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New archaeogastropod limpets from hydrothermal vents: new family Peltospiridae, new superfamily Peltospiracea

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Seven new species of limpets from hydrothermal vents are described in five new genera in the new family Peltospiridae (new superfamily Peltospiracea). Limpets in this family are known only from the hydrothermal vent community at two sites, near 21°N and 13°N, on the East Pacific Rise. New genera and species are: *Peltospira*, type species *P. operculata* from both sites, and *P. delicata* from 13°N; *Nodopelta*, type species *N. heminoda* from both sites, and *N. subnoda* from 13°N; *Rhynchopelta*, type species *R. concentrica* from both sites; *Echinopelta*, type species *E. fistulosa* from 21°N; *Hirtopelta*, type species *H. hirta* from 13°N. These limpets are associated with the Pompei worm *Alvinella*, except for Rhynchopelta, which is associated with the vestimentiferan worm *Riftia*.

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Introduction

The hydrothermal vent community of the East Pacific has now been known for a decade, following the first discovery of this community at the Galapagos Rift in 1977 (Lonsdale 1977). Archaeogastropod limpets are exceptionally well represented in mollusk fauna of this community (McLean 1985, 1988*b*). Although descriptions of the new families are only partially published (Fretter 1988; Fretter *et al.* 1981; McLean 1981, 1988; McLean & Haszprunar 1987), the hydrothermal vent limpets are tentatively assigned to eight different families in seven superfamilies (McLean 1988*b*).

This paper gives the taxonomic descriptions of seven new species in five new genera of the new family Peltospiridae in the new superfamily Peltospiracea. Species in this family have earlier been mentioned by Hickman (1983) as the "Group-A" limpets and by McLean (1985) as the "tapersnout" hydrothermal vent limpets. With one exception these species do not have an expanded tip to the snout, as is true of most other archaeogastropod limpet families; hence the vernacular name.

Only brief information about the anatomical characters of the group is given here, as a detailed report on the anatomy of these seven species is soon to be published separately by V. Fretter. However, external features of mantle margin and epipodium provide characters useful in generic discrimination and are therefore treated here.

One coiled member of this new group, *Melanodrymia aurantiaca*, has been described earlier by Hickman (1984), who did not propose any higher level classification, but tentatively assigned the genus to the superfamily Trochacea. Additional coiled members are described concurrently by Warén & Bouchet (1989) in the same issue of this journal. Protoconchs and immature shells of unidentified peltospirid limpets, other hydrothermal vent limpets and coiled gastropods were illustrated by Turner & Lutz (1984), Turner *et al.* (1985) and Lutz *et al.* (1986), who also discussd the potential for larval dispersal in hydrothermal vent mollusks. Reproduction in vent mollusks was also discussed by Berg (1985).

Materials and methods

Although coiled members of the family are known from most hydrothermal sites, the peltospirid limpets have been found at only two of five localities in the eastern Pacific for which limpets have been reported (McLean 1985). These are the two major sites on the East Pacific Rise, near 21°N and 13°N. Peltospirid limpets have not been collected at the Galapagos Rift, the Guaymas Basin or the Juan de Fuca Ridge.

The site near 21°N was first visited in November 1979 (RISE Expedition, *Alvin* dives 976-981). This site was again visited in April-May 1982 (OASIS Expedition, *Alvin* dives 1209-1230). The initial account of the biological community was that of Spiess *et al.* (1980); Hessler *et al.* (1985) discussed ecological relationships. Fourteen limpet species were reported at 21°N (McLean 1985); four of these are peltospirid species described herein; three of these occur also at 13°N. One, *Echinopelta fistulosa*, is known only from 21°N.

The site near 13°N on the East Pacific Rise was first visited in March 1982 (BIOCYATHERM Expedition, *Cyana* dives 82-33 to 82-37) and again in March 1984 (BIOCYARISE Expedition, *Cyana* dives 84-32–84-38). General accounts are given by Desbruyères *et al.* (1982) and Desbruyères & Laubier (1983). This site also has 14 limpet species (McLean 1985), of which six are peltospirids treated here. Three of these species occur also at 21°N; another three, *Peltospira delicata, Nodopelta subnoda* and *Hirtopelta hirta*, are known only from 13°N.

Jones *et al.* (1985) gave station data for all dives made by these submersibles through 1985.

Except for the species described here as *Rhynchopelta concentrica*, the peltospirid limpets were collected only on sulfide crust deposits, particularly the walls of the superheated black smoker vents, where they were associated with the tubes of the polychaete *Alvinella pompejana* Debruyères & Laubier, 1980. *Rhynchopelta concentrica* was collected with specimens of the large vestimentiferan tube worm *Riftia pachyptilia* Jones, 1981, which were removed with the mechanical arms of the subsmersibles.

Specimens were preserved upon reaching the surface and were fixed for 24 h in 10% seawater–formalin buffered with sodium borate, washed in fresh water and transferred to 70% ethanol (for details of collecting procedures see Turner *et al.* 1985). Preserved specimens collected by the

Alvin were sorted and counted at Woods Hole Oceanographic Institution, following which the limpets were sent to me. Specimens collected by the *Cyana* were sorted at the Centre National de Tri d'Oceanographic Biologique, Brest, France, and sent to P. Bouchet at the Muséum National d'Historie Naturelle, Paris, and subsequently loaned to me for this study.

Transverse and sagittal histological sections were prepared at the Los Angeles County Museum of Natural History and loaned to V. Fretter for her work on anatomy. Radulae and juvenile shells were examined with SEM, without removal of organic growths. Protoconch lengths were taken directly from scale indications for the SEM micrographs.

Shell microstructure is not treated here, as this is being studied by Marie-Pierre Triclot of the Université Paris-Sud, Orsay, France, who will report separately on it.

Repositories of the major series of type material are the Los Angeles County Museum of Natural History (LACM), the United States National Museum of Natural History (USNM) and the Muséum National d'Histoire Naturelle, Paris (MNHN). All figured specimens other than holotypes of the three species endemic to 13°N are deposited at the LACM.

Systematic descriptions

PELTOSPIRACEA superfam.n.

Peltospiridae fam.n.

A single family is here recognized; the diagnosis that follows serves for that of the superfamily and family.

Diagnosis. Shell lacking nacreous layer, periostracum thick, often broadly enveloping apertural edge. Shell coiled with complete peristome and multispiral operculum, or of limpet form with apex posterior, usually offset to right and below highest elevation of shell. Shell sculpture varied. Protoconch sculpture of longitudinal ridges or net-pattern, length 160-260 μm; protoconch II lacking. Muscle scar in limpet members horseshoe-shaped, narrowed posteriorly, where usually located on adapical side of thickened ridge (columellar edge) on shell interior.

Snout tapered, oral disc reduced. Cephalic tentacles thick at base, lacking papillae; left and right tentacles equal in most genera (left larger in *Melanodrymia*, see Warén & Bouchet 1989). Eyes lacking. Epipodium and mantle margin variously modified but not with long epipodial tentacles of trochaceans. Mantle cavity deep, single (left) ctenidium bipectinate, free tip overlying head, lamellae of left side of axis half the length and dorsal to those of right, afferent and efferent membranes present. Heart monotocardian. Sexes separate. Left kidney only, not like papillary sac of trochaceans.

