MORPHOLOGY AND DEVELOPMENT OF THE SEX ORGANS IN THE SNAIL *POMATIOPSIS CINCINNATIENSIS* (LEA)

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MORPHOLOGY AND DEVELOPMENT OF THE SEX ORGANS IN THE SNAIL *POMATIOPSIS CINCINNATIENSIS* (LEA)[1]

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Recent investigations of two common American operculates of the genus *Pomatiopsis* show that this genus is almost identical in its morphology to all four of the Oriental *Oncomelania*. As was anticipated, the similarity extends to ecology (van der Schalie and Dundee, 1957 and 1959; van der Schalie and Getz, *in press*) and to life-histories (van der Schalie and Walter, 1957). More recently it was possible to produce hybrids between these two nominal genera (van der Schalie, Getz, and Dazo, *in press*). Morphological work with American *Pomatiopsis* was covered in a broad and basic way by E. G. Berry (1943). The internal anatomy was presented in some detail in a paper on *Pomatiopsis cincinnatiensis* by H. van der Schalie and D. S. Dundee (1956) and in another report on *P. lapidaria* by D. S. Dundee (1957)

The importance of the genus *Oncomelania* as the snail intermediate host of *Schistosoma japonicum* has prompted a series of malacological studies. Several investigations have been directed toward obtaining a better understanding of the anatomy and morphology of these particular snails. One of the earliest papers on this subject (G. C. Robson, 1921) gives a lucid account of the general anatomy of *Hypsobia* (=*Oncomelania*) *nosophora*. Since that time some of the more important anatomical studies of *Oncomelania nosophora*, as that species is now known, include publications by Nakamoto (1923), Itagaki (1955), and Roth and Wagner (1957; 1960). Pesigan *et al.* (1956–1957) studied the morphology of *Oncomelania quadrasi* in the Philippines. Fu-Ching Li (1934) worked on the Chinese *Oncomelania hupensis*. Roth (1960) described the structure and function of the seminal receptacle and *bursa copulatrix* of *Oncomelania formosana*.

Although it is now clear that the basic anatomy of all of the *Pomatiopsis* and *Oncomelania* examined is essentially the same, several details relating structure to function have been difficult to resolve. The available reports have not been helpful in clarifying matters involving the relationship of several of the organs in the female genital tract. In view of this fact, two extensive series of *Pomatiopsis cincinnatiensis* snails were taken from their natural habitat and prepared for study. From collections made every hour, beginning at 11:30 A.M., August 2, until 1:30 A.M., August 3, 1960, some 74 specimens were relaxed, killed and fixed; the shell length of each was measured and then the shell removed with Bouin's fixative. The snails were then serially sectioned and stained for microscopic examination to determine the course of the eggs through the female tract. Another series of 238 snails was collected on October 20, 1959, and similarly studied. This later collection contained animals in all stages of growth and development (van der Schalie and Getz, *in press*). The maturity of the sex organs in both males and females could be compared, therefore, with the size of the individual.

The data from these studies have been arranged into three major categories, as follows: (1) development of the male and female reproductive systems; (2) the relation of organs as determined by the course of the eggs through the female genital tract; and (3) females with a male characteristic, *i.e.*, a verge or penis, which probably represents an anomalous development.

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Development of the Male and Female Reproductive Systems

The Male System.—While the general relations of the organs in the male and female reproductive systems have been shown in some detail (van der Schalie and Dundee, 1956), little is known about the development of the gonads and the degree of maturity reached prior to hibernation in the winter season. The gross morphology of an adult is essentially as illustrated in an earlier publication (van der Schalie and Dundee, 1956: Pl. V). It was found in the present study that, whereas the gonad of a half-grown male already shows a considerable amount of development (Pl. I, Fig. A), it is not until the animals reach the three-quarter to full-grown stages that sperm are produced and the gonads and seminal vesicles become packed with sperm (Pl. I, Figs. B and C).

The prostate gland also is not well-developed until the animal attains the three-quarter-grown stage (Pl. I, Fig. D); in the full-grown stage it is found as a relatively large gland (its upper portion, Pl. I, Fig. E; the lower portion, Pl. I, Fig. F).

In all instances, the verge is present almost as soon as the snail hatches from its egg. The process of sexing even the very young animals therefore, was, relatively easy. The developmental stages of the verge, from recently hatched individuals to adults, are shown in Plate V.

