On the Opisthobranch Genus *Haminoea* Turton & Kingston[1]

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ABSTRACT: A study was made of *Haminoea zelandiae, H. solitaria, H. cymbalum,* and *H. crocata.* The reproductive systems show a close similarity to that of *Aplysia* and lack of important anatomical differences show that *Haloa* and *Lamprohaminoea* are unnecessary genera. The mantle cavity, alimentary canal, and nervous system show the relationship of *Haminoea* to *Atys* and *Smaragdinella.*

THE HERBIVOROUS OPISTHOBRANCH GENUS *Haminoea* Turton & Kingston, 1830 is found throughout the temperate and tropical regions of the world. The genus is characterized by the thin bubble-shaped shell which is partially enclosed by lateral extensions of the foot, the development of the posterior edge of the mantle floor into a functional accessory foot, the wide radula of hook-shaped teeth, and the large gizzard containing three ridged chitinous plates.

Haminoea zelandiae was commonly found both on sandy mud flats and on the coralline turf of rocky shores around Auckland. Specimens of *Haminoea cymbalum* were collected by Mrs. A. Neads of Fiji and sent alive to me. Preserved specimens of *Haminoea crocata* and *H. simillima* (= *H. cymbalum*) from Hawaii were made available by Dr. E. Alison Kay, and preserved specimens of *H. solitaria* from the Atlantic coast of North America were sent by Dr. D. Franz and Dr. J. Steinberg.

In temperate waters the species are usually drably colored in mottled grays and browns—*H. zelandiae* Gray, 1843: (Rudman, 1971); *H. antillarum* (d'Orbigny, 1841): (Marcus and Marcus, 1967); *H. hydatis* (Linné, 1758): (Vayssière, 1885), while in tropical waters species are often brilliantly colored, as in the case of *H. cymbalum* (Quoy & Gaimard, 1835) which is lime green with orange and purple markings.

In this work, I describe the anatomy of a number of species from around the world, among which I found great anatomical similarity. The form and functioning of the alimentary canal has been adequately described elsewhere (Fretter, 1939; Rudman, 1970), and this study is restricted to the form and function of the external features, the mantle cavity, and the reproductive system. An anatomical description of the nervous system is also included.

EXTERNALS AND MANTLE CAVITY

The headshield is large, the anterior edges form temporary funnels directing water down over the Hancock's organs on either side of the head. The posterior end of the headshield is usually divided into a pair of short posterior lobes. In *Haminoea elegans* (Gray, 1825) and *Haminoea zelandiae* (Gray, 1843), there is only a small median notch on the posterior border of the headshield (Marcus, 1957; Rudman, 1970). In *Haminoea zelandiae* a large mucous gland opens into a vestibule below the mouth. The foot is short, extending posteriorly halfway down the shell. Large lateral lobes, the parapodia, fold up and over the shell. An extension of the posterior edge of the floor of the mantle cavity, the infrapallial lobe, forms a large accessory foot extending some distance behind the shell and also encloses the posterior end of it (Fig. 1). The Hancock's organs are large brown-yellow sensory regions, lying on either side of the head. They are usually slightly folded (Fig. 2*D*).

When the animal is moving, it encloses itself in a mucous tube produced by the subepithelial glands of the foot and headshield, and also by the mucous gland opening below the mouth. The mucous sheet collects and holds the silt or sand particles of the substrate. By the action of its heavily ciliated epidermis, the

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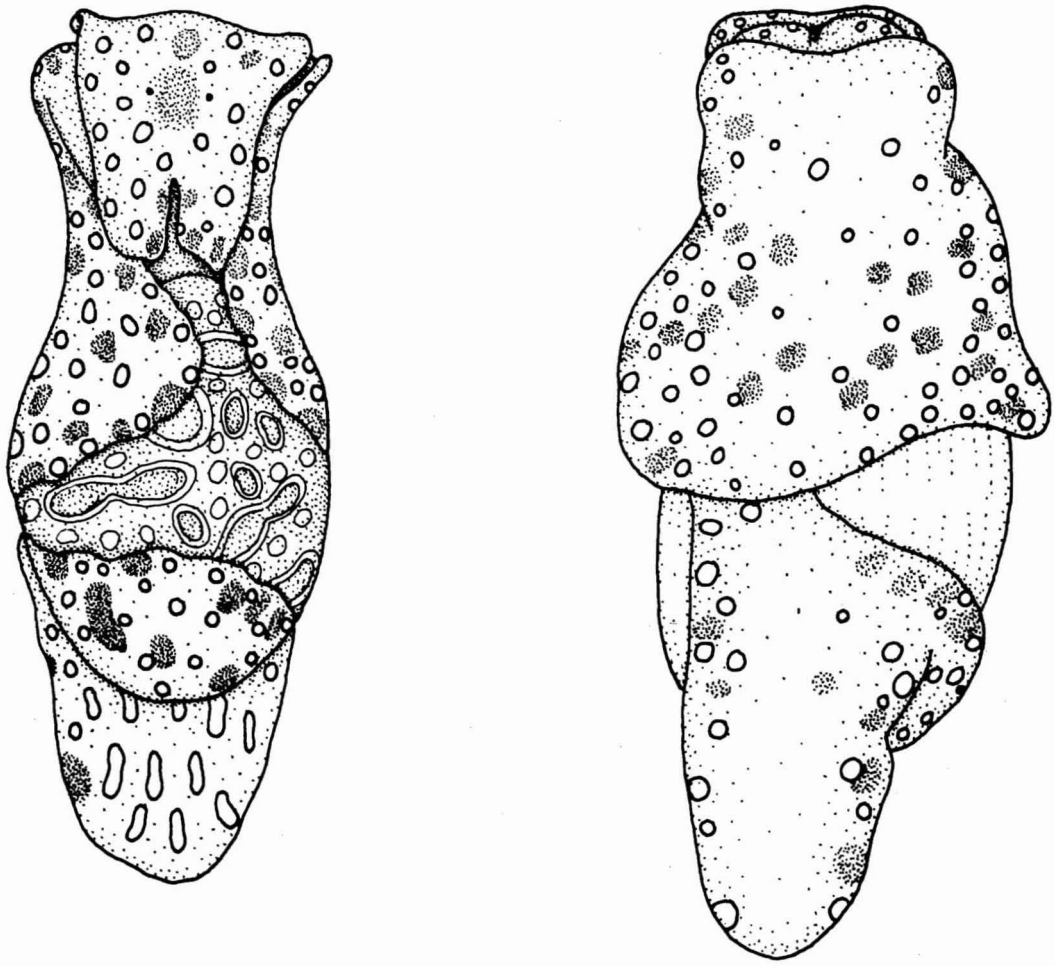

FIG. 1. *Haminoea cymbalum* (Quoy & Gaimard) from Fiji.

animal glides through this continuously produced mucous tube and does not become clogged with mud and detritus. The mantle cavity is typical of the type found in the lower opisthobranchs. The following description is for *H. zelandiae*. The large gill is only slightly ciliated and the mantle water flow is caused by the raphae, a pair of large ciliated ridges. The lower raphe (Fig. 3) runs from the posterior or right edge of the mantle opening, describing a wide arc, spiralling above itself at the right inner corner of the mantle cavity. At this inner end, the blind caecum into which it spirals is probably homologous to the pallial caecum described by Fretter and Graham (1954) for *Acteon tornatilis* (L). From the inner end of this caecum, the upper raphe runs out along the mantle, above the lower raphe. A wide mucous gland runs along the inner side of the curve of both raphae.

