MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 100

Aspects of the Biology of *Pomatiopsis lapidaria* (Say) (Mollusca: Gastropoda: Prosobranchia)

BY
DEE SAUNDERS DUNDEE

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
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CONTENTS

ILLUSTRATIONS

PLATES

(Plates I-XIV follow page 37)

FIGURES IN THE TEXT

MAPS

ASPECTS OF THE BIOLOGY OF *POMATIOPSIS LAPIDARIA* (SAY)* (MOLLUSCA: GASTROPODA: PROSOBRANCHIA)

INTRODUCTION

SNAILS of the genus *Pomatiopsis* are of special interest because of their potentials for serving in North America as intermediate hosts of *Schistosoma japonicum*, the human blood fluke which produces in the Orient a widespread disease, schistosomiasis (Stunkard, 1946; Ward, Travis, and Rue, 1947; Berry and Rue, 1948). The United States Public Health Service is satisfied that there is no immediate danger of the disease becoming established in this country, but the importance of accurate and detailed information concerning potential vectors cannot be overestimated. This genus is also of interest because it is one of the few prosobranchs known to live on land. Studies on the biology of *Pomatiopsis* have revealed numerous similarities in the morphology and ecology of this genus and *Oncomelania*, the Oriental snail vector for schistosomiasis. The present investigation is designed to increase knowledge of the life history and morphology of *Pomatiopsis lapidaria.* Abbott (1948: 57), who initiated a similar program, stated: "Whether or not, with the accidental introduction of schistosomiasis into this country, the snail (*P. lapidaria*) would become of medical importance in the future, it seems wise at this time to record what we know of its distribution, habits and morphology."

Pomatiopsis lapidaria is a rather small, operculate snail, with maximum height of less than 8 mm. It is a member of the large group of gastropods, the prosobranchs, characterized by having the heart posterior to the gill, the visceral commissures of the nervous system crossed, and the sexes separate. For some time there were several different opinions about the taxonomic position of this genus, but in 1929 Thiele placed it in the family Hydrobiidae and in the subfamily Truncatellinae, which also includes *Oncomelania*, among other genera. Since that time other shifts in the generic classification have been made, but the classification proposed by Thiele seems most logical on the basis of the close relationship between *Pomatiopsis* and *Oncomelania.*

A survey of the biological literature on *Pomatiopsis lapidaria* reveals that five major articles have been published; several others include incidental information about this species. F. C. Baker (1931) concerned himself with some of the ecological aspects of *P. lapidaria* in an attempt to settle an issue as to whether this species was amphibious or aquatic. In 1938 D. J. Ameel published his "Observations on the Natural History of *Pomatiopsis lapidaria* Say." That work was done on colonies found in the Ann Arbor area. A brief summary of the available knowledge about *Pomatiopsis lapidaria* was given by R. T. Abbott (1948) in a paper entitled, "A Potential Snail Host of Oriental Schistosomiasis in North America (*Pomatiopsis lapidaris*)." In the same year a paper was presented at the twenty-third meeting of the American Society of Parasitologists by E. G. Berry

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and R. E. Rue, in which they first described the egg and told of their tests of the susceptibility of *Pomatiopsis* to infection with *Schistosoma japonicum.* The last of the major papers concerning this species was that of W. B. DeWitt (1952). In it he discussed aspects of the biology of *P. lapidaria* in the Washington, D. C. area and gave information about rearing these snails in the laboratory. Also of interest with respect to *Pomatiopsis* in Michigan is the paper "Amnicolidae of Michigan: Distribution, Ecology, and Taxonomy" by E. G. Berry (1943). In it he included a discussion of *Pomatiopsis*, even though he considers this genus to belong to a family of its own rather than to a subfamily of the Amnicolidae.

The data to be presented are arranged under four main topics: distribution, habitats, life history, and anatomy. In each of these categories past findings are integrated with present results, and an attempt is made in the last three to compare much of the available knowledge of *Pomatiopsis lapidaria, Pomatiopsis cincinnatiensis*, and the three better known species of *Oncomelania.*

Acknowledgments

For continued help and interest in the course of this investigation, I want to express my appreciation to Dr. Henry van der Schalie. I am also grateful to Drs. Elzada Clover, Frank Eggleton, Theodore Hubbell, and Norman Kemp for their constructive suggestions in the writing of the manuscript.

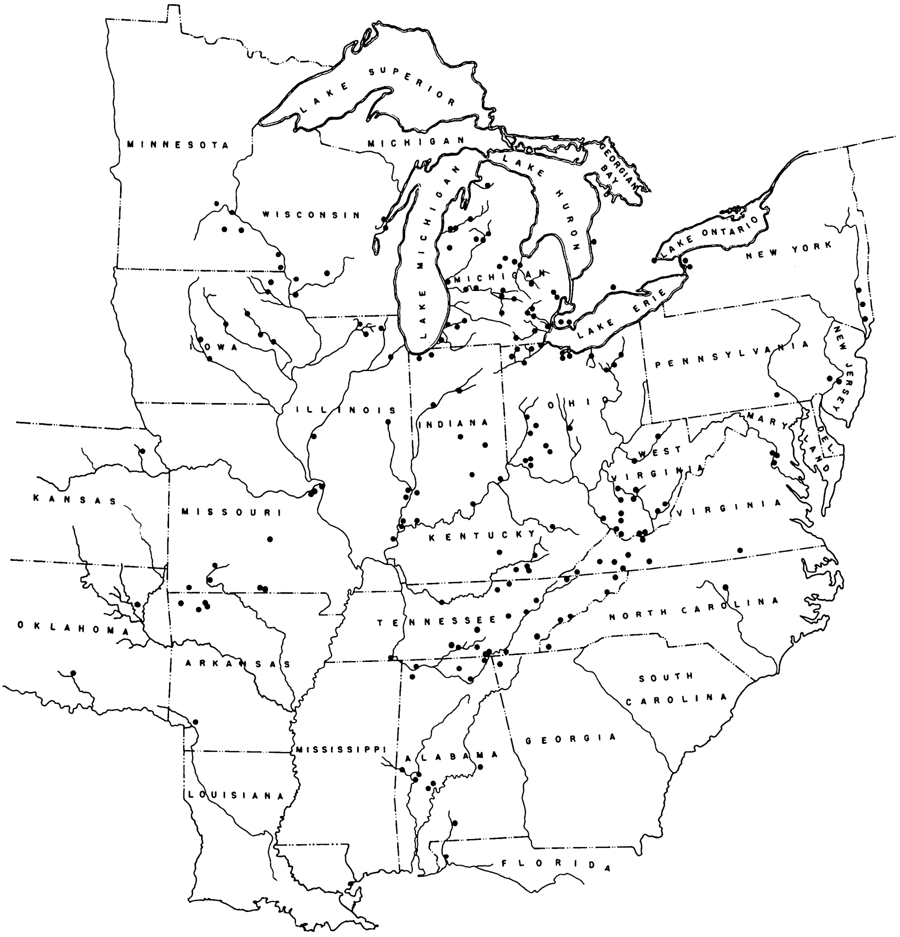
Mr. William Brudon prepared several of the figures; Mr. William Cristanelli drafted the maps and the histograms.

Some locality records provided by Mr. Leslie Hubricht were valuable in plotting distribution.

DISTRIBUTION

Time.—Three species of *Pomatiopsis* are known from the Pleistocene. One, *Pomatiopsis scalaria*, is believed to have existed from Yarmouth to Early Wisconsin time, when it presumably became extinct (Baker, 1931). Likewise, *P. lapidaria* has been found in Yarmouthian deposits. More recent findings (Leonard, 1952) have shown that *Pomatiopsis cincinnatiensis* existed in the late Kansan and early Yarmouthian periods. Stimpson (1865) and Cooke (1895) have suggested that the group of closely allied prosobranchs which includes, among others, *Hydrobia, Cincinnatia, Amnicola, Pomatiopsis, Oncomelania, Truncatella, Bithynia, Paludestrina,* and *Somatogyrus* is closely related to, and was probably originally derived from, the Littorinidae, a marine family inhabiting the intertidal zones of all oceans. The earliest known occurrence of any member of this group is that of *Hydrobia* which is recorded from the Jurassic. It is possible, then,. that *Pomatiopsis* had its origin sometime between the Jurassic and early Pleistocene where it is first found; possibly in the Cretaceous when such other forms as *Melania, Valvata, Neritina, Planorbis, Carychium,* and *Physa* appeared.

Space. — *Pomatiopsis lapidaria* has a rather wide distribution (Map 1) over much of the eastern half of the United States extending northward into southern Ontario. Its known westward limits are indicated by the following records: Atchison County, Kansas; Cherokee and Murray counties, Oklahoma; and Socorro County, New Mexico. Along the eastern coast its known range extends in a spotty manner from southeastern New York southward to Durham County, North Carolina. On the north it ranges from Minnesota eastward through southern Ontario. In the south its true distribution is obscured by a lack of collections. Many records are known from Alabama, a few from Arkansas, and one from Florida, but there are none from Louisiana, Mississippi, Georgia, or South Carolina. Abbott (1947, 1948) and Ameel (1934) have both mapped the distribution of this species. Map 1 not only adds localities to those which they have already plotted, but represents an attempt to plot the range more accurately. It was not possible to include the Socorro County, New Mexico, record on this map.



Map 1. Distribution of *Pomatiopsis lapidaria* in the United States.

In Michigan (Map 2) *Pomatiopsis lapidaria* has been reported as far north as Charlevoix County in the lower peninsula. It is widely scattered over the eastern and western parts of the state south of the Grand-Saginaw drainage, but there are relatively few localities known to the north of those basins.

P. lapidaria, in contrast to *P. cincinnatiensis,* seems to require a much wetter environment. It can be found in abundance in certain marshy areas; for example, those occurring along the Huron River near Ann Arbor. It may also live in various other habitats such as the wooded flood plains of small creeks; for example, the one found at the Hogback station considered here. Occasionally, it may be observed in the same habitat as *P. cincinnatiensis* (van der Schalie and Dundee, 1955). Such an association occurs within Warren Woods in Berrien County, Michigan, as well as along the Little Miami River at Yellow Springs, Greene County, Ohio. *P. lapidaria* has also been reported from the banks of a few lakes (Reed's Lake, Kent County, Michigan, by Charles D. Nelson—UMMZ 56361; Thumb Lake, Charlevoix County, Michigan, no collector given—UMMZ 42707). Because of the present limitations of knowledge it is extremely difficult to say just what are the factors influencing its distribution. Although *P. cincinnatiensis* seems to inhabit the banks of sizable streams ranging from a large creek to a river, *P. lapidaria* appears not to be limited by stream size, since it has been reported from bodies of water varying from temporary streams, which may be dry part of the year, to rivers as large as, or larger than, the Grand River in Michigan.

HABITATS

Two stations near Ann Arbor and within the Huron River drainage in southeastern Michigan were chosen for making regular observations. These sites were visited at bimonthly intervals (except during the dormant or winter season) over a period of two and one-half years for the purpose of making collections, observing the behavior of the snails, and studying the habitats.

Barton station. —This station is approximately one-fourth mile east of Barton Dam along the Huron River Drive and about two miles northwest of Ann Arbor, Washtenaw County, Michigan. In the ensuing discussion it will be referred to merely as "Barton." It consists of an area approximately 40 yards long and 20 yards wide and is a cattail marsh (Pl. I, Fig. 1). It is bounded on the north by the Huron River and on the south by a high embankment supporting the main road. The dominant plant is the cattail, *Typha latifolia.* During the active growing season a number of plants, such as *Dipsacus sylvestris*, *Impatiens capensis*, and *Symplocarpus foetidus*, may be found; however, the one associated plant which seems most characteristic in a *Pomatiopsis lapidaria* habitat is the moss, *Amblistegium varium.* It was observed here and in nearly every site where *P. lapidaria* occurred.

The soil at Barton is a sandy loam and throughout the year it remains saturated with water supplied by rains, by the river itself, and by a small seepage stream that drains into the habitat from the hill above the road.

Map 2. Distribution of *Pomatiopsis lapidaria* in Michigan.

In view of the fact that other *Typha* stands in nearby areas do not have colonies of *Pomatiopsis* or at best have only a few individuals, it seems likely that seepage is an important factor in making this a suitable area for the species. At no time during the two and one-half years of observation did the river actually flood the area. The pH of this soil generally ranged between 7.5 and 8.0.

Other associated snails found in this habitat are listed in order of decreasing abundance, as follows: *Stenotrema monodon, Oxyloma retusa, Stenotrema hirsutum, Polygyra multilineata, Gastrodonta ligera, Succinea ovalis, Mediappendix vagans, Euconulus fulvus,* and *Discus cronkhitei.*

Since *Typha* is a perennial, a heavy mat of dead cattail leaves covered the habitat at Barton and undoubtedly gave protection to the snails during the more rigorous seasons (Pl. I, Fig. 2). In warm periods and when the vegetative mat was sufficiently moist, many *P. lapidaria* were often found crawling about on the exposed surfaces of these leaves. When conditions were dry and during cold weather, these snails sought shelter below the surface of the mat; they were then much more difficult to find. Sometimes it was necessary to dig down two to three inches under the mat in order to obtain them.

That part of the Barton habitat directly opposite the seepage zone contained much more standing water than the rest. This wetter area supported very few *P. lapidaria,* and it was obvious that they were much more abundant in the peripheral zones. During unusually heavy rains the entire *Typha* mat was covered with water. Most of the snails were then submerged for hours without any apparent harm. Occasionally, they were found crawling upon the living *Typha,* but this activity was most evident during early morning hours or in cloudy, wet weather. They were never seen higher than a foot from the base of the stock on the few occasions when climbing was observed.

At this station *Typha latifolia* itself had a predictable annual cycle. It first appeared above the ground in the latter part of February. By the second week of June it had grown to about six feet in height. Flowers appeared about June 20 and by the second week of July the stand had reached a maximum height of approximately seven feet. In the latter part of July it started to turn brown, and by the last of September it began to fall. From autumn until February the plants were entirely brown, and as the season progressed more and more stalks were knocked down. The snails usually resumed activity on the mat when the new plants appeared in early spring.

Hogback station. —The conditions at this station were in sharp contrast to those at Barton. Located on Hogback Road about four miles east of Ann Arbor in Washtenaw County, it consists of the wooded flood plain (Pl. II, Fig. 1) of a small stream, the Pittsfield Drain, which has a channel approximately three feet wide in this part of its course. The vegetative cover here includes elms (*Ulmus americanus*), willows (*Salix* sp.), dogwood (*Cornus racemosa*), and a variety of smaller plants such as *Laportea canadensis, Stellaria media, Thalictrum* sp., and *Ranunculus arborvitus,* which together with some grasses make up the ground herbage.

The creek itself did not dry completely at any time during the two and one-half years of observation, although it was reduced to a width of six inches in August and September, 1953. Since this stream is heavily polluted, it often has a milky appearance and a vile odor. In the area adjacent to the stream there are three rivulets which form connections between bends of the main stream. These expansions are filled during rains and by overflow from the stream, but are dry for much of the year. The heavier concentrations of *Pomatiopsis lapidaria* are found along these rivulets, although they can also be collected in the low grassy areas and along the main stream. In the latter situation they are usually found about a foot or so from the water's edge; seldom are they on the part of the bank closest to the stream. The snails associated with *Pomatiopsis lapidaria* at this station include many *Zonitoides nitidus* and *Cionella lubrica* and an occasional *Gastrodonta ligera*, *Zonitoides arboreus*, and *Lymnaea humilus*. The soil in this habitat is sandy and well drained. The soil pH generally runs 7.5, whereas the pH of the water in the main stream is 8.0.