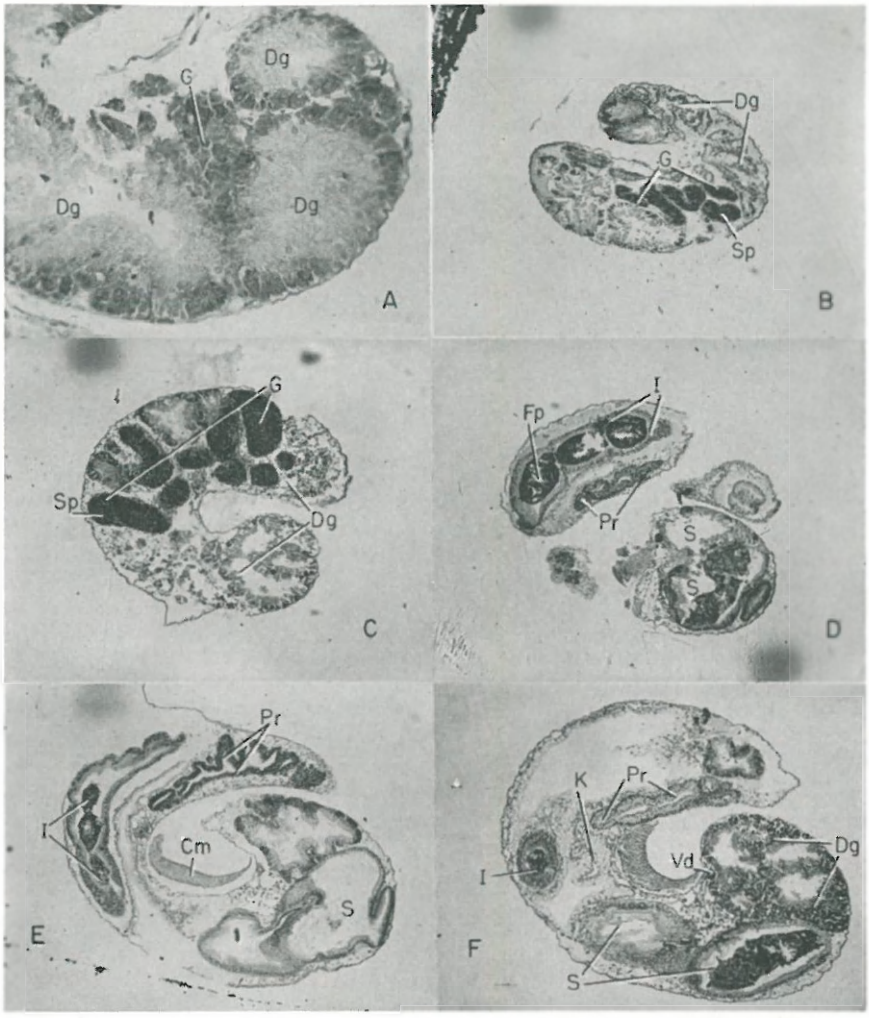
The Female System.—The structure of some of the organs in the female reproductive system are shown in Plate II. In contrast to the males, in which the gonad did not exhibit much sperm production until the animal was about half-grown, the females all had small but clearly defined eggs in the ovary when the animals were only one-fourth grown (Pl. II, Fig. A). Growth of the female snail is reflected in the corresponding increase of egg size (Pl. II, Figs. B and C). At the full-grown stage of development the eggs were several times the size of those in half-grown specimens and were at the same time surrounded by a large mass of yolk (Pl. II, Fig. D).

One of the prominent organs in the female, even at the half-grown size, is the accessory gland (Pl. II, Fig. E); this structure becomes particularly massive in the adult female (Pl. II, Fig. F).

The Relation of Organs in the Female Genital Tract

In the publications dealing with both *Oncomelania* and *Pomatiopsis* there has been confusion in the names, as well as the functions, of the organs in the adult female reproductive system. The existing uncertainty is shown through several errors committed in reports by van der Schalie and Dundee (1956), by Roth and Wagner (1957), and by Roth (1960). The difficulties are due mainly to a lack of understanding as to what course the eggs take as they are oviposited. With the large amount of serially-sectioned material now available, it is possible to clarify some of the inconsistencies.

