

## The Evolution of Vermetid Gastropods

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SEVERAL FAMILIES of prosobranch gastropods are preadapted, by the possession of efficient cleansing mechanisms—the cilia and mucous tracts of the pallial cavity—to adopt a method of ciliary feeding. It is thence a natural development to take on an immobile habit, either buried beneath the surface of soft sand or mud (as in the Turritellidae [Yonge, 1946] or the Struthiolariidae [Morton, 1951a]); or attached firmly to a hard substratum (Calyptraeidae, Capulidae, and Vermetidae, [Yonge, 1938]). The gastropods known collectively as the vermetids are one of the most specialised of the latter groups: they have altogether abandoned the regular coiling of the typical gastropod and the shell has become untwisted and vermiform, attached to, or embedded in the substratum. In previous papers (1951a, 1951b, 1951c, 1953) the present writer has dealt in some detail with the structure and systematics of the vermetids, and it has been demonstrated that the classically recognised family Vermetidae must be broken into two very distinct groups—the Vermetidae s. str. and the Siliquariidae. Each of these has been derived, probably separately, from a free-moving regularly-coiled prosobranch stock. It has been thought useful here to sum up in a short space the adaptive features of these

two families and to discuss the separate evolutionary trends they have followed.

### THE VERMETIDAE

The first detailed accounts of the feeding habits or adaptive morphology of vermetids were given by Boettger (1930) with a description of *Serpulorbis gigas*, followed by Yonge (1932) with a discussion of *Vermetus novae-hollandiae* of the Great Barrier Reef. Yonge concluded, on the basis of the widely different feeding mechanisms revealed in *Serpulorbis gigas* and *Vermetus novae-hollandiae* (see also Yonge and Iles [1939]) that these two vermetids belonged to widely separate groups, and that "the taxonomy of the Vermetidae clearly requires revision in the light of these results." Yet in this series of genera, the result of further work (Morton, *op. cit.*) on *Serpulorbis* and *Novastoa* and a fuller knowledge of *Aletes* (McGinitie and McGinitie, 1949: 366) was to bring together a large range of forms into a single sequence and to show that the ciliary feeding in *Vermetus novae-hollandiae* and the mucous trap feeding of *Serpulorbis gigas* are the extreme forms in a single evolutionary process.

Of the genera now included within the Vermetidae s. str. seven are dealt with here, namely *Vermetus*, *Petalconchus*, *Novastoa*, *Spiroglyphus*, *Bivonia*, *Aletes*, and *Serpulorbis*. Of the two examples selected from *Serpulorbis*, *S. gigas*

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is a mucous trap feeder, and *S. zelandicus* differs widely from it, still making considerable use of its ciliary feeding mechanism.

We may regard *Vermetus novae-hollandiae* of Yonge's account (1932) as the most primitive known type of the Vermetidae (Fig. 1*a*). It is entirely a ciliary feeder, which must have been the original mode of life of all the Vermetidae after their development of the attached position; it lives cemented to coral or to calcareous algae on the wave-beaten shore line of the Great Barrier Reef and the tropical Pacific. Its shell tube is stout and straight with the sculpture concealed by encrusting growth. The foot is short and plug-shaped and bears a broad, saucer-shaped, chitinous operculum, overlapping a good deal at the sides of the foot. The gill is very large, and the ciliary currents, especially of the lateral and frontal fields, are very powerful. The filaments are, however, primitively triangular in shape, and form the least modified type of gill among the ciliary feeders discussed by Yonge (1938). There is a large pedal gland extending backwards from the haemocoel of the foot into the cavity of the head and trunk, below the buccal mass and alongside the oesophagus. The sole of the foot, which formed the original creeping surface, is now greatly reduced, forming a small triangular area immediately in front of the mouth. Mucus is discharged from the pedal gland upon this area of the foot through a duct opening immediately in front of the foot; its aperture is flanked by a pair of short, stout pedal tentacles, unciliated except for a groove along their mesial sides, by which mucous secretion is carried to their tips. So far as can be ascertained the mucus of the pedal gland has little or no connection with feeding in *Vermetus novae-hollandiae*—it appears to perform a role of cleansing the surface of the head and foot adjacent to the mouth and carrying away rejected particles. Within the mantle cavity, extending along the right side of the roof and the right side of the floor respectively, are two further mucous glands forming wide epithelial tracts.

The first is the hypobranchial gland forming a normal part of the pallial equipment in all prosobranchs and apparently little concerned with feeding in *Vermetus*. The other forms a food tract by which collected food particles deposited by the gill on the right side of the pallial floor are swept forward by long cilia to the region of the mouth, where they are seized, in small mucous boluses, by the radula.

Though powerfully ciliated, the gill filaments of *Vermetus novae-hollandiae* are otherwise little specialised, and it is probable that the Vermetidae first originated as ciliary feeders of a type like this species. In rough water on a wave-beaten shore ciliary feeding is obviously much more efficient than the use of mucous traps. Calm water and some amount of shelter are required, in order to allow the use of the pedal gland in feeding; which is done to some extent by almost all the remaining members of the family. In retaining the more primitive feeding mechanism of the family, *Vermetus novae-hollandiae* has remained well-adapted to life in rough water.