Comparison of *Oncomelania* and *Pomatiopsis* habitats.—Throughout the course of this work with *Pomatiopsis* a striking similarity was evident in its habitats when compared with those of *Oncomelania* which have been described by a number of investigators, as follows:

> Snails [*Oncomelania quadrasi*] were most frequently found in grassy ponds or slowly moving water. They do not normally live in swifty flowing water, although floods may transport [them] .... These mollusks were found on the stems of emergent vegetation, particularly reeds, often as much as four inches above the surface. However, this was true only in the early morning and part of the evening. During the hotter part of the day they migrated beneath the water surface and were especially abundant in the shade of overhanging trees and shrubs (Avery, 1946: 5).
>
> ...small, slowly flowing, fresh-water creeks or boggy areas which are being constantly supplied with a fresh flow of water. The snail is amphibious but never absent from shady and moist, if not actually flooded, creek beds (Abbott, 1946: 41).
>
> ...found living under variable conditions.... These areas are alluvial plains not much above sea level, with meandering streams, and a great deal of the terrain is swampy or boggy and overgrown with grass.... The snails live in places kept wet in the process of rice culture, or in seepages at the bases of the mountains that form the walls of the valleys ....During the dry season most of the snails are on the surface of the moist soil in these grassy, shaded areas. They are sometimes found where there are sedges but the grass habitat is more typical. They are also found in adjacent streams and pools where they are on decaying palm fronds, coconut shells, grass, water hyacinths, etc....they are also found beneath the water and on the muddy bottom (McMullen, 1947: 260-61).
>
> [*Oncomelania nosophora*] live in brooks and ditches used mainly for the purpose of irrigation where the water current is slow or nearly stagnant and dries up in winter seasons. They do not exist in such ditches where the water is abundant all the year round and rapidly flows, or where a spring supplied cold water.... These snails rarely stay in deep water ... they are usually found in or on moist soil just above the water's edge of the brook, or on moist vegetable matter above the apparent level of the water.... They also inhabit the rice fields and the ridge between the fields (Sugiura, 1933: 3-4).
>
> In warm weather they [*Oncomelania hupensis*] prefer to live close to the edge of, or even under, the surface of relatively clear, still, fresh water. During certain seasons these snails are plentiful along the banks of the canal, while at other times they are found under the surface of the water attached to stalks of water-grass, other aquatic plants, or stones (Watt, 1936: 435-36).

Pomatiopsis cincinnatiensis is found along banks of large creeks or rivers "where the mud or matted root system on which the animals live retains a considerable amount of moisture" (van der Schalie and Dundee, 1955: 120). Also present are a band of grass and/or weeds which provides shade for the snails and a soil composed of a mud-sand mixture.

Pomatiopsis lapidaria is found in a variety of habitats such as marshes, wooded flood plains of small creeks, grassy hummocks in low, wet pastures, in the habitat described above for *P. cincinnatiensis,* and in upland artesian-fed marshes. The features common to all *P. lapidaria* habitats seem to be: (1) a very moist substratum with enough sand to prevent it from becoming muck, (2) shade, (3) fresh water. As with all of these general descriptions of habitats, one must keep in mind the seasonal factor—that these habitats are drier at certain times of the year.

Both groups of snails are amphibious and yet capable of withstanding considerable dessication. Both *Oncomelania* and *Pomatiopsis* live on moist soil close to the edge of relatively quiet, fresh-water streams; both apparently need shade. *Oncomelania*, however, is found on emergent vegetation much more frequently than *Pomatiopsis,* and some species of *Oncomelania* seem to live where they are subject to submergence much more often. On the basis of the published figures it appears that *Pomatiopsis* is subjected to a somewhat higher pH than *Oncomelania.* This apparent difference may not be real since the tests were made by different people who probably used different methods. The figures obtained from available information are as follows: *Oncomelania nosophora,* water pH 6.2-7.0 (Sugiura, 1933); *Oncomelania quadrasi,* water pH 6.2-7.0 (McMullen, 1947); none for *O. hupensis; P. lapidaria,* wet soil and water pH 7.5-8.0; *P. cincinnatiensis,* soil pH 8.0 (van der Schalie and Dundee, 1955).

So far as habitat selection is concerned, *Pomatiopsis* may be somewhat more advanced in that it has succeeded in adapting itself to life on land better than has *Oncomelania.* Avery (1946) reported that *O. quadrasi* in the Philippines spent the warmer part of the day under water; Watt (1936) stated that in Chekiang Province, China, *O. hupensis* lived close to, or even under, water. Within the *Pomatiopsis* group itself, *P. cincinnatiensis* appears to be better adapted to life out of water than *P. lapidaria* since it maintains itself on the banks of the stream well above the water level. This tendency may be indicated by the progressive decrease in the number of gill filaments from *Oncomelania* with 40-60 filaments, to *P. lapidaria* with 15-20 filaments, to *P. cincinnatiensis* with 10-15. Abbott (1948) also indicated that the mucous glands become more abundant in a similar sequence. Even between *P. lapidaria* and *P. cincinnatiensis* such a glandular increase is apparent.

LIFE HISTORY

Population size.—The discontinuous or "spotty" nature of the pattern of distribution in *Pomatiopsis* emphasizes the fact that these animals usually occur in colonies. The size of a colony varies tremendously, and its dimensions may reflect the length of time a colony has been established in an area. Some colonies, such as those at Barton and Hogback, have been under observation by local malacologists for at least twenty years. In both stations thousands of snails were available over an extended period. It has been difficult to obtain figures on the size of these populations, since the animals are not randomly distributed over the area which they occupy. Other habitats are much less productive and may contain relatively few individuals. Observations have shown that usually specimens of *P. lapidaria* are not so abundant within a colony as are those of *P. cincinnatiensis*. This difference can undoubtedly be attributed to the tendency for the latter species to occupy the stream banks in a more linear pattern.

Adult.—*Pomatiopsis lapidaria* shows a sexual dimorphism which becomes most apparent when a series of specimens is examined. The adult males are smaller, tend to appear less inflated, have a much sharper apex, and have a higher average whorl count than the adult females. This dimorphism, however, is not so clear-cut that one can determine with complete accuracy the sex of any individual merely upon casual observation of external features. The largest female found during this study was 8.5 mm. long, 3.5 mm. wide, and had 7.5 whorls; the largest male was 7.0 mm. long, 3.0 mm. wide, and had 6.5 whorls. When the lengths of individuals in various population samples are plotted, the results show bimodal curves. A mode at 4.5-5.0 mm. indicates the size of the bulk of the mature male population and includes part of the young females; the mode at 5.5-6.0 mm. includes most of the adult females plus a few males of more than average size. Measurements (Table I) are provided to establish the average width and number of whorls for given sizes (in lengths) of males and females at the Barton station.

TABLE I

Average Dimensions (Length and Width in mm.)
and Whorl Counts of Males and Females at the Barton Station

Females	Length	Width	Whorls	Males	Length	Width	Whorls
27	0.50	0.50	2.25	14	0.50	0.50	2.41
30	1.00	0.72	2.69	12	1.00	0.71	2.70
34	1.50	1.00	3.18	20	1.50	1.00	3.33
20	2.00	1.50	3.83	15	2.00	1.25	3.87
20	2.50	1.50	4.00	11	2.50	1.48	4.21
23	3.00	1.93	4.59	15	3.00	1.87	4.62
26	3.50	1.92	4.75	10	3.50	2.00	5.25
23	4.00	2.21	5.21	10	4.00	2.00	5.45
20	4.50	2.35	5.73	20	4.50	2.50	5.50
42	5.00	2.49	5.84	25	5.00	2.46	5.87
32	5.50	2.68	6.00	10	5.50	2.58	6.00
33	6.00	2.87	6.11	4	6.00	3.00	6.50
19	6.50	3.00	6.50	0	....	....	....
8	7.00	3.25	6.50	1	7.00	3.00	6.50
1	7.50	3.50	7.00	....	....	....	....
2	8.00	3.50	7.00	....	....	....	....

Movements. —Movement of the colony as a whole is restricted to periodic, short-distance shifts which are correlated with changes in the moisture content of the habitat. A series of quadrat samples was taken at the Hogback station during the bimonthly visits from May to September, 1954. Each observation was made with the quadrat (40 by 12 inches and marked off into 20 rectangles, each measuring 4 by 6 inches) placed in exactly the same place within the habitat. The relative positions of the snails were used to establish the nature of their movements. As the water disappeared from the rivulets, the snails moved nearer to their lower level; when the rivulets dried to the moist mud stage many snails were found moving over the damper parts. When these rivulets again were filled with water following rains or the melting of snows or because of overflow from the main stream, the snails moved out of the water and up onto the adjacent banks. At Barton, where conditions were totally different from those at Hogback, movement was in a more vertical direction so that when the land was dry, the snails went below the *Typha* mat to reach the moisture, but during wet periods they could be found crawling about on the upper surface of the mat.

In terms of migration individuals apparently do not voluntarily move more than about six feet throughout their entire life span. Marked specimens were never recaptured at a greater distance beyond the point of their release. Although experimental data are lacking, it seems reasonable to assume that new colonies do become established at different points along the stream during floods. On September 4, 1954, after a heavy four-day rainy period in which some three inches of rain fell, the habitat at the Hogback station assumed quite an unusual aspect. The entire area showed the effects of being washed by the heavy current resulting from the overflow of the main stream. Specimens of *P. lapidaria* could not be found in their usual places, but rather were concentrated in drift which had been stacked against objects. Doubtless others were washed farther downstream. Even a month later (October 14, 1954) the specimens there were still scattered and not so abundant as usual in the rivulets. On another occasion, June 20, 1953, under similar circumstances many of the mollusks in that area, including *P. lapidaria*, were found washed downstream to a point where one of the rivulets joins the main channel and where there are usually no snails.

These observations seem to indicate that spreading may occur in such a passive manner; however, if one considers the places in which this species is found in nature, it becomes evident that not all such fortuitous dispersals are successful. The ecological requirements of these snails are such that they cannot live at every location even along the same stream; rather, they need a suitable habitat before new colonies can be established. As a consequence, despite such excellent possibilities for distribution as the drift dispersal just cited, *P. lapidaria* usually maintains itself in small and highly localized colonies that keep their identities and show little tendency to spread unless the animals find the right combinations of habitat requirements.

Dormancy. —In Michigan there are two major dormant periods in the yearly cycle of *P. lapidaria*, one during the cold months (November through February) and another during the hot and dry summer weather (last week of June and the month of July). Neither period is continuous. Should a few days of rain occur during one of them, the snails may again become temporarily active. During most of the winter the animals are dormant and are found lying beneath fallen vegetation, in crevices, and under objects with their opercula well inserted into the apertures of their shells. In summer they are similarly inactive, but are found lying more on the surface of the ground. Evidently, dormancy ensues when there is a lack of sufficient available moisture.

Moisture relations. —There has been considerable controversy as to the amphibious versus the terrestrial nature of *P. lapidaria* (see DeWitt, 1952, for summary). It should be emphasized that throughout the course of this work *P. lapidaria* was not found living under water as was reported by Baker (1931). This species is undoubtedly amphibious since it is found in marshy areas as well as under somewhat drier conditions. Several tests were run to determine how long these snails can and will remain submerged. Whenever stream water was brought into the laboratory and the snails were placed in it, they crawled out if they possibly could. If, however, they were forced to remain submerged, they died within a few days (as was also pointed out by Pilsbry, 1896). If they were placed in a stream in a wire basket, as was done several times during this study and previously by Berry (1943), they tended to live considerably longer than under the laboratory conditions. Their tolerance has not been accurately measured, but they cannot remain immersed indefinitely. The problem exists as to whether they perish because of a lack of food in the cages or solely by drowning. Ameel (1938) reported that he observed *P. lapidaria* submerged for a week during a flood period and that the animals made no effort to crawl out of the water. Such submergence, particularly during spring floods, must be experienced by many colonies. It is possible that the differences in survival in these various experiments are correlated with the seasonal temperatures. Berry's experiment, for example, was conducted from February to May when the temperatures were lower, whereas some of the other observations were made in warmer seasons. Since cool water has a higher oxygen content than warm water, perhaps *P. lapidaria* can withstand submergence better in early spring and late fall.

Concerning the relation of normal daily activity to shade, Ameel (1938) stated: "On bright days, the snails remain hidden under the leaves and other cover but expose themselves on dull days or in well shaded situations provided their cover is well saturated with moisture." The need for shade in order to help maintain a sufficiently high humidity for activity was repeatedly observed in the course of this study.

Reproductive period. —*Pomatiopsis lapidaria* begins mating and egg laying soon after it becomes active in the spring. The time, of course, depends entirely on the weather. In 1953 snails at Barton were first found mating on May 9, whereas in 1954 mating was first seen on April 30. In the same year several mating pairs were seen on March 25 at Hogback after a heavy rain. Mating activity seems to occur throughout most of the warm season. Pairs have been seen in March, April, May, June, and early July. Mating was not observed between the second week in July and the last week in August at either station. Copulation was resumed near the second week of August and continued until the last week of October when the dormant period began. The first egg-laying period in early spring began about mid-March or a little sooner. Although it was found that matings occur in late fall, even to the last week of October, there is not sufficient time at that season to permit laying and hatching of eggs before cold weather sets in. Consequently the sperm are presumably stored within the seminal receptacle.

Young snails, 1.5 mm. in length, were found by June 15 of each year. A calculation of the possible elapsed time since those young were in the egg stage would indicate that they developed from the first (about mid-March) spring eggs. Such young (less than 2 mm.) appeared in nature until the end of July. Very small individuals did not appear again until late September. Hence, *P. lapidaria* apparently has two periods in which the young appear: one from about mid-May through late June; the other from the second week of September until frost. An interesting aspect of the reproductive state was revealed in the serial sections. Males contained apparently mature sperm during all seasons of the year; females seemed to have mature ova only during the warm seasons.

Copulation.—Copulation was observed at various hours of the day and at night. More mating was seen on damp and cloudy days or after rains than at any other time. It is possible that during mating, when the head-foot part of the female is out of the shell for a considerable period, damper conditions are most favorable for a mating process occurring on land. The snails remained in copulation for an extended time, as is true of many other mollusks. Although no exact calculations were made, pairs were observed in copulation from two to ten hours. Not only did the duration vary, but the site for copulation was also apparently fortuitous. Pairs were seen on flat mud surfaces, on rough slopes, on or under fallen vegetation, and in similar situations. Copulating pairs, however, were never seen in water.

The activities prior to mating are as follows: The female assumes a normal "sitting" position with her foot and head slightly protruding from the shell. The male crawls onto her shell and assumes such a position as to place his shell and body at right angles to hers; he is then facing the right side of her body. He then appears to rasp with his radula at the very edge of the dorsal surface of the aperture of her shell. Gradually, he works downwards to the lower right edge of her aperture, where he remains with his shell paralleling hers and with the aperture of his shell somewhat facing the right side of hers. It is in this position that mating occurs. Although numerous attempts have been made to kill and fix a pair in the actual process of mating, none have been successful since these snails withdraw the instant they are disturbed. Boiling water, hot fixatives, and dry-ice alcohol mixtures have all been used in vain.

Eggs.—The egg of *Pomatiopsis lapidaria* (Pl. II, Fig. 2) was described by Berry and Rue (1948). Structurally, it is almost identical in appearance with that of *P. cincinnatiensis* (van der Schalie and Dundee, 1955). The only difference observed is one of size; the egg of *P. lapidaria* is usually about 0.25 mm. larger than that of *P. cincinnatiensis*. The eggs are laid on soil near the water or, as at the Hogback station, in the damp soil at the center of rivulets which had started to dry. Eggs laid in the laboratory were always found on the soil in the dishes and never on the extremely wet parts of the containers or on their walls. In contrast to *P. cincinnatiensis*, which seems to require a more or less vertical surface on which to deposit its eggs, *P. lapidaria* will deposit them on flat areas. Also, eggs of *P. lapidaria* are not camouflaged as well as those of *P. cincinnatiensis* in that they do not seem to be surrounded by as much soil and they often are found on the surface of the soil rather than in small depressions; however, their sandy husk blends with the soil, making them extremely difficult to find. The egg-laying process and the method by which the snail makes the sand husk are much the same as described for *Oncomelania quadrasi* by Abbott (1946).

The number of eggs laid during the season by an individual was quite variable. All of the evidence available at present is based upon laboratory findings. One female, isolated after mating, produced forty-two eggs, all of which hatched. Another, which was isolated in a container with the male after the pair had been found mating, produced only twenty-six eggs. The data obtained during a year of observations on these snails are

TABLE II

Observations on Egg Laying of *Pomatiopsis lapidaria* in Vivaria

Date	2C-Female Alone		Date	2B-Mating Pair	
	Number Observed	Largest Individual (In mm.)		Number Observed	Largest Individual (In mm.)
April 1	1 egg		April 4	3 eggs	
May 4	12 eggs		April 18	4 eggs	
May 8	14 eggs		April 26	11 eggs	
May 16	16 eggs		May 10	13 eggs	
June 12	1 young	0.50	May 16	20 eggs	
June 12	32 eggs		May 26	1 young	0.50
June 21	8 young	0.75	May 31	4 young	0.50
June 21	34 eggs		June 12	19 young	1.00
June 28	15 young		July 9	26 young	1.00
June 28	27 eggs		July 21	26 young	1.50
July 9	31 young	1.50	Aug. 10	26 young	1.50
July 9	11 eggs		Aug. 30	26 young	1.75
Aug. 10	42 young	1.50	Sept. 21	26 young	2.00
Aug. 30	42 young	2.00	Oct. 17	26 young	2.75
Sept. 21	42 young	2.00	Nov. 30	21 young	3.25
Oct. 17	42 young	2.00	Dec. 20	21 young	4.00
Nov. 30	42 young	3.00			
Feb. 12	20 young				
May 2	20 young	5.00♀ 4.75♂			

summarized in Table II. In the case of the isolated female (2C) the total time for deposition of the 42 eggs was between 73 and 82 days (April 1 to June 21). In another vivarium with a pair (2B) 20 eggs were laid in 37 to 43 days (April 4 to May 16). Essentially, the time necessary to produce an equal number of eggs is the same as in 2C; that is, half as many appeared in about half the time.

