

A Preliminary Study of the Land Operculate *Murdochia pallidum* (Cyclophoridae, Mesogastropoda)

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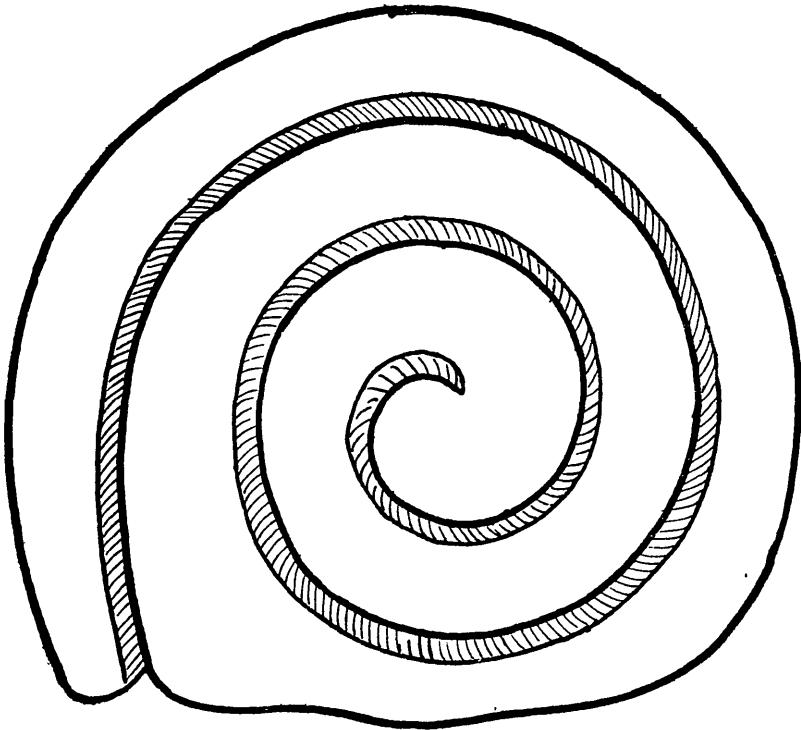
Summary

THIS paper gives a detailed description of the digestive and reproductive systems of the New Zealand land operculate *Murdochia pallidum* (Family Cyclophoridae), with a discussion on the morphological changes involved in the transition from the sea to a land habitat. The Cyclophoridae have accomplished the transition from the sea to a land habitat with relatively few modifications of their primitive structure.

THE Cyclophoridae represent one of several groups of terrestrial molluscs that have evolved from the marine gastropods belonging to the Sub-class Prosobranchiata. They are wholly distinct from the later-derived pulmonate stock, remaining much more generalised in the structure of the animal, and being conveniently referred to collectively as the "land operculates." Three such families are represented in the New Zealand fauna, the Hydrocenidae, which originated among the Neritacea; the Cyclophoridae; and the Realiidae. The two last-named families are generally held to have arisen from littorinid-like marine ancestors; they are probably only distantly related, though by Thiele (1935) the two groups, together with a long list of other terrestrial mesogastropods are loosely associated in the Stirps Archaeotaenioglossa. Of the structure of the Cyclophoridae we have little detailed knowledge, although from Bouvier's picture (1882) of the nervous system of *Cyclophorus tigrinus*, with persistent ladder-like pedal ganglionic cords, it has long been inferred that they are highly primitive among mesogastropods. The New Zealand members of the Cyclophoridae belong to the genus *Murdochia*, and are all of small size, seldom exceeding 5 mm. in length. The family has a wide distribution in S.E. Asia and the East Indies, Central America and the West Indies; some of the tropical species are of temptingly large size, and would be especially suitable for the detailed work on living gut and genitalia, which will be required before a confident assessment of the group is able to be made. But in view of the present lack of anatomical work, and the interest of the genus *Murdochia* among neozelanic land mollusca, it was felt that the following observations would prove of some value. It is hoped in a later paper to expand the present account, especially as regards reproductive activities, and also to provide a description of the New Zealand genera *Hydrocena* and *Realia*.

Material of *Murdochia pallidum* was dissected alive after removal of the shell, fixed in Bouin's and dissected preserved, also sectioned at 8μ and stained in Delafield's haematoxylin and Van Gieson's picrofuchsin. Mr. C. B. Trevarthen kindly collected several batches of living *Murdochia*, and his assistance is gratefully acknowledged. The writer is also indebted to Dr. W. D. Reid, of the Plant Diseases Division, D.S.I.R., Owairaka, Auckland, for carrying out a culture trial with the spirochaetes from the stomach.

The described species of *Murdochia* are 13 in number (Powell, 1946) and seem to have a rather localised distribution in New Zealand rain-forests. The species most commonly encountered near Auckland is *M. pallidum* (see Suter, 1913); it is 5 mm. in length, 3.25 mm. in greatest diameter, turbinate, conical, horny brown in colour, with the operculum silvery-white (Text-fig. 1). The most typical habitat is in the deep, ensheathing leaf bases of *Rhopalostylis*, and also of *Collospermum* and *Freyzenetia*. Pfeiffer's term "cryptozoic" admirably describes the mode of life of these animals, avoiding the light and seeking moisture. This fauna includes a wide range of small invertebrates, such as pulmonate snails (flamulinids), slugs (*Athoracophorus*), arachnids and myriapods, and insects—especially coleoptera and collembola. Most of these are vegetarians, taking into the gut fragments of food of varied detrital nature, including pieces of decaying leaves and wood pulp, and much unrecognisable plant material. In many cases, including *Murdochia*, a high proportion of the food is made up of fungal mycelia scraped off the moist substratum with the radula. *M. pallidum* seems to be more or less a specialist in its diet, and a similar preference for fungi is reported in the case of the tropical American cyclophorids (de la Torre, Bartsch, and Morrison, 1942).



