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Shell Structure of the Galapagos Rift Limpet *Neomphalus fretterae* McLean, 1981, With Notes on Muscle Scars and Insertions

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ABSTRACT

The principal shell layers of *Neomphalus fretterae* McLean, 1981, are an inner concentric crossed-lamellar and an outer complex crossed-lamellar layer. The protoconch is unusual in being composed of four layers rather than one or two as in most other gastropods. The narrow, high-angled crossed-lamellae of the inner principal layer are nearly identical with those of advanced mesogastropods, rather than the broader, low-angled archeogastropod crossed-lamellae. This, along with

shell shape, ornament, and the presence of a muscle platform suggests a closer relationship with the mesogastropod limpets than with the archeogastropods. Muscle attachment is by direct muscle fiber insertion, forming tubules in the shell, and also by myo-adhesive epithelial cells which may form a myostracal layer. Based on the multiple layers found in the protoconch, I speculate on the possibility that the larval stage may have remained planktonic for an extended period.

INTRODUCTION

A description of the shell structure of the Galapagos Rift limpet *Neomphalus fretterae* McLean, 1981, and a peripheral discussion of the ontogeny of the shell structure and the nature of muscle insertions is presented in this study. *Neomphalus fretterae* is a deep-water limpet encountered at various hydrothermal vents in the Eastern Pacific (fig. 1). It is classed as an archeogastropod, but possesses a combination of archeogastropod and mesogastropod character complexes. McLean (1981, pp. 309-325) assigned this new genus and species to a new, monospecific ar-

cheogastropod superfamily, Neomphalacea, and new suborder, Euomphalina of the primitive archeogastropod order Macluritina. With the exception of the new superfamily, the Euomphalacea and Macluritacea are restricted to pre-Jurassic time. Thus *N. fretterae* will serve as yet another example of a living fossil.

This study, based on two adult specimens sent to me by Dr. J. H. McLean, includes a description of the ontogenetic development of the shell ultrastructure and a discussion of the significance of the animal in the system-

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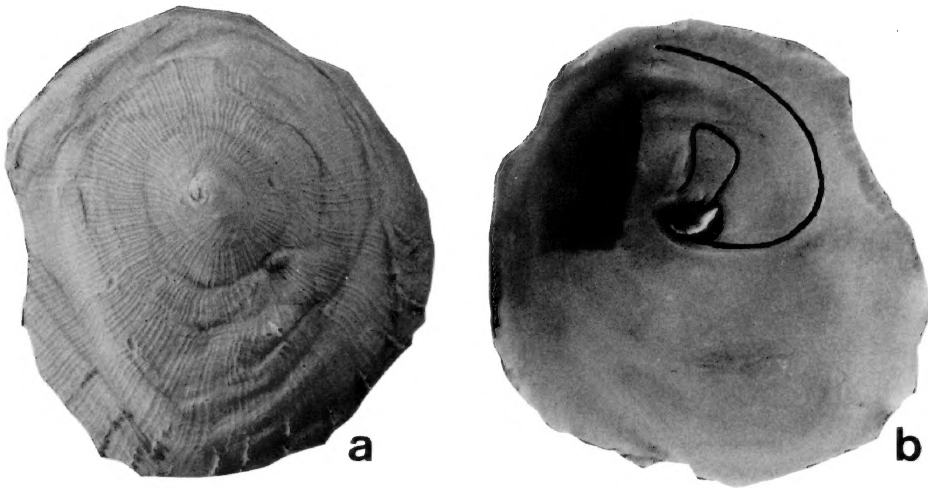


FIG. 1. Shell of *Neomphalus fretterae* McLean, 1981. a. Exterior view, showing numerous circumferential breaks and subsequent shell repair, anterior of shell is down. $\times 3$. b. Interior view, showing the shell ridge just under the apex, the triangular muscle field immediately beneath the shell ridge, and the large arcuate, crescent-shaped muscle field which occupies most of the southeast quadrant of the shell. The boundaries of the muscle fields have been inked in for emphasis. $\times 3$.

atics of higher gastropod categories. The relationship of the muscle scar fields to the underlying shell structure is also described and discussed.

The study specimens were retrieved from the Galapagos Rift vent field called the *Garden of Eden* on *Alvin* dive 733 in February 1977. This vent field is typical of the thermal springs along the spreading axis of the Galapagos Rift (see Corliss et al., 1979 for location and details).

For a detailed description and discussion of the shell, the anatomy, and taxonomy of *Neomphalus fretterae*, see McLean (1981).

ACKNOWLEDGMENTS

I thank the following people: Dr. James H. McLean of the Los Angeles County Museum for sending me specimens of *N. fretterae* and for his advice, encouragement, and review of my manuscript; Mr. Robert Koestler for his advice and help in using the Cambridge Stereoscan S4; and Ms. Joan Whelan for her help in using the new Cambridge S 250, obtained by the American Museum of Natural History with a grant from the National Science Foundation (# DEB 801206). Dr. Richard A. Lutz of Rutgers University reviewed this paper and made important recommendations.

MATERIALS AND METHODS

The two specimens were fixed in 4 percent buffered formalin on site and later transferred to 70 percent ethyl alcohol. Both specimens retained only small portions of the periostracum, mostly in the outer third of the adult shell.

The specimens were prepared for SEM examination by scribing the inner and outer surfaces with a diamond style and fracturing in the vicinity of the scribed lines, but not precisely along them. Four fractured sections of each of the adult shells were made at 90-degree intervals. The early coiled shell was fractured through the protoconch and through the coiling axes of the postprotoconch whorls. The resulting fragments were mounted on standard SEM stub mounts and coated with 500 Å of gold. Studies were then made using a scanning electron microscope (Cambridge Stereoscan 250 Mark II).