Hatching.—In the laboratory the average time between egg laying and hatching seems to be about forty-eight days, or roughly seven weeks. The room temperatures during these observations were between 60° and 65° F. This observed incubation period is much longer than the "nearly three weeks" reported by Berry and Rue (1948). This difference in incubation time is probably directly related to the differences in room temperatures. Reports on incubation among species of *Oncomelania* are also variable. For *Oncomelania nosophora* incubation is reported to be 11-13 days (Sugiura, 1933); *O. hupensis*, 3-4 weeks (Rose and Koh, 1934); and for *O. quadrasi*, 15 days (Abbott, 1946). Evidently these differences in incubation periods are related to differences in temperature, but the accompanying data in all the instances cited were insufficient to provide temperature records. It is likely, however, that the incubation time for *Pomatiopsis* will prove to be less in the field than is reported here for the laboratory. In the hatching process the young snail rasps a hole through both the egg coat and its sand husk (Pl. II, Fig. 2) and then crawls through it.

TABLE III

Growth Rates in Laboratory Colonies of *Pomatiopsis lapidaria*

Date	Height (In mm.)	Time Elapsed (Days)	Growth (In mm.)
Experiment I			
26 May - 31 May	0.50-0.75	5	0.25
31 May - 12 June	0.75-1.00	12	0.25
12 June - 21 June	1.00-1.00	9	none
21 June - 9 July	1.00-1.50	18	0.50
9 July - 21 July	1.50-1.50	12	none
21 July - 10 Aug.	1.50-1.75	20	0.25
10 Aug. - 30 Aug.	1.75-2.00	20	0.25
Total		96	1.50
Average			0.109 per week
Experiment II			
12 June - 21 June	0.50-0.75	9	0.25
21 June - 28 June	0.75-0.75	7	none
28 June - 9 July	0.75-1.50	11	0.75
9 July - 21 July	1.50-1.50	12	none
21 July - 10 Aug.	1.50-1.50	20	none
10 Aug. - 30 Aug.	1.50-2.00	20	0.50
Total		79	1.50
Average			0.132 per week

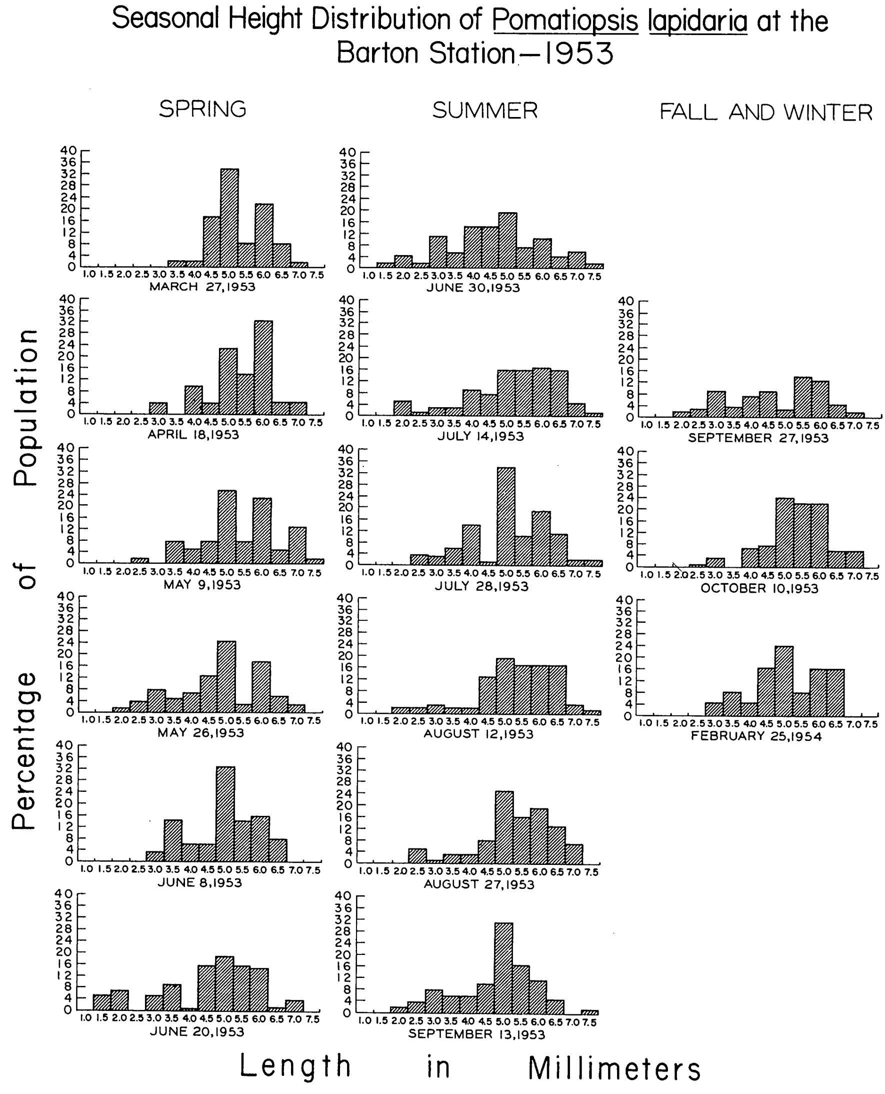


Fig. 1

The size of the newly hatched young is 0.5 mm. long by 0.5 mm. wide, and it has from 2 to 2.25 whorls. As compared with *P. cincinnatiensis*, which has a growth rate of 0.25 mm. per week under laboratory conditions (van der Schalie and Dundee, 1955), *P. lapidaria* has a more erratic growth. These irregularities in development are noticeable in Table III in which growth for some individuals is shown to be rapid (Expt. I, May 26-31), although other individuals show no growth at all

(Expt. II, July 9-21). When the total amount of growth is determined for the total time, the increment appears to be 0.1+ mm. per week. As with incubation time, growth rate will depend on temperature, for, as the histograms (Fig. 1) show, the growth rate in nature is slightly faster than in the laboratory and averages about 0.19 to 0.20 mm. per week. This rate, however, is slow compared with figures given for *Oncomelania.* For example, *O. nosophora* is reported to grow 0.66 mm. per week for the first six weeks (based on table given by Sugiura, 1933), whereas *O. hupensis* apparently grows only at a rate of approximately 0.38 mm. per week (based on information given by Rose and Koh, 1934). Similar data are, as yet, unavailable for *O. quadrasi* and *O. formosana.*

Sex ratio.—The ratio of females to males in *Pomatiopsis lapidaria* averaged 2.9 females to 1 male, or roughly 3 to 1. These figures are based on population samples collected at the two stations from February through August, 1954. One group of young hatched in the laboratory (all from one female) had a ratio of 2.3 females to 1 male.

Longevity.—On May 26, 1953, some marked or painted specimens were transplanted from Barton to Clinton, the station on the Raisin River where both *P. cincinnatiensis* and *P. lapidaria* were found. Unfortunately, the cage was discovered by someone, and in its destruction the snails were scattered. One of them was recovered on April 21, 1955, a year and eleven months later. Since the smallest snail in that marked group was 2.5 mm. in length, or about five months old, a recaptured individual must have been at least two years and five months old. Additional evidence bearing on the length of life of *P. lapidaria* was available from another marked specimen at Hogback. That one had been marked along with others on April 18, 1953. It was recovered on April 25, 1955. Therefore, it was at least two and one-half years old. More observations are necessary to establish the actual life span of this species. Additional experiments are projected in which large numbers of snails of known sizes will be marked, and it would seem advisable to sex the planted specimens so as to distinguish males from females among the recovered specimens.

To date, little has been published regarding the longevity of *Oncomelania.* Sugiura (1933) reported recovering *O. nosophora* in the fourth year after they were marked. Considering the age at the time of marking, they had a life span of at least five years. McMullen (1947), on the other hand, found evidence of "at least 1 year" for the life span of *O. quadrasi.*

Parasites.—Ameel (1939) reported several trematode parasites from *P. lapidaria.* Abbott (1948) in his consideration of *Oncomelania* and *Syncera* stated: "The same two commensal ciliates are found abundantly in the mantle cavity of these two genera but are absent from snails that have no attraction for Schistosoma japonicum miracidia." He failed, however, to name those ciliates. It was of interest to find that both *P. lapidaria* and *P. cincinnatiensis* also have commensal ciliates in their mantle cavities. These ciliates have been tentatively identified as members of the genus *Cochliophilus*

Both species of *Pomatiopsis* have also been found infected with minute nematode worms which may be the cause of many deaths among laboratory stocks. It was noticed that numerous snails observed soon after they had died contained many nematodes in the vicinity of their mantle cavities. This possibility that nematodes are destructive may prove of value as a means of natural control.

TABLE IV

Comparative Data on the Life Histories of Species of *Pomatiopsis* and *Oncomelania*

Snail	Copulation	Eggs	Number Laid	Development Time of Egg	Hatching	Growth Rate
P. *lapidaria*	March to early July; Sept. to Oct.; on soil, leaves, etc.	Laid singly; husk of soil and fecal pellets; each 1 mm; laid on or in soil; mid-Mar. to mid-May; again in late August	Maximum number known is 42	Approx. 7 wks. in lab. at temp. of 60°-65° F.	L., W., Whorls 0.5-0.5-2.25; some young throughout yr., except for late July and August	Average 0.1 mm. per wk. in lab., 0.19-.2 mm. in field
P. cincinnatiensis	April and May; fewer throughout warm season; many pairs again in Sept.; on soil	Laid singly; husk as above; 0.75-1.0 mm.; laid on or in soil	Not yet determined	5-7 wks. in lab. at temp. of 60°-65° F.	L., W., Whorls 0.5-0.5-2.25; large number of young in Aug.; some later through early fall.	Average is 0.25 mm. per wk. in lab.
O. nosophora	April, May, June, Oct.; both on land and in water (Sugiura, 1933)	Laid singly; husk or no husk; each 1 mm.; laid on floating objects, wood, but with some soil; May to June (Sugiura, 1933)	1-27 (1) ave. 18 (2)ave. 5 (Sugiura, 1933); ave. 33 (Ritchie, 1951)	11-13 days (Sugiura, 1933); 12-35 days with 2 peaks of hatching at 16-19 and 24-27 days (Ritchie, 1951)	0.5-0.8 mm. and 1.5-2.5 whorls; hatch early June throughout early July; 1-2 months after copulation (Sugiura, 1933)	0.66 mm. per wk. (Sugiura, 1933)
O. hupensis	Late April; mid-Oct.; on soil (Watt, 1936); Feb., Mar., Oct. to Dec.; on soil; 1 pr. in water (Rose and Koh, 1934)	Mid-April (Rose and Koh, 1934)	15-30 (Li, 1934)	2 weeks, (Vogel, 1948); 3-4 wks. (Rose and Koh, 1934)	May 10, 12-21 young found; stay in water month after hatching (Rose and Koh, 1934)	0.34 mm. per wk. (Rose and Koh, 1934)
O. quadrasi	On soil coating cocoanut husks (Abbott, 1946)	Laid singly; have husk; 1-1.5 mm; laid on cocoanut husk, leaves, etc. (Abbott, 1946)	No information	15 days (Abbott, 1946)	Mean time 18.38 days (Ritchie, 1951); some young throughout yr.; large nos. at diff. times in diff. areas (Mc Mullen, 1947)	No information

In view of the scattered nature of available information, Table IV was prepared to summarize the available information on the life histories of both species of *Pomatiopsis* studied, as well as on those of the three common species of *Oncomelania*.

LABORATORY PROCEDURE

With the use of large (12 inch diameter), clay flowerpot saucers these snails were easily maintained in the laboratory. The saucers, containing soil from the habitat, were set on a water table at an angle so that part of the saucer touched the water and part was supported above it. The saucers were then covered with glass. The soil was thus kept at a proper moisture level, and a high humidity was maintained within the terrarium. Occasionally, a saucer became too wet and it was then removed from the water for a sufficient time to allow some drying. Sometimes it was necessary to change to a less porous saucer.

The food used consisted of pieces of blotter or paper toweling on which ground rat food (pellets) was placed. It was also found advantageous to add a drop or so of an aqueous solution of calcium carbonate ($CaCO_3$) to the pieces of paper since some of the shells began to show erosion at their apices. Such erosion was not observed after the calcium carbonate was provided with the food.

In general, this method proved quite successful for raising these animals. Stocks were maintained for many months, and satisfactory reproduction was obtained. Recently, smaller (3 inch diameter and 1 inch depth) saucers were used. They proved better in that they were less cumbersome for routine examinations under a dissecting microscope than were the larger containers.

The temperature of the laboratory was maintained at 60°-70°F., depending upon the season of the year. Snails were sexed by the method described by Wong and Wagner (1954). Good relaxation of specimens which were to be sectioned was obtained by using Nembutal as described by van der Schalie (1953).

ANATOMY

The external appearance of *Pomatiopsis lapidaria* has been described by several authors (Say, 1817; Stimpson, 1865; Abbott, 1948; Berry, 1943); therefore, a description need not be included here. A view of the animal (Pl. III) as it appears in the living condition is given for orientation. In the following discussion of the internal anatomy the organs and systems are considered in the order in which they appear when one dissects from the outermost parts inward.

Mantle cavity. —The mantle cavity lies above the head-foot region and contains the gill filaments, the osphradium, and three openings—the female genital pore or (in the male) the verge, the anus, and a renal pore.

The wall of the mantle cavity on the left side is greatly folded to form the gill filaments, which extend posteriorly from a short distance behind the mantle collar to the renal pore located in the left dorsoposterior part of the mantle cavity. In fresh specimens the pore appears as a pair of whitish tumid lips. The gill is composed of 15-20 filaments (Pl. IV, Fig. 1). Each filament is enlarged near its distal end; cilia occur distally for a short distance from this area of enlargement (Pl. VIII, Fig. 1). Paralleling the left anterior half of the gill is the osphradium consisting of two ridges forming an oval depression with a groove through the middle. The inner epithelium of the mantle itself contains many mucous cells, as does the epithelium of the head region.

The anus lies on the right side of the mantle cavity just behind the collar (Pl. IV, Fig. 1). It appears as a transverse slit. The genital pore is slightly anterior and to the right of it in a female, and may also be described as a slit at the very end of the pallial oviduct. In males the penis, or verge, is contained within the mantle cavity. It represents an extension of the middorsal surface of the body wall. Under normal conditions the penis remains within the mantle cavity where it rests in a U-shaped curve over the posterior part of the head. The penis of *Pomatiopsis lapidaria* does not have a filament as does that of *Pomatiopsis cincinnatiensis.* In a serial section the penis has a layer of longitudinal muscle just below the epithelium and a heavy layer of circular muscle surrounding the vas deferens, which is centrally placed. The connective tissue layer between the two muscle layers is amply supplied with circulatory sinuses.

The main differences (Table V) in the mantle cavities of *Pomatiopsis lapidaria* and *Pomatiopsis cincinnatiensis* are readily understood when they are arranged in tabular form.

