

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

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

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

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

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

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

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

PALAEOTROCHACEA: Again there is no

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

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

APPENDIX 2: Suppression of Superfamilies Craspedostomatacea and Amberleyacea

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

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

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

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

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

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

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

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

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

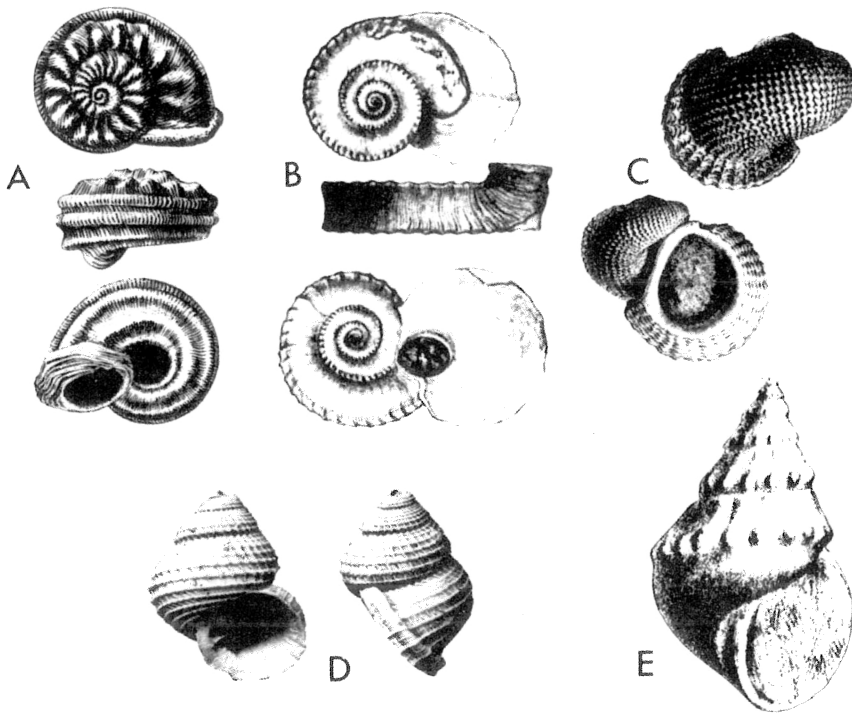


FIG. 18. Trochacean genera mentioned in Appendix 2. A) *Dichostasis complex* Yochelson, 1956, Permian (Liotiidae), $\times 5.1$. B) *Anisostoma suessi* (Hörnes, 1855), Triassic (Liotiidae), $\times 1.7$. C) *Crespedostoma spinulosum* Lindström, 1884, Silurian (Craspedostomatidae), $\times 1.7$. D) *Danilia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

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

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

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

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

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

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

been very different.

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