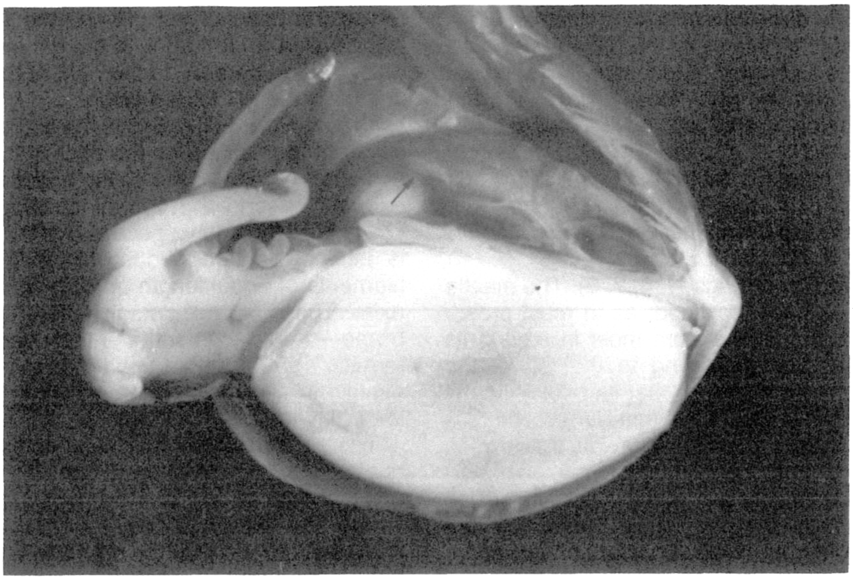

FIG. 6. *Neomphalus fretterae.* Left-ventral view of male specimen after cutting ventrally along the floor of the mantle cavity adjacent to the foot and folding up the ctenidium, showing the enlarged left cephalic tentacle adjacent to the left neck groove. The mouth is a vertical slit between the oral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

neck is long, wide, and flattened, so that its thickness is only about ¼ 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 ⅔ 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 posteriormost 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 between 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

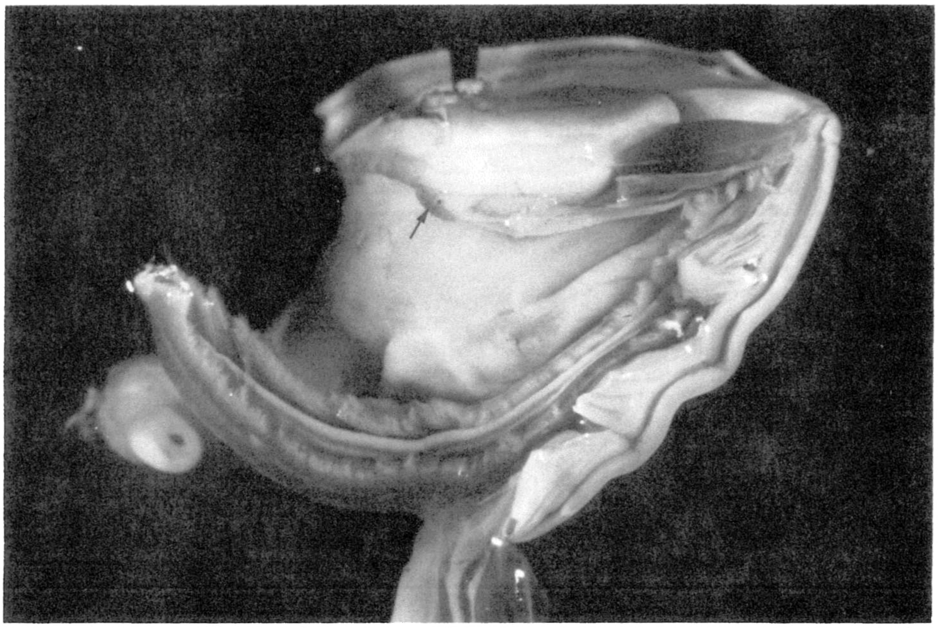

FIG. 7. *Neomphalus fretterae.* Female specimen from left side after cutting the mantle skirt between the visceral mass and the pallial vein; tips of ctenidial filaments excised to show the afferent side of the ctenidial axis. Arrow points to the female opening.

