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THE SYSTEMATIC RELATIONSHIP OF POMATIOPSIS LAPIDARIA (SAY) AND ONCOMELANIA HUPENSIS FORMOSANA (PILSBRY AND HIRASE) (GASTROPODA:HYDROBIIDAE)

by

George Morgan Davis

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan
1965

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INTRODUCTION

This paper is concerned with the systematic relationship of the American genus Pomatiopsis (Say, 1817) and the Oriental genus Oncomelania (Pilsbry and Hirase, 1905). Interest was first generated in determining to what extent these prosobranch snails were related to each other when Stunkard (1946), Ward, Travis, and Rue (1947) and Berry and Rue (1948) demonstrated that Pomatiopsis lapidaria was capable of serving as an intermediate host of the human blood fluke, Schistosoma japonicum. Abbott (1948) stated that malacological studies showed that P. lapidaria was "strikingly similar" to species of Oncomelania. Dundee (1957) stated that anatomically P. lapidaria was "quite similar" to Oncomelania and that differences appeared "to be minor." H. van der Schalie et al. (1962) reported success in hybridizing 2 species of Oncomelania with P. lapidaria which "strengthened" their "contention that these genera are rather closely related." Burch (1960a) considered the genera to be synonymous but later, after a detailed cytological study, separated them as closely related genera (Burch, 1964).

In this paper Pomatiopsis lapidaria and Oncomelania formosana were chosen as representatives of the 2 genera. Their

comparative anatomy, potential for hybridization, electrophoretic properties, and laboratory ecology were studied. The investigation was undertaken to determine to what extent differences coupled with existing knowledge of the other species of each genus would serve to establish the degree of relationship between Pomatiopsis and Oncomelania, i.e., whether or not Pomatiopsis and Oncomelania are congeneric, closely related but distinct genera, or genera more widely separated than has previously been considered.

Dundee (1957) discussed the major papers pertaining to Pomatiopsis, i.e., ecology, systematics, general distribution, and anatomy. Aside from a few anatomical details including a discussion of variability in the radula presented by Abbott (1948a) Dundee published the only anatomical study on P. lapidaria giving details which can be used in a general comparative manner on the generic level. H. van der Schalie and Dundee (1956) presented the basic anatomy of P. cincinnatiensis enabling certain specific comparisons with P. lapidaria, and the so-called species of Oncomelania.

Oncomelania formosana was chosen as a representative of its genus because it appeared to be a form intermediate in the Oncomelania species complex. Burch (1964) studied cytological aspects of the currently recognized species of Oncomelania and their hybrids, and, in light of his findings coupled with the fact that there was no reduced viability on the F1 and F2 hybrids, he stated that the 4 species were no more than geographic populations or races of

the same species. Davis et al. (1965) were of the same opinion due to success in hybridization studies where only 1 abnormal snail was found among thousands of hybrids observed. They felt that the genetic compatability involved was of a con-specific or sub-specific nature. In shell shape, there is a north-south cline with O. nosophora from Japan having a long, slender shell; O. quadrasi from the Philippines having a relatively more short and broad shell; with O. formosana from Taiwan being intermediate. This intergradation was noted by Abbott (1948b), who stated that 5% of the Formosan specimens could not be distinguished from O. quadrasi while 10% were the same shape and size of many O. nosophora from Japan and China. Studies by Kuo and Mao (1957) indicate that O. hupensis and O. nosophora from China are all O. hupensis and that there was "no clear-cut line of demarcation between them," i.e., between the smooth shelled O. nosophora type and ribbed O. hupensis type. In all following discussion in this thesis, the so-called Oncomelania "species" of most previous authors will be considered subspecies.

There are a number of anatomical papers describing various features of the subspecies of Oncomelania. Heude (1880), Li (1934), and Kuo and Mao (1957) discussed various aspects of the anatomy of O. hupensis hupensis; Robson (1921), Nakamoto (1923), Itagaki (1955), Williams (Fide Ritchie, 1955, in referring to the (1954, 1955) Professional Reports of the 406 General Medical Laboratory), and Roth and Wagner (1957) presented material on

O. hupensis nosophora. As far as is known, no anatomical studies have been published on O. hupensis formosana aside from that of Roth (1960), who described the female reporductive anatomy and Davis (1964) who depicted the structure of the female gonad. Abbott (1945) provided some anatomical notes on O. quadrasi.

SYSTEMATIC DISCUSSION

Pomatiopsis and Oncomelania are representatives of the family Hydrobiidae (Troschel, 1857) subfamily Pomatiopsinae (Stimpson, 1865). As shown in Table 1, there has been a considerable difference of opinion concerning the proper family and subfamily designation for Pomatiopsis since 1862. Oncomelania was not named until 1881 and this genus generally has been placed in the same subfamily with Pomatiopsis.

Pomatiopsis lapidaria was described by Say (1817) as a species of Cyclostoma, a genus currently split into several genera of the Pomatiasidae (Wenz, 1938-1944). Tryon (1862) recognized the basic differences between the viviparid and hydrobiid types of snails and subsequently created the family Amnicolidae. In the same paper he separated Pomatiopsis as a subgenus of Amnicola because he felt that "A. lapidaria" differed from the small globose shells of Amnicola by "shell elongate, spire (of about 6 whorls) much exceeding the length of the aperture . . . ." Tryon (1862) did not give a family diagnosis for the Amnicolidae. Gill (1863), in a noteworthy paper, defined the family but stated that Pomatiopsis (i.e., P. lapidaria) was possibly an aciculid snail.[1] He asserted

[1] Wenz (1938-1944) used Acmeidae for this family, but according to opinion 344 of the International Commission on Zoological Nomenclature, the correct designation is Aciculidae.

TABLE 1.

The Family and Subfamily Status of Pomatiopsis as Indicated by Various Authors

Author		Amnicolidae		*	Hydrobiidae		Pomatiopsidae	Rissoidae	Truncatellidae
		Pomat.	Hydr.	___	Pomat.	Trun.	Pomat.	Pomat.	Pomat.
Tryon	1862			x					
Gill	1863			x					
Stimpson	1865							x	
Binney	1865							x	
Gill	1871						x		
Fischer	1885				x				
Tryon	1883							x	
Call	1898	x							
Baker	1902	x							
Pilsbry and Ferris	1906						x		
Hannibal	1812			x					
Walker	1918	x							
Annandale	1924							x	
Baker	1926						x		
Thiele	1928					x			
Baker	1928						x		
Thiele	1929					x			
Wenz	1938								x
Berry	1943						x		
Abbott	1948		x						
Dundee	1957					x			
Davis	1965				x				

Pomat. = Pomatiopsinae Hydr. = Hydrobiinae Trunc. = Truncatellinae

*____ = no subfamily mentioned

that the "validity" of Pomatiopsis as defined by Tryon was doubtful and the Amnicolidae contained 3 genera: Amnicola, Chilocyclus, and Somatogyrus. Chilocyclus, proposed by Gill (1863) is a synonym for Pomatiopsis as the genus is currently understood and was used to separate Cyclostoma cincinnatiensis (now P. cincinnatiensis) from species of Amnicola.

Stimpson (1865) rejected Gill's family definition for the following reasons: the definition was almost an exact translation of Moquin-Tandon's (1855) definition of Bythinia, and the definition did not apply to the American forms of the group founded at that time on the genus Amnicola, e.g., the verge is not bifid in all species, the tentacles of Amnicola proper are not setacious, etc. Aside from the fact that the family was poorly diagnosed, laws of priority exclude Amnicolidae from being used as a family name. H. B. Baker (1960) reviewed this situation and pointed out that if one accepts Bithyniidae and Truncatellidae as separate families, Hydrobiidae is the legal name for the family under discussion. Bithyniidae is distinct (Taylor and Davis, in preparation). A number of features described for Truncatella indicate separate family status. The great reduction in the ctenidium contrasts the well-developed ctenidium of the Hydrobiidae; concentrated cerebral, pleural, and parietal ganglia in Truncatella are in contrast to the widely separated cerebral and parietal ganglia of the Hydrobiidae; shortened tentacles with eyes at

their bases on the mid-line, or displaced medially in the former, is in contrast with eyes at the outer base of generally elongate tentacles in the latter. The elongated gonopericardial duct and the connection of the bursa copulatrix with the left kidney are unknown in the Hydrobiidae. The modified, small, pedestal-like foot of Truncatella contrasts the elongate, broad foot of the Hydrobiidae. In the Truncatellidae the corneous operculum is sub-spiral and characteristically, though not infallibly, with a thick, outer, calcarious layer. The central tooth of the radula is triangular and supports a single, anterior, triangular cusp (drawings in Fischer, 1880-1887; Binney, 1865; Clench and Turner, 1948). The hydrobiid operculum is corneous, usually paucispiral, sometimes multispiral, but not subspiral to the degree shown in Truncatella. The central tooth of the radula is trapezoidal or rectangular, the anterior edge supporting more than one cusp. As discussed below, the mode of progression found in the Truncatellidae is distinctly different compared with that in the Pomatiopsinae.

Stimpson (1865), in an outstanding paper, presented a broad diagnosis for the family Rissoidae so that it included the currently recognized families Rissoidae, Hydrobiidae, and Bithyniidae. The Truncatellidae were excluded on the basis of radula, eye position, and the nature of the "breathing organ." The Rissoidae is currently characterized as follows: marine, a filament arising from the operculigerous lobe and/or the presence of a pallial tentacle; foot more

narrow and agile than that of the Hydrobiidae; the shell may be smooth but is more characteristically ribbed, with spiral cords, or canacellate. The aperture below may be bent outwards (Fretter and Graham, 1962).

The Hydrobiidae is a separate family of freshwater snails with a few marine, brackish water, amphibious, and terrestrial forms. The shell is characteristically smooth but not infallibly so; the aperture is not bent out below. No filament arises from the operculigerous lobe and a pallial tentacle is known only for Hydrobia ulvae. The difference in the foot has been mentioned. Fretter and Graham (1962) state that the pleuroparietal connectives of the nervous system are long in the Hydrobiidae and comparatively shortened in the Rissoidae.

In light of the above discussion, it is clear that Pomatiopsis cannot be placed in the Amnicolidae, Rissoidae, or Truncatellidae. Stimpson (1865) gave excellent reasons for establishing the subfamily Pomatiopsinae. The principal character used was what he called "lateral sinuses" which separated the foot into anterior and posterior parts. Other distinguishing characteristics were: (1) the terrestrial habitat, (2) the peculiar mode of progression, (3) the central tooth of the radula had basal denticles, not lateral or basolateral cusps as in the Hydrobiinae. Due to Stimpson's influence, most authors have considered Pomatiopsis distinctly

separate from other hydrobiid snails and have placed it either in a separate family or in a distinct subfamily (Table 1).

The question raised is: Does Pomatiopsis deserve to be separated from the Hydrobiidae in a separate family, Pomatiopsidae? Gill (1871) raised Pomatiopsis to family rank without a diagnosis; Pilsbry and Ferriss (1906) did likewise. F. C. Baker (1902) recognised the subfamily Pomatiopsinae but later (1926, 1928) used Stimpson's subfamily characteristics to justify family status. Berry (1943) considered family status justified, especially on radular characteristics.

A reanalysis of Stimpson's subfamily characteristics in light of current studies on (1) morphology and (2) mode of progression, is necessary in order to determine whether or not Stimpson was correct in establishing the subfamily, and, if so, to determine whether or not even a family status is warranted.

1. Lateral Sinuses of the Foot. The following discussion pertains to Plate 1, Figs. 2 and 5, in which the right lateral view of the head-foot region of P. lapidaria is shown with the animal expanding its foot in preparation for advancing (Fig. 2) and with the comple - tion of a "step" or forward advancement (Fig. 5). The head-foot region is characterized by a number of folds, grooves, and creases. The ventral edge of the operculigerous lobe (Op) continues anteriorly as the suprapedal fold (P) and sweeps upwards towards the posterior

Plate I

HEAD AND FOOT OF POMATIOPSIS LAPIDARIA

Fig. 1. Dorsal view of the head.

Fig. 2. Right lateral view of the head. The animal extending the fore foot in the first movement of a "step."

Fig. 3. Sole of the foot without pronouced lateral indentation.

Fig. 4. Sole of the foot showing pronounced lateral indentations.

Fig. 5. Right lateral view of the head. The foot is contracted showing completion of a "step."

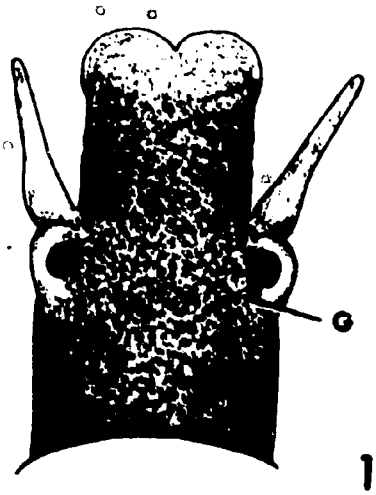
Fig. 6. Sole of the foot where the fore foot is beginning to expand forward.

Fig. 7. The sole of the foot in various stages of "stepping." A. The foot is contracted; B, the fore foot expands while the hind foot remains firmly attached to the substrate; C, the hind foot is drawn up to the contracted state.

Figs. 8, 9. Variations found in the shape of the flexible foot.

At. anterior foot
G. glandular units
L. lateral indentation
M. point where the mantle covers the "neck."
Ms. mucoid slit
O. operculum
Om. omniphoric groove
Op. operculigerous lobe
P. suprapedal fold
Pc. pedal crease
Ps. posterior foot
R. rostrum
S. subocular lobe
So. subocular groove
Su. suprapedal lobe
x. mid-region of the foot under the pedal haemocoel.

Plate 1



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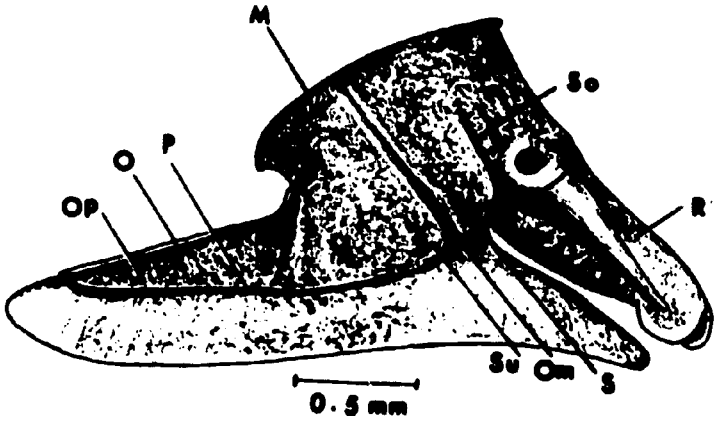

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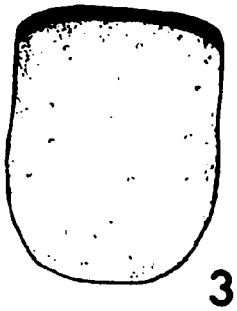

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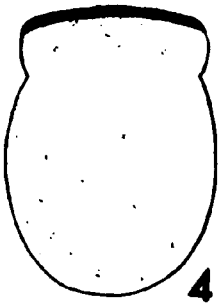

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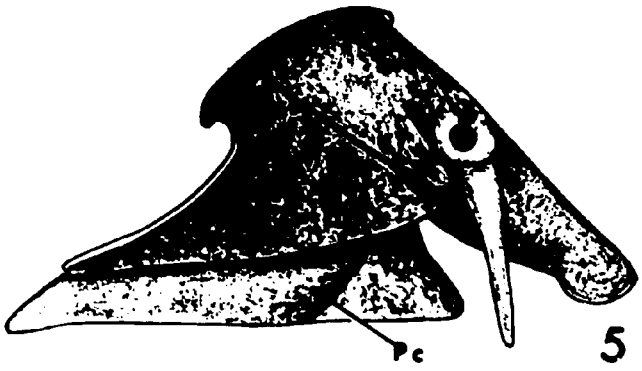

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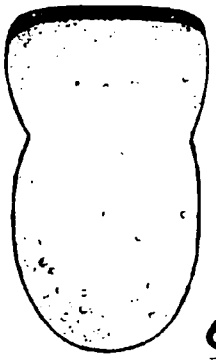

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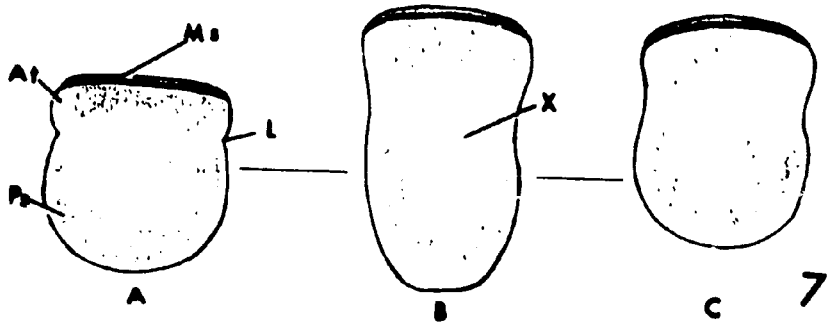

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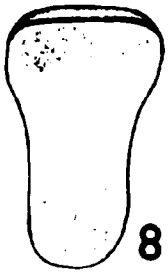

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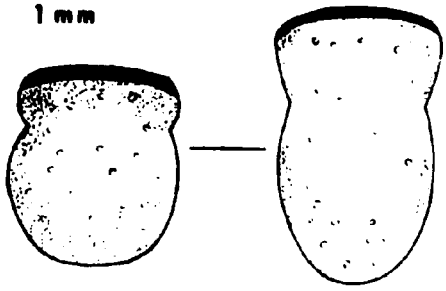

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part of the rostrum (R). Anteriorly the fold is interrupted by the anterior termination of the omniphoric groove (Om). As shown, the groove arises under the mantle on the right side of the "neck" and runs obliquely down towards the anterior border of the suprapedal fold. The groove is highly ciliated and serves to move fecal pellets along its path as well as particles and mucoid strings from the mantle cavity. The terminal end of the groove juts out over the antero-lateral portion of the foot onto which the fecal pellets and particles fall or are swept by ciliary currents. The groove undoubtedly serves to transport eggs to the anterior foot prior to their final encasement in a soil capsule. An identical groove is found on the left side. From time to time a particle may be seen moving anteroventrally along the groove. More dynamic, however, are the ciliary currents sweeping into the left side of the mantle cavity. These currents are created, in part, by cilia on the lateral surfaces of the head.

As the animal moves about it is evident that the groove is plastic and, due to stretching of the lateral skin, may disappear. Certain movements accentuate the groove and the anterior edges of the groove appear lobed, the suprapedal lobe (Su) ventrally and the subocular lobe (S) dorsally. Another groove, the subocular groove (So), is evident below the eye, arising from the suprapedal fold. The subocular groove terminates just posterior to the eye. With the exception of the suprapedal fold which is always distinct, the other

structures discussed are pliable; they appear and disappear as the animal moves about, stretching its head and body in various positions. In relaxed or preserved specimens only the suprapedal fold is evident. Dundee's figure (1957, Plate 3) is of a narcotized specimen as evidenced by the swollen and disproportionate head. The suprapedal fold is continuous directly with the rostrum with no sign of the omniphoric or subocular grooves.

The pedal crease (Pc) shown in Fig. 5 is equivalent to the lateral sinus of the foot described by Stimpson (1865) and the vertical fold mentioned by Baker (1928). This crease is evident only upon completion of a "step" (Fig. 5) where the full weight of the animal presses down on the fully contracted foot. With reduced contraction the pedal fold becomes less evident or nonexistent. Muscular contraction bringing the posterior foot forward causes a bunching of muscles which in turn creates the crease or fold. Pigmented epithelium concentrated by this contraction accentuates the crease. Stimpson (1865) was correct in stating that the pedal crease was dependent upon "the peculiar mode of movement." Abbott (1948) stated that both Oncomelania and Pomatiopsis have the same mode of progression and produce "folds in the flesh of the foot due to the weight of shell and body."

The folds and grooves described above were illustrated by Stimpson (1865; p. 33, Fig. 25; p. 34, Fig. 26; p. 31, Fig. 22).

Stimpson's figures were partially correct but failed to consider the plasticity of the organism. His Fig. 26 is quite misleading as current studies show that the pedal crease is not evident when the fore foot is expanding or expanded. Table 2 shows the extent to which Stimpson's figures were copied and his influence felt. The figures depicted the crease as a most prominent and rigid structure, which in his words was a truly "distinct fold separating the foot into an anterior and posterior part . . . ." Abbott (1948a) correctly stated that previous accounts of the divided foot . . . are misleading." Pelseneer (1906) was led to assert that a transverse furrow which crosses the anterior half of the foot was found in Pomatiopsis, a statement which is unfounded as the sole of the foot is simple and undivided. Annandale (1924) felt that the external anatomy of Pomatiopsis might differ from that of Blanfordia as Stimpson's drawing of the sub ocular and supra-pedal lobes led Annandale to state that the former genus had a "triangular process behind the true tentacle" which did not apply to the latter genus. Actually, the same lobes are found in both genera with about the same degree of development. Annandale (1924) was led by Stimpson's drawings and description of the lateral sinus to separate Oncomelania into a new subfamily, Triculinae, where there was no divided foot, contrasting the Pomatiopsinae where the foot was divided by "a transverse furrow."

TABLE 2.

References to Reproductions of Stimpson's 1865 Figures of *Pomatiopsis lapidaria*

Author	Page	Plate	Figure
Binney (1865)	93		187
Call (1896)		8	16
Baker (1898)	345		127
Walker (1918)	34		120
Annandale (1924)	273		1
Baker (1928)	166, 167		77, 78

TABLE 3.

Cusp Formulae for the Teeth of *Pomatiopsis lapidaria* Previously Presented or Discussed in the Literature

Author	Central	Lateral	Inner Marginal	Outer Marginal
1. Stimpson (1865)	$\frac{1-1-1}{2-2}$	1-1-2	5	5
2. Binney (1865)	copied from Stimpson			
3. Baker (1902)	copied from Stimpson			
4. Walker (1918)	copied from Stimpson			
5. Annandale (1924)	$\frac{2-1-2}{2-2}$	2-1-3	10	10
6. Thiele (1928)	$\frac{1-1-1}{2-2}$	2-1-3	6	5
7. Baker (1928)	$\frac{1-1-1}{1-1}$	1-1-3	6	9
8. Thiele (1929)	$\frac{1-1-1}{2-2}$	2-1-3	4-6	3-5
9. Abbott (1948)	$\frac{1-1-1}{2(3)-(3)2}$	2-1-2 (3-4)	7(6)	5
10. Dundee (1957)	$\frac{1-1-1}{2-2}$	2-1-3		

2. Mode of Progression. The underside of the foot was examined by placing specimens on a glass slide in a drop of water, waiting until the animal began moving over the slide, inverting the slide, and supporting it above the stage of a dissecting scope. Mucoid secretions of the foot and supportive action of the surface film of water served to keep the snail from dropping from the slide. The snails moved freely across the slide enabling a study of foot shape, structure, and mode of progression.

When the animal is at rest the foot is slightly contracted and a lateral indentation is noted on either side of the foot (Plate 1, Fig. 7, L). This indentation corresponds to the ventrolateral end of the pedal crease and corresponds to an area separating anterior and posterior portions of the foot. The latter, as Stimpson (1865) observed, is about twice the length of the former. The degree of indentation varies considerably from individual to individual and depends a great deal upon the amount of muscular contraction. In Plate 1, Fig. 3, for instance, only a slight bend of the lateral margins indicated the position of the indentation. At this point the foot is capable of greater contraction. In Fig. 7, the foot at position A is fully contracted. To advance, the anterior portion of the foot (At) expands forward during which the lateral indentation becomes progressively less evident as this area also expands forward. When the fore foot is fully extended (position B) the point corresponding to the lateral

indentation has moved forward from 0.36 to 0.42 mm. In this expansion of the fore foot, the posterior portion (Ps) remains firmly attached to the substrate (position B). The extended fore foot then becomes attached to the substrate and the foot musculature contracts in the area marked x (Fig. 7) drawing the posterior foot foreward until the foot again assumes the shape shown in position A. These movements constitute a "step." While the snail is engaged in a series of "steps" the foot does not become fully contracted (position C, Fig. 7).

Stimpson (1865) stated that in progression and as part of the stepping process the "snout" was thrust forward and its "disc-like extremity affixed to the ground as far ahead as possible." With the "snout" and the posterior portion of the foot solidly in place, "the anterior part of the foot becomes free and is thrust forward to the disk of the rostrum where it is again planted." He considered 3 points of support to be used in progression, the two parts of the foot and the rostral tip. In studying numerous specimens of this species it is evident that the rostrum is not used for support nor does it ever become "affixed" to the substrate. The rostrum is only used for feeding as is described more fully below. The animal is supported only by the foot with the greatest points of support associated with the mid- and posterior foot. The snail is quite capable of stretching the anterior foot forward and lifting it off the substrate while solidly supported by the mid- and hind foot. The various movements of

Pomatiopsis lapidaria over rough and smooth substrates are classified and described below.

A. Movement and feeding on moist filter paper. Filter paper serves as a roughened but unyielding surface on which the movement of the snail is normal and unstrained. When the animal is not actually feeding, the basic movements of the foot described above operate smoothly. Here the extending fore foot expands beneath the tip of the rostrum and beyond it often as far as 0.6-0.8 mm. The contraction drawing up the hind foot is most often followed by a contraction of the columellar muscle which tends to raise the spire of the shell as well as pull it forward. On a smooth level substrate the last movement may not be pronounced but its occurrence gives the snail the appearance of hunching forward. With completion of the hunching movement the rostral tip is again brought before the front edge of the foot. Often the rostrum sweeps from one side to the other without touching the substrate.

While feeding, the animal may rasp the substrate within an arc limited by the extensibility of the rostrum. In initiating a step while the animal is browsing, the fore foot is extended to the tip of the rostrum but not beneath it. Completion of a "step" automatically causes an advance of the rostrum. With the advance, the rostrum may remain near the substrate, the radula rasping here and there, or, with the hunching motion stretch straight out and, subsequently,

rasping the substrate as it is drawn straight back to the body. Occasionally with the hunching movement the rostrum is raised and the whole head stretched upward at an angle of about 60°. The rostrum is fully extended and then lowered to the substrate as far ahead of the body as possible. In all these movements the foot is coordinated with the actively probing rostrum but the animal is not dependent upon the rostrum for support.

B. Movements on soil. On loose soil, especially on a sharp incline, the step-like movement may appear less evident due to back sliding and the crumbling of soil beneath the foot. Where greater exertion is necessary the hunching movement becomes quite pronounced.

C. Movement in water. While moving across glass and submerged under water, this species does not simply glide as stated by Abbott (1948a). Water greatly reduces resistance to movement due to the weight of shell and visceral mass. Glass affords such a smooth substrate that ciliary activity facilitates a slight glide. The main movement is achieved, however, by what appears to be an almost effortless short extension of the fore foot and subsequent contraction at mid-foot as described above. The "step" is not at all pronounced due to the reduced pressures on the foot. Under water the hunching movement is greatly reduced and the ciliary action as well as undulations of the margin of the fore foot are more pronounced.

Pomatiopsis lapidaria was observed moving upside down, adhering to the surface film of water. The fore foot was extended and cupped, thus forming a deep concavity. Ciliary currents swept into the concavity and the animal glided over the surface of the water. Only occasionally did the mid-foot contract or the snail make a hunching movement.

The point to be made here is that the foot of Pomatiopsis lapidaria is like that of the Hydrobiidae while the mode of progression is evidently an adaptive change enabling movement on land where the buoying effect of water is lost and the increased weight on the foot makes ciliary movement impossible. The pedal crease is a result of accentuation of certain muscles enabling the step-like mode of progression and is accentuated in Pomatiopsis by pigmentation on the lateral foot surface below the suprapedal fold. Weight of body and shell also serve to accentuate the crease.

The basic difference between the mode of progression of members of the Pomatiopsinae and that of members of the Truncatellidae was pointed out by Stimpson (1865) who stated that in Truncatella there were only 2 points of support and that progression in Truncatella should be called "looping" as opposed to "stepping" in Pomatiopsis. Fretter and Graham (1962) give the following description for the mode of progression in Truncatella. It "extends the snout, which is very extensible, and grips the substratum with its tip (page 598,

Fig. 315); it then pulls the foot up to grasp the ground just behind the snout, dragging the shell in its rear, releases the snout and starts the process once again. Sometimes the foot slides along the surface of the ground as it is drawn forward, sometimes it is lifted clear." They state that the small rounded foot and the expanded tip of the snout are related to this movement.

3. Radula. Stimpson (1865) figured the radula of Pomatiopsis lapidaria. As shown in Table 3, this drawing was extensively copied. Additional figures were prepared by Annandale (1924), Baker (1928), Thiele (1928), and Abbott (1948). The radula of P. cincinnatiensis was figured by Troschel (1863) under the synonym of Amnicola sayana and subsequently copied by Stimpson (1865) and Binney (1865). Baker (1928) and Berry (1943) provided new figures, those of the last being the best.

Stimpson (1865) states that the radula of the Pomatiopsinae is distinct from that of the Hydrobiinae in that the basal cusps (denticles) of the central tooth are placed in the former at or near the base. In this view Stimpson is correct. In the Hydrobiidae the basal cusps are often attached to a thickened ridge along the lateral angle of the central tooth (V Plate 19). This arrangement is particularly noted in genera such as Amnicola and Hydrobia. In the Pomatiopsinae the supports for the cutting edge of the basal cusps do not arise from a thickened ridge along the lateral angle but from moulded

thickenings of the tooth running straight back from an anterior point on the lateral angle posteriorly (X, Plate 19). By changing focus on the lateral angle it is evident that the thickened support causes a slight undulation to the lateral angle where it arises (Plate 19, central 6). The most prominent of the supports arises just lateral to the outer anterior cusp (or cusps) flanking the large central cusp (V, Plate 19). Baker (1926) in the first diagnosis of the Pomatiopsidae used the following radular characteristics as having major importance; "radula with its few cusps of large size and the large denticles on the base of the central tooth." Baker (1928) stated in the family diagnosis "central tooth of the radula with but one large basal denticle; denticles of the lateral and marginal teeth very large and few in number, proportionally much larger than in the Amnicolidae." Berry (1943) states that the radula is "very different from the Amnicolidae. The central tooth has the basal wing terminating as a cusp and a single basal denticle down from the lateral ridge. The few large cusps on the central, lateral, and marginal teeth are distinct characters of Pomatiopsis, and not Amnicolidae."

The radulae of Pomatiopsis and Oncomelania are described in detail in the section on anatomy. A few comments must be made here, however, as they relate radular structure to family or subfamily taxon characters. Baker (1926, 1928) was mistaken in using a single pair of basal cusps as part of the criterion for defining the

family Pomatiopsidae. P. lapidaria has 2 or 3 pairs of basal denticles (Thiele, 1928; Abbott, 1948a). P. cincinnatiensis has two pairs of basal denticles (Berry, 1943), as do the radulae of P. californica and P. binneyi which I have observed. In studying the radula collection of P. cincinnatiensis at the University of Michigan Museum of Zoology (UMMZ), it was evident that the basal portion of the lateral angle did not terminate as a cusp although the outer basal cusp was definitely at a more basoexternal position contrasted with that of P. lapidaria. It was possible to discern basolateral to the outer basal cusp a well-defined termination of the lateral angle. The support for the basal cusp arose quite anteriorly on the edge of the lateral angle.

The radulae found in the Pomatiopsinae are clearly included in the range of types found in the Hydrobiidae throughout the world. They are similar in that the central is wider than long, it has basal cusps, the anterior edge is narrower than the posterior (basal) edge, the anterior cusps are more than one. The shape and denticulation of the laterals and marginals are compatible with those found in the family Hydrobiidae.

The pomatiopsid radula is distinctive in that the cusps of the laterals and marginals are generally fewer and larger contrasted with most hydrobiids. P. cincinnatiensis is extreme in having only 3-4 large cusps on the marginals. P. lapidaria has up to 9 cusps on

inner marginal while P. binneyi has up to 11. In the last species, the cusps of the marginals are small and needle-like as in many hydrobiid species. The central is distinctive in having only 1 or 2 cusps on either side of the central cusp on the anterior edge of the tooth. Other hydrobiids generally have 3 or more cusps on either side of the central cusp. The distinctive nature of the supports for the basal cusps has been mentioned.

When the radulae of other prosobranch families are compared with those of the Hydrobiidae, it is evident that the radula of Pomatiopsis is a hydrobiid type. While members of the Bithyniidae (e.g., Bithynia tentaculata) have a radula seemingly more similar to some hydrobiids than that of Pomatiopsis, the former possesses numerous major morphological differences which clearly separate the group from the Hydrobiidae. In the Truncatellidae the unusual triangular central tooth with the single anterior cusp is distinctive. In the Littorinidae and Pleuroceridae the central lacks basal cusps. In assiminiid radulae the central and outer marginals have shapes which are distinctly different from those found in the Hydrobiidae. The length of the central is greater than its width. The central is without the lateral angle characteristic of the hydrobiid radula and is often without basal cusps. The outer marginal is exceptionally wide compared with the relatively slender type found in the Hydrobiidae. Radular characteristics are clearly not sufficient to separate

Pomatiopsis from members of the family Hydrobiidae.

The Pomatiopsinae represents a subfamily including several genera outside the United States; e.g., Tomichia from South Africa, Blanfordia from Japan, as well as Oncomelania. In these genera the shell is elongated and turreted contrasting the globose type of Amnicola or the bulimoid shape of Littoridina. The tendency in the group is towards an amphibious to terrestrial habitat. Correlated with the amphibious habitat is a step-like mode of progression. A crease develops in the anterolateral foot upon full contraction of the foot. Eggs, laid singly, are covered with a mud capsule (not known for Tomichia). The radula has fewer and larger cusps on the marginal teeth compared with other hydrobiid snails. The anterior cusps on either side of the central cusp of the central tooth are 1 or 2 in number. The basal cusps of the central teeth have a distinctive type of support and are generally 2 or 3 in number. The eye is in a pronounced swelling at the base of the tentacle contrasting the species of the genus Hydrobia where the eye is in a slight swelling of the tentacular base.

Characters in common with other hydrobiids are the simple verge (hydrobiids have simple verges or ones with various appendages), paucispiral corneous operculum, a broad simple foot which is truncate in front and gently rounded behind. The foot has an anterior transverse mucous slit. The rostral shape and tip, and basic internal anatomical features are hydrobiid.

MATERIALS AND METHODS

The body of this paper is divided into four major sections: anatomical, hybridization studies, electrophoretic, and laboratory ecology. Methods pertaining to each of these sections will be discussed under those 4 headings. The snails used throughout these studies were all fully mature adults as indicated by shell size in Pomatiopsis and varix formation in Oncomelania. The only exceptions were the newly hatched young used in the growth experiments.

Field collected Pomatiopsis lapidaria were utilized for anatomical studies and electrophoretic experiments. These were obtained from the Barton and Hog Back stations described by Dundee (1957) as well as the Parker Mill station discussed by van der Schalie and Dundee (1959). These stations are within 5 miles of Ann Arbor, Michigan.

Oncomelania subspecies used were F_1 or F_2 laboratory reared snails of field collected parental stock. O. hupensis formosana came from Pu Yen village, a small farming community a few miles south of the city of Changhua. O. hupensis nosophora were sent from the Kofu Valley in the Yamanashi Prefecture of Japan. O. hupensis quadrasi were sent from Palo, Leyte, in the Philippines.

COMPARATIVE ANATOMY

A. Introduction

One encounters several major problems in attempting to make detailed comparisons from published anatomical material. The material is often stylized and portrays organ systems in a general manner omitting exact contours, dimensions, variations, and positional relationships with other organs. Homologous organs are presented in different views by the various authors making comparisons difficult or impossible.

In this study the gross anatomy of the muscular, nervous, reproductive systems, parts of the alimentary system, and the external morphology are discussed. The systems and organs of both species are presented in the same manner of orientation thereby facilitating comparisons. The systems and organs were studied in order to determine in a comparative manner (1) the presence or absence of a structure, (2) qualitative differences in the structure of homologous organs, and (3) quantitative differences or similarities in organs or structures.

This is not a complete anatomical description, as details of the excretory and circulatory systems are not covered. The systems investigated were chosen because of their potential in providing characters which could be readily used in a systematic discussion.

Pomatiopsis lapidaria will be discussed first, followed by a similar treatment of Oncomelania hupensis formosana. Comparisons between the two species will be discussed with each anatomical section presented for O. hupensis formosana.

B. Material and Methods

Dissections were carried out under magnifications of 40X and 60X using a Nippon Kogaku dissecting scope. Measurements of all structures were made using a standard ocular micrometer. Proportions and structural dimensions in all drawings were checked against the specimen using this micrometer. A 9 cm. Petri dish filled with parafin and blackened with norite served as the container and substrate for all dissections.

Tools used for dissections were "minuten naddeln" embedded in solid glass rods, iridectomy scissors of the finest grade, jeweler's forceps with extra fine points, and pliers for cracking the shell.

Well over 200 snails were used for the anatomical studies of each species. The snails were studied while living or just freshly preserved. Living animals were most useful in studying the organs and ducts of the reproductive systems. Aqueous neutral red was very useful in accentuating the tubes of the reproductive systems as well as nerves and ganglia. Aqueous methyline blue aided in

staining the visceral ganglia and associated nerves in the living snail.

In studying freshly killed snails the animals were removed from the shells, pinned out in the desired position under water, the water was poured off, and Bouin's fixative was added full strength. Structures in the head were more readily studied in the freshly killed snail as mucoid secretions were a hindrance in the living animals. Studies on nerves were facilitated by dissecting under Bouin's solution as minute nerves stood out prominantly in that fluid under direct illumination. Muscles were studied in the contracted state where the smaller muscles were more prominent as well as providing a very uniform condition.

Radula. Radulae were dissected from the buccal mass and placed in a 10% solution of KOH for varying amounts of time (about 24 hours). Upon dissolution of attendant membranes the cleaned radula was placed on a slide with a drop of 4% acetic acid. The acid loosened the lingual membrane (radular shield) within an hour so that the radula could be readily flattened out as well as facilitating removal of separate teeth or bunches of teeth from the membrane. With the radula flattened out, measurements were made of the length and width of the radula and the number of rows of teeth were counted. Measurements and counting were carried out under 150X using a Nippon Kogaku compound microscope. At this point, the radular ribbon

was mounted whole or teeth were stripped from the membrane to facilitate a study of each tooth. The acid was allowed to dry on the slide and then a drop of CMC-10, a non-resinous mounting medium was added and a coverslip applied. In 24 hours the CMC-10 dried and the edge of the coverslip was ringed with clear fingernail polish assuring the permanency of the slide. Detailed studies of the teeth were readily made without need for stain as the smallest cusp readily stood out. Drawings of the radular teeth were made using oil immersion (1000X) and camera lucida.

Jaws. The buccal mass was removed and the area of the outer lips cut free with iridectomy scissors. This separated anterior end of the buccal mass was placed on a slide and opened from the dorsal surface, thus exposing the oral tube and the anterior part of the buccal cavity. A drop of CMC-10 was placed on the tissue, the tube was opened, and a coverslip was applied. The jaws, fully exposed, were studied under the compound microscope. They were drawn using a camera lucida.

Shell. Shells were boiled in chlorox to remove the periostracum and all occluding matter such as algae, dirt, etc. Cleaned in this manner, the sculpture, shell surface, apical whorls, and sutures were readily studied.

Anatomical orientation. There is no problem in discussing features of the head as the foot is ventral and the rostrum points anteriorly. However, the remainder of the organism is coiled within the shell and orientation becomes a problem when discussing anatomical features. As Fretter and Graham (1962) state for Littorina, "as the animal lies in its shell the outer part of each whorl corresponds to the dorsal surface of the body, and the inner to the ventral." The inside of the coil or ventral surface is that which is appressed to the columella.

All anatomy presented here was described from the uncoiled snail, uncoiled so that the head was to the right; the body surface presented here is the columellar or ventral. Treating the body as an uncoiled tube, and for convenience, "posterior" means towards the apex, "anterior" towards the head. "Ventral" means the side of the body tube presented, i.e., the columellar side and dorsal is through the tube at any level stated towards the opposite side. Left lateral is towards the bottom of the drawings wherever the term is used, and right lateral is towards the top of any given figure.

C. Pomatiopsis lapidaria

1. Shell. Say (1817) described the shell in the type descriptions as "turreted, subumbilicate, with 6 volutions, which are obsoletely wrinkled across. Suture impressed. Aperture longitudinally ovate-

orbicular, rather more than 1/3 of length of shell. Length about 1/5 of an inch."

F. C. Baker (1928) possibly made the foremost elaboration of Say's original description, but more detail and discussion of the shell is necessary. The shell (Pate 2) is indeed elongate and turreted. Adult shells have 6.5-7.0 whorls. Shells of 7.5 whorls are rare in non-fossil material. The nuclear whorls are 2.0-2.75 in number, glassy, and in cleaned material may appear amber thereby set off from the brownish or yellow-brown horn color of the remainder of the shell. In uncleaned material the nuclear whorls may appear glistening or dull white. The first nuclear whorl, as Baker (1928) pointed out, is usually not emergent and is partially "embraced by the second whorl." This often gives the apex a flattened appearance.

The sutures of the whorls are deeply impressed and the whorls correspondingly very convex. The aperture is "elongate, ovate, somewhat narrowed and angled above" (Baker, 1928). The inner lip is connected with the outer lip by a parietal callus. In some specimens the callus is so thickened that it appears as if the inner lip continues into the outer lip. Occasionally a specimen is found where the inner lip is not adenate to the parietal wall. The inner lip is slightly reflected over the umbilicus. The parietal callus varies in length, the greater the length, the more occluded the um-

bilicus. The outer lip is sharp, strong, and does not form a varix. Observing the edge of the outer lip with the aperture rotated 90° to the left of apertural view, one observes that it is straight, not sinuate (Plate 3, Fig. 5). The apical part of the outer lip may have a slight sinuation in some cases but this is not as nearly pronounced as the sinuation found in Oncomelania hupensis formosana. (Plate 3, Fig. 4)

The umbilicus is very pronounced and deep (Plate 3, Figs. 1-3). As shown in these same figures, the base of the shell is rounded. Without magnification the whorls of the cleaned shells appear smooth and glistening. Under 6 to 16 magnifications it is evident that the surface of the whorls are wrinkled by growth lines which are irregular in diameter, vary in prominence, and are closely packed. The overall effect is to give the shell a roughened microsculpture. The coarse growth lines start immediately after the nuclear whorls.

A series of measurements are discussed below which are felt to be of use in specific comparisons. Others could be made, but those presented are adequate for the comparisons intended. A series of 62 specimens collected from the Barton, Parkers Mill, and Hog Back stations were studied conchologically without reference to sexual dimorphism. Length, width, aperture length, parietal callus length, width of the first nuclear whorl, and width of the tip of the nuclear

Plate 2

SHELLS OF POMATIOPSIS LAPIDARIA AND ONCOMELANIA HUPENSIS FORMOSANA

The top row of shells is P. lapidaria. The lower row is O. hupensis formosana.

Plate 2

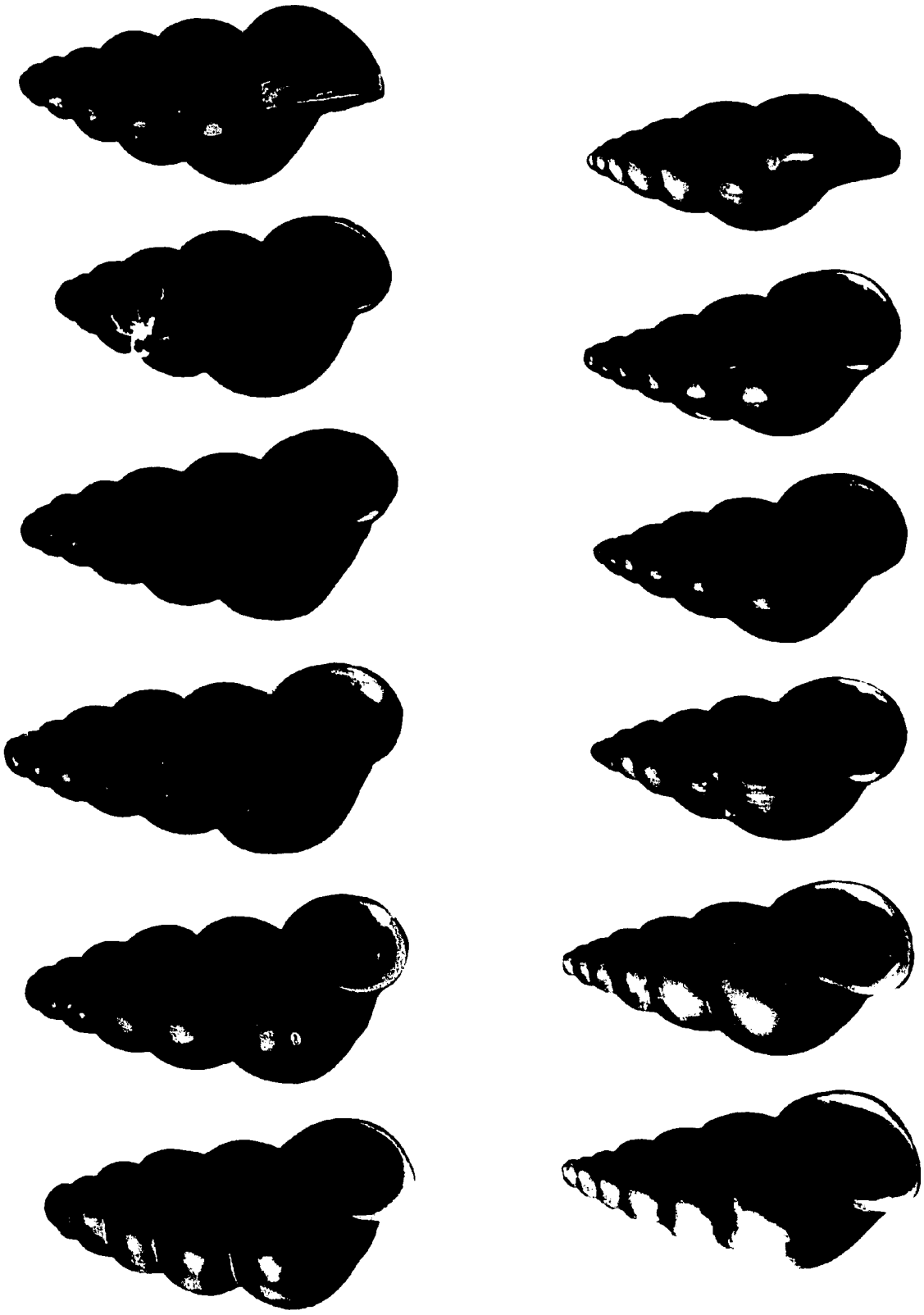


Plate 3

FEATURES OF THE SHELL OF *POMATIOPSIS LAPIDARIA* AND *ONCOMELANIA HUPENSIS FORMOSANA*

Figs. 1, 2, 3. Apertural view of the shell of *P. lapidaria* showing the wide umbilicus and the shortened parietal callus.

Fig. 4. Shell of *O. hupensis formosana* showing the sinuate outer lip and the varix.

Fig. 5. Shell of *P. lapidaria* showing the straight outer lip with no varix.

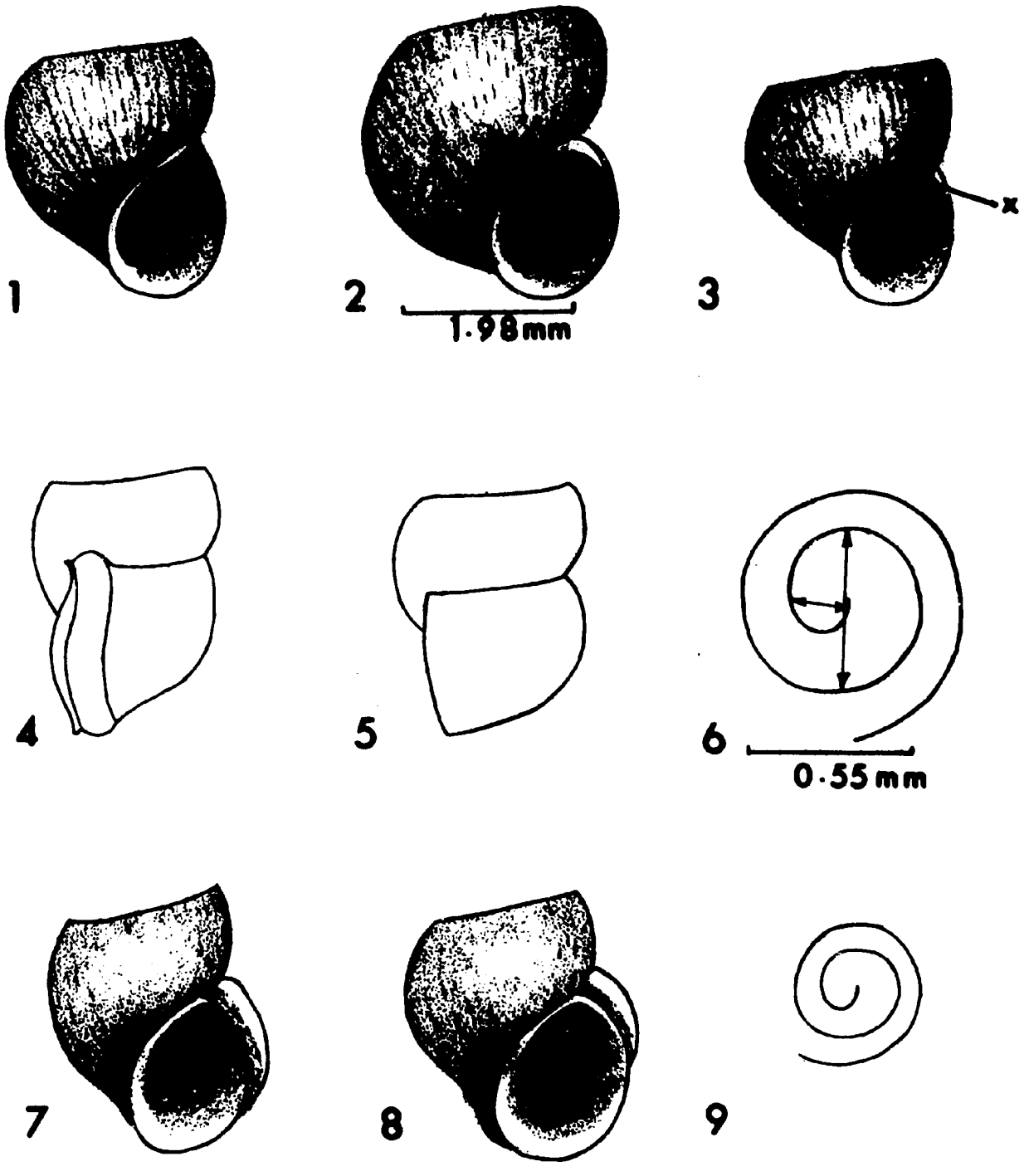
Fig. 6. Apical whorls of *P. lapidaria*. The short arrow points out the width of the tip of the apical whorl; the long arrow points out the width of the first whorl.

Figs. 7, 8. Apertural view of *O. hupensis formosana* showing the relatively narrow umbilicus and elongate parietal callus.

Fig. 9. Apical whorls of *O. hupensis formosana*.

x. parietal callus

Plate 3



whorl (Plate 3, Fig. 6) were measured. These were recorded with the corresponding whorl count. The results are shown in Table 4. Shells of 6 whorls had an average length of 5.5 mm. and an average width of 2.9 mm; those 6.5 whorls were 6.2 mm and 3.1 mm, respectively; shells of 7.0 whorls were 6.7 and 3.2 mm, respectively. No shells with 7.5 whorls were found among several hundred additional snails observed. The average length of the aperture for snails of 6.0 to 7.0 whorls was 2.1 mm. These dimensions were compared with those gathered from several lots of this species housed at the UMMZ (Table 5). These lots represented populations scattered over the extensive range of this species (distribution map in Abbott, 1948a). No significant difference was found for the parameters of shell length, width, or aperture length among these populations.

The first nuclear whorl (Plate 3, Fig. 6) varied but little (Table 4) with a width of 0.53 mm. The tip of the first whorl averaged 0.19 mm and this likewise was extremely constant. These features did not deviate significantly among the populations studied. The length of the parietal callus, however, did vary quite a bit in length and significantly so between populations (Table 5). The Ann Arbor snails of the current studies had an average callus length of 0.6 mm. This was the shortest of all the populations studied. Correlated with this was an unusually pronounced umbilicus. As shown

Table 4

Conchological Measurements of Pomatiopsis lapidaria from Ann Arbor, Michigan

Structures Measured	Number of Snails	Length in mm			Number of Snails	Width in mm		
		$\bar{X}$	S	Se		$\bar{X}$	S	Se
Shell 6.0 whorls	24	5.5	0.32	0.07	24	2.9	0.20	0.04
Shell 6.5 whorls	30	6.2	0.27	0.01	30	3.1	0.11	0.02
Shell 7.0 whorls	8	6.7	0.36	0.04	8	3.2	0.18	0.06
Aperture	62	2.1	0.10	0.01				
Apical Whorl					26	0.53	0.04	0.008
Tip of Apical Whorl					26	0.19	0.03	0.006

S = Standard Deviation

Se = Standard Error of the Mean

$\bar{X}$ = The Mean

Table 5

The Average Callus Length for Lots of *Pomatiopsis lapidaria* from Various Wide-Spread Localities

Locality	No. Specimens	Average callus length
Alabama, Florence; Lauderdale Co.		
Lot. UMMZ 69912 topotypes of *P. hinkleyi*	16	0.72
Florence; Bolder Falls; Lauderdale Co.		
Lot. UMMZ 91487 paratypes of *P. hinkleyi*	4	0.96
Indiana, New Harmony; Posey Co.		
Lot. UMMZ 69915 Fossil Material	11	0.72
Iowa, Marion; Linn Co.		
Lot. UMMZ 132464	11	0.84
Michigan, Ann Arbor; Washtenaw Co.		
Lot. UMMZ 91559 Barton Station	9	0.90
Lot. UMMZ 183219 Barton Station, 1952	12	0.66
Lot. UMMZ 183217 Hog Back Station, 1952	16	0.84
North Carolina; Broad River, Point Rock		
Lot. UMMZ 91495	6	0.72
Ohio; Miami Co.		
Lot. UMMZ 59325 Drift off Big Miami River	8	0.84
Wisconsin; Baraboo; Sauk Co.		
Lot. UMMZ 143721	9	0.84

in Table 5, the average callus length population ranged from 0.6 mm to 0.96 mm. These differences are possibly related to growth patterns which deviate under different environmental conditions. Variations in length of parietal callus is shown in Plate 3, Figs. 1-3.