TEXT-FIG 1—The operculum, upper surface.

The animal when removed from the shell is found to be quite unspecialised in its structure. The foot is long, truncate, and squarish in front, rounded behind. The margin of the sole is surrounded by a wide strip of black-pigmented epithelium, thrown into small, regular, puckered folds; the central tract of the plantar surface is covered with short-celled smooth epithelium, deeply enfolded in the middle of the sole to give exit to the secretion of the pedal gland. Other sources of mucous secretion are present, in the mantle cavity—a broad hypo-

branchial gland extending along the right side of the pallial roof, unaltered in histological structure from that of marine prosobranchs; and a narrow zone of sub-epithelial gland cells encircling the mantle just within its margin; these probably serve to seal the closed operculum, during prolonged withdrawal of the animal into the shell. The colour of the exposed parts of the head and foot is greyish-black, and the head, snout and short, paired tentacles are jet black. The pallial wall is divided into regions, the respiratory area occupying the left half, the hypobranchial gland to the right, and behind it the yellowish renal sac. The visceral mass is largely occupied by the digestive gland, composed of a mass of stout reddish-brown lobules, investing the stomach, which is seen from the surface as a translucent white sac. The gonad is quite large, forming a spacious undivided sac, applied to the convex surface of the digestive gland. It is white in the male, deep yellow in the female.

THE DIGESTIVE SYSTEM

The snout is deeply cleft at the tip, and the mouth is a vertical slit opening directly into the buccal bulb, which occupies most of the cephalic haemocoel. The anterior half of the bulb is equipped with a pair of chitinous jaws, triangular plates close together in the dorsal mid-line, diverging ventrally, and secreted by the buccal epithelium. Their anterior edges project sharply from the buccal wall, serving to grip firmly an object during abrasion by the protractor strokes of the radula. Each jaw is broken up by diagonal striations into a series of lozenge-like teeth, slightly overlapping and with their acute tips forwards. The odontophore is short and wide, supported by a single median cartilage formed of large squarish or spherical vacuolated cells. The cartilage is deeply excavated behind, forming a chair-like depression through which the radula passes. The radular caecum is long and slender, passing backwards along the ventral side of the oesophagus, and becoming involved in the torsion of the gut, so that its slightly expanded tip finally curves around to the right side. The median and two lateral teeth are of the taenioglossan rasping type, the former with three bluntly rounded cusps, the latter with a row of five. The two pairs of marginals are sharp, curved and prehensile. The salivary glands are minute, sending forward a pair of well-defined ducts embedded in the connective tissue of the folds bounding the dorsal oesophageal channel. The salivary cells are stained uniformly purple with haematoxylin, having no apparent enzyme contents and probably serving merely for secretion of mucus. The oesophagus preserves no trace of its lateral glandular pouches, proceeding straight to the stomach, as a uniformly narrow, ciliated tube. Mucus cells are everywhere abundant, and the ciliated cells are largest along the broad dorso-lateral folds, keeping up a strong aboral current.

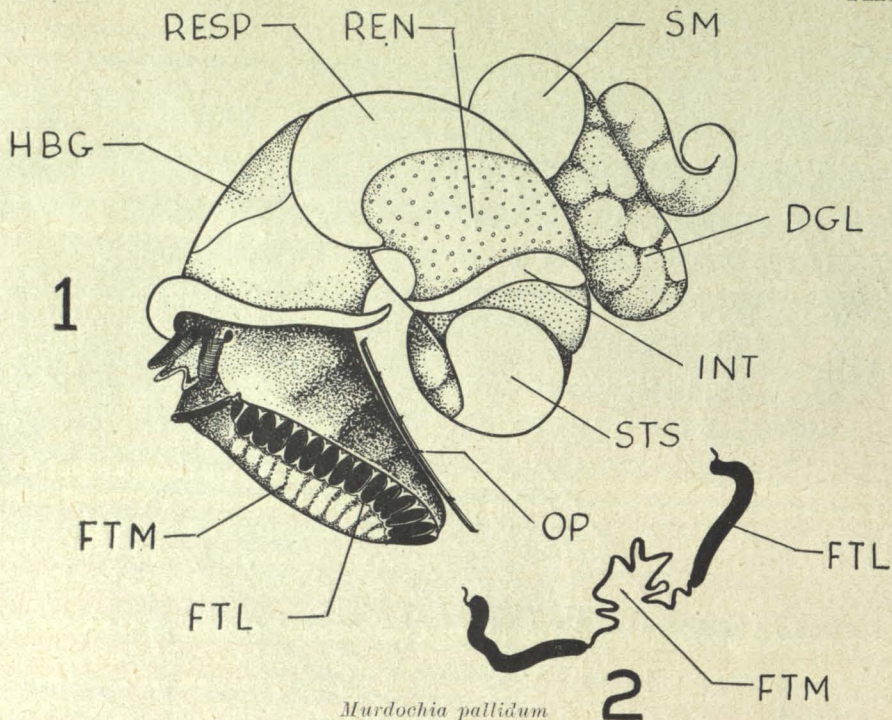
The stomach in *Murdochia* is a rather long tubular sac curved around the first visceral whorl. The oesophagus opens into its rounded posterior end, and the intestine issues from the narrow extremity of the stomach in front. The structure of the sac, is of the simplest type, showing two histological regions. The longer posterior portion is lined with a thin transparent cuticle, save for a strip of short-celled ciliated epithelium which runs forward in a groove along the ventral wall. This groove originates at the posterior tip of the stomach from two or three folds of ciliated epithelium leading from the mouth of the oesophagus. The anterior third of the stomach is slightly constricted off from the cuticulate portion, and forms a small thimble-shaped sac, meeting the posterior chamber at an obtuse angle. Its lining epithelium is of the densely ciliated type, characteristic of the style sacs of mesogastropods and lamellibranchs, the bristle-