The accessory gland is perhaps the largest and most prominent structure in the female reproductive system. Whereas its function has not been properly determined, the concensus is that it is composed of two clearly defined tissues (Pl. III, Fig. E), an upper portion which may produce albumen, and a portion lower down in the tract which probably secretes the mucous used to form the prominent capsule or husk that surrounds each egg. Only a more careful study, using histochemical techniques, can clarify the function of this gland. In the many serial sections examined, however, it is clearly indicated that the accessory gland does not function as an "oviduct" and is not a "pallial oviduct" as erroneously labeled by H. van der Schalie and D. S. Dundee (1956), and by A. Roth and E. Wagner (1957). The error was again repeated in a more recent article by Roth (1960). While it is true that this latter study concerns *Oncomelania formosana*, there was no indication that eggs had been observed passing through the "pallial oviduct."



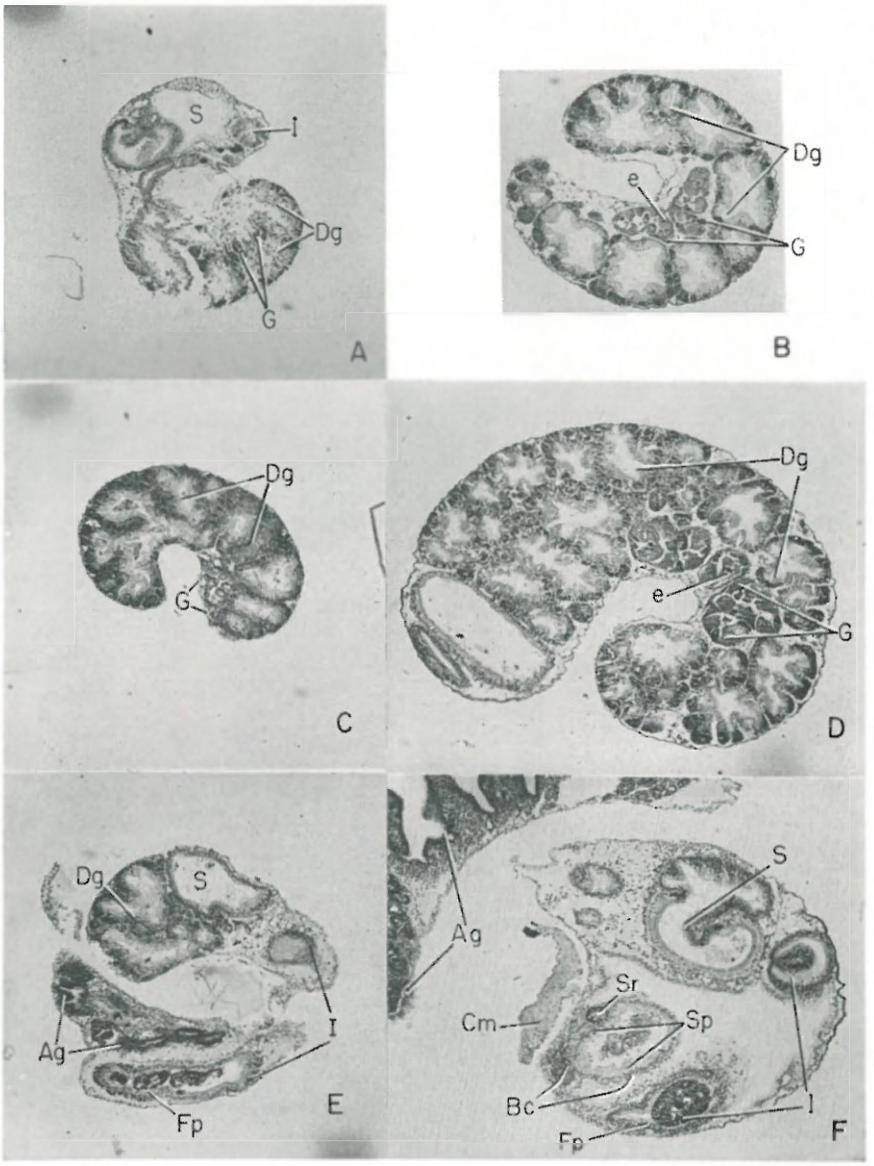
ABBREVIATIONS

Ag., albumen gland
Ac., accessory gland
Bc., *bursa copulatrix*
c., connection between convoluted tubules and accessory gland
C., columella
Cg., capsule gland
Cm., columellar muscle
Ct., convoluted tubules
Dg., digestive gland (liver)
e., egg
Fp., fecal pellet
G., gonad
Ga., genital aperture
H., heart
I., intestine
K., kidney
O., ovary
Ov., oviduct
Pr., prostate
S., stomach
Sp., sperm
Sd., spermathecal duct
Sr., seminal receptacle
Ss., style sac
T., tentacle
Vd., *vas deferens*

EXPLANATION OF PLATE I

Development of the male reproductive system; all animals were collected October 20, 1959

FIG. A. Gonad of a half-grown male showing early stages in development. (250×).
FIG. B. Gonad of male three-quarters grown with sperm already well developed. (60×).
FIG. C. Gonad and seminal vesicles of a full-grown animal showing the large increase both in the size of the organ and the sperm it contains. (60×).
FIG. D. Animal same as in B above, showing development of the prostate. (60×).
FIG. E. Upper portion of prostate of full-grown male. (60×).
FIG. F. Lower prostate of same animal as shown in E. (60×).



Development of sex organs in female system of *Pomatiopsis cincinnatiensis* (Lea); all specimens collected October 20, 1959.

FIG. A. Young female only a fourth grown with eggs already recognizable in gonad. (60×).
FIG. B. Female about three-quarter stage of develpoment with the gonad and eggs quite clearly defined. (60×).
FIG. C. Half-grown female with eggs more clearly defined. (60×).
FIG. D. Gonad of a full-grown female. (60×).
FIG. E. Half-grown female showing early development of accessory gland. (60×).
FIG. F. Organs of full-grown female; accessory gland greatly enlarged, bursa and seminal receptacle already filled with sperm. (60×).