COMMENTS ON SHELL MORPHOLOGY

McLean (1981, p. 295) has described and illustrated details of the shell of *Neomphalus fretterae* (fig. 1). For review purposes I make the following additional observations. The relatively small size of the early coiled shell

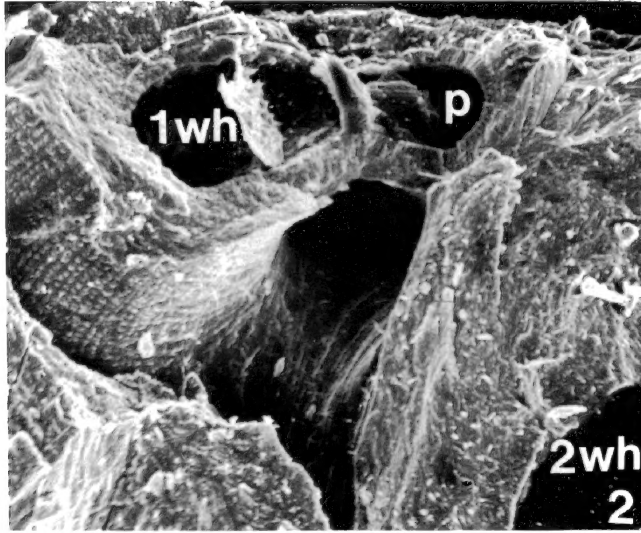


FIG. 2. Fractured cross section of the first two postprotoconch whorls and the cap-shaped protoconch. Note the spiral, beaded ornament on the orthostrophically coiled postprotoconch whorls; the protoconch is in the upper right-hand portion of the micrograph. $\times 200$.

suggests that the veliger could be planktonic; see Jablonski and Lutz (1980, pp. 329–334) for a discussion on the recognition of larval types. The protoconch and the first postprotoconch whorl lie in a plane (fig. 2); they are similar in shell shape to that of the stomatellid trochid *Praestomatia* Cox, 1960 (in Knight, Batten, and Yochelson, 1960, fig. 169, p. 1263). I use protoconch here to mean the cap-shaped larval shell terminating at the first growth line. In most gastropods this is usually less than one whorl. In other gastropods, where more than one whorl is developed during the larval stage, the terms protoconch I and protoconch II are used.

The second postprotoconch whorl expands rapidly so that the apertural and translation rates appreciably change the shape of the juvenile pre-limpet stage of the shell to mimic that of *Praestomatia* which also has rapidly expanded whorls with a flattened upper whorl surface. This second whorl is ornamented by a closely packed and evenly developed system of spiral ribs which are beaded as a result of the overlay of impressed collabral elements. The pattern is similar to that of the sculpture of *Tegula pellisserpentis* Wood, 1828 (see Knight, Batten, and Yochelson, 1960, p. 1254, fig. 163). It also resembles the sculpture of the juvenile shell of *Cellana eu-cosmia* Pilsbry.

By the third postprotoconch whorl the shell aperture has expanded into a full limpet shape so that additional shell growth involves omnidirectional accretion in a typical limpet mode. At this stage the predominant ornament pattern is radial ribbing (for further discussion and description of the shell see McLean, 1981).

ULTRASTRUCTURE DESCRIPTION

THE PROTOCONCH: The shell of the protoconch consists of four layers; a thin outer one, an inner layer, and two medial layers, herein referred to as the principal outer layer and the principal inner layer. The outermost layer is very thin and composed of what appears to be prisms (layer a, fig. 3). It is preserved in both of the specimens available for this study; however, the exact nature of the prisms is not known owing to poor preservation, perhaps because of some form of dissolution alteration, since this locality is below the aragonite compensation depth level.

The principal outer layer (layer b, fig. 3) directly beneath the outermost prismatic layer is a transitional structure between asymmetrical prismatic and complex crossed-lamellar (fig. 6). Neither component is well organized, but corrosion has emphasized the complex crossed-lamellar aspect. The con-

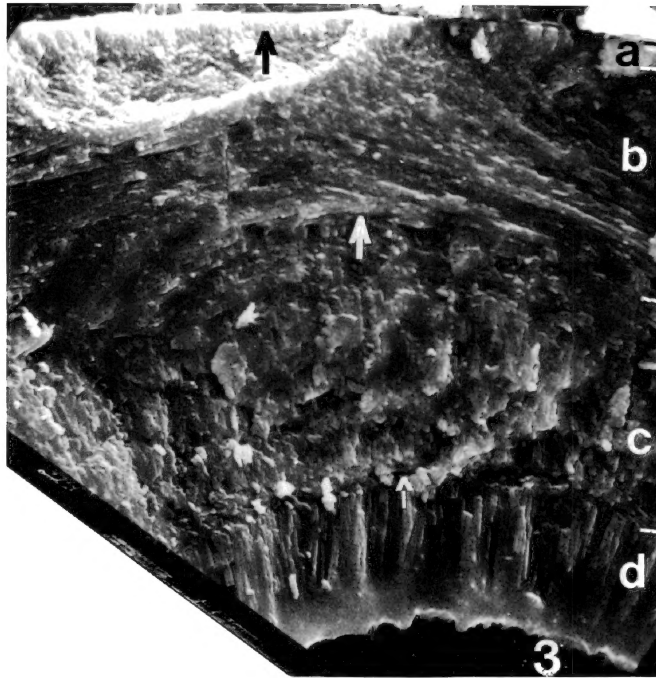


FIG. 3. Fractured cross section of the protoconch, inked lines indicate the boundaries between the four shell structure layers; layer a is a thin outermost prismatic layer; layer b is an upper (outer) transition layer with a complex crossed-lamellar component; layer c is the lower (inner) transitional layer with a crossed-lamellar component, note the intercalated myostracal layers; layer d is the innermost asymmetric prismatic layer. Arrows point to layer boundaries. $\times 1800$.

tact between this layer and the outermost prismatic layer (a) is obscure but appears to be an intergrading one (fig. 3).