like cilia reaching as much as two-thirds the height of the stout columnar cells. Along the ventral wall of this sac, the shorter ciliated longitudinal tract is continued from behind, interrupting the denser cilia, and passing imperceptibly into the intestinal epithelium in front. There is a single digestive diverticulum, opening just behind the ciliated sac, on the ventral wall of the stomach, close alongside the longitudinal ciliated tract. Its mouth is surrounded by ciliated cells whose currents appear to aid the entry of fine particles, and perhaps also the outward passage of egesta. At the angle of the stomach and along the margin of the ciliated groove, the cuticle becomes heavily thickened, forming a stouter ridge representing the gastric shield of style-bearing molluscs.

In the living *Murdochia*, the stomach is filled with a viscid mucous rope, continuous behind with the less coherent food string entering from the oesophagus, and passing in front directly into the narrower string occupying the lumen of the intestine. The mucous contents of the stomach are thus divisible into two portions. The ciliated anterior chamber is filled with a short, opaque rod, whitish and quite free from food particles. This is inserted behind into a longer cord of mucus, permeated with dark-coloured ingested material, and extending through the rest of the stomach. It is constantly augmented by the inward passage of particles from the oesophagus. In addition to a good deal of unrecognisable detritus, material of plant origin such as leaf fragments, broken fern sporangia, and—in particular—numerous short segments of fungal mycelia, are almost always present. *Murdochia* must be to some extent non-selective, using the radula for scraping up the rich nutritive film overlying the damp surfaces within the leaf sheaths and similar locations. The general movement of stomach contents is apparent from figure 5.

The chief impetus to particles is conveyed by the colourless anterior portion of the mucous rod, which is rotated by the transverse beat of the "style sac" cilia. This has the effect of rotating the whole attached mass of food contents within the cuticulate chamber, while in addition, the shorter cilia of the ventral tract evidently impart sufficient forward motion to carry the contents slowly towards the intestine. This movement must be very gradual, permitting of sufficient time for such preliminary digestion as may occur while the mucous rod is rotated within the stomach. As suggested by Graham (1939) in the case of the land operculate *Pomatias elegans*, the long posterior chamber of the stomach evidently serves as a storage region, and—though feeding seems to be almost continuous in *Murdochia*—may help to even out irregularities in the flow of food through the stomach.

It is evident that the functioning of the stomach in *Murdochia* typifies what must have been the simplest and earliest condition of the style sac form of molluscan stomach. The mass of whitish mucus within the style sac—if we may call it such—is an example of what the writer has called elsewhere (1951b) a "protostyle." Its chief role appears to be to transmit rotatory movement, imparted by the style sac cilia, backwards to the rest of the stomach contents—a function which is of obvious importance in the activity of the stomach. By this means, ingested food is drawn through the stomach at a slow, uniform speed by the action of the very robust cilia, concentrated in the style sac. Stomach contents are thoroughly admixed with such digestive enzymes as may be present. The smallest, finely divided particles are repeatedly rotated alongside the opening of the digestive diverticulum, into which they are received, in part by ciliated action, in part probably by compression movements of the sparsely muscular



Murdochia pallidum

FIG. 1—The entire animal, removed from the shell, viewed from the left side.

FIG. 2—Diagram of transverse section of sole of foot.

DGL, digestive gland; FTL, lateral tract of sole; FTM, median tract of sole; HBG, hypo-branchial gland; INT, intestine; OP, operculum; REN, renal organ; RESP, respiratory surface of mantle; SM, posterior (cuticulate) portion of stomach; STS, 'style' sac.