The interrelations of the organs in the female system are shown in Plate IV. This figure is slightly modified from that previously published (van der Schalie and Dundee, 1956: Pl. VI). In that account, serial sections revealed a connection (Fig. D) between the spermathecal duct and the accessory gland, but in the gross anatomical work (Fig. C) the tubes were too fine to be seen clearly. The availability of so many serial sections permits a more accurate reconstruction of the interconnecting tubules as shown in Plate IV. The confluence of the convoluted tubules below the *bursa copulatrix* (Pl. III, Fig. C) was observed in several specimens, and it was not uncommon to find that a few sperm actually invaded the upper portion of the accessory gland. That the oviduct and the spermathecal duct join (Pl. III, Fig. D) and continue as the spermathecal duct is now also well-established.

Many specimens were studied carefully to determine whether eggs do pass through the accessory gland. All of these observations emphasize that this structure is glandular in nature and does not serve to convey eggs; in no sense should it be referred to as an "oviduct." The difficulty seems to stem from the fact that eggs will line up in the oviduct above the junction with the spermathecal duct, but only seldom does one find an egg in the lower tract. Obviously, the eggs pass through that lower region quickly. It was possible to find one section, however, (Pl. III, Fig. F) in which an egg was far down the common tract or spermathecal duct. Its position in the lower tract is verified by the characteristic lower or capsule gland tissue of the accessory gland appearing in the same section. While the relation of structure to function in this organ system is not worked out satisfactorily, the path the eggs take as they progress through the female genital tract seems clear. It also appears that the so-called "spremathecal duct" serves both as the avenue by which sperm get to the *bursa copulatrix* and the seminal receptacle, as well as the tube through which the eggs pass as they are deposited or laid.

In studies involving both *Pomatiopsis* and *Oncomelania* it has been emphasized repeatedly that these animals have an ability to control egg-laying that is quite remarkable. For example, unless a vivarium contains soil to serve as husk for the egg the animal will not oviposit. Evidently this control can also be used when a variety of other unfavorable conditions may be present. Because of this ability to withhold egg-laying and because of the fact that the eggs pass through the lower genital tract rather quickly, it has been difficult among the many specimens serially sectioned to locate eggs in the spermathecal duct.

