma race snails. These were massed on sticks, clam shells and rocks. A few alpha race snails were found with 3.5-5.5 whorls. Mud-coated egg capsules of *"L." aperta* were plastered on the shells of some of the snails.

Both alpha and gamma races have been collected from Khong Island. The gamma race predominates along the eastern side of the island. Snails are found in shallow water on rocks, leaves and sticks which rest on the mud substrate. Occasionally snails are found in the mud itself, under rocks. Water may be only 4-5 cm deep, with little or no current, and warm, i.e. 26° to 27°C. The shallow environment is quickly changed with the onset of heavy rains when a strong current develops. Then snails are found beneath rocks. Habitats are totally inaccessible at the height of the rainy season.

Four collection sites on Khong Island are shown in Fig. 2. *"L." aperta* was found at all 4 sites. Human infections with the Mekong schistosome appear to be derived principally from site 2 where people frequent the shallows to bathe, wash clothes, and defecate. The center of Khong Town is less than 1/4 mi SW of site 2.

METHODS

Anatomical data on the alpha race were derived from snails collected at locality 1 (Fig. 1) on 5 June 1973. Shells of this population have the Academy of Natural Sciences of Philadelphia catalog number 331949. Data on the gamma race were obtained from snails collected at Khong Island (locality 5) and maintained in the laboratory of the Faculty of Tropical Medicine in Bangkok until they matured. Dissections of alpha race snails were done in Philadelphia; gamma race snails were studied in Thailand. No shells of the laboratory-maintained gamma populations survived to be catalogued after the anatomical study. During the course of this anatomical study, no live beta race snails were seen.

Anatomical procedures employed are those given in detail by Davis & Carney (1973). Aqueous solutions of neutral red and methylene blue were used as vital stains for studying the reproductive system. The nervous system was dissected out in a dilute solution of Bouin's fixative. Radulae were mounted unstained in CMC-10, a non-resinous mounting medium.

Confirmation of duct openings was made by studying histological sections. The serial sections were cut at 7 μm and stained in hematoxylin and eosin.

MORPHOLOGY

Shell

A summary of shell traits distinguishing the 3 races is given in the first 5 traits listed in Table 11.

ALPHA RACE (Table 1, Fig. 3A-B).—

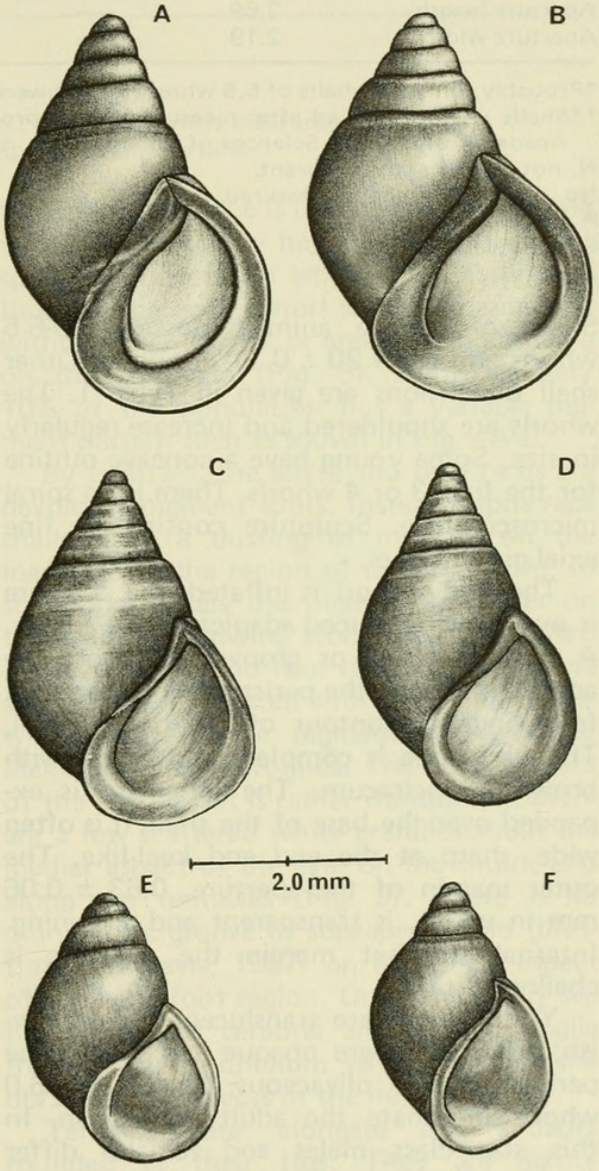


FIG. 3. Shells of the 3 races of *"Lithoglyphopsis" aperta.* A-B, alpha race, ANSP catalog number 331949; C-D, beta race, ANSP no. 332316; E-F, gamma race, ANSP no. 330925.

TABLE 1. Analyses of shells from living animals of alpha race *"Lithoglyphopsis" aperta* (measurements in mm).

Shell trait**	Females		Males		S.D.	P
	$\bar{X}$	Sd	$\bar{X}$	Sd		
6.0 whorls (No. = 9)						
Length	4.20	0.11	4.03	0.10	N	>0.05
Width	2.79	0.08	2.72	0.16	N	>0.05
Length of body whorl	3.15	0.11	2.81	0.30	S	<0.05
Aperture length	2.62	0.09	2.49	0.10	S	<0.01
Aperture width	2.13	0.09	1.96	0.10	S	<0.01
6.5 whorls (No. = 8)						
Length	4.22	—	4.18	0.06	N*	—
Width	2.81	—	2.90	0.27	N*	—
Length of body whorl	3.26	—	2.90	0.22	S*	—
Aperture length	2.69	—	2.60	0.08	N*	—
Aperture width	2.19	—	2.03	0.08	S*	—

*Probably, only 2-3 shells of 6.5 whorl females were found.

**Shells were destroyed after measurement to procure the animals for anatomy. Remaining shells in The Academy of Natural Sciences of Philadelphia, no. 331949.

N, not significantly different.
No., number of shells measured.
P., probability level.
S, significantly different.
Sd, standard deviation.
S.D., significant difference.
$\bar{X}$, mean.

Shells of mature animals possess 6.0-6.5 whorls and are 4.20 ± 0.11 mm long. Other shell dimensions are given in Table 1. The whorls are shouldered and increase regularly in size. Some young have a concave outline for the first 3 or 4 whorls. There is no spiral microsculpture. Sculpture consists of fine axial growth lines.

The body whorl is inflated; the aperture is pyriform, produced adapically like a beak. A distinct crease or groove runs from the adapical limit of the peristome into the shell following the contour of the body whorl. The peristome is complete and edged with brown periostracum. The inner lip is expanded over the base of the shell; it is often wide, sharp at the end and keel-like. The outer margin of the aperture, 0.63 ± 0.06 mm in width, is transparent and glistening. Internal to that margin the aperture is chalky white.

Young shells are translucent and yellowish; adult shells are opaque and white. The periostracum is olivaceous. Shells with 6.0 whorls dominate the adult population. In this size class males and females differ significantly in length of body whorl, aperture length and width.

BETA RACE (Table 2, Fig. 3C-D).—Shells of mature animals have 6.0-6.5 whorls and are significantly smaller than those of the alpha race. The greatest length observed for an uneroded shell with 6.5 whorls is 3.81 mm. Shells also differ from those of the alpha race in having flat-sided whorls or a smoothly concave spire outline. The suture is very shallow. Raised spiral microsculpture is pronounced in 58% of the shells, faint in 25% and absent in 17% (40 specimens).

GAMMA RACE (Table 2, Fig. 3E-F).—Animals mature with a shell primarily of 5.5 whorls; few reach 6.0 whorls. Females taken from Khong Island and maintained in the laboratory for several months matured with an average shell length of 2.93 mm (standard deviation, 0.16 mm; standard error of the mean, 0.06 mm). An insufficient number of males was available for comparison.

Living mature animals have thus far not been collected and preserved in the field to enable accurate shell measurements. Several collections of dead shells were made at Khemarat (locality 1). The shells were collected in pockets in the river where currents had deposited them. Their position with regard to living immature snails suggested that they were of the same population but of a previous generation. Data from 2 of these populations are given in Table 2. Shell apices were so badly eroded that shell lengths were not measured. Mature shells

TABLE 2. Shell dimensions of beta and gamma race *"Lithoglyphopsis" aperta.* Males and females are mixed.

Whorls	Length	Width	Lbw	Lap	Wap
Beta Race—ANSP 332316+					
Complete Shells					
6.0	3.44	2.00	2.63	1.88	1.31
6.5	3.81	2.56	2.94	2.31	1.81
Eroded Shells					
6.0 est. (No.=8)	——*	2.23 ± 0.13	2.68 ± 0.10	2.06 ± 0.13	1.52 ± 0.12
6.5 est. (No.=11)	——	2.46 ± 0.11	2.95 ± 0.04	2.34 ± 0.07	1.73 ± 0.06
Gamma Race—ANSP 330925					
5.5 to 6.0 (No.=7)	——	2.29 ± 0.17	2.68 ± 0.18	2.11 ± 0.22	1.66 ± 0.19
Gamma Race—ANSP 327506					
5.0 est. (No.=7)	——	1.91 ± 0.20	2.32 ± 0.12	1.76 ± 0.17	1.44 ± 0.14

*Eroded, measurement useless.
±, Standard deviation.
+, catalog number in The Academy of Natural Sciences of Philadelphia.
Lap, length of aperture. No., number of shells measured.
Lbw, length of body whorl. Wap, width of aperture.

were readily recognized because of the fully developed aperture with pronounced parietal shelf and keel-like appearance of the edge of the expanded inner lip. Estimates of whorl number were derived from the 1 or 2 nearly entire shells.

As seen in Table 2, from Fig. 3E-F, and from the data on laboratory-reared specimens, there is great variability in shell size of mature gamma race snails. This has been observed both within and between populations. As seen in Table 2, the length of body whorl and width of gamma race snails (ANSP 330925) equaled those of eroded beta race snails with the same estimated whorl number. Most populations of gamma race snails seen, however, have been significantly smaller. Influence of sex on shell size in the beta and gamma races has yet to be determined.

The whorls are slightly convex and thus there is only a shallow suture. The base of the inner lip meets the base of the shell in a sharp keel. The translucent outer margin of the aperture is 0.25-0.30 mm wide; the area within the aperture is the usual chalky white. There is a tendency in this race to have a less developed beak-like adapical projection of the aperture and a less developed parietal shelf as compared with alpha race snails. Shells have no spiral microsculpture.

External Features

The gamma race is unique among Mekong River hydrobiids by having 4 black pigment spots on the mantle which are clearly seen through the body whorl when the animal is withdrawn (Fig. 4F), or emerged and moving on the substrate (Fig. 5). Approximately 10% of the population has a variable pigment pattern such as shown in Fig. 4A-E.

By contrast, the alpha and beta races are devoid of pigment spots. Instead, alpha race snails have a dusting of melanin on the mantle over the region of the ctenidium. In some individuals the pigment is denser on the mantle following along each gill leaflet.

Head, neck, and foot regions of the races studied are not dusted with black melanin or with yellow-orange pigment as are many Mekong River hydrobiids. The dorsal aspect of the head-snout is rather transparent; there are a few scattered white granules about the medial aspect of the eye, on the snout, and along the tentacles (Fig. 9). There is no omniphoric groove or suprapedal fold (illustrated in Davis, 1967) on the lateral aspect of the head-foot region. One can readily see the pigmented cerebral and pleural ganglia through the epithelium when studying the dorso-lateral aspects of the head (Fig. 9).

Tentacles are elongate and broadly rounded at their tips. They are lightly ciliated and without pronounced tufts or clusters of cilia. The sole of the foot is white. When extended, its length varies from 2.5-2.9 mm. At rest, the length is about 2.0

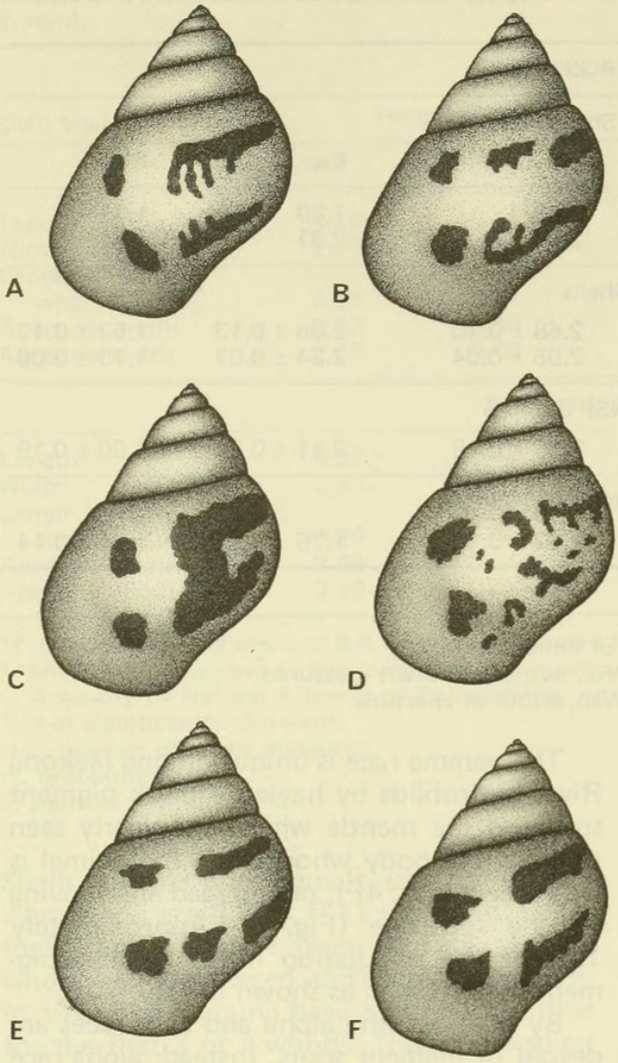


FIG. 4. Variation in pigment patterns on the mantle as seen through the shell of gamma race snails.

mm. The posterior end is rounded; the anterior end is blunt, 1.2 mm wide, and has the typical rissoacean mucous slit across the entire front edge (see Davis, 1966, fig. 4a). Viewing the antero-dorsal edge of the foot, one can observe, in alcohol-preserved specimens, characteristic mucous glands (Fig. 6B). The mid-central gland is largest of these. Results of histological studies of these glands are given in Fig. 16F-I. The central gland projects farthest upward into the pedal haemocoel. The highly secretory nature of the gland cells is seen particularly well in Fig. 16G. These glands, which pour their mucous secretions into the anterior pedial slit, are more pronounced in this species than in other taxa in which these glands have been studied, i.e. *Tricula* and *Oncomelania hupensis*.

The dorsal aspect of the stomach and digestive gland are densely pigmented with melanin. Salmon pink granules give the posterior areas of the living animal, especially the digestive gland, a pink sheen.

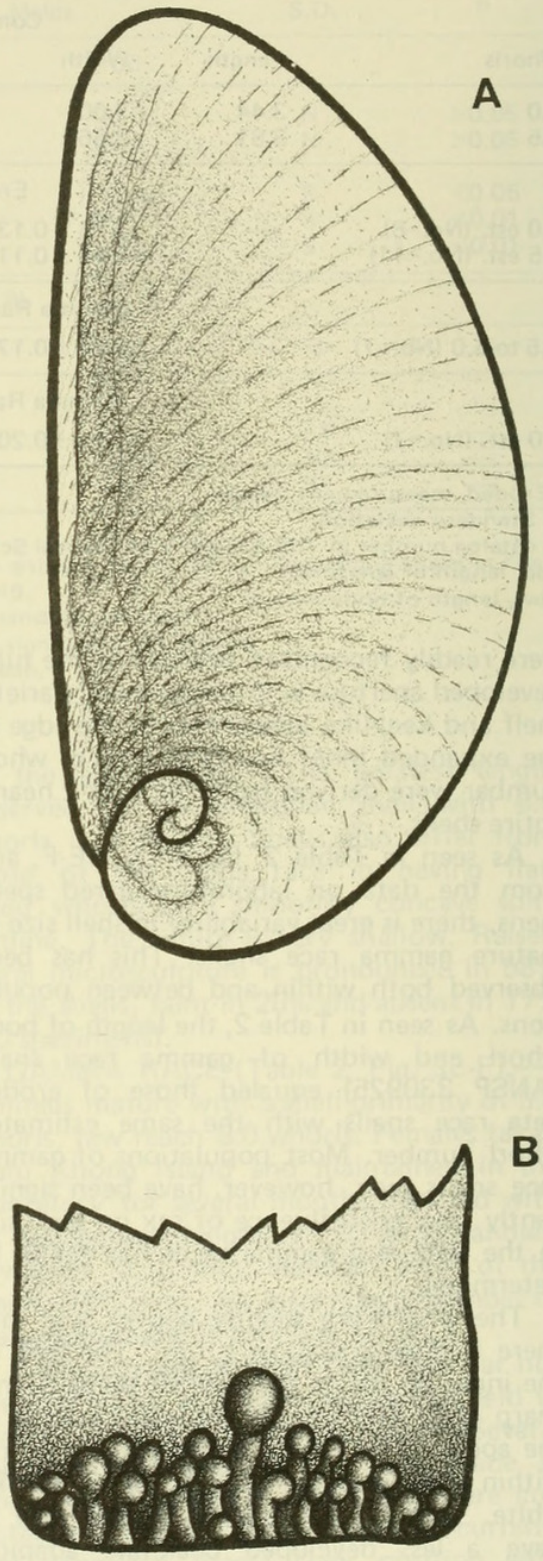


FIG. 6. A. Operculum, 1.20 mm long, from a gamma race individual. B. Glands along the anterior edge of the foot as seen (dorsal view) through the epithelium of an alcohol-preserved specimen. Note that the central gland is longest. See Fig. 16, F-I.

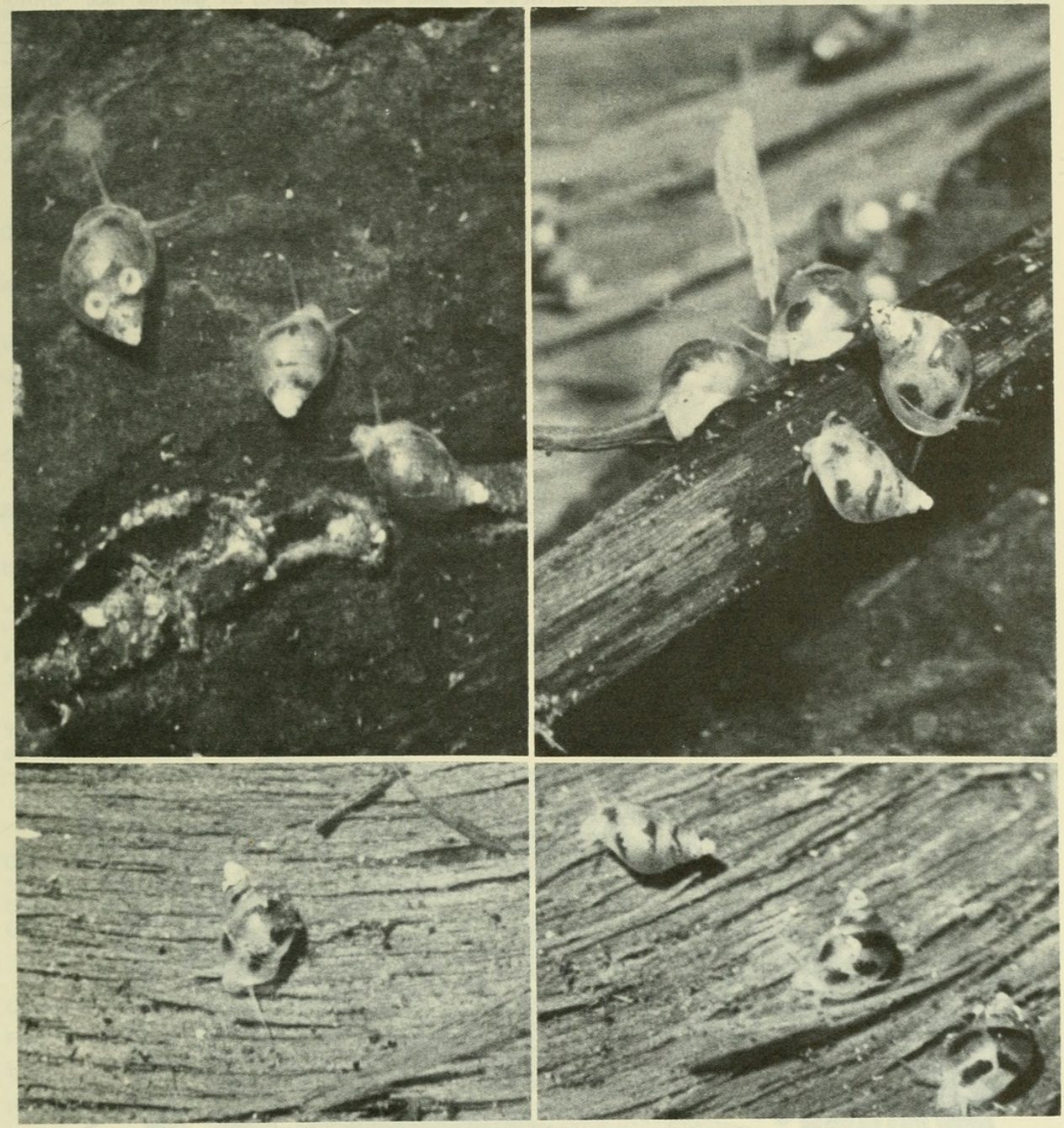


Fig. 5. Gamma race snails crawling over the substrate.

Operculum (Fig. 6A)

The operculum is thin, corneous and paucispiral. The nucleus is eccentric, nearly marginal. In gamma race snails, the left posterior margin spirals out over the columellar edge of the operculum. Growth striations are very faint. Dimensions are given in Table 3.

The operculum of alpha race snails differs slightly from that of the gamma race in that the edge of the operculum has a smooth contour, i.e. the growth spiral from the nucleus does not extend out beyond the columellar edge. As seen in Table 5, the operculum is larger than that of the gamma race, a correlate of greater shell size.

Mantle Cavity (Figs. 7, 9)

Structures in the mantle cavity are typically rissoacean. There is sexual dimorphism in the number of gill filaments; males have fewer (Tables 3-4). The length of the row of gill filaments is 1.83 mm ± 0.47 in the gamma race and 2.10 mm ± 0.17 in the alpha race. Correlated with this is the greater number of gill filaments in the alpha race (Tables 3-5).