Rachidian with long shaft and projecting lateral extensions at mid-length, overhanging cusp tapered. Lateral teeth four pairs, overhanging cusps tapered like that of rachidian, each lateral tooth with inwardly directed flange extending behind rachidian or adjacent lateral tooth, an indentation on inner side to accommodate lateral extension of rachidian or adjacent lateral tooth, a projecting nub on exposed side at position of interlock and a projecting lateral extension like that of rachidian on outer side. Fourth lateral tooth with sharp denticulation on outer edge of cusp; cusps of other lateral teeth smooth. Lateromarginal plate and marginal basal plate lacking. Marginals numerous, shafts spatulate, very long, cusps finely denticulate. Tooth rows broadly spaced in central field, exposing narrow bases of rachidian and laterals. Position of cusps of central field only slightly descending away from rachidian, but shafts of lateral teeth increasing in length. Marginal teeth rows steeply descending and not matching rows in central field; shafts of outermost marginals often fused.

Remarks. Ten genera are presently recognized: *Melanodrymia* Hickman, 1984; four described concurrently by Warén & Bouchet (1989): *Depressigyra, Pachydermia, Lirapex* and *Solutigyra*; five described here: *Peltospira, Nodopelta, Rhynchopelta, Echinopelta* and *Hirtopelta*. The limpet members of this family have been earlier referred to as the "tapersnout" limpets (McLean 1985) owing to the long, tapered snout (except in *Hirtopelta*), unlike that of the Patellacea and Lepetodrilacea, which have an expanded oral disk, or that of the Cocculinacea or Lepetellacea, which have lappets lateral to the mouth.

The limpet genera range from relatively large-shelled to small, compared to the coiled genera, all of which are small to minute. Ornamentation includes spaced axial elements, projecting nodes, tubular spines or concentric ridges. Elaboration of the epipodium and mantle margin in the limpets is diverse. Generic characters are provided by shell form and sculpture and the condition of the mantle margin and epipodium.

Intact protoconchs have been examined in only three of the seven species of limpets (*Peltospira operculata, Nodopelta subnoda* and *Rhynchopelta concentrica*). All appear to be coloured dark brown and are weakly or apparently not calcified. In some specimens that appeared to have protoconchs, the protoconch scar area was packed with a dark substance that provides the dark color and the protoconch itself was missing. For those species that have been examined, protoconch size ranged from 160 μm in *Nodopelta subnoda* to 260 μm in *Melanodrymia aurantiaca* (see Warén & Bouchet 1989), with intermediate sizes for *Peltospira operculata* (180 μm) and *Rhynchopelta concentrica* (225 μm). Protoconch sculpture in three limpet genera consisted of strong ridges. In contrast, only *Lirapex* of the four coiled genera proposed by Warén & Bouchet (1989) has similar protoconch sculpture; the others have net-sculpture.

An operculum is retained in mature specimens of *Peltospira operculata* and *Hirtopelta hirta*. Opercula were also noted on juvenile specimens of *Rhynchopelta concentrica* (Fig. 37) and are assumed to be present in juveniles of all species. Retention of the operculum in the adult is not a good generic character by itself, as it is retained in *P. operculata* but not in *P. delicata*.

Four of the five limpet genera have radulae that conform to the radular diagnosis given above. The interlock between lateral teeth is best illustrated in Fig. 48, in which the lateral projection of the third lateral and the flange of the fourth is revealed by the folding back of the fourth lateral. The radula of *Hirtopelta* follows the basic plan but differs in details. Three of the coiled genera proposed by Warén & Bouchet (1989) also agree; one (*Solutigyra*) does not, but was provisionally admitted to the family (see Warén & Bouchet 1989). Radular characters are treated further in the Discussion section of this paper.

Intact peltospirid limpet specimens are easily distinguished from lepetodrilid limpets (McLean 1988*a*) in having strikingly different epipodial features, rather than the single anterior and double posterior pair of that family. However, shells of peltospirid limpets resemble lepetodrilid limpets in having the inturned periostracum, the muscle scar narrow posteriorly and posterior apices below the highest elevation. Some species in both families have the posterior transverse ridge on the shell interior. If shells have intact protoconchs, there is one clear means of distinguishing peltospirids from those of lepetodrilids: peltospirid limpets (at least those for which the protoconch is known) have protoconch sculpture of strong ridges, whereas the protoconch of lepetodrilid limpets is finely pitted.

The family is presently known only from hydrothermal sites in the eastern Pacific. It is evidently dependent upon sulfide-rich water that is toxic to most other families in the ambient deep sea.

The family name is based on the new genus *Peltospira*, which means 'shield-spire'. Species of *Peltospira* are essentially coiled but have inflated apertures that suggest the limpet form. Because the family has a nearly equal representation of coiled and limpet members, this genus is selected as the one on which to base the family name.

Generic diagnoses that follow treat only the characters important for comparison between the five genera, whether or not the genus is presently monotypic. Species descriptions, however, repeat generic characters.

Key to limpet genera based on shell characters

1.	Sculpture of broadly spaced nodes or spines	2
	Sculpture lacking nodes or spines	4
2.	Sculpture of elongate spines	*Echinopelta*
	Sculpture of scattered nodes	3
3.	Nodes crescent shaped	*Nodopelta*
	Nodes irregular, elongate	*Hirtopelta*
4.	Sculpture of axial ridges on early teleoconch	*Peltospira*
	Sculpture of fine concentric ridges	*Rhynchopelta*

Peltospira gen.n.

Type species. Peltospira operculata sp.n.

Diagnosis. Shell thin, limpet-like, coiling nearly disjunct, rapidly expanding, apical whorl overhanging posterior margin on right. Periostracum strong, forming axial sculpture and enveloping shell edge. Protoconch sculpture of ridges where known. Multispiral operculum present or lacking.

External anatomy. Mantle edge with thin fold extending under periostracum, exposed edge thickened, puckered. Epipodial ridge bearing pronounced club-shaped processes of irregular size.

Radula characteristic of family, tapered cusps of rachidian and laterals relatively long, tooth bases broadly exposed, nubs prominent, outer marginals fused.

Remarks. Two species of *Peltospira* are described here, the type species *P. operculata* from both sites on the East Pacific Rise and *P. delicata*, known only from 13°N. A third species, *P. lamellifera*, known only from a single, probably immature shell from 13°N, is described concurrently by Warén & Bouchet (1989). Of the two species described here, a major difference is that *P. operculata* has an operculum and *P. delicata* lacks it, but the two are clearly congeneric in having a similar shell form, a periostracum with raised ridges and very similar epipodial elaboration. Shell form in this genus is essentially coiled, and comparable to that of stomatelline trochids with expanded apertures. The shell retains a columellar wall, unlike the condition in *Nodopelta, Rhynchopelta* and *Echinopelta*, in which the columellar wall is replaced by a posterior ridge on the shell interior.

Sculpture formed by periostracum and not by the shell was also reported by Warén & Bouchet (1989) in the coiled peltospirid *Lirapex granularis*.

Peltospira operculata sp.n. (Figs. 1–8)

"Opercular tapersnout limpet"; McLean 1985, p. 160.

Type locality. East Pacific Rise at 21°N (20°50.0′N, 105°06.0′W), 2615–2622 m. Probably associated with the pompei worm *Alvinella*.