TABLE V

Comparison of the Mantle Cavities of
Pomatiopsis lapidaria and *Pomatiopsis cincinnatiensis*

Mantle Cavity	*P. lapidaria*	*P. cincinnatiensis*
Gill	Compact, neat, crescent-shaped 15-20 filaments Filaments close	Ragged, somewhat crescent-shaped 10-15 filaments Filaments spread apart
Osphradium	One-half length of gill	Less than one-half length of gill
Openings	Anus transverse Female genital pore oval	Anus transverse Female genital pore oval
Mantle	Very little black pigment	Considerable black pigment

Head-foot. —On the lower surface and in the extreme anterior part of the foot large mucous glands, the pedal glands, secrete directly to the exterior on the anteroventral surface (Pl. VIII, Fig. 2). They provide most of the mucous used during movement. In addition, mucous cells are scattered along the exterior surface of the foot, and the entire ventral surface is ciliated. The foot itself consists largely of supporting connective tissue interwoven with numerous circulatory sinuses. Interspersed are longitudinal muscle fibers. The columellar muscle starts at about the middle of the operculum and extends upwards along the columella. In the head region long muscle strands extend from the columellar muscle to the buccal mass and the proboscis.

Nervous system (Pl. V). —This system is considered only in relation to the ganglia and the nerves connected with them. All of these nerves eventually split into numerous finer branches amply supplying the various parts of the body. A detailed analysis of their ultimate innervations was not undertaken. The nerves on the right side tend to be smaller than those on the left. It is important to realize that these structures vary considerably among individuals with regard to their size and their course.

In the dorsal part of the head and surrounding the esophagus are three pairs of ganglia (Pl. V): the cerebral, immediately posterodorsal to the buccal mass; the pleural, posterior to the cerebral; and the esophageal (supra- and sub-), connected with the pleural by rather long commissures. The right pleuro-supraintestinal commissure crosses over the shorter left pleuro-subintestinal to form the middle piece of the figure eight characteristic of all prosobranch nervous systems. Nerves originating from the dorsal or lateral surfaces of a cerebral ganglion are as follows: from the dorsolateral the optic nerve goes directly to the eye area before branching; the tentacular nerve arises in a small nodelike projection at the anterior end of the cerebral ganglion and at a short distance from it divides into two major parts, one branching further and innervating the tentacle, and the other dividing again to supply the lateroventral surface of the rostrum. The remaining cerebral nerves originate from the ventral surface of the cerebral ganglion, as follows: from the anterior part a nerve soon divides, one branch supplying the anteroventral part of the buccal mass; the other, the mouth. The latter immediately branches again, and this third nerve innervates the lateral area of the rostrum. Only one other major nerve originates from the cerebral ganglion and it supplies the buccal mass. A nerve from the left pleural ganglion innervates part of the mantle.

The supraesophageal ganglion on the left side of the animal has a nerve extending posterolaterally to join a ganglion adjacent to the osphradium. The other branch of this nerve follows a posterior course to the visceral ganglion found in the whorl above the body whorl and very close to the heart. The subesophageal ganglion has, on the other hand, three branches: a large one innervating the mantle and two smaller divisions, one going to the ventral surface of the head and the other joining the visceral ganglion as does its counterpart on the right side of the body.

The lower part of the main nervous system is represented by the paired pedal ganglia connected with both the cerebral and pleural ganglia by means of commissures. These pedal ganglia are found immediately ventral to the junction of the head and foot.

Sense organs. — *Pomatiopsis lapidaria* has an eye on the outer side of the base of each tentacle (Pl. VIII, Fig. 4). It is a rather complex organ in that it has a cornea-like layer, a lens which lies in a fluid-filled chamber, a pigment layer lining that chamber, and a layer of presumably sensitive cells which is in direct contact with the optic nerve.

Two otocysts are present on the posterodorsal surfaces of the pedal ganglia (Pl. VIII, Fig. 3). Each of these consists of a sphere of flattened, thin epithelium the cells of which have round, basal nuclei. Inside each sphere is a small body, the otolith, which is composed of concentric layers of material. It lies free in the fluid-filled cavity and apparently as it touches cells of various parts of the chamber wall, the animal receives stimuli which aid it in maintaining proper balance.

Digestive system. (Pl. VI). — In relaxed specimens the mouth appears as a dorsoventral slit. A short tube, composed of columnar epithelium with a heavy muscular layer beneath it, connects the mouth with the buccal cavity. A cuticular layer lines the oral region and extends to the anterior part of the buccal mass, where a lateral enlargement forms the buccal cavity. The jaws are found at the entrance to the buccal cavity. Each jaw consists of a series of cuticular plates (25-30 in *P. lapidaria*), which occupy the upper half of the lateral walls of the tube (Pl. VII, Fig. 1).

Within the lower part of the buccal cavity are two odontophoral cartilages of the buccal mass. The radular sac lies ventrally between them. The radula was figured by Stimpson (1865), Baker (1928), and Abbott (1948). It is usually seen extending from its sac, lying over the dorsal surface of the buccal mass, and reaching the mouth. From a lateral view it is S-shaped.

Emptying into each side of the dorsal part of the pharyngeal cavity is a salivary gland. These are cylindrical long white glands extending posteriorly from their point of entrance and lying over the cerebral ganglia. They are composed of tall columnar cells with basal nuclei (Pl. VII, Fig. 2). Their contents, consisting of fine granular secretions, empty into a central lumen.

The esophagus (about 3.25 mm. long in adult specimens) is a tube passing over the dorsal surface of the buccal mass through the body whorl to join the posteroventral part of the stomach. All of its inner lumen has ciliated columnar epithelium.

The stomach (Pl. VII, Fig. 3) is a large organ occupying the whorl above the body whorl and is similar structurally to that described in *Pomatias elegans* and *Bithynia tentaculata* by Graham (1939). The posteroventral part contains openings to the esophagus and the digestive gland. Internally and near the entrance of the esophagus the stomach has a kidney-shaped papilla apparently used to direct incoming food toward the posterior part of the stomach, where there are prominent cilia. The style sac projects from the anterior end of the stomach. Its epithelium (Pl. VII, Fig. 5) has tall columnar cells with extremely long cilia. The style itself is a clear, gelatine-like rod (Pl. VII, Fig. 7), the head of which rotates against the gastric shield (Pl. VII, Fig. 6). The latter appears as a clear cuticular mass covering the epithelium of the anterior dorsal part of the stomach (Pl. VII, Fig. 4). The stomach opens into the intestine near the columellar side of the style sac.

The digestive gland (Pl. V) enters the stomach just posterior to the entrance of the esophagus. This large gland occupies most of the apical whorls, and the ovary or testis is usually surrounded by its glandular tissue. This major gland consists of numerous branching tubules with gland cells of two major kinds: (1) tall club-shaped cells with basal nuclei produce secretions which appear as droplets at their distal ends; the cytoplasm is vacuolated; (2) much shorter, triangular-appearing cells, also with basal nuclei, but containing within their prominent vacuoles brown spherules of various sizes. These dark bodies appear scattered throughout the periphery of the gland and tend to give it a characteristic stippled outline. These spherules are evidently similar to those described in *Bithynia tentaculata* by Lilly (1953: 92). She explained their function as follows:

> The excretory cells of the digestive gland have a broad base lying against the haemocoel, and taper distally so that each of the cells has a conical shape. They are much shorter than the digestive cells. The cytoplasm is dense and vacuolated, and there is one exceedingly large vacuole which contains an aggregation of excretory matter. Such aggregations have been found in the faecal pellets, showing that these cells discharge their contents into the gut, so that they leave the body in the faeces. The contents of the excretory cells appear as dark reddish-brown deposits when living tissue is examined.

The intestine contains a typhlosole (Pl. VII, Fig. 8) extending from the stomach to the level of the posterior end of the gill. That part of the intestine is heavier in appearance than the remainder. Cilia are found throughout the length of the intestine. The anal opening is situated near the mantle collar and on the right side of the mantle cavity. The fecal pellets with their characteristic elliptical shape may fill the whole length of the intestine.

When the digestive systems of *Pomatiopsis lapidaria* and *Pomatiopsis cincinnatiensis* are compared, as in Table VI, it is interesting to see that, although *P. cincinnatiensis* is generally a smaller snail, in many respects its system is larger and sometimes has an extra loop in the tract. The reason for this increase in the length of the tract is unknown, but it may be associated with the fact that *P. cincinnatiensis* is the more terrestrial of the two species. It is also of interest to observe that in laboratory studies *P. lapidaria* fed directly on the ground rat food as well as on the blotting paper, but *P. cincinnatiensis* seemed to eat only the blotter. Perhaps the latter species is better adapted to a diet containing more cellulose.

Heart-kidney. —The circulatory system is an open type and consists of a heart with one auricle and one ventricle, a system of arteries, and a network of venous sinuses. The heart (Pl. VIII, Fig. 5) is an opaque, thin-walled sac which lies in the whorl above the body whorl and is close to the anterior end of the stomach. It is contained in a pericardial cavity. The pericardium is composed of flattened epithelium with circular muscle

TABLE VI

Comparison of Digestive Organs of
Pomatiopsis lapidaria and *Pomatiopsis cincinnatiensis*

Organ	*P. lapidaria*	*P. cincinnatiensis*
Radula	Formulae: $\frac{1\text{-}1\text{-}1}{2\text{-}\text{-}\text{-}2}$; 2-1-3	Formulae: $\frac{1\text{-}1\text{-}1}{2\text{-}1\text{-}2}$; 1-1-3 or 2-1-3
Jaws	25-30 cuticular plates	15-20 cuticular plates
Salivary Glands	Somewhat cylindrical	Somewhat club-shaped
Esophagus	About 3.25 mm. long in adults	About 3.75 mm. long
Stomach	Somewhat rectangular Style sac about 0.5 mm. long About 1.5 mm. long	Somewhat ovoid Style sac about 0.75 mm. long About 1.25 mm. long
Digestive Gland	Finger-like Often black pigment externally	Cluster-like Without black pigment externally
Intestine	No extra loop About 3.25 mm. long	Extra loop sometimes below hairpin loop over stomach About 3.75 mm. long

fibers interspersed and lies directly against the base of the kidney epithelium (Pl. IV, Fig. 2). The heart itself is composed of a network of muscle fibers which form the wall. From the left ventral part of the ventricle extends a short truncus arteriosus, which in turn divides into an anterior and a posterior aorta. The former runs forward over the intestine, and the latter seems to extend beneath the rectum. Only portions of the remainder of the system have been found. It probably is similar to the system of many other gastropods in that the anterior aorta breaks into two major arteries, one supplying the intestine and the other the foot, whereas the posterior aorta divides into two lateral trunks, left and right pallial arteries. The blood eventually reaches the venous sinuses, which are easily seen in *Pomatiopsis lapidaria,* and then circulates through the gill for aeration before returning to the heart via the vessel which extends from the gill to the auricle. No valve was found between the auricle and ventricle. At 70° F. the heart of a *P. lapidaria* was observed to have the following counts per minute: (1) snail extended from shell—89, 63, 91; (2) snail withdrawn into shell—22 and 28. It was of interest to find that if the snails are disturbed greatly the heart will stop beating entirely for a minute or longer.

The kidney (Pl. IV, Fig. 2) is a large, lobate, saclike structure readily distinguished by its whitish appearance and by the minute white granules (uric acid?) appearing within its lumen when it is cut. The renal aperture lies at the posterior end of the mantle cavity near the posterior part of the gill; it is surrounded by a muscular sphincter. From this aperture the kidney extends posteriorly for approximately two whorls and appears to mold itself to the shape of the various organs. The epithelium of the kidney (Pl. VIII, Fig. 6) is cuboidal and has a distinctive appearance. The nuclei are basal as is most of the cytoplasm, but the entire distal part of each cell is extremely vacuolated.

Female reproductive system. —Since the functions of the parts of this system have not been studied, the names applied to the various organs must be considered as tentative. Published studies on the reproductive system of closely related species have provided a variety of names for similar organs. The female system in this group appears to be sufficiently complex to indicate the need for studying the function of these organs in order to determine which nomenclature should apply. Table VII and Plates IX and X have been prepared to indicate the names used and their relations to other terms given to similar organs by various investigators. Obviously, the systems are not identical in the several species, but that fact has been taken into account. It may be seen from Table VII that there is general agreement on ovary and oviduct. Beyond that, however, there is confusion.

It would appear that the evolutionary trend was from a seminal receptacle which was part of the oviduct to its present position as a separate blind sac connected to the oviduct. Where the table reads "none," this does not necessarily mean that the organ in question is lacking; it may mean either that it was not found or that it was called by another name. Bursa, like the seminal receptacle, is a term which has been applied to various organs, as Table VII indicates. The large glandular mass called pallial oviduct in this study is especially difficult to consider as a unit since, in most cases, it is divided into two distinct halves, both of which are glandular. The names of organs in the following discussion were selected after comparing those of *Pomatiopsis* with equivalent structures in other groups. The system adopted is nearest to that used by some of the more recent workers (Creek, 1951, 1953; Itagaki, 1955).

In *Pomatiopsis* the ovary (Pl. XI; Pl. XII, Fig. 1) is yellow and lies embedded in the columellar side of the digestive gland at the third whorl below the apex. The ovary of *P. lapidaria* is much less branched than that of *P. cincinnatiensis*. The renal oviduct (Pl. XII, Fig. 2) also appears yellow when it contains many ova. It extends along the columella from the ovary to a point near the level of the posterior part of the stomach where it becomes highly convoluted and disappears under the bursa copula-

TABLE VII

Partial Summary of Nomenclature of Female Genital Organs in Certain of the Prosobranchs

* Indicates that organ is called same name as that listed at the top of column.

Species	Literature Source	Taxonomic Position (Thiele, 1929)	Ovary	Oviduct	Seminal Receptacle	Bursa	Pallial Oviduct		Spermathecal Duct
							Albumen Gland	Capsule Gland	
		ORDO=MESOGASTROPODA. STIRPS=LITTORINACEAE							
Littorina littorea	Linke, 1934	Fam.Littorinidae	*	*	*	Albumen gland	Capsule gland	Gelatine gland	None
Pomatias elegans	Creek, 1951	Fam.Pomatiasidae	*	*	Part of oviduct	*	*	*	None
Acme fusca	Creek, 1953	Fam. Acmidae	*	Gonadial duct	Part of gonadial duct	*	*	*	None
		STIRPS RISSOACEA							
Paludestrina jenkensi	Robson, 1920	Fam.Hydrobiidae	*	*	None	None	*	Brood pouch	Vagina
Paludestrina jenkensi	Krull, 1935	Fam.Hydrobiidae	*	*	*	*	Drüsenmasse	Uterus	Vagina
Paludestrina ventrosa	Robson, 1922	Fam.Hydrobiidae	*	*	*	Oviducal gland	Accessory	Gland	Vagina
P. ventrosa	Krull, 1935	Fam.Hydrobiidae	*	*	*	*	Drüsenmasse		None
Lithoglyphus naticoides	Krause, 1949	Fam.Hydrobiidae	*	*	*	Posterior oviduct gland	Vaginales lumen of the oviduct	Vaginales lumen of the oviduct	Sperm conducting lumen of oviduct
Lithoglyphus naticoides	Krull, 1935	Fam.Hydrobiidae	*	*	*	*	Anhangsdrüse of the oviduct	Anhangsdrüse of the oviduct	None
Bythinella dunkeri	Bregenzer, 1915	Fam.Hydrobiidae	*	*	*	Albumen gland	Anhangsdrüse	Anhangsdrüse	Vagina
Pomatiopsis lapidaria	Dundee,	Fam.Hydrobiidae	*	*	*	*	*	*	*
Oncomelania nosophora	Robson, 1921	Fam.Hydrobiidae	*	*	None	Spermatheca	Accessory gland	Uterus	Oviduct
O. nosophora	Itagaki, 1955	Fam.Hydrobiidae	*	*	Fertilization chamber	Spermatheca	Mass membrane gland	Mass membrane gland	*
O. hupensis	Li, 1934	Fam.Hydrobiidae	*	*	None	*	Uterus	Uterus	None
Bithynia tentaculata	Lily, 1953	Fam.Hydrobiidae	*	*	None	Seminal receptacle	Pallial Oviduct	Bursa	None
Assemania grayana	Krull, 1935	Fam.Micromelanidae	*	*	*	*	Drüsenmasse	Drüsenmasse	None

trix. There it is enveloped in kidney tissue. This convoluted part of the renal oviduct consists of an outer layer of circular muscle and an inner epithelial layer of tall ciliated columnar cells with central nuclei.