On the mantle roof is a small gland (M. GL.M.) opening alongside the upper raphe and in from the center of the mantle edge. Sections of this gland (Fig. 2*A*), which in life appears as a cluster of white granules, show that it consists of a collection of large vacuoles surrounding a central secretory area (S.D.). In relation to the size of the vacuoles, which store

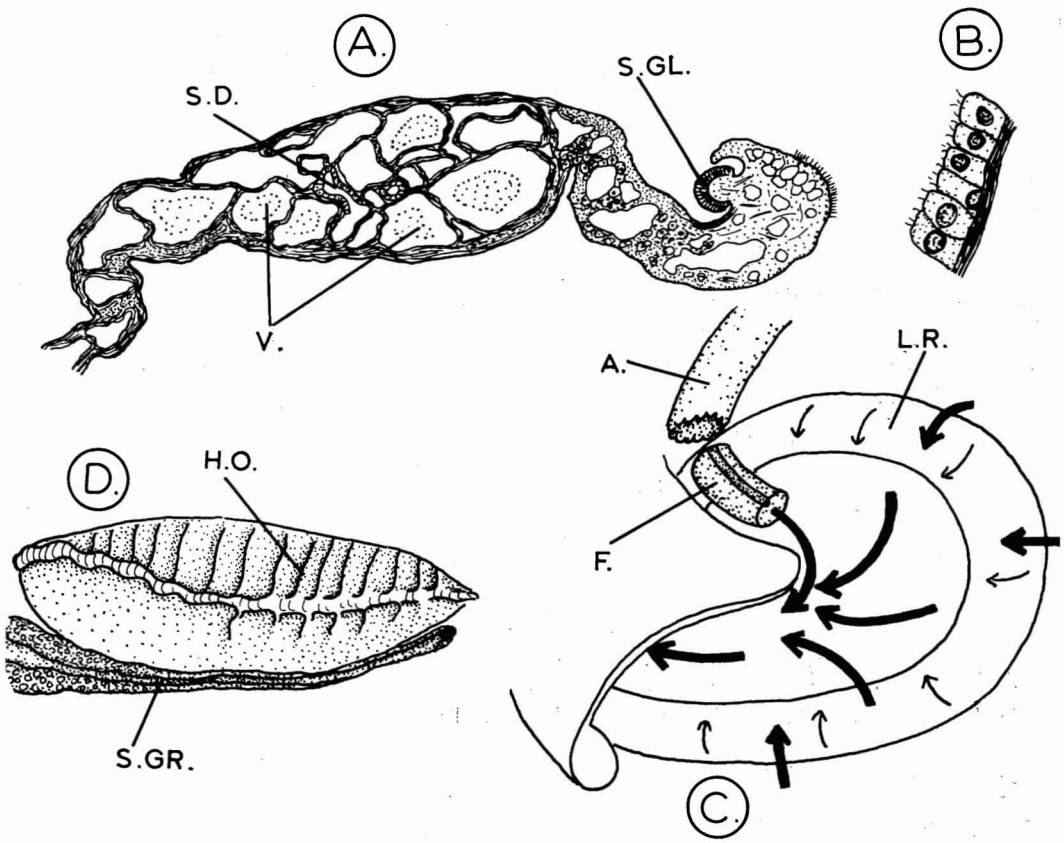

FIG. 2. *A-C, Haminoea zelandiae* Gray: *A*, section of mantle; *B*, cells of secretory duct of mantle gland; *C*, currents of raphal region; *D, Haminoea cymbalum* (Quoy & Gaimard): Hancock's organ.
SYMBOLS: A., anus; F., fecal pellet; H.O., Hancock's organ; L.R., lower raphe; S.D., secretory duct of mantle gland; S.GL, shell gland; S.GR., seminal groove; V., storage regions of mantle gland.

the milky white secretion, the duct, which forms the secretory region and opens into each vacuole and also into the mantle cavity, is quite small. On persistent irritation of the mantle, a small amount of white secretion is extruded from the gland. Apart from the raphal mucous glands and the small glandular cluster, however, the mantle is devoid of glands. Large glands, similar to the repugnatorial glands of *Siphonaria* (Fretter and Graham, 1954), are scattered over the foot, but their viscous white secretion is extruded only when the foot is actually damaged.

The kidney occupies the left third of the roof of the mantle cavity, the pericardial cavity being found at the left posterior corner of the mantle cavity, extending partly on to the outer edge of the digestive gland. Alongside the pericardium is a diffuse gland with many branching lobes. The histology of this gland is similar to that of the pericardial gland described in a separate study on *Hydatina.*

The anterior mucous gland of the pallial gonoduct runs across the floor of the mantle cavity, at the left edge, to open at the mantle opening. The external seminal groove runs from the genital opening along the right side of the head to enter the penial sac just below the anterior edge of the Hancock's organ (Fig. 2*D*). The brown gametolytic sac sits near the pericardium and the long posterior mucous gland of the genital gland mass lies at the back of the mantle

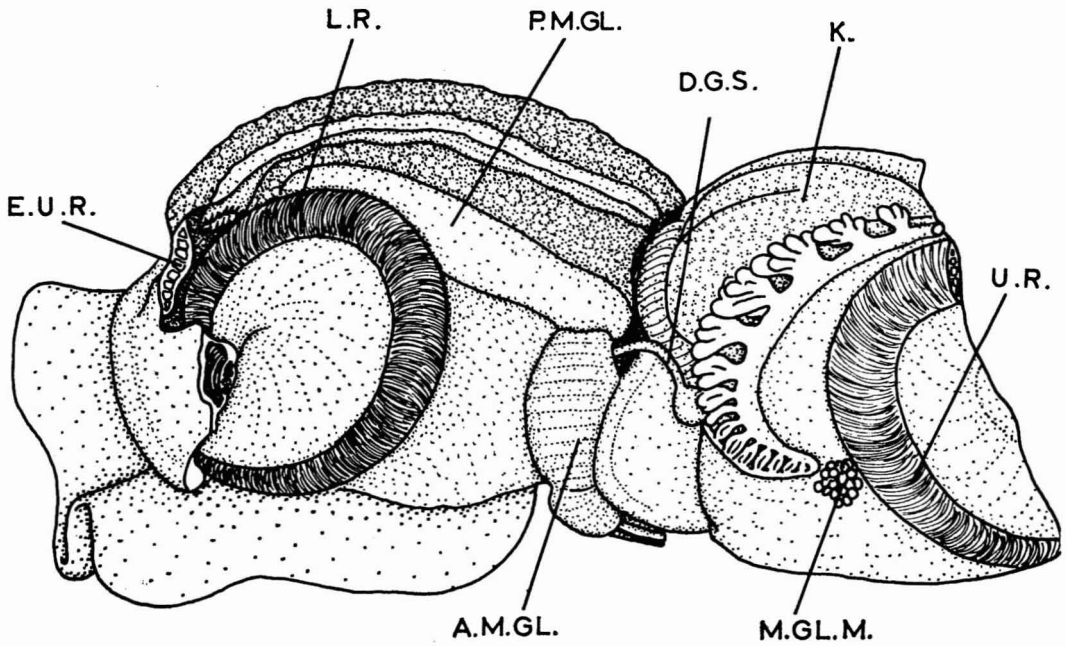

FIG. 3. *Haminoea zelandiae* Gray: mantle cavity. A.M.GL., anterior mucous gland of genital system; D.G.S., duct of gametolytic sac; E.U.R., cut edge of upper raphe; K., kidney; L.R., lower raphe; M.GL.M., mantle gland mass; P.M.GL., posterior mucous gland of genital system; U.R., upper raphe.

cavity. The anus opens at the right inner corner of the mantle cavity just above the lower raphe. As can be seen in Fig. 2*C*, the currents of the raphae sweep fecal pellets out at the right edge of the mantle opening.

REPRODUCTIVE SYSTEM

Serial sections of the reproductive system of *Haminoea zelandiae*, prepared at different times of the breeding cycle, and subsequent dissections of the genital gland mass of *H. cymbalum*, *H. solitaria* Say, 1822, and *H. crocata* Pease, 1860 suggest that the reproductive system is constant within the genus. The penis, however, varies in structure from species to species. The following description of the genital gland mass is based on *Heminoea zelandiae*.