TABLE 3. Dimensions (mm) or number of non-neural organs and structures of gamma race *"Lithoglyphopsis" aperta.*

Organ or structure		No.	$\bar{X}$	Sd	Range
Operculum	L	5	1.20	0.01	1.18-1.22
	W	4	0.68	0.03	0.68-0.70
Gill filaments					
males		4	26.8	6.07	20-34
females		9	35.7	2.17	32-40
Buccal mass	L	1	0.60	—	—
Osphradium	L	2	0.85	—	0.80-0.90
	W	1	0.14	—	—
Prostate	L	3	1.33	0.15	1.20-1.50
	W	1	0.56	—	—
Verge	L	3	2.03	0.20	1.85-2.25
Pallial oviduct	L	3	1.73	0.32	1.50-2.10
	W	1	0.34	—	—
Bursa copulatrix	L	3	1.09	0.10	1.00-1.20
	W	2	0.31	—	0.30-0.32

L, length. W, width.
No., number of snails. $\bar{X}$, mean.
Sd, standard deviation.

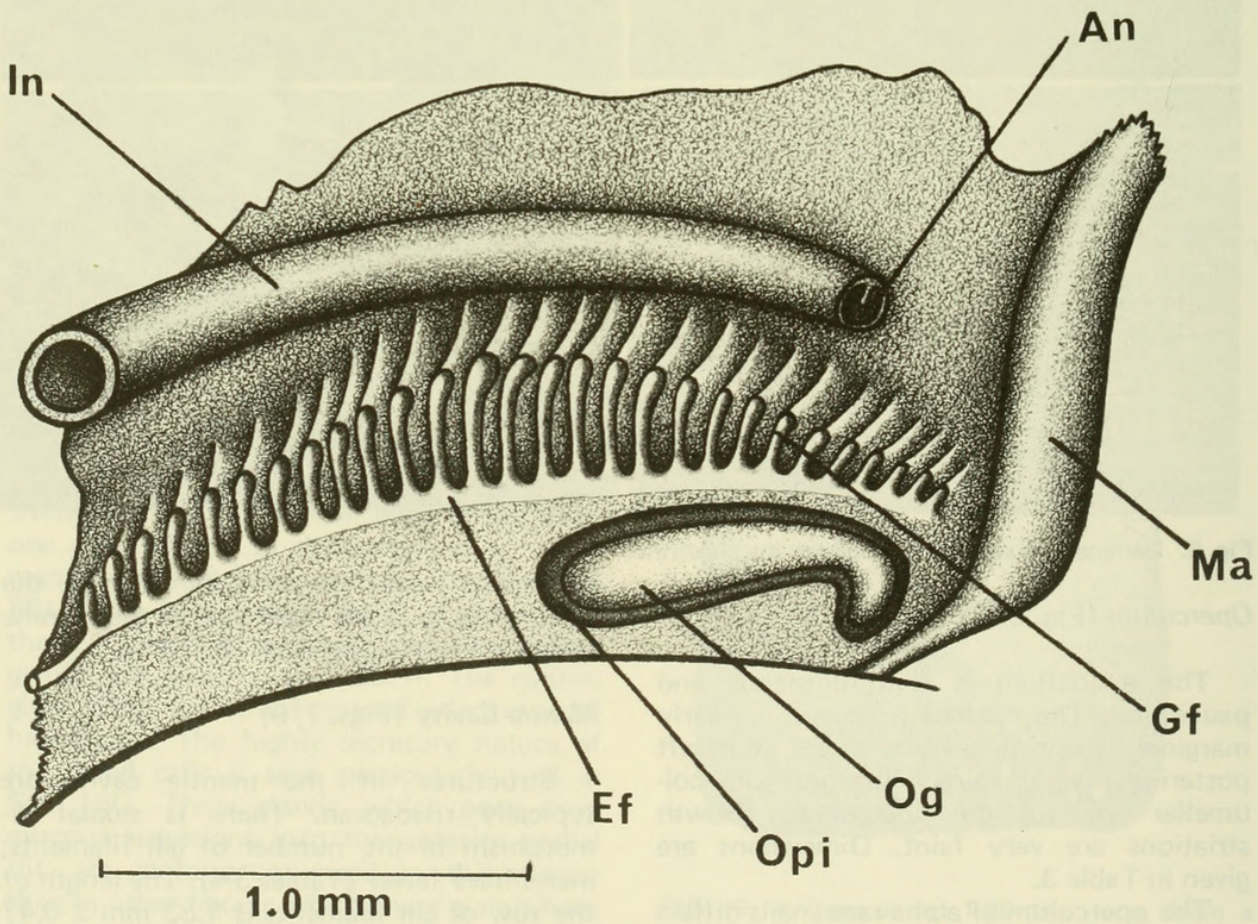


FIG. 7. Anterior end of the mantle cavity opened to reveal the relationships of the intestine, ctenidium, osphradium and mantle edge. **An**—anus; **Ef**—efferent branchial vessel; **Gf**—gill filament of the ctenidium; **In**—intestine; **Ma**—mantle edge; **Og**—osphradial ganglion; **Opi**—osphradial pit.

TABLE 4. Dimensions (mm) or numbers of non-neural organs and structures of alpha race *"Lithoglyphopsis" aperta.*

Organ or structure		No.	$\bar{X}$	Sd	Range
Operculum	L	6	1.62	0.09	1.48-1.72
	W	6	0.92	0.06	0.85-1.02
Gill filaments					
males		10	43.6	3.66	38-48
females		4	49.8	1.50	48-51
Osphradium	L	4	1.01	0.08	0.96-1.14
	W	3	0.21	0.06	0.16-0.29
Prostate	L	8	1.18	0.25	0.85-1.45
	W	8	0.36	0.08	0.21-0.48
Verge	L	8	1.63	0.33	1.16-2.42
Gonad	L	9	1.96	0.39	1.57-2.42
(m)	W	4	0.44	0.06	0.41-0.48
(f)	L	3	0.61	—	0.61-
Digestive gland	L	12	2.96	0.57	1.82-3.63
(m + f)	W	9	0.70	0.15	0.48-1.02
Pallial oviduct	L	6	2.26	0.14	2.06-2.42
	W	6	0.29	0.20	0.15-0.68
Bursa copulatrix	L	7	0.84	0.20	0.61-1.09
	W	7	0.16	0.07	0.12-0.29

f, female. No., number of snails. $\bar{X}$, mean.
L, length. Sd, standard deviation.
m, male. W, width.

TABLE 5. Statistical comparison of lengths or numbers of selected structures of the alpha and gamma races of *"Lithoglyphopsis" aperta.*

Organ or structure	Significant difference	P.	Alpha race has greater (G) lengths or numbers	Difference is correlated (+) with larger size of alpha race
Operculum	+	0.01	G	+
Gill filament no.				
males	+	0.01	G	+
females	+	0.01	G	+
Osphradium	+	0.01	G	+
Prostate	—	0.10		
Verge	—	>0.01		
Pallial oviduct	—	>0.01		
Bursa copulatrix	—	>0.01		

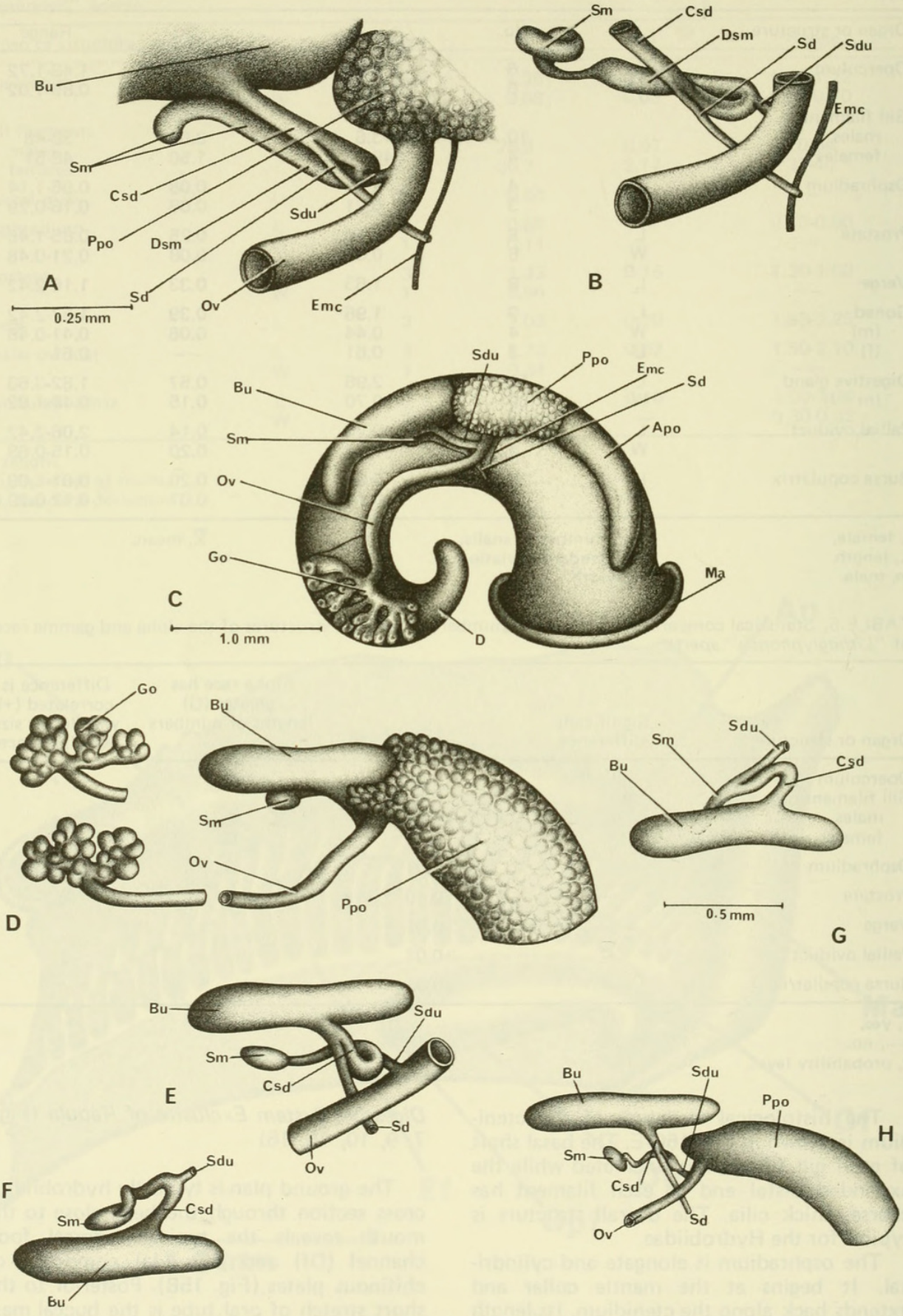
+, yes.
—, no.
P, probability level.

The histological structure of the ctenidium is shown in Fig. 16C-E. The basal shaft of each gill filament is unciliated while the expanded distal end of each filament has coarse, thick cilia. The overall structure is typical for the Hydrobiidae.

The osphradium is elongate and cylindrical. It begins at the mantle collar and extends back along the ctenidium. Its length is 46% the length of the ctenidium (measurements from 10 individuals).

Digestive System Exclusive of Radula (Figs. 7, 9, 10, 15, 16)

The ground plan is typically hydrobiid. A cross section through the head close to the mouth reveals the typically dorsal food channel (Df) and jaws (Ja) composed of chitinous plates (Fig. 15B). Posterior to the short stretch of oral tube is the buccal mass containing the odontophoral apparatus (Fig. 15C). The longitudinal section shows the


Bu
Sm
Csd
Ppo
Dsm
Sdu
Sd
Ov
Emc
A
0.25 mm
Sm
Csd
Dsm
Sd
Sdu
Emc
B
Sdu
Ppo
Emc
Sd
Bu
Sm
Apo
Ov
Go
Ma
C
1.0 mm
D
Go
Bu
Sm
Ov
Ppo
Sdu
Sm
Bu
Csd
0.5 mm
G
Bu
Sdu
Sm
Csd
Sd
Ov
E
Sdu
Sm
Csd
Bu
F
Bu
Sdu
Ppo
Sm
Csd
Sd
Ov
H

entire radula from tip of radula sac to the bending plane over the cartilage (Ca). The salivary glands, a single pair, are unbranched simple tubes which run back dorsal to the nerve ring. Ducts of the gland are shown in Fig. 16A.

The esophagus has a pronounced dorsal food groove bounded on each side by a pronounced dorsal fold. Just posterior to the cerebral ganglia several smaller folds appear in the region where the dorsal food groove is located (Fig. 15D) and the right dorsal fold becomes less pronounced until it resembles the other folds of the esophagus. Thus, only the left dorsal fold persists, as a structure twice the size of the other 8 to 9 folds. Torsion in the gut, which occurs just posterior to the cerebral ganglia, is seen by following the rotation of the left dorsal fold to a ventro-lateral position.

The stomach is like that described in *Oncomelania, Pomatiopsis,* and other hydrobiids. The topography of the ventral surface is shown in Fig. 10A, B, D. The section shown in Fig. 15E shows both the entrance of the deeply crypted esophagus (Es) into the stomach and passage from the stomach to the digestive gland (Ed).

The intestine leaves the stomach at the left ventro-lateral aspect of the style sac, coils as a U-shaped tube over the end of the style sac, and then doubles back to run anteriorly to the end of the mantle cavity. There is no slit-like communication between the style sac and the intestine. The whole length of the U-shaped portion of intestine contains an extremely pronounced typhlosole (Fig. 15G). This highly ciliated structure undoubtedly serves to send a constant stream of particles to the fecal pellet compressor located in the sharp bend where the intestine begins to run anteriorly.

The extremely strong and well-organized cilia of the style sac are shown in Fig. 15F (top row of cells) in contrast to the less organized cilia lining the roof of the anterior chamber of the stomach which slightly overlies the style sac (lower row of cells).

Radula (Fig. 11, gamma race female)

The radula is typically taenioglossate. Radular dimensions and counts of teeth are given in Table 6. Numbers of cusps on each of the 4 different teeth are quite variable, as documented in Table 7. The most generalized formulas for the alpha and gamma races are given in Table 8.

Although its shell is longer, the alpha race has a significantly shorter radula than the gamma race. There are, however, significantly more teeth on the radula (Table 6). The width of the base of the central tooth of the alpha race is greater.

No alpha race snail has been found with a central tooth formula of $\frac{4\text{-}1\text{-}4}{5\text{-}5}$, but this formula predominates in 67% of the radulae of gamma race snails. The most characteristic features of this species are: 1) the 4 to 7 cusps on the basal lateral angle of the central tooth; 2) the largest basal cusps of the

FIG. 8. Female reproductive system. The whole reproductive system in the uncoiled snail (minus head) is shown in Fig. 8C. The ventral surface of the snail is exposed. Key reference points are the anterior end of the mantle cavity (Ma) and the posterior end of the mantle cavity (Emc). The reproductive system is drawn as seen through the epithelium of the living animal.

A-B. Expanded views of the ducts associated with the bursa copulatrix (Bu) and posterior pallial oviduct (Ppo) with the snail's epithelium and kidney tissue removed. Variation in twisting of the U-shaped duct running from the bursa to the seminal receptacle is shown.

A-C were drawn from gamma race snails. D-H were drawn from alpha race snails.

D-F. The tissues of the posterior pallial oviduct shown in D are stripped away in E to reveal the interrelationships of ducts. In F, the bursa was rotated 180° to expose the nature of the coiling of the duct of the seminal receptacle and the origin of the sperm duct (Sdu).

G. The bursa rotated as in F but in this individual the seminal receptacle is a blind duct and the sperm duct is very elongate, arising near the seminal receptacle instead of the usual position at the end of the duct of the seminal receptacle.

H. An immature individual. Note the positional relationship of the anterior end of the bursa copulatrix. and the pallial oviduct. Compare with Fig. 17 C-E.

Figs. 8A and B are at the same scale, and so are Figs. 8D-H.

Apo—anterior pallial oviduct;
Bu—bursa copulatrix;
Csd—common sperm duct;
D—digestive gland;
Dsm—duct of the seminal receptacle;
Emc—posterior end of the mantle cavity;
Go—gonad;
Ma—anterior end of the mantle;
Ov—oviduct;
Ppo—posterior pallial oviduct;
Sd—spermathecal duct;
Sdu—sperm duct;
Sm—seminal receptacle.

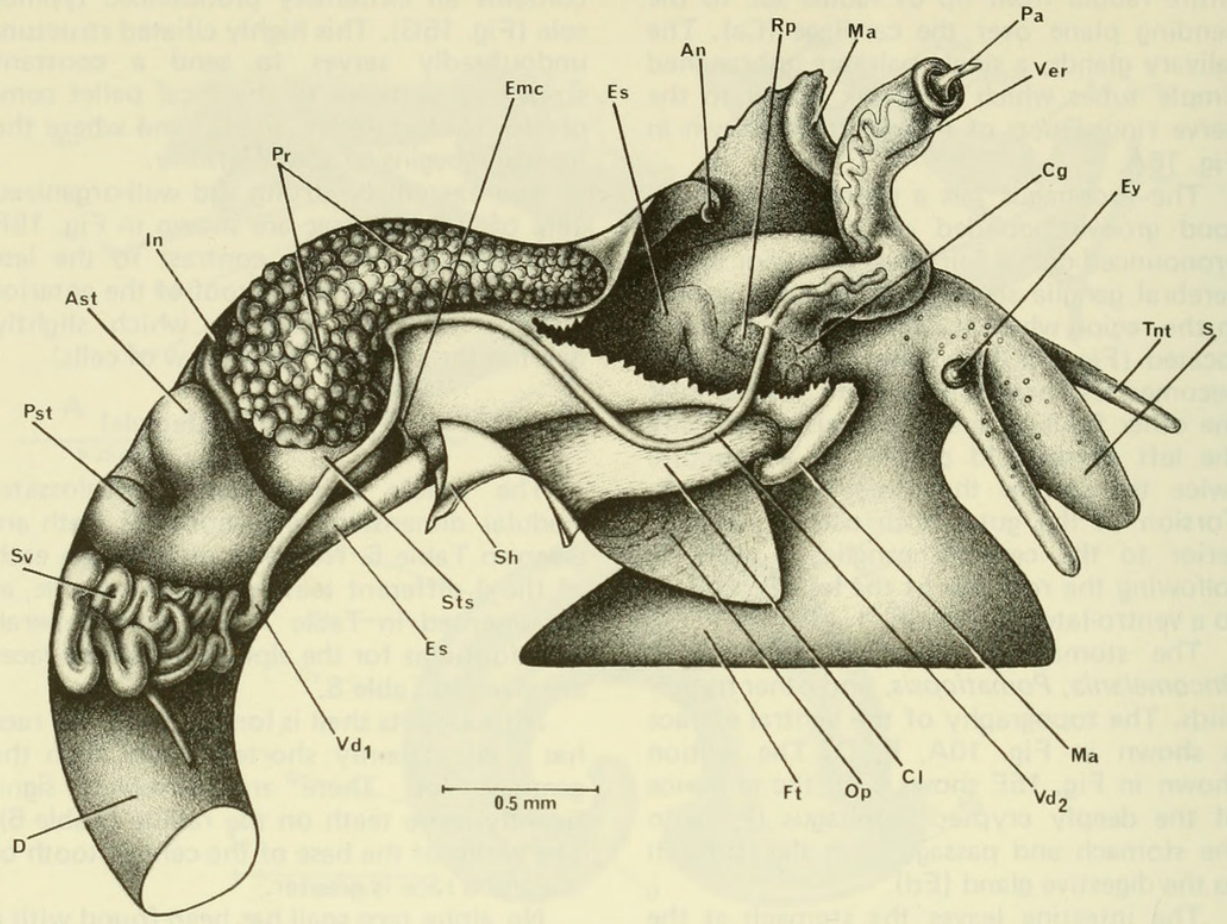


FIG. 9. Male snail of the gamma race uncoiled to reveal the ventral surface. The digestive gland (D) has been partially removed and the gonad is not shown. The mantle cavity has been opened to show the anus (An), origin of the penis (Ver = verge), and structures readily seen beneath the epithelium of the neck such as the esophagus (Es), right pleural ganglion (Rp) and cerebral ganglion (Cg). Note that the prostate (Pr) overlies the posterior end of the mantle cavity (Emc) and that the seminal vesicle (Sv) consists of very heavy coils pressed against the posterior chamber of the stomach (Pst).

An—anus;
Ast—anterior chamber of the stomach;
Cl—columellar muscle;
Cg—cerebral ganglion;
D—digestive gland;
Emc—posterior end of the mantle cavity;
Es—esophagus;
Ey—eye;
Ft—foot;
In—intestine;
Ma—anterior edge of the mantle;
Op—operculum;
Pa—papilla;
Pr—prostate;
Pst—posterior chamber of the stomach;
Rp—right pleural ganglion;
S—snout;
Sh—shell;
Sts—style sac;
Sv—seminal vesicle;
Tnt—tentacle;
Vd_1—posterior section of the vas deferens;
Vd_2—anterior section of the vas deferens;
Ver—verge.

central tooth arise from the face of the tooth; 3) the central anterior cusp of the central tooth is flanked by 3 or more cusps, and 4) the lateral tooth usually has 4 or more cusps on the inner side of the dominant cusp.

Female Reproductive System (Fig. 8A-H)

The system is rissoacean in that there is an interrelationship of bursa copulatrix, seminal receptacle, and a bipartite pallial oviduct (i.e. albumen gland [Ppo] and capsule gland [Apo]). The reproductive system is shown in Fig. 8C in relation to the general body shape and regions. Points for orientation are the mantle edge (Ma), posterior end of the mantle cavity (Emc), and digestive gland (D).

When the living animal is pinned out to expose its uncoiled ventral surface and stained with neutral red, one observes an amazingly large bursa copulatrix (Bu), the pallial oviduct (Ppo and Apo), gonad (Go) and oviduct (Ov) extending to the posterior section of the pallial oviduct (Ppo). A vague

TABLE 6. A comparison of radular traits of alpha and gamma race *"Lithoglyphopsis" aperta* using 9 individuals of each.

	alpha race		gamma race			
Radular trait	$\bar{X}$	Sd	$\bar{X}$	Sd	S.D.	P.
Length*	0.41	0.016	0.65	0.04	S	<0.01
Width	0.06	0.002+	0.09	0.03	S	<0.01
No. rows of teeth	103.8	3.73	77.9	4.09	S	<0.01
No. rows forming	7.4	2.15	9.3	3.16	N	>0.10
Width of base of central tooth	0.031**	0.001	0.027	0.001	S	<0.01

* Measurements in mm.
** No. radulae = 10.
+, highly invariable width resulting in an extremely low standard deviation.
N, not significantly different.
P, probability level.
S, significantly different.
Sd, standard deviation.
S.D., significant difference.
$\bar{X}$, mean.

impression of a tube from the bursa copulatrix running towards the oviduct is seen. Careful dissection, with removal of membranes, kidney tissue, and excessive glandular tissue of the posterior pallial oviduct, reveals a unique arrangement of tubes (Fig. 8A-B).