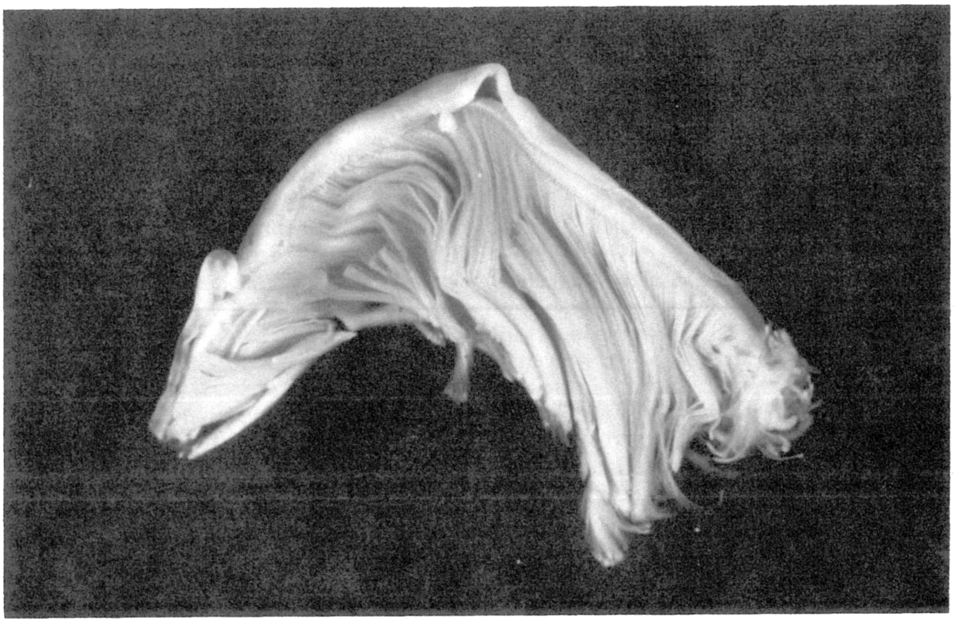

FIG. 8. *Neomphalus fretterae.* Ctenidium from specimen in Fig. 4, showing the close spacing and rounded tips to the filaments and the bend to the right midway along the axis. Filaments that arise beyond the bend terminate in a line coresponding to the position of the food groove where it traverses the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

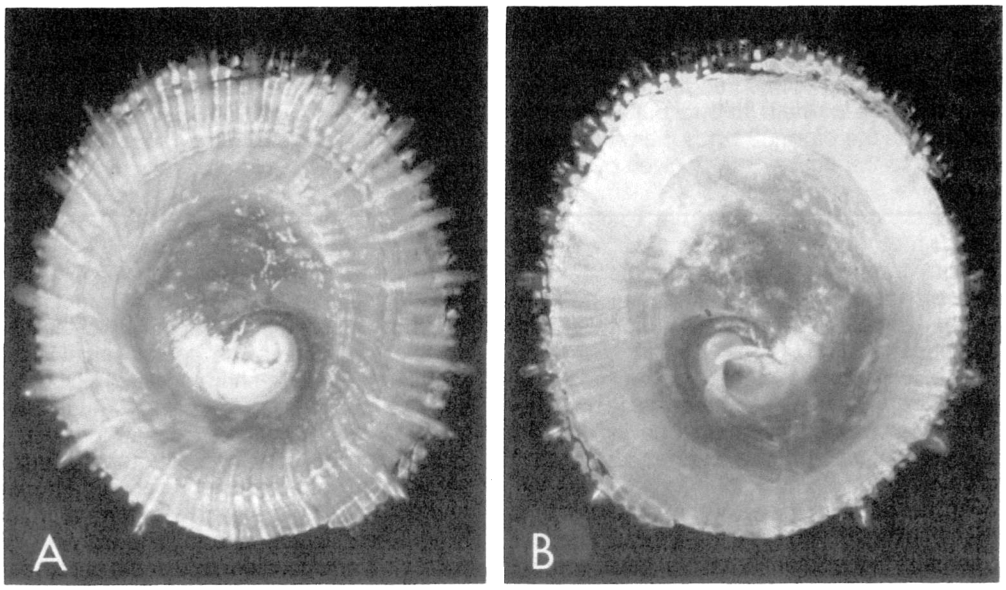

FIG. 9. *Neomphalus fretterae.* Juvenile shell of female, dive 733, Garden of Eden, diameter 7.0 mm. A) Exterior, anterior at top, showing flat-lying coil of early whorls. B) Interior, anterior at top, showing abandoned columella from the early coiled phase, the muscle scar and the shell ridge now positioned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