The narrow spermoviduct leaves the ovitestis on the inner side of the visceral whorls and soon widens into the large, folded, ampullar region of the duct. Here endogenous sperm and ova pack the lumen. The epithelial lining of the ampulla is quite complex. Two-thirds of the epithelium consists of cubical cells, each of which has a large nucleus which almost completely fills the cell. It appeared that these cells are ciliated but, because the duct was packed with sperm, it was difficult to be certain. The other third of the lining consists of low strongly ciliated cells forming a longitudinal ciliated channel. On either side of the channel is a ciliated ridge of cells which do not stain in either Weigert's iron haemotoxylin and van Gieson or Mallory and Heidenhain. Near the genital gland mass the spermoviduct narrows into a thin-walled, ciliated duct with a simple folded epithelium (Fig. 4), and this runs beneath the gland mass. Under the gland mass, a small caecum (S.S.) (the opening has a large sphincter muscle) joins the ovitestis duct. The walls of the caecum are ciliated and nonglandular and its function now is unknown. The ciliated spermoviduct (S.SP.OV.D.) then opens into a vestibule. Opening into this vestibule is the exogenous sperm sac; also both incurrent and excurrent sperm grooves end here. From this chamber the eggs travel along another duct which passes into a large sac which I consider to be the fertilization chamber. The epithelium

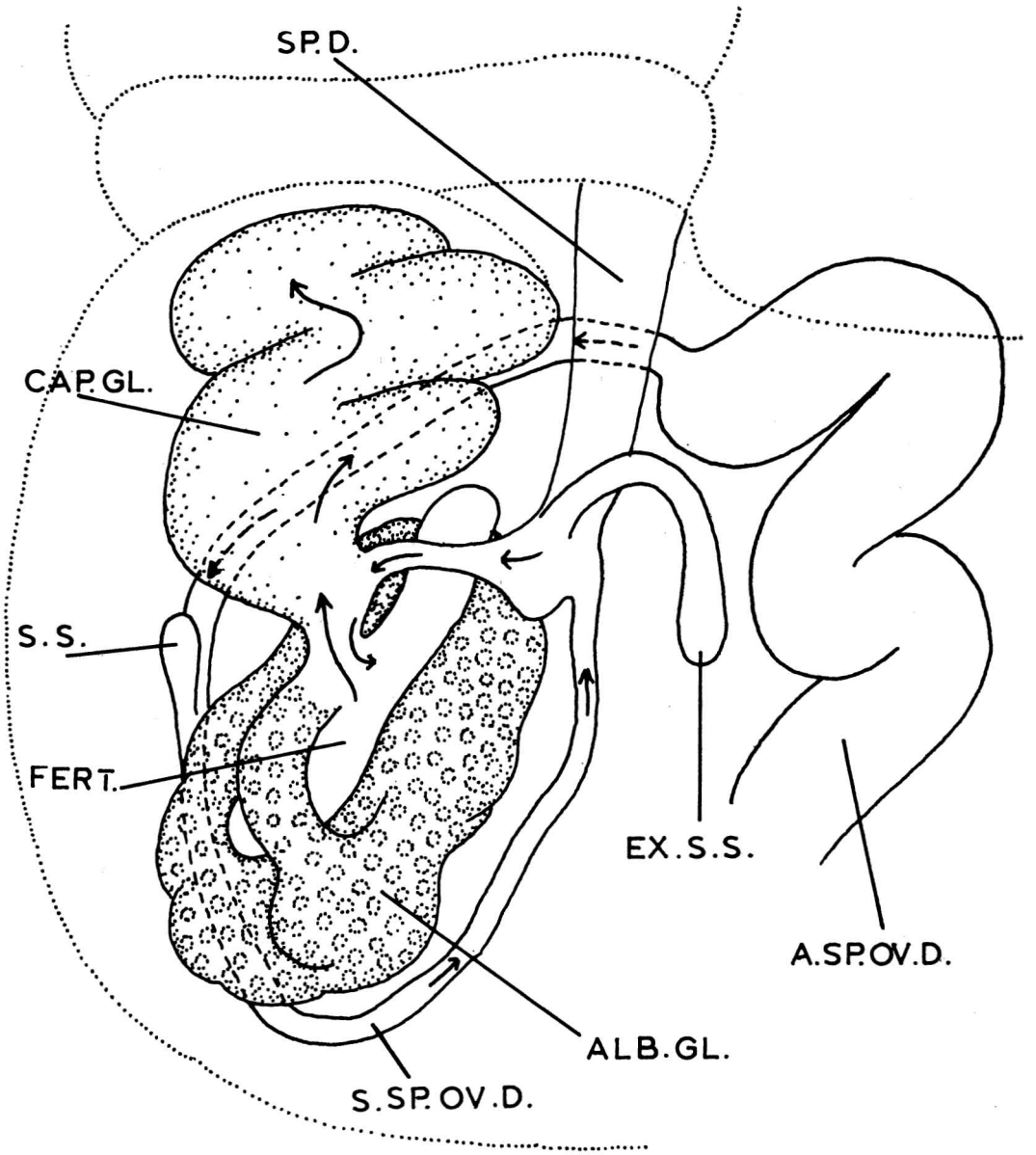

FIG. 4. *Haminoea zelandiae* Gray: ducts of genital gland mass. ALB.GL., albumen gland; A.SP.OV.D., ampullar region of spermoviduct; CAP.GL., capsule gland; EX.S.S., exogenous sperm sac; FERT., fertilization chamber; SP.D., sperm duct; S.S., small sac of unknown function; S.SP.OV.D., small spermoviduct.

is lined with tall, closely packed, ciliated cells. The upper quarter of the cell stains blue in Mallory and Heidenhain and brown in Weigert's iron haemotoxylin and van Gieson (Figs. 4, 5*B*). At the center of the fertilization chamber are openings from the albumen gland and the capsule gland. The cells of the albumen gland are loosely packed, and in Mallory and Heidenhain the nucleus stains dark blue with a bright red nucleolus. The cytoplasm is packed with spherules staining light blue. In Weigert and van Gieson the nuclei are dark brown, the