Sperm enter the system from within the posterior recess of the mantle cavity (Emc) and travel in the spermathecal duct (Sd, called receptacular duct in Davis, 1968b) to enter the common sperm duct (Csd). The spermathecal duct is very pronounced and easily dissected to the end of the mantle cavity. Sperm then travel to the bursa copulatrix (Bu) or to the seminal receptacle (Sm). The spermathecal duct runs dorsal to, and at right angles to the oviduct.

The bursa copulatrix is unusual for a hydrobiid because of its great length and bulk. It is, on the average, 63% the length of the pallial oviduct in the alpha and gamma races. In *Tricula* it is 24-25% (Davis, 1968b); in *Oncomelania* it is 18-24% (Davis & Carney, 1973). The anterior end is, in mature animals, slightly overgrown by the filmy glandular tissue of the posterior pallial oviduct (Fig. 8C, D). In immature animals (Fig. 8H) the anterior end of the bursa is antero-lateral to the posterior end of the pallial oviduct.

Substructures of the bursa copulatrix and its relationship to the pallial oviduct in early development are seen in histological sections (Fig. 17 A-E). Internally, the bursa has highly secretory columnar cells. Vacuoles with secretory product dominate the cells and are seen from the basal nucleus to the point of disruption into the lumen (Fig. 17G). It is clearly seen in Fig. 17C-E that the anterior end of the bursa is anterolateral to the end of the posterior pallial oviduct. When the latter matures as the fully secretory albumen gland it will surround the anterior end of the bursa as shown in Fig. 8C, D.

There is a greater tendency in the alpha race (Fig. 8D) for the bursa to be deeply embedded in the mature albumen gland. Contrast the condition seen in the gamma race (Fig. 8C).

A pronounced key trait of this species is the U-shaped common sperm duct (Csd,

TABLE 8. Formulae for the most common cusp arrangements in *"Lithoglyphopsis" aperta.*

Tooth	Formula	% Radulae with formula
	Alpha race	
Central	$\frac{4(5)\text{-}1\text{-}(5)\text{-}4}{6\text{-}6}$	100
Lateral	5(6)-1-6	66
Inner marginal	18-21	100
Outer marginal	15-17	100
	Gamma race	
Central	$\frac{4\text{-}1\text{-}4}{5(6)\text{-}(6)5}$	89
Lateral	4-1-4(5)	89
Inner marginal	17-20	100
Outer marginal	15-17	100

TABLE 7. The various cusp arrangements in the 4 types of taenioglossate teeth from the radulae of 7 alpha race and 9 gamma race *"Lithoglyphopsis" aperta.*

Central (% of radulae)			Lateral (% of radulae)		
anterior cusps / basal cusps	alpha	gamma	Cusps	alpha	gamma
4-1-4 / 5-5	—	67	4-1-5	17	67
			4-1-4	—	67
4-1-4 / 6-6	57	56	5-1-6	50	—
			5-1-4	—	44
5-1-5 / 6-6	57	44	6-1-6	33	—
			4-1-3	—	22
5-1-5 / 5-5	29	44	3-1-5	—	22
			3-1-4	—	22
5-1-5 / 7-7	29	—	4-1-6	17	—
			4-1-7	17	—
3-1-3 / 5-5	—	33	5-1-7	17	—
			5-1-8	17	—
3-1-3 / 6-6	—	33	6-1-7	17	—
			5-1-5	17	11
3-1-3 / 7-7	14	—	7-1-6	17	—
			7-1-7	17	—
4-1-4 / 7-7	—	11	5-1-3	—	11
4-1-4 / 4-4	—	11			

Inner Marginal (% of radulae)			Outer Marginal (% of radulae)		
No. cusps	alpha	gamma	No. cusps	alpha	gamma
18	67	33	16	57	89
21	67	22	17	57	67
17	17	56	15	71	44
20	50	22	18	43	—
19	33	33	19	29	—
22	33	33	14	—	22
15	—	22	13	—	11
24	22	—	12	—	11
16	17	—			
23	17	—			
25	—	11			

FIG. 10. Male reproductive system. Alpha race, A-G; gamma race, H.

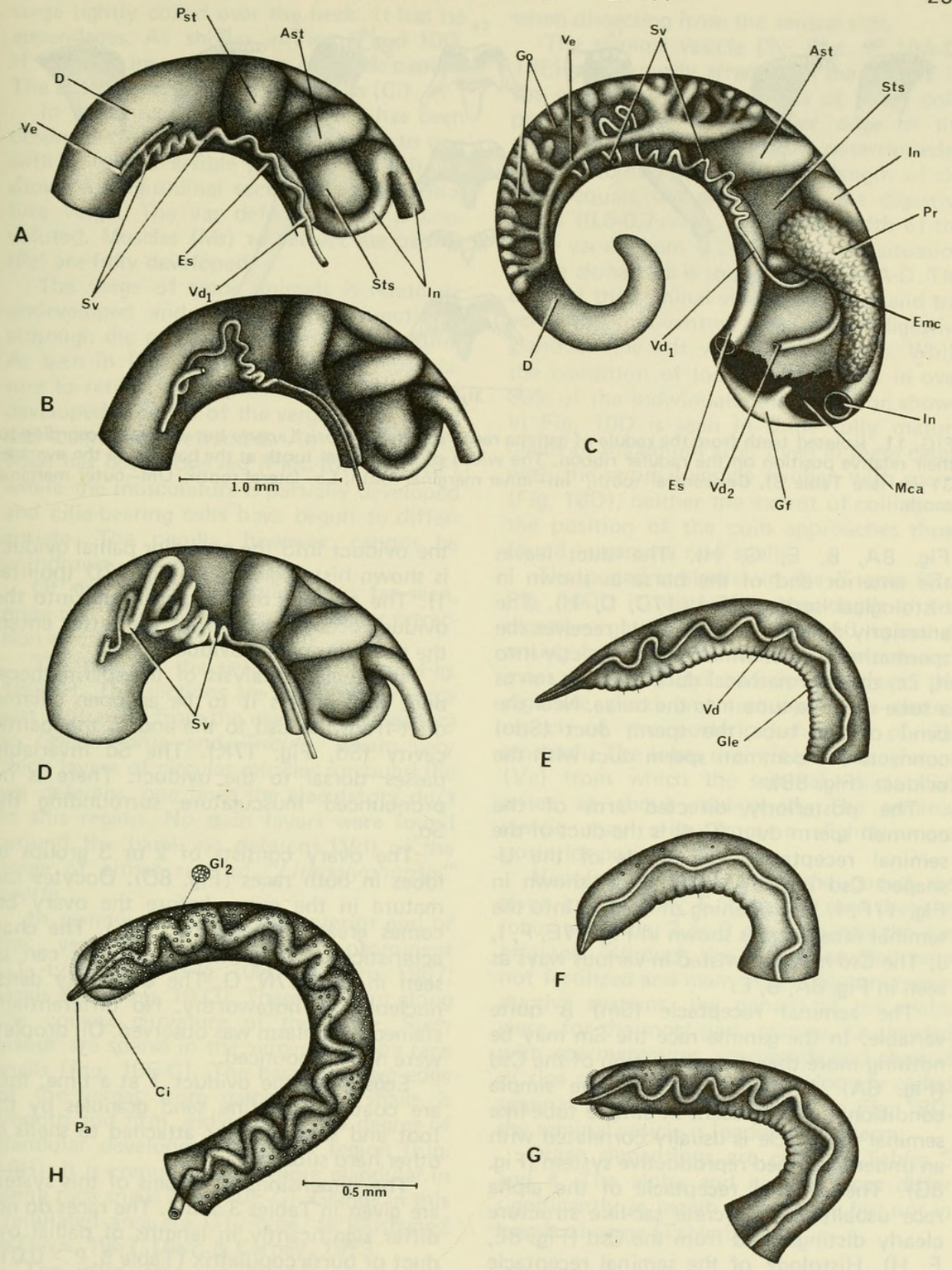
A, B, D. Variation in coiling of the seminal vesicle (Sv) shown from different individuals.

C. An uncoiled snail with the ventral surface exposed. The anterior end has been sliced off to reveal the mantle cavity (Mca), the intestine (In) and a gill filament (Gf). The loosely coiled seminal vesicle (Sv) is shown in relation to the gonad.(Go). Note that the anterior end of the gonad overlies the posterior chamber of the stomach.

E-G. Various stages in the development of the verge in alpha race snails. In E there is no papilla, only a slender prong without retractile musculature. In F there is an incipient papilla. Cilia are lacking in these early developmental stages although some solitary non-motile cilia are seen. Full development is shown in G, with a fully retractile papilla and ciliary bands.

H. Verge from gamma race snail with numerous $G1_2$ type glands, cilia and retractile papilla.

Figs. 10A-D are at the same scale, and so are Figs 10E-H.



Ast—anterior chamber of the stomach;
Ci—cilia;
D—digestive gland;
Emc—posterior end of the mantle cavity;
Es—esophagus;
Gf—gill filament;
Gle—glandular scalloped edge of the verge;
Gl_2—gland type 2 of the verge;
Go—gonad;
In—intestine;
Mca—mantle cavity;
Pa—papilla;
Pr—prostate;
Pst—posterior chamber of the stomach;
Sts—style sac;
Sv—seminal vesicle;
Vd_1—posterior section of the vas deferens;
Vd_2—anterior section of the vas deferens;
Ve—vas efferens.

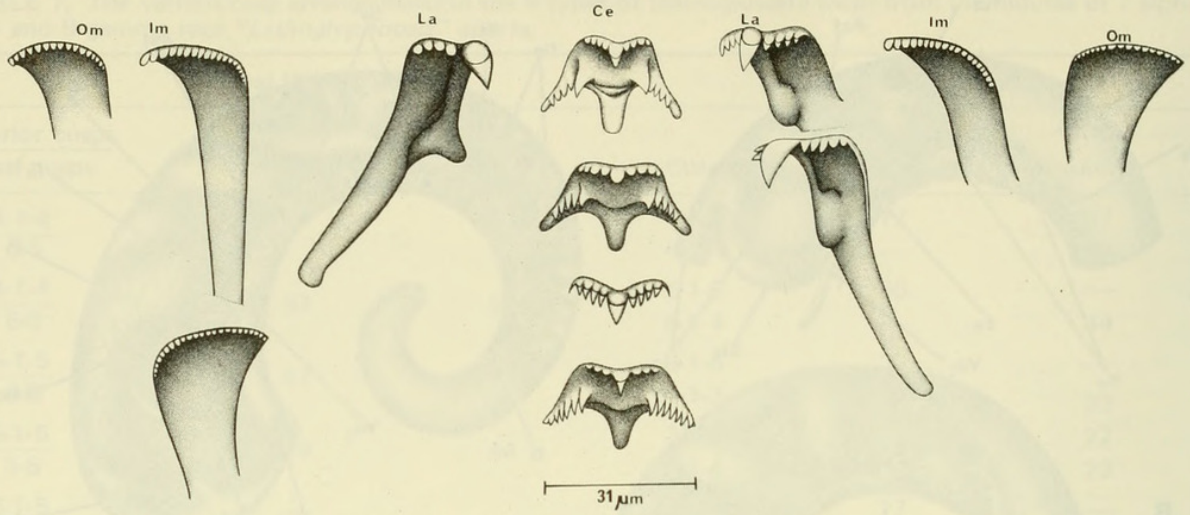


FIG. 11. Isolated teeth from the radula of gamma race *"Lithoglyphopsis" aperta* but arranged according to their relative position on the radular ribbon. The width of the central tooth at the base is, on the average, 31 µm (see Table 8). **Ce**—central tooth; **Im**—inner marginal tooth; **La**—lateral tooth; **Om**—outer marginal tooth.

Fig. 8A, B, E, G, H). The duct leaves the anterior end of the bursa as shown in histological section (Fig. 17C, D, H). The anteriorly directed arm of the U receives the spermathecal duct which opens directly into it, i.e. the spermathecal duct does not run as a tube-within-a-tube into the bursa. Near the bend of the tube, the sperm duct (Sdu) connects the common sperm duct with the oviduct (Fig. 8B).

The posteriorly directed arm of the common sperm duct (Csd) is the duct of the seminal receptacle. The whole of the U-shaped Csd is heavily ciliated as shown in Fig. 17F, I. The opening of the Csd into the seminal receptacle is shown in Fig. 17E, F, I, J. The Csd may be twisted in various ways as seen in Fig. 8A, B, E.

The seminal receptacle (Sm) is quite variable. In the gamma race the Sm may be nothing more than a continuation of the Csd (Fig. 8A). In the alpha race the simple condition is rarely seen. A simple tube-like seminal receptacle is usually correlated with an underdeveloped reproductive system (Fig. 8G). The seminal receptacle of the alpha race usually is a discrete sac-like structure clearly distinguished from the Csd (Fig. 8E, F, H). Histology of the seminal receptacle (Fig. 17E, F, J) reveals a simple unciliated cuboidal epithelium.

The posterior pallial oviduct (Ppo) appears highly glandular in gross dissection (Fig. 8C, D) and functions as the albumen gland. It is sharply set off from the smooth, firm anterior pallial oviduct (Apo) which functions as a capsule gland. The opening of the oviduct into the posterior pallial oviduct is shown histologically in Fig. 17D (pointer 1). The opening of the sperm duct into the oviduct occurs just before the latter enters the posterior pallial oviduct.

Histological analysis of the spermathecal duct (Sd) shows it to be an open ciliated duct from the Csd to the end of the mantle cavity (Sd, Fig. 17K). The Sd invariably passes dorsal to the oviduct. There is no pronounced musculature surrounding the Sd.

The ovary consists of 2 or 3 groups of lobes in both races (Fig. 8D). Oocytes can mature in the ovary before the ovary becomes greatly lobed (Fig. 17L). The characteristics of fully mature oocytes can be seen in Fig. 17N, O. The extremely dense nucleolus is noteworthy. No differentially stained cytoplasm was observed. Oil droplets were not pronounced.

Eggs leave the oviduct 1 at a time; they are coated with fine sand granules by the foot and subsequently attached to shells or other hard substrates.

The dimensions of organs of this system are given in Tables 3 and 4. The races do not differ significantly in lengths of pallial oviduct or bursa copulatrix (Table 5; $P > 0.01$).

Male Reproductive System (Figs. 9, 10)

The male reproductive system has the standard hydrobiid ground plan. The verge (Ver, Fig. 9) arises from the side of the neck to the right of the mid-line and behind the right tentacle. The living animal carries the

verge tightly coiled over the neck. It has no appendages. As shown in Figs. 9 and 10G, H, the mature verge has an eversible papilla. The anterior end is covered by cilia (Ci).

In alpha race snails a transition has been observed from a non-papillate verge to one with a fully eversible papilla. Fig. 18B, D, shows a longitudinal section through a mature verge. The vas deferens (Vd) is convoluted. Muscles (Ms) to retract the papilla (Pa) are fully developed.

The verge of some animals is relatively undeveloped and probably not functional although the prostate and testes are mature. As seen in Figs. 10E and 18I, the musculature to retract the papilla and cilia have not developed. The tip of the verge is drawn out and cannot be retracted. An intermediary stage has been observed (Figs. 10F and 18F) where the musculature is partially developed and cilia-bearing cells have begun to differentiate. The papilla, however, cannot be withdrawn.

Of the gamma race snails thus far seen, none had immature stages of papillar retraction or cilia.

The base of the verge is shown in Fig. 18G, H. The sections are through the verge just as it arises from the neck. In such genera as *Oncomelania* and *Tricula,* where very thick layers of circular muscles surround the vas deferens, one finds the ejaculatory duct in this region. No such layers were found around the basal vas deferens (Vd) of the verge of either race of *"Lithoglyphopsis" aperta*.

In gamma race snails the anterior end of the verge is packed with prominent $G1_2$-type glands (Fig. 10H; see Davis, 1967; Davis & Carney, 1973). These thin out along the convex curvature of the verge. Such glands are sparse in the verges of alpha race snails (Fig. 10E-G). The basal concave edge of the verges from gamma race snails is smooth and firm, indicating a low degree of glandular development in that region (Fig. 10H); it is crenulated and more glandular in alpha race snails (Fig. 10E-G). Glands in this crenulated area are $G1_3$-type, as illustrated in Davis, 1967; Davis & Carney, 1973.

The intra-verge vas deferens is central, thick, and undulating.

In both races the prostate (Pr, Figs. 9, 15A) overlies the posterior end of the mantle cavity. The posterior section is ventral to the style sac of the stomach so that the prostate hides the style sac from view when dissecting from the ventral side.

The seminal vesicle (Sv, Figs. 9, 10A-D, 18E) is differently arranged in the 2 races. In the gamma race it is a mass of heavy coils pressed against the anterior edge of the digestive gland and against the posterior edge of the stomach (Fig. 9). The length of the mass equals the diameter of the digestive gland (0.6-0.7 mm), while the width of the mass varies from 0.2-0.4 mm. The situation in the alpha race is shown in Fig. 10A-D. The coils of the seminal vesicle are loose and traverse the mid-ventral area of the digestive gland or the left ventro-lateral edge. While the condition of loose coils is seen in over 80% of the individuals, the condition shown in Fig. 10D is seen in some fully mature males of maximum size. Even in these cases, with the seminal vesicle swollen with sperm (Fig. 18D), neither the extent of coiling nor the position of the coils approaches those found in gamma race snails.

The gonad is similar in the 2 races (Go, Fig. 10C); it nearly fills the length of the digestive gland. There are 8-10 branches arising from the vas efferens. The anteriormost lobes expand anteriorly beyond the digestive gland and rest upon the ventral aspect of the posterior chamber of the stomach. The lobes drain into a vas efferens (Ve) from which the seminal vesicle (Sv) arises at about mid-gonad. The seminal vesicle may arise from a slightly more posterior position.

Histological sections of the gonad are given in Fig. 18A, E. It can be seen that the lobes are wide, 2 or 3 draining into the vas efferens. Although the females studied were not fertilized and many had immature reproductive systems, the gonads of the males were, for the most part, mature, i.e., loaded with spermatocytes, spermatids and clusters of ripe sperm. Sections of the loosely coiled seminal vesicle (Sv) are shown in Fig. 18D; the seminal vesicle is loaded with sperm.

Organ dimensions are given in Tables 3 and 4. The alpha and gamma races differ significantly in length of prostate but not in length of verge (Table 5).

Nervous System (Figs. 12-14)

The nervous system is typically hydrobiid. Measurements of the lengths of the primary neural structures are given in Table 9. The races are similar. Distinctive aspects of the nervous system of this species are:

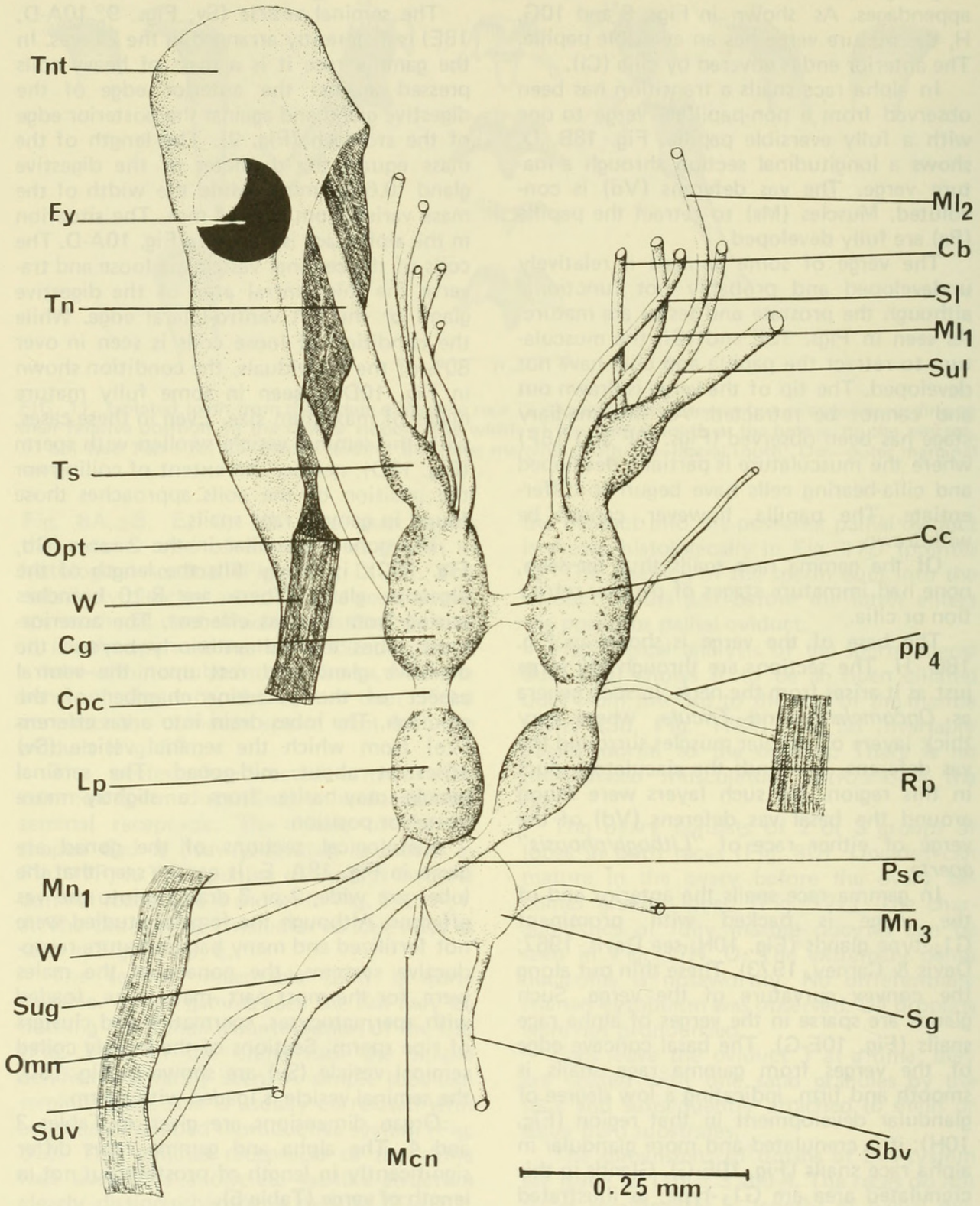


FIG. 12. Central nervous system seen from dorsal aspect. Note the great amount of melanin on the cerebral (Cg) and pleural (Rp and Lp) ganglia as well as the swelling of the tentacular nerve (Ts). A portion of the tentacle (Tnt) is shown.