Hubricht (1960) studied the shells of Pomatiopsis lapidaria from a number of localities and stated that the species appeared modified by different ecological conditions; "slender, thick shells occur in dry habitats, obese thinner shells in wet ones. This is especially true in the South." In this paper Hubricht considers P. praelonga Brooks and MacMillan and P. hinkleyi Pilsbry synonyms of P. lapidaria. I agree with Hubricht in synonymizing these forms. Certainly P. hinkleyi (Table 5) showed no shell characteristics significantly different from P. lapidaria from many localities except that in length of parietal callus, a character which is shown to be variable.

A lot of fossils from the same locality as Pomatiopsis scalaris (Baker, 1927) was studied (Table 5). P. scalaris, a Pleistocene fossil, was described as "strikingly" different compared with P. lapidaria as it was longer, with 1 more whorl, and with very deep sutures. The lot of fossils studied from the UMMZ formed a series which graded from P. lapidaria studied in Ann Arbor to P. scalaris, i.e., the fossil material had shells of 7.0, 7.5 whorls (P. scalaris was described as having 8 whorls). Many of the recent

specimens of P. lapidaria had the very deeply impressed sutures and convex whorls attributed to P. scalaris. Occasional specimens of recent P. lapidaria from various parts of the country can be found with 7.5 whorls and the characteristics of P. scalaris although they are comparatively rare. The umbilicus of P. scalaris and the fossil series studied from the UMMZ appeared more rounded, wider, and deeper than found in recent P. lapidaria from many localities. These features are correlated with a pronounced tendency for a short parietal callus and an inner lip which is barely reflected. These same characters are quite pronounced in current populations of P. lapidaria found in the Ann Arbor area. The width of the apical whorl in the fossil material was the same as that found in recent P. lapidaria. As a result of these studies, P. scalaris is considered an early extreme of P. lapidaria and synonymous with it.

2. External morphology and topography. The folds and grooves of the head have been mentioned. The head, dorsal and lateral, is black to grey-black due to heavy pigmentation (Plate 1, Figs. 1, 2, and 5). The edges of the foot below the supra pedal fold are dusted with pigment although more lightly than the dorsal surface. Pigmentation continues along the neck into the mantle cavity but fades out towards the base of the "neck." On the anterodorsal edge of the foot pigmented patterns appear to outline channels in the foot (Plate 4) which probably coincide to the mucous ducts figured by Abbott (1948a).

The sole of the foot (Plate 1, Figs. 3, 4, 6-9) appeared to have 2 color patterns when studied under direct illumination. The periphery of the sole was a light slate grey to blue-grey while the central area appeared opaque white to yellow-white. The central area, on the average, was 0.5 mm from the front edge of the foot, 0.96 mm from the posterior end, and about 0.40 mm in from each side. This area corresponds to a position over the pedal haemocoel.

White granular units of about 25 micra diameter were especially crowded in the posterior part of the foot, becoming sparse along the sides. Granules were sparse in the central area. In addition to the relatively large granules, the sole was covered with small whitish bodies appearing as tiny rods all perpendicular to the sole (observed 40 X). These tiny rods were closely packed at the anterior edge of the foot, becoming less dense posteriorly.

Viewing the living animal through the shell (apertural view with snail retracted) the pattern of pigmentation on the outer or dorsal side of the body tube is readily observed. The intestine filled with fecal pellets is clearly discerned crossing the body whorl underlined by a thin band of pigment 0.24-0.40 mm wide. This band continues along the dorsal surface becoming wider above the body whorl (0.48-0.72 mm). In the apical whorls this band of pigment becomes more slender again (0.25-0.40 mm). Dundee (1957, Plate 6) shows this pattern in the apical whorls. The band is generally positioned

on the periphery of the coil or displaced towards the aperture on each whorl. The band is not neatly delineated with parallel side but irregularly scalloped, flamulate at the edges, especially the edge towards the apex. This pattern is observable in both males and females. From the ventral aspect some of the pigment is observed curling over from the dorsal surface (Plates 5 and 6). In Plate 4 the ctenidium is demonstrated. The exterior epithelium covering this area is pigmented and the pigmentation tends to outline the position of each gill filament.

Abbott (1948a) states that in Pomatiopsis lapidaria "the most distinguishing color markings are the bright splotching of yellow or yellowish-white granular dots over each eye forming false "eyebrows." These glandular units (Plate 1, Figs. 1, 2, and 5; Plate 4, Plate 11; Fig. 1) partially surround the eye and occlude the medial, posterior edge of the eye. Collectively they are a mass about 0.36 mm long with the greatest width of 0.17 mm. Coloration varies from white to yellow-white.

Tentacles and Eyes. The eyes are in large, distinct swellings at the outer base of each tentacle (Plate 1, Fig. 1). Viewed ventrally these swellings appeared continuous with the tentacles but from the dorsal surface they appear as units fused with the tentacles and set off from them by a slight crease. In any event, the ocular units are not the simple swellings in the outer tentacular

bases seen in Hydrobia and others of the Hydrobiinae and Rissoidae. The characteristic shape of the tentacles is shown in Plate 1, Fig. 1. They are highly contractile and pliable but can most often be seen with a swelling at their base anterior to the ocular units.

General Topography. In the uncoiled snail with the columellar side exposed, one can observe, in addition to the head, 3 general areas: (1) the region of the mantle cavity which extends from the mantle edge (M) where it encircles the "neck" (Plate 4) back to a point just posterior to the tip of the visceral ganglion (Vg); (2) the mid-body region extending from the end of the mantle cavity to the posterior portion of the stomach and in which are observed the stomach (St; Pst, Ast), kidney (K), part of the intestine (I), a segment of the esophagus (Ss), and a portion of the oviduct or vas deferens (Ov or VD_1, respectively); (3) the digestive gland (D) which continues posteriorly from the stomach and contains the gonad (Go) in its left ventral surface beneath the epithelium just posterior to the stomach.

In the female, the pronounced pallial oviduct (Po) traverses the anterior portion of the mid-body and the length of the mantle cavity. In the male, the prostate (Pr) overlays the 2 areas but does not extend anteriorly the whole length of the mantle. The bursa copulatrix (B) is prominent in the mid-body of the female. The columellar muscle (Cl) emerges from the "neck" area of the

Plate 4

HEAD, FOOT, AND MANTLE REGION OF POMATIOPSIS LAPIDARIA

A	anus
B	bursa copulatrix
Cl	columellar muscle
Ct	ctenidium
Ctn	cut edge of the mantle
F	fecal pellet
G	glandular units
I	intestine
K	cut edge of the kidney
K_1	ventral surface of the kidney
M	edge of the mantle
O	operculum
Om	omniphoric groove
Oo	opening of the pallial oviduct
Op	operculigerous lobe
Ov	oviduct
Os	osphradial ganglion
P	suprapedal fold
Pc	pedal crease
Pe	pericardium
Po	pallial oviduct
R	rostrum
Sd	spermathecal duct
Sd_1	sperm duct
Si	subintestinal sinus
Ss	esophagus
St	stomach
V	blood vessel

Plate 4

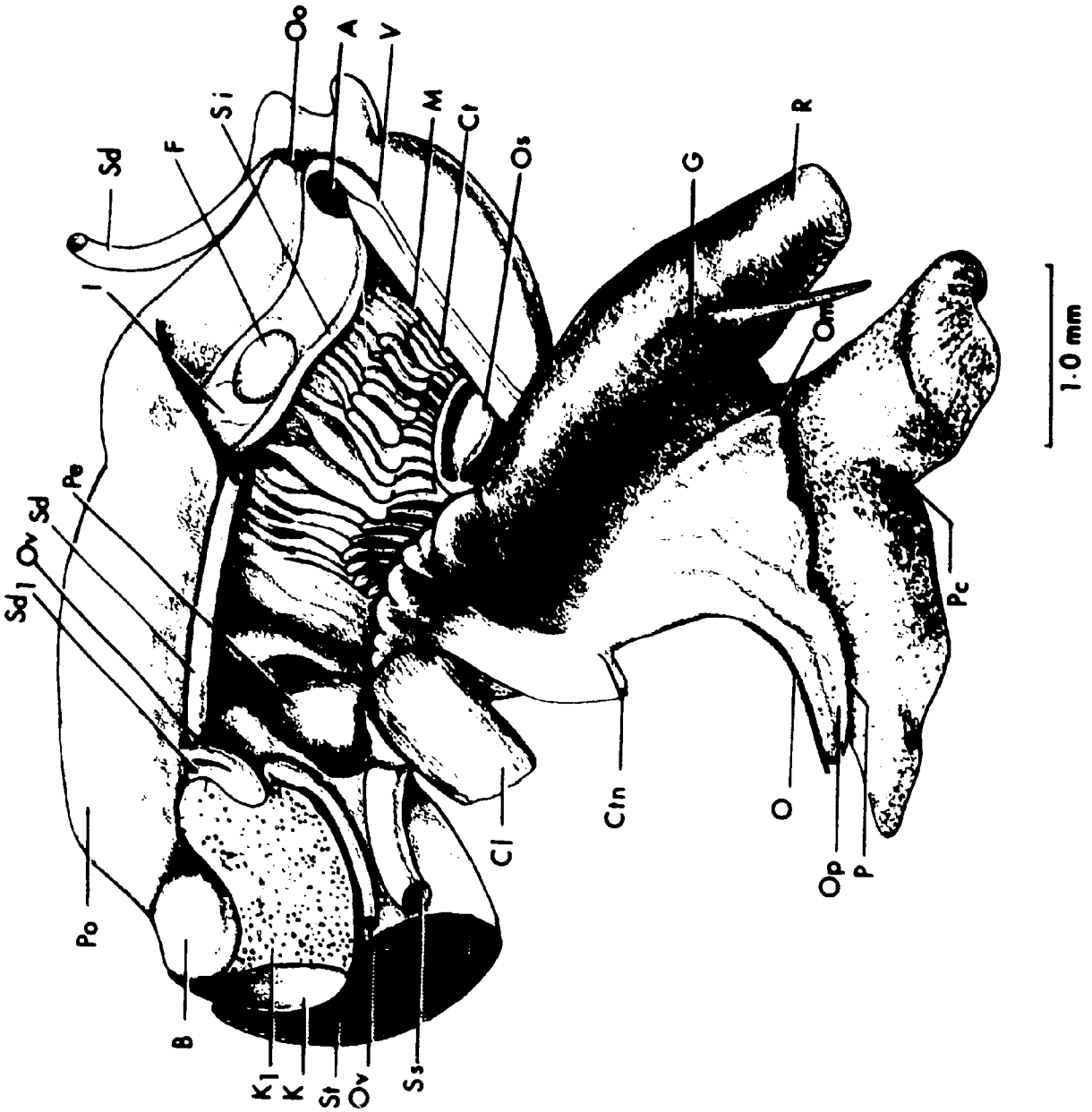

Oo
A
V
M
Ci
Os
Si
F
Sd
I
R
G
Om
Pe
Sd
Ov
Sd
Pc
Cln
O
Op
P
Cl
Po
B
K1
K
St
Ov
Ss
1.0 mm

Plate 5

UNCOILED FEMALE *POMATIOPSIS LAPIDARIA* SHOWING PARTS OF THE FEMALE REPRODUCTIVE SYSTEM

Fig. 1. Uncoiled female *P. lapidaria*. The oviduct (Ov) is broken due to the stress of uncoiling the snail.

Fig. 2. The portion of the reproductive system uncovered by peeling away the connective tissue and kidney tissue between the bursa copulatrix (B) and the edge of the mantle cavity (x).

Ast	anterior chamber of the stomach
B	bursa copulatrix
Cl	Columellar muscle
D	digestive gland
Go	gonad
Gp	gonopericardial duct
K	ventral surface of the kidney
M	edge of the mantle
Mc	ventral wall of the mantle cavity
Ov	oviduct
Ov_2	portion of the oviduct passing ventral to the spermathecal duct to enter the pallial oviduct
Pe	pericardium
Pi	pigment band showing the flamulate pattern at the edge
Po	pallial oviduct
Pst	posterior chamber of the stomach
Sd	spermathecal duct
Sd_1	sperm duct
Ss	esophagus
Vg	visceral ganglion
x	the posterior end of the mantle cavity

Plate 5

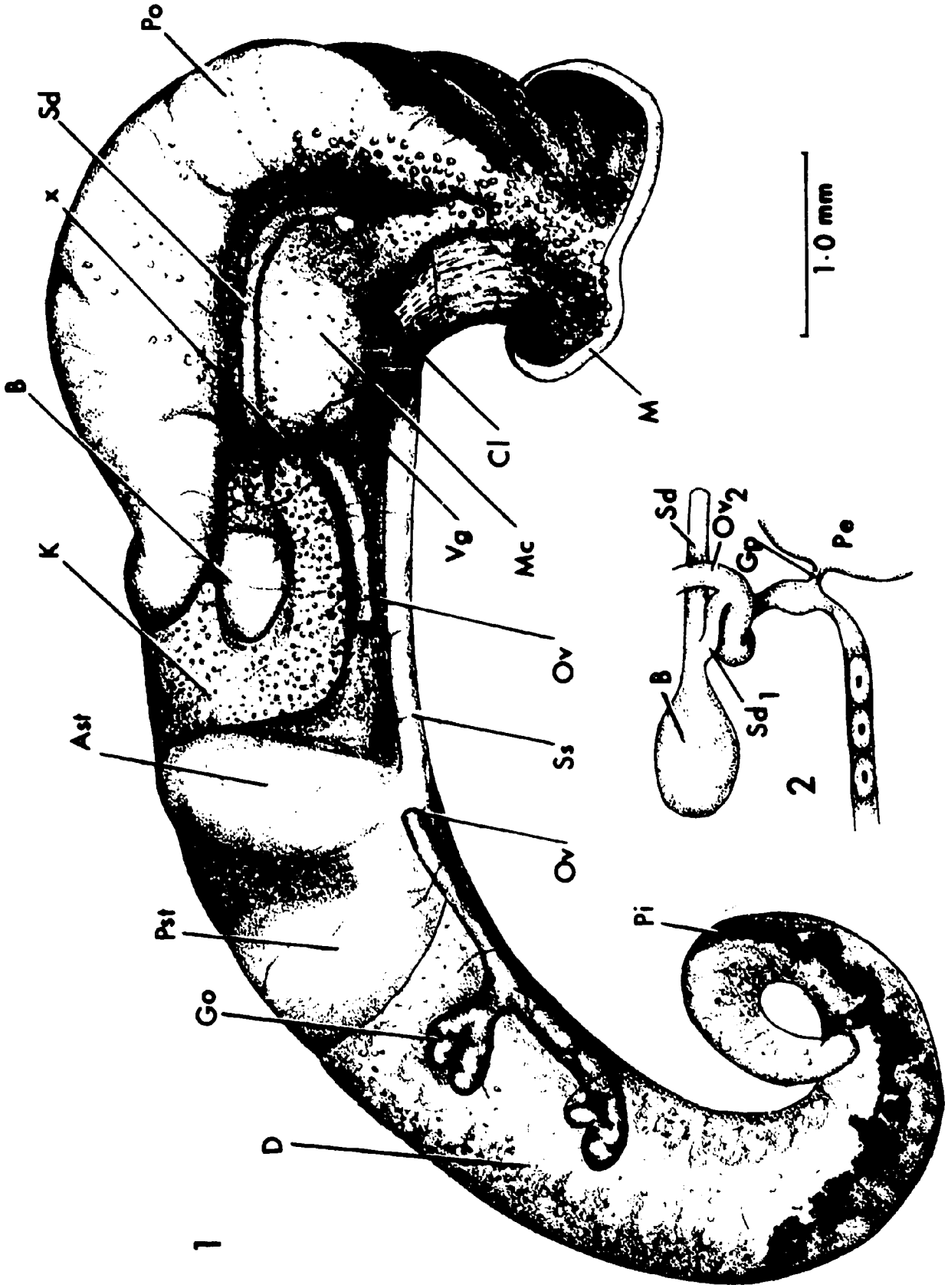

Po
Sd
x
B
K
Ast
Pst
Go
D
1
Vg
Mc
Cl
M
Ov
Ss
Ov
Pi
1·0 mm
Sd
Ov2
Gg
Po
B
Sd1
2

Plate 6

UNCOILED MALE *POMATIOPSIS LAPIDARIA* SHOWING PARTS OF THE MALE REPRODUCTIVE SYSTEM

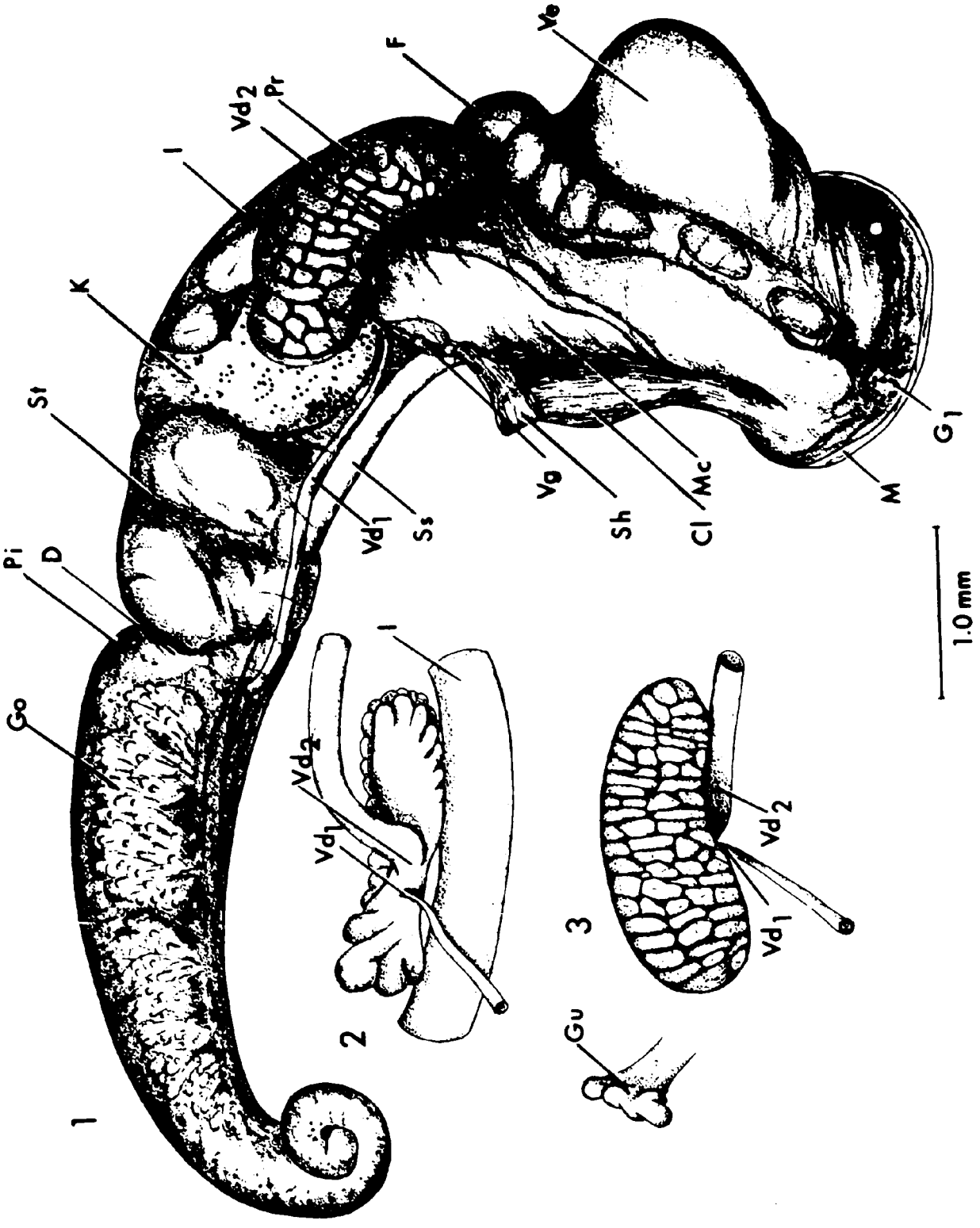
Fig. 1. The uncoiled snail.

Fig. 2. The prostate pressed against the intestine and turned over to expose the point of entrance of the posterior portion of the vas deferens in relationship to the point of exit of the anterior portion of the vas deferens.

Fig. 3. The prostate as viewed in Fig. 1 where the connective tissue was cleared away to show the posterior vas deferens passing under the edge of the prostate.

F	fecal pellet
Cl	columellar muscle
D	digestive gland
G_1	large, white "granular" units
Go	gonad
Gu	a single glandular unit from the prostate
I	intestine
K	kidney
M	edge of the mantle
Mc	ventral wall of the mantle cavity
Pi	pigment
Pr	prostate
Sh	shell
Ss	esophagus
St	stomach
Vd_1	posterior portion of the vas deferens
Vd_2	anterior portion of the vas deferens
Ve	verge covered by mantle wall
Vg	visceral ganglion

Plate 6


Ve
F
Vd2
Pr
I
K
St
Pi
D
Go
Vd1
Ss
Va
Sh
Cl
Mc
M
G1
1.0 mm
1
I
Vd2
Vd1
2
Pa2
Pa1
3
Gu

head (Plate 4) on the ventral surface and is pressed against the ventral exterior mantle cavity wall which is exposed in Plates 5 and 6. Connective tissue usually binds the columellar muscle in place but this has been torn and the muscle pulled away from the mantle cavity wall to expose that area and the associated structures, i.e., the visceral ganglion (Vg), anterior section of the vas deferens in the male (Vd_2) and the spermathecal duct in the female (Sd).

The various organs which were pointed out in the plates discussed above are readily observed although no connective tissue has been removed because of their position just beneath the connective tissues, their size and bulk, or color and texture. The gonads in the living animals stand out bright yellow, as does the bursa copulatrix (Plate 5). The kidney (K) is visible because the ventral tissues of this organ are rather transparent. The organ is sac-like and filled with fluid. Numerous white granules are in constant agitation and can be observed through the membranes. The total effect is that the kidney appears quite white compared with the surrounding tissues of other organs.

The mantle cavity and pallial oviduct are flecked with pigment. Imbedded within the connective tissue all over the ventral surface are what appear to be white granules (some appear under the compound microscope to be glandular as shown in Plate 11, Fig. 6). These are particularly concentrated in several areas--the triangular

area from the mantle edge to the point where the anterior portion of the pallial oviduct disappears into the mantle cavity (Plate 5), the connective tissue sheet between the bursa copulatrix, and the posterior edge of the mantle cavity (Plate 5). The space over the style sac between the left edge of the anteroventral arm of the kidney and the esophagus is frequently crowded with granules as is the V-shaped area between the anterior (Ast) and posterior (Pst) chambers of the stomach. Granules are scattered over the ventral tissue of the digestive gland.

The reduced size of the male prostate compared with the female pallial oviduct permits a clearer external view of the intestine crossing the mantle cavity from left to right often filled with fecal pellets in a characteristic manner (Plate 6, Fig. 1). Likewise, characteristic for the male, from an external view, is the dorsal swelling of the mantle cavity corresponding to the large verge coiled within.

3. The Mantle Cavity. The mantle cavity was opened by cutting posteriorly along the right lateral margin of the mantle wall where it fuses with the "neck" (Plate 4) or posteriorly just to the right of the mid-dorsal mantle wall (Plate 11, Fig. 1). In Plate 4 the columellar muscle is shown pulled away from the mantle cavity wall and downward; the mantle edge (M) is pulled forward to stretch the left wall, enabling a clear view of the ctenidium (Ct) and

osphradium (Os).

Organs and structures associated with the mantle cavity are the ctenidium, osphradium, anterior wall of the pericardium (Pe), opening of the kidney (Plate 8, Fig. 1, Or), openings of the Anus (A), pallial oviduct (Oo), and spermathecal duct (Plate 9, Figs. 4 and 7, Osd). In males, the verge is housed within the cavity. The reproductive structures and their association with the mantle cavity will be discussed in sections dealing with the reproductive systems.

Ctenidium. The ctenidium is composed of triangular gill filaments characteristically of a hydrobiid nature (Plate 11, Fig. 1; Plate 13, Fig. 3). Dundee (1957) stated that there were 15-20 filaments while Abbott (1948a) stated that there were 27-29 lamellae. In a study of over 50 mature specimens without regard to sex the number found varied between 20-28 with an average of 24. Males characteristically had fewer lamellae than females, an average of 22 ± 2 for the former and 25 ± 3 for the latter. This difference is correlated with sexual dimorphism, the males being smaller than the females. A blood channel (V, Plate 4) is noted in the mantle collar connected with a blood sinus (Si) running along the anterior intestine. Near the anus the tissues of the sinus make a collar around the intestine and send a tubular passage to the blood channel in the mantle edge. The gill lamellae connect with the sinus (subintestinal sinus). The base of each lamella connects with a vessel which runs to the

auricle (Plate 11, Fig. 1).

Osphradium. The osphradium is an elliptical grove or pit located at the base of the gills near the anterior end of the mantle cavity as shown in Plate 4; 11, Fig. 1. The edges of the groove are swollen and lip-like, packed with small white granules (possibly glands). Swelling up within the groove is the osphradial ganglion covered with an epithelium which itself appears fluid filled and swollen (Os, Plate 4; 11, Fig. 1). The osphradial nerve enters the ganglion just anterior to the mid-ventral line as shown in Plate 11, On. The osphradium is 0.59 ± 0.12 mm long and 0.33 ± 0.02 mm wide.

Visceral ganglion. The visceral ganglion is observed, imbedded within the tissues of the floor of the mantle cavity at the base of the "neck." (Plate 11, Fig. 1) As mentioned previously, the ganglion is just as readily observed from the external surface of the ventral mantle wall imbedded in the connective tissues (Plates 5 and 6). The subvisceral and supervisceral commissures (Sbv and Suv) are observed running anteriorly on either side of the "neck" to disappear into the epithelium covering the anterolateral portions of the "neck."

Mucoid glands. There is no distinct hypobranchial gland, per se, which serves for producing a copius supply of mucous. Such a gland is figured by Fretter and Graham (1962) for Littorina littorea.

There are, however, posterior to the gills at the posterior mantle cavity, under the area hidden by the spermathecal duct (Plate 4), numerous, individual, large, spheroidal, glandular units within which one can observe, under the compound microscope, numerous tiny granules all in high agitation. Mucous is liberated upon disrupting these units. In many cases these glandular units are so thick that they appear coalesced into a large glandular sheet covering the epithelium of the intestine and right wall of the mantle within the posterior recess of the cavity.

Posterior Mantle Cavity. The mantle cavity narrows posteriorly and its terminal epithelium is appressed against two organs, the pericardium and the kidney. In Plate 11, Fig. 1, the pericardium appears at the posterior end of the "neck." The opening of the kidney (not shown) is, in this figure, above the pericardium. In Plate 8, Fig. 1, one can see that these organs are appressed against the dorsal surface of the body tube and that the pericardium lies on the left dorsolateral curvature while the anterior kidney wall arises from the right dorsolateral curvature. The wall of the kidney abuts the pericardium. The opening of the kidney (Or) is a slit-like aperture bounded by a pair of "whitish tumid lips" (Dundee, 1957). The lips are provided with a sphinctor muscle.

4. Female Reproductive System. Dundee (1957) provides a useful table of terms used by various authors for the different organs of the female reproductive system as found in prosobranch snails. Further comparative material is found in Fretter and Graham (1962) where the schematic diagrams of reproductive systems from various prosobranch genera are presented. In the overall scheme, eggs pass from the gonad and travel along the oviduct past the entrance of the seminal receptical and sperm duct to enter the posterior end of the pallial oviduct. In theory they travel down the pallial oviduct to emerge over the omniphoric groove. Actually, no one has recorded the passage of an egg through the pallial oviduct. Sperm enter the spermathecal duct which opens into the mantle cavity near the anterior end of the pallial oviduct. They travel to the bursa copulatrix or pass into the sperm duct at the entrance of the bursa and move into the oviduct and then into the seminal receptacle. The spermathecal duct and the pallial oviduct are not fused but separate structures.

Gonad. (Plate 5, 10) The female gonad is a plastic tubular structure about 1.2 to 1.5 mm long and 0.59 to 0.57 mm. wide. It is characterized by few branches, the style of branching being plastic and variable (Plate 10). The outer epithelium was removed from one of the gonads (Plate 10) to demonstrate how the gonad can be gorged with eggs. The epithelium of the gonad is often extremely stretched

by gonadal products. The anterior edge of the ovary is generally not further than 0.2 mm to 0.3 mm from the posterior edge of the stomach. The oviduct runs anteriorly from the gonad as shown (Plate 5) and crosses the edge of the stomach at a point beneath which the stomach opens into the digestive gland. Passing over the posterior portion of the esophagus (Ss) the oviduct runs below the left ventrolateral edge of the kidney and seems to disappear at the posterior end of the mantle cavity. Up to this point, all along the oviduct, eggs can be frequently observed characteristically squeezed and flattened into elongate spheres (Plate 5, Fig. 2; Plate 7, Fig. 2). Along this length (1.4 mm - 1.8 mm.) the oviduct is about 0.06 mm. to 0.10 mm wide. The mid-region of the body, the anterior portion of which seemingly engulfs the oviduct, is complex in its interrelationships of organs. The juxtaposition of kidney, pericardium, nerves, reproductive tubes, and connective tissue layers is of such a complex nature that some space is devoted to describe this region.

Mid-Region of the Body. (Plates 5, 7, 8) The posterior end of the mantle cavity is readily defined by a marked crease where the mantle cavity wall folds dorsally along with the distinctive kidney tissue of the ventral anterior arm of that organ (Plate 5). At the edge of the pallial oviduct between the bursa copulatrix (B) and the mantle cavity (Mc) one observes a thick layer of connective tissue which occludes the posterior portion of the spermathecal duct (Sd).

This tissue is generally full of large white granules; it runs as a sheet to the left ventral curvature of the body tube and folds under the area traversed by the esophagus (Ss). It is into this connective tissue that the oviduct turns dorsally just at the edge of the mantle cavity.

The ventral surface of the kidney on the right side stretches between the edge of the anterior portion of the stomach and the posterior end of the pallial oviduct. It surrounds the posterior end of the bursa copulatrix (B) and sends an arm anteriorly between the left edge of the bursa and the oviduct. This ventral anterior arm, like the oviduct, turns dorsally at the posterior edge of the mantle.

In Plate 7, Fig. 1, the connective tissue sheet between the bursa and the mantle was peeled away. Staining the living organism with neutral red aided in revealing more clearly the underlying structures. The spermathecal duct (Sd) runs dorsal to the point where the oviduct (Ov_2) enters the pallial oviduct (Po). At the junction of the spermathecal duct and the bursa copulatrix, from the left side, a tube arises which first turns left, then turns to the right over the spermathecal duct, then left again to enter the oviduct. This is the sperm duct (Sd_1).

As previously described, the kidney is a thin walled, fluid filled sac. It is molded around and between organs from the posterior edge of the mantle to the anterior chamber of the stomach (Ast). As the

Plate 7

MID-BODY REGION OF POMATIOPSIS LAPIDARIA

Fig. 1. The ventral surface of the kidney (K) is shown. Connective tissue was removed to reveal the point where the sperm duct and spermathecal duct connect and their relationship to the bursa copulatrix (B).

Fig. 2. The ventral wall of the kidney was slit open to reveal the cavity of the kidney. The bursa copulatrix (B) was pulled out of the cavity to show how it and the coiled oviduct (Ov) were wrapped in kidney tissue.

B bursa copulatrix
Cl columellar muscle
E egg
Ek cut edge of kidney wall
F fecal pellet
Gn gonadal nerve
I intestine
K kidney
K_1 portion of kidney wall resting on the style sac
Mcn external mantle nerve 3
Ov coiled portion of the oviduct
Ov_1 oviduct posterior to the gonopericardial duct
Ov_2 portion of the oviduct entering the pallial oviduct
Po pallial oviduct
Sbv subvisceral commissure
Sd spermathecal duct
Sp the deep crevice between the right edge of the style sac and the anteroventrally running intestine. This is the deepest portion of the kidney.
Ss esophagus
St stomach
Suv supervisceral commissure
Vg visceral ganglion

Plate 7

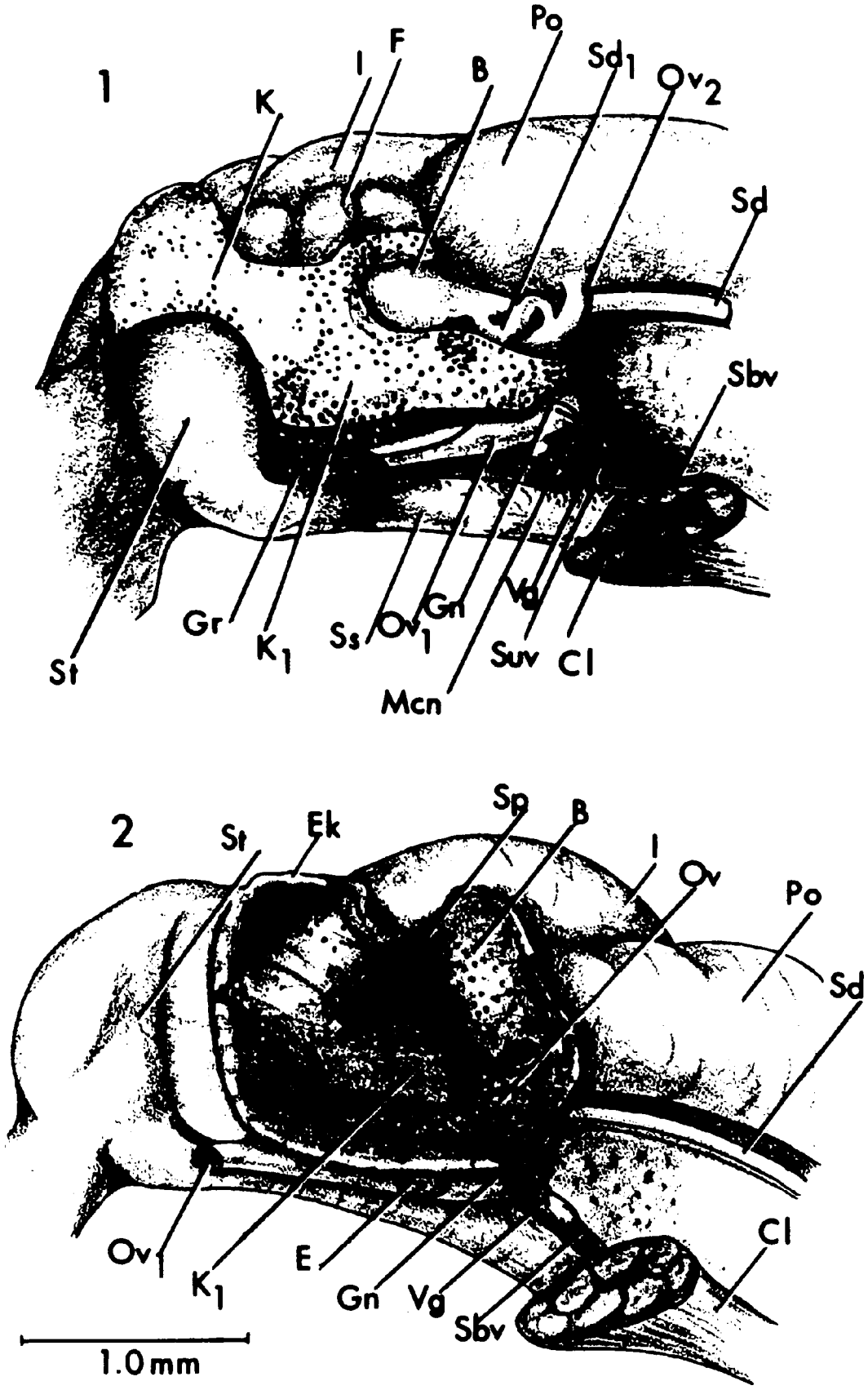

1
K
I
F
B
Po
Sd1
Ov2
Sd
Sbv
St
Gr
K1
Ss
Ov1
Gn
Vg
Suv
Cl
Mcn
2
St
Ek
Sp
B
I
Ov
Po
Sd
Ov1
K1
E
Gn
Vg
Sbv
Cl
1.0mm

Plate 8

FEMALE REPRODUCTIVE SYSTEM OF POMATIOPSIS LAPIDARIA

Fig. 1. The ventral wall of the kidney was removed as well as the ventral wall of the mantle cavity. All kidney tissue was removed from the reproductive structures. The pallial oviduct and spermathecal duct were cut and the posterior portion of the reproductive system was lifted from the body tube to show underlying structures.

Fig. 2. The bursa copulatrix with the left lateral "crest" showing, and the oviduct between the bursa and gonopericardial duct pulled out like a spring to show the nature of coiling.

Fig. 3. The ventral surface of the bursa copulatrix exposed with the oviduct pulled out as in Fig. 2.

Fig. 4. The relationship of the seminal receptacle to the bursa copulatrix is shown as well as the coiled portion of the oviduct.

Fig. 5. The relationship of the sperm duct and bursa copulatrix showing the position of the opening of the seminal receptacle into the oviduct.

Au	Auricle
B	bursa copulatrix
Cl	columellar muscle
Dmc	dorsal wall of the mantle cavity
Gp	gonopericardial duct
I_1	portion of the intestine circling over the tip of the style sac
I_2	intestine anteroventral to the pellet compressor
I_3	intestine running along side the pallial oviduct
Ke	cut edge of the kidney wall
Oi	the point where the intestine arises from the posterior portion of the style sac
Or	opening of the kidney into the posterior mantle cavity
Osm	opening of the seminal receptacle into the oviduct
Ov_1	oviduct posterior to the gonopericardial duct
Ov_2	portion of the oviduct entering the pallial oviduct
Po	pallial oviduct
Sd	spermathecal duct
Sd_1	sperm duct
Sm	seminal receptacle
Sts	style sac
V	vein draining the ctenidium and leading to the auricle
W	posterior wall of the mantle cavity abbutting the kidney

Plate 8

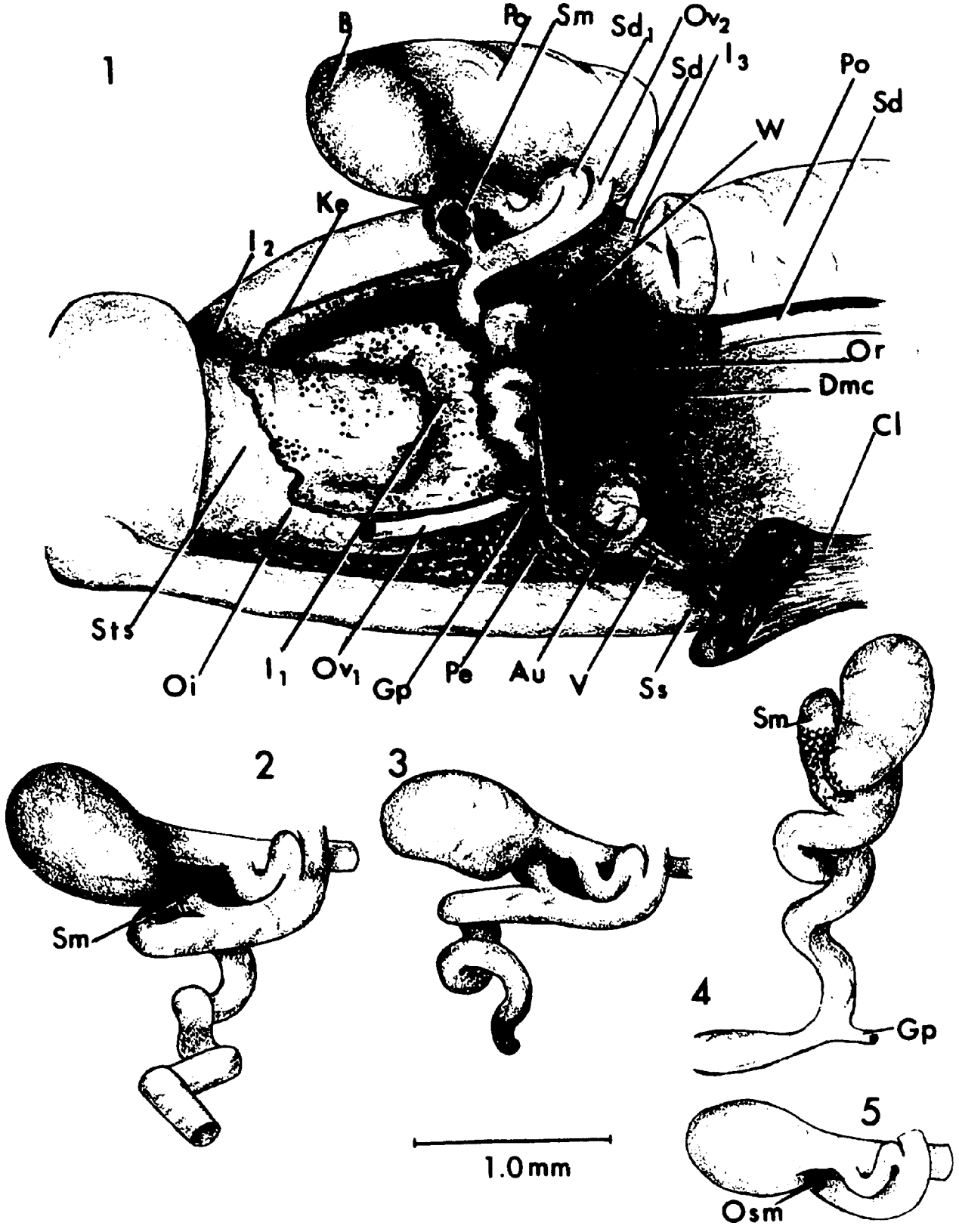

1
B
Po
Sm
Sd1
Ov2
Sd
I3
Po
Sd
W
Ke
I2
Or
Dmc
Cl
Sts
Oi
I1
Ov1
Gp
Pe
Au
V
Ss
2
Sm
3
Sm
4
Gp
5
Osm
1.0mm

Plate 9

FEMALE REPRODUCTIVE SYSTEM OF POMATIOPSIS LAPIDARIA

Figs. 1,2. Different views and variations of the bursa copulatrix and associated ducts.

Fig. 3. Variation in the seminal receptacle.

Fig. 4. The pallial oviduct and the spermathecal duct oriented to show the opening of the spermathecal duct and the dense connective tissue sheets binding the spernathecal duct to the pallial oviduct.

Fig. 5. The pallial oviduct and the spermathecal ducts as they appear in Plate 4 but with greater detail.

Fig. 6. The pallial oviduct oriented to show the opening as well as the connective tissue "tubes" encircling the lips and running into the mantle tissue.

Fig. 7. The pallial oviduct and spermathecal duct oriented to show the opening of the spermathecal duct.

Con	connective tissue sheets
Oo	opening of the pallial oviduct
Osd	opening of the spermathecal duct
Osm	opening of the seminal receptacle
Sd	spermathecal duct
Vas	vascular channels in the connective tissue sheets

Plate 9

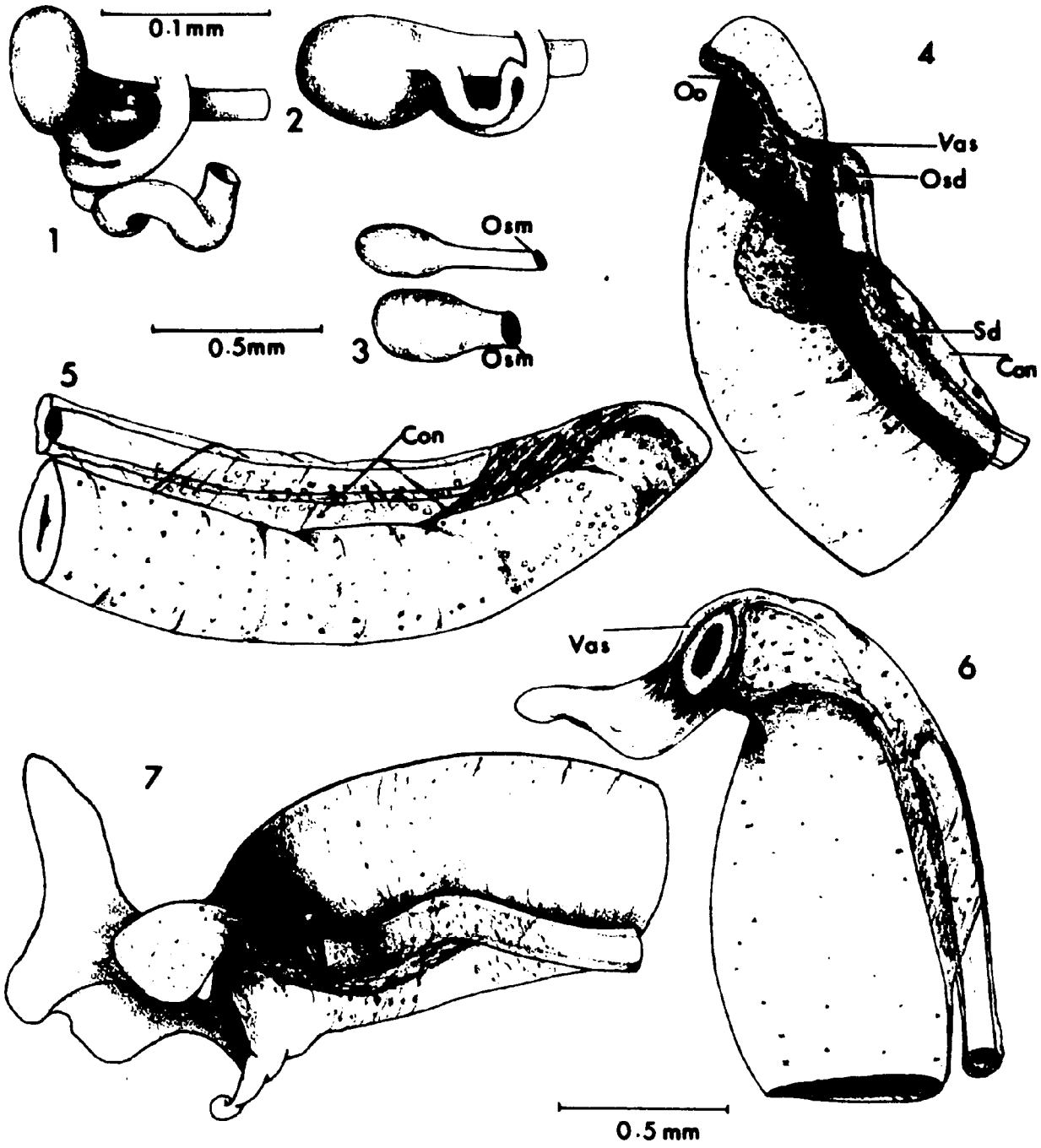
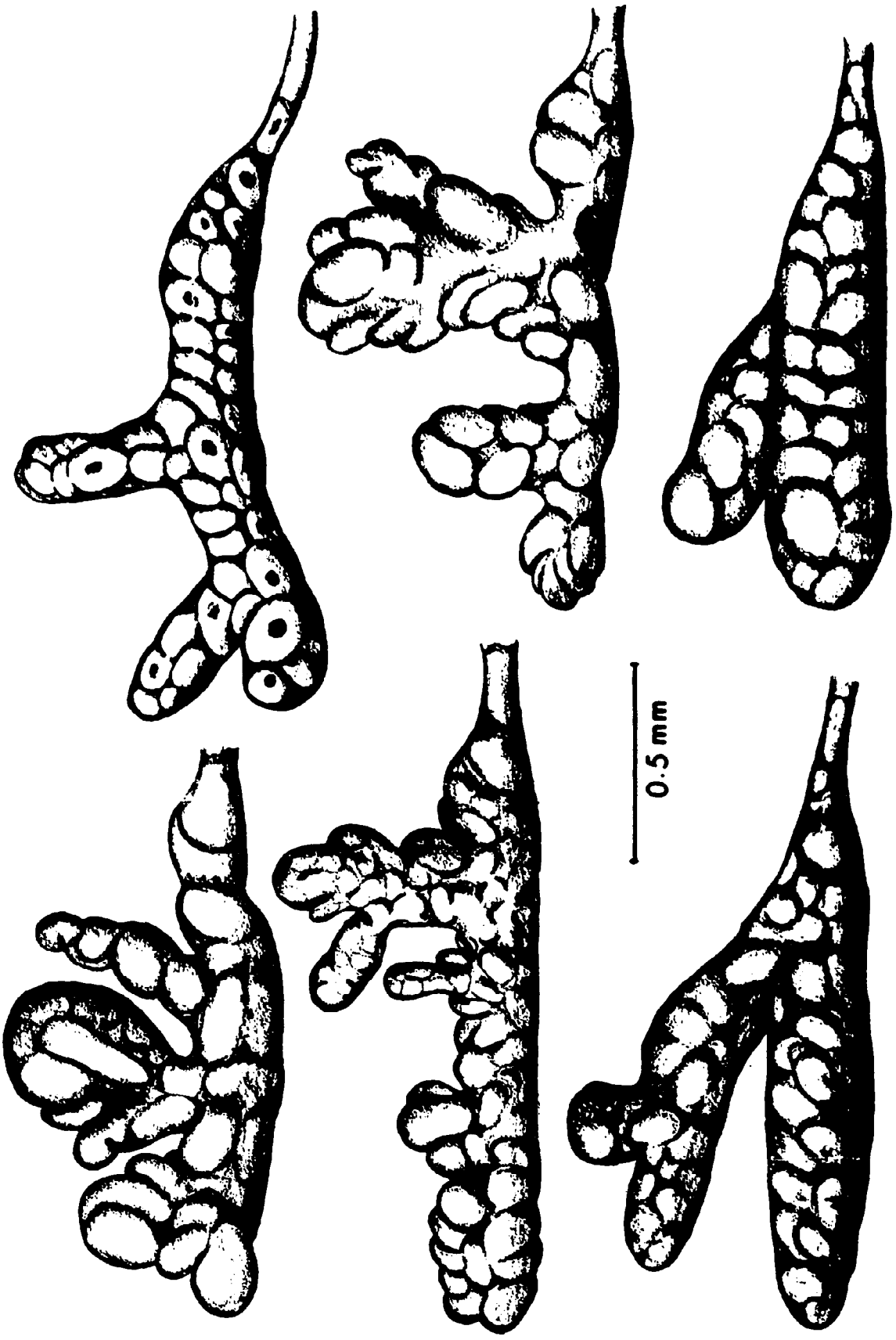


Plate 10

VARIATIONS IN THE GONAD OF FEMALE
POMATIOPSIS LAPIDARIA

Plate 10



kidney fills the residual space within the bounds described, it is like a second body cavity, the ventral wall of which is shown in Plates 4-7. Opening the ventral wall and peeling it away (Plate 7, Fig. 2) exposes the cavity of the kidney. The bursa copulatrix (B) is shown pulled slightly outward and rotated about 45° to the right. The postero-ventral and all of the dorsal surface of the bursa are covered with kidney wall. Pulling the bursa outwards exposes the oviduct lying coiled dorsal to the bursa, likewise wrapped in kidney tissue. The dorsal wall of the kidney under the area marked K_1 in Plate 7 covers the style sac, the latter better shown in Plate 8, Fig. 1, Sts. The style sac arises from the anterior chamber of the stomach, runs about 1.44 mm anteriorly not quite reaching the end of the mantle cavity. This structure is about 0.96 mm wide at its posterior end. From its left ventrolateral surface about 0.45 mm from the edge of the anterior chamber of the stomach, the intestine arises (Oi) with a width of 0.36 mm. The intestine runs anteriorly, swings over the rounded ventral tip of the style sac (I_1) and turns dorsoposteriorly still appressed against the style sac. The intestine then makes a sharp turn swinging anteroventrally again (I_2). The fecal pellet compressor is located in this sharp turn. The dorsal wall of the kidney is appressed and molded around these structures. A deep crevice is formed to the right of the point where the intestine turns dorsoposteriorly over the style sac. The crevice runs down towards

the dorsal surface (Sp, Plate 7, Fig. 1). This deepened portion of the kidney extends anteriorly up to the anterior wall of the kidney abutting the rear of the mantle cavity.

In Plate 8, Fig. 1 the kidney tissue was cleared from the oviduct, the pallial oviduct (Po) was cut anterior to the point where the oviduct (Ov2) entered the former organ, and the posterior portion of the pallial oviduct with bursa copulatrix and tubes was lifted up and outward thereby exposing structures otherwise hidden by that complex. In that same figure the ventral wall of the mantle cavity was removed. The anterior wall of the kidney is shown abutting the epithelium of the posterior mantle cavity (W). The left edge of the anterior wall abuts the pericardium (Pe), the right edge abuts the intestine (I_3). The opening of the kidney is shown to the right of the pericardium (Or).

The pericardium lies anterior to the style sac (Sts) and pushes out into the mantle cavity (Dmc). The auricle (Au) is shown and the vessel (V) which brings blood from the ctenidium to the auricle. Just posterolateral to the point where the auricle joins the ventricle a thin tube, the gonopericardial duct (Gp), connects the pericardium with the oviduct. This structure has not been previously mentioned for Pomatiopsis. The gonopericardial duct arises from the dorsal surface of the oviduct where the latter turns into the body tube under the anteroventral arm of the kidney (Plate 7,

Fig. 1). This area is generally occluded by pigmented connective tissue and the go nadal nerve (Gn) which runs posteriorly over the oviduct at this point and is bound to the latter by tenacious connective tissue.

Lifting the bursa and the pallial oviduct and displacing them (Plate 8, Fig. 1) reveals the coiled nature of the oviduct between the gonopericardial duct and the bursa copulatrix. In this plate the relationship of the seminal receptacle (Sm) is shown to the bursa copulatrix and the point where the sperm duct (Sd_1) enters the oviduct. The coiled portion of the oviduct readily fits into the space between the end of the style sac and the posterior slope of the pericardium. As can be seen in Plate 5, Fig. 2, all of the coils of the oviduct are packed dorsolaterally to the point where the spermathecal duct enters the bursa copulatrix.

Gonopericardial Duct to the Pallial Oviduct (Plates 5, 7-9).

Gonopericardial Region and Coiled Oviduct. The oviduct narrows just posterior to the gonopericardial duct (Plate 8, Fig. 4). Eggs have not been seen past this point although they may be found lined up, one behind the other, posteriorly into the gonad. The small section of the gonad from which the gonopericardial duct arises is distinct in that it is characteristically swollen (Plate 5, Fig. 2) and is about 0.24 mm long and 0.19 mm wide. The duct penetrates connective tissue layers to enter the pericardium and is

open at both ends. It measures about 0.096 mm long and 0.048 mm wide. The connective tissues occluding the reproductive tract between the bursa copulatrix (B) and the oviduct (Ov) shown in Plate 5, Fig. 1, were removed. The exposed structures (Plate 5, Fig. 2) are presented as observed with one exception. The gonopericardial duct arises more dorsally than is shown and would, therefore, be barely visible. The duct is shown to demonstrate the proportional relationship of the duct with the pericardium and the oviduct.

The coiled portion of the oviduct forms a very compact cylinder some 0.31 mm in diameter and 0.48 - 0.36 mm in length depending upon whether there are 4 or 3 coils in the tube. The width of the tube in the coil is thick, up to 0.17 mm in diameter. Uncoiled, the length of the oviduct between the gonopericardial duct and the point of entry of the seminal receptacle into the oviduct is about 2.0 mm. Coiling may be regular or with irregular twists. In Plate 8, Figs. 1-4, the oviduct has been slightly stretched out as one would stretch a spring to demonstrate the nature of the coils and twists commonly found in that section.