Two relatively primitive genera of the Vermetidae, which, like *Vermetus novae-hollandiae*, retain a fully developed operculum are the New Zealand *Novastoa* (Fig. 1*b*) and the American *Spiroglyphus*. From the structure of the operculum, the radula, and the embryonic shell, these two genera are evidently very closely related (Morton, (1951*c*)). A similar level of evolution has evidently been reached by the American *Petalconchus* which the writer has handled only as fixed material, and has not watched feed. In *Novastoa lamellosa*, which we may take as a stage of evolution next advanced upon *Vermetus novae-hollandiae*, the chief means of food collection is still by cilia, and this species frequents disturbed water where mucous traps would be liable to dislodgment (Cranwell and Moore, 1938). The filaments of the gill are triangular and rather unspecialised and the pallial cavity has a ciliated food tract along its right floor. Here, in addition, the pedal gland is a long, well-developed strap passing well backwards into

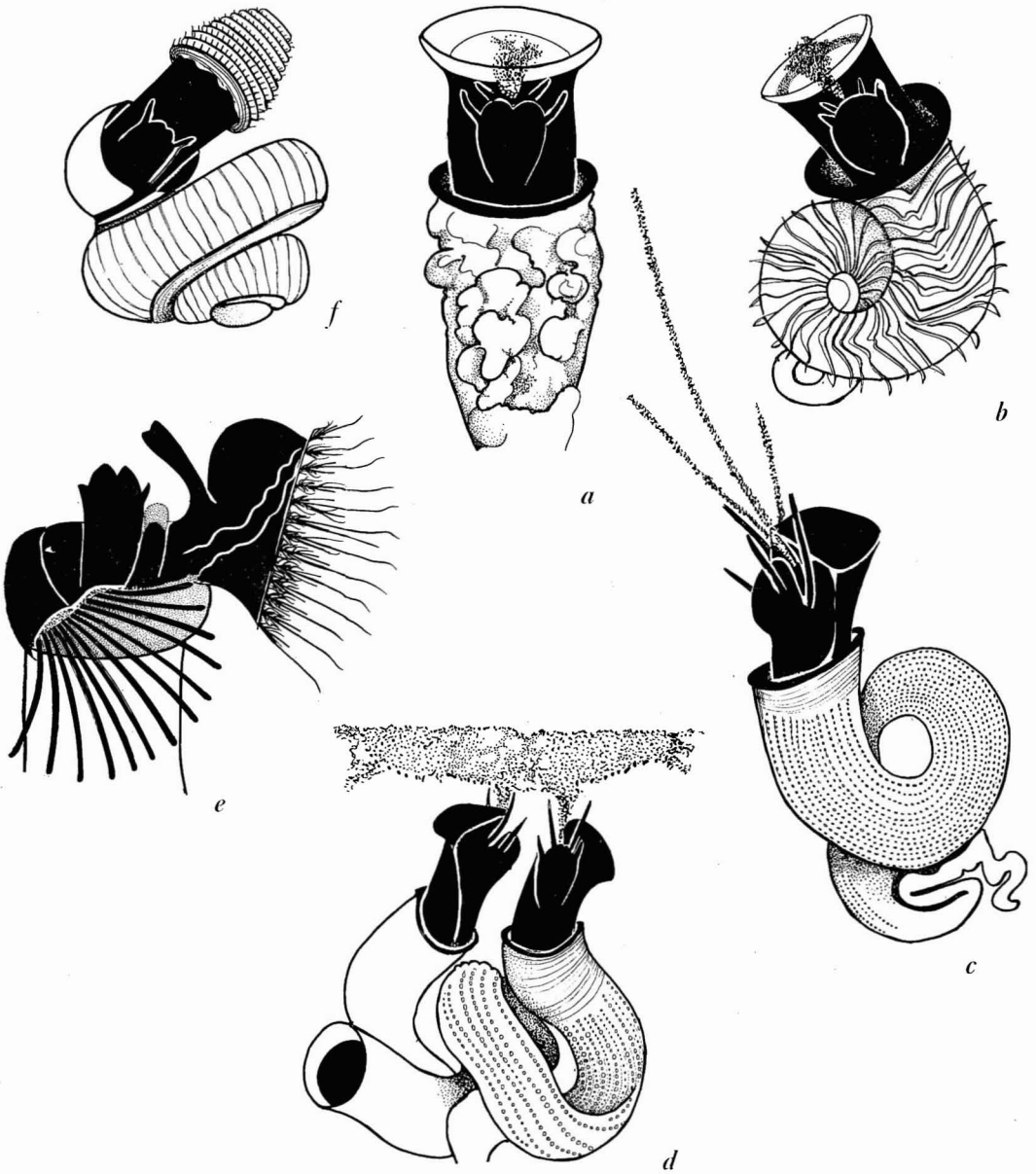


FIG. 1. Semidiagrammatic views of the animal and shell in four genera of Vermetidae and two genera of Siliquariidae. *a*, *Vermetus*, based on *V. novae-bollandiae*; *b*, *Novastoa*, (*N. lamellosa*); *c*, *Serpulorbis*, (*S. zelandicus*, with mucous trap extended during feeding); *d*, *Aletes*, (a pair of *A. squamigerus* with portion of the communal mucous sheet); *e*, *Stephopoma* (*S. roseum*, with the feeding fringe of gill filaments extended); *f*, *Siliquaria* (based on *S. maoria*).

the haemocoel of the trunk. Fairly constantly, while the animal is feeding, the gland extrudes a small triangular or conical mass of mucus which hangs indecisively over the edge of the foot. The mucous gland of the foot is here evidently beginning to develop a feeding as well as a cleansing function; but although the animals were watched during a long period of feeding by the aid of water goggles, the mucous traps with their collected particles were never seen to be ingested and the disturbance of the water surface by wave action often impeded their proper formation.

