

THE GALAPAGOS RIFT LIMPET *NEOMPHALUS*: RELEVANCE TO
UNDERSTANDING THE EVOLUTION OF A MAJOR
PALEOZOIC-MESOZOIC RADIATION¹

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ABSTRACT

Neomphalus fretterae, new species, genus, family, and superfamily, was first collected in 1977 at the vents of thermal springs along the Galapagos deep-sea spreading center at depths of 2,478 to 2,518 m. Shells reach 30 mm in diameter and are cap-shaped with a horizontally lying initial coiled phase. The shell is protected by periostracum and is composed of lamellar aragonite. In form and function *Neomphalus* is convergent with the Calyptraeidae, having a flattened neck and a deep mantle cavity on the left with long gill filaments extending to the food groove on the right. *Neomphalus* is the first known gastropod with a bipectinate gill modified for filter feeding.

As further detailed in the adjoining paper on internal anatomy (Fretter, Graham & McLean, 1981), *Neomphalus* has such archaeogastropod characters as a rhipidoglossate radula, bipectinate ctenidium, epipodial tentacles, and anterior loop of the intestine. Features of the mesogastropod level of organization include loss of the right pallial complex, a monotocardian circulatory system, expanded left kidney, and glandular gonoducts. Unique features are: 1) a dorsal food groove, which leads to the mouth over the right cephalic tentacle rather than under it as in all other filter-feeding gastropods, 2) a mantle cavity not enveloped by the shell muscle on the left side, 3) posteriorly directed cephalic tentacles, 4) reproductive specializations: the male with the left tentacle enlarged to form a copulatory organ, and the female with a separate seminal receptacle.

The first postprotoconch whorl is coiled; growth stoppage in the second postprotoconch whorl on the columellar lip prevents the muscle from enveloping the mantle cavity on the left, but forces lip expansion on the right to produce the limpet shell form.

There are no living relatives, nor has any fossil record of *Neomphalus* been found, yet the ctenidium is so adaptive that a radiation on this theme must have taken place, and the highly specialized *Neomphalus* can only represent one ultimate expression of this basic plan. Paleontologists have recently hypothesized that the extinct Euomphalacea, which underwent a major radiation in the Paleozoic and declined in the Mesozoic, were filter feeders because their discoidal or open coiled shells with radial apertures differ from those of motile gastropods having tangential apertures and the capacity to balance the shell over the cephalopedal mass. The anatomy of *Neomphalus* could function in a coiled shell and would explain the euomphalacean anatomy, the differences between *Neomphalus* and euomphalaceans being about equivalent to differences between calyptraeids and turritellids. As in turritellids the operculum of euomphalaceans would loosely block the aperture in feeding position. The columellar muscle in the euomphalaceans would be at the right of the cephalopedal mass, instead of ventral to it as in those motile gastropods that balance the shell over the cephalopedal mass. The coiling axis in euomphalaceans has to shift relative to the substrate from horizontal to vertical during growth, as shell-balancing capacity is lost and filter feeding replaces grazing. Because the position of the columellar muscle in *Neomphalus* is to the right of the cephalopedal mass and because *Neomphalus* also shifts the coiling axis of its initial whorls, *Neomphalus* is the logical limpet derivative of an euomphalacean.

The discoidal euomphalaceans became extinct in the Cretaceous, having no defense against shell-crushing predators that arose in the Mesozoic, but the limpet derivative is protected against such predators and exploits the abundant chemosynthetic bacterial food source not accessible to soft-substrate-dwelling animals. During the Mesozoic, hydrothermal vents may have been accessible along rift zones in shallow water, providing stepping stones to deep-water rift systems. The rift-vents in deep water fortuitously lack such usual molluscan predators as drill snails

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and sea stars; thus, the rift-vent habitat has been a stable refugium for a relict family at least since the Cretaceous, the period of the last surviving euomphalaceans.

Only the Pleurotomariidae share with the Neomphalidae the absence of afferent support to the ctenidium. The Euomphalacea can be independently derived from the Pleurotomariacea, upon loss of the right pallial complex, probably from an early pleurotomariacean stock of flat-lying discoidal shells with a slit on the upper whorl surface, as the Ordovician *Lesueurilla*. The unique dorsal food groove of *Neomphalus* is here interpreted as a primitive character. The tips of filaments from paired ctenidia, modified for filter feeding, could have converged upon a dorsal food groove in this group of early pleurotomariaceans, the shells of which are no better designed for locomotion than those of euomphalaceans.

The new archaeogastropod suborder Euomphalina, to include the superfamilies Euomphalacea and Neomphalacea, is proposed, an independent line derived from early pleurotomariaceans. It has attained the mesogastropod level of advancement in its circulatory and reproductive systems but retains the primitive characters of the rhipidoglossate radula and the bipectinate ctenidium.

Possible affinities of other extinct archaeogastropods are discussed in Appendix 1, with the conclusion that Macluritacea and Clisospiracea are lineages apart from Euomphalacea and Trochacea. Pseudophoracea, Platyteratacea, Anomphalacea, Microdomatacea, and Palaeotrochacea may have had the pallial complex of the Trochacea.

In Appendix 2 the Liotiidae are recognized in the Paleozoic, making the Trochacea older than previously supposed, and the Craspedostomatacea and Amberleyacea are merged with the Trochacea.

INTRODUCTION

Strange new deep-sea communities associated with thermal springs along sea-floor spreading centers have recently been discovered both at the Galapagos Rift (Ballard, 1977; Lonsdale, 1977; Corliss & Ballard, 1977; Corliss et al., 1979; Crane & Ballard, 1980) and the East Pacific Rise (Corliss et al., 1979; Spiess et al., 1980). Chemosynthetic bacterial production deep within the springs provides a source of food (Rau & Hedges, 1979; Karl et al., 1980; Jannasch & Wirsén, 1979, 1981). Another source of food derived from photosynthetic sources may be made accessible by advection currents through the vents (Enright et al., 1981). The hydrothermal vent communities are richly provided with filter-feeding animals, predators, and a conspicuous gutless animal—the vestimentiferan pogonophoran *Riftia pachyptila* Jones, 1981. Questions in the fields of ecology, physiology, reproduction, dispersal, and taxonomic origins of the rift-vent species have engendered an extraordinary interest among marine biologists. Nearly all members of the rift-vent community are new species.

Mollusks are conspicuous members of these communities. In addition to two large bivalve species, a mytilid and the large white clam, *Calyptogena magnifica* Boss & Turner, 1980, there are several limpets. The largest of the limpets from the Galapagos Rift is described here as the new genus and species *Neomphalus fretterae*. Its anatomy is so un-

like that of any living gastropod that it can not be assigned to an existing superfamily or even to a suborder in the Gastropoda.

The external anatomy resembles that of the mesogastropod family Calyptraeidae, having a similar flattened neck, a deep mantle cavity on the left side, and long gill filaments converging upon a food groove. Unlike the calyptraeids, in which the gill is monopectinate, *Neomphalus* has a bipectinate gill, with filaments on both sides of the axis. Bipectinate gills are characteristic of the Archaeogastropoda, the oldest and most primitive order of prosobranchs. Additional archaeogastropod features include the epipodial tentacles surrounding the foot and the rhipidoglossate radula. Unlike such other single-gilled, rhipidoglossate archaeogastropods as the Trochacea and Neritacea, the neomphalid heart is monotocardian, having but a single auricle as in mesogastropods. Other mesogastropod-like features of *Neomphalus* include expansion of the left kidney to serve as a cavity in which some organs lie, and reproductive advancements that include glandular gonoducts, a copulatory organ in males and a seminal receptacle in females. The internal anatomy of *Neomphalus* and its affinity to other living gastropods is treated in a separate paper in this issue of MALACOLOGIA (Fretter, Graham & McLean, 1981).

One must assume that *Neomphalus* represents an evolutionary line that underwent an adaptive radiation, as have nearly all animal

groups in which a morphological innovation, in this case the unique filter-feeding ctenidium, has opened a new feeding zone to exploitation.

The absence of living relatives suggests that the radiation must have taken place in the past. Yet, no fossil record of this limpet has been found. However, because all limpets derive from coiled predecessors, the search for relatives may be directed to the extinct coiled groups. Archaeogastropods were the dominant gastropods in the Paleozoic, the period in which the origins of all other higher categories of living archaeogastropods took place.

Because the limpet shell form imposes few constraints upon anatomy, many features of limpet anatomy are likely common to the coiled predecessor. There are some groups of Paleozoic gastropods that seem so poorly designed for locomotion that they have recently been considered to have been sedentary and therefore likely to have been filter feeders. These groups, the Macluritacea and the Euomphalacea, are prime candidates as predecessors to *Neomphalus*. The discussion section of this paper presents the case for *Neomphalus* as a limpet derivative of the Euomphalacea. The neomphalid mantle cavity is suited to function within a coiled shell. Apart from the ease with which the neomphalid mantle cavity can account for filter feeding in euomphalaceans, there are clues in the shell ontogeny of *Neomphalus* that also suggest a derivation from the Euomphalacea.

The two superfamilies Macluritacea and Euomphalacea have been united in the suborder Macluritina (Cox & Knight, 1960), but this relationship has recently been questioned by paleontologists; the differences are sufficiently pronounced that subordinal separation can be justified. As this has not yet been done, the formal proposal of the suborder Euomphalina, to include the superfamilies Euomphalacea and the new superfamily Neomphalacea, is given at the conclusion to the discussion section in this paper.

Some other extinct superfamilies of archaeogastropods were considered as possible predecessors to *Neomphalus*. My opinions about feeding modes and affinities of these groups are given in Appendix 1. Because the Euomphalacea have shell characters that overlap those of the Trochacea, an effort has been necessary to define the shell characters that distinguish the two groups.

Few arguments could be found to preclude many of the extinct groups from having the pallial complex of the Trochacea. The evidence seems sufficient to merge the Craspedostomatacea and Amberleyacea with Trochacea, as discussed in Appendix 2.

MATERIALS AND METHODS

The thermal springs along the spreading axis of the Galapagos Rift were first observed from the deep submersible research vessel ALVIN in February 1977. Although biological collecting had not been anticipated, pieces of volcanic rock (Fig. 12A) were retrieved with the mechanical arm of ALVIN. Limpet specimens ranging in diameter from 7 to 30 mm were removed aboard the support ship and were transmitted to me in June 1977. These came from the vent-fields named Oyster Bed (dives 723 and 726) and Garden of Eden (dive 733).

Second and third expeditions were made to the Galapagos Rift site in February and December 1979 by biologists from Woods Hole Oceanographic Institution and Scripps Institution of Oceanography (Ballard & Grassle, 1979). Small specimens of *Neomphalus* were recovered from samples of the mytilid collected at the Garden of Eden vent-field (dive 884) and were transmitted to me.

All specimens were originally fixed in 4% buffered formalin and were subsequently transferred to 70% ethyl alcohol. Some specimens were dissected. Transverse and sagittal sections of males and females were made. Material for sectioning was embedded in paraffin; sections were cut at a thickness of 15 μm and stained with Mayer's hematoxylin and eosin. Shells of two small specimens were examined with a scanning electron microscope (SEM), and the intact animals of two others were critical-point dried for SEM examination. The radula was also examined with the SEM.

The internal anatomy of *Neomphalus*, its bearing on feeding and reproduction and the relationship to other living gastropods is treated separately by Fretter, Graham & McLean in this issue of MALACOLOGIA. The discussion section in the present paper therefore follows the discussion in the joint paper.

A report on the shell structure by Roger L. Batten, American Museum of Natural History, is in preparation and will be published separately.

In this paper frequent references are made to extinct genera and families of archaeogastropods. All are diagnosed and illustrated in the archaeogastropod volume of the *Treatise on Invertebrate Paleontology* (1960), in which the Paleozoic groups were treated by J. B. Knight, R. L. Batten & E. L. Yochelson, those of the Mesozoic by L. R. Cox, and those of the Cenozoic by A. M. Keen and R. Robertson. Knight's (1941) "Paleozoic Gastropod Genotypes" provides photographic illustrations useful for comparison with the shell drawings in the *Treatise*. Authors, dates, and type-species of genera are not given here; citations are readily available in these works.

SYSTEMATICS AND DESCRIPTIONS

NEOMPHALACEA McLean, new superfamily

Diagnosis: Having the characters of the family as follows:

NEOMPHALIDAE McLean, new family

Diagnosis: Shell cap-shaped, composed of lamellar aragonite and having an adherent periostracum; protoconch and first postprotoconch whorl with coiling axis perpendicular to final aperture; first whorl rounded, suture deep; conversion to limpet form in second postprotoconch whorl by process of lip expansion on upper half of whorl and growth stoppage on columella; radula rhipidoglossate; foot with anterior mucous gland and epipodial tentacles bunched along posterior sides of foot; shell muscle crescent-shaped, enveloping the visceral cavity but not the mantle cavity or pericardial cavity; mantle cavity deep, extending entire length of animal on left side; heart monotocardian, ventricle not traversed by rectum; right ctenidium and auricle lacking but represented by prominent efferent pallial vein in mantle skirt; left ctenidium lacking afferent membrane, attached to floor of mantle cavity by thickened efferent membrane; elongate gill filaments arching over flattened neck to food groove, which cuts over top of head directly to mouth; left kidney enlarged to form body cavity; gonads discharging through glandular gonoducts; left cephalic tentacle of male enlarged to serve as copulatory organ; seminal receptacle in female unconnected to genital duct.

Neomphalus McLean, new genus

Diagnosis: With the characters of the family plus shell features that include a nearly central position of the apical whorls, sculpture of fine radial ribs, and an internal shell ridge within the area of the muscle scar that increases the area for muscle insertion.

Type-species: *Neomphalus fretterae*, new species. Other species are yet unknown but may be expected at other rift-vent sites.

Etymology: The generic name combines the Greek prefix *neo* (new), and the generic name *Euomphalus* J. Sowerby, 1814, in keeping with my theory that the Neomphalidae are limpet derivatives of the Euomphalacea. The specific name honors Dr. Vera Fretter, of the University of Reading, in recognition of her contributions to our understanding of the relationships among prosobranchs.

Neomphalus fretterae McLean, new species
Figs. 1–12

Material: 115 specimens in the initial series, 69 ♀ and 46 ♂ from 3 dives of the ALVIN at the Oyster Bed and Garden of Eden vent-fields on the Galapagos Rift: Dive 723, Oyster Bed, 27 February 1977, 0°47.5'N, 86°08.0'W, 2478–2490 m, 15 ♀, 5 ♂; Dive 726, Oyster Bed, 9 March 1977, same coordinates and depths, 17 ♀, 18 ♂; Dive 733, Garden of Eden, 16 March 1977, 0°47.69'N, 86°07.74'W, 2482–2518 m, 37 ♀, 23 ♂. Position of Oyster Bed from the 1977 expedition, that of Garden of Eden from the 1979 expeditions; depths from ranges recorded on the 1979 expeditions, courtesy Fred Grassle.

Type Material: The holotype (Figs. 3A, B), an intact ♀ attached to the shell, from dive 723, Oyster Bed, is deposited in the U.S. National Museum of Natural History, Washington (USNM), no. 784637. Designated paratypes from dives 723, 726, and 733, as follows: USNM no. 784638, 3 ♀, 2 ♂; Los Angeles County Museum of Natural History (LACM), no. 1966, 17 ♀, 8 ♂, including specimens illustrated in Figs. 1, 4–9, some specimens dissected, 5 specimens sectioned; Museum of Comparative Zoology, Harvard University, Cambridge (MCZ), no. 280321, 5 ♀, 5 ♂. Additional paratype lots preserved with the body attached to the shell, have been sent to the mollusk departments of the following museums, the lot consisting of either two ♀ and one ♂ or one ♀ and one ♂, each specimen

individually labeled by sex and dive number: Academy of Natural Sciences, Philadelphia; American Museum of Natural History, New York; Field Museum of Natural History, Chicago; California Academy of Sciences, San Francisco; Department of Paleontology, University of California, Berkeley; Scripps Institution of Oceanography, La Jolla; National Museum of Canada, Ottawa; Museo Nacional de Historia Natural, Santiago; British Museum (Natural History), London; National Museum of Wales, Cardiff; Royal Scottish Museum, Edinburgh; Museum National d'Histoire Naturelle, Paris; Zoological Museum, Copenhagen; Zoological Museum, Amsterdam; Rijksmuseum van Natuurlijke Historie, Leiden; Forschungs-Institut Senckenberg, Frankfurt; Zoological Institute, Academy of Sciences, Leningrad; P. P. Shirshov Institute of Oceanology, Moscow; National Science Museum, Tokyo; Australian Museum, Sydney; National Museum of Victoria, Melbourne; Western Australian Museum, Perth; National Museum of New Zealand, Wellington; Auckland Institute and Museum, Auckland.

Additional Material: USNM 784639, dive 733, 23 specimens, 12 ♀ and 11 ♂, associated with the vestimentiferan *Riftia*, frozen and thawed in Bouin's fixative (which destroyed the shells) by M. Jones; MCZ 280323, 9 specimens, 1977 expedition, dive number not re-

corded; LACM 67728, Dive 884, Garden of Eden, 25 January 1979, 17 small specimens removed from shells and residue associated with the mytilid bivalve, including specimens illustrated in Fig. 10. Specimens from dives 723, 726, and 733 not designated as paratypes have been sent to Dr. Vera Fretter, Dr. Roger L. Batten, and Dr. Richard A. Lutz.

Geographic Range: Oyster Bed, Garden of Eden, Rose Garden, and Mussel Bed vent-fields at the Galapagos Rift. Although specimens from the latter two vent-fields have not been examined, *Neomphalus* has been identified by Dr. Fred Grassle and Ms. Linda Morse-Porteous in the collections from these vent fields that were made on the January-February, 1979, expedition.

Description

Shell (Figs. 1, 3, 9, 10): Maximum diameter of females 30.0 mm, of males 25.5 mm. The initial series had 30 females 22 mm in diameter or larger but only 3 males that size or larger. Shell height 0.23 to 0.33 times diameter. Dimensions of holotype: Maximum diameter 30.0, lesser diameter 26.7, height 7.8 mm.

The shell is white under a light-brown periostracum, moderately elevated and irregular in outline. The adult shell is composed

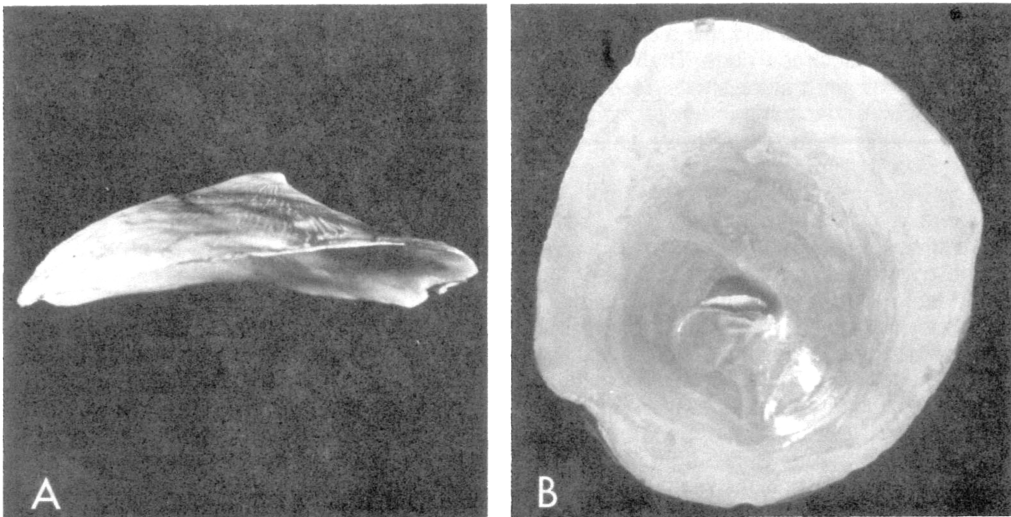


FIG. 1. *Neomphalus fretterae* McLean. Shell of mature female, dive 733, Garden of Eden, maximum diameter 26.6 mm, maximum height 6.5 mm. A) Lateral view from left side, showing the irregular shell margin. B) Interior view, anterior at top, showing the crescent-shaped muscle scar in the lower left quadrant and the shell ridge within the anterior arm of the muscle scar.

of two layers of lamellar aragonite, an outer complex crossed-lamellar layer and a thicker inner radial crossed-lamellar layer.² The lamellae of the inner layer are readily visible under low magnification, running parallel to lines of growth. The light-brown periostracum is thin but persistent. It projects beyond the margin of the shell and has prominent ridges corresponding to the radial sculpture.

The apex is posterior and slightly to the right of center, positioned at 0.6 the shell length from the anterior margin. The protoconch (Figs. 10A, B) has 1.2 rounded whorls and is sculptured with an irregular network of low ridges. The maximum protoconch diameter is 0.2 mm. The first post-protoconch whorl is rounded and the suture deeply incised; on the second whorl the area next to the suture has a flattened appearance, and faint spiral sculpture appears. The growth line trace on the second whorl continuously increases its extent with growth until it makes a full circle as the shell diameter reaches 1.8 mm. Further growth takes place along the entire margin.