The 80 specimens thus sectioned also revealed that copulation takes place among the fully developed snails belonging to the young-of-the-year age class (Pl. III, Figs. A and B). In the specimen illustrated (collected October 20), the *bursa copulatrix* and the seminal receptacle are filled with sperm. Roth (1960) in his study of *Oncomelania formosana*, failed to take into account the fact that this relationship of the *bursa* and seminal receptacle was previously described (van der Schalie and Dundee, 1956: 13–14); it is illustrated again here. The functional relation appears to be exactly as reported in all of the species of the two nominal genera. As previously stated and now figured, the sperm in the seminal receptacle are arranged perpendicular to its wall with the sperm heads embedded *en masse* in the wall tissue (Pl. III, Fig. B).

Anomalous Development of Two Females

Two specimens were discovered with an unusual development of the male sex organ or verge (penis). The animals were clearly females as determined by their larger size and general appearance. Also, the verges were both not normal in size and development as illustrated (Pl. V, Figs. G H). One of them (shown in Fig. G) was serially sectioned and stained. The gonad was that of a normal female and and there was no evidence of an hermaphroditic or ovotestis arrangement as might

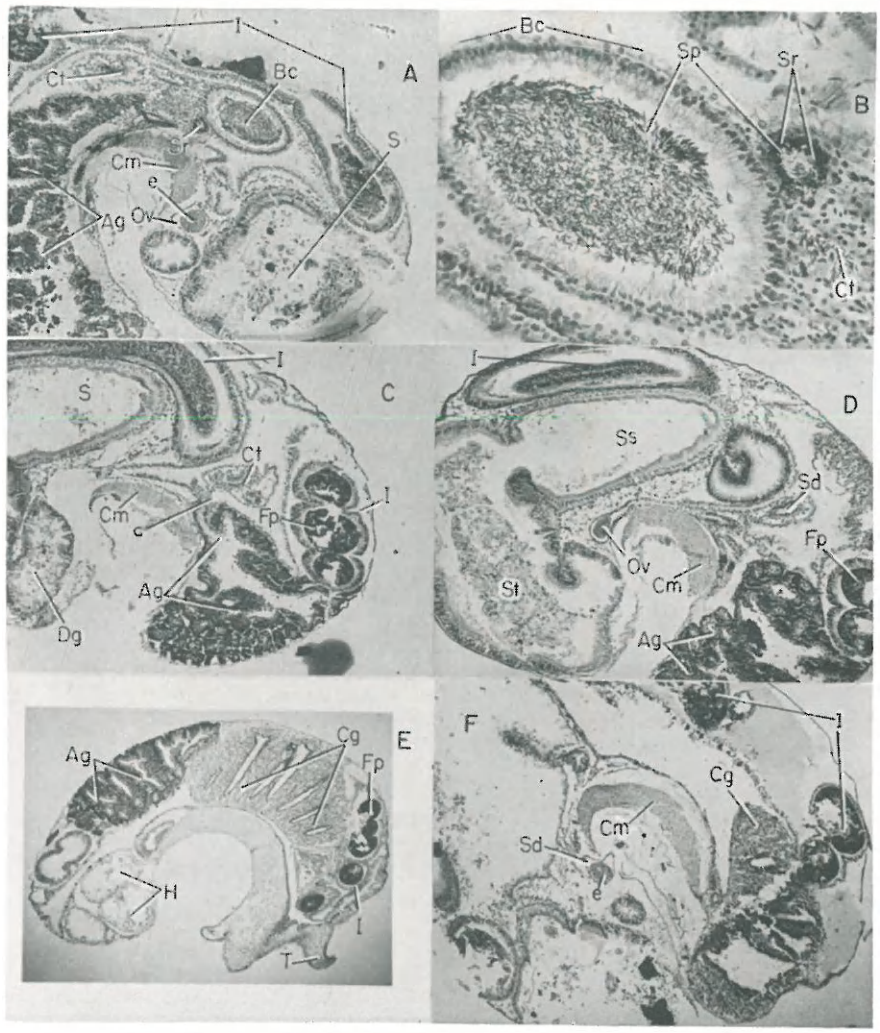


PLATE III

Relation of female reproductive organs in adult *Pomatiopsis cincinnatiensis* (Lea); animals collected October 20, 1959.

FIG. A. Orientation of *bursa copulatrix*, seminal receptacle, convoluted tubules, oviduct and accessory gland. (60×).