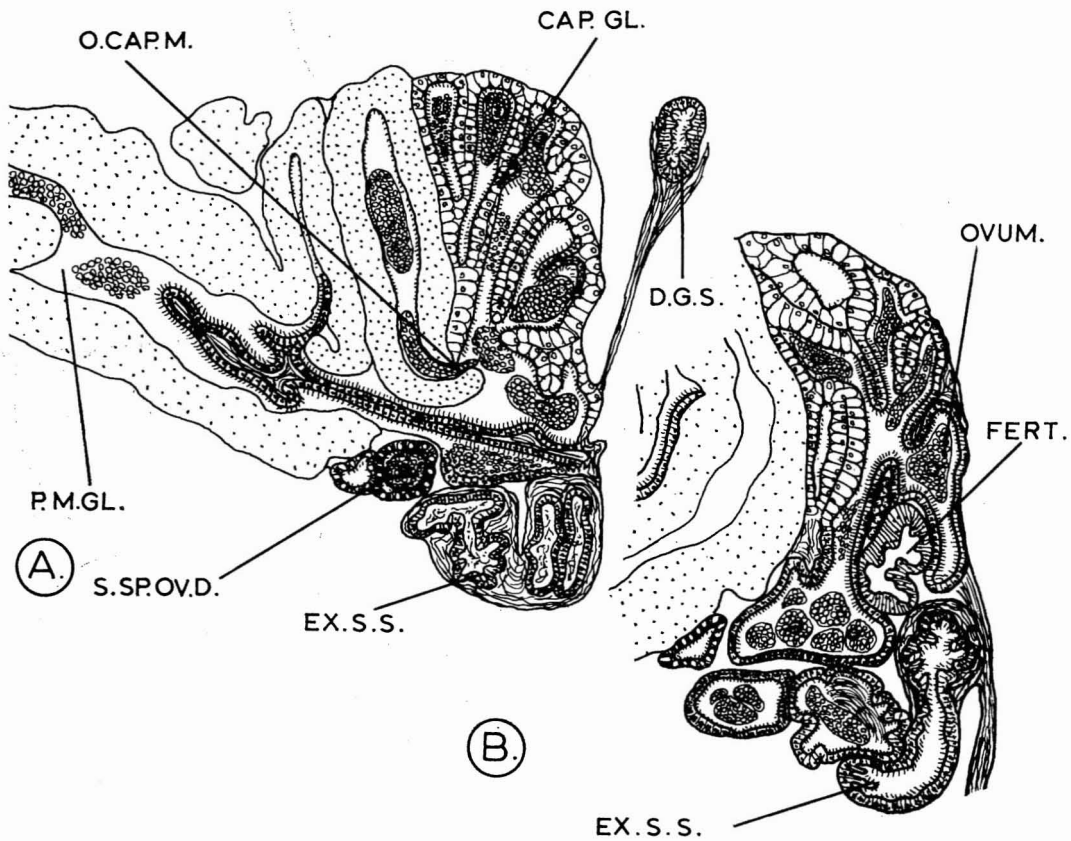

FIG. 5. *Haminoea zelandiae* Gray: *A*, genital gland mass showing junction between mucous gland and capsule gland; *B*, genital gland mass showing junction between gonoduct and fertilization chamber.
SYMBOLS: CAP.GL., capsule gland; D.G.S., duct to gametolytic sac; EX.S.S., exogenous sperm sac; FERT., fertilization chamber; O.CAP.M., opening between capsule and mucous glands; P.M.GL., posterior mucous gland; S.SP.OV.D., small spermoviduct.

nucleolus black, and the spherules light brown or colorless.

The capsule gland is a wide, folded, ciliated tube (Figs. 4, 5, 6) with closely packed columnar secretory cells. The cytoplasm stains black or dark purple in Weigert's iron haemotoxylin and van Gieson and pale blue in Mallory and Heidenhain. The capsule gland opens at the inner end of the anterior mucous gland, just anterior to the vestibule into which the spermoviduct, exogenous sperm sac, and egg duct to the fertilization chamber open. The posterior mucous gland also opens near the capsule gland opening and inside has a large, double fold along its length (Figs. 5, 6). The anterior mucous gland consists of large folds of mucous cells all opening into a small channel along the left posterior edge. This channel, the pallial gonoduct, is oval in section and has one ciliated groove along the left edge. This channel is probably a sperm groove but I was unable to determine whether it was used as both an excurrent and an incurrent channel. At the genital opening, however, just outside the mantle opening, this groove joins the external seminal groove to the penis—thus suggesting that it serves at least as an excurrent channel.

From the genital opening, a long ciliated duct runs back alongside the anterior mucous gland to the brown gametolytic sac located in the posterior left corner of the mantle cavity. The cells lining this sac are tall and thin, and

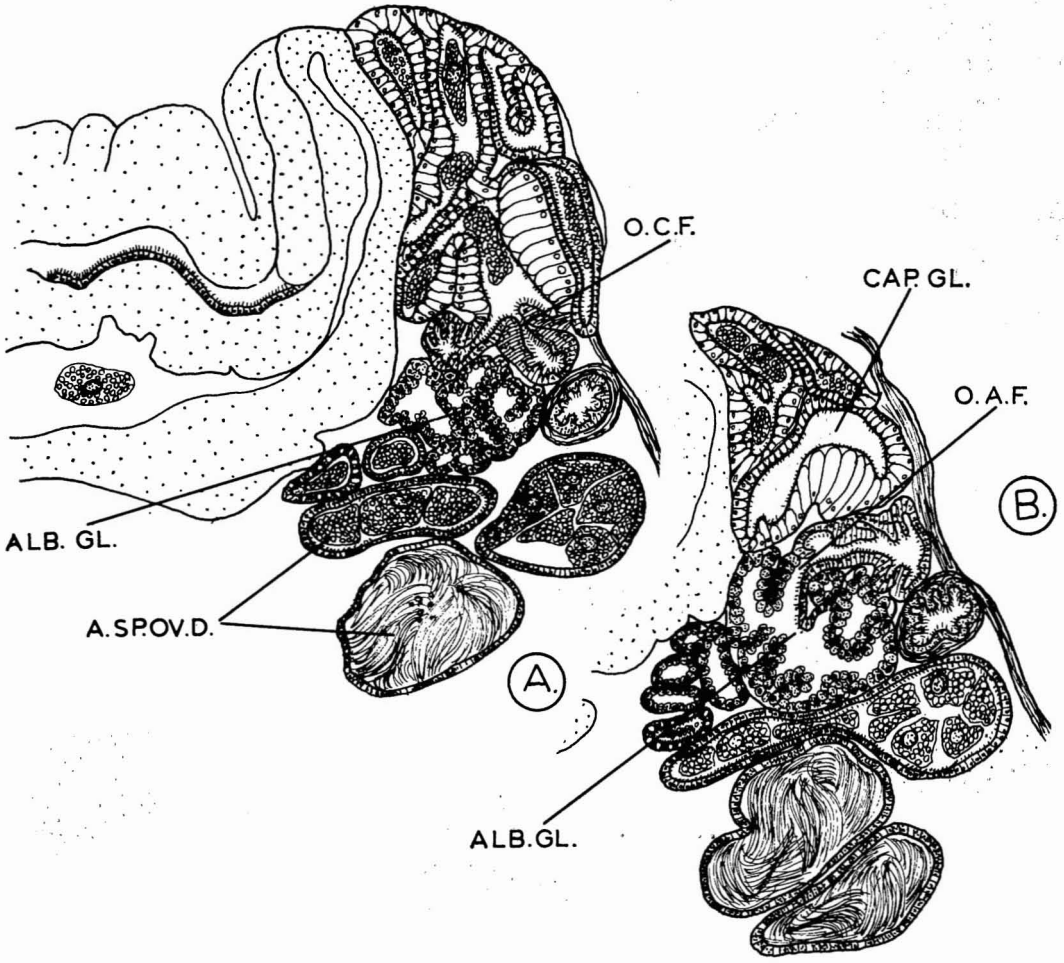

FIG. 6. *Haminoea zelandiae* Gray: *A*, genital gland mass showing junction between capsule gland and fertilization chamber; *B*, genital gland mass showing junction between albumen gland and fertilization chamber. SYMBOLS: ALB.GL., albumen gland; A.SP.OV.D., ampullar region of spermoviduct; CAP.GL., capsule gland; O.A.F., opening between albumen gland and fertilization chamber; O.C.F., opening between capsule gland and fertilization chamber.

the granular cytoplasm stains light purple in Mallory and Heidenhain and light brown in Weigert and van Gieson. During the breeding season it is usually packed with unorientated sperm and other, unidentifiable, matter.

From serial sections of an animal laying an eggmass, it was possible to determine the route the ova follow through the genital gland mass. From the opening of the spermoviduct, the eggs are moved to the fertilization chamber. From there, moved along by ciliary action, they are passed to the opening of the albumen gland, but do not enter it. After receiving a coating of albumen they are directed through the winding glandular capsule gland. Here each ovum is encapsulated, usually one to a capsule, but sometimes two; and the capsules are joined together by a short string. The string of eggs then moves out of the capsule gland and through the posterior mucous gland, by action of a powerfully ciliated ridge running the length of the gland. At the outer end of the posterior mucous gland the string turns to travel down the other side of the gland which is divided by the

previously mentioned double fold. Here it receives its inner mucous coat. On entering the anterior mucous gland, near the capsule gland opening, the egg string is slowly coiled into a spiral and is surrounded by an outer mucous coat. As the mucous coat of the egg mass comes in contact with seawater, the mucous swells to form the large sausage-shaped egg mass, up to 30 mm long and 10 mm wide (Fig. 7*B*). The egg string appears as a coil of yellow beads packed into a transparent mass.

The penis is a complex structure showing great variation from species to species. The penis of the species studied will be described separately.