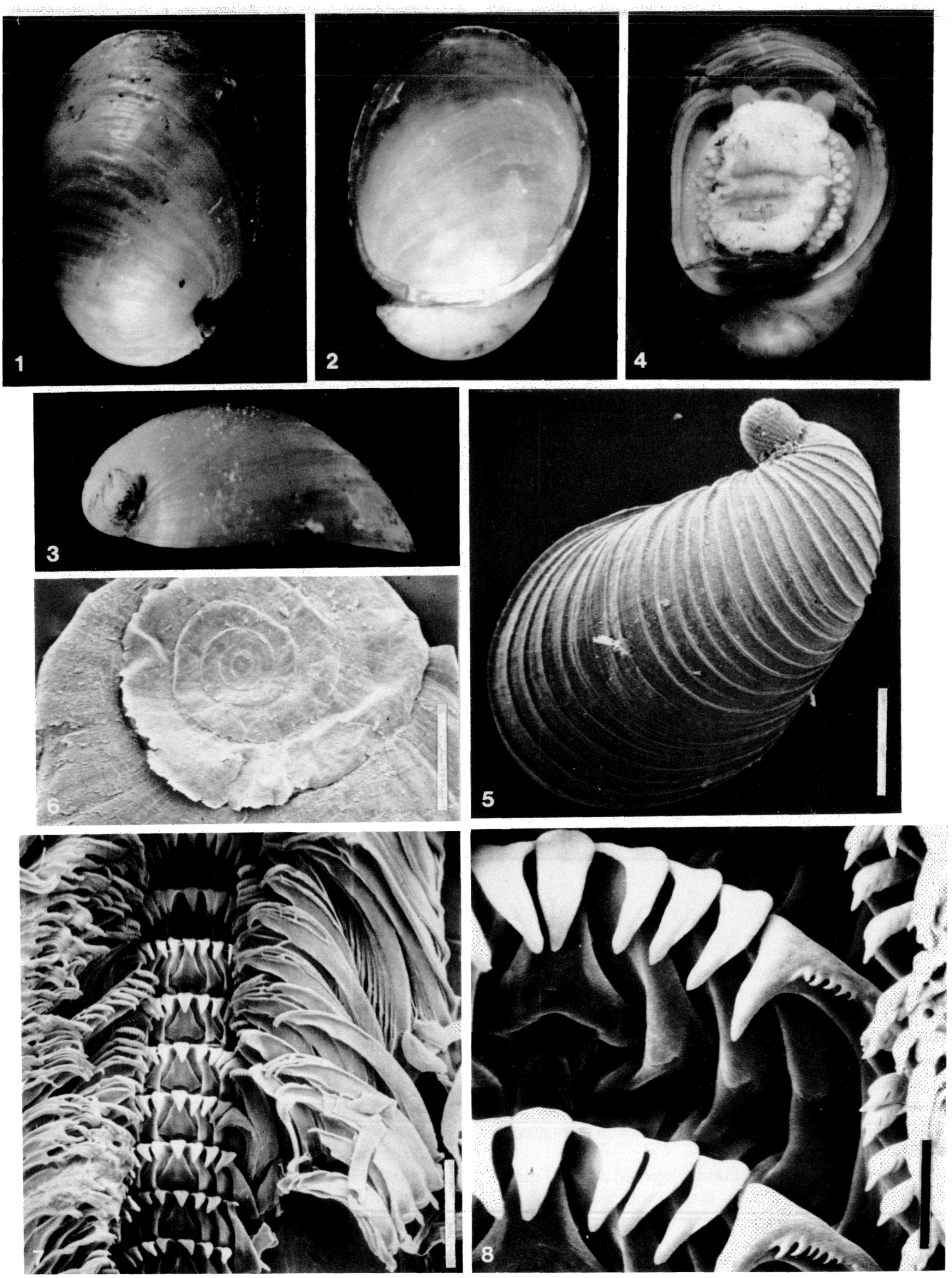
Holotype. LACM 2307, *Alvin* dive 1213 at type locality, 19 April 1982.

Paratypes. From 4 *Alvin* dives at type locality: dive 1213, 2 specimens, LACM 2308; dive 1219, 1 specimen, USNM 859934; dive 1223, 20 specimens, LACM 2309, USNM 859935, MNHN; dive 1226, 60 juvenile specimens, LACM 2310, USNM 859936, MNHN. From 11 *Cyana* dives at East Pacific Rise at 13°N (12°48.6′N, 103°56.7′W), 2630–2635 m: dive 82-33, 3 specimens, MNHN; dive 82-34, 1 specimen, MNHN; dive 82-35, 22 specimens, LACM 2311, USNM 859937, MNHN; dive 82-36, 2 specimens, MNHN; dive 84-32, 2 specimens, MNHN; dive 84-34, 5 specimens, MNHN; dive 84-37, 8 specimens, MNHN; dive 84-38, 51 specimens, MNHN; dive 84-41, 14 specimens, MNHN; dive 84-43, 11 specimens, MNHN; dive 84-46, 27 specimens, MNHN.

Description. Shell (Figs. 1–3) of moderate size for family (maximum length 10.1 mm), teleoconch coiled through one and a quarter whorls, suture deeply impressed; aperture length seven times breadth of previous whorl. Outline of aperture oval, anterior broader that posterior. Apical whorl overhanging posterior margin on right. Periostracum strong, yellow-green, enveloping shell margin, including columellar lip. Protoconch dark brown, length 180 μm, sculpture of longitudinal ridges (Fig. 5). Early sculpture of teleoconch appearing at shell length of 0.4 mm, of sharp, raised, axial ridges formed by periostracum; strength and spacing of ribs slightly irregular; microscopic spiral striae also formed by periostracum at this stage. Most axial and spiral sculpture lost after shell attains length of 2 mm; mature sculpture of growth irregularities only. Shell interior glossy, muscle scar not apparent. Operculum half the diameter of aperture, brown, multispiral, final volution broader, edge of earlier volution projecting (Fig. 6). Dimensions of holotype: length 7.8, width 5.6, height 3.3 mm.

External anatomy (Fig. 4). Foot oval, anterior with broad transverse groove marking opening of pedal gland, operculum attached to posterior surface. Snout tapered, cephalic tentacles thick at base, tapered (contracted in all specimens), equal in size. Mantle edge with thin fold extending under periostracum, exposed edge puckered. Epipodial ridge with packed club-shaped processes of irregular size (retracted in all specimens), complete posteriorly but not extending to snout.

Radula (Figs. 7, 8). Typical for family, cusps of rachidian and laterals exceptionally long, nubs of laterals



Figs. 1–8. Peltospira operculata sp.n., all from 21°N—*1–3*. Holotype shell, exterior and interior (anterior at top) and lateral (right side) views. Length 7.8 mm.—*4*. Ventral view of paratype body in shell, showing operculum attached.—*5*. Juvenile shell with intact protoconch, scale bar 200 μm.—*6*. SEM view of operculum, scale bar 400 μm.—*7*. SEM view of radular ribbon, scale bar 40 μm.—*8*. SEM view showing rachidian, 4 laterals and tips of marginals, 4th lateral with denticulation matching that of marginals, scale bar 10 μm.

prominent; denticulation on outer edge of fourth lateral matching that of marginals; shafts of outer marginals prominently fused.

Remarks. In addition to the opercular difference, this species is larger and has a more inflated final whorl than its congener *P. delicata*.

The operculum is of sufficient size to serve as a pad shielding the upper part of the foot from contact with the coiled portion of the shell.

The specimens sorted at Woods Hole were labeled from "*Calyptogena* and *Alvinella* wash", but all specimens had associated particles of iron sulfide, suggesting that they came from the base of the black smokers where *Alvinella* forms large colonies.