1) There is heavy pigment on the cerebral and pedal ganglia, and usually also on the pleural ganglia. 2) The origin of the tentacular nerve is far anterior on the cerebral ganglion, and the tentacular nerves have prominent pigmented swellings (Ts, Fig. 12). 3) The pedal commissure is elongate compared with that known in other hydrobiids (Pc, Fig. 14). 4) In some individuals the pleural ganglia are not tightly fused against the cerebral ganglia, i.e. there is a distinct cerebro-pleural connective (Cpc, Fig. 12).

General intrapopulation variation in neural structures is similar to that discussed by Davis & Carney (1973).

Histological sections (Fig. 16A, B) reveal the darkly pigmented cerebral and pedal ganglia. Note the elongate pedal commissure (Fig. 16B). The statocyst (Stc) with a single statolith is shown in Fig. 16B.

A condition where the connectives are short relative to the size of the animal and size of the nervous system is considered an advanced or highly evolved state. This is based on the assumption that a condensed nervous system is more efficient in neuromuscular coordination and neuro-regulatory functions. By contrast, elongate connectives and a "loose" nervous system is considered primitive (Fretter & Graham, 1962).

Few drawings of hydrobiid and rissoid nervous systems exist where one can find a measurement scale or have confidence that the drawings were accurately proportioned. Where data seem accurate, taxa of the 2 families appear to vary considerably in the lengths of the osphradio-mantle nerve and the supraesophageal connective.

In order to assess the degree of condensation of the supraesophageal nerve tract, particularly the closeness of the supraesophageal ganglion to the right cerebral ganglion, we have established the length of the connective divided by the sum of the lengths of the right pleural ganglion, the pleuro-supraesophageal connective, and the supraesophageal ganglion. Data derived from this study and the literature are given in Table 10. The higher the value, the greater the relative length of the connective. As seen from the data, in spite of different shell lengths, taxa of the Pomatiopsinae and Triculinae thus far studied have rather similar values, ranging from 0.40 to 0.49. We consider this length intermediate. The connective of taxa placed in the Hydrobiinae varies from elongate in *Hydrobia* (50 to 63% of the total length) to short in *Lithoglyphus* (7%). The 1 species of *Rissoa* for which data were available has a connective of rather intermediate length. The connective of *Littorina littorea* (Linnaeus) is exceptionally elongate.

DISCUSSION

Races or Species?

The summary of differences between the 3 races of *"Lithoglyphopsis" aperta* given in Tables 5 or 11 or discussed in the text suggest that there may be 3 species. Differences include shell size and microsculpture, pigment patterns, radular traits, coiling of the seminal vesicle, and attributes of the verge.

Further weight is given to the hypothesis that the taxa are either species or subspecies when one considers factors of environment and differential rates of maturation. The beta race has only been found at 1 locality, the Mun River below Pibun Mangsahan. The Mun River flows into the Mekong River at the islands near Ban Dan, locations inhabited by gamma race *"L." aperta.* Living beta race snails were collected from the undersides of boulders in swift rapids at Ban Hin Lart near

---

Cb—cerebro-buccal connective;
Cc—cerebral commissure;
Cg—cerebral ganglion;
Cpc—cerebro-pleural connective;
Ey—eye;
Lp—left pleural ganglion;
Mcn—mid-columellar nerve;
Ml_1—median labial nerve—1;
Ml_2—median labial nerve—2;
Mn_1—mantle nerve—1;
Mn_3—mantle nerve—3;
Omn—osphradio-mantle nerve;
Opt—optic nerve;
pp_4—lateral nerve—4;
Psc—pleuro-supraesophageal connective;
Rp—right pleural ganglion;
Sbv—subvisceral connective;
Sg—subesophageal ganglion;
Sl—supralabial nerve;
Sug—supraesophageal ganglion;
Sul—sublabial nerve;
Suv—supravisceral connective;
Tn—tentacular nerve;
Tnt—tentacle;
Ts—swelling of the tentacular nerve;
W—left wall of the neck.

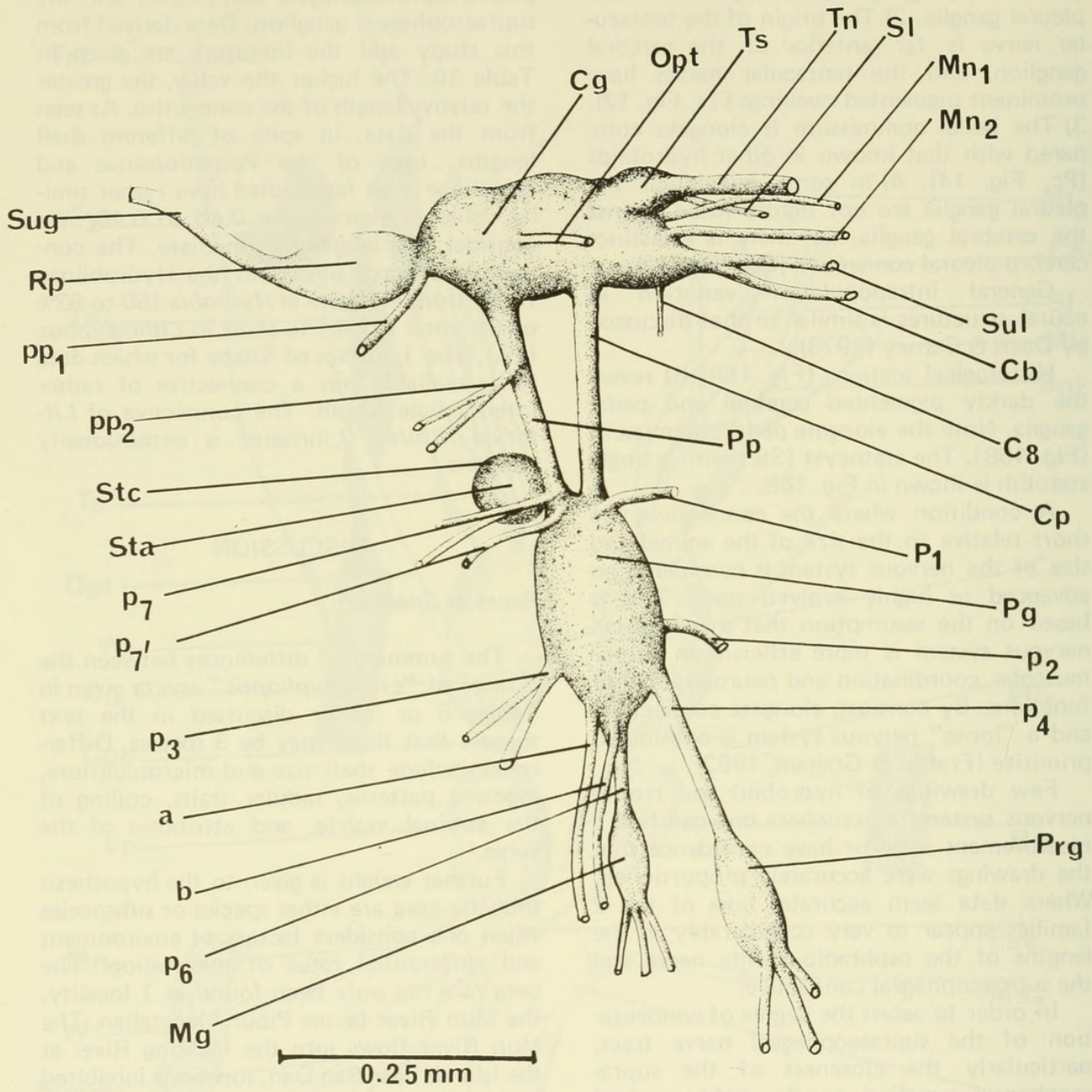


FIG. 13. Lateral view of the cerebro-pedal nerve complex.

a—nerve from p_6;
b—nerve from p_6;
c_8—cerebro-tensor nerve;
cb—cerebro-buccal connective;
Cg—cerebral ganglion;
Cp—cerebro-pedal connective;
Mg—metapodial ganglion;
Mn_1—median labial nerve—1;
Mn_2—median labial nerve—2;
Opt—optic nerve;
P_1—lateral retractor nerve;
P_2—nerve to antero-ventral wall of the pedal haemocoel;
P_3—major lateral nerve of the pedal ganglion;
P_4—propodial connective;
P_6—metapodial connective;
P_7—dorso-lateral pedal nerve;
P_7'—secondary dorso-lateral pedal nerve;
Pg—pedal ganglion;
pp—pleuro-pedal connective;
pp_1—lateral nerve—1;
pp_2—lateral nerve—2;
Prg—propodial ganglion;
Rp—right pleural ganglion;
Sl—supralabial connective;
Sta—statolith;
Stc—statocyst;
Sug—supraesophageal connective;
Sul—sublabial nerve;
Tn—tentacular nerve;
Ts—swelling of the tentacular nerve.

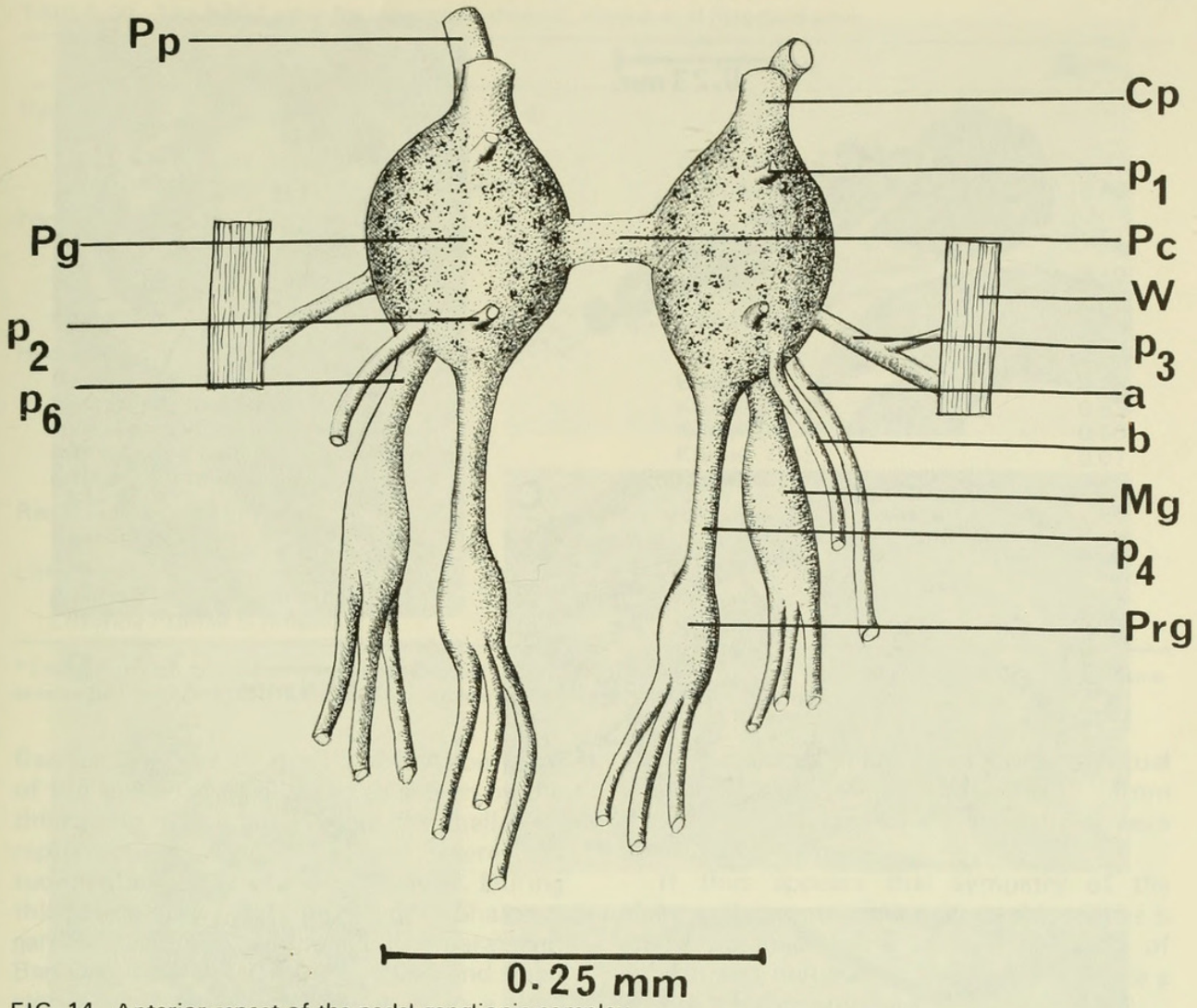


FIG. 14. Anterior aspect of the pedal ganglionic complex.

a—nerve from p_6;
b—nerve from p_6;
Cp—cerebro-pedal connective;
Mg—metapodial ganglion;
p_1—lateral retractor nerve;
p_2—nerve to antero-ventral wall of the pedal haemocoel;
p_3—major lateral nerve of the pedal ganglion;
p_4—propodial connective;
p_6—metapodial connective;
Pc—pedal commissure;
Pg—pedal ganglion;
Pp—pleuro-pedal connective;
Prg—propodial ganglion;
W—wall of the pedal haemocoel.

TABLE 9. Measurements (mm) of lengths of neural structures of gamma race *"Lithoglyphopsis" aperta.*

Structure	No.	$\bar{X}$	Sd	Range
Cerebral ganglion	4	0.23	0.02	0.20-0.24
Cerebral commissure	2	0.045	——	0.04-0.05
Pleural ganglia				
Right	4	0.12	0.02	0.10-0.14
Left	4	0.12	0.01	0.10-0.12
Pleuro-supraesophageal connective	4	0.16	0.04	0.10-0.20
Supraesophageal ganglion	4	0.12	0.02	0.10-0.14
Osphradio-mantle nerve	3	0.26	0.05	0.20-0.30
Subesophageal ganglion	3	0.11	0.01	0.10-0.12
Pedal ganglion	2	0.18	——	0.16-0.20
Pedal commissure	3	0.07	0.002	0.06-0.08

No., number of snails.
Sd, standard deviation.
$\bar{X}$, mean.

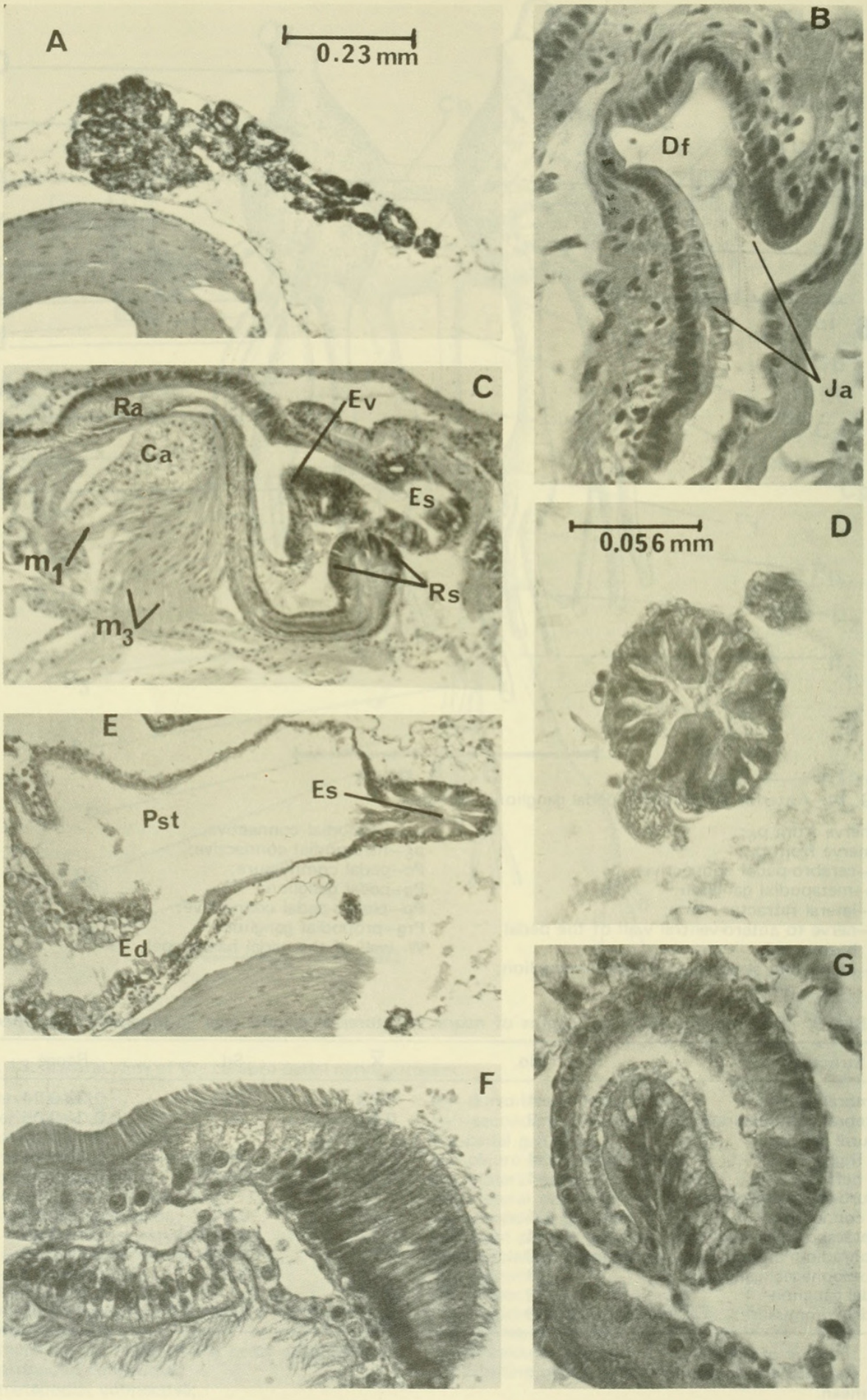

A
0.23 mm
B
Df
Ja
C
Ra
Ca
Ev
Es
m_1
m_3
Rs
D
0.056 mm
E
Es
Pst
Ed
F
G

TABLE 10. The RPG* ratio for selected hydrobiid, rissoid, and littorinid taxa.

Taxon	Reference	RPG
Hydrobiidae		
Triculinae		
Tricula bollingi Davis	Davis, 1968b	0.47
"Lithoglyphopsis" aperta Temcharoen	this paper	0.40
Pomatiopsinae		
Oncomelania hupensis chiui (Habe & Miyazaki)	Davis, 1968a	0.49
O. h. lindoensis Davis & Carney	Davis & Carney, 1973	0.40
Pomatiopsis lapidaria (Say)	Davis, 1967	0.42
Hydrobiinae		
Bythinella dunkeri (Frauenfeld)	Bregenzer, 1916	0.18
Hydrobia ulvae (Pennant)	Krull, 1935	0.63
Hydrobia ventrosa (Montagu)	Krull, 1935	0.50
Lithoglyphus naticoides (Fér.) Pfeiffer	Krause, 1949	0.07
Semisalsa dalmatica Radoman	Radoman, 1974	0.36
Rissoidae		
Rissoa inconspicua Alder	Johansson, 1939	0.32
Littorinidae		
Littorina littorea (Linnaeus)	Johansson, 1939	0.72
Littorina littorea (Linnaeus)	Fretter & Graham, 1962	0.84

*The length of the pleuro-supraesophageal connective divided by the sum of the lengths of the supra-esophageal ganglion, pleuro-supraesophageal connective and right pleural ganglion.

Ban Sai Mun on 26 April 1974. About 10% of the shells were full-sized as shown by the thickening of the outer lip of the shell. The reproductive systems, however, were too rudimentary for anatomical analysis. During this same low water period, alpha and gamma races were found at Khemarat and Ban Dan, clustered on sticks, shells and small stones in shallow quiet water or in a slow current. Gamma race snails collected from Ban Dan during the same week were only 1/3 grown; those collected from Khong Island in mid-May, 1974, were not yet 1/2 grown.

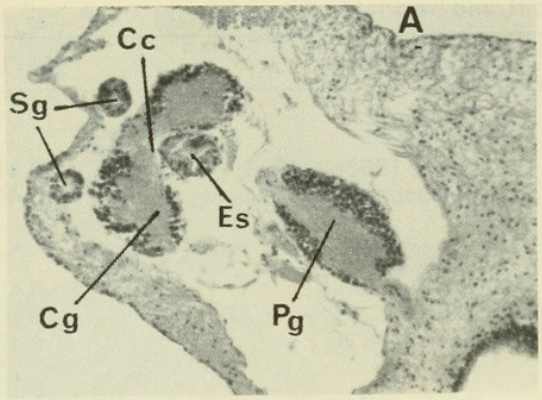
Alpha race snails collected from Khemarat in June 1973 had fully developed shells and nearly mature reproductive systems. Some males had reached sexual maturity. Gamma race snails from Khemarat, collected at the same time, were about half grown.

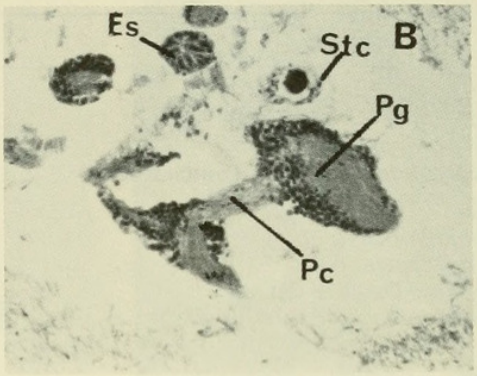
It thus appears that sympatry of the alpha and gamma races at several localities is made possible by a differential rate of growth and maturation which might create a barrier to cross breeding.