Haminoea zelandiae (Fig. 8)

The penis is large, opening at the right side of the head. The penis sac is as long as the buccal bulb and lies to the right of it. From the posterior end of the penis sac, a short duct runs over the esophagus to the bright yellow

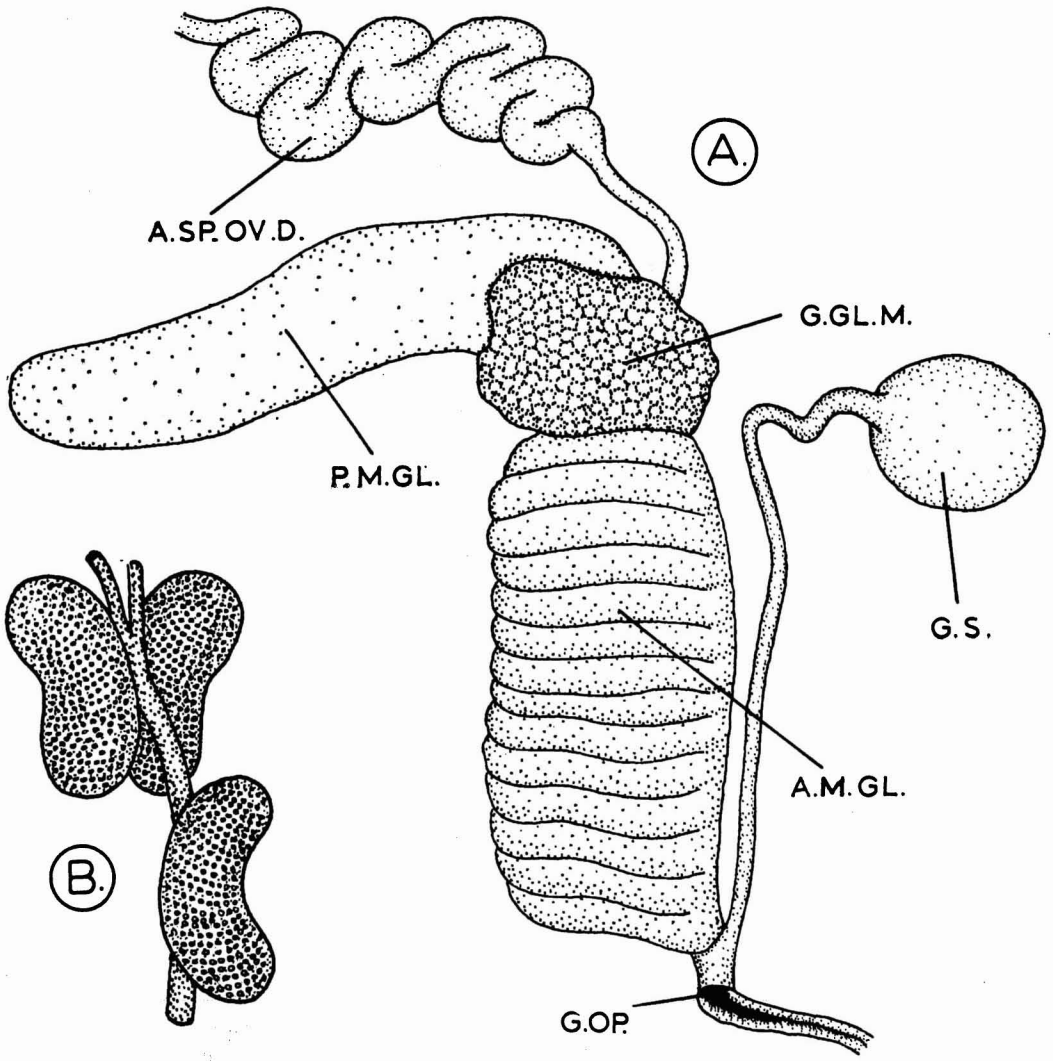

FIG. 7. *Haminoea zelandiae* Gray: *A*, reproductive system; *B*, egg masses.
SYMBOLS: A.M.GL., anterior or pallial mucous gland; A.SP.OV.D., ampullar region of spermoviduct; G.GL.M., genital gland mass (albumen, capsule gland); G.OP., genital opening; G.S., gametolytic sac; P.M.GL., posterior mucous gland

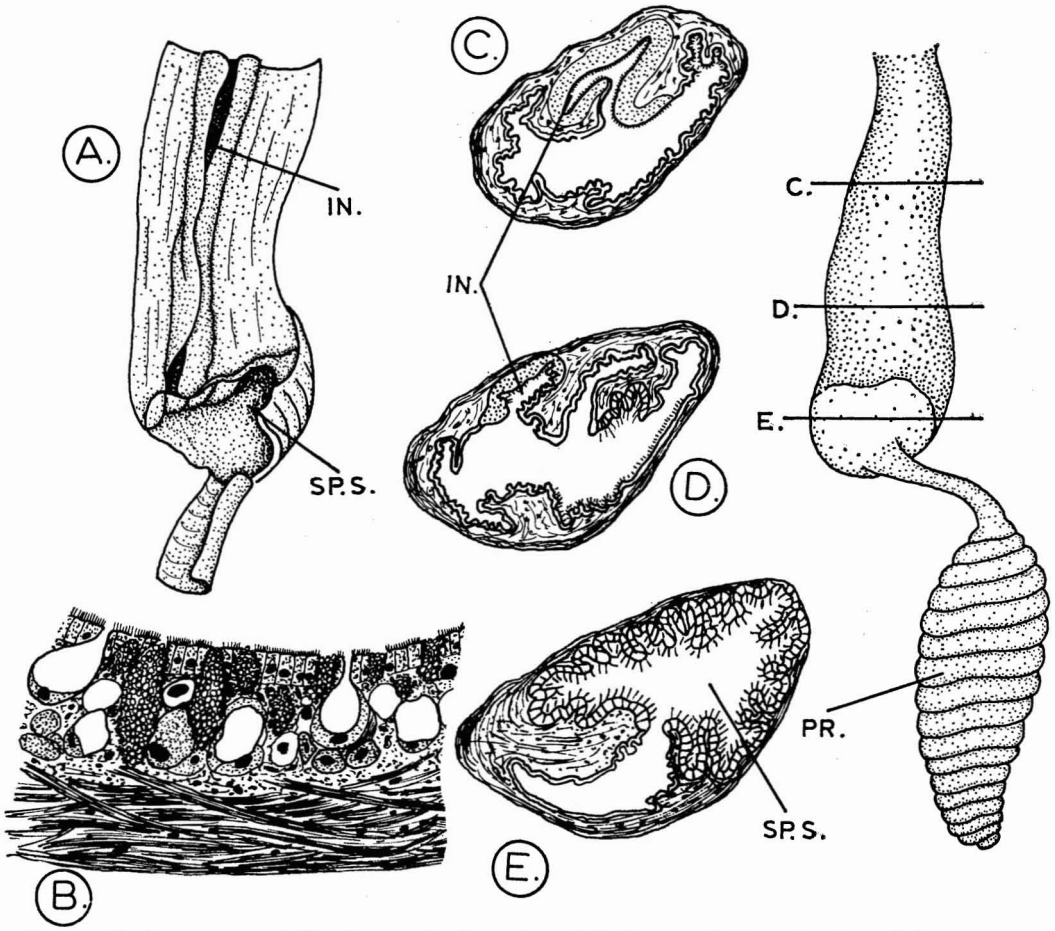

FIG. 8. Penis structure of *Haminoea zelandiae*: *A*, penis bulb, opened; *B*, section through incurrent sperm groove; *C, D, E,* sections through penis bulb, as indicated.
SYMBOLS: IN., incurrent sperm groove; PR., prostate, SP.S., sperm sac.

prostate gland lying on the left of the cavity. The penis sac is black with a light yellow patch at the posterior end.