The shell is sculptured with radial ribs that appear at a shell diameter of about 2 mm. Ribs are well defined, slightly curved until the shell diameter reaches about 7 mm, then more or less straight. Rib surfaces are rounded, with the interspaces about equal to the width of the ribs. Secondary ribs emerge in the rib interspaces after the shell attains a diameter of about 7 mm. Every 6th to 10th rib is stronger than the rest and has a correspondingly strong periostracal ridge. There are 23 to 25 strong ribs on mature shells. Most shells have irregular concentric interruptions representing resting stages or growth rings, the first interruption at a diameter of 6 to 7 mm, the second at a diameter of 9 to 13 mm. The periostracal ridges are stronger after crossing the first concentric interruption.

The growing edge of the shell is very thin and fragile and extends in short digitations corresponding to the rib pattern reflected in the overhanging periostracum.

The muscle scar (Figs. 1B, 9B) is crescent-shaped and located entirely within the lower left quadrant. The scar extends left from the apical pit and curves to the right, its closest approach to the shell margin about $\frac{1}{4}$ the radius. A shell ridge that is twice as high as wide originates at the deepest point on the apical depression. It extends along the inner

border of the muscle scar crescent for a distance of about $\frac{1}{4}$ the length of the inner margin of the crescent. The ridge may be 4 mm in length in large specimens. Its position is entirely within the area of the muscle scar; thus, it serves to increase the area available for muscle insertion.

Although thin, the shell of *Neomphalus* offers highly effective protection. None of the specimens showed any loss of periostracum or shell erosion. Specimens remain intact when dried, although the shell margin and periostracum may crack.

Similar overhanging periostracum is known in limpets of the families Capulidae and Hipponicidae. These limpets are immobile—the overhanging periostracum may function to provide a tighter seal along the margin.

Shell structure of lamellar aragonite is known in at least the innermost layer of the Fissurellidae, Scissurellidae, Skeneidae, Phasianellidae, Neritidae, Phenacolepidae, Cocculinidae and the extinct Bellerophonacea (Bøggild, 1930; MacClintock, 1963, 1967; Batten, 1975; Gainey & Wise, 1980). This is in contrast to the nacreous aragonitic internal layer of Pleurotomariidae, Haliotidae, Trochidae, Turbinidae, and Seguenziidae (Bøggild, 1930; Batten, 1972; Bandel, 1979; Gainey & Wise, 1980), and to the complex layering in the Patellacea (MacClintock, 1967).

The protoconch lacks the pointed tip illustrated for trochacean species by Bandel (1975), Rodriguez Babio & Thiriot-Quévieux (1975), and Fretter & Graham (1977). The diameter of the protoconch is well within the size limits for archaeogastropod protoconchs tabulated by Bandel (1979).

Radula (Figs. 2A, B, C, D, E): The radula is rhipidoglossate, with a monocuspitate rachidian, five monocuspitate laterals, and about 20 marginal teeth. The rachidian has a long main cusp that overhangs half its height, its tip sharp-pointed and its sides serrate and concave. The base is three times the width of the overhanging tip and has lateral and basal protrusions that fit in corresponding sockets on the adjacent lateral teeth. The first lateral has a basolateral extension and a longer overhanging tip than the rachidian. The second lateral has a longer overhanging tip than the first lateral and an even broader lateral extension. Bases of the lateral teeth are notched to provide space for the overhanging tips of

²Roger L. Batten, *in litt.*

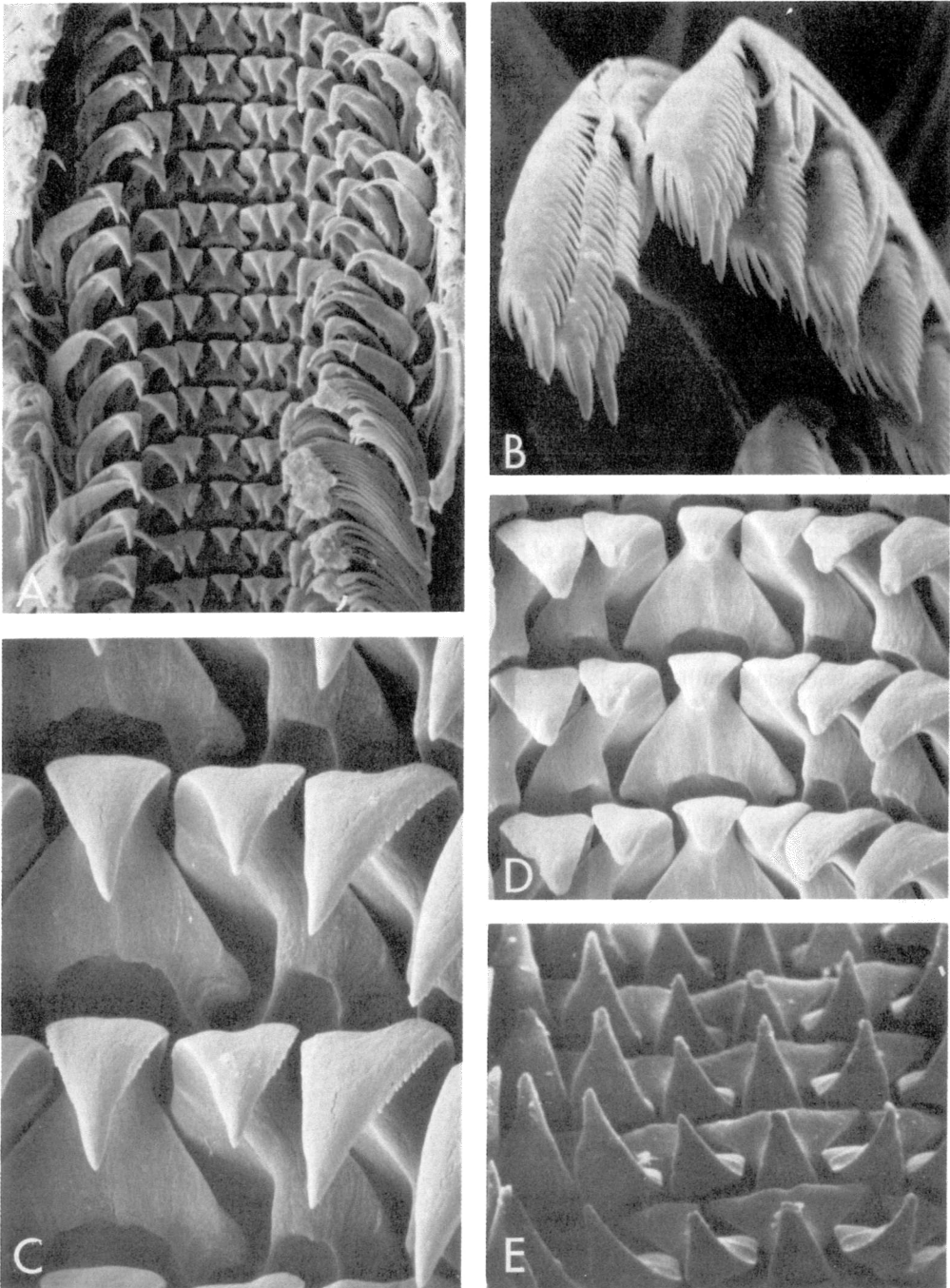


FIG. 2. *Neomphalus fretterae*. SEM views of radula. A) Full width of ribbon, showing rachidian, 5 laterals, and sheaths of incompletely separated marginal teeth. $\times 160$. B) Finely fringed tips of marginal teeth. $\times 1700$. C) Rachidian and first three laterals, showing fine denticulation on both sides of the main cusp of the rachidian but only on the outer sides of the main cusp of the laterals. $\times 950$. D) Rachidian and first three laterals showing tooth wear. $\times 575$. E) Intact radular ribbon projecting from mouth of preserved specimen.

the lateral teeth in the row below. The third lateral tooth has a narrow overhanging cusp about as long as that of the first lateral and a long, curved basal portion with a central strengthening ridge. The fourth lateral is similar to the third, and the fifth lateral is thin throughout and has only a sharp-pointed tip. The overhanging tips of the marginal teeth have a large, pointed denticle at the tip, with as many as 21 smaller comblike denticles on the sides.

The shafts of the marginal teeth have a tendency not to separate completely, producing an irregular arrangement, as has been noted by Hickman (1980b: 292, fig. 6C), who suggested that this may be due to a partial loss of function for these marginal teeth. The size of the radula is comparable to that of the Calyptraeidae and not to that of a grazing archaeogastropod, in which it is about ten times larger. The shortness of the radular ribbon indicates that the teeth are not rapidly used and replaced. The main function of the radula must be to rake in the food string, as in the Calyptraeidae.

The radula of *Neomphalus* is unlike any other rhipidoglossate radula. Elongation of the third, fourth and fifth laterals is unusual, recalling the elongate teeth in the Pleuro-

tomariidae (Woodward, 1901; Bouvier & Fischer, 1902; Fretter, 1964), but there is not the multiplicity of the lateral teeth in that family. There is no enlarged first marginal as in fissurellids and some trochaceans. The radular morphology of *Neomphalus* is so different from that of other archaeogastropods that it offers no useful phylogenetic clues.

External Anatomy in Ventral View (Figs. 3A, 4A, 5B, 6): Shrinkage resulting from preservation has retracted the mantle margin away from the growing edge of the shell, in most specimens decreasing the diameter of the animal by about a third (Fig. 3A). (In the following description of the ventral surface all references to left and right sides are from the normal dorsal aspect.)

Along the retracted mantle margin very fine mantle tentacles in nearly retracted condition are visible under high magnification on the outer edge; these tentacles correspond to grooves in the overhanging periostracum. Larger projections correspond to the major periostracal ridges on the shell.

The sole of the foot is oval except for its obtusely pointed posterior tip. It projects slightly on all sides, the anterior edge projecting to the greatest extent, where there is a straight edge and a prominent transverse fur-

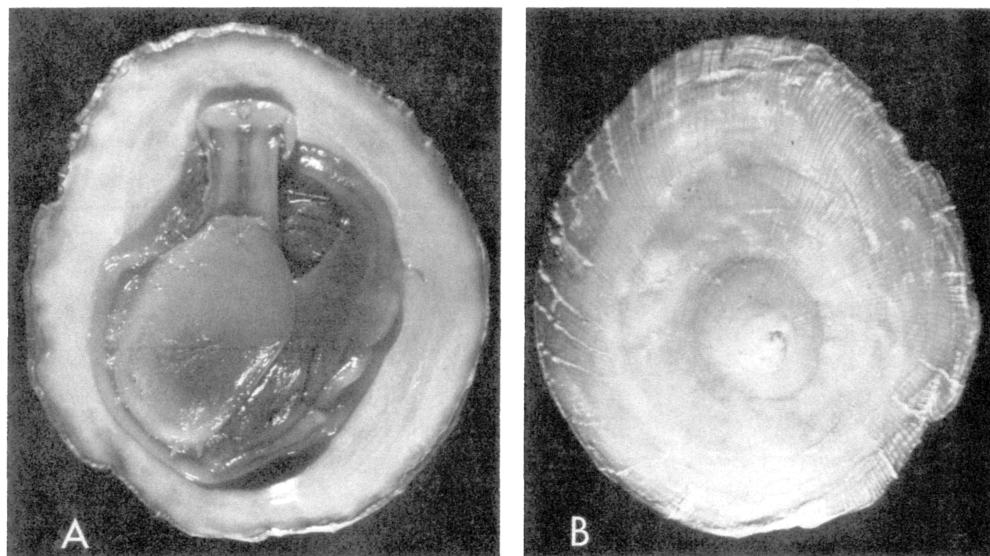


FIG. 3. *Neomphalus fretterae*. Holotype, USNM 784637, mature female attached to shell, dive 723, Oyster Bed, maximum diameter 30.0, maximum height 7.8 mm. A) Ventral view, showing the contraction of the body away from the shell margin and the projecting periostracum. The broad mid-ventral line on the neck is an artifact from shrinkage, marking the position of the esophagus. B) Exterior view, anterior at top, showing the periostracal ridges.

row, the opening of the anterior pedal mucous gland.

A thin epipodial ridge encircles the foot and extends forward on the ventral sides of the neck, where it fades and disappears. Tentacles are borne on this ridge only posteriorly. Those on the right side occur on the posterior third of the epipodium, the anteriormost concentrated on a projecting lobe bearing 4 to 9 short, stubby tentacles, with another two more broadly spaced tentacles between this group and the posterior tip of the foot. Tentacles on the left side (the mantle cavity side) are more limited, occurring only on the posterior fifth of the epipodium, the anteriormost being in a closely spaced group of 5 or 6, of which the first is the shortest; beyond this group are two longer and more broadly spaced tentacles.

The mantle cavity fills a space adjacent to the foot along the entire left side of the animal, extending posteriorly to a point opposite the foot tip. Adjacent to the foot the mantle cavity is closed and the gill axis shows through as a

supporting rod on the floor of the cavity. Adjacent to the neck the floor of the cavity is open and the gill filaments arch over the neck. The open portion of the mantle cavity extends over the head to a corresponding point on the right side.

Epipodial tentacles are prominent features in archaeogastropods other than Pleurotomariidae, Neritacea, and Patellacea. In no other family is there a similar elaboration in which they are entirely restricted to the posterior region and bunched together.

The pedal mucous gland is prominent in Pleurotomariidae, Scissurellidae and some trochaceans but is lacking in Haliotidae and Fissurellidae.

External Anatomy in Dorsal View (Figs. 4B, 5A): Upon removal of the shell the crescent-shaped columellar muscle is exposed. It surrounds the visceral mass except at the left side. No portion of the mantle cavity is enveloped by the shell muscle. A slit in the anterior portion of the muscle marks the position of

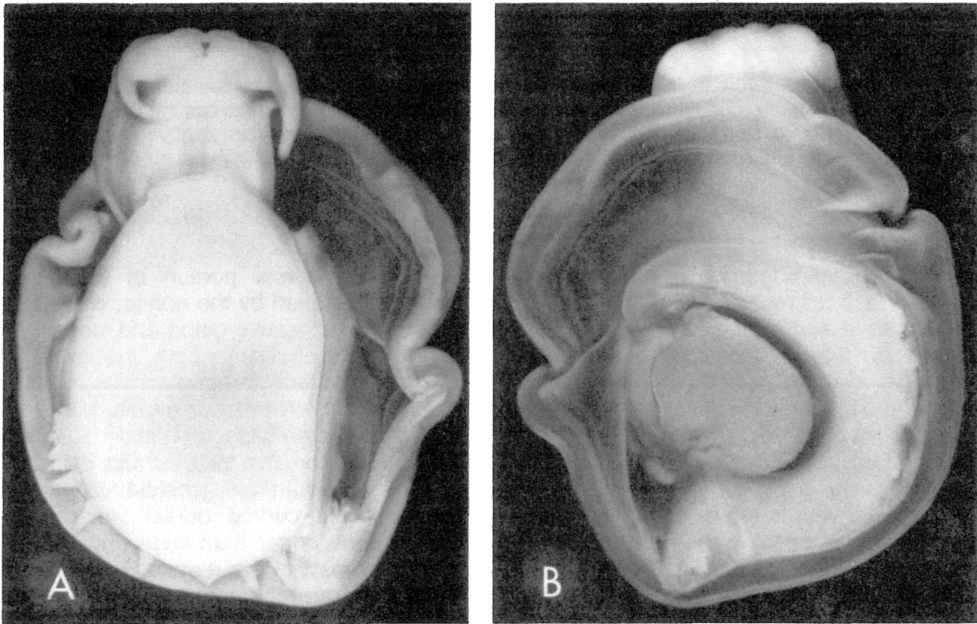


FIG. 4. *Neomphalus fretterae*. Mature female removed from shell, the ctenidium and its skeletal support on the floor of the mantle cavity excised. A) Ventral view, showing the epipodial tentacles bunched along the posterior sides of the foot, the obtusely pointed tip of the foot, and the opening of the anterior pedal mucous gland. Oral lappets extend on either side of the mouth, ventral to the posteriorly directed cephalic tentacles. B) Dorsal view, showing the efferent pallial vein in the mantle skirt, the food groove cutting diagonally toward the mouth, the crescent-shaped shell muscle surrounding the visceral mass except at the left side. The dorsal surface of the visceral mass is covered by the ovary on the right and the narrow, three-chambered glandular gonoduct on the left. The triangular pericardial cavity is left of the posterior arm of the shell muscle, containing the large, dark-appearing auricle on the left, and the smaller, lighter-appearing ventricle on the right.

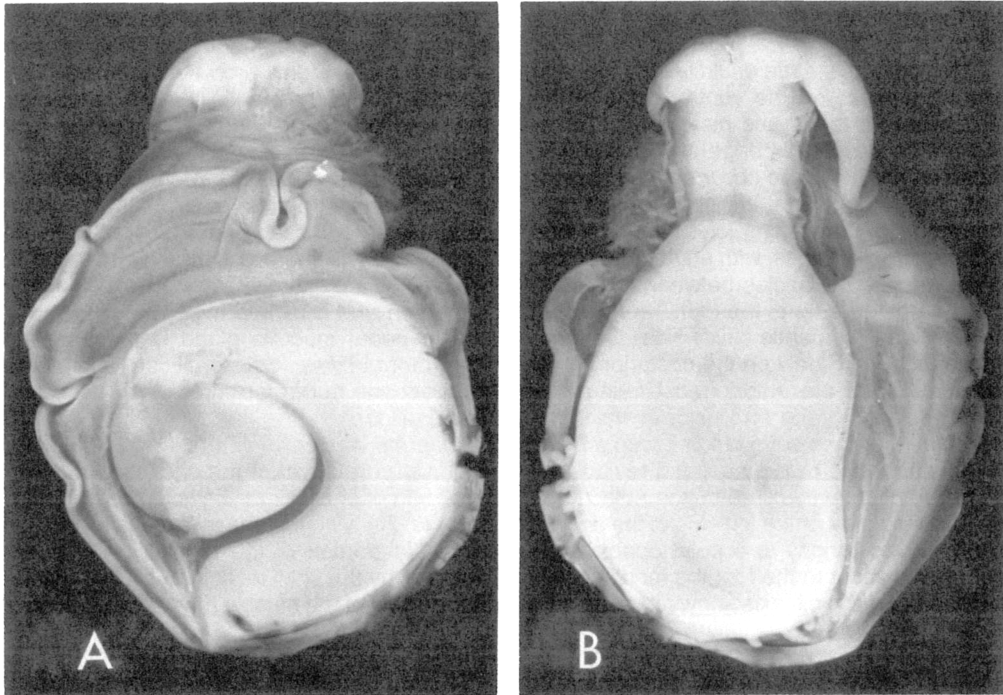


FIG. 5. *Neomphalus fretterae*. Mature male removed from shell. A) Dorsal view, showing the crescent-shaped shell muscle surrounding the visceral mass, which is covered by the testis on the right and prostate on the left. The mantle skirt is contracted and folded. The free tip of the ctenidium lies over the neck and the filaments extend to the right. B) Ventral view, showing the enlarged left cephalic tentacle adjacent to the left neck groove; other structures as in the female, Fig. 4A.

the interior shell ridge, which provides additional surface for muscle insertion.

The mantle skirt is relatively thin, apart from a thickened margin. It extends laterally in all directions; it is narrow to the right of the shell muscle and broad to the left where it roofs the mantle cavity, and broad anteriorly where it overlies the gill filaments that extend to the right above the neck.

The pallial vein is prominent in the mantle skirt, having its origin in the right anterior region of the mantle skirt and running midway along the roof of the mantle cavity on the left side of the animal. It extends to the posterior-most region of the mantle cavity, where it enters the auricle.

The triangular pericardial cavity is bordered on the right by the posterior arm of the shell muscle, on the left by the mantle cavity, and anteriorly by the visceral mass. The auricle is elongate, lying within the left side of the pericardial cavity; the shorter ventricle fills the right side.

The right-dorsal portion of the visceral mass is occupied by the gonad, entirely concealing the digestive gland and stomach beneath. Tubules within both the ovary and testis are visible externally, converging in both sexes at the left anterior region. Males (Fig. 5A) have a large bilobed prostate gland left of the testis; in females the glandular duct region is narrower than the prostate of the male, presenting a curved dorsal surface about three times longer than wide (Fig. 4B). The glandular duct of the female is comprised of three separate chambers, as detailed in the description of internal anatomy (Fretter, Graham & McLean, 1981).

Aside from the unique arrangement by which the shell muscle envelops only the visceral mass and not the mantle cavity, the dorsal position of the gonad is unusual; in other rhipidoglossate limpets the gonad shares the dorsal position with the digestive organs.

Head and Neck (Figs. 3A, 4, 5, 6, 7): The



FIG. 6. *Neomphalus fretterae*. Left-ventral view of male specimen after cutting ventrally along the floor of the mantle cavity adjacent to the foot and folding up the ctenidium, showing the enlarged left cephalic tentacle adjacent to the left neck groove. The mouth is a vertical slit between the oral lappets. Arrow points to the male genital opening.

neck is long, wide, and flattened, so that its thickness is only about $\frac{1}{4}$ the height of the shell muscle. It lies at the level of the foot, the space above filled by the ctenidium. The anterior end of the head is blunt—nothing projects beyond the base of the cephalic tentacle—a snout is therefore absent.