The gill in the Vermetidae never becomes more specialised than at the *Vermetus-Novastoa* level; on the contrary two other trends have begun to appear, to a greater or lesser extent, in all the other members of the family: a loss of reliance on the pallial organs in feeding, and the exploiting of the pedal mucous gland, which in every member of the family is already prominently developed.

*Serpulorbis zelandicus* (Fig. 1c) is probably typical of the Vermetidae which are beginning to undertake mucous feeding. This species undoubtedly uses the gill in feeding to a major extent (Morton, 1951a) and also puts out long slender mucous strings from the pedal gland, which are evidently drawn in by the pedal tentacles or the radula, and ingested after they have become loaded with microscopic particles. The pedal gland is very stout in *Serpulorbis zelandicus*, much more so than in *Vermetus novae-hollandiae* or *Novastoa lamellosa* (where it is still relatively narrow) and more nearly resembles in extent that of *Serpulorbis gigas*. The ciliary feeding mechanism of the pallial cavity has, however, undergone hardly any reduction as yet; the gill filaments are large and triangular and prominently ciliated, and although, as is always the case in Vermetidae, there is no glandular "endostyle" running along the gill axis the ciliated and mucus-producing food tract is strongly developed. The cross-section (Fig. 3) across the trunk and pallial cavity illustrates the lo-

cation of the glandular tracts; the hypobranchial gland is well-developed too, although it plays little part in supplying mucus for food collecting.

The serpulorbids have two further modifications which can be regarded as being associated with the feeding adaptations. First, the operculum is entirely lost and the terminal disc of the foot is naked and generally bright coloured. Its edge is very thin and mobile and may easily be indented or retracted at any point so that the formation of mucous strings and their employment is not impeded, as would be the case in the presence of the rigid edge of a projecting operculum. The sole of the foot is also very small in *Serpulorbis*, and relatively much less conspicuous than in *Vermetus novae-hollandiae* or *Novastoa lamellosa*. The loss of the operculum makes necessary the power of quick retreat into the shell; and this is probably correlated in turn with the tendency of the shell in *Serpulorbis*, *Aletes*, and *Bivonia* to become long and vermiform, of far greater length than is normally occupied by the animal. However, other factors no doubt enter into the determining of shell form, or lack of it, in vermetids; thus in genera such as *Novastoa* and *Spiroglyphus* which do not retreat deeply, but rely on large opercula, the shell also tends to become elongated. Moreover, in some of the species of *Serpulorbis* the deeper parts of the shell are cut off by septa. The length of the visceral mass also increases in the species of *Serpulorbis*, whereas in *Vermetus* and in many specimens of *Novastoa lamellosa* the visceral mass, including the posterior lobe of the digestive gland, is rather short and blunt.

A related adaptive trend in the evolution of the Vermetidae is the development of a long median slit in the mantle of the female; this is associated with the protection of the eggs, which in all genera of the family are retained in capsules within the mantle cavity until the emergence of the crawling benthic embryo with its regular spiral shell. In *Novastoa*, *Petalococonchus*, and *Vermetus*, and almost

certainly in *Spiroglyphus*, the egg capsules remain unattached, lying freely within the mantle cavity. But in the nonoperculate forms which retreat quickly into narrower parts of the shell, egg capsules so retained would be liable to damage during the rapid withdrawal of the head and foot into the mantle cavity as the animal darts into the shell. By means of the pallial slit a row of three or four egg capsules can be attached directly to the inner surface of the shell by short stalks. On the retreat of the animal, the capsules remain attached near the mouth of the shell; as the animal again expands the mantle wall extends forward around them.

The genus *Bivonia*, of which the Mediterranean species *triqueter* is the best known example, appears to have reached the *Serpulorbis zelandicus* stage of evolution. The operculum however remains as a small button-like vestige upon the terminal disc of the foot. The shell is long, irregular, and vermiform, and the animal retreats deeply and has a slit mantle in the female. According to Yonge (1932), mucous traps are formed by the pedal gland, but in addition the gill remains well-developed.

The most advanced group of Vermetidae, in feeding habits, is probably that typified by *Serpulorbis gigas*, whose feeding mechanism has been described in great detail by Boettger, and *Aletes squamigerus*, of which the McGinities (1949) have given an account. There is also a brief general description of the feeding habits of the latter and a good figure in Ricketts and Calvin (1948). In both these species mucous traps have entirely replaced the cilia of the pallial cavity in feeding. The gill is very small and insignificant, and the ciliary tracts and glandular region of the pallial floor much reduced in importance. No doubt strong inhalant and exhalant currents, if present at the opening of the mantle cavity, would impede the full employment of mucous traps. In *Serpulorbis gigas*, mucous strings are extruded, which reach 8 or 9 inches in length, i.e. several times the average length of the animal. These are waved about gently with

the slight movements of the surrounding water and presently withdrawn and ingested with the food particles that have become attached to them. It is claimed by Boettger that *S. gigas* captures small zooplankton in this way, and in one case, the presence in the stomach of numerous small shells of gastropods (possibly veliger larvae?) was reported. Yonge (1932) maintained that the crystalline style and gastric shield were lost, with the abandonment of ciliary feeding. Later Yonge and Iles (1939) reported the presence of a small gastric shield of greatly reduced extent. A dissection of fixed *Serpulorbis gigas* by the present writer reveals a style sac and gastric shield of similar proportions to that of *Serpulorbis zelandicus*; in *Aletes*, too, the stomach has its normal structure with a prominent style sac and shield. The loss or reduction of the crystalline style is thus evidently not an accompaniment of this type of mucous feeding in vermetids, and the mode of action of the stomach conforms to that of style-bearing prosobranchs in general, as discussed by Morton (1952).