A simple unciliated epithelium lines the penis sac. A large ciliated incurrent sperm groove (Fig. 8*A*, *C*) running the length of the sac is lined with a complex of subepithelial gland cells. These consist of large flask-shaped cells with a granular cytoplasm staining light brown in Weigert and van Gieson and purple in Mallory and Heidenhain. Some of these cells contain a large clear vacuole. The other type of cell has brightly staining spherules—red in Mallory and Heidenhain and yellow in Weigert and van Gieson. Scattered amongst these cells are clusters of granules colored green in both of the stains used. At the posterior end a lateral fold forms an enclosed region in which the epithelium is ciliated and nonglandular (SP.S.); this is a sperm storage region. From the sperm sac a short duct runs back to the large prostate gland. The histology of the prostate gland cells shows them to be similar to those I have observed in *Pupa kirki* and *Hydatina physis*. In Mallory and Heidenhain the cells are packed with light blue spherules, and the nucleus is purple and the large nucleolus bright red. In Weigert and van Gieson the spherules stain orange-brown and the nucleus dark brown.

Haminoea cymbalum (Fig. 9)

The penis complex lies over the buccal bulb and esophagus. It consists of an anterior tubular portion, in which the incurrent sperm groove

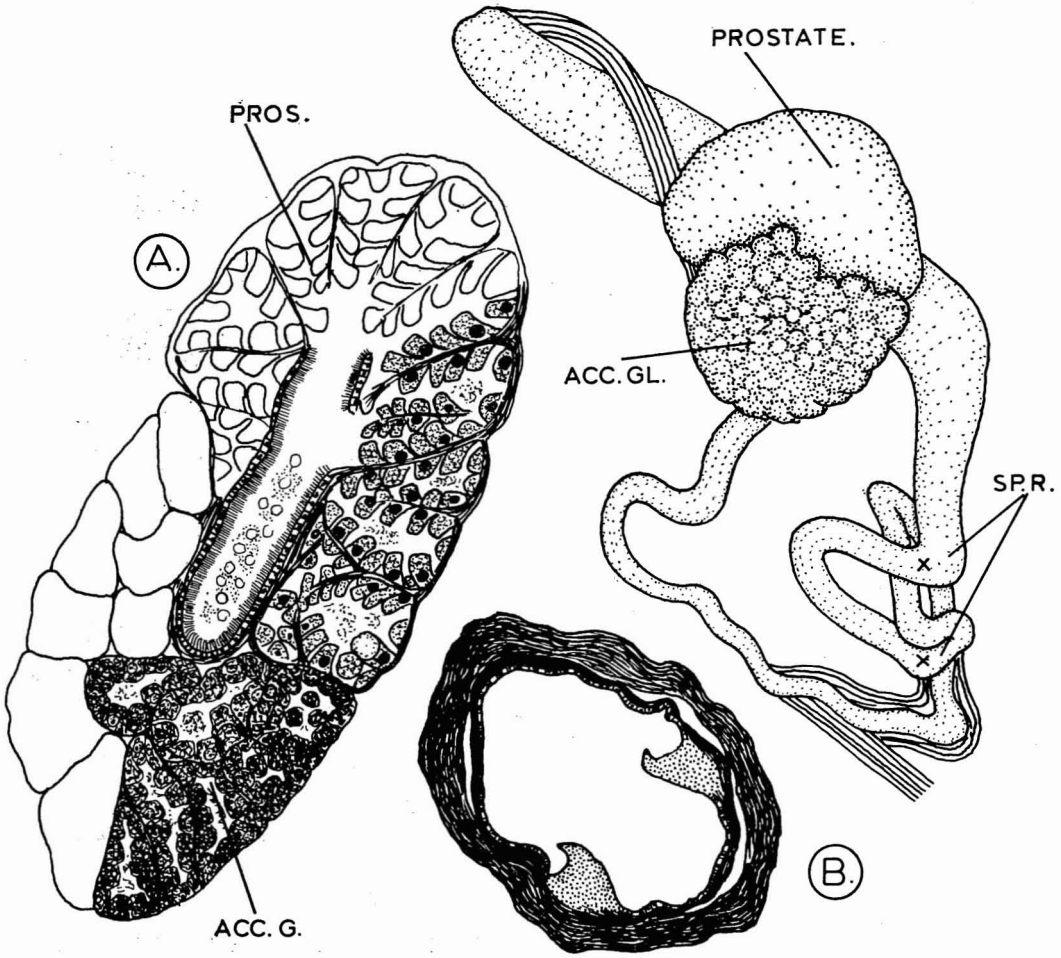

FIG. 9. Penis structure of *Haminoea cymbalum* (Quoy & Gaimard): *A*, section through gland mass; *B*, section through armed region of penis.

SYMBOLS: ACC.GL., accessory gland; PROS., prostate; SP.R., region with chitinous spines (delimited by X).

is not well developed. A thin muscular duct runs from the anterior tube to the prostate and accessory glands. The anterior portion of this duct (SP.R.) is thin-walled and armed with sparsely scattered chitinous spines (Fig. 9*B*). The remainder of the duct is surrounded by a band of circular muscle and is lined with a simple ciliated epithelium. The accessory gland, yellow in life, is anterior to the lime-green prostate gland. The histology of the prostate gland is the same as that of *H. zelandiae*. The histology of the accessory gland is somewhat different. The cells are cubical rather than elongate. In Weigert and van Gieson the nuclei do not stain as deeply and the cytoplasm is granular, staining a light brown. In Mallory and Heidenhain, the granular cytoplasm stains dark blue. Both glands open into the common ciliated duct (Fig. 9*A*).

Haminoea crocata (Fig. 10*A*)

The penial armature of this species is greatly developed. The anterior end of the penis is strongly muscular and a deep incurrent seminal groove covered with a dorsal flap is present. Behind this is a large, thin-walled tube bearing