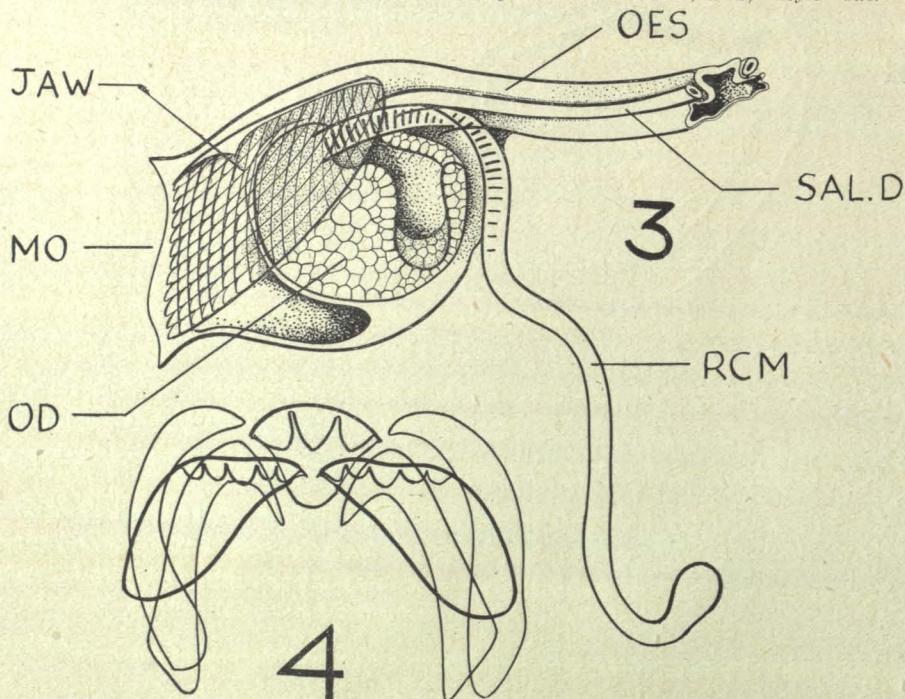
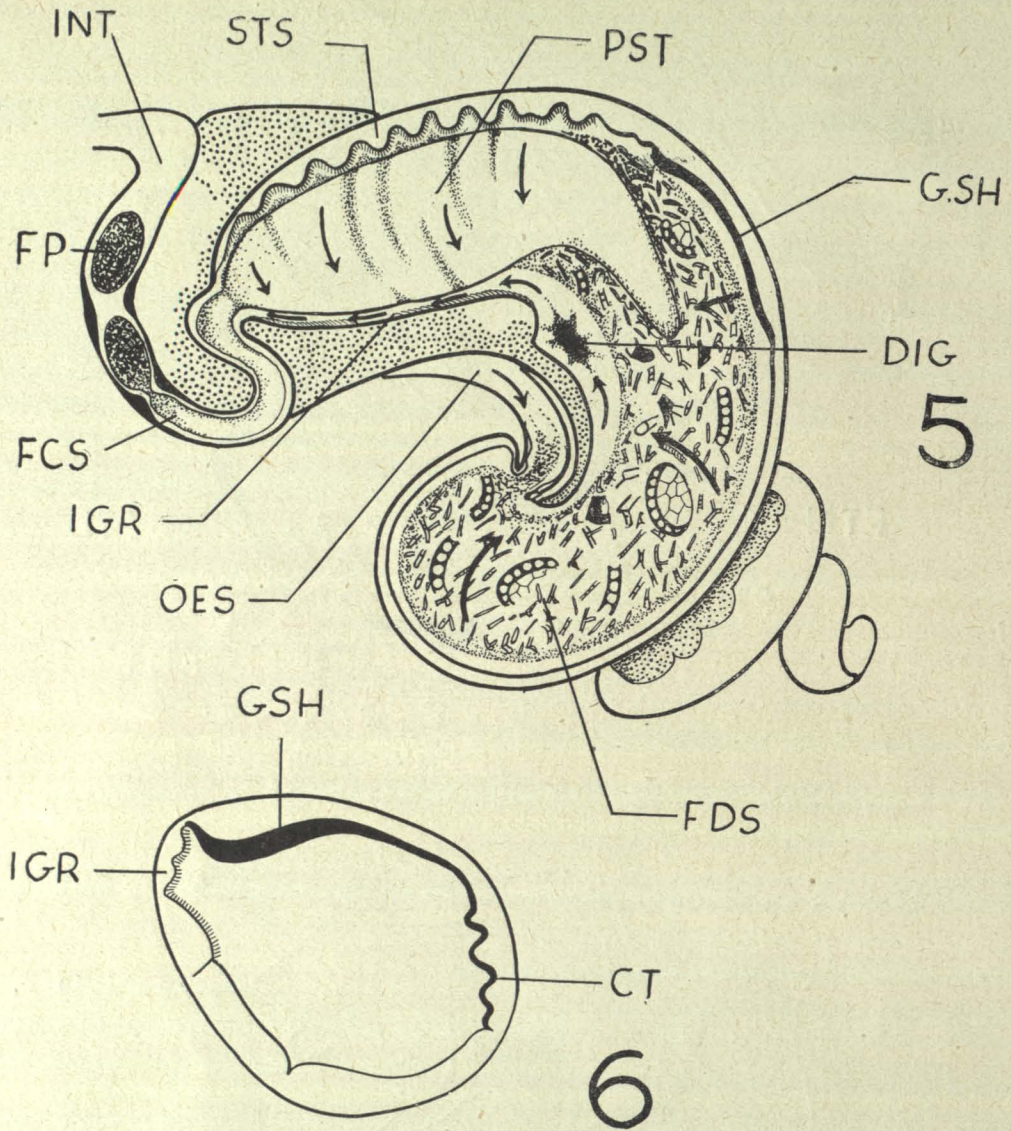


FIG. 3—The buccal bulb, viewed as a transparent object from the left side, showing the disposition of jaw, radula, and odontophoral cartilage.

JAW, left jaw plate; MO, mouth; OD, odontophoral cartilage; OES, oesophagus; RCM, radular caecum; SAL.D, left salivary duct.

FIG. 4—A single row of radular teeth.



Murdochia pallidum

FIG. 5—The stomach in longitudinal section, somewhat diagrammatic, showing the disposition of contents and the arrangement of ciliary currents.

FIG. 6—Transverse section of stomach, through the region of the gastric shield, just behind the digestive diverticulum.