The mouth is a recessed vertical slit at the ventral anterior edge of the head. Some specimens are preserved with the inner lips closed, the mouth appearing as a slit between the outer lips; in others the outer lips are parted and the buccal mass, jaw, and radula protrude.

The dorsal anterior region of the head is continuous with a pair of posteriorly directed cephalic tentacles. Eyes are lacking. In males of all sizes the left cephalic tentacle is larger than the right and may extend along the opening of the mantle cavity for $\frac{2}{3}$ the length of the neck. In most females the left tentacle is the same size or only slightly larger than the right tentacle. One specimen was observed in which the left tentacle was sufficiently large to suggest that it was male, but it proved on gonad inspection to be female; thus, tentacle dimorphism is not fully reliable for sex determination.

The neck has lateral extensions or lobes on both sides. The right neck lobe is simple and

flaplike, its connection to the neck defined along most of its length by the food groove. Anteriorly the food groove arcs across the dorsal surface of the cephalic lobe, cutting deeply toward a notch directly above the mouth. The right neck lobe merges with the base of the right cephalic tentacle anteriorly.

The left neck lobe borders the opening to the mantle cavity and is comprised of two ridges with a deep channel between. The ventral ridge is straight and smooth, and the dorsal ridge is somewhat more ruffled or contracted (at least in preserved material). Anteriorly the ridges rise above the base of the left tentacle and fade dorsally where the tentacle emerges from the head. No direct groove leads to the mouth. Posteriorly the channel margins terminate against the foot side, below the ventral opening to the mantle cavity.

The head and neck of *Neomphalus* are highly modified in relation to filter feeding and thus are not comparable to the head and neck in other archaeogastropod limpets. Neck lobes in trochaceans are considered to be forward extensions of the epipodium, but this seems not the case in *Neomphalus* because the neck lobes are not continuous with the epipodial ridge. The flattened head and neck is more like that of the Calyptraeidae but exhibits the following unique features: 1) the

posteriorly directed cephalic tentacles, 2) the enlarged left tentacle of the male (which certainly has a copulatory function), 3) the dorsal route taken by the food groove (in the Calyptraeidae and all other filter-feeding prosobranchs it passes beneath the right cephalic complex rather than over it), 4) and the depth of the left neck channel (the Calyptraeidae have a left neck groove, but it is shallow in comparison).

Mantle Cavity (Figs. 4, 6, 7, 9): The mantle cavity lies over the head, as in most prosobranchs, but differs from most in having its closed portion extending to the left of the cephalopedal mass, so that its total shape is that of an inverted "L." In most limpets there is a horseshoe-shaped shell muscle that is open anteriorly and fully envelops the posterior-most extent of the mantle cavity, but in *Neomphalus* the opening in the muscle envelops only the visceral mass, and the opening is shifted 90° to the left. The anterior portion of the shell muscle lies directly between the neck and all of the visceral cavity. Access to the right side of the animal is thereby unavailable to the mantle cavity organs normally associated with the right side.

Structures within the mantle cavity can be observed either by cutting into it ventrally be-

tween the base of the gill and the foot (the mantle skirt folded up with the gill attached), or by cutting dorsally to the right of the pallial vein and the gill folded down.

The ctenidium (Fig. 8) fills the entire mantle cavity. It is attached on the floor of the deep, enclosed portion of the cavity and its free tip extends beyond the ventral opening of the cavity to fill the entire space above the head. It is bipectinate throughout, with long narrow filaments of equal length on both sides of the axis. There is no dorsal (afferent) membrane—the attachment is entirely ventral (efferent). The thickened ventral axis continues along the free tip, providing support for the long filaments.

The gill axis within the closed portion of the mantle cavity is placed so that afferent and efferent vessels are aligned nearly vertically; where the cavity opens ventrally the axis makes a 120° bend to the right and turns to lie flat. Here the two vessels are horizontally aligned and the filaments from both sides of the axis are directed over the neck. Water currents thus may pass through filaments on both sides of the axis.

On a large specimen 190 separate leaflets were counted on each side of the gill axis. Those that emerge deep in the mantle cavity

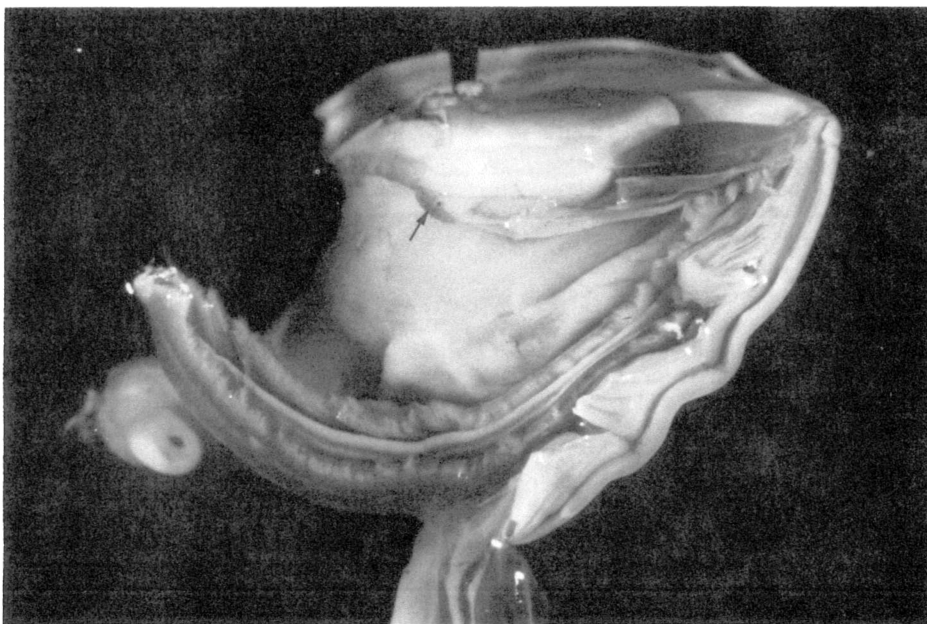


FIG. 7. *Neomphalus fretterae*. Female specimen from left side after cutting the mantle skirt between the visceral mass and the pallial vein; tips of ctenidial filaments excised to show the afferent side of the ctenidial axis. Arrow points to the female opening.

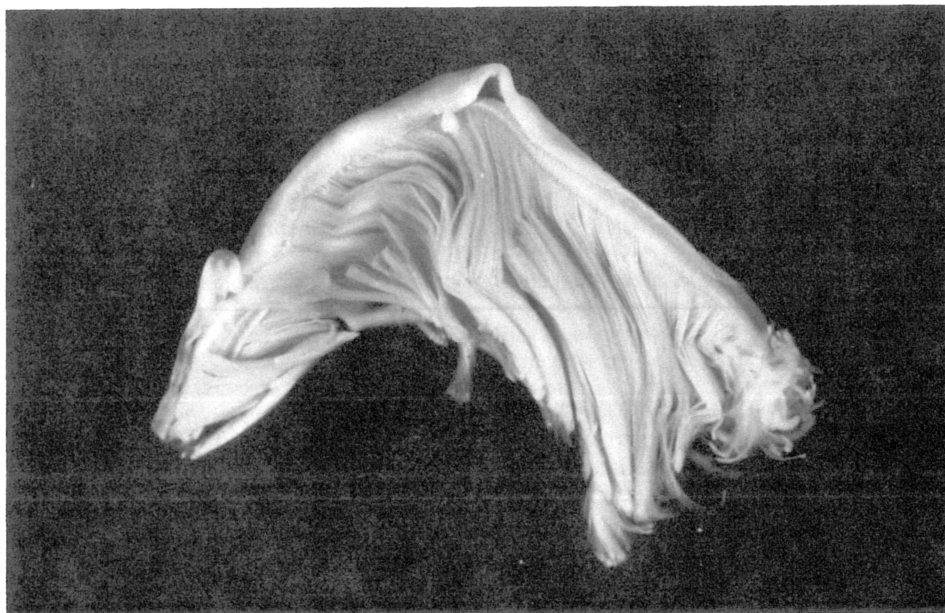


FIG. 8. *Neomphalus fretterae*. Ctenidium from specimen in Fig. 4, showing the close spacing and rounded tips to the filaments and the bend to the right midway along the axis. Filaments that arise beyond the bend terminate in a line corresponding to the position of the food groove where it traverses the neck.

are short and do not reach the opening. Filaments arising closer to the bend are longer, and those that emerge at the end are the longest. Tips of all the filaments impinge upon the food groove. On a large specimen the longest filament measured 9 mm in length and 0.4 mm in width throughout its length, which was therefore 22 times the width, comparable to the figure of 26:1 given by Yonge (1938) for *Crepidula*. Tips of the filaments are rounded. The filaments are not easily separated; a single filament cannot be removed without tearing the adjacent filaments. The cilia on the filaments and the skeletal rods within are treated in detail by Fretter, Graham & McLean (1981).

The food groove may be traced from the posterior end of the right neck lobe to near the innermost part of the mantle cavity, though sometimes appearing as a ridge rather than a groove. From the neck lobe it runs to the left over the dorsal surface of the head-foot and then backward, ventral to the anus, the genital opening, the ciliated area alongside that in females, and the kidney and pericardial cavity.

The osphradium consists of two elongated patches of dark-staining sensory epithelium at the base of the gill within the closed portion of

the mantle cavity behind the separation of the free tip to the ctenidium. This position is compatible with the normal position of the osphradium in aspidobranch gastropods, in which it is located at the leading edge of the efferent membrane that supports the free tip to the ctenidium. In *Neomphalus* the efferent membrane is thick and extends through the free tip, so that the osphradium has to be partitioned on both sides of the ctenidial axis to retain its usual position.

The left kidney opening is a tiny pore deep on the dorsolateral wall of the mantle cavity slightly posterior to the ventral inhalant opening and just within the anterior limb of the shell muscle. In females the genital opening has prominent rosette-shaped lips; from their base a series of fine, ciliated ridges and grooves runs posteriorly, dorsal to the food groove, to the opening of the receptaculum seminis. In males the opening is recessed, and the lips curve forwards to form a groove lying ventral to the rectum. The extreme leftward shift and considerable depth of the mantle cavity has the important consequence of keeping the genital openings on the left side of the body, unlike the condition in all other single-gilled prosobranchs, in which the reproductive functions are entirely performed at

the right side of the head. The displacement of the genital opening to the left side explains why it is the left rather than right cephalic tentacle of the male that is modified as a copulatory organ.

The rectum, upon emerging from the kidney cavity at about the position of the genital opening, is suspended dorsally in the mantle cavity, running adjacent to the shell muscle. The anus is positioned directly over the mid-point of the neck. A rod of fecal material continues in a groove in the mantle skirt adjacent to the shell muscle, which carries the fecal rod to the right, where it can be expelled when the shell edge is raised.

No distinct region in the mantle skirt can be regarded as hypobranchial gland, although scattered subepithelial gland cells are present. This is in striking contrast to the prominent ridged and convoluted development of discrete left and right hypobranchial glands in the pleurotomariids, haliotids and trochaceans. In these groups left and right hypobranchial glands are separated by the rectum in the mantle skirt. In *Neomphalus* the rectum does not traverse the mantle skirt. Hypobranchial gland development comparable to that of *Neomphalus* occurs in the Fissurellidae, in which gland cells are present in the

mantle skirt but do not form a discrete organ with a folded surface.

The ctenidium of *Neomphalus* is unique in the Gastropoda. It is the only ctenidium bipectinate throughout its entire length in which the filaments are elongate and the afferent membrane is lacking. Its length and mass is no doubt greater than that of any other living gastropod. Only in bivalves may the length of the gill be equal to that of the animal. The afferent membrane is lacking in one other family in the Archaeogastropoda—the Pleurotomariidae. Pleurotomariid ctenidia differ in being paired, the filaments not elongated, the efferent membranes not thickened. The pleurotomariid mantle cavity extends even deeper than that of *Neomphalus*, past the ctenidial origin.

Growth and Shell Ontogeny: Four small specimens, having shell diameters of 1.7, 3.2, 3.8, and 4.0 mm, were collected on the second expedition in February 1979. The shell of the 1.7 mm specimen was mounted for SEM examination of the aperture (Fig. 10C); the 3.2 mm specimen remains intact; the 3.8 mm specimen was critical-point dried for SEM examination of the animal (Fig. 10D); and the 4.0 mm specimen was used for SEM study of its exterior (Figs. 10A, B).

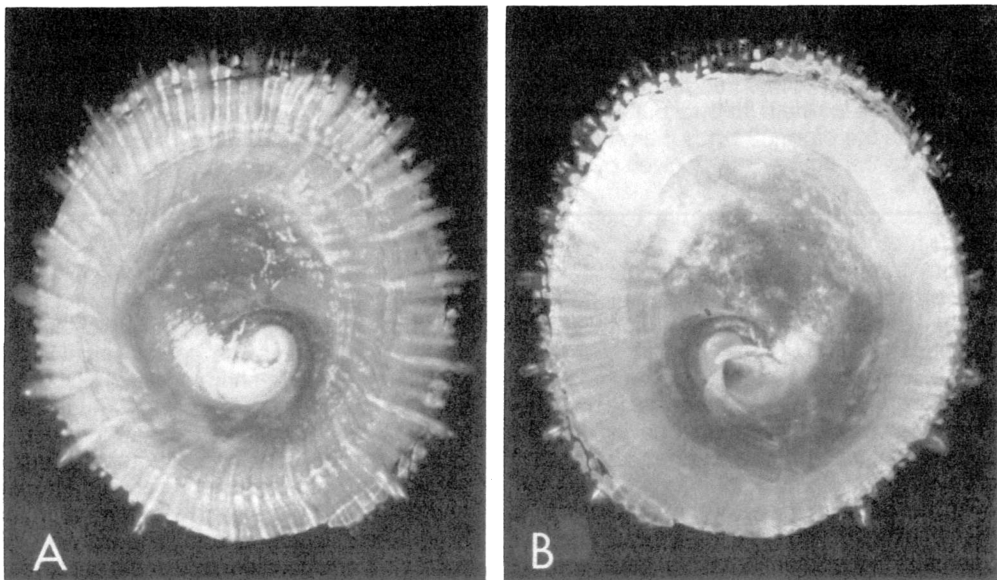


FIG. 9. *Neomphalus fretterae*. Juvenile shell of female, dive 733, Garden of Eden, diameter 7.0 mm. A) Exterior, anterior at top, showing flat-lying coil of early whorls. B) Interior, anterior at top, showing abandoned columella from the early coiled phase, the muscle scar and the shell ridge now positioned directly over the base of the early shell.

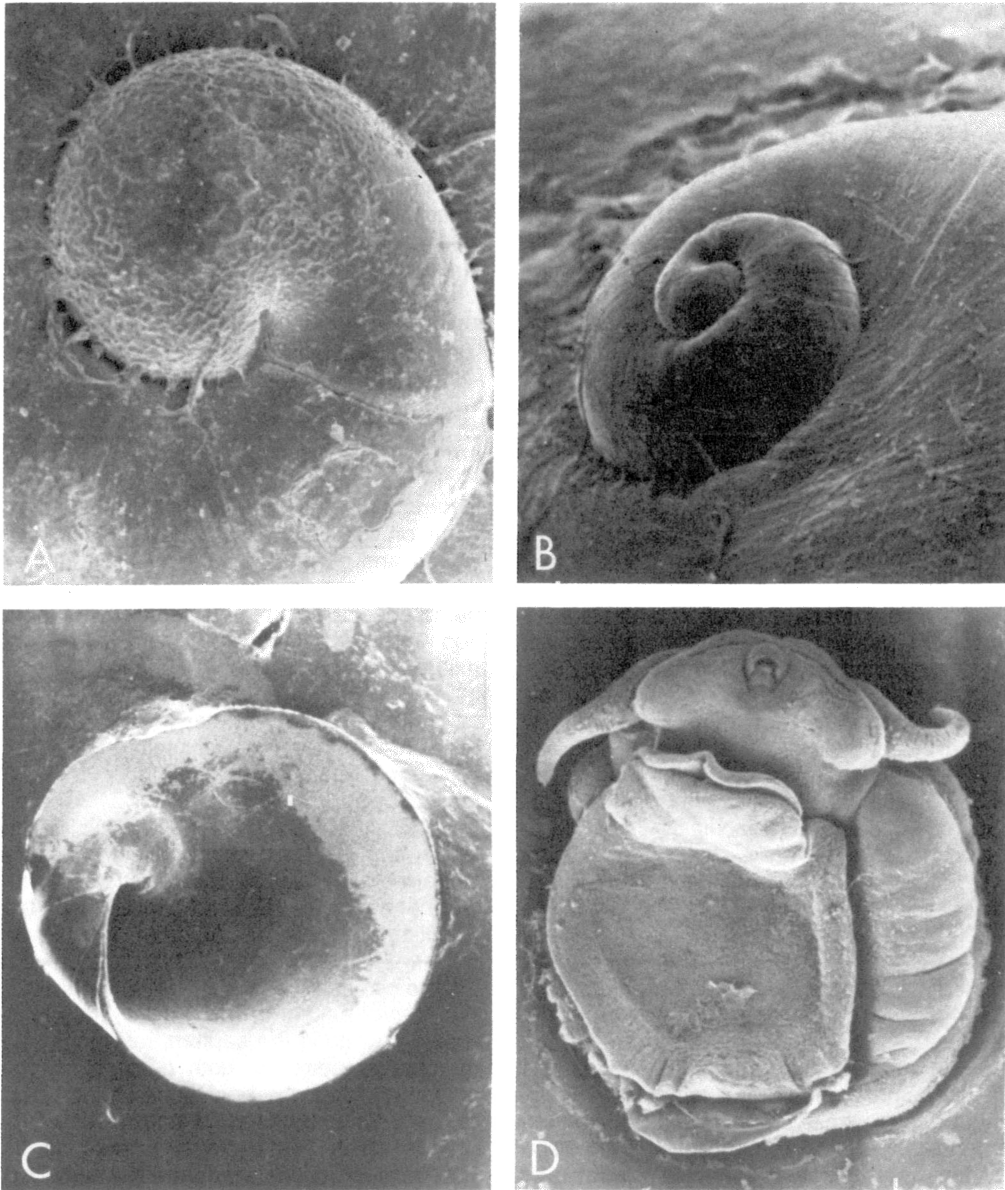


FIG. 10. *Neomphalus fretterae*. SEM views of early stages. A) Protoconch, maximum diameter 0.2 mm. B) Oblique view of protoconch and first two postprotoconch whorls, same specimen as Fig. 10A. C) Basal view of coiled juvenile shell 1.7 mm in diameter, showing the rudiment of the shell ridge, the rounded columellar lip along which growth has stopped, and the encirclement by lip growth on the right $\frac{3}{4}$ complete. D) Ventral view of critical-point-dried juvenile attached to shell, shell diameter 3.8 mm, showing larval operculum 0.8 mm in diameter, the prominent opening of the anterior pedal mucous gland, jaws and other adult features, except that the neck is short, the mantle cavity not open on the left and the gill filaments not in evidence.

The critical-point dried specimen (Fig. 10D) shows the larval operculum attached vertically at the rear of the foot, its diameter 0.8 mm. It has a tight central coil of 5 whorls and a paucispiral final whorl. Epipodial tentacles, jaws, the oral lappets, and the anterior pedal gland are well developed. Major differences from the adult are that the neck is relatively short, the gill filaments are not visible, and the mantle cavity opening ventral and left of the neck is not apparent nor is the left neck groove. Cephalic tentacles are laterally directed. The larval operculum of *Neomphalus* reaches a larger size and persists through more advanced stages of development than in limpets of any other family.

Neomphalus is also unique among limpets in the manner in which it makes the transformation from a coiled juvenile to the adult shell form. The transformation takes place in the second postprotoconch whorl, and results from cessation of growth of the columellar lip and accelerated growth along the suture and upper margin of the lip. A new suture is laid upon the periphery of the *Lamellaria*-like shell until the lip extends a full 360°. The stage at which the process begins is not marked by a line of transition on the external surface. This transformation is nearly complete on the 1.7 mm diameter specimen (Fig. 10C), in which the columellar lip is rounded and the base of the shell exposed, as yet uncovered with callus deposits. The total cessation of growth on the columellar lip is clearly indicated in larger juvenile shells (Fig. 9B), in which the old columella remains visible in the apical position of the shell interior.

The transformation to the limpet form involves a 90° shift in the orientation of the animal relative to the initial axis of coiling. Such a change is inferred because the larval stage in the 0.2 mm long protoconch would have the orientation common to all veliger stages with the head balanced relative to the axis of coiling. Because the animals in all the small specimens are oriented perpendicular to the plane of the aperture, they must have completed this 90° shift during the growth of the second postprotoconch whorl, coinciding with cessation of growth on the columellar lip.

Cessation of coiling fixes the orientation of the head and columellar muscle at an early stage. The columellar muscle of the coiled juvenile would be just inside the columellar lip; the cessation of coiling forces the growing muscle to emerge and assume a position on the base of the shell, where it expands with

growth. The rudiments of the shell ridge are apparent on the 1.7 mm specimen (Fig. 10C).

