

THE GALAPAGOS RIFT LIMPET *NEOMPHALUS*: RELEVANCE TO  
UNDERSTANDING THE EVOLUTION OF A MAJOR  
PALEOZOIC-MESOZOIC RADIATION<sup>1</sup>

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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

<sup>1</sup>Contribution number 17 of the Galapagos Rift Biology Expedition, supported by the [United States] National Science Foundation.

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  $\mu\text{m}$  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

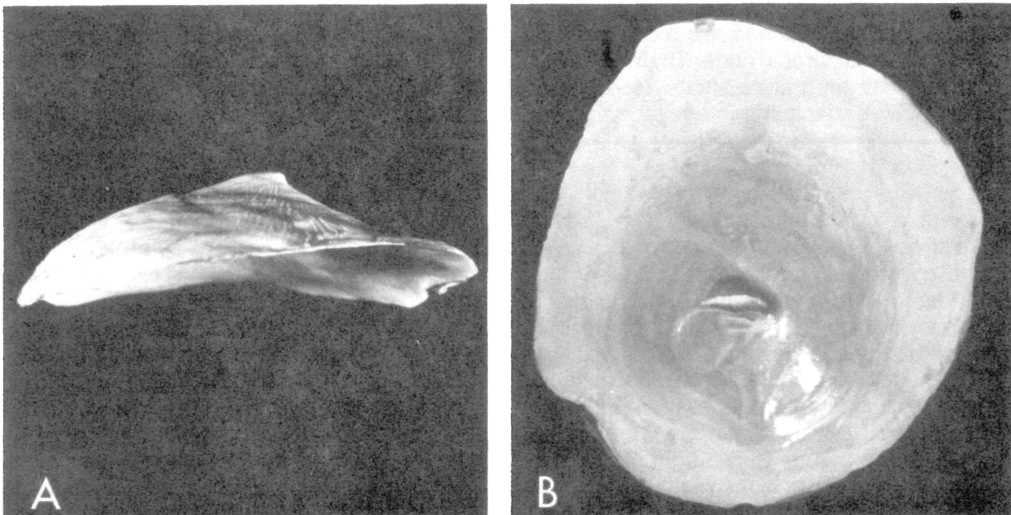


FIG. 1. *Neomphalus fretterae* McLean. Shell of mature female, dive 733, Garden of Eden, maximum diameter 26.6 mm, maximum height 6.5 mm. A) Lateral view from left side, showing the irregular shell margin. B) Interior view, anterior at top, showing the crescent-shaped muscle scar in the lower left quadrant 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.<sup>2</sup> 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-Quievreux (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