CT, cuticle; DIG, digestive diverticulum; FCS, faecal string; FDS, food string within the stomach; FP, faecal pellet; GSH, gastric shield; IGR, intestinal groove; INT, intestine; PST, protostyle; STS, "style" sac.

stomach wall. In addition, the larger, coarse particles near the periphery of the food string are swept across the longitudinal groove (IGR) and caught by its cilia to be rapidly carried forward into the intestine. Though the clear mucus of the protostyle must also be slowly carried into the intestine, where it forms the matrix of the faecal string, yet the strongest forward flow is along the ventral ciliated groove. This forms a channel whereby particles too large to enter the digestive diverticulum are able to by-pass the protostyle, and find their way directly into the intestine. The longitudinal groove in *Murdochia* is the sole representative of the ciliary sorting area in this snail. *Pomatias*, similarly, shows an almost total reduction of the sorting plicae typical of the stomachs of marine prosobranchs. The mode of feeding of marine microherbivorous gastropods, generally on a continuous stream of poorly sorted bottom deposits, is a habit calling forth a high development of sorting and grading mechanisms within the stomach. In terrestrial prosobranchs, such as *Murdochia* or *Pomatias*, the problem is not so much one of sorting, as of breaking up larger fragments of plant material and rendering them finally suitable for absorption by the digestive gland epithelium.

According to Graham (1939), the opaque mucous contents of the style sac in *Pomatias* constitute a true crystalline style—this is gradually thrust into the stomach towards the gastric shield, by a backwardly directed ciliary current within the style sac. No such current could be detected within the much smaller stomach of *Murdochia*; from the whole appearance of the mucous rod, including its direct merging into the faecal string, we may conclude it is not properly speaking a crystalline style. Amylase tests are not mentioned in Graham's account of *Pomatias*. In *Murdochia* the spotting tests for amylase were difficult to carry out satisfactorily because of minute size, but gave negative results. No doubt the chief function of the protostyle in *Murdochia* is its mechanical role of rotating the stomach contents.

It is unlikely that any digestion takes place in *Murdochia* in the part of the gut anterior to the stomach. Particles of food, including fragments of fungal hyphae, are too large to enter the digestive diverticulum intact, and recognisable hyphal or other food particles were never detected either within the lumina of the digestive tubules, or within the cytoplasm of the digestive cells. The structure of the digestive gland is in no way dissimilar from that of other phytophagous prosobranchs, or lamellibranchs already investigated; ingestion of fine particles evidently occurs, followed by intracellular digestion. The question arises, how—and to what extent—are large particles, such as fragments of hyphae, first broken up within the stomach? There is little evidence that mechanical trituration occurs. The muscle layer of the stomach wall is not conspicuous, and the cuticle is for the most part not robust. It is possible that particles are pressed, by the rotation of the prostyle, against the stout ridge of cuticle (GSH) and thus become slowly comminuted, perhaps assisted by a squeezing action of the stomach wall as suggested by Yonge in the protobranchiate bivalves (1939).

Further, in the cyclophorids, such as *Murdochia*, which feed to a large extent on fungal mycelia (see also de la Torre *et al.*, 1942), a high proportion of cellulose-like substances must be included in the diet. If this carbohydrate is to be successfully utilised, a digestive problem is presented that has in only a few cases been successfully surmounted by molluscs. A possible clue to the means of cellulose break-down is obtained by microscopic examination of the opaque mucoid mass of the style sac. The colloidal matrix is here invariably packed with long, highly

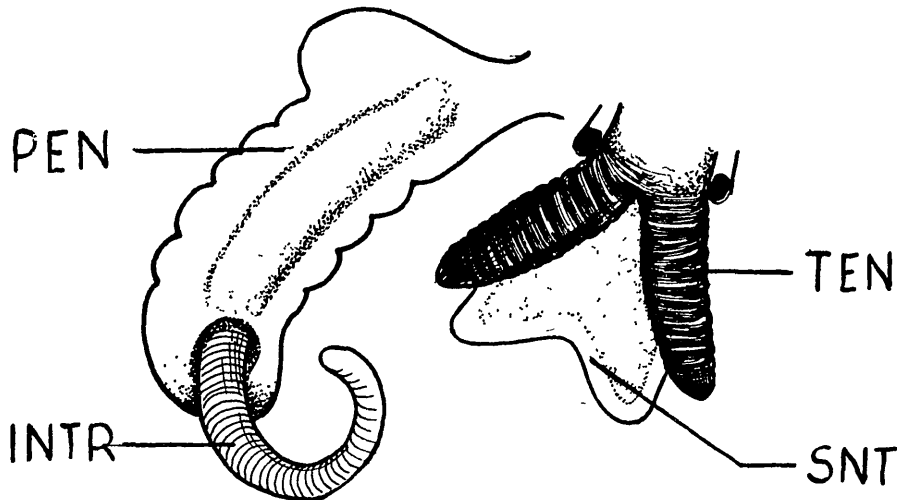
motile spirochaetes, progressing through the medium in constant vibratile movement, and especially densely concentrated at the boundary between clear mucus and food material. It may be suspected that these organisms, occurring in pure state with such regularity, are not without some role in the digestive process of the mollusc.

Large spirochaetes assigned to the genus *Cristispira* have been briefly recorded as living "commensally" in the stomachs and crystalline styles of a fairly long list of lamellibranchs. Yonge (1926) refers to the presence of spirochaetes in the style substance of *Ostrea edulis*, while Breed, Murray and Hitchens (1948) list occurrences in no less than 13 families of bivalves. There would appear to be no previous record of spirochaetes from a gastropod style sac; nor has any explanation been hazarded as to the role they may play. Results of great interest may be expected from further inquiry into the spirochaetes of style sacs, especially from a survey of their occurrence among molluscs, and their powers of breaking down complex carbohydrates. An analogy might be suggested with *Spirochaeta cytophaga*, a free-living cellulose-digesting organism, whose activity has been investigated by Walker and Warren (1938). As regards the snail, *Murdochia*, some amount of simpler carbohydrate is probably available within the lumen of the gut for direct absorption, after external bacterial or autolytic breakdown of cellulose and other plant substances; but the problem of the fungal hyphae—so conspicuous in stomach contents but apparently quite absent in the faecal pellets—remains to be solved.

