On Melanochlamys Cheeseman, 1881, a Genus of the Aglajidae (Opisthobranchia, Gastropoda)¹

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ABSTRACT: Melanochlamys Cheeseman, 1881, long considered to be a synonym of Aglaja Renier, 1807, is shown to be a distinct genus of the Aglajidae differing from other genera in external body form, shape of shell, alimentary canal, and reproductive system. Specimens of the type species, M. cylindrica Cheeseman, 1881, are compared with M. lorrainae (Rudman, 1968), M. queritor (Burn, 1958), and M. diomedea (Bergh, 1893).

It is suggested that Aglaja dubia O'Donoghue, 1929, A. ezoensis Baba, 1957, A. henri Burn, 1969, A. nana Steinberg & Jones, 1960, and A. seurati Vayssière, 1926, also belong to Melanochlamys.

IN 1881, Cheeseman described a new species of aglajid from New Zealand, and, because of differences in the external form of the body and nature of the shell, he erected a new genus *Melanochlamys*. From that date all subsequent workers (Pilsbry, 1896; Eliot, 1903; Bergh, 1907; O'Donoghue, 1929) have considered this name to be a junior synonym of *Aglaja* Renier, 1807. However, after an extensive study of the family, I have come to the conclusion that *Melanochlamys* should be reinstated.

The following comparative account of Melanochlamys cylindrica Cheeseman, 1881, M. lorrainae (Rudman, 1968), M. queritor (Burn, 1957), and M. diomedea (Bergh, 1894) is the first of a series of separate studies on the genera of the Aglajidae.

EXTERNAL FEATURES AND MANTLE CAVITY

The body form and structure of the mantle cavity are constant within the genus and the following description, therefore, is applicable to any of the four species studied. The body is cylindrical and the parapodial extensions of the foot are small, usually tightly pressed against the sides of the body and reaching up to the edge of the dorsum. The headshield occupies

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the anterior half of the dorsum and posteriorly the edge is rounded forming a small loose flap. Sometimes there is a small central indentation on the posterior edge of the headshield. A slightly visible median line runs from the anterior end to halfway down the headshield. The posterior half of the dorsum forms a posterior shield. The hind end of this shield overhangs the posterior end of the body and encloses the reduced shell. It folds under on either side to form the mantle cavity (Figs. 1, 2A, B). On the right posterior end of the body, below the posterior shield, is the large genital opening (G.OP.); running from it, along the right side of the body to the penial opening, is the ciliated seminal groove (S.GR.). The Hancock's organs are large yellowish brown patches on either side of the head.

On either side of the mouth, below the anterior edge of the headshield, is a large mound bearing retractile sensory bristles (S.BR., Figs. 1, 3C). Both below and above the mouth is a deep groove into which large mucous glands open. In a sagittal section of the head region (Fig. 3C) it can be seen that these glands run back some distance, above and below the buccal bulb, in the body wall. They consist of two different types of cells. One gland (L.G.L.1) consists of cells staining deep blue in Mallory and Heidenhain and light pink in Weigert's iron haemotoxylin and van Gieson. Each cell is enveloped in a fibrous coat. The other gland (L.GL.2) lying outside the former does not

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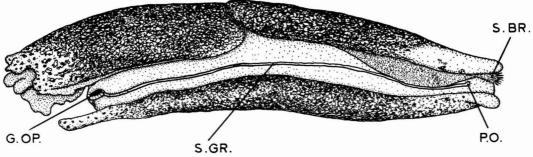


FIG. 1. Melanochlamys lorrainae, dark form. SYMBOLS: G.OP., genital opening; P.O., opening of penial sac; S.BR., sensory bristles; S.GR., external seminal groove.

