

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.

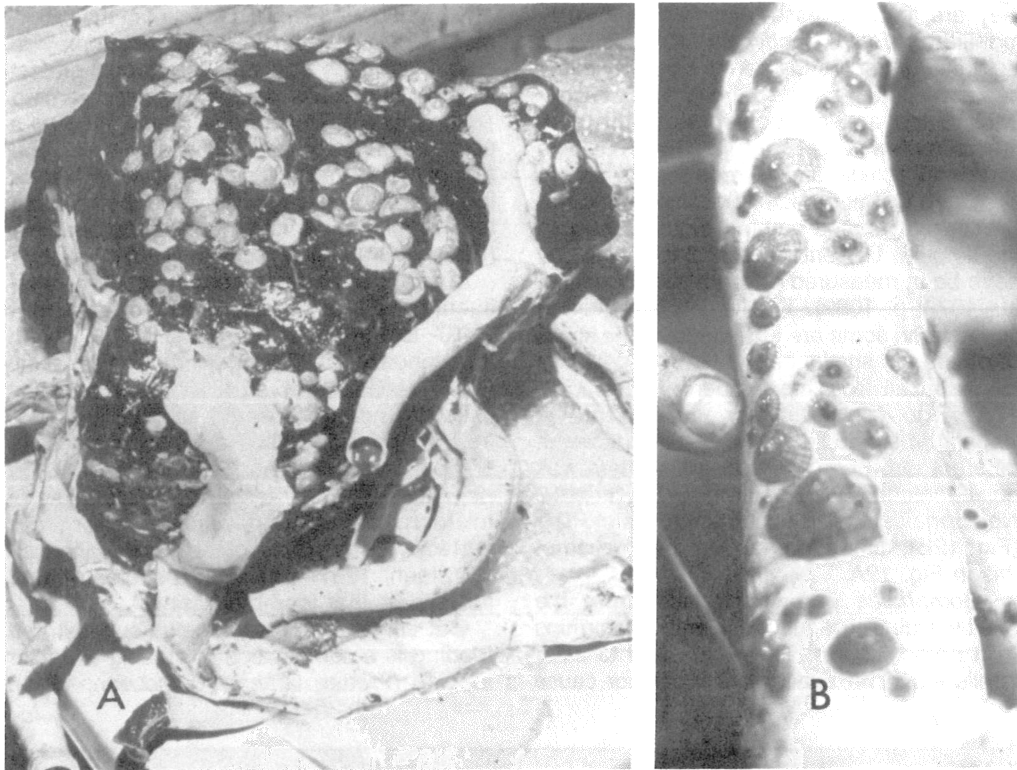


FIG. 12. A) 72 lb fragment of pillow basalt from dive 733, Garden of Eden, photographed on deck of support ship, showing *Neomphalus* in place and tubes of the vestimentiferan, *Riftia*. B) Tube of *Riftia* with attached *Neomphalus* in place, from 1979 expeditions, dive number unknown.

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).

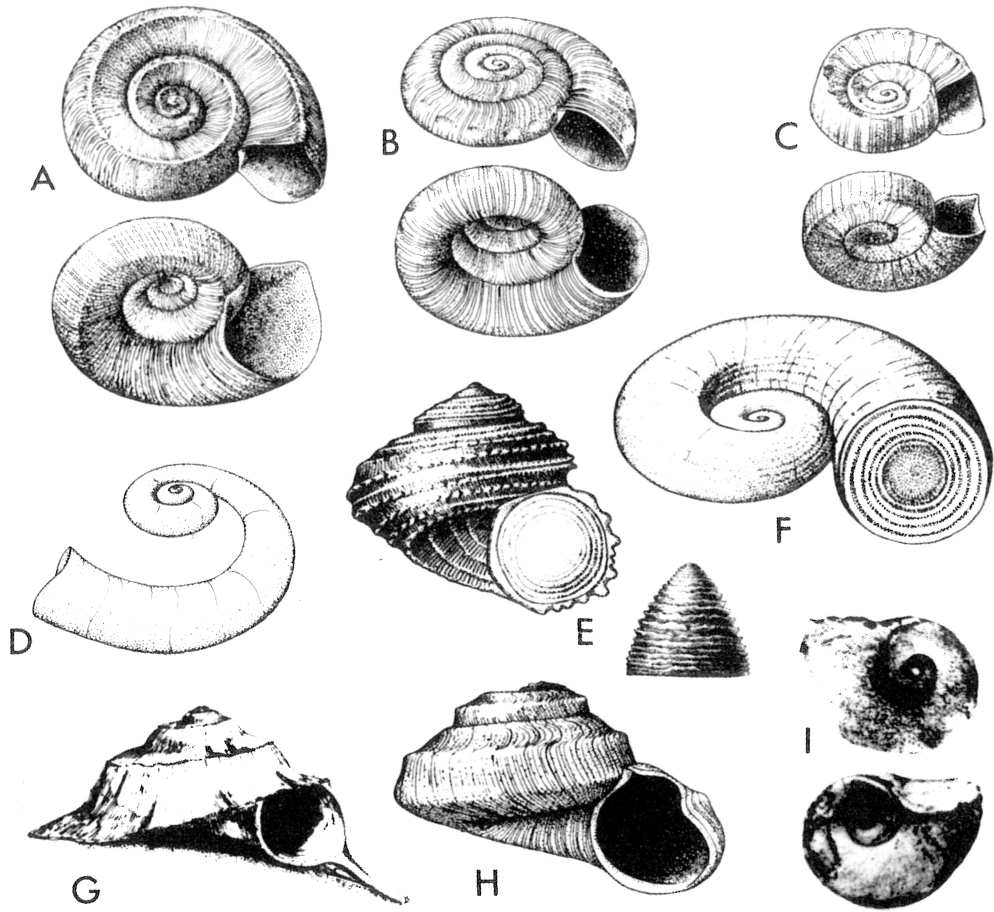


FIG. 13. Euomphalacean shells. A) *Euomphalus pentangulatus* J. Sowerby, 1814, Carboniferous (Euomphalidae), $\times 0.9$. B) *Straparollus laevis* (Archiac & Verneuil, 1842), Devonian, with attachment scars for shell fragments (Euomphalidae), $\times 1.5$. C) *Amphiscapha reedsi* (Knight, 1934), Pennsylvanian (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