Seminal Receptacle. The seminal receptacle is not observable from the ventral surface (Plate 5, Fig. 2; Plate 8, Fig. 5; Plate 9, Fig. 2) although the point where it enters the oviduct may be seen (Plate 8, Fig. 5). This small, sperical, sac-like organ

is bound to the anterior dorsal surface of the bursa copulatrix by a connective tissue sheath which is often heavily imbedded with numerous white granules (Plate 8, Fig. 4). The seminal receptacle does not communicate directly with the bursa copulatrix. By slowly rotating the bursa from its normal position (Plate 5, Figs. 1,2), like turning the page in a book, one gradually exposes the seminal receptacle (sequence in Plate 8, Figs. 5,3,2,4, but with different specimens).

The shape of the seminal receptacle varies greatly depending upon the extent to which it is gorged with sperm and fluid. It may be elliptical or circular with gradations between (Plate 8, Figs. 4 and 1, respectively). It often appears to have a dense hard core (Plate 8, Fig. 1). The duct leading to the oviduct varies in length as shown in Plate 1, Figs. 1-4; Plate 9, Fig. 3. The length varies between 0.12 mm and 0.25 mm while the width varies between 0.06 mm to 0.15 mm. The longer slender duct is most commonly encountered. The spherical portion of the organ varies in length from 0.20 mm to 0.24 mm and the width from 0.17 mm to 0.24 mm. The duct enters the oviduct about 0.48 mm from the opening of the sperm duct as shown in Plate 8, Figs. 1, 3, 5; Plate 9, Fig. 1.

Sperm Duct. The sperm duct (Sd_1, Plate 8, Fig. 1) varies in length from 1.2 mm to 0.4 mm but is, on the average and

most commonly 0.70 mm. The width varies between 0.14 mm to 0.09 mm. It may arise abruptly at the juncture of the spermathecal duct and the bursa copulatrix (Plate 9, Figs. 1,2) or out along the spermathecal duct as far as 0.5 mm from the anterior portion of the bursa (Plate 8, Fig. 2). The degree of convolution of the sperm duct varies between the condition shown in Plate 8, Fig. 1, and Plate 5, Fig. 2; the latter condition is rather rare.

The oviduct, beyond the entry of the sperm duct (Ov_2, Plate 8), is short, some 0.17 mm long and 0.12 mm wide. It passes into the pallial oviduct (Po) 1.0 mm to 1.7 mm from the posterior end of the pallial oviduct, not in the mid-length of that organ as stated by Dundee (1957). This point is 0.65 mm ± 0.16 mm from the posterior end of the bursa copulatrix and is covered by the sheet of connective tissue discussed above (Plate 5, Fig. 1). The oviduct passed ventral to the spermathecal duct and does not communicate with it although both are closely bound together by connective tissue.

Bursa Copulatrix. The bursa copulatrix as viewed from the ventral aspect overlays the anterior tip of the style sac with part of the curvature often within the kidney space on the right of the style sac (Plate 5, Fig 1; Plate 7, Figs. 1,2; Plate 8, Fig. 1). As shown in Plate 5, Fig. 2, the ventral surface is evenly rounded. The mediolateral surface is not rounded but narrows to a crest

(Plate 8, Figs. 1,2; Plate 9, Fig. 1). This organ is characteristically appressed against the posterior end of the pallial oviduct as shown in Plate 8, Fig. 1. At times the end of the bursa projects beyond the edge of the pallial oviduct (Plate 7, Fig. 1) but this is rare. Another variation is where the tip of the pallial oviduct swings slightly away from the bursa (Plate 5, Fig. 1). The bursa has never been found posterior to the tip of the pallial oviduct as shown by Dundee (1957, Plate 11). The general positions of the bursa and the pallial oviduct in relationship to the organs in the mid-body region shown in Plates 5, 7, and 8 were found to be invariable. The length of the bursa along its ventral surface averaged 0.72 mm ± 0.14 mm and the width averaged 0.48 mm ± 0.03 mm.

Pallial Oviduct and Spermathecal Duct (Plates 5, 7, 8, 9).

Spermathecal duct. The spermathecal duct arises from the anterior tip of the bursa copulatrix as a tube 0.096 mm to 0.168 mm wide. It runs anteriorly, closely appressed to the ventromedial edge of the pallial oviduct and passes dorsal to the oviduct (Ov_2, Plate 8, Fig. 1) where the latter enters the pallial oviduct. Passing over the end of the mantle cavity the spermathecal duct narrows to 0.07 mm - 0.10 mm and becomes separated from the pallial oviduct by 0.02 mm to 0.07 mm. As shown in Plate 5, the spermathecal duct (Sd) is readily observed following the curve of the pallial oviduct (Po) imbedded within the ventral superficial tissues of the mantle cavity wall. Anteriorly, with the sharp curve

of the mantle cavity and pallial oviduct, the spermathecal duct turns towards the pallial oviduct, becomes more slender, and disappears under the ventromedial edge of the pallial oviduct. The area where the spermathecal duct disappears from view is about 0.48 mm from the point where the pallial oviduct is observed to disappear within the mantle cavity (Plate 5, Fig. 1).

In Plate 4, the mantle cavity is shown opened and the gross aspects of the relationship between the termination of the spermathecal duct and pallial oviduct may be observed. It appears from this gross aspect that the spermathecal duct enters the tip of the pallial oviduct. About 0.7 mm posterior to the opening of the pallial oviduct (Oo) the spermathecal duct becomes closely bound to the pallial oviduct by sheets of connective tissue. The opening of the spermathecal duct is not evident. A number of whole mount slides were prepared using CMC-10 (Michelson, 1960) where only the anterior 1.0 mm portion of the spermathecal duct, pallial oviduct, and intestine were utilized. Water mounts were also made in studying the same area. Studied under the compound microscope it was found that the spermathecal duct did not open onto the pallial oviduct via a common pore as stated by Dundee (1957), but quite differently.

In Plate 4, the spermathecal duct appears to continue into the tip of the pallial oviduct because stout connective tissue

layers bind the spermathecal duct to the pallial oviduct and the connective tissue continues to the tip if the pallial oviduct beyond the point where the spermathecal duct has opened to the mantle cavity. In Plate 9, Fig. 5, the structures under discussion are shown as they appear in Plate 4. In Plate 4 the opening of the pallial oviduct is shown only to demonstrate the point where it opens. In reality what would be seen is the lip-like tip of the pallial oviduct appressed to the mantle wall. This lip-like tip shown in Plate 9, Fig. 5, is the outer lip which is appressed against the inner mantle wall by muscular contraction thereby sealing off the opening of the pallial oviduct. Both lips around the opening (Plate 9, Fig. 6) are muscular, and thickened by connective tissue strands which encircle the edges of the lips. The connective tissue anterior to the opening of the spermathecal duct is heavily pigmented, full of whitish granules, and forms the tubular channel for vascular flow to the tip of the pallial oviduct and around the lips (Plate 9, Fig. 4). This vascular tube is thick and dense enough so that it is with the greatest difficulty that one can perceive where the spermathecal duct ends and the connective tissue tube begins (Plate 9, Fig. 5). The vascular channels running down each side of the lips of the pallial oviduct end in sinuses within the mantle edge.

By rotating the connected spermathecal duct and pallial oviduct shown in Plate 4, and 9, Fig. 5, as turning a page in a book

from left to right, one can observe with the aid of a bright light, that the spermathecal duct terminates about 0.48 mm from the tip of the pallial oviduct. The opening of the spermathecal duct is permanent and not distinct due to the rather thin edge of the tube at this point (Plate 9, Figs. 4, 7). Note that the opening of the spermathecal duct is not in the same quadrant as that of the pallial oviduct. In Plate 4, while the opening of the pallial oviduct is appressed against the mantle wall, the opening of the spermathecal duct is rotated 90° above. In the intact animal, where the mantle is in its normal position, the opening of the pallial oviduct is appressed against the right ventrolateral mantle wall while the spermathecal duct opens towards the "neck."

The opening of the spermathecal duct is about 71 micra in length and 25 micra width. In some specimens it appears slit-like with a length of about 60 micra and a width of 12 micra; in others the aperture was round with a diameter of 35 micra. In Plate 9, Fig. 6, the tips of the organs are rotated still further, exposing the thickened lips of the opening of the pallial oviduct but causing the opening of the spermathecal duct to disappear from sight.

Pallial Oviduct. The pallial oviduct is the largest organ of the body with a length of 4.3 mm to 5.0 mm and a width of 0.72 mm towards the posterior regions. In the living animal the organ appears

divisible into 2 parts of equal length; the posterior half appears greyish, thick, and quite glandular, the anterior portion is whitish, narrower and more smooth. These observations correspond to Dundee's (1957) histological findings.

5. Male Reproductive System

A male snail is shown uncoiled in Plate 6 as was the female previously described. Sperm from the gonad (Go) travel via the vas deferens (Vd_1) to the prostate (Pr), enter the prostate, and leave through the anterior portion of the vas deferens (Vd_2) which travels into the base of the verge, along the length of the verge to exit at its tip (Plate 11, Fig. 1).

Gonad (Plates 6, 12). The gonad, observed through the ventral epithelium of the digestive gland, does not appear as distinct as did the gonad of the female (Plate 6, Fig. 1). The reason for this vagueness is that the lobes of the gonad are small and the gonad is finely branched. The main collecting duct, the vas deferens, is dorsal to the gonad and therefore hidden from sight until it turns ventrally near the edge of the stomach. Peeling off the ventral epithelium reveals the structure of the testis (Plate 12, Fig. 1). It is longer than the female gonad with a length of about 2.4 mm to 2.8 mm. The width of the gonad at its widest part, which is usually in the anterior third of the gonad, is about 0.7 mm. From a narrow collecting duct (0.05 - 0.09 mm wide), the vas efferens (Ef), there

Plate 11

MALE REPRODUCTIVE SYSTEM OF POMATIOPSIS LAPIDARIA

Fig. 1 Head, verge, and mantle cavity. The verge is shown uncoiled and partially extended.

Fig. 2 Head of the gland shown in Fig. 3.

Fig. 3 Longitudinal view of the glands which pack the area between the vas deferens and the concave curvature of the verge Ge of Fig. 5.

Fig. 4 Gland type commonly found near the tip of the verge, appearing dense or black under direct illumination. They are oriented with the circular muscle fibers.

Fig. 5 Verge showing the vas deferens and glandular areas.

Fig. 6 Gland type clustered about the vas deferens.

A	anus
Ct	ctenidium
Cm	cut edge of the mantle
F	fecal pellet
G	glandular units around the dorsomedial surface of the eye
Ge	gland type shown in Figs. 2, 3
Gl_1	gland type shown in Figs. 2, 3
Mvd	thick layers of circular muscle encircling the vas deferens at the base of the verge
On	osphradial nerve
Os	osphradial ganglion in the osphradial pit
Pe	pericardium
Pr	prostate
R	rostrum
Sbv	subvisceral commissure
Suv	supervisceral commissure
Vd_2	anterior portion of the vas deferens
Ve	verge
Vg	visceral ganglion

Plate 11

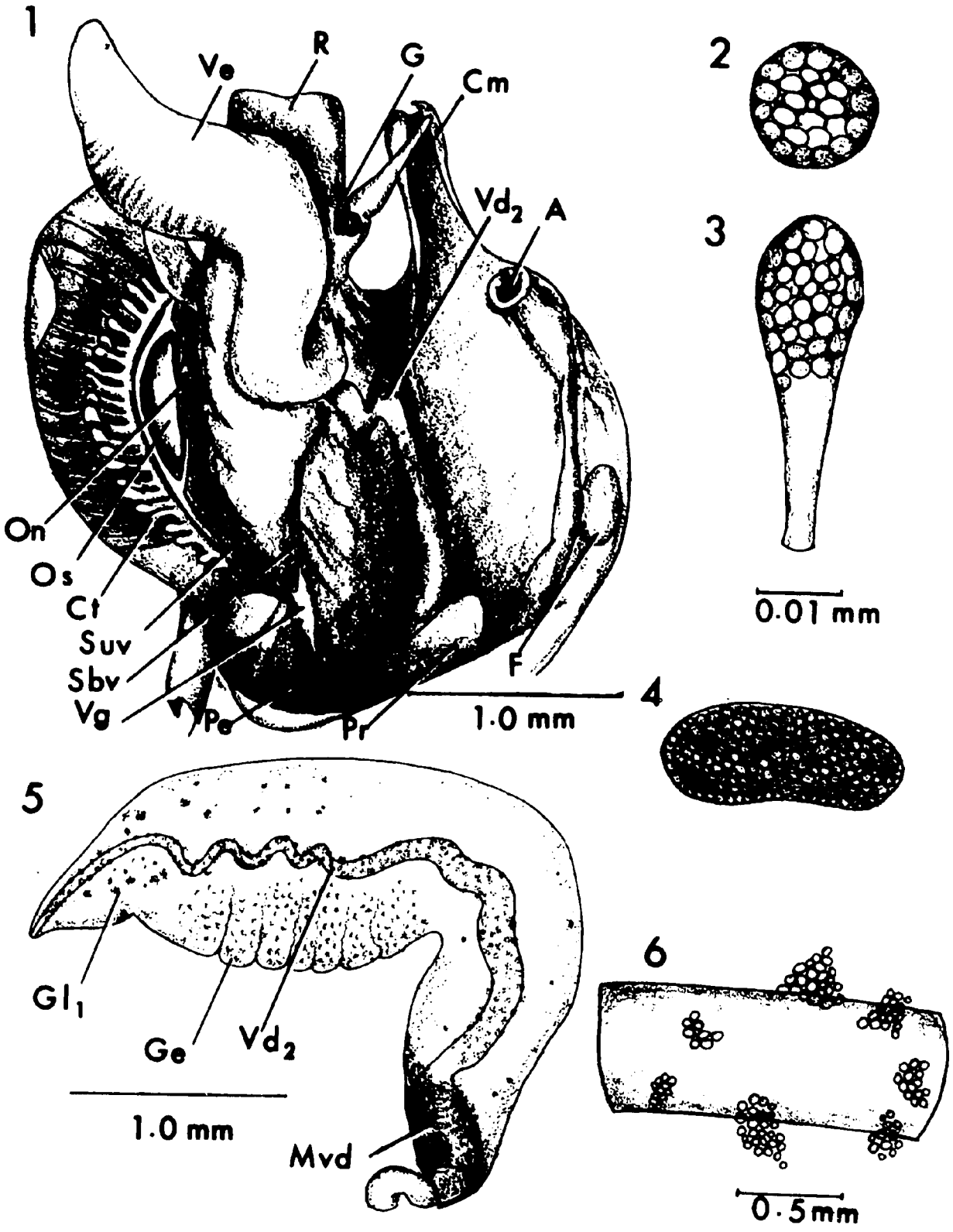

1
Ve
R
G
Cm
Vd2
A
On
Os
Ct
Suv
Sbv
Vg
Pe
Pr
F
1.0 mm
2
3
0.01 mm
4
5
Gl1
Ge
Vd2
1.0 mm
Mvd
6
0.5mm

Plate 12

MALE REPRODUCTIVE SYSTEM OF POMATIOPSIS LAPIDARIA

Fig. 1 Gonad showing 9 multibranched units and the coiled "seminal vesicle" behind.

Fig. 2 A single multibranched unit arising from the vas efferens.

Figs. 3,4,5 Variation in the coiling of the "seminal vesicle."

Fig. 6 An enlarged view of a single multibranched unit supporting testicular lobes.

Fig. 7 Variation in the structure of the testicular lobes seen laterally.

Fig. 8 A multibranched unit showing testicular lobes and how the lobes are vascularized.

Ar artery to the testicular lobes
Br branch arising from the vas efferens
Ef vas efferens
O_1 point where the vas deferens arises from the vas efferens and leads to the "seminal vesicle"
T testicle lobe

Plate 12

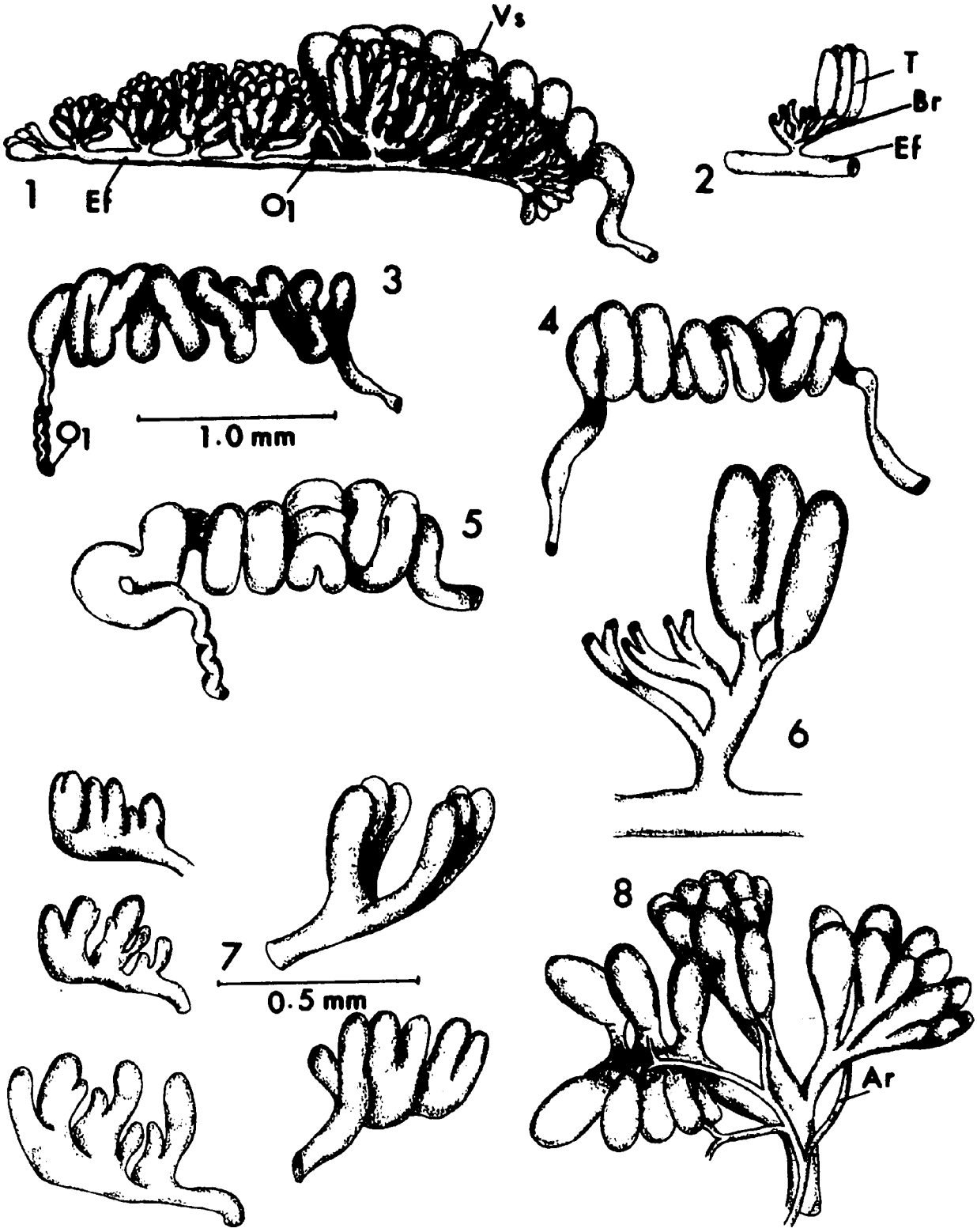


Plate 13

STRUCTURES OF THE MUSCULAR, RESPIRATORY, REPRODUCTIVE, DIGESTIVE, AND NERVOUS SYSTEMS

Fig. 1 Muscles arising in the pedal haemocoel at a level below the pedal ganglion. The drawing was made from O. hupensis formosana and shows a cross section through the pedal haemocoel. The pedal ganglion on the right is transected. The right propodial and metapodial ganglia are shown. The main structures to be pointed out are the mid-ventral protractors arising from the anterior wall of the pedal haemocoel.

Fig. 2 The verge of P. lapidaria showing a rarely found penial lobe (a).

Fig. 3 The structure of 2 gill filaments from P. lapidaria.

Fig. 4 Variation in the salivary glands of P. lapidaria.

Fig. 5 Variation in the nerves associated with the buccal ganglion.

a Fig. 1. anterior wall of the pedal haemocoel
Fig. 2. rare penial lobe

b_1 dorsal buccal nerve

b_2 esophageal nerve

b_3 central buccal nerve

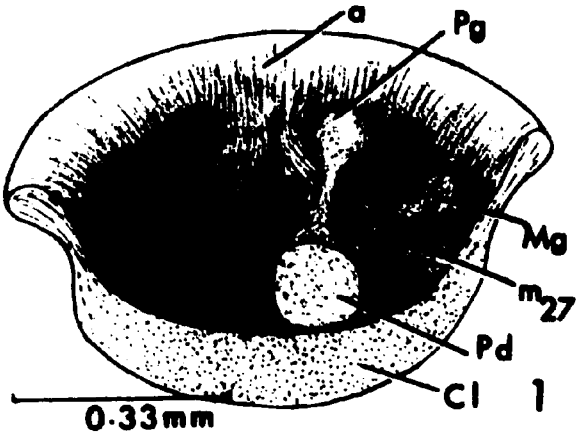
b_4 anterior buccal nerve

b_5 odontophoral nerve

b_6 posterior buccal nerve

Bc buccal commissure
Bg buccal ganglion
Cb cerebrobuccal commissure
Cl columellar muscle
Mg metapodial ganglion
m_{27} mid-ventral protractor
Pd pedal ganglion
Pg propodial ganglion

Plate 13



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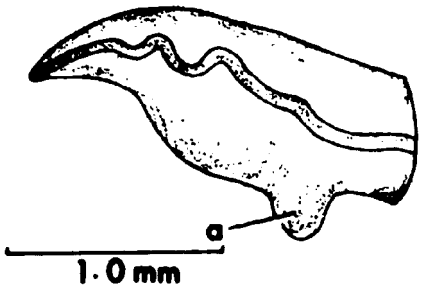

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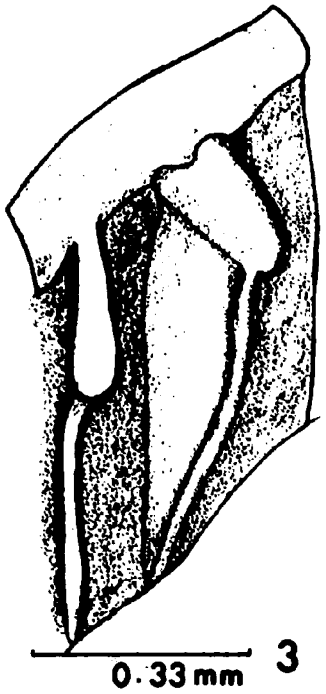

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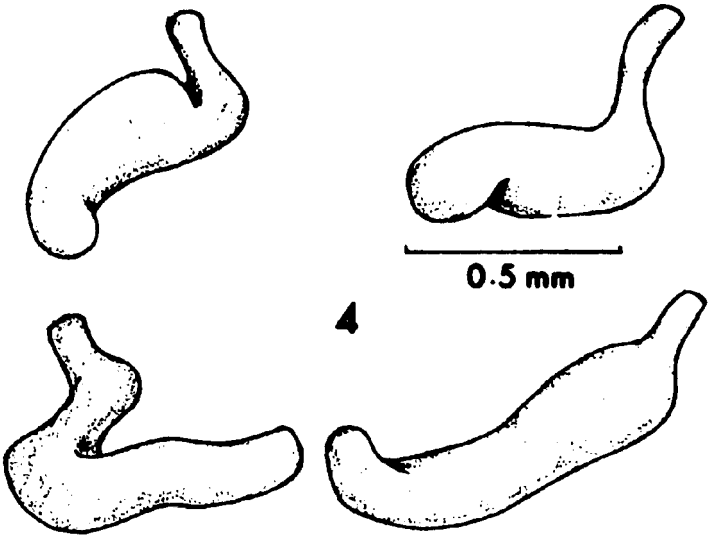

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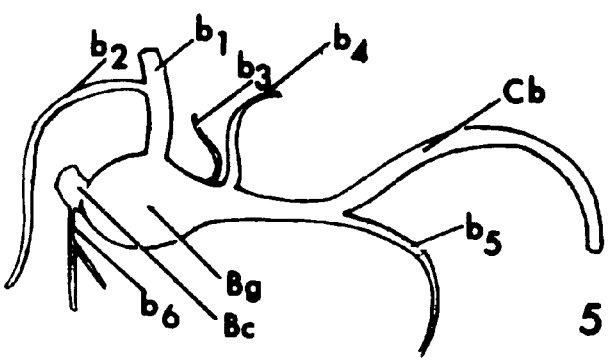

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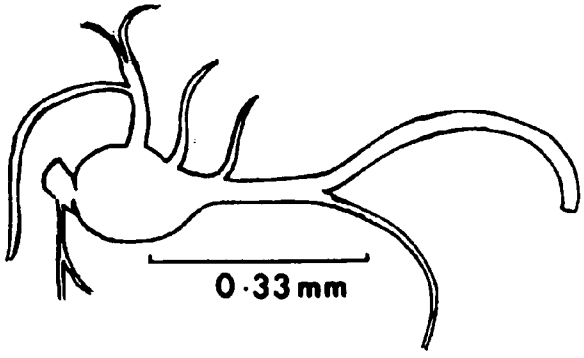


arise 8-9 multibranched units. The nature of these branched units is shown in Plate 12, Figs. 2, 6, and 8). At the end of each branch are lobes of varying size. The lengths and widths of the lobes depend upon the degree to which they are filled with gonadal products. A single tubular branch may support several interconnecting lobes (Plate 12, Fig. 8). The whole gonad appears very bright yellow when all of the testicular lobes are productive. In Plate 12, Fig. 8, vascularization of three groups of testicular lobes is shown.

Posterior Vas Deferens (Plates 6, 12). A narrow tube (0.048 mm diameter), which is extremely convoluted in most cases, arises just anterior to the mid-length of the vas efferens. This is the beginning of the section of the posterior vas deferens called the "seminal vesicle" by Dundee (1957). As shown in Plate 12, Fig. 1, the tube (O_1) arises at a place which would otherwise be filled by a multibranched unit. Removing the anterior testicular units reveals the structure of the "seminal vesicle" (Plate 12, Figs. 3, 4, 5). The "seminal vesicle" is coiled in a characteristic manner. The convoluted portion arising from the vas efferens becomes a thickened uncoiled tube within 0.6 mm of the vas efferens. The thickened tube enters a series of regular coils like a spring when the tubes are not overloaded with gonadal products (Plate 12, Figs. 3, 4). When fully loaded, however, some of the coils bulge out of position so as to disrupt the neatly coiled pattern (Plate 12, Fig. 5). The length of

the "seminal vesicle" is (measuring just the length of the coil) 1.4 mm to 1.9 mm; the width is about the same as that of the gonad. An individual tube within the coil may have a diameter of 0.24 mm. Fully uncoiled, the tubing making up the "seminal vesicle" measures up to 6.0 mm in length. At the anterior end of the testis the "seminal vesicle" narrows to about 0.07 mm and turns ventrally to appear from the dorsal side of the gonad as shown in Plate 6. The vas deferens has an anterior course as did the oviduct toward the rear of the mantle cavity. At the place where the oviduct turned dorsally, the vas deferens continues along the ventral surface across the body tube, posterior to the mantle cavity, without coiling, connecting with the pericardium, or great involvement with kidney tissue. The vas deferens moves to the prostate to enter that organ just posterior to the place where the anterior portion of the vas deferens (Vd_2) is seen leaving (Plate 6, Fig. 1). The tube is difficult to see because it becomes more slender as it approaches the prostate and it is surrounded in connective tissue. As shown in Plate 6, Fig. 2, the prostate was turned over to reveal the point of entry of the vas deferens into its dorsal surface. At this point the vas deferens (Vd_1) measures about 0.024 mm in diameter.

Prostate (Plates 6, 11). As seen from the ventral surface, the prostate is a kidney shaped organ, white in color, situated in the same position as the female pallial oviduct but not as long as that

organ. The prostate is 1.68 mm to 1.75 mm long and the greatest width is about 0.70 mm. The posterior end projects beyond the mantle cavity about 0.48 mm and the end is encircled by kidney tissue as was the female bursa copulatrix and pallial oviduct.

In contrast to the pallial oviduct, the prostate surface is quite irregular due to discrete glandular units which were readily separated (Plate 6, Fig. 3). Viewing the opposite side of the prostate it is evident that the glandular units drain into a narrow tubular collecting tube (Plate 6, Fig. 2). The posterior portion of the vas deferens (Vd_1) enters the collecting tube of the prostate 0.60 mm from its posterior end while the larger anterior portion of the vas deferens (Vd_2) leaves the prostate 0.17 mm anterior to the entry of Vd_1.

Anterior Vas Deferens (Plates 6, 11). Viewing Plate 6, the anterior vas deferens (Vd_2) emerges from the dorsal side of the prostate as a tube 0.96 mm to 0.12 mm wide. It usually follows along the edge of the prostate until the anterior end of that organ before running obliquely over the mantle cavity towards the columellar muscle but occasionally it diverges immediately upon leaving the prostate as shown in Plate 6, Fig. 1. The vas deferens enters the mantle cavity behind the columellar muscle, 1.4 mm from the edge of the mantle. In Plate 11, Fig. 1, the anterior tip of the prostate (Pr) and anteriorly running vas deferens (Vd_2) are shown. The vas deferens runs

anteriorly on the floor of the mantle cavity along the right side of the "neck" to a point slightly anterior to the base of the verge (Ve) and then turns back and enters the "neck" under the base of the verge.

Verge (Plates 11, 13). The verge of Pomatiopsis lapidaria is very characteristic for the species. The verge would be called simple in much of the malacological literature as it has no appendages and the vas deferens terminates at the tip which has no papilla. The verge has, however, a number of significant details of importance to a systematic discussion. As Dundee (1957) stated, the verge is very flattened; it is relatively thin bladed. It arises from the "neck" to the right of the mid-line and is carried, coiled counter-clock-wise over the "neck." It measures up to 3.4 mm in length in the extended condition but it can possibly be expanded further. The animal shown in Plate 11, Fig. 1 is a relatively small snail; the verge shown in Fig. 5 is from a larger male.

Abbott (1948a) described the verge as varying considerably, "ranging from a simple, flattened, tapering cylinder to a prong with a "meatchopper blade on one side." I found the "simple" verge only in immature males. In adults the verge is characteristically of the shape shown in Figs. 1 and 5. In very rare cases (less than 1 per cent) the inner curvature near the anterior end has a fleshy lobe (Plate 13, Fig. 2, a) reminiscent of a penial appendage common in some hydrobiid snails. The inner margin of the mid-verge is

swollen out into a convex curve which appears scalloped. As shown in Plate 11, Fig. 5, the scalloped effect is due to the rounded ends of blunt lobes which are finger-like, with parallel sides. The verge was cut from the body deep at its base so as to include the vas deferens where it entered. This organ was studied by placing it in a drop of saline, gently placing a coverslip on it, and viewing it through the compound microscope. The vas deferens runs along the base of the verge before turning up into the mid-portion of that organ. The basal portion of the vas deferens is greatly thickened due to a pronounced layer of dense circular muscles (Mvd, Fig. 5). Beyond the base, the vas deferens has an anterior course along the mid-line of the verge or slightly displaced towards the outer curvature. It does not run pressed against the outer curvature. The tube, loosely undulating, begins to narrow noticeably about mid-verge. At the tip the vas is only about 0.024 mm wide.

The area of the verge between the crenulated edge and the vas deferens is highly glandular with ducts and fissues running beneath the epithelium, along the edges of the "lobes," towards the edge of the verge. At 150 X distinct glandular units were noted pushing against the epithelium so that the whole area seemed pustulate. The glands (Plate 11, Figs. 2, 3) were club-shaped, the diameter of the heads (Fig. 2) measuring 10-30 micra. The head of such a gland appears full of vesicles (8-20 per head) measuring

2-10 micra in diameter. The length of the glands measured about 160 micra; the basal portions were without vesicles (Fig. 3). The whole area was full of these glands, the whole length of which could often be seen lying under the epithelium.

Anteriorly, the verge has a characteristic indentation on the inner curvature (Plate 11, Figs. 1, 5). The edge of the verge appears to have no cilia when viewed at 600 X. Two other glandular types can be found in the verge. Along the vas deferens are numerous crowded groups of vesicles (Plate 11, Figs. 5 (Gl_2), 6). Also near the anterior end of the verge one sometimes finds dense spheres of minute vesicles which look like black spots under the dissecting scope (Plate 11, Fig. 5 (Gl_1), Fig. 4). The longitudinal axis of these dense spheres are oriented lengthwise with the circular muscle fibers encasing the verge.

6. Buccal Mass.

In Plate 14 the rostrum is shown opened along the mid-dorsal line. The epithelium of the "neck" was slit open revealing the wide, powerful columellar muscle (Cl). Structures are shown as they appeared upon opening this area with 2 exceptions. First, the salivary glands (Sa) are usually folded and tucked ventrolaterally around and about the cerebral commisure (Cc), esophagus (Ss), and cerebral ganglia (Cg) in a variable manner (Plate 15, Fig. 1). They

were pulled upward and straight back to permit at least a limited view of the relationships of the buccal mass (Bm) with the dorsal area above the cerebral ganglia (Cg), esophagus (Ss), and underlying musculature. Second, the area dorsal to the cerebral ganglia (Cg), esophagus (Ss) and pleuro-supraesophageal commissure (Psc) is occluded by transverse strands of connective tissue just beneath the roof of the cephalic area. These strands support the cephalic aorta which travels along the esophagus, dorsal to it, crossing from left to right to descend, near the right cerebral ganglion, into the pedal haemocoel. These structures were removed to enable one to observe the underlying organs.

The dorsal aspect of the buccal mass (Bm) is somewhat pyriform. In the contracted state it varies in length from 0.85-1.08 mm; in width from 0.79-0.84 mm. It fills the rostral portion of the cephalic haemocoel. The posterior end turns sharply ventrally at the beginning of the esophagus, the mid-posterior curve of which is pressed against the posteroventral part of the buccal mass (Plate 15) by the cerebral commissure (Cc). The position of the cerebral commissure corresponds to the mid dorsoventral axis of the posterior buccal mass. The esophagus turns dorsally again under the pleuro-supraesophageal commissure (Psc) and swings left to follow the left edge of the columellar muscle (Cl) posteriorly, lying on that muscle. The esophagus is a large tube 0.31-0.24 mm in diameter.

Muscles arising from the dorsal and dorsolateral surface of the buccal mass (m17) are irregularly placed and serve to suspend the buccal mass from the rostral roof. The dorsal posterior portion of the buccal mass appears fleshy and laced with only a few muscle fibers. The mid-dorsal aspect appears as if two fleshy folds were pressed together and bound in position by superficial layers of connective tissue. Each lip-like edge is the dorsal termination of a hemisphere of tissue arising from the lateral and ventrolateral aspects of the buccal mass. Studying the lateral aspect of the buccal mass (Plate 15, Fig. 1) one observes that the anterior, lateral, and dorsolateral regions are highly muscular (m8, m9, m6).

The buccal mass may be considered a composite of 2 main parts; (1) the pharyngeal tube and attendant muscles which swell between the mouth and the esophagus; (2) the odontophore apparatus which projects into the ventral posterior portion of the pharyngeal tube (Plate 16, Fig. 4). The odontophore is a neatly delineated structure made up of the buccal cartilages, musculatures binding the cartilages together as well as the odontophore to the pharyngeal tube, radula, and radular sac. Connected to the posterior dorsal region of the buccal mass are the paired salivary glands which drain into the pharyngeal tube over the dorsolateral aspect of the odontophore apparatus.

Salivary Glands. The salivary glands are characteristically simple, flattened structures as shown in Plate 14. They are delicate and easily damaged. As shown in Plate 15, Fig. 1, they arise from the dorsolateral surface of the buccal mass 0.24-0.36 from the mid-dorsal line. The duct leading from the main expanded glandular blade varies in length and is closely appressed to the tissue of the buccal mass. The anterior 0.36 mm is generally covered by a sheet of connective tissue. The total length of gland and duct may be 1.37 mm but is generally less, about 1.0 mm. The width varies considerably about 0.20 mm. Variation in the shape of these glands is shown in Plates 13, Fig. 4; 14; 15, Fig. 1.

Interior Buccal Mass. Slitting the epithelium between the dorsal lips of the buccal mass and pulling aside the hemispheres of the pharyngeal tube exposes the inner regions of the tube and the odontophore apparatus (Plate 17, Fig. 4). The large triangularly shaped odontophore, upon full contraction of the buccal mass, causes the dorsal lips of the buccal mass to stretch apart (Plate 14). The odontophore imparts shape to the buccal mass and gives support to the pharyngeal tube and the initial portions of the esophagus.

Shown schematically in a cross section of the pharyngeal tube (Plate 16, Fig. 4), the long axis of the cartilages runs obliquely from posteroventral to anterodorsal. The radula runs along the mid-dorsal surface of the odontophore (Plate 17, Fig. 4) and bends over

the anterior odontophore tip called the bending plane of the radula (Plate 16, Fig. 4). The radula teeth are formed on a chitinous membrane, the radular shield which tightly caps the anterior, anterolateral, and dorsolateral portion of the odontophore (Plate 16, Fig. 4; Plate 17, Fig. 4).

Posteriorly, the radula emerges from the radular sac. The latter bends ventrally between the cartilages (Plate 16, Fig. 4) and turns dorsally again at its tip. The ventral aspects of the radular sac and odontophore are shown in Plate 18. The radula and radular sac form a backward S as shown in Plate 16, Fig. 4. There is a fleshy papilla, the collostyle tip (Carriker, 1946a) at the point where the radula leaves the sac (Plate 17, Figs. 2, 4). The collostyle is an elongate plug of dense white tissue between the radular teeth and the posterodorsal curvature of the radular sac epithelium. Only the tip protrudes beyond the opening of the radular sac.

A sheet of membranes from both posterolateral sides of the inner buccal mass meet, coalesce, and form the radular sac. The posterolateral continuation of this sheet thickens noticeably and forms the esophageal valve (Plate 16, Figs. 1, 4; Plate 17, Figs. 2,4). This structure, quite variable in form between individuals, is extensively discussed by Fretter and Graham (1962). The anterodorsal edge of the valve is pressed against the radular sac. It and the collostyle tip serve to keep material from dropping into

the radular sac or other ventral spaces behind the odontophore. The lateral portions of the valve send membrano-tendonous folds of tissue anteroventrally along either side of the odontophore on the sides of the pharynx (Plate 16, Fig. 1; Plate 17, Fig. 4). These cross over the odontophore divaricator muscles (m3) to run into the loosened membranes arising from the pharynx floor in front of the odontophore under the sublingual space (Sp). Part of this same membrane system sweeps over the divaricator muscles to join the radular sac.

The dorsal aspect of the esophageal valve may be folded with an internal anterior lip (anterior portion of Ev, Plate 17, Fig. 2). The dorsal valvular structure may be folded in various ways as shown in Plate 16, Fig. 1; Plate 17, Figs. 2, 4). The esophageal valve also serves as the floor for the initial portion of the esophagus.

The mouth is bounded by the outer lips (Ol,, Plate 16, Fig. 4; Plate 17, Fig. 4). It opens into a short oral tube (Ot) which terminates at the two lateral outswellings of the pharynx wall, the inner lips (Il), and a pronounced transverse ventral fold (Vf). The inner lips bear the paired jaws (J). The ventral fold is centrally grooved (Gr) and is the threshold to the buccal cavity, the latter being the entire space of the pharyngeal tube. That portion of the buccal cavity beneath the anterior tip of the odontophore is the

sublingual space (Sp).

The ventral fold is traversed on either side by ventrolateral ciliated grooves, the food grooves (Plate 16, Fig. 1; Plate 17, Fig. 4). They traverse the ventrolateral edge of the pharyngeal tube, pass up and over the large odontophore divaricator muscles, and over the lateral edges of the esophageal valve into the dorsal portion of the anterior section of the esophagus.

Jaw. F. C. Baker (1928) showed a small section of the jaw which appeared like bricks in a wall. Dundee (1957) stated that the jaw consisted of 25-30 cuticular plates. She derived this number from a longitudinal, histological view of the jaw area which included the inner lips. A camera lucida drawing of each jaw is shown in Plate 20, Fig. 10. The edge of each jaw is composed of at least 27 plates. The whole jaw is composed of many cuticular plates arranged in a narrow sheet. The length of this sheet is 0.13 mm to 0.16 mm and the width varies around 0.06 mm.

Radula. The radula is the typical taenioglossate type, i.e., numerous rows of teeth with each row consisting of a central flanked on either side by a lateral, an innner and outer marginal. There are 7 teeth per each row.

Nine radular ribbons were straightened out on slides and studied. The statistics on radular length, width, total rows of teeth, and rows of teeth in the formative stage are presented in Table 6.

Table 6

Radular Statistics

Statistics	*Pomatiopsis lapidaria*			*Oncomelania hupensis formosana*		
	$\overline{X}$ (mm)	S	Se	$\overline{X}$	S	Se
Radular Length	1.133	0.085	0.016	0.976	0.098	0.024
Radular Width	0.125	0.005	0.002	0.120	0.008	0.002
No. of Rows of Teeth	94	8.6	2.5	84	7.5	1.9
No. of Rows in the Formative Stage	19	5.6	1.9	19	5.3	1.4

$\overline{X}$ = The Mean

S = Standard Deviation

Se = Standard Error of the Mean

Table 7

A General Formula for the Most Common Cusp Arrangement in *Pomatiopsis lapidaria*

Tooth	central	lateral	inner marginal	outer marginal
Cusp formula	$\frac{1\text{-}1\text{-}1}{3\text{-}3}$	2-1-2(3)	6 ± 1	5-6
Per cent of snails from 3 populations where the cusp arrangement for an individual tooth was found	62	75	84	90

Table 8

The Total Types of Cusp Arrangement Found for Each Tooth in *Pomatiopsis lapidaria* and the Percentage of Radulae Showing That Arrangement

Central	%	Lateral	%	Inner Marginal	%	Outer Marginal	%
$\frac{1\text{-}1\text{-}1}{3\text{-}3}$	62	2-2-2	40	6	60	5	90
		2-1-3	39				
				7	60	6	56
$\frac{1\text{-}1\text{-}1}{2\text{-}2}$	40	1-1-2	18	8	16	4	6
$\frac{1\text{-}1\text{-}0}{2\text{-}2}$	2	2-1-3	6	5	13	7	6
$\frac{1\text{-}1\text{-}2}{3\text{-}3}$	2	2-1-4	6				
$\frac{2\text{-}1\text{-}2}{3\text{-}3}$	2	2-1-2 on one side					
$\frac{1\text{-}1\text{-}2}{2\text{-}2}$	2	2-1-3 on the other side					
0	2		12				

Rows of teeth at the tip of the radular sac and a little toward the sac opening are in various stages of formation, those closer to the end of the sac being the least formed. In this area the central may not be formed although the peduncles of the laterals could be counted. The total rows were found by counting all the centrals until they became too indistinct to count and then all the remaining rows of peduncles. Rows of teeth in the formative stages were counted until a row was found where all the cusps could be discerned on each of the 7 teeth.

Each of the 7 teeth is characterized by a varying number of cusps. The formulas for the cusp arrangements has been considered important throughout systematic molluscan literature. Reviewing this literature it is evident that on the one hand it is not generally appreciated that the variability in the number of cusps per tooth may be considerable not only between specimens from a single population but also along the same radular ribbon. The variability discussed here is not that due to wear which is readily observed for what it is. On the other hand, many who have observed variability often discredit the use of cusp arrangement as a major characteristic of either genera or species.

Knowledge of variability is essential and the presence of variation is not a problem if all the classes of variation can be adequately accounted for. It is, therefore, not sufficient to describe

1, 2, or even a dozen radulae until the full range of variation is documented. In the study of this species it was necessary to study about 50 radulae from 3 distinct populations in order to adequately encompass variation in cusp number.

In addition to cusp number, basic tooth morphology may vary between taenioglossate radulae of various genera, subfamilies, and families. Some of the variation in the morphology of the central tooth was discussed above in the section on systematics.

In Plate 19, the top row of teeth depicts the relationship between teeth as seen on the lingual ribbon, i.e., of tooth folded over tooth. All other teeth are shown disarticulated from the membrane and were drawn from various planes and views. The teeth were chosen to represent variations observed among the centrals and laterals. A series of inner and outer marginals is shown in Plate 20. For an accurate count of the cusps on the laterals and marginals it is advisable to have the teeth folded back far enough to expose all the cusps, e.g. Plate 19, lateral 5; Plate 20, teeth 2-4, 7-9.

Each cusp is composed of a thickened, rounded supporting piece (Sup) and a thin, blade-like cutting edge (Cu). In radular preparations the cutting edges are often torn away leaving only the supports (Plate 20, tooth 6). Where the cutting edge is drawn, the edge of the underlying support is represented by a dashed line. The body of the

central tooth (Ce) supports both anterior and basal (posterior) cusps. The supports for the basal cusps of the central have been discussed in the section of systematics. In Plate 19, central 6, note the characteristic shape of the posterior edge of the support (x). The supports for the large medial basal cusps give the face of the tooth a square appearance. There is no thickened tongue-like projection from the face of the central tooth. As shown in central 6, the posterior contour of the lateral angle sweeps medially and then bows posteriorly as a tongue-shaped structure. The latter is the membranous attachment for the posterior edge of the tooth. It is not thickened and is not an obvious structure.

The laterals and marginals are attached to the membrane by the base of the slender peduncle (Pd, Plate 19, Plate 20, tooth 1). The lateral tooth has a distinctive thickening (y, Plate 19, lateral 3). As shown, the medial 3 cusps of the lateral are born on a swelling which continues posteriorly over the face of the tooth as a molded thickening or ridge.

In Table 7, the arrangement of cusps for each tooth most commonly found is shown along with the percentage of radulae on which that arrangement was found to be present in at least 90 per cent of the teeth. Only 61 per cent of the snails had this representative formula although teeth could be found in these radulae which were not of the representative types. In Table 8, every cusp

arrangement found per tooth type is tabulated with the per cent of radulae on which it was found, regardless of the frequency with which it occurred. The only significant difference found between populations was found in the central tooth. Centrals from the radulae of snails from the Parker Mill population had a formula of $\frac{1\text{-}1\text{-}1}{2\text{-}2}$ in 61 per cent of the population, while in the Hog Back and Barton populations 80 per cent of the snails had a central with a formula of $\frac{1\text{-}1\text{-}1}{3\text{-}3}$. A rare case was found which had no centrals at all. An unusual percentage had a lateral tooth formula of 2-1-3 on one side of the central and 2-1-2 on the other side. This arrangement would continue the length of the ribbon.

Variation within the same lingual ribbon was greatest among the cusps of the marginal teeth. In 60 per cent, variation within a ribbon was limited to the marginals. Whether a marginal had 7 or 8 cusps would often depend on the presence or absence of a tiny lateral spur as shown in Plate 20, tooth 7. In only 20 per cent of the radulae did there appear to be only minor variation, i.e., a few outer marginals varying between 5 or 6 cusps. In the 40 per cent of the snails where the central or lateral tooth varied along the ribbon, a small stretch of about 10 centrals might have one formula while the next stretch of 15 or so would have another. In other cases only 5 or 6 centrals would vary along the whole ribbon.

Plate 14

DORSAL BUCCAL MASS AND ASSOCIATED ORGANS IN POMATIOPSIS LAPIDARIA

Bg	buccal ganglion
Bm	buccal mass
Cc	cerebral commissure
Cg	cerebral ganglion
Cl	columellar muscle
m_5	buccal protractor muscle
m_{16}	preventral dilator muscles
m_{17}	suspensors of the buccal mass
m_{22}	lateral cephalic retractor muscle
Ml_1	median labial nerve 1
Ml_2	median labial nerve 2
Mn_2	mantle nerve 2
On	osphradial nerve
Opt	optic nerve
pp_3	lateral nerve 3
Psc	pleuro-supraesophageal commisure
Sa	salivary gland
Sl	superlabial nerve
Ss	esophagus
Sug	superesophageal ganglion
Suv	supervisceral commissure
Tn	tentacular nerve

Plate 14

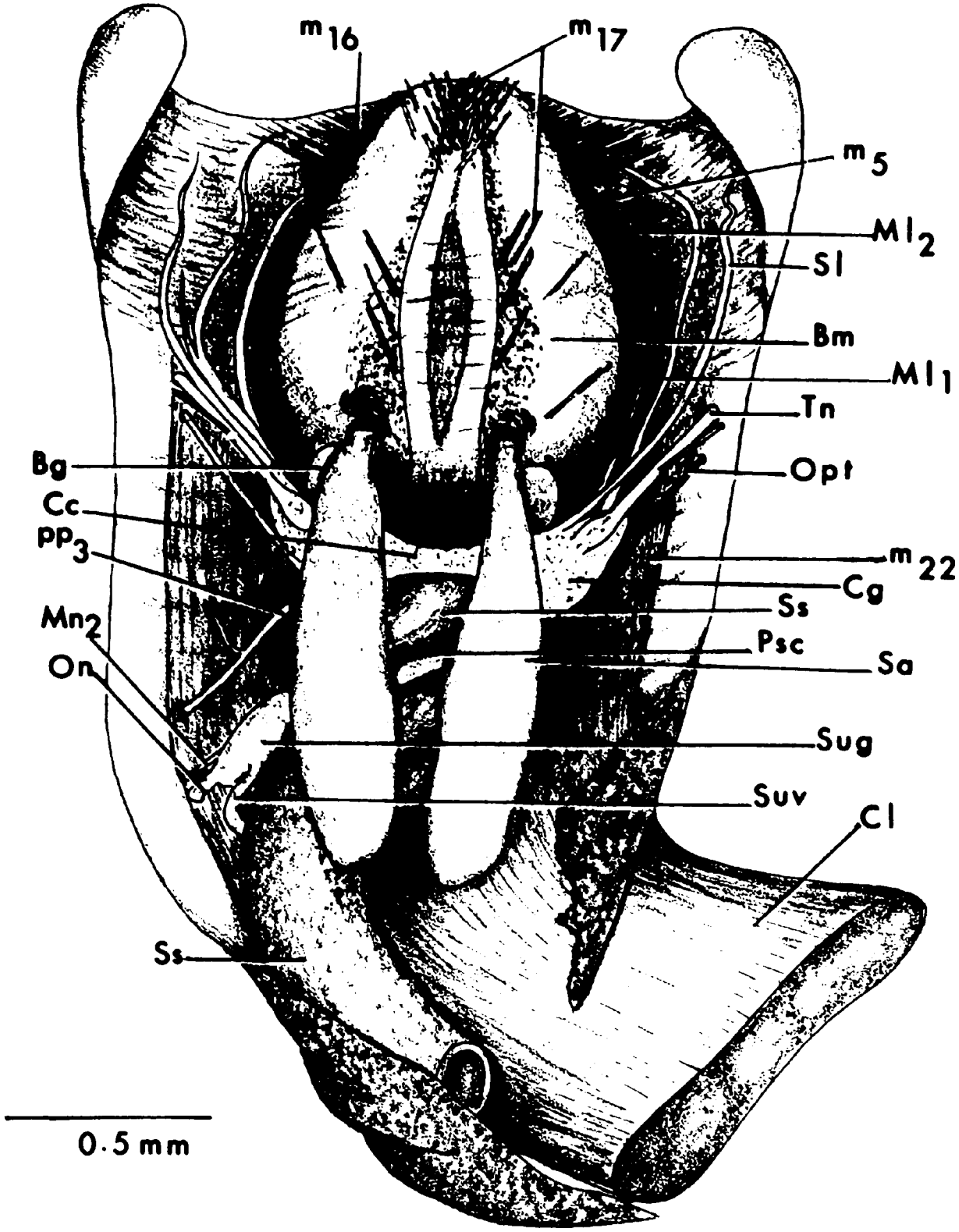

m16
m17
m5
Ml2
Sl
Bm
Ml1
Tn
Opt
Bg
Cc
pp3
m22
Cg
Ss
Mn2
Psc
Sa
On
Sug
Suv
Cl
Ss
0.5 mm

Plate 15

MUSCULAR, NERVOUS, AND DIGESTIVE SYSTEMS OF POMATIOPSIS LAPIDARIA

Fig. 1 The lateral aspect of the buccal mass with associated neural structure.