The bursa (Pl. XI) mentioned above usually appears as a yellow sac lying adjacent to the posterior end of a very large glandular mass, the pallial oviduct. The yellow color is apparently imparted to this organ by the male fluid which it often contains; the sac itself is not yellow. The bursa has two openings; one leads from it to the renal oviduct; the other enters it from the exterior via a long tube, the spermathecal duct (Pl. XII, Fig. 5). Both of these openings are on the anterior part of the bursa and are close enough to each other to give the impression of a common duct. Sperm found in the bursa seem to have no particular orientation. The wall (Pl. XII, Fig. 3) is composed of an outer layer of circular muscle with interspersed longitudinal fibers and an inner lining of tall columnar cells with basal nuclei. No cilia have been seen within the bursa. The cells of the wall are vacuolated. Some of the material within the bursa appears the same as that found within these cells; they may be glandular in nature.

In the seminal receptacle (Pl. XI), on the other hand, the sperm are often extremely thickset and are oriented with their heads toward the outer wall. The seminal receptacle lies either ventral to, or to the left of, the bursa. It usually looks white and opaque and is approximately one-fourth the size of the bursa. A very short duct leads from the seminal receptacle into the tube connecting the bursa and renal oviduct. The seminal receptacle is lined with tall, nonglandular columnar cells (Pl. XII, Fig. 4), and a thin layer of circular muscle surrounds this epithelium. Nuclei are large and basal. No cilia have been seen in this sac. Sperm found in the female tract stain an intense blue with haematoxylin or a bright red with Mallory's Triple Stain.

The renal oviduct itself crosses under the spermathecal duct and continues to a point about one-half the distance from the posterior end of the large glandular mass, the pallial oviduct (Pl. XI), where it appears to enter that mass. This connection is extremely small, fragile, and very difficult to see.

The pallial oviduct is the largest organ in the female genital tract. It is an opaque, whitish, kidney-shaped mass which extends from the anterior region of the stomach and parallels the rectum down to the right side of the anus where it opens through a muscular terminal pore. Its interior has very deep folds throughout its length. It is divided into two distinct halves, an upper or posterior and a lower or anterior. The epithelium of the upper part of the pallial oviduct (albumen gland?) consists of conical columnar cells with basal nuclei and ciliated supporting cells. These cells stain light blue with haematoxylin, whereas their abundant secretion, which occurs in the form of various-sized droplets, stains very dark blue. In some specimens the secretion is so abundant that it obscures much of the epithelium. By contrast, the lower part (capsule gland?) stains a lighter shade, and its secretions always outline the folds of the gland rather than obscure them. The cells are also tall and columnar. The secretions are in the form of uniform, minute droplets. The entire pallial oviduct is ciliated.

Paralleling the pallial oviduct for its entire length on the columellar side is the spermathecal duct. It connects the bursa with the exterior via a common opening with the genital pore at the anterior end of the pallial oviduct. It is a very tiny tubule, but may be seen easily even with the naked eye. It, too, is lined with a tall ciliated epithelium.

When one considers the histology of the female genital tract, it is possible to speculate upon the probable function of the various parts. It is not possible to consider their function with any degree of certainty, however, until physiological studies have been made. The observations made in the course of this work suggest that when copulation occurs, the tip of the verge of the male is inserted into the sphermathecal duct (in *P. cincinnatiensis* the penetration could be much deeper since the verge has a long filament on its terminal end). Sperm travel up this duct and are deposited in the bursa perhaps along with a male secretion (prostatic?). There a glandular secretion from the female is mixed with the male component (nourishment for the sperm?), and eventually the sperm are transferred from the bursa to the seminal receptacle by means of pressure exerted by the circular muscle layer around the bursa. Since the receptacle is only about one-fourth the size of the bursa, it seems likely that excess sperm are stored in the bursa. It was suggested by Krause (1949) that in *Lithoglyphus naticoides* the sperm get into this organ accidentally during copulation and are destroyed there. He believes that this organ (called "posterior oviducal gland" by him) contributes to the gelatinous coverings of the deposited eggs. No evidence of destruction of sperm has been seen in this species either in the bursa or in the seminal receptacle, as suggested by Creek (1951) in *Acme fusca.*

Sperm have been seen in the convoluted part of the renal oviduct and in the upper part of the pallial oviduct, as well as in the bursa, the seminal receptacle, and the spermathecal duct. Consequently, it is not clear just where fertilization occurs. It is likely that it may occur in the convoluted part of the oviduct since that is the part nearest the seminal receptacle.

It is significant that despite the large numbers of specimens examined (including females of mating pairs and females which appeared to be preparing to deposit an egg) no eggs have been seen in the tract anywhere from the convoluted part of the renal oviduct down to the genital aperture. In an examination of many female specimens of *P. cincinnatiensis* a fellow worker observed only one egg in that part of the tract. The results of that study will be reported in another paper now in preparation. It appears likely that once an egg starts to move through the tract, it may pass in a matter of a few minutes; also it is probable that in most cases this occurs at night.

The fertilized egg probably enters the pallial oviduct through the small duct (lower end of the renal oviduct), which is so difficult to see. Once in the pallial oviduct, it receives a layer of albumen and an outer coat of a somewhat harder and stickier substance (perhaps conchiolin in mucous as reported in *Pomatias* by Creek, 1951). It then leaves the body via the genital pore, and the snail adds a husk composed of material from fecal pellets and soil.

Male reproductive system (Pl. XIII). —As is seen in Table VIII the distinctive feature of this system in contrast to that in *P. cincinnatiensis* is the lack of a long filament on the verge. In its extended state the verge of *P. lapidaria* merely has a very short projection on its distal end. When in the resting condition it lies in a U-shaped curve within the mantle cavity and against the dorsal surface of the head. This verge (Pl. XIV, Fig. 6) is flattened dorsoventrally and in section has an outer columnar epithelium which is underlain by a heavy layer of longitudinal muscle. Beneath this is

TABLE VIII

Comparison of Reproductive Organs of
Pomatiopsis lapidaria and *Pomatiopsis cincinnatiensis*

Reproductive Organ	*P. lapidaria*	*P. cincinnatiensis*
Female		
Ovary	Slightly branched	With several branches
Oviduct	Many convolutions	Few convolutions
Bursa	Kidney-shaped, tending toward oval	Kidney-shaped
Seminal receptacle	Oval, saclike	Oval, saclike
Pallial oviduct	Slender	Rather thick
Spermathecal duct	Straight	Often wavy
Genital pore	Slit bounded by muscular lips	Slit bounded by muscular lips
Male		
Verge	No filament	Very long filament
Testis	Cluster-like	Cluster-like
Vas deferens	Many convolutions	Few convolutions
Prostate	Short, kidney-shaped	Short, kidney-shaped

the connective tissue mass; running directly through the center of it and thus forming a "core" is the vas deferens (Pl. XIV, Fig. 6), which is surrounded by a thick circular muscle layer. Its epithelium consists of small cuboidal cells which are heavily ciliated. The vas deferens (Pl. XIV, Fig. 4) leaves the base of the verge, passes along the left part of the junction of the head and mantle cavity, and continues posteriorly to a point about midway along the prostate gland. There it enters that gland. The prostate (Pl. XIV, Fig. 3) is the kidney-shaped, light colored mass which lies adjacent to the right side of the rectum in the body whorl. Its appearance is much like that of the pallial oviduct in the female. The epithelium of this gland is very tall. The nuclei are basal, and often the cells are vacuolated immediately distal to them. The contents of the cells are apparently emptied directly into the lumen. The testis (Pl. XIII), often yellow in color, lies embedded in the columellar side of the digestive gland. It appears as a cluster of follicles (Pl. XIV, Fig. 1), all of which have a common exit into the vas deferens. The upper or posterior part of the vas deferens is much enlarged and extremely convoluted. It lies as a compact white mass (Pl. XIII) just beneath the ventral edge of the testis. Spermatozoa (Pl. XIV, Fig. 5) are often so compacted within this duct that in sections it has the appearance of containing a solid mass of material (Pl. XIV, Fig. 2). The epithelium of this seminal vesicle (Pl. XIV, Fig. 2) consists of short nonciliated cells, the boundaries of which are difficult to discern. Below this white convoluted seminal vesicle the duct becomes much narrower, its cells slightly higher and ciliated. This part, the renal vas deferens, follows the columella down to the point where it enters the prostate, thus receiving secretions from the latter.

SUMMARY

Pomatiopsis lapidaria is found in most of the eastern half of the United States and extends northward into southern Ontario. It is limited to the vicinity of fresh water. Generally, it is an inhabitant of marshy seepage areas along banks and flood plains of streams.

Pomatiopsis appears better adapted for life on land than does its Oriental relative, *Oncomelania.* On the other hand, among the American species of *Pomatiopsis, P. lapidaria* appears to have a greater affinity for water than does *P. cincinnatiensis.* This tendency is indicated by the number of gill filaments, the degree of submergence tolerated, the abundance of pedal glands, the size of intestine, and the nature of the habitat.

A comparison of the habitats of *Pomatiopsis* and *Oncomelania* indicates that they are extremely similar. In this respect *Pomatiopsis lapidaria* resembles *Oncomelania nosophora* more closely than it does any of the other species of *Oncomelania;* the similarities among species in both genera are remarkable.

Pomatiopsis lapidaria is sexually dimorphic. Males usually have a slightly higher whorl count than females and tend to be slightly more slender; the largest female measured 8. 5 mm. in length, and the largest male 7 mm.

Based on field collected material, the sex ratio averaged 2. 9 females to 1 male; among laboratory hatched specimens it was 2. 3 to 1.

In this area *Pomatiopsis lapidaria* has two dormant periods; one in the winter, the other during summer drought. The animals during these periods remain inactive under fallen vegetation, in crevices, or beneath objects, with the aperture closed by the operculum.

The life span of *Pomatiopsis lapidaria* appears to be about three years. There are two major mating periods each year: March to early July and from the last week of August to the last week of October. Egg laying usually begins in March and continues throughout the warm season, although there is a period from the last of July until late September when no newly hatched young appear.

Copulation may occur at almost any time of the day or night; it is more frequent when the humidity is very high. The site for copulation is apparently fortuitous, since pairs have been seen under many different circumstances.

Eggs are laid singly and coated with a husk composed of soil and fecal pellets. They are deposited on soil; sometimes they are partly buried so that it is extremely difficult to see them.

The incubation time was from 5 to 7 weeks in the laboratory at temperatures of 60°-65°F. Other investigators have reported hatching in three weeks; since *Oncomelania* requires four weeks or less (depending on the species), *P. lapidaria* in nature may also have a shorter incubation period.

The size of newly hatched individuals is about 0.5 mm. wide by 0.5 mm. long; they have 2.25 whorls. Growth rate was approximately 0.1+ mm. per week in the laboratory and 0.19 to 0.20 mm. per week in nature.

Anatomically *P. lapidaria* is quite similar to *Oncomelania;* differences appear to be minor. The main structural features of *P. lapidaria* are as follows: (1) gill present and renal pore located in the mantle cavity at the posterior end of gill; (2) crystalline style present; (3) spermathecal duct in female completely separated from pallial oviduct in contrast to other closely related Hydrobiids, such as *Lithoglyphus naticoides*, in which these two organs have communicating lumens; (4) the male genital system is a closed and complete system; (5) the female has two saclike pouches, the seminal receptacle and bursa, in contrast to species in which the renal oviduct serves as the seminal receptacle. These features, as well as the external appearance of the shell and operculum, indicate a relationship between *Pomatiopsis* and other Rissoids; it seems to belong in the family Hydrobiidae (of Thiele).

The main anatomical differences between *Pomatiopsis lapidaria* and *Pomatiopsis cincinnatiensis* aside from size and shape are the following: (1) 15-20 gill filaments in *P. lapidaria* in contrast to 10-15 for *P. cincinnatiensis;* (2) *P. cincinnatiensis* has only 15-20 cuticular plates in its jaws, *P. lapidaria* has 25-30; (3) the intestine of *P. cincinnatiensis* is relatively longer than that of *P. lapidaria;* (4) the verge of *P. cincinnatiensis* has a long filament at its tip, that of *P. lapidaria* lacks it.

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PLATE I

Fig. 1. The Barton station looking northeast, with the Huron River in the background and the study area in the foreground.

Fig. 2. The *Typha latifolia* mat which covers the ground in the Barton area; snails are found both on this mat and below it.

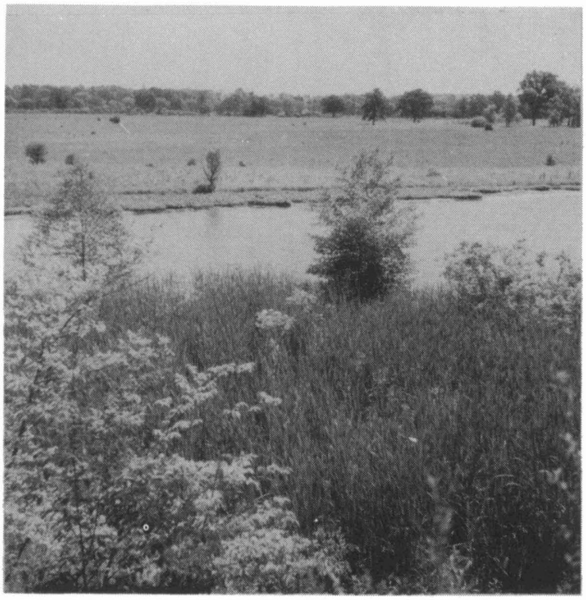


Fig. 1

Fig. 2

PLATE II

Fig. 1. The Hogback study area. Pittsfield Drain is at the lower right and the study area proper lies among the trees.

Fig. 2. The husk of an egg of *Pomatiopsis lapidaria* showing the hole through which the young escaped. Magnified *ca.* 20 times.

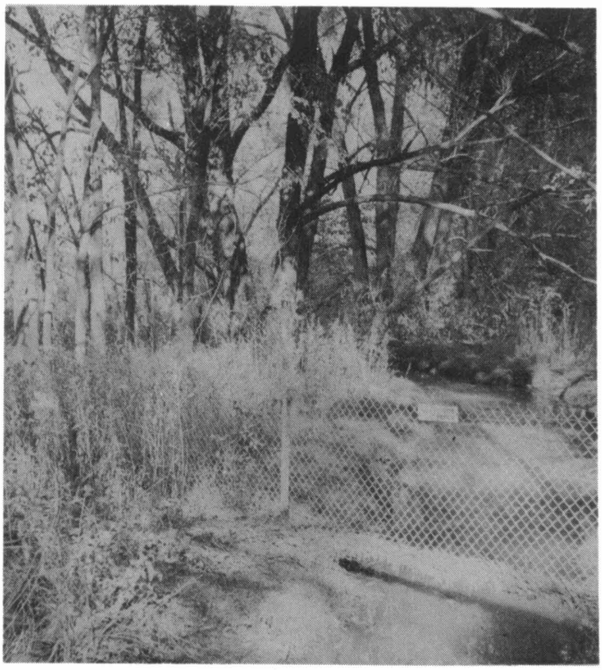


Fig. 1

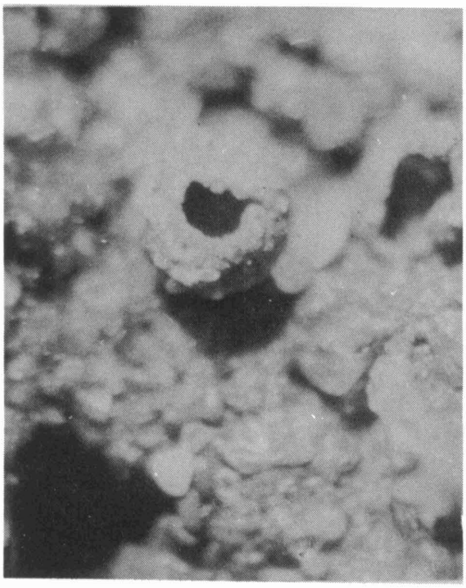


Fig. 2

PLATE III

Pomatiopsis lapidaria (Say) as it appears in the living condition. The animal is in the process of turning with its body moving away from the observer and its shell swinging towards him. Approx. 18X.

Inset shows the operculum of this species.