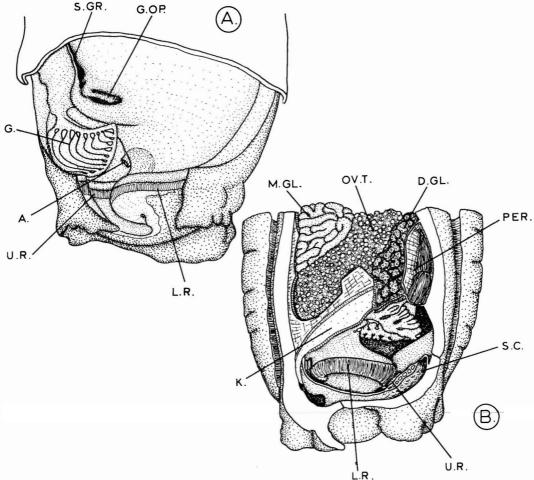


Fig. 2. Melanochlamys cylindrica, mantle cavity. A, ventral view, B, dorsal view, with roof of mantle cavity and visceral cavity removed.

SYMBOLS: A., anus; D.GL., digestive gland; G., gill; G.OP., genital opening; K., kidney (partly removed); L.R., lower raphe; M.GL., mucous gland (of genital system); OV.T., ovotestis; PER., pericardial cavity; S.C., shell cavity; S.GR., seminal groove; U.R., upper raphe.

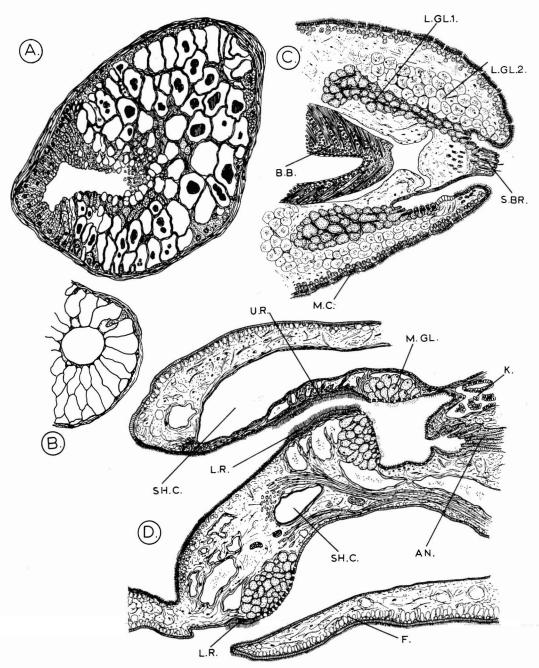


Fig. 3. Melanochlamys cylindrica. A, longitudinal section through yellow gland; B, transverse section of yellow gland; C, longitudinal section through head region, just off-center; D, sagittal section through mantle cavity.

SYMBOLS: AN., anus; B.B., buccal bulb; F., foot; K., kidney; L.GL., labial glands; L.R., lower raphe; M.C., mucous cells; M.GL., mucous gland; S.BR., sensory bristles; SH.C., shell cavity.

take up either stain. From a separate study (Rudman, in press) on the method of feeding in *Melanochlamys cylindrica* it is suggested that these labial glands are not involved in the feeding process and in fact produce the large quantities of mucus required to produce the mucous tube in which the animal slides along. The whole of the body is ciliated and below the epithelium are many small mucous cells (M.C.) staining identically to the cells of the first labial gland.

The structure of the mantle cavity can be seen in Figs. 2A, B and 3D. The shell is strongly calcified and is reduced to the body whorl and a small columellar region (Rudman, 1968, Fig. 2 D-H). It lies enclosed in a shell cavity above the mantle, and a narrow strongly ciliated duct runs from the shell cavity to open on the left side at the posterior end of the shield. I have observed a similar duct in other genera of the Aglajidae and in species of Philine. This duct is probably a relic structure recording the phylogenetic past when the shell was exposed. The left posterior edge of the body, forming the left wall of the mantle cavity, is developed into a large spiralling ridge on which sits the wide lower raphe (LR.). The upper raphe runs across the roof of the mantle cavity, above the lower raphe, and down the right side to the mantle opening. These raphae form an extraction device at the extreme posterior end of the body, sucking water in between the parapodia and down over the gill and through the reduced mantle cavity. Following each raphe round on the anterior edge is a large mucous gland (M.GL.), the cells of which stain pink in Weigert's iron haemotoxylin and van Gieson and blue in Mallory and Heidenhain. The wall of the mantle cavity inside the raphae has small scattered cilia. The anus opens almost in the midline, a small section of the intestine jutting out into the cavity. The kidney opens alongside the anus and lies dorsally, partly over the body cavity and partly above the anterior end of the mantle cavity (K.).