Fig. 2 The posterodorsal portion of the pedal haemocoel showing the relationship of the columellar muscle (Cl), mid-columellar supportive (m23), and pedal ganglia.

a nerve characteristically arising from p_6

b nerve characteristically arising from p_6 ventral to a

b_1 dorsal buccal nerve

b_2 esophageal nerve

b_3 central buccal nerve

b_4 anterior buccal nerve

Bg buccal ganglion

Cb cerebrobuccal commissure

Cg cerebral ganglion

Cl columellar muscle

Cp cerebropedal commissure

C_8 cerebro-tensor nerve

Eo external odontophore membrane

m_5 buccal protractor muscle

m_6 preventral protractors

m_8 anterior jugalis

m_9 buccal constrictor

m_{11} dorsolateral buccal protractor

m_{12} buccal retractor

m_{13} membranous jugalis

m_{16} preventral dilators

m_{17} suspensors of the buccal mass

m_{20} rostral retractors

m_{22} lateral cephalic retractors

m_{23} mid-columellar supportive

m_{25} dorsal pedal tensor

m_{26} dorsal propodial retractor

Mg metapodial ganglion

Ml_1 median labial nerve 1

Ml_2 median labial nerve 2

Opt optic nerve

p_1 lateral retractor nerve

p_2 pedal nerve to the anteroventral wall

p_3 major lateral nerve

p_4 propodial commissure

p_5 mid-propodial nerve

p_6 metapodial commissure

p_7 dorsolateral pedal nerve

Pd Pedal ganglion

Pg Propodial ganglion

Pp pleuropedal commissure

pp_1 lateral nerve 1

pp_2 penial nerve

pp_3 lateral nerve 3

pp_4 lateral nerve 4

Rp right pleural ganglion

Sa salivary gland

Sl superlabial nerve

Ss esophagus

Sta statolith

Stc statocyst

Sul sublabial nerve

Tn tentacular nerve

Plate 15

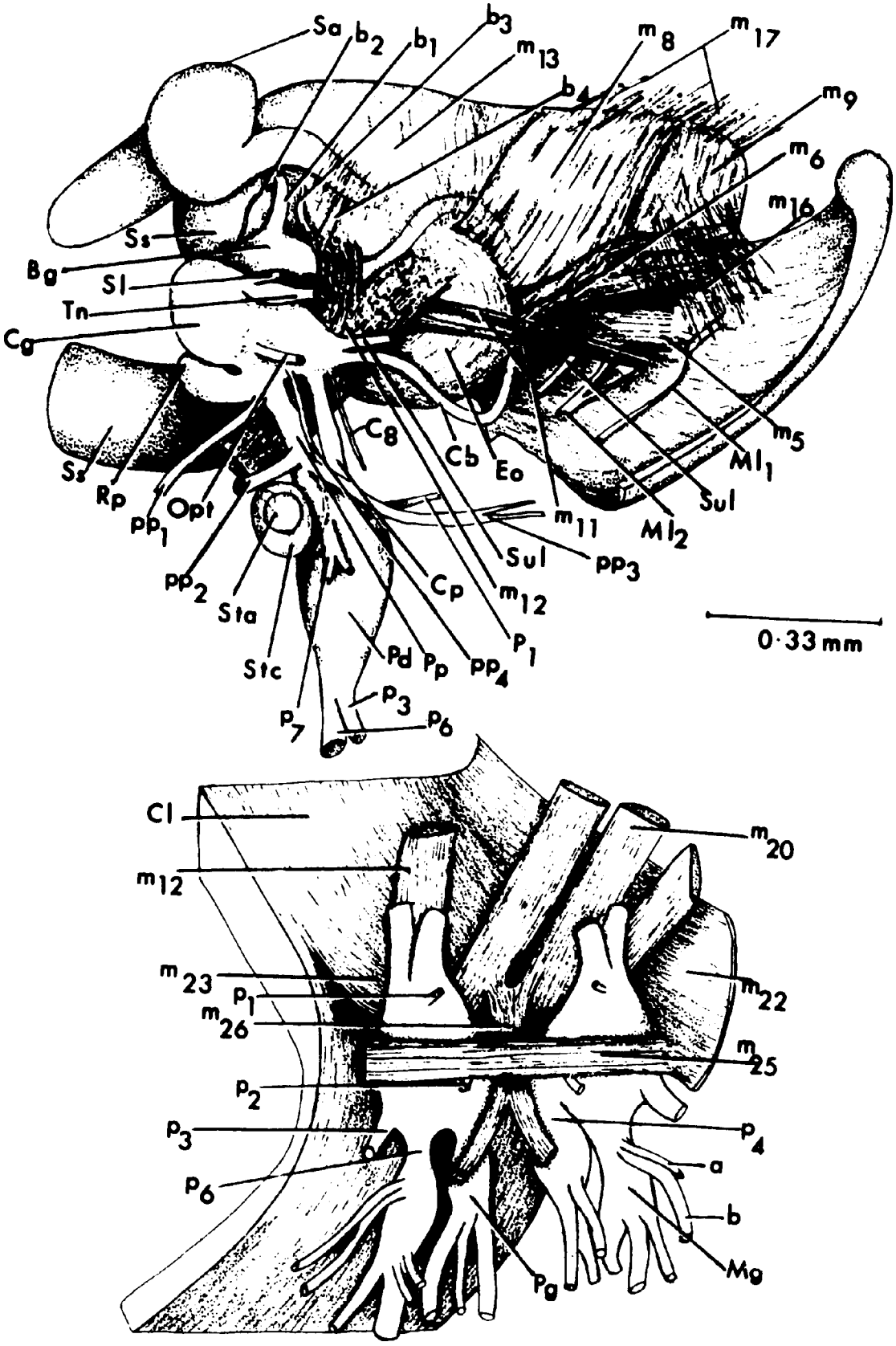

Sa
b2
b1
b3
m13
b4
m8
m17
m9
m6
m16
Ss
Ba
Sl
Tn
Cg
C8
Cb
Eo
m5
Ml1
Sul
Ss
Rp
pp1
Opt
m11
Ml2
pp2
Sta
Sul
pp3
Cp
m12
P1
Stc
Pd
Pp
pp4
P3
P7
P6
0·33 mm
Cl
m20
m12
m23
P1
m22
m26
m25
P2
P3
P4
a
P6
b
Mg
Pg

Plate 16

MUSCULATURE AND PHARYNGEAL STRUCTURES IN POMATIOPSIS LAPIDARIA

Fig. 1 Posterior portion on the pharyngeal tube showing the dorsal aspect of the odontophore with the radula removed.

Fig. 2 Left buccal cartilage from the dorsal view wrapped in intrinsic muscles. Muscle m_1 is not shown.

Fig. 3 Lateral aspect of the left buccal cartilage showing muscles arising or inserting on the cartilage. The position of the cartilage is shown as in Fig. 4.

Fig. 4 Schematic representation of the odontophore within the posterior portion of the pharyngeal tube. The left side of the odontophore is shown.

Fig. 5 The fused cup-like muscles making up the mediolateral cartilage tensor (m_2) and the subradular membrane which continues from this muscle. The medial radular retractor arises from the postero ventral curvature of this muscle.

a	thickened portion of the subradular membrane
Bca	buccal cavity
Bf	floor of the pharyngeal tube
Ca	cartilage
Ev	esophageal valve
Fg	food groove
m_1	lateral cartilage tensor
m_2	mediolateral cartilage tensor
m_3	odontophore divaricator
m_4	medial radular retractor
m_5	buccal protractor
m_6	preventral protractor
m_{15}	suspensor of the radular sac
m_{17}	suspensor of the buccal mass
m_{20}	rostral retractor
m_{21}	oral sphincter
Mo	mouth
Ot	oral tube
Ra	radula
Ras	radular shield
Rb	pharyngeal roof, or roof of the buccal mass
Rf	roof of the rostrum
Rpc	rostral portion of the cephalic haemocoel
Sp	sublingual space
Sr	subradular membrane
Ss	esophagus
Vf	ventral fold

Plate 16

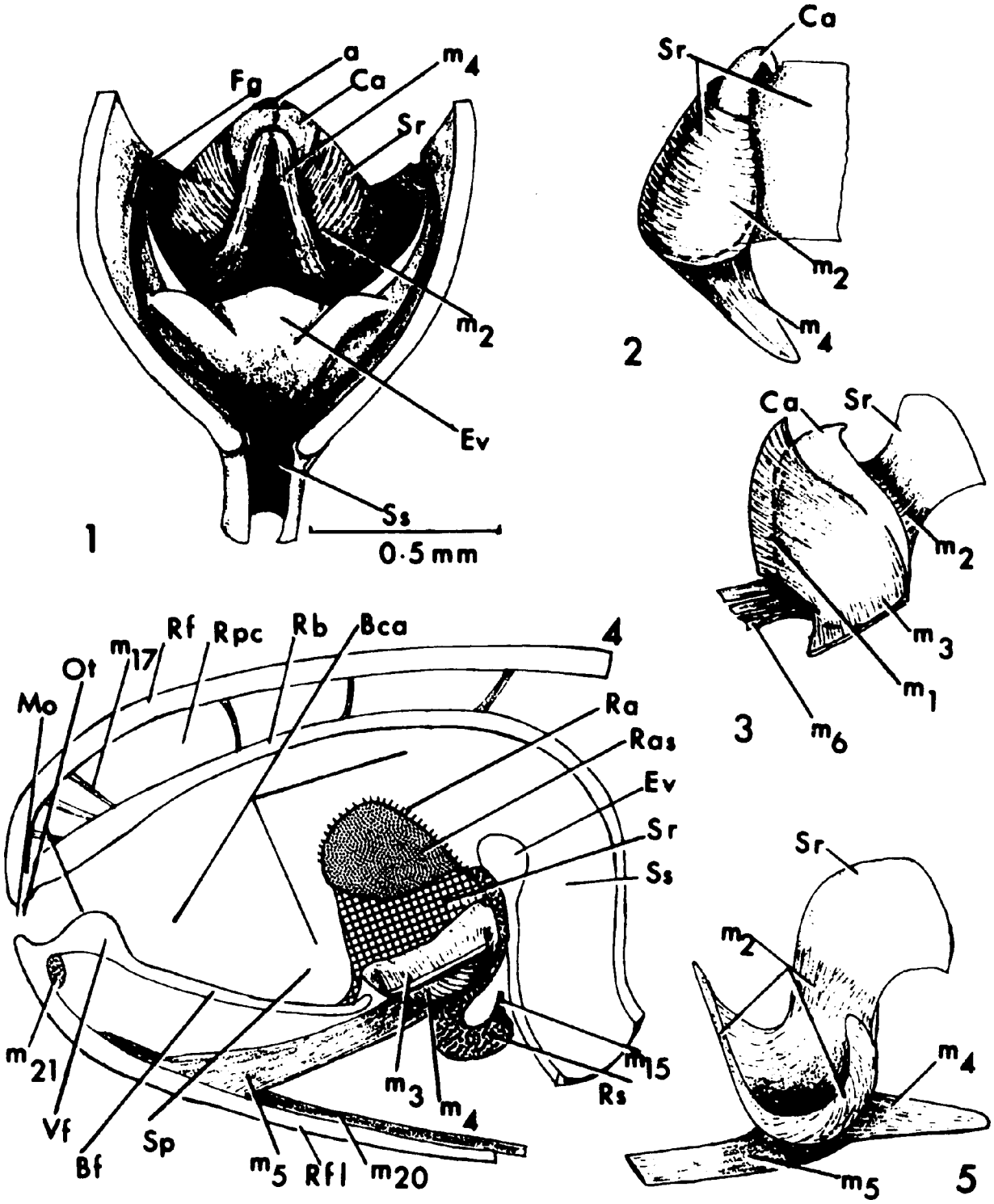

a
Fg
Ca
m4
Sr
m2
Ev
Ss
0·5 mm
1
Ca
Sr
m2
m4
2
Ca
Sr
m2
m3
m1
m6
3
Rf
Rpc
Rb
Bca
4
m17
Ot
Mo
Ra
Ras
Ev
Sr
Ss
m21
Vf
Bf
Sp
m5
Rf1
m20
m3
m4
m15
Rs
Sr
m2
m4
m5
5

Plate 17

MUSCULATURE OF POMATIOPSIS LAPIDARIA

Fig. 1 Muscles arising from the mid-columellar supportive muscle (m_{23}).

Fig. 2 Dorsal view of the odontophore before removing the radula.

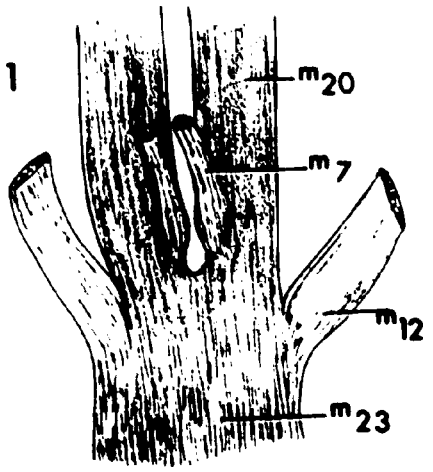
Fig. 3 Dorsal view of the odontophore with the radula removed and the medial radular retractor pulled backwards from the odontophore.

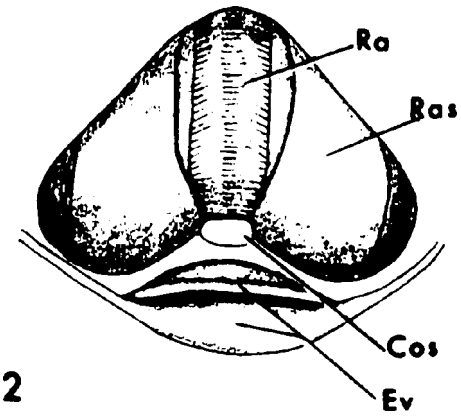
Fig. 4 Dorsal aspect of the opened pharyngeal tube showing the odontophore.

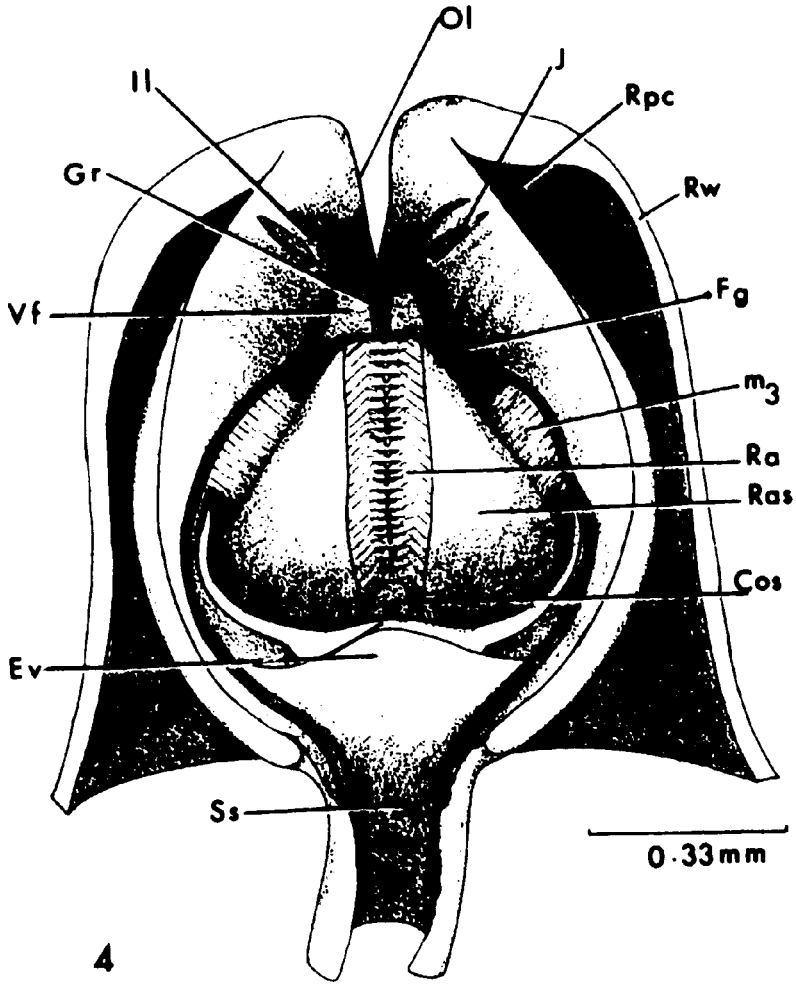
Fig. 5 The cartilages are shown separated and folded out to show the medial surface of the cartilages wrapped in the mediolateral cartilage tensor muscle.

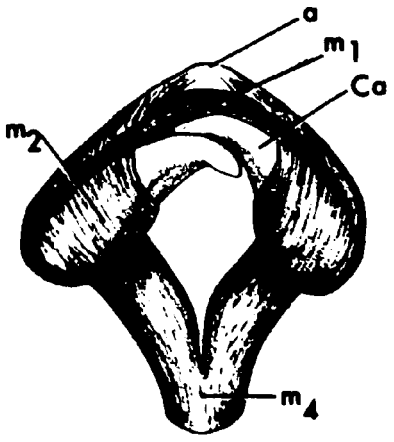
a thickened anterior portion of the subradular membrane
Ca cartilage
Ev collostyle tip
Ev esophageal valve
Fg food grove
Gr central groove in the ventral fold
Il inner lip
J jaw
m_1 lateral cartilage tensor
m_2 mediolateral cartilage tensor
m_3 odontophore divaricator
m_4 medial radular retractor
m_7 radular protractor
m_{12} buccal retractor
m_{20} rostral retractor
m_{23} mid-columellar supportive
Ol outer lip
Ra radula
Ras radular shield
Rpc rostral portion of the cephalic haemocoel
Rw rostral wall
Ss esophagus
Vf ventral fold

Plate 17


1
m20
m7
m12
m23


Ra
Ras
Cos
Ev
2


Ol
J
II
Rpc
Gr
Rw
Vf
Fg
m3
Ra
Ras
Cos
Ev
Ss
0·33mm
4


a
m1
Ca
m2
m4
3

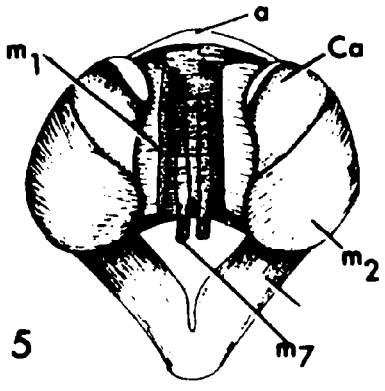

a
m1
Ca
m2
m7
5

Plate 18

MUSCULATURE OF POMATIOPSIS LAPIDARIA

The buccal mass was pulled out of the rostrum to expose the muscles and nerve endings ventral to the buccal mass.

a	area where the floor of the rostrum slopes downward as the anterior wall of the pedal haemocoel
b	posterodorsal gap of the pedal haemocoel
b_6	posterior buccal nerve
Bc	buccal commissure
Bg	buccal ganglion
Cb	cerebrobuccal commissure
Cl	columellar muscle
Eo	external odontophore membrane
m_5	buccal protractor
m_6	preventral protractor
m_7	radular protractor
m_{11}	dorsolateral buccal protractor
m_{12}	buccal retractor
m_{20}	rostral retractor
m_{22}	lateral cephalic retractor
m_{23}	mid-columellar supportive
m_{24}	tensor magnus
Mb	membrane around the radular sac
Ml_1	median labial nerve 1
Ml_2	median labial nerve 2
p_1	lateral retractor nerve from the pedal ganglion
Rs	radular sac
Sul	sublabial nerve

Plate 18

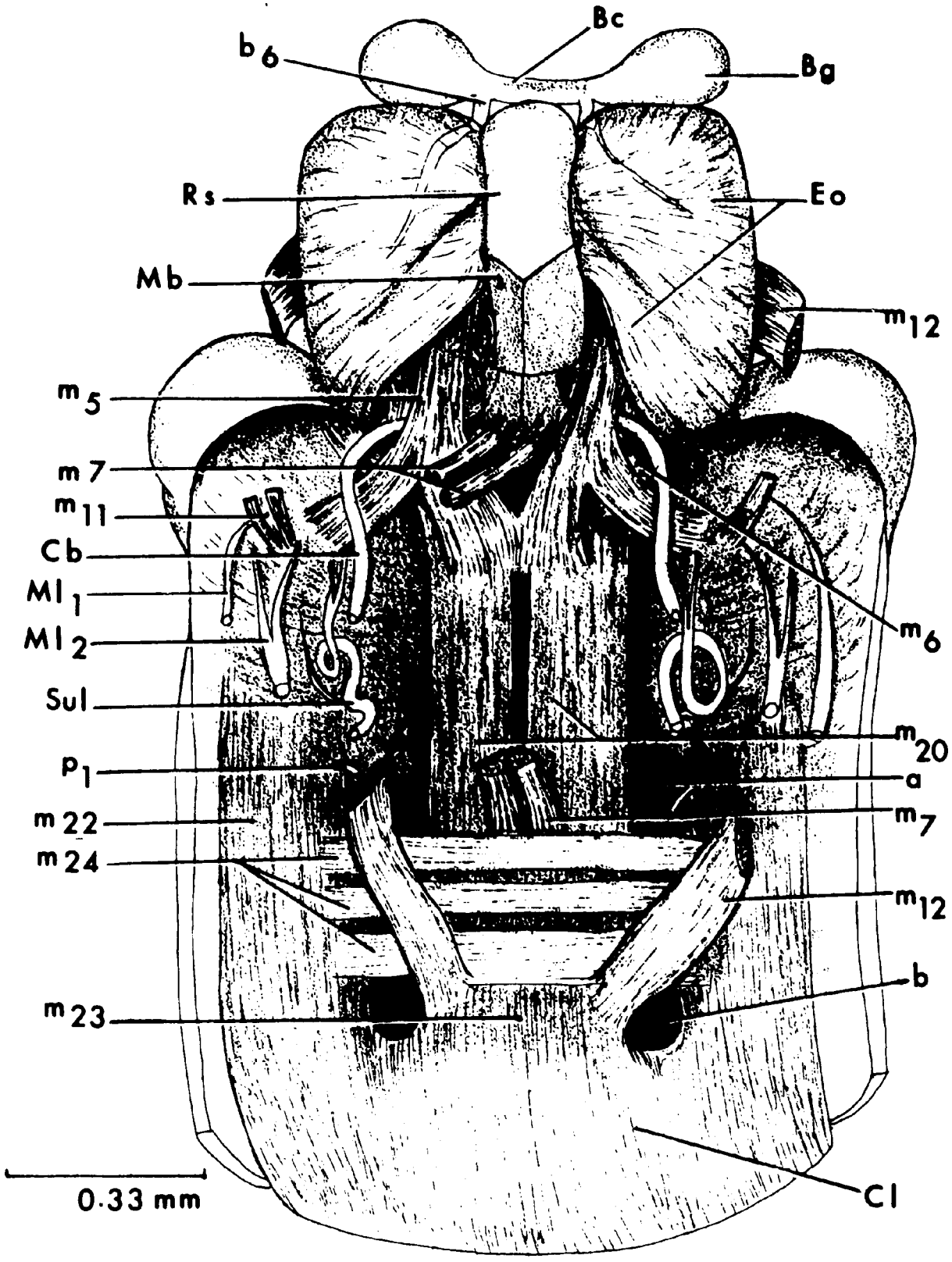

Bc
b6
Bg
Rs
Eo
Mb
m12
m5
m7
m11
Cb
Ml1
Ml2
m6
Sul
m20
p1
a
m22
m7
m24
m12
b
m23
Cl
0.33 mm

Plate 19

RADULA OF POMATIOPSIS LAPIDARIA

Ce	central tooth
Cu	cutting edge of a cusp
Im	inner marginal tooth
La	lateral tooth
Oma	outer marginal tooth
Pd	peduncle
Sup	supportive for the cutting edge
U	anterior edge of the tooth
V	lateral angle
W	posterior edge or basal edge of the tooth
X	supportive for the large medial, basal cusp of the central tooth.
Y	molded thickening which gives the anterior medial part of the lateral tooth a distinct curvature

Plate 19

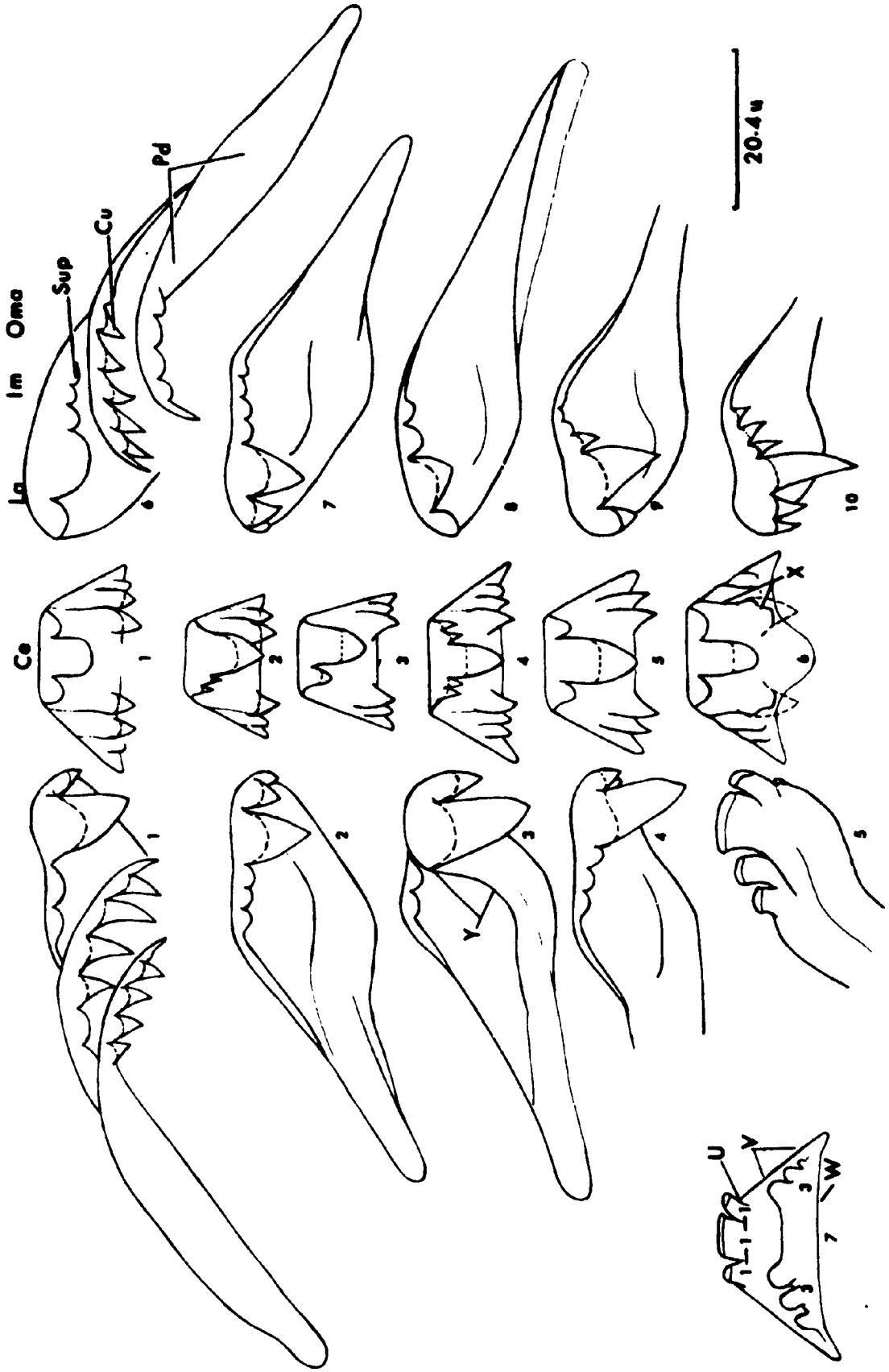


Plate 20

RADULA OF POMATIOPSIS LAPIDARIA

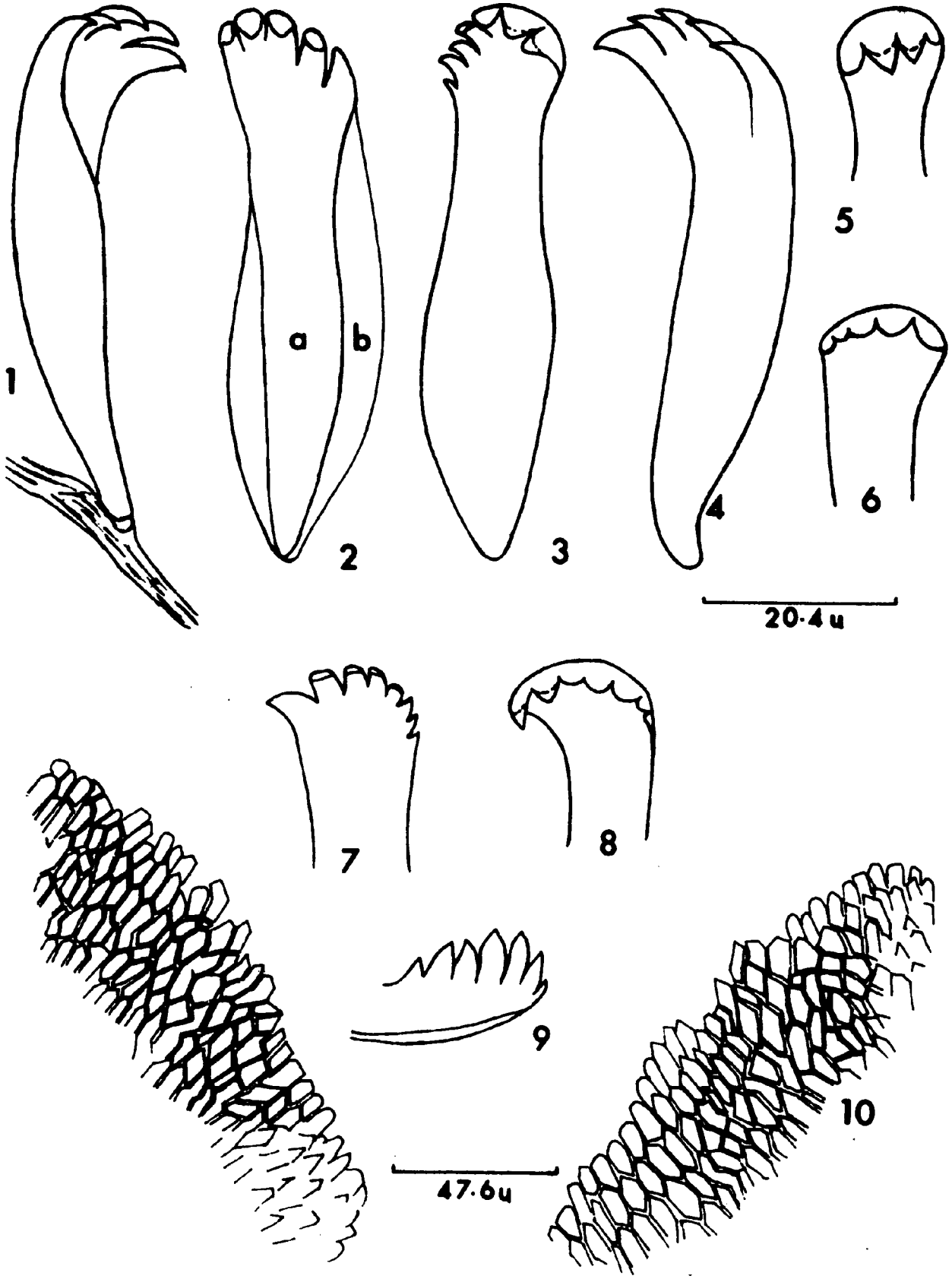
Figs. 1-6 Variations in the outer marginal teeth.

Figs. 7-9 Variations in the inner marginal teeth.

Fig. 10 The jaw.

a thickened central core of the peduncle
b thin, wing-like expanded portion of the peduncle

Plate 20



In Table 3 are listed the authors who have previously figured or discussed the radula of Pomatiopsis lapidaria. Also shown are the formulas they have figured or presented. The variations discussed in this paper encompass the formulas presented by Stimpson (1865), Thiele (1928), Abbott (1948a), and Dundee (1957). Baker (1902) studying the work of Stimpson (1865), discusses the 2 incurved basal denticles on each side of the central tooth. In 1926, however, in his family diagnosis for the Pomatiopsidae, he mentions only 2 large basal denticles for the central and it is this arrangement he figures in 1928, i.e., one large basal cusp on either side of the central. In the light of the weight of evidence of other workers [Stimpson (1865), Thiele (1928), Abbott (1948), and Dundee (1957)], it is evident that Baker (1926, 1928) either did not observe the other cusps which were present or he studied an extremely rare variant. Likewise, he reversed the inner and outer marginals; it is more likely that the inner marginal had 9 and the outer marginal 6 cusps in the specimen that he studied.

Annandale (1924) reports the highly improbable number of 10 cusps for the inner and outer marginals. These can only be considered misinterpretations. The central tooth formula for the anterior cusps, i.e., 2-1-2 , could only represent a rare variant. Thiele (1929) gives a formula intended for the genus, thereby including Pomatiopsis lapidaria and P. cincinnatiensis. Inner and

outer marginals with 4 and 3 cusps, respectively, are characteristic of P. cincinnatiensis.

7. Musculature.

Muscles of the Odontophore and Buccal Mass.

It is beyond the scope of this paper to attempt the detailed study on buccal mass musculature and function as presented by Carriker (1946a) for Lymnaea stagnalis appressa (Say) or by Nesbit (1953) as presented by Fretter and Graham (1962) on the functional relationships in Monodonta lineata. For a full review of the literature pertaining to the buccal mass musculature one should consult Herrick (1906), Carriker (1946a), and Fretter and Graham (1962). There is not much literature on the buccal mass musculature of taenioglossate snails. Johansson (1939) presented a noteworthy paper on the musculature of Littorina littorea; Krause (1949) discussed the anatomy of Lithoglyphus naticoides. Fretter and Graham (1962) show several figures of the buccal mass musculature of Viviparus viviparus. The last authors review other literature which pertains to this group. As much of the musculature shown by these authors apparently does not pertain to the muscles described in this study, muscle nomenclature becomes a problem. Johansson (1939) avoided this problem by numbering the muscles. I have named all the muscles discussed on the basis of position or inferred function.

Intrinsic Muscles of the Odontophore.

The intrinsic muscles of the odontophore are those intimately associated with the cartilages. Removing the radula, radular shield, and radular sac from the odontophore (Plate 16, Fig. 1) and viewing the dorsal aspect, one observes two muscles (m_4) each running from a posterior, ventrolateral position towards the mid-anterodorsal line of the odontophore. They fuse and form a trough which supports the radular sac. This muscle, the medial radular retractor, is readily lifted from the odontophore and pulled backward exposing the tips of the buccal cartilages (Plate 17, Fig. 3). The tips of the cartilages overlap as shown with either the right over the left tip or the reverse. Each cartilage is about 0.6 mm long. The shape of the medial surface of the cartilages is shown in Plate 17, Fig. 5. The dorsal outline of the cartilage (left) seen through the occluding musculature is shown in Plate 16, Fig. 2. Each cartilage swells posteriorly reaching a width of 0.26 mm. The height of the cartilages is about 0.35 mm. As shown in Plate 17, Fig. 3, the posterior ends of the cartilages are widely separated leaving adequate room for the radular sac to nestle between.

1. Lateral Cartilage Tensor. (Plate 16, Fig. 3; Plate 17, Figs. 4,5) The lateral cartilage tensor passes as an arc-like band about 0.36 mm wide about the ventroanterior end of the 2 cartilages binding the cartilages together. The muscle fastens along

the exterior lateral edges of the cartilages (Plate 16, Fig. 3).

2. Mediolateral Cartilage Tensor (Plate 16, Figs. 1,2,3,5; Plate 17, Figs. 3,5) The mediolateral cartilage tensor is a pronounced muscle seen arising from the ventral edge of each cartilage as well as the ventral and posterolateral edge thus forming a cup-like structure encasing the posterior end of each cartilage (Plate 16, Fig. 5; Plate 17, Fig. 5). The muscle runs dorsally and anteriorly over the medial surface of each cartilage and appears thickened at the dorsal edge of the cartilages. From this thickening appears to arise a membranous continuation which continues as a wide, thin band down laterally, and around the anterior edge of the cartilages covering the lateral cartilage tensor (Plate 16, Figs. 2,4; Plate 17, Figs. 4,5). This membranous portion is called the subradular membrane (Sr). The mid-ventral crest of the membrane is thickened (a, Plate 17, Figs. 3,5) and serves as the place for the insertion of the radular protractor muscles (m_7, Plate 17, Fig. 5). The radular shield (Ras) is tightly appressed to the subradular membrane (Plate 16, Fig. 4). Ventrally, the subradular membrane is continuous with the floor of the pharynx to which it becomes tightly and inseparably appressed (Plate 46, Fig. 4).

On either side of the ventral crest of the subradular membrane a thin muscle inserts (this muscle is not figured). Its origin is on the posteroventral edge of the cartilages. This muscle, m_{18},

is the lateral membrane protractor.

3. Odontophore Divaricator. (Plate 16, Figs. 3,4; Plate 17, Fig. 4) The odontophore divaricator arises from the posterolateral edge of each cartilage. The muscle is a band which runs laterally to the pharynx wall and serves, in part, as the major source of support and attachment of the pharynx wall to the odontophore.

4. Medial Radular Retractor. (Plate 16, Figs. 1,2,4,5; Plate 17, Figs. 3,5). The origin of this muscle is from the posterior, ventrolateral portion of the mediolateral cartilage tensor. As mentioned above, this muscle runs dorsally between the cartilages, over the medial surface of the mediolateral cartilage tensor, fuses with the counterpart from the other cartilage, and rests with the anterodorsal tip on the crossed anterior ends of the buccal cartilages. They insert on the anterior, ventrolateral portion of the radular sac at a point 1/5 the way posteroventrally from the tip of the muscle. The muscle is trough-like and serves to support the radular sac as well as retract it.

Not figured is a pair of thin muscles (m_{19}) which run from the mid-ventrolateral edge of the style sac, between the cartilages, under the anteroventral edge of the lateral cartilage tensor, where they insert on the subradular membrane to either side of the radular protractor. This pair of tiny muscles is the ventral

membrane protractor.

Extrinsic Muscles of the Odontophore.

5. Buccal Protractors. (Plate 14; Plate 15, Fig. 1; Plate 16, Figs. 4,5; Plate 18) The origin of these paired muscles is shown in Plate 18. There are characteristically 2 slips for each of the protractors; one from the rostral retractor (m_{20}) and the other from the anterior, ventrolateral rostral wall. The slips arising from the rostral retractors are usually fused as shown. Occasionally all the slips are fused in a single arc of muscle, but this is rare in this species. Each muscle inserts partially on the posteroventral surface of the medial radular retractor and partially on the mediolateral cartilage tensor (Plate 16, Figs. 4,5). These broad, heavy muscles serve to pull the odontophore anteriorly as well as depress the posterior end of the odontophore.

6. Preventral Protractors. (Plate 15, Fig. 1; Plate 16, Fig. 3; Plate 18) The origin of these muscles is at the tip of the rostrum immediately adjacent to the oral aperture (Plate 15, Fig. 1). They insert on the posterior ventrolateral edge of each cartilage (Plate 16, Fig. 3). These bands of muscle are most readily observed from the lateral, external view of the buccal mass (Plate 15). They serve to protract the odontophore as well as the pharyngeal walls. The number of muscle bands is variable.

7. Radular Protractor (Plate 17, Figs. 1, 5; Plate 18) The paired radular protractors arise from the base of the rostral protractors as shown in Plate 17, Fig. 1. They run anteriorly side by side bound in a connective tissue sheath with the main vascular supply to the buccal mass. They pass over the point where the fuxed medial slips of the buccal protractors separate (Plate 18), pass into the connective tissue sheet which surrounds the radular sac (Mb), run between the cartilages to insert on the central crest of the sub-radular membrane (Plate 17, Fig. 5). These muscles serve to depress the tip of the odontophore while protracting the radula slightly over the bending plane of the odontophore.

Extrinsic Muscles of the Buccal Mass

8. Anterior Jugalis (Plate 15, Fig. 1) Arising from the anterior dorsal crest of the buccal mass, this muscle band, about 0.40 mm wide, runs obliquely posteroventrally covering the posterior portion of the buccal constrictor (m_9). It inserts about the odontophore divaricator and the ventrolateral edge of the cartilage. The cerebrobuccal commissure passes between this muscle and the buccal constrictor.

9. Buccal Constrictor (Plate 15, Fig. 1) The buccal constrictor wraps the anterior end of the buccal mass from the anterior end of the odontophore forward. The posterior portion of this muscle is covered by the anterior jugalis.

10. Odontophore Levator (not figured) The odontophore levator runs obliquely from the odontophore to the dorsal portion of the buccal constrictor between the buccal constrictor and the anterior jugalis. This is a slender muscle and overlies the cerebrobuccal commissure as does the anterior jugalis. The insertion is with the anterior jugalis.

11. Dorsolateral Buccal Protractor (Plate 15, Fig. 1; Plate 18) The origin of this muscle is from the anterolateral rostral wall as shown in Plate 18. The muscle (m_{11}) arises from each side as a single thin strand or 2 thin strands which run parallel to an insertion on the lateral edge of the cartilage or the odontophore divaricator. The insertion of this muscle is covered by the buccal retractor (Plate 15, Fig. 1, m_{12}). Commonly the protractor bifurcates, the anterior slip fusing with the anterior slip of the retractor with both inserting on the divaricator muscle. The posterior protractor slip runs posteroventrally over the exterior odontophore membrane to fuse with fibers from the tensor membranous mentioned below.

12. Buccal Retractor (Plate 15, Figs. 1,2; Plate 17, Fig. 1; Plate 18) These pronounced paired muscles (m_{12}) arise from the basal part of the mid-columellar supportive (m_{23}, Plate 17, Fig. 1; Plate 18). They run anteriorly passing the medial surfaces of the cerebral ganglia, the pleuro-pedal and the cerebro-pedal commissures to insert on the divaricator muscle or the lateral car tilage surface. Before inserting this broad muscle bifurates sending the

anterior slip to an insertion on the odontophore; the posterior slip sends fibers into the membranous jugalis (m_{13}).

13. Membranous Jugalis (Plate 15, Fig. 1; Plate 14) Posterior to the anterior jugalis (m_8) and dorsal to the external odontophore membrane (Eo), the buccal mass is more fleshy and only sparsely laced with muscle fibers. The salivary glands enter this tissue; the esophagus arises from posterior continuations of this tissue.

14. Tensor Membranous Muscle (not figured) The lateral musculature of the odontophore bulges outward making the contour of the odontophore evident to one observing the lateral buccal mass (Plate 15, Fig. 1). This musculature is hidden from view as it is wrapped in a membrane, the external odontophore membrane (Eo), which is continuous between the 2 halves of the odontophore. Posteroventrally this membrane passes between the ventral, protruding, recurved end of the radular sac and the odontophore musculature (Eo, Plate 18).

A slender muscle, the tensor membranous, runs from side to side across the external odontophore membrane through the angle formed by the emerging esophagus and the membrane. This muscle sends branches over the ventrolateral surface of the membrane.

15. Suspensor of the Radular Sac (Plate 16, Fig. 4) The origin of this muscle (m_{15}) is the thickened tensor membranous muscle (m_{14}) at the point where the latter passes over the recurved ventral tip of the radular sac. It inserts on the membranes of the tip of the radular sac. The muscle may be forked with a common point of insertion, the origins slightly separated on the tensor membranous muscle.

16. Preventral Dilator Muscles (Plate 14; Plate 15, Fig. 1) Numerous thin muscle strands run from the buccal constrictor muscle and the preventral protractors to the anterolateral rostral wall.

17. Suspensors of the Buccal Mass. (Plate 14; Plate 15, Fig. 1; Plate 16, Fig. 4) Irregularly placed muscle strands run from the dorsal and dorsolateral surface of the buccal mass to the rostral roof. Anteriorly, from the dorsal crest of the buccal constrictor and anterior jugalis, these muscles are more dense and some of them undoubtedly serve to protract the buccal mass.

18. Lateral Membrane Protractor (discussed under 2).

19. Ventral Membrane Protractor (discussed under 4).

Body Musculature.

The principal muscle of the body is the columellar muscle (Cl). In Plates 5 and 6 this muscle is observed emerging from the ventral mantle tissue behind the collar (M). Only a portion of

this wide muscle is shown. As previously mentioned, the muscle is normally pressed and bound to the ventral wall of the mantle cavity. It is fused with the columella of the shell at a level corresponding to the posterior end of the mantle cavity.

In Plate 4, the muscle is shown emerging from the epithelium covering the "neck." In Plate 14, the rostral and "neck" epithelium are slit and folded back to reveal this broad muscle which is the basis of support for the head-foot region. The esophagus was cut at the level of the pleuro-supraesophageal commissure (Psc), the cerebral commissure was cut, and the posterior region of the buccal retractors (m_{12}) was cut. The posterior end of the buccal mass was then pulled upward out of the rostral portion of the cephalic haemocoel and forward using the origins of the buccal protractors as a hinge (Plate 18). The radular protractors (m_7) were then cut enabling the completion of pulling the buccal mass forward. Finally, removing the dorsal nervous system, one could observe the musculature underlying the organs shown in Plate 14.

The columellar muscle, beneath the point where the pleuro-supraesophageal commissure crosses the esophagus (Plate 14) sends 3 pronounced slips anteriorly while it sweeps ventrally in an arc as shown in Plate 15, Fig. 2. The 3 slips are the 2 lateral cephalic retractors (m_{22}) and the centrally positioned mid-columellar supportive (m_{23}, Plate 18).

The mid-columellar supportive muscle serves as the origin for a number of important muscles. On either side of the origin of the columellar supportive is noted a cavity (b, Plate 18). These cavities lead into the posterior portion of the pedal haemocoel where the ventrally curved columellar muscle forms the posterior wall and the mid-columellar supportive forms the roof. Laterally there is a space between the mid-columellar supportive and the lateral cephalic retractors which marks the dorsolateral edges of the pedal haemocoel. The mid-columellar supportive bifurcates anteriorly into 2 band-like muscles which continue across the dorsal pedal haemocoel and run anteriorly over the floor of the rostrum (Plate 17, Fig. 1; Plate 18). These are the rostral retractors (m_{20}).

Johansson (1939) has an excellent photograph of a gross dissection of the rostral area of Littorina littorea showing these paired muscles running toward the oral aperture as they do in Pomatiopsis lapidaria. Anteriorly the rostral retractors pass beneath the point where the medial slips of the buccal protractors take their origin; they send numerous inserting slips around the oral aperture on the rostral floor.

The origin of the radular protractors is at the dorsomedial base of the rostral retractors (Plate 17, Fig. 1). They are characteristically slightly swollen at their base. The origin of the

buccal retractors (m_{12}) is shown in Plate 17, Fig. 1 and Plate 18. They arise at the dorsal, posterolateral base of the mid-columellar supportive muscle.

Around the oral aperture at the rostral tip is a thin circular band of muscles best observed by clearing the rostral floor of the buccal protractors (m_5). This band is the labial sphinctor (Plate 16, Fig. 4, m_{21}). Anterior to the origin of the buccal retractors is a sheet of muscles running from side to side between the lateral cephalic retractors (m_{20}). Characteristically this sheet, the tensor magnus (m_{24}) is split up into 3 to 5 discrete bands (Plate 18). The sheet is 0.36 mm wide and about 0.96 mm long. It rests upon the mid-columellar supportive muscle as well as the posterior portion of the rostral retractors and supports the posterior portion of the contracted buccal mass as well as providing a supportive framework for the cerebral ganglia. The tensor magnus and the mid-columellar supportive form a sort of roof over the pedal haemocoel separating it in a loose manner from the cephalic haemocoel. The paired pleuropedal commissures, one on either side of the mid-columellar supportive, pass from the cerebral area between the posterior and mid-slips of the tensor magnus down into the pedal haemocoel to connect with the pedal ganglia. The cerebropedal commissures do likewise, passing between the mid and anterior slips of that muscle (Plate 18). The origin of the buccal retractor

(m_{12}) is sometimes split so that an anterior slip appears to arise from the posterior slip of the tensor magnus (Plate 18).

The lateral cephalic retractors are powerful slips (m_{22}) giving support to the posteroventral wall of the rostrum. They terminate at about the point where the rostral floor turns ventrally forming the anterior wall of the pedal haemocoel (Plate 18). The relationship of the ventrally curving columellar muscle (Cl), mid-columellar supportive (m_{23}), and lateral cephalic retractor (m_{22}) is shown with regard to the posterior pedal haemocoel and the pedal ganglia (Plate 17, Fig. 2). The columellar muscle sweeps ventro-posteriorly beneath the operculum. Where the rostral floor slopes down to form the anterior wall of the pedal haemocoel some transverse muscle fibers are noted passing between the lateral cephalic protractors. These muscles, the dorsal pedal tensors (m_{25}) lie against the anterior wall of the pedal haemocoel and pass across the mid-anterior surface of the pedal ganglia or a little dorsal to the mid-length of these ganglia.

A single muscle arises from the ventral origin of the rostral retractors, the dorsal propodial retractor (m_{26}, Plate 15, Fig. 2). This muscle passes anteroventrally between the pedal ganglia over the pedal commissure, forks, and sends a slip ventro-laterally to the anterior haemocoel wall beneath the dorsal pedal tensor.

At the level of the propodial ganglia, from the mid-anterior haemocoel wall, arises a muscle about 0.15 mm wide which bifurates and sends a slip laterally, right and left respectively, under the point where the propodial ganglia enter the anterior musculature, back under the metapodial commissure, to the posterolateral wall of the descending columellar muscle. This is the mid-ventral protractor (m_{27}) shown for Oncomelania hupensis formosana, which has the same arrangement (Plate 13, Fig. 1).

8. Nervous System.

In the study of neural anatomy for comparative, systematic use, considerable attention was directed towards the position of ganglia and their dimensions, the number of nerves and their respective points of origin on a given ganglion, the lengths of the major commissures, and especially the amount of variation encountered in all of the above. Secondary and especially tertiary branches of nerves were found to be highly variable and were not generally considered for this comparative study.

The previous work on the neural anatomy of Pomatiopsis lapidaria (Dundee, 1957) contained major discrepancies with my own observations. The work presented here is derived entirely from my own observations made on over 100 snails dissected especially for neural structure. A classical, extensive study on comparative

Plate 21

NERVOUS SYSTEM OF POMATIOPSIS LAPIDARIA

Fig. 1 Dorsal aspect of the "brain" or central portion of the nervous system lifted out of the rostrum.

Fig. 2 Anterior aspect of the pedal ganglia.

Fig. 3 A rare variant in that a distinct pleuro-subesophageal commissure is found between the left pleural ganglion and the subintestinal ganglion.

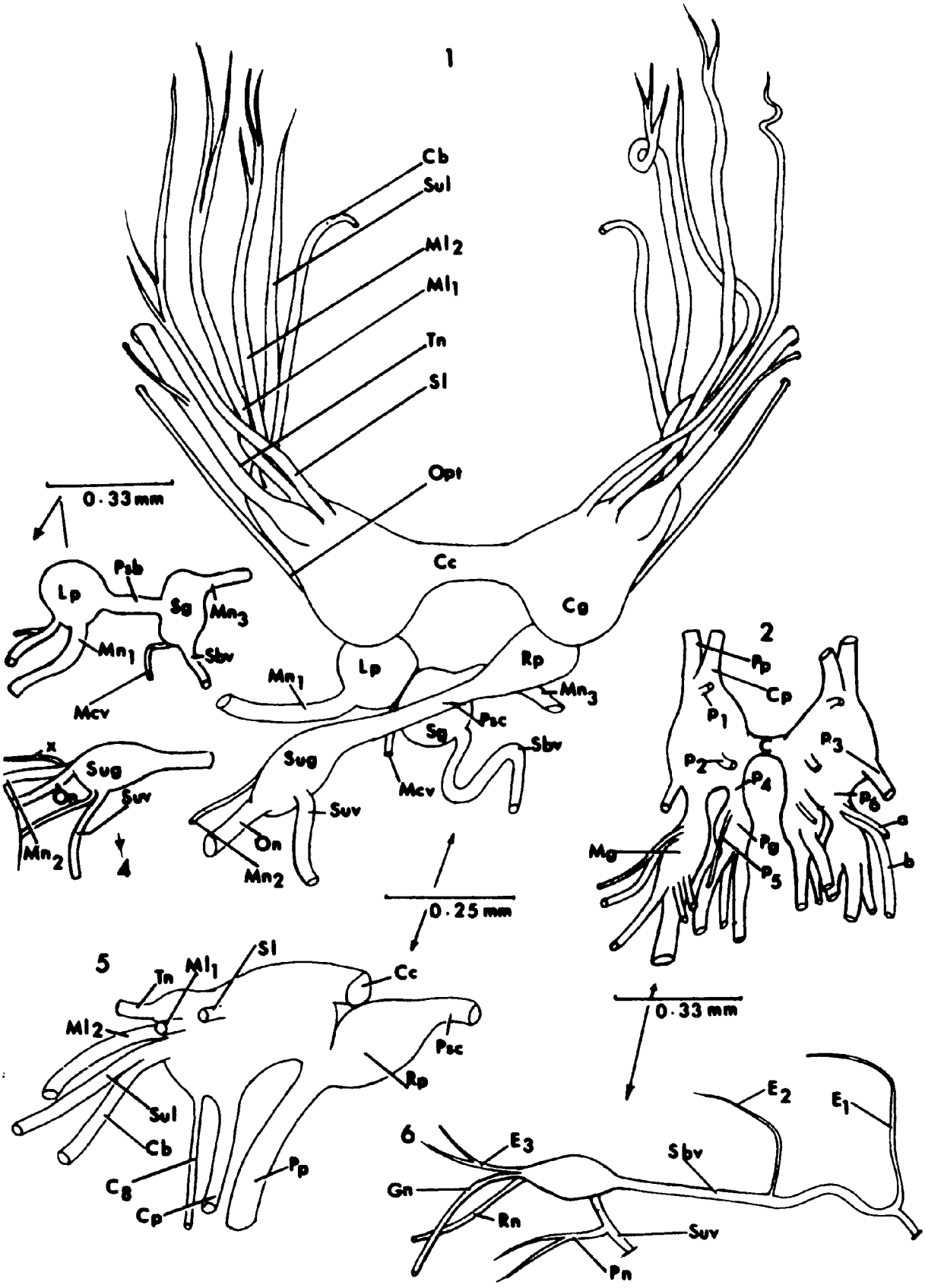
Fig. 4 A variant in the arrangement of nerves leaving the superintestinal ganglion.

Fig. 5 Medial surface of the right cerebral ganglion showing the exact positions where the nerves from that ganglion arise.

Fig. 6 Visceral ganglion viewed from the ventral aspect.

a nerve from p_6
b nerve from p_6
C pedal commissure
Cb cerebrobuccal commissure
Cc cerebral commissure
Cg cerebral ganglion
Cp cerebropedal commissure
C_8 cerebro-tensor nerve
E_1 external mantle cavity nerve 1
E_2 external mantle cavity nerve 2
E_3 external mantle cavity nerve 3
Gn gonadal nerve
Lp left pleural ganglion
Mcv mid-columellar nerve
Mg metapodial ganglion
Ml_1 median labial nerve 1
Ml_2 median labial nerve 2
Mn_1 mantle nerve 1, from the left pleural ganglion
Mn_2 mantle nerve 2, from the superintestinal ganglion
Mn_3 mantle nerve 3, from the subintestinal ganglion
On osphradial nerve
Opt optic nerve
p_1 lateral retractor nerve, from the pedal ganglion
p_2 nerve to the anteroventral wall of the pedal haemocoel
p_3 major lateral nerve of the pedal ganglion
p_4 propodial commissure
p_5 mid-propodial nerve
p_6 metapodial commissure
Pg propodial ganglion
Pn pericardial nerve
Pp pleuropedal commissure
Psc pleuro-supraesophageal commissure
Psb pleuro-subesophageal commissure
Rn renal nerve
Rp right pleural ganglion
Sl superlabial nerve
Sg subintestinal ganglion
Sbv subvisceral commissure
Sug superintestinal ganglion
Sul sublabial nerve
Suv supervisceral commissure
Tn tentacular nerve

Plate 21


1
Cb
Sul
Ml2
Ml1
Tn
Sl
Opt
Cc
Cg
0·33mm
Psb
Lp
Sg
Mn3
Mn1
Sbv
Mcv
Mn1
Lp
Rp
Mn3
Psc
Sg
Sbv
Sug
Suv
Mcv
On
Mn2
x
Sug
On
Suv
Mn2
4
0·25mm
2
Pp
Cp
P1
P2
P3
P4
P6
P5
Mg
a
b
0·33mm
5
Tn
Ml1
Sl
Cc
Ml2
Psc
Rp
Sul
Cb
Cg
Pp
Cp
6
E2
E1
E3
Sbv
Gn
Rn
Suv
Pn

prosobranch neural anatomy was that of Bouvier (1887). General prosobranch neural anatomy is reviewed by Fretter and Graham (1962). Johansson (1939) presented some unique photographs of gross dissections of the central nervous system of Littorina littorea. Krull (1935) presented data on prosobranch nervous systems and their relevance to prosobranch phylogeny. Krause (1949) presents excellent drawings of the nervous system of Lithoglyphus naticoides. Further references are reviewed by these authors.

