

FORM AND FUNCTION IN THE  
EVOLUTION OF THE VERMETIDAE



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	Page
I. INTRODUCTION . . . . .	585
2. GENERIC REVIEW . . . . .	588
(i) Genus <i>Dendropoma</i> . . . . .	588
(ii) Genus <i>Petalconchus</i> . . . . .	597
(iii) Genus <i>Serpulorbis</i> . . . . .	603
(iv) Genus <i>Vermetus</i> . . . . .	608
3. EVOLUTIONARY TRENDS IN THE VERMETIDAE . . . . .	612
(i) The Apex . . . . .	615
(ii) The Adult Shell . . . . .	616
(iii) The Operculum . . . . .	617
(iv) Ciliary and Mucous Feeding and Related Adaptations . . . . .	618
(v) Reproductive system . . . . .	622
(vi) The Radula . . . . .	622
(vii) Phylogeny . . . . .	625
4. ABSTRACT . . . . .	628
5. ACKNOWLEDGMENTS . . . . .	629
6. REFERENCES . . . . .	630

## I. INTRODUCTION

AN awareness of the living animal is always important to the evolutionary morphologist : it is nowhere more so than in the mesogastropod family Vermetidae, which have lost all external traces of snail form and produce loosely coiled worm tubes welded to or embedded in the substrate. In a literal sense vermetids are tied to their environment and their adaptations to this new mode of life are peculiarly intimate and far-reaching. The study of structure as reflecting function was for long neglected in the Vermetidae. The pioneering papers are those of Boettger (1930) on mucous feeding in *Serpulorbis gigas*, and Yonge (1932) on ciliary feeding in an Australian species. They were followed by Yonge and Iles (1939), a brief description in MacGinitie & MacGinitie (1949), and Morton (1951a ; 1955).

Yet a study of adaptive morphology, however rewarding, is not in itself sufficient for an understanding of evolutionary history. Adaptive features are unreliable as guides to natural arrangement and the classifier must look for conservative characters unlikely to be too much influenced by evolutionary convergence, which becomes more frequent and confusing as the mode of life becomes more specialised. The conchologist must usually have the last word in taxonomy at the generic level, not only because shell characters are the most accessible to study in collections, but chiefly because the features in which he is interested are more likely to be immune from convergence due to similar modes of life. Till the present time vermetid

taxonomy has proceeded upon the evidence of the shell, usually in the absence of the apex and of the operculum. Compilers of faunas and check-lists have approached this family with a distaste evoked by no other, and have hastily left it after a decent minimum of provisional re-arrangement.

Dr. Myra Keen's paper (1961) has now given us the first firmly grounded generic classification of Vermetidae, on the basis of the coiling pattern, apex and operculum throughout the family. For the first time it is possible to consider the impact of adaptation to mode of life in validly drawn generic groups. At intervals from 1949 onwards I have had the advantage of correspondence and later of personal discussions with Dr. Keen. She has generously provided me with preserved animals and kept me in constant touch with the progress of her taxonomic studies. From investigation of the Vermetidae from our different points of view has now emerged a broad-based agreement in our ideas upon evolution and generic relationships.

The progress in vermetid classification during the last 30 years will be apparent on comparing Thiele's (1929) arrangement of the family with that possible today. Of two genera conservatively adopted by him, one, *Tenagodus (Siliquaria)*, has become the basis of another family with only a convergent resemblance to true Vermetidae. Into the Siliquariidae has passed also one of six subgeneric groups of Thiele's *Vermetus* s.l. (each more usually regarded as a genus)—namely *Stephopoma*; while a second of these six, *Vermicularia*, belongs close to the Siliquariidae, preferably in a separate family, Vermiculariidae. These two families show close affinities with Turritellidae.

Dr. Keen has recognised five genera in the family Vermetidae as now restricted, namely *Vermetus*, *Serpulorbis*, *Petaloconchus*, *Dendropoma* and the new genus *Tripsysha*. The last is monotypic, and gives recognition to the peculiar mode of coiling, in a closely wound hollow cone, of *Vermetus tripsysha* Pilsbry and Lowe, 1932, a form evidently closely allied to *Petaloconchus*. The four large groups have been adequately studied malacologically, and can be seen to make up a homogeneous and workable family, with a series of well-marked evolutionary trends.

The Vermetidae have no clear annectant features with any other group known at present. There is no reason to break up their loose association with the other families of Thiele's large and loosely defined Stirps Cerithiacea.

It is too early yet to give a definite account of vermetid functional morphology or evolution. My object here is to bring together what we at present know of the malacological features of each genus of Vermetidae, and of their adaptive peculiarities and possible evolution. In addition to living material of *Dendropoma (Novastoa) lamellosum*, *Serpulorbis aotearoicus* and *S. zelandicus*, I have examined preserved material of representative species, including several examples of each genus. For a few species, my material was crudely preserved, and in the crucial species *V. adansonii* was resuscitated after drying! Here it was a matter of being grateful for what facts I could cull; I have at least learned from experience to get the best from such specimens as I had. I shall not deal exhaustively with the anatomy of any one species here: it is hardly useful to attempt this in the absence of observations from life. With each genus I have attempted to give representative figures showing the



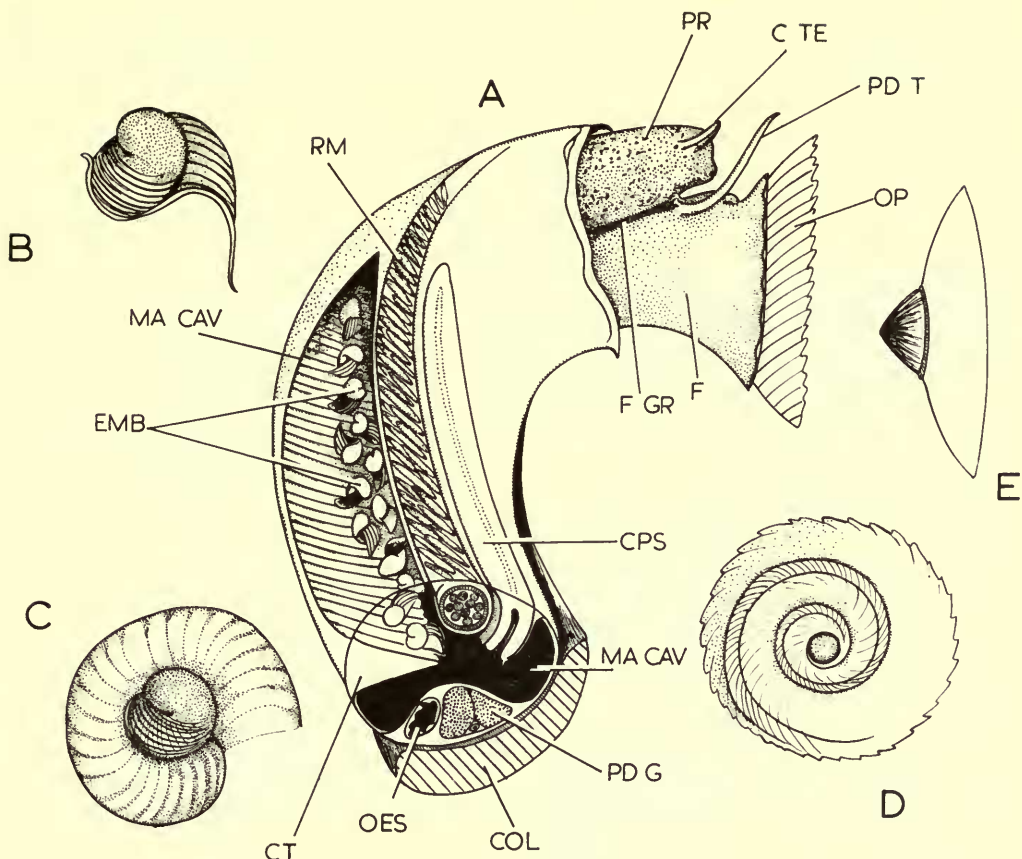


FIG. 1. *Dendropoma marchadi*. A. The anterior part of the animal illustrated diagrammatically, with the incision of the mantle to show its contents. B. The apex at the beginning of post-embryonic growth. C. The apex showing the embryonic shell encircled by the first post-embryonic whorl, shown from beneath after detaching from the substrate. D. Operculum in upper view. E. Operculum in side view.

nature and location of the structures chiefly involved in the differentiation of the group, especially in the cephalic, pedal and pallial regions. The figures of the animal, operculum and nuclear whorls of *Dendropoma marchadi* show pretty well the key characters that are important in any examination of new vermetid material. Reference to the diagrammatic sagittal sections of *Dendropoma maximum*, (Text-fig. 2c), *D. (Novastoa) lamellosa* (Text-fig. 3g) and *Serpulorbis squamigerus* (Text-fig. 9a) will also be helpful in illustrating the range of structure and adaptations of the soft parts shown within the family.

It is unlikely that I shall have an early opportunity to work again with living vermetids; and this paper will have achieved its purpose if it makes clear that Dr. Keen's four generic groups stand out equally naturally upon the evidence of the

animal as on conchological features. I offer my present findings as a starting point for a student on some shore more favoured by these reticent but charming gastropods.

## 2. GENERIC REVIEW

### (i) Genus *DENDROPOMA* Mörch, 1861

#### *Species examined :*

1. *D. (Dendropoma) leucozonias* (Mörch, 1861) ; West Africa. B.M. (N.H.) Reg. No. 195926.
2. *D. (Dendropoma) lituella* (Mörch, 1861) ; California.
3. *D. (Dendropoma) maximum* (Sowerby, 1825) ; Queensland, Australia. B.M. (N.H.) Reg. No. 1856.9.24.45. B.M. (N.H.) Reg. No. 1870.13.23.21. B.M. (N.H.) Reg. No. 1952.1.29.290.
4. *D. (Dendropoma) rastrum* (Mörch, 1861) ; California. B.M. (N.H.) Reg. No. 195916.
5. *D. (Dendropoma) marchadi* Keen & Morton, 1960 ; East Africa.
6. *D. (Novastoa) lamellosum* (Hutton, 1873) ; New Zealand.
7. *D. (Novastoa) irregulare* (Orbigny, 1842) ; Jamaica.
8. *D. (Novastoa) corallinaceum* (Tomlin, 1939) ; South Africa. B.M. (N.H.) Reg. No. 1953.3.12.93-94.
9. *D. (Novastoa) ghanaense* Keen & Morton, 1960 ; Ghana.
10. *D. (Novastoa) tholia* Keen & Morton, 1960 ; Mozambique.
11. "*Dendropoma B*" : Undescribed sp. from South Africa (see Keen & Morton, 1960).

Keen (1961) has clearly set out the diagnostic features of this genus, including the brown-coloured, one to two-whorled inflated nucleus, characteristic modes of coiling and sculpture, and the prevalence of the corroding habit. The operculum, though showing a wide range of variation in shape and proportions, is always greater in diameter than the foot and has a distinctive character in the axial mamilla which constitutes its centre and is only occasionally wanting.

The operculum is the most obvious and accessible classificatory character provided by the *Dendropoma* animal, and the species of this genus could be arranged upon opercular characters in three groups, not necessarily however coinciding with their natural descent or with subdivisions upon other anatomical grounds. First there are those species with the operculum upwardly concave, forming a thin and sharp-edged saucer or bowl, either with the axial mamilla very prominent as in *D. lamellosum*, much reduced as in *D. lituella* and *D. marchadi*, or almost or entirely lacking as in *D. leucozonias* and *D. maximum*. Secondly, the operculum may be flat or only very slightly concave, with the mamilla small or lacking and the insertion surface strengthened by a polished annular thickening, as in *D. corallinaceum* and *D. rastrum*. The third group of species, typified by *D. tholia*,

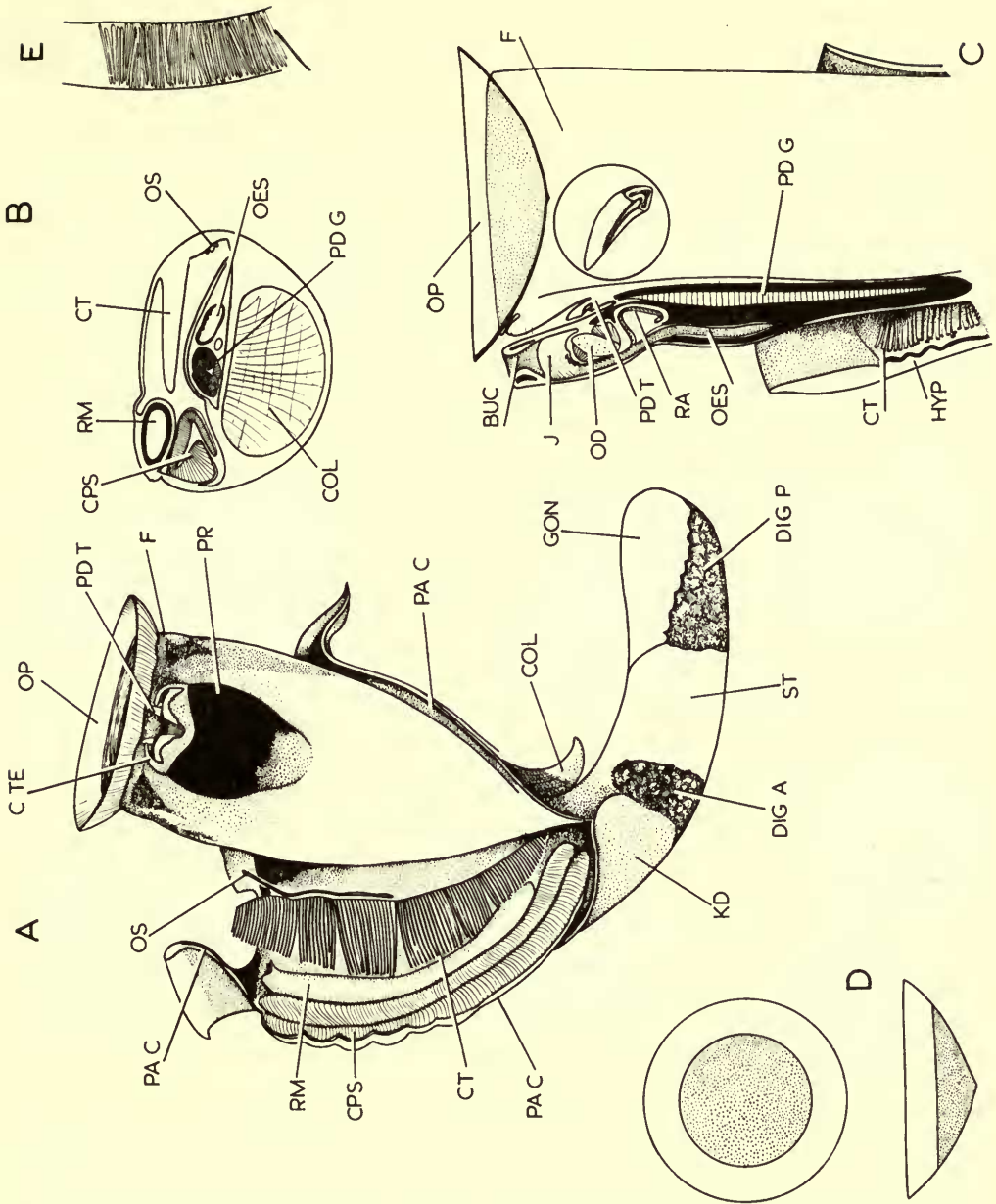


FIG. 2. *Dendropoma maximum*. A. The entire female animal removed from the shell and with the mantle cavity opened along the right side, ventrally to the glandular genital tract. B. Diagrammatic transverse section through the pallial region. C. The head foot and mantle in sagittal section, showing the relative proportions of the parts for comparison with Text-figs. 9 and 3 for *Serpulorbis squamigerus* and *Dendropoma (Novastoa) lamellosa*. D. The operculum in external and in lateral view. E. Detail of the rectum showing the form of the faecal pellets.

*D. irregulare* and *D. ghanaense*, show an operculum externally convex, built up into a solid dome, and concave beneath where the axial mamilla emerges to form a plug inserted into the foot.

The dendropomatid operculum has the typical structure of a spirally wound band of chitin, in which by appropriate maceration—as in dilute caustic potash—the overlapping whorls may be dissociated as shown in Text-fig. 3D for *D. lamellosa*, leaving the more resistant mamilla at the centre. In opercula with a built-up dome, the successive coils of the chitinous band are strongly thickened, and of a mahogany red hue, narrowly triangular in section and superimposed to form a convex structure of great solidity. (See page 617 for discussion of the operculum in Vermetidae generally, and Text-fig. 15 for range of opercular structure in *Dendropoma*).<sup>1</sup>

On opercular characters the first and most primitive of the dendropomatids are probably among those with thin, concave, saucer-shaped opercula. In *D. marchadi* (Keen & Morton, 1960) the saucer is ornamented in its upward exposed concavity with an upstanding spiral lamina of two to three volutions. This character—not observed in any other dendropomatid studied—shows an affinity with the opercula of *Petalococonchus* and *Vermetus* s.s. *D. marchadi* has a tiny axial mamilla; but in *D. maximum* this structure is generally lacking, being represented perhaps as a scarcely visible thickening of the chitin, at the bottom of the deep opercular bowl, which rests in a corresponding concavity in the muscular mass of the foot. The mamilla, though small, is quite obvious in *D. megamastum* while in the concave operculum of *D. lamellosum*, the mamilla forms a very large cylindrical peg running right through the operculum to appear freely above and below. It is flatly truncated on top, and underneath forms a round-tipped plug deeply inserted into the musculature of the foot. The mamilla shows the same deep foot insertion in the species with massively domed opercula; but there the operculum is concave beneath and grips the muscular mass of the foot all-round. In these species, the mamilla does not emerge above but is smoothed off in the contour of the upper surface. Around the axial mamilla, the operculum in *D. irregulare*, *D. tholia* and *D. ghanaense* is built up of deep reddish-brown chitinous whorls, strongly thickened and opaque. The outermost whorl overspreads the edge of the foot in a reddish marginal zone; outside that is a sharp peripheral lamella of transparent horn. For *D. irregulare*, the operculum of two stages of the non-adult is illustrated, showing the solid biscuit-shaped plate that is finally built into the convex dome.