Specimens from 13°N agreed in all particulars with the type material from 21°N, although the largest specimen noted was 6.2 mm in length, compared to the maximum length of 10.1 mm at 21°N.

***Peltospira delicata* sp.n.** (Figs. 9–16)

"Delicate tapersnout limpet", McLean 1985, p. 160.

Type locality. East Pacific Rise at 13°N (12°48.6′N, 103°56.7′W), 2630–2635 m.

Holotype. MNHN, *Cyana* dive 84-38 at type locality, 15 March 1984.

Paratypes. From 5 *Cyana* dives at type locality: dive 84-37, 9 specimens, MNHN; dive 84-38, 44 specimens, MNHN, LACM 2312, USNM 859938; dive 84-41, 7 specimens, MNHN; dive 84-43, 1 specimen, MNHN; dive 84-46, 35 specimens, MNHN.

Description. Shell (Figs. 9–11) size medium for family (maximum length 6.5 mm), teleoconch coiled through one whorl, suture moderately impressed, aperture length nine times breadth of previous whorl. Outline of aperture slightly raised relative to ends. Apical whorl overhanging posterior margin on right. Periostracum strong, enveloping shell margin, including columellar lip. Protoconch length 180 μm (presence of sculpture not known). Early sculpture of teleoconch appearing at shell length of 0.3 mm, of sharp, raised, somewhat irregular axial ridges, formed by periostracum, persisting through shell length of less that 1 mm. Spiral sculpture lacking.

Mature sculpture lacking in some specimens; some with strong, irregularly spaced periostracal ridges (as in holotype). Shell interior glossy, muscle scar narrow except for broadly inflated anterior terminations, extending slightly more anterior on left side. Operculum lacking. Dimensions of holotype: length 5.2, width 3.3, height 1.7 mm.

External anatomy (Fig. 12). Foot oval, anterior with broad transverse groove marking opening of pedal gland. Snout tapered, cephalic tentacles thick at base, tapered (contracted in all specimens), equal in size. Mantle edge with thin fold extending under periostracum, exposed edge thickened. Epipodial ridge with packed, club-shaped processes of irregular size (contracted in all specimens), extending forward only to region of muscle attachment.

Radula (Figs. 15, 16) typical for family, cusps of rachidian and laterals long, curved inwardly, nubs of laterals prominent; denticulation on outer edge of fourth lateral like that of marginals; shafts of outermost marginal markedly fused.

Remarks. Peltospira delicata differs from *P. lamellifera* Warén & Bouchet, 1989, in lacking the spiral sculpture of that species, and from *P. operculata* in lacking the operculum at maturity, smaller size, lower profile, lack of spiral sculpture and greater elongation of the aperture and lesser anterior extent of the epipodial ridge. In its lack of the operculum and more elongate aperture it has achieved a greater shift to the limpet form than has the type species.

Although specimens appeared to have intact, dark colored protoconchs, under SEM examination the protoconch itself was missing, but a trace of its former position and size was apparent (Fig. 14).

Many of the specimens are decalcified at the anterior margin and held together only by the persistent periostracum. Specimens varied greatly in the amount of axial sculpture. Some specimens had attached iron sulfide particles, indicating that this is also a species more closely associated with the black smokers than with the vestimentiferan *Riftia*.

***Nodopelta* gen.n.**

Type species. Nodopelta heminoda sp.n.

Diagnosis. Shell of limpet form, apex close to posterior margin but not overhanging it; sides raised relative to ends; interior with strong posterior ridge. Periostracum, thick, enveloping shell edge. Sculpture finely clathrate, with scattered imbricate nodes. Protoconch sculpture (where known) of strong longitudinal ridges.

External anatomy. Mantle margin with thin fold extending under periostracum, exposed surface of mantle margin with transverse ridges aligned perpendicular to mantle edge. Epipodium a single row of low tubercles, extending to anterior end of foot.

Radula typical for family, cusps of rachidian long or short, nubs of laterals prominent, denticulation on outer edge of fourth lateral fine or matching that of marginals, shafts of outermost laterals fused.

Remarks. This is the only peltospirid limpet genus to have any modification of the middle lobe of the mantle margin. The ridges are superficially comparable to the development of branchial gills in the Patellacea, but have a glandular rather than respiratory function (V. Fretter, pers. commun.).

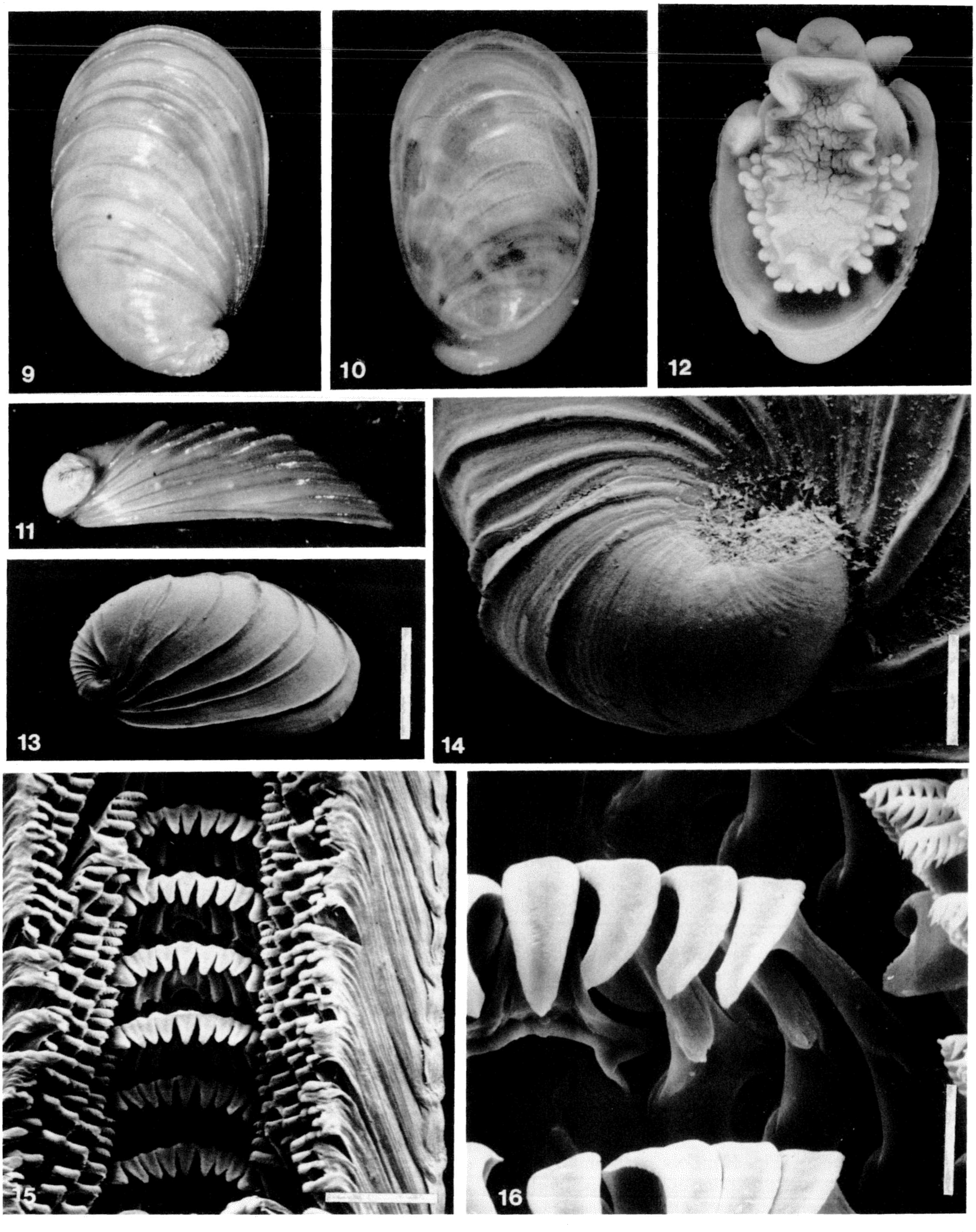
Although there is a major size difference between the two species *Nodopelta heminoda* and *N. subnoda*, they have a clear affinity in sharing sculptural and mantle margin characters. The two species differ in radular characters, as detailed in the comparisons under each species. The protoconch is known only for *N. subnoda*.