A large gland sac sitting in the posterior end of the body cavity opens just to the left of the anus and extrudes a bright yellow secretion on some occasions when the animal is disturbed. In section (Fig. 3 A, B) we can see that this

gland consists of columnar chambers opening into a central channel. The walls of these chambers have no epithelial lining and in fresh material are shining translucent white. At the proximal end, near the gland opening and sparsely scattered on the walls of the sac, are cells with a large nucleus. The granular cytoplasm stains light brown in Weigert's iron haemotoxylin and van Gieson and reddish brown in Mallory and Heidenhain. Some cells contain secretion spherules staining yellow in the first stain and blue in the second. The vacuoles often contain large amounts of this secretory material. This yellow secretion was collected from the mantle cavity of Melanochlamys cylindrica and placed in a watch glass of fresh seawater. Polychaete worms, up to 50 mm in length, the normal food of this species, were paralyzed in a few seconds when placed in this, but would recover if removed within 30 seconds. The worms would die within two or three minutes. One must be cautious, however, in considering that this yellow gland is defensive or offensive in function; the secretion was only sometimes extruded on irritation and, since the mantle cavity is at the rear, it would provide little meaningful protection for the animal. Chapman and Fox (1969) have produced evidence to show that the secretion of the purple gland in Aplysia, usually considered a defensive mechanism, is probably merely a waste product. Aplysioviolin, the purple secretion, is a derivative of phycoerythrin and is only produced in Aplysia californica when on a diet of red algae. It becomes facultatively de-inked on a diet of brown algae. The structure of the aplysiid purple gland is similar to that of the aglajid yellow gland and it may be that the yellow secretion is a waste product, its offensive nature being secondary to its primary function.

The large plicate gill is attached at the upper right corner of the mantle cavity and folds down and under. The pericardium lies farther forward on the right above the posterior end of the body cavity. As described earlier, the genital opening is on the lower right body wall at the anterior end of the mantle cavity. Completely closing off the open ventral side of the mantle cavity is the free posterior end of the foot. Water, therefore, can enter the mantle

cavity only by running down the gaps between the sides of the body and the parapodia and leave the cavity only through the funnel formed by the raphae.

In the midline, at the back of the posterior shield, just below the lip of the notum is a small gland. It consists of a central opening surrounded by gland cells arranged in a radial pattern. I have found a similar gland in species of *Chelidonura* and *Philine*. It is also found (Brown, 1934) in *Philine aperta* and was called by Pelseneer (1894) the "fossette glandulaire."

BODY CAVITY AND ALIMENTARY CANAL

An illustration of the arrangement of the organs in the body cavity of Melanochlamys cylindrica is given in a separate paper (Rudman, in press); the same study also includes a full description of the structure and functioning of the alimentary canal. Subsequent investigation of the three other species of the genus show that the arrangement of the body cavity and the gut are constant within the genus and a brief review is presented below. With the loss of spiral visceral whorls, the digestive gland and ovotestis have moved down into the body cavity. In this genus, a fibrous diaphragm, running vertically from the roof to the floor, separates the anterior body cavity containing the foregut, central nervous system, and penis from the posterior body cavity containing the viscera which, in spirally shelled types, form the visceral whorls.

The buccal bulb is a huge, bulbous, muscular organ, approximately half as long as the animal and is held to the body wall by five pairs of protractor muscles. It is devoid of jaws and radula and acts as a suction pump, sucking in polychaete and nemertine worms. The esophagus, expanded into a large crop, fills the posterior half of the anterior body cavity. At the end of the crop the esophagus narrows, running through the diaphragm to the small reduced stomach lying under the digestive gland mass. The intestine loops through the digestive gland to open in the mantle cavity. In mature animals the brownish orange digestive gland is overlain by a large, yellow, diagonally placed

gland, the ovotestis (Fig. 2B). To the left of this and underneath the viscera sit the glands of the reproductive system. The gametolytic sac is brown, and is usually visible at the right anterior edge of the digestive gland. A small diffuse white gland, the pericardial gland, similar in histological features to that described separately for *Hydatina* and *Haminoea*, lies just in front of the pericardium.