The digestive diverticula in *Murdochia* contain both digestive and excretory cells. The former are wedge-shaped or clavate, filled with granular cytoplasm, consisting of colourless refractile particles easily liberated by cell maceration. Ingested material appears to be taken up in an extremely fine state of division, and the digestive cells contain little or no coloured egesta for return to the stomach. Enzyme droplets are not detectable.

The excretory cells are broad-based and pyramidal, brown-staining with Van Gieson's. They apparently extract chlorophyllous or other absorbed pigments from the blood, passing their contents to the lumen in the form of large droplets, sometimes equipped with little tails, or drumstick-shaped, as they emerge from the cell. The intestine is of simple structure throughout, describing a short S-shaped course after leaving the stomach, and crossing to the right side around the edge of the renal sac. The rectum is slightly wider (70μ in diameter).

Each faecal pellet occupies the whole width of the intestine, and is stoutly ovoid in shape, being nipped off from the mucous string by repeated peristaltic constrictions of the intestinal wall, which is provided with a narrow coat of circular muscle, several fibres thick. Muscular action plays the most important part in faeces formation, both in *Murdochia* and evidently in mesogastropoda in general. While it is broadly true—as stated by Yonge (1936 and elsewhere)—that the gut in microphagous prosobranchs performs little muscular action, yet the small but definite peristaltic movements of the intestine have generally been overlooked. As well as in *Murdochia*, peristalsis has been observed by the present writer in *Struthiolaria* (1951), *Suterilla* (unpublished) and in *Serpulorbis* (1951a). *Murdochia* is reminiscent of marine mesogastropods in the care taken for the consolidation of faecal pellets, as a precaution against the fouling of the pallial cavity in gill-breathing animals. Mucus is liberally secreted by fusiform gland cells, interspersed between the narrow ciliated cells of the intestinal epithelium,



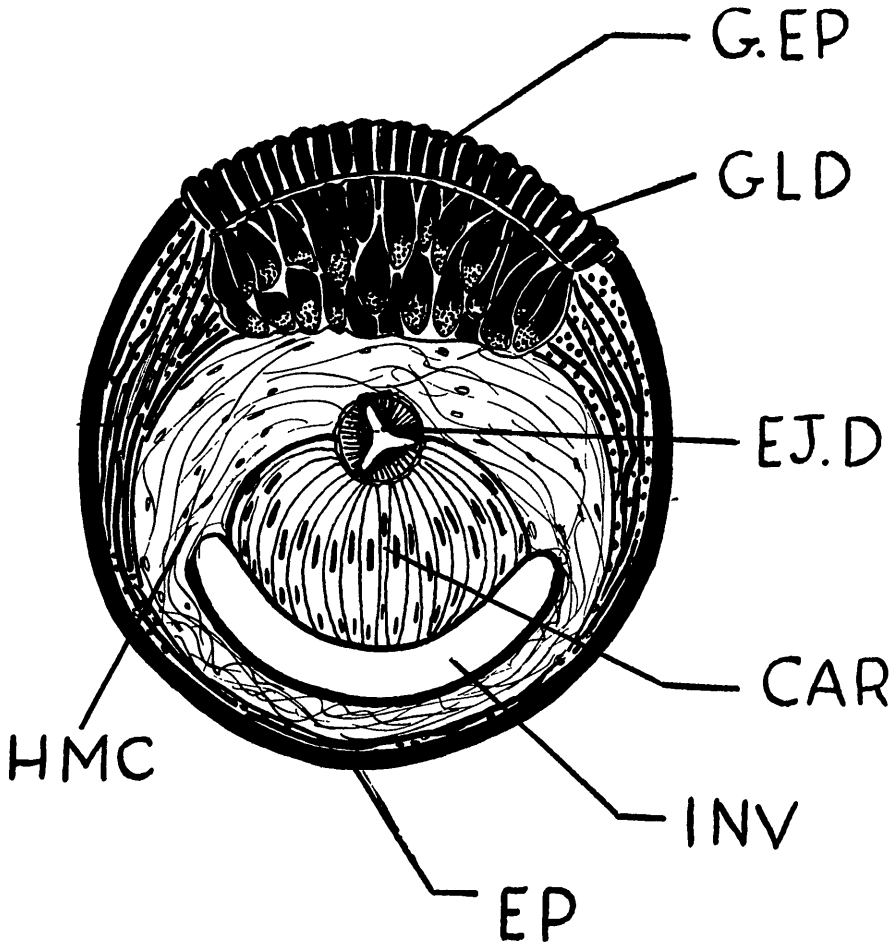
TEXT-FIG. 2.—The head, snout and penis.