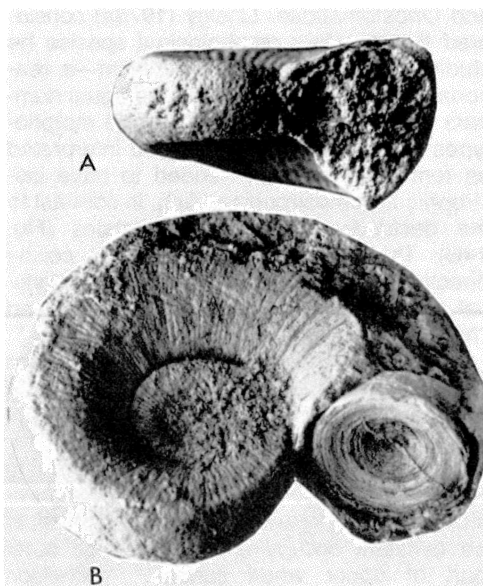


FIG. 14. *Liomphalus northi* (Etheridge, 1890), Devonian, Lilydale Limestone, Lilydale, Victoria, Australia. Showing the omphalocirrid operculum in place and coiling differences attributed to sexual dimorphism by Linsley (1978a). A) Apertural view of specimen thought to be an immature female, diameter 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 opisthocline, as in *Omphalotrochus* (Fig. 13H), although *Weeksia* (Fig. 13I), with a prosocline lip, is an exception. The trochacean lip is usually prosocline.

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 mineralogic 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 $\frac{1}{3}$ 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).

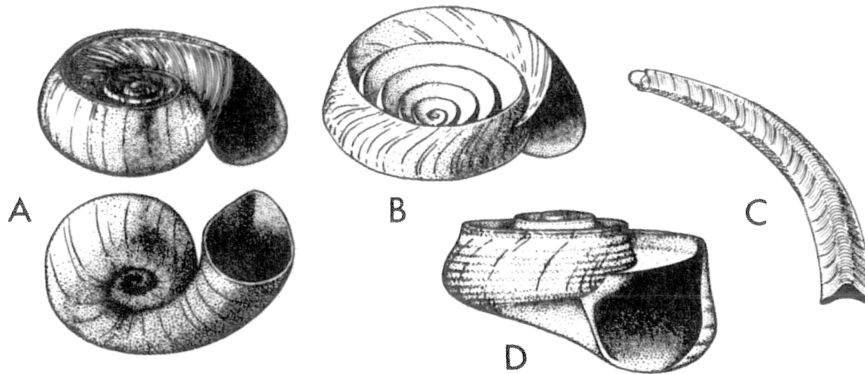


FIG. 15. Early Paleozoic genera now excluded from the Euomphalacea for having a prominent raised slit or selenizone. This group of genera is now regarded (Yochelson manuscript) as the low-spired pleurotomariacean group ancestral to the Euomphalacea. A) *Lesueurilla infundibulum* (Koken, 1896), Ordovician, $\times 1.1$. 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 *Umbronium* 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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⁹Salvini-Plawen's (1980: 261) suborder Vetigastropoda for superfamilies "Macluritoidea, Pleurotomarioidea, Cocculinoidea, 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

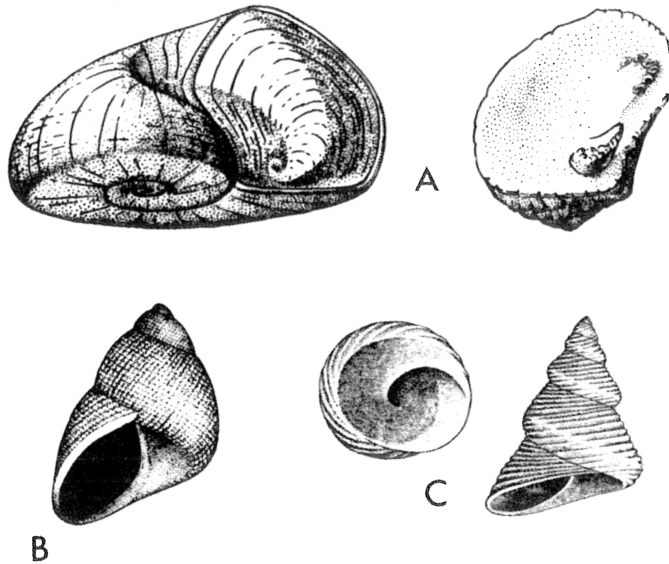


FIG. 16. Macluritacea and Clisospiracea. A) *Maclurites logani* (Salter, 1859), with internal view of operculum, Ordovician (Macluritacea: Macluritidae), $\times 0.6$. B) *Onychochilus physa* Lindström, 1884, Silurian (Clisospiracea: Onychochilidae), $\times 8.4$. C) *Mimospira cochleata* (Lindström, 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. *Omphalocirrus* 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.