The flat or but slightly concave opercula of *D. corallinaceum* and *D. rastrum* differ from either of the previous types by the rather papery thinness and irregularity of the projecting rim and the raised polished ring of thickened chitin upon the insertion surface. *D. corallinaceum* shows a small central mamilla. In *D. rastrum* there is no trace of this, and the upper surface has the successive whorls overlapping and irregularly jagged at the free margin.

In a previous paper, Keen & Morton (1960) have described the anatomy of a species of the concave opercular type (*D. marchadi*), and of one of the domed type

<sup>1</sup> D'Arcy Thompson in "Growth and Form" (1942) (page 777) is incorrect in stating that the operculum of *Siphonium* (= *Dendropoma*) shows concentric growth and forms an exception to the general spiral rule



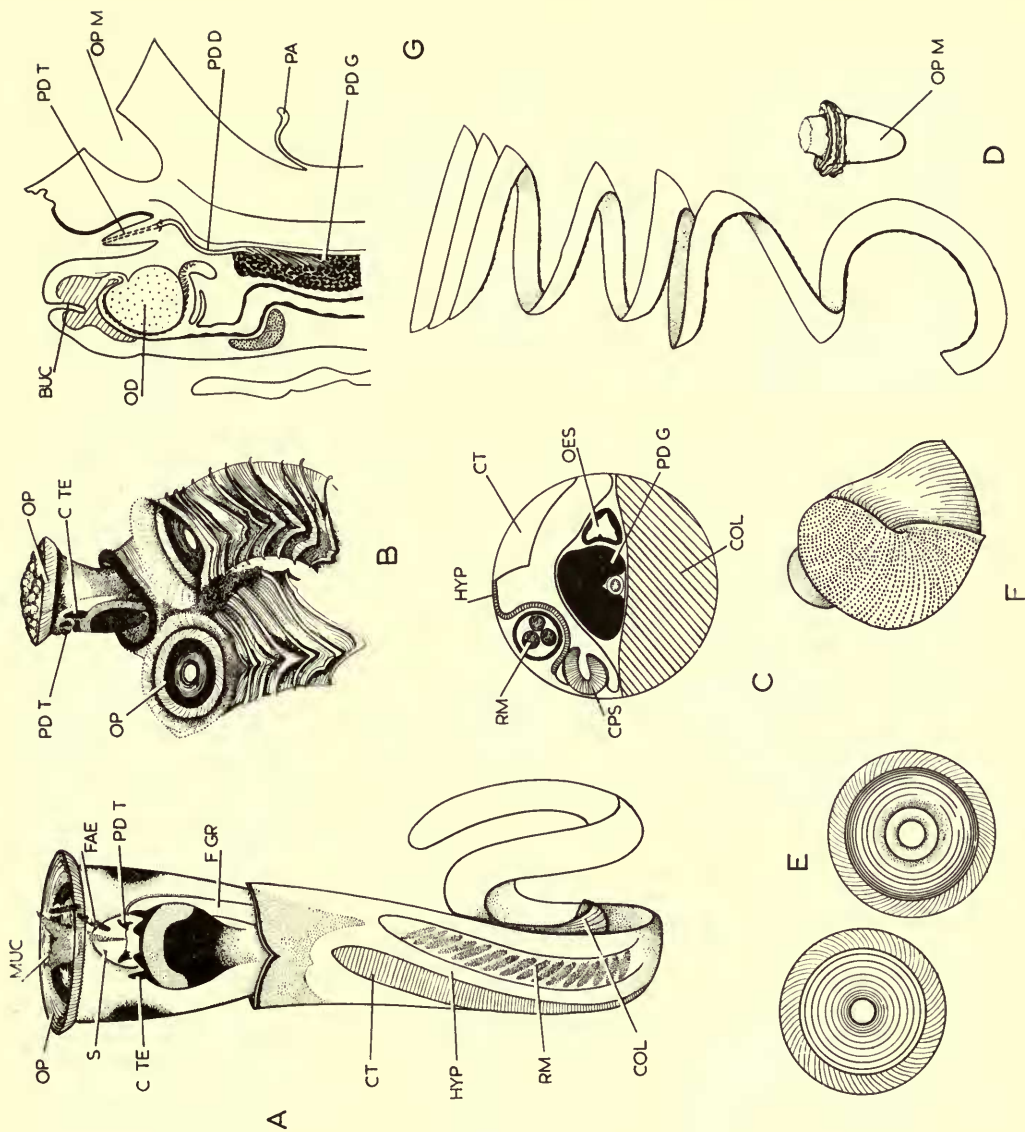
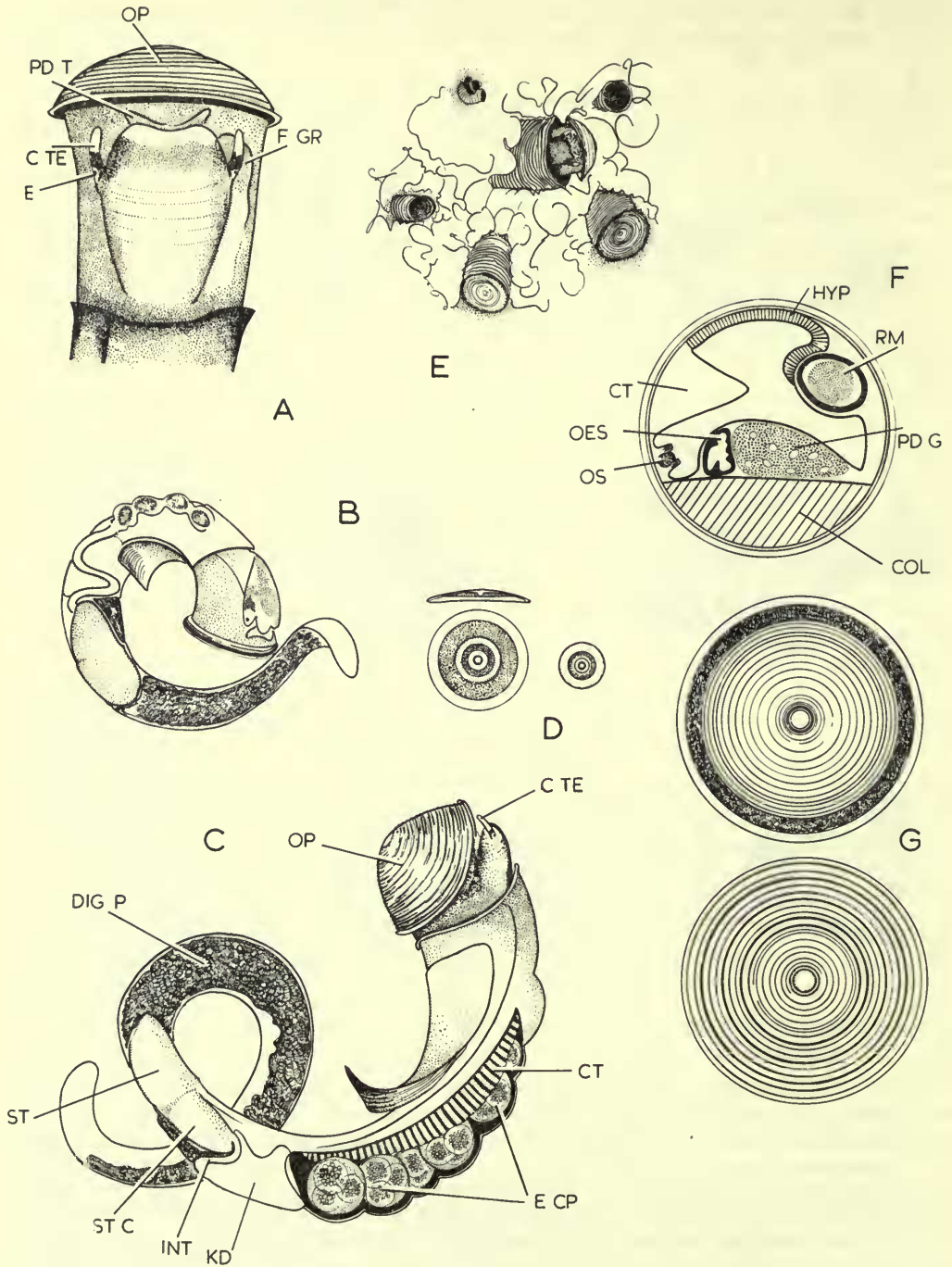


FIG. 3. *Dendropoma (Novastoa) lamellosa*. A. The entire animal removed from the shell and viewed from the dorsal surface. B. A cluster of animals showing one with the foot and head extended and the others withdrawn into the shells. C. Diagrammatic transverse section of the pallial region. D. The spirally wound strip of the operculum as displayed in extended view after maceration with caustic potash, and the axially mamilla separately shown. E. The operculum in inner (left) and outer (right) view. F. The embryonic shell with the beginnings of post-embryonic growth. G. The head and foot in sagittal section, showing the relative proportions of the parts, for comparison with Text-figs. 1 and 9.





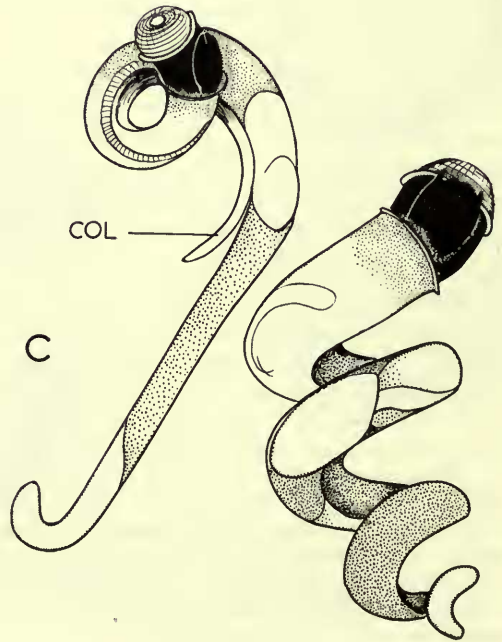
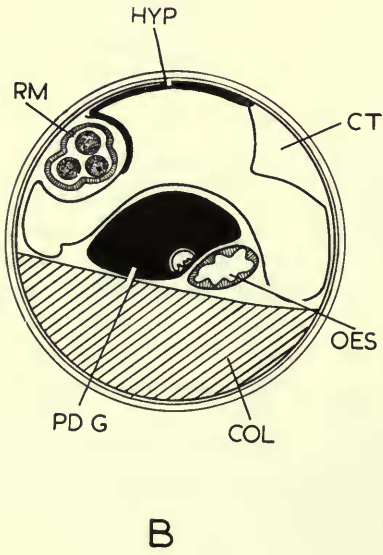
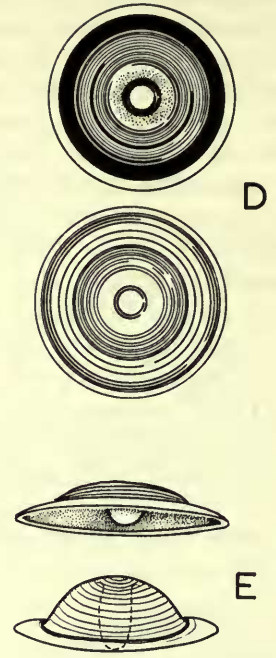
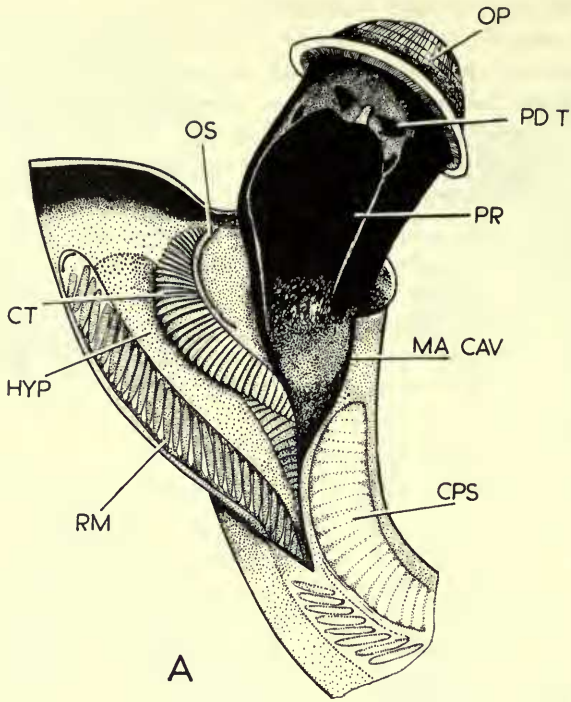
(*D. tholia*). The mode of life and feeding mechanism has been described for *D. maximum* by Yonge (1932) and for *D. lamellosa* by Morton (1951a). Robertson (*in litteris*) has recently communicated observations on feeding in *D. irregulare*.

In most species of *Dendropoma* the body retains its primitive habit of growth, being wound in an open dextral gyre of several whorls, widening regularly from the apex. An operculum is never lacking and is always the most conspicuous feature of the animal viewed from outside, crowning the strong muscular plug of the foot. The operculum can be withdrawn only a short distance into the shell, as it closely approaches in diameter the widest and most recently formed section of the tube (see Text-fig. 3B for *D. lamellosum*). It serves effectively for the protection of the animal from attack, as it swiftly darts back to close the mouth of the shell. Deep retreat into the tube is precluded by the rather low insertion of the columellar muscle, that is, relatively near the head, marking the deepest point of attachment towards which the animal can be withdrawn.

In some species, as for example *D. irregulare*, the spire tends to have fewer whorls coiled in one or two widely open volutions, and in some specimens of *D. lamellosum* the distal part of the animal has a tendency to straighten out, as the latter part of the shell tube loses its original curved growth pattern. Sometimes, as in some adult specimens of *D. lamellosum*, the visceral spire may shorten abruptly after one or one-and-a-half turns and the top of the spire, formed by the digestive gland, is then bluntly truncated, the earlier parts of the shell being cut off by septa (see Keen, 1961, page 198). This tendency is carried furthest in *D. maximum*, by far the largest-sized species of the genus. As is evident from the work of Yonge (1932) on the anatomy of the animal, this is a species marked off in many ways from other *Dendropomas* (Text-fig. 2). As well as being very large, its shell forms in the adult a straight or only slightly curved tube. The body of the animal is thick and cylindrical, about the diameter of a man's small finger, with a short, blunt-tipped and only slightly curved visceral mass (Text-fig. 2A).

Both in the structure of the animal and in its exclusively ciliary feeding habits, the large-sized species *D. maximum* appears to fall furthest apart from other members of the genus. Its head and the exposed parts of the foot are handsomely pigmented in deep blue-black and light brown. The exposed mantle margin has a wide, blue-black band, and the operculum is of golden coloured translucent chitin. Much of the anatomy of the head and mantle cavity may be correlated with Yonge's description of the feeding habits of *D. maximum*. The head, as shown in longitudinal section in Text-fig. 2C, shows very different proportions in relation to the foot, from that of *Serpulorbis* species (see *S. squamigerus* for comparison) or even other species

FIG. 4. *Dendropoma (Novastoa) irregulare*. A. Detail of the head and foot in dorsal view. B. A young animal taken from a recently attached shell. C. The whole female animal removed from the shell, with the mantle cavity opened to show the mode of carriage of the brood. D. Stages in the growth of the operculum in early settled animals. E. A group of specimens *in situ* showing the perforating habit of the shell, embedded in encrusting lithothamnion. F. Diagrammatic transverse section through the pallial region. G. The operculum, viewed (above) from within and (below) from the outer surface.



of *Dendropoma*. The head is much less massive than the foot and relatively shallow dorso-ventrally, with a buccal bulb of rather modest size. It appears likely that the size and muscular development of the buccal bulb are reduced in a ciliary feeder, which does not employ the radula for pulling back towards the mouth the heavy mucous traps extruded from the pedal gland of other species.

The pallial cavity contains by far the largest and best developed ctenidium seen in any vermetid investigated. The gill filaments have increased in length to form attenuated triangles, somewhat approaching to the parallel-sided and linear condition found in highly advanced ciliary feeders such as the Calyptraeidae (see Yonge, 1938). The filaments extend across the hypobranchial gland to conceal it completely from below, and they reach as far as the rectum on the right side of the pallial cavity roof. They have a ratio to the width of the pallial cavity of approximately 3 : 5. Yonge (1932, 1938) has described the action of the lateral ciliary fields in drawing a water current through the mantle cavity and of the frontal and abfrontal cilia in carrying collected particles to the tips of the filaments. These particles are projected from the tips of the gill filaments on to a ciliated tract on the right side of the mantle cavity floor. Here ciliary currents sweeping obliquely forward carry them to the neighbourhood of the right side of the head. Yonge (1932) identifies a weakly defined food groove forming a ciliated gutter at the right side of the head. From the preserved material figured here, this could not be separately detected (Text-fig. 2A). The particles brought to the front of the head by the cilia of the food groove come under the influence of mucus being extruded from the pedal gland, which embeds and binds the collected food, in preparation for its ingestion by the regular plucking strokes of the radula. The opening of the pedal gland is flanked by two short tentacles, carrying a ciliated groove along their medial edges. These tentacles are very short and slender; in preserved material they usually curve inwards towards the centre line, although—as in other dendropomatids—they may diverge laterally in life. They appear to have the function of transporting or guiding the cone or small irregular mass of mucus that generally hangs from the mouth of the pedal gland, or rises from the surface of the foot in front of the mouth. The mucous mass is of smaller size in *D. maximum* than was figured in life for *D. lamellosa* by Morton (1951a), where it is suspected to be employed in direct mucous food collecting. With the reduced size of the mucous mass in *D. maximum*, we may correlate the reduction of the pedal gland (illustrated in transverse section in Text-fig. 2B and in longitudinal section in Text-fig. 2C). This has the smallest relative extent observed in any of the vermetids; with a ratio of only 1 : 6 or 7 to the total body diameter, in contrast with the larger pedal glands, not only of *Serpulorbis* and *Petalococonchus* but also of other species of *Dendropoma*.

