Description. Shell (Figs. 49–51) of limpet form, large for family (maximum projected length 12 mm); outline elongate with parallel sides. Margin of aperture not in same plane, sides markedly raised relative to ends. Anterior slope convex, lateral slopes convex until shell breadth of 5 mm, then nearly at right angles to anterior slope. Apex posterior, position uncertain (apical whorl not represented in present material). Protoconch characters unknown. Periostracum thick, shaggy, not enveloping shell edge. Sculpture of fine radial ribs, beaded at intersections with growth lines. Nodes represented by irregular, elongate swellings along growth lines. Muscle scar narrow, left arm of scar extending more anteriorly that right; posterior insertion unknown (posterior portion of shell not represented in present material). Operculum (Figs. 52, 53) multispiral, diameter greater than that of (contracted) breadth of body; opercular volutions few, last volution of equal diameter to all previous volutions. Dimensions of incomplete holotype: length 11.5, width 6.5, height 4.1 mm.

External anatomy (Figs. 52–53). Foot oval, rounded posteriorly; anterior with opening of pedal gland. Snout not tapered, slightly expanded at tip. Cephalic tentacles thick at base, contracted in present material, equal in size. Mantle edge simple, epipodial ridge projecting, extending to head, ventral to cephalic tentacles, bearing single row of low tubercles. Ctenidium extremely large, occupying most of dorsal surface under mantle skirt.

Radula (Figs. 54, 55) as described under generic heading.

Remarks. Lack of an apical portion of the shell makes it impossible to properly characterize this species, although there should be little difficulty in recognizing it when intact specimens may be found. Both specimens were originally of about the same size. Mature length probably attains at least 13 mm; the largest fragment of the second specimen (length 6.2) is also an anteriormost piece. Black particles of iron sulphide adhere to the foot (Figs. 52, 53). It is apparent that this species is closely associated with the black smokers, although the heavy coating of rust colored mineral deposits on the shell may indicate that it lives outside the burrows of *Alvinella*, in contrast to *Nodopelta heminoda*, shells of which tend to be relatively clean of mineral deposits.

The specific name is a Latin adjective meaning shaggy or rough.

Discussion

Provisional classification

Superfamilial distinctions in prosobranchs are generally based upon major differences in anatomical organization. It is admittedly premature to draw conclusions about the superfamilial placement of the hydrothermal vent archaeogastropods because the anatomy of all members is not yet known. Although such workers as Fretter, Warén and Haszprunar are currently engaged in filling this gap, it may be some time before the information is published and synthesized and a consensus reached. Meanwhile,

Warén & Bouchet (1989) have preferred to place the peltospirids and the neomphalids together in Neomphalacea, pending a better understanding of anatomy in all members of both groups. On the other hand, I follow an earlier course (McLean 1985) in which a superfamilial distinction was drawn between *Neomphalus* and the peltospirid limpets, based largely on preliminary comparisons of anatomical characters made by V. Fretter, who will shortly report on the anatomy of the limpets and still continues to regard the two groups as different at the superfamilial level (pers. commun.).

The peltospirid radula, like the neomphalid radula, has the rachidian and laterals with long, tapered cusps and a similar arrangement of basal interlock between the rachidian and subsequent lateral teeth. However, the peltospirid radula differs from that of *Neomphalus* in several important way, as noted by Hickman (1984). There is a broader separation between rows in the central field of the peltospirid radula, which exposes the narrow bases of the rachidian and laterals below the main shaft of each tooth. The marginal tooth rows descend more sharply and the rows are not aligned with tooth rows in the central field. The prominent nubs on the shafts of the laterals are not reported in any of the neomphalid genera (*Neomphalus, Cyathermia* and *Lacunoides*). *Neomphalus* lacks the sharp denticulation on the fourth lateral, although this feature is apparent in the radula of *Cyathermia* and *Lacunoides*. Warén & Bouchet (1989) have considered the shared features of the peltospirid and neomphalid radulae to be archetypal or plesiomorphic among archaeogastropods. If that is the case, the fact that there are similarities in the radulae between the two groups does not preclude their separation at the superfamily level.

In my view, the difference in the shape of the head between the neomphalids and the peltospirids can, for now, be acknowledged at the superfamily level. The long, flattened neck and lappets of *Neomphalus*, with a food groove that cuts dorsally above the right cephalic tentacle (McLean 1981), contrasts sharply with the tapered snout of the peltospirids (Fig. 36). Such differences must reflect a profound difference in buccal musculature and radular cartilages between the two groups. Although *Cyathermia* and *Lacunoides* have the head and oral lappets shaped like that of *Neomphalus*, I expect that family level distinctions within the Neomphalacea may be necessary when anatomy of the coiled species is better understood.