The contact between layer b and the inner principal asymmetric prismatic layer (layer c, fig. 3) is irregular, partly transitional and discontinuous. This inner layer (c) is composed of elongated asymmetric prisms. Inserted within this layer is a series of repeated pallial myostracal sub-layers which are composed, in turn, of irregular smaller, simple prisms marking unconformities in the growth of the elongated asymmetric prisms (fig. 6). A better example of these inserted or intercalated layers can be seen in the postprotoconch layer illustrated in figure 4.

The innermost layer (layer d, fig. 3) is about equal in thickness to the outer principal layer b and is composed of coarse, bladed, asymmetric prisms different in appearance from those described in layer c. The opposing adjacent terminals of the prisms are lined into incipient second order crossed-rods (see

fig. 6); see Batten (1982, p. 36) for a complete definition of crossed-rod structure.

To explain briefly: crossed-rod structure is a form of crossed-lamellar structure in which the third order lamellae are tablets with axes at right angles to the axes of second order structure (fig. 11). In normal crossed-lamellar structure the third order elements are elongate with their axes parallel to the second order lamellae (see fig. 17). This layer has much coarser prisms than in layer c, suggesting that they were formed more slowly.

There are several unconformities within layer d where crystal growth has been interrupted, but these are not as well developed as in layer c. These are marked by simple myostracal prisms which are confined to the upper half of the layer. No myostracal interruptions are found below the middle of the layer. This is a critical observation because it indicates that the layer probably formed during the larval stage and was not added as a thickening during postlarval time. The low-

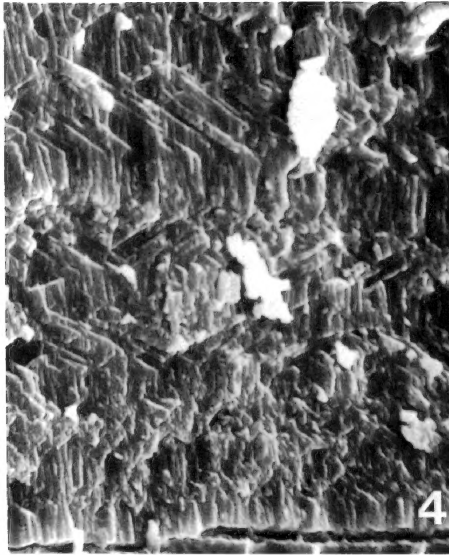


FIG. 4. Fractured cross section of the inner concentric crossed-lamellar (CXL) layer of the second postprotoconch whorl; the vertical prisms are myostracal layers marking interruptions in the growth of the CXL crystals. These intercalations are similar to those in the protoconch c layer. $\times 1800$.

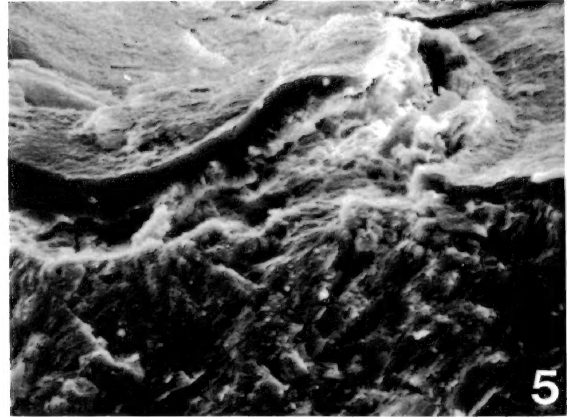


FIG. 5. Vertical fractured cross section (second postprotoconch whorl) of a break in the periostracum and the underlying prismatic layers showing that the break does not appear to involve the crossed-lamellar shell layers. $\times 500$.

er half of this layer would also have the interruptions if it were formed as postlarval thickening.

INTERPRETATION OF INTERCALATED MYOSTRACAL LAYERS: These myostracal interruptions probably indicate a pause in the formation of the shell layers. They are found throughout the coiled portion of the shell. This suggests that the organism might have remained in an arrested larval, or in the coiled pre-limpet stage, for a relatively long period of time. Interruptions in the deposition of a particular shell structure result in the formation of a pallial myostracum. The reason for the deposit of this type of myostracum is that the pallium becomes temporarily attached to the inner surface of the shell and secretion of irregular prisms is initiated. Clearly, these myostracal deposits are extraneous to layers formed in mantle folds or in the protoconch. The pallium is the second method by which additional shell layering can be formed. I qualify this statement because in the larval stage the mantle *per se* is not present; but a thin tissue extending into velar lobes probably serves as a mantle and capable of producing shell secretion.

Interruptions in the shell structure layers can be either periodic or episodic (Batten, 1972, pp. 23–25; Taylor, Kennedy, and Hall, 1969, p. 54). Lutz and Rhoads (1980, p. 245) have suggested that interruptions in the growth of the complex crossed-lamellar layer by insertion of pallial myostracal layers in the bivalve *Arctica islandica* (Linnaeus), develop when anaerobic respiration occurs during burrowing. In any event, these repeated pauses mark a change in the physiological environment of shell deposition. These interruptions support my speculation of the extended time that the veliger larval stage, represented by the protoconch, remained in the plankton. The principal argument for an extended larval stage, however, is the presence of four layers.