REPRODUCTIVE SYSTEM

The penis is relatively small, lying on the floor of the body cavity either under or to the right of the buccal bulb. It consists of a thinwalled penis sac and an unpaired prostate gland. In all cases a large incurrent sperm groove runs from the penial opening down to the inner end of the sac near the opening of the prostate. Attached to the wall of the sac is a large muscular flap developed posteriorly into the penial papilla. In Melanochlamys cylindrica and M. lorrainae the muscular flap is attached along its posterior half to the sac wall (Fig. 4A) and at the posterior end it extends into a muscular papilla lying free in the penial sac. In Fig. 4B we can see that the incurrent sperm groove (IN.) runs down to the posterior end of the base of the muscular flap. At this point the prostate gland opens and a large excurrent (EX.) groove runs out along the edge of the papilla. The muscular flap and papilla have large internal hemocoelic spaces (Fig. 5F). In M. queritor the penis is similar but the posterior end of the muscular flap is not developed into a papilla. The penis of M. diomedea is, on first appearances, quite different in shape, but in basic form it is similar to that of the other three species (Fig. 4C). The anterior end of the muscular flap extends into a conical structure with a chitinous tip, while the posterior papilla is a thin muscular extension folding in on each side to form a wide channel. A small thin-walled sac (SP.B) opens near the prostate gland opening. This sac is sometimes considered to be a secondary branch of the prostate gland (Marcus, 1961) but it is not glandular and probably stores sperm. The penis structure of M. diomedea is thus rather different from that of the other species; it also differs considerably

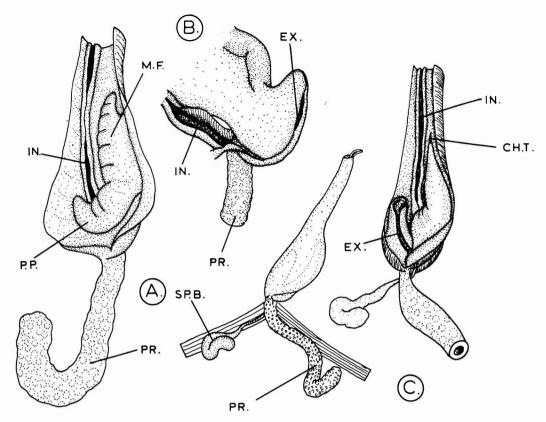


Fig. 4. Penis structure: A, Melanochlamys cylindrica, with penial sac opened; B, M. cylindrica, muscular flap folded to the right to show excurrent sperm groove; C, M. diomedea, left, showing opened penial sac. Symbols: CH.T., chitinous tip; EX., excurrent sperm groove; IN., incurrent sperm groove; M.F., muscular flap; P.O., penial papilla; PR., prostate; SP.B., spermatic bulb.

from the forms found in the other genera of the Aglajidae. Because in all other characters it conforms with *Melanochlamys* I consider it to be a slightly specialized form of this genus.

The genital gland mass lies under the digestive gland at the rear of the body cavity. Its structure is characteristic of the genus. A study of serial sections of the genital gland mass of specimens of *M. cylindrica* forms the basis of the following description. Dissection of this system in the other three species showed it to be identical in each case. The protandrous ovotestis lies over the digestive gland. From its ventral surface arises the spermoviduct which soon widens into a large folded ampulla in which the duct is distended with tightly packed endogenous sperm. The duct narrows, forming the small spermoviduct which runs around the al-

bumen-capsule gland complex, and then forks -one branch, the sperm duct, runs straight to the vestibule at the genital opening, while the other, the oviduct, opens into a wide albumen gland. The albumen gland describes two loops and then runs into the capsule gland which folds around and opens, with the mucous gland, into the vestibule at the genital opening. The mucous gland has one long curved arm which lies on the floor of the body cavity and a short arm at the genital opening. Two other ducts leave the genital vestibule, a short one to the large exogenous sperm sac and a long one which runs forward, in the body wall, to the gametolytic sac lying at the upper right corner of the digestive gland. The histology of these regions is discussed separately.