Of the mucus secreting sources within the mantle cavity, Yonge (1932) recognises

FIG. 5. *Dendropoma* "B" from West Africa (see Keen & Morton, 1960). A. The head, foot and pallial region of the animal removed from the shell and with the mantle cavity opened. B. Diagrammatic transverse section through the pallial region. C. Two views of the entire animal removed from the shell. D. The operculum from its inner face (above) and its outer aspect (below). E. Two oblique side views of opercula showing variations in height of the dome in different individuals.



an "endostyle" (so-called in the rather unsatisfactory terminology of Orton, 1914) running along the gill axis. Although in this part of the mantle wall mucus is probably diffusely secreted from the general integument, there appears to be no such highly specialised endostylar tract, with well demarcated zones of secretory and ciliated cells, as has been described for the ciliary feeding families Calyptraeidae (Orton, 1912), Struthiolariidae (Morton, 1951), and Siliquariidae (Morton, 1951a).

In the remaining and smaller-sized species of *Dendropoma* the pedal gland is in every case better developed. The transverse sections of the pallial region illustrated for *D. irregulare*, *D. tholia* and *D. lamellosum*, show a large pedal gland, semicircular in section, bulging through the pallial floor and massively displacing the narrower oesophagus to the left side. Morton (1951c) has suggested that mucus contributes to food collecting in *D. lamellosa* and Keen & Morton have advanced the same view for *D. tholia* and *D. marchadi*. More recently, Robertson (*in litteris*) has given a useful account of feeding in *D. irregulare*, and has kindly allowed me to quote in anticipation of a more detailed account by him. "Mucus produced by the enlarged pedal gland is formed into threads and spread out radially from the aperture of the shell with the pedal tentacles. Plankton, organic detritus and numerous sand grains in suspension are entangled and the threads are then drawn into the mouth with the radula."

The pedal tentacles in *Dendropoma* species are, however, seldom larger or much more prominent than in *D. maximum*. They remain short, club-shaped or pointed processes, well hidden beneath the tip of the snout and the rim of the operculum. Only in *D. marchadi* do they appear—from preserved material—to be longer and more mobile. With respect to the elongation of the gill filaments, the only other species found during my own work to show any tendency to the form shown in *D. maximum* is *D. marchadi*, where they are narrowly triangular, with a ratio of slightly more than 1 : 2 to the diameter of the mantle cavity. In *D. irregulare*, *D. tholia*, and *D. ghanaense* they are typically triangular, with no trace of elongation. In *D. lamellosa* the filaments are especially short, forming broadly based triangles, seemingly ill-adapted for ciliary food collecting. Nevertheless, both the species, *D. lamellosum* and *D. irregulare*, investigated living, show some ability to feed by ciliary means with the ctenidium. A well-developed ciliated food tract runs along the right side of the mantle cavity floor in *D. lamellosum* carrying particles bound in mucus for ingestion at the mouth. *D. tholia* has a food tract lined with thickened ciliated and mucus-producing epithelium, well demonstrated in sections. Of *D. irregulare*, Robertson states that there is a broad ciliary tract on the right side of the animal which carries particles gleaned from the ctenidium forward to the mouth. Though some food is obtained in this way the amount is held to be small.

From the study of fixed material alone, in spite of the unspecialised appearance of the gill filaments, or the apparent small size of the pedal tentacles, it must be unsafe to exclude the possibility of either type of feeding habit. Judgment must be reserved until living material may be examined; and we must keep in mind the probability that both ciliary and mucous methods of food collecting may frequently be employed together.

The transverse sections of the pallial region in *Dendropoma* illustrate also the mode of incubation of the eggs and the disposition of the female genital duct (Text-figs. 1A, 2B, 3C). The mantle margin of the female is always entire in the dorsal mid-line, never slit backwards as in *Serpulorbis* or *Vermetus*; and the egg capsules are never attached to the shell but are carried in the mantle cavity in a single row of up to 12, as in the smaller sized *D. tholia* or *D. irregulare*, or in a double row as in the larger *D. marchadi*. Such a simple incubation method is only compatible with the lack of deep retreat of the animal into the upper reaches of the tube; the eggs can here be held freely in the mantle cavity without risk of sudden crushing during emergency withdrawal of the animal into the tube. For *D. maximum* we have as yet no information either about the mode of brood carrying or the form of the embryonic shell. With the extrusion of a long line of egg capsules directly into the mantle cavity in *Dendropoma*, the long distal section of the female genital duct, the capsule gland, runs as a glandular furrow of uniform width for most of the length of the pallial cavity. It lies immediately to the right of and ventrally to the rectum, and—as may be seen from the sections—it forms a thick-walled trench open along its whole length. Its extended slit-like aperture offers a more extended entry to current-borne sperm, (the male vermetid is aphyllid), and allows the emergence of a long row of egg capsules placed end to end throughout the mantle cavity. In *D. maximum* the capsule gland is especially elongated, and contiguous with the whole ventral aspect of the rectum.

The digestive system appears to provide no distinctive generic features for *Dendropoma*. A typical vermetid stomach has been described (Morton, 1951a) for *Serpulorbis zelandicus*. This shows a close agreement in the relations of style sac, gastric shield, sorting area and digestive diverticula, with the stomachs of *Dendropoma lamellosum* (Morton, 1951a) and of *D. maximum*, described by Yonge in 1932.

The radula has a characteristic appearance for the genus *Dendropoma* (see Text-figs. 13A–F). The general form of the median tooth is rectangular, somewhat wider in the transverse dimension, with posterior corners built out into short, curved, horn-like flanges. These are fairly strongly chitinized and fit into concavities on the lateral teeth. The lateral teeth are as typically in vermetids, with their main cusp as long as the median cusp of the central, with three smaller cusps laterally to it. The first marginal tooth bears at either margin two low cusps and towards the tip a stronger spine-like cusp directed terminally. The second tooth is smooth save for a similar spine-like cusp.

## (ii) Genus *PETALOCONCHUS*

### *Species examined:*

1. *P. (Macrophragma) montereyensis* (Dall, 1919); California.
2. *P. (Macrophragma) nigricans* (Dall, 1919); Florida.
3. *Vermetus (Thylaeodus) contortus* (Carpenter, 1857); Tropical West America (see Keen, 1960, p. 201). B.M. (N.H.) Reg. No. 57.6.4.1490.

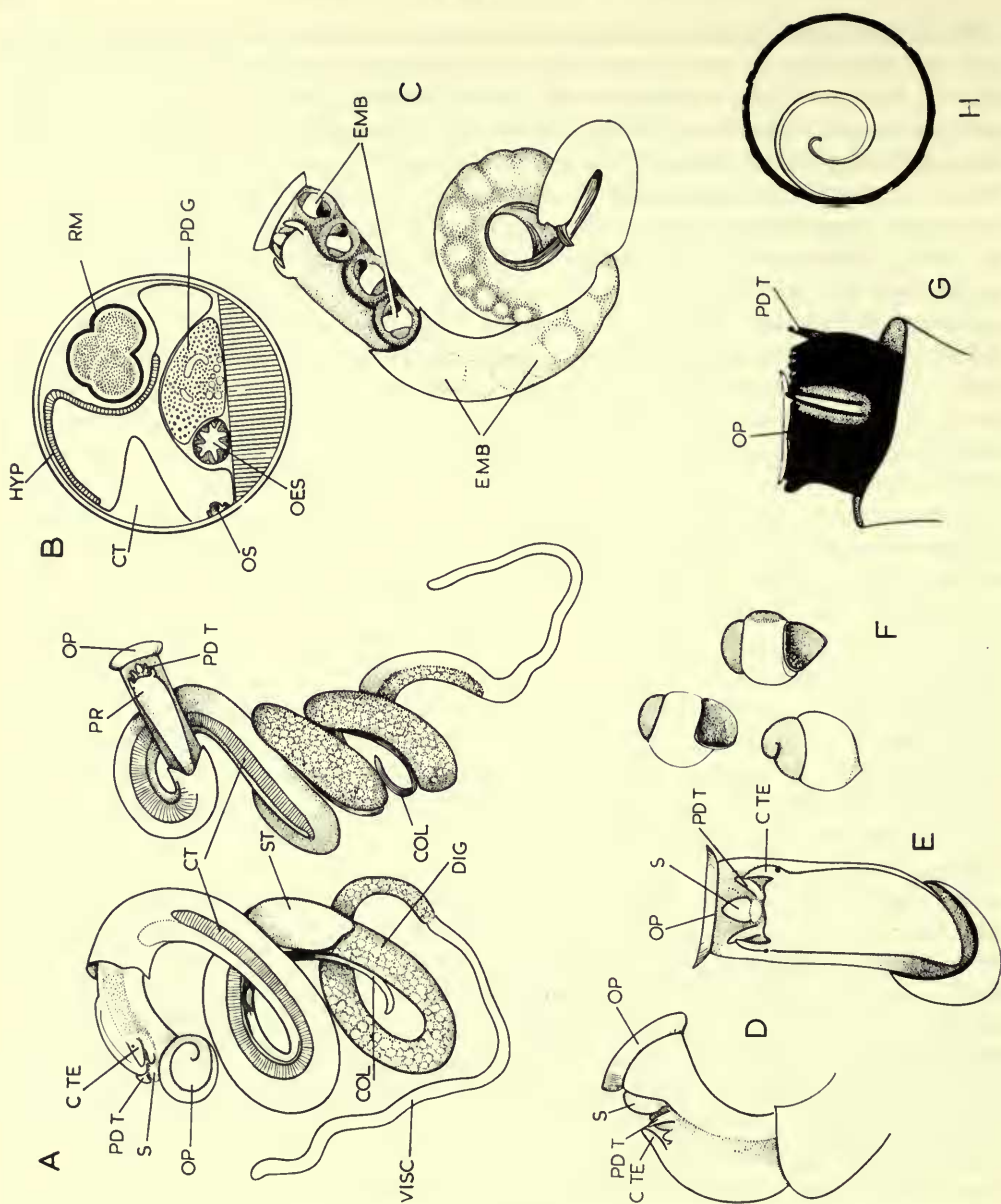


FIG. 6. A-F *Petalocochus montereyensis*. A. Two views of the entire animal with the head shown (left) from the left side and (right) in dorsal view. B. Diagrammatic transverse section through the pallial region. C. Female animal showing the location of the eggs and shelled embryos within and in front of the mantle cavity. D. Detail of the head and foot in right side view. E. The head and foot in dorsal view. F. Embryo shells shortly before liberation.

G-H *Petalocochus nigricans*. G. The head, foot and operculum from the left side. H. The operculum in surface view.



The chief diagnostic feature of the genus *Petalconchus* is shown by Keen (1961) to be the development in the earlier part of the tube of a pair of spiral lamellae of varying complexity, partly subdividing or restricting the space occupied by the animal. In addition, the subgenus *Macrophragma* (the *Petalconchus* of most authors, to which belong the great majority of the species, including *P. montereyensis* and *P. nigricans* examined here) is characterized by a distinctive coiling pattern, the whorls being laxly superimposed on each other like a "Turritella squeezed sideways" to quote Carpenter's description. The nucleus too is strongly diagnostic, having 2-4 whorls, more than in *Dendropoma*, but being of smaller actual size. It is never brown, but ivory white to waxy yellow in colour, and conical to rather distinctively cylindrical or barrel-shaped in outline (see Text-fig. 6F). The operculum is always present, though never so elaborate as it may become in *Dendropoma*. It is shallowly concave with an upstanding spiral lamina of one or two volutions. Though it generally covers the foot and may slightly overspan the sides, it is always considerably smaller than the diameter of the aperture.

Species of *Petalconchus* are seldom of great size as compared with the largest of *Dendropoma* or with a typical *Serpulorbis*; the body of the animal when removed from the shell is found to be long and extremely slender, having the general appearance of the sideways displaced spiral coils of the shell. In *P. montereyensis*, which has a very typical development of internal spiral lamellae, these greatly restrict the internal diameter of the earlier whorls of the adult tube. The body of the animal is produced to a long tail, of uniform thickness of about half the rest of the body, and running right through the part of the shell occupied by the lamellae. This tail appears to consist wholly of gonadial tissue displaced backwards from its usual site alongside the digestive gland. The columellar muscle (see Text-fig. 6A) is of very different shape from that of *Dendropoma*; it is attached far back in the shell at a depth of at least two full volutions, alongside the visceral mass of the animal, and forms an attenuated narrow strip running for a good distance free of the rest of the body. Such an arrangement equips the animal for a deep protective retreat into the shell. Unlike that of *Dendropoma*, the operculum is scarcely massive enough to serve for protection and is somewhat too narrow to close the aperture. In my specimens of *P. nigricans* it does not in fact cover the whole top of the foot.

The exposed parts of the head and foot are jet black in *P. nigricans* with the cephalic tentacles long and ornamented with a lighter stripe. The inner surface of the mantle skirt is also broadly black edged. In *P. montereyensis* the animal in spirit is yellowish white or pale-coloured, with no prominent pattern or colour markings. The operculum in *P. montereyensis* (Text-fig. 6D) is a thin concave saucer, bearing a spiral lamina in its concavity and strongly overlapping the sides of the foot. The head and the proboscis do not appear to show the massive size sometimes found in *Serpulorbis*, and the head and foot present no special features very unlike those of *Dendropoma*. The pedal tentacles lie beneath the proboscis, being somewhat longer than the cephalic tentacles in preserved material, and forming incurved or divergent papillae, with a small, pale-coloured patch of integument between them

that represents the sole of the foot. Despite the small size of the pedal tentacles, the pedal mucous gland, as illustrated for *P. montereyensis*, is of very large size. It extends backwards for the whole length of the mantle cavity (about half that of the entire animal) and bulges strongly through the mantle cavity floor as a thick, dorsally convex, glandular strap.

The considerable size of the pedal mucous gland suggests that its secretion must clearly be employed for the formation of mucous traps, though there is no such pronounced development of the pedal tentacles as in *Vermetus* s.s. and in *Serpulorbis*. Robertson (*in litteris*) describes a similar mode of mucous feeding in *P. nigricans* to that observed in *D. irregulare*. The mucous threads are as long as 12–15 cm. The pallial cavity has no clearly defined food groove, but its forward ciliary currents on the right side are stated to be stronger than in *D. irregulare*. The gill filaments are equilaterally triangular in shape. A ciliary method of food collection, by the action of the gill and the ciliated tract, must supplement the action of the mucous traps, particularly at times when the erect apertural tube of the shell is broken off and repaired, the rest of the tube being meanwhile almost closed by a thin convex shelly septum, rendering the deployment of mucous traps impossible.

The genus *Petalococonchus* has been little studied in life, and as with *Dendropoma*, an investigation of the feeding habits of some of the fairly easily available American species would be highly rewarding.

The arrangements for the retention and brooding of the eggs in *Petalococonchus* hardly appear to differ from those of *Dendropoma*. The mantle skirt is entire, being never slit in the middle line in the female, and the eggs and embryos are retained in a row extending backwards for the whole length of the mantle cavity, those furthest forward being the most advanced in development. Text-fig. 6c for *P. montereyensis* illustrates the mode of carriage of the eggs and embryos; and Text-fig. 6D shows the form of the embryonic shell. The oldest embryos at the front of the row, lying against the head, have not yet attained their full number of whorls, as found in the finished embryonic shell; it would be interesting to discover whether the veliger acquires its extra whorl during a final interval of free-swimming, after the conclusion of incubation and before settlement. (Cf. the mesogastropod *Struthiolaria* (Morton, 1951) for a similar succession of an incubatory phase by a short free-swimming episode.) The capsule gland of the female *Petalococonchus* forms a long, thick-walled trench, with an extended opening, much as was found in *Dendropoma*.

In any consideration of the genus *Petalococonchus* the status of the small, slender-tubed species, *Vermetus contortus* of Carpenter (1857) falls to be assessed. This Southern Californian species was first regarded by Dr. Keen as a *Petalococonchus*, but was later removed into the subgenus *Thylaeodus* of Mörch (1861) under the genus *Vermetus* s.l., on account of its lack of internal spiral laminae. The operculum (see Text-fig. 7E) is characteristically that of a *Petalococonchus*, slightly overlapping the sides of the foot though not reaching the diameter of the aperture. It carries in its shallowly concave upper surface a spiral flange of one-and-a-half volutions. The embryonic shell too is typical of *Petalococonchus* as characterized by Keen (1961).

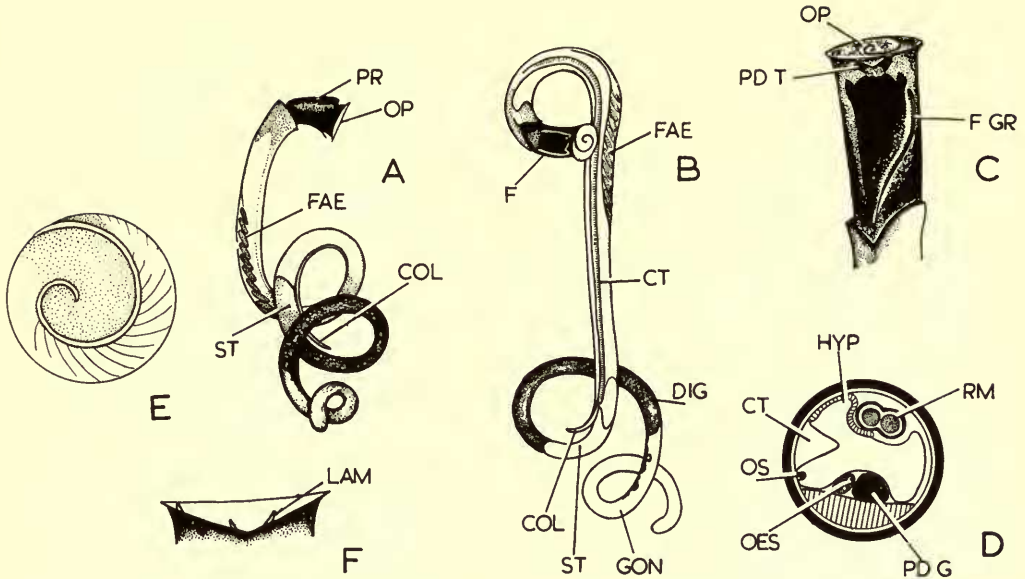


FIG. 7. *Vermetus (Thylaeodus) contortus*. A, B. Two views of the whole animal removed from the shell. C. The head and foot in dorsal view. D. Diagrammatic transverse section through the pallial region. E. Operculum in surface view from above. F. Diagram of the operculum in position upon the foot in sectional view.