It is possible that the pallial myostracum has its origin in the basic crystal fabric of the included ultrastructure types, to be discussed later. As observed by Mutvei (1978), some forms of pallial myostracum may be the source of some types of ultrastructures, as is the case of the stacked nacre of *Nautilus*, derived from complex prismatic structure. In *Neomphalus* the interruptions in the depo-

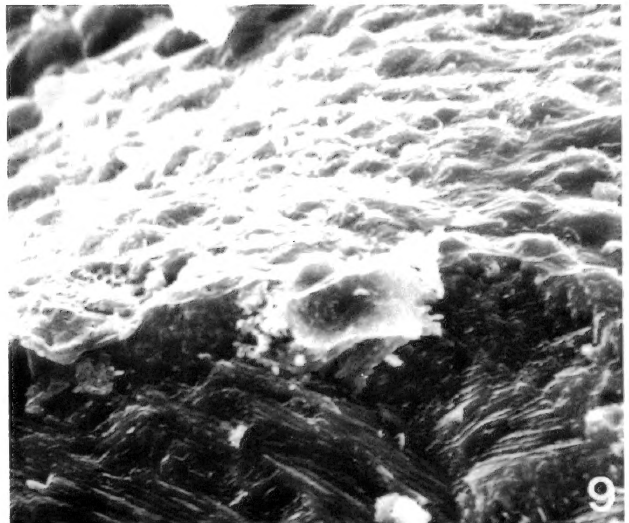
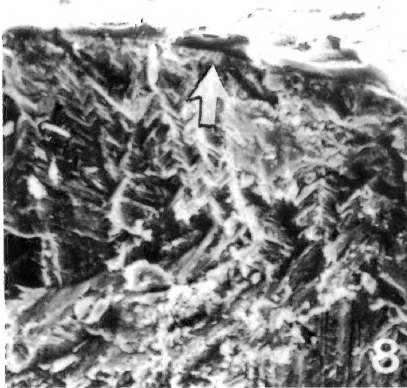
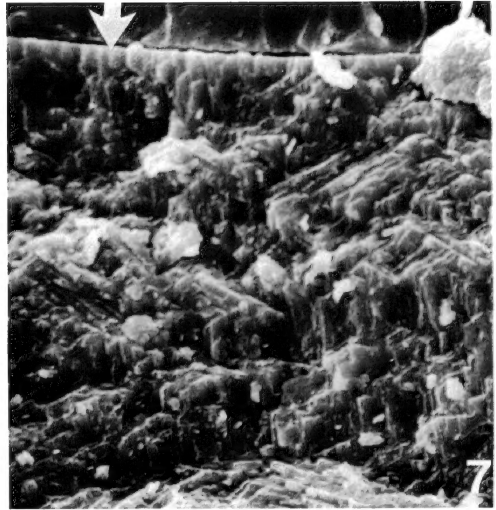
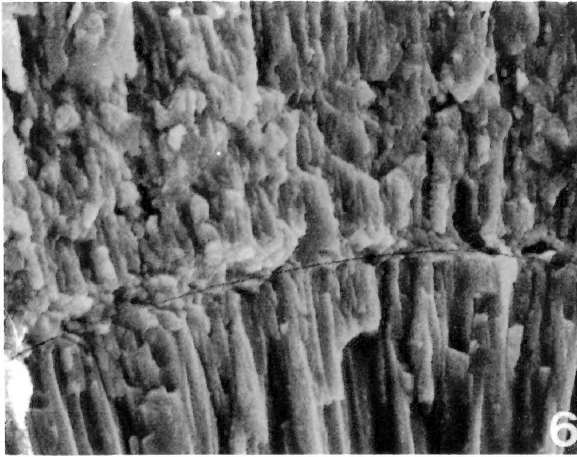


FIG. 6. A detail of figure 5 showing the contact between the transitional layer (c) and the innermost asymmetric prismatic layer (d); the diagonal crystal boundaries represent the incipient first order crossed-roads in the lower layer. An inked line marks the boundary between the two layers. $\times 4500$.

FIG. 7. Fractured cross section of the second postprotoconch whorl (see arrow) showing the innermost prismatic layer at the top of the figure, beneath it is the inner crossed-rod layer showing several pallial myostracal units. $\times 1900$.

FIG. 8. A fractured cross section of the adult shell with the shell surface exposed at the top, showing the outer prism-like portion of the complex crossed-lamellar (CCL) layer with each "prism" a first order lamella. A small portion of the outermost and thin asymmetric prismatic (AP) layer is shown just to the left of center at the top of the micrograph, marked by the arrow. $\times 150$.

FIG. 9. View of the shell surface showing the rounded knobs of complex crossed-lamellae with the lower portion showing a fractured cross section of the inner portion of the CCL layer showing the broad, curved and cone-shaped appearance of the first order lamellae. $\times 1800$.

sition of shell structure layers, represented by changes of the crossed-lamellar to myostracal layers (fig. 4), are apparently unrelated to the numerous shell breaks and subsequent repairs.

Figure 5 shows a break of the periostracum and outermost prismatic layer, with the underlying complex crossed-lamellar (CCL) shell layer unaffected by the break. This indicates that the shell breaks occur only at the outer edge of the shell involving the outermost, thin, prismatic layer when it has been formed by the mantle fold.