The cessation of growth along the basal part of the columellar lip explains why the columellar muscle does not form the encompassing horseshoe-shaped shell muscle of most other limpets. In transitional forms between normally coiled trochids and auriform limpet-like stomatellid trochaceans, the columella is lengthened, as is the columellar muscle. This expansion of the columellar muscle along the left side (viewing the animal dorsally) envelops the mantle cavity on the left, producing, upon further reduction of coiling, the horseshoe-shaped muscle that entirely envelops the visceral mass posteriorly and the mantle cavity anteriorly. In *Neomphalus* the left arm of the muscle is not stretched along an expanding columella and thus does not envelop the mantle cavity on the left side.

Thus many of the unusual features of *Neomphalus* can be traced to growth stoppage on the juvenile columella, which halts coiling and generates the limpet form, at the same time preventing the mantle cavity from being enveloped on the left side. The orientation of the animal relative to the columella and axis of coiling is forced to change.

Shell ontogeny in the Calyptraeidae, recently described by Fretter (1972), follows a different course: the columellar lip of the protoconch expands, altering the axis of coiling, followed by the addition of a projecting peripheral rim on all sides, producing the limpet shell. Folds of the mantle produce the calyptraeid septum by adding a flange to the original columella. *Neomphalus* differs in that the limpet shell results from progressive rather than simultaneous encirclement and the old columella is completely abandoned. In the calyptraeid the columellar muscle is drawn out along the septum, retaining major attachment points at both ends; hence the calyptraeid has the horseshoe-shaped muscle with its extremities at both sides of the mantle cavity, as in most limpets. In the Patellacea, Fissurellacea, and the Neritacean limpets, the horseshoe-shaped muscle results from fusion of the left and right muscles; only minor changes in the orientation of the animal relative to the axis of coiling are involved.

Life habits

Neomphalus limpets live clustered near and extending into the vents (Fig. 11), where

they are in close association with the vestimentiferan *Riftia pachyptila* Jones (1981). Vent effluent at the Garden of Eden vent-field has a maximum temperature of 17°C, in contrast to the ambient bottom temperature of approximately 2°C. Vent effluent contains hydrogen sulfide and is reported as anoxic above 10°C, but presumably mixes sufficiently with oxygenated ambient water to sustain the limpets. Current flows of 2 to 10 cm/sec have been measured (all data from Corliss et al., 1979, p. 1082). The limpets are often in contact and some are positioned on the shells of others, as shown on the large fragment of pillow basalt from the Garden of Eden (Fig. 12A). The broad anterior surfaces of the limpets on the boulder (Fig. 12A) are facing in different directions, indicating that there was no orientation with reference to currents. *Neomphalus* may attach to the tubes of *Riftia* (Fig. 12B), although there is no indication of this in Fig. 12A.

Neomphalus is primarily sedentary; the shell margin is irregular, evidently conforming to a particular site. Those attached to other shells leave no attachment scars nor cause

any damage to the periostracum of the lowermost shell. The periostracum should provide a seal along the shell edge that would protect it from the claws of the brachyuran crab *Bythograea thermydron* Williams (1980), a potential predator at the Galapagos Rift. The foot of *Neomphalus* is sufficiently muscular for locomotion. Some motility would be required for the mating we deduce from the anatomy (Fretter, Graham & McLean, 1981).

Suspended bacterial cells in the rift-vent effluent have been measured in the range of 5×10^5 to 10^6 per ml (Karl et al., 1980) during the January 1979 expedition; Corliss et al. (1979) reported a count of 10^8 to 10^9 bacterial cells per ml in preserved samples from the 1977 expedition. Thus there is a sufficient source of suspended food to sustain large populations of filter-feeding animals. Mats of microorganisms also develop on shell or rock surfaces in the vicinity of the vents (Jannasch & Wirsen, 1981), providing a source of food for limpets that feed by grazing.

Gut contents in *Neomphalus* suggest that feeding is a combination of grazing and filter feeding (Fretter, Graham & McLean, 1981).



FIG. 11. Oyster Bed vent-field, dive 726, showing the vestimentiferan, *Riftia pachyptila*, the brachyuran crab *Bythograea thermydron* in upper center, the galatheid crab at lower left, and numerous *Neomphalus fretterae* on all exposed surfaces.

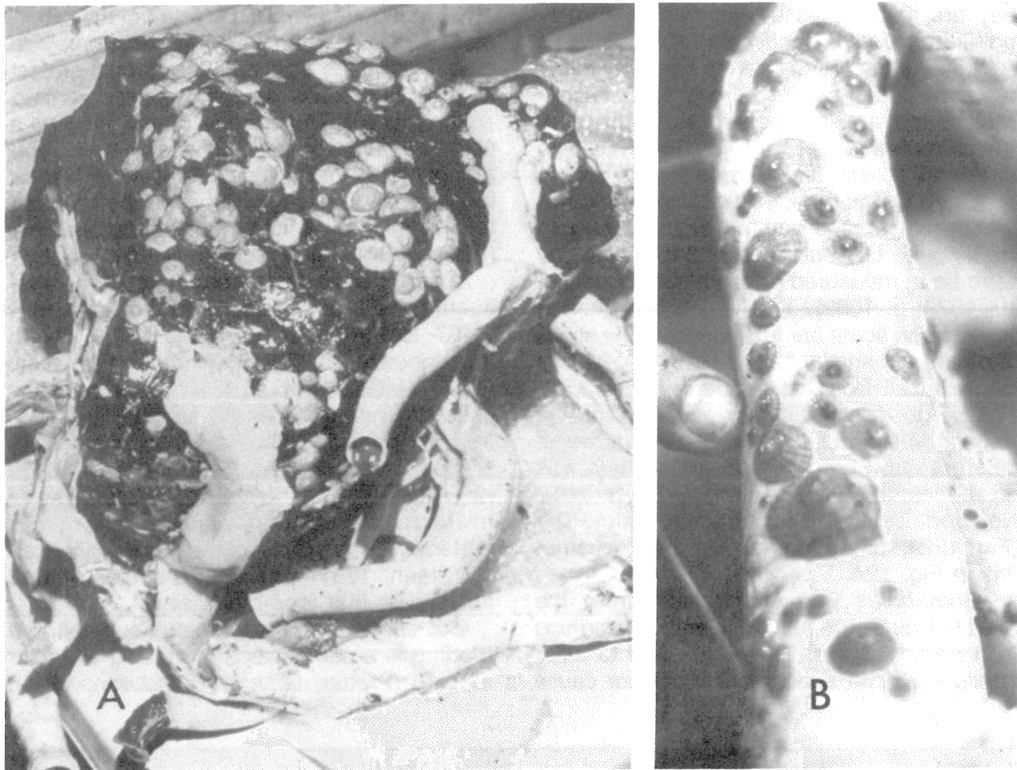


FIG. 12. A) 72 lb fragment of pillow basalt from dive 733, Garden of Eden, photographed on deck of support ship, showing *Neomphalus* in place and tubes of the vestimentiferan, *Riftia*. B) Tube of *Riftia* with attached *Neomphalus* in place, from 1979 expeditions, dive number unknown.

Wear on the rachidian and lateral teeth (Fig. 2D) provides additional evidence that the radula is used for grazing. The prominence of the jaw and buccal development and retardation of the gill development in juvenile specimens (Fig. 10D) suggests that grazing is the exclusive feeding mode of young stages. A retention of the grazing capacity and a combination of the two feeding modes in adults is therefore not surprising.

Sectioned specimens examined by Fretter, Graham & McLean (1981) showed ripe gonads with gametes in all stages of development, indicating that reproduction is a constant process throughout the year, in agreement with observations that in the absence of seasonal stimuli, most deep-sea invertebrates spawn throughout the year (Rokop, 1974; Rex et al., 1976).

The reproductive anatomy of *Neomphalus* indicates that copulation must take place, that sperm are stored in a receptaculum seminis, that fertilization probably takes place in the

proximal arm of the genital duct, and that fertilized eggs receive a coating of jelly-like material before extrusion from the distal arm of the genital duct (Fretter, Graham & McLean, 1981). Egg capsules have not been collected; thus, the next step is unknown and it is uncertain whether individually encapsulated eggs are released freely or attached to the substratum. A sufficient number of females have been collected to rule out the possibility that developing young are brooded under the shell. Egg masses have apparently not been found attached to the boulders from which the specimens were collected. The free release of coated eggs therefore seems most likely.

A coated egg, upon expulsion from the mantle cavity might settle in a crevice or perhaps become entangled by the byssal threads of the rift-vent mytilid. A postprotoconch larval shell with a sharp transition preceding the onset of adult sculpture is lacking, indicating that there is no planktotrophic veliger stage (Shuto, 1974; Robertson, 1976). Plankto-

trophic veligers are unknown in archaeogastropods (Fretter, 1969) and *Neomphalus* is no exception. Direct development through the trochophore and veliger stages probably takes place within the egg coating; crawling juveniles would emerge. During the growth of the first and second postprotoconch whorls, the juvenile *Neomphalus* would be active but would remain in crevices or among the byssal thread of the mytilids. When the transformation to the limpet is completed by the end of the second postprotoconch whorl, the limpets would take up a more sedentary, primarily filter-feeding existence where exposed to the strong flow of the rift-vent effluent. Those juvenile specimens received were recovered from residue samples associated with the mussels. The mature mussels live in a zone further away from the vents; thus there is some evidence that the early life of the juvenile takes place away from the vents.

The hypothesized course of development should enable the continuation of populations at each vent site, but it does not account for a mechanism of dispersal to more distant vent sites. Individual vent fields have been postulated to have a rather brief, ephemeral existence of several hundred years, necessitating the colonization of the new vent sites that emerge along the spreading sea floor.

Unlike *Neomphalus* the mytilid from the Galapagos Rift seems to have an effective dispersal mechanism. Because it has a well-defined larval shell, Lutz et al. (1979) inferred that there is a planktotrophic larval stage capable of long-range dispersal via bottom currents, its metamorphosis indefinitely delayed because of lower metabolic rates at ambient bottom temperatures. For *Neomphalus*, however, the colonization of new vents may be a matter of passive transport via larger, as yet unknown animals that may move between the springs.

DISCUSSION

As discussed by Fretter, Graham & McLean (1981), the neomphalid anatomy is an extra-

ordinary combination of archaeogastropod and mesogastropod characters combined with some unique features. That it is a highly modified and specialized archaeogastropod cannot be doubted, for it has such primitive archaeogastropod characters as a rhipidoglossate radula, a bipectinate ctenidium, epipodial tentacles, and the anterior loop of the intestine. Its features at the mesogastropod level of organization include the nearly complete reduction of the right pallial complex, a monotocardian circulatory system, expansion of the left kidney and formation of a nephridial gland, a copulatory organ in the male, and glandular gonoducts in both sexes. Unique features include the split osphradia, absence of a snout, dorsal position of the food groove, posteriorly directed cephalic tentacles, the enlargement of the left tentacle to form a copulatory organ, and an unusually positioned receptaculum seminis in the female.

Fretter, Graham & McLean (1981) discuss the leftward rotation on the anterior-posterior axis and the 90° of further torsion, so clearly shown in the placement of the internal organs, that accounts for many of the unusual aspects of the anatomy. These shifts and rotations can be understood as resulting from the early ontogeny, as described here, in which growth stops along the columella, forcing the columellar muscle to emerge to the base of the shell, and changing the orientation of the animal from its initial axis of coiling. Can it be shown that some of the features of this ontogeny occur in the evolutionary history of *Neomphalus*? Although *Neomphalus fretterae* is the only known member of a group that can be assigned to no family, superfamily, or suborder with living representatives, its evolutionary history can be sought in the fossil record, even though no fossil record of the genus itself has been found.³

Argument for an Archaic Origin

The neomphalid ctenidium is a departure from other gastropod ctenidia. It is a morphological innovation, an effective adaptation for filter feeding. The course of evolution is

³Four poorly known Devonian genera, *Procrucibulum*, *Paragalerus*, *Progalerus*, and *Protocalyptraea*, have names that imply some similarity to the shell form of calyptraeids. An affinity of these genera to the Calyptraeidae, which appeared in the Cretaceous (Hoagland, 1977) has to be ruled out. However, these genera are of interest as possible precursors to the Neomphalidae. Except for *Paragalerus*, drawings of reconstructed shells were illustrated in the Treatise (Knight et al., 1960). Each genus is known only from the type-species (Yochelson, personal communication), holotypes of which were described and illustrated by Knight (1941). The first three are represented by internal molds that lack information about protoconchs and muscle scars. *Protocalyptraea* is based on a small incomplete specimen (see also Linsley et al., 1978: 111), in which the peripheral frill would seem to preclude it as a precursor for *Neomphalus*. Affinity of these genera with the Neomphalidae cannot be completely dismissed, but it cannot be discussed further until better material is known.

marked by adaptive radiations, proliferations of new taxa following the introduction of successful morphological innovations (Simpson, 1953; Stanley, 1979). Thus, the neomphalid ctenidium should either have given rise to experimentation or be an end result of experimentation that has already taken place. Because *Neomphalus* has many unique and very specialized features and because it occurs in an environment with many limiting parameters, it surely must represent a single twig of a larger branch in a group having the same ctenidial structure. Its predecessors need not be limpets, for limpets are evolutionary dead ends, giving rise to adaptive radiation within a family or superfamily, but not serving as raw material for the further evolution of higher categories.

The limpet form has been derived from coiled predecessors with some frequency in gastropods. Among archaeogastropods, mesogastropods, opisthobranchs, and pulmonates there are many families of limpets. One example is known in a siphonostomate neogastropod—that of *Concholepas*. Except for the docoglossate patellaceans, for which a convincing derivation has never been offered, the limpet families are closely related to families or superfamilies having regular coiling, particularly those in which the shell aperture is holostomate rather than siphonostomate.

In some families or superfamilies—for example the trochacean Stomatellidae—there are limpet derivatives in which the entire progression from a trochiform to auriform and to a limpet shell form is represented. In others, like the Patellacea and the Calyptraeidae, there are no clues as to the shell form of the closest relatives. In these groups the derivation may have been sudden, in a process of paedomorphosis, a phylogenetic derivation in which reproductive maturity is attained in a stage before the development of adult characters (see Gould, 1968; Stanley, 1979). Normal adult coiling does not take place; rather, shell growth expands the aperture of the juvenile shell. In each case the limpet's anatomy, though modified by loss of coiling, retains a sufficient number of characters common to its ancestor (shared primitive characters) to permit its taxonomic placement. The external features of any limpet animal—for instance the modifications of the head for its generally constant retention under the protective shield of the shell—have some similarity from one family to another, but there are so many diverse anatomies represented in limpet fami-

lies that it is apparent that the form itself imposes few constraints upon the internal anatomy. Thus, the major features of a limpet's anatomy must be a reflection of primitive characters in its coiled predecessor.

In the absence of a living coiled group with anatomy comparable to that of a particular limpet, one may hypothesize the anatomy of the coiled predecessor, basing the reconstruction around the characters displayed by the limpet that are assumed to be primitive and not a consequence of the limpet mode.

Although the ctenidial filaments of *Neomphalus* are highly modified for filter feeding, the basic configuration of the neomphalid gill—aspidobranch with afferent attachment lacking—is a character that would be shared with the coiled predecessor. The only comparable condition in which an aspidobranch gill lacks an afferent membrane occurs in the Pleurotomariidae, in which the gills are paired. The Pleurotomariidae are regarded as the most primitive living gastropods. The superfamily Pleurotomariacea has a fossil record that is continuous from the Upper Cambrian. The possible affinity of *Neomphalus* to the extinct groups contemporary with the early pleurotomariaceans must be considered.

Although the subordinal classification of archaeogastropods proposed by Cox & Knight (1960) for use in the *Treatise* (Knight et al., 1960) is due for modification, all of the major divisions they recognized are traceable to the early Paleozoic, the only remaining doubt being that surrounding the appearance of the Patellina—whether early or late in the Paleozoic. Most of the living archaeogastropod families made their appearance by the early Mesozoic, well in advance of the burst of evolution in the Neogastropoda during the Cretaceous. If all other high-level, subordinal origins and initial radiation of archaeogastropod taxa took place in the Paleozoic, it is logical to assume that the subordinal distinction in *Neomphalus* also had a Paleozoic origin.

Excluding the living and fossil groups for which there is reasonable certainty that the gill condition was dibranchiate, and excluding the neritaceans, a completely divergent line (Fretter, 1965), for which the fossil record is well understood, those extinct, conspirally coiled archaeogastropods that may have had a unibranchiate mantle cavity were placed by Knight et al. (1960) in two of the suborders of Cox & Knight—the Macluritina and the Trochina. In that classification the extinct

superfamilies in the suborder Macluritina were the Macluritacea and Euomphalacea; in the suborder Trochina there were four extinct superfamilies: Platyceratacea, Microdomatacea, Anomphalacea, and Oriostomatacea. In addition there were five superfamilies of "doubtful subordinal position," for which single gills were likely: the Clisospiracea, Pseudophoracea, Craspedostomatacea, Palaeotrochacea, and Amberleyacea. These represent major evolutionary lines for which there is no direct information about their anatomies. Implicit in the ranking of these groups as families and superfamilies is the assumption that they had anatomical differences comparable to those that distinguish the living families for which the anatomy is known. Was there in fact as great a diversity in anatomies as is implied by the number of available supraspecific categories?

In the Trochacea, the only superfamily of the suborder Trochina recognized as living, many authors (Risbec, 1939, 1955; Yonge, 1947; Clark, 1958; Graham, 1965) have found the structure of the ctenidium to be virtually identical among species examined in all trochacean families, including the Trochidae, Stomatellidae, Turbinidae, and Phasianellidae.⁴ In its most familiar condition the trochacean ctenidium has a free tip with a strong ventral skeleton and gill leaflets of equal size on both sides of the axis. Posterior to the free tip about $\frac{2}{3}$ the length of the ctenidium is supported by both dorsal afferent and ventral efferent membranes (Fretter & Graham, 1962, figs. 53, 170). Here the leaflets on the right side of the axis, where there is more space, are larger than those of the left side, which are confined in a deep narrow chamber (see Yonge, 1947, fig. 25). The number of leaflets in the deepest reaches of this chamber may be reduced compared to those on the right. There are two modifications of this basic plan, that of *Umboonium* (Fretter, 1975) in which the entire gill is monopectinate and fused to the mantle wall throughout its length, and that noticed in *Margarites* (Fretter, 1955: 161) in which "the long aspidobranch gill lies freely in the mantle

cavity, and both afferent and efferent membranes are short. . . ." I have found that this latter condition is true of several other trochacean groups, as will be discussed further in a separate paper (McLean, in preparation).

All three of these different expressions of the trochacean gill have in common the transverse pallial vein, an additional conduit to the afferent ctenidial vessel, requiring at least a short afferent membrane for support (except in *Umboonium*). The left gill of the trochacean differs in this way from the left gill of the pleurotomariid, which lacks the transverse pallial vein and thereby has far less efficient circulation to the ctenidium. The trochacean pallial complex has evidently been highly effective from its inception, for the Trochacea are the most successful of living archaeogastropods in numbers of extant species and diversity of habitat. The extent of adaptive radiation possible for a group with the trochacean pallial complex has probably been attained.

The anatomical similarity of trochacean families is a remarkable fact, considering the diversity of shell shape, shell structure, and opercular structure. The close anatomical relationships between families with nacreous interiors and the Skeneidae and Phasianellidae, in which the primitive nacre is replaced by lamellar aragonite, would seem to belie the frequently emphasized principle that shell structure is a conservative character (for example, Batten, 1972, 1975). It is entirely possible that many of the extinct groups could have had anatomies that would place them in the Trochacea. The diversity of shell form in the Trochacea is broad enough to encompass the extremes of shell shape in some, though not all, of the extinct superfamilies. The problem can be approached by asking how the shell features in extinct groups would impose functional constraints upon their anatomies.

The Trochacea are dated from the Triassic by Knight et al. (1960: 247), but there is no clear argument in the literature to exclude many older extinct families or even super-

⁴The Skeneidae, doubtfully considered trochaceans a short time ago (Fretter & Graham, 1962: 618), are now shown to have trochacean anatomy (Fretter & Graham, 1977: 81). I have examined the pallial complex in Liotiidae and have found a gill condition like that described by Fretter (1955: 161) for *Margarites*. The Seguenziidae, however, despite the nacreous interior and modified rhipidoglossate radula (Bandel, 1979) have, in addition to the right subocular peduncle often occurring in trochids (see Crisp, 1981), a very large penis behind the right cephalic tentacle, as well as a fully monopectinate ctenidium (personal observation on a preserved specimen). This suggests, pending study of the internal anatomy, that mesogastropod-like specializations in the reproductive system have been attained and that a superfamily apart from Trochacea may be required.

families from the Trochacea. In Appendix 1, I show that a Permian group assigned to the Craspedostomatacea cannot be distinguished from extant trochacean Liotiidae, which suggests that the trochacean anatomy was well established in the Paleozoic.