There are 6 major gangliar complexes; the cerebral, buccal, pedal, pleural, parietal, and visceral. The parietal is composed of 3 ganglia, the supra and sub-esophageal ganglia and the osphradial ganglion.

Cerebral Complex.

A. Dorsal Aspect. Opening the rostral cavity from the dorsal aspect one exposes the buccal mass and associated structures. Particularly noticeable is the heavy pigment dusted over the ganglia and nerves seen from the dorsal surface. The paired cerebral ganglia (Cg, Plate 14; Plate 21, Fig. 1) connected by the cerebral commissure (Cc) are pressed against the mid-posterior curvature of the esophagus where the latter bends ventrally (Plate 15, Fig. 1). The anterior tips of the ganglis press against the mid or ventral, posterolateral wall of the buccal mass, in particular against the anterior end of the buccal retractor muscle (m_{12}, Plate 15, Fig. 1).

The cerebral commissure (Cc) is 0.14 mm long but in some specimens a length of 0.19 mm was found. The width is 0.05 mm to 0.06 mm. The dorsal aspect of the cerebral ganglia is 0.36 mm to 0.29 mm long. From the cerebral ganglion 7 nerves run anteriorly and an 8th ventrally. Five of the 7 nerves can be seen from the dorsal surface.

1. Tentacular Nerve. The tentacular nerve (Tn) is the most prominent nerve rising from the cerebral ganglion (Plate 14; Plate 15, Fig. 1; Plate 21, Figs. 1, 5). It arises from a pronounced swelling, the tentacular bulb, on the anterodorsal end of each cerebral ganglion and runs anterolaterally into the lateral rostral wall, through the wall and into the tentacle. Arising from the tentacular nerve about half way out towards the rostral wall is a slender nerve which runs into the rostral wall apart from the entry of the tentacular nerve. Occasionally 1 or 2 other nerves are seen emerging from the tentacular nerve at a point 0.24 mm beyond the tentacular bulb. These last mentioned nerves are rarely found. When they occur they enter the rostral wall posterior to the tentacular nerve.

2. Optic Nerve. This nerve (Opt) arises from the mid, ventrolateral surface of each ganglion and runs anteroventrally to enter the rostral wall about 0.12 mm posterior to the tentacular nerve. The nerve is quite slender. It innervates the eyes (Plate 14; Plate 15, Fig. 1; Plate 21, Fig. 1).

3. Supralabial Nerve. In order to show the origins of the remaining nerves which arise from the cerebral ganglia, Plate 21, Fig. 5, was prepared which shows the medial surface of the right cerebral ganglion. The supralabial nerve (Sl) sweeps dorsally from the anteromedial surface of the cerebral ganglion, crosses over the other nerves from the ganglion, and runs dorsolaterally to the rostral wall. It becomes bound to the dorsolateral rostral wall about 0.12 mm anterior to the point where the tentacular nerve (Tn) enters the wall. Travelling anteriorly, dorsal to the other labial nerves, it becomes more slender and undulates near its anterior end due to the contracted state of the rostrum (Plate 14, Sl). The nerve terminates more posteriorly than the other labial nerves. The supralabial often sends off a small branch near the point where it fuses with the rostral wall (Plate 21, Fig. 1).

4. Median Labial 1. Arising slightly anteroventrally of the previous nerve (Plate 21, Fig. 5), the median labial (Ml_1) runs anteriorly unfused with the rostrum but usually laying against the rostral wall. Anteriorly it passes above the origin of the dorsolateral buccal protractor (m_{11}) and runs to the tip of the rostrum beneath the preventral dilators (m_{16}, Plate 15, Fig. 1; Plate 18; Plate 21, Figs 1, 5).

5. Median Labial 2. Median labial 2 (ml_2) arises from the anterior edge of the cerebral ganglion beneath the tentacular bulb

(Plate 21, Fig. 5). It runs anteroventrally to median labial 1, likewise unfused with either the rostral wall or buccal mass. It characteristically forks anteriorly sending a root to either side of the origin of the dorsolateral buccal protractor; one root innervates this muscle.

6. Sublabial Nerve. This nerve (Sul) arises closely appressed to the cerebro-buccal connective (Cb) and sometimes these 2 nerves arise as a fused, inseparable trunk before branching. The sublabial travels freely along the floor of the rostrum. In the contracted rostrum, the nerve coils and from the coil a branch arises to innervate the anterior rostral floor (Plate 18). Anteriorly the nerve forks; one slip passes to the origin of the buccal protractor (m_5) while the other passes beneath the buccal protractor to travel anteriorly to the rostral tip. (Plate 15, Fig. 1; Plate 18; Plate 21, Figs. 1, 5).

7. Cerebro-Buccal Commissure. This nerve (Cb) runs anteriorly over the lateral edge of the rostral retractor (m_{20}, Plate 18), up under and behind the buccal protractors (m_5) before the latter disappear beneath the external odontophore membrane. As shown in Plate 15, Fig. 1, the cerebro-buccal commissure travels between the anterior jugalis and the buccal constrictor over the anterolateral edge of the odontophore, emerges over the surface of the membranous jugalis (m_{13}) to run posteriorly into the anterior

tip of the buccal ganglion (Bg). Before reaching the buccal ganglion it passes beneath the inserting fibers of the posterior slip of the buccal retractor.

Nerves 1 to 7 may appear, upon opening the rostrum, jumbled, intermixed, or appressed to the buccal mass. In all cases, however, they are easily untangled and separated from the buccal mass. In a rare case the right salivary gland was found running down between the cerebral ganglion and the buccal mass intertwined in the nerves.

8. Cerebro-Tensor Nerve. This nerve (C_8) arises from the anteroventral edge of the cerebral ganglion (Plate 21, Fig. 5). It is a slender nerve which runs directly ventral to innervate the anterior slip of the tensor magnus muscle (m_{24}).

B. Right Lateral Aspect of the Cerebral Complex. As shown in Plate 15, Fig. 1, and Plate 21, Fig. 5, 2 commissures leave the ventral surface of the cerebral ganglia, drop ventrally, and converge on the dorsal surface of the pedal ganglia (Pg). The posterior commissure is the pleuro-pedal (Pp), the anterior one is the cerebro-pedal (Cp). The former is about 0.19-0.22 mm long and 0.048-0.050 mm wide. The latter is about 0.19 mm long with a width of about 0.03 mm. The cerebro-pedal commissure is devoid of nerves arising from along its length. From the juncture of the pleuro-pedal commissure and the cerebral ganglion arises the pleural

ganglion (Rp, Plate 15, Fig. 1; Plate 21, Figs. 1, 5). A few nerves arise from the pleuro-pedal commissure.

pp1. Lateral Nerve 1. At the ventral juncture of the pleural ganglion with the commissure a nerve arises (pp_1) which runs ventrolaterally under the penial nerve (pp_2) to enter the musculature of the rostral wall just above the lateral insertion of the posterior slip of the tensor magnus in the lateral cephalic retractor. This nerve may not be present and when it is found one observes that the thickness varies considerably. It is 0.024 mm in diameter or thinner.

pp2. Penial Nerve. In males this nerve (pp_2) is greatly thickened (0.036 mm wide). It arises from the mid-length of the commissure (in some cases slightly lower, e.g. Plate 15, Fig. 1). Passing posteriorly as well as dorsolaterally to the cephalic wall above pp_1, it becomes narrower and passes to the mid-cephalic roof and then into the basal musculature of the verge. In females the nerve is slender, about 0.024 mm wide, and passes dorsolaterally to the cephalic wall.

pp3. Lateral Nerve 3. Slightly ventral and lateral to pp_2 a nerve arises (pp_3) which travels initially anteriorly and ventrolaterally, then dorsolaterally. Near its end it forks and sends each branch into the lateral rostral wall just posterior to the point where the tentacular nerve enters the wall. The optic nerve occasionally

passes between the bifurcation (Plate 15, Fig. 1). The points where the branches of this nerve enter the wall are variable and may be ventral or posterior to the positions described. The nerve itself is markedly variable. Instead of a single nerve arising from the commissure, 2 closely associated nerves often arise and run directly to the lateral rostral wall. In rare instances 2 minute nerves just ventral to pp_3 arise from the commissure and run laterally to the rostral wall.

pp4. Lateral Nerve 4. When dissecting under Bouin's solution with the aid of a very bright light, I often found arising from the ventral surface of the cerebral ganglion between the pleuro-pedal commissure and the cerebro-pedal commissure a thin strand (pp_4) appressed or fused with the pleuro-pedal commissure, or distinctly separate so as to traverse the space between the commissures (Plate 15, Fig. 1, pp_4). When this nerve was not observed it was suspected that it was incorporated within the pleuro-pedal commissure. The nerve passed into the area where the pp_2 and pp_3 nerves arose but its final destination was not ascertained with certainty.

C. Left Lateral Aspect of the Cerebral Complex. The counterpart of pp_1 found on the right side was rarely present. When it was found it was a thin strand running ventrolaterally into the lateral cephalic retractor (m_{22}) near the posterior edge of the attachment of the tensor magnus (m_{24}). The counterpart of the

penial nerve is regularly encountered. It runs dorsalaterally to enter the cephalic wall just behind the entrance of the optic nerve where the latter enters the wall. The counterpart to pp_3 runs laterally and only slightly dorsally, bifurcates, each branch entering the ventrolateral cephalic wall opposite the pleuro-pedal commissure or posterior to that point (Plate 14, pp_3). Again, variation is commonly encountered in the arrangement of these lateral nerves from the pleuro-pedal commissure. In unusual instances one finds no pp_1 but a nerve arising from the posterior surface of the pleuro-pedal commissure below the point where the pleural ganglion arises. The nerve runs ventrally and innervates the posterior slip of the tensor magnus. Contrasting the right side, pp_2 and pp_3 arise from the ventral portion of the commissure.

Pedal Complex.

The paired pedal ganglia are quite large and fill the pedal haemocoel beneath the tensor magnus (m_{24}). Each ganglion seen from the anterior aspect (Plate 15, Fig. 2; Plate 21, Fig. 2) is about 0.31 mm long and 0.24 mm wide. They are connected, as shown, by a commissure which varies in length from 0.08 mm to 0.04 mm. The right and left ganglia are similar with regard to the number of nerves which arise, their position, and variability. The description below pertains to either ganglion.

P1. Lateral Retractor Nerve. The lateral retractor

nerve (p_1) arises anteroventrally with respect to the cerebro-pedal commissure as a slender nerve. It runs anteriorly to enter the lateral cephalic retractor at the latter's ventral edge near the area where the ventral retractors emerge from beneath the tensor magnus (m_{24}, Plate 15, Fig. 1; Plate 18; Plate 21, Fig. 2).

P2. Nerve to the Anteroventral Wall. A slender nerve (p_2) arises from the anterior face of the pedal ganglion dorsal and medial to the propodial commissure. It runs anteriorly to the anterior wall of the pedal haemocoel beneath the dorsal pedal tensor.

P3. Major Lateral Nerve. This stout nerve (p_3), often 0.048 mm wide, arises from the ventrolateral edge of the pedal ganglion and runs posterolaterally back through the musculature to an area beneath the operculum. The minor lateral nerve (not figured) was found only a few times. It arises between p_3 and the metapodial commissure (p_6) on the lateral edge of the ganglion and follows p_3 into the lateral musculature of the foot.

P4. Propodial Commissure. This short, stout connective (p_4) joining the pedal ganglion to the propodial ganglion arises from the ventromedial edge of the former. It is devoid of emergent nerves. Within about 0.07 mm from the pedal ganglion it swells into the propodial ganglion which is about 0.12 mm in diameter or slightly less. The commissure usually swings dorsally from the

long axis of the pedal ganglion and enters the anteroventral foot musculature (Plate 13, Fig. 1). The foot musculature forms a spheroidal cavity encasing the propodial ganglion. From the distal tip of that ganglion 3 nerves arise of about equal size. These nerves are, however, variable and at times only 1 of them is particularly pronounced.

P5. Mid-Propodial Nerve. A thin nerve (p_5) emerges from the anterior, mid surface of the propodial ganglion. It runs anteroventrally into the foot musculature.

P6 Metapodial Commissure. This stout connective (p_6) between the pedal ganglion and the metapodial ganglion arises lateral to the propodial commissure and runs ventrolaterally to it. Between the pedal and metapodial ganglia 2 slender nerves arise from the commissure. Commonly they arise next to each other at the dorsal end of the metapodial commissure, although the exact position where they arise is quite variable. The dorsal strand (a, Plate 21, Fig. 2) may actually, at times, arise at the point where the pedal ganglion gives rise to the commissure and at the posterior side. The ventral strand (b, Plate 21, Fig. 2) may arise from the mid-anterior commissure near the pedal ganglion. These 2 nerves are tightly appressed to each other and against the commissure, the metapodial ganglion, and nerves leaving the distal end of the metapodial ganglion.

The metapodial ganglion is not spherical as the propodial ganglion, but more like an elongate swelling of the commissure. It measures about 0.19 mm long and 0.10 mm wide. Nerves leaving the distal tip vary as to number and thickness. Generally, the

ganglion narrows to a central wide and thin band flanked on either side by a thinner nerve. Often the medial of the thinner nerves is replaced by 2 nerve stands. The metapodial ganglion and distal nerves enter a well-defined, roomy channel in the ventrolateral wall of the pedal haemocoel below the level of the more medially placed propodial ganglion (Plate 13, Fig. 1).

P7. Dorsolateral Pedal Nerve. Viewing the lateral aspect of the pedal ganglion (Plate 15, Fig. 1) one notices a nerve (p_7) arising just ventral to the point where the pleuro-pedal commissure joins the pedal ganglion. This point of origin is just anterior to the mid-point of the statocyst (Stc) where the latter is pressed against the dorsoposterior wall of the pedal ganglion. The nerve soon bifurcates and each branch runs laterally to the haemocoel wall. The nerve is variable and 2 nerves might arise from the ganglion instead of 1. In one case, p_7 arose from the pleuro-pedal commissure just dorsal to the pedal ganglion as a thick, single nerve. It ran posteroventrally 0.07 mm and then branched into 3 distinct nerves each of which traveled laterally to the haemocoel wall.

The statocyst is 0.12 mm in diameter and contains a single statolith 0.07 mm in diameter. Upon full contraction of the rostrum these spheres slide up within the openings (b) shown in Plate 18, lateral to the base of the mid-columellar supportive (m_{23}).

Buccal Complex.

From the dorsal aspect, the buccal ganglia are just visible in each angle of the anterodorsal cerebral ganglion and the outer edge of the salivary glands (Plate 14, Bg). It is evident from the lateral view (Plate 15, Fig. 1) that these ganglia lie in the depression where the esophagus presses against the posterior buccal mass just after the origin of the former. The ganglia are not circular but slightly elongate, the long axis generally projecting slightly anterodorsally when the buccal mass is horizontal. Each ganglion is about 0.19 mm with a width of 0.14 mm. The cerebro-buccal commissure has been discussed. A number of nerves arise from these ganglia and the cerebro-buccal commissure.

b1. Dorsal Buccal Nerve. This nerve (b_1) arises from the mid-dorsal surface of the buccal ganglion as a stout strand which runs dorsally and bifurcates beneath the emerging salivary glands. Each branch runs to the dorsal crest of the buccal mass over the area of the esophageal valve (Plate 15, Fig. 1; Plate 13, Fig. 5).

b2 Esophageal Nerve. The esophageal nerve (b_2) arises from the dorsal buccal nerve before the latter passes beneath the salivary gland. It runs posteriorly along the mid-esophageal surface (Plate 15, Fig. 1).

b3 Central Buccal Nerve. This nerve (b_3) is variable in position. It may arise from the anterodorsal surface of the

ganglion, from the posterior base of b_4, or as a branch of b_4. The nerve runs dorsally to enter the buccal mass just posterior to the root of the salivary gland.

b4. Anterior Buccal Nerve. This nerve (b_4) arises from the dorsal surface of the emerging cerebro-buccal commissure. It runs dorsally to disappear beneath the root of the salivary gland.

b5. Odontophore Nerve. About 0.19 mm anterior to the buccal ganglion a nerve (b_5) emerges from the ventral surface of the cerebro-buccal connective. This nerve curves over the external lateral odontophore musculature beneath the external odontophore membrane (Plate 13, Fig. 5).

b6. Posterior Buccal Nerve. The buccal ganglia are connected by the buccal commissure which is about 0.24 mm long and 0.048 mm wide. The commissure passes between the esophagus where it leaves the buccal mass and the posterior buccal mass. The commissure is shown ventrally in Plate 18 (Bc). At the point where each ganglion gives rise to the commissure a nerve (b_6) emerges from the commissure to run ventrally over the external odontophore membrane (Plate 13, Fig. 5; Plate 18).

Pleural Complex.

The pleural ganglia arise from the pleuro-pedal commissure immediately at the juncture of the cerebral ganglia and the commissure and, therefore, the former are partially pressed

beneath the posteroventral curvature of the cerebral ganglia. As shown in Plate 21, the pleural ganglia are intimately associated with the cerebral ganglia. As a result of the characteristic prosobranch streptoneurous condition the posterior tip of the right pleural ganglion is drawn up over the edge of the esophagus (Plate 5, Fig. 1) where it gives rise to the pleuro-supraesophageal commissure (Psc). The commissure crosses the esophagus to the left side of the body. The shape of the ganglion, corresponding to this stretching, is not round but drawn out with a length of 0.24 mm and width of 0.12 mm. The pleuro-supraesophageal commissure often lies in a crease in the esophagus, crossing 0.24 mm or less behind the cerebral commissure (Plate 14). The commissure has a length of 0.34 mm ± 0.048 mm. It enlarges at the left lateral extremity into the supraintestinal ganglion (Plate 15; Plate 21, Figs. 1).

The left pleural ganglion, resting on the mid-columellar supportive muscle is round with a diameter of 0.17 mm. Posteriorly it gives rise to a pronounced nerve, mantle nerve 1 (Mn_1, Plate 21, Figs. 1,3). Mantle nerve 1 runs laterally to the left ventrolateral cephalic wall and enters it at a point just anterior to the point where mantle nerve 2 from the supraesophageal ganglion enters the wall. The left pleural ganglion is tightly appressed to and connected with the subintestinal ganglion. The latter is characteristically not separated from the former by more than 0.04 mm. In only one

instance was a short, pronounced pleuro-subintestinal commissure noted (Plate 21, Fig. 3). In that same instance an unusual second nerve arose from the left pleural ganglion just anterolateral to mantle nerve 1 and ran to the left ventrolateral cephalic wall. No corresponding mantle nerves arise from the right pleural ganglion.

Parietal Complex.

The superintestinal ganglion is about 0.24 mm long and 0.12 mm wide. The tip of the ganglion is very close to the ventrolateral cephalic wall as shown in Plate 14. The tip of the ganglion is generally only 0.12 mm or less from the wall. From the area of the ganglion tip a few nerves arise in a variable fashion. The supervisceral commissure (Suv) leaves the posterolateral surface of the ganglion (Plate 14; Plate 21, Figs. 1,4). This commissure consistantly leaves the ganglion at this point, travels posteriorly along the left edge of the columellar muscle against the base of the "neck" wall, emerges from the left side of the "neck," and runs posteriorly to join the visceral ganglion, thereby completing one side of the "visceral loop" (Plate 11, Fig. 1; Plate 14, Plate 21, Figs. 1,4).

The osphradiomantel nerve arises from the anterior tip of the ganglion and bifurcates. The point of bifurcation is quite variable. The nerves resulting from this bifurcation are the osphradial nerve (On) and mantle nerve (Mn_2). In Plate 21, Fig. 1, the mantle nerve 2 and osphradial nerve arise separately, the former

emerging from the ganglion as a very thin fiber. This condition is quite rare. Commonly the two nerves emerge, equally thick, as separate but closely associated trunks. Equally common, a single large trunk emerges from the ganglion and immediately bifurcates before entering the cephalic wall. Occasionally bifurcation occurs within the wall.

The osphradial nerve (On) runs laterally to the osphradium to enter the mid-ventral surface of the osphradial ganglion (Plate 11, Plate 14, Plate 21). The mantle nerve (Mn_2) runs anteriorly towards the mantle edge after it enters the lateral cephalic wall. This nerve sends a branch to connect in a dialuneury with mantle nerve 1 from the left pleural ganglion. One extreme varient is shown in Plate 21, Fig. 4, where the branch of mantle nerve 2 arose from the nerve at a point where the mantle nerve 2 emerged from the supraintestinal ganglion. In this same rare varient, a nerve arose from the base of the supervisceral commissure and ran laterally to the cephalic wall.

The subintestinal ganglion is of the same dimension as the left pleural ganglion. It lies beneath the esophagus closely appressed against the left pleural ganglion as previously mentioned. Three nerves characteristically pass from this ganglion.

1. The subvisceral commissure arises (Sbv) from the posterolateral curvature as shown in Plate 21, Fig. 1. It forms a

loop when the rostral area is contracted and then runs posteriorly along the mid-line of the columellar muscle or slightly to the right of the mid-line. It enters that muscle in the posterior "neck" region and appears emerging from the "neck" on the right side (Plate 11, Fig. 1). The commissure runs to the visceral ganglion thereby completing the other arm of the "visceral loop."

2. Mantle nerve 3 (Mn_3) arises from the anterolateral curvature of the ganglion as a strong nerve running laterally across the columellar muscle just as the columellar muscle turns ventrally to form the posterior wall of the pedal haemocoel. This nerve tends to slope downward at the right edge of the columellar muscle and then turns to enter the right wall (Plate 21, Figs 1,3).

3. The mid-columellar nerve (Mcv) arises from the left, ventral curvature of the subintestinal ganglion as a slender fiber which slips around the left edge of the mid-columellar supportive (m_{23}), turns ventrally and enters the columellar muscle.

The osphradial ganglion was discussed in the section on the mantle cavity.

Visceral Complex.

The visceral ganglion is a single structure about 0.24 mm long and 0.096 mm wide. Studying the uncoiled snail as shown in Plate 6, by pulling back the columellar muscle one would expose the subvisceral commissure (Sbv) where it emerges dorsal to that

muscle and runs into the ganglion (Plate 21, Fig. 6). Two nerves are seen arising from the subvisceral commissure. They arise at points usually covered by the columellar muscle. The most pronounced is the anterior nerve, exterior mantle nerve 1(E1), which runs directly over the mantle cavity towards the right edge of the cavity often crossing the spermathecal duct to the pallial oviduct in thefemalesor to the intestine in the males. The posterior nerve, external mantle nerve 2(E2) is variable in size and at times is not present. It arises about 0.32 mm posterior to E1 and runs to the mid-ventral external wall of the mantle cavity, turns posteriorly, becomes slender and finely branched. Between these 2 nerves the subvisceral commissure is characteristically kinked or undulating.

The supervisceral commissure (Suv) arises from the dorsal surface of the visceral ganglion near its anterior end (Plate 21, Fig. 6; Plate 7, Fig. 1). About 0.07 mm from the ganglion the pericardial nerve (Pn) arises from the supervisceral commissure and runs posteriorly over the pericardium, forks, and sends 2 branches over the pericardial surface. In Plate 21, Fig. 6, the visceral ganglion is shown as observed in Plates 5-7. From the posterior tip of the ganglion 2 major nerves and one minor nerve arise. Most readily observed is the ventrally located gonadal nerve (Gn) which travels along the vas deferens or oviduct towards the gonadal area (Plate 7, Fig. 1).

Arising along side of the gonadal nerve or as an early branch of the gonadal nerve is a minor nerve, the external mantle nerve 3 (E3). It runs over the area covering the end of the mantle cavity towards the right.

The renal nerve (Rn) can only be observed from the ventral surface by cutting the gonadal nerve and lifting the posterior tip of the visceral ganglion up. From the dorsal surface of the ganglion near the posterior tip this stout nerve arises and runs into the body tube between the posterior mantle cavity epithelium and the kidney epithelium pressed against the posterior wall of the mantle cavity. The nerve passes to the dorsal surface of the body tube and bifurcated sending roots to the kidney.

Occasionally very fine fibers were observed emerging from the right lateral surface of the ganglion which ran onto the external mantle cavity epithelium.

D. Oncomelania hupensis formosana

1. Shell. Pilsbry and Hirase (1905) described this species as Blandfordia formosana. The shell was "perforate, light brown, rather solid, turrite-conic, the outline of the spire straight, apex rather acute. Whorls 6-3/4, quite convex and parted by well-impressed sutures, smooth except for faint growth lines. The last whorl has a rounded and rather strong crest or varix behind the outer

lip. The aperture is ovate, brown within; peristome brown-edged, the columella concave and somewhat thickened, whitish. Length 7, diam. 3.25 mm., length of aperture with peristome 2.8 mm."

Others who described the shell of this species were primarily Bartsch (1916) Annandale (1924), and Abbott (1948b). Annandale (1924) included Blandfordia formosana, Katayama nosophora, and Oncomelania hupensis within the single genus Oncomelania. Abbott (1948b) also included the genus Schistosomophora within Oncomelania. The descriptions presented by these authors need to be enhanced and in some cases modified.

Adult shells, i.e., those with a varix, have 7.0-7.5 whorls (Plate 2). The nuclear whorls are 2.5, white, glossy, set off from the yellow-horn of the remaining whorls. The first nuclear whorl is emergent.

The sutures are moderately impressed and the whorls slightly convex. Pilsbry and Hirase (1905) correctly stated that the outline of the spire was straight; the comparatively flattened whorls aid in giving this impression. The aperture is ovate, elongate, narrowed apically. The inner lip is slightly reflected over the narrow umbilicus and is connected with the outer lip by a long parietal callus (Plate 2; Plate 3, Figs. 7,8). The outer lip is thin and strong. Observing the outer lip with the shell rotated 90° to the left of the apertural view, one observes that it is sinuate as is the thickened

varix behind the lip (Plate 3, Fig. 4).

The base of the shell, as shown in Plate 3, Figs. 7 and 8, is not rounded but appears truncate. The surface of the shell has fine growth lines in contrast to the roughened microsculpture of Pomatiopsis lapidaria. Occasionally a line here and there is more pronounced but these are minor. Cleaning the shell with chlorox removes the periostracum and the "brown-edged" peristome.

Shells with 7.5 whorls had an average length of 6.3 mm and a width of 3.0 mm; those of 7.0 whorls measured 5.76 mm and 2.82 mm, respectively (Table 9). The average length of the aperture for 7.5 mm shells was 2.4 mm and the average callus length was 1.08 mm. The width of the first nuclear whorl was 0.34 mm and the tip of first nuclear whorl measured 0.12 mm in diameter (Table 9). The width of the tip of the first nuclear whorl was almost constant.

Several features of the shell of Oncomelania hupensis formosana separate this species from Pomatiopsis lapidaria:

1. The apical whorls of P. lapidaria are considerably larger than those of O. hupensis formosana (Plate 3, Figs. 6, 9).

2. The straight lip of the former contrasts with the sinuate lip of the latter.

3. The lack of varix formation in the former differs considerably as compared with the pronounced varix in the latter.

Table 9

Conchological Measurements of Oncomelania hupensis formosana

Structures Measured	Number of Snails	Length in mm			Number of Snails	Width in mm		
		$\overline{X}$	S	Se		$\overline{X}$	S	Se
Shell 7.0 whorls	6	5.76	0.58	0.23	6	2.82	0.34	0.14
Shell 7.5 whorls	25	6.30	0.25	0.05	25	3.00	0.22	0.04
Aperture	25	2.40	0.19	0.04				
Callus	25	1.08	0.14	0.03				
Apical Whorl					25	0.34	0.03	0.005
Tip of Apical Whorl					25	0.12	-	-

S = Standard Deviation

Se = Standard Error of the Mean

$\overline{X}$ = The Mean

4. The wide umbilicus and short parietal callus in P. lapidaria contrast the narrow umbilicus and long parietal callus in O. hupensis formosana.

5. The roughened microsculpture, deeply impressed sutures, and pronounced convex whorls of the former are in contrast to the comparatively smooth shell, moderately impressed sutures, and moderately convex whorls of the latter.

6. Although the adult shells of both species may not differ significantly in length, O. hupensis formosana has one more whorl, i.e., 6.5 whorls as compared with 7.5 whorls.

2. External Morphology and Topography.

The folds and grooves of the head as well as the mode of progression are the same as those described for Pomatiopsis lapidaria. The pattern of pigmentation is somewhat different. Oncomelania hupensis formosana shows sexual dimorphism in that the apical whorls of the male have an intense black pigment which is lacking in the females. This was initially evident looking at the whorls through the shell. The apical whorls of the male appeared black while those of the female appeared light brown and peppered with the usual white granular bodies.

In the males the pronounced band of pigment starts at the beginning of the digestive gland (Plate 25, Fig. 2) with a width of 0.48 mm. The apical edge of the band is smooth and regular in

contrast to the flamulate pattern found in Pomatiopsis lapidaria. The lower edge of the band is irregular but not deeply lobed or flamulate.

Anteriorly the dorsal surface of the stomach is lightly dusted with pigment. No pigmented strip underlies the intestine crossing the body whorl. Viewing the animal through the shell from an apertural view one notes a very dark pigmented area to the left. This corresponds to the dorsal surface of the mantle which is densely pigmented all the way back to the rear of the ctenidium. This same mantle area is deeply pigmented in females.

The dorsal rostrum and head are gray-black, the intensity of the pigment varying between individuals. The pigment is evenly dusted over the epithelial surfaces. Below the suprapedal fold on the sides of the foot there is very light pigmentation contrasting the darker pigment found in Pomatiopsis lapidaria. Lack of dark pigment in this area is one reason for the decreased prominence of the pedal crease.

The sole of the foot appears different when compared with Pomatiopsis lapidaria. The entire surface appears white due to the densely packed large, white, glandular units which were found mainly at the posterior part of the foot in Pomatiopsis lapidaria. The lateral indentation is slightly less pronounced.

Tentacles and Eyes. The tentacles of Oncomelania hupensis

formosana are more elongate than those of Pomatiopsis lapidaria. A series of adult specimens were placed under water with adult P. lapidaria, observed as they moved about, and the tentacular length beyond the eye measured. The tentacles of both species, although capable of great expansion and contraction, are carried in a characteristic fashion, usually just short of full extensibility. In O. hupensis formosana the length measured between 0.96 mm to 1.20 mm; in P. lapidaria the length varied between 0.60 mm to 0.90 mm. The width of the tentacle at the base was about 0.12 mm in both species.

The "glandular units" partly occluding the dorsomedial surface of the eyes formed units about the same length and width in both species. The glandular patches vary in size. They may continue anterior to the eye as much as 0.09 mm. Abbott (1948b) described these granules as bright yellow in this species just as he found them in Oncomelania hupensis quadrasi. In reality, the color varies from light, pale yellow to a white-yellow. Very few individuals have been found which have the bright yellow colored glandular units found in O. hupensis quadrasi. While the yellow tinge is not common in Pomatiopsis lapidaria, pure white granules are very uncommon in O. hupensis formosana.

General Topography. The position and arrangement of organs in both species are the same. The detailed descriptions of

the relationships of organs in Pomatiopsis lapidaria likewise pertain to this species. Differences between the species are mainly ones of structural or dimensional modifications of homologous organs. The descriptions which follow deal mainly with those features which are different compared with P. lapidaria. The organ systems of Oncomelania hupensis formosana are presented in Plates 22-32 so that a general comparison with P. lapidaria can be readily made.

One feature of the digestive gland of this species deserves attention. One is impressed with the way the vascular elements stand out beneath the external epithelium (Plate 21, 25, V). The blood vessels are evident as they are outlined by pigment as well as the white "granules" imbedded in the ventral surface of the digestive gland. The artery supplying this portion of the vascular system runs under the epithelium above the left ventral edge of the digestive gland. In this position the artery runs over the edge of the gonad and can be traced to an area on the stomach where the anterior and posterior chambers of the stomach join (Plates 21, 25). At this point there is a slight depression covered by dense epithelium studied with numerous "granules." From here the artery can be traced anteriorly to the right where it parallels the esophagus and gonoduct until the mid-region of the right anterior arm of the kidney beneath which it disappears. It passes over the style sac under the kidney tissue, beneath the intestine where the intestine loops over the tip

of the style sac, and connects with the aorta soon after the aorta sends a main branch anteriorly towards the head. This artery is present in Pomatiopsis lapidaria but never stood out prominently as it did in this species.

The vessels from the artery running along the gonad pass from left to right, perhaps branching once before passing over the right edge of the digestive gland. These same vessels are not pronounced in Pomatiopsis lapidaria and are discerned with comparative difficulty. The pronounced pigmented outlines are lacking in P. lapidaria.

3. Mantle Cavity.

The number of gill filaments are numerous, 46 ± 4. Abbott (1948b) stated that 40-60 ctenidial filaments are characteristic for the genus Oncomelania. The osphradium is 0.5 mm ± 0.09 mm long and the width is about 0.14 mm ± 0.024 mm. The osphradium (Plate 25, Fig. 1) of this species is definitely more narrow than that of Pomatiopsis lapidaria.

4. Female Reproductive System.

The uncoiled female is shown in Plate 22, Fig. 1. The general arrangement of organs and tubes of the reproductive system is similar to that described for Pomatiopsis lapidaria. There are, however, distinct differences to be found in the structure of the gonad,

Plate 22

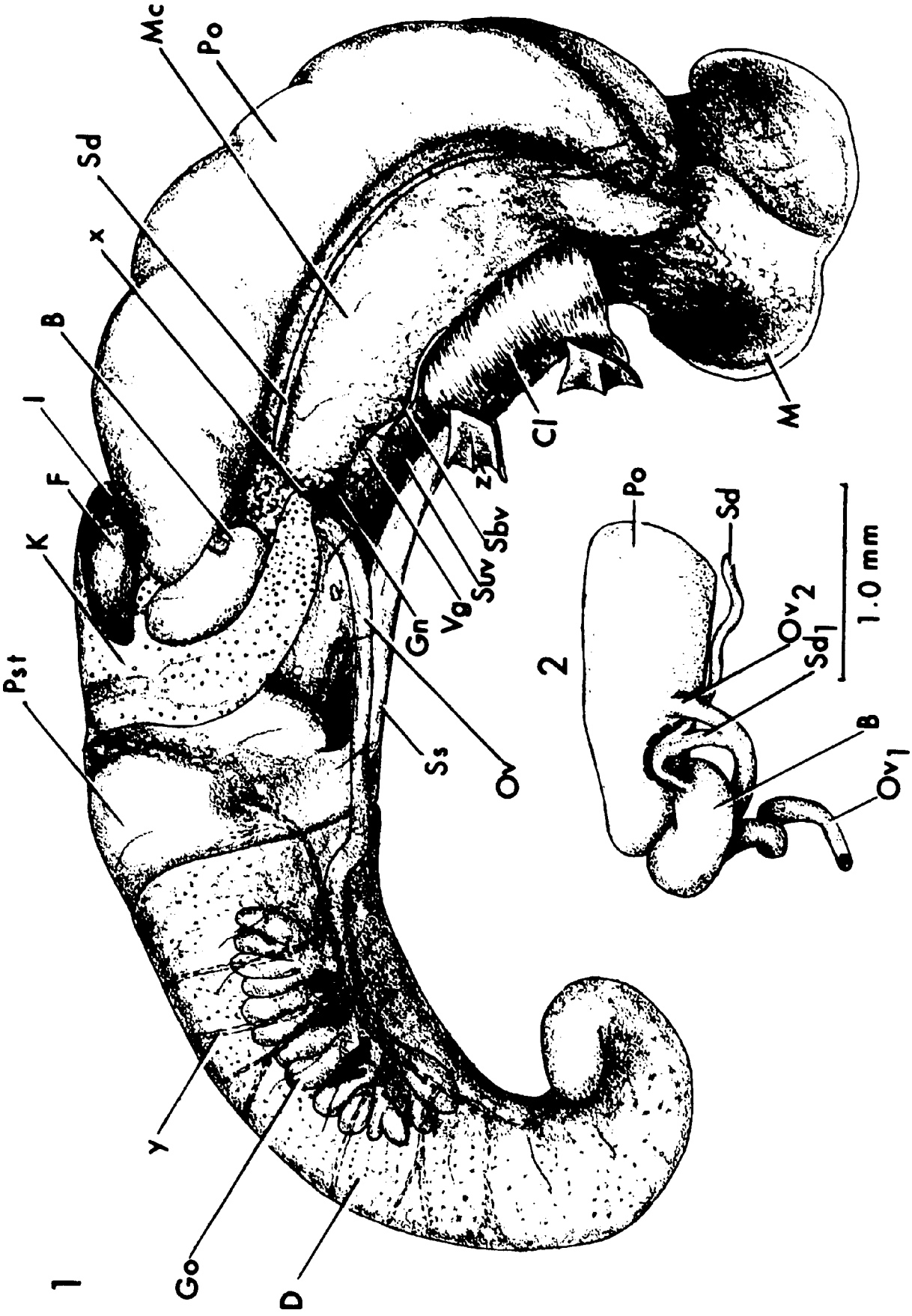
UNCOILED FEMALE ONCOMELANIA HUPENSIS FORMOSANA

Fig. 1. The uncoiled female. Numerous organs are evident through the epithelium.

Fig. 2. A portion of the female reporductive system made evident by removing connective tissue and kidney tissue evident in Fig. 1 anterior to and to the left of the bursa copulatrix (B). A portion of the pallial oviduct is cut away to show the tubes of the spermathecal and sperm ducts which are overgrown by tissue of the pallial oviduct.

B bursa copulatrix
Cl columellar muscle
D digestive gland
F fecal pellet
Gn gonadal nerve
I intestine
K kidney
M edge of the mantle
Mc ventral wall of the mantle cavity
Ov oviduct
Ov_1 coiled portion of the oviduct
Ov_2 portion of the oviduct passing into the pallial oviduct
Po pallial oviduct
Pst posterior chamber of the stomach
Sbv subvisceral commissure
Sd spermathecal duct
Sd_1 sperm duct
Suv supervisceral commissure
Vg visceral ganglion
x end of the mantle cavity
y vascular element running laterally over the digestive gland
z shell

Plate 22


1
Mc
Po
Sd
x
B
I
F
K
Pst
Gn
Va
Sdv
Sbv
z
Cl
M
Ss
Ov
Y
Go
D
2
Po
Sd
Ov2
Sd1
1.0 mm
B
Ov1

the coiling of the oviduct posterior to the bursa copulatrix, and the arrangement of the ducts leaving the bursa.

Gonad. The gonad is multibranched (Plate 22, Fig. 1). The average length of this organ is about 1.39 ± 0.19 mm and the width is 0.53 mm ± 0.096 mm at the widest portion. The lobed nature of the gonad of Oncomelania hupensis quadrasi was shown schematically by Abbott (1948b). Roth and Wagner (1957) showed a schematic drawing of the gonad from O. hupensis nosophora. Roth (1960) presented a schematic diagram for the female reproductive tract of this species depicting a gonad composed of lobed-like structures.

Variation in the size and shape of the gonad is shown in Plate 23. Gonads in Figs. 2 and 3 show rudimentary development although the gonads were taken from otherwise adult specimens. The gonads of both of the species investigated showed no variation corresponding to the time of the year, i.e., no swelling or decrease in productivity throughout the year.

The gonad is rather delicate compared with that of Pomatiopsis lapidaria (Plate 10). The branches of the latter species arise from a large swollen tube while those in the former arise from a slender collecting duct. The fully matured ovaries of Oncomelania hupensis formosana have 5 or 6 branched units, each supporting several terminal lobes. The posterior end of the gonad ends in one of the multibranched units.

Plate 23

FEMALE REPRODUCTIVE SYSTEM IN ONCOMELANIA HUPENSIS FORMOSANA

Fig. 1 Mature gonad.

Figs. 2,3 Underdeveloped gonads from adult sized snails.

Figs. 4,5 Mature gonads

Fig. 6 The relationship of the spermathecal duct, pallial oviduct, and intestine in the area where the ducts open into the mantle cavity.

A anus
F fecal pellet
I intestine
Oo opening of the pallial oviduct
Osd opening of the spermathecal duct
Sd spermathecal duct
Si subintestinal sinus

Plate 23

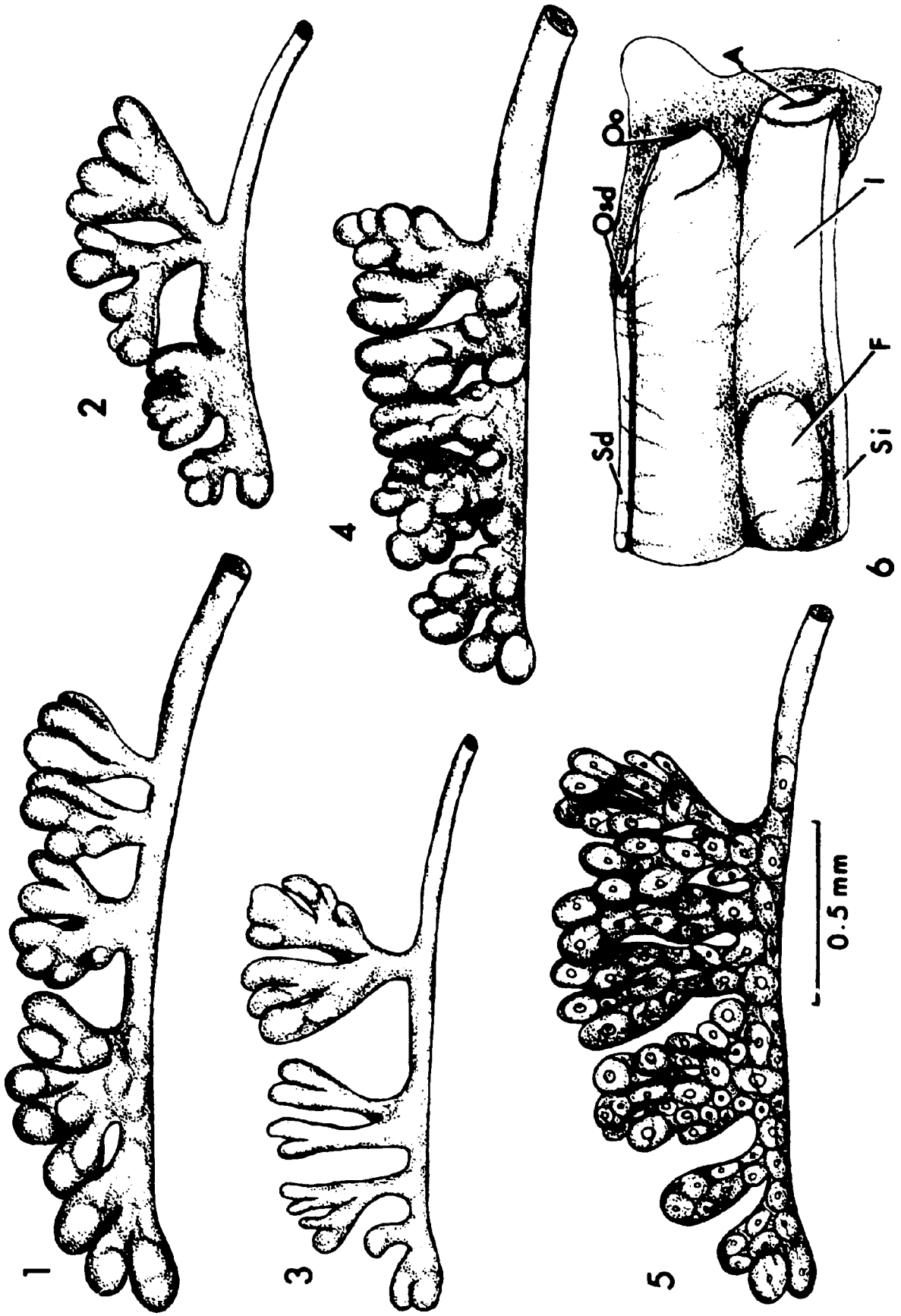


Plate 24

FEMALE REPRODUCTIVE SYSTEM OF ONCOMELANIA HUPENSIS FORMOSANA

Fig. 1 The terminal portions of the anus, pallial oviduct, and the spermathecal duct.

Fig. 2 Mid-body region cleared of kidney tissue showing the relationship of the tip of the style sac (Sts) to the pericardium (Pe) Note the point where the gonopericardial duct enters the pericardium (Gp). Note how the commonly bound spermathecal and sperm ducts leaving the bursa (z) seem to enter the pallial oviduct.

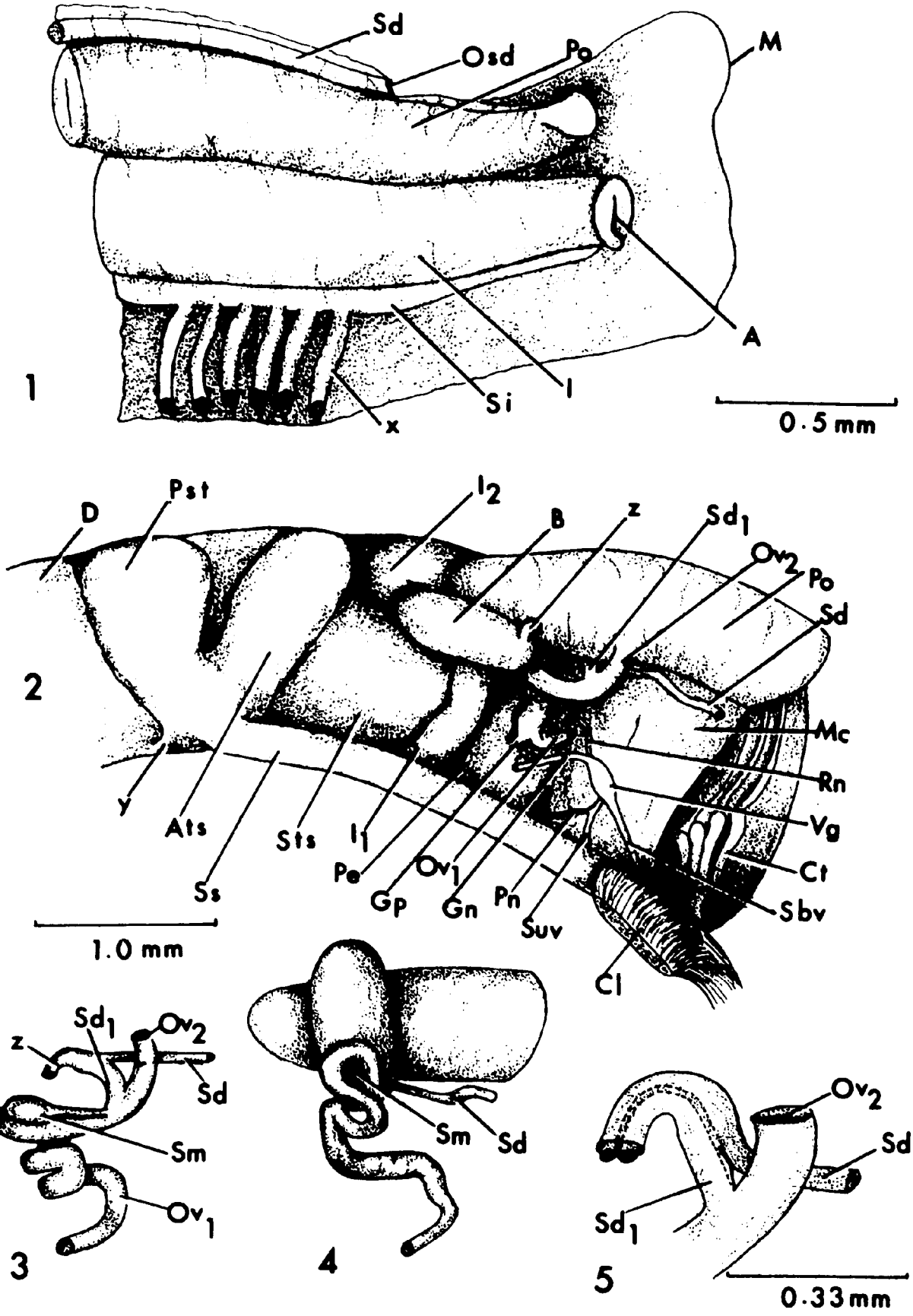
Fig. 3 The bursa has been removed to show the relationship of tubes and structures associated with the bursa. Note the coil about the seminal receptacle (Sm).

Fig. 4 The bursa has been rotated to show how the oviduct coils about the seminal receptacle.

Fig. 5 The point where the sperm duct and the spermathecal duct enter the common connective tissue sheath is shown. The tubes are separate within the sheath (dashed lines).

A	anus
Ast	anterior chamber of the stomach
B	bursa copulatrix
Cl	columellar muscle
Ct	ctenidium
D	digestive gland
Gn	gonadal nerve
Gp	gonopericardial duct
I	intestine
I_1	intestine starting to swing over the tip of the style sac
I_2	intestine at the hairpin turn, the point of the pellet compressor
M	edge of the mantle
Mc	ventral wall of the mantle cavity
Osd	opening of the spermathecal duct
Ov_1	coiled section of the oviduct beyond the genopericardial duct
Ov_2	portion of the oviduct entering the pallial oviduct
Pe	pericardium
Pn	pericardial nerve
Po	pallial oviduct
Pst	posterior chamber of the stomach
Rn	renal nerve
Sbv	subvisceral commissure
Sd	spermathecal duct
Sd_1	sperm duct
Si	subintestinal sinus
Sm	seminal receptacle
Ss	esophagus
Sts	style sac
Suv	super visceral commissure
Vg	visceral ganglion
x	gill filaments
y	passage from the stomach to the digestive gland
z	tubes leaving the bursa copulatrix

Plate 24


Sd
Osd
Po
M
A
Si
I
x
1
0.5 mm
D
Pst
I2
B
z
Sd1
Ov2
Po
Sd
Mc
Rn
Vg
Ct
Sbv
Cl
Suv
Pn
Gn
Gp
Pe
Ov1
I1
Sts
Ats
Ss
y
2
1.0 mm
Sd1
Ov2
z
Sd
Sm
Ov1
3
Sm
Sd
4
Ov2
Sd
Sd1
5
0.33mm

The oocytes of Pomatiopsis lapidaria are distinctly larger than those of this species. In the former the larger oocytes measured about 0.17 mm while in the latter they were about 0.11 mm in diameter.

Coiled section of the oviduct. The length of the oviduct between the gonopericardial duct and the opening of the seminal receptacle into the oviduct measures about 1.7 mm to 2.1 mm. The tube is narrower than that of Pomatiopsis lapidaria; the diameter measures up to 0.12 mm. The convoluted oviduct in this region does not form the relatively compact cylinder found in P. lapidaria. It forms 1 or 2 irregular loops as shown in Plate 24, Fig. 3. In Figs. 3 and 4 the oviduct is shown just beyond the gonopericardial duct. After making 2 irregular coils the oviduct circles under the bursa and encircles the seminal receptacle which is appressed against the bursa. The oviduct does not encircle the seminal receptacle in P. lapidaria (Plate 8, Figs. 2, 3). Roth and Wagner (1957) show the coil encircling the seminal receptacle in a similar manner in Oncomelania hupensis nosophora.

Seminal Receptacle. The seminal receptacle (Plate 24, Figs. 3,4) varies in shape and dimension as it does in Pomatiopsis lapidaria. The spherical or elliptical portion of the organ varies in length from 0.17 mm to 0.31 mm and the width from 0.12 mm to 0.24 mm. A dense central core is often observed within the central portion of the

organ. The duct leading to the oviduct varies in length from 0.14 mm to 0.19 mm. It is slender with a width of 0.048 mm. The duct enters the oviduct about 0.14 mm from the opening of the sperm duct. In one case (Plate 24, Fig. 3) the duct entered the oviduct right at the base of the entrance of the sperm duct (Sd_1).

Bursa Copulatrix. The bursa, viewed from the ventral surface (Plate 22, Figs. 1,2; Plate 24, Figs. 2,4) measures 0.84 mm ± 0.096 mm in length and 0.38 mm ± 0.048 mm in width. The spermathecal duct does not arise from the anterior tip of the bursa as it does in Pomatiopsis lapidaria. It arises with the sperm duct from the right anterior tip of the bursa 0.12 mm from the end of that organ (Plate 22, Figs. 1,2; Plate 24, Fig. 2). Studying this area mounted as a whole mount in CMC-10 revealed that the spermathecal duct and the sperm duct emerge from the bursa as 2 distinct tubes bound together in a common sheath of connective tissue. At magnifications of 60 X they appeared as 1 tube (Plate 24, Fig. 2). The 2 tubes loop to the right and anteriorly. They emerge from the connective tissue sheath just posterior to the point where the oviduct passes ventral to the spermathecal duct (Plate 22, Fig. 2; Plate 24, Figs. 2, 3, and 5). In Plate 24, Fig. 5, the tubes within the connective tissue sheath are shown as dashed lines. In one specimen the sheath was lacking altogether. Where the tubes loop anteriorly, they are overgrown by tissue of the pallial oviduct (Plate 22, Fig. 2). The sperm

duct, as it enters the oviduct, measures about 0.12 mm in diameter. Upon entering the common sheath with the spermathecal duct it narrows noticeably to 0.048 mm. Both tubes emerging from the bursa have a collective diameter of about 0.036 mm.

Roth and Wagner (1957) describe the spermathecal duct as the "vagina" and the sperm duct as the "duct of the bursa." They figure the ducts arising from the mid-portion of the bursa in Oncomelania hupensis nosophora. A more thorough investigation of that species has verified that the arrangement of tubes leaving the bursa is as described for O. hupensis formosana.

Pallial Oviduct and the Spermathecal Duct. The spermathecal duct is a slender tube in this species with a diameter of about 0.048 mm. The opening (Plate 23, Fig. 6; Plate 24, Fig. 1) is quite evident with general observations at 60 X. The complications found in Pomatiopsis lapidaria with the thick connective tissue sheets which are heaviy pigmented are not encountered here. The opening of the duct is 0.48 mm to 0.57 mm posterior to the opening of the pallial oviduct. The opening of the spermathecal duct is 25 micra surrounded by lips 12.5 micra thick.

The pallial oviduct is about 3.36 mm to 4.00 mm long and up to 0.60 mm wide. This organ is distinctly smaller than that of Pomatiopsis lapidaria. The width of the pallial oviduct at the anterior end in this species is 0.14 mm contrasting the width of 0.27 mm for

the same structure in P. lapidaria. For a distance of 0.12 mm posterior to the opening, the pallial oviduct is very slender and non-glandular.

In both species, snails of adult size may possess an underdeveloped pallial oviduct which is only 0.28 mm wide the whole length. The occurrence of this phenomenon is more pronounced in Oncomelania hupensis formosana.

There has been some confusion concerning the area where the oviduct (Ov_2) passes ventral to the spermathecal duct. Itagaki (1955) shows the ducts intercommunicating in Oncomelania hupensis nosophora. Current investigations as well as those of Roth and Wagner (1957) clearly show that these ducts do not intercommunicate. Itagaki (1955) does not mention the sperm duct. He states that the spermathecal duct enters the pallial oviduct near the latter's terminus as did Dundee (1957) for Pomatiopsis lapidaria. As Roth and Wagner (1957) showed, this is not the case in O. hupensis nosophora; the spermathecal duct and the pallial oviduct have separate openings into the mantle cavity.