Dr. Keen finds the conchological distinction between *Thylaeodus* and *Vermetus* s.s. slight and predicts that the separate groupings may be unjustifiable. The animal of Carpenter's *contortus* is illustrated here (Text-fig. 7); and as a result of this investigation, it would appear to have little in common with either of the other two species referred to *Vermetus* s.s., including the type *adansonii*. Except for its neglect to develop internal lamellae and the consequent narrow "tail", Carpenter's *contortus* has every other qualification needed for *Petalococonchus*, such as the conic-cylindrical character of the nucleus, the "squeezed sideways coiling pattern", and the narrow body with the columellar muscle forming a long slender strip stretching far back to allow deep insertion within the tube. The pedal tentacles are small, dark-pigmented, divergent papillae, and the whole of the exposed head and foot are black-pigmented. The pedal gland, as shown (Text-fig. 7D) in cross section of the pallial cavity, is massive and semicircular in section. The operculum differs by its large size from the spirally laminate one of *Vermetus* s.s. which is always a vestigial button.

The radula of *P. contortus* moreover agrees with that of *P. montereyensis* and departs from that of other genera; it is strikingly different, for example, from that of *V. adansonii*. The central tooth in *Petalococonchus* is a transverse rectangle, wider in its cross dimension, and with side projections or peg-like lobes similar to those of *Dendropoma* but somewhat stronger and more peg-like. The lateral teeth are much as in *Dendropoma* or *Serpulorbis*. The first marginal tooth shows—as



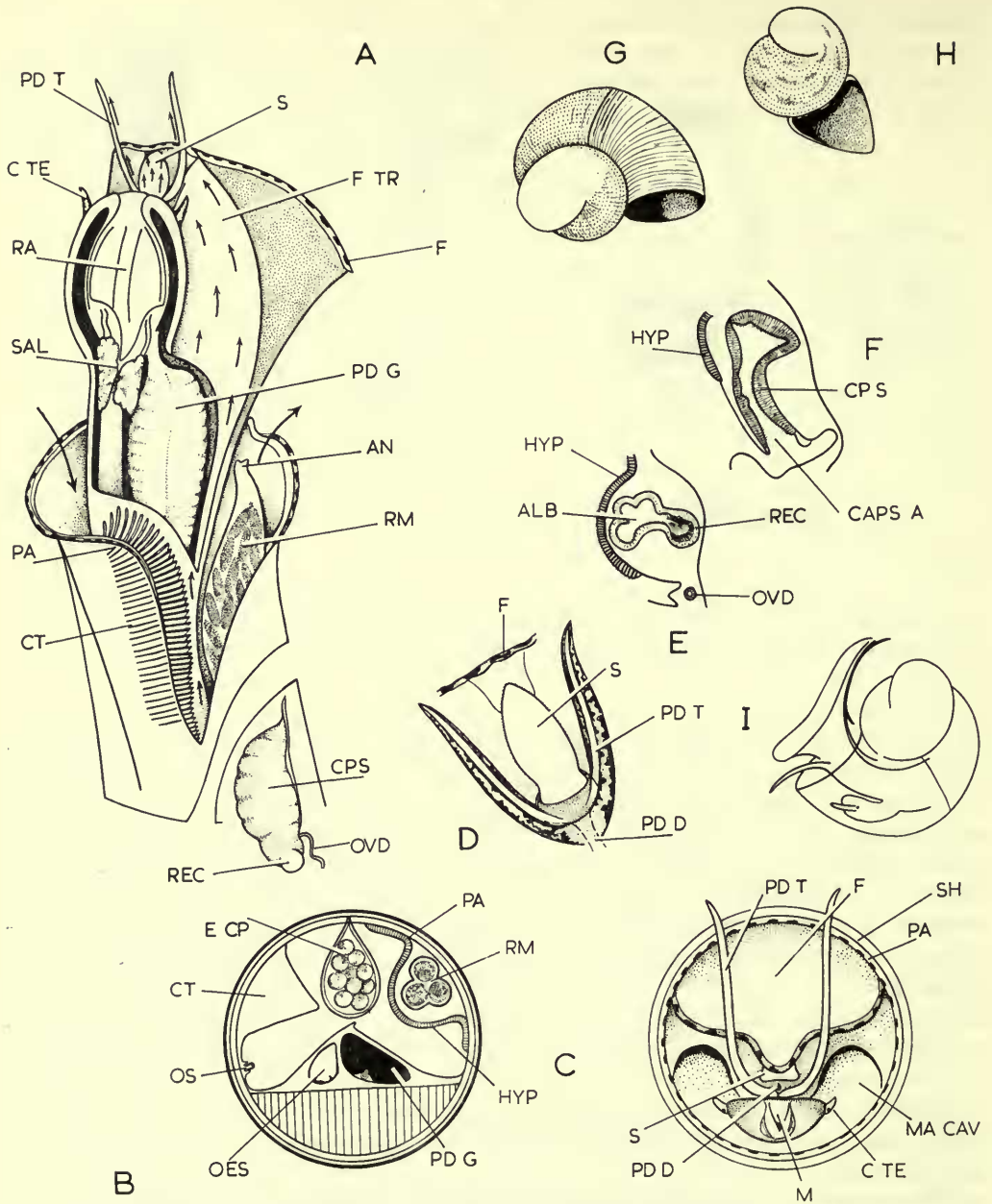


FIG. 8. *Serpularbis zelandicus*. A. Head, foot and pallial cavity of the female. The pallial cavity is shown without dissection, as viewed through the median slit. The body wall of the proboscis and of the head immediately behind it has been dissected to show the internal structures. The arrows indicate ciliary currents within the mantle cavity. B. Diagrammatic transverse section through the pallial region. C. The head and foot as partly retracted within the pallial cavity, viewed looking down upon the shell aperture.

well as the distally-directed spine-like cusp—a row of four or five weaker cusps on either margin a little further back. The second marginal tooth, which is smooth in *Dendropoma* except for its spine-like tooth, has in *Petalocochnus* a row of four or five weak cusps at either side.

### (iii) Genus *SERPULORBIS*

#### *Species examined :*

1. *S. (Serpulorbis) gigas* (Bivona-Bernardi, 1832) ; Mediterranean.
2. *S. (Serpulorbis) squamigerus* (Carpenter, 1857) ; California.
3. *S. (Serpulorbis) zelandicus* (Quoy & Gaimard, 1822) ; New Zealand.
4. *S. (Serpulorbis) aotearoicus* Morton, 1951 ; New Zealand.

By comparison with either *Dendropoma* or *Petalocochnus*, any species of *Serpulorbis* presents a number of differences in the outward appearance of the animal, which at once set it off as easily referable to this genus. First, there is no operculum, and the flat top of the foot is soft and often brightly coloured. The disc of the foot is highly sensitive to tactile stimuli and its margin is very labile and deformable by small local muscular contractions. The foot musculature appears much less solid than in the firm cylindrical plug which bears the operculum in *Dendropoma* ; and the head and proboscis, containing a very large buccal mass, are much more massive in proportion to the foot as compared with *Dendropoma*, especially with the species *maximum*. That this is a real difference of proportion, even allowing for the greater shrinkage upon preservation of the foot, where its shape is not maintained by the hard operculum, is amply apparent from comparison of the animals in life. The greater massiveness of the buccal mass in a predominantly mucous feeding group is probably to be attributed to the important function of the radula in hauling back for ingestion the quite extensive mucous sheets or traps.

The second obvious feature of *Serpulorbis* is the generally much greater prominence of the pedal tentacles. These are no longer inconspicuous appendages at the opening of the pedal gland, but are very long, attenuated filaments, standing erect above the front edge of the foot and no longer overshadowed by the brim of an operculum. The ciliated groove on their mesial side runs from the opening of the pedal gland to the tentacle tip. Besides being sensitive tactile structures the pedal tentacles seem to be chiefly responsible for deploying the mucous strings in *S. zelandicus*, *S. aotearoicus*, and *S. gigas*. The pedal tentacles of *S. gigas* are deeply incised by their mesial ciliated groove ; they curve outwards in horseshoe shape from the aperture of the pedal gland, and may be extended a good deal further than the figure by Yonge & Iles (1939), or my Text-fig. 10F, of retracted tentacles, would

D. Detail of the sole of the foot, the opening of the pedal gland and the pedal tentacles, somewhat more contracted than in A. E, F. Transverse sections of the female genital duct at a posterior level (E) through the albumen gland and more anteriorly (F) through the capsule gland. G. The embryonic shell with the first portion of the post-embryonic tube already formed. H. The embryonic shell taken from one of the capsules within the mantle cavity. I. Early post-embryonic stage, showing the temporary operculum

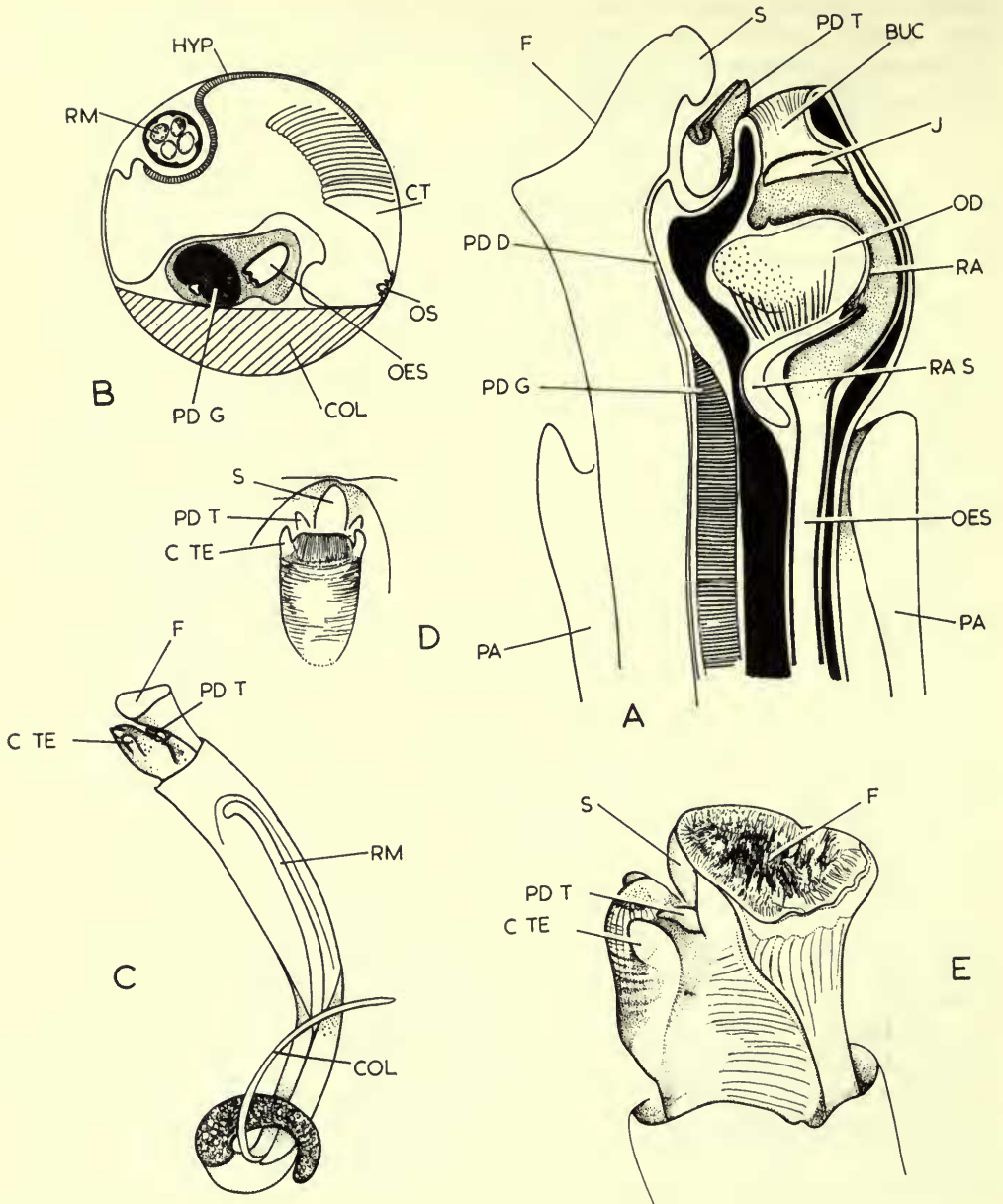


FIG. 9. *Serpuloorbis squamigerus*. A. Diagrammatic sagittal section of the head, foot and mantle cavity for comparison with Text-figs. 1 and 3, of *Dendropoma (Novastoa) lamellosa* and *Dendropoma maximum*. B. Diagrammatic transverse section through the pallial region. C. The entire animal removed from the shell and viewed from the right side. D. Detail of the head, sole of the foot and pedal tentacles from above. E. Detail of the head and foot from the right side.



suggest. The smaller size of the pedal tentacles in my specimen of *S. squamigerus* must to some extent be a preserving artefact ; Johnson & Snook (1935) show them, for example, much longer than in any observed *Dendropoma* or *Petalococonchus*, though relatively shorter than in *S. gigas* or *S. zelandicus*. This may perhaps be

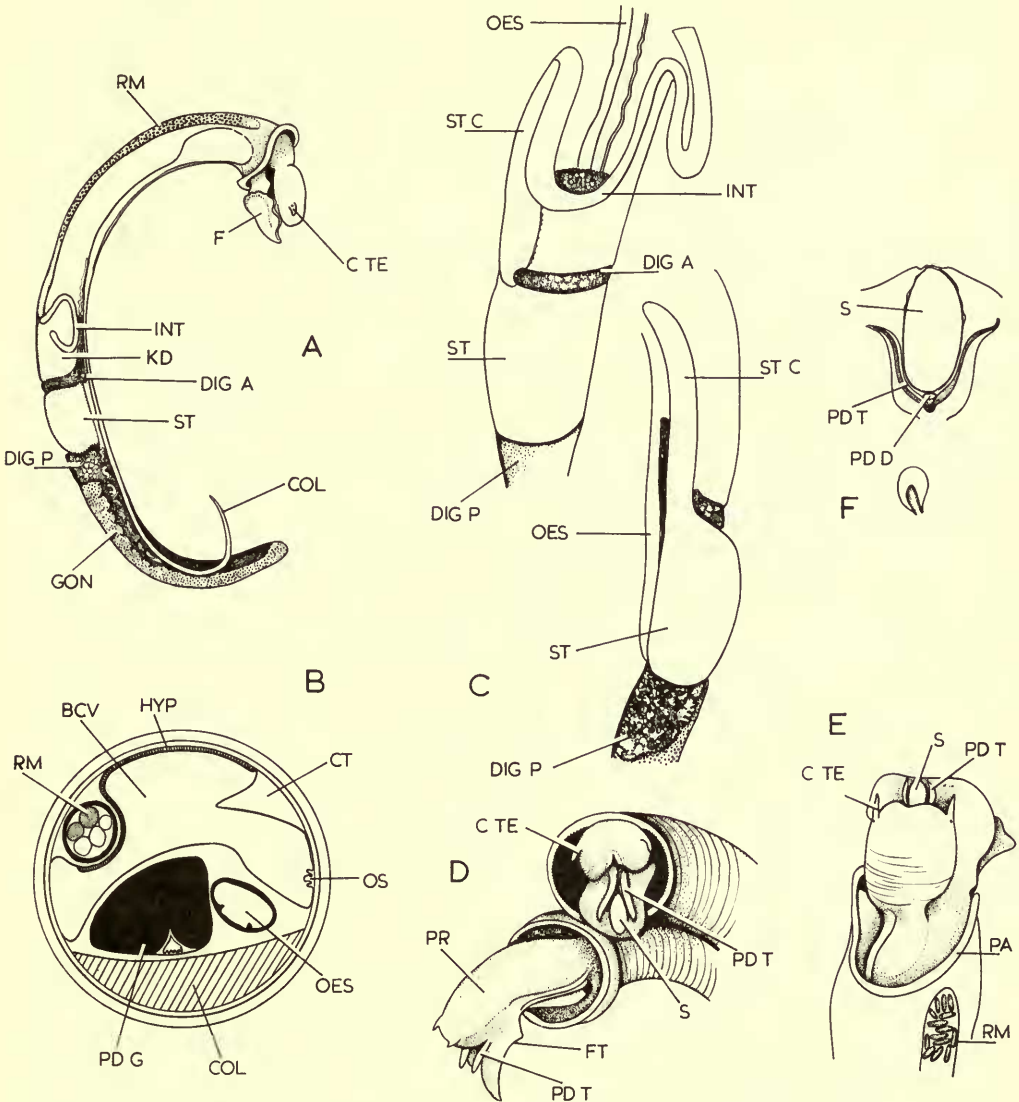


FIG. 10. *Serpulatorbis gigas*. A. The entire animal removed from the shell and viewed from the right side. B. Diagrammatic transverse section through the pallial cavity. C. The stomach, style sac and intestine, viewed from the left side (below) and the right side (above). D. Two animals with the head and foot partly extended from the shell. E. Detail of the head and foot viewed from above. F. Detail of the sole of the foot, and the aperture of the pedal gland with the pedal tentacles (one shown in section).

correlated with the habit of *S. squamigerus* of constructing a communal mucus sheet serving as a "mess-table" for an agglomeration of animals, rather than deploying individual mucus strings by means of the pedal tentacles (see MacGinitie & MacGinitie, 1949).