In *Aletes squamigerus*, (Fig. 1*d*) the reduction of the gill has been accompanied by great development of the pedal gland as in *Serpulorbis gigas*, but here, instead of the formation of long separate strings, the extruded mucus takes on the form of a continuous sheet and feeding becomes the combined activity of a large cluster of gregarious individuals. As described by the McGinities (1949), "When the animals occur in clusters, the fan-shaped sheets of mucus they put out become entangled, and the table with its bill of fare becomes a community affair. When one member in such a group begins to eat the mucus sheet, all the others start swallowing. The sheets of mucus may extend upward into the water for five or six inches."

The demarcation of genera in the *Aletes-Serpulorbis* series is at present a very uncertain proceeding. There would appear to be no well-marked conchological characters to discriminate between forms such as *Serpulorbis*

*zelandicus*, which have continued to make good use of the gill in feeding, mucous trap feeders like *S. gigas*, and mess-table feeders like *Aletes squamigerus*. The adult shells are markedly similar and devoid of diagnostic features. Evolution in sculptural detail has tended to become retrograde and is moreover often obscured by encrusting organisms or becomes obsolete on the older parts of the shell. The radulae in the above three species are extremely similar and thus unhelpful. The most natural means of separation would at present appear to be by reference to the condition of the gill and the ciliary tracts of the mantle cavity, which is of small help to the conchologist faced with a range of cabinet material. Perhaps the most valuable character will be found in the sculpture of the embryonic shell; and here the careful work of Dr. Myra Keen on the American vermetids will be eagerly awaited. It is possible that the *Aletes-Serpulorbis* group should have the status of a single worldwide genus, when judged on shell characters; if this is so, it will be a genus in which evolution of the animal and its mode of life has greatly outrun the changes in conchological features.

#### THE SILIQUARIIDAE

In the second family now recognised, the Siliquariidae, the shell never loses its roughly spiral general form; though as a general rule the spire loosens up to become open and corkscrew-shaped. The tube is never cemented to the substratum along the whole of one side, as in the most advanced and least regularly coiled members of the Vermetidae; it is usually, as in *Stephopoma*, loosely immersed in the encrusting growth on rocks, or, as often in *Siliquaria*, embedded in sponges. Mucous traps are not used in feeding and the pedal gland does not become greatly enlarged as it is in all the Vermetidae. In all cases the ctenidial filaments are employed in food collecting and they have become much more modified than the primitively triangular fila-

ments of the vermetid type. The pedal tentacles are never present, and the sole of the foot, while reduced in extent, is usually clearly recognisable in the adult and considerably more conspicuous than in the Vermetidae.

The account by Morton, (1951*b*) describes in detail the mode of feeding of a member of the Siliquariidae, *Stephopoma roseum*. The more normal method of food collecting, with the gill retained in the pallial cavity, is clearly not very different from that of *Turritella* (Graham, 1938). The gill is also however employed in a "sweeping fringe" type of feeding activity, which has not been observed and recorded in any other gastropods. The gill filaments have become narrow and cirriform, and lie across the pallial cavity to form an oblique lamina extending from its insertion on the left across to the food groove on the right. A continuous water current is drawn into the pallial cavity by the action of the lateral cilia of the ctenidium, and is passed between the filaments from the ventral (frontal) to the dorsal (abfrontal) side. Food particles themselves, entangled in mucus secreted by the endostyle, are carried along the filaments to the right side of the pallial cavity, chiefly by the frontal cilia, to a lesser extent by the abfrontals. The "food groove" does not form a wide glandular sheet as in the Vermetidae, and correspondingly less mucus is derived from it. The greater part of the binding substance of the food string comes from the endostyle and, as in the Vermetidae also, the hypobranchial gland appears to contribute little if any mucus to the food string. The tips of the ctenidial filaments are rounded, somewhat expanded, and bulbous, and anterior filaments crowd like a cluster of fingers into the wider portion of the food groove.

During normal feeding, a number of ctenidial filaments protrude across the free edge of the mantle, and when the animal is fully extended from its tube a fringe of radiating filaments forming about one-fourth to one-third of the total length of the gill projects from the mantle. Frequent sweeping move-



ments are performed with this fringe which, because of the flexibility of the filaments, is curved downwards below the margin of the shell, and then, more rapidly, the fringe is suddenly flexed. Particles engaged by the separate filaments travel towards the apices by the action of the frontal cilia, embedded in a copious secretion of mucus from the axial endostyle, which secretion appears to be immediately induced by the contact stimulus of the particles upon the surface of the filament. At the same time the lateral cilia, normally in rapid motion, become motionless; this is of obvious advantage during the "sweeping fringe" type of feeding, in preventing the loss of the endostylar mucous secretion by passage between the filaments during the beat of the lateral cilia. At the tips of the filaments another set of cilia, arranged in long apical tufts and generally kept inert, now comes vigorously into play. The cord of particles collected in mucus, which now extends from tip to tip around the fringe of filaments, is carried by the apical cilia towards the mouth where it may either be accepted for ingestion or, as is usually the case with experimental carmine particles, cast off the filaments and rejected.