THE UNUSUAL PROTOCONCH: The apparent complicated ultrastructure of the protoconch is in contrast to the far simpler structure found in the protoconchs of most archeogastropods (see Batten, 1975, fig. 9), which consists of one or two layers of asymmetric prisms. In the mesogastropods (*ibid.*, 1975, fig. 25), the ultrastructure of the protoconch consists of a prismatic and a crossed-lamellar layer, excepting the fissurellid *Emarginula* which also has a four layered protoconch.

It is possible that the multiple layers of the *Neomphalus* protoconch layers could be an artifact of mechanical fracturing resulting from sectioning and preparation of the two specimens. However, these layers were consistent in every fragment. Further, there is a traceable transition of these layers into the shell layers of the postprotoconch whorls.

THE FIRST AND SECOND POSTPROTOCONCH WHORLS: By the beginning of the first postprotoconch whorl, the outer complex crossed-lamellar layer b (CCL), becomes well organized and occupies the outer third of the wall, with layer c and d equal in thickness. It is conceivable that layer b and c, could be shell thickening formed in post-metamorphosis time. However, it is apparent that these layers were formed before layer d (the innermost layer); therefore, layers b and c could not form in postprotoconch time since layer d is present only in the protoconch and in the early part of the first whorl. Layer d could not have formed after metamorphosis because the early whorls are sealed off when the limpet stage is formed.

The outermost, thin asymmetric prismatic (AP) layer disappears by the completion of the first postprotoconch whorl, but reappears

in the adult whorl, although this observation may either be a sampling problem or the lack of preservation of this layer between the two whorls. This outer layer could also be an artifact of fracturing. However, it is also found in later stages therefore, I believe it is less likely to result from trauma. In contrast to most other gastropods, the beaded, embryonic whorl sculpture reflects the curved complex crossed-lamellae (figs. 2 and 9). By the completion of the second postprotoconch whorl, the inner crossed-rod layer c, and the outer (CCL) layer b are equal in thickness.

Starting at the junction of the first postprotoconch and the protoconch, the innermost asymmetric prismatic layer d thins rapidly and disappears during the formation of the first whorl, either becoming a thin coating in succeeding whorls being succeeded by a different thin, inner prismatic layer (fig. 7). During the growth of the first protoconch whorl, this thinning of layer d is accompanied by an increase of a crossed-rod component, as evidenced by opposing diagonal boundaries on the crystal faces (fig. 7). Its space is apparently replaced by the lower portion of the inner concentric crossed-rod layer c, which becomes the thickest layer of the second whorl. As layer d thins, the second order crossed-rods are converted into irregular myostracal prisms, similar prisms are seen in the Pennsylvanian archeogastropod *Shan-siella carbonaria* (Norwood and Pratton, 1855 (see Batten, 1972, fig. 17). The interruptions containing myostracal layers mentioned above are fully developed in this layer c (see fig. 4). There is a general trend of these myostracal layers to be spaced increasingly farther apart going from the inside of the layer to the outside, but there does not seem to be any regularity in the progressive pattern. In the adult whorl, the pallial myostracal layers thin and disappear completely and are absent from the outer one-third of the adult shell.

THE ADULT WHORL: The adult wall of the shell consists of two principal layers, an outer complex crossed-lamellar layer (CCL) and an inner concentric crossed-lamellar layer (CXL). The third order elements of the crossed-rod structure of what was layers c and d are converted to fine acicular needles, so that the third order lamellae have their axes

parallel to the second order lamellae. Third order lamellae with axes parallel to the second order lamellae are the usual condition found in crossed-lamellar structure as has been shown by Carter (1983, appendix C). Thus, there is a transition in *N. fretterae* from the crossed-rod type of crossed structure in early growth to a crossed-lamellar type. This situation is identical with that found in the heteropods as discussed by Batten and Dumont (1976, p. 270). Batten (1975, p. 21) also showed that crossed-rod structure could be converted into crossed-lamellar structure during ontogeny from the embryonic whorls to the adult limpet stage in *Emarginula* Lamarck, 1801, and other fissurellids. It appears likely that this is an ontogenetic phenomenon or a function of shell thinness (Batten, 1975, p. 21). Crossed-rod structure is also found in very thin-shelled adults of the scissurellids and the heteropods (Batten and Dumont, 1976).

Finally, there is no evidence for the transition or conversion of the CCL second order elements to second order CXL elements, the contact between the two layers is unconformable.

The layers of the adult shell of *Neomphalus* are similar to those found in shells of patellids, as described by MacClintock (1967) in that the multiple layers thicken and thin to maintain an even overall thickness from near the apex to the shell periphery. However, not all limpets display this feature. For example, the calyptraeids tend to have the same layer thicknesses, but the myostracum does vary, thinning from the muscle field toward the periphery. In *Neomphalus*, there does appear to be a thin outermost (AP) layer present which overlies the CCL layer (fig. 8). In the adult stage, the CCL layer is reduced to occupying one-third of the shell wall thickness; the second order lamellae are in the form of cones which are convex up. In addition, the CCL layer is composed of two different structural expressions. The inner two-thirds of the CCL layer is formed of broad irregular stacks of CCL cones with curved second order lamellae (see fig. 9). The outer one-third of the layer has cones, which are narrow and sharply defined, so that the first order lamellae form prism-like structures (fig. 8).

The inner CXL layer of the adult whorl is

composed of concentric crossed-lamellar structure of the type that Carter (1983) classified as *linear* crossed-lamellar (fig. 10). Second order lamellae in adjacent first order lamellae are at a very high angle to each other and are clearly linear crossed-lamellae (fig. 10).