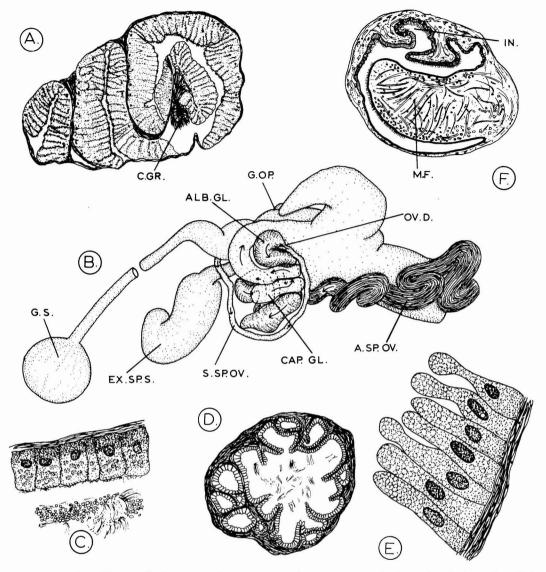


FIG. 5. Melanochlamys cylindrica, reproductive system. A, T.S. mucous gland; B, dorsal view of genital gland mass; C, E, cells of gametolytic sac; D, T.S. of distal end of exogenous sperm sac; F, T.S. of penial sac. SYMBOLS: ALB.GL., albumen gland; A.SP.OV., ampullar region of spermoviduct; CAP.GL., capsule gland; C.GR., ciliated, grooved ridge of mucous gland; EX.SP.S., exogenous sperm sac; G.OP., genital opening; G.S., gametolytic sac; IN., incurrent sperm groove; M.F., muscular flap; OV.D., oviduct branch of spermoviduct; S.SP.OV., small spermoviduct.

Spermoviduct and Sperm Duct

The ampullar region is lined with a thin epithelium which has a wide ciliated track running its length. From the ampulla the spermoviduct narrows and the walls become slightly folded and ciliated. It is separated from the

final section of the small spermoviduct by a large sphincter. This final section is shown in Fig. 5B; it is lined with a glandular, lightly ciliated epithelium (Fig. 6C). The oval glandular cells stain grey in Weigert's iron haemotoxylin and van Gieson and light blue in

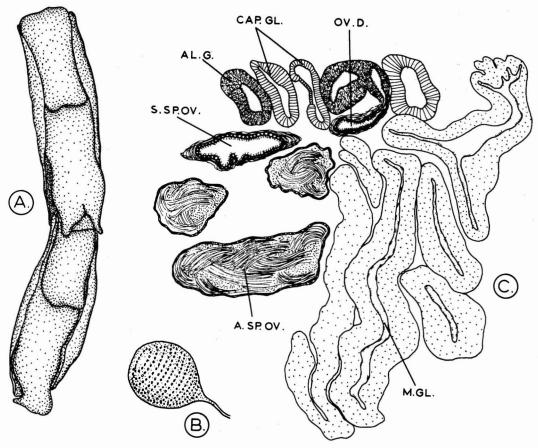


FIG. 6. Melanochlamys cylindrica. A, copulation; B, egg mass; C, section through genital gland mass. SYMBOLS: AL.G., albumen gland; A.SP.OV., ampullar region of spermoviduct; CAP.GL., capsule gland; M.GL., mucous gland; OV.D., oviduct at junction with albumen gland; S.SP.OV., small spermoviduct.

Mallory and Heidenhain. Scattered either singly or in groups between the gland cells are small ciliary cells. From the opening of the albumen gland the male branch of the spermoviduct runs straight to the genital opening. The sperm duct is narrow and ciliated and the epithelium contains large scattered gland cells staining bright orange in Mallory and Heidenhain and yellow-brown in Weigert and van Gieson.