5. Male Reproductive System.

Gonad. The gonad appears as indistinct as that of Pomatiopsis lapidaria when viewed through the ventral epithelium of the uncoiled digestive gland (Plate 25, Fig. 2). The distinctly outlined vascular pathways further tend to occlude the gonad. The structure of this organ is revealed by removing the ventral epithelium from the

digestive gland (Plate 26, Fig. 2). Comparison of the gonad of P. lapidaria (Plate 12) with the gonad of this species shows several differences. Although there are about the same number of multi-branched units (7 to 9) arising from the vas efferens (Ef), the units of Oncomelania hupensis formosana lack the many finely branched tubes supporting testicular lobes at their tips. The testicular lobes in this species are thick and elongate, tending to rise from wider, more basal branches very close to the vas efferens (Plate 26, Fig. 5). The difference in testicular lobes between the 2 species is observed by comparing Plate 25, Fig. 5, with Plate 12, Figs. 6, 7.

The length of the gonad is 1.92 mm ± 0.24 mm and the width is 0.55 mm ± 0.10 mm. The vas deferens arises from the vas efferens at a position similar to that described for Pomatiopsis lapidaria. The initial tube is not tightly coiled but runs directly into the "seminal vesicle." The "seminal vesicle" is very characteristic for this species. It never forms the neatly deliniated coil described for P. lapidaria (Plate 12, Figs. 3, 4) but forms a knot, a spherical mass of intertwined tubes bound together by connective tissue strands and laced with vascular elements (Plate 26, Fig. 1). The left edge of this confused mass of tubing is generally visible projecting out from the dorsal surface of the gonad (Plate 26, Fig. 2). The tubes of the "seminal vesicle" are quite narrow, only about 0.096 mm wide but are often more slender. The "knot" is about 0.60 mm long and 0.40 mm

wide. Uncoiled, the vas deferens, up to the prostate, is about 2.4 mm long.

Prostate Gland. The prostate measures 2.20 mm to 2.25 mm in length and 0.62 mm to 0.72 mm wide. The relationship of the anterior and posterior portions of the vas deferens to the prostate is the same as that found in Pomatiopsis lapidaria (compare Plate 26, Fig. 4, with Plate 6, Figs. 2,3).

Verge. Although the verge is characterized as "simple" in the literature, it has a number of distinctive features which are of value for comparative purposes. The length of the extended verge is 3.36 mm ± 0.12 mm and the greatest width (near the tip) is about 0.80 mm. The verge is thicker and more muscular than that of Pomatiopsis lapidaria. The anterior end is so muscularly thickened that it has a pronounced convex curvature (Plate 25, Fig. 1; Plate 26, Fig. 6). The anterior portion of the verge has a distinct pinkish, salmon color which was also observed by Itagaki (1955) for Oncomelania hupensis nosophora. In this area longitudinal muscle strands are readily observed. The tip is blunt and flattened, or in the contracted state, a little concave (Plate 25, Fig. 1).

When the verge is expanded a distinctly fleshy papilla is pushed beyond the tip of the verge (Plate 26, Figs. 6,7). When studying the verge at 600 X, it is evident that the tip of the verge is ciliated to either side of the papilla as shown in Plate 26, Fig. 7. The ciliary

Plate 25

MALE REPRODUCTIVE SYSTEM OF ONCOMELANIA HUPENSIS FORMOSANA

Fig. 1 Head, verge, and mantle cavity.

Fig. 2 Stomach and digestive gland as observed without removal of external epithelia. Note the "seminal vesicle" (Vs) irregularly coiled and protruding from behind the gonad (Go).

A	anus
Ast	anterior chamber of the stomach
Ct	ctenidium
D	digestive gland
F	fecal pellet
Go	gonad
M	edge of the mantle
N	the "neck"
Os	osphradial ganglion in the osphradial pit
Pe	pericardium
Pi	pigment
Pr	prostate
Pst	posterior chamber of the stomach
R	rostrum
Sbv	subvisceral commissure
Ss	esophagus
Suv	supervisceral commissure
V	visceral artery
Vd_1	posterior portion of the vas deferens
Vd_2	anterior portion of the vas deferens
Ve	verge
Vg	visceral ganglion
Vs	seminal vesicle

Plate 25

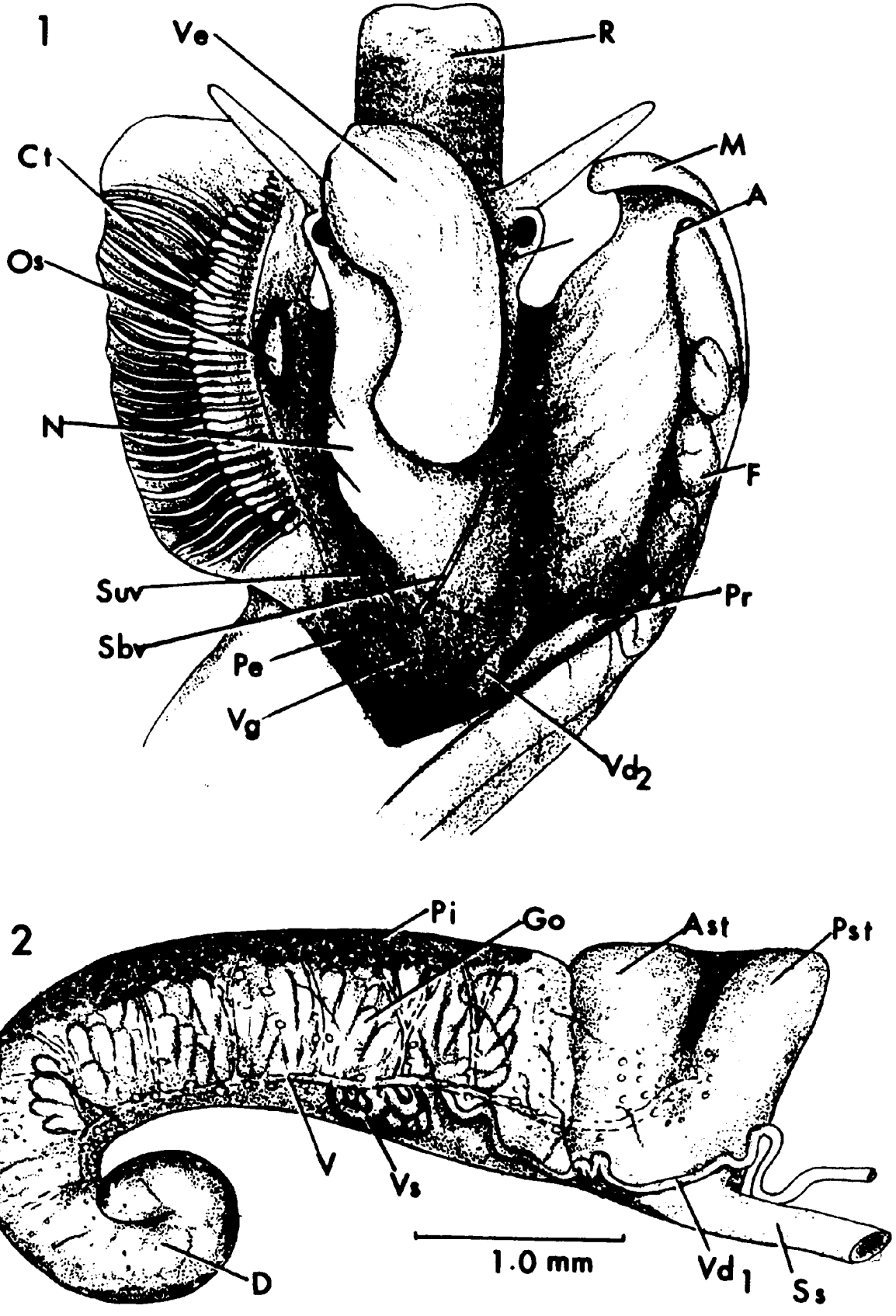

1
Ve
R
Ct
M
A
Os
N
F
Suv
Pr
Sbv
Pe
Vg
Vd2
2
Pi
Go
Ast
Pst
V
Vs
D
1.0 mm
Vd1
Ss

Plate 26

MALE REPRODUCTIVE SYSTEM OF ONCOMELANIA HUPENSIS FORMOSANA

Fig. 1 The gonad with several of the multibranched units removed to reveal the structure of the seminal vesicle.

Fig. 2 The gonad as viewed from the ventral surface.

Fig. 3 The single glandular type found in the verge.

Fig. 4 The prostate as seen from the ventral surface A and turned over, B, to show the points where the vas deferens enters and leaves the organ. The scale is the same as Fig. 2.

Fig. 5 The structure of the testicular lobes.

Fig. 6 Verge.

Fig. 7 The tip of the verge magnified several times to show the strips of cilia on either side of the papilla.

Ef vas efferens

Mvd thick layer of circular muscles encircling the vas deferens at the base of the verge.

O_1 initial portion of the vas deferens

Pa papilla at the end of the verge

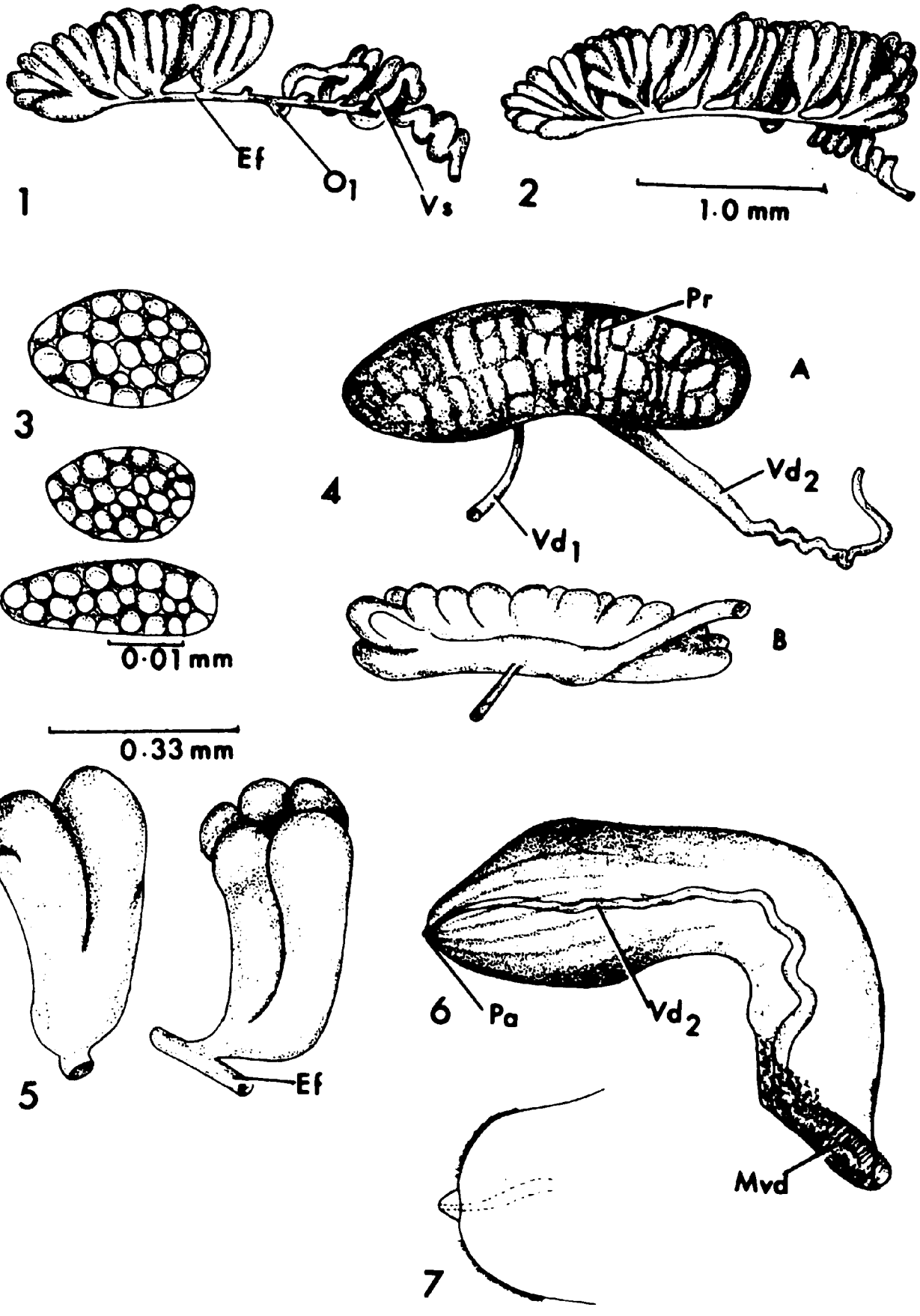
Pr prostate

Vd_1 posterior portion of the vas deferens

Vd_2 anterior portion of the vas deferens

Vs seminal vesicle

Plate 26



bands extend, invariably, only about 50 micra on each side of the papilla; they project beyond the epithelium by 3.8 micra and actively beat from anterior to posterior.

The inner curvature of the verge does not have the expanded glandular area so pronounced in Pomatiopsis lapidaria. Only 1 glandular type was found scattered throughout the verge (Plate 26, Fig. 3). The verge differs from that of P. lapidaria in the following:

(1) The tip is ciliated; (2) it possesses a distinct papilla; (3) there is 1 glandular type; (4) there is a pronounced musculature which is "pink" in color; (5) it lacks the glandular edge; and (6) the anterior end is not crimped thereby set off from the rest of the verge (compare with P. lapidaria, Plate 11, Fig. 5).

Roth and Wagner (1957) noted the papilla at the tip of the verge as well as the "several small white lines running parallel to the axis of the penis . . . in the tapering portions" for Oncomelania hupensis nosophora. Those "white lines" represent fibers of longitudinal muscle.

6. Buccal Mass.

The buccal mass and associated structures are similar in the 2 species under consideration. The most noticeable difference is one of size. Oncomelania hupensis formosana is uniformly smaller when one compares dimensions of the buccal mass, ganglia, muscles,

etc. The length of the buccal mass is 0.79 mm ± 0.07 mm and the width is 0.53 mm ± 0.05 mm. The dorsal view of the buccal mass is shown in Plate 27; the opened pharyngeal tube in Plate 29, Fig. 2.

Jaw. The jaws are similar to those of Pomatiopsis lapidaria with the exception of being slightly longer. The plates of the jaw are comparatively larger (compare Plate 31, Fig. 7, with Plate 20, Fig. 10).

Radula. The structure of the radula is the same in both species. A series of 16 radulae were straightened out on slides and studied (Table 6). It can be seen that the radula of this species is shorter, less wide, and has fewer rows of teeth than Pomatiopsis lapidaria. There was no significant difference in the number of rows of teeth in the formative stages.

The most commonly encountered cusp formula for each tooth is presented in Table 10, along with the percentage of radulae on which the arrangement was found for at least 90 per cent of each tooth type. Only 53 per cent of the 50 snails investigated had this representative formula. In Table 11 each cusp arrangement found per tooth type is tabulated with the percentage of radulae on which it was found at least once.

Studies on the radulae of the subspecies of Oncomelania by Abbott (1948b), Mao and Li(1948), and Kuo and Mao (1957) point up the fact that variation in radular formulas for a single subspecies

Table 10

A General Formula for the Most Common Cusp Arrangement in Oncomelania Hupensis Formosana

Tooth Type	central	lateral	inner marginal	outer marginal
Cusp formula	$\frac{1-1-1}{2-2}$	2-1-2(3)	8(9)	6(5)
Per cent of snails where the cusp arrangement for each tooth type was found	62	74	100	91

Table 11

The Total Types of Cusp Arrangement Found for Each Tooth in Oncomelania Hupensis Formosana and the Percentage of Radulae Showing that Arrangement

Central	%	Lateral	%	Inner Marginal	%	Outer Marginal	%
$\frac{1-1-1}{2-2}$	70	2-1-3	50	9	100	6	90
$\frac{1-1-1}{3-3}$	30	2-1-2	40	10	20	5	60
$\frac{2-1-2}{2-2}$	20	2-1-4	10	11	40	4	10
$\frac{2-1-2}{3-3}$	10	2-1-0	10	8	4		
$\frac{1-1-2}{2-2}$	30	3-1-3	10				
$\frac{1-1-2}{3-3}$	10	3-1-4	10				
$\frac{3-1-2}{3-3}$	10	one side central 2-1-2; other side, 2-1-3	20				
		one side, 2-1-3; other side 2-1-4	10				

of Oncomelania include the cusp arrangements of the other subspecies as well as Pomatiopsis lapidaria. Those studies did not generally consider the frequency of occurrence of cusp arrangement. As shown in Table 10, 70 per cent of the centrals of Oncomelania hupensis formosana had a formula of $\frac{1-1-1}{2-2}$ while only 40 per cent of P. lapidaria had the same formula. Considering the inner marginals, 84 per cent of P. lapidaria had 5-7 cusps while 100 per cent in O. hupensis formosana had 8-9 cusps. The question arises, do other populations of Oncomelania conform to the pattern in the laboratory population studied here? For the most part that question remains unanswered with the exception of some data presented by Mao and Li (1948) for O. hupensis hupensis in China. They presented data for 1 population. The central had a formula of $\frac{1-1-1}{2-2}$ for 75 per cent of the population. Centrals with 3 basal denticles occurred in only 26 per cent of the snails. There were 8-9 cusps on the inner marginals in 87 per cent of the population with the remainder having 7.

In spite of the overlapping variations between the subspecies of Oncomelania and Pomatiopsis lapidaria, it appears that P. lapidaria is separable from Oncomelania on the basis of cusp formula in that there is a pronounced tendency in the former to have 3 basal cusps on each side of the central and 8-9 cusps on the inner marginal.

Plate 27

DORSAL ASPECT OF THE BUCCAL MASS AND ASSOCIATED STRUCTURES IN ONCOMELANIA HUPENSIS FORMOSANA

Bg	buccal ganglion
Bm	buccal mass
Cc	cerebral commissure
Cg	cerebral ganglion
m_5	buccal protractor
m_{11}	dorsolateral buccal protractor
m_{16}	preventral dilators
m_{17}	suspensors of the buccal mass
m_{22}	lateral cephalic retractor
Ml_1	median labial nerve 1
Ml_2	median labial nerve 2
Mn_1	mantle nerve 1
Omn	osphradiomantle nerve
Opt	optic nerve
pp_3	lateral nerve 3
Psc	pleuro-supraesophageal commissure
Rp	right pleural ganglion
Sa	salivary gland
Sl	superlabial nerve
Ss	esophagus
Sug	superesophageal ganglion
Suv	supervisceral commissure
Tn	tentacular nerve

Plate 27

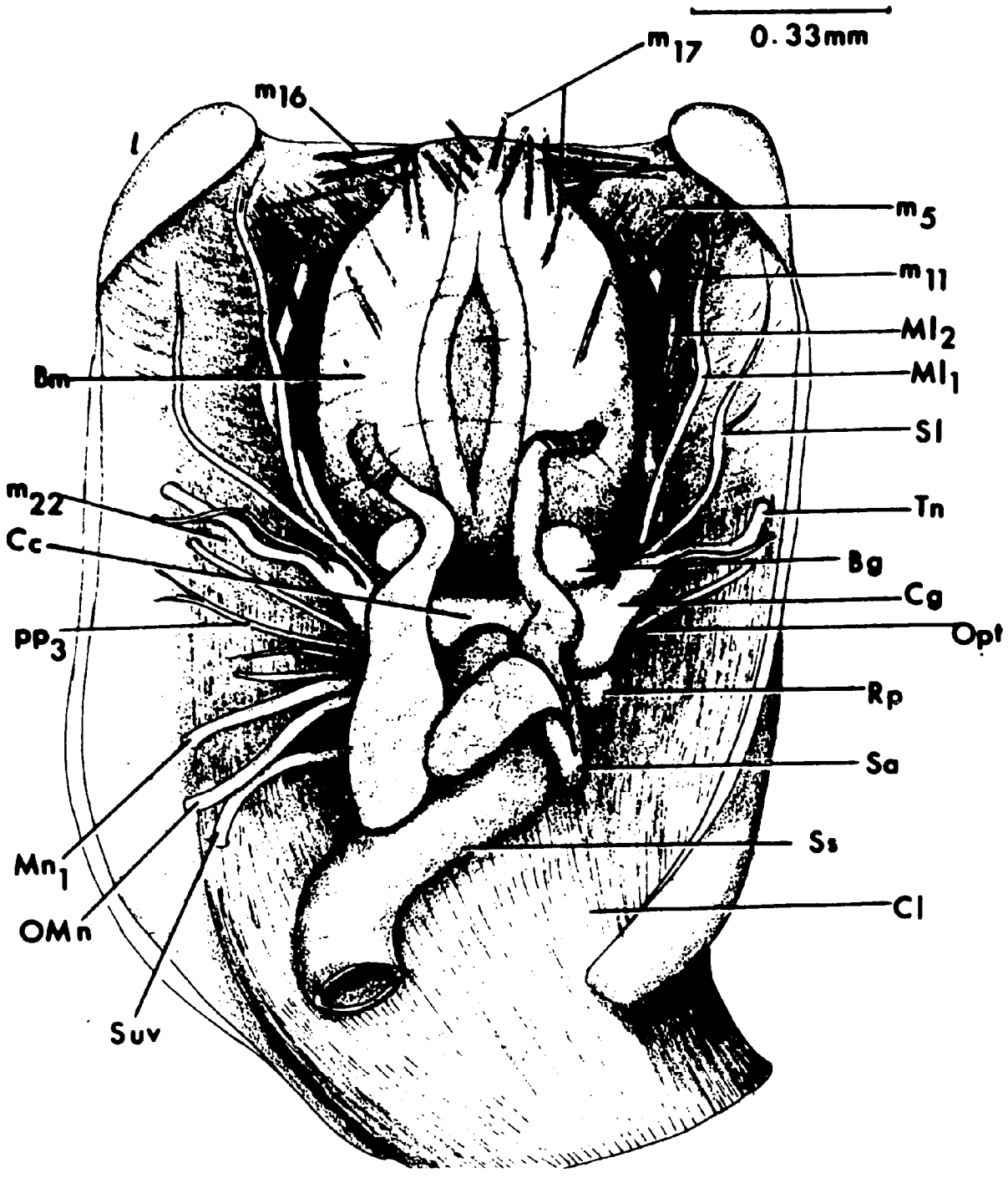

0.33mm
m17
m16
m5
m11
Ml2
Ml1
Sl
Tn
Bg
Cg
Opt
Rp
Sa
Ss
Cl
Bm
m22
Cc
pp3
Mn1
OMn
Suv

Plate 28

MUSCULATURE OF ONCOMELANIA HUPENSIS FORMOSANA

b	posterodorsal gap of the pedal haemocoel
Bc	buccal commissure
Bg	buccal ganglion
Cl	columellar muscle
Eo	external odontophore membrane
m_5	buccal protractor
m_6	preventral protractor
m_7	radular protractor
m_{11}	dorsolateral buccal protractor
m_{12}	buccal retractor
m_{20}	rostral retractor
m_{22}	lateral cephalic retractor
m_{24}	tensor magnus
Mb	membrane around the radular sac
Ml_1	median labial nerve 1
Ml_2	median labial nerve 2
pl	lateral retractor nerve from the pedal ganglion
Rs	radular sac
Ss	esophagus
Sul	sublabial nerve

Plate 28

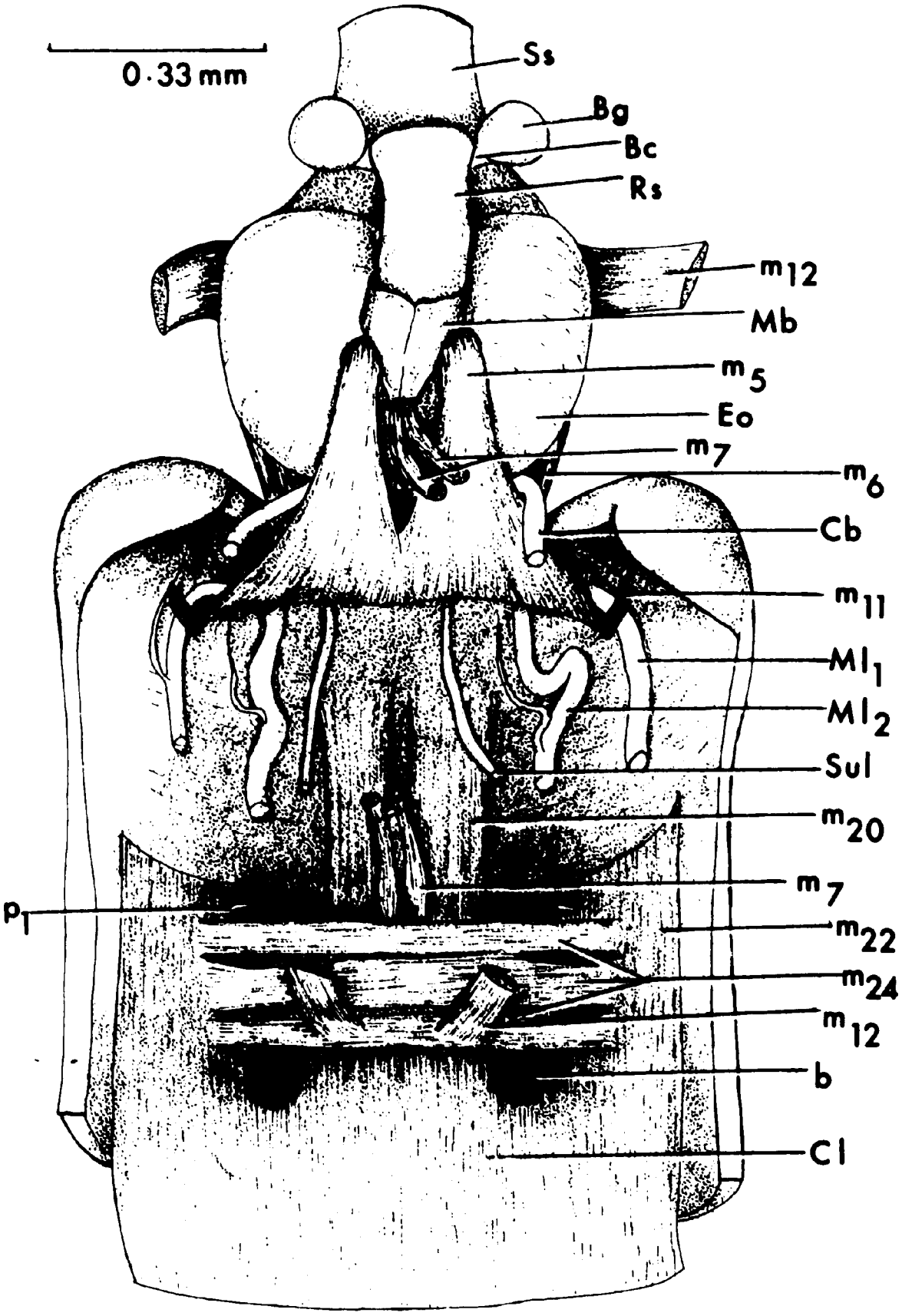

0·33 mm
Ss
Bg
Bc
Rs
m12
Mb
m5
Eo
m7
m6
Cb
m11
Ml1
Ml2
Sul
m20
m7
p1
m22
m24
m12
b
Cl

Plate 29

MUSCULAR AND NERVOUS SYSTEMS OF ONCOMELANIA HUPENSIS FORMOSANA

Fig. 1 The lateral aspect of the buccal mass showing the lateral view of the central portion of the nervous system.

Fig. 2 The dorsal aspect of the opened pharyngeal tube showing the dorsal odontophore.

Fig. 3 The right buccal cartilage and intrinsic muscles associated with the cartilage.

Fig. 4 The overlapping tips of the cartilages are pulled apart and the medial surfaces of the cartilages exposed, wrapped in the intrinsic muscles of the odontophore.

b_1	dorsal buccal nerve
b_4	anterior buccal nerve
b_5	odontophoral nerve
Bg	buccal ganglion
Ca	cartilage
Cb	cerebrobuccal commissure
Cg	cerebral ganglion
Cos	collostyle tip
Cp	cerebropleural commissure
Eo	external odontophore membrane
Ev	esophageal valve
Fg	food grove
Gr	central groove in the ventral fold
Il	inner lip
m	circular muscle running over the medial slips of the buccal protractors
m_1	lateral cartilage tensor
m_2	mediolateral cartilage tensor
m_3	odontophore divaricator
m_4	medial radular retractor
m_5	buccal protractor
m_6	preventral protractor
m_7	radular protractor
m_8	anterior jugalis
m_9	buccal constrictor
m_{11}	dorsolateral buccal protractor
m_{12}	buccal retractor
m_{13}	membranous jugalis
m_{16}	preventral dilators
m_{17}	suspensors of the buccal mass
Ml_1	median labial nerve 1
Ml_2	median labial nerve 2
Ol	outer lip
Opt	optic nerve
p_1	lateral retractor nerve
p_2	nerve to the anteroventral wall
p_3	major lateral nerve
Pd	pedal ganglion
Pp	pleuropedal commissure
pp_1	lateral nerve 1
pp_2	penial nerve
pp_3	lateral nerve 3
pp_4	lateral nerve 4
Ra	radula
Ras	radular shield
Rp	right pleural ganglion
Rpc	rostral portion of the cephalic haemocoel
Rw	rostral wall
Sa	salivary gland
Sr	subradular membrane
Ss	esophagus
Sta	statolith
Stc	statocyst
Sul	sublabial nerve
Tn	tentacular nerve
Vf	ventral fold

Plate 29

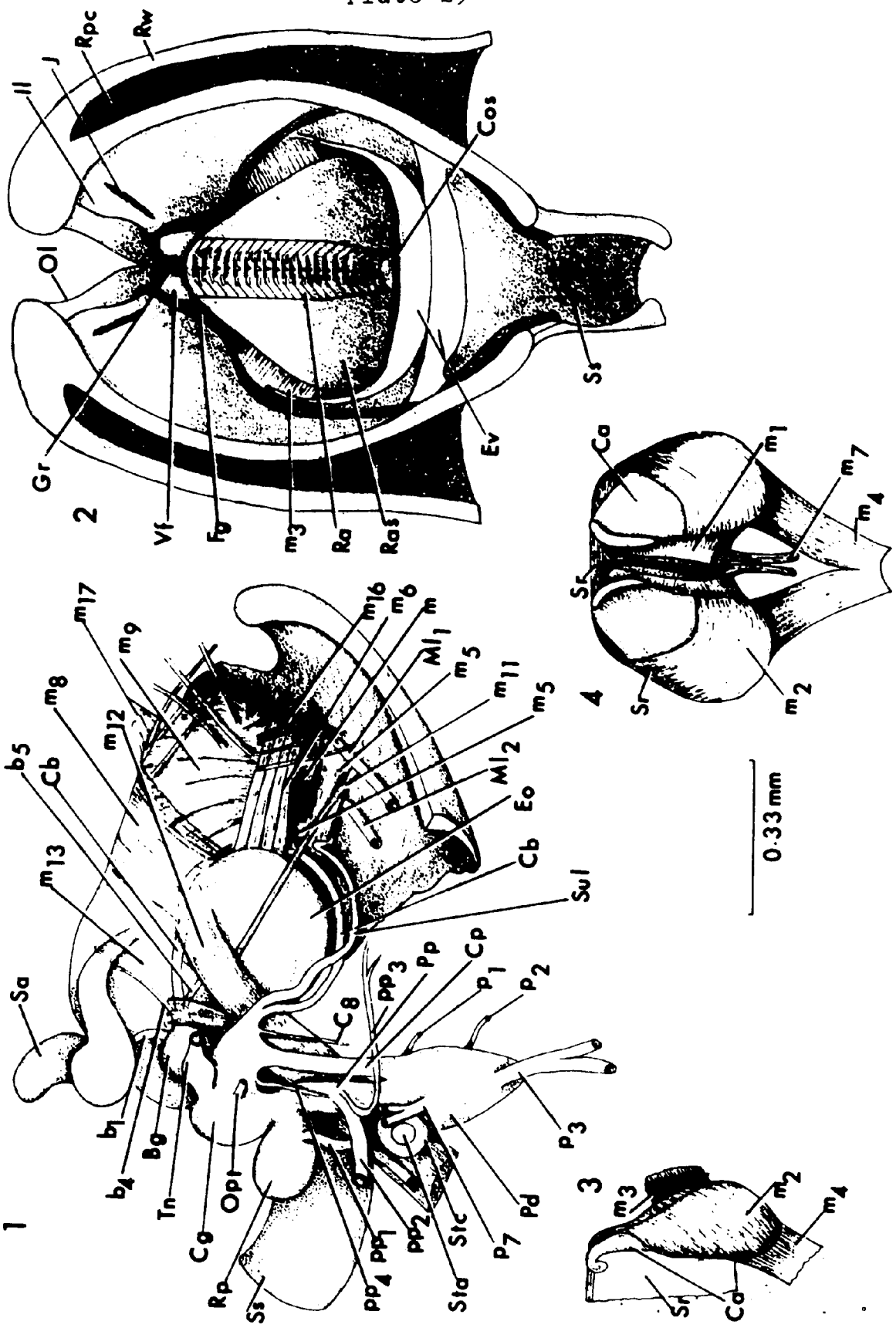

Rpc
Rw
J
Cos
Ol
Gr
Ev
Ss
Vf
Fg
m3
Ra
Ras
2
Ca
m1
m7
m4
Sr
m2
4
m17
m9
m16
m6
m
Ml1
m5
m8
m12
m11
m5
b5
Cb
Ml2
Eo
Cb
m13
Sul
Sa
Pp
Cp
Pp3
p1
p2
C8
b1
b4
Bo
Tn
Co
Opi
Rp
Ss
pp4
pp1
pp2
Sta
Stc
p7
Pd
p3
1
3
m3
m2
m4
Sr
Ca
0.33 mm

Plate 30

RADULA OF ONCOMELANIA HUPENSIS FORMOSANA

Ce	central
Im	inner marginal
Oma	outer marginal
La	lateral

Plate 30

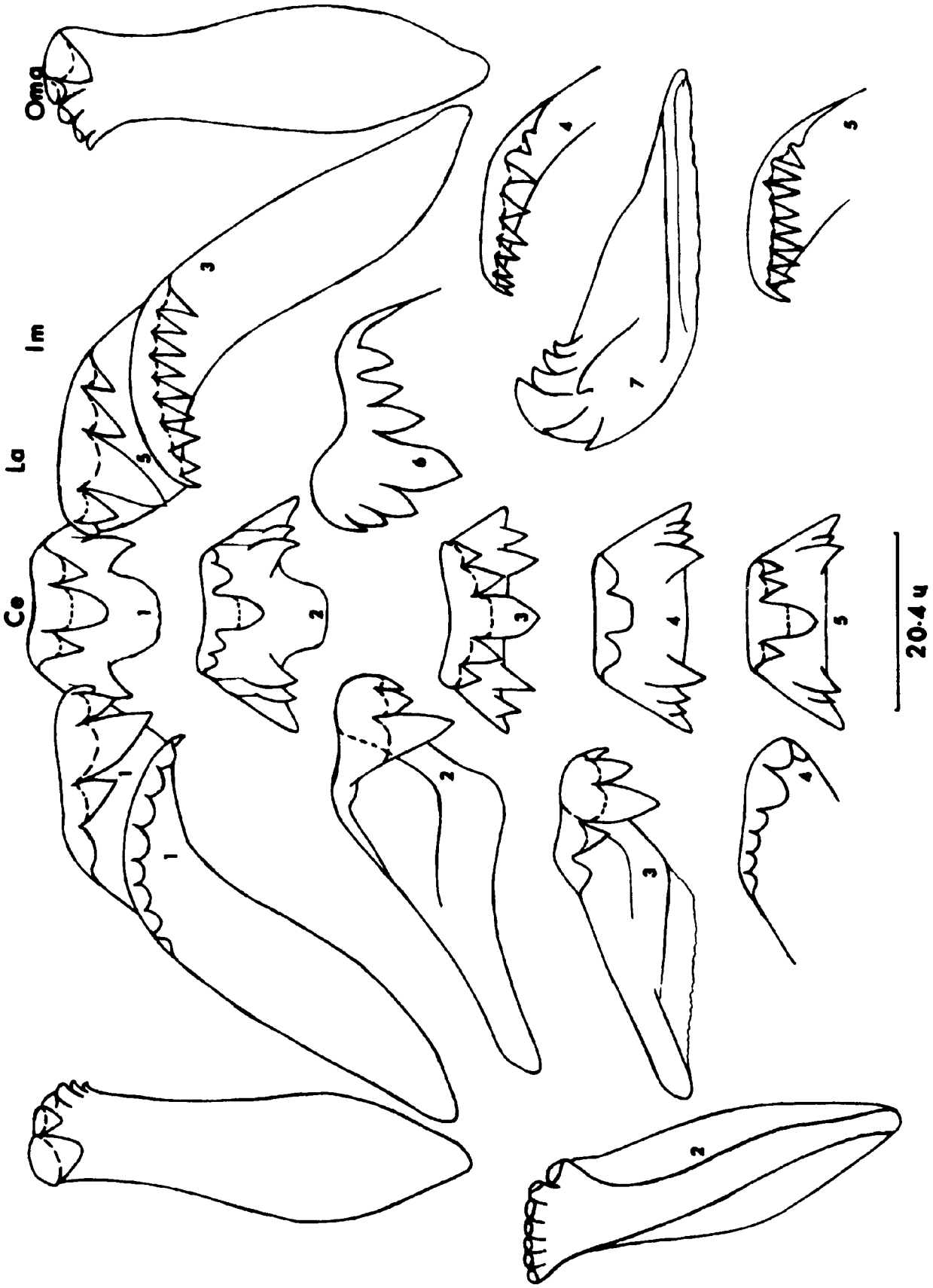
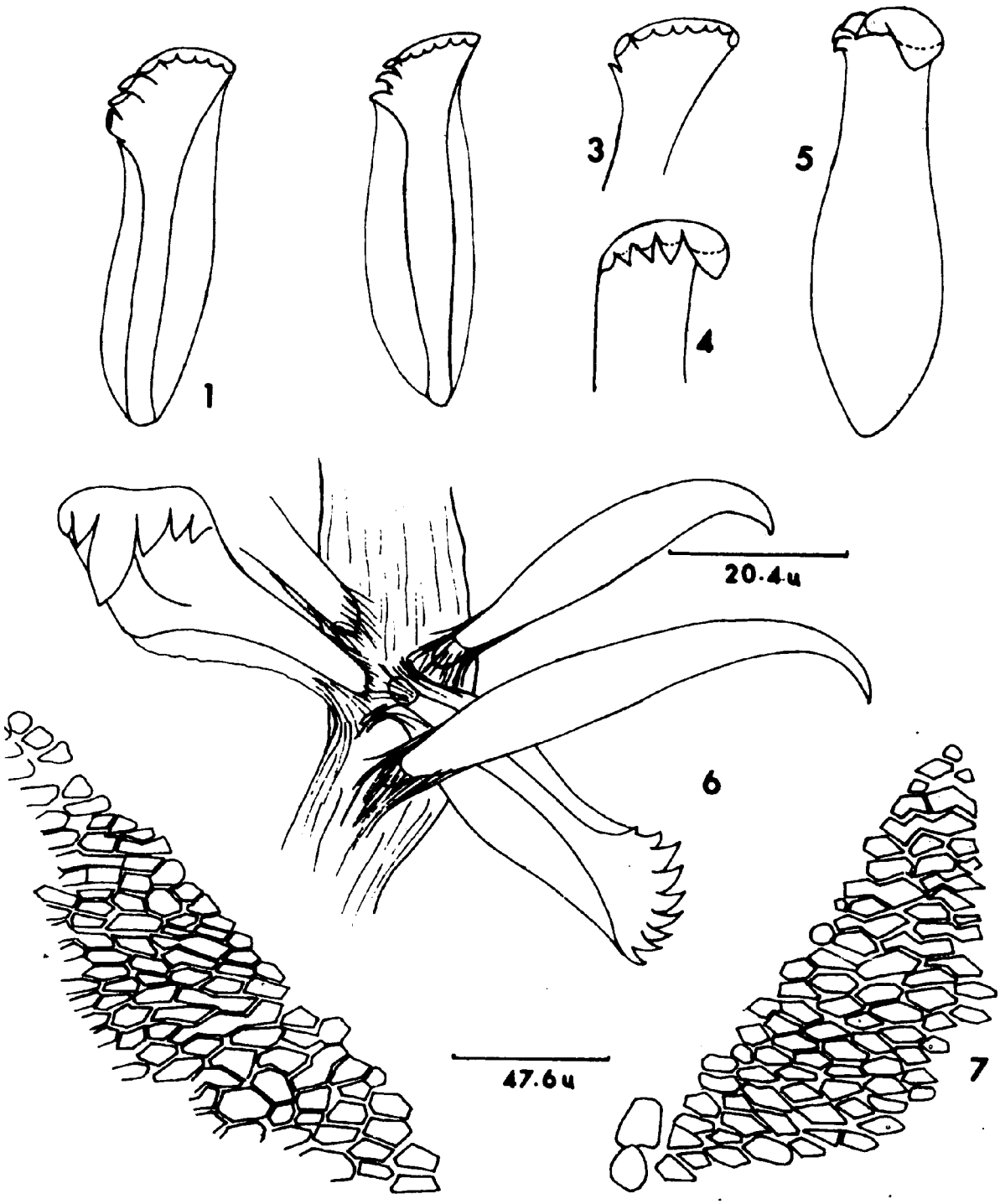


Plate 31

RADULA OF ONCOMELANIA HUPENSIS FORMOSANA

Figs. 1,2,3	inner marginals
Figs 4,5	outer marginals
Fig. 6	the manner in which the teeth are attached to the radular membrane
Fig. 7	jaw

Plate 31



Aside from the differences in length, width, and number of rows of teeth, there are 2 other small differences. The large mediobasal cusps of Oncomelania hupensis formosana are more widely separated than those of Pomatiopsis lapidaria (compare Plate 19 with Plate 30). Also, there is a pronounced tendency in the outer marginal to have an enlarged and swollen outer cusp (Plates 30, 31), a condition rarely observed in P. lapidaria.

The manner in which the teeth in both species are attached to the membrane is shown in Plate 31, Fig. 6.

7. Musculature.

The musculature is shown in Plates 13, 27-29. The patterns and arrangements of muscles are the same in both species with few exceptions. There are grades of variation in muscular structures which reach extremes in Oncomelania hupensis formosana. The preventral protractors (Plate 29, m_6) tend to be more strongly developed than in Pomatiopsis lapidaria, although this is variable. The suspensors of the buccal mass (Plate 27; Plate 29, m_{17}) tend to be more stout and fewer in number than found in P. lapidaria, although there is a gradation to the exact condition found in the latter species. In several cases stout muscle strands from the anterior jugalis (m_9) were observed running anterodorsally to the anterior rostral roof, a condition never observed in P. lapidaria.

There are 3 distinct differences between the musculature of these 2 species: (1) The rostral retractors (Plate 28, m_{20}) terminate shortly after passing over the pedal haemocoel. They do not pass under the buccal protractors to insert about the oral aperture at the floor of the tip of the rostrum as they do in Pomatiopsis lapidaria. (2) The buccal protractors commonly fuse in a single sheet of muscle which have their origin from the rostral floor (Plate 28, m_5). This is in contrast to the condition normally found in P. lapidaria (Plate 18, m_5). There is a mediolateral slip which has its origin on each side of the oral aperture which runs posteriorly and then dorsally to unite with the buccal protractor near the rostral floor before the muscle bifurcates as shown in Plate 28. As these slips are anterior to the main sheet of m_5 in Plate 28, they cannot be observed. Each m_5 label in Plate 29, Fig. 1, refers to the medial slip and the posterolateral sheet, respectively. The mediolateral slips are not found in P. lapidaria. (3) The mediolateral slips are crossed by a circular band of muscles (Plate 29, m) which arise from the floor of the rostrum at either side of the oral aperture and sweep around in an arc over the mediolateral slips of the buccal protractors. This muscle band does not correspond to the oral sphincter muscle. Usually this arc of muscle is posterior to the oral sphincter.

8. Nervous System.

Several differences are found between the species with regard to the nervous system. (1) Upon opening the rostral cavity one notices that the ganglia and nerves are not dusted with the heavy pigment as was found in Pomatiopsis lapidaria. (2) The length of the cerebral commissure (Cc, Plate 32) is short in Oncomelania hupensis formosana. It measures 0.07 mm ± 0.024 mm long and about 0.06 mm wide. In P. lapidaria the commissure measures at least 0.12 mm long and 0.07 mm wide. This difference is not necessarily due to the generally smaller structures in O. hupensis formosana.

(3) The pleuro-supraesophageal commissure is short, 0.168 mm ± 0.048 mm long compared with a length of at least 0.288 mm in Pomatiopsis lapidaria. As a result of the shortened commissure, the supraesophageal ganglion rests on the dorsolateral surface of the esophagus. The osphradiomantle nerve (Omn) and the supervisceral commissure (Suv) arise from the tip of the ganglion and travel about 0.39 mm to the left lateral wall (Plate 27, Plate 32, Fig. 1). In P. lapidaria, due to the lengthened commissure, the tip of the ganglion almost touches the lateral wall (Plate 14). The supervisceral commissure arises from the posterior side of the ganglion near its tip, but not from the tip. The osphradial nerve and the mantle nerve barely leave the ganglion when they enter the lateral wall.

NERVOUS SYSTEM OF ONCOMELANIA HUPENSIS FORMOSANA

Fig. 1 The dorsal aspect of the central nervous system or "brain."

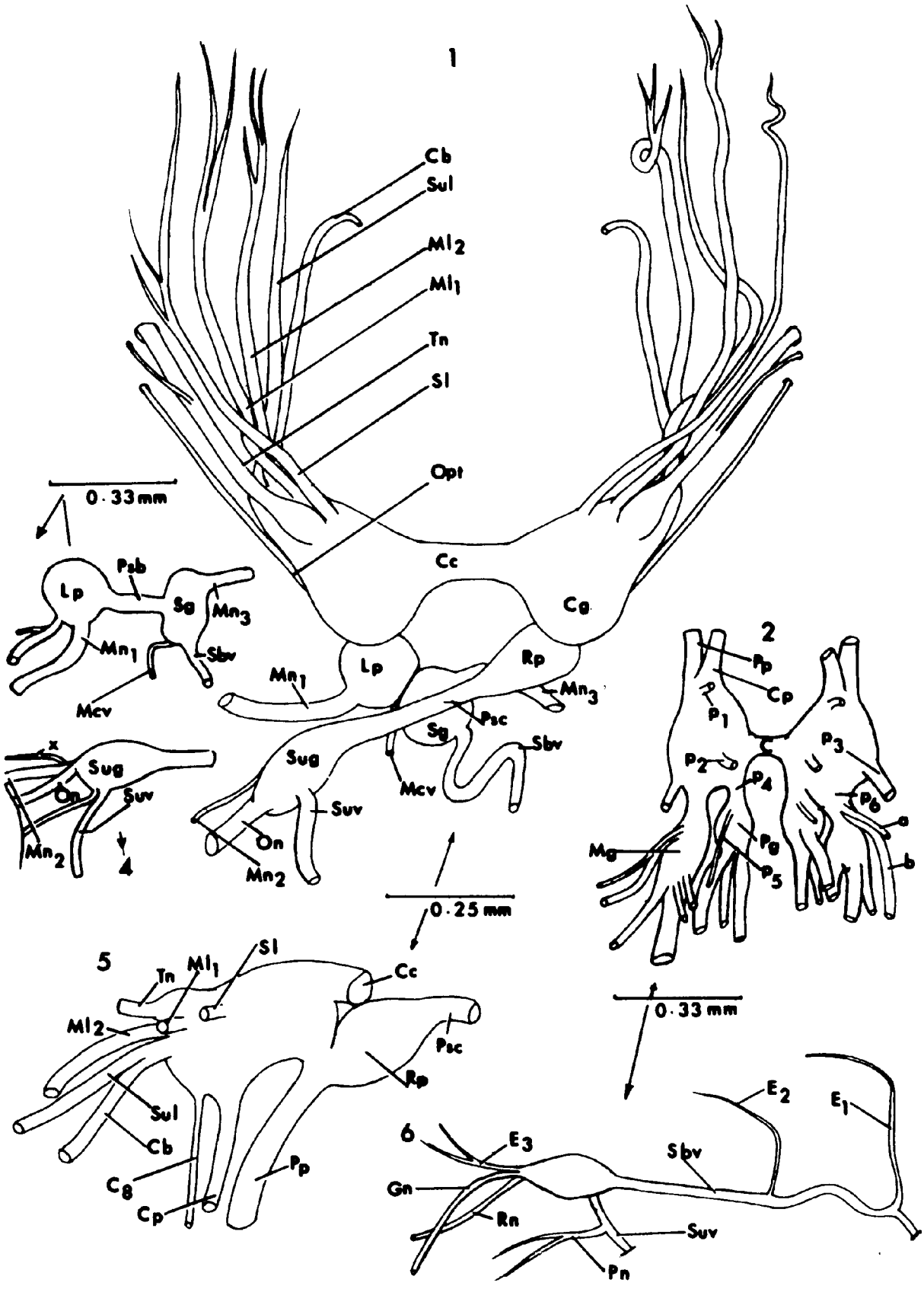
Fig. 2 The anterior aspect of the pedal ganglia.

Fig. 3 The medial aspect of the right cerebral ganglion showing the position where each nerve arises.

Fig. 4 The ventral aspect of the visceral ganglion and associated nerves.

a	nerve from p_6
b	nerve from p_6
C	pedal commissure
Cc	cerebral commissure
Cb	cerebrobuccal commissure
Cg	cerebral ganglion
Cp	cerebropedal commissure
C_8	cerebro-tensor nerve
E_1	external mantle cavity nerve 1
E_2	external mantle cavity nerve 2
E_3	external mantle cavity nerve 3
E_4	external mantle cavity nerve 4
Gn	gonadal nerve
Lp	left pleural ganglion
Mcv	mid columellar nerve
Mg	metapodial ganglion
Ml_1	median labial nerve 1
Ml_2	median labial nerve 2
Mn_1	mantle nerve 1, from the left pleural ganglion
Mn_3	mantle nerve 3, from the subintestinal ganglion
Omn	osphradiomantle nerve
Opt	optic nerve
p_1	lateral retractor nerve, from the pedal ganglion
p_2	nerve to the anteroventral wall of the pedal haemocoel
p_3	major lateral nerve of the pedal ganglion
p_4	propodial commissure
p_6	metapodial commissure
p_8	minor lateral nerve of the pedal ganglion
Pg	propodial ganglion
Pn	pericardial nerve
Pp	pleuropedal commissure
Psc	pleuro-supraesophageal commissure
Rn	renal nerve
Rp	right pleural ganglion
Sl	superlabial nerve
Sg	subintestinal ganglion
Sbv	subvisceral commissure
Sug	superintestinal ganglion
Sul	sublabial nerve
Suv	supervisceral commissure
Tn	tentacular nerve

Plate 32


1
Cb
Sul
Ml2
Ml1
Tn
Sl
Opl
Cc
Cg
0·33mm
Psb
Lp
Sg
Mn3
Mn1
Sbv
Mcv
Mn1
Lp
Rp
Mn3
Psc
Sg
Sbv
Mcv
Sug
Suv
On
Mn2
4
x
Sug
On
Suv
Mn2
0·25mm
2
Pp
Cp
P1
P3
P2
P4
P6
a
Mg
P5
b
0·33mm
5
Tn
Ml1
Sl
Cc
Ml2
Psc
Rp
Sul
Cb
Cg
Cp
Pp
6
E2
E1
E3
Sbv
Gn
Rn
Suv
Pn

(4) The main branch of the tentacular nerve (Tn, Plate 32) arises from the basal swelling of the tentacular nerve, not from the mid-length of the nerve as in Pomatiopsis lapidaria. (5) Buccal nerve 3 was not found in Oncomelania hupensis formosana.

The other differences are mainly ones of size (compare Plates 32 and 21). A few minor differences might be mentioned. The minor lateral nerve (Plate 32, Fig. 2, p_8) from the pedal ganglion was frequently encountered in Oncomelania hupensis formosana while it was infrequently found in Pomatiopsis lapidaria. The external mantle nerve (Plate 32, Fig. 4, E_4) was observed although it varied in strength and was sometimes absent. It ran anterolaterally over the mantle wall epithelium. This nerve was not observed in P. lapidaria.

E. Summary and Discussion

Abbott (1948a) stated that the reproductive and nervous systems of Pomatiopsis and Oncomelania showed few differences. Actually, the major differences found between the species were in these systems. In Table 12 are listed those differences which I feel are important in defining the generic separation of Oncomelania and Pomatiopsis. Differences of a specific nature are listed in Table 13. In the latter many of the characters are unknown for the other species of Pomatiopsis as well as the subspecies of Oncomelania. Future

Table 12

Anatomical Differences between Pomatiopsis lapidaria and Oncomelania hupensis formosana Felt to be of Major Importance

Character	P. lapidaria	O. hupensis formosana
Shell		
1. umbilicus	wide	narrow
2. varix	-	+
3. sutures	deep	moderately deep
4. apex	wide	narrow
5. lip	straight	sinuate
6. whorls	6.5-7.0	7.0-7.5
Gill filaments	30 or less	35 or more
Tentacles	short	long
Female Reproductive System		
1. gonad branches	few	several
2. gonad collecting duct	wide	slender
3. oviduct coils encircle the seminal receptacle	-	+
4. bursa copulatrix	spermathecal duct leaves anterior end	sperm and spermathecal duct leave laterally
Male Reproductive System		
1. verge with papilla	-	+
2. verge ciliated	-	+
3. verge with glandular edge pronounced	+	-
4. verge with pronounced musculature	-	+
5. seminal vesicle	thick, neatly coiled	slender, knotted tube
Nervous System		
1. cerebral commissure long	+	-
2. pleuro-supraesophageal commissure long	+	-
3. supervisceral commissure	posterolateral surface	from the tip
4. osphradial nerve	short	long

Table 13

Anatomical Differences between Pomatiopsis lapidaria and Oncomelania hupensis formosana Indicative of Specific Rank

Characteristic	P. lapidaria	O. hupensis formosana
Pigmentation	no dimorphism	sexual dimorphism
Glands at edge of eyes	white-yellow white	yellow white-yellow
Digestive gland with prominent vascularization	-	+
Radula		
1. length	1.13 mm	0.98 mm
2. width	0.13 mm	0.12 mm
3. total rows of teeth	94	84
Size of organs	larger	smaller
Osphradium	wider	narrower
Muscles		
1. short rostral retractor	-	+
2. mediolateral slip from buccal protractor	-	+
3. circular muscle over buccal protractor	-	+
Male Reproductive System		
1. gland types in verge	3	1
2. testicular lobes	short and slender	elongate and thickened
Female Reproductive System		
1. opening of the spermathecal duct obscure	+	-
2. ova	larger	smaller
Nervous System		
1. buccal nerve 3	+	-
2. external mantle nerve 4	-	+
3. branch of tentacular nerve arises	mid nerve	basal

investigations of these other forms may serve to give those characters greater weight, i.e., they may represent a condition representative of the genus as a whole.