The trochaceans share so many characters with the living Pleurotomariidae—nacreous interior, left kidney a large papillary sac, spiral caecum in the stomach, paired auricles, skeletal rods in the ctenidial filaments, large paired hypobranchial glands—that their derivation from a pleurotomariacean stock is readily understood (Fretter, 1964, 1966). However, the pallial condition of the Trochacea with the transverse pallial vein is not what would remain after a change amounting to little more than the loss of the right ctenidium.

Between the dibranchiate Pleurotomariacea and the unibranchiate Trochacea, *Neomphalus* is the only living form that is transitional in having a single bipectinate ctenidium with supporting skeletal rods in the filaments, no afferent support, and thereby no additional afferent conduits to the auricle.⁵ Except for its modification for filter feeding, the neomphalid ctenidium represents what remains after the loss of the right ctenidium of a pleurotomariacean. With or without the filament elongation, the pallial condition of *Neomphalus*, if it existed in a coiled shell, would be an alternative anatomy that could provide an explanation for the anatomies of some extinct Paleozoic groups. This pallial complex, like the trochacean pallial complex, would also impose constraints upon the diversity attained by adaptive radiation in some extinct groups.

As discussed in the section that follows, paleontologists have recently hypothesized that filter feeding was the likely feeding mode in the extinct Macluritacea and Euomphalacea. The neomphalid ctenidium provides a mechanism by which these archaic gastropods could have been filter feeders. Apart from the ease with which the neomphalid ctenidium may be invoked to account for filter feeding, there are clues about the coiled predecessor in the shell, for *Neomphalus* has a coiled phase in its first postprotoconch whorl. The ontogeny of *Neomphalus* provides clues to its phylogeny. My theory is that the Neomphalidae are limpet derivatives of the Euomphalacea.

The Euomphalacea, along with the Macluritacea, have been regarded as comprising the archaeogastropod suborder Macluritina (Knight et al., 1960). Yochelson (manuscript) provides arguments that a close affinity between the two groups is no longer tenable and that subordinal separation can be justified. A suborder Euomphalina is therefore necessary to include the superfamily Euomphalacea and the new superfamily Neomphalacea. Formal proposal of the new suborder is given in the concluding section of this paper. The Macluritacea are discussed further in Appendix 1.

In the section that follows, I summarize what is known of the Euomphalacea, with a particular effort to contrast the group with the Trochacea. This is followed by a review of the recent work that proposed a filter-feeding mode for the Euomphalacea.

Current Understanding of the Euomphalacea (Fig. 13)

Diagnosis: Shell low-spined to discoidal, broadly umbilicate, some genera open-coiled; coiling dextral, some discoidal genera with the coiling rising slightly above the apical whorl rather than descending below; peritreme complete, upper lip trace usually sinuous but not with slit or selenizone; aperture radial, its plane passing through the coiling axis; operculum (where known) calcified, external pattern multispiral, inner surface with adventitious layers.

Included Families: Euomphalidae de Koninck, 1881 (Middle Ordovician to Triassic); Euomphalopteridae Koken, 1896 (Silurian); Oriostomatidae Wenz, 1938 (Upper Silurian to Lower Devonian); Omphalocirridae Wenz, 1938 (Devonian); Omphalotrochidae Knight, 1945 (Devonian to Upper Triassic); Weeksiidae Sohl, 1960 (Triassic to Cretaceous).

The above diagnosis reflects an altered concept of the Euomphalacea, which is consistent with the paleontological literature that has appeared since the last attempt at full classification by Knight et al. (1960). They recognized three constituent families (Helicotomidae, Euomphalidae, and Omphalotrochidae) in contrast to six recognized earlier by Wenz in 1938 (Euomphalidae, Omphalo-

⁵A short afferent membrane is present in both neritaceans and the acmaeid patellaceans; both groups also differ from the Pleurotomariidae in lacking skeletal rods in the ctenidial leaflets (Yonge, 1947; Fretter, 1965). The cocculinid gill is not bipectinate and there are no skeletal rods (Thiele, 1903).

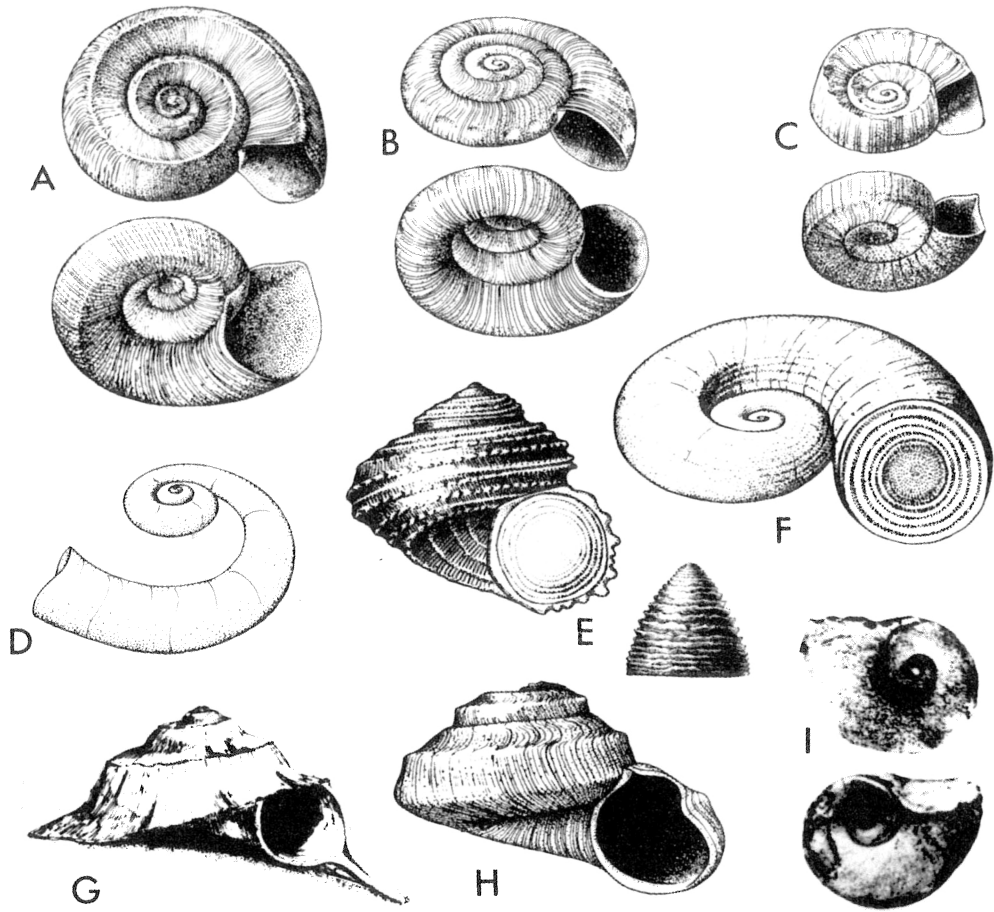


FIG. 13. Euomphalacean shells. A) *Euomphalus pentangulatus* J. Sowerby, 1814, Carboniferous (Euomphalidae), $\times 0.9$. B) *Straparollus laevis* (Archiac & Verneuil, 1842), Devonian, with attachment scars for shell fragments (Euomphalidae), $\times 1.5$. C) *Amphiscapha reedsi* (Knight, 1934), Pennsylvanian (Euomphalidae), $\times 1.1$. D) *Serpulospira centrifuga* (F. A. Roemer, 1843), Devonian (Euomphalidae), $\times 1.1$. E) *Oriostoma coronatum* Lindström, 1884, with operculum (identified by Lindström to genus) in lateral view, Silurian (Oriostomatidae), $\times 1.7$. F) *Beraunia docens* (Perner, 1903), Silurian (Oriostomatidae), $\times 1.1$. G) *Euomphalopterus alatus* (Wahlenberg, 1821), Silurian (Euomphalopteridae), $\times 0.6$. H) *Omphalotrochus whitneyi* (Meek, 1864), Permian (Omphalotrochidae), $\times 1.1$. I) *Weeksia lubbocki* Stephenson, 1941, Cretaceous (Weeksiidae), $\times 1.7$. After Knight et al. (1960), except operculum in E, after Lindström, 1884, and G, after Linsley et al., 1978.

cirridae, Platyacridae, Cirridae, Oriostomatidae, Poleumitidae, and Macluritidae). Two recognized by Wenz—the Omphalocirridae and Oriostomatidae—are now returned to the list. Of the other families recognized by Wenz, Platyacridae and Cirridae are here regarded as trochacean (see Appendix 2), Poleumitidae is synonymous with Euomphalidae (Knight et al., 1960) and Macluritidae is dis-

cussed in Appendix 1. In the absence of an overall revision of the Euomphalacea, the important changes since 1960 may be summarized as follows:

Omphalocirrus was regarded by Wenz (1938) as a sinistral euomphalacean, but by Knight et al. (1960) as macluritacean; Yochelson (1966) returned it to the Euomphalacea (Euomphalidae) as a dextral form with the

spinose projections on the under rather than the upper side; Linsley (1978a) independently proposed a family Omphalocirridae to include also the genus *Liomphalus* (Fig. 14), which lacks the spinose projections, neglecting to note that Wenz (1938) had previously proposed the family.

Euomphalopterus (Fig. 13G) had been treated as pleurotomariacean, until its peripheral frill was no longer regarded as the site of a selenizone by Linsley et al. (1978), who transferred its family to the Euomphalacea.

Oriostoma (Fig. 13E), with its multispiral operculum and nacreous interior, was given family and superfamily status in the Trochina by Knight et al. (1960); Linsley (1978a) suggested the transfer of Oriostomatidae to the Euomphalacea, in which it had been previously placed by Wenz (1938). Opercular characters support this assignment, as discussed in the section that follows.

Euomphalid genera of the Mesozoic included by Knight et al. (1960) require further attention: some may need to be reassigned to the Trochacea. Sohl (1960) proposed the euomphalacean family Weeksidae for three biangulate, discoidal genera—*Weeksia* (Fig. 13I), *Discohelix*, and *Amphitomaria*—differing from euomphalids in having a prosocline upper whorl surface. He also noted that *Hippocampoides* is a magiliniid (i.e., coralliophilid). I assign *Anosostoma*, which had a greatly expanded final lip (Fig. 18B) to the trochacean Liotiidae in Appendix 2; no genera with expanded apertures remain in the Euomphalacea.

Yochelson (manuscript) removes *Lesueurilla* (Fig. 15A) and other genera with a slit or slit-like feature on the upper lip to the Pleurotomariacea, and suggests that all such genera should be reconsidered. Rohr & Smith (1978) have treated *Odontomaria* (Fig. 15C) as pleurotomariacean. I propose that *Helicotoma* (Fig. 15D) with its elevated slit be included in this transfer, thereby removing the Helicotomidae of Knight et al. (1960) from the Euomphalacea. Transfer of such genera to the Pleurotomariacea is in essence a return to the classification of Wenz, who associated them with the raphistomatid pleurotomariaceans.

The Euomphalidae have been reduced since 1960 by the removal of groups mentioned above. The content of the Omphalotrochidae (Fig. 13H) remains unchanged.

It is beyond the scope of this review even to

estimate the number of euomphalacean taxa. Additional genera have been proposed since 1960, and there are several entries per year in the *Zoological Record* pertaining to the group. In the monographic series on Permian gastropods of the southwestern United States (Yochelson, 1956, 1960; Batten, 1958), 45 bellerophontacean species, 32 pleurotomariacean species, and 31 euomphalacean species were treated. All the other archaeogastropods (Patellacea, Trochonematacea, Pseudophoracea, Anomphalacea, Craspedostomatacea, and Platyceratacea) together totaled only 21 species. It is therefore clear that the Euomphalacea comprised a major share of the Paleozoic gastropod fauna.

Shell characters: Shell structure has heretofore been an important part of the diagnosis for the Euomphalacea, but it is omitted here because the admission of the nacreous Oriostomatidae (Lindström, 1884; Knight et al., 1960) changes the previous concept that the Euomphalacea were entirely non-nacreous. As discussed above, the inclusion of families with different shell structure is currently accepted in the Trochacea. Thus, the inclusion of nacreous and non-nacreous families in the Euomphalacea is not without precedent.

Bøggild (1930: 301), in his classic survey of the shell structure of mollusks, reported on the Euomphalidae as follows: "In the shells of this old family the aragonite is, of course, never preserved but it seems to have existed originally. In most members examined by me there is a prismatic layer which is sometimes rather regular and which indicates that the shell, in such instances, must have possessed an upper calcitic layer." Knight et al. (1960: 189) essentially repeated Bøggild's remarks in their superfamilial diagnosis.

The calcitic layer need not have great taxonomic significance, for Bøggild (1930: 298) noted that it "must be said to be a rather accidental element," for it occurs "in a great number of families," and may be lacking altogether in some genera within families where it is otherwise known.

Shell structure would be an extremely useful character in archaeogastropod classification if it were always possible to determine the original structure of fossil shells. Little can be said of most Paleozoic and Mesozoic genera and nothing can be established for those of the Cambrian and Ordovician. Presumably, as in the Trochacea, nacreous interiors would be primitive in the Euomphalacea, persisting

only in the family Oriostomatidae, a group unknown past the Devonian.⁶

Although the range of possible shell forms in the Trochacea overlaps that of the Euomphalacea (see Appendix 2), the euomphalaceans are generally lower spired. Some, like the genus *Serpulospira* (Fig. 13D), are open-coiled, defined by Yochelson (1971: 236) as "shell forms that fail to have some or all of the whorls in contact but that do not obviously deviate from logarithmic factors in rate of coiling." Open coiling occurs with some frequency in the Euomphalacea, but in a review of living forms that are open-coiled, Rex & Boss (1976) reported no trochaceans with this mode of coiling.

The diagnosis for Euomphalacea given here omits reference to the mode of coiling as either orthostrophic or hyperstrophic, as in Knight et al. (1960). Hyperstrophic coiling was defined by Cox in Knight et al. (1960: 131) as: "dextral anatomically, but shell falsely sinistral. . . ." This is a concept easily understood in conspirally coiled forms in which there is dextral anatomy within a sinistral shell, as diagrammed by Cox in Knight et al. (1960: 111) for the ampullariid genus *Lanistes*,⁷ but it is here (on the advice of Yochelson) considered as an inappropriate term to describe the coiling in such discoidal euomphalacean genera as *Beraunia* (Fig. 13F), *Amphiscapha* (Fig. 13C) and *Liomphalus* (Fig. 14), in which the coiling rises slightly above the apex instead of below it. Living gastropods that are anatomically dextral have an operculum with a counterclockwise spiral on the external surface (Pelseneer, 1893; Robertson & Merrill, 1963). Opercula with a counterclockwise spiral are known in such euomphalacean genera as *Liomphalus* (Fig. 14), providing the evidence generally accepted by paleontologists that

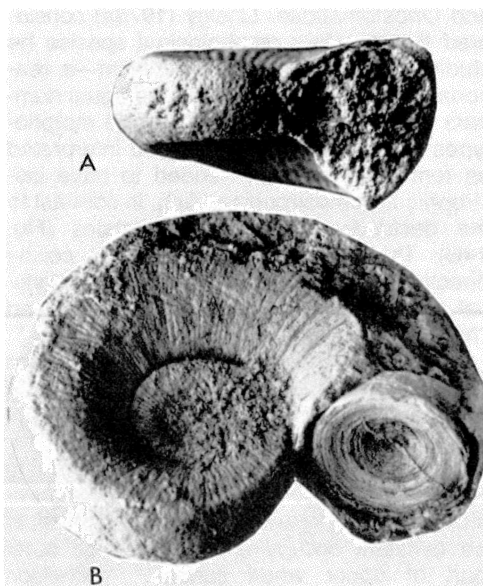


FIG. 14. *Liomphalus northi* (Etheridge, 1890), Devonian, Lilydale Limestone, Lilydale, Victoria, Australia. Showing the omphalocirrid operculum in place and coiling differences attributed to sexual dimorphism by Linsley (1978a). A) Apertural view of specimen thought to be an immature female, diameter 20 mm, coiling essentially orthostrophic. B) Oblique apical view of specimen considered a mature male, diameter 75 mm, operculum in place, coiling "hyperstrophic." Photos courtesy R. M. Linsley, specimens in the National Museum of Victoria.

this and similar "hyperstrophic" genera for which opercula are unknown were anatomically dextral.

"Hyperstrophic" coiling has been used as a generic-level character in some members of the families Euomphalidae, Omphalocirridae

⁶Quinn (1981) has suggested that the nacreous Seguenziidae (see also Bandel, 1979) could have been derived from the Omphalotrochidae, a family here included in the Euomphalacea. Because nacre is unknown in the Omphalotrochidae, such a derivation would require the unlikely reversion to nacre.

⁷Hyperstrophy is known in two living mesogastropod families—in the larval stages of architectonicids and in the African ampullariid genus *Lanistes* (see Wenz, 1938). In architectonicids it is normally limited to the planktotrophic veliger stage (Robertson, 1964), although rare abnormal specimens have been found in which hyperstrophy persists in the adult (Robertson & Merrill, 1963). Normally the coiling changes to orthostrophic in the first teleconch whorl. In *Lanistes* it is apparent that these moderately high-spired forms carry the shell directed to the left rear as in sinistral gastropods, but that water currents move in the mantle cavity from left to right as in dextral gastropods (Lang, 1891: 368, fig. 21, copied in part by Cox in Knight et al., 1960, fig. 67). Andrews (1965: 71) studied *Lanistes* and noted that its mantle cavity is deeper than that of orthostrophic members of the family, but she did not discuss the functional advantage of hyperstrophy in *Lanistes*. Hyperstrophy raises some questions, for, according to descriptions of torsion (Crofts, 1955), the normal course of development leads to dextral orthostrophic coiling. Crofts showed that in the archaeogastropods *Haliotis*, *Patella*, and *Calliostoma*, the first phase of torsion involves a delayed development of the left compared to the right post-torsional retractor muscle, which imposes an immediate asymmetry upon the protoconch, causing the direction of coiling to proceed in the usual dextral manner. In sinistral gastropods the anatomical sinistrality may be traced to the first stages of cleavage, as recently reviewed by Verdonk (1979). Discussions of torsion (Lever, 1979, and references therein) make no mention of hyperstrophy. How hyperstrophy in architectonicids and *Lanistes* can follow torsion is worthy of further investigation.

and Oriostomatidae. Linsley (1978a) considered that the four omphalocirrid species he studied showed sexual dimorphism—a reasonable conclusion based on the equal numbers of supposed male and female morphotypes in each species. Those he interpreted as females (Fig. 14A) tended to have isostrophic to orthostrophic coiling, in contrast to the decidedly “hyperstrophic” males (Fig. 14B). This intraspecific variability in coiling direction indicates that there was no anatomical difference between orthostrophic and “hyperstrophic” euomphalaceans.

There are no families or genera in the Euomphalacea in which there is a thickened final lip or abrupt change in coiling direction, as in the Trochacea (see Appendix 2).

The diagnosis for the Euomphalacea in Knight et al. (1960, p. 189) included the provision: “commonly with channel presumed to be exhalant occupying angulation on outer part of upper whorl surface.” Yochelson (manuscript) now notes that most euomphalaceans do not have a prominent shoulder and that in those that have an angulation the shell is thickened in that area and there is no interior channel to be regarded as an exhalant route. Thus, this provision of the diagnosis is no longer included. It is to be noted that the growth line on the upper lip of many euomphalaceans is often sinuous and opisthoclinal, as in *Omphalotrochus* (Fig. 13H), although *Weeksia* (Fig. 13I), with a prosoclinal lip, is an exception. The trochacean lip is usually prosoclinal.

Euomphalacean protoconchs were described by Yochelson (1956: 195) as “commonly discoidal,” but to my knowledge have not been illustrated. Dzik (1978) illustrated protoconchs of some Ordovician gastropods that resemble those of modern archaeogastropods. However, it is not certain whether any of those he figured are referable to the Euomphalacea.

The concept of the “radial aperture” was introduced by Linsley (1977: 196), defined as “an aperture whose plane passes through the axis of coiling and thus lies along a radius from the coiling axis to the shell periphery.”

Radial apertures are characteristic of all families in the Euomphalacea. Apertures in the Trochacea tend to be oblique, or—in Linsley’s terminology—tangential, defined as “an aperture whose plane is tangent to the body whorl,” so that it and the ventralmost part of the body whorl lie in one plane.