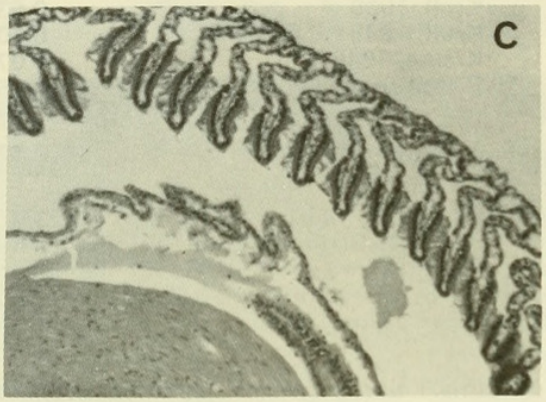
What are the factors that weaken the case for species status for the 3 taxa? There are several populations where snails were fully mature. These are most difficult to obtain, as full sexual maturity occurs in late May or in June after the rainy season has begun and populations are several meters under swift current. The data presented here for

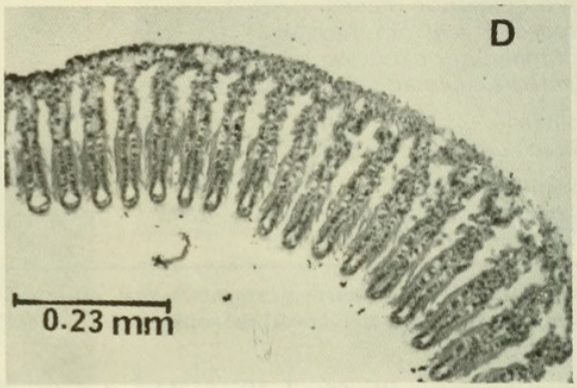
FIG. 15. Histology of the male reproductive system (A) and digestive system (B-G).
A. Prostate in an early stage of development with the columellar muscle seen below.
B. Oral aperture sectioned through the jaws (Ja).
C. Buccal mass featuring the odontophore apparatus with cartilage (Ca), radula (Ra), radular sac (Rs) and intrinsic muscles m_1, m_3.
D. Cross section of the esophagus.
E. Section showing the entrance of the esophagus (Es) into the stomach, and the entrance of the stomach (Ed) into the digestive gland.
F. Heavily ciliated columnar cells lining the style sac are shown above while less densely organized cilia shown below line the roof of the anterior chamber of the stomach.
G. Cross section of the intestine with pronounced typhlosole.
Figs. 15A, C and E are at the same scale, and so are Figs. 15B, D, F, and G.

Ca—cartilage;
Df—dorsal food groove;
Ed—entrance of stomach to the digestive gland;
Es—esophagus;
Ev—esophageal valve;
Ja—jaws;
m_1—lateral cartilage tensor;
m_3—odontophore divaricator;
Pst—posterior chamber of the stomach;
Ra—radula;
Rs—radular sac.

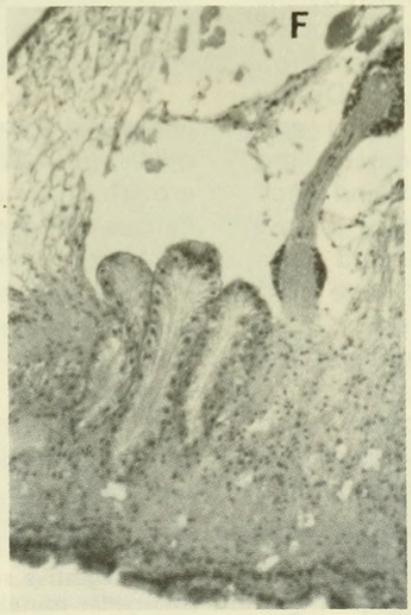

A
Cc
Sg
Es
Cg
Pg

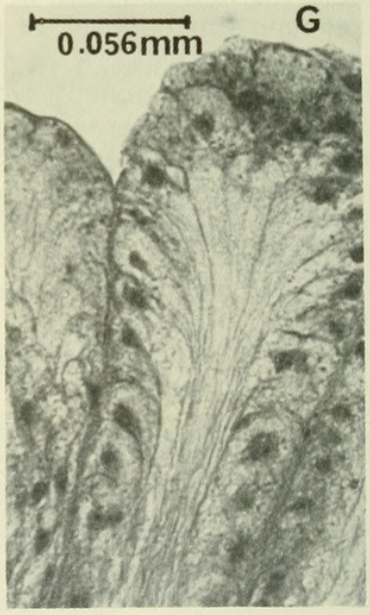

Es
Stc
B
Pg
Pc

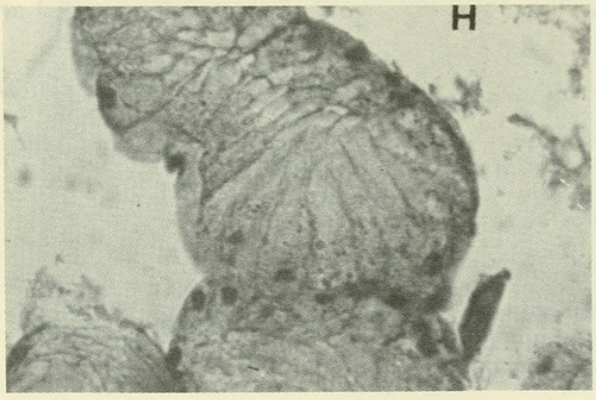

C


D
0.23 mm


E


F


0.056mm
G


H

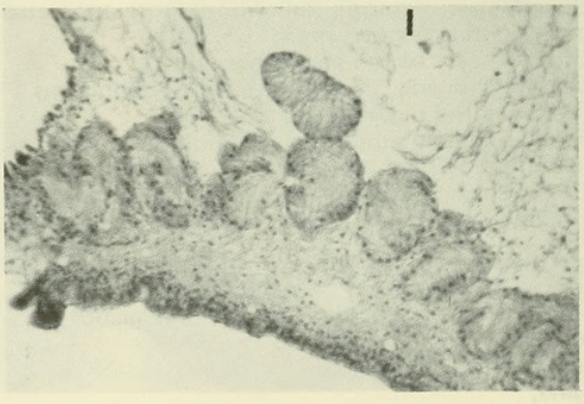

I

TABLE 11. Summary of differences between the races of *"Lithoglyphopsis" aperta*. See text for details.

Trait	alpha	beta	gamma
1. Shell length (mm)	3.15-3.26	2.94-2.95	2.68
2. No. whorls	6.0-6.5	6.0-6.5	5.5-6.0
3. Concave outline to spire	–	+	–
4. Shouldered whorls	+	–	+
5. Shell microsculpture	–	+	–
6. Pigment spots on mantle	–	–	+
7. Contour operculum smooth and continuous	+	?	–
8. Length of ctenidium (mm)	2.10	?	1.83
9. No. gill filaments	44-50	?	27-36
10. Radular length (mm)	0.41	?	0.65
11. No. rows central teeth on radula	104	?	78
12. Width central tooth (mm)	0.031	?	0.027
13. Central tooth formula			
$\frac{5\text{-}1\text{-}5}{6\text{-}6}$	+	?	–
$\frac{4\text{-}1\text{-}4}{5\text{-}5}$	–	?	+
14. Seminal receptacle a discrete sac	+	?	–
15. Seminal vesicle a coiled mass against digestive gland	–	?	+

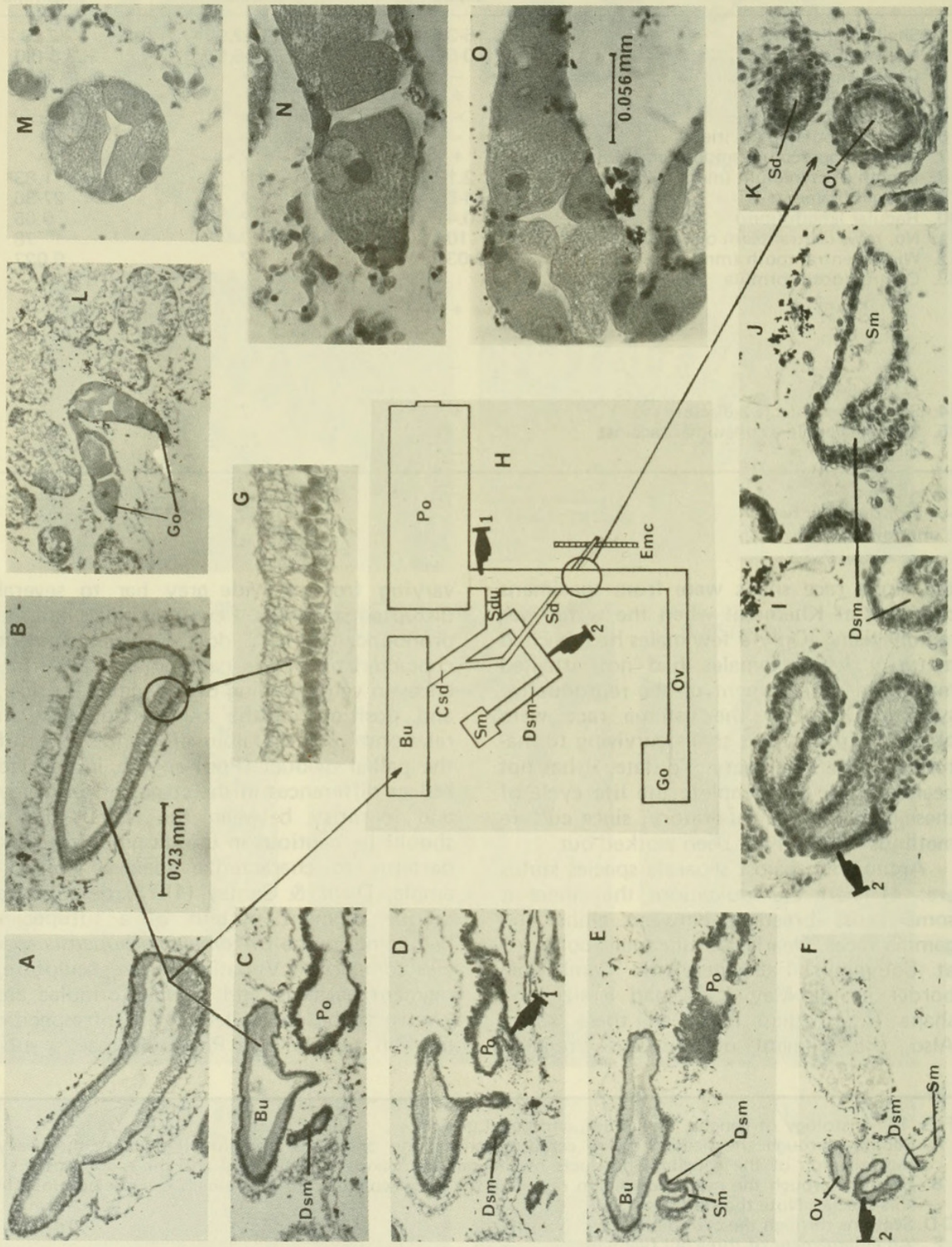
+, yes or has.
–, no or does not have.
?, unknown.

the alpha race snails were from specimens collected at Khemarat when the water was rapidly rising. Only a few males had reached maturity while females had not attained maximum development of the reproductive system. Data for the gamma race were obtained from those snails surviving to maturity in the laboratory. To date, it has not been possible to complete the life cycle of these snails in the laboratory, since culture methods have not yet been worked out.

Arguments against separate species status are: 1) There are indications that there is some cross breeding between alpha and gamma races. Nearly mature snails collected at Sompamit Falls near the Cambodian border in mid-May 1974 had a size and shape intermediate between these races. Also, the pigment pattern was irregular, varying from a wide grey bar to several disrupted splotches. Few individuals had the pronounced 4 to 5 dots of black pigment characteristic of the gamma race. 2) Differences in verge, coiling of the seminal vesicle, and position of the bursa copulatrix in relationship to the albumen gland section of the pallial oviduct (Ppo) appear, in part, to reflect differences in the stages of ontogeny and maturity between the races. 3) One should be cautious in using unique pigment patterns to characterize species. For example, Davis & Carney (1973) described a unique pigment pattern of a subspecies belonging in the *Oncomelania hupensis* species complex. 4) Variation in size, sculpture, pigment patterns, and radular formulae are known to be controlled at the infraspecific level in taxa of the Pomatiopsinae, a sub-

FIG. 16. Histology of ganglia, ctenidium, and pedal glands.
A. Section through the head showing cerebral ganglia and one pedal ganglion (Pg). Note the heavy melanization of the ganglia. The ducts of the salivary glands are seen (Sg) and the esophagus (Es).
B. Section through the head-foot region revealing the pedal commissure (Pc) which is especially long in this species. Note the statocyst (Stc).
C-D. Sections through the ctenidium.
E. An enlargement of three gill filaments.
F-I. Sections of the mucous glands at the anterior edge of the foot shown in Fig. 6B. The central gland is elongate and projects into the pedal haemocoel. Enlargements of these glands are given in G and H.
Figs. 16A-D, F and I are at the same scale, and so are Figs. 16E, G and H.

Cc–cerebral commissure;
Cg–cerebral ganglion;
Es–esophagus;
Pc–pedal commissure;
Pg–pedal ganglion;
Sg–duct of salivary glands;
Stc–statocyst.



Bu—bursa copulatrix;
Csd—common sperm duct;
Dsm—duct of seminal receptacle;
Emc—posterior end of the mantle cavity;
Go—gonad;
Ov—oviduct;
Po—pallial oviduct;
Sd—spermathecal duct;
Sdu—sperm duct;
Sm—seminal receptacle.

family closely allied geographically, and possibly genetically, to the Triculinae (Davis, 1967; 1968a; 1968b; 1971; Davis & Carney, 1973; Davis & Ruff, 1974). For example, Davis & Ruff (1974) demonstrated that ribbing in *Oncomelania* is controlled by a dominant gene and that the degree of ribbing appears to be controlled by multiple alleles. Likewise, the variation in microsculpture in a single population of the beta race suggests control by multiple alleles.

Variation in cusp formulae in polytypic *Oncomelania hupensis* is notorious (Davis & Carney, 1973). The same magnitude of variation is seen for *"L." aperta* in Table 7. It is expected that, as more populations of *"L." aperta* are studied, apparent differences between races will lessen.

The tradition in malacology has been to present cusp formulae from 1 row of teeth from 1 radula (Bartsch, 1936). Little attention to variation is usually given (Brandt, 1968, 1970; Thompson, 1968). However, if variability is not adequately studied, one may repeat mistakes exemplified by Bartsch (1936) who separated taxa, now considered *Oncomelania hupensis,* into various genera and species on the basis of cusp formulae. For example, he considered *Katayama* to have 3-3 basal denticles on the central tooth while *Oncomelania* and *Schistosomophora* had 2-2. He stated that the anterior cusps of the central tooth numbered 3 in *Katayama.* We know today that a population of *O. h. quadrasi* (previously considered *Schistosomophora quadrasi*) can have a central tooth formula of $\frac{1\text{-}1\text{-}1}{3\text{-}3}$, $\frac{2\text{-}1\text{-}2}{3\text{-}3}$, or $\frac{1\text{-}1\text{-}1}{2\text{-}2}$. The anterior edge of the central tooth of *O. h. nosophora* (Robson) (previously considered *Katayama nosophora*) can have 1-1-1 or 2-1-2 cusps.

Davis & Carney (1973: 32) suggested that cusping in *Oncomelania* is under genetic control, that patterns of variability in cusp formulae serve to characterize populations, and that the distribution of those genes governing cusp formation could be analyzed by population studies. It is possible that cusp formation on the central tooth of the radula is governed by 2 genes, where 1 gene governs anterior cusps while the 2nd controls basal cusps (anterior and posterior numbers vary independently). Interaction between the alleles of these genes could account for variability scored for the central tooth seen in Table 7. The formula can vary on the same radula, indicating lack of rigid control in the individual. However, one formula may be present in 2% of population A and of 50% of population B. This difference is reproducible, i.e. on the population level, variability appears to be held within genetically defined bounds from 1 year to the next. Individual versus population variability is open to techniques of analysis of variance.

Species Easily Confused with "L." aperta

One species, *Manningiella conica* Temcharoen (1971), has been confused with *"L." aperta.* Shells of *M. conica* are illustrated in Fig. 19. Temcharoen (1971) stated that the species looks like young *aperta;* as the anatomy was not described, the species was only tentatively placed in *Manningiella. M. conica* was described as having a shell

FIG. 17. Histology of the female reproductive system. The schematic representation (H) of the reproductive system was derived from Fig. 8.

A, B. Longitudinal sections of the bursa copulatrix (Bu). These bursas are fully developed and ready to function. The highly secretory columnar cells with dense basal nuclei and pronounced vacuoles are seen in G.

C-E. The positional relationships of the bursa, pallial oviduct (Po), and seminal receptacle (Sm) are shown in the sections of three different levels. Note that the pallial oviduct has not matured. Fertilization has not occurred because the bursa and the seminal receptacle are devoid of sperm. The entrance of the oviduct into the pallial oviduct is shown in D (1; compare with H).

F, I. The pronounced U-shaped tube from the bursa to the seminal receptacle (2) is greatly ciliated throughout. One arm of the tube is the duct of the seminal receptacle (Dsm, E, F, I, J).

E, F, J. The sac-like seminal receptacle is composed of simple unciliated cuboidal cells.

K. Cross section of the greatly ciliated oviduct (Ov) and ciliated spermathecal duct (Sd) at a position close to the posterior end of the mantle cavity (Emc). Compare with H.

L. The ovary (Go) embedded in the digestive gland in a relatively early stage of development as it is unbranched. However, it contains mature oocytes.

M-O. Cross section of the ovary with three oocytes. Enlargement of the oocytes, compared with these shown in L, is given in M-O. Note the markedly dense nucleolus in the mature oocytes.

Figs. 17A-F and L and are at the same scale, and so are Figs. 17G, I-K, M-O.

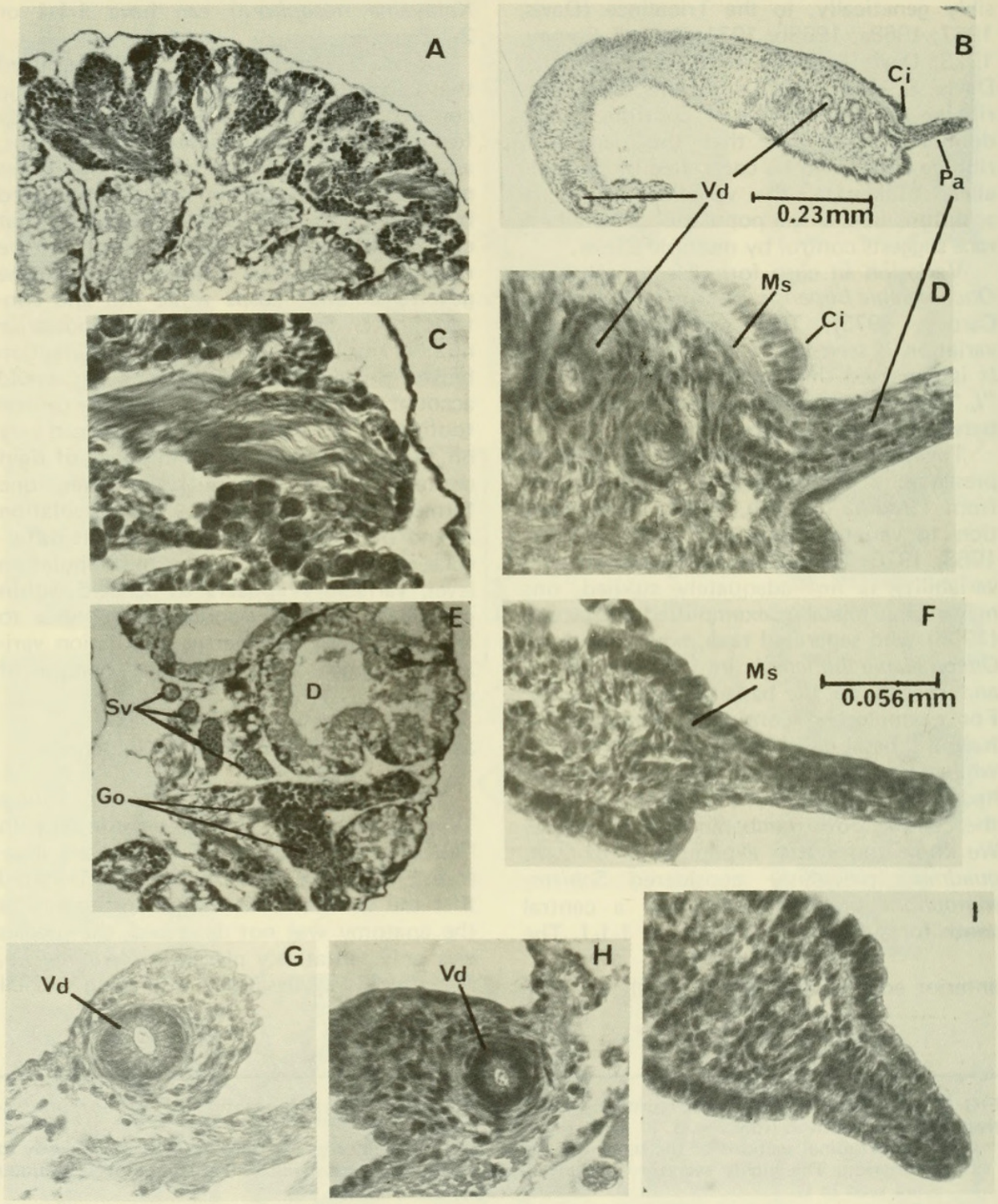


FIG. 18. Histology of the male reproductive system.

A. Lobes of the testis packed with spermatids and sperm.
B. Longitudinal section through the verge showing the pronounced papilla and some coils of the vas deferens.
C. Masses of sperm and spermatocytes.
D. Enlarged view of B showing the ciliated cells (Ci), the fully-developed papilla retractor muscles (Ms) and the vas deferens (Vd).
E. A section demonstrating regions of the sperm-packed, coiled seminal vesicle (Sv).
F. Anterior end of verge in which the papilla is not yet retractible and the papilla retractor muscles have not yet become fully developed. A verge with a very undifferentiated papillar area is shown in I.

G-H. The vas deferens (Vd) where it leaves the neck and enters the base of the verge. Note that there are sparse circular muscles surrounding the vas deferens.

Figs. 18A, B and E are at the same scale, and so are Figs. 18C, D, F-I.