INTR, terminal invaginable intromittent portion of penis. PEN, basal portion of penis, SNT, snout, TEN, cephalic tentacle

REPRODUCTIVE SYSTEM

The structure of the genitalia in *Murdochia pallidum* may be outlined briefly. In the male, the vas deferens is a narrow tube closed throughout its whole length, as far as the tip of the prominent cephalic penis. It leaves the thin-walled testis sac as a lightly coiled, non-glandular tube, which emerges ventrally to the renal organ, to run the whole length of the pallial cavity, just below the rectum, along the attachment of the mantle to the trunk musculature. The closure of the pallial portion of the vas deferens—primitively an open ciliated groove—is to be regarded as correlated with the terrestrial habit. The wall of the pallial vas deferens is thickened and glandular, as far forward as the base of the penis, its lumen narrow, rounded or slightly flattened. This portion of the male duct evidently performs the role of a "prostate" gland: its lining cells are stoutly columnar, filled with minute, non-staining secretion granules, and having rounded, basal nuclei. Regularly alternating with the glandular cells are narrow, darkly compressed, ciliated cells, about half the length of the secreting cells, and with dark-staining elongate nuclei. Their distal surfaces are narrow, and cilia are borne also by the glandular cells, the whole of the lumen being uniformly lined. The penis is attached to the head immediately behind the right tentacle, forming a stout muscular column, flattened or cylindrical, with strong annular rugae, and yellowish-white in colour. It is generally reflected back within the pallial cavity, lying transversely across the trunk, or along the right side. It is perforated throughout by a narrow ejaculatory duct, continuous with the vas deferens, proceeding to the distal tip of the penis, which becomes narrow and cylindrical, and forms the intromittent part of the male organ. This structure is freely extensible, and can be withdrawn into the haemocoelic blood space enclosed by the stouter basal portion of the penis (Fig. 3.) It can be strongly protruded by the pressure of the muscular wall of the basal part of the penis on the blood contained in the haemocoelic space. The terminal intromittent portion of the penis is supported by a flexible rod of elastic connective tissue, which runs alongside, and finally extends completely around the ejaculatory duct. It is made up of long, vacuolated cells, radially inserted at the base of the

epithelium of the ejaculatory duct. The basal part of the penis has a stout layer of muscle fibres, circular and longitudinal elements intermingled, and its external surface is traversed along one side by a broad tract of glandular epithelium, mucus being produced by rounded, subepithelial secretory cells, sending up narrow ducts between the cells of the columnar epithelium.



TEXT-FIG. 3—Transverse section of the penis, with the terminal intromittent portion invaginated.

CART, cartilage-like supporting rod; EP, external epithelium of the penis; EJ.D, ejaculatory duct; G.EP, tract of glandular epithelium, GLD, subepithelial gland cells; HMC, haemocoel occupied by sparse connective tissue, INV, Invagination

The female genital duct is divisible into two portions—an extremely narrow, much convoluted posterior part, leading forward from the ovary to open into the stouter, glandular-walled pallial oviduct. The functions of the pallial oviduct have not yet been properly ascertained. It appears to combine the secretory role of both the albumen gland and the capsule gland as recognised by Fretter (1946) for marine prosobranchs. But the two regions are not structurally separable in *Murdochia*.

On leaving the ovary, the posterior portion of the female duct is at first very narrow, thin-walled and translucent, the cells lightly staining, and with long cilia; the duct is here strongly distensible with the passage of eggs. A little further forward the proximal oviduct becomes thrown into a number of coils and closely convoluted, opaque white in appearance. It is here noticeably muscular, its coat of circular fibres being well developed and the epithelial lining being thrown into 4-5 longitudinal folds by cell height differences. The epithelium contains plump, ovoid gland cells, with basal nuclei and mucous contents staining lightly in haematoxylin. Ciliated cells are also present, especially at the crests of the folds, centrally constricted and with rod-like central nuclei. The posterior-most part of the coiled oviduct is of different structure from the rest, and functions as a receptaculum seminis. The epithelium here is not folded, and the cells are of one type only, regularly columnar, clear or lightly staining, with a single row of basal nuclei. A coating of close-pressed sperm heads is found attached to the distal surfaces of the cells, the tails occupying the middle of the lumen. It is presumably in this part of the duct that fertilisation takes place before the addition of glandular secretions to the egg.

The pallial oviduct runs forward immediately below the rectum. It is pale yellow in colour, thick-walled and laterally compressed, thrown into a succession of deep transverse folds which project into the lumen as ridges of the glandular wall. The epithelium is extremely regular, the gland cells tall and narrowly columnar, with basal nuclei, and with small triangular or wedge-shaped ciliated cells inserted between their tips. The character of the secretion changes about halfway along the duct. Posteriorly the cells are filled with rows of large, finely granular vesicles or spherules, each occupying the whole width of a cell, and staining light pinkish-brown with Van Gieson's. Further forward, the secretion is in little droplets, much smaller, and staining deeper purplish, with a stronger affinity for haematoxylin. The aperture of the pallial oviduct lies far forward, just below the anus, and near the opening the histology changes. The wall becomes somewhat folded by differences in the length of the cells. The ciliated cells are longer with their cilia more prominent, and the contents of the gland cells—in the basal two-thirds—are tiny refractile spherules, staining deeply black with haematoxylin.