The modifications undergone by the foot in *Stephopoma* can be best appreciated by reference to Figure 2*b* which represents an embryo recently liberated from the maternal pallial cavity and just beginning its brief period of free crawling. In the adult *Stephopoma*, the foot is prolonged in front of the mouth into a long, flattened or spatuliform lobe, the pre-pedal process. This displays a rather complicated set of ciliary currents which evidently assist in the ingestion of the mucous cord from the food groove, or in the rejection of loose particles alighting near the mouth, probably both. It is formed by the large anterior margin of the foot which is squarish, strongly ciliated, and very labile in the embryo. In the adult, it becomes narrowly constricted from the rest of the sole of the foot which remains in the form of a broad cushion of whitish, ciliated and glandular epithelium, lying in

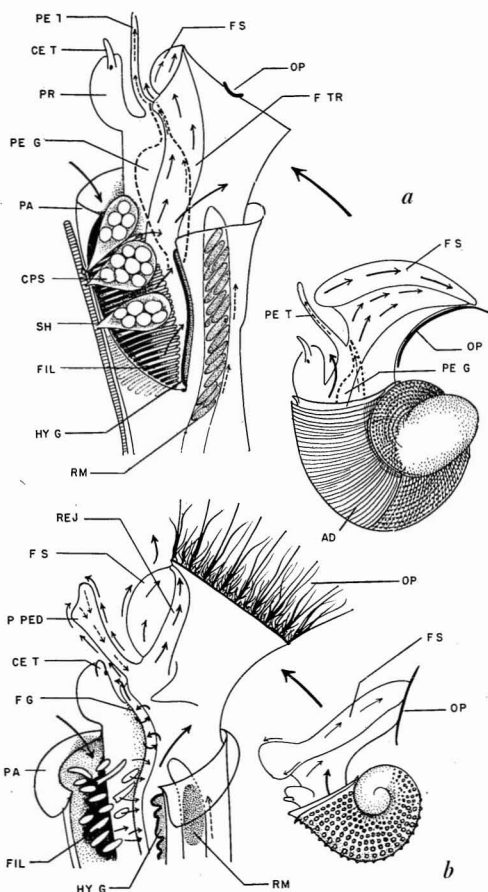


FIG. 2. Diagrams illustrating the structural differences between the families Vermetidae and Siliquariidae. *a*, *Serpularbis*. Section of the head and foot and the free crawling embryo; *b*, *Stephopoma*. Section of the head and foot and the free crawling embryo. In the figure of *Serpularbis*, the contents of the pallial cavity are displayed through the natural cleft in the female, through which the egg capsules are attached to the shell. In *Stephopoma*, the pallial cavity has been opened by the removal of a portion of its right wall, to display the tips of some of the ctenidial filaments in end view. The arrows indicate the directions of the principal ciliary currents. In the embryos note the spirally coiled embryonic shell, and compare with the figures of the adults, to see the modifications involved in the development of the head and foot.

AD, Adult portion of the shell added to the nuclear shell in *Serpularbis*; CE T, cephalic tentacle; CPS, egg capsules; F G, food groove in *Stephopoma*; FIL, gill filaments; F S, sole of the foot; F TR, food tract in *Serpularbis*; HY G, hypobranchial gland; OP, operculum; PA, mantle; PE G, pedal gland; PE T, pedal tentacle; P PED, pre-pedal process in *Stephopoma*; PR, proboscis; REJ, rejectory tract of foot; RM, rectum with faecal pellets; SH, shell.

the normal position of the parts, in front of the proboscis. At the sides of this cushion, excurrent grooves carry particles of detritus and rejected debris off the surface of the sole. The anterior lobe of the foot contains a nest of mucous glands in the embryo, which—far from becoming enlarged in the adult—appears to be lost almost entirely. The epithelial covering is, however, well-supplied with mucous glands which serve for the cleansing of the foot. The whole of the mucous supply for food collecting is produced in the pallial cavity, chiefly from the endostyle.

In the embryo of *Stephopoma* the operculum is a simple chitinous disc, slightly concave, carried on the back of the still functional foot. In the adult it becomes very large, overlapping the border of the foot, and densely setose. It consists of a spirally coiled chitinous band, each whorl fringed with long, branched setae, those on the final whorl the longest and extending far beyond the edge of the disc. The present writer has fully described elsewhere this operculum and the structure of its bristles (1951*b*) and has discussed a possible adaptive explanation of its structure. When the bristles are in contact with the edge of the shell aperture they have a screening and filtering action which prevents larger particles entering the pallial cavity. The animal may apparently feed for considerable periods of time in this position with the disc of the operculum close against the aperture and the sweeping fringe of gill filaments not extended. Deep withdrawal into the tube is a feature of some of the siliquariids as well as of the true vermetids. In *Stephopoma* it is made possible by the flexibility of the opercular bristles, which may be recurved upwards against the inner wall of the shell when the animal is fully retracted although their full spread is considerably wider than the aperture. Whether the adaptive explanation of opercular specialisation is the full one is rather doubtful. Quite possibly the elaborate form of the bristle crown, and especially the interspecific differences in the bristles in *Stephopoma* (see the old

paper of Mörch, 1861), is, as must be the structure of the operculum in *Siliquaria*, a non-adaptive specialisation—one of those extravagances of evolution which seem so often to recur among gastropods at the level of family and generic systematic characters.

The second section of the Siliquariidae contains those wormlike gastropods truly assigned to the genus *Siliquaria* (s. lat.). Here the shell may be long, slender, and corkscrew-shaped, delicate and translucent as in the subgenus *Pyxipoma*, or squat and much heavier as in the *Agathirses* series. In all cases, however, its spiral shape is retained, and along the right side runs a long spiral slit (reduced in some cases to a row of holes) corresponding with an internal fissure along the exhalant side of the pallial cavity. *Pyxipoma weldii*, from New Zealand and Australian waters, was the only siliquariid studied alive. It corresponds very closely in organisation with *Stephopoma*, and the latter genus was placed alongside the fissured "vermetids" in the Siliquariidae by Morton (1951*b*). Characters in common are the structure of the foot, its absence of pedal gland and tentacles, and the nature of the ctenidial filaments which are narrow and linear, quite distinct in form from those of the Vermetidae. In *Pyxipoma* the supplementary mode of feeding by means of the "sweeping fringe" has not been observed, though the general arrangement of the pallial organs makes such a mechanism quite to be expected. The food groove, as in *Stephopoma*, forms a deep ciliated gutter, with no great development of mucous glands. The "endostyle" along the gill axis is large and highly glandular.