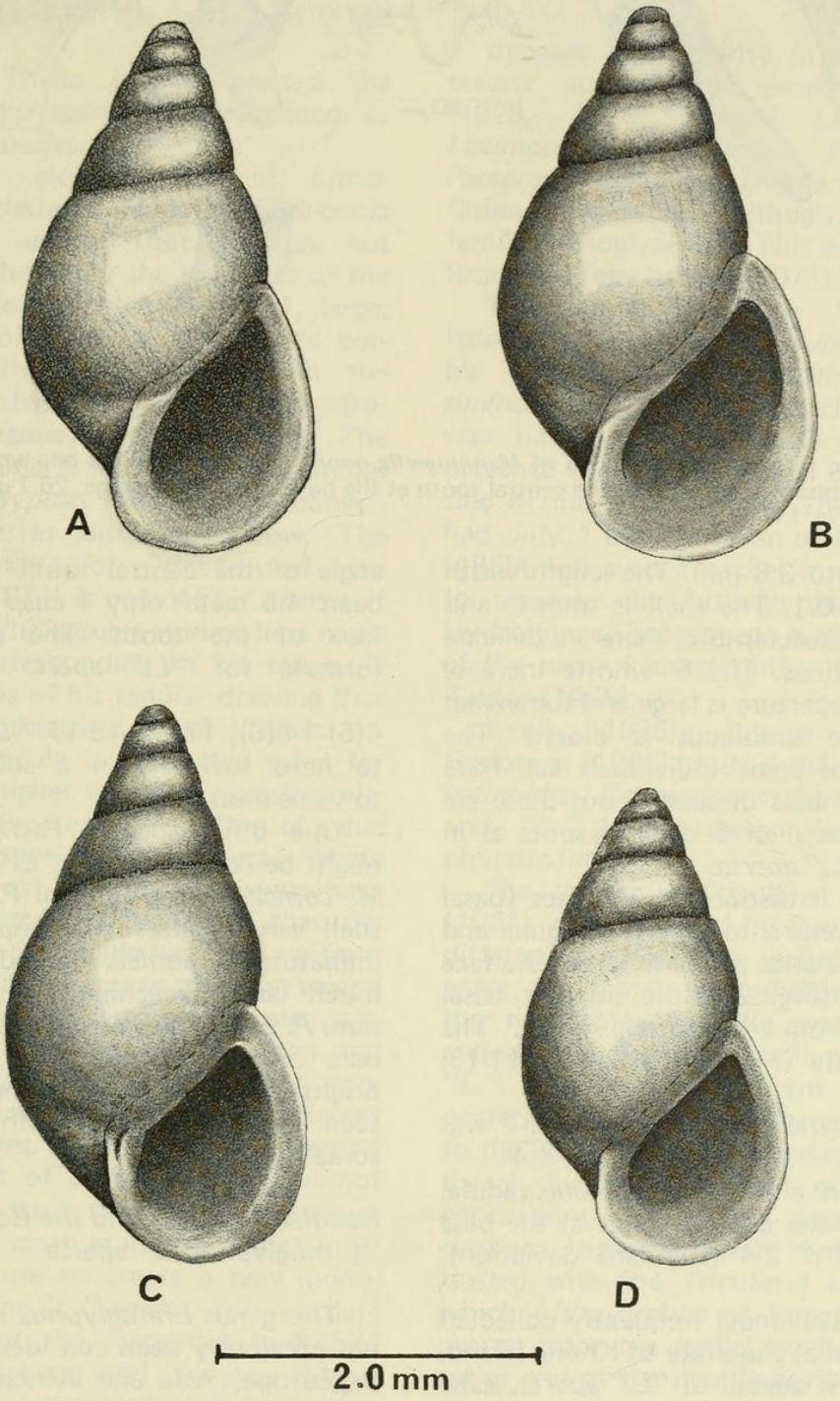


FIG. 19. Shells of *Manningiella conica*. Khong Island; location 5, site 3, 25 May 1973. ANSP 332467.

Ci—cilia;
D—digestive gland;
Go—gonad;
Ms—muscles;
Pa—papilla of the verge;
Sv—seminal vesicle;
Vd—vas deferens.

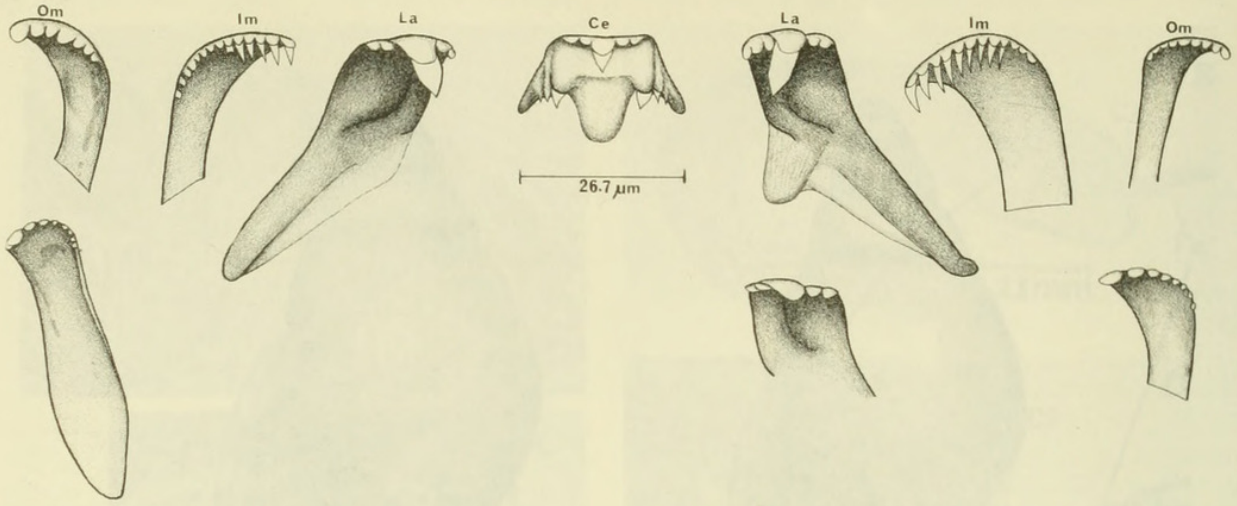


FIG. 20. Isolated teeth from the radula of *Manningiella conica* but positioned as one would observe them on the radular ribbon. The width of the central tooth at the base is, on the average, 26.7 µm. Abbreviations the same as for Fig. 11.

length of 3.0 to 3.8 mm. The length/width ratio is 1.8 ± 0.1. The shell is smooth and lacks spiral microsculpture; there are delicate axial growth lines. The 5 whorls increase regularly, the aperture is large and somewhat expanded; the umbilicus is closed. The mantle edge of some individuals can have black pigment bars or specks, but these are not grouped as 4 or 5 distinct spots as in gamma race *"L." aperta.*

The radula is distinctive. The face (basal plate) of the central tooth is rectangular and the basal cusps arise primarily from the face of the tooth (Fig. 20); the smallest basal cusp arises from the lateral angle. The radular formula is $\frac{2\text{-}1\text{-}2}{3\text{-}3}$, 3(2)-1-2, 11-13, 8-10. The central tooth formula $\frac{2\text{-}1\text{-}2}{4\text{-}4}$ was found only on a few teeth of one radula. The width of the central tooth at the base was 2.67 µm ± 2.4 (standard deviation); (n = 7).

M. conica was most frequently collected by sieving sand at the shore of Khong Island, an environment devoid of *"L." aperta.* Like *"L." aperta, M. conica* matures late, i.e. during the onset of the rainy season in June. For this reason it has not yet been possible to obtain mature animals for anatomical study in order to clarify the generic status of *M. conica.*

"L." aperta differs from *M. conica* in that the shell is wider, the length/width ratio being 1.50 ± 0.1. The lip is widely flaring and expanded in *"L." aperta.* The gamma race has distinct pigment spots while the alpha race is devoid of pigment. The lateral angle of the central tooth of *"L." aperta* bears 4-5 teeth; only 1 cusp arises from the face of the tooth. The general radular formula for *"L." aperta* is $\frac{4(5)\text{-}1\text{-}(5)4}{6(5)\text{-}(5)6}$, 4(5)-1-5(6), 17-21, 15-17. *"L." aperta* clings to hard surfaces on a substrate tending towards mud.

One other species, *Pachydrobia bavayi* might be confused with *"L." aperta* or with *M. conica.* The young of *P. bavayi* have a shell very similar in all respects to that of immature *M. conica.* The adult, however, is much larger, reaching a length of 5.0-7.8 mm. *P. bavayi* has no pigment dots or black bars on the mantle. The mantle appears bright pink. However, some pink color is seen on the mantle of both *M. conica* and some *"L." aperta.*

Radular Structure and the Generic Status of "Lithoglyphopsis" aperta

The genus *Lithoglyphus* Hartman (1821) has previously been considered to have taxa in Europe, Asia and Africa (Thiele, 1928, 1929; Wenz, 1939). The type-species, *L. naticoides* (Fér.) Pfeiffer (1828) is European. The designation of *L. naticoides* as type-species is discussed in Appendix I. Placement of taxa from diverse geographic regions in the genus is based on shell similarity, i.e. these freshwater snails have globose to cap-shaped, fairly thick shells.

Thiele (1928), studying the radula of *L. naticoides* and Asian *"Lithoglyphus",* noted that the central tooth formula of the former

was $\frac{3\text{-}1\text{-}3}{3(4)\text{-}(4)3}$ while that of some species (i.e. *L. tonkinianus* Bavay & Dautzenberg and *L. modesta* (Gredler) of the latter had $\frac{0\text{-}1\text{-}0}{2\text{-}2}$. Accordingly, Thiele (1928) created the genus *Lithoglyphopsis* and designated *L. modesta* type-species.

The rather globose shell of *Lithoglyphopsis modesta* is unlike the ovate-conic shell of *"L." aperta.* That they are not congeneric is shown by the structure of the central tooth of the radula. The 1, large, smooth anterior cusp of *L. modesta* corresponds to the condition seen in the Mekong River hydrobiid genera *Pachydrobiella, Hydrorissoia,* and *Lacunopsis.* The radula of *"L." aperta* more closely resembles that of *Lithoglyphus naticoides,* a convergent similarity as discussed below. The radular illustration presented by Temcharoen (1971) is not of *"L." aperta.* It is definite that the radulae studied here came from snails corresponding to his taxon. It was on the basis of his radular drawing that he placed the species in *Lithoglyphopsis.*

While the radula is of limited value for characterizing higher taxa and assessing relationships between taxa, it is often of value for defining species and genera. Where several species of a hydrobiid genus have been studied carefully, we note that the ground-plan of the radula has been uniform for the genus. It is of course true that several genera may have the same ground-plan, e.g. the radular structure of *Hubendickia* and *Paraprososthenia* is similar. However, congeneric species do not have vastly different radular structures. A species with a central tooth like that of *L. modesta* would not belong in the same genus with a species having a central tooth as in *"L." aperta.*

It is premature to create a new monospecific genus for *"L." aperta.* Too few data are available for the numerous hydrobiid taxa of the Mekong and Yangtze Rivers. Thus, *aperta* is temporarily left in *"Lithoglyphopsis."* The problem of generic placement will be solved when we know more of the anatomy of several species of each of the hydrobiid genera in the Mekong. The specific information needed is on the anatomy of the female reproductive system. This will be correlated with shell, radula, and habitat characters. Much of the problem would be clarified by anatomical data from Yangtze River *Lithoglyphopsis* and *"Lithoglyphus."*

Subfamily Status

Because of similarity in shell structure, several authors but prominently Thiele (1928, 1929), placed *Lithoglyphopsis, Lacunopsis, Pachydrobia, Pachydrobiella, Paraprososthenia* and *Tricula* of SE Asia and China in the tribe Lithoglypheae or subfamily Lithoglyphinae. This was followed by Brandt & Temcharoen (1971).

The subfamily name "Lithoglyphi," based on the genus *Lithoglyphus,* was given by Troschel (1857) to *Lithoglyphus, Assiminea,* and *Tomichia.* Troschel's subfamily was based on 1 character, namely the presence of 2 or more basal cusps on either side of the central tooth. The "Hydrobiae" had only 1 basal cusp on each side. Fischer (1885) followed Troschel in using this trait to separate the Lithoglyphinae from the Hydrobiinae. Subsequent history of the use of the name Lithoglyphinae is reviewed by Taylor (1966).

Krull (1935), Krause (1949), and Radoman (1966) studied the anatomy of *L. naticoides.* Comparisons show that *Tricula* and *"L." aperta* belong in a different phyletic line.

The subfamily Triculinae of Annandale (1924) was redefined by Davis (1968b). Its differential characters include how sperm enter the female reproductive system and the morphology of the system. The Triculinae is an Asian subfamily which includes *"L." aperta,* where sperm enter at the posterior end of the mantle cavity and travel to the bursa copulatrix through the spermathecal duct. This passage may be via the pericardium or it may bypass the pericardium. In the subfamily Hydrobiinae (contrasted with the Triculinae in Fig. 21) to which *Lithoglyphus* of Europe is assigned, sperm enter the pallial oviduct at the anterior end of the mantle cavity and travel to the bursa via a ciliated gutter. There is no spermathecal duct. It is thus evident that there is a fundamental difference between female reproductive systems in these 2 subfamilies. Characteristics of the male reproductive system are of little value in defining these subfamilies. For example, numerous taxa of both have a simple verge with 1 duct.

Similarities in the structure of the central tooth of *"L." aperta* and *Lithoglyphus naticoides* are superficial and derived by

convergent evolution.

Relationships of "Lithoglyphopsis" aperta *Within the Rissoacea*

Higher Category Relationships—*"L." aperta* conforms to the grade of anatomical organization which is rissoacean and hydrobiid. On the basis of mode of sperm entrance into the female reproductive system and the ontogeny of the female reproductive system it is evident that the Triculinae differ from the Hydrobiinae phylogenetically.

A duct leading from the upper end of the pallial oviduct to the proximal end of the mantle cavity is known from only a few non-triculine mesogastropods. Creek (1953) described such a duct in the terrestrial littorinacean *Acicula fusca* (Montagu). Johansson (1953) reported its occurrence in the marine cerithiacean *Triphora perversa* (Linnaeus); Fretter & Graham (1962) discuss its presence in the marine rissoacean *Barleeia rubra* (Montagu).

Johansson (1953) and Fretter & Graham (1962) considered the connection between the oviduct and proximal end of the mantle cavity to reflect a primitive state. Only in the Triculinae has a morphological ground plan evolved where the primitive route of fertilization has been uniformly retained. The triculine taxa possibly differ from the above named taxa in that there is evidence of a close association between the spermathecal duct and pericardium, e.g. sperm reach the spermathecal duct of *Tricula bollingi* Davis by passing through the pericardium.

The salivary glands of *"L." aperta* are dorsal to the cerebral commissure and have their origin anterior to the nerve ring. Fretter & Graham (1962) and Ponder (1973) make a point of differentiating monotocardian gastopods from neogastropods by stating that the ducts of the salivary glands run through the nerve ring in the former while the glands and ducts are in front of the cerebral commissures and thus do not pass through the nerve ring in the latter.

"L." aperta, however, is not unique among monotocardian gastropods. The dorsal anterior position of the duct is seen in the Pomatiopsinae (Davis, 1967, 1968a) and Assimineidae [*Assiminea brevicula* (Pfeiffer)], Truncatellidae [*Truncatella guerinii* A. & J. B. Villa], Bithyniidae [*Bithynia manchurica* Bourguignat], and Hydrobiidae [*Amnicola limosa* (Say)] (dissected by Davis along with *"L." aperta* specifically for this trait). Too few papers dealing with rissoacean anatomy give details on the interrelationships of organs, and thus the status of the salivary glands relative to the cerebral commissures is unknown for over 50 taxa discussed in the literature (Henking, 1894; Bregenzer, 1916; Robson, 1920, 1921, 1922; Krull, 1935; Johansson, 1939, 1956; Krause, 1949; Lilly, 1953; Radoman, 1955a, 1955b, 1974; Dundee, 1957; Bole, 1970, 1971; Winterbourn, 1970; Pezzoli & Girod, 1971).

It is not appropriate to use the trait in question to differentiate monotocardian gastropods from the neogastropods. Contrary to the explanation given by Fretter & Graham (1962), it is evident that in certain lineages of mesogastropods there was a backward shift of the cerebral ganglion-commissure complex *not* accompanied by a backward shift of the salivary glands and correlated elongation of the salivary ducts.

"L." aperta does not possess a hypobranchial gland, in contrast to the usual mesogastropod condition. The same lack of this gland is observed in the pomatiopsines *Oncomelania* and *Pomatiopsis.* Too few rissoacean taxa have been examined for this trait to make useful statements concerning the distribution of the hypobranchial glands among the various families.

The Triculinae are most closely allied with the Pomatiopsinae both in anatomy and zoogeography. One of us (Davis) considers the subfamily Pomatiopsinae to have evolved from the same basal stock giving rise to both *"L." aperta* and *Tricula.* This is an important consideration as *Oncomelania hupensis* of the Pomatiopsinae and *"L." aperta* of the Triculinae transmit human, Asian schistosomes. While the ancestral Triculinae were aquatic, the present day Pomatiopsinae are amphibious or terrestrial. The adaptation to the amphibious-terrestrial environment is seen in the pedal crease of the foot and the step-like mode of progression; both traits resulted from bearing the weight of the turreted shell in the absence of water. The aquatic Triculinae move by ciliary glide. Both pomatiopsine and triculine snails lay eggs singly and coated with sand grains or mud. The central tooth of the radula of the Pomatiopsinae closely resembles that of certain taxa now placed in the Triculinae, e.g., *Manningiella conica* (Fig.

20).

The pomatiopsine female reproductive system (Fig. 21) could have been derived from the triculine condition seen in *"L." aperta* and *Tricula burchi* Davis (Fig. 22). The bursa would have rotated 90° to 180°, bringing the conditions shown in Fig. 22A to those given in Fig. 22B, i.e. bringing the openings of the spermathecal duct and sperm duct into the bursa from the left ventro-lateral side to the right anterolateral aspect. With the rotation, the spermathecal duct elongated along the pallial oviduct to open at the anterior end of the mantle cavity. The duct of the seminal receptacle migrated to open directly into the oviduct. Continued rotation of the bursa yielded the pomatiopsine condition (Fig. 22C). It is a distinct advantage to pomatiopsine snails to have the opening of the spermathecal duct at the anterior end of the mantle cavity rather than at the posterior end when one considers the mechanics of copulation in the amphibious or terrestrial environment.

Oncomelania hupensis is the most widespread and abundant representative of the Pomatiopsinae in Asia. As discussed by Davis (1971) and Davis & Carney (1973), fossil *Oncomelania* have been found in Pleistocene beds of the northern Shan States of Burma (Annandale, 1919). This establishes that *Oncomelania* has existed in an arc overlapping the Mekong and Yangtze Rivers. From this area taxa of the genus radiated to Japan, the Philippines, and Sulawesi (= Celebes).

It is, of course, possible that the Pomatiopsinae evolved independently of the Triculinae. The presence of a gonopericardial duct in *Oncomelania* and *Pomatiopsis* of the former subfamily (Davis, 1967) and absence of the duct in the latter may support this view.

The pomatiopsine female reproductive system could not have been derived from the hydrobiine type described in the section on "Subfamily Status". The spermathecal duct of the former did not arise by closure and separation of the ciliated ventral groove of the pallial oviduct of the latter. In the Hydrobiinae the ciliated gutter is formed during ontogeny by the closure of the open pallial oviduct (Johansson, 1956). In the Pomatiopsinae (e.g. *Oncomelania hupensis*) one of us (Davis) has observed that the pallial oviduct forms by cavitation in a solid core of developing tissue and the spermathecal duct elongates from a bud of the bursa copulatrix.

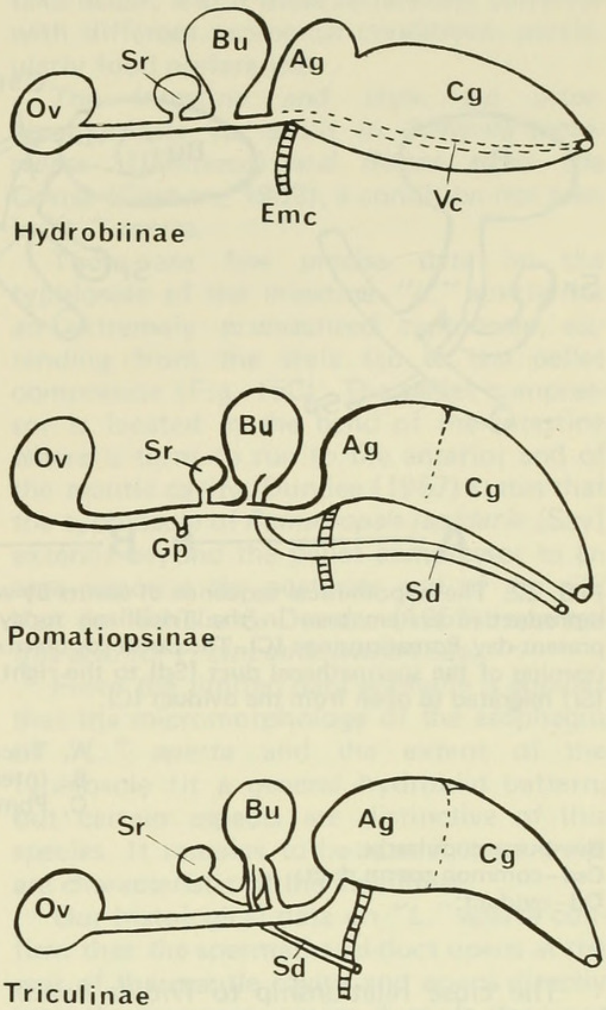


FIG. 21. Schematic drawings of the female reproductive systems of three subfamilies of the Hydrobiidae showing essential similarities and differences.

Ag—albumen gland = posterior pallial oviduct;
Bu—bursa copulatrix;
Cg—capsule gland = anterior pallial oviduct;
Emc—posterior end of the mantle cavity;
Gp—gonopericardial duct;
Ov—ovary;
Sd—spermathecal duct;
Sr—seminal receptacle;
Vc—ventral channel of the pallial oviduct.

Lower Category Relationships—*"L." aperta* is, of taxa thus far known, most closely related to *Tricula burchi*. In both *"L." aperta* and *T. burchi* there is a U-shaped common sperm duct from the bursa copulatrix to the seminal receptable. In both taxa the spermathecal duct (labeled Rd in Davis, 1968b) bypasses the pericardium and joins the common sperm duct close to the bursa copulatrix.