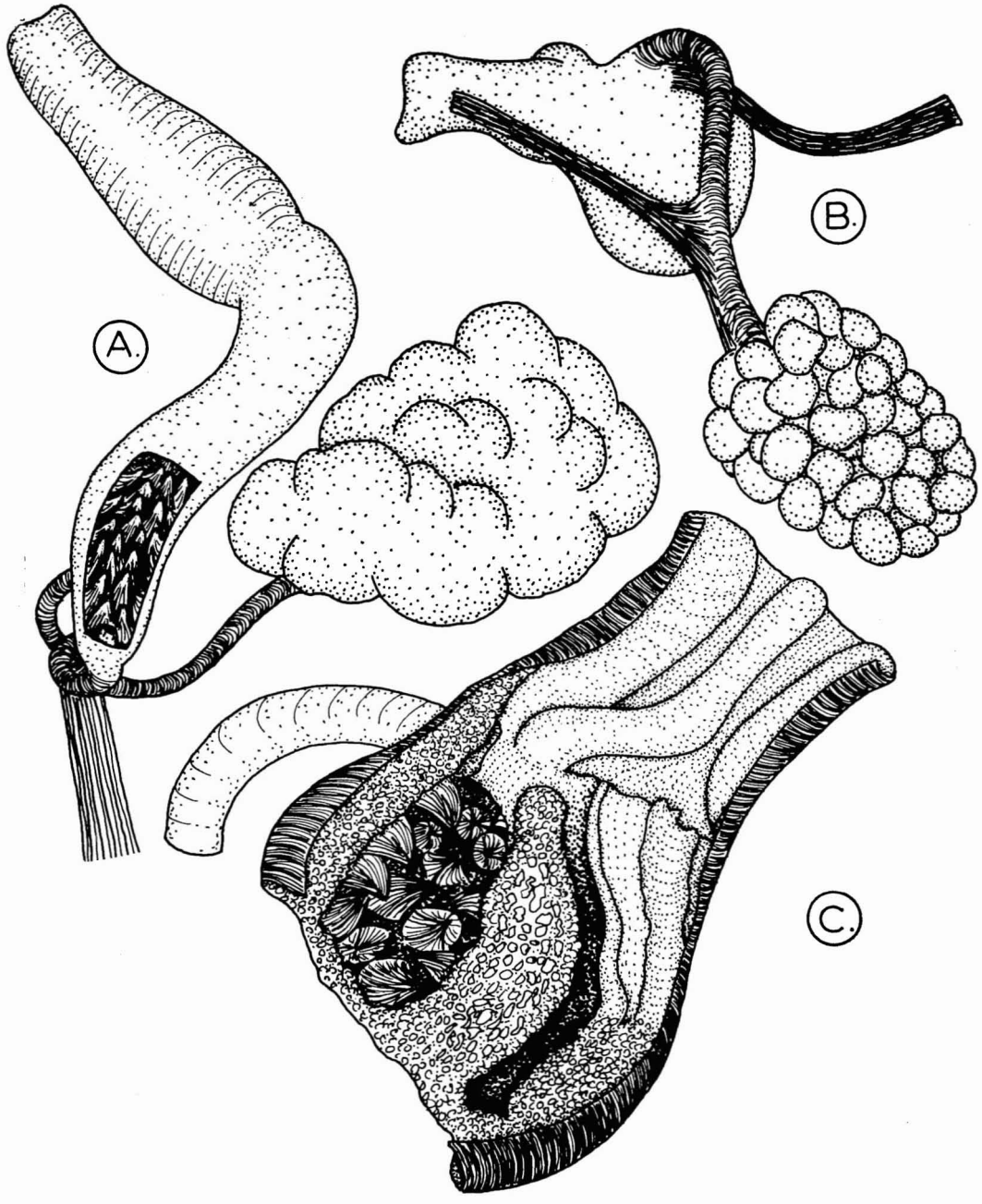

FIG. 10. Penis structure: *A, Haminoea crocata* Pease, opened to show spiny region; *B, Haminoea solitaria* Say; *C, Haminoea solitaria* Say, showing opened penis bulb.

large, closely packed, chitinous spines. At the posterior end of this region the muscular duct of the prostate gland opens through a short papilla. An histological study was not undertaken but the posterior gland mass appeared to be of one tissue.

Haminoea solitaria (Fig. 10*B*, *C*)

The anterior end of the penis sac is short, the incurrent seminal groove being covered by a large dorsal flap. The posterior end of the sac is enlarged and here there is a pocket of large chitinous spines and a large glandular region probably associated with sperm storage. The large prostate gland is connected to the penis sac by a muscular tube. The state of preservation made an histological study impossible.

NERVOUS SYSTEM

An investigation of the nervous systems of the four species of *Haminoea* studied showed no differences. The following account is of the nervous system of *H. zelandiae*.

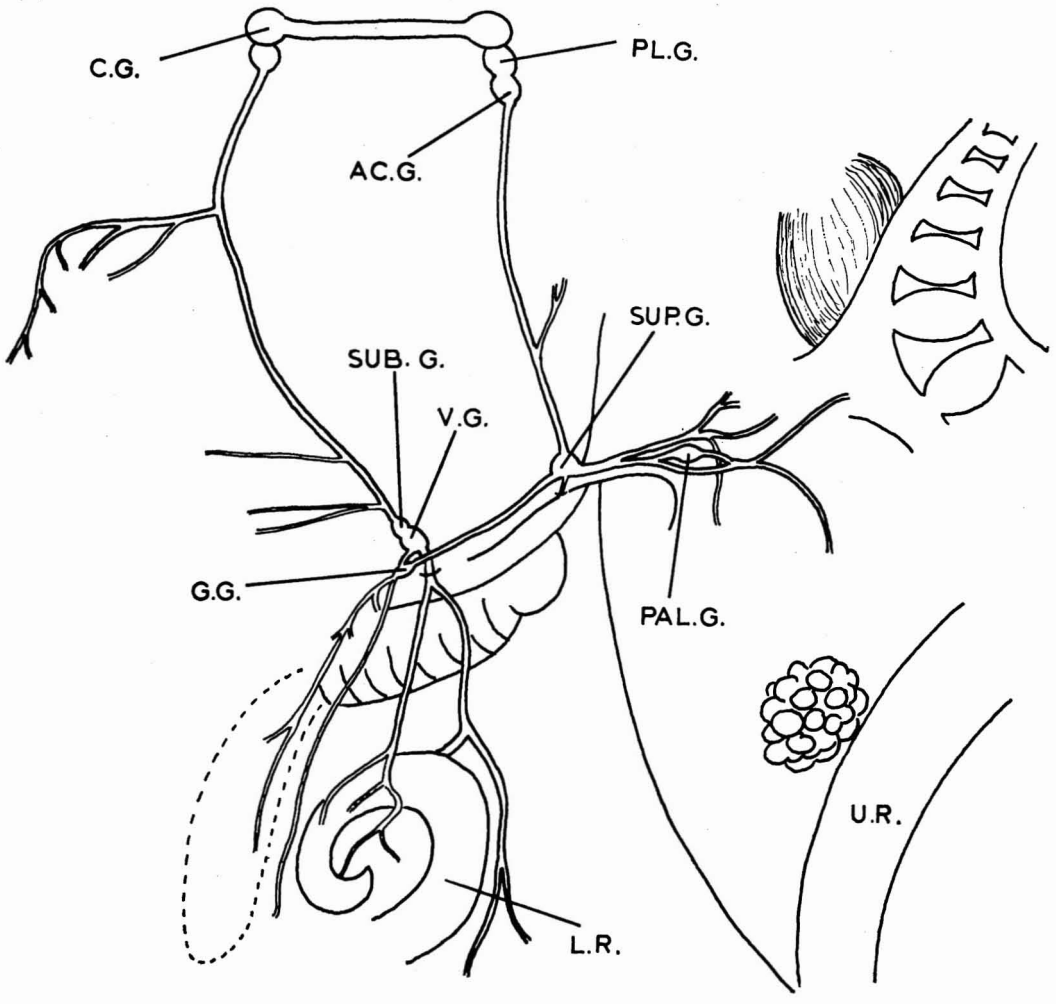

FIG. 11. *Haminoea zelandiae* Gray: central nervous system. AC.G., accessory ganglion; C.G., cerebral ganglion; G.G., genital ganglion; L.R., lower raphe; PAL.G., pallial ganglion; PL.G., pleural ganglion; SUB.G., subesophageal ganglion; SUP.G., supraesophageal ganglion; U.R., upper raphe; V.G., visceral ganglion.

The nerve collar runs around the anterior end of the buccal bulb. The cerebral ganglia are joined by a long commissure and lie midway down the side of the buccal bulb. They are joined to the respective pedal ganglion by a short connective; the two pedal ganglia are joined by a long commissure. The pleural ganglia are joined to the respective cerebral ganglion and, on the right side, an accessory ganglion, sometimes called a pallial (Guiart, 1901) or a parietal ganglion (Marcus, 1958), also joins the pleural ganglion. The subesophageal and visceral ganglion are joined to each other and lie on the floor at the posterior end of the body cavity. The long connective between the left pleural and the subesophageal ganglia has a large nerve branching off it halfway down, which runs into the body wall and innervates the posterior half of the roof of the body cavity.

From the visceral ganglion a large nerve runs back under the anterior mucous gland and divides. One of the branches innervates the columellar muscle and the infrapallial lobe which forms the accessory foot; the other innervates the lower raphe (Fig. 11). Above the visceral ganglion, and connected to it by a short cord, is a small ganglion, the genital ganglion, which is attached to the posterior body wall. Two thin nerves arise from this and branch to innervate the genital gland mass. The supraesophageal ganglion, sitting in the right posterior corner of the body cavity, is joined to the genital ganglion and the right accessory ganglion by long connectives. A large nerve from the supraesophageal ganglion runs into the mantle roof (Fig. 11) and supplies the gill, the heart, the upper raphe, and other organs of the mantle. A ganglion, joined at both ends to a branch of this nerve, lies buried at the anterior edge of the mantle. This ganglion has been described as an osphradium (Guiart, 1901) and an osphradial ganglion (Marcus, 1958), but as there is no region of the mantle cavity comparable to the prosobranch osphradium these terms are inaccurate. This ganglionic thickening (PAL.G.) is associated with the nerves innervating the organs of the mantle. Although the term "pallial ganglion" has been used (Guiart, 1901) for the accessory ganglia between the pleural and esophageal ganglia, I have used it for the ganglia described here. My observations show that a similar ganglion is present in the Philinidae and Aglajidae.