With the loss of the protective operculum, the foot takes on a variety of bright colours, and these are shared by the head and proboscis and the widely exposed rim of the mantle, extending freely over the margin of the shell. Yellows, reds and blacks appear to predominate (see Morton, 1951a for the New Zealand species). In *Dendropoma* species also there is a preponderance of jet black on these parts of the body, relieved at the mantle and tip of the snout and tentacles by either yellow or red. It may not be too fanciful to suspect that these conspicuous colours are aposematic; comparison may be made with the Nudibranchia (Garstang, 1890), where a naked skin surface assumes an array of bright colours, and is accompanied by distasteful properties to predators (Thompson, 1960).

The chief means of protection available to the animal of *Serpulorbis* is, however, by deep retreat into the shell tube which can be effected with lightning rapidity when the animal is disturbed. This habit has its effect in the design of many of the parts of the body enclosed within the tube. First, the body of the animal when removed from the shell is quite limp, and can only be described as vermiform; it lacks any permanent or well-defined spiral configuration. The columellar muscle does not as in *Dendropoma* form a short, broad strap lending its shape to the overlying body, but for the most part runs free of the body as a long, narrow slip inserted very far back in the shell, often at the level of the tip of the visceral spine (see Text-fig. 9c). This position of attachment allows a long retraction of the animal, and the limpness of the body facilitates its passage through the often irregularly wound volutions of the shell.

Deep retreat into the narrower reaches of the shell is made possible by the lack of an operculum and the extreme compressibility of the soft foot. Compression of the mantle cavity, or the withdrawal of the head and foot into it, would not, however, be possible with the egg capsules lying freely within the mantle cavity as in *Dendropoma* and *Petalococonchus*. The capsules are instead attached to the interior of the shell, shortly within the mouth (see Text-fig. 8B). The mantle of the female is slit backwards in the median line along the line of attachment of the row of capsules (see p. 621).

The principal trend shown by the pallial organs in *Serpulorbis* is the reduction in the size and functional importance of the gill, more especially in those exclusively or predominantly mucous trap feeders such as *S. gigas*, and *S. squamigerus* that form the most advanced section of the genus. The gill filaments in all species examined are equilaterally triangular, and—although the gill extends the whole length of the mantle cavity—it may become extremely narrow, the filaments having in *S. gigas* a ratio of only 1 : 5 to the total diameter of the mantle cavity. In *S. squamigerus* and *S. gigas* the ctenidium appears to be partly enclosed in a separate narrow compartment on the left side of the mantle cavity by the tendency to develop a high longitudinal ridge down the median line of the mantle cavity floor. Cor-

related with the importance of mucous trap feeding, the pedal gland like the pedal tentacles, in *Serpulorbis* reaches its greatest development among the Vermetidae.

The earliest and fullest account of mucous trap feeding in *Serpulorbis* is that of Boettger (1930) for *S. gigas*. The pedal gland and the action of the pedal tentacles have been well described for the same species by Yonge & Iles (1939), who provide a detailed comparison with the same organs in *Dendropoma maximum* under the name of *Vermetus novae-hollandiae*. The same structures are described and illustrated by me for *S. aotearoicus* (Morton, 1951a). The typical appearance of the pedal gland in transverse section is shown in Text-fig. 6B, my Fig. 4 (1951a) being drawn too far posteriorly to represent adequately the bulk of the gland.

In *Serpulorbis gigas*, dependent entirely on mucous traps, long ropes are put out, reaching more than a foot in length, and become loaded with planktonic organisms before being pulled back and grasped by the radular teeth and by the pair of sharp-edged jaws. The pedal tentacles evidently assist in carrying the extruded mucus upwards and clear of the body as it is put out from the pedal gland and formed into the feeding trap. The tentacles may also have a manipulatory power over the spread out mucous cone or threads, and may assist in hauling it in when it is loaded with food for ingestion.

The colonial species *Serpulorbis squamigerus* (see MacGinitie & MacGinitie, 1949) makes a different use of mucus: here a communal sheet of mucus is contributed by the glands of many individuals and the food caught up in it is afterwards ingested as portions of the sheet are plucked off by the radulae of the separate animals.

In *S. gigas*, the gill reaches the smallest proportions found in any vermetid examined, with the exceptions of *Vermetus adansonii* and *V. triqueter*, where it has suffered equal reduction. *Serpulorbis squamigerus* has a somewhat wider gill, with filaments of greater area; this fact is perhaps related to the need to draw in the pallial water current through the loose mucous meshwork of the overlying communal feeding table in a way that cannot be required with the longer and loosely deployed mucous traps of *V. gigas*.

Despite their unspecialized triangular gill filaments, and the lack of the further refinements of ciliary feeding adaptations, it is clear that some serpulorbids resort to a considerable degree of ciliary feeding along with the use of mucous traps. Thus in *S. aotearoicus* and *S. zelandicus* slender mucus strings are sometimes found issuing from the pedal gland but are generally elusive and difficult to observe. In these species, the triangular gill filaments are relatively well-developed for a *Serpulorbis*, drawing a current into the mantle cavity by powerful lateral cilia. Frontal cilia carry particles towards the right side of the mantle cavity, where they are projected off the gill on to a smooth, wide tract of the pallial cavity floor, sweeping round the right side of the foot to the neighbourhood of the mouth. This has powerful anteriorly-directed cilia, and uniformly tall mucus-secreting epithelial cells. The more general mucus source, the hypobranchial gland, is still present upon the roof of the mantle cavity to the right of the gill, but does not seem to be peculiarly or at all closely associated with feeding. On the other hand, the gill axis bears no "endostyle" so-called, of the kind developed in more specialized ciliary feeders,

lacking the pedal mucous gland (i.e. Crepidulidae, Siliquariidae and Struthiolariidae). The long and slenderly tapering pedal tentacles in all species of *Serpulorbis* rise well above the level of the terminal disc of the foot. They can be freely moved about as sensitive tactile and exploratory organs, being much larger and more active than the head tentacles which are raised towards the tip of the bulbous snout; the chief tentacular sensitivity is thus shifted from the head to the new food-getting region, which is the part of the foot in the vicinity of the pedal gland aperture.

The female genital ducts of *Serpulorbis zelandicus* were described by Morton (1951a). The ovarian duct opens into a proximal albumen gland to which is attached a pouch-like receptaculum seminis. The capsule gland is no longer as in *Dendropoma* a thick-walled groove prolonged the length of the mantle cavity, but a purse-shaped sac, open by a slit upon its longer side, and able at one time to secrete and place in position on the shell a single capsular envelope.

(iv) Genus **VERMETUS** s.s. Daudin, 1800

*Species examined* :

1. *V. (Vermetus) triqueter* (Bivona-Bernardi, 1832); Mediterranean.
2. *V. adansonii* Daudin, 1800; West Africa.

Preserved animals of the type species, *Vermetus adansonii*, Adanson's original "le vermet", have been collected and kindly presented to Dr. Keen and myself by M. Marche-Marchad, from the type locality, Senegal, French West Africa. Three specimens examined after careful soaking out from the dried state gave a clear indication of the anatomical features necessary for generic assignation, though rather few of the finer histological details. For *Vermetus triqueter* I have had fixed material collected at the Oceanographic Institute, Monaco; and have also had much help from the description and figures of Lacaze-Duthier's memoir of 1860 which, couched in the convention of another age, are beautifully detailed and clear and go unerringly to the features still of salient interest to the student of a century later.

Both these species have a profound resemblance to *Serpulorbis* in the features of the animal; and were it not for their vestigial operculum mounted on the disc of the foot, there would be few if any malacological objections to throwing *Serpulorbis* into Adanson's original genus *Vermetus*.

The body of *V. triqueter* when removed from the shell is limp and serpentine, the long posterior lobe of the digestive gland occupying half its length. The columellar muscle is a long narrow slip with a deep insertion in the shell and the animal is able to retreat a considerable way. Apart from its small operculum the foot is that of a *Serpulorbis*; its very prolonged pedal tentacles and the disposition of the head and pallial organs suggest that *V. triqueter* is an accomplished mucous trap feeder (see also Yonge & Ilse, 1939). It approaches closest in this respect to *Serpulorbis gigas*. The pedal tentacles appear, however, even longer than in *gigas*, being extremely slender and tapered, with a ciliated groove running along their mesial sides as far as the tip. They diverge from the median opening of the very



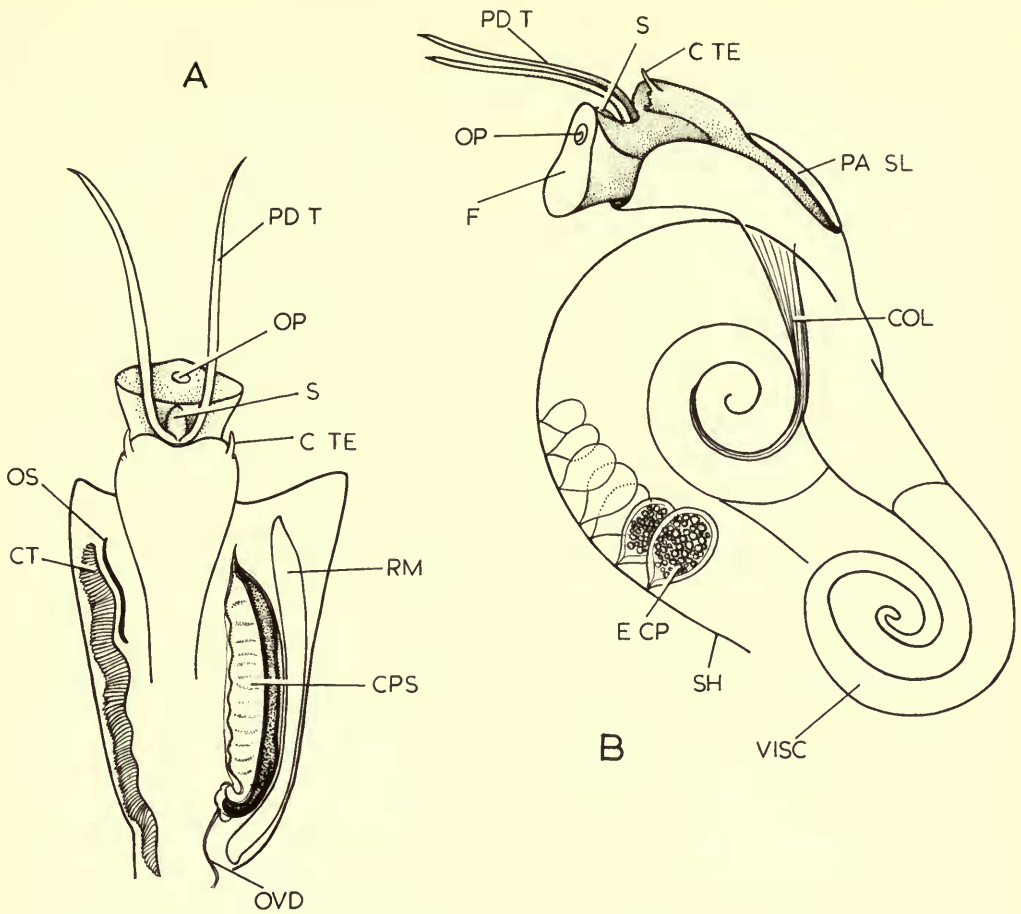
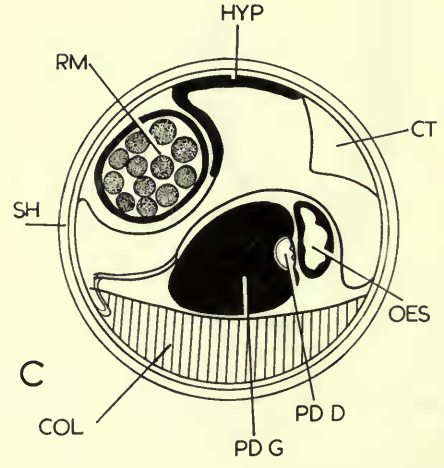
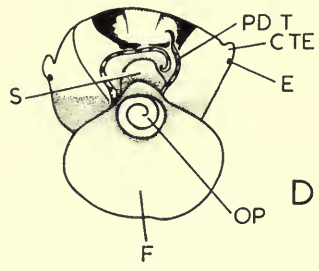
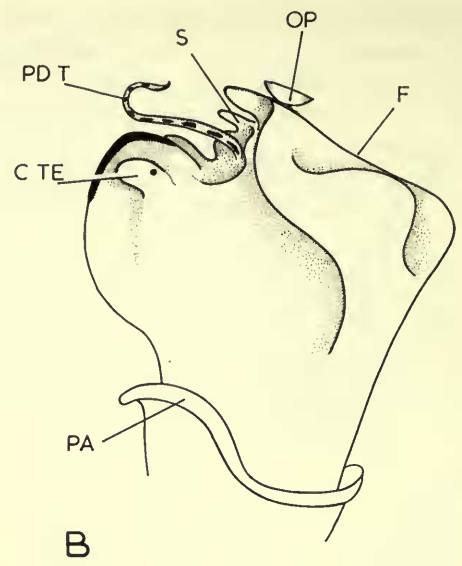
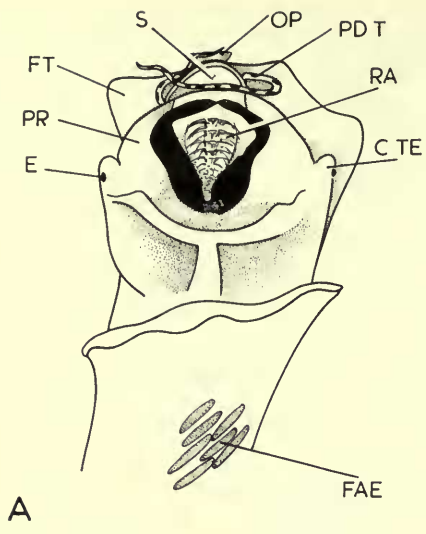


FIG. 11. *Vermetus triqueter*. A. The anterior part of the animal showing the head, foot and pallial cavity of the female after opening the pallial cavity in the dorsal midline. B. Diagrammatic view of the whole animal with the visceral mass slipped out of the shell which is shown in section to illustrate the mode of attachment of the eggs.

Both figures are adapted from Lacaze-Duthiers (1860).

large pedal gland, in front of which and between the tentacles is the small ovoid area representing the sole of the foot. The large and bulbous head is crowned with very short cephalic tentacles. The head has no trace of a deepened food groove upon the right side, nor of a flat food tract, such as is found in *Serpulorbis zelandicus*. The possibility of ciliary feeding is further negated by the exceedingly small dimensions of the gill filaments. Although the gill extends the full length of the mantle cavity, it is as narrow as that of *S. gigas*, and its filaments form tiny equal-sided triangles. The wide area of the hypobranchial gland is left entirely uncovered by the small gill at its left.

*V. triqueter* displays the same reproductive adaptation as *Serpulorbis* in enclosing the eggs in thin, teardrop-shaped capsules affixed in a single row to the lining of





the shell of the female. The pallial skirt is in the same way deeply incised in the dorsal middle line. The female reproductive tract is extremely similar to that of *Serpulorbis zelandicus*: the capsule gland does not run the length of the mantle cavity, but forms an ovoid purse ventrally slit open, and evidently capable of secreting and affixing a single capsule at one time. Lacaze-Duthiers figures seven capsules and states the egg number in each to be 10–30. The embryo has the conical to globular shell characteristic of *Serpulorbis*, with 1–2 whorls; the velum is reduced and the liberated embryo settles at once, without any stage of free-swimming.

*Vermetus adansonii*, as illustrated in Text-figs. 12A–D has a head and foot greatly recalling those of *Serpulorbis*. The head with its contained buccal mass is undoubtedly massive in life, but its great size relatively to the foot may be in part the result of unequal shrinkage of the latter in drying. The foot is naked on the terminal disc except for a small concave saucer-shaped operculum, about one quarter the diameter of the foot after preservation. Though smaller, it is a typical operculum derived from the *Petalocochnus* type with an upstanding spiral flange of 1–2 volutions. The very similar operculum of *V. triqueter* is illustrated in Text-fig. 11. There is no *a priori* reason for expecting the reduction (or total loss) of the operculum to be a monophyletic happening in the Vermetidae; but there does in fact appear to be a strong affinity between these two species assigned to *Vermetus* s.s. and to all the *Serpulorbis* species examined.

The pedal tentacles of *V. adansonii* are especially long, and are finely tapered and whip-like. A further resemblance to *V. triqueter* is seen in the mantle cavity (Text-fig. 12C) where the gill is of the smallest proportions, with equilaterally triangular filaments, and the pedal gland as revealed in cross section is very large, one of the best developed among all the Vermetidae.

I could examine no female specimen of *V. adansonii*, and thus can report nothing about the condition of the capsule gland, or as to whether the mantle edge is deeply incised as in *V. triqueter*. A single embryo shell obtained is illustrated as Text-fig. 12E and exhibits a strong general resemblance to the conic-globose apex of *Serpulorbis* (see Keen, 1961).

The radulae of several species of *Serpulorbis* and of *Vermetus adansonii* share a strong similarity and are easily distinguishable from radulae of *Dendropoma* or of *Petalocochnus*. The median tooth is not rectangular with the addition of postero-lateral horns, but is roughly trapezoidal, with straight or somewhat convex sloping sides and a long median cusp. The postero-lateral corners are of even thickness with the rest of the tooth and are never built out into horn-like projections. The lateral teeth are not greatly different from those of *Dendropoma*, and the second marginal teeth are smooth of cusps or have a distally-directed spine rather less prominent than that of *Dendropoma*. They lack the four or five denticles of these teeth in *Petalocochnus*.

FIG. 12. *Vermetus adansonii*. A. The head, foot and anterior part of the pallial region in dorsal view. B. The same structures viewed from the right side. C. Diagrammatic transverse section through the pallial cavity. D. The head and foot viewed from above. E. The embryonic shell. F. A single row of teeth of the radula, omitting the marginals on the right side.