THE MUSCLE FIELD AND TUBULES

THE TUBULES: The shell ridge or inner septum lies entirely within the muscle field and within that field there are at least three separate regions. Just posterior of the ridge there is a triangular, well-developed muscle field, represented by a scar. Immediately to the right of that field there is a low, sharply defined ridge. Surrounding these features is the principal, broad crescent-shaped muscle scar field occupying the posterior left quadrant of the inner surface of the shell (fig. 1b).

Within the large crescentic muscle field there are numerous tubules, of two sizes: (1) a smaller order that I will call fine tubules (averaging about 0.1 μm in diameter) rather than microtubules which has been used by Waller (1980) and others, which are found primarily in the muscle field but also scattered throughout the shell, and (2) large tubules (averaging about 1.0 μm in diameter) which are confined to the triangular region adjacent to and posterior of the shell ridge.

The distribution of the large tubules and the fact that they penetrate the interior surface of the shell suggests that they are muscle insertion sites. The fine tubules penetrate the inner surface of the shell and through the two principal adult shell layers. Not all of them penetrate the outer shell surface; some terminate just below the thin myostracum that covers the triangular region (see fig. 12). They are, as in the arcoid bivalves, probably formed by protuberances of the mantle epithelium, (Waller, 1980). Both sets of tubules are straight and regular and are readily distinguished from irregular infestation borings (by bryozoans, sponges, algae, etc.). Oberling (1955), and Shibata (1979), provide more details of these tubules in other molluscs. They are not restricted to the muscle field but are less commonly encountered in other parts of the shell.

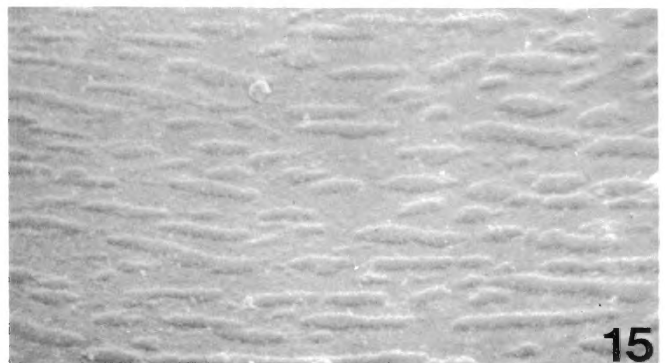
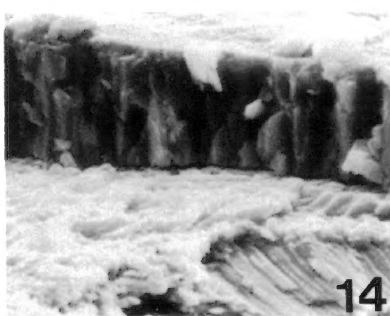
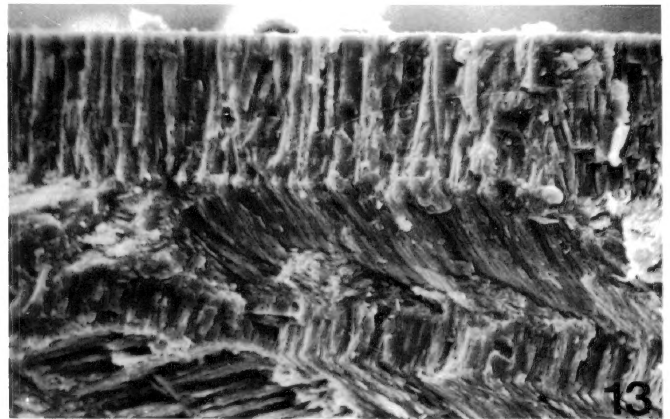
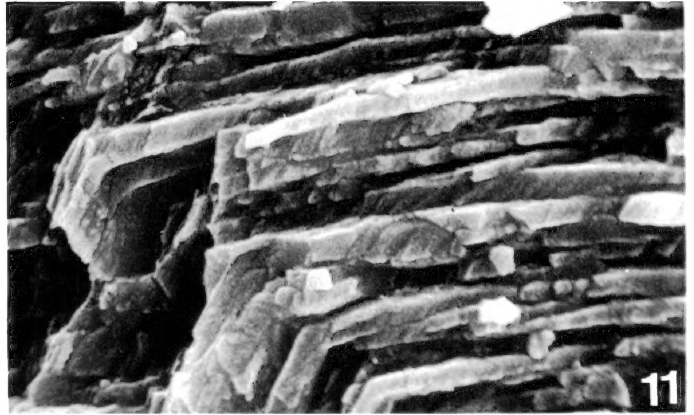
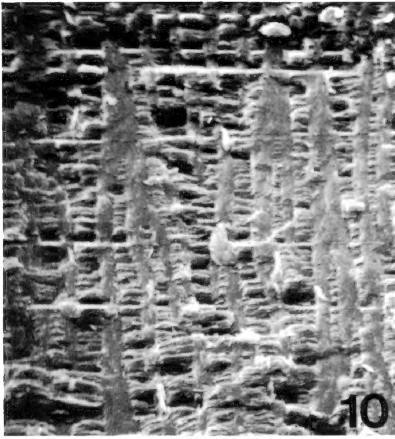


FIG. 10. Fractured horizontal surface of the inner concentric crossed-lamellar layer (CXL), showing the long, narrow and parallel sided first order lamellae. $\times 250$.

FIG. 11. Detail of the second order lamellae showing the vertical third order lathlike lamellae, in a fractured cross section at the juncture of the third postprotoconch and adult whorls. $\times 6750$.

FIG. 12. Fractured cross section of the outer CCL layer, showing a number of micro-tubules. $\times 500$.