There are also indications that anatomical differences among some of the genera currently recognized as peltospirids may require family level recognition. The existence of an enlarged left tentacle in *Melanodrymia* (see Warén & Bouchet 1989) suggests that it may function in copulation, as in *Neomphalus*, but this may have developed independently in the two groups. A better understanding of anatomy may necessitate the establishment of family level recognition for *Melanodrymia*. *Hirtopelta* and *Pachydermia* differ from other peltospirids in snout morphology and on radular characters, having the cusps of the rachidian and laterals markedly serrate and lacking the strong nubs on the laterals. As noted under the description of *Hirtopelta*, there may also be family level characters for consideration here. Warén & Bouchet

(1989, figs. 57, 58) noted that *Solutigyra* exhibits a major departure in radular characters from other peltospirids; further anatomical comparisons may warrant a reconsideration of the family level classification of *Solutigyra*.

Warén & Bouchet distinguished two kinds of protoconch sculpture in coiled peltospirids and neomphalids, those with net-sculpture (*Melanodrymia, Pachydermia, Depressigyra, Solutigyra*) and one (*Lirapex*) with longitudinal ridges. In the limpet members of Peltospiridae only the longitudinally ridged protoconch has been detected (*Peltospira, Nodopelta* and Rhynchopelta). Intact protoconchs have not been observed in *Echinopelta* or *Hirtopelta*. It is likely that *Echinopelta* will have a ridged protoconch, but more likely that *Hirtopelta* will have a protoconch with net-sculpture, considering the radular and snout morphology characters that it shares with *Pachydermia*, which has a protoconch with net-sculpture. The three known neomphalids (*Neomphalus, Cyathermia,* and *Lacunoides*) all have net-sculpture in the protoconch. The significance of this distinction is unknown, but these data should be useful in future attempts at classification of the vent archaeogastropods.

Generic diversity

The family Peltospiridae, with ten genera, is the most diverse family known from hydrothermal vents. Species per genus are few: three in *Peltospira*, including *P. lamellifera* Warén & Bouchet, 1989, and two each in *Nodopelta, Depressigyra* and *Lirapex*. Six genera are as yet monotypic. This contrasts with the Lepetodrilacea, for which there are fewer genera but larger numbers of species per genus; six species in *Lepetodrilus* and three in *Gorgoleptis* (McLean 1988*a*). The low number of species in peltospirid genera may be an artifact of collecting and should be increased when the mollusk fauna of other hydrothermal sites becomes known. Nevertheless, it is evident that many members are likely to remain in monotypic genera.

Distribution

The extensive radiation of peltospirids in the hydrothermal vent community is correlated with habitat specialization. Warén & Bouchet (1989) reported that some of the coiled peltospirids live in sediment pockets. The limpets require firm substrates, as do all limpets. *Rhynchopelta* is associated with the ventimentiferan *Riftia*, on which it probably grazes bacterial films, thereby invading the chief habitat of the extremely abundant *Lepetodrilus* species (McLean 1988*a*). However, most other peltospirid limpets have taken advantage of the thick mass of tubes provided by the Pompei worm *Alvinella*, which lives on the walls of the black smoker chimneys. This microhabitat is remarkable in its chemical and thermal parameters. Black smoker chimneys discharge hydrothermal fluid at 350°C or higher. The animals at the base of these chimneys "live under a constant rain of sulfide particles precipitated from the smoker effluent" (Baross & Deming 1985, and references therein). These authors considered that the thermophilic bacteria discharged in smoker effluents colonize the available surfaces on the chimneys, and provide

the source of food for *Alvinella*. This same food source is evidently available to the limpets. The tubes and burrows of *Alvinella* provide a major habitat for most of the peltospirid limpets, in the same way that *Riftia* provides the major habitat for the lepetodrilid limpets.

The fact that peltospirid limpets are known only from the two major localities on the East Pacific Rise, the site at 21°N and the site at 13°N, is evidently due to the distribution of the black smokers at these sites and not at such other sites as the Galapagos Rift, the Guaymas Basin and the Juan de Fuca and Explorer Ridges. The two localities on the East Pacific Rise at 13°N and 21°N have the largest total number of limpet species (14 species at each site; McLean 1985) especially because black smokers as well as warm water vents occur. Of the peltospirid limpets only *Rhynchopelta concentrica* could conceivably extend its distribution to the Galapagos Rift, where the habitat provided by *Riftia pachyptila* is available. Among the coiled genera, *Melanodrymia* was initially collected from the black smoker habitat (Hickman 1984). *Depressigyra*, at least, is not a member of the black smoker community, as it occurs at the Juan de Fuca Ridge.