Two thick nerves (H) issue from each cerebral ganglia, branch and bifurcate, and innervate the Hancock's organ. One branch from the anterior nerve (L.N.) innervates the ridge on either side of the mouth. Another thick cerebral nerve arises above the anterior Hancock's organ nerve and branches, innervating the overlapping anterior edge of the head. When *H. zelandiae* is crawling, this edge of its head is constantly rippling and touching the sub-

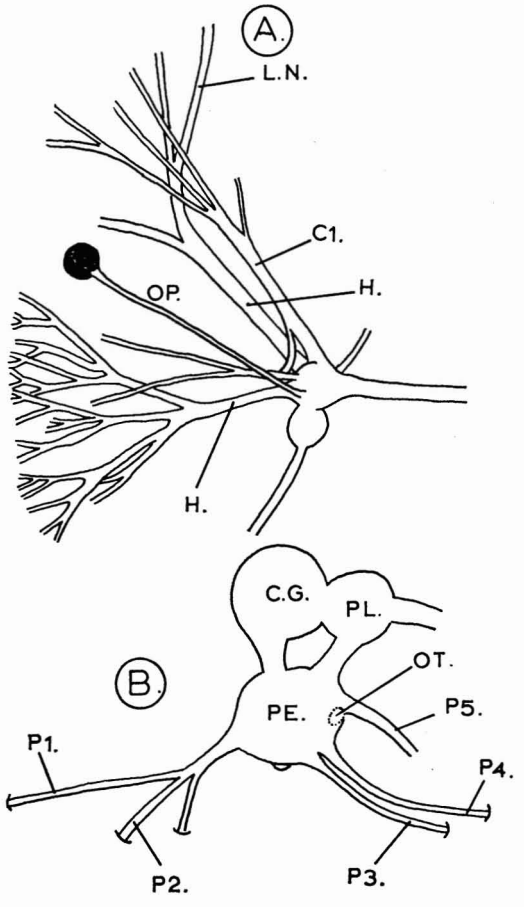

FIG. 12. *Haminoea zelandiae* Gray: *A*, cerebral nerves to head region; *B*, pedal nerves to left side.

SYMBOLS: C., cerebral nerve; C.G., cerebral ganglion; H., nerve to Hancock's organ; L.N., labial nerve; OP., optic nerve; OT., otocyst; P., pedal nerve; PE., pedal ganglion; PL., pleural ganglion.

strate, suggesting some sensory function. The optic nerve is long and the large black eyes are embedded just below the surface. One other cerebral nerve, thin and branching, runs back into the body wall.

The five main pedal nerves are illustrated in Fig. 12*B*. P_1 innervates the head region of the foot and body wall; P_2, the anterior region of the parapodia; and P_3, the posterior region of the parapodia. The central and posterior areas of the foot are innervated by P_4, and P_5 innervates the longitudinal muscle straps running the length of the body.

DISCUSSION

Pilsbry (1893) lists over 50 species of *Haminoea*, and a study of more recent literature shows that at least 20 more species have been described. In all but a very few cases, only the shell, typically thin and bubble-shaped, is described. In a number of species, features of the alimentary canal are mentioned, showing that the wide radular ribbon with many hook-shaped teeth and the three transversely ridged, chitinous gizzard plates are typical of the genus. The following radular formulas are not recorded in the literature. *Haminoea solitaria*, 15.1.15; *Haminoea vesicula*, 40.1.40; *Haminoea crocata*, 10.1.10; *Haminoea cymbalum* (Fiji), 10.1.10 and 13.1.13; and *Haminoea simillima* (Hawaii) (= *H. cymbalum*), 9.1.9.

On the basis of the shell, Pilsbry (1920) divided the genus *Haminoea* into three sections: *Haloa, Liloa,* and *Haminoea.* Subsequent workers (Habe, 1952) gave these generic status. In the case of *Haloa*, Pilsbry named *H. crocata* Pease as the type species. My observations on *H. crocata* show no distinguishing characters for *Haloa*, and Habe's distinction (1952) that there are two cusps on the first marginal tooth of the radula in *Haloa*, is not the case for the type species *H. crocata.* I would therefore consider *Haloa* Pilsbry, 1920 to be a junior synonym of *Haminoea* Turton & Kingston, 1830. A subgenus of *Haloa, Vitreohaminoea* Kuroda & Habe, 1952 is distinguished by the presence of only one cusp on the first marginal tooth. As this is the normal form in the genus *Haminoea*, this subgenus is also invalid. Another new subgenus of *Haloa, Sericohaminoea* Habe, 1952 was not accompanied by an account of its distinguishing features and was merely noted in the description of a new species *Haloa yamagutii* Habe, 1952. This subgenus, whether it is a natural group (which I doubt) or not, does not fulfill the requirements of the International Code of Zoological Nomenclature.

Although the external form of the reproductive system has been described for some species (Guiart, 1901; Marcus, 1958), no full account has been published before on the histology and anatomical detail. It is typically monaulic and in basic plan is identical to that of *Aplysia* (Eales, 1921; Quattrini, 1967; Thompson and Bebbington, 1969). It does differ, however, in having the prostate associated with the penis rather than with the anterior gonoduct, as is the case in *Aplysia.* From Thompson and Bebbington's account of the histology of the winding gland of *Aplysia*, it is possible to homologize this structure with the capsule gland of *Haminoea.* The penis shows great variability in form, from the saclike penial bulb and simple prostate gland in *Haminoea zelandiae* to the armed form with prostate and accessory gland found in *H. cymbalum.* The penis of *H. musetta* Marcus & Burch, 1965 and of *H. linda* Marcus & Burch, 1965 are similar to that of *H. cymbalum.* In *Haminoea virescens* (Sowerby, 1833) and *H. elegans* (Gray, 1825) the unarmed penis has a large papilla (Marcus, 1961; Marcus, 1958).

In this widespread herbivorous genus the major distinctions between species are to be found in the soft parts of the animal. In some species, such as *H. cymbalum*, the radular formula is variable and in most cases the variations between shells are difficult to determine. In some cases the color of the body is constant and can be employed as a characteristic; in others, such as *H. zelandiae*, it ranges from almost black to a mottled grey-brown. In the present study one case of taxonomic confusion arose. Specimens of *Haminoea* with a green body, spotted with bright orange and blotches of purple, were obtained from Fiji. This species was identified as *H. cymbalum* (Quoy & Gaimard, 1835). In 1952 another new genus, *Lamprohaminoea* Kuroda & Habe, 1952 was erected with this species as a type. Again this

genus is invalid, both because the type species differs little from *Haminoea* and because no separate differentiation of the taxon was given. Similarly colored specimens from Hawaii were studied, and proved to be identical to *H. cymbalum* from Fiji. The differences in radular formula, mentioned earlier, are not considered significant. Pease (1868) described the Hawaiian form as a distinct species, *H. simillima*, but this species must be considered a junior synonym of *H. cymbalum*.

Separate studies of *Atys, Liloa, Smaragdinella*, and *Phanerophthalmus* show that this group, to which *Haminoea* belongs, occupies different levels of evolutionary development ranging from *Atys* with the large solid shell, through *Haminoea*, to *Phanerophthalmus* with a thin internal shell and a body form reminiscent of the Aglajidae. Their herbivorous habits and reproductive systems show a closer relationship to the Aplysiomorpha than to many of the Bullomorpha, and this tends to suggest that the Bullomorpha are an unnatural grouping.

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