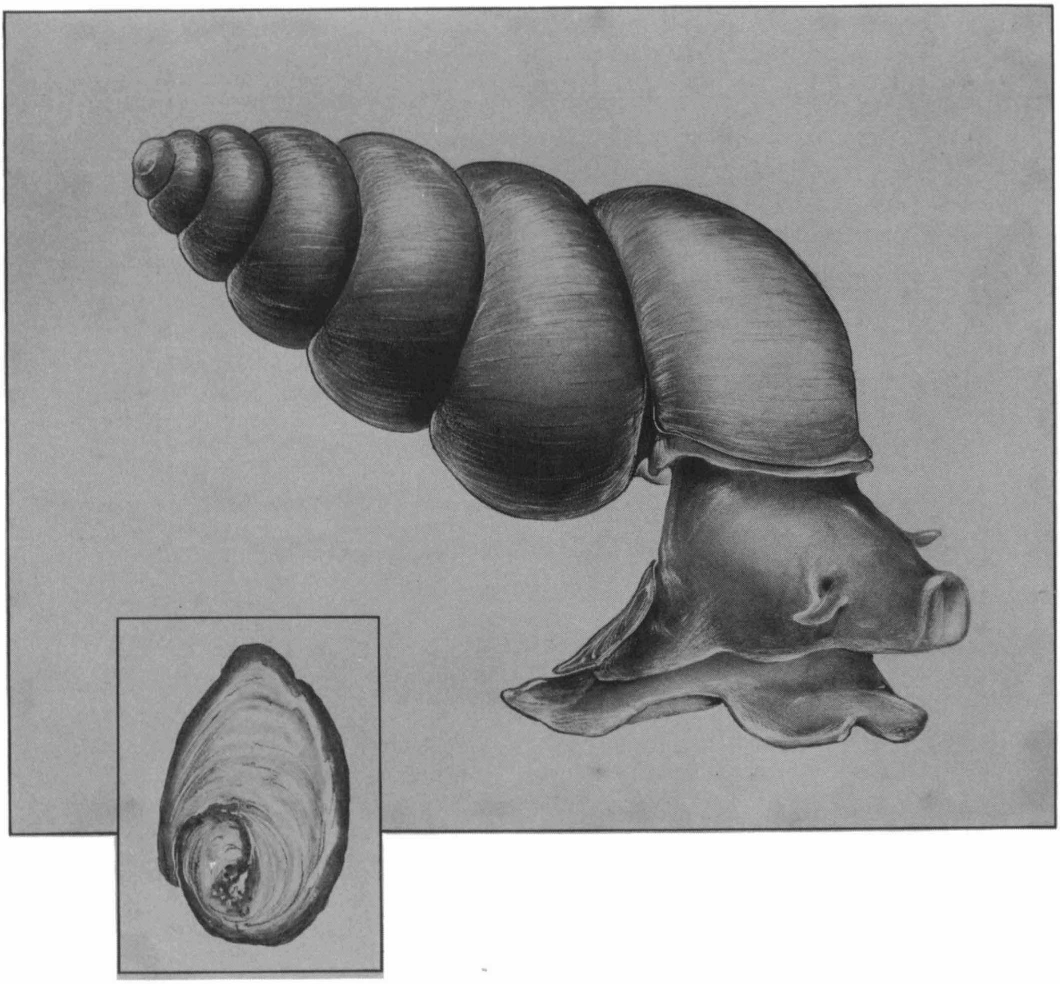
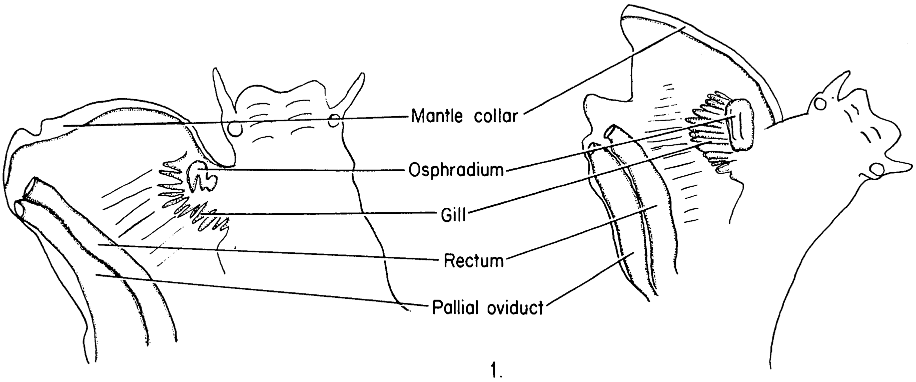


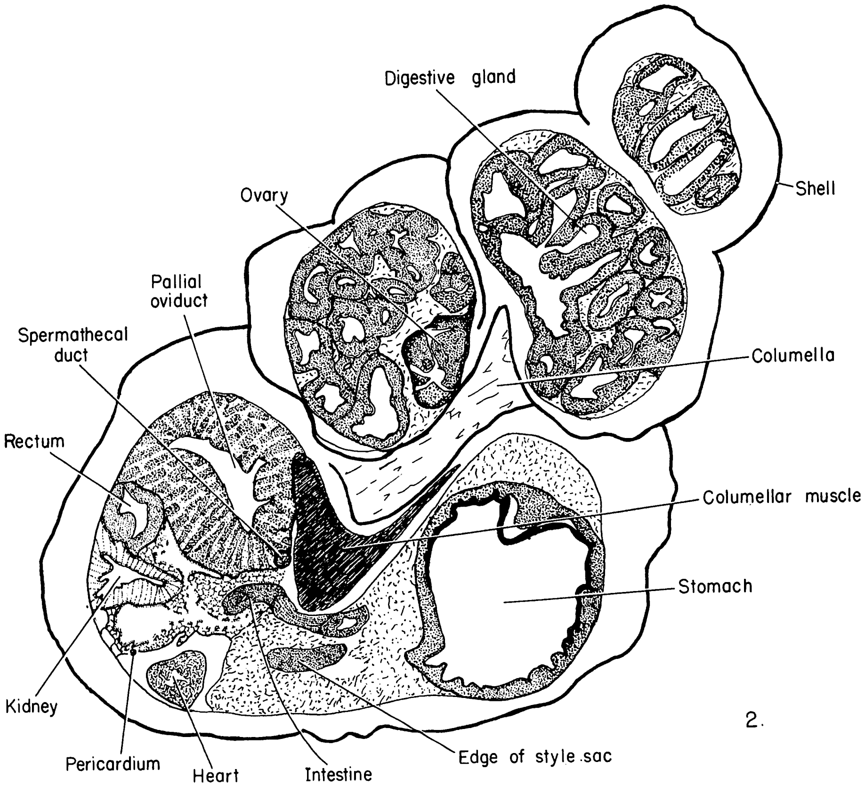
PLATE IV

Fig. 1. Sketch of mantle cavities of *Pomatiopsis cincinnatiensis* (Lea) (left) and *Pomatiopsis lapidaria* (Say) (right), showing osphradium and gill comparisons. The mantle has been cut along the body wall close to the right side and unfolded to the left to show the interior.

Fig. 2. Sagittal section showing relationships of various organs of *Pomatiopsis lapidaria* (Say). Approx. 25X.


Mantle collar
Osphradium
Gill
Rectum
Pallial oviduct

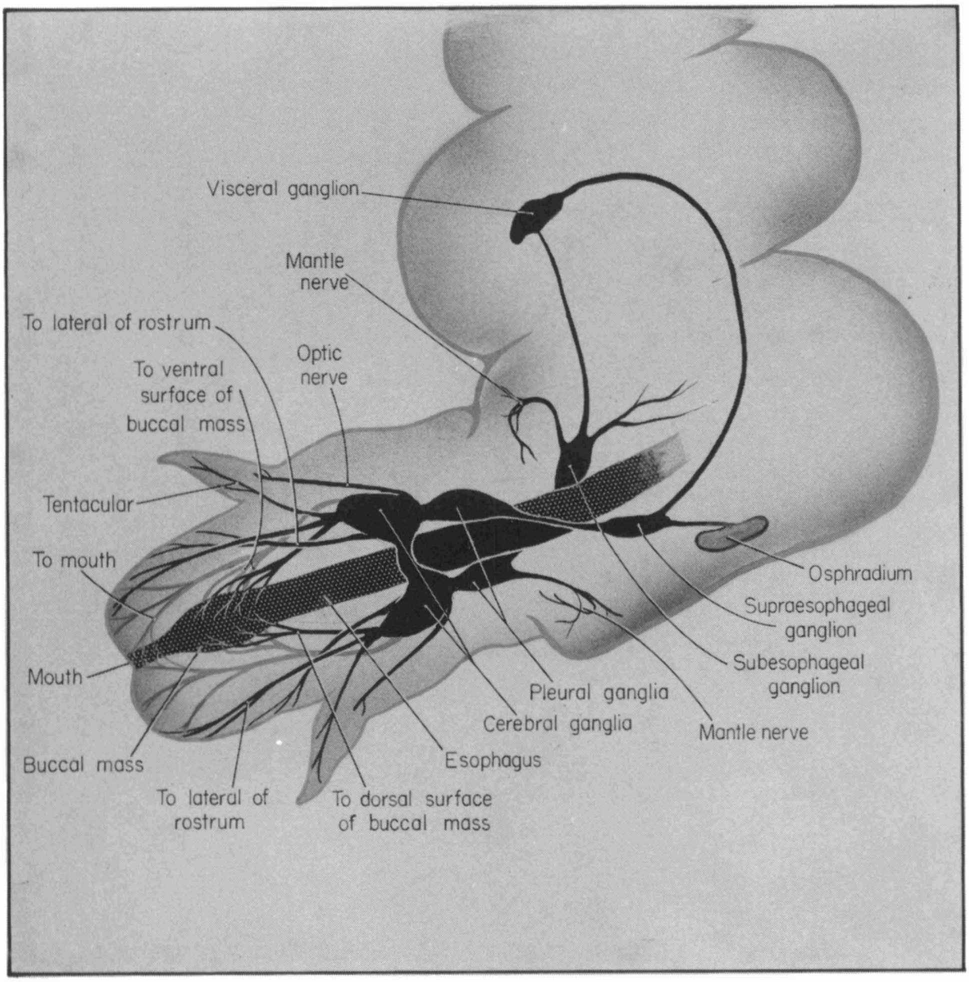
1.


Digestive gland
Shell
Ovary
Pallial oviduct
Spermathecal duct
Columella
Rectum
Columellar muscle
Stomach
Kidney
Pericardium
Heart
Intestine
Edge of style sac

2.

PLATE V

Dorsal view of the central nervous system of *Pomatiopsis lapidaria* (Say).



Visceral ganglion
Mantle nerve
To lateral of rostrum
To ventral surface of buccal mass
Optic nerve
Tentacular
To mouth
Mouth
Buccal mass
To lateral of rostrum
To dorsal surface of buccal mass
Esophagus
Cerebral ganglia
Pleural ganglia
Mantle nerve
Subesophageal ganglion
Supraesophageal ganglion
Osphradium

PLATE VI

The digestive system of *Pomatiopsis lapidaria* (Say).

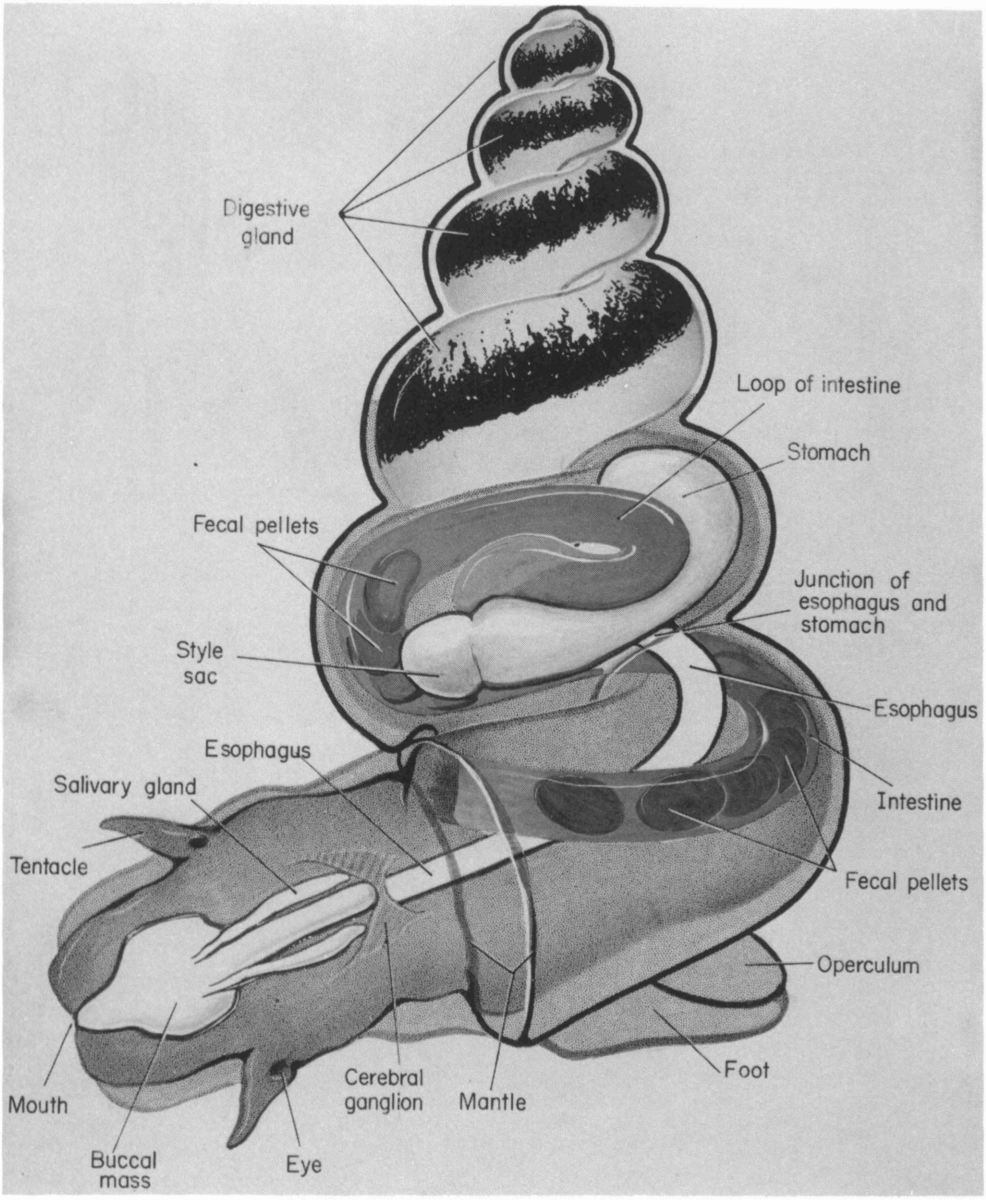

Digestive gland
Loop of intestine
Stomach
Fecal pellets
Junction of esophagus and stomach
Style sac
Esophagus
Esophagus
Salivary gland
Intestine
Tentacle
Fecal pellets
Operculum
Foot
Mouth
Cerebral ganglion
Mantle
Buccal mass
Eye

PLATE VII

DETAILS OF THE DIGESTIVE SYSTEM

Fig. 1. Cross section of esophagus to show jaws. Approx. 37X.

Fig. 2. Longitudinal section of salivary gland. Approx. 92X.

Fig. 3. View of interior of stomach showing various openings. Arrow points to area against which the head of the crystalline style rotates. 32X.

Fig. 4. Cross section of stomach and style sac. Approx. 40X.

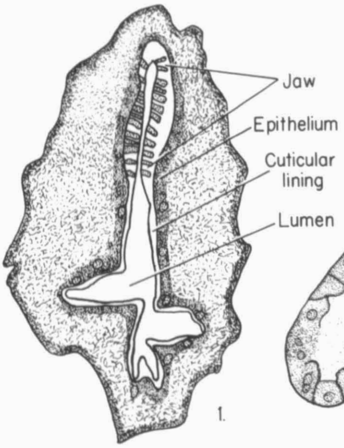
Fig. 5. Epithelium lining the style sac. Approx. 40X.

Fig. 6. Two views of the gastric shield. The upper represents the lower one inverted. The arrows on the upper one indicate the point at which the shield was folded down during dissection. Approx. 36X.

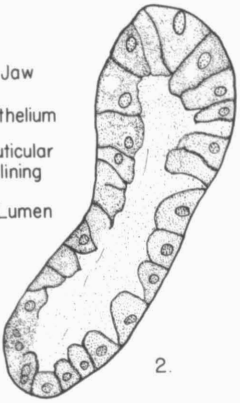
Fig. 7. The crystalline style. Lighter part to the right of the dark band rotates against the gastric shield. Approx. 32X.

Fig. 8. Cross section of the intestine to show the typhlosole. 54X.