The name means noded-shield.

***Nodopelta heminoda* sp.n.** (Figs. 17–23)

"Half-node tapersnout limpet"; McLean 1985, p. 160.

Type locality. East Pacific Rise at 21°N (20°50.0′N, 105°06.0′W), 2615–2622 m. In burrows and tubes of Pompei worm *Alvinella* at base of 'black smokers'.

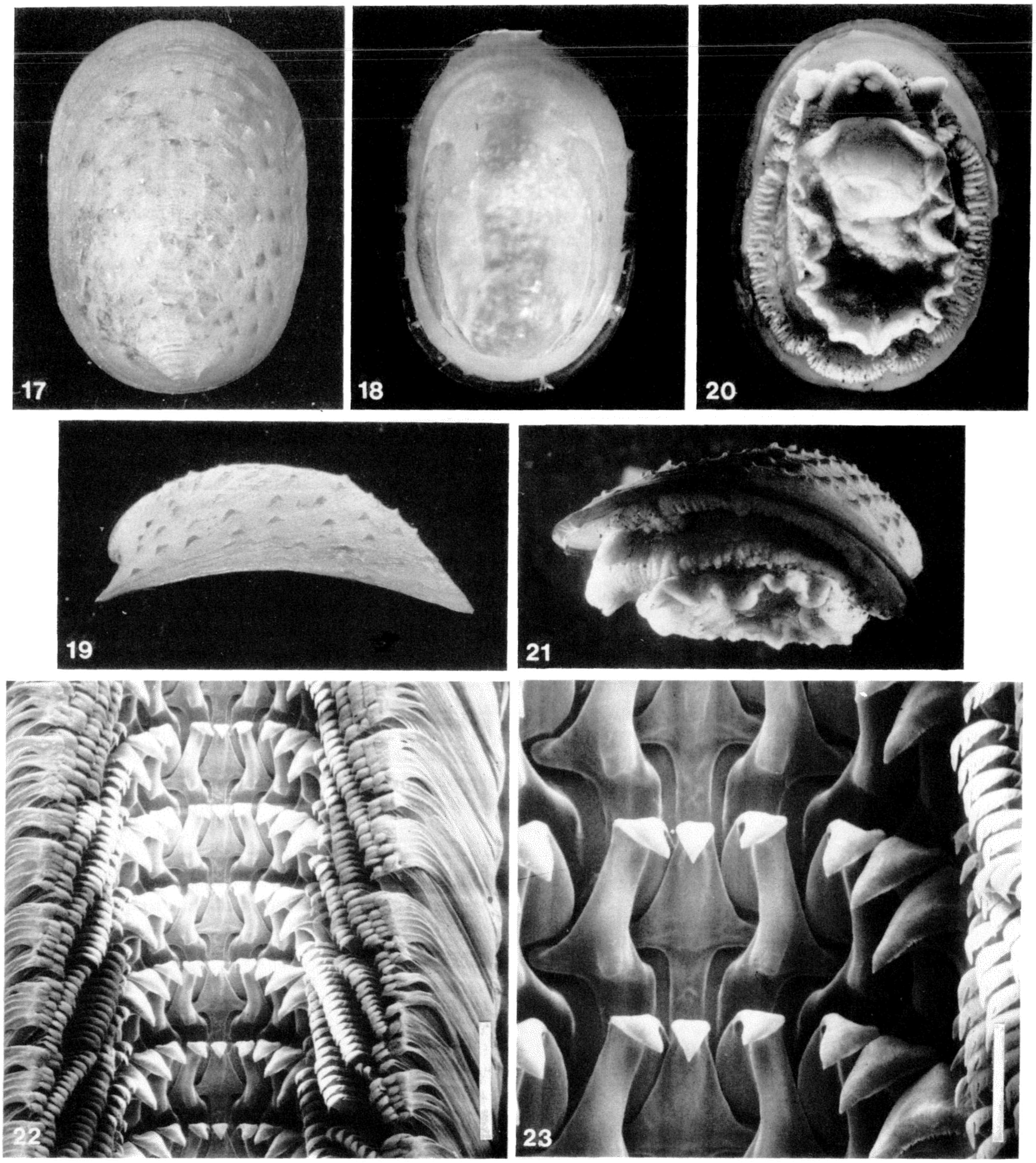


Figs. 9–16. Peltospira delicata sp.n. from 13°N.—*9–11.* Holotype shell, exterior and interior (anterior at top) and lateral (right side) views. Length 5.2 mm.—*12.* Ventral view of detached paratype body.—*13.* SEM view of juvenile shell, scale bar 1 mm.—*14.* Apical area of same specimen showing protoconch scar, scale bar 100 μm.—*15.* SEM view of radular ribbon, scale bar 40 μm.—*16.* SEM view showing rachidian, 4 laterals and tips of marginals, scale bar 4 μm.

Holotype. LACM 2313, *Alvin* dive 978 at type locality, 2 March 1979.

Paratypes. From 4 *Alvin* dives at type locality: dive 978, 13 specimens, LACM 2314, USNM 859939, MNHN; dive 1211, 1 specimen, USNM 859940; dive 1223, 26 specimens, LACM 2315, USNM 859941, MNHN; dive 1225, 4 specimens, USNM 859942. From 4 *Cyana* dives at East Pacific Rise at 13°N (12°48.6′N, 103°56.7′W), 2630-2635 m: dive 82-33, 3 specimens, MNHN; dive 84-38, 12 specimens, LACM 2317, USNM 859943; dive 83-41, 13 specimens, MNHN; dive 84-43, 1 specimen, MNHN.

Description. Shell (Figs. 17-19) of limpet form, produced through one half whorl of growth, large for family (maximum length 19.0 mm). Outline of aperture oblong



Figs. 17–23. *Nodopelta heminoda* sp.n., all from 21°N.—*17–19.* Holotype shell, exterior and interior (anterior at top) and lateral (right side views). Length 17.5 mm.—*20, 21.* Ventral and lateral (left side) views of paratype body in shell.—*22.* SEM view of radular ribbon, scale bar 100 μm.—*23.* SEM view showing rachidian, 4 laterals and tips of marginals, scale bar 40 μm.

oval, anterior slightly broader than posterior. Margin of aperture not in same plane, sides markedly raised relative to ends. All slopes except posterior convex, becoming flat toward margin in large specimens. Apex posterior, slightly right of midline, projecting, 7/8 shell length from anterior end. Protoconch scar dark brown, right side remaining visible; surface sculpture of protoconch unknown (juvenile shells not available). Early teleoconch growth lacking on posterior (columellar) slope until shell length of 2 mm; subsequent growth along posterior margin raises apex above margin. Periostracum strong, tightly adhering, light brown, inturned at shell edge. Background sculpture of fine radial and concentric ribs beaded at intersections, arising in early teleoconch. Noded sculpture arising at shell length of 4 mm; nodes prominent, large, projecting, crescent-shaped; nodes aligned in curved rows, lacking on posterior slope; development of nodes subdued at final growth stages. Shell interior with strong angular ridge posteriorly, interior surface glossy. Muscle scar relatively broad, extending anteriorly 2/3 shell length, tips expanded inwardly, inserting posteriorly on inner edge of angular ridge; left arm of scar extending slightly more anteriorly than right. Dimensions of holotype: length 17.5, width 11.9, height 6.6 mm.