Differences in the shell clearly separate Oncomelania from the species of Pomatiopsis. P. binneyi, however, has a shell quite unlike those of either Oncomelania or the other species of Pomatiopsis. It is tiny, about 3.0 mm high; imperforate, and the inner and outer lips are continuous, i.e., there is no parietal callus and the lips are slightly separated from the body whorl. P. binneyi will be discussed in the final summary statements as this form is aberrent in a number of ways when compared with the other species of Pomatiopsis.

The verges of all the species of Pomatiopsis do not have the terminal papilla found in Oncomelania, Blanfordia, and Tomichia. Two species of Pomatiopsis, P. cincinnatiensis and P. californica, have penial filaments. Penial filaments are unknown in Blanfordia Tomichia, or Oncomelania.

Oncomelania and Blanfordia have the characteristic ciliation of the tip of the verge described for O. hupensis formosana. Tomichia ventricosa has the same active cilia but in this species the bands of cilia extend half way back along the verge. In these 3 genera the cilia are about 4 micra in length and beat actively.

The verges of Pomatiopsis lapidaria and P. cincinnatiensis

lack cilia. In initial studies on P. binneyi and P. californica, I found that the tips of the verges have bristle-like cilia. Unlike those of Oncomelania, they are not active, a cilium here or there beating slowly once in a while. They were bushy, irregularly oriented, and 6-7 micra in length. In P. californica they extended part way out on the penial filament.

The relative number of gill filaments clearly separate Oncomelania from species of Pomatiopsis. All the species of Pomatiopsis have the short tentacles relative to the length of the rostrum compared with Oncomelania.

The manner in which the tubes arise from the right, ventrolateral surface of the bursa copulatrix and not from the tip is characteristic for Oncomelania, Blanfordia, and Tomichia. The condition found in Tomichia is somewhat intermediate between that found in Pomatiopsis lapidaria and Oncomelania. In Tomichia ventricosa the bursa copulatrix is about twice as long as that of P. lapidaria and the subspecies of Oncomelania. The spermathecal duct arises from the right, mid, ventrolateral surface of the bursa as a single tube which runs anteriorly along the pallial oviduct. The sperm duct arises and coils in the same manner described for P. lapidaria. How the tubes arise from the bursa is unknown for P. californica and P. binneyi.

The slender collecting duct of the ovary and the numerous branches separate Oncomelania from Pomatiopsis lapidaria and P. cincinnatiensis. The condition is unknown for P. californica and P. binneyi.

The oviduct coils around the seminal vesicle in a characteristic manner in the subspecies Oncomelania hupensis quadrasi, O. hupensis formosana, and O. hupensis nosophora. The condition is unknown in O. hupensis hupensis. This arrangement does not occur in Pomatiopsis lapidaria and P. cincinnatiensis. The condition is unknown for P. californica and P. binneyi.

The pleuro-supraesophageal commissure in all the subspecies of Oncomelania is relatively short as described. This is also the condition in Blanfordia japonicum. The osphradial nerve and the mantle nerve are correspondingly long. H. van der Schalie and Dundee (1956) showed an elongate commissure for Pomatiopsis cincinnatiensis. I found that P. binneyi had a commissure like that found in P. lapidaria. The supervisceral commissure likewise arose from the superintestinal ganglion from the posterolateral surface near the tip. In these species of Pomatiopsis the mantle nerve and osphradial nerve were correspondingly very short. The condition in P. californica is unknown.

HYBRIDIZATION STUDIES

The success of hybridizing the subspecies of Oncomelania was reviewed by Davis et al. (1965). H. van der Schalie et al. (1962) reported success in hybridization experiments where male Pomatiopsis lapidaria were placed in culture with virgin female O. hupensis quadrasi and O. hupensis formosana. They did not have success with crosses involving female P. lapidaria and male Oncomelania.

Crosses were again established between male Pomatiopsis lapidaria and virgin females of the various subspecies of Oncomelania in order to obtain hybrids for anatomical studies. Three different sets of experiments were established over a total of 26 months in which adult, male P. lapidaria were maintained under various culture conditions with virgin female Oncomelania. In all the experiments males which died were replaced. Females that died were removed from the culture but not replaced. Cultures which deteriorated due to soil erosion, mold, or algal accumulation were replaced with fresh cultures. The deteriorated cultures were maintained for at least 1 month in order to observe if any young had hatched from eggs laid just prior to changing the culture. All cultures were maintained at $24^{\circ} \pm 2^{\circ}C$.

Experiment 1.

A. Seven plastic tray cultures (van der Schalie and Davis, unpublished) were established with 10-20 females in each along with 13-40 males so that each culture had about 50 snails. The plastic tray aquaterrarium was 28 cm x 19 cm x 6.5 cm. At one end was a soil bank and the other a reservoir with about 250 cc capacity. Water in the reservoir was constantly aerated. The tray was covered by a sheet of plexiglass bored with many small holes to permit gaseous exchange. Filter paper was added as food as prescribed by van der Schalie et al. (1962). The cultures were maintained in normal room level light during the day and were in the dark at night.

One culture was set up with Oncomelania hupensis nosophora, 2 with O. hupensis quadrasi, and 4 with O. hupensis formosana.

B. Eight cultures were set up and maintained exactly as those described by van der Schalie et al. (1962). Five specimens of each sex were maintained in the cultures. Only Oncomelania formosana was used.

In both A and B the cultures were routinely serviced each day along with the 80 other stock cultures on hand. Within 3-7 months 5 of the plastic tray cultures contained young. Upon redetermining the sex of all the adults in the cultures (methods of Wong and Wagner, 1954) it was determined that in every case where young were produced,

1 or 2 males of Oncomelania hupensis formosana or O. hupensis quadrasi were found. This contamination occurred in 2 cultures in the 7th month after the sexes of all the snails had been rechecked in the 5th.

In the 7th month all the cultures were placed in isolation and serviced with tools set aside for only the cross cultures. These cultures in which contamination occurred were discontinued. When these precautions were taken, no further young were produced, although the cultures were maintained and constantly observed until the 20th to 26th month.

Experiment 2.

Thirteen medium clay pot cultures were established. These cultures were unglazed clay pots with a diameter of 13 cm and a depth of 4 cm. A central mound of mud was placed on a large disc of filter paper. The bottom of the culture was covered with water so that an excess of 5-6 cc was present. H. van der Schalie and Davis (unpublished) found that this container provided optimal conditions for the production of young Oncomelania.

Five specimens of each sex were placed in each culture. Two of the cultures contained Oncomelania hupensis quadrasi; 11 of the cultures contained O. hupensis formosana. Five of the cultures were maintained under constant light provided by cool, white, flourescent bulbs. The intensity of light was 75 ft. candles. All

cultures were carefully maintained in isolation. The experiment was discontinued in 14 months. No young were produced. All control cultures with Oncomelania produced young within 2 to 3 months of being established. Male Pomatiopsis lapidaria were observed in copulation with the Oncomelania many times and spot examination of the male gonads showed them to be fully mature and productive.

Experiment 3.

A total of 16 medium clay pot cultures were established. The 16 cultures were separated into blocks of 4, each block established with males from a different population. The males were collected and placed in culture in the spring, a time of year when Pomatiopsis lapidaria exhibits pronounced sexual activity. Two cultures of each block were established with virgin Oncomelania hupensis quadrasi and 2 with virgin O. hupensis formosana. Two females were uniformly used in all the cultures while alternately 2 or 4 males were used. The cultures were maintained in isolation. Copulation was noted frequently but no young were produced over a period of 5 months. At the end of 5 months the cultures were discontinued.

Females removed from the terminated cultures were fixed in Bouin's solution, sectioned, stained with standard Hematoxylin and Eosin, and studied to determine if the ovaries were productive and if the seminal receptacles were storing sperm. In no case was sperm noted in the seminal receptacle or bursa copulatrix.

Oocytes posterior to the gonopericardial duct often showed signs of atrophy and deterioration.

Summary and Discussion.

As a result of these experiments it was concluded that Pomatiopsis lapidaria will not produce an hybrid F_1 generation when interbred with Oncomelania. It is felt that the results of previous experiments reporting success in such crosses were possibly due to contamination of the cultures with male Oncomelania during routine mantenance.

Burch (1960b) reported that the spermatagonial cells of Pomatiopsis lapidaria have 33 chromosomes, 16 pairs and "a heterochromatic chromosome, presumably a sex chromosome." The oogonial cells of Oncomelania hupensis quadrasi and O. hupensis nosophora had 34 chromosomes. The spematogonial cells of P. cincinnatiensis have 32 pairs of chromosomes plus a heteromorphic pair. Patterson (1963) states that 2n = 34 in Oncomelania; the sex determining mechanism in P. lapidaria is of an XO type while in P. cincinnatiensis the sex determining mechanism appears to be an XY type. Although a cross between individuals with 2n = 32 and 2n = 34 is possible, a successful cross between P. cincinnatiensis (2n = 32) with a heteromorphic pair of chromosomes (presumably sex chromosomes) and Oncomelania (2n = 34) which lacks a corresponding heteromorphic pair is highly improbable. Karyotipic

differences in the chromosomes of these species indicate that there would not be a sufficient number of similar homologues between the 2 species to permit successful hybridisation (Burch, personal communication).

ELECTROPHORETIC STUDIES

A. Introduction

Very little is known about the use of electrophoresis as it pertains to molluscan systematics. Cheng (1964) reviews previous work pertaining to mollusks. Cheng used a Bekman Durrum-type migration chamber to investigate the serum proteins of several species of marine and freshwater gastropods as well as a few marine pelecypods (also 1 Sphaeriid). The gastropods were widely separated taxonomically. Using serum, he obtained up to 5 fractions although there were generally only 1-3 fractions. From his results he concluded that each "species" can be identified by its serum electrophoretic pattern. He states that "undoubtedly much more extensive surveys of the serum proteins of mollusks must be made before useful taxonomic information will be obtained."

Wright and Ross (1959) found that quantities of protein in snail blood are small and satisfactory separations were not obtained on paper. Using cellulose acetate they succeeded in separating a few fractions from the blood of Australorbis glabratus. Wright and Ross (1963) published data showing that blood proteins and haemoglobin varied considerably both quantitatively and qualitatively with progressive growth and development of sexual maturity in

Australorbis glabratus. They state they confirm earlier doubts concerning the taxonomic value of molluscan blood proteins and indicate that molluscan egg proteins might be more useful.

Davis and Lindsay (1964) studied foot muscle protein and blood from Helix pomatia using disc electrophoresis. With the use of muscle, there was no significant qualitative or quantitative difference in the 19 separated protein components between individuals from the same population. Age composition of the population did not affect qualitative or quantitative results. Seven components were isolated from the blood. The migrational position of the components remained constant over a range of different sized snails but the density varied inversely with size.

Davis and Lindsay (1964) reported that "distinct species have distinct patterns," and that disc electrophoresis is sensitive enough to demonstrate variations between populations when such differences occur. Disc electrophoresis was used to study the "fingerprint" patterns of Pomatiopsis lapidaria and Oncomelania hupensis formosana in order to determine whether distinct and different patterns could be obtained. This investigation was undertaken as a preliminary step for comparative studies involving the other subspecies of Oncomelania and species of Pomatiopsis.

B. Materials and Methods

In the disc electrophoresis technique used, proteins were separated in a tube of 7-1/2 per cent polyacrylamide. The buffer used was a tris-glycine mixture with a pH of 8.2-8.4. A constant current of 5 ma per tube was passed through each tube (Plate 33). The progress of the run was checked by the advance of the visible brom phenol blue dye front through the gel column. This dye was added to the buffer prior to the beginning of each run. When the dye front had moved 1-1/4 inches into the separating (lower) gel the run was terminated. The gel was immediately fixed in Amido-Schwartz stain for several hours and then destained in acetic acid. The gel was placed in a Calalco microdensitometer, Model E, which graphed the position of each fraction as well as integrated and recorded the area under each curve.

Fresh snail foot muscle was chosen as a source of protein as it was (1) more readily obtained from small mollusks than blood; (2) a tissue more often free from parasites and was readily observed for parasites; (3) compared with grinding up the whole snail, the foot represented a relatively homogeneous tissue although it admitedly included nerve fiber, mucous glands, and haemolymph.

Using large snails such as helicids and lymnaeids, one snail provided enough foot tissue to make one run possible (5-10 tubes). In such cases 0.3 gm of tissue were homogenized in

2.0 ml. Carriker's (1946) physiological saline using a Servall microhomogenizer (50,000 r.p.m.). The tissue was homogenized for 30 seconds and then checked to see whether all the shreds of tissue were "taken." If some pieces remained the muscle was homogenized for another 30 seconds.

Using small gastropods such as planorbids or hydrobiids 2 different procedures were used depending upon the amount of material available. When 20-50 snails of Pomatiopsis lapidaria or Oncomelania hupensis formosana were available, 0.15 gm were homogenized in 1.0 ml of saline using the microhomogenizer. Often only a few snails were available in which case 0.03 gm were homogenized by grinding the tissue by hand in a small glass well to which were added a "pinch" of silicon carbide and 150 lambda of saline. Maceration of the tissue was accomplished by hand using a small glass pestle. All operations were carried out at temperatures of 2°-3°C. accomplished by use of ice baths. The homogenate was centrifuged in a refrigerated centrifuge at 1200 r.p.m. for 5 minutes. Prior to the use of the refrigerated unit, a standard clinical centrifuge was used where the tubes with the homogenate rested in a sleeve packed with ice. The results using both procedures were comparable.

It was important to determine how much of the homogenized material remained in the supernatant after centrifugation and

how much was actually separated in the electrophoretic runs. The Folin-Ciocalteu reagent test, using colorimetric procedures, was used to determine the relative weight of protein in the supernatant and electrophoretic runs. Shreds of foot tissue were weighed on a Mettlar microbalance and subsequently submitted to the Folin test. Wet weight of tissue was plotted against Klett colorometric readings (Plate 34). From the resulting curve it was possible to determine the amount of protein in the supernatant relative to the initial wet weight of tissue. The tissue, of course, was not entirely protein, since water and mucoid material added weight which was not involved in the Folin test. The relative approximation of weights only gives one a useful indication of the fate of the homogenized tissue. It was determined that 27 per cent of the initial weight of tissue remained in the supernatant after homogenization. Increasing the weight of tissue for the 2.0 ml of saline will not "load" the supernatant with more protein. The available volume in each tube for the sample (mixed 1 parts supernatant with 2 parts upper gel) was such that only 3,300 micrograms relative weight was available for each tube. Of this amount 45 per cent was too crude to pass into the spacer gel, 21 per cent remained in the spacer gel, and 33 per cent was separated in the lower gel (Plate 33).

At least 20 runs were made using the foot muscle of each species. Each run consisted of 4 to 5 tubes loaded with

aliquots of a single muscle preparation.

C. Results

The results of these experiments are shown in Plate 35. Figs. 1 and 2, represent Pomatiopsis lapidaria and Oncomelania hupensis formosana, respectively. The lines beneath the peaks of the graphs represent the linear arrangement of protein components. Each electrophoretic run varies slightly in length and this difference is magnified about 4 times by the densitometric tracings. It is evident that it is difficult to make a one to one comparison between tracings because of this fact. To avoid this problem the bands on the gels are measured with a ruler which is accurate to 0.5 mm. The mm distance from the origin of the run to each band was recorded and the accuracy of the measurements was checked against the densitometric tracing. A ratio of the distance to each band and the distance to the front was made (Rf) thereby offsetting the slight shifts in band position due to small differences in run length (0.5 mm - 1.0 mm).

The greatest error for measurements with different persons measuring the same components was 3 per cent or an Rf value of 0.014. This same degree of error was found for measurements of the same components in tubes from different runs.

The Rf values for the protein components shown in Plate 35 are listed in Table 14. The "fingerprint" pattern for

Table 14

Rf Values for the Separated Protein Components Shown in Plate 35

Species	Band 1	2	3	4	5	6	7	8	9
Pomatiopsis lapidaria	.014	.056	.099	.141	.197	.254	.296	.380	.451
Oncomelania hupensis formosana	.014	.042	.070	.098	.155	.211	.296	.310	.408

Species	Band 10	11	12	13	14	15	16	17
Pomatiopsis lapidaria	.507	.563	.606	.662	.718	.802	.858	1.00
Oncomelania hupensis formosana	.437	.507	.620	.647	.775	.817	.873	1.00

Plate 33

DIAGRAMMATIC SET UP FOR DISC ELECTROPHORESIS

Plate 33

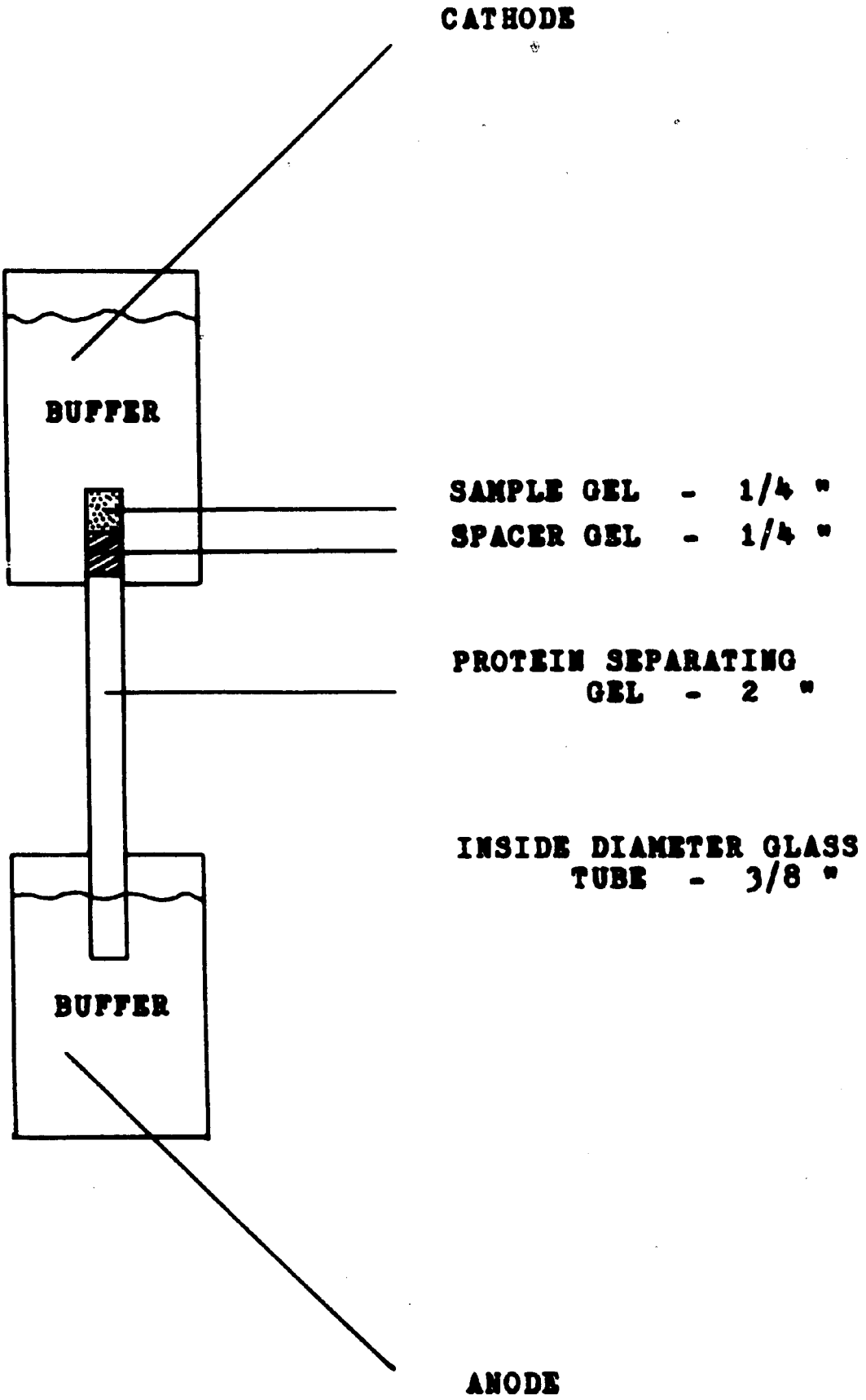

CATHODE
BUFFER
SAMPLE GEL - 1/4 "
SPACER GEL - 1/4 "
PROTEIN SEPARATING GEL - 2 "
INSIDE DIAMETER GLASS TUBE - 3/8 "
BUFFER
ANODE

Plate 34

ESTIMATION OF PROTEIN IN FOOT MUSCLE TISSUE

Plate 34

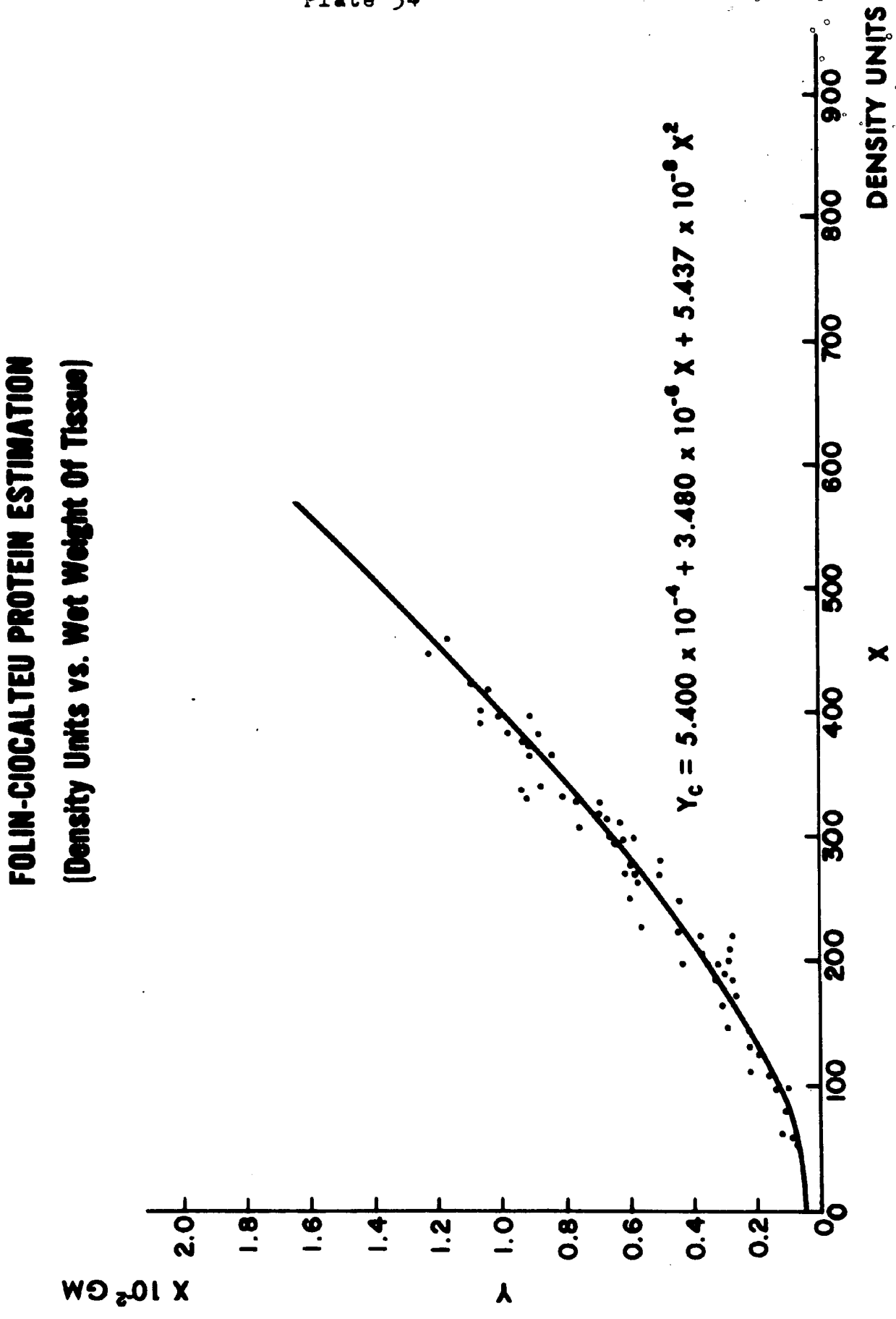

FOLIN-CIOCALTEU PROTEIN ESTIMATION
(Density Units vs. Wet Weight Of Tissue)
$Y_c = 5.400 \times 10^{-4} + 3.480 \times 10^{-6} X + 5.437 \times 10^{-8} X^2$
Y
X 10² GM
X
DENSITY UNITS
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
100
200
300
400
500
600
700
800
900

Plate 35

ELECTROPHORETIC COMPARISON OF *POMATIOPSIS LAPIDARIA* AND *ONCOMELANIA HUPENSIS FORMOSANA*

The lines beneath the densitometric tracings represent the separated components from the foot muscle. The photographs above each tracing were prepared by using the stained gels as negatives and placing them under the enlarger. Prints were made directly from the gels.

Plate 35



Pomatiopsis lapidaria (Fig. 1) varied in a number of small ways not recorded in the Rf values or in the densitometric tracings. At times bands 7 and 8 as well as 9 and 10 appear very close together or fused. Occasionally a faint band can be observed between bands 3 and 4 with an Rf value of 0.111.

In Oncomelania hupensis formosana faint bands can sometimes be resolved between bands 8 and 9 with Rf values of 0.356 and 0.366, respectively. A faint band is often resolved between bands 6 and 7 with an Rf of 0.239. In several runs bands 7 and 8; 9 and 10 appeared almost fused as a single band.

Aside from the difference in Rf values, several distinct features separate the 2 species. (1) In Pomatiopsis lapidaria bands 1 and 2 are extremely dense and close together. Oncomelania hupensis formosana has 2 equally dense bands near the origin but these are separated and have a very thin band between (Fig. 2, Bands 1-3). (2) There is a low density region beyond band 13 in P. lapidaria. Bands 14 and 15 are very low density and at times difficult to resolve. Within this region, O. hupensis formosana has a particularly outstanding component in width and density (Band 14). In the initial phase of studying the other subspecies of Oncomelania it was found that all the subspecies have 1 or 2 dense, fast moving proteins in this area usually with Rf values exceeding 0.75. (3) P. lapidaria has greater density in the slow moving components up to an Rf value of 0.500.

D. Discussion.

The patterns shown in Plate 35 are highly species specific. Some of the Rf values are similar or overlap between the 2 species but these do not necessarily infer homology. As the results stand, one can only say that there is a species difference represented which is readily reproduced and consistent. Initial studies with the other subspecies of Oncomelania indicate that they have "finger-prints" quite similar to that of O. hupensis formosana. They are all uniformly different from Pomatiopsis lapidaria by possessing 1 or 2 dense components with Rf values exceeding 0.75.

LABORATORY ECOLOGY

A. Introduction

Modifications of Vogel's (1948) aquaterrarium have been used with varying degrees of success for rearing the subspecies of Oncomelania. References to such vivaria are found in Stunkard (1946), Ward et al. (1947), Dewitt (1952), Wagner and Wong (1956), and Moose et al. (1962). These and others have noted a marked contrast between success in maintaining species of Pomatiopsis in the laboratory and rearing Oncomelania.

Stunkard (1946) noted that Pomatiopsis cincinnatiensis did not survive well in the laboratory and although P. lapidaria remained alive many weeks, reproduction was not obtained. Ward et al. (1947) failed to maintain P. lapidaria on moist mud in shallow pans. They employed large aquaterraria with a sloping mud bank covered with dry maple leaves but found that stocks died after several months. Berry and Rue (1948) stated in an abstract that laboratory breeding of P. lapidaria was successful. They noted egg laying followed after 3 weeks by hatching. No other data were given. DeWitt (1952) stated that he was successful in maintaining P. lapidaria from 1944 to 1952 using an "aquaterrarium." He gave no data on reproduction, growth of young, or if an F_1 generation was reared to maturity in the laboratory.

Dundee (1957) described a large flower pot container (12 inches in diameter) which she used "successfully" as a vivarium. She reported reproduction and egg hatching but did not mention whether the young were reared to maturity. H. van der Schalie and Dundee (1955), Van der Schalie et.al. (1962), van der Schalie and Getz (1962, 1963) discuss various aspects relating to the difficulties in maintaining species of Pomatiopsis in the laboratory.

There has been little quantitative data presented comparing Oncomelania and Pomatiopsis with regard to survival in the laboratory, natality, growth rates of the young produced, or survival of the young in the laboratory. H. van der Schalie and Getz (1963) provided comparative data on temperature and moisture responses between species of the 2 genera.

In this study the survivorship of field collected Pomatiopsis lapidaria and Oncomelania hupensis formosana was investigated when these snails were placed in different standard vivaria. The production of young was noted and the growth rates of the young recorded. Records were maintained on the survivorship of the young in culture.

B. Materials and Methods

1. Vivaria Unitilized in the Investigations.

a. Plastic tray container (PT). The PT vivarium is a modification of the aquaterrarium used by DeWitt (1952) and was described in detail by H. van der Schalie and Davis (in press). It is briefly described in the section of hybridization studies.

b. Tall clay pot (TCP). The unglazed, tall, clay flower pot vivarium was described by van der Schalie and Getz (1962). It was designed to decrease or regulate soil moisture as other vivaria with saturated soils were particularly detrimental to Pomatiopsis cincinnatiensis. This unit, 7 inches in diameter at the top and 5-1/2 inches deep, was modified slightly for this study. The filter paper wick was replaced with a thick roll of cheesecloth which projected up into the pot about 2 inches. The pot was filled with sand up to within 3 inches of the top. The sand was covered with 1-1/2 inches of loam. The packed loam was dusted with finely ground dried loam to provide a surface of particularly fine particles.

c. Battery jar (BJ). Battery jars 10 inches deep and 8 inches in diameter were utilized. The bottom of each jar was covered with a double thickness of No. 500 filter paper. A glass plate 3" x 4" was placed in the center of the jar and was used to support a small mound of mud. The filter paper was continually soaked with water so that a residue of 15-20 cc was present. The

jar was covered with a plate of glass.

d. Petri dish culture (PDC). Nine centimeter Petri dishes were used as cultures as described by van der Schalie and Davis (in press). A mound of soil was placed in the center of the dish so that a space of 1.5 cm remained between the edge of the soil and the walls of the dish. About 40 ml of pond water were added to the culture. This type of vivarium was used only for rearing the young, newly-hatched snails to maturity. The vivarium was maintained under a 40 watt, white, "cool," flourescent tube suspended 10 inches above the cultures. The light, providing 100-150 ft. candles, was cycled 10-12 hrs. per day.

e. Medium clay pot (MCP). Wong and Wagner (1956) used unglazed flower pots 5 inches in diameter in which a slope of "soil" was packed "high on one edge and terminating before reaching the other edge." The "soil" was a mixture containing soil, gravel, and sand mixed in the ratio of 2:1:1. Filter paper and dried leaf were added as food.

H. van der Schalie and Davis (in press) reported that a modification of the Wong-Wagner vivarium provided optimal conditions for the production of young Oncomelania. This vivarium type was described in general terms in the section on hybridization studies. Five males and 5 females were maintained in this culture.

2. Conditions of Temperature and Light.

The cultures, with the exception of the Petri Dish cultures, were maintained at 24° ± 2° C. As the Petri Dish vivaria were maintained under different lighting conditions, the temperature was generally 25° ± 2°C.

The cultures were maintained under different lighting conditions. Those maintained in room level light were exposed to 60 ± 10 ft. candles over an 8-hour period. They were in the dark at night. Cultures under "alternating light" were exposed to 100 ± 10 ft. candles for periods of 10-12 hours. Those under constant light (not the PDC) were exposed to 140 ± 20 ft. candles each 24 hours.

3. Routine Maintenance and Collection of Data.

All cultures were routinely checked each day to secure proper water levels, knock down the snails from the sides of the vivaria (these snails show a pronounced negative geotropism), and observe general culture conditions. Every 2 weeks each culture was thoroughly examined (except the PDC). Dead snails were removed and recorded; young were removed and the number at each whorl stage was recorded. At this time reservoirs clogged with soil particles were cleaned. The young were placed in Petri Dish cultures where they remained at least 8 weeks. In some cases 2-5 young were placed in medium clay pots and observed.

In the growth experiments young of Oncomelania hupensis formosana were measured every 3 days using a dissecting scope and a Nippon Kogaku sliding ocular micrometer. The young of Pomatiopsis lapidaria were initially measured every 3 days but it soon became evident that monthly measurements were sufficient.

C. Experiments

1. Survivorship.

a. Oncomelania hupensis formosana. From a shipment of about 2000 specimens received from Taiwan, 1,788 adults were sorted out, i.e., animals with shells possessing varices. Shells showing extreme erosion were not used. From the adult size and condition of shell it was assumed that the snails were about 1 year old. There appears to be some validity for this assumption. Although Sugiura (1933) demonstrated that O. hupensis nosophora was capable of living about 5 years in the field and McMullen et al. (1951) stated that this subspecies could live more than 2 years, other evidence indicates that the average life expectancy for subspecies of Oncomelania reaching maturity is less than 2 years. Li (1953) states that although it was not possible to indicate how long field Oncomelania hupensis formosana lived, his data indicated that a large number of adults of the previous year died during or soon after the most active breeding season. From his data he calculated the life span to be about 1 year

for the vast majority of snails.

Pesigan et al. (1958) stated that the average rate of daily mortality for field females of Oncomelania hupensis quadrasi was 0.76 per cent, and that the average female lived 65.8 days after reaching maturity. From their data on the growth rate of this subspecies, the average female would succumb in about the 7th to 8th month in life. From the growth rates for O. hupensis formosana in the field (Li, 1953), it was calculated that the adults received in the collection were at least 5 months old. From the condition of the shells it was felt that the minimal age was most likely 7-8 months.

The snails were placed in Battery Jar and Plastic Tray vivaria; the latter were maintained under alternating light. The total number of snails placed in each culture along with the total number of cultures are tabulated in Table 15. The initial number of females in each culture varied between 47 per cent to 55 per cent. The percentage of adults surviving each month is shown in Plate 36. It is evident that a constant fraction of the snails in the Plastic Tray vivarium died each month (exponential rate of 0.127). The snails maintained in the Battery Jars showed an increasing rate of mortality. The latter condition is indicative of an unfavorable environment. The snails were apparently less able to subsist in that environment with advancing age although the cultures were cleaned every 2 weeks and the filterpaper was regularly replaced. Extreme erosion of the

Table 15

The Arrangement of Vivaria and the Number of Snails Used Per Culture

Species	Culture Condition	Light Condition	No. of Cultures	Total no. of Snails	No. of Snails per Culture
Oncomelania hupensis formosana	PT	Alternating	5	600	120
	BJ	Room level	7	1188	170
Pomatiopsis lapidaria	PT	Alternating	6	156	26
		Constant	11	286	26
	BJ	Room level	5	500	100
	MCP	Alternating	5	50	10
		Constant	9	90	10
		Room level	21	210	10
	TCP	Alternating	14	140	10
Pomatiopsis cincinnatiensis	PT	Alternating	6	156	26
		Constant	5	130	26
	MCP	Alternating	5	50	10
		Constant	6	60	10
		Room level	5	50	10
	TCP	Alternating	15	150	10
		Constant	7	70	10

BJ = Battery Jar
MCP = Medium Clay Pot
PT = Plastic Tray
TCP = Tall Clay Pot

shells for snails maintained in the Battery Jars 8 to 9 months was evidence that this environment was not suitable for optimal survival. As a result of the poor environment, 50 per cent of the adults died within 4 months and only 1 per cent survived until the 32nd month. In the former environment, 50 per cent survived until the 6th month and 2 per cent were surviving at the end of 38 months.

b. Pomatiopsis lapidaria. Adults of this species were collected from the stations previously mentioned. Dundee (1957) presented data indicating that the growth rate of this species in nature was 0.20 mm per week. At this rate of growth, adults used in this study were at least 7-1/2 months old. As the snails overwinter and are inactive for at least 4 months, the snails were most likely a minimal 11-1/2 months of age. Dundee (1957) indicated that the life span in thefield is about 2 years for this species. As the adults were collected primarily in July and August, they had overwintered and had presumably grown from young hatched in June or July of the previous year. The snails were thus assumed to be 11-12 months of age.

The survivorship of Pomatiopsis lapidaria was not tested in the laboratory until a year after Oncomelania was established in the laboratory. During that period of time van der Schalie and Davis (unpublished) found that Oncomelania hupensis formosana and the other subspecies of Oncomelania survived better and produced

more young per female when cultured in the Medium Clay Pot vivaria. It was found that while all the subspecies of Oncomelania survived equally well in the Plastic Tray vivaria, O. hupensis hupensis produced no young and O. hupensis nosophora produced very few. Production of young was greatly increased for all the subspecies when they were placed in the Medium Clay Pot vivaria.

It was about this same period of time when van der Schalie and Getz (1936) produced the Tall Clay Pot vivarium type which proved more suitable for rearing Pomatiopsis cincinnatiensis. Consequently, P. lapidaria and P. cincinnatiensis were tested in a larger array of vivaria types than Oncomelania hupensis formosana. Additional field specimens of Oncomelania were not available for testing survivorship and productivity in the Medium Clay Pots and Tall Clay Pots.

Table 15 lists the number of snails placed in each culture as well as the number of cultures used under the varying conditions of light. The sex ratio was 1 in all these cultures. The survivorship curves for this species in 6 different environments are presented in Plates 37 and 38. It is clear that the lowest rate of mortality was found where the snails were maintained in Medium Clay Pots in either room level or alternating light. In these environments the exponential rate of mortality was 0.177 over the first 10 months after which time the rate of mortality progressively increased.

In Table 16 are listed the exponential rates and finite rates of mortality for Pomatiopsis lapidaria in the 6 environments tested. The rates were calculated for the first 4 to 7 months in culture. It is evident that optimal survivorship is correlated with the Medium Clay Pot vivarium type. It also appears that constant light is correlated with increased mortality.

Survivorship in the Medium Clay Pot in room level or alternating light was compatible with the 2 year life expectancy in the field. The increasing rate of mortality after the snails were about 2 years old perhaps reflects the natural consequence of old age rather than deteriorating culture conditions. All the other enviroments are clearly unsuitable for maintaining Pomatiopsis lapidaria. Mortality rates were rapid, the exponential rate exceeding 0.40 per month, i.e., a finite rate of greater than 33 per cent of the snails per month.

c. Pomatiopsis cincinnatiensis. Data presented by van der Schalie and Dundee (1955) indicated that there is a decrease in adults in the field at the end of August. The vast majority of young hatch early in August. Their data show that the life span is 16-18 months. Adults were collected in July and August; a few cultures were established with snails collected in May. These snails had presumably hatched in August or October of the previous year and had overwintered. The snails were considered to be about 10 to 12 months old. The number of snails per culture type is listed in

Table 16

Exponential and Finite Rates of Mortality for *Pomatiopsis lapidaria*, *P. cincinnatiensis*, and *Oncomelania hupensis formosana* under varying Environmental Conditions

Species	Exponential* Death Rate per Month (first 4-7 months)	Finite† Death Rate per Month (%)	Vivarium Type	Light Condition
O. hupensis formosana	0.127	12	PT	Alt.
P. lapidaria	0.177	16	MC	Room
	0.177	16	MC	Alt.
	0.42	34	MC	Con.
	0.60	45	PT	Alt.
	0.66	49	TC	Alt
	1.08	66	PT	Con.
P. cincinnatiensis	0.17	16	MC	Con.
	0.40	33	PT	Con.
	0.42	34	MC	Alt.
	0.60	45	TC	Con.
	0.60	45	PT	Alt.
	0.60	45	TC	Alt.
	0.92	60	MC	Room

* $\ell x = e^{-ax}$

† $1 - e^{-a}$

MC = Medium Clay
PT = Plastic Tray
TC = Tall Clay

Alt. = Alternating
Con. = Constant
Room = Room Level

Table 15. The sex ratio was 1. Survivorship curves for P. cincinnatiensis in 7 different environments are presented in Plates 39, 40, and 41.

Optimal survivorship was obtained in the Medium Clay Pot cultures under constant light (Plate 40) where the exponential rate of mortality was 0.17 for the first 3 months and then 0.82 thereafter. Only 10 per cent of the snails were alive at the end of 6 months. In Table 16 cultures and lighting conditions are listed in order of increasing exponential rates of mortality. It is evident that survivorship is correlated with lighting conditions and not culture type. Optimal survival occurred under constant light. The least favorable environment was that of room level light in a vivarium which provided optimal survival in constant light, i.e., the Medium Clay Pot. In all but the 1 optimal condition, the finite rate of mortality was 33 per cent or greater per month. By 6 months cultures were down to 1-4 snails with the exception of those maintained under constant light where there were 6 to 10 snails per culture.

The patterns of survival of Pomatiopsis cincinnatiensis in the laboratory indicate that this species is an "annual" as observed by van der Schalie and Dundee (1955) for this species in the field. Constant high rates of mortality might be expected for adults collected at the end of summer.

d. Pomatiopsis californica and P. binneyi. Nothing is known of the life history of these snails which are native to California. Although exact data were not kept for these species, attempts at maintaining them in Plastic Tray or Medium Clay Pot vivaria have not been successful so far. No young were produced nor did survival generally exceed 5 months. Over 200 specimens of each species were involved in attempts to establish these species in the laboratory.

e. Interspecific comparisons. It is of value to compare the survivorship curves of the different species in the same environment. In only 1 case was a comparison possible between the 2 species of Pomatiopsis and Oncomelania hupensis formosana. In this case they were in the Plastic Tray vivarium under alternating light; a condition providing only an intermediate type of survivorship for the species of Pomatiopsis (Plates 38 and 41). The finite rate of mortality for O. hupensis formosana was 12 per cent per month while the rate was 45 per cent per month for both species of Pomatiopsis.

Survivorship curves for Pomatiopsis cincinnatiensis and P. lapidaria are compared for 5 different environments in Plates 42 to 45. P. lapidaria is distinctly separated from P. cincinnatiensis on the basis of superior survivorship only when the former is maintained in the Medium Clay Pot vivarium under alternating or room level light. P. cincinnatiensis has the same survivorship as P. lapidaria for 3 months in the Medium Clay Pot vivarium under constant light but the

Plate 36

SURVIVAL OF O. HUPENSIS FORMOSANA IN VARIOUS VIVARIA

Plate 36

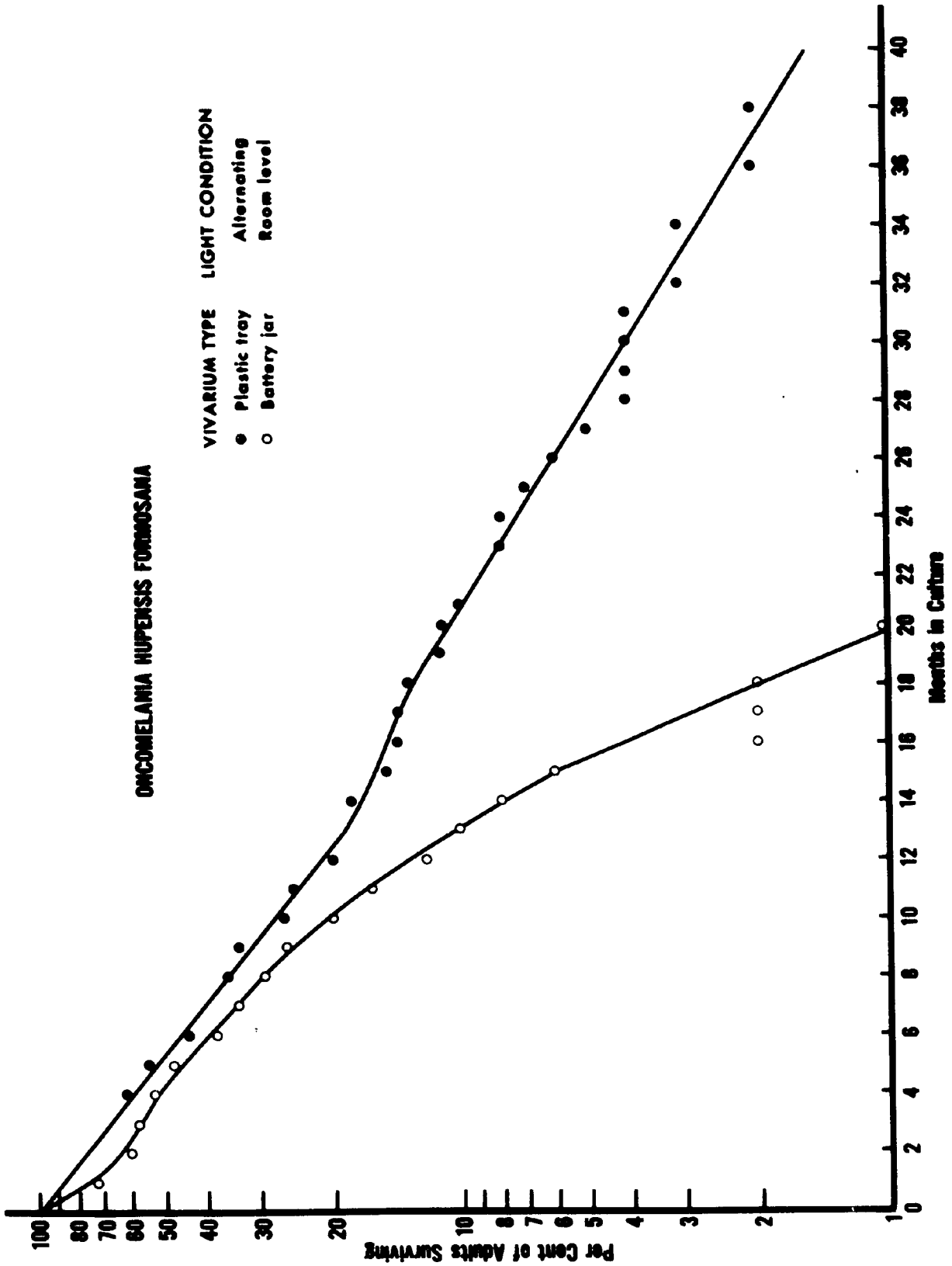

ONCOMELANIA HUPENSIS FORMOSANA
VIVARIUM TYPE
Plastic tray
Battery jar
LIGHT CONDITION
Alternating
Room level
Per Cent of Adults Surviving
Months in Culture
100
80
70
60
50
40
30
20
10
8
7
6
5
4
3
2
1
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40

Plate 37

SURVIVAL OF *POMATIOPSIS LAPIDARIA* IN MEDIUM CLAY POTS UNDER VARYING CONDITIONS OF LIGHT

Plate 37

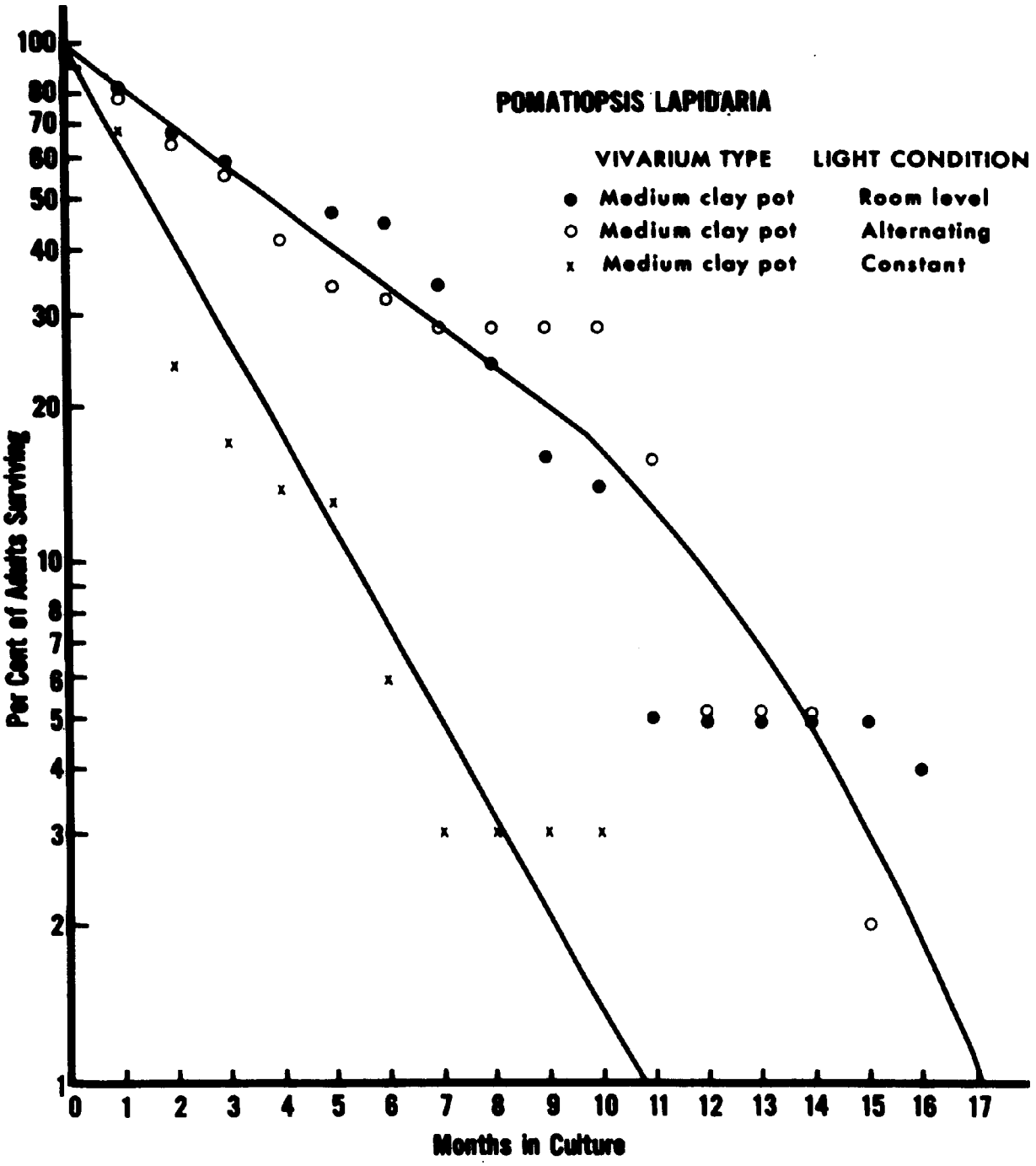

POMATIOPSIS LAPIDARIA
VIVARIUM TYPE
LIGHT CONDITION
Medium clay pot
Room level
Medium clay pot
Alternating
Medium clay pot
Constant
Per Cent of Adults Surviving
100
80
70
60
50
40
30
20
10
8
7
6
5
4
3
2
1
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
Months in Culture

Plate 38

SURVIVAL OF POMATIOPSIS LAPIDARIA IN VARIOUS VIVARIA

Plate 38

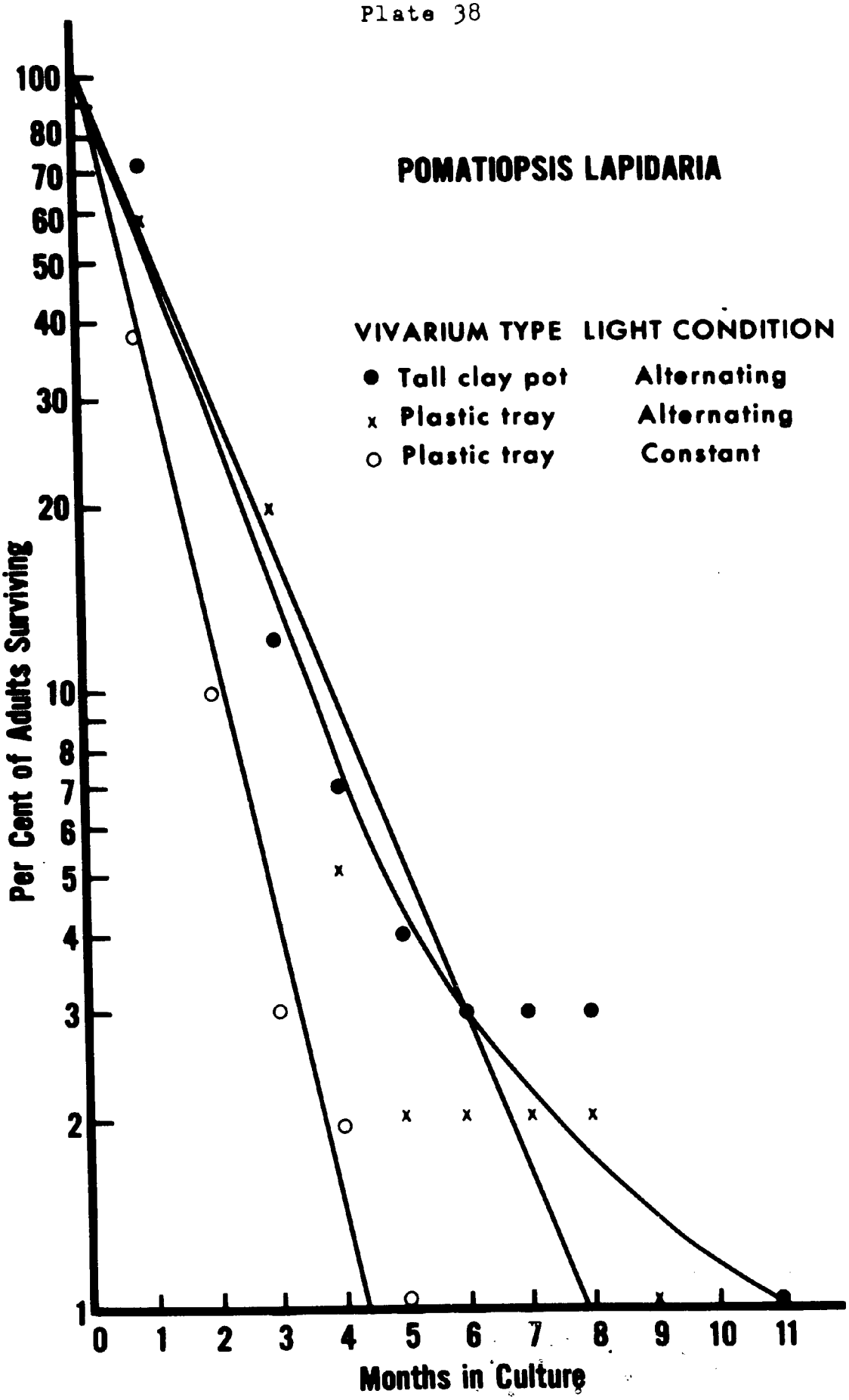

POMATIOPSIS LAPIDARIA
VIVARIUM TYPE
LIGHT CONDITION
Tall clay pot
Alternating
Plastic tray
Alternating
Plastic tray
Constant
Per Cent of Adults Surviving
100
80
70
60
50
40
30
20
10
8
7
6
5
4
3
2
1
0
1
2
3
4
5
6
7
8
9
10
11
Months in Culture