Albumen Gland

The albumen gland is in the form of a wide tube and the eggs traverse its lumen. The cells are long and columnar (Fig. 6C), the granular cytoplasm staining a light brown in Weigert's iron haemotoxylin and van Gieson, and the granules are light blue in Mallory and

Heidenhain. Small triangular ciliary cells are wedged between the upper edges of the gland cells.

Capsule Gland

The capsule gland is also a wide tube, the long columnar cells staining a deep grey-blue in Weigert's iron haemotoxylin and van Gieson and light blue in Mallory and Heidenhain. As in the albumen gland, small wedge-shaped ciliary cells are squeezed between the gland cells. Although no specimens were sectioned during egg-laying, the position of this gland and histological similarity of the cells to those of the capsule gland in *Haminoea zelandiae* suggest that it serves a similar function in *Melanochlamys* (Rudman, 1971).

Mucous Gland

The major branch of the mucous gland is extensively folded internally, the major fold bearing a large strongly ciliated ridge (Fig. 5A). The mucous cells are long and columnar, staining lightly in both stains used. Interspersed at intervals are small groups of ciliary cells.

Exogenous Sperm Sac

This large sac has a short duct opening into the vestibule at the genital opening. It is brown in fresh material. The wall is developed into laminae and at the distal end these plates form a honeycomb arrangement (Fig. 5D). The epithelium consists of small cells, their cytoplasm staining blue in Mallory and Heidenhain and dark brown in Weigert and van Gieson. Sections were cut of this sac from specimens acting either as a male or female and fixed immediately or after 24 hours in isolation. In two specimens acting as females, and fixed immediately after copulation, this sac was packed with sperm and prostatic fluid. Some of the sperm were attached by the head to the wall. In "female" specimens kept in isolation for 24 hours after copulation and then fixed, all the spermatozoa were tightly packed with their heads attached to the wall. No loose sperm were observed. In those specimens acting as male and either immediately fixed or left for 24 hours, there was considerable variation from some in which the sperm were tightly packed and attached to the wall to some in which the sac was almost empty. These observations confirm that this sac receives exogenous sperm at copulation and stores it. It would appear that some time elapses before all the spermatozoa are able to attach themselves to the sac wall.

Gametolytic Sac

The histology of the epithelial cells is similar to that of a similar sac described separately for *Pupa kirki* and *Haminoea zelandiae*. The cytoplasm is vacuolated, staining a grey-brown in Weigert and van Gieson and a light redbrown in Mallory and Heidenhain. Although the cells are of the same nature, they vary considerably in shape from low cubical cells (Fig. 5C) to tall cells with rounded tips (Fig. 5E). This variation of shape is probably caused by

changes accompanying stages of either secretory or absorptive activity. In the region around the opening of the duct the cells bear short cilia. The duct is a narrow muscular ciliated tube. In specimens acting as females and fixed immediately after copulation only a few scattered spermatozoa were observed in the gametolytic sac; after 24 hours only unidentifiable homogenous matter was present. In specimens acting as males, sperm and yellow spherules (possibly "yolk" spherules) (Fig. 5C) were found immediately after copulation and unidentifiable matter was found 24 hours later. This gives further support to the view that this sac, often called the bursa copulatrix, does not function as such.

The following pattern of movement of eggs and sperm through the reproductive system is suggested. Endogenous sperm are stored in the ampullar region of the spermoviduct and ova are moved down from the ovitestis along the ciliated track. Movement of gametes from the ampulla is controlled by the sphincter halfway along the small spermoviduct. From the opening of the albumen gland the eggs move down through the gland and into the capsule gland. Thompson and Bebbington (1969) are doubtful as to whether the winding gland of Aplysia acts as a capsule gland as has been suggested by Ghiselin (1965), and state that the capsules did not appear until the distal part of the mucous gland. In sectioned material I found it was very difficult to see the capsule because it did not stain, but after a mucous coat was present some process of reflection or refraction of light or perhaps change in the chemical composition of the capsule itself allowed it to be seen more easily. Other indirect evidence to support the idea that this tissue produces the capsule is my discovery of a gland of similar appearance in Haminoea and other atyiid opisthobranchs and in other genera of the Aglajidae. In these forms the eggs are individually encased. However, in Pupa and Bullina, in which each egg is not encased, I found no sign of this gland.