FIG. 13. Fractured cross section showing two myostracal layers (the layers with vertical prisms) of the mesogastropod limpet *Cheilea cepacea* (Broderip), 1834. $\times 630$.

FIG. 14. A fractured cross section of *Fissurella rosea* (Gmelin), 1791 in the arcuate muscle field showing the thin myostracal layer as the upper layer. $\times 2000$.

FIG. 15. Oblique view of the interior shell surface of the mesogastropod limpet *Trochita trochiformis* (Born), 1778, showing the elongate muscle bosses in the muscle field. $\times 100$.

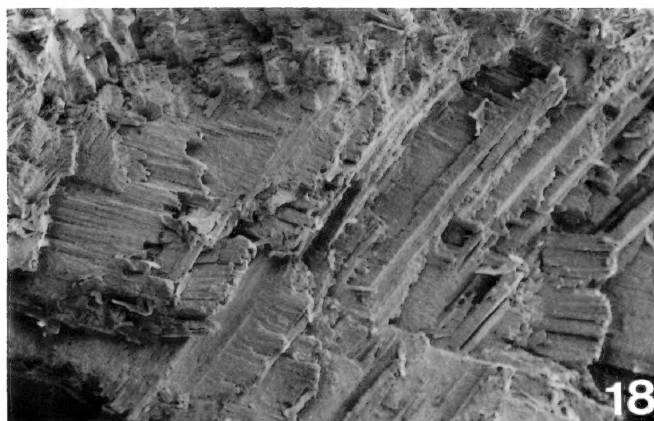
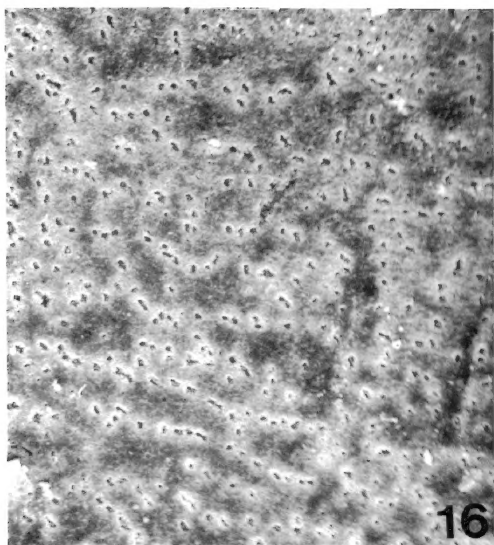


FIG. 16. Looking down on the interior shell surface of *Neomphalus fretterae* showing muscle pits on the triangular muscle field. $\times 500$.

FIG. 17. The medial crossed-lamellar layer of the Pennsylvaniaian *Straparollus amphiscapha catilloides* (Conrad), 1842, note that the opposing sets of second order lamellae are about 45 degrees to each other. $\times 185$.

FIG. 18. A cross section of a shell of *Cerithium* sp. showing the opposing sets of second order lamellae at 90 degrees to each other in the crossed-lamellar layer. $\times 120$.

THE PITS: A large number of circular to ovoid pits consistently appear to penetrate partially through the inner shell layer only and are found in the whole of the muscle field including the shell ridge (see fig. 16). The pits, which average $2.0 \mu\text{m}$ in width, appear randomly distributed and relatively widely scattered except in two locations. First, on the distal sides of the shell ridge the pits are closer

together and form a linear pattern normal to the base of the shell ridge. Second, they are at their densest along the outer one-eighth of the muscle field to the right of the shell ridge where they are linear with the axes parallel to the shell margin. I am unsure of the exact origin of the pits, but since they are absent from the rest of the shell, I assume they are epithelial in origin or sites of muscle cell pen-

etration. Their size is about right for accommodating either. These pits are not the same as in the large tubules described earlier which are smaller averaging about $1.0\ \mu\text{m}$ in diameter.

MUSCLE FIELDS: The method by which the muscles attach to the shell surface and the effects of such attachments have not been previously studied, to my knowledge, in limpet gastropods. Mutvei (1964) observed that the muscle fibers were modified into myo-adhesive epithelium in *Nautilus pompilius* Linnaeus, 1758, and that the fibers are not directly attached to the shell surface, but the epithelium bears microvilli of about $1.0\ \mu\text{m}$ in diameter which do penetrate the shell. This has also been observed by Hubendick (1958) in the freshwater limpet *Acroloxus lacustris* (Linnaeus, 1758). In most instances, particularly in the bivalves, the ultrastructure under the muscle impressions consists of irregular prisms termed *myostracum* by Taylor, Kennedy, and Hall (1969, p. 53); the term itself was coined by Oberling (1955, p. 128).

The muscle fields present a rather complex picture in *Neomphalus fretterae*. In the bottom of the muscle field trough, adjacent to the left wall of the shell ridge, is the only region where a true muscle-formed myostracal layer was found as a very thin ($7.0\ \mu\text{m}$) irregular prismatic layer.

My observations of pleurotomarian gastropods (Batten, 1972) have shown that the muscle impression type of myostracum differs significantly from pallial myostracum. The pallial myostracum tends to be thinner and composed of finer prisms, which can be either regular or offset, depending on the nature of the adjacent type of ultrastructure. The nature of the myostracum and its relation to the muscles and the mantle is in need of extensive investigation, particularly among the gastropods.