<sup>2</sup>Roger L. Batten, *in litt.*

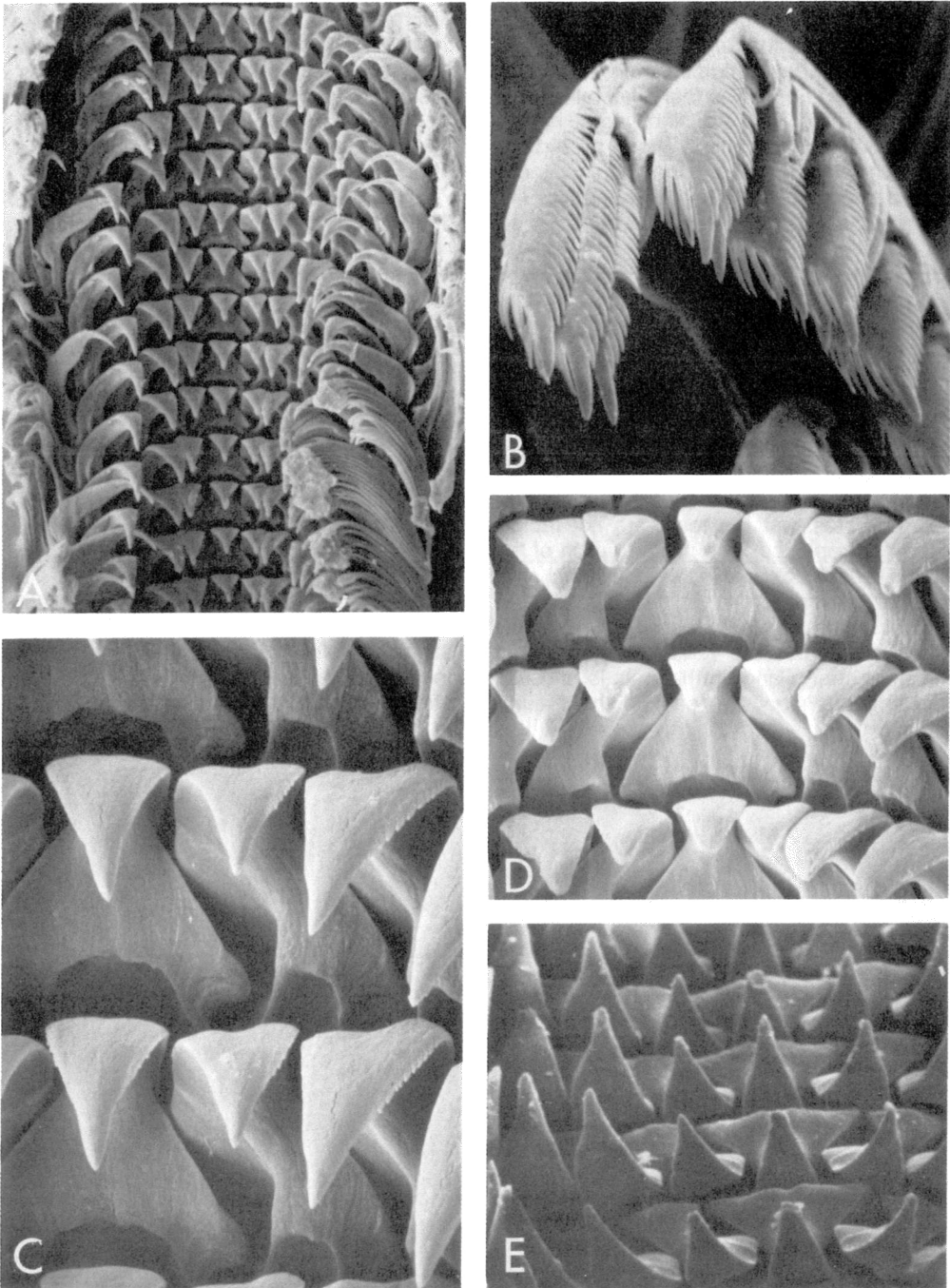


FIG. 2. *Neomphalus fretterae*. SEM views of radula. A) Full width of ribbon, showing rachidian, 5 laterals, and sheaths of incompletely separated marginal teeth.  $\times 160$ . B) Finely fringed tips of marginal teeth.  $\times 1700$ . C) Rachidian and first three laterals, showing fine denticulation 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-

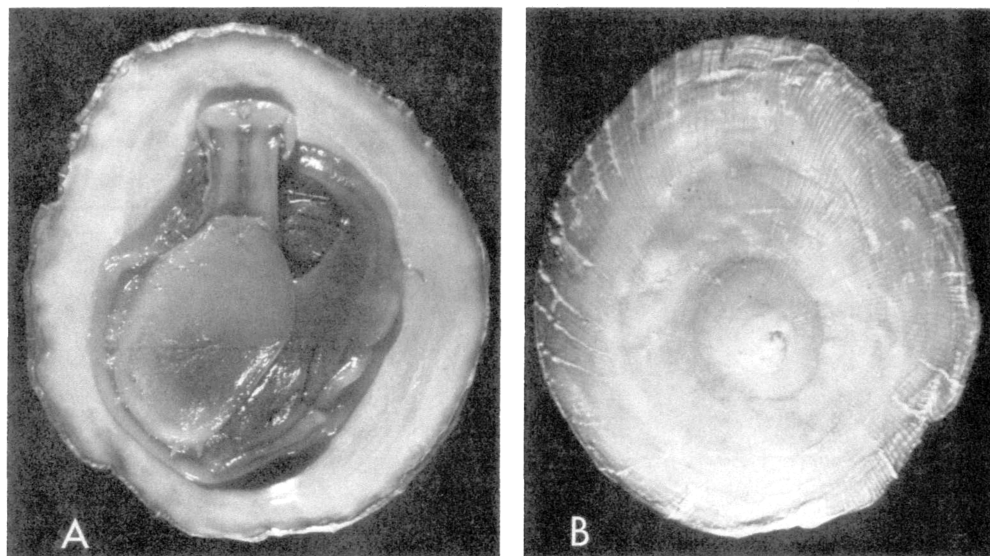


FIG. 3. *Neomphalus fretterae*. Holotype, USNM 784637, mature female attached to shell, dive 723, Oyster Bed, maximum diameter 30.0, maximum height 7.8 mm. A) Ventral view, showing the contraction of the body away from the shell margin and the projecting periostracum. The broad mid-ventral line on the 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