The fissured shell is of much less taxonomic importance in marking the limits of the siliquariid group than has been hitherto supposed. The present writer proposed (1951*b*) to take as the chief diagnostic feature of the family the embryo shell, which is one and one-half whorled, coiled in an almost plane spiral, with a wide, slightly effused trumpet mouth, marking it off clearly from the adult shell,



with which it is set in the same axis, in strong contrast to the condition in the Vermetidae. The general mode of coiling of the shell, which is never internally septate, as well as the form of the dentition, are also good distinguishing characters of the Siliquariidae. The structure of the operculum, which is always prominently retained, is equally typical; it consists always of a spirally coiled band, bearing a fringe of setae, elaborate in *Stephopoma*, much more simple in *Pyxipoma*. In the latter genus, the operculum is raised to form a tall dome, built up of a spirally rolled band, enclosing a core of triangular cells arranged about a central axis. The setae here are never elaborate, and the operculum fits tightly over the aperture so that the animal is unable to retreat deeply into its tube.

The significance of the spiral shell fissure in the siliquariids is perhaps not yet fully understood; but it is undoubtedly in part an adaptation of the same type as the primitive shell fissure in many Archaeogastropoda, by which the exhalant water current is released. Such a feature is not of course a primitive one in the Siliquariidae, but rather a reacquired character in members of a highly specialised group. Extra efficiency of the exhalant water current is an obvious advantage in a siliquariid living, as is common, in turbid waters on a highly sedimented substratum; moreover, the siliquariids lack the protective straining mechanism which may be provided by the long opercular bristles in *Stephopoma*. The presence of an exhalant slit is perhaps also of adaptive value in the sudden and rapid withdrawal of the animal, which frequently darts back into the tube and closes the operculum tightly over the aperture. No expulsion of water is possible between the bristles of an opercular fringe as in the case in *Stephopoma*. Such an explanation of the shell fissure appears the most probable one in *Agathirses* and those siliquariids which do not deeply embed themselves in the substratum. Its presence makes much less sense in *Pyxipoma* which is in its habit more specialised, spending its whole life embedded in a

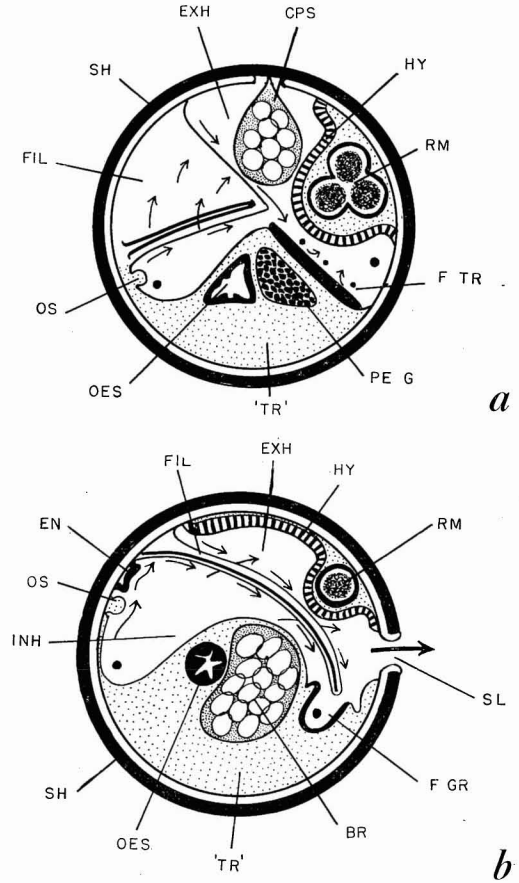


FIG. 3. Diagrammatic transverse sections to illustrate differences between the vermetid and siliquariid organisation of the pallial cavity. *a*, *Serpulorbis* (Vermetidae); *b*, *Pyxipoma* (Siliquariidae). The arrows show the direction of the principal ciliary currents. These figures should be examined together with the diagrams of Figure 2.

BR, Brood pouch in *Pyxipoma*; CPS, egg capsule in *Serpulorbis*; EN, endostyle; EXH, exhalant chamber of pallial cavity; FIL, gill filament with tract of lateral cilia indicated; F GR, food groove in *Pyxipoma*; F TR, food tract in *Serpulorbis*; HY, hypobranchial gland; INH, inhalant chamber of pallial cavity; OES, oesophagus; OS, osphradium; PE G, pedal gland; RM, rectum with faecal pellets; SH, shell; SL, exhalant slit in *Pyxipoma*; 'TR,' muscular region of "trunk" formed by columellar muscle flooring haemocoel.

mass of sponge, as far as the extreme edge of the aperture. Any advantage once derived from an accessory exit from the pallial cavity would seem here to have been entirely sacri-

ficed, especially as the slit in the shell becomes very narrow, at times almost obsolete, and is always occluded by the overgrowth of sponge tissue and spicules across it.