Multispiral calcareous opercula are known in the families Omphalocirridae (Fig. 14) and Oriostomatidae (Figs. 13E, F). Other euomphalacean families may have had multispiral opercula that were uncalcified, or their original aragonitic opercula may have preserved poorly compared to the calcitic shell. Such mineralogical differences between shell and operculum are known in some Recent turbinids and neritids (Adegoke, 1973). The omphalocirrid operculum is best known in *Liomphalus northi* (Fig. 14). It has recently been described by Yochelson & Linsley (1972) and Tassell (1976: 9). This type of operculum varies in thickness, is disc-shaped, slightly concave externally, beveled to fit tightly within a circular aperture, and has numerous externally visible volutions and internal laminar layers. It is quite similar to the *Cyclosporgia* operculum, an operculum first thought to be a sponge, but redetermined by Solem & Nitecki (1968) as a gastropod operculum from an unknown shell.⁸ External surfaces of opercula are known in two other omphalocirrids treated by Linsley (1978a). The oriostomatid operculum is known in *Beraunia* (Fig. 13F) (see also Knight, 1941, pl. 80) and in *Oriostoma* (Fig. 13E) (see also Lindström, 1884, pl. 17, and Kindle, 1904, pls. 11, 14). Externally, the oriostomatid operculum is conical, in some cases higher than broad, the central nucleus projecting, the succeeding whorls descending and having raised edges. The mode of formation of both the omphalocirrid and oriostomatid opercula would be similar, with accretions at the edge produced in the opercular groove on the animal’s foot, and adventitious layers added on the underside, as it rotates in a clockwise direction to produce the counterclockwise coil of the external surface. These opercula are unlike the turbinid operculum, in which a

⁸Yochelson & Linsley (1972) considered that the *Cyclosporgia* operculum matches the operculum described by Tyler (1965: 348, pl. 48, figs. 19–25) and assigned by Tyler to his species *Turbinilopsis anacarina*. That assignment violates the well-reasoned hypothesis of Solem & Nitecki that the shell of *Cyclosporgia* must have been a “planorbiform, depressed helicoidal, or helicoidal shell possessing a circular aperture, deep sutures. . . .” *Turbinilopsis* as applied by Tyler is assigned to the Anomphalacea. In my opinion, such a shell is wholly inappropriate for the *Cyclosporgia* operculum because it has a tangential aperture and lacks an umbilicus. I cannot agree with Yochelson & Linsley (1972) that an operculum as discrete as those of *Liomphalus* and *Cyclosporgia* can be convergent in widely different families. I am certain that a euomphalacean shell eventually will be found for the *Cyclosporgia* operculum.

paucispiral or multispiral pattern is preserved on the inner surface but is obliterated on the external surface where it is enveloped by the animal's foot. The omphalocirrid and orio-stomatid opercula differ from the trochid, turbinid and liotiid opercula in depositing adventitious layers on the internal surface. Thus, the euomphalacean and trochacean opercula, though both multispiral, are entirely different. There is convergence in shell form in the Trochacea and Euomphalacea, but the distinction may be clearly drawn between those members in which opercula are known.

Feeding and locomotion: During the preceding decade a number of papers have considered possible modes of locomotion and feeding in the Euomphalacea. The theme has been developed that these gastropods rested with the aperture perpendicular to the substratum, unlike the trochaceans in which the shell is balanced over the cephalopedal mass and the aperture maintained in a position parallel to the substratum.

Yochelson (1971) discussed open coiling and septation in the Devonian euomphalid *Nevadispira* (which is similar to *Serpulospira*, Fig. 13D). He suggested that it had a sedentary life mode because an animal with open coiling would have great difficulty balancing the shell for locomotion, the septation that shortened the body mass would further hamper locomotion, the open coiling would increase the area of contact with the substratum, and the "hyperstrophic" coiling would raise the aperture above the sediment. Thus, this "would appear to be a natural response in shape change for a coiled animal living a sedentary life on a mud bottom." He suggested that euomphalids may have been deposit feeders rather than herbivores and that the open-coiled members "may have further specialized toward ciliary feeding." This suggestion was in contrast to the traditional dictum that all archaeogastropods are herbivorous.

Linsley & Yochelson (1973) discussed Devonian members of *Straparollus* (Fig. 13B) and *Euomphalus* that had the habit of attaching foreign matter to the shell in a way comparable to that of the modern Xenophoridae. They concluded (1973: 16) that these euomphalids were unlikely to have balanced the shell like trochaceans, it being "most unlikely that *Straparollus laevis* could have held its shell motionless in the normal carrying position for the several hours required" for implantation of objects. This was further evidence

that euomphalaceans were sessile animals resting on the base of the shell.

Peel (1975a) also discussed the probability that open-coiled Paleozoic gastropods were sedentary. He contrasted open-coiling with the uncoiling of higher-spired forms, which also suggests a sedentary existence (see also Gould, 1969). He concluded that "Paleozoic gastropods were more diverse in their feeding habits than comparison with extant gastropods would suggest."

Linsley (1977, 1978b, 1978c, 1979) developed the concept of the radial aperture—in which the plane of the aperture would pass through the coiling axis. Gastropods with radial apertures would have difficulty balancing the shell over the cephalopedal mass. His "law of radial apertures" states (1977: 109): "Gastropods of more than one volution with radial apertures do not live with the plane of the aperture parallel to the substrate. Most typically it is perpendicular to the substrate." Few living gastropods have radial apertures. In one major example, the Architectonicidae, the animals are mostly sedentary and "usually lie with the shell on the substrate" (Linsley, 1977). For the Euomphalacea he stated (1977: 204): "I suggest that all had adopted a rather atypical gastropod posture of lying with the shell flat on the sediment, rarely if ever hoisting it above the cephalopedal mass in the stance associated with the majority of modern forms." The only possible means of locomotion would be what Linsley has called "shell dragging." In view of the sedentary habit, Linsley has considered suspension feeding to be the most likely feeding mode, "either by filtering with their gill(s) or by casting mucous nets" (1979: 251).

Schindel (1979) found encrusting epibionts on the exposed apical cavity surface of the "hyperstrophic" euomphalid *Amphiscapha* (Fig. 13C), whereas the basal surfaces were free of encrustations. This indicates that the basal surface was never exposed as would happen if the life mode involved shell balancing. This provides further confirmation for Linsley's principle.

I can here add the observation that the orio-stomatid operculum precludes locomotion by shell balancing in that group. Shell-balancing gastropods use the operculum as a protective pad placed between the shell and the foot. In the turbinids the dorsal surface of the foot envelops the external surface of the operculum, keeping it smooth, or in some species producing intricate sculpture. The

turbinid operculum is not so thick that it cannot be carried in the usual position between the foot and the shell. However, the conical orio stomatid operculum, which may be higher than broad (Fig. 13E), was not enveloped by the foot (which would have altered its sharp sculpture) and is too large and sharply pointed in the center to have been carried between the foot and the shell during locomotion.

Extinctions: Euomphalacean genera and species proliferated in the Paleozoic. Few stocks survived the mass extinctions at the close of the Permian. Vermeij (1975, 1977) correlated their further decline in the Mesozoic with the appearance of such shell-crushing predators as teleosts, stomatopods and decapod crustaceans. The broadly umbilicate or openly coiled euomphalacean shells are poorly constructed to resist crushing. There are few broadly umbilicate forms among modern marine gastropods. Shells tend to be sturdier, with narrower apertures, often having such modification as apertural dentition or spiny external surfaces to strengthen the shell.

More recently Thayer (1979) has discussed a trend in the evolution of marine benthic communities. Paleozoic communities on soft sediments were dominated by immobile suspension feeders such as articulate brachiopods, dendroid graptolites, tabulate and rugose corals, bryozoa, cystoids, and blastoids. In the Mesozoic and Cenozoic, the soft-bottom benthic communities are dominated by infaunal deposit feeders that include protobranch bivalves, irregular echinoids, certain crustaceans, holothurians, and annelids. The disruption or bioturbation of the sediments by the large infaunal deposit feeders would foul or bury the soft-substrate suspension feeders, particularly their juvenile stages. This, in addition to their vulnerability to shell-crushing predators, could also account for the demise of the soft-substrate living Euomphalacea, a group not mentioned by Thayer.

Previous interpretations of euomphalacean anatomy: The Euomphalacea have been variously interpreted as either dibranchiate or unibranchiate. Knight (1952: 40), in his classic paper on primitive gastropods concluded that in "hyperstrophic" forms there was "very little room for a right ctenidium" and assumed that it and the associated organs had been lost. Yochelson (1956: 195) considered that the Euomphalacea were dibranchiate: "The characteristic keel on the upper whorl surface

probably was the locus of an anus as in the Macluritacea, and the distance of this keel from the suture would have allowed ample space in the mantle cavity for paired ctenidia." Cox & Knight (1960: 262) took a position on middle ground: "Right ctenidium inferred to have been reduced and in some forms possibly absent." Golikov & Starobogatov (1975) included the "Order Macluritida" among the dibranchiate gastropods.

Linsley (1978c: 440) suggested that Macluritacea and Euomphalacea "had only one inhalant and one exhalant stream and probably only a single gill," and that the shape of the aperture "makes sense if these forms did not undergo torsion." Thus, they "therefore should not be considered gastropods." Linsley's theory has not as yet been fully detailed. It seems to me, however, that the euomphalacean operculum strongly suggests gastropod affinities.

Yochelson (manuscript) now advocates the removal of genera with a slit from the Euomphalacea and finds no indication of an exhalant canal in those that remain; he therefore finds no evidence of paired gills.

My theory for the anatomical reconstruction of the Euomphalacea includes torsion, allows both orthostrophy and "hyperstrophy," and reconstructs them as unibranchiate, as originally proposed by Knight (1952). Peel (1975a: 218) understood that bipectinate ctenidia modified for filter feeding would entail some essential differences from the ctenidia of modern filter feeders: "The effects of this difference in the structure or even number of ctenidia upon the form of a mantle cavity adapted to ciliary feeding are perhaps impossible to estimate. It is certainly possible that another arrangement of ctenidia and mantle cavity was required and that this was at variance with the elongate ctenidium and long narrow mantle cavity of the Recent species." The neomphalid mantle cavity now provides the best model for the reconstruction of the euomphalacean mantle cavity. There is little essential difference between the filter-feeding mantle cavities of calyptraeid limpets and the coiled turritellids. The placement of the neomphalid feeding mechanism within the euomphalacean shell is equally plausible. I therefore accept the filter-feeding mode of life for the euomphalaceans recently suggested by Yochelson, Peel, and Linsley.

Apart from the ease with which the neomphalid mantle cavity could be construed as having been possible within a coiled shell,

there is a strong correlation between the musculature and ontogenetic development of the shell in *Neomphalus* and that of the euomphalaceans, as discussed in the section that follows.

Neomphalus as a Euomphalacean Derivative

Evidence has been presented in the preceding section that their radial apertures precluded the euomphalaceans from balancing the shell over the cephalopedal mass. Thus they had to rest the shell on its base, which was concave for orthostrophic shells or flat for "hyperstrophic" shells. This is in complete contrast to the life mode of the trochaceans.

Trochaceans have tangential apertures—the tangential aperture exposes less body surface than the radial aperture when the animal is attached to a hard substratum. The shell is balanced over the cephalopedal mass and the columellar muscle is ventral to it during locomotion. Even when retracted within the shell, the cephalopedal mass remains dorsal to the columellar muscle, which means that the animal actually rests upon its left side when the shell is resting upon the base. Thus the head always maintains a position that is perpendicular to the axis of coiling. When the animal extends, a twist in the alignment of the head of approximately 45° is necessary to balance the shell, tilting the spire up and to the right rear.

What can be said about the position of the head relative to the axis of coiling in the extinct euomphalaceans? In the absence of shell balancing, there is no reason to assume that the cephalopedal mass of mature animals was aligned to the coiling axis. In normal feeding posture the head of any animal needs to be balanced relative to the substratum. If the head and body of a euomphalacean animal in retracted condition was aligned toward the coiling axis, a 90° twist would be required to place it in a feeding posture, an unnecessary requirement for an animal that never needs to balance its shell. Moreover, the feeding posture of a filter-feeding gastropod is one in which the head remains within the shell aperture, as in *Turritella*. Most likely the head would be permanently aligned relative to the substratum. The columellar muscle would therefore be lateral rather than ventral to the cephalopedal mass. Modern gastropods with irregular coiling have abandoned coiling and thereby dissociated the columellar muscle from the axis of coiling. For the Euom-

phalacea, my supposition is that regular coiling continues, but the alignment of the body relative to the coiling axis shifts by 90°. Mechanical considerations require that the major area for muscular insertion on any discoidal shell be on the inner, columellar wall. Muscle attachment on any other surface would be unnecessary. For an animal oriented to the substratum in a flat-lying shell, this will mean that the right side of the body assumes the entire muscle attachment function. There is no need for a left columellar muscle. The left side of the body is therefore available for a long, deep mantle cavity.

Neomphalus is the logical result of the conversion of the euomphalacean body plan to the limpet form. One of the most significant features of *Neomphalus* is the occlusion by columellar muscle of the entire right side of the body posterior to the neck. The columellar muscle is lateral to the body mass, just as it must have been in a euomphalacean.

Veliger stages of all gastropod larvae are similar in having the shell balanced over the cephalopedal mass. Post-veliger euomphalaceans would be motile, would balance the shell, and would feed by grazing. Growth of the columellar muscle would be programmed to shift the muscle to the right of the cephalopedal mass, causing the animal to lose the shell-balancing capacity and assume the filter-feeding mode.

In its protoconch and first postprotoconch whorl, the neomphalid animal must carry its shell with the coiling axis and plane of the aperture parallel to the substratum. Its transformation to the limpet form involves cessation of coiling and a 90° shift of the shell to place the coiling axis perpendicular to the substratum. The same 90° shift in the placement of the coiling axis is presumed to occur in the ontogeny of all the extinct euomphalaceans in which the regular coiling continues. The euomphalacean alters the orientation of the animal within the shell; the neomphalacean effects the change by growth stoppage along the columellar lip; in both cases the initial coiling axis becomes perpendicular to the substratum. This is the essential requirement in euomphalacean and neomphalacean ontogeny that distinguishes these superfamilies from all other living archaeogastropods, whether coiled or limpet derivatives of coiled forms.

The relatively large size of the neomphalid larval operculum and its vestigial retention in juvenile sizes far larger than that of other

limpets is additional evidence that a coiled ancestry is phylogenetically close. The presence of epipodial tentacles only near the site of the operculum is consistent with the idea that euomphalaceans were filter feeders in which the head and foot were kept within the shell in feeding position. There would be no use of epipodial structures away from the operculum in euomphalaceans.

The origin of *Neomphalus* may have been a rapid event brought about by a relatively simple alteration of the developmental process, one that inhibited growth along the basal portion of the columellar lip, forcing continued growth to produce lip expansion and the formation of a limpet in much the same process as revealed in the ontogeny of *Neomphalus*. If such an event in an euomphalacean stock took place near an active rift-vent site, the new limpet would be especially adapted to utilize the abundant sulphur bacteria in this rocky environment. *Neomphalus* represents a highly successful response to an abundant food supply, entailing no loss of body size, using less calcium than that required by a coiled shell, and affording some protection from shell-crushing predators. The limpet conversion represented by the Neomphalidae was perhaps the only as yet untested morphological theme in a stock already specialized for filter feeding.

The Mesozoic euomphalacean family Weeksidae, proposed by Sohl (1960), has some features in common with *Neomphalus*. Characters shared by *Neomphalus* and the Cretaceous *Weeksia* (Fig. 131) mentioned by Sohl (1960: 50) are: "ornament usually poorly developed . . . growth lines prosocline on upper surface . . . moderately large shell with raised naticoid protoconch." The discoidal shell of *Weeksia* has an orthostrophic protoconch whereas the later whorls are faintly "hyperstrophic." The early shell ontogeny of *Neomphalus* does not include a stage having the biangulate lateral profile of weeksiid genera. However, I have examined specimens of the similarly constructed biangulate euomphalacean *Amphiscapha* and note that the earliest whorls are unsculptured. Thus the postprotoconch whorls of *Weeksia* and *Neomphalus* can be considered far less different than the mature teleoconch whorls. If the juvenile shells are to provide the only characters in common, it is unlikely that the direct ancestor of *Neomphalus* will ever be known.

If *Neomphalus* was derived from weeksiid euomphalaceans, the minimal age for the family would be Cretaceous. Because the euomphalaceans were the dominant unibranchiate gastropods in the Permian, it can be argued, however, that the Paleozoic, when numerous stocks were present, is the most likely time of origin of the Neomphalidae.

Entry of *Neomphalus* into the Rift-Vent Community

The rift-vent habitat has probably been available over long periods of geologic time, because it is likely that hydrothermal vents have accompanied tectonic movements throughout the entire history of the earth. The oceanic rift system is global in magnitude (Corliss et al., 1979: 108), although the full extent of hydrothermal activity along it is unknown. Vents have not yet been found along the mid-Atlantic Rift, but at least two widely separated sites in the Pacific are now known.

As stated by Spiess et al. (1980: 1424): "The similarity of the East Pacific Rise and Galapagos Rift fauna suggests that these vent communities are widespread and that their species are equipped with sophisticated dispersal mechanisms well suited for the detection of the discontinuous and ephemeral vent conditions." This similarity also suggests stability of the community. Invasions of species from other habitats must be of rather infrequent occurrence. Possible barriers to new colonizations of the community include the differing chemical conditions, cold water masses separating the warm environment of the habitat from other warm environments, and the scarcity of hard substrates to serve as stepping stones from shallow water into a deep-sea hard-substrate environment. Molluscan predators such as sea stars and drill snails are not known to be present. In the absence of these predators, the rift-vent community seems well suited to provide refuge for an archaic molluscan group specialized for filter feeding.

Modern filter-feeding gastropods, the turritellids and the calyptraeids, occur in shallow water from the intertidal zone to the continental shelf, with none known from continental slope or abyssal depths. This evidently reflects a scarcity of sufficient suspended food for these relatively large forms under normal conditions at abyssal depths. A filter-feeding gastropod the size of *Neomphalus* would

have to have a shallow-water origin, from which it would make the transition to the rift-vent community with no interruption in abundance of the food source, through rift-vent sites in progressively deeper water. A shallow-water origin for the Neomphalidae is also consistent with findings by Clarke (1962) that no molluscan families have originated in the deep sea. Shallow water occurrences at one time are known for all deep-sea mollusks with continuous Paleozoic to Recent fossil records.

There is precedence for the interpretation of a rift-vent community member as a relict species. Newman (1979) considered the stalked barnacle *Neolepas zevinae*, which he named from hydrothermal vents on the East Pacific Rise at 21° N latitude (see Grassle et al., 1979; Spiess et al., 1980), to represent a stage of barnacle evolution attained in the Mesozoic.

Newman's hypothesis for the origin of *Neolepas* is as follows (Newman, 1979: 153): "Habitat also favors the interpretation that *Neolepas* is a relict form, having found refuge near deep, hydrothermal springs. Such a refuge may have been attained in the late Mesozoic when predation pressures on sessile organisms are inferred to have dramatically increased. Though immigration into the hydrothermal environment by deep-sea stocks is a distinct possibility, in the present case, the route appears more likely to have been from relatively shallow waters of warm and tropical seas where tectonically active rifts intersect continental crust, and perhaps where islands are forming along ridge crests."

This explanation provides for both the antiquity and the route into the rift-vent community for *Neolepas zevinae*. It is also the best hypothesis to account for the presence of *Neomphalus* in the rift-vent community. If the origin of *Neomphalus* was quickly followed by submergence, as postulated by Newman for *Neolepas*, a fossil record of *Neomphalus* in shallow water would be elusive. Fossil records of deep-sea mollusks are all but unknown because of the solubility of calcium carbonate shells at abyssal depths (Berger, 1978; Killingley et al., 1980).

According to my supposition, the origin of the Neomphalidae took place at some point between Late Paleozoic to Late Mesozoic, giving it an age in the range of 70 to 250 million years. If a fossil record for the family could verify such an age, it could be called a

"living fossil," a term limited by Eldredge (1975) and Stanley (1979: 258) to "taxa that have persisted for long intervals of time with little evolutionary change and that are primitive or archaic in comparison with living taxa of the same class or phylum." It can be argued that the neomphalid gill can only be archaic, since it is not represented in any other family in normal marine habitats.

If there were a fossil record of the family, the Neomphalidae could be compared to the nautiloid cephalopods, the neopilinid monoplacophorans, the pleurotomariid archaeogastropods, and the abyssochrysid loxonemataceans, recently added to the list of living fossils by Houbrick (1979). These families were once diverse in shallow seas of the Paleozoic and Mesozoic but survive now at the lower limits of the continental shelf to the abyss. Each family is still represented by several species. Speciation events have apparently kept pace with extinctions. The average duration—the Lyellian curve—for marine gastropod longevity is about 10 million years (Stanley, 1979: 237). Even if a neomphalid species could endure as long as 20 or 30 million years, numerous speciation events should have occurred, and other species (or genera) are likely to be living now at other rift-vent systems. An effective dispersal mechanism for *Neomphalus* is unknown. This is a factor that should increase its speciation potential, because new colonies would stay isolated the longer. The possibility that a single species has represented the family throughout its entire existence seems the least plausible alternative.

Reconstruction of Euomphalacean Anatomy

An attempt to reconstruct the anatomy of euomphalaceans can be based upon two models: *Neomphalus* and *Turritella*. Because *Turritella* is a mostly sedentary filter-feeding animal on soft bottoms (Graham, 1938; Yonge, 1946), there should be many parallels. Differences between the mesogastropod Calyptraeidae and the Turritellidae should be about equivalent to the differences between *Neomphalus* and the euomphalaceans.