No fertilization chamber is present but it is probable that both exogenous and endogenous sperm use the sperm duct from the opening of the albumen gland to the genital vestibule, eggs being fertilized at the opening of the albumen gland. It is possible that the distal region of the small spermoviduct, from the sphincter to the albumen gland, could function as a fertilization chamber. From the capsule gland, eggs are coated with mucus and deposited in a spherical egg mass attached either in sand or among coralline turf by a long thread (Fig. 6B). Specimens of Melanochlamys cylindrica are found laying eggs from late June to the end of October, the height of activity being in September and October. Normally they were only found copulating in pairs (Fig. 6A) with the partner acting as male wedging its head between the posterior shield and the foot, the penis on the right of the head being everted by blood pressure and inserted in the genital vestibule of the other partner. However, when large numbers are collected during this period and placed in a small container, chains of up to 10 copulants occur.

NERVOUS SYSTEM

The detailed arrangement of the nervous system can be seen in Figs. 7 and 8. The nerve collar lies around the anterior end of the buccal bulb, long commissures linking the pairs of pedal and cerebral ganglia. The pleural ganglia are joined to the respective cerebral ganglion and separated from the respective pedal ganglion by a short connective. The supraesophageal ganglion is joined to the right pleural ganglion and gives rise to a long pallial nerve running back in the body cavity to the right anterior edge of the mantle cavity alongside the gill. Here, it branches (Fig. 7C), one short nerve ending in a pallial ganglion innervating the heart and the gill, and another nerve branching to the kidney, the upper raphe, and other parts of the mantle. On the posterior floor of the body cavity the subesophageal, visceral, and genital ganglia lie joined together. From the visceral ganglion a large nerve runs back to supply the lower raphe, the columellar muscle, and the posterior end of the mantle region. The genital ganglion, an extension of the visceral ganglion, gives rise to three branches, two innervating the genital gland mass and the third running up and along the mantle.

There are eight major pedal nerves innervating the foot and body wall. The origins of each

of these nerves and the pattern of branching (Fig. 7A) are reasonably constant both within each species and within the genus. The cerebral nerves (C_1) which innervate the upper anterior packed radiating nerves in the anterior region of the body (Fig. 8). A group of large thick cords (H) supply the Hancock's organs and above them are a number of thin branching nerves (C_1) which innervate the upper anterior edge of the headshield. The mounds of sensory bristles are innervated, on each side, by a thick branching nerve, called here the labial nerve (L.N.). The otocysts, one sitting on each pedal ganglion, are innervated from the cerebral ganglia.

DISCUSSION

Of the 90 or so described species of the Aglajidae most have been characterized by the shape of the shell and the external body features (often after preservation). None of the genera of this family have been defined adequately and various authors have different interpretations of what constitutes the genera Aglaja Renier, 1807, Chelidonura A. Adams, 1850, and Navanax Pilsbry, 1895 (Bergh, 1900, 1905, 1907; Burn, 1966; Eliot, 1903; Marcus and Marcus, 1960, 1966; Rudman, 1968; White, 1945). The purpose of the present study is to define adequately and describe the genus Melanochlamys. The other genera of the family will be defined separately; of these, one account will contain a full comparison of the genera of the Aglajidae.

In Cheeseman's original description of the genus Melanochlamys (1881), he differentiated the genus from Aglaja on the external form of the body noting that in Melanochlamys "the side-lobes of the foot [are] closely appressed to the sides of the animal, and [are] not spreading." In live material it is possible to distinguish members of this genus immediately by the shape of the body. The body is usually cylindrical, the parapodia small and tightly held against the side of the body, the posterior end of the headshield rounded sometimes with a small median indentation. No processes are developed from the rear of the posterior shield although there is usually a median notch. In the four species