External anatomy (Figs. 20, 21). Foot oval, rounded posteriorly, with opening of pedal gland at anterior end. Snout tapered, cephalic tentacles thick at base (contracted in present material), equal in size. Mantle margin with thin fold extending between shell and inturned periostracum, exposed surface of mantle margin with numerous transverse ridges, aligned perpendicular to edge. Epipodium a single row of faint tubercles. Mantle cavity extending more than half length of shell muscle; ctenidium bipectinate, lamellae elongate and broad, tips spatulate, free tip extending over head, afferent and efferent membranes pronounced, lamellae on left side of axis (uppermost) half as long as those on right side.

Radula (Figs. 22, 23) typical for family, cusps of rachidian and inner laterals relatively short, denticulation on outer side of fourth lateral fine, unlike that of marginals, nubs of laterals prominent, shafts of outer marginals fused.

Remarks. The original association of these limpets with the substratum was described as follows: "recovered from sulfide samples knocked loose from a 'black smoker'—edifices up to 6 m high with 350°C water exiting from the top. The samples were riddled with tubes and burrows, constructed by a polychaete called the Pompei worm by geologists. The limpets were found inside the surface furrows. The samples were collected from older parts of the black smoker—presumably well away from the superheated water." (William Smithey, *in litt.* 21 January 1980). All specimens have associated iron sulfide particles, the black particles visible in Figs. 20 and 21.

This is the largest member of the Peltospiridae, reaching a length of 19.0 mm, considerably larger than the maximum for *Rhynchopelta concentrica*, which reaches a maximum length of 12.6 mm. The exceptionally large size of this species may be correlated with the protection afforded by the burrows of the Pompei worm *Alvinella*.

Specimens from 13°N are of similar size as those from 21°N; no apparent differences were noted. Juvenile specimens have not been recognized; the smallest specimen examined (length 6.7 mm) came from 13°N.

The name is a Latin rendition of the vernacular name 'half-node', denoting the truncate, crescent-shaped nodes.

Nodopelta subnoda sp.n. (Figs. 24–31)

"Elongate tapersnout limpet", McLean 1985, p. 160.

Type locality. East Pacific Rise at 13°N (12°48.6′N, 103°56.7′W), 2630–2635 m.

Holotype. MNHN, *Cyana* dive 84-83 at type locality, 15 March 1984.

Paratypes. From 7 *Cyana* dives at type locality, dive 82-35, 2 specimens, MNHN; dive 82-36, 2 specimens, MNHN; dive 84-34, 2 specimens, MNHN; dive 84-38, 83 specimens, LACM 2317, USNM 859944; dive 84-41, 15 specimens, MNHN; dive 84-44, 1 specimen, MNHN; dive 84-46, 11 specimens, MNHN.

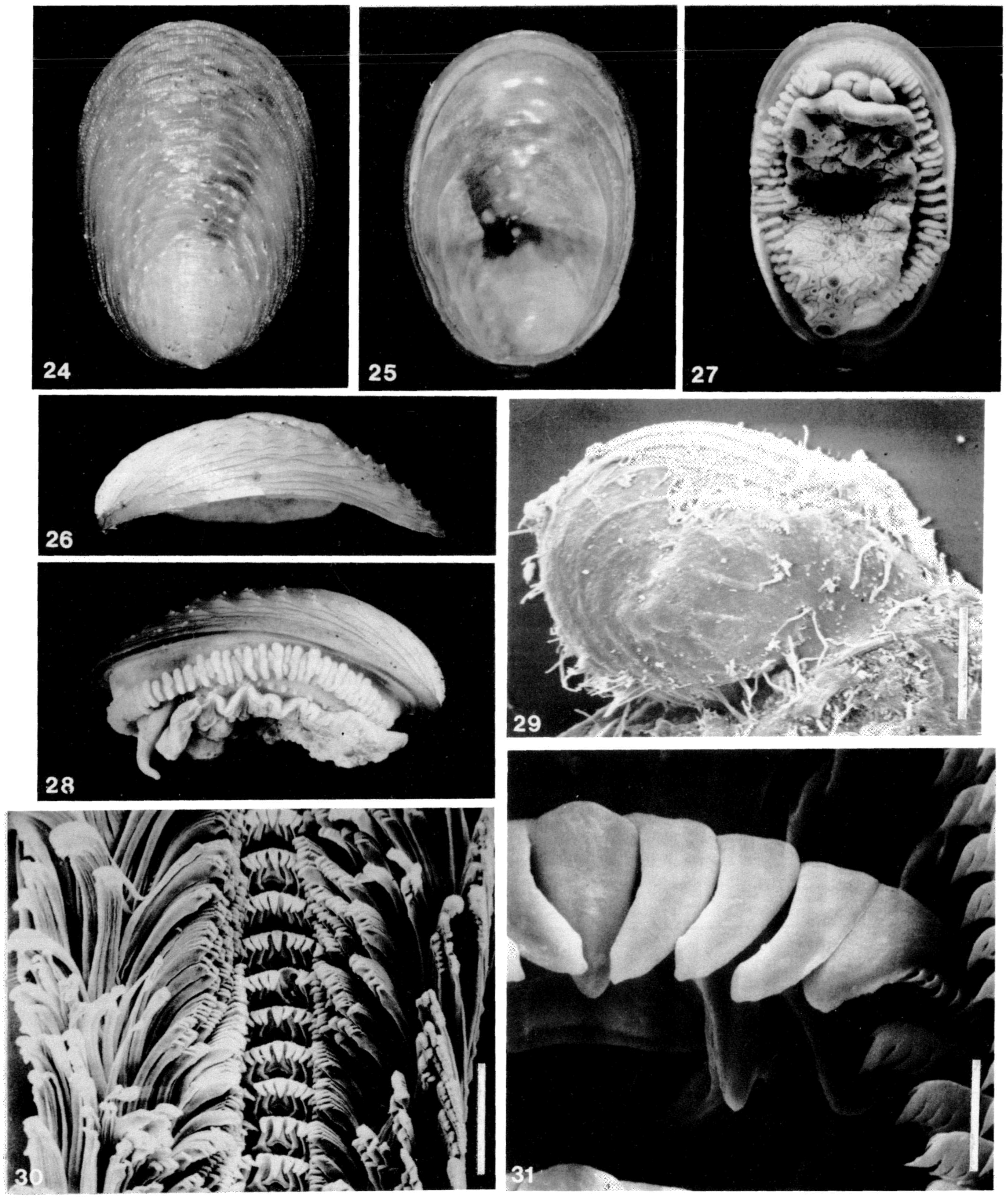
Description. Shell (Figs. 24-26) of limpet form, produced through one half whorl of growth, medium sized for family (maximum length 9.6 mm); outline oblong oval, anterior markedly broader than posterior. Margin of aperture not in same plane, sides markedly raised relative to ends. All slopes except posterior convex. Apex posterior, slightly right of midline, slightly above level of margin and projecting slightly beyond posterior margin. Protoconch dark brown, weakly or not calcified, diameter 160 μm, right side remaining visible, surface sculpture of longitudinal ridges (Fig. 29). Early teleoconch growth lacking on posterior (columellar) slope at all growth stages. Periostracum strong, tightly adhering, light brown, inturned at shell edge, greatly thickened at posterior margin where it not only envelops shell edge but extends nearly to level of protoconch. Background sculpture of fine radial and concentric ribs, beaded at intersections, arising in early teleoconch. Noded sculpture arising at shell length of 4 mm; nodes represented by narrow, alternating, longitudinal swellings along line of growth; nodes aligned in curved rows. Shell interior with strong angular ridge posteriorly, interior surface glossy. Muscle scar relatively broad, close to edge of shell, extending anteriorly 2/3 shell length, tips expanded inwardly and tapered anteriorly, inserting posteriorly on inner edge of angular ridge; left arm of scar extending slightly more anteriorly than right. Dimensions of holotype: length 9.5, diameter 6.7, height 3.2 mm.