FIG. B. Enlarged bursa copulatrix and seminal receptacle from same section as A above to show orientation of sperm. (250×).

FIG. C. Convoluted tubules just below *bursa copulatrix* to show connection between tubules and accessory gland. (60×).

FIG. D. Confluence of oviduct (containing egg) with sperm duct. (60×).

FIG. E. Accessory gland showing its two characteristic tissues, presumably the albumen gland and the capsule gland. (60×).

FIG. F. Section with an egg in the spermathecal duct; eggs are seldom found in this tube while they are not uncommon in the oviduct before it reaches the spermathecal duct. (60×).

have been expected in a female specimen with a verge. The eggs found in the oviduct appeared normal in development. Whereas other females taken in this same collection had copulated, as determined by the presence of sperm in the *bursa copulatrix* and the seminal receptacle, this specimen contained no sperm and had not mated. The other specimen (shown in Fig. H) was stained and cleared as a whole mount preparation. There was no *vas deferens* to the verge, neither in this specimen nor in the one serially sectioned, indicating that the male organ was non-functional. There was also no evidence that either specimen had mated although both animals were equipped to function as normal females.

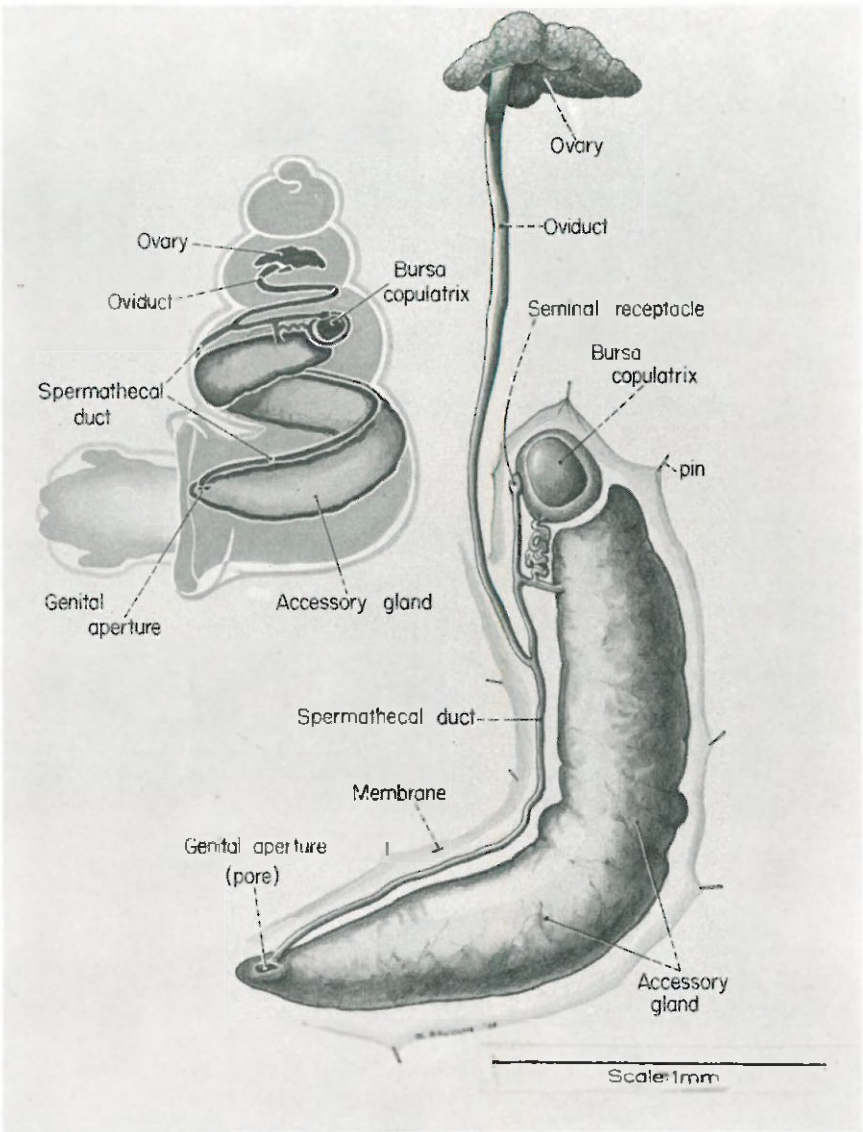


PLATE IV

The female reproductive system of *Pomatiopsis cincinnatiensis* (Lea)