Although many deep sea archaeogastropods probably remain to be discovered, it is most unlikely that any vent-associated species of Neomphalacea, Lepetodrilacea and Peltospiracea will be discovered away from the hydrothermal vent habitat. Ten years have elapsed since the hydrothermal vent community was first discovered. A number of new sites of hydrothermal activity have been discovered and other deep sea habitats continue to produce new species, but there have been no exceptions to the above generalization.

Possible fossil affinity

A fossil record of peltospirids is, as yet, unknown. There are, however, many extinct families of presumed archaeogastropods in the late Paleozoic and Meozoic for which relationships to modern archaeogastropods can only be surmised. The following families diagnosed and illustrated in Knight *et al.* (1960) have non-siphonate apertures and are thought to be single gilled archaeogastropods: Euomphalidae, Omphalotrochidae, Holopeidae, Platyceratidae, Anomphalidae, Oriostomatidae and Tubinidae. Some have been placed in the 'suborder Trochina' and are thereby implied to have had some anatomical features in common with Trochacea. Considering the range of size, shell form and sculpture of the hydrothermal vent archaeogastropods, it is equally logical to hypothesize that anatomy in some of these families was comparable to living hydrothermal vent archaeogastropods in the Neomphalacea, Lepetodrilacea and Peltospiracea. Nacre is unknown in living species, but fossil shells with nacreous interiors need not be more likely to have been trochacean predecessors, as nacre may be readily lost, considering that there are some trochacean genera that lack it.

There is one possible direct link that should be further pursued. *Rhynochopelta concentrica* closely resembles the illustration of the Triassic *Phyrx* (Knight *et al.* 1960, fig. 144-2), which has been placed in the Symmetrocapulidae along with the Jurassic *Symmetrocapulus*. The

muscle scar of *Phyrx* is unknown, but the muscle scar of *Symmetrocapulus* indicates that the apex is posterior rather than anterior (Kase 1984, pl. 24, fig. 6). I have already discussed the potential relationships of this extinct family (McLean 1988a), concluding that these asymmetrical limpets with posterior apices have more in common with either the Lepetodrilidae or the limpet members of the Peltospiridae than any other possible affinity. Direct comparisons of specimens of *Phyrx* and *Symmetrocapulus* with lepetodrilid and peltospirid limpets would be useful in the future.

As discussed earlier (McLean 1985), it should be possible to trace a fossil record of mollusks in the hydrothermal vent community itself, as fossil vestimentiferan burrows in hydrothermally deposited iron ore formations have already been noted (Haymon *et al.* 1984; Haymon & Koski 1985). This suggests that limpet and other gastropod fossils should also eventually be discovered in such formations, although fossils would likely be trace impressions, rather than preserved shell, considering that calcium carbonate of dead shells is dissolved in the hydrothermal vent environment (Lutz *et al.* 1985).

Hypothesis of age and origin

I have earlier offered my views concerning age and origin of the new families of hydrothermal vent limpets (McLean 1981, 1985, 1988*a*, *b*, and references therein) and will therefore summarize rather than repeat the details of the same arguments here. I note again that all hydrothermal vent limpets are derived from archaeogastropod stocks to the clear exclusion of mesogastropod stocks.

The broadly defined Neomphalacea, Lepetodrilacea and Peltospiracea all differ at the superfamily level from living archaeogastropod superfamilies. Their origin must therefore be placed in the same time frame as the origin of other living archaeogastropod superfamilies, which are traceable to the late Paleozoic and early Mesozoic. This was a time at which archaeogastropods were the dominant component of the gastropod fauna, and a time at which there was probably a greater diversity at the family level than today. The ancestors of the Neomphalacea, Lepetodrilacea and Peltospiracea would have escaped the extinction that befell other shallow water members of their groups by invading the hydrothermal vent community.

Ancestors of the superfamilies that are now limited to the hydrothermal vent habitat would have entered the community first by colonizing hydrothermal sites in shallow water and dispersing to successively deeper hydrothermal sites.

The hydrothermal vent community has existed throughout geological time (Skinner 1983). Invasions of new predators should be infrequent, due to the toxicity of the sulfide environment; this should promote stability over geologic time, providing a refuge for archaic forms and enabling their continued radiation in the hydrothermal vent habitat. Newman (1985) has argued that there is evidence for similar patterns of evolution in other invertebrates of the hydrothermal vent community.

Acknowledgements

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