Coiling differences are reflected in the orientation of the turritellid and euomphalacean mantle cavities. The mantle cavity of the extremely high-spired *Turritella* has to turn like a corkscrew through at least one full whorl; that of the euomphalacean maintains a

horizontal position but has to curve to the right. It may be a requirement that filament tips of a bipectinate ctenidium have to relate to a horizontally aligned food groove; the single rack of filaments of a pectinibranch filter-feeder should have no difficulty relating to the food groove, whatever the orientation.

Although the columellar muscle of *Turritella* is ventral to the cephalopedal mass as in motile gastropods, the extremely high-spined shell is too heavy to be balanced for locomotion. In *Turritella* the early whorls are made heavy and are partially filled by septation and deposition of callus (Andrews, 1974). A similar process of septation and deposition in the early whorls is also characteristic of euomphalacean shells (Yochelson, 1971). Stability on soft bottoms is thus enhanced in both groups.

There are remarkable parallels between *Turritella* and the euomphalaceans in aperture shape and structure of the operculum. In both groups the aperture is radial and the operculum multispiral. The sinuous whorl side of *Turritella* marks the position of a dorsal excurrent siphon; a similar opisthocline sinus in the upper lip of some euomphalaceans, particularly the omphalotrochids, can also be interpreted as the excurrent sinus.

In feeding posture *Turritella* lies partially buried on soft bottoms so that the operculum nearly blocks the aperture. The exceptionally small foot (Yonge, 1946) remains contracted, sole up, directly behind the operculum (Fretter & Graham, 1962, figs. 57, 64), except when used to clear an incurrent depression in the substratum (Yonge, 1946, fig. 1). Continuous inhalant and exhalant currents are maintained unless the foot and operculum are fully retracted.

Placement of the neomphalid anatomy in the euomphalacean shell would require the foot to curl forward so that it comes to lie, sole up, underneath the long neck, which would position the operculum so that it loosely blocks the aperture, as in turritellids. In most euomphalaceans the foot must have been contained entirely within the aperture, for there is no ventral gape in the shell. Like the turritellid foot, the euomphalacean foot would be relatively small. Because the aperture is so far to the side of the shell's center of gravity, the euomphalaceans were probably no better adapted for burrowing than for locomotion.

The euomphalacean would have its entire visceral mass deep within the coils of the shell. The columellar muscle would be at-

tached about 1/3 of a whorl behind the aperture and the mantle cavity would extend at least another third of a whorl deeper. The neck and head would extend forward of the area of muscle attachment and would be broad and flattened as in *Neomphalus* because of compression from above and below. The space above is taken by the free tip to the ctenidium and the space below is taken by the foot. A deeply channelled left neck groove like that of *Neomphalus* would help to keep some open space at the left and to provide a rejection and cleansing channel for the mantle cavity.

In *Turritella* pallial tentacles provide a coarse filter for the incurrent stream. In euomphalaceans, tentacles of either pallial or epipodial origin would be used for that purpose. Other features of the mantle cavity should be like those of *Neomphalus*: a bipectinate ctenidium would extend the length of the mantle cavity, attached ventrally to the mantle skirt, the free tip emerging near the region of columellar attachment and extending over the neck: the split osphradium located at the separation of the free tip; the dorsal afferent membrane lacking, so that the filament tips from both sides of the gill axis can reach the food groove; the food groove extending the full length of the mantle cavity, running anteriorly over the dorsal surface of the long neck and cutting directly to the mouth.

Because both *Turritella* and the calyptraeids have eyes and anteriorly directed cephalic tentacles, it is likely that the euomphalacean head would have such features, having a need for greater sensory contact outside of the shell than that of *Neomphalus*. However, the dorsal food groove precludes the presence of a snout, so the most reasonable assumption is that the head and neck were structured much like that of *Neomphalus*.

In *Neomphalus* a fecal groove extends well beyond the mid-dorsal anus, the ctenidial filaments keeping the fecal groove in the mantle skirt well separated from the food groove on the neck. The same arrangement must have obtained in the euomphalacean, the general pattern of water currents in the mantle cavity being ventral to dorsal, rather than left to right.

The euomphalacean mantle cavity is completely asymmetrical, extending laterally and ventrally rather than dorsally over the cephalopedal mass. This asymmetry would also work to dislodge the primitive juxtaposition of the rectum and ventricle, so that the complete

monotocardian condition is a necessary consequence of the euomphalacean body plan. In the absence of a similar leftward displacement of the mantle cavity, the Trochacea and Neritacea have remained diotocardian, despite their loss of the right ctenidium.

Although the monotocardian condition is a likely consequence of the leftward shift of the mantle cavity, the mesogastropod level of reproductive advancement need not be. It is problematic whether these features were primitive to euomphalaceans or represent an adaptation of *Neomphalus* to the rift-vent environment. It is clear that the genital opening in euomphalaceans would have to be within the mantle cavity on the left side. If a copulatory appendage was present, it would have been on the left side because this is the side close to the genital opening and there would be more space for it on the left than the right. The likely immobility of euomphalaceans makes it improbable that they could have moved to copulate effectively. There is no reason to suggest that broadcast spawning through an unmodified left kidney would not be suitable for an immobile animal in concentrated shallow-water populations.

If my basic assumption—that the columellar muscle is positioned to the right rather than ventral to the body mass of the euomphalacean—is valid, then the variable expression of “hyperstrophy” or orthostrophy can be considered a result of the shift in position of the body relative to the columellar muscle. The direction of coiling then becomes entirely a matter of convenience to elevate or lower the aperture above the substratum as an adaptation to particular bottom conditions. Thus the hyperstrophy hypothesized for the Euomphalacea is unlike that of larval architectonicids or *Lanistes* in the Ampullariidae, in which the columellar muscle is always ventral to the cephalopedal mass. This justifies the rejection of the term hyperstrophy with reference to the Euomphalacea.

My theory predicts that ontogeny in a euomphalacean involves these changes: 1) the columellar muscle shifts, relative to the cephalopedal mass, from the ventral position in the postveliger to the right lateral position in the adult, 2) the feeding mode changes from grazing to filter-feeding, which involves lengthening of the gill filaments, and a corresponding decrease in the relative size of the radula. The extent to which these changes were effected could have varied in different lineages. An incomplete shift in the position of

the muscle would enable retention of shell-balancing mobility and could account for some of the more high-spined euomphalaceans with shell shapes that converge upon those of the Trochacea (some oriostomatids, some euomphalids, some omphalotrochids). If the radula retained its early prominence, the initial grazing capacity would be retained.

The relatively high-spined euomphalaceans could have behaved like the freshwater mesogastropod *Viviparus*. Though quite capable of normal shell-balancing, locomotion and rasping with the radula, *Viviparus* also employs a filter-feeding stance in which the shell lies half buried, aperture up, the operculum partially blocking the aperture (Cook, 1949; Freter & Graham, 1978).

The fossil chronology indicates that the earliest euomphalaceans were low-spined and discoidal. This suggests that the monotocardian condition with a fully bipectinate ctenidium was primitive to all euomphalaceans. Given this premise, many different expressions of the basic body plan were possible.

Origin of the Euomphalacea

Although Knight (1952) did not mention the Euomphalacea in his classic paper on primitive gastropods, he discussed a derivation of Macluritacea from the Bellerophonacea. Two years later, Knight, Batten, and Yochelson (1954) diagrammed a phylogeny of Gastropoda in which the Macluritacea were derived from the Bellerophonacea and the Euomphalacea in turn derived from the Malcuritacea, a view also followed by Knight et al. (1960).

Yochelson (manuscript) has a new theory that seems more compatible with my reconstruction for the Euomphalacea. He speculates that they could have been derived in the Ordovician from a *Lecanospira*-like pleurotomariacean following the loss of the right ctenidium in a way comparable to the separate derivation of the Trochacea. *Lecanospira* (Fig. 15B) had previously been regarded by Knight et al. (1960) as a macluritid, but Yochelson presents convincing arguments that it and genera like *Lesueurilla* (Fig. 15A) with a deep V-shaped notch in the upper aperture are best interpreted as pleurotomariaceans. This group of genera was limited to the early Paleozoic, none being represented in the extensive euomphalacean fauna of the Permian (see Yochelson, 1956).

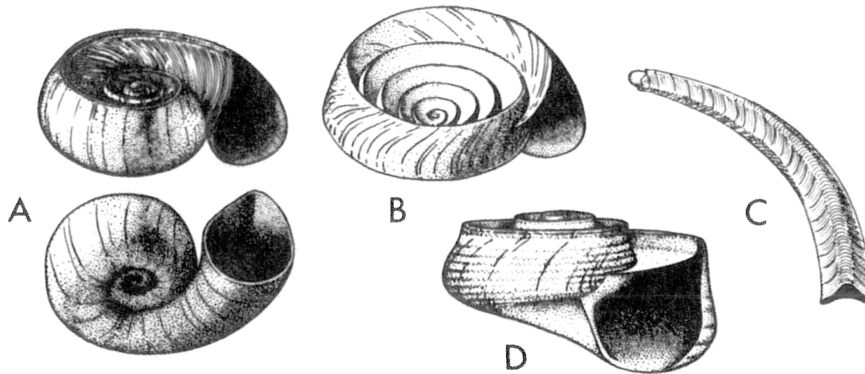


FIG. 15. Early Paleozoic genera now excluded from the Euomphalacea for having a prominent raised slit or selenizone. This group of genera is now regarded (Yochelson manuscript) as the low-spired pleurotomariacean group ancestral to the Euomphalacea. A) *Lesueurilla infundibulum* (Koken, 1896), Ordovician, $\times 1.1$. B) *Lecanospira compacta* (Salter, 1859), Ordovician, $\times 1.1$. C) *Odontomaria elephantina* C. F. Roemer, 1876, Devonian, $\times 0.8$. D) *Helicotoma planulata* Salter, 1859, Ordovician, $\times 1.6$. All after Knight et al. (1960).

Like euomphalaceans, such genera are low-spired and discoidal. Open coiling is represented in *Odontomaria* (Fig. 15C) (see also Rohr & Smith, 1978). *Lecanospira* and *Lesueurilla* are "hyperstrophic," like some euomphalaceans. This shell form, whether represented in a unibranchiate or a dibranchiate gastropod, presents the same constraints for locomotion already discussed. Thus these genera were probably sedentary forms resting for the most part on their flat bases. Assuming that they were dibranchiate pleurotomariaceans, the question arises: could these forms have been filter feeders?

The food groove of *Neomphalus* provides a relevant clue, for *Neomphalus* is the only known prosobranch in which the food groove takes a dorsal route to the mouth. In pectinibranch filter feeders and even in the trochid *Umboium* the right lateral food groove has developed independently in several families by "conversion of the tract on the right of the mantle cavity, along which the food particles are led to the mouth, into a deep gutter . . . which runs across the whole of the floor of the mantle cavity to a point just under the right cephalic tentacle" (Fretter & Graham, 1962: 100). They noted that no living gastropods with paired gills are known to be ciliary feeders: "The reason for this in zeugobranchs is most likely to be found in the disposition of the currents within the mantle cavity—so long as there are two sets of these, right and left, converging upon the mid-line, it will prove impossible for the material which they carry in

suspension to be collected into a place where the gastropod may use it. It is only when the water current is the transverse stream of the mesogastropod that this happens" (Fretter & Graham, 1962: 98).

The possibility that the food groove in a dibranchiate filter-feeder could take a dorsal route over the head to the mouth has not heretofore been considered. Lengthened ctenidial filaments arising from both gills could converge upon a central food groove. The food groove of *Neomphalus* is deflected toward the right before arching toward the mouth, but this could be a vestige of its primitive mid-dorsal position. Many of the unusual features of the body plan of *Neomphalus* can be understood in terms of additional torsion and rotation on the anteroposterior axis, as discussed by Fretter, Graham & McLean (1981), but no such shifts could account for a migration of the food groove (or a corresponding ciliated tract) across the right cephalic complex to a dorsal position. One way to account for the dorsal position of the food groove is to consider it a primitive character shared by the dibranchiate ancestor. Thus there is good reason to suggest that filter feeding in a group of low-spired Ordovician pleurotomariaceans preceded the derivation of the Euomphalacea.

Diagnosis of the New Suborder Euomphalina

The preceding account of the relationships between the Euomphalacea and Neomphal-

acea is concluded with the proposal of a new suborder for the two superfamilies, coordinate in detail with the subordinal definitions of Cox & Knight (1960) and Knight et al. (1960).

EUOMPHALINA McLean, new suborder

Diagnosis: Shell low-spired to discoidal, or cap-shaped; coiled shells broadly umbilicate, aperture radial; operculum (where known) calcified, multispiral externally, with adventitious layers internally; radula rhipidoglossate; left ctenidium entirely bipectinate, afferent membrane lacking; right ctenidium and right auricle lacking; ventricle not traversed by rectum; columellar muscle lateral to cephalopedal mass.

The subordinal classification of archaeogastropods in the Treatise (Knight et al., 1960) has been both inflated (Golikov & Starobogatov, 1975) and deflated (Salvini-Plawen, 1980).⁹

I prefer to follow a middle ground, more or less equivalent to that of Cox & Knight, recognizing for now three suborders of living unibranchiate rhipidoglossates: Euomphalina, Trochina, and Neritina, each of which has undergone major radiations that exploited the evolutionary potential of their very different body plans.¹⁰

The addition of *Neomphalus* to the ranks of molluscan classification is a major milestone in malacology. New finds with as much to contribute to our knowledge of molluscan diversity and evolution are unusual events. Not since the discovery of *Neopilina* has there been an animal that could fuel so many lines of speculation. Few living malacologists have been as privileged as I in having free rein over

such an exciting find.¹¹ Now it is to be hoped that *Neomphalus*, like *Neopilina*, will inspire others to offer alternative or modified interpretations. One cannot approach the subject of phylogeny without some preconceived notions, and I could hardly expect that all of those expressed here will endure.

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Serial sections were expertly prepared by my volunteer laboratory technician, Jo-Carol Ramsaran. Superb photography of whole and dissected specimens was done by museum volunteer Bertram C. Draper. Scanning electron micrographs of the radula were provided by Dr. Carole S. Hickman, University of California, Berkeley (NSF Grant DEB77-14519). SEM micrographs of the juvenile shells were made with the assistance of David R. Lindberg, University of California, Santa Cruz.

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⁹Salvini-Plawen's (1980: 261) suborder Vetigastropoda for superfamilies "Macluritoidea, Pleurotomarioidea, Coccuinoidea, Trochoidea, and Murchisonioidea," "defined by the dominant presence of the (posttorsional) right dorso-ventral retractor muscle as well as the right excretory organ and bilamellate ctenidia with skeletal rods," has these difficulties: *Neomphalus* with its skeletal rods in the ctenidium lacks the right kidney, and *Cocculina* has no right kidney, no skeletal rods, nor even a true ctenidium (Thiele, 1903).

¹⁰Too little is now known of the Cocculinacea, Lepetellacea and Seguenziacea to include them in this scheme.

¹¹Over the three years that I have had *Neomphalus* under consideration, my conclusions about it have undergone some major changes. Progress reports have been given at meetings, which occasioned the entry of abstracts in the literature, some of the statements in which are no longer supported. The first abstract (McLean, 1979) submitted in 1978, drew no firm conclusion, although I announced at the Geological Society of America meeting in San Jose, California, on 9 April 1979 that I assigned the limpet to the suborder Macluritina as then understood. On 21 May 1979 I discussed the limpet at the Symposium on the Biology and Evolution of Mollusca at the Australian Museum, Sydney. The abstract (1980a), which was completed in April 1979, did not mention the unpaired left kidney (so large and thin-walled that it was mistaken for a body cavity), but it incorrectly stated that the gonads discharge through the right kidney. In 1980 I developed my current view that the musculature of *Neomphalus* is the necessary consequence of its ontogeny and phylogeny. On 5 September 1980, for the Seventh International Malacological Congress in Perpignan, France, my abstract (1980b) incorrectly stated that the left kidney was vestigial. Fortunately for this novice anatomist, Drs. Fretter and Graham examined the serial section in September, 1980, and agreed to add their expertise to the account of the internal anatomy, resulting in the adjoining paper. The excretory and reproductive systems proved to be more advanced than I had realized, leaving *Neomphalus* with fewer of the archaeogastropod characters than I had originally claimed for it.

ence (though not necessarily agreeing with all of my conclusions) include: R. L. Batten, K. J. Boss, G. M. Davis, J. F. Grassle, R. R. Hessler, C. S. Hickman, R. S. Houbrock, M. L. Jones, D. R. Lindberg, R. M. Linsley, R. A. Lutz, N. J. Morris, W. A. Newman, J. Pojeta, Jr., W. F. Ponder, R. Robertson, B. Runnegar, L. v. Salvini-Plawen, R. S. Scheltema, D. E. Schindel, and R. D. Turner.

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APPENDIX 1: Possible Affinity of Other Extinct Superfamilies

The search for fossil predecessors to *Neomphalus* has led me to consider the relationships and possible feeding modes of some other extinct groups. My conclusions are given in this section.

Shell characters in the Macluritacea and the Clisospiracea, as in the Euomphalacea, exceed the limits of diversity now expressed in the Trochacea. Reasons to dissociate these two superfamilies from the Euomphalacea are given here. The Oriostomatacea have been synonymized with the Euomphalacea in the body of this paper. Reasons to synonymize the Craspedostomatacea and Amberleyacea with the Trochacea are given in Appendix 2. The remaining extinct superfamilies recognized by Knight et al. (1960) and thought to be unibranchiate are the Pseudophoracea, Platyceratacea, Anomphalacea, Microdomatacea, and Palaeotrochacea. Commentary on these groups is directed to the question: Do the shell characters exceed the limits now expressed in the Trochacea?

MACLURITACEA: The Ordovician genus *Maclurites* (Fig. 16A) had an exceptionally large "hyperstrophic" shell that could only have rested on its flat base (see Banks & Johnson, 1957; Knight et al., 1960: 188). A heavy, protruding operculum fits the aperture. Internally the operculum has two roughened areas that have been interpreted as attachment scars for right and left retractor muscles; externally it is paucispiral with one counter-clockwise volution, which provides the evidence that led Knight (1952) to interpret its anatomy as dextral. The *Maclurites* operculum is analogous to that of the Neritacea, upon which left and right columellar muscles insert, preventing it from rotating to produce a multispiral pattern. Horn-shaped opercula of a somewhat different type are known in the macluritacean genus *Teiichispira* (Yochelson & Jones, 1968). The shell of *Teiichispira* is poorly known, but Yochelson (1979a: 40) has concluded that it had a flattened base like that of *Maclurites*. Yochelson (in preparation) will report on the recently discovered operculum of the macluritid genus *Palliseria*.

Linsley (1978b, fig. 10) has depicted *Maclurites* as a filter-feeding form with the operculum loosely blocking the aperture in feeding position. Shells are heavy and the center of gravity is offset from the aperture. Linsley has therefore concluded that any

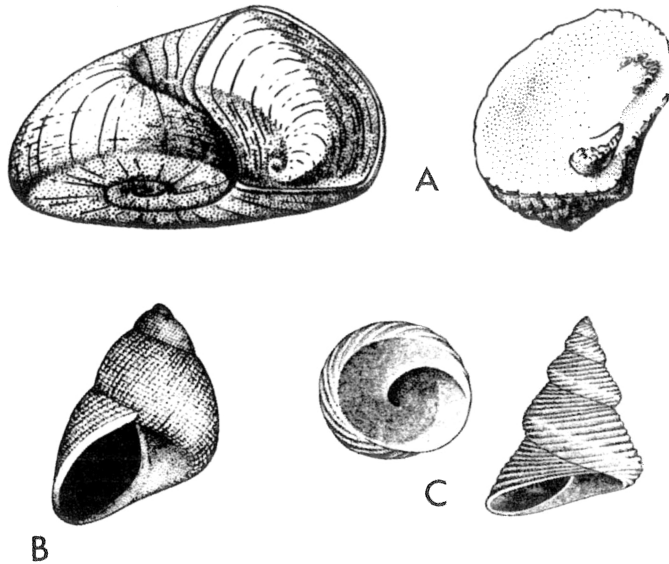


FIG. 16. Macluritacea and Clisospiracea. A) *Maclurites logani* (Salter, 1859), with internal view of operculum, Ordovician (Macluritacea: Macluritidae), $\times 0.6$. B) *Onychochilus physa* Lindström, 1884, Silurian (Clisospiracea: Onychochilidae), $\times 8.4$. C) *Mimospira cochleata* (Lindström, 1884), basal and apertural views, Silurian (Clisospiracea: Clisospiridae), $\times 3.4$. A & B after Knight et al. (1960), C after Wängberg-Eriksson (1979).

locomotion was by shell dragging. *Maclurites* may have had the pallial configuration of *Neomphalus*, but the paired musculature that has been assumed would entail some major differences from the Euomphalacea. As noted earlier, Linsley (1978c: 440) has a theory, not as yet fully detailed, that the Macluritacea (in addition to the Euomphalacea) were untorted and not gastropods. Yochelson (1979b: 347) has mentioned the possibility that the small Cambrian *Pelagiella* could be ancestral to the Macluritacea, though he now (manuscript) favors retention of Macluritacea as a gastropod lineage apart from Euomphalacea, rather than their predecessors, as implied by Knight et al. (1960).