SUMMARY

Serial sections of two extensive series of *Pomatiopsis cincinnatiensis* (Lea) were used not only to study the development of the male and female reproductive systems but also to clarify structural relations to the function of organs in the female tract. Males were easily recognized since the verge (penis) was present soon after the animal hatched in August; the gonad and prostate are usually fully developed and functional before the animals hibernate in the fall. In leaving the body, the eggs pass through the same tube, the so-called spermathecal duct,

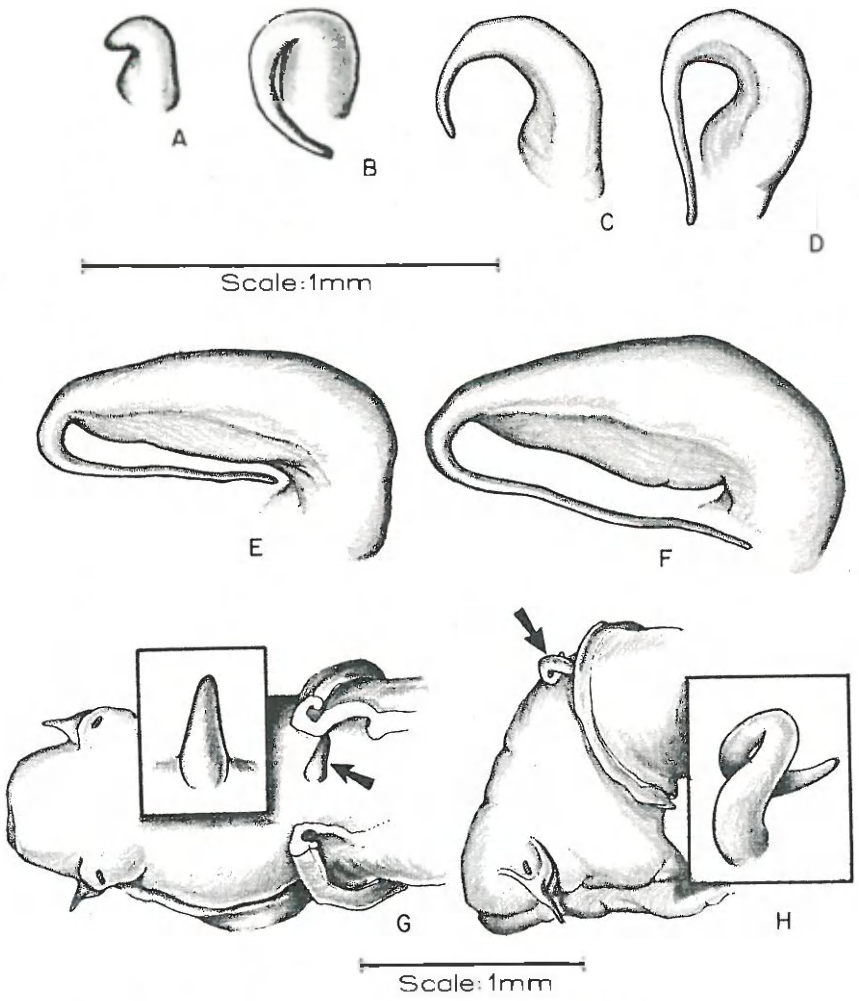


PLATE V

Development of male reproductive system
in *Pomatiopsis cincinnatiensis* (Lea)

FIGS. A to F. Stages in the development of the verge (penis) at various ages as shown for the nearly hatched young (Fig. A) to that of the fully matured adult (Fig. F).

FIGS. G and H. Females with verges (enlarged in insert drawings); verges poorly developed and not normal for adults (compare verges G and H with a normal fully developed one shown in F.

used by sperm to gain access to the *bursa copulatrix* and seminal receptacle. Contrary to earlier published reports, the incorrectly designated "pallial oviduct" is in reality an accessory gland which does not serve to convey eggs about to be oviposited. Two females were discovered with poorly developed verges; an examination of their reproductive organs failed to indicate any bisexual or hermaphroditic characteristics and their gonads appeared quite normal.

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