External anatomy (Figs. 27, 28). Foot oval, rounded posteriorly; anterior pedal gland not conspicuous. Snout tapered, cephalic tentacles thick at base (contracted in present material), equal in size. Mantle margin with thin fold extending between shell and inturned periostracum, exposed surface of mantle edge with numerous transverse ridges, aligned perpendicular to mantle edge. Epipodium a single row of projecting tubercles. Mantle cavity extending to half depth of muscle; ctenidium bipectinate, lamellae elongate and broad, tips spatulate, free tip extending over head, afferent and efferent membranes pronounced, lamellae on left side of axis (uppermost) half as long as those on right side.

Radula (Figs. 30, 31) typical for family, cusps of rachidian and laterals long, curved inwardly; nubs of laterals prominent; denticulation on outer edge of fourth lateral like that of marginals; outer marginals not prominently fused.

Remarks. Nodopelta subnoda is about half the size of *N. heminoda*, but differs chiefly in having almost no posterior slope, which places the apex at the level of the margin and slightly overhanging it. Also, the nodes of *N. subnoda* are narrower and lack the swelling that precedes the nodes of *N. heminoda*. The radula of *N. heminoda* is like that of most limpet members of the family, differing from that of *N. heminoda* in having longer cusps on the rachidian and laterals and having the dentition on the outer edge of the fourth lateral matching that of the marginals.

Specimens of *N. subnoda* have adhering iron sulfide particles and it is likely that the species is also associated with the Pompei worm *Alvinella* in its habitat at 13°N. Juvenile shells have not been examined, which is also the case for *N. heminoda*. The smallest shell in the present material is 7.5 mm in length.



Figs. 24–31. Nodopelta subnoda sp.n., from 13°N.—*24–26.* Holotype shell, exterior and interior (anterior at top) and lateral (right side) views. Length 9.5 mm.—*27, 28.* Ventral and lateral (right side) views of paratype body in shell.—*29.* Protoconch from right side, scale bar 40 μm.—*30.* SEM view of radular ribbon, scale bar 100 μm.—*31.* SEM view showing rachidian, 4 laterals and tips of marginals, scale bar 10 μm.

Rhynchopelta gen.n.

Type species. Rhynchopelta concentrica sp.n.

Diagnosis. Shell of limpet form, apex projecting, close to posterior margin, interior with strong posterior ridge. Periostracum thick, enveloping shell edge. Sculpture of radial striae and fine concentric ridges that bifurcate. Periostracum with longitudinal ridges.

External anatomy. Mantle edge with thin fold extending under periostracum, exposed surface of mantle edge puckered; epipodium a single row of low tubercles.

Radula typical for family, cusps of racchidian and laterals long, nubs of laterals prominent, denticulation on outer edge of fourth lateral like that of marginals, outer laterals fused.

Remarks. A monotypic genus for the species *Rhynchopelta concentrica* is proposed on the combination of unique sculpture and the condition of the mantle margin and epipodium. The mantle margin does not have the pronounced transverse ridges of *Nodopelta*, and the epipodium is the least developed in the five limpet genera. The name means snout-shield—to make reference to 'tapersnout', the vernacular name previously used for this family (McLean 1985).

Warén & Bouchet (1989) noted that two species of the coiled genus *Lirapex* share longitudinal ridges on the protoconch similar to that of *Rhynchopelta concentrica* and on that basis considered the two genera to be more closely related than to other peltospirids.

Rhynchopelta concentrica sp.n. (Figs. 32–40)

"Concentric tapersnout limpet"; McLean 1985, p. 160.
"Unnamed limpet"; Turner *et al.* 1985, p. 172, figs. 5a–c.
"Concentric Group-A species"; Berg 1985, p.192.

Type locality. East Pacific Rise at 21°N (20°50.0′N, 105°06.0′W), 2615–2622 m.

Holotype. LACM 2318, *Alvin* dive 1214 at type locality, 20 April 1982.

Paratypes. From 4 *Alvin* dives at type locality: dive 1214, 288 specimens plus 33 juvenile specimens, LACM 2319, USNM 859945, MNHN; dive 1219, 7 specimens plus 3 juvenile specimens, USNM 859946; dive 1221, 8 specimens, USNM 859947; dive 1223, 2 specimens, USNM 859948. From 3 *Cyana* dives at East Pacific Rise at 13°N (12°48.6′N, 103°56.7′W), 2630–2635 m: dive 84-39, 11 specimens, MNHN; dive 84-41, 4 specimens, MNHN; dive 84-42, 159 specimens, LACM 2320, USNM 859949, MNHN.

Description. Shell (Figs. 32–36) of limpet form, produced through one half whorl of growth, relatively large for family (maximum length 12.6 mm); outline of aperture evenly elliptical; anterior slope convex, posterior slope concave, lateral slopes convex but concave near margin; highest point of shell 2/3 distance from anterior margin. Margin of aperture nearly in same plane, sides slightly raised relative to ends. Apex posterior, on mid-dorsal line, 9/10 shell length from anterior margin. Protoconch (Figs. 37, 38) brown, diameter 225 μm, with strong ridges perpendicular to lip, right side of protoconch remaining visible. Early teleoconch growth lacking on posterior slope until shell length of 2 mm; subsequent growth along posterior margin raises apex above margin. Periostracum thin but tightly adhering, faintly yellow-green, inturned at shell edge. Early sculpture of teleoconch nearly smooth for first millimeter of length; mature sculpture of extremely fine concentric ridges that bifurcate along lateral slope so that there are more ridges on anterior slope than on lateral slopes. Radial sculpture fine and overriding concentric sculpture, under magnification appearing evenly clathrate. Shell interior white, showing fine lamellar pattern under magnification. Interior with sharp, angular posterior ridge. Muscle scar relatively broad anteriorly, narrowed posteriorly; muscle inserting on inner side of angular ridge. Dimensions of holotype: length 11.0, width 8.3, height 4.1 mm.