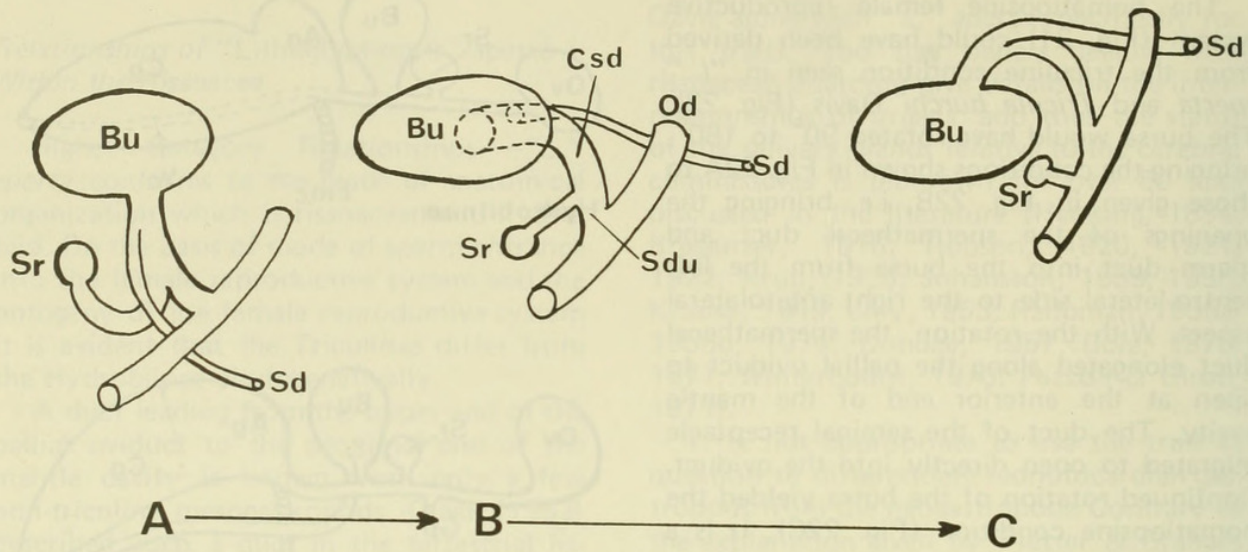


FIG. 22. The hypothetical sequence of events by which the arrangement of ducts and organs of the female reproductive system seen in the Triculinae today (A) modified to produce the condition seen in the present-day Pomatiopsinae (C). The bursa copulatrix in A rotated through 90° (B) to 180° (C), bringing the opening of the spermathecal duct (Sd) to the right antero-lateral edge of the bursa. The seminal receptacle (Sr) migrated to open from the oviduct (C).

A. Triculinae.
B. Intermediate stage.
C. Pomatiopsinae.

Bu—bursa copulatrix;
Csd—common sperm duct;
Od—oviduct;
Sd—spermathecal duct;
Sdu—sperm duct;
Sr—seminal receptacle.

The close relationship to *Tricula burchi* suggests that *Tricula* might be a suitable genus for *"L." aperta.* Unfortunately, the anatomy of the type-species of *Tricula* Benson (1843), i.e. *T. montana* Benson (1843), is unknown. *T. montana* has not been found since it was discovered in Bhimtal, India (Prashad, 1921 a, b; Rao, 1928). The anatomical concept of *Tricula* is currently based on *T. burchi* and *T. bollingi* (Davis, 1968b).

"L." aperta differs from *T. burchi* and *T. bollingi* in several characters. Species placed in *Tricula* have turreted shells with 5 or more whorls, the inner lips are simple, sharp, and not reflected over the base, the length to width ratio is 2.0 to 2.26, and there is no columellar shelf. There is no eversible papilla in the verge of either *T. burchi* or *T. bollingi.* As previously mentioned, the taxa differ from *"L." aperta* in size and shape of the bursa copulatrix and the relative position of the seminal receptacle to the bursa. The central tooth of *Tricula* has a "basal bar" not seen in *"L." aperta.*

Tricula bollingi differs from both *"L." aperta* and *T. burchi* in that the seminal receptacle does not arise from the common sperm duct, but from the oviduct. Also, the spermathecal duct enters the pericardium and there is a passage from the pericardium to the rear of the mantle cavity.

Aside from *"L." aperta* and *T. burchi,* the bursa copulatrix and seminal receptacle have separate openings into the oviduct in rissoids and hydrobiids thus far studied.

We consider the fundamental condition or primitive state of triculine snails to be seen in the morphology of *"L." aperta* and *T. burchi,* i.e. where there is a common sperm duct through which the bursa copulatrix and seminal receptacle communicate independent of the oviduct. The sequence in the secondary and tertiary derived states involves the migration of the seminal receptacle to open into the oviduct posterior to the opening of the duct of the bursa. A third stage, not yet observed, would have the seminal receptacle lost and the storage of sperm within the coils of the oviduct. Also, a stage might be found fixed in some living species where the seminal receptacle opens into the duct running from the bursa into the oviduct.

Histological Data

Histological data presented here are baselines for comparisons with other Mekong River hydrobiids and rissoaceans in general. Very few papers have been published illustrating even limited histological aspects of rissoacean taxa. Henking (1894) presented a few drawings of sections through the buccal mass of *Hydrobia ulvae* (Pennant). Bregenzer (1916) gave an excellent account of *Bythinella dunkeri* with 28 drawings of sections. Vague information is given by Robson (1920) for *Potamopyrgus jenkinsi* (Smith), by Robson (1921) for *Oncomelania hupensis nosophora* (Robson), and by Robson (1922) for *Hydrobia ventrosa* (Montagu). Johansson (1939) provided numerous photographs and drawings of sections for 4 species of Rissoidae. Krause (1949) gave an excellent account of the anatomy of *Lithoglyphus naticoides* which included 12 drawn sections.

From the information available, it appears that there are differences between rissoacean snails in micro-morphology of the digestive system. Graham (1939) summarized the available data on the alimentary canal of style-bearing prosobranchs. In *Hydrobia ventrosa, H. ulvae,* and *Pomatopyrgus jenkinsi* the dorsal food channel of the esophagus is bounded by dorsal folds so high that they contact the opposite wall, thereby seeming to divide the tube into 3 chambers. The posterior esophagus has numerous folds, 1 of which is a continuation of the left dorsal fold. In *Bythinella dunkeri* (Frauenfeld) the dorsal food groove of the anterior esophagus is closed ventrally by the meeting of the ends of the dorsal folds; the posterior esophagus is thrown into folds.

In *"Lithoglyphopsis" aperta* the dorsal food groove of the anterior esophagus is almost closed ventrally except that the ends of the dorsal folds do not quite meet. The left dorsal fold continues to the stomach, while the right 1 becomes indistinguishable from the several other folds which are about 1/2 the height of the left dorsal fold. The transition occurs posterior to the nerve ring. The persistence of the left dorsal fold as a structure twice the size of the other 8 to 9 folds is thus far unique among hydrobiid snails. It has yet to be determined whether these traits described for *"L." aperta* are species-specific or characteristic of all triculine snails. The functional significance of these folds is unknown. It is important to determine if differences between triculine taxa occur, and if these differences correlate with different ecological conditions, particularly food preferences.

The intestine and style sac intercommunicate via a slit in *Bithynia tentaculata* (Linnaeus) and *Rissoa parva* (da Costa) (Graham, 1939), a condition not seen in *"L." aperta.*

There are few precise data on the typhlosole of the intestine. *"L." aperta* has an extremely pronounced typhlosole, extending from the style sac to the pellet compressor (Fig. 15C). The pellet compressor is located in the bend of the intestine where it turns to run to the anterior end of the mantle cavity. Dundee (1957) states that the typhlosole of *Pomatiopsis lapidaria* (Say) extends beyond the pellet compressor to an area opposite the posterior end of the gill; Van der Schalie & Dundee (1956) reported this also for *P. cincinnatiensis* (Lea).

From the limited data available it appears that the micromorphology of the esophagus of *"L." aperta* and the extent of the typhlosole fit a general hydrobiid pattern, but certain aspects are distinctive of this species. It remains to be seen if these traits are characteristic of the Triculinae.

Our histological data on *"L." aperta* confirm that the spermathecal duct opens at the rear of the mantle cavity and opens directly into the common sperm duct. It does not travel as a tube-within-a-tube to the bursa copulatrix. In *Oncomelania* the spermathecal duct and sperm duct both enter the spermathecal sheath for a short distance before they enter the bursa (Css, fig. 27, Davis, 1969a). The wrapping of these ducts in a sheath is here considered to be derived from the sheathless state because the tubes are not wrapped in *"L." aperta,* because morphology of the bursa-seminal receptacle complex in *"L." aperta* is considered, and because we feel that *Oncomelania* evolved from early triculine stock where taxa had an *"L." aperta*-like bursa-seminal receptacle complex.

Analysis of the ontogeny of the penis sheds light on how the papillate condition is derived from the "simple" penis. The degree of papilla formation corresponds to the degree of development of the penial muscles at the free end of the penis attaching to the blunt nipple-like tip (Fig. 18 I, F, D, B). As the muscle bundles thicken, strands extend into the papilla and the papilla becomes more slender. Muscles bunch up around the

base of the papilla essentially forming a cylinder through which the papilla can be retracted.

Nervous System

Clearly, more data from additional triculine and pomatiopsine species are needed to confirm or reject the hypothesis indicated by the available data that there is no relative reduction of the supravisceral connective in taxa of these subfamilies. As the species increase in size, so does the connective.

We consider the relative length of the supraesophageal connective thus far seen in the triculine-pomatiopsine lineage to be intermediate in the Rissoacea (Table 10). In the Hydrobiinae there is a great spectrum of values ranging from elongate connectives *(Hydrobia)* to near fusion of supraesophageal and right pleural ganglia *(Lithoglyphus).* Thus there is, in the monophyletic assemblage of the Hydrobiinae, a distinct trend towards concentration of the nervous system. Brackish-water *Hydrobia* is considered most like the rissoacean marine ancestor of the Hydrobiinae. *Bythinella* is a more highly evolved type while *Lithoglyphus* represents the most advanced condition. The latter genera inhabit fresh water.

We consider the Littorinidae to be more generalized in its nervous system than the Rissoidae or Hydrobiidae because of the very elongate connective (the RPG ratio being 0.72 in *Littorina littorea*) as seen in Johansson, 1939, and 0.84 as seen in Fretter & Graham, 1962). The former ratio was derived from measuring a photograph of the dissected nervous system; the latter was derived from a drawing.

It has yet to be learned if triculine snails radiating into environments requiring specialization have evolved a more concentrated nervous system. For example, do species of *Lacunopsis* which resemble (in shell) *Lithoglyphus* of Europe and which live in rapids have a concentrated nervous system? Have arboreal pomatiopsine snails likewise evolved such a nervous system?

Conservative- and Non-Conservative Organ Systems

Our anatomical and histological data reveal a conservative hydrobiid ground plan in the circulatory, excretory, nervous, digestive and male reproductive systems. The arrangement of folds in the esophagus of *"L." aperta* is a variant within the hydrobiid ground plan and thus far unique.

As is evident from the discussions of the female reproductive systems of the Triculinae, Pomatiopsinae, and Hydrobiinae, this system is non-conservative. Aside from the fact that the females of the 3 subfamilies have a bursa, seminal receptacle, and pallial oviduct, there is no common ground plan. Where data are available for pomatiopsine and triculine taxa (Davis, 1967, 1968a, b, 1969a; Van der Schalie & Dundee, 1956) it is evident that this 1 organ system has changed markedly in taxa radiating into new environments and geographic regions. We have yet to see an end to the variation of how the bursa, seminal receptacle, spermathecal duct and oviduct interconnect. It is evident that selective pressures adapted reproductive strategies to very different ends in coping with new environments while feeding strategies (as seen in the structure of the digestive system) were adapted to the same end, i.e. feeding structures did not diversify but held to the same general type. This is the converse of the course of events in the neogastropod radiation where reproductive structures are quite similar from genus to genus or between families, while fore-gut structural differences are profound.

We need both qualitative and quantitative data for organ systems in order to provide data of value for systematics in the Rissoacea, i.e. shell, and reproductive, digestive, and nervous systems, as well as external features of the head-foot region and mantle cavity structures. It takes little additional effort to record quantitative data while observing qualitative aspects of an organ, e.g. recording dimensions of major organs. It is obvious that such measurements must be made with regard to a well established marker indicating stage of development, e.g. using only fully mature animals where the shell has reached maximum development.

It is important to be able to compare taxa in the relative sizes of organs. While this is obvious to a student of vertebrate biology or one investigating races of mankind, it has been generally ignored by students of molluscan systematics and evolution. It should be obvious that when taxon A has a shell length of 5 mm and a length of pallial oviduct of 2.0 mm while congener B has a

shell length of 4 mm and a pallial oviduct 2.5 mm long, quantitative analysis is of value in discriminating between taxa. In the absence of the quantitative data one has a usual assessment; the shells differ in size, the external aspects of the pallial oviduct are the same. Obviously, meaningful information is lost. With such data one can often make assessments of subtle infraspecific variation. This was done by Davis & Carney (1973) in distinguishing *O.h. lindoensis* of Sulawesi from small subspecies of *O. hupensis* from Taiwan and the Philippines.

While quantitative data serve to characterize a taxon and increase the data base for inter-taxon comparisons, they are also of value for analyses of function or evolutionary strategies for coping with the environment, obtaining energy, reproduction, etc. For example, the length of the osphradium of *"L." aperta* is 46% of the length of the ctenidium. The relative length of the osphradium in other Hydrobiidae (where known, Davis, 1969a) varies from 26 to 40%. With the length of shell as a standard of size, the relative length of the osphradium is 24% in *"L." aperta* as against 8 to 13% in *Oncomelania minima, O.h. chiui,* and *O.h. formosana.* The estimated value for *Tricula burchi* and *T. bollingi* is 10%. A quick check of the osphradia of taxa of other hydrobiid genera in the Mekong River showed that they, likewise, had an elongate osphradium. *Tricula,* closely allied genetically to *"L." aperta* but outside the Mekong River drainage, has a short osphradium as indicated above. The elongate osphradium correlates with habitation of the Mekong River. A hypothesis to explain this is that: The Mekong River has an exceptional silt burden. Sensory perception with a small nerve center might be ineffectual under such conditions. Enhancement of sense discrimination where silt burden could overload the sensory system might be achieved by increasing the volume of the nerve elements in the osphradium. The elongation of the osphradial ganglion would cause an increase in surface area and volume and hence cause a markedly increased capacity for sensory perception. That there is a selection advantage for an elongate osphradium is shown by the fact that the species checked of such divergent Mekong dwelling genera as *Hubendickia* and *Pachydrobia* possess the elongate osphradium.

Quantitative Data, Ecological Parameters, and "r"-Selection

Analysis of quantitative data for the bursa copulatrix and pallial oviduct shows that the former is 63% the length of the latter. In other hydrobiids (where known) the % varies from 18 to 25. The pallial oviduct of *"L." aperta* and these other hydrobiids has a length relative to shell length of 54 to 66%. Correlated with the extremely large bursa is a correspondingly large seminal receptacle-common sperm duct complex. We suggest that these relative size differences are related to ecological parameters and reproductive strategy.

"Lithoglyphopsis" aperta, when found in nature, are gregarious and extremely limited in movement. They are found densely crowded on solid objects such as sticks, shells, and stones. Populations of growing young are extremely dense, e.g. 10 per cm^2 on a stick or shell. Because of their substrate preference and their tendency to move little while grazing, it is evident that the population in a given area is composed of those snails hatching within the area. During their growth to maturity there is probably little recruitment from extralimital areas and nearly zero emigration. As snails mature, and with increased flooding from July on, some snails are probably transported on sticks to different localities.

The species has 1 breeding cycle per year. We have collected no living specimens, but thousands of dead shells, in early March. Newly hatched young are collected in April. The following are probable: 1) Females lay their eggs in late January or early February and subsequently die. Eggs are coated with sand grains and attached to hard substrates such as shells of living mollusks, sticks, stones, shells of dead animals. The numerous shells of dead animals collected in March probably do not come from animals dying in November or December, but in January and February. The raging currents which scour the river bottom would sweep these downstream; they would be ground to small particles by the action of sand and pebbles carried in the current. Also, the shells collected in March are in the same area where the populations of young are found in April. 2) The young crowd every piece of substrate available, e.g. surfaces of leaves, sticks, etc. Young seem to be substrate limited, as there are frequently scant solid objects in the area,

otherwise composed of silt, mud or mud-sand. Many do not reach maturity, as evidenced by the fact that collecting these animals by fine sieves, empty *"L." aperta* shells of 3.0 whorls are common.

Males mature ahead of females, i.e. in May. By mid-May, alpha race females have oocytes in the gonad. We project that full maturity in females is reached in late June or possibly in early July, and that copulation occurs at this time when the river level has begun to rise. If the reproductive pattern follows what is known for *Oncomelania hupensis* and generally for hydrobiids, once copulation has occurred females can store sperm for prolonged times in the seminal receptacle. Sexual dimorphism, frequently seen in hydrobiids, is usually represented by a smaller shell in males; the shells have one half to a full whorl less than that of the female. This is correlated with a more rapid maturation rate of the males. There is no selective pressure on males for prolonged life beyond copulation. It is suspected that males die before females in *"L." aperta.* This is the case in *Manningiella expansa* Brandt which also lives in the Mekong River. We note that functional males of *M. expansa* have not been found in late April or May although functional females have been found. The indication is that the reproductive system deteriorates, the penis atrophies, that the small males die off before the females. Likewise, in *Pachydrobia,* we have seen females with functional reproductive systems in April; males were fewer in number, the verges were atrophied and the rest of the reproductive system was degenerating.

The indications are that female *"L." aperta,* once fertilized, store sperm and do not release oocytes for fertilization during the six months of great environmental trauma when the Mekong River is in flood. As the animals have limited mobility and are substrate-limited it is almost certain that large numbers of the population are swept away and destroyed annually. We have seen areas heavily populated one year that were totally disrupted the following year due to the floods. The extremely large bursa-seminal receptacle complex would thus be necessary to store copious quantities of sperm in the viable state and manage this resource throughout the environmentally disrupted period by continuously destroying weakened or inviable sperm. The bursa copulatrix functions in regulating the catabolism of sperm. The bursa of hydrobiids, after fertilization has occurred, is full of a brown-yellow mass of sperm in various stages of decomposition and elimination. Snails surviving the period of trauma by location in rock crevices and beneath rocks unmoved by the floods produce prodigious numbers of young per female and thus need a large reservoir of viable sperm. The dense populations of young seen in April and May substantiate the high reproductive capacity per female.

Populations are often restricted to several small patches within a larger area. This is due to discontinuity of suitable substrates and of relatively sheltered areas characterized by a slow current and zone of deposition. For example, 1 population at Ban Khee Lek of Khemarat was located within an area of 4,000 m^2 and another population was not found until 1/2 mi upstream. In other regions such as Khong Island, the population may be continuous for 2-3 miles along the shore of the island with nodes of increased density reflecting a greater abundance of suitable substrates in protected shallow water areas. It has thus been evident over 4 years of collecting *"L." aperta* from various regions in the Mekong River that certain areas in the river are relatively stable over a number of years as evidenced by *"L." aperta* being found in the same locality year after year. Other regions are unstable in that the population is found at a locality 1 year and not in the next, the difference attributed to complete alteration at the locality due to flooding.

Taking these facts as a group it is evident that *"L." aperta* has 2 major "strategies" for survival. 1) The species acts as a colonizer, living in unstable habitats which may be destroyed and new ones created. The mechanism for invasion of a freshly created suitable environment must be the survival of some individuals or encapsulated eggs on dead shells or sticks which are swept by the gentler currents in the periods prior to, or after peak flooding. The sand grain encrusted eggs are sturdy. There must be a strong selection for such egg capsules because all the triculine snails in the Mekong thus far observed have this trait. *"L." aperta* is a colonizer or fugitive species in the sense of Wilson (1965) in that it survives . . . "indefinitely within the kaleidoscopically changing environments of single regions." By considering the fugitive species concept one

may account for the origin of the genetic differences seen in the 3 races and the invasion of new environments as exemplified by the beta race. An additional reason (to the ones previously given) that the races are probably not species derive from Wilson's (1965) speculation that a colonizer which permits speciation generates its own competitors which reduces the rate of——or potential to——colonize. Considering the predictable annual cycle of environmental disruption in the Mekong River it would seem to be a distinct selective advantage for survival if trends toward speciation were dampened. However, considering the number of species of other triculine genera which are also likely colonizers it is probable that a balance has been achieved between the ability to speciate and the ability to colonize and to maintain gene flow with other transient populations, thus assuring survival. 2) *"L." aperta* is an *r*-strategist (MacArthur, 1962; MacArthur & Wilson, 1967; Hairston et al., 1970) in that there is a high density-independent mortality, apparently much of its resources are applied towards reproduction, the energy expended per young produced is very low, and the number of young produced per time is very high compared with pomatiopsine species.

King & Anderson (1971) discussed the fact that there are simultaneously *r* and *k* components in selection and their interaction with regard to genotype and initial population structure determines the pattern of population growth and changes in gene frequencies. They demonstrated via simulations that as the number of breeding cycles for each environmental cycle is reduced, the *r*-components come ". . . to determine both equilibrium gene frequencies and population size." In their model the threshold for *r*-selection was 13 breeding cycles per environmental cycle. *"L." aperta* has 1 breeding cycle per environmental cycle and thus clearly is within King & Anderson's (1971) concept of an *r*-selected species.

The *k*-components of selection in *"L." aperta,* i.e. density dependent factors, are active during the growth phase when young increase in size on a limited substrate and crowding occurs. Not all young will survive to maturity; there is not sufficient room. There is then selective pressure in relation to those surviving to reproduce.

Transmission of Mekong Schistosoma *sp.*

One of us (Kitikoon) has established (unpublished) that all 3 races of *"L." aperta* can experimentally transmit the Mekong schistosome. We consider this schistosome to be a different species than *S. japonicum.* The interaction between the Mekong schistosome and *"L." aperta* is highly specific. The Mekong schistosome and *S. japonicum* have probably evolved from a common ancestor.

The evolution of host-parasite interactions involves sets of complex factors. On the one hand it is clear that molluscan genes operating at the interspecific level control the potential for schistosome miracidia to successfully penetrate and infect a population of snails. This has been established for *Schistosoma mansoni* Sambon of Africa and South America (Richards, 1970), and *S. japonicum* of Asia (Chi et al., 1971; Davis & Ruff, 1974). On the other hand it is clear that genetic factors inherited by the parasite are important if a successful infection in the snails is to occur (Wright, 1974).

Schistosoma japonicum is transmitted by subspecies of *Oncomelania hupensis* of the Pomatiopsinae. There are populations on Taiwan of *O.h. formosana* which lack genes for transmission (Davis & Ruff, 1974). Only *O.h. hupensis* of mainland China and *O.h. chiui* of Taiwan have populations through which all geographic strains of *S. japonicum* can be transmitted.