## 3. EVOLUTIONARY TRENDS IN THE VERMETIDAE

With knowledge of a wide enough range of characters, convergent evolution should be no impediment to natural arrangement. Convergence affects characters and seldom whole organisms, and though several characters may often be linked in an adaptive complex (here for example the gill, pedal gland and pedal tentacles concerned in feeding), and there generally remain some features not implicated in adaptation, and forming signposts to the lines of natural cleavage. The organism is a mosaic of characters evolving at different rates, and there is not one character which—studied alone—may not be misleading in classification. And insofar as the recognition of lines of descent is a respectable object of study, it is—like the delimitation of species—a product of the judgment of the investigator; there seems no formula by which the evolutionary importance of particular characters, or of degree of progress in different trends, can be made the objects of measurement. The phenotypic extent of a particular character may have no necessary correspondence with length of evolutionary time, or phylogenetic separation.

To discuss the evolution of a homogeneous family such as the Vermetidae, one must consider the *evolutionary trends* running through the group: a number of these will be separately recognizable, usually proceeding without detailed correspondence with each other. Trends are characterized by direction; and to recognize the primitive condition and direction of advance is again a matter of judgment. With hard parts one could look ideally at the fossil record, but this is frequently lacking and always so with soft tissues. Several rules may, however, be followed, whether by analogy with other prosobranch groups, or from correlation of structure with known function in the Vermetidae itself. Evolution proceeds from the general to the novel, from structures widely possessed to structures specially adapted. For example, gill filaments narrow and linear may reasonably be derived from broad triangular ones characteristic of prosobranchs as a whole. The mantle slit of the female *Serpulorbis* is an advanced feature as compared with the lack of it. A multispiral apex is generally held to have given rise to a paucispiral one and not the reverse (see Finlay, 1931; Thorson, 1950), and is in turn to be correlated with a change from free-swimming veligers to retained young. Both the high elaboration and the loss of the operculum may be regarded as conditions subsequent to the possession of a normal sized unelaborated operculum.

Table 1 sums up the evolutionary trends that will be considered in the following discussion. The presumed primitive condition is set out in the central column, and the columns to left and right show the one or more derived conditions represented in various parts of the family. The content of the "derived" columns of the left and right will be found—on reference to the schematic diagram on the opposite page—to be selected according to the views advanced in this paper as to the derived condition of *Dendropoma* and *Serpulorbis* with respect to the more "central" genera within the Vermetidae. The shading conventions, whether black or vertical or cross-hatched are chosen to represent differently specialized conditions of each character, corresponding to different genera.

## (i) THE APEX

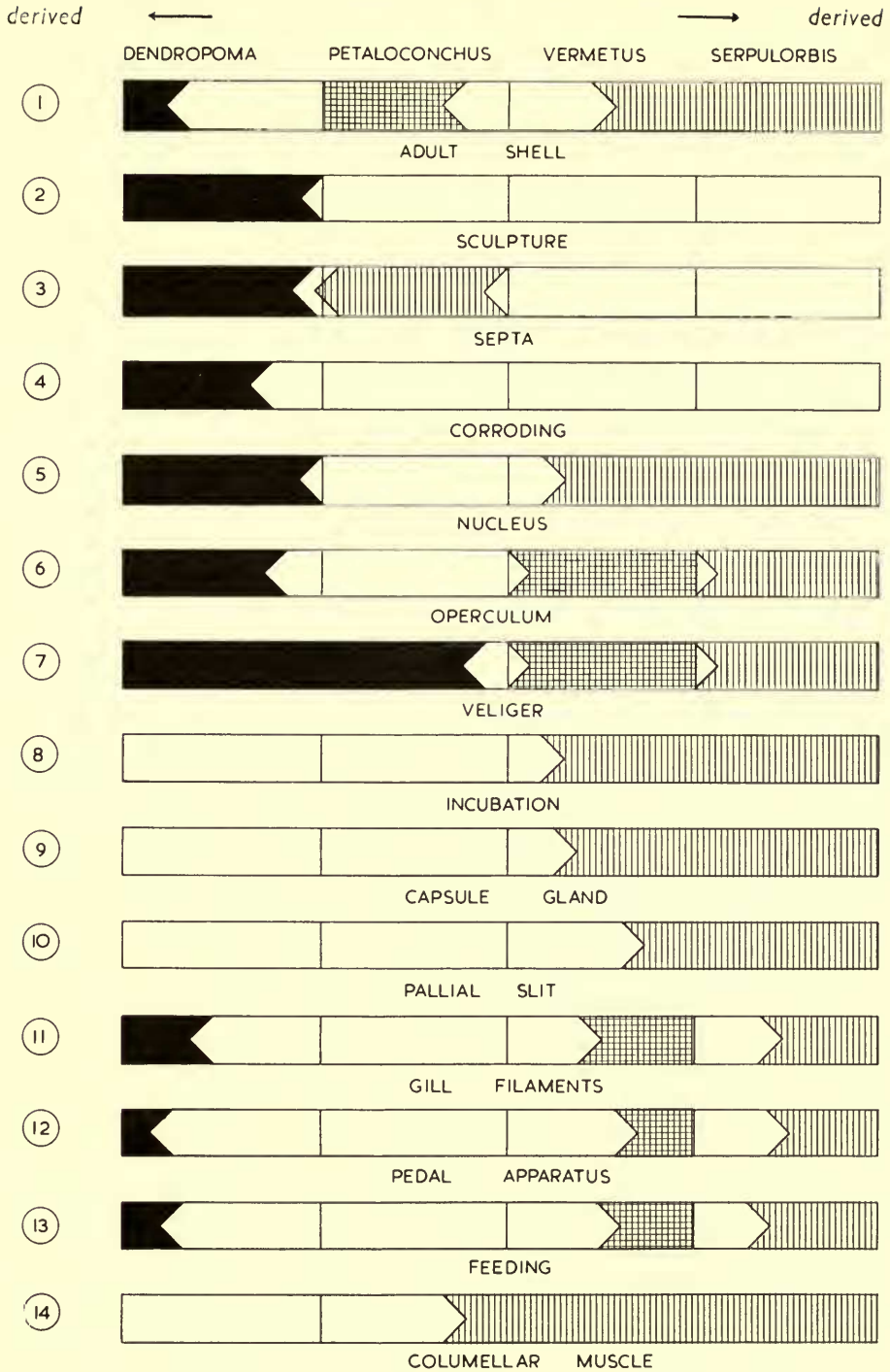
The young vermetid just before settlement is closer in form than it will ever be afterwards to more normal gastropods. As Dr. Keen has shown, the first vermetid peculiarity appears at the time of attachment when the helicoid embryo shell settles upon its side and the direction of coiling is changed, as the first post-embryonic whorls become attached to the substrate. Such a movement of the axis of volution through  $90^\circ$  is the salient distinguishing feature of the apex of a true vermetid. The apex would seem, moreover, to provide one of the most reliable taxonomic characters at generic and specific level, yet even this is not wholly free from adaptive involvements. Finlay (1931), Thorson (1950) and others have shown the correlation for prosobranchs in general of a smaller multispiral apex with smaller sized eggs and free-swimming veligers, and of a larger paucispiral apex with larger eggs and the suppression of free-swimming. In the Vermetidae we find apices with the largest number of whorls (3-4) in *Petalocochnus*. *Serpulorbis* has usually two to three whorls and the larger apex of *Dendropoma* has typically one-and-a-half whorls. Finlay has postulated that the reduced paucispiral apex never gives rise to the multispiral but that evolution in the other direction frequently occurs. We know accurately the life history of very few vermetids. For *Serpulorbis aotearoicus*, I have shown conclusively (Morton, 1951a) that there is no free-swimming stage and that the actively crawling embryo attaches very shortly after emergence from the maternal shell (see Text-fig. 8G). The eggs are few (c. 10) and large. We may clearly infer the same condition for *Vermetus triqueter*, and so far as we can tell this appears to be the more general vermetid rule. There is a relative lack of any records of known vermetid larvae from the plankton (see, however, Lebour, 1945). We have, however, the interesting case of *Serpulorbis imbricata* which releases free-swimming larvae with well-developed four-lobed vela. The eggs here are very much smaller and more numerous than in *S. aotearoicus*, lying in a row of 20-30 attached capsules, each with some 70 or 80 eggs of which some are devoured as nurse eggs by other embryos. The apex of *S. imbricatus* is long-spined for a *Serpulorbis*, with three-and-a-half whorls at settlement. *S. aotearoicus* settles with only two whorls. Its velum, though small and not divided into lobes, is still prominent, with its cilia beating while still within the embryonic capsule; larval retention is evidently a phylogenetically recent development in this genus. *Vermetus triqueter* exhibits retained veligers at much the same level of development. If we may take the number of apical whorls as a provisional index to the type of life history, we would expect in *Dendropoma*—a derived group with a large paucispiral apex—to find no free-swimmers. The New Zealand *D. (Novastoa) lamellosum* certainly hatches crawling embryos direct (Morton, 1951a). *Petalocochnus* has a small rather cylindrical apex, regularly of three to four whorls; *Serpulorbis* has a rather more conical to ovoid apex, with the whorl number two to three and subject to reduction. From the apex of *Petalocochnus* we should be tempted to look in this genus for species with free-swimming veligers<sup>1</sup>; the oldest embryos retained in the mantle cavity

<sup>1</sup> Since this was written, Robertson (*in litteris*) advises me that he has observed the free-swimming veligers of *Petalocochnus nigricans* at Bimini, Bahamas.

TABLE I. EVOLUTIONARY TRENDS

<i>Derived</i>		<i>Primitive</i>	<i>Derived</i>
Adult shell a straight upright tube	1	Adult shell an open, sometimes irregular spiral of several turns	
Sinous growth lines predominate, often with sharp ridges or toothed keel	2	Sculpture both transverse and longitudinal, often cancellated	
Shell with internal transverse septa	3	Shell lacking internal subdivision	Shell with internal longitudinal lamellae
Shell corroding the substratum	4	Shell applied to surface of substratum	
Nucleus reduced to 1-2 whorls	5	Nucleus small and multi-spiral, of 4-5 whorls	
Operculum with an axial mamilla and variously enlarged and strengthened	6	Operculum a thin saucer, sometimes with a spiral flange	Operculum reduced to a button or lost in adult
Free-swimming stage lost, eggs larger and few	7	Numerous small egg and free-swimming veligers	
	8	Egg capsules lie freely in the mantle cavity	Egg capsules attached to inside of shell
	9	Capsule gland a long furrow	Capsule gland short and purse-like
	10	Mantle of female entire	Mantle of female with median incision
Gill filaments narrow and tending to elongate	11	Gill filaments large and triangular	Gill filaments triangular but reduced in size
Gland and tentacles reduced	12	Pedal gland large and tentacles moderately long	Gland and tentacles very large
Ciliary feeding predominates	13	Mixed ciliary and mucous feeding	Mucous feeding predominates
	14	Columellar muscle short and inserted far forward	Columellar muscle a long strap deeply inserted





of *P. montereyensis* had only two to two-and-a-half whorls, suggesting a further pre-settlement period, possible free-swimming, before the growth of the embryo shell is completed. In *Serpulorbis* free-swimming is to be suspected in those species with more whorls (as in *imbricata*) and the free-swimming habit was perhaps abandoned in other *Serpulorbis* species more recently than in *Dendropoma*. The greatest gap in our knowledge is of the life history of *Petalconchus*: fortunately there are several American species from which this may be remedied.

#### (ii) THE ADULT SHELL

The disposition and coiling of the post-embryonic and adult tube is—as Dr. Keen has shown—of a characteristic type for each of the vermetid genera. This pattern is seldom likely to have adaptive significance, although the straight upturned terminal part of the tube is probably so disposed as to assist the putting out of mucous traps with the minimum of impediment from the substratum or from adjacent tubes. It is not easy to discern evolutionary trends in coiling pattern: each type, as for example the Greek key of *Dendropoma* or the Turritella pushed sideways of *Petalconchus*, may be regarded as something *sui generis* and distinctive to its particular group. It is doubtful too whether the colonial habit and massive crowding of tubes is of any phylogenetic value. This occurs in some species of both *Petalconchus* and *Dendropoma* (in the latter Dr. Keen has suggested it as a character in the recognition of the subgenus *Novastoa*). The larger tubes of *Serpulorbis* tend more often to be solitary or more loosely clustered; but crowded aggregates may be found as, for example, in *S. squamigerus* where this habit is associated with the communal mess table contributed by the pedal glands of many individuals.

Certain other features of the shell in *Dendropoma* may, however, be regarded as specialised and advanced. The corroding habit is very characteristic and is exclusive to this genus; so too is the tendency to a greater or lesser degree to straighten up the adult shell into a long cylinder as in *D. maximum*. Further, we find in *Dendropoma* the most specialised sculptural characters: the emphasis of transverse ribbing with sharp upstanding incremental growth lines, to the exclusion of longitudinal sculpture, and the frequent development of spines or beaked projections, well seen, for example, in *D. (Novastoa) lamellosa* (Text-fig. 3A). In the remaining genera both transverse and longitudinal sculpture is very generally retained, equally and moderately developed, with a tendency towards cancellation.

Internal septation of the shell is most frequent in *Dendropoma*. The early parts of the tube become cut off by apertually concave septa, associated with the shortening of the visceral mass, often seen in *Novastoa* and particularly characteristic of *D. maximum*, so that the animal is plump and finger-shaped, no longer occupying the earlier convolutions of the tube. This in turn may be correlated with the large operculum which cannot be withdrawn into the shell and prevents deep retreat into the disused earlier portions. Another type of closing off of the earlier shell is practised in *Petalconchus*, which lays down two longitudinal lamellae dividing the earlier tube into two passages communicating by a narrow slit. Only one of these appears to be occupied by the "tail" of the animal which carries (see Text-fig. 6A)

a long narrow extension into which the gonad may extend beyond the tip of the digestive gland.

### (iii) THE OPERCULUM

The earliest operculum of the vermetid embryo is a circular, flat or shallowly concave, chitinous plate covering and overlapping the back of the foot. It is illustrated for *Serpulorbis aotearoicus* in Text-fig. 8J, and for *Dendropoma irregulare* in Text-fig. 4B. In those adults that possess it the operculum is also circular, and in *Petalconchus* extends slightly, in *Dendropoma* considerably, beyond the edges of the foot. In *Vermetus* s.s. the operculum is reduced to a tiny button, towards the centre of the foot and in *Serpulorbis* it is wholly lost. In the re-organised adult foot the upward-facing disc that bears the operculum is not, of course, the sole, but corresponds to the back of the metapodium; the true sole is reduced to a narrow triangular area, squeezed up in the middle line between the terminal disc and the proboscis. It is flanked by the two pedal tentacles, between which, and in front of the sole, opens the duct from the pedal gland. In adult *Petalconchus* the operculum remains thin and fragile, forming a transparent saucer, not too greatly overlapping for the foot to be withdrawn deeply into the tube. Its line of spiral coiling is raised into a sharp, upstanding spiral flange. The reduced operculum of *Vermetus* s.s. is of the same type which appears to be the earliest and simplest found in a vermetid adult.

In *Dendropoma* the operculum usually becomes highly elaborated and is always large, overlapping the foot and sealing the aperture to such an extent that the animal can retreat only slightly or not at all into the tube. Mörch's valid generic name is descriptively inappropriate; the animal is quite innocent of any branching structure on the operculum. (Could the author have taken for a *lituellus* operculum that of a *Stephopoma* species having multifid opercular setae? Or were the opercula of his specimens bedecked, as occasionally happens, with calcareous algae?) The dendropomatid operculum may be massively thickened, sometimes built up into a solid dome and often calcified. The earliest species show affinities with the opercula of *Petalconchus*, as in *D. senegalense*, where the operculum still carries a spiral flange, but is deeply concave, inserted into the foot by a broad conical base. This is strengthened by the development of a dense axial mamilla, projecting upwards as a rounded boss in the exposed concavity. *D. megamastum* shows a similar operculum without, however, the spiral flange and *D. maximum* has the same concave bowl, but with neither spiral flange nor mamilla, or the latter very small. On the other hand, *D. (Novastoa) lamellosum* has the mamilla greatly enlarged to form an axial pillar with its rounded tip deeply inserted into the foot below, and its exposed end bluntly truncate. A further group of *Dendropoma* species, especially some of those colonial forms of smaller size, have the operculum convexly built up on top by the thickening of its own substance. In *D. irregulare*, *D. tholia*, and *D. ghanaense*, it forms a convex dome with the axial pillar running through it. (See Text-fig. 15 for range of opercular structure in *Dendropoma*.)

The reduction and loss of the operculum in *Vermetus* s.s. and *Serpulorbis* is clearly

a derived condition ; so is its elaboration in *Dendropoma*, with the domed opercula of *corrodens*, *tholia* and *corallinaceum* evidently most advanced. It is suggested that the primitive adult operculum is most closely approached by species of *Petaloconchus*, where the spiral flange—though possibly not primitive—has been found in all representatives studied. The embryonic operculum is an even simpler concave plate.

(iv) CILIARY AND MUCOUS  
FEEDING AND RELATED ADAPTATIONS

In the following species only is the mode of feeding known from direct observations of the living animal :—

Species	Feeding	Authority
<i>Serpulorbis gigas</i>	Entirely mucous	Boettger, 1930
<i>Serpulorbis aotearoicus</i> and <i>S. zelandicus</i>	Mixed ciliary and mucous	Morton, 1951a
<i>Serpulorbis squamigerus</i>	Entirely mucous with a communal mess-table	MacGinitie & MacGinitie, 1948
<i>Petaloconchus nigricans</i>	Ciliary mucous with a smaller amount of ciliary	Robertson (1959), ( <i>in litt.</i> )
<i>Serpulorbis</i> sp.	Mucous ; ciliary not observed	Keen (1959), ( <i>in litt.</i> )
<i>Dendropoma maximum</i>	Entirely ciliary	Yonge, 1932
<i>Dendropoma lamellosa</i>	Chiefly ciliary, with a smaller amount of mucous	Morton, 1951a
<i>Dendropoma irregulare</i>	Mixed mucous and ciliary	Robertson (1959), ( <i>in litt.</i> )

In *Serpulorbis gigas*, and *Serpulorbis squamigerus* (and also probably in *Vermetus triqueter*) on the one hand, and in *Dendropoma maximum* on the other, there is thus reported to be exclusive reliance on one feeding method with the abandonment of the other. The other species studied grade between these two extremes. In vermetids not yet investigated in life, the methods of feeding available are often a matter of reasonable inference from the anatomy : there are fortunately a number of structural characters that appear to be correlated with the predominance of one method or the other, though care should be taken not to exclude either method even upon what appear to be reasonable anatomical grounds.