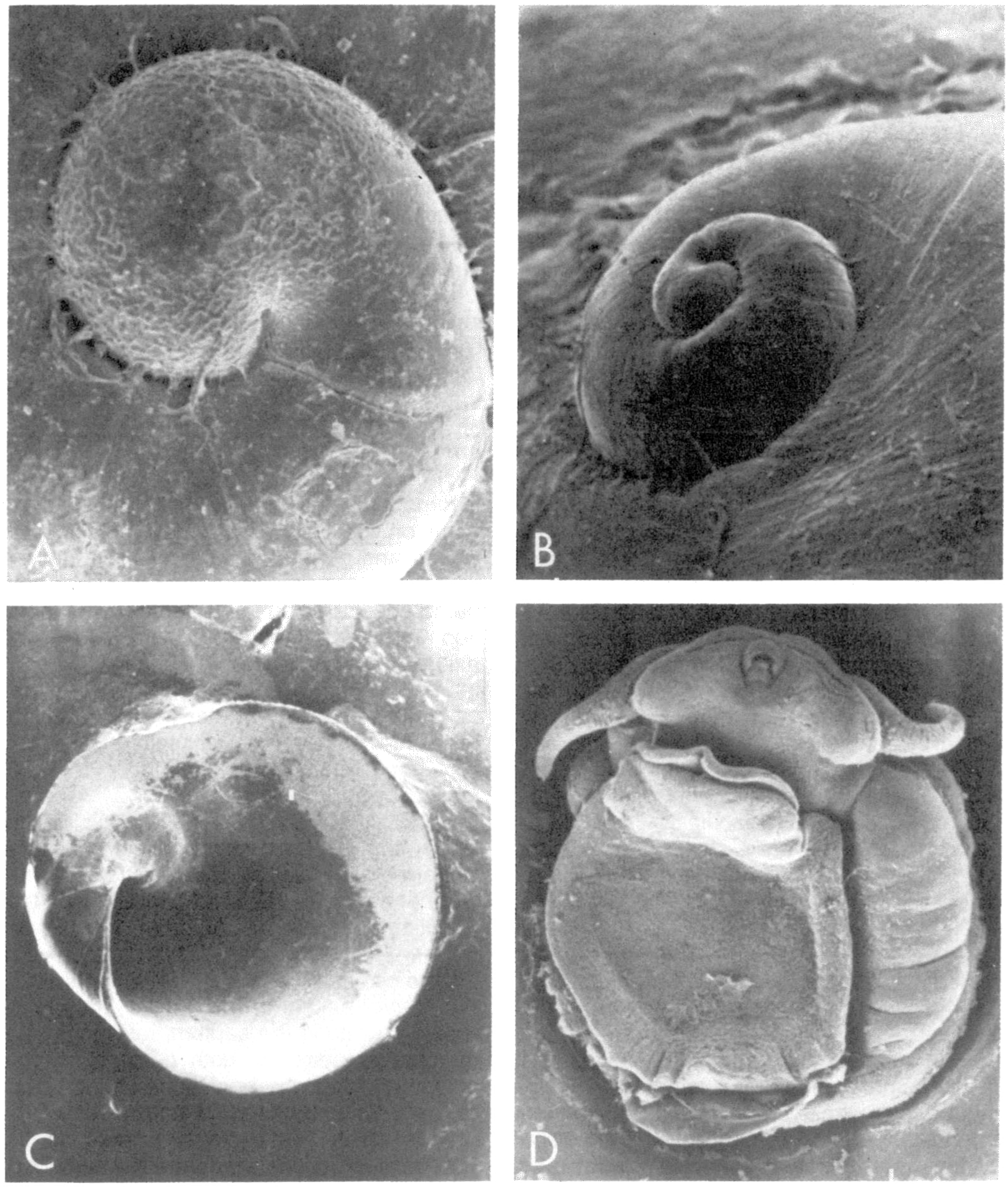

FIG. 10. *Neomphalus fretterae.* SEM views of early stages. A) Protoconch, maximum diameter 0.2 mm. B) Oblique view of protoconch and first two postprotoconch whorls, same specimen as Fig. 10A. C) Basal view of coiled juvenile shell 1.7 mm in diameter, showing the rudiment of the shell ridge, the rounded columellar lip along which growth has stopped, and the encirclement by lip growth on the right ¾ 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