Lo et al. (1971) have shown that no subspecies of *O. hupensis* can be infected with the Mekong schistosome. This indicates that the Mekong parasite does not have genes enabling penetration and infection of polytypic *Oncomelania hupensis* and that the genetic composition of *O. hupensis* marshals against infection. This does not negate the potential of miracidia of *S. japonicum* to infect *"L." aperta.* Even if the latter should be demonstrated, it is evident that the Mekong parasite is now genetically isolated from *S. japonicum* by its inability to develop in *O. hupensis.*

Iijima et al. (1971) studied adult Mekong schistosome worms and compared them with the Japanese strain of *S. japonicum.* They concluded that the Mekong schistosome is different from all strains of *S. japonicum.* It would appear that the Mekong schistosome is a sibling species of *S. japonicum* because

of the general morphological resemblance. We note, however, that the eggs of the Mekong parasite are smaller and rounder; the worms are significantly longer than those of *S. japonicum;* the ovaries are relatively larger.

The ecology of transmission is different. *S. japonicum* is transmitted by an amphibious snail. Transmission can occur in dew-wet fields of rice, in small drainage ditches and pools. *"L." aperta* is found only in the river, one which is in flood for much of the year. As *"L." aperta* grows to infective size and matures in late May or June, man can become infected only in the dry season from perhaps late May to June or July, and after the September peak floods, from December to late February when the adults die. With the May rains, the river rises some 40 ft and becomes a raging torrent. The current is too swift for man or animal to venture into the river and is too swift to enable the delicate larval cercariae to infect man. It appears that the annual floods keep this parasite in balance as a relict species from Khong Island to Kratie, Cambodia. That the parasite is not more prevalant throughout the range of *"L." aperta* is probably due to the patchiness and population dynamics of the species discussed earlier, which are so tightly coupled with the hydrodynamics of the Mekong River.

The Mekong schistosome and *S. japonicum* probably evolved from a common ancestor. Several million years ago both triculine and pomatiopsine snails existed in an arc from India to the upper Yangtze drainage. As pomatiopsine snails evolved from the early triculine-pomatiopsine stock, genes governing the transmission of a generalized schistosome parasite were inherited by some taxa of both lineages of snails. Genetic control over transmission would not have been nearly as specific as it is today. With time, as new species and genera of snails evolved, genes governing transmission would have become more restricted to some taxa than to others. Precursors to present day *Oncomelania hupensis* evolved with a greater genetic affinity for schistosome transmission while only a few triculine snails retained genes for transmission.

With extinction of *Oncomelania* in the headwaters of the Mekong during the Pleistocene, and with the subsequent radiation of *Oncomelania hupensis* throughout the Yangtze basin, Taiwan, the Philippines, Sulawesi and Japan, the evolving interaction with the parasite, now *S. japonicum,* became highly specific. As the snail evolved so did the parasite if it were to survive in the snail (Davis, 1969b). As the subspecies of *O. hupensis* altered genetically in the separated regions of its range, so did the parasite. The strains of *S. japonicum* occurring today differ somewhat in morphology, egg dimensions, pathogenicity, etc.

The triculine snails radiated both into the Mekong and the Yangtze. As far as we know today, the human schistosome of the Mekong is transmitted only by *"L." aperta. Tricula* and *"L." aperta* are allied in having genetic potential to transmit mammalian schistosomes, as Davis (1969a) found an undescribed mammalian schistosome in *T. bollingi*. It has yet to be discovered whether species of *"Lithoglyphus"* of China are involved in schistosome transmission or have potential to transmit the Mekong schistosome. Much has yet to be learned of *Tricula* from India, Burma, and China regarding the potential to transmit schistosomes.

APPENDIX I

DESIGNATION OF THE TYPE-SPECIES OF *LITHOGLYPHUS*

Hartman (1821: 57) listed *"Lithoglyp. eburneus"* in his catalog of German gastropods. His footnote indicates that *eburneus* is a manuscript name and, without description, a nomen nudum ["(Megerle ab Mühlfeld) nov. spec."].

Pfeiffer (1828) formally described a manuscript name of Férussac, i.e. *Paludina naticoides,* and the manuscript name *Lithoglyphus fuscus* of Ziegler, i.e. *Paludina fusca.*

Cristofori & Jan (1832) list both *naticoides* and *fusca* under *Paludina (Lithoclypus). "Lithoclypus"* is an error for *Lithoglyphus.*

Herrmannsen (1846) designated *L. naticoides* as type of the genus *Lithoglyphus* preceding Gray's (1847) designation of *L. fuscus.* Subsequent authors have used *naticoides* (Fér.) Pfeiffer as the type-species (e.g. Stimpson, 1865; Thiele, 1929; Wenz, 1939).

ACKNOWLEDGMENTS

We express our thanks to Drs. Chamlong Harinasuta and Santasiri Sornmani of the Faculty of Tropical Medicine, Mahidol Uni-

versity, Bangkok, for providing space and assistance in Bangkok and for providing assistance in the field. We are grateful to the Ubon Ratchathani Provincial Public Health Service for providing housing facilities at Khemarat, and to the Thomas A. Dooley Foundation for the use of facilities on Khong Island. Special thanks to Mr. Samai Rodpai—field technician.

We are grateful to Drs. Vera Fretter, Elaine Hoagland, and Arthur J. Cain for reading and criticizing this manuscript. We are also grateful to Dr. Curt Schneider, Bangkok administrator of the Smithsonian Institution Water-Borne Disease Project for his generous support and his critical reading of this manuscript. We, however, accept full responsibility for the content of the paper.

Particular thanks go to Mr. William Eilers, principal investigator of the Smithsonian project for making this study possible.

Histological preparations were made by Mr. Edward Kepner and Ms. H. Hopkins. All drawings except those of the shells were made by one of us (Davis). Final rendering of the nervous system was done by Mr. Pluem Kidkian of the Faculty of Tropical Medicine, Bangkok. Final rendering of the other anatomical drawings was done by Ms. Vicky Pritchard. The shells of *"L." aperta* were done entirely by V. Pritchard while those of *M. conica* were done by Ms. H. Hopkins.

The manuscript was typed and edited by Ms. Margie Skedzielewski.

LITERATURE CITED

ANNANDALE, N., 1919, The gastropod fauna of old lake beds in upper Burma. *Rec. Geol. Surv. India,* 50: 209-240, 3 pls.

ANNANDALE, N., 1924, The molluscan hosts of the human blood fluke in China and Japan, and species liable to be confused with them. *In* Faust, E. C. & Mekeney, H. E., Studies on schistosomiasis japonica. *Amer. J. Hyg. Monogr. Ser.,* No. 3: 269-294, 1 pl.

AUDEBAUD, G., TOURNIER-LASSERVE, C., BRUMPT, V., JOLLY, M., MAZAUD, R., IMBERT, X. & BAZILLIO, R., 1968, Premier cas de bilharziose humaine observé au Cambodge. *Bull. Soc. Pathologie Exotique,* 61: 778-784.

BARBIER, M., 1966, Determination d'un foyer de bilharziose arterio-veineuse au Sud-Laos (Province de Sithandone). *Bull. Soc. Pathologie Exotique,* 59: 974-982.

BARTSCH, P., 1936, Molluscan intermediate hosts of the Asiatic blood fluke *Schistosoma japonicum* and species confused with them. *Smithson. misc. Collect.,* 95(5): 1-60, 8 pls.

BENSON, W. H., 1843, Description of *Camptoceras,* a new genus of the Lymnaeidae, allied to *Ancylus,* and *Tricula,* a new type of form allied to *Melania. Calcutta J. natur. Hist.,* 3: 465-468.

BOLE, J., 1970, Prispevek k poznavanju anatomije in taksonomije podzemeljskih hidrobiid (Gastropoda, Prosobranchia). *Razprave; Slovenska Akademija Znanosti in Umetnosti academia scientiarum et artium Slovenica.* Classis IV, *Historia Naturalis et Medicina,* 13(2): 87-111.

BOLE, J., 1971, O anatomiji in taksonomiji rodu *Litthabitella* Boeters, 1970 (Gastropoda, Hydrobiidae). *Razprave; Slovenska Akademija Znanosti in Umetnosti academia scientiarum et artium Slovenica.* Classis IV, *Historia Naturalis et Medicina,* 14(3): 79-91.

BRANDT, R. A. M., 1968, Descriptions of new non-marine mollusks from Asia. *Arch. Molluskenk.,* 98: 213-289.

BRANDT, R. A. M., 1970, New freshwater gastropods from the Mekong. *Arch. Molluskenk.,* 100: 183-205.

BRANDT, R. A. M. & TEMCHAROEN, P., 1971, The molluscan fauna of the Mekong at the foci of schistosomiasis in South Laos and Cambodia. *Arch. Molluskenk.,* 101: 111-140.

BREGENZER, A., 1916, Anatomie und Histologie von *Bythinella dunkeri. Zool. Jahrb. (Anat.),* 39: 237-292, 1 pl.

CHERNIN, E., 1968, Interference with the capacity of *Schistosoma mansoni* miracidia to infect the molluscan host. *J. Parasitol.,* 54: 509-516.

CHERNIN, E. & PERLSTEIN, J. M., 1969, Further studies on interference with the host-finding capacity of *Schistosoma mansoni* miracidia. *J. Parasitol.,* 55: 500-508.

CHI, L. W., WAGNER, E. D. & WOLD, N., 1971, Susceptibility of *Oncomelania* hybrid snails to various geographic strains of *Schistosoma japonicum. Amer. J. trop. Med. Hyg.,* 20: 89-94.

CREEK, G. A., 1953, The morphology of *Acme fusca* (Montagu) with special reference to the genital system. *Proc. malacol. Soc. Lond.,* 29: 228-240.

CRISTOFORI, J. & JAN, G., 1832, *Catalogus in IV Sectiones Divisus.* Section II, *Conchyliologica;* Part I, *Conspectus Methodicus Molluscorum;* Fasc. I. *Testacea Terrestria et Fluviatilia.* 1-8, 1 p. supp.

DAVIS, G. M., 1966, Notes on *Hydrobia totteni. Venus,* 25: 27-42.

DAVIS, G. M., 1967, The systematic relationship of *Pomatiopsis lapidaria* and *Oncomelania hupensis formosana* (Prosobranchia: Hydrobiidae). *Malacologia,* 6: 1-143.

DAVIS, G. M., 1968a, A systematic study of *Oncomelania hupensis chiui* (Gastropoda: Hydrobiidae). *Malacologia,* 7: 17-70.

DAVIS, G. M., 1968b, New *Tricula* from Thailand. *Arch. Molluskenk.,* 98: 291-317.

DAVIS, G. M., 1969a, Reproductive, neural and other anatomical aspects of *Oncomelania minima* (Prosobranchia: Hydrobiidae). *Venus,* 28: 1-36.

DAVIS, G. M., 1969b, *Oncomelania* and the transmission of *Schistosoma japonicum:* A brief review. *In:* Harinasuta, C. (ed.), *Proceedings of the Fourth Southeast Asian Seminar on Parasitology and Tropical Medicine, Schistosomiasis and other Snail-Transmitted Helminthiasis.*

Bangkok, p. 93-103.

DAVIS, G. M., 1971, Mass cultivation of *Oncomelania* (Prosobranchia: Hydrobiidae) for studies of *Schistosoma japonicum. In:* Hubert, A. (ed.), Culturing *Biomphalaria* and *Oncomelania* (Gastropoda) for Large-Scale Studies of Schistosomiasis. *Bio-Medical Report of the 406th Medical Laboratory,* No. 19: 85-161.

DAVIS, G. M. & CARNEY, W. P., 1973, Description of *Oncomelania hupensis lindoensis,* first intermediate host of *Schistosoma japonicum* in Sulawesi (Celebes). *Proc. Acad. natur. Sci. Philad.,* 125: 1-34.

DAVIS, G. M. & RUFF, M. D., 1974, *Oncomelania hupensis* (Gastropoda: Hydrobiidae): Hybridization, genetics and transmission of *Schistosoma japonicum.* Malacol. Rev., 6: 181-197.

DUNDEE, D. S., 1957, Aspects of the biology of *Pomatiopsis lapidaria* (Say) (Mollusca: Gastropoda: Prosobranchia). *Misc. Publs. Mus. Zool., Univ. Mich.,* No. 100: 1-37, 14 pls.

FISCHER, P., 1885, *Manuel de Conchyliologie et de Paléontologie Conchyliologique.* Savy, Paris, p. 689-784.

FRETTER, V. & GRAHAM, A., 1962, *British Prosobranch Molluscs.* Ray Soc., London. 755 p.

GRAHAM, A., 1939, On the structure of the alimentary canal of style-bearing prosobranchs. *Proc. zool. Soc. Lond.,* 108: 75-112.

GRAY, J. E., 1847, A list of the genera of Recent Mollusca, their synonyma and types. *Proc. zool. Soc. Lond.,* "1847": 129-219.

HAIRSTON, N., TINKLE, D. & WILBUR, H., 1970, Natural selection and parameters of population growth. *J. Wildlife Management,* 34: 681-690.

HARINASUTA, C., SORNMANI, S., KITIKOON, V., SCHNEIDER, C. R. & PATHAMMAVONG, O., 1972, Infection of aquatic hydrobiid snails and animals with *Schistosoma japonicum*-like parasites from Khong Island, Southern Laos. *Trans. Roy. Soc. trop. Med. Hyg.,* 66: 184-185.

HARTMAN, W., 1821, System der Erd- und Susswasser Gasteropoden Europa's. *In*: J. Sturm (ed.), *Deutschlands Fauna,* VI, part. 5, Nürnberg, 60 p., 3 pls.

HENKING, H., 1894, Beiträge zur Kenntniss von *Hydrobia ulvae* Penn. und deren Brutpflege. *Ber. Naturf. Ges. Freiburg,* 7: 89-122, pl. 4.

HERRMANNSEN, A. N., 1846, *Indicis Generum Malacozoorum Primordia.* Vol. 1. Cassell, xvii + 637 p.

IIJIMA, T., LO, T. C. & ITO, Y., 1971, Studies on schistosomiasis in the Mekong Basin. I. Morphological observation of the schistosomes and detection of their reservoir hosts. *Jap. J. Parasitol.,* 20: 24-33.

ITO, J., 1964, A monograph of cercariae in Japan and adjacent territories. *In: Progress of Medical Parasitology in Japan,* Vol. 1. Meguro Parasitol. Mus., Tokyo, p. 397-538.

JOHANSSON, J., 1939, Anatomische Studien über die Gastropodenfamilien Rissoidae und Littorinidae. *Zool. Bidr. Upps.,* 18: 287-396, pls. 1-11.

JOHANSSON, J., 1953. On the genital organs of some mesogastropods: *Cerithium vulgatum* Brug., *Triphora perversa* (L.) and *Melanella (Eulima) intermedia* (Cantr.). *Zool. Bidr. Upps.,* 30: 1-23.

JOHANSSON, J., 1956, Genital organs of two *Alvania* species and a comparison with related families (Moll. Pros.). *Ark. Zool.,* 9: 377-387.

KING, C. E. & ANDERSON, W., 1971, Age-specific selection. II. The interaction between r and K during population growth. *Amer. Natur.,* 105: 137-156.

KITIKOON, V., SCHNEIDER, C. R., SORNMANI, S., HARINASUTA, C. & LANZA, G., 1973, Mekong schistosomiasis: 2. Evidence of the natural transmission of *Schistosoma japonicum,* Mekong strain, at Khong Island, Laos. *Southeast Asian J. trop. Med. Public Health,* 4: 350-358.

KRAUSE, H., 1949, Untersuchungen zur Anatomie und Ökologie von *Lithoglyphus naticoides* (C. Pfeiffer). *Arch. Molluskenk.,* 78: 103-148.

KRULL, H., 1935, Anatomische Untersuchungen an einheimischen Prosobranchiern und Beiträge zur Phylogenie der Gastropoden. *Zool. Jahrb. (Anat.),* 60: 399-464.

LILLY, M., 1953, The mode of life and the structure of functioning of the reproductive ducts of *Bithynia tentaculata* (L.). *Proc. malacol. Soc. Lond.,* 30: 87-110.

LO, C. T., BERRY, E. G. & IIJIMA, T., 1971, Studies on schistosomiasis in the Mekong Basin. II. Malacological investigations on human *Schistosoma* from Laos. *Chin. J. Microbiol.,* 4: 168-181.

MACARTHUR, R. H., 1962, Some generalized theorems of natural selection. *Proc. Natn. Acad. Sci.,* 48: 1893-1897.

MACARTHUR, R. H. & WILSON, E. O., 1967, *The Theory of island biogeography.* Princeton Univ. Press, N.J., U.S.A., 203 p.

MALEK, E., 1962, *Laboratory Guide and Notes for Medical Malacology.* Burgess, Minn., U.S.A., iv + 154 p.

PATHAMMAVONG, O., 1969, Schistosomiasis in Laos. *In* Harinasuta, C. (ed.), *Proceedings of the fourth southeast Asian seminar on parasitology and tropical medicine, schistosomiasis and other snail-transmitted helminthiasis, Manila, 24-27 February, 1969,* Bangkok, p. 65-66.

PEZZOLI, E. & GIROD, A., 1971, *Frauenfeldia lacheineri* (Küster) e *Bythinella schmidti* (Küster) in Lombardia. *Natura,* Milano, 62: 369-395.

PFEIFFER, C., 1828, *Naturgeschichte deutscher Land- und Süsswasser-Mollusken.* Weimar, 84 p, 8 pls.

PONDER, W. F., 1973, The origin and evolution of the Neogastropoda. *Malacologia,* 12: 295-338.

PRASHAD, B., 1921a, Reports on the freshwater gastropod mollusks of Lower Mesopotamia. III. The families Neritidae, Hydrobiidae, and Melaniidae. *Rec. Ind. Mus.,* 18: 215-227.

PRASHAD, B., 1921b, The Indian species of the genus *Tricula,* Benson. *Rec. Ind. Mus.,* 22: 67-69.

RADOMAN, P., 1955a. Prilog izučavanju malakološke faune pribrežnih voda Ohridskog Jezera. Srpsko Biolosko Drustvo. *Archiv Bioloskih Nauka,* 7: 105-113.

RADOMAN, P., 1955b, Morfološko-sistematska istrazivanja Ohridskih Hidrobida. Srpsko Biolosko Drustvo. *Posebna Izdanja,* 1: 1-106.

RADOMAN, P., 1966, The zoogeographical and phylogenetic inter-relations of the genera *Lithoglyphus* and *Emmericia. Bull. Mus. Hist. Nat. Belgrade,* Ser. B, 21: 43-49.

RADOMAN, P., 1974, Some new gastropod representatives from the brackish waters of the Adriatic and Aegean seasides. *Veliger,* 16: 283-288.

RAO, H. S., 1928, The aquatic and amphibious mollusks of the Northern Shan States, Burma. *Rec. Ind. Mus.,* 30: 399-468, 3 pls.

RICHARDS, C. S., 1970, Genetics of a molluscan vector of schistosomiasis. *Nature,* 227: 806-810.

ROBSON, G. C., 1920, On the anatomy of *Paludestrina jenkinsi. Ann. Mag. natur. Hist.,* ser. 9, 5: 425-431.

ROBSON, G. C., 1921, On the anatomy and affinities of *Hypsobia nosophora. Ann. Mag. natur. Hist.,* ser. 9, 8: 401-413.

ROBSON, G. C., 1922, On the anatomy and affinities of *Paludestrina ventrosa,* Montagu. *Quart. J. microsc. Sci.,* 66: 159-185.

SORNMANI, S., KITIKOON, V., HARINASUTA, C. & PATHAMMAVONG, O., 1971, Epidemiological study of schistosomiasis japonica on Khong Island, southern Laos. *Southeast Asian J. trop. Med. Public Health,* 2: 365-374.

SORNMANI, S., KITIKOON, V., SCHNEIDER, C. R., HARINASUTA, C. & PATHAMMAVONG, O., 1973, Mekong schistosomiasis: 1. Life cycle of *Schistosoma japonicum,* Mekong strain in the laboratory. *Southeast Asian J. trop. Med. Public Health,* 4: 218-225.

STIMPSON, W., 1865, Researches upon the Hydrobiinae and allied forms; chiefly upon materials in the museum of the Smithsonian Institution. *Smiths. misc. Collect.,* (201): iii, 1-59.

STUNKARD, H., 1946, Possible snail hosts of human schistosomes in the United States. *J. Parasitol.,* 32: 539-552.

TAYLOR, D. W., 1966, A remarkable snail fauna from Coahuila, Mexico. *Veliger,* 9: 152-228.

TEMCHAROEN, P., 1971, New aquatic molluscs from Laos. *Arch. Molluskenk.,* 101: 91-109.

THIELE, J., 1928, Revision des Systems der Hydrobiiden und Melaniiden. *Zool. Jahrb. (Syst.),* 55: 351-402, pl. 8.

THIELE, J., 1929, Handbuch der systematischen Weichtierkunde. Teil I. Jena, Fischer, 1-376 p.

THOMPSON, F., 1968, *The aquatic snails of the family Hydrobiidae of peninsular Florida.* Univ. Florida Press, Gainesville, xv + 268 p.

TROSCHEL, F. H., 1857, Das Gebiss der Schnecken zur Begründung einer natürlichen Classification . . . Bd. I, Berlin, Nicolaische Verl.

UPATHAM, E. S., 1972, Interference by unsusceptible aquatic animals with the capacity of the miracidia of *Schistosoma mansoni* Sambon to infect *Biomphalaria glabrata* (Say) under field-simulated conditions in St. Lucia. *J. Helminth.,* 46: 277-283.

UPATHAM, E. S. & STURROCK, R. F., 1973, Field investigations on the effect of other aquatic animals on the infection of *Biomphalaria glabrata* by *Schistosoma mansoni* miracidia. *J. Parasitol.,* 59: 448-453.

VAN DER SCHALIE, H. & DUNDEE, D., 1956, The morphology of *Pomatiopsis cincinnatiensis* (Lea), an amphibious prosobranch snail. *Occ. Paps. Mus. Zool., Univ. Mich.,* No. 579: 1-17, 7 pls.

WENZ, W., 1939, *Handbuch der Paläozoologie,* vol. 6 (O. H. Schindewolf, ed.) Gastropoda, Part 3, *Prosobranchia.* Berlin, Borntraeger, p. 481-720.

WILSON, E. O., 1965, The challenge from related species, *In:* H. G. Baker & G. L. Stebbins (ed.), *The Genetics of Colonizing Species,* Academic Press, N.Y., p. 7-24.

WINTERBOURN, M., 1970, The New Zealand species of *Potamopyrgus* (Gastropoda: Hydrobiidae). *Malacologia,* 10: 283-321.

WRIGHT, C. A., 1974, Snail susceptibility or trematode infectivity? *J. Nat. Hist.,* 8: 545-548.