The Macluritidae are now limited to genera with horn-shaped opercula; these genera are known only from the Ordovician. *Omphalocirus* was transferred to the Euomphalacea by Yochelson (1966) and *Lecanospira* (Fig. 15B) to the Pleurotomariacea (Yochelson manuscript). The Ordovician *Ceratopea* is another genus with a horn-shaped operculum of yet another kind. Its poorly known shell was first associated with its well-known operculum by Yochelson & Wise (1972). The shell is orthostrophic, thereby differing from other macluritids, but I would be more inclined to

place it in a family within the Macluritacea because of its horn-shaped operculum, than to relate it (as suggested by Yochelson & Wise) to the suborder Pleurotomariina. In living pleurotomariaceans (families Pleurotomariidae and Scissurellidae), the operculum is multispiral. Wenz (1938: 211) placed *Ceratopea* in Macluritidae.

The family Onychochilidae, included by Knight et al. (1960) in the Macluritacea, is here transferred to the Clisospiracea, as discussed under the following heading.

CLISOSPIRACEA: The Clisospiridae (Fig. 16C) and Onychochilidae (Fig. 16B), both moderately to extremely high-spired and apparently sinistral, are here united in the superfamily Clisospiracea. Although Knight (1952) included *Clisospira* among the supposedly hyperstrophic genera related to *Maclurites*, this position was reversed by Knight et al. (1960), who interpreted *Clisospira* as sinistral. The Clisospiracea, then containing only Clisospiridae, were grouped among those superfamilies of "doubtful subordinal position." The Onychochilidae were regarded as dextral-hyperstrophic and were included in the Macluritacea, apparently in the belief that there were transitional forms leading to *Maclurites*. More recently, Horný (1964), Peel

(1975b), and Wängberg-Eriksson (1979) have found transitional forms between the Onychochilidae and the Clisospiridae. This led again to the assumption that clisospirids were hyperstrophic like the onychochilids and therefore to the assignment of both families to the Macluritacea. However, because opercula are unknown in both families, there is no direct evidence of hyperstrophy, and the entire assumption is open to question.

Whether the two families were sinistral or dextral-hyperstrophic, they differ from Macluritacea and Euomphalacea in having tangential rather than radial apertures. Onychochilids and clisospirids would have been able to clamp to the substratum and some should have been capable of more effective locomotion than that of a "shell dragger." The ontogenetic change in orientation, which would be required in euomphalacean and macluritacean development, was not a component in onychochilid and clisospirid development. The tangential rather than radial aperture plus the lack of the appropriate opercula is sufficient reason to exclude them from either the Macluritacea or Euomphalacea.

The Clisospiridae, exemplified by *Mimospira* (Fig. 16C), have moderately high-spired shells with smooth, concave bases. The only possible interpretation of the relation of such a shell to the substratum is that it attached, limpet-like, to hard surfaces. Hyperstrophy by definition means that the internal anatomy is dextral, with water currents flowing left to right, despite the sinistrality of the shell. Dextral anatomy is entirely possible within a high-spired sinistrally coiled shell like the ampullariid *Lanistes* (see Cox, 1960: 110, fig. 67), in which the plane of the aperture is nearly parallel to the axis of coiling, but it is not possible in a shell form in which the axis of coiling is perpendicular to the plane of the aperture (Fig. 16C). The left ctenidium under such an impossible condition would be forced to curve backwards around the columella. Thus the Clisospiridae could only have been sinistral in both shell and anatomy. If there is a transition between the Clisospiridae and the Onychochilidae, as has been proposed by Horný, Peel and Wängberg-Eriksson, then it follows that the Onychochilidae were also anatomically sinistral. The Devonian Progalierinae (see footnote 3) were regarded by Knight et al. (1960) as dextral clisospirids. It is possible that there were dextral as well as sinistral clisospiraceans, although there are

too few progalerine specimens known to enable any firm conclusions.

This analysis, however, is complicated by the fact that some *Mimospira* species have heterostrophic (not hyperstrophic) protoconchs (Peel, 1975b: 1528): "The protoconch is an open-coiled half whorl which, by way of a perpendicular change in direction of the axis of coiling from horizontal to vertical, assumes the hyperstrophic form of the teleconch." Because heterostrophic protoconchs are unknown in Recent archaeogastropods, I offer no further speculation. Linsley (1977: 204, fig. 7; 1978b: 201, fig. 9; 1978c, figs. 3, 12) has depicted *Onychochilus* (Fig. 16B) as carrying the shell with the spire directed anteriorly over the head of the animal. Such an unorthodox interpretation presumably is explained in his theory (1978c) that the entire group comprising the Macluritacea and Euomphalacea was untorted. The Onychochilidae appeared in the Upper Cambrian and thus are among the earliest known gastropods. A convincing explanation of their form and function would be of great importance to an understanding of gastropod phylogeny.

PSEUDOPHORACEA: Linsley et al. (1978) have discussed the life habits of pseudophorid genera (Fig. 17A) that have a peripheral frill, an extension of the base of the shell serving to raise the position of the aperture above the substratum. As in the Euomphalacea the coiling axis is perpendicular to the substratum, but the lip growth is prosocline and the aperture is tangential, so that the base of the shell is shielded on all sides. They concluded that the frill-bearing pseudophorids could have lived on a firm, but not hard, substratum, much as in the extant deposit-feeding Xenophoridae. Retention of spiral sculpture on the base of the Permian *Sallya* (Fig. 17A) precludes the limpet-like mode of the living calyptraeid *Trochita*, in which the entire base of the shell is smooth. The absence of inhalant access in the shell is no hindrance to filter-feeding limpets on hard substrates, but the example of *Turritella*, as well as that hypothesized for the Euomphalacea, suggests that filter feeders on soft substrates would not provide a tentlike shield over the head. I therefore think that the best hypothesis is that pseudophorids were deposit feeders. Although there are no living trochaceans with a peripheral frill, there are deposit-feeding trochaceans. I can think of no argument that would preclude the Pseudophoracea from having the trochacean pallial complex.

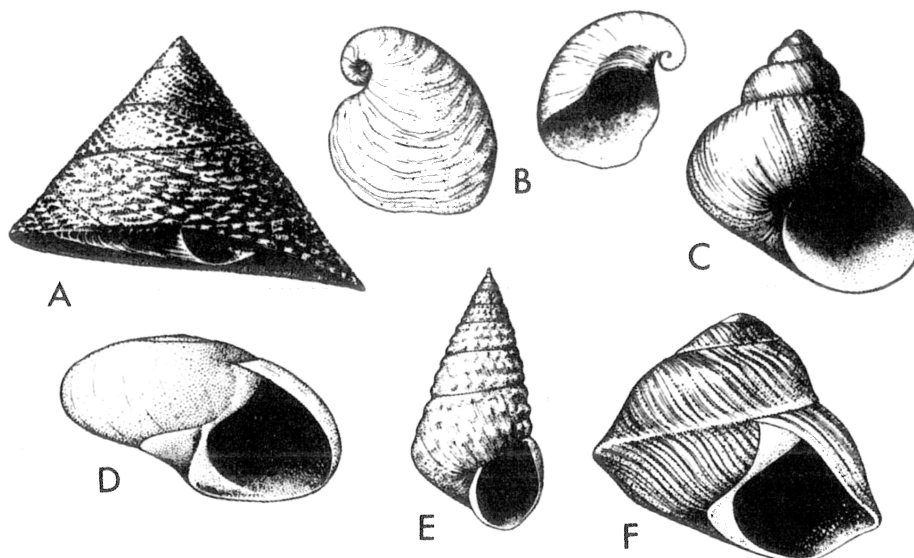


FIG. 17. Representative genera of extinct superfamilies discussed in Appendix 1, suborder Trochina. A) *Sallya linsa* Yochelson, 1956, Permian (Pseudophoracea: Pseudophoridae), $\times 3.4$. B) *Platyceras vetustum* J. C. Sowerby, 1829, Mississippian (Platyceratacea: Platyceratidae), $\times 0.6$. C) *Holopea symmetrica* Hall, 1847, Ordovician (Platyceratacea: Holopeidae), $\times 2.3$. D) *Anomphalus rotulus* Meek & Worthen, 1867, Carboniferous (Anomphalacea: Anomphalidae), $\times 8.4$. E) *Microdoma conicum* Meek & Worthen, 1867, Carboniferous (Microdomatacea: Microdomatidae), $\times 5.7$. F) *Palaeotrochus kearneyi* (Hall, 1861), Devonian (Palaeotrochacea: Palaeotrochidae), $\times 0.6$. All after Knight et al. (1960).

PLATYCERATACEA: The Platyceratid limpets (Fig. 17B) have long been understood to have been coprophagous on crinoids and cystoids (Bowsher, 1955). Their presumed coiled predecessors, the Holopeidae (Fig. 17C), had an ordinary trochiform appearance.

Platyceratid limpets had a horseshoe-shaped muscle scar (see Yochelson, 1956, pl. 23, figs. 25, 30); the right columellar muscle of *Platyceras* was evidently large enough to envelop the mantle cavity as well as the visceral mass. This provides the argument that serves to eliminate the group as a possible predecessor for *Neomphalus*. The configuration of the platyceratid muscle scar suggests that their derivation as limpets was parallel to that of the trochid family Stomatelidae, in which the single right columellar muscle is stretched along the columella as the whorl expands. There is no evidence to preclude the Platyceratacea from having a mantle cavity like that of the Trochacea.

Yochelson & Linsley (1972) described a calcareous operculum for the Devonian "*Cyclonema*" *lilydalensis* Etheridge, 1891. They noted that the platyceratid genus

Cyclonema was inappropriate for this species, a problem treated recently by Tassell (1980), who proposed for it the genus *Australonema* in the Holopeidae. Of most interest here is the fact that the holopeid operculum is unlike any now known in the Trochacea. This provides the most useful argument to justify the retention of Platyceratacea as a superfamily separate from Trochacea.

ANOMPHALACEA: The smooth, mostly non-umbilicate shells of the Anomphalacea (Fig. 17D) are streamlined like those of the Naticidae and *Umbonium*. They could have been partially or completely enveloped by the mantle to enable burrowing in sand. There are no clues as to feeding habits; probably they were deposit feeders although the filter feeding of *Umbonium* cannot be ruled out. Nothing precludes their having the trochacean mantle cavity.

MICRODOMATACEA: I find no argument to preclude this small-shelled nacreous group with tangential apertures (Fig. 17E) from having a mantle complex like that of the Trochacea.

PALAEOTROCHACEA: Again there is no

argument to preclude a mantle complex like that of the Trochacea in this large-shelled group (Fig. 17F) with tangential apertures. A nacreous shell interior has not been demonstrated, but may prove to have been present.

Conclusion: It is entirely possible that the trochacean pallial complex, which is so uniform in the diverse living trochaceans (Risbec, 1939, 1955; Graham, 1965), could have accounted for all extinct single-gilled archaeogastropod superfamilies other than the Euomphalacea, Macluritacea, and Clisospiracea.

APPENDIX 2: Suppression of Superfamilies Craspedostomatacea and Amberleyacea

Two superfamilies proposed by the Treatise authors in 1960, the Craspedostomatacea and the Amberleyacea, were grouped by the authors with other superfamilies of "doubtful subordinal position." Evidence for the synonymization of these categories with the Trochacea is presented as follows:

CRASPEDOSTOMATACEA: This was proposed (Knight et al., 1960: 298) as a "probably polyphyletic and artificial group," mostly having in common the "expanded apertures in gerontic stages." Three families were included: the Craspedostomatidae, Upper Ordovician to Silurian; the Codonocheilidae, Upper Silurian to Middle Jurassic; and the Crossostomatidae, Middle Triassic to Middle Jurassic.

Expanded apertures are diagnostic for one living family in the Trochacea, the Liotiidae. In addition to the expanded aperture, which is more of a varix than a completely flared aperture, the family Liotiidae may be recognized by its flat spire in at least the early whorls, and predominating axial sculpture of spaced major ribs and sharp lamellar increments. The final lip is usually preceded by descent of the suture, making the aperture more oblique than that of early stages, in which the aperture is more nearly radial.¹² The Liotiidae can be traced to the Permian in the genera *Dichostasia* (Fig. 18A) and *Brochidium* (see

Yochelson, 1956: 207, 257, and Batten, 1979: 110). These genera have the characteristic sculpture of liotiids, and are hereby transferred to the Liotiidae, which places the origin of the Liotiidae as early as the Permian.

Craspedostoma (Fig. 18C) lacks the spaced axial ribs of the Liotiidae but has a similar kind of imbricate sculpture that suggests a sufficiently close relationship with the Liotiidae to warrant placement of the family Craspedostomatidae in the Trochacea.

In first proposing *Craspedostoma*, Lindström (1884: 182) remarked: "I have placed this genus with the Turbinidae in consequence of the congruence of its shell with several of the Liotidae [sic]." Cossmann (1918) continued the close association of Liotiidae and *Craspedostoma* in adjacent families. Wenz (1938) separated the two families, placing the Craspedostomatidae in the Trochonematacea and the Liotiinae as a subfamily of Turbinidae. This led to further separation in the raising of Craspedostomatidae to the superfamily Craspedostomatacea in Knight et al. (1960), leaving it to the students of this day to rediscover the affinity between *Craspedostoma* and the Liotiidae.

A thickened final lip is present also in the living trochid genus *Danilia* (Fig. 18D; see also Beu & Climo, 1974: 315), as well as in some small homalopomatine turbinids and some skeneids. Thus, a thickened final lip is a recurring theme in the Trochacea. The two Mesozoic genera in Cox's family Crossostomatidae may easily be encompassed within the Trochacea; so also at least for the Mesozoic genera included within the Codonocheilidae. Accordingly, I recommend that the Craspedostomatacea be synonymized with Trochacea, and that the trochacean pallial complex be considered to have been well established by the Silurian, the time of appearance of *Craspedostoma*.

AMBERLEYACEA: This was proposed by Cox in Knight et al. (1960: 303) for four families thought to have been limited to the Triassic through Oligocene. It was characterized as "a single new superfamily (that) serves to bring together a number of genera with obvi-

¹²The Triassic *Anisostoma* (Fig. 18B), thought by Koken (1897) and Knight et al. (1960) to be euomphalacean, has the final lip inflated to match the diameter of all previous whorls of the discoidal shell. Its quadrate shell profile resembles that of the architectonicid *Pseudomalaxis*. *Anisostoma* is so bizarre that its true affinity would remain unknown were it not for *Ilaira evoluta* (Reeve), a liotiid with a quadrangular whorl profile and a completely flat spire. In this species, according to Pilsbry (1934: 380), "the minute axial thread-lineolation usual in Liotiidae is well developed, but other axial sculpture is reduced to tuberculation of the four subequidistant carinae—at suture, base, and two at periphery." This description applies equally well to *Anisostoma*. In both *Anisostoma* and *Ilaira* the suture descends on the third whorl, though more abruptly in *Anisostoma*. In *Ilaira* there is no flaring of the lip, but it may be that mature examples with flared lips are yet unknown. The removal of *Anisostoma* from the Euomphalacea limits the euomphalaceans to genera that do not have a final varix.

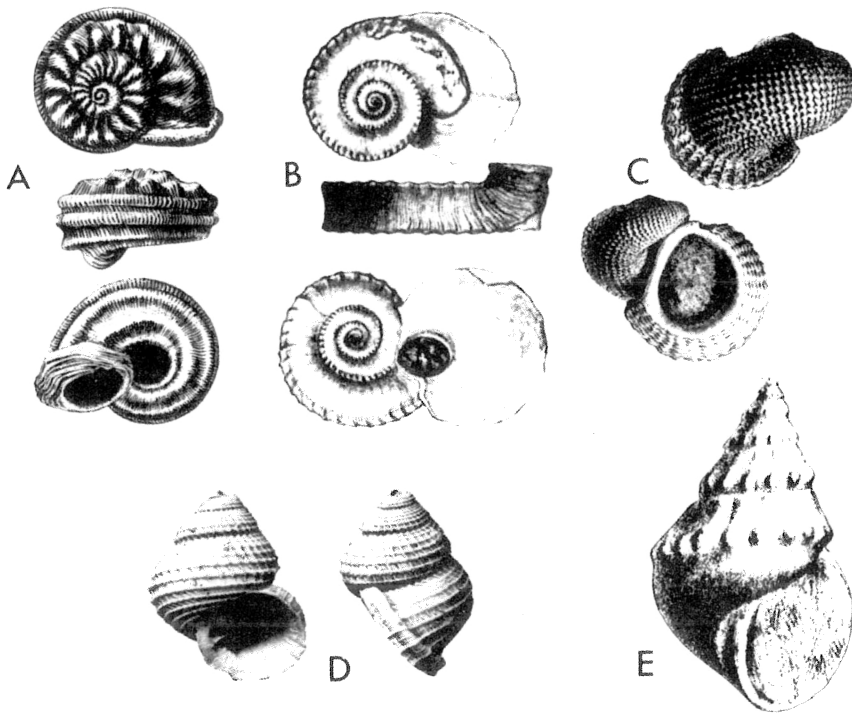


FIG. 18. Trochacean genera mentioned in Appendix 2. A) *Dichostasis complex* Yochelson, 1956, Permian (Liotiidae), $\times 5.1$. B) *Anisostoma suessi* (Hörnes, 1855), Triassic (Liotiidae), $\times 1.7$. C) *Crespedostoma spinulosum* Lindström, 1884, Silurian (Craspedostomatidae), $\times 1.7$. D) *Danilia insperata* Beu & Climo, 1974, Recent Trochidae, $\times 1.2$. E) *Amberleya bathonica* Cox & Arkel, 1948, Jurassic (Trochidae: Amberleyinae), $\times 0.8$. Fig. C after Lindström, 1884; Fig. D after Beu & Climo, 1974; others after Knight et al. (1960).

ous similarities." Unifying features were the nodose or cancellate sculpture and the resemblance to the Littorinacea, presumably because of the incomplete peritreme in Amberleyidae. Nacre was verified only in the Amberleyidae; the shell of the other groups may yet prove to have been nacreous.

Genera in the Amberleyidae have a striking resemblance to a group of modern genera that includes *Bathybembix*, *Cidarina*, and *Calliotropis*. *Bathybembix* species look like the Jurassic *Amberleya bathonica* Cox & Arkel (Fig. 18E) and many Jurassic species assigned to *Amberleya* by Huddleston (1887–1896) could readily be grouped in the Recent *Cidarina*. No reason can be advanced not to recognize the Recent taxa as a continuation of this Mesozoic lineage. This lineage has been in need of subfamilial recognition in the Trochidae (Hickman, 1980a: 16, and personal communication), based upon unifying radula and sculptural characters. The modern line-

age is hereby assigned to the trochid subfamily Amberleyinae (reduced from the Amberleyidae).

Removal of Amberleyidae from the Amberleyacea leaves three other originally included families for consideration—the Platyacridae, Cirridae, and Nododelphinulidae. The Platyacridae were characterized in having planispiral early whorls, which led Cossmann (1915) and Wenz (1938) to place them in the Euomphalacea. Mature shells are trochiform. Because planispiral early whorls occur in the Liotiidae, I have no hesitation in considering this group as trochacean. Because of its discoidal final whorl, the sinistral *Cirrus* was thought to be euomphalacean by Cossmann (1915) and Wenz (1938). However, it and other genera included in the Cirridae have the spinose sculpture of the Amberleyinae. I doubt that Cirridae is a natural group, for few prosobranch families are completely sinistral. Because of the close re-

semblance between *Amberleya* and *Cirrus*, the Cirridae are easily encompassed within the Trochacea. The five genera of Cox's Nododelphinulidae exhibit many sculptural features of both the Liotiidae and the genus *Angaria*; these genera are also easily placed within the Trochacea.

Conclusions: A comparison of treatments by Cossmann (1915, 1918), Wenz (1938) and the Treatise authors (1960), leads me to believe that taxonomic inflation of supraspecific categories has obscured some relationships. The Treatise authors introduced two new superfamilies with very weak justifications. They evidently followed Wenz's dogma that the Trochacea arose in the Triassic; therefore, everything occurring in the Paleozoic had to be placed elsewhere. If Wenz or the Treatise authors had pursued Lindström's or Cossmann's recognition of an affinity between *Craspedostoma* and *Liotia*, the accepted classification of today would have

been very different.

The suprageneric classification of the Trochacea is greatly in need of revision. I suggest that as a prelude to a new understanding of the Trochacea, the available families and subfamilies of the currently recognized Craspedostomatacea and Amberleyacea be reconsidered as possible familial or subfamilial lineages in the Trochacea. Many of the Mesozoic genera now uncomfortably left in the Euomphalacea also need to be reconsidered as possible trochaceans. The roots of the great radiation of the Trochacea are in the Paleozoic, as evidenced by the clear presence of the Liotiidae in the Permian and the likelihood that the Silurian *Craspedostoma* was also trochacean. Some members of other Paleozoic superfamilies also need to be considered as possible trochaceans, because few arguments can be advanced to disprove an affinity with the Trochacea (see Appendix 1).