Every known vermetid possesses a well-marked pedal mucous gland extending into the haemocoel alongside the oesophagus and opening in front of the foot between the two pedal tentacles. Yonge and Iles (1939) have well described its two extremes of development in *Serpulorbis gigas* and *Dendropoma maximum*. The homologies of the pedal gland are uncertain. In certain Rissoacea there is also an important pedal mucous gland of such a size as to have become haemocoelic in position ; Graham & Fretter regard this as a highly developed ventral pedal gland from the position of its opening upon the surface of the sole. In the Vermetidae, so far as the morphology of the vestigial foot can be regarded as clear, the mucous gland would appear to open at the anterior edge of the foot upon what corresponds to the metapodium, and its closest resemblances to be with the anterior pedal gland, generally and to a varying extent developed in prosobranchs. The Vermetidae have no very close known relatives to which we might turn for any clue as to the original



or intermediate condition of their mucous gland. Equally strikingly, it is present well-developed in every vermetid examined.

The homogeneity of this structure within the family, and the evidence of feeding habits within each of the four genera make it overwhelmingly likely that the gland was at its first appearance developed as a means of food-collecting. Contrary to the tentative view I have previously expressed (Morton, 1955), there seems every likelihood that mucous trap feeding was an early and probably an original activity of the Vermetidae. Of all mesogastropod families that are able to practise ciliary feeding, the Vermetidae have undergone the least specialization in the filaments of the gill or the other food collecting structures of the mantle cavity: ciliary feeding is a condition to which—as a family—they have never become deeply committed. With the exception of *Dendropoma maximum* it is probably the exclusive habit of rather rather few species. Nearly all vermetids probably make use of both methods of feeding.

Nevertheless, the most extreme development of mucous feeding, with the greatest enlargement of the mucous gland and—in particular—the elongation of the pedal tentacles and the reduction in extent of the gill are evidently a later feature confined to *Vermetus* s.s. and *Serpulorbis*. Even in species where this would seem anatomically unlikely, particles are collected within the mantle cavity and carried forward on the right side to the neighbourhood of the mouth in a food groove or open tract of varying elaborateness.

The retention of an operculum spreading widely beyond the margin of the foot, and the small or even rudimentary condition of the pedal tentacles, cannot have favoured development of mucous feeding, and where we find this condition, as in *Petalococonchus* and particularly in *Dendropoma*, an admixture of ciliary with mucous feeding has generally been shown to occur. More evidence on the feeding habits of species of *Petalococonchus* will be eagerly awaited, in particular the publication of Robertson's full report. The pedal gland of both *P. montereyensis* and also of *V. (Thylaeodus) contortus*, though narrow, is very large as a result of the great prolongation of the pallial region. Here the operculum overlaps the foot only relatively slightly; and in *P. nigricans*, reported by Robertson to feed by mucous traps, there is no overlap at all. There would appear to be little in the anatomy of the genus *Petalococonchus* to disable its members from either type of feeding. The provisional view may be taken that the original feeding habit of the Vermetidae included resort to both mucous and ciliary means, and that the genus *Petalococonchus* most nearly represents this condition. In their feeding organs, as in much of the rest of their anatomy, the two species of *Vermetus* s.s. examined come very close to *Serpulorbis* and cannot be considered unspecialized. At the other extreme, the genus *Dendropoma* has in many of its species retained a primitive ability to collect food by ciliary means, and has in at least one species developed this method exclusively.

It has often been suggested, as by Yonge and Iles (1939), and in my own papers on New Zealand vermetids, that there is an ecological correlation with the mode of feeding. Without more knowledge of the distribution of feeding habits within the

family, it is difficult to generalise. In exposed situations with continually broken waters and wave disturbance, mucous traps might be difficult to put out or to maintain successfully and ciliary feeding might be expected to be best developed. The outstanding example is *Dendropoma maximum*, living on the surf-beaten outer ramparts of the Great Barrier Reef. In general it may be said of *Dendropoma* that the typical ecological form is that of small to medium-sized vermetids, frequently colonial and zone-forming on the exposed surfaces of open shores, and often deeply impacted in coralline algae or eroding the substrate during their growth. *D. (Novastoa) lamellosa* in New Zealand is an intertidal animal diagnostic of exposed off-shore islands with considerable wave attack. *D. irregulare* in the West Indies would appear to be an inhabitant of coralline-encrusted, very wave-exposed rocks. On the other hand, these two species, like *Petalconchus nigricans*, also occurring in rough water, are able to practise varying amounts of mucous feeding.

In *Serpulorbis* and *Vermetus* s.s. on the other hand, we may recognise a general preference for quieter and more sheltered situations, though there are numerous exceptions. These vermetids are frequently solitary or semi-solitary, grow to a larger size, with the shells often emergent above the substratum, never corroding and seldom becoming encrusted. They are frequently found beneath rocks or protected by ledges where mucous traps could best be employed without disturbance, extending freely into still water until hauled in. The under-stones or sheltered habitat is so far as I know unrecorded for species of *Dendropoma*.

Reduction and loss of the operculum is correlated in *Serpulorbis* and *Vermetus* s.s. with a greater perfection of mucous feeding. Whether the condition of the operculum has had a "pre-adaptive" influence in determining the mode or predominance of feeding, it is difficult to determine. These different adaptive trends are obviously interwoven, but to discern any simple cause and effect relation between them may be to oversimplify.

But the condition of the operculum carries in its train other adaptive implications. Thus, in *Dendropoma*—with an operculum as wide as the shell tube—the animal cannot retreat for long distances into the tube, although its quickness of response in darting back and closing the tube with the operculum is very striking. In *Petalconchus* with the operculum not quite so wide as the tube, and in *Vermetus* and *Serpulorbis* with it reduced or lacking, the animal on disturbance retreats deeply into the earlier reaches of the tube and with the loss of the operculum this is the chief protection from attack. *Dendropoma* will then retain a more or less constant position of the animal in the distal and later formed part of the tube. The columellar muscle is a short and thick strap forming the structural support of the pallial region as it runs forward to become continuous with the foot. It attaches somewhat distally to the tube at the level of the anterior half of the body. In *Petalconchus* and *Serpulorbis* the columellar muscle is more slender, plays less part in the structural support of the pallial region of the body, and becomes drawn out into a narrow strip that extends far backwards into the tube alongside and independent of the rest of the body. Its posterior insertion marks the deepest point towards which the anterior half of the body can be drawn back, with the visceral mass sliding freely behind it.

This reaction takes place in a flash when the animal is disturbed and disappears beyond sight into the earlier coils of the shell. In correlation with the lesser use made of the deeper parts of the tube, we find the tendency in many species of *Dendropoma* to cut off the earlier parts of the tube by aperturally concave septa. In this way the body of the animal may become considerably foreshortened. Compare, for example, the finger-shaped body of *D. maximum* with the limp, vermiform visceral mass in most *Serpulorbis*, or the many-coiled, slenderly elongate animal of *Petalococonchus*. In some specimens of most *Dendropoma* species, the visceral mass is truncate and foreshortened, in other specimens the full visceral spiral will be found. This tendency seems to have proceeded furthest in *D. maximum*, where the animal is hardly if at all curved, and lies entirely in the straight terminal part of the tube. The formation of shell septa is unusual in *Serpulorbis*, being not mentioned as a diagnostic character by Keen (1961), though I have found aperturally concave septa in *Serpulorbis zelandicus* (see Morton, 1951a, page 4).

Deep retreat into the tube has its effects in turn on the mode of protection of the eggs, which in this family can take place in one of two main ways. First, in *Dendropoma* and *Petalococonchus* up to a dozen egg clusters lie freely in the mantle cavity of the female, in a single row reaching from near the mantle edge to the top of the mantle cavity, beneath or to the right of the rectum, on the side away from the gill. In *Vermetus* s.s. (at least in *V. triqueter*) and in all species of *Serpulorbis* I have seen, the egg capsules are contained in a row of teardrop-shaped capsules attached by short stalks to the inner surface of the shell of the female. These lie in a median row of a dozen or fewer, reaching nearly to the aperture of the tube. The mantle of the female is deeply incised to allow the egg capsules, while remaining fixed to the shell, to lie within the mantle cavity of the expanded animal. On retreat the animal leaves the attached eggs unguarded near the shell aperture and darts back without them. Eggs retained fully in the mantle cavity as in *Dendropoma* would be crushed or damaged on retreat by the retraction into the mantle space of the foreshortened and thickened head and foot. There would be no room for both. In *Serpulorbis* the foot is softer and more flexible than the muscular plug of *Dendropoma* and can be contracted away from the egg capsules as it passes them on going down into the shell. In *Petalococonchus* deep retreat is still, however, possible with eggs lying freely in the mantle cavity and carried back with the animal. Here—as will be seen from Text-fig. 6A, B—the mantle cavity is usually much longer than in *Serpulorbis* and the egg capsules are not individually so bulky, each appearing to contain a single embryo only. The head too seems to have a smaller bulk and to lie flatter against the contour of the foot than in *Serpulorbis*. It must on retreat present less obstruction to the eggs which—as in *M. montereyensis*—lie to one side of it, on the right of the mantle cavity. The prominent bulge of the head in *Serpulorbis*—it may be almost as large as the foot—is (as has been mentioned) due to the enlargement of the buccal mass, which in mucous trap feeders serves not only to rake in food boluses but in addition to haul downwards the bulky mucous traps before ingesting them.



## (v) REPRODUCTIVE SYSTEM

A thorough examination of the structure and action of the genital ducts in female vermetids is much needed ; only the short account for *Serpulorbis* by Morton (1951a) has given this system more than glancing mention. Like other attached and non-motile prosobranchs (except the Calyptraeidae) the Vermetidae are aphyllic. Gregarious habits will ensure that sperm released into the water by the male is carried into the mantle cavity of the female in her inhalant current ; and the pallial genital duct of the female consists of a glandular tube widely slit open down one side to receive the sperm (see Fretter (1946) on *Turritella*). The ovary leads into a narrow prominal ovarian duct carrying the ova to a small spherical albumen gland lying at the posterior end of the mantle cavity on the right side. This opens into the much longer, ventrally open capsule gland. At the junction of these two glands, open one or more tiny rounded pouches, forming together a receptaculum seminis where incoming sperm lie oriented by their heads to the lining epithelium.

In *Dendropoma*, see for example *D. maximum*, the capsule gland is a very long furrow, lined with a thick secreting wall on either side and open in the ventral line. It extends forward along the mantle wall ventrally to the rectum and reaches as far as the anus. It secretes the thin horny capsules round the long row of eggs or egg clusters that first lie within it, and are then turned out to remain freely within the right side of the mantle cavity until the crawling shelled embryos emerge. The female of *Petalconchus* has a similar genital duct. (See Text-fig. 6B, c).

In *Serpulorbis* on the other hand, the capsule gland is a short semicircular pouch open along its straight side, and much more confined to the posterior part of the mantle cavity. It is situated just behind and to the right of the median pallial incision. A single egg capsule at a time is elaborated in it and completely fills its lumen. These capsules are one by one attached to the lining of the shell, the oldest lying in front. The ventral opening of the capsule gland can by means of the pallial incision be brought into direct contact with the lining of the shell as the egg capsules are extended.

## (vi) THE RADULA

Where uniformity of diet within a family can be known or reasonably assumed, the radula is often found to provide detailed taxonomic differences apparently unrelated to differences in habit. Sometimes, as for example in the ciliary feeding mesogastropod family Struthiolariidae, the diagnostic differences in the cusp pattern of the reduced radula must have been developed well below the minimum size level of adaptive play (Morton, 1956b). In the Vermetidae, though the radula is short and "S"-shaped, with the upturned tip of its sac hidden beneath the buccal mass, the teeth are still somewhat robust. As in most ciliary feeding gastropods, the erectile laterals and marginals serve to seize boluses of mucus-bound food. In mucous trap feeders especially the paired, sharp-edged lateral jaws play an active role in grasping the food bolus ; a medium-sized *Serpulorbis* will firmly seize and hold a needle tip placed between the jaws.

The radula is a conservative structure within the family Vermetidae, and is in



the first place useful in confirming the homogeneity of the family as a unit to the exclusion of *Stephopoma*, *Siliquaria* and *Vermicularia*. The main subdivision within the family is indicated by the shape of the central tooth. In the first group consisting of the operculate genera *Dendropoma* and *Petalococonchus*, the base of the central tooth is a squarish to rectangular transverse plate, with its posterior corners drawn out into very distinct curved or peg-like projecting horns. In the second group, consisting of the genera *Vermetus* s.s. and *Serpulorbis*, this central plate is distinctly trapezoidal in shape, a good deal wider across the posterior than the anterior edge, and its posterior corners are provided with prominent horns. The

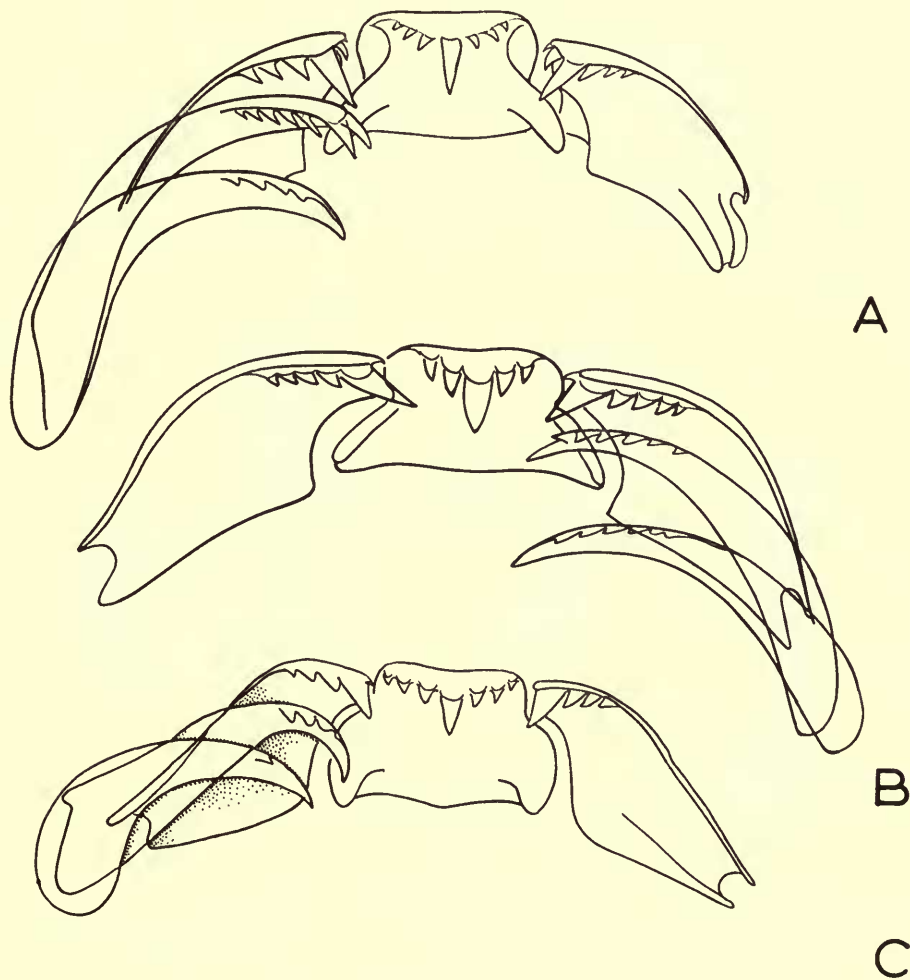


FIG. 13. Single rows of teeth from the radula of selected species of Vermetidae. The marginal teeth are variously omitted from one or other side. A. *Vermetus* (*Thylaeodus*) *contortus*. B. *Petalococonchus montereyensis*. C. *Dendropoma corallinaceum*.