DISCUSSION

The Cyclophoridae have accomplished the transition from the sea to a land habitat with relatively few modifications of their primitive structure. They have occupied a peculiarly favourable ecological niche, and like all terrestrial molluscs—save a few xerophilic pulmonates—they are confined to conditions of high humidity. The retention of the operculum closing the shell aperture prevents water loss. The air-filled pallial cavity remains widely open anteriorly and there is, properly speaking, no development of a lung, respiration taking place merely through the smooth vascularised epithelium of the pallial roof; gill filaments are lost and there are no folded respiratory lamellae. The lumen of the renal organ is small and restricted; its opening into the pallial cavity was not traced in sections, and there is no forward prolongation running alongside the rectum to form a "ureter" leading to the pallial margin, as has become the case in pulmonates. The lining cells of the renal sac are filled with yellowish granules—it would be of interest to know whether the animal has become uricotelic, and whether there is a periodic discharge of renal contents into the mantle cavity, or whether, as seems more probable, the renal organ functions as a kidney of

accumulation. The mode of reproduction has not yet been fully worked out, but the animals are bisexual and the genital ducts relatively simple, as in the lower prosobranchs in general. The landward migration of marine gastropods has become possible only in those that have evolved about the rhipidoglossan level, and in which the gametes are no longer discharged by way of the right kidney. Fertilisation now becomes internal, and a closed pallial genital duct has been developed. In the males the sperms are conducted forwards by a closed channel to a well-developed cephalic penis; in the female, a closed glandular oviduct, derived from secretory tissue of the pallial wall, runs forward to open alongside the rectum.

In *Murdochia*, the alimentary canal combines a primitive structure with certain specialised features. The absence of oesophageal pouches or other sources of enzyme secretion within the oesophagus is evidently an advanced feature, paralleling the condition described in the specialised *Turritella* (Graham, 1938). The salivary glands are likewise devoid of enzyme cells, and *Murdochia* would appear to have been singularly improvident in abandoning all its sources of extra-cellular digestive enzymes, probably before the landward migration of the family. Whether or not the spirochaetes in the protostyle have taken on an accessory role in digestion remains to be determined. The small size of the animal—as well as its primitiveness—may be a contributing factor to the simplicity of structure of the stomach. The loss of the ciliary sorting area is probably correlated with the terrestrial habit and the changed nature of the food. The primary function of the stomach is no longer sorting, but the breaking down, whether by digestion or mechanically, of particles of plant material still too large for entry into the digestive diverticulum. The extreme posterior position of the opening of the oesophagus into the stomach is to be regarded—following Graham (1949)—as a highly primitive feature. In almost all other mesogastropods it has migrated some distance forwards towards the intestinal aperture. The long, backwardly directed sac in the stomach of *Pomatias* (Graham, 1939), *Littorina* (Graham, 1949), *Melarhaphé* and *Risellopsis* (present writer, unpublished), would appear to be directly homologous with the cuticulate chamber of the stomach in *Murdochia*, after the forward migration of the oesophagus, to open shortly behind the style sac—intestinal chamber. In *Murdochia*, the formation of firm, mucus-bound faecal pellets in the intestine is a relic of ancestry among marine prosobranchs, where the compacting of the faeces serves as a device for prevention of fouling of the respiratory water of the pallial cavity. In a terrestrial prosobranch it is probably equally necessary in the absence of a cleansing current passing continuously through the pallial cavity.

REFERENCES TO LITERATURE

1. BOUVIER, E. L., 1887. Systeme nerveux, morphologie generale et classification des Gastropodes prosobranches. *Ann. des Sci. Nat. (Zool.)*, 7, iii.
2. BREED, R. S., MURRAY, E. G. D., and HITCHENS, A. P., 1948. *Manual of Determinative Bacteriology*, Bergery, 6th Edn., London.
3. DE LA TORRE, C., BAERTSCH, P., and MORRISON, J. P. E., 1942. The Cyclophorid Operculate Land Molluscs of America. *U.S. Nat. Mus. Bull., Smithsonian Inst., Washington, D.C.*
4. FRETTER, VERA, 1946. The Genital Ducts of *Theodoxus*, *Lamellaria* and *Trivia*, and a Discussion on their Evolution in the Prosobranchs. *J. Mar. Biol. Ass. U.K.*, 26, 312-351.
5. GRAHAM, A., 1938. On a Ciliary Process of Food-collecting in the Gastropod, *Turritella communis* Risso. *Proc. Zool. Soc. London A*, 108, 453.
6. ——— 1939. On the Structure of the Alimentary Canal in the Style-bearing Prosobranchs. *Ibid., B*, 109, 75.

7. GRAHAM, A., 1949. The Molluscan Stomach. *Trans. Roy. Soc. Edin.*, 61, 737.
8. MORTON, J. E., 1951. The Ecology and Digestive System of the Struthiolariidae (Gastropoda). *Quart. Journ. Micr. Sci.*, 92, (1), 1-25.
9. ——— 1951a. The Structure and Adaptations of the New Zealand Vermetidae. Pt. 1. Genus *Serpulorbis*. *Trans. Roy. Soc. N.Z.*
10. ——— 1951b. The Role of the Crystalline Style. *Proc. Malacol. Soc. Lond.* (in the press).
11. POWELL, A. W. B., 1946. *New Zealand Shellfish*, Auckland, 2nd Edn.
12. SUTER, H., 1913 *Manual of the New Zealand Mollusca*. Govt. Printer, Wellington. (With Atlas of Plates, 1915)
13. THIELE, J., 1931. *Handbuch der systematischen Weichtierkunde*, I. Jena, Fischer.
14. WALKER, E., and WARREN, F. L., 1938. Decomposition of Cellulose by *Cytophaga*. *Biochem. J.*, 32, 1, 31.
15. YONGE, C. M., 1927. Structure and Physiology of the Organs of Feeding and Digestion in *Ostraea edulis*. *J. Mar. Biol. Ass. U.K.*, 14, 295-386.
16. ——— 1936. On Some Aspects of Digestion in Ciliary Feeding Animals. *Ibid.*, 20, 341-346
17. ——— 1939. The Protobianchiata Mollusca. a Functional Interpretation of their Structure and Evolution. *Phil. Trans. Roy. Soc., Lond. B.*, 230, 79.