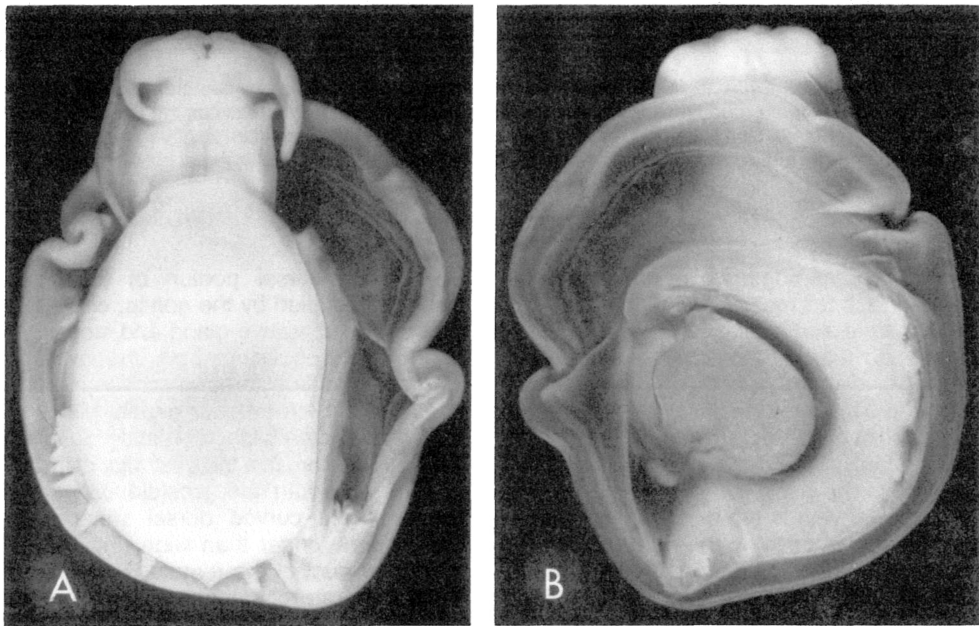


FIG. 4. *Neomphalus fretterae*. Mature female removed from shell, the ctenidium and its skeletal support on the floor of the mantle cavity excised. A) Ventral view, showing the epipodial tentacles bunched along the posterior sides of the foot, the obtusely pointed tip of the foot, and the opening of 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.

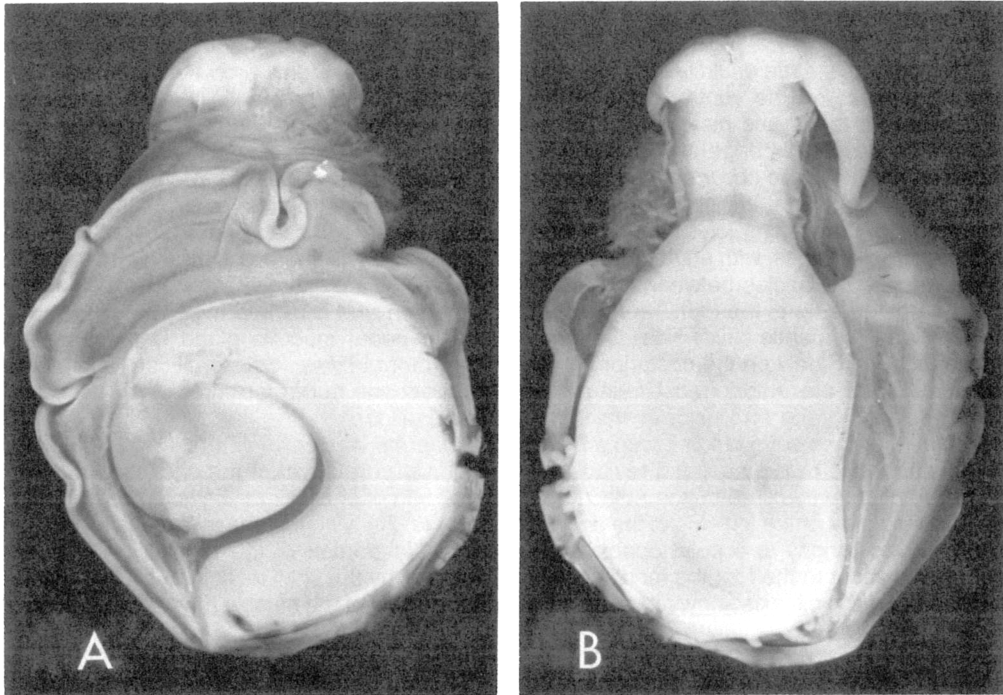


FIG. 5. *Neomphalus fretterae*. Mature male removed from shell. A) Dorsal view, showing the crescent-shaped shell muscle surrounding the visceral mass, which is covered by the testis on the right and prostate on the left. The mantle skirt is contracted and folded. The free tip of the ctenidium lies over 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