Plate 39

SURVIVAL OF POMATIOPSIS CINCINNATIENSIS IN VARIOUS VIVARIA

Plate 39

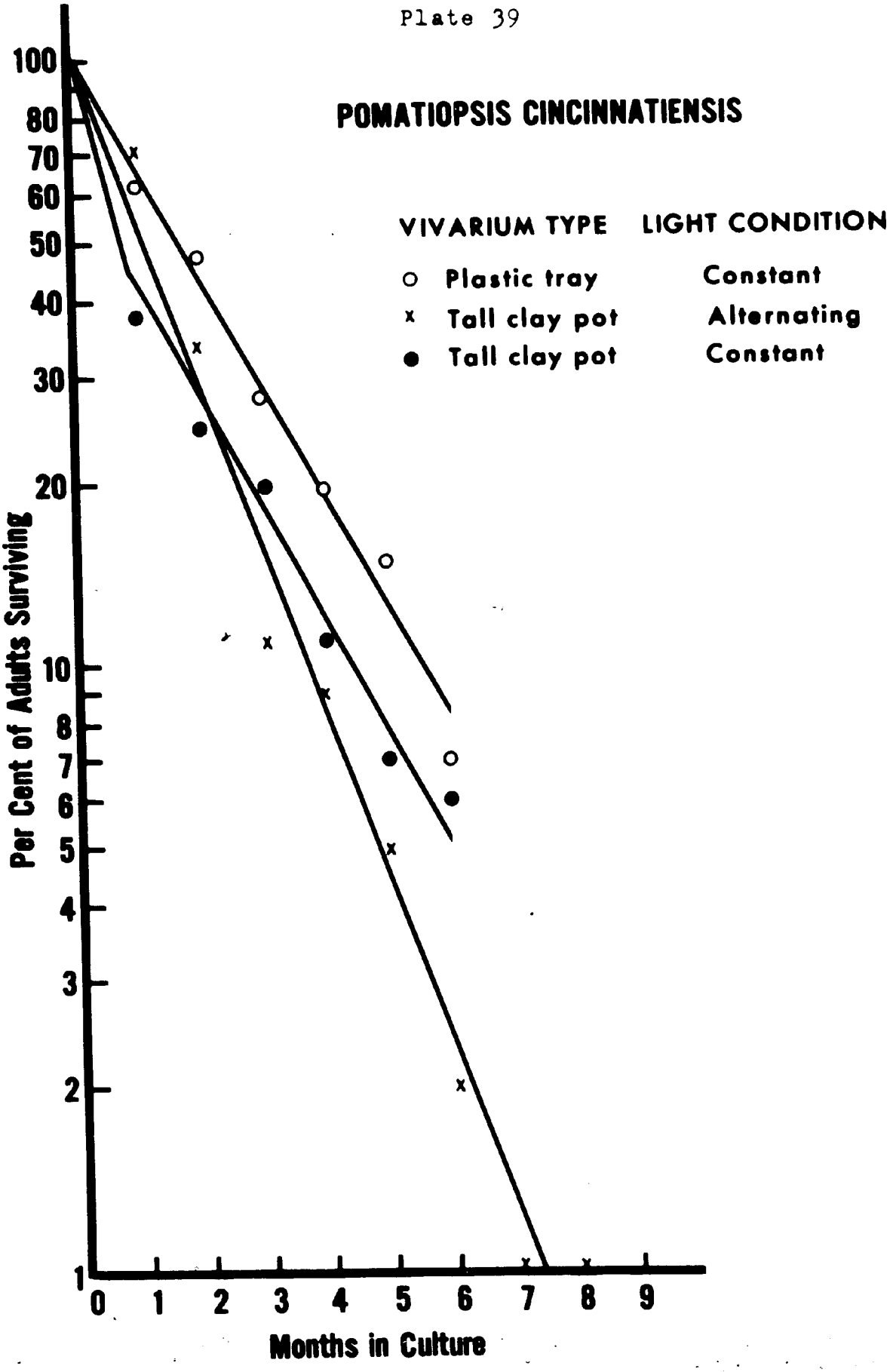

POMATIOPSIS CINCINNATIENSIS
VIVARIUM TYPE
LIGHT CONDITION
Plastic tray
Constant
Tall clay pot
Alternating
Tall clay pot
Constant
Per Cent of Adults Surviving
100
80
70
60
50
40
30
20
10
8
7
6
5
4
3
2
1
0
1
2
3
4
5
6
7
8
9
Months in Culture

Plate 40

SURVIVAL OF POMATIOPSIS CINCINNATIENSIS IN MEDIUM CLAY POTS UNDER VARYING CONDITIONS OF LIGHT

Plate 40

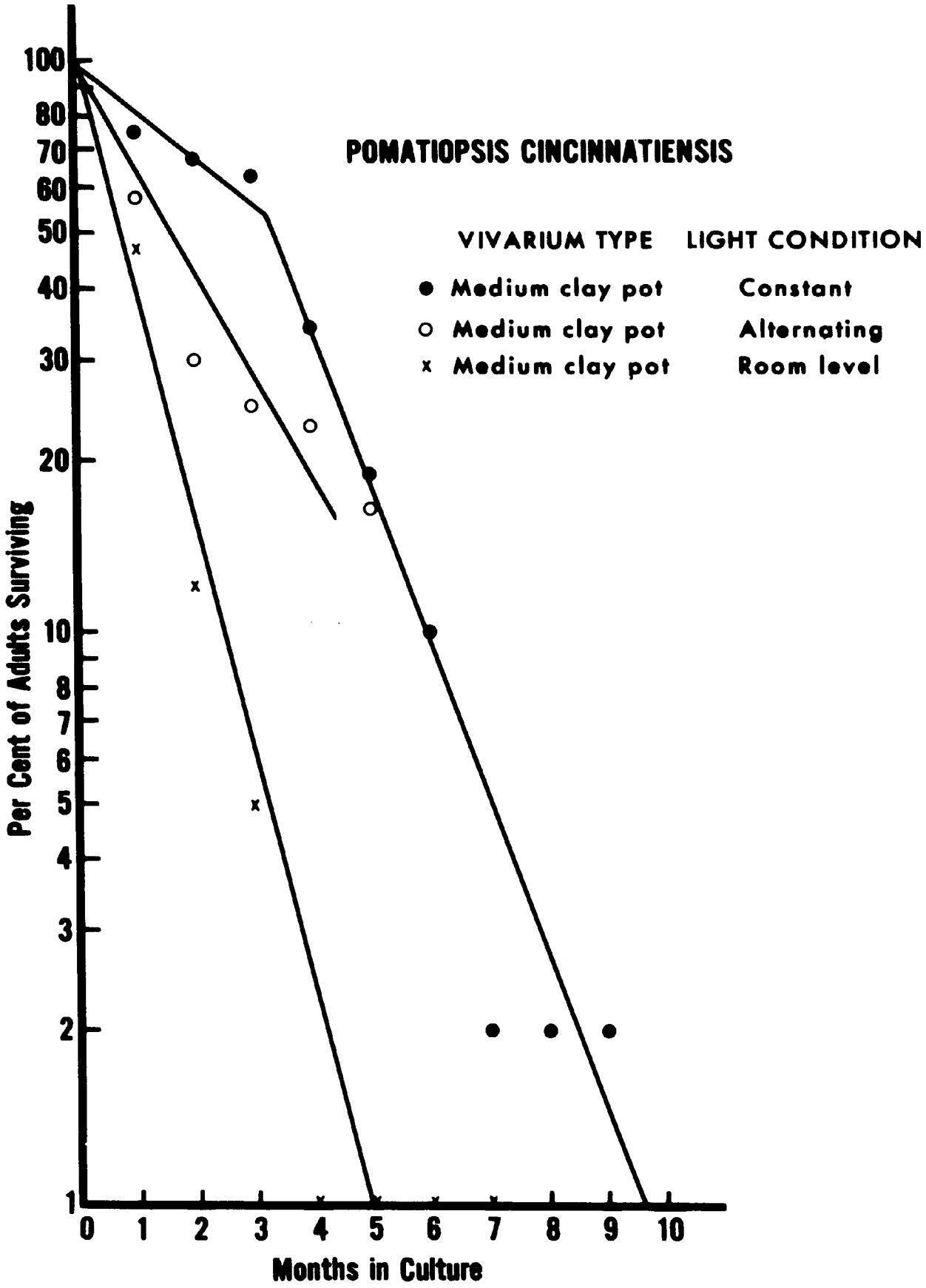

POMATIOPSIS CINCINNATIENSIS
VIVARIUM TYPE
LIGHT CONDITION
Medium clay pot
Constant
Medium clay pot
Alternating
Medium clay pot
Room level
Per Cent of Adults Surviving
100
80
70
60
50
40
30
20
10
8
7
6
5
4
3
2
1
0
1
2
3
4
5
6
7
8
9
10
Months in Culture

Plate 41

COMPARATIVE SURVIVORSHIP IN THE PLASTIC TRAY VIVARIA UNDER ALTERNATING LIGHT

Plate 41

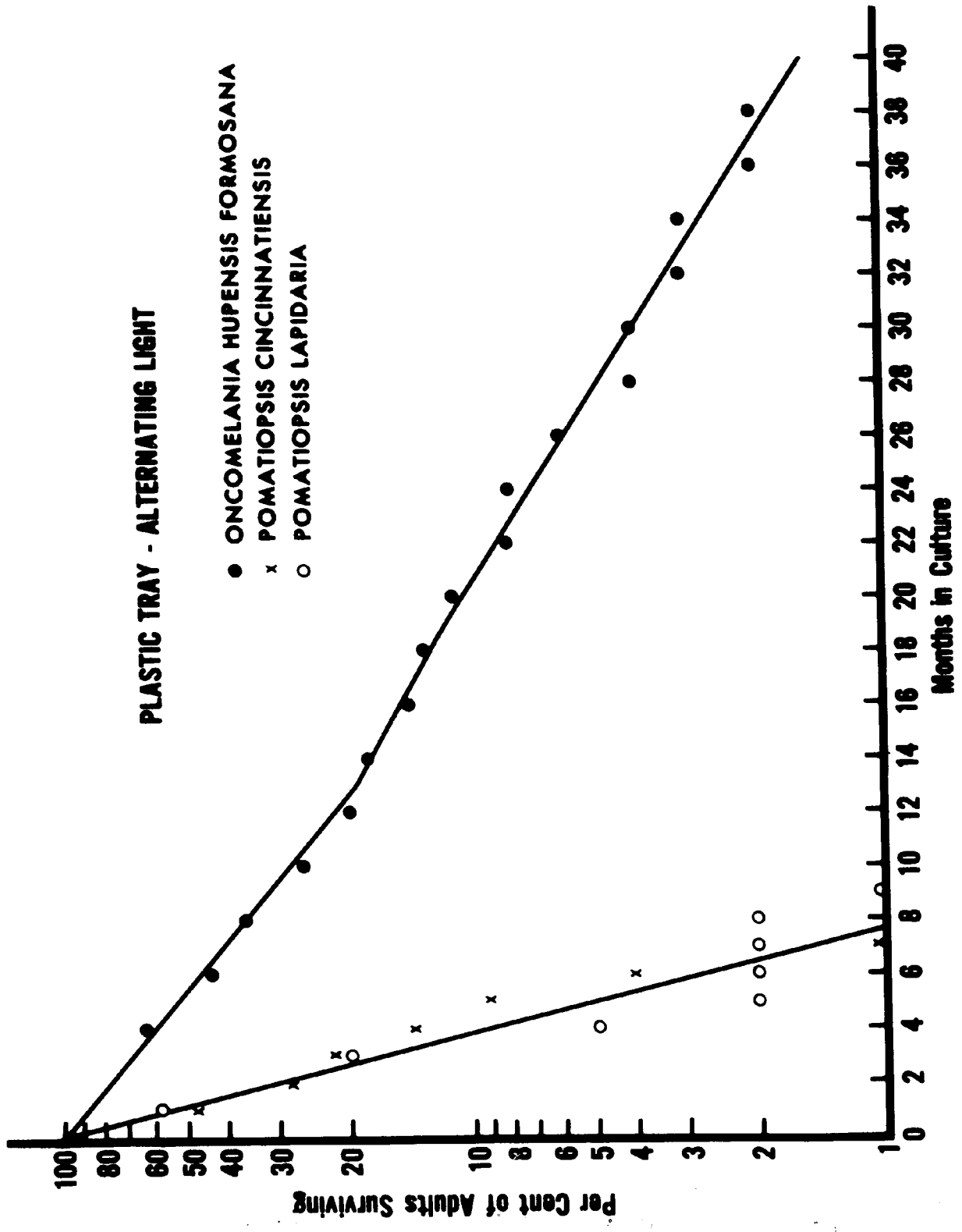

PLASTIC TRAY - ALTERNATING LIGHT
ONCOMELANIA HUPENSIS FORMOSANA
POMATIOPSIS CINCINNATIENSIS
POMATIOPSIS LAPIDARIA
Per Cent of Adults Surviving
100
80
60
50
40
30
20
10
8
6
5
4
3
2
1
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
Months in Culture

Plate 42

COMPARATIVE SURVIVORSHIP IN MEDIUM CLAY POT VIVARIA UNDER DIFFERENT LIGHTING CONDITIONS

Plate 42

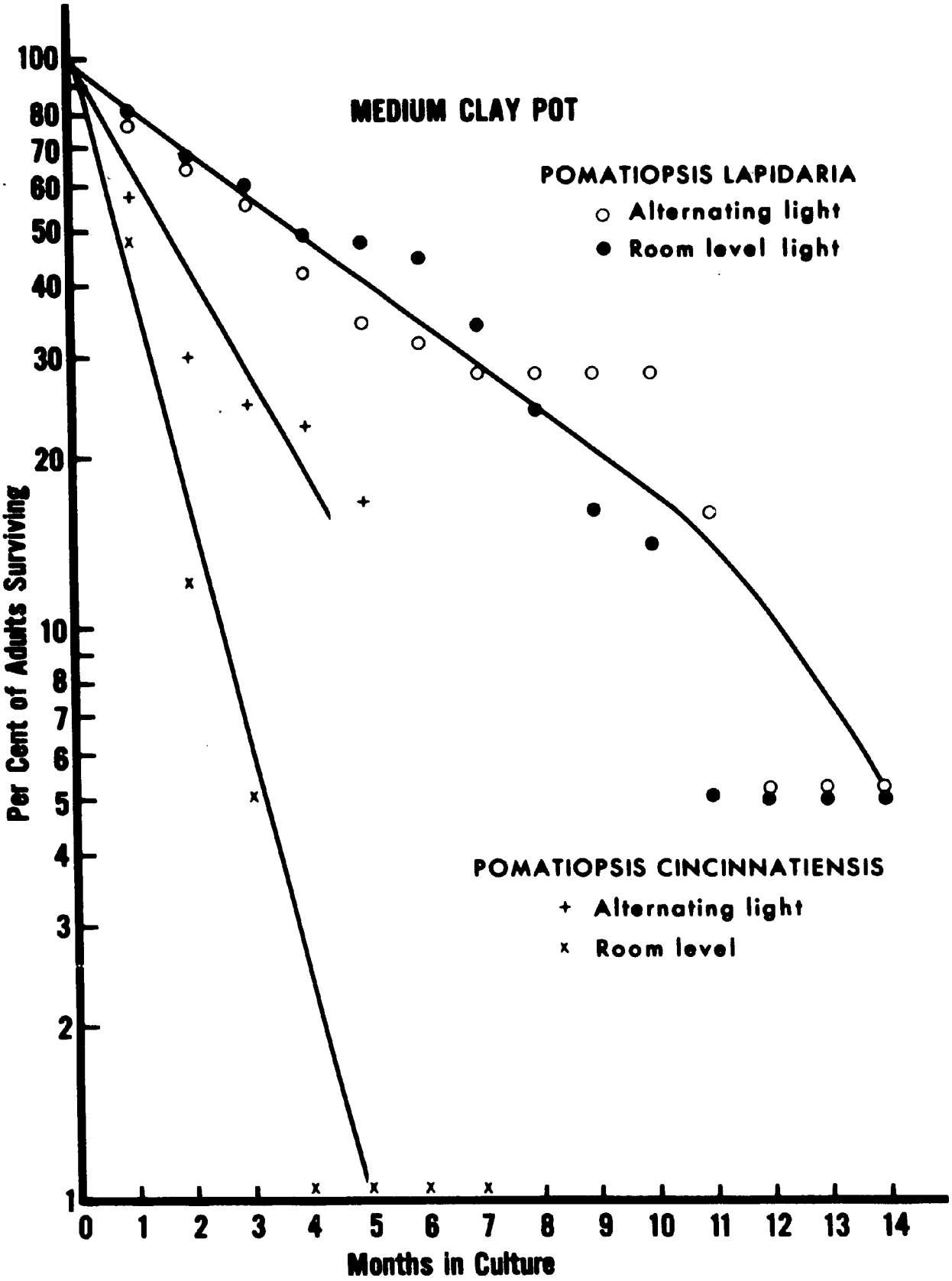
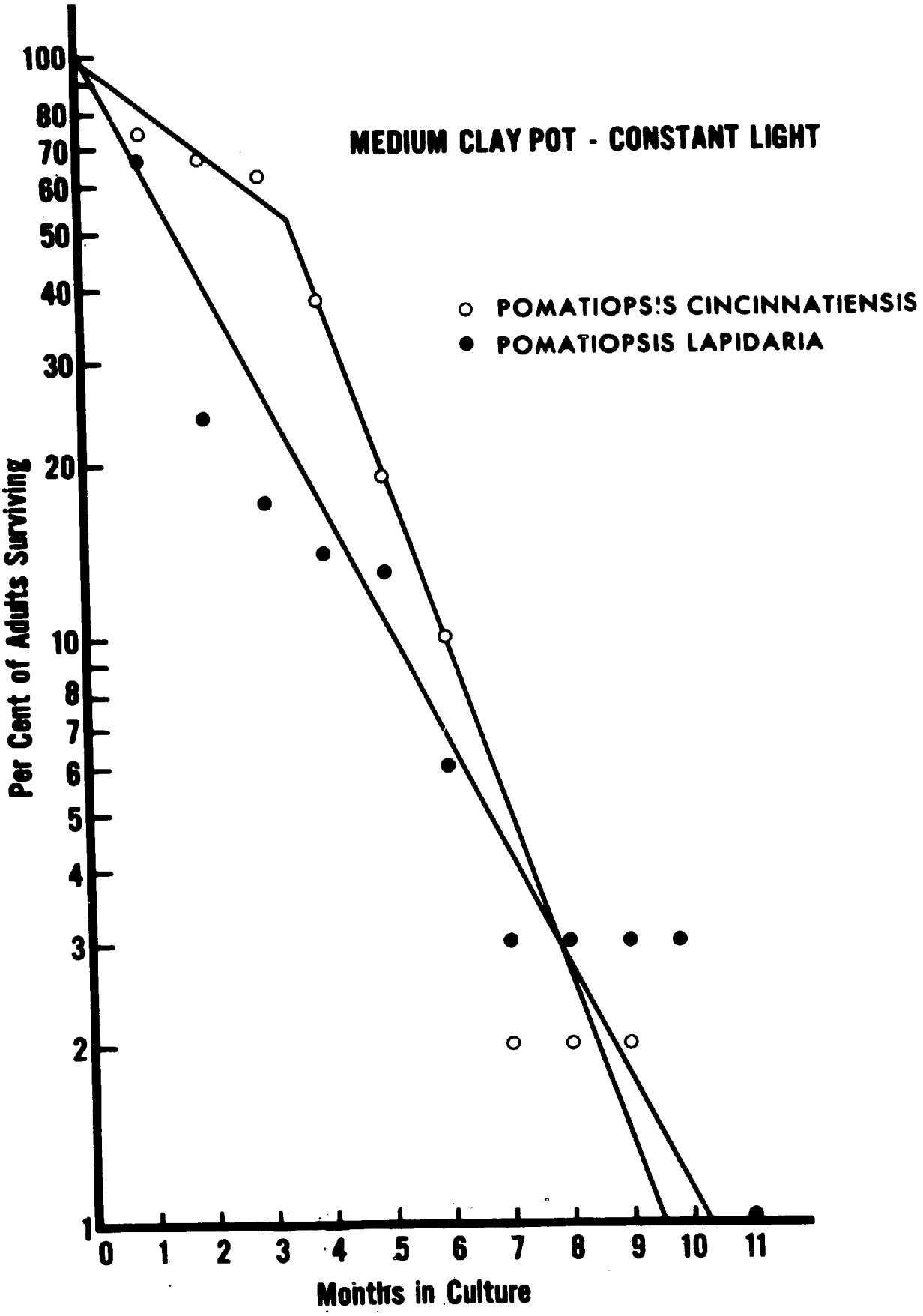

MEDIUM CLAY POT
POMATIOPSIS LAPIDARIA
Alternating light
Room level light
POMATIOPSIS CINCINNATIENSIS
Alternating light
Room level
Per Cent of Adults Surviving
100
80
70
60
50
40
30
20
10
8
7
6
5
4
3
2
1
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14
Months in Culture

Plate 43

COMPARATIVE SURVIVORSHIP IN MEDIUM, CLAY POT
· VIVARIA UNDER CONSTANT LIGHT

Plate 43


MEDIUM CLAY POT - CONSTANT LIGHT
POMATIOPSIS CINCINNATIENSIS
POMATIOPSIS LAPIDARIA
Per Cent of Adults Surviving
100
80
70
60
50
40
30
20
10
8
7
6
5
4
3
2
1
0 1 2 3 4 5 6 7 8 9 10 11
Months in Culture

rate of mortality increases markedly in the 4th month. This indicates that the 2 species have the same rate of mortality in their respective optimal environments but that the specific differences in longevity account for the difference in rates of mortality after the 4th month. In the first few months both species have a finite rate of mortality of 16 per cent per month compared with that of 12 per cent per month for Oncomelania hupensis formosana in the Plastic Tray vivarium.

Pomatiopsis lapidaria has greater rates of mortality than P. cincinnatiensis when both are maintained in the same vivarium under constant light (Plates 43, 44). Constant light was as detrimental for P. lapidaria in the Plastic Tray culture as room level light was for P. cincinnatiensis in the culture condition proving to be optimal for the former, i.e., the Medium Clay Pot (Plates 42, 44).

Plastic Tray and Tall Clay Pot vivaria under alternating light provided an environment in which an intermediate type of survivorship occurred for both species, an exponential rate of mortality of about 0.60 where the finite rate of mortality was about 45 per cent per month (Plates 41, 45).

The survivorship of Pomatiopsis lapidaria under optimal conditions very closely approximated the survivorship of Oncomelania hupensis formosana in the Battery Jar vivarium, a condition which was detrimental to the latter species. In the Battery Jar

Plate 44

COMPARATIVE SURVIVORSHIP IN PLASTIC TRAY VIVARIA UNDER CONSTANT LIGHT

Plate 44

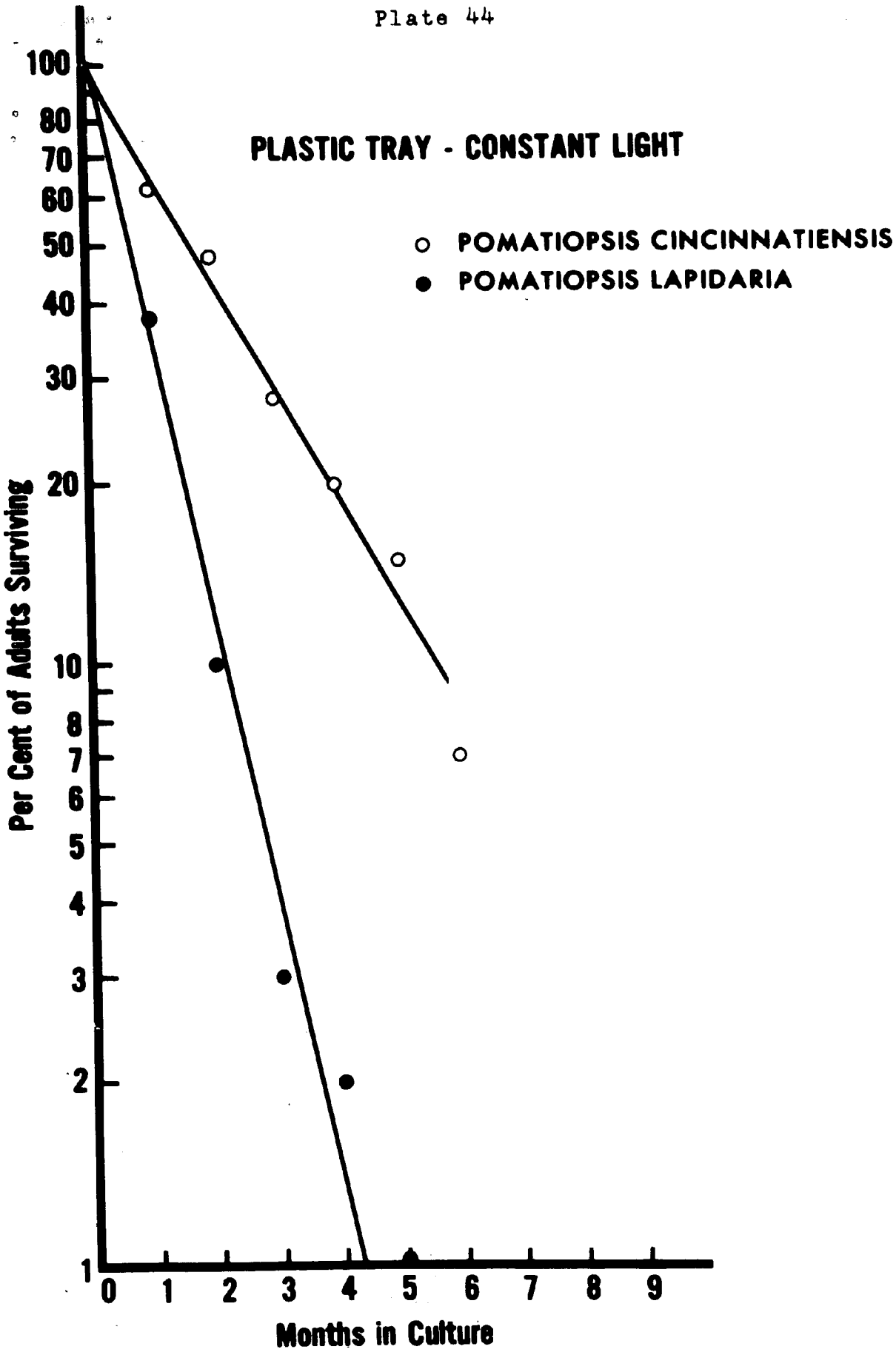
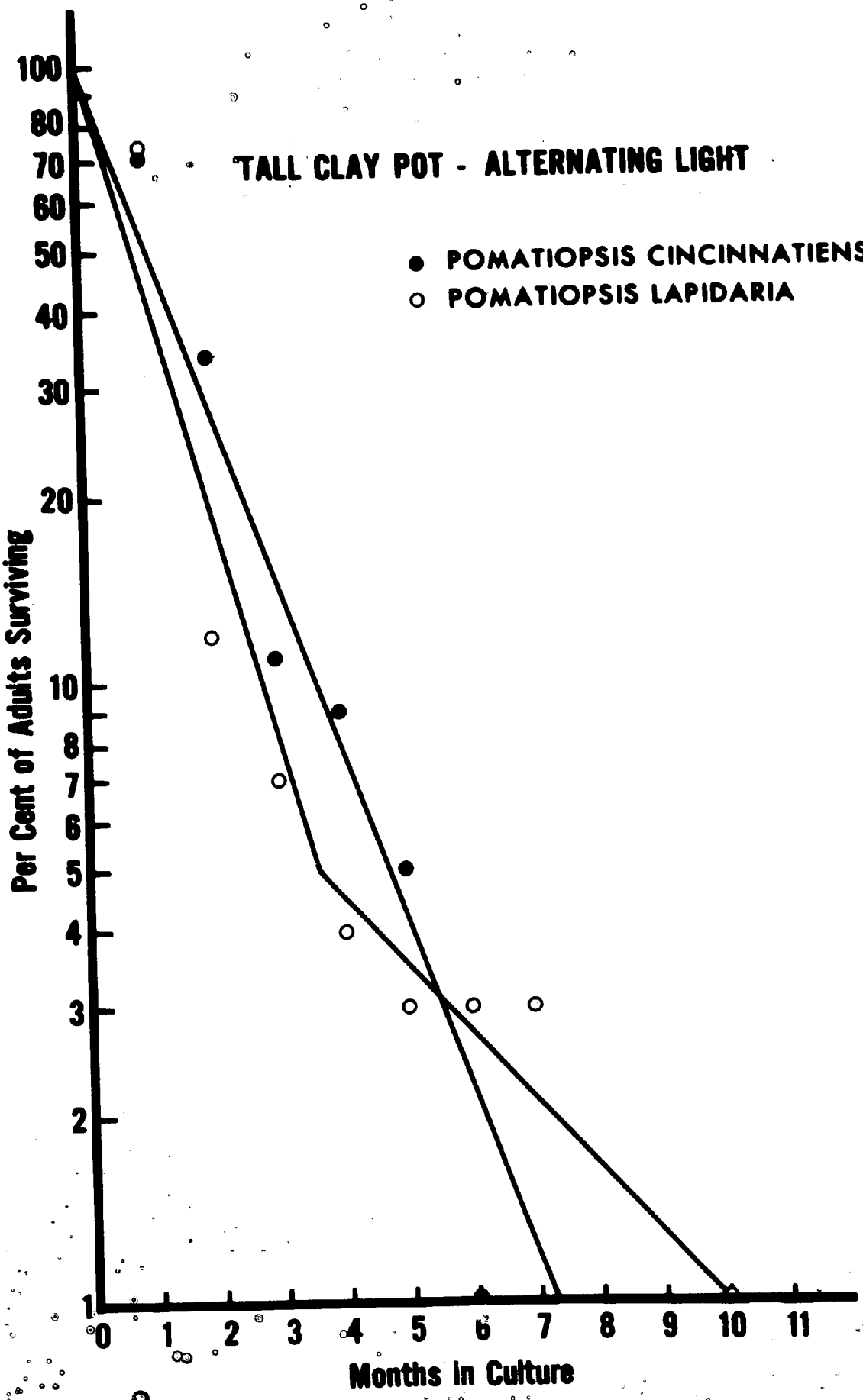

PLASTIC TRAY - CONSTANT LIGHT
POMATIOPSIS CINCINNATIENSIS
POMATIOPSIS LAPIDARIA
Per Cent of Adults Surviving
100
80
70
60
50
40
30
20
10
8
7
6
5
4
3
2
1
0 1 2 3 4 5 6 7 8 9
Months in Culture

Plate 45

COMPARATIVE SURVIVORSHIP IN TALL CLAY POT VIVARIA UNDER ALTERNATING LIGHT

Plate 45


TALL CLAY POT - ALTERNATING LIGHT
POMATIOPSIS CINCINNATIENSIS
POMATIOPSIS LAPIDARIA
Per Cent of Adults Surviving
100
80
70
60
50
40
30
20
10
8
7
6
5
4
3
2
1
0 1 2 3 4 5 6 7 8 9 10 11
Months in Culture

environment, P. lapidaria suffered a 50 per cent mortality within 1 month and none survived past 4 months.

2. Productivity.

The production of young is a function of survivorship of the female, the capacity of the females to lay a relative number of eggs per unit time over her lifespan, and a suitable environment which encourages egg laying and hatching.

In Table 17 are listed for each species the per cent of each vivarium type in which young were produced, the percentage of the total young found in each vivarium type along with the average number of young found per producing vivarium.

Young of Oncomelania hupensis formosana were produced in 100 per cent of each vivarium type; 54 per cent of the young were produced in Plastic Tray cultures and 46 per cent in Battery Jar cultures. The average number produced per culture was 243 in the former and 148 in the latter in spite of the fact that there were more initial femals in the latter cultures.

Considering Pomatiopsis lapidaria, only 50 per cent of the Medium Clay Pots in room level light produced young, while 40 per cent of the Medium Clay Pots in alternating light produced young. Only a relatively small percentage of the other culture types produced young. Young from producing Medium Clay Pots in room level light accounted for 68 per cent of all the young produced

with an average of 9.4 per culture. The second highest percentage was 19, the result of 1 Plastic Tray culture in alternating light which produced 27 young. Although survival of P. lapidaria in Medium Clay Pots in alternating light was about equal to survival in Medium Clay Pots in room level light, only 1 per cent of the young were produced in the former while 68 per cent were produced in the latter. In terms of the percentage of young produced per initial female in the 2 conditions, there was 0.04 per cent for the former and 0.65 per cent for the latter showing that the difference in the initial number of females did not account for the higher production of young in the 1 culture type.

Of the vivaria housing Pomatiopsis cincinnatiensis, 60 per cent of the Plastic Tray vivaria in constant light produced young while 67 per cent of the Tall Clay Pots in alternating light were producers. Only 16 per cent of the young were produced in the former while 80 per cent were produced in the latter. An average of 8.3 young were produced in each of the producing cultures of the former while an average of 14.2 were found in the latter. The initial number of females per culture type were about equal although there were about 2 times as many females per culture in the Plastic Tray vivaria. The greatest production of young occurred in a vivarium where there was an intermediate rate of mortality. No young were produced in the culture providing the best rate of survival, i.e.,

Table 17

Vivaria in Which Young Were Found

Species	Vivarium Type	Light Condition	Percent of Each Vivarium Type producing Young	Percent of Total Young Found in Producing Vivarium	Average No. Young Found per Producing Vivarium
Oncomelania hupensis formosana	PT	Alt.	100	54	243
	BJ	Room	100	46	148
Pomatiopsis lapidaria	PT	Alt.	17	19	27
		Con.	0	0	0
	BJ	Room	0	0	0
	MCP	Alt.	40	1	1
		Con.	22	7	4.5
		Room	50	68	9.4
	TCP	Alt.	21	5	2.5
P. cincinnatiensis	PT	Alt.	17	2	4.0
		Con.	60	16	8.3
	MCP	Alt.	0	0	0
		Con.	0	0	0
		Room	25	2	2
	TCP	Alt.	67	80	14
		Con.	0	0	0

BJ = Battery Jar
MCP = Tall Clay Pot
PT = Plastic Tray
TCP = Tall Clay Pot

Alt. = Alternating
Con. = Constant
Room = Room level

Medium Clay Pots in constant light.

These comparisons become more meaningful when the number of young produced per female per unit time is considered. Young per female per month were calculated for those cultures producing 46 per cent or more of the young (Table 18). The calculations are based on the survivorship of the females. Exact survivorship for the females was not recorded but spot checks on the cultures indicated a general trend of equal rates of mortality for the sexes. The data presented in Table 18 is, therefore, only a rough estimate but nonetheless serves to show real differences between the 3 species listed. Oncomelania hupensis formosana shows sustained production of young at much higher numbers of young per female per month than found for the other species. In the month where the greatest number of young were produced per female, Pomatiopsis lapidaria produced 5.0 y/f/m; O. hupensis formosana produced 10.0 y/f/m.

Accurate data was available for each of the 4 subspecies of Oncomelania maintained in Medium Clay Pots in room level light. With snails at 1 year of age the greatest production of young per female per month in a given month was O. hupensis hupensis, 23; O. hupensis nosophora, 22; O. hupensis quadrasi, 51; O. hupensis formosana, 44.

It appears that the peak productivity of young in the field at a given season does not carry over in the laboratory (Table 19). In

Table 18

The Production of Young per Female per Month in Cultures Which Produced 46 per cent or More of the Young

Species	Culture Condition	Light Condition	y/f/m	No. months in production	Highest y/f/m in a given month
Oncomelania hupensis formosana	PT	Alt.	0.88	26	2.91
	BJ	Room	2.12	21	10.0
Pomatiopsis lapidaria	MCP	Alt.	0.22	2	0.22
		Room	0.22	9	0.64
	PT	Alt.	...	1	5.0
P. cincinnatiensis	PT	Con.	0.39	3	0.48
	TCP	Alt.	0.50	1.5	1.29

BJ = Battery Jar
MCP = Medium Clay Pot
PT = Plastic Tray
TCP = Tall Clay Pot

Alt. = Alternating
Con. = Constant
Room = Room level

Table 19

The Percentage of the Total Young Produced Each Month of the Year

Species	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Oncomelania hupensis formosana	5	8	8	5	7	11	18	10	7	3	9	9
Pomatiopsis lapidaria	16	10	11	1	11	17	10	7	3	3	3	31
P. cincinnatiensis	31	1	1	0	0	26	9	0	0	0	9	24

Table 19 the percentage of the total young produced each month is listed for Oncomelania hupensis formosana, Pomatiopsis lapidaria, and P. cincinnatiensis. It was found that young of P. lapidaria appeared in culture 4-5 months after the culture was initiated. As the preponderance of the cultures were established in July or August the greatest percentage of young were found in December and January. Young produced by P. cincinnatiensis were found in cultures 3-4 months after the cultures were established in August or September. Six cultures were set up in May and young appeared 1-2 months after these were started. Due to rapid rates of mortality in the adults there were no young produced in several months.

3. Growth Rates and Survivorship of Young.

H. van der Schalie and Davis (1964) found that newly hatched young of Oncomelania hupensis formosana maintained 1 or 2 per Petri Dish culture grew more rapidly than snails reared in any other fashion. Petri Dish vivaria provided an environment where the snails grew, on the average, 0.65 mm per week for the first 8 weeks with a mortality below 10 per cent. In Plate 46 the growth curves for male and female O. hupensis formosana are presented. The measurements were made using 25 snails of each sex. The snails were maintained 1 per dish under constant light. It was later found that alternate light stimulated the same optimal growth.

Young Pomatiopsis lapidaria grew at a slow rate with a high mortality in PDC vivaria. Within 3 months 50 per cent were dead and little growth had taken place (Plate 47). Only 15 per cent were alive at the end of 6 months. At the end of 1 year 5 per cent remained of the 40 snails which started. In 6 months the average weekly increment in length was 0.13 mm. This rate is about the same given by Dundee (1957) for the growth of this species in the laboratory. When the relative growth rates of the 2 species were compared between 1 and 1.5 months, Oncomelania hupensis formosana was growing at a rate of 0.95 mm per week compared with 0.20 mm per week for P. lapidaria.

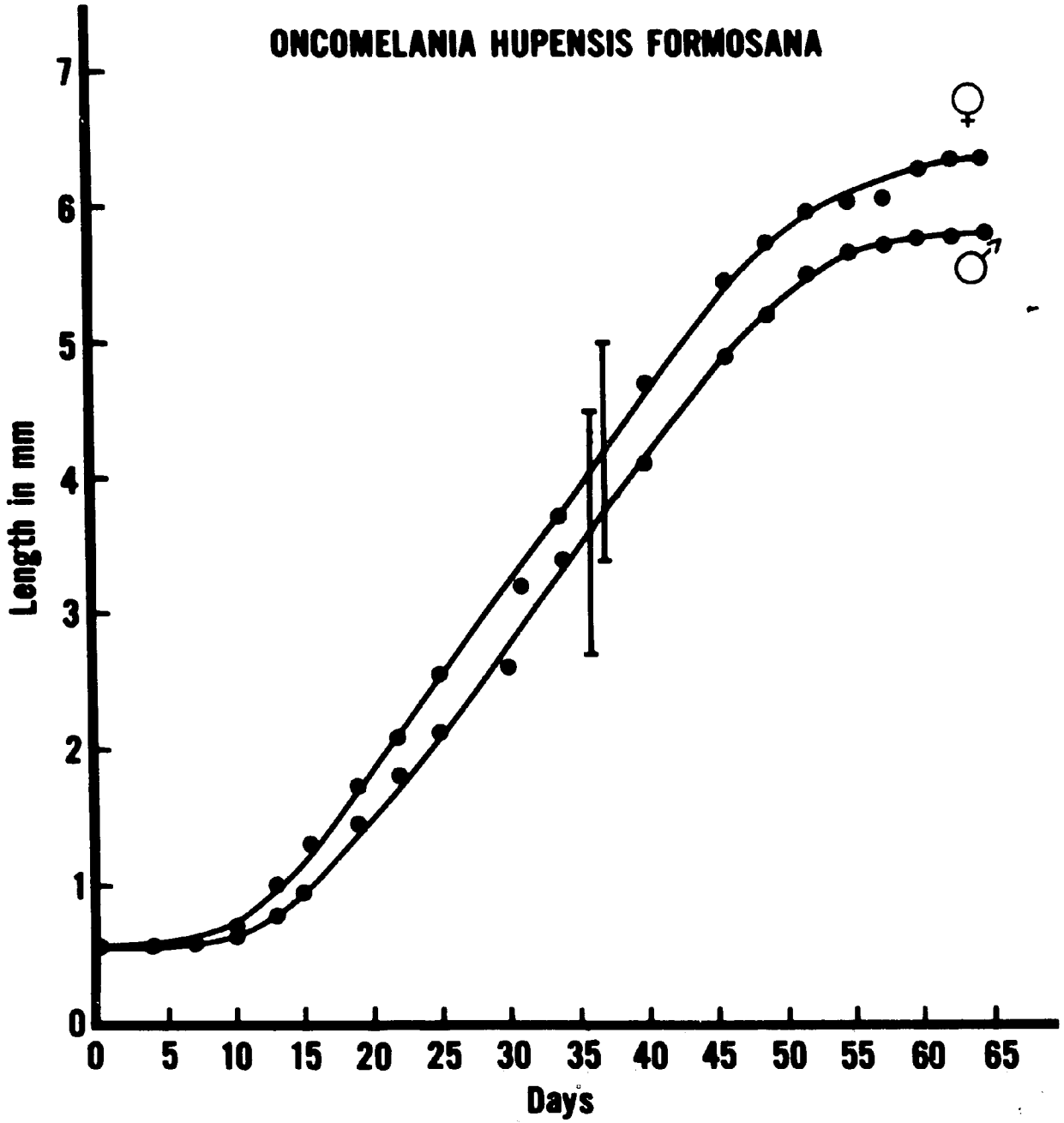
It was discovered that placing 5 young Pomatiopsis lapidaria in a MCP in room level light or by leaving the young in the parental cultures increased the survivorship of the young snails. Of 15 snails observed in these conditions, 50 per cent survived until the 9th month and at the end of 13 months 40 per cent were still surviving. The growth rate was somewhat lower, however, about 0.10 mm per week for the first 6 months.

P. cincinnatiensis barely lasted 5 months in Petri Dish vivaria. Of the 20 young snails studied, 50 per cent were dead in 3.5 months and none survived past 5 months. In that period the average increment in length was 0.12 mm per week.

Plate 46

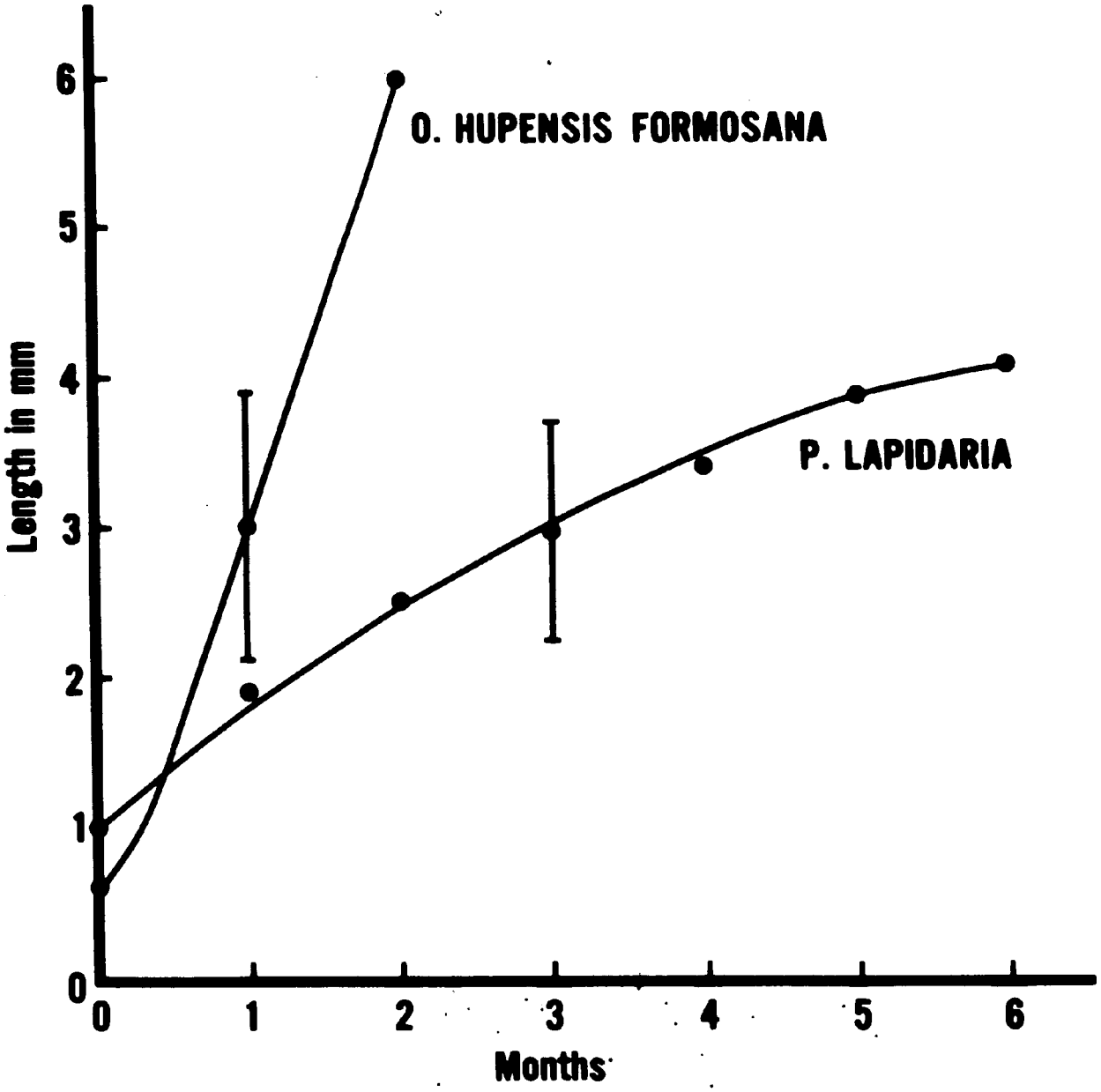
GROWTH CURVES FOR MALE AND FEMALE ONCOMELANIA HUPENSIS FORMOSANA

Plate 46


ONCOMELANIA HUPENSIS FORMOSANA
Length in mm
0
1
2
3
4
5
6
7
0 5 10 15 20 25 30 35 40 45 50 55 60 65
Days
♀
♂

GROWTH CURVES FOR POMATIOPSIS LAPIDARIA AND ONCOMELANIA HUPENSIS FORMOSANA

Plate 47


O. HUPENSIS FORMOSANA
P. LAPIDARIA
Length in mm
Months
0
1
2
3
4
5
6

D. Discussion

As has been reported by a number of authors, the subspecies of Oncomelania can survive and reproduce under a variety of conditions which are not optimal environments. Oncomelania hupensis formosana survived well in the vivaria provided and produced young at an adequate rate to assure survival of the species in the laboratory. H. van der Schalie and Davis (unpublished) found that survivorship and productivity increased when the four subspecies were maintained in Medium Clay Pot vivaria.

There was a uniform, large gap between Oncomelania and Pomatiopsis with regard to longevity, production of young, growth rates of young, and survival of the young in the laboratory. The 4 species of Pomatiopsis did not survive well in any of the vivavia provided with 2 exceptions. Pomatiopsis lapidaria and P. cincinnatiensis showed survivorship in optimal environments (Medium Clay Pot, room level light for the former; Medium Clay Pot, constant light for the latter) corresponding to what might have been predicted from knowledge of their survivorship in the field.

Pomatiopsis lapidaria produced more young per female in the environment which provided optimal conditions for survival. Although P. cincinnatiensis survived better under constant light, this species produced more young per female in the Tall Clay Pot vivarium type under alternating light, an environment in which the adults had an intermediate type of survivorship.

Data on the production of young per female per month as well as the greatest production per female for any given month indicate that 1 or several critical factors in the laboratory environments were either absent or detrimental. For instance, in the field Pomatiopsis cincinnatiensis reproduces throughout the summer with pronounced hatches of young in August and October. In August, I found 20 females and 155 young in a quadrat 2 feet wide and 3 feet long. The following month I found in the same quadrat 24 females and 525 young. This condition could be duplicated up and down the river banks for 30 feet in either direction and concerned a population known to be in a steady state for over 10 years. It is obvious that production of young per female per month in the field was many times that found for this species in the laboratory.

The 4 subspecies of Oncomelania appear more closely allied in their performance in the laboratory than the 2 species of Pomatiopsis discussed in detail. Data from the laboratory studies show that P. lapidaria survives best under room level light, produces the greatest number of young in this optimal environment, and had a finite rate of mortality of 16 per cent over 8-9 months. P. cincinnatiensis survives best under constant light but produces more young in a Tall Clay Pot under alternating light, a condition where the finite mortality rate was 49 per cent per month for 7 months.

CONCLUDING DISCUSSION

A large number of similarities between Oncomelania and Pomatiopsis have been discussed in generalities by many authors. These similarities have mainly pertained to subfamily characteristics. Such characteristics are the general arrangement of organs in the body, an amphibious mode of existence, eggs laid singly out of water and coated with a mud capsule, a distinctive manner of progression, and a particular structural arrangement for the central tooth of the radula.

Enough data is available to state that Oncomelania and Pomatiopsis are distinct genera within the Pomatiopsinae, a subfamily which includes Tomichia from South Africa, Blanfordia from Japan, and Oncomelania from the Orient. Whether or not Tricula from the Orient belongs to this subfamily must be determined.

H. van der Schalie and Getz (1963) pointed out that Pomatiopsis lapidaria and P. cincinnatiensis were more tolerant of low temperatures (-5° to -7° C.), less tolerant of high temperatures (41° to 44° C.), and less resistent to drowning than Oncomelania. From the laboratory ecological data of this study it is evident that Oncomelania is characterized by the comparative ease with which it adapts to laboratory culture and by the rapid growth of the young.

Pomatiopsis does not adapt to the laboratory environment in which Oncomelania thrives; the growth rate of the young is extremely slow.

The genera will not hybridize. Reference was made to the cytological differences between Oncomelania and P. lapidaria and P. cincinnatiensis in the section on hybridization studies.

Major anatomical differences are listed in Table 12. Anatomical differences of a specific nature are listed in Table 13. Many of the specific differences are not given greater weight due to lack of comparative data for other species of Pomatiopsis and subspecies of Oncomelania. The electrophoretic differences are on the order of specific differences although initial data for the other subspecies of Oncomelania indicate similarities in the dense, fast moving proteins which P. lapidaria does not have.

Davis (1964) indicated that a basic difference existed between Pomatiopsis lapidaria and Oncomelania hupensis formosana in the potential of the 2 forms for shell regeneration. O. hupensis formosana rapidly regenerated a shell in the apical whorls with low mortality, while P. lapidaria had a high mortality and showed no signs of shell regeneration.

A discussion and generic diagnosis for Oncomelania and Pomatiopsis are given below. The relative terms pertaining to morphological structures may be checked against the drawings provided for the 2 forms discussed in this paper. It is to be expected

that the generic diagnosis for Pomatiopsis may need alteration in 1 or 2 places when the anatomy of P. californica and P. binneyi become better known.

Oncomelania is a genus with but 1 species and 4 subspecies. The subspecies of Oncomelania do not differ greatly in their internal anatomy. External differences are mainly those of size, ribs on the shells of some populations of O. hupensis hupensis, and variance in the intensity of external pigmentation and the yellow coloration of the granules surrounding the medial surface of the eye.

Oncomelania is a genus in which the shell is usually smooth (excepting the above mentioned ribs), with moderately deep sutures and with moderately convex whorls. The outer lip of the shell has a tendency to form a varix which is usually quite pronounced. The umbilicus is narrow and the apical whorl narrow. The parietal callus is elongate. There are at least 35 or more gill filaments, usually 45 or more. The verge is muscular, the tip has short strips of actively beating cilia, and the tip has a distinct papilla. The pleurosupraesophageal commissure is short. The osphradial and mantle nerves arise from the tip of the superesophageal ganglion and are elongate. The sperm and spermathecal ducts arise together from the ventral, right anterolateral surface of the bursa copulatrix. The female gonad is multibranched and the collecting duct of the gonad relatively slender. The seminal vesicle is composed of a slender

tube which is characteristically knotted. The cerebral commissure is short. The tentacles are elongate relative to the length of the rostrum.

Pomatiopsis is a genus composed of 4 distinct species of which only P. lapidaria and P. cincinnatiensis are known in terms of anatomy and life history. P. californica and P. binneyi are virtually unknown except for general habitat and shell. A 5th species, P. chacei, is most like P. californica as the type description given by Pilsbry (1936) is not sufficient to separate this form as a separate species. P. robusta (Walker) was listed by Abbott (1948a) with Pomatiopsis. Pilsbry (1933) had removed this species from Pomatiopsis with justification as the radula is clearly not of the type found in the Pomatiopsinae.

Pomatiopsis binneyi is different from the other species in the genus on the basis of shell and habitat although there are similarities on the basis of some subfamily characteristics. The shell is only about 3 mm high, without an umbilicus, and the inner and outer lips meet without forming a parietal callus and are generally slightly separated from the parietal surface of the body whorl. The species lives high on Mt. Tamalpais in Marin County, California. The snails live in dense shade on the surfaces of rocks and leaves either in the path of trickling water or sprayed by water streaming down steep canyon slopes. This habitat is markedly different from

those inhabited by the other species of Pomatiopsis. P. californica lives on shallow mud banks and marshy seepages leading into shallow streams. The area I observed was a low land habitat on the edge of Bolinas Bay, Marin County, California. P. cincinnatiensis lives on a narrow margin of river bank while P. lapidaria survives in marshy Typha swamps, grassy seepages leading into rivers, or wooded lowlands seasonally swampy due to stream overflow. Much of the swampy areas inhabited by P. lapidaria closely resemble the habitat of Oncomelania hupensis quadrasi observed in the Philippines.

Because Pomatiopsis binneyi appears so different on the basis of shell and habitat it should be studied thoroughly to determine whether it is, indeed, a species of Pomatiopsis.

Pomatiopsis is currently defined as a genus in which the shell has a roughened microsculpture, the lip is sharp and there is no tendency to form a varix. The apical whorls are wide. The umbilicus is wide and pronounced. The sutures are deeply impressed and the whorls very convex. There are less than 30 gill filiments. The verge does not have the pronounced musculature or papilla found in Oncomelania and cilia are lacking in 2 species. Where cilia are found they are bushy and generally not active. Two species have penial filaments, a condition not found in Oncomelania, Blandfordia, or Tomichia. The pleuro-supraesophageal commissure is elongate. The osphradial nerve and the mantle nerve are quite short. The

spermathecal duct arises from the anterior end of the bursa copulatrix. The female gonad is little branched and the collecting duct is very wide. The seminal vesicle is a thick tube. The tentacles are relatively short relative to the length of the rostrum.

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