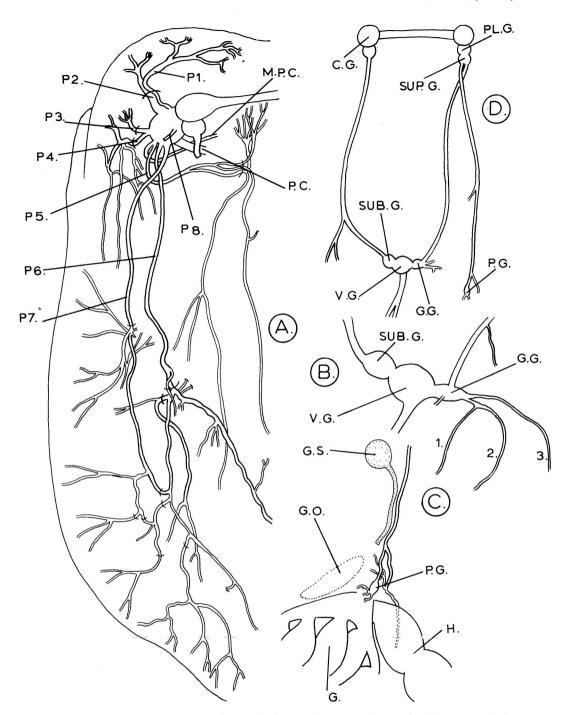


Fig. 7. Nervous system: A, Melanochlamys cylindrica, pedal nerves of the left side; B, M. cylindrica, pos-

terior ganglia; C, M. queritor, pallial region; D, M. cylindrica, central nervous system.

SYMBOLS: C.G., cerebral ganglion; G., gill; G.G., genital ganglion; G.O., genital opening; G.S., gametolytic sac; H., heart; M.P.C., minor pedal commissure; P., pedal nerves; P.C., pedal commissure; P.G., pallial ganglion; PL.G., pleural ganglion; SUB.G., subesophageal ganglion; SUP.G., supraesophageal ganglion; V.G., visceral ganglion.

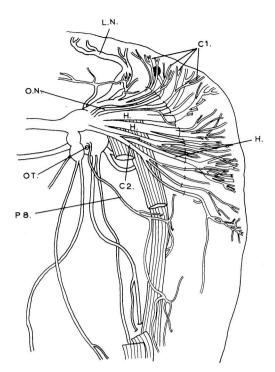


FIG. 8. M. cylindrica, right cerebral nerves. SYMBOLS: C., cerebral nerves; H., nerves to Hancock's organ; L.N., labial nerve; O.N., optic nerve; OT., otocyst; P., pedal nerves.

studied, *M. cylindrica* is totally black, *M. lorrainae* ranges from white to a mottled grey, *M. queritor* is black with white anterior patches, and *M. diomedea* is mottled grey or brownish black (Steinberg and Jones, 1960). *Aglaja diomedea* illustrated by MacFarland (1966, Pl. 2, Fig. 4) is in fact *A. ocelligera* (Bergh, 1893). Other species which I consider belong to this genus will be listed later. In all cases they also fall into this color range. The shell is also characteristic, being small, strongly calcified, and curved.

The large rigid buccal bulb is not eversible as in the other genera, and the tubular nature of the albumen-capsule gland complex, the short duct to the exogenous sperm sac, and the form of the penis are characteristic. Illustrations of the whole living animal of a number of species which probably belong to this genus appear in the literature. They are:

Aglaja dubia O'Donoghue, 1929; South Africa. Aglaja ezoensis Baba, 1957; Japan.

Aglaja henri Burn, 1969; Southeastern Australia

Aglaja nana Steinberg & Jones, 1960; California.

Aglaja seurati Vayssière, 1926; Mediterranean.

MATERIAL

Melanochlamys cylindrica was collected commonly around Auckland on coralline-covered rocky reefs. Specimens of M. queritor from Pt. Lonsdale, Victoria, Australia, were made available by Mr. R. Burn and M. diomedea from Morro Bay, California, by Mr. G. MacDonald. M. lorrainae is uncommon and a few specimens were collected at Whangateau Harbour on the east coast just north of Auckland and at Parengarenga Harbour in the extreme north of New Zealand.

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