Adaptations for the protection of the embryos must be briefly mentioned for the Siliquariidae. In *Stephopoma*, the embryos with their trumpet-mouthed shells, enclosed in a thin egg capsule, are simply held freely in the mantle cavity of the parent, as is the case in the more primitive members of the Vermetidae. In *Pyxipoma* there is a spacious brood pouch excavated in the cavity of the head, immediately below the buccal mass and the oesophagus. It opens to the exterior by a small circular aperture on the right side at the termination of the ciliated oviducal groove running forwards from the female aperture, and close to the termination of the food groove below the right tentacle.

No species of the genus *Vermicularia* appears to have been examined from living material. The present writer (1951*b*) suggested reasons for its transfer to a position alongside the siliquariids, pointing out that in its structure it was certainly unlike any of the gastropods properly belonging to the Vermetidae. Following access to a better supply of preserved material of *Vermicularia spirata*, the close relationship of this genus with both the Siliquariidae and the Turritellidae is fully confirmed. It forms an interesting example of a form intermediate in structure, and presumably in habits, between the freely moving, ciliary feeding turritellids and the fixed or embedded siliquariids as has been indicated in a more recent discussion (Morton, 1953):

*Vermicularia* then has close relationships with *Turritella* in the pallial tentacles, and the structure of the gill, the food groove and the foot; as well as in the radula, the embryo shell, the operculum and the ontogeny and sculpture of the adult shell. On the other hand, it is close to *Stephopoma* in many features, such as the uncoiled shell, the sessile "vermetid" habit, and the greater elongation of the gill filaments . . . In choosing with which family the genus *Vermicularia* should most properly be placed, we should probably select the Turritellidae, which would enable the Siliquariidae to be reserved for those sessile forms with

reduced, trumpet-mouthed apices. But the relationship of *Vermicularia* to both is very close and there can be little reason to doubt that the genus is near the point at which a deposit feeding prosobranch with a turritellid organisation gave rise to one or more lines of sessile, uncoiled derivatives.

#### DISCUSSION

To "define" a group of organisms at the family level in terms useful to the systematist is a problem rather different from "characterising" it in such a way as to bring out its interest to the evolutionist. In this case we are concerned less with extreme cases or with anomalies in marginal form, and more with the central pattern of organisation that unifies the family, and with the evolutionary trends being followed within it. These trends would appear in many cases to be of two rather different kinds: there is first the phenomenon of "adaptive radiation" between different genera, and this must account for many of the characteristics of the Vermetidae and Siliquariidae, especially the modifications of the foot and pallial cavity; but there are, further, a number of trends running through each family, often apparently developed convergently in different genera, which seem to be much less closely, if at all, related to adaptation.

It must be obvious that in the vermetid and siliquariid stocks we are dealing with two fundamentally different groups of Mesogastropoda. The writer has already (1951*b*) outlined at length the differences between the two families, and has suggested that the Siliquariidae approach rather closely to the Turritellidae in their affinities. It is much less clear from which group the Vermetidae may have originated, and there seem to be no living mesogastropods which at all clearly suggest an ancestral form. In the development of ciliary feeding within the Siliquariidae and the more primitive section of the Vermetidae, we would seem to have no more than an instance of parallel adaptation. There are moreover several other apparently unrelated groups of prosobranch gastropods which have devel-

oped the ciliary feeding habit as an evolutionary climax feature as mentioned earlier in this paper. They all fall within the wide series of Mesogastropoda bearing crystalline styles or protostyles, and relying strongly upon the action of cilia and mucus in the functioning of both the pallial cavity and of the digestive tract; they are preadapted to give rise to ciliary feeders. A similar potentiality separately realised in different groups is the development of an enzyme-carrying crystalline style (Graham, 1938; Morton, 1952). A common structural pattern and mode of functioning of the stomach is inherited by all of those molluscs, both gastropod and lamellibranch, derived from possessors of a protostyle. The enzymic action of the crystalline style was doubtless acquired separately within these groups in a number of parallel cases.

The diagrams (Fig. 2*a, b*) make sufficiently clear the differences in adaptations of the Vermetidae and Siliquariidae, both in the modifications developed in the foot of the adult and the pallial structures present in the embryo. A common ancestor among the microphagous mesogastropods must have had the following structures, or the potentiality to develop them: (1) a crystalline style sac in the stomach, and the mucous string mode of food transport; (2) a pallial cavity with a well-developed gill equipped with strong ciliated tracts for current-producing, cleansing and rejection, and (potentially) three longitudinal glandular tracts within the pallial cavity, a hypobranchial, basibranchial ("endostylar") and infrabranchial (nuchal tract or food groove); (3) a mucous gland of the foot opening anteriorly to the sole, and potentially able to become very large; (4) a small, strong radula of the grasping type, with sharply pointed teeth; and (5) a foot bearing a simple, circular, saucer-shaped operculum. Obviously almost any family of microphagous mesogastropods would satisfy these requirements, and there is very little to indicate that the Vermetidae and the Siliquariidae arose close together.