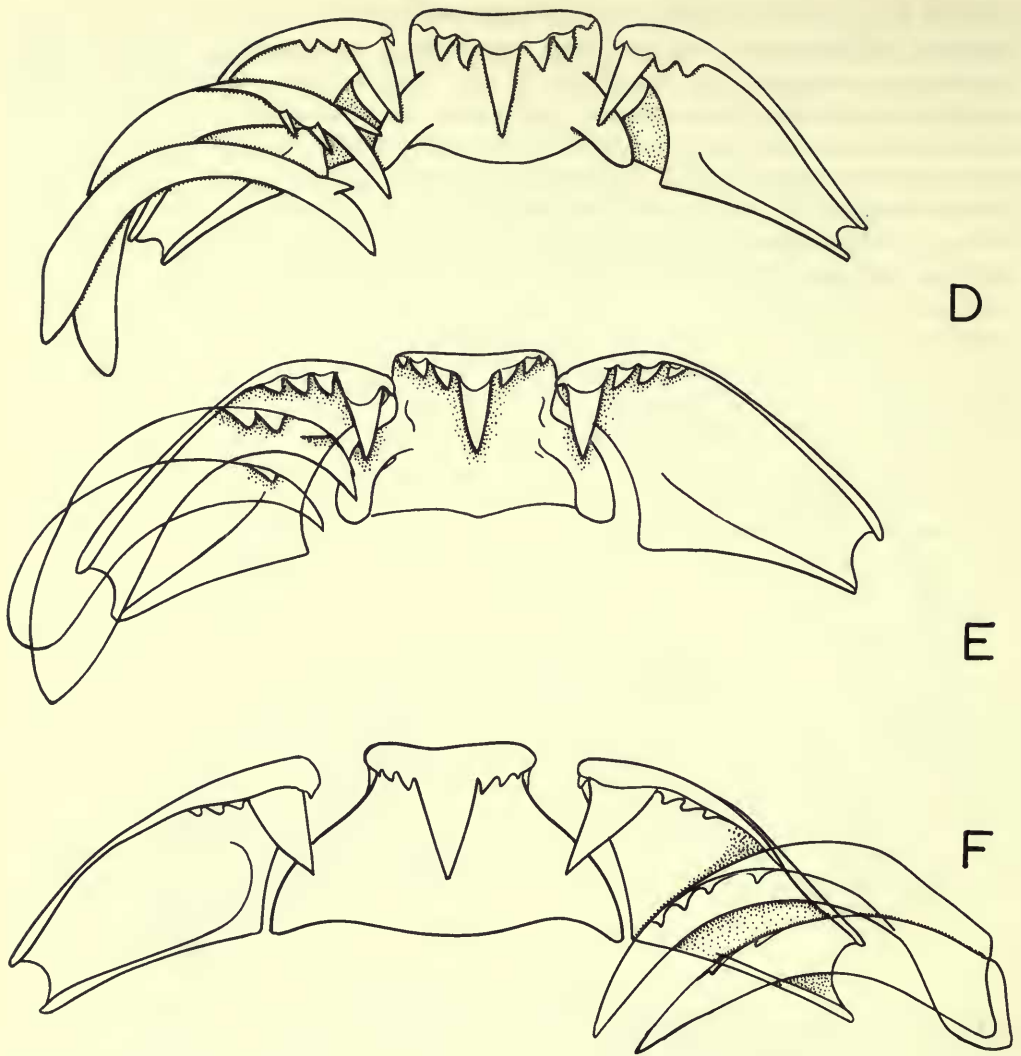


FIG 13 (continued)

D. *Dendropoma ghanaense*. E. *Dendropoma tholia*. F. *Serpulorbis zelandicus*.

(Compare also with *Vermetus adansonii*, Text-fig. 12F)

marginal teeth provide a further distinction between *Dendropoma* and such species as *Petalconchus* as I have been able to examine. In *Dendropoma*, the first marginal bears just behind the tip a group of usually two sharp serrations on either side, distally to which is a spine-like apically-directed denticle. The second marginal bears this denticle alone, lacking other serrations. In the first marginal of *Petalconchus* the serrations are five in number on either side of the tooth, with the spine-like denticle again directed apically. The second marginal has no spine-like

denticle, only a line of five very reduced serrations at either edge. In *Serpulorbis* the first marginal bears two or three serrations at either edge, and the second marginal a reduced spine-like denticle alone. (See Text-figs. 13A-F for generically typically radulae.)

## (vii) PHYLOGENY

The facts now established about the animals of 20 species of the Vermetidae, and such insight as we have gained into the relation of structure to habits, invite some consideration of the possible lines of descent and relationships of the vermetid genera. In my shorter review of vermetid adaptations (Morton, 1955), after severing the Siliquariidae and *Vermicularia* from the Vermetidae, I proposed a dichotomy of the family into two lines, the one characterized by predominantly ciliary feeding and retaining the operculum (the "genera" now grouped in *Dendropoma* and *Petalocochus*), and the other comprising chiefly mucous feeders with reduction or loss of the operculum (now *Vermetus* s.s. and *Serpulorbis*). While such a division still broadly holds good, certain of my previous conclusions require modification, after access to a wider range of species. First, I can no longer advocate the basically primitive position assigned to "*Vermetus novae-hollandiae*" (= *Dendropoma*

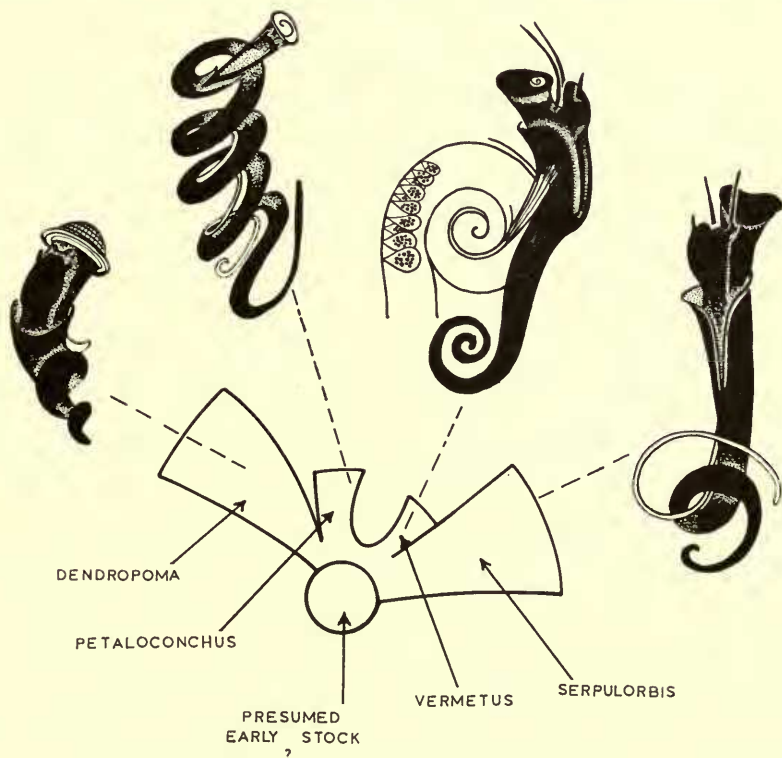


FIG. 14. A diagram of the evolutionary radiation of the genera of the Vermetidae as suggested in the accompanying discussion.

*maximum*), on the basis of its feeding habits and operculum. This species has proved in many ways a misleading example of its genus, giving little indication of the full extent of opercular evolution now disclosed in *Dendropoma*. Its operculum is shallowly concave with neither the calcified mamilla nor the high development of the chitinous disc found in most members of the genus. It recalls much more indeed the simple opercular type found in the embryos of the vermetids in general. Further, the advanced sculptural features of the shell, the corroding habit and the very characteristic nucleus, together with the late appearance—so far as is known—of the genus in time, must clearly disqualify *Dendropoma* as a whole from any primitive relation with the rest of the vermetids. This genus, on the one hand, and the mucous-feeding *Serpulorbis* on the other, represent advanced forms that have followed divergent paths.

The derived condition of *Dendropoma* throws doubt in turn on my assumption that ciliary feeding was the sole primitive habit of the Vermetidae. In particular, such a view would leave unexplained the presence of a pedal mucous gland and pedal tentacles in every vermetid studied. I suggested previously that the function of this gland in its relatively small state in *Dendropoma maximum* was merely to cleanse the surface of the foot of waste particles alighting upon it, and that in *D. lamellosa* it had begun to assume some role in the feeding process. I think it safer, however, until we have actual observations of feeding in more living vermetid material, to suppose that the most general and primitive condition included the ability to collect food by both ciliary and mucous means (see page 619). Such a condition is indeed found in *D. lamellosa*, *D. irregularis*, *Petaloconchus nigricans*, *Serpulorbis zelandicus* and *S. aotearoicus*. The exclusive or predominant use of ciliary feeding would then be a later development of a few species like *Dendropoma maximum*, while among the most advanced species of *Serpulorbis* the gill has become very small and the animal develops by contrast a total reliance on mucous trap feeding.

The primitive features of *Dendropoma* are indeed much more apparent in the status of the animal than of the shell. They include the retention of the operculum the relatively small size of the mucous gland and pedal tentacles, the lack of reduction of the gill, and the lack of a pallial fissure or of shell attachment of the eggs in the female. All these features are, however, equally characteristic of *Petaloconchus*, a genus of which I have had little chance till recently for full examination of animals. *Petaloconchus*, moreover, lacks the advanced character of the operculum and the apex. Here the operculum is thin and fragile, only slightly, if at all, overlapping the foot, capable of withdrawal into the shell and distinguishable from the larval operculum only in the raised spiral flange of its free surface. The apex is multispiral, with three to four whorls. In *P. montereyensis* and in *P. nigricans* the pedal mucous gland and pedal tentacles are of moderate size and the gill shows primitively triangular filaments with little sign of reduction. There is no channelled food groove as in some *Dendropoma*, and it is a fair inference from anatomy that most *Petaloconchus* possess both modes of food collecting, neither excessively developed.

*Petaloconchus* has several features removing it from fully primitive rank, in particular the characteristic shell coiling which there is no reason to suppose was an



early feature in the family and the possession of a long tailpiece secreting longitudinal internal lamellae. In addition, there is no record of its early representation among fossil vermetids. The specialised features of the internal lamellae are avoided by forms like *Vermetus* (*Thylaeodus*) *contortus*, (otherwise a good *Petalococonchus*), *Vermetus adansonii* and *V. triqueter*, with long pedal tentacles and large mucous gland, and (at least in *V. triqueter*), with mantle slit, and shell attachment of eggs, seem thoroughly committed in the *Serpulorbis* direction of evolution.

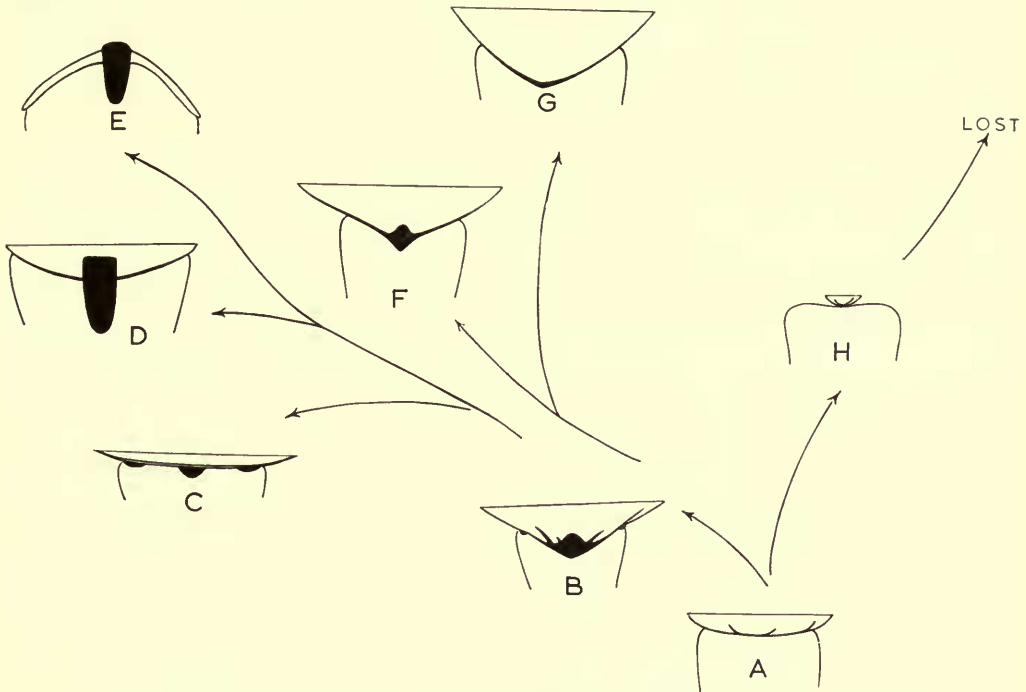


FIG. 15. A suggested sequence in the evolution of the operculum of the Vermetidae. A generalized basic form (lower right) represented by *Petalococonchus* species, is shown giving rise to the reduced condition in *Vermetus* and to the variant conditions found in *Dendropoma*. A. *Petalococonchus*. B. *Dendropoma marchadi*. C. *D. rastrum*. D. *D. lamellosa*. E. *D. thalia*. F. *D. megamastum*. G. *D. maximum*. H. *Vermetus*.

A more reliable approach to phylogeny, based on non-adaptive features, may stem from the evidence of the operculum and the apex; these features harmonise very well (see Text-figs. 14, 15), and they moreover agree with the tentative dichotomy—based on a study of the animal—suggested by me in 1955. On this basis, the multispiral apex of *Petalococonchus* would denote a central and primitive position, giving rise to the somewhat shorter-spined apex of most *Serpulorbis* and of *Vermetus* s.s. and to the large and paucispiral apex of *Dendropoma*. With differences in apex are to be expected differences in the life history and habits of the veliger. The genus *Dendropoma* is likely to have lost the free-swimming habits, but a free-swimming stage persists in at least one *Serpulorbis* species (*S. imbricata*) and should

be looked for in species of *Petalococonchus*.<sup>1</sup> Similarly with the opercula, *Petalococonchus* differs only from the larva in the spiral lamella acquired by its thin fragile operculum ; *Vermetus* s.s. has a similar operculum reduced to a vestigial button ; *Serpulorbis* has lost the operculum altogether and *Dendropoma* has become greatly specialized in the operculum, which develops a calcified axial mamilla and may consist of a concave bowl, a flat disc or a strong elevated dome. *Dendropoma marchadi* combines the characters of *Dendropoma* and *Petalococonchus*, with a concave bowl provided with both a mamilla and a spiral flange. As well as in the reduction of the operculum, *Vermetus* s.s. runs close to *Serpulorbis* in the high development of the pedal gland and pedal tentacles and in the pallial fissure and mode of attachment of the eggs. The radula abundantly confirms the relationship of *Serpulorbis* with *Vermetus* s.s. and also the approximation of *Petalococonchus* towards *Dendropoma*.

Evolution of vermetids is a mosaic affair ; and a common ancestor with the whole complex of assumed primitive characters we shall not expect to find ; the phyletic morphologist must be content if he can discern something of the direction and extent of the various evolutionary trends. This much can be tentatively claimed ; that the earliest vermetids must have possessed many of the features of the operculum and apex of *Petalococonchus* ; they must have already possessed pedal gland and pedal tentacles, employed for putting out feeding mucous traps to assist the ciliary action of the gill ; the gill retained its normal mesogastropod form, with the filaments unspecialized and triangular ; the foot carried a full-sized operculum, thin and flatly concave, possibly with a spiral flange ; the mantle of the female was entire, with the eggs lying unattached in the mantle cavity ; the shell had equally developed longitudinal and spiral sculpture, and showed neither corroding habit nor internal septa ; and the larva very probably showed a period of free-swimming.

*Serpulorbis*, according to Keen, appears earliest in time, in the Eocene. Species with the *Petalococonchus* mode of coiling are found first in the Early Miocene, *Dendropoma* doubtfully in the Oligocene. Palaeontological evidence would generally be allowed great weight in determining the early or primitive section of the Vermetidae. Yet in view of the lack of the apex or operculum in fossils, such evidence cannot be conclusive ; and the problem must be attacked independently by comparative morphology in its own right. In the sculpture and mode of coiling of the shell (as well as in the multispiral apex) *Serpulorbis* is suitably unspecialized for an early vermetid. Yet, as pointed out earlier, the animal discloses many advanced features. The operculum is lost, the pedal tentacles and mucous gland are highly emphasized, the mantle is slit in the female and the eggs are attached to the interior of the shell. The condition of *S. gigas*, with the gill reduced and functionless in feeding, may be held to represent the ultimate advance characteristic of this evolutionary line.

#### 4. ABSTRACT

The adaptive morphology of the Vermetidae is considered in the light of our knowledge of the habits and functions of the living animal, especially in relation to the mechanisms of mucous and ciliary feeding and the mode of brood protection.

<sup>1</sup> See Robertson's observation on *P. nigricans* (page 615).

In a larger range of species a comparative study has been made of the anatomical features of the animal, including the operculum, the organs of the pallial cavity, the radula and the rest of the digestive system, and the reproductive system. The bearing of this evidence upon evolution and phylogeny has been supported with a consideration of the embryonic shell.

The nature and direction of the evolutionary trends operating within this family has been discussed and a broad picture of the suggested generic relationships and divergence is presented. The family, as properly restricted, has been found to consist of a few well-marked genera ; and the naturalness of the four main genera, *Vermetus*, *Dendropoma*, *Petalococonchus* and *Serpulorbis*, in the sense proposed by Dr. Myra Keen, has been amply confirmed from the malacological standpoint.

#### 5. ACKNOWLEDGMENTS

During the whole course of my study of the Vermetidae, I have had access to the kindness and sound counsel of Dr. Myra Keen and have had the pleasure of collaborating with her both in correspondence and during her visit to London. My views upon the evolution of the Vermetidae owe very much to Dr. Keen's profound insight into the conchology and history of the family.

I wish also to acknowledge the courtesy and help of the Trustees and officers of the British Museum (Natural History) in making available for my study the whole range of the vermetid material represented in their spirit collections.

#### REFERENCES TO FIGURE CAPTIONS

ALB	albumen gland	M	mouth
AN	anus	MA CAV	mantle cavity
BCV	body cavity	MUC	mucus from pedal gland
BUC	buccal cavity	OD	odontophore
CAPS A	aperture of capsule gland	OES	oesophagus
COL	columellar muscle	OP	operculum
CPS	capsule gland	OP M	opercular mamilla
CT	ctenidium	OS	osphradium
C TE	cephalic tentacle	OVD	oviduct
DIG	digestive gland	PA	mantle
DIG A	anterior lobe of digestive gland	PA C	cut edge of mantle
DIG P	posterior lobe of digestive gland	PA SL	pallial slit of female
E	eye	PD D	duct of pedal mucous gland
E CP	egg capsules	PD G	pedal mucous gland
EMB	embryos	PD T	pedal tentacle
F	foot	PR	proboscis
FAE	faecal pellets	RA	radula
F GR	food groove	RA S	radular sac
FL	gill filament	REC	receptaculum seminis
F TR	food tract	RM	rectum
GON	gonad	S	reduced sole of foot
HYP	hypobranchial gland	SAL	salivary gland
INT	intestine	SH	shell
J	jaw	ST	stomach
K	kidney	ST C	style sac
LAM	spiral lamella of operculum	VISC	visceral mass

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