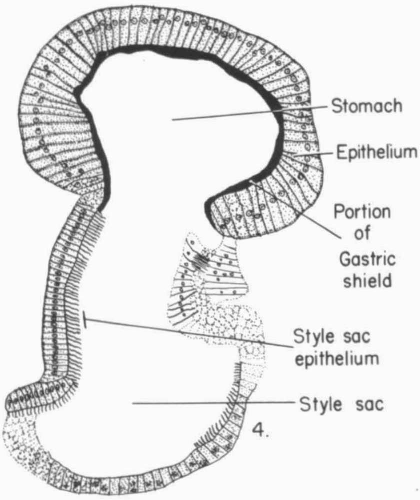
Fig. 9. Epithelium of the digestive gland. 88X.


Jaw
Epithelium
Cuticular lining
Lumen

1.

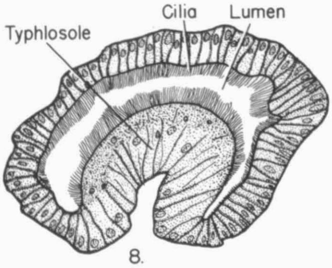


2.

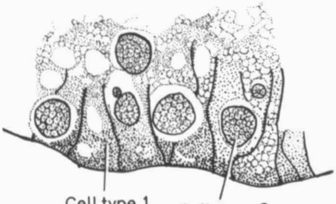

Stomach
Epithelium
Portion of Gastric shield
Style sac epithelium
Style sac

4.

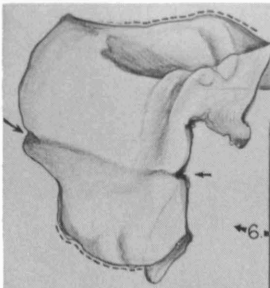
5.


Typhlosole
Cilia
Lumen

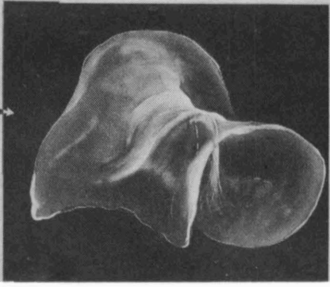
8.

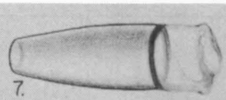

Cell type 1
Cell type 2

9.



6.





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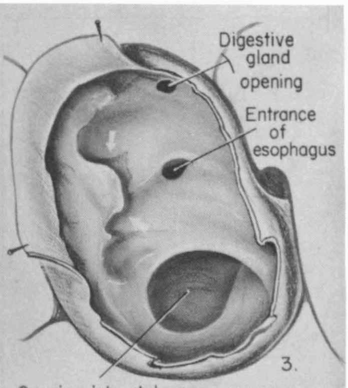
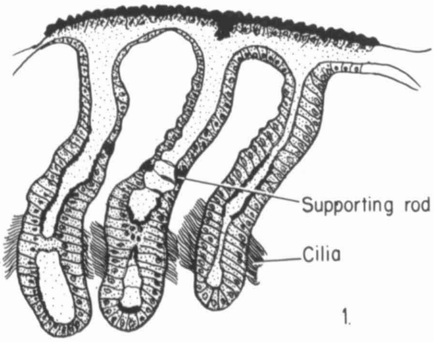

Digestive gland opening
Entrance of esophagus
Opening into style sac

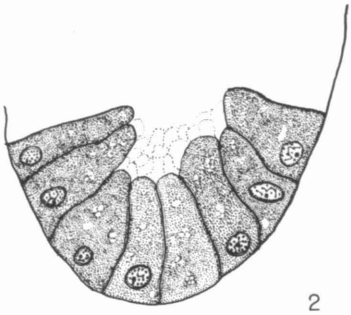
3.

PLATE VIII

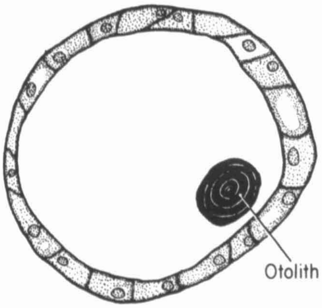
Fig. 1. Gill filaments. 29X.
Fig. 2. Epithelium of the pedal gland. 55X.
Fig. 3. An otocyst. 40X.
Fig. 4. An eye. 30X.
Fig. 5. Cross section of the heart. 45X.
Fig. 6. Epithelium of the kidney. 45X.


Supporting rod
Cilia

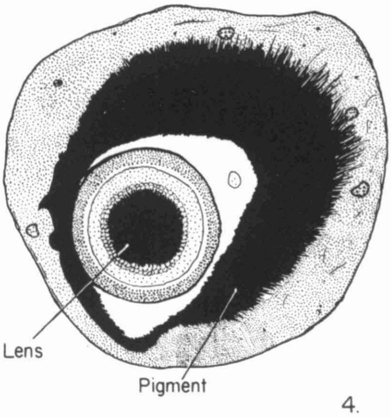
1.



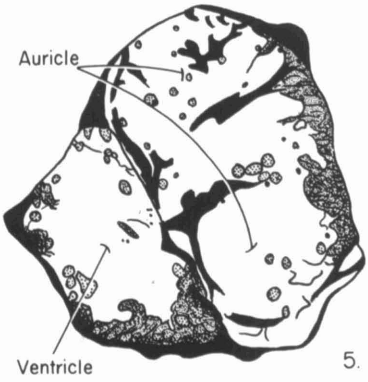
2


Otolith

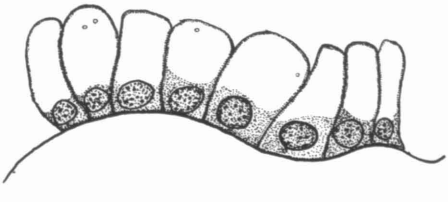
3.


Lens
Pigment

4.


Auricle
Ventricle

5.



6.

PLATE IX

FEMALE GENITAL SYSTEMS

All figures on this plate are taken directly from the originals.

Fig. 1. From Linke, 1934, p. 167. *Littorina littorea.* *D*, intestine; *Ewd*, albumen gland; *Gad*, gelatine gland; *Kad*, capsule gland; *M*, middle-intestinal gland; *Mw*, mantle collar; *Od*, oviduct; *Ov*, ovary; *Rs*, seminal receptacle; *Sch*, columellar muscle.

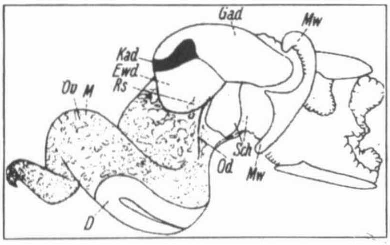
Fig. 2. From Creek, 1951, p. 604. *Pomatias elegans.* *OV*, ovary; *DG*, digestive gland; *RS*, seminal receptacle; *BC*, bursa copulatrix; *AG*, albumen gland; *LI*, thin anterior lip of bursa; *RC*, renal oviduct; *SL*, lip of albumen gland; *EC*, egg conducting groove; *CL*, capsule gland.

Fig. 3. From Creek, 1953, p. 232. *Acme fusca.* *O*, ovary; *GD*, gonadial duct; *RG*, renal oviduct; *RS*, receptaculum seminis; *BC*, bursa copulatrix; *AG*, albumen gland; *CD*, common duct; *CG*, capsule gland; *OM*, copulatory opening to mantle cavity.

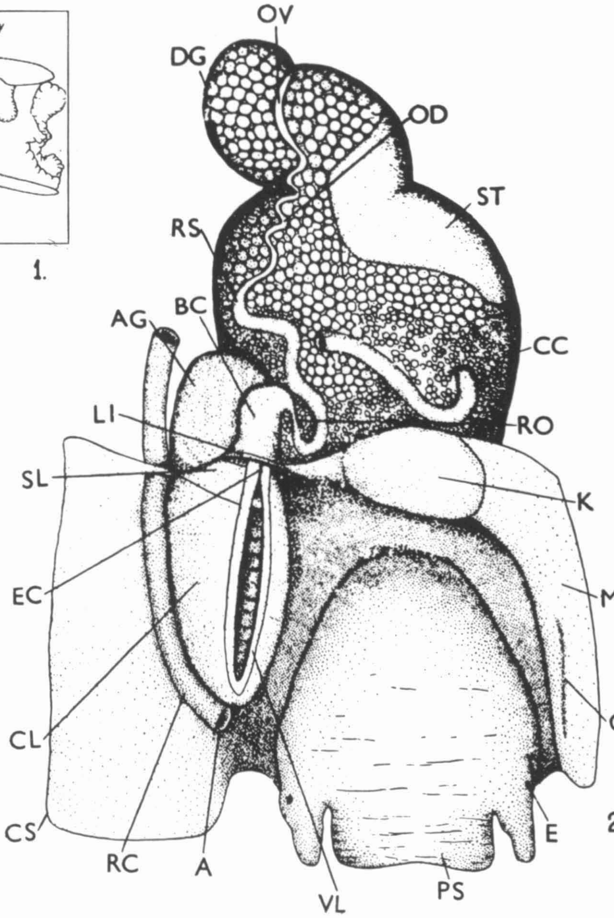
Fig. 4. From Robson, 1920, Pl. XV, Fig. 8. *Paludestrina jenkensi.* *ag*, albumen gland; *v*, vagina; *od*, oviduct; *av*, junction between spermatheca and vagina.

Fig. 5. From Krull, 1935, p. 443. *Paludestrina ulvae.* *ovd*, oviduct; *rs*, receptaculum seminis; *bc*, bursa copulatrix, *dr*, Drüsenmasse, *gp*, gonoporus.

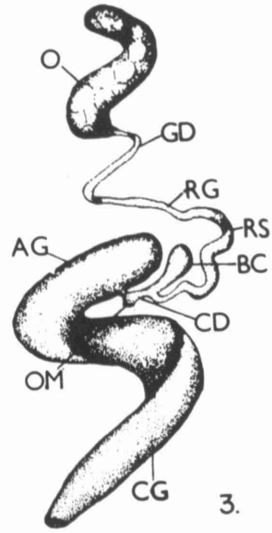
Fig. 6. From Robson, 1922, p. 176. *Paludestrina ventrosa.* *a*, accessory gland; *o*, oviduct; *og*, oviducal gland; *rs*, receptaculum seminis; *v*, vagina.


Gad
Mw
Kad
Ewd
Rs
Ov
M
Sch
Od
Mw
D

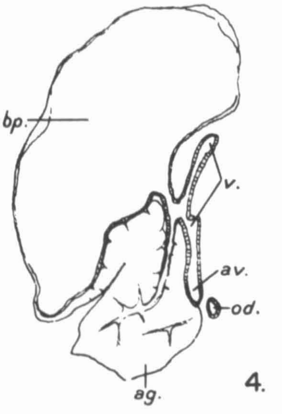
1.


OV
DG
OD
ST
RS
AG
BC
CC
LI
RO
SL
K
EC
MF'
OS
CL
CS
RC
A
VL
PS
E

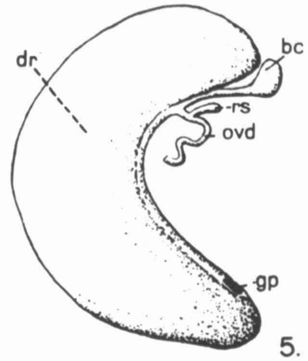
2.


O
GD
RG
RS
AG
BC
CD
OM
CG

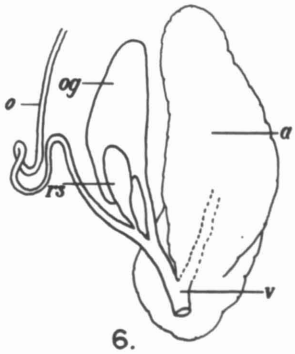
3.


bp.
v.
av.
od.
ag.

4.


dr
bc
-rs
ovd
-gp

5.


o
og
a
rs
v

6.

PLATE X

FEMALE GENITAL SYSTEMS

Fig. 7. From Krull, 1935, p. 443. *Paludestrina ventrosa. ovd,* oviduct; *rs,* receptaculum seminis; *bc,* bursa copulatrix; *dr,* Drüsenmasse, *gp,* gonoporus.

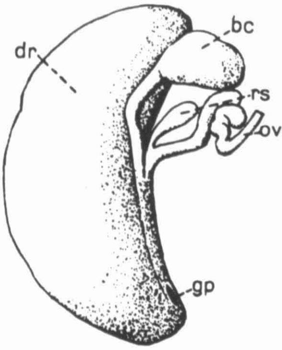
Fig. 8. From Krull, 1935, p. 436. *Lithoglyphus naticoides. ov,* ovary; *ovd,* oviduct; *gpg,* gonopericardial opening; *rs,* receptaculum seminis; *bc,* bursa copulatrix; *ado,* Anhangsdrüse of the oviduct; *gp,* genital pore.

Fig. 9. From Robson, 1921, p. 410. *Oncomelania nosophora.* ......, ovary; oviduct, and spermatheca; ------, accessory gland and uterus; -.-.-., rectum.

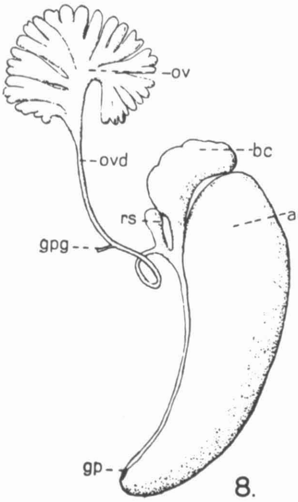
Fig. 10. From Itagaki, 1955, Pl. 2, Fig. 2. *Oncomelania nosophora. ov,* ovary; *od,* oviduct; *sp,* spermatheca; *spd,* spermathecal duct; *mmg,* mass membrane gland; *an,* anus; *st,* stomach; *oe,* esophagus.

Fig. 11. From Itagaki, 1955, Pl. 2, Fig. 3. *Oncomelania nosophora, od,* oviduct; *fch,* fertilization chamber; *spd,* spermathecal duct; *mmg,* mass membrane gland; *sp,* spermatheca; *m,* intestine.

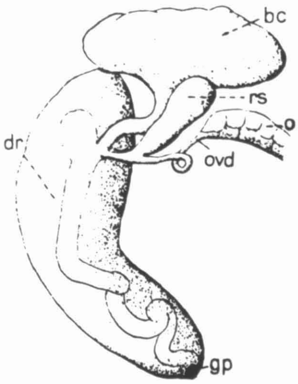
Fig. 12. From Krull, 1935, p. 449. *Assemania grayana. Ovd,* oviduct; *O,* egg; *Rs,* receptaculum seminis; *Bc,* bursa copulatrix; *Dr,* Drüsenmasse; *Gp,* gonopore.


dr
bc
rs
ovd
gp

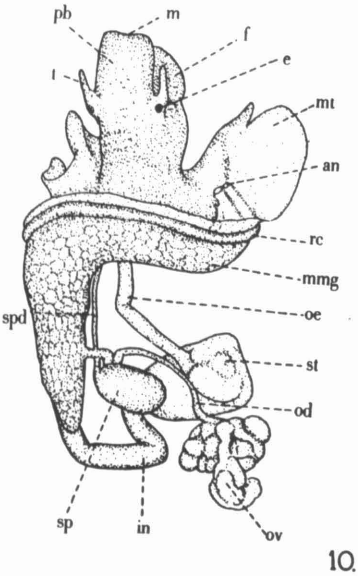
7.


ov
ovd
bc
rs
ado
gpg
gp

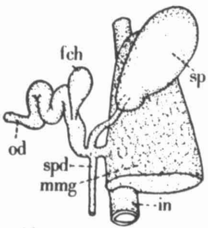
8.


bc
rs
o
dr
ovd
gp

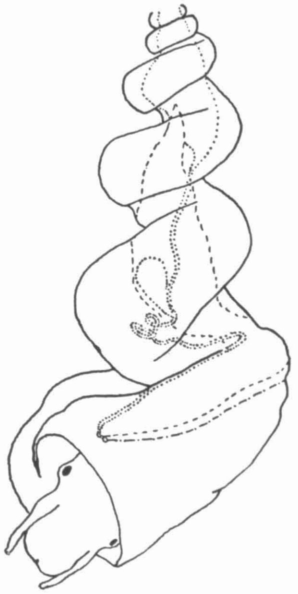
12.


pb
m
f
t
e
mt
an
rc
mmg
oe
spd
st
od
sp
in
ov

10.


fch
sp
od
spd
mmg
in

11.



9.

PLATE XI

The female reproductive system of *Pomatiopsis lapidaria* (Say).