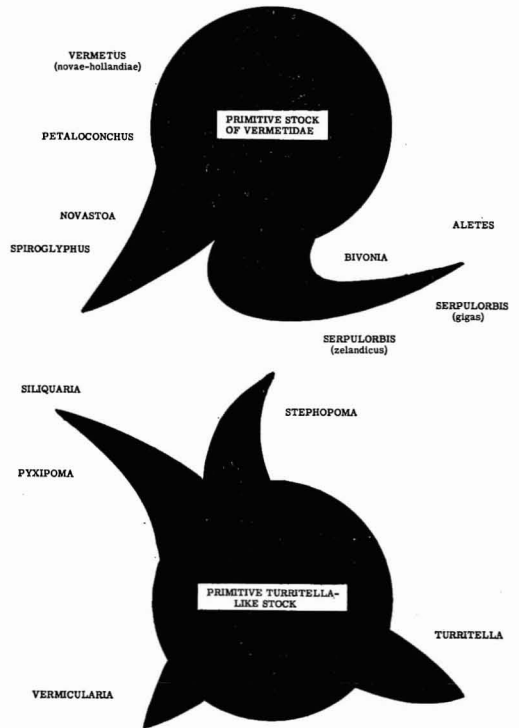


FIG. 4. Scheme to express the relationships and course of evolution of the vermiform gastropods included in the Vermetidae and the Siliquariidae.

The evolution of the two series (Fig. 4) shows first a convergence in the parallel development of ciliary feeding, and then a swinging away of the vermetid line towards more highly specialised mucous feeding. On the one hand, ciliary feeding is continued, with increasing specialisation of the pallial organs (Siliquariidae), on the other, the pedal gland at an early stage assumes a share in the provision of mucus for food collecting. The gill filaments in this series never lose their original triangular form, and in the furthest evolved members of the Vermetidae, the pedal gland is enormously enlarged and the gill tiny and vestigial. In the siliquariids the operculum becomes large and very elaborate; in the vermetids it is finally lost altogether. Parallel with the enlargement of the pedal gland and

the reduction of the gill, the shell in Vermetidae becomes elongated and very irregularly coiled: with the loss of the operculum the animal becomes able to retreat deeply into the shell, and the mantle in the female becomes medianly slit as described above, as an adaptation for fixing the egg capsules directly to the shell. This modification seems always to be associated with the loss of the operculum and the consequent need for deep protective retreats into the shell. The reduction or loss of the operculum may itself be primarily a consequence of the mucous feeding habit, enabling the animal to put out its mucous traps unimpeded by the edge of the operculum, as suggested by Yonge and Iles (1938).

In the group including the Siliquariidae, the Vermiculariidae, and the Turritellidae, we may imagine an ancestral form with a potentiality to develop both elaborate opercular setae and also pallial tentacles—these are the chief diagnostic features of this assemblage, which has been shown to share a large number of structural characters in common. In the genera so far investigated, *Turritella* retains both the opercular setae and the pallial tentacles, *Vermicularia* loses the setae, and in the Siliquariidae the pallial tentacles are not represented. We should not perhaps regard the loss of tentacles or setae in one or other of these groups as being too literally a phylogenetic event; or suppose that an ideal common ancestor possessing each of them ever existed. All that the facts entitle us to suggest is the existence of a common stock which had a tendency to produce evolutionary forms, either of the siliquariid or the vermulariid type. The Turritellidae perhaps comes closest, among surviving families, to such an ancestral stock but this family is in itself undoubtedly specialised upon a distinct line, and almost certainly gave rise directly to neither.

In the evolution of a radiating group such as the prosobranch gastropods, we are likely

to find different adaptive patterns almost from family to family; and the two groups of vermiform mesogastropods illustrate this principle very well. At the level, however, at which families are diversified into genera, it would appear that evolution due obviously to adaptive changes has relatively much less effect. Such a conclusion is best illustrated by the details of shell sculpture and dentition, and, in the present case, by the characters of the nuclear shell and the operculum; and it is in part because of their nonadaptive character that these structures have come to be the most useful ones in a reliable classification. The evolution of other molluscan groups seems often to tell a similar story. We find first a series of adaptive characters setting off a family or a group of families from neighbouring ones, such as, in the vermetids, adaptations to ciliary or mucous feeding. Then, most often at the generic or interspecific level, evolutionary diversity of a different kind seems to enter the picture. In two others groups of gastropods examined by the writer in some detail, the Strombacea (1951*d*) and the Ellobiidae (in press), a similar situation has appeared, and further examples might easily be cited from other groups.

Mollusca evolving at the generic level are uneasy ground for the dogmatic selectionist. In some cases there appear to be features of an "orthogenetic" kind (though this is a word that has acquired some objectionable shades of meaning) running in a parallel way through different, but related series of genera. Many of these trends may force themselves into expression in the history of a group so as to dominate much of its evolution. Thus it happens that many molluscan groups present beautiful examples of adaptive evolution at the family level, and may then become permeated with what appears to be functionally meaningless minor trends, often, as in the case of shell structure, aesthetically pleasing and always interesting to the taxonomist. The selectionist's plea will be that most of these characters, at present inexplicable on adaptive

lines, may on fuller investigation be found to be genetically linked with advantageous features or developmental patterns. Such a stand is less likely to appeal to one looking at, for example, the variety of sculpture found in the nuclear whorls of vermetids or siliquariids, the sculpture pattern of the adult shells, the structure of the operculum in *Siliquaria*, or of its bristles in *Stephopoma*. The selectionist's view has the merit of removing a problem one stage further away; but to try to argue with our present knowledge, any general relation between adaptive influences and the evolution of molluscs at the generic or specific level, is probably to go further than reliable evidence will allow.

In this paper I have given no critical attention to generic nomenclature, but have employed as genera, according to prevailing practice, each of the subgeneric groups recognized by Thiele (1931), in his rather conservative arrangement of the Vermetidae (s.l.). Dr. Myra Keen, of the Department of Geology, Stanford University, California, has recently (August, 1954) outlined to me in correspondence a revision of the genera of Vermetidae (properly so-called) which she will shortly make. From my own study of the soft parts and biology of the family I am in agreement with Dr. Keen's proposals.

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