In patellacean limpets such as *Lottia gigantea* (Sowerby), MacClintock (1967, p. 51) reported that the myostracum is composed of complex prisms. In the limpets, the myostracum, for the most part, is formed by the muscle fields as they migrate with the growth of the shell (fig. 13), as in *Cheilea* Modeer, 1793. There are several distinct muscle patterns within the limpets. In *Fissurella* Brugiere, 1789 (Fissurellacea) and *Trochita*

Schumaker, 1817 (Calyptraeacea) the muscle attachments are raised bosses (see fig. 15). *Fissurella rosea* (Gmelin), 1791, and *Cheilea cepacea* (Broderip), 1834 both have a thin myostracum in the muscle band (see fig. 14). Cross sections of these raised areas show no penetration of muscle pits or tubes. Direct attachment was probably by adhesive epithelial cells located at the end of the muscle fibers, as described by Hubendick (1958) in the freshwater snail *Acroloxus lacustris* (Linnaeus), 1758.

NOTES ON THE TAXONOMY OF *NEOMPHALUS*

McLean's placement of *Neomphalus* in the suborder Euomphalina is based, in part, on a number of soft anatomical structures of the living *Neomphalus*, particularly that of the bipectinate gill, epipodial tentacles and radula. This data is combined with suggestions by Linsley (1978) on the theoretical reconstruction of the ctenidia and feeding mechanism of the Macluritina. McLean (1981, pp. 309–325) assigned *N. fretterae* to a separate new superfamily Neomphalacea and proposed a new suborder Euomphalina to include the new superfamily along with the Paleozoic-Mesozoic Euomphalacea. Previously, the Euomphalacea, along with the Macluritacea, were placed in the suborder Macluritina by Knight, Batten, and Yochelson (1961). See McLean (1981, pp. 312–318) for a detailed discussion of the general shell morphology of the euomphalaceans.

My observations suggest that the general shell features and the shell structure of *Neomphalus* are comparable to those of other limpets, regardless of their systematic position. The crossed-lamellar structure of *Neomphalus* is closer to that found in patellid archeogastropods or mesogastropods (fig. 18) rather than that of the Euomphalacea which have a medial, broad crossed-lamellar layer (fig. 17). Even though narrow crossed-lamellar structure is primarily restricted to advanced gastropod groups, it can also be found in some archeogastropods. For example, it is present in the bellerophontids (the most primitive group of gastropods) which has a wide range of shell structures within families.

An additional problem of assigning *N. fret-*

terae to the Euomphalacea is that this group is characterized by having an autapomorphic outer calcitic shell layer (Batten, in press). In brief, I believe that the Neomphalacea should be considered as an advanced archeogastropod or primitive mesogastropod group, hence removed from the primitive Macluritina on the basis of shell structure.

SUMMARY AND CONCLUSIONS

The most important observation made here is that the narrow, straight, high-angled linear crossed-lamellar structure of the inner principal layer of *N. fretterae* is quite similar to that seen in advanced gastropods such as the calyptraeans, particularly that of *Trochita* Schumacher, 1817, and *Capulus* Montfort, 1810 or a number of other groups of meso or neogastropods (fig. 17). As to be expected, among the archeogastropod patellaceans, *Acmaea* Escholtz, 1830 does have a linear crossed-lamellar layer, but the first order lamellae are broad. In many archaeogastropod and mesogastropod groups crossed-lamellar ultrastructure tends to consist of broad, short, low-angled first order lamellae however, there is much variation (Batten, in press, p. 36) (fig. 18). For example, within the primitive bellerophonitids there is a range of variation, *Retispira* Knight, 1945 has linear crossed-lamellae with relatively narrow first order lamellae compared with *Euphemites* Warthin, 1930 that has short, broad first order lamellae. In the Euomphalacea the structure consists of low-angled, short, first order crossed-lamellae. The wall structure of *Neomphalus*, the shell ridge, and shell ornament, and shell shape all suggest to me that this genus is a sister group of the calyptraeids.

As in other gastropods, such as the mesogastropod heteropods and the archaeogastropod fissurellids, there is an ontogenetic change in *Neomphalus* from a crossed-rod structure in the larval shell to a crossed-lamellar structure in the adult shell. This is probably related to a thin-shelled condition because crossed-rod structure is found in adult heteropods. It may be that the crossed-rod structure provides greater strength in thin-walled shells.

There is an indication, based on the observations made of the inner layers of *Neom-*

phalus, that the pallial myostracum is probably derived from the basic crystal fabric of the included ultrastructure type.

The larger of the two sets of tubules and the pits found within the muscle field are possibly the sites for muscle cell insertion. This is unusual in the molluscs since the common method of attachment is by means of myo-adhesive epithelial cells.

Interruptions during the formation of the inner layers of the shell, particularly the early shell, are marked by the consequent deposition of pallial myostraca, suggesting that the organism may have remained in a coiled juvenile stage for a relatively long time. Another explanation is that there have been alternating physiological changes produced by respiration (or other activity) causing these deposits. In addition, I speculate that the multiple protoconch shell layers may indicate that the veliger larval stage may have an extended planktonic mode. However, Lutz (personal commun., 1983) is not convinced that the larval shell indicates that the larvae were planktonic, in part, because of the lack of a protoconch II stage. Because the rift vents appear to be ephemeral, there may be a distinct advantage to a longer veliger stage so that the larvae could be carried to new vents.

McLean (1981) placed *Neomphalus* in the Macluritina based on such features as the bipectinate ctenidia, rhipidoglossate radula, epipodial tentacles and anterior loop of the intestine, all archeogastropod features and he combined this with Linsley's (1978) speculation about the nature of the ctenidia in the Macluritina. The shell structure suggests that the Neomphalacea should not be associated with the Euomphalacea. However, McLean's analysis and conclusions are based on strong evidence and more study is surely necessary, particularly of shell structure in the Macluritina.

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