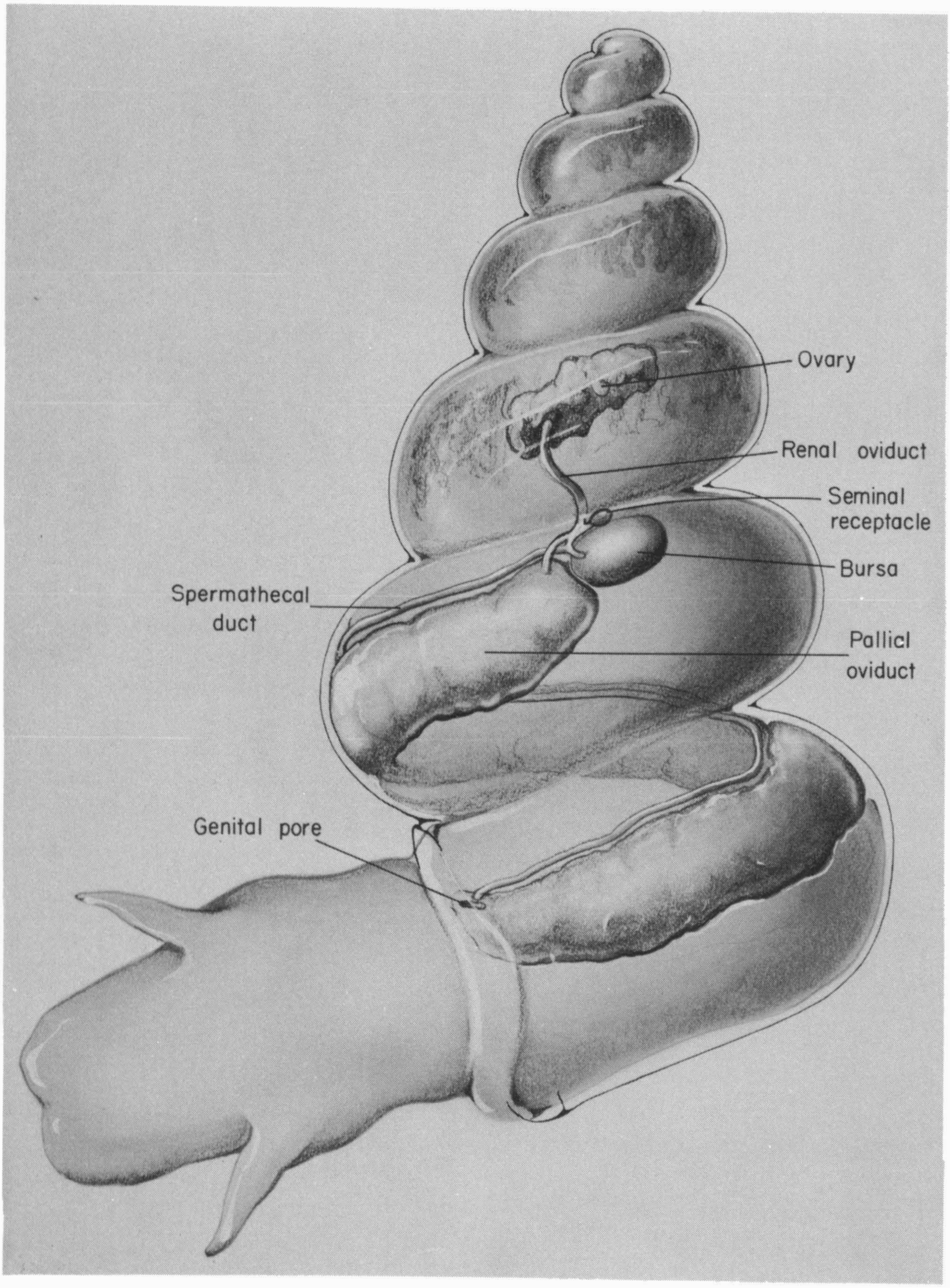

Ovary
Renal oviduct
Seminal receptacle
Bursa
Spermathecal duct
Pallicl oviduct
Genital pore

PLATE XII

DETAILS OF THE FEMALE REPRODUCTIVE SYSTEM

Fig. 1. Cross section of branch of ovary showing ova in various stages of development. 68X.

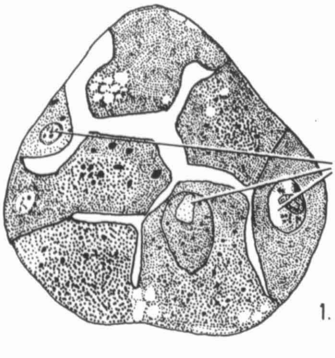
Fig. 2. Cross section of renal oviduct with ovum in the lumen. 135X.

Fig. 3. Epithelium of the bursa showing unoriented sperm in the lumen. 135X.

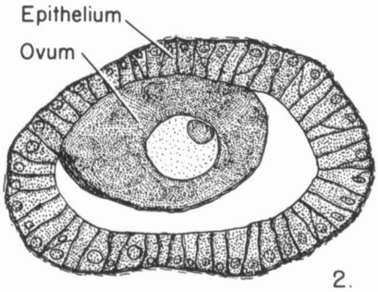
Fig. 4. Cross section of seminal receptacle showing sperm with the heads oriented towards the epithelium. 135X.

Fig. 5. Cross section of spermathecal duct. 293X.

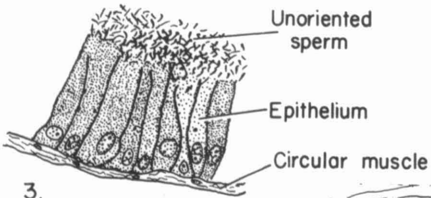
Fig. 6. Sagittal section of pallial oviduct showing the difference in the upper (albumen gland) and lower (capsule gland) portions. 15X.


Ova

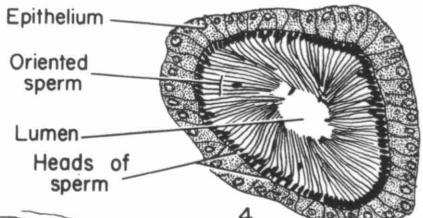
1.


Epithelium
Ovum

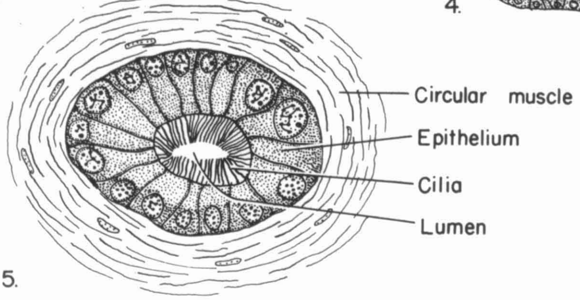
2.


Unoriented sperm
Epithelium
Circular muscle

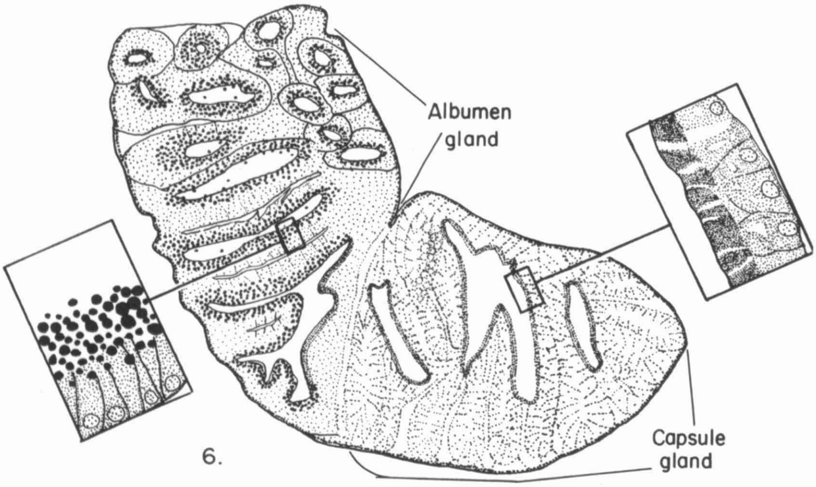
3.


Epithelium
Oriented sperm
Lumen
Heads of sperm

4.


Circular muscle
Epithelium
Cilia
Lumen

5.


Albumen gland
Capsule gland

6.

PLATE XIII

The male reproductive system of *Pomatiopsis lapidaria* (Say).

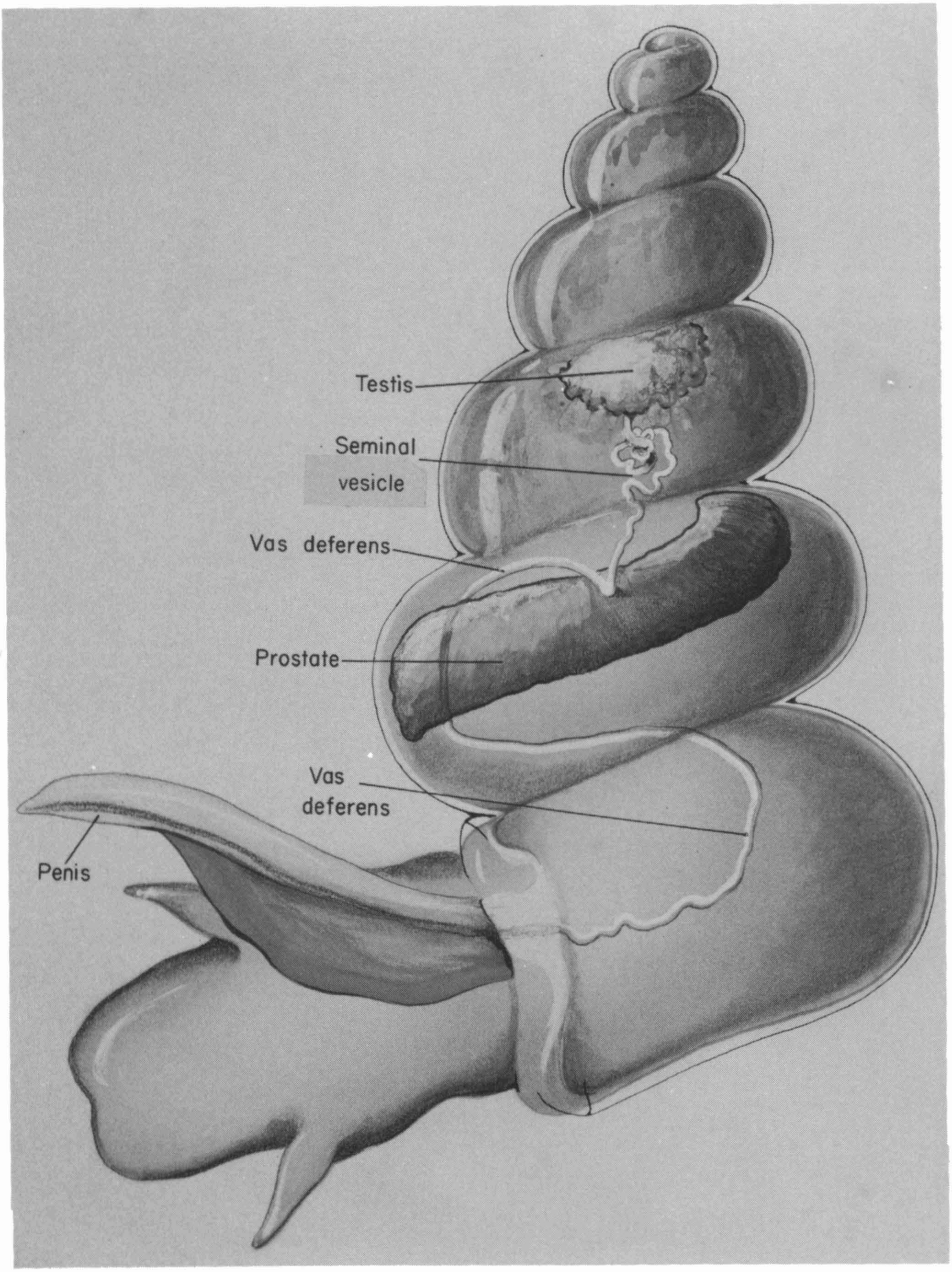

Testis
Seminal vesicle
Vas deferens
Prostate
Vas deferens
Penis

PLATE XIV

DETAILS OF THE MALE REPRODUCTIVE SYSTEM

Fig. 1. Part of the testis. 279X.

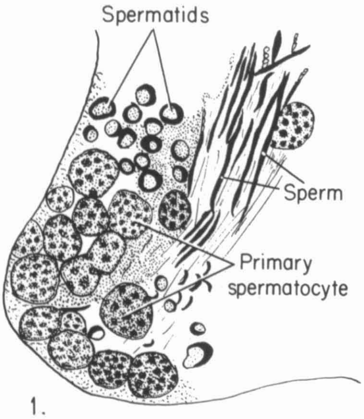
Fig. 2. Cross section of the seminal vesicle to show the sperm packed within it. 279X.

Fig. 3. Cross section of the prostate gland to show type of epithelium. 128X.

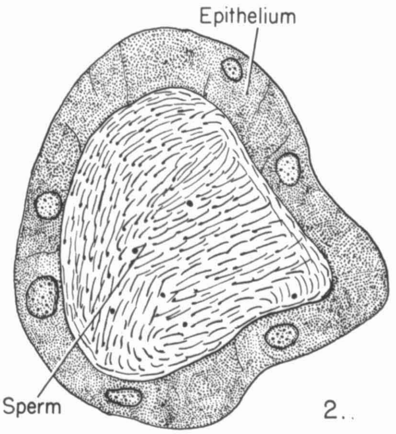
Fig. 4. Cross section of the vas deferens. 279X.

Fig. 5. A sperm showing the characteristic manner in which the tail is wound about the body. 838X.

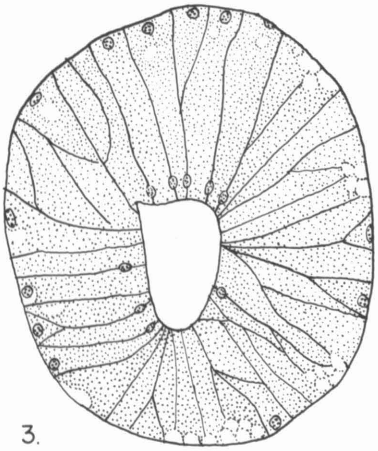
Fig. 6. Cross section of the verge. 128X.


Spermatids
Sperm
Primary spermatocyte

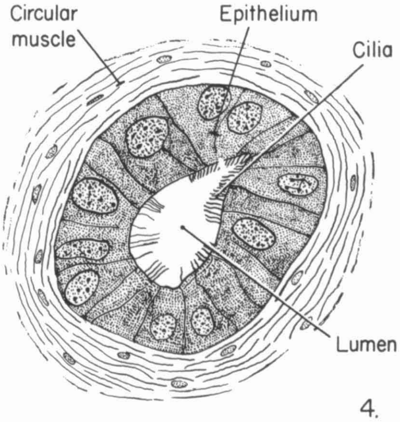
1.


Epithelium
Sperm

2.

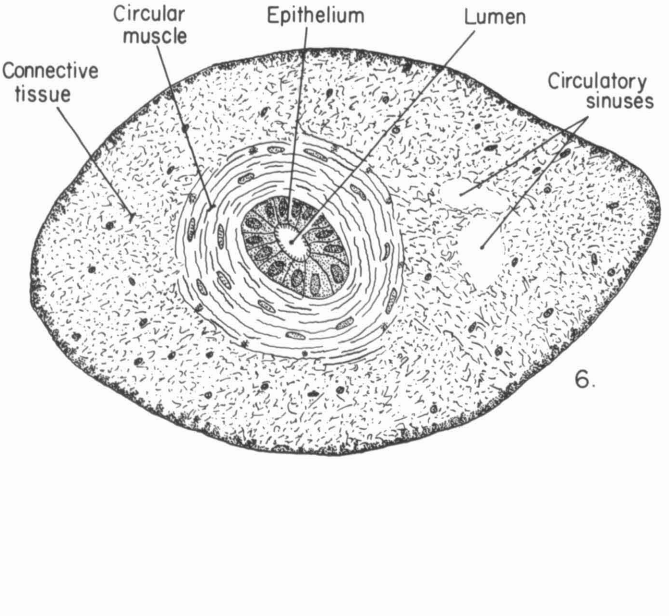


3.


Circular muscle
Epithelium
Cilia
Lumen

4.

5.


Circular muscle
Epithelium
Lumen
Connective tissue
Circulatory sinuses

6.

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