External anatomy (Figs. 35, 36). Foot oval, rounded posteriorly, opening of anterior pedal gland not prominent. Snout with tapered tip. Mantle edge with thin fold extending between shell and inturned periostracum, exposed surface thick, puckered, having no apparent elaboration. Epipodium a row of very faint, retracted tubercles, extending forward to lateral extremities of foot, with a more prominent pair of tubercles close together posteriorly. Mantle cavity deeper than half length of shell muscle limb; ctenidium bipectinate, gill lamellae of left (dorsal) side half length of right (ventral) side; gill lamellae of free tip broad and thick on right side.

Radula (Figs. 39,40) as described above for genus.

Remarks. Rhynchopelta concentrica is not easily confused with any other limpet, considering its unique shell sculpture, protoconch sculpture of longitudinal ridges, reduced epipodium and lack of modification to the mantle margin.

Specimens from 13°N collected by the *Cyana* were as robust as those from 21°N and no differences were detected. The "unknown organism" mentioned by McLean (1988*a*) on *Lepetodrilus* species and Warén & Bouchet (1989) on some species of coiled peltospirid species is also prevalent on *Rhynchopelta concentrica* from 13°N. Berg (1985) gave data on egg dimensions for this species.

This species is clearly associated with the vestimentiferan *Riftia pachyptila*, as relatively large numbers of specimens were recovered from '*Riftia* washings', from *Alvin* dive 1214. Iron sulfide particles are absent, unlike the condition for most of the other peltospirid limpets, in which the sulfide particles indicate an affinity with the sulfide crust deposits.

Although the above mentioned count of 288 mature specimens from *Alvin* dive 1214 suggests that this species is relatively common, it is much less abundant than two lepetodrilid limpets associated with *Riftia*. Counts of *Lepetodrilus pustulatus* and *L. elevatus* at dive 1214 were 1853 and 14,574, respectively (McLean 1988*a*).

Echinopelta gen.n.

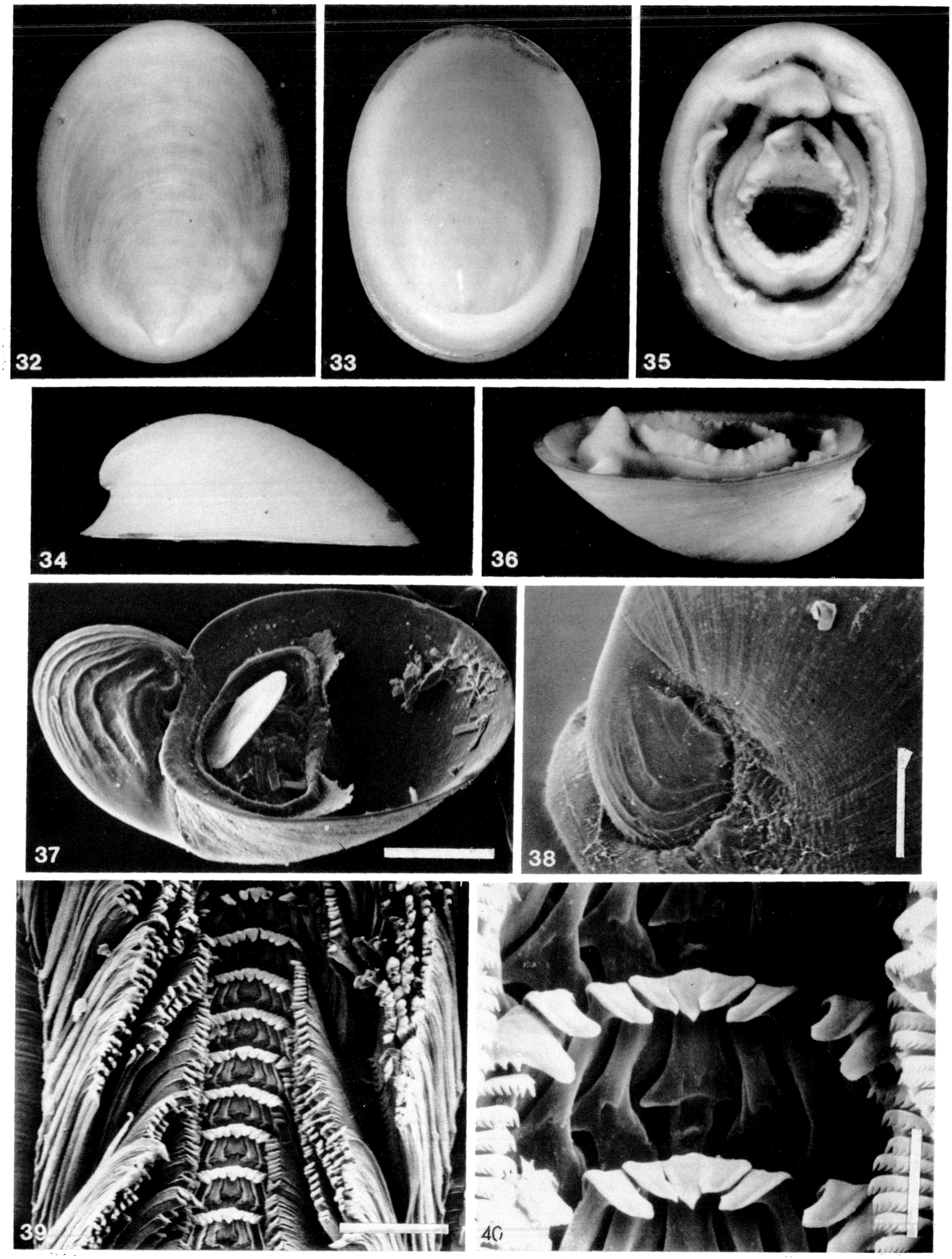
Type species. Echinopelta fistulosa sp.n.

Diagnosis. Shell of limpet form, apex close to posterior margin but left of center; interior with strong posterior ridge. Periostracum thick but only slightly enveloping shell edge. Sculpture finely pustular with spaced tubular spines.

External anatomy. Mantle edge unmodified, epipodial ridge extending anteriorly to position of muscle extension, projecting, bearing numerous elongate tentacles.

Radula typical for family, cusps of rachidian and laterals long, nubs of laterals moderately prominent; denticulation of outer edge of fourth lateral like that of marginals, shafts of marginals fused.

Remarks. Although the sculptural elements of *Echinopelta fistulosa* could qualify for inclusion in *Nodopelta*, and it shares the angular ridge of the interior and the tips of the muscle scar broader on the inside, this



Figs. 32–40. Rhyncopelta concentrica sp.n., all from 21°N.—*32–34*. Holotype shell, exterior and interior (anterior at top) and lateral (right side) views. Length 11.0 mm.—*35, 36*. Ventral and lateral (right side) views of paratype body in shell.—*37*. Early juvenile showing ridged protoconch and operculum, scale bar 100 μm.—*39*. SEM view of radular ribbon, scale bar 100 μm.—*40*. SEM view showing rachidian, 4 inner laterals and tips of marginals, scale bar 20 μm.

genus differs from the other peltospirid limpet genera in having the following unique characters: periostracum with slight wrapping around shell edge, apex displaced to left of midline and hollow spines. The epipodial development is most like that of *Peltospira*, although the epipodial processes are far less prominent. Intact protoconchs have not been observed.

The generic name is a Latin compound meaning spiny-shield.

***Echinopelta fistulosa* sp.n.** (Figs. 41–48)

"Archaeogastropod limpet"; Turner & Lutz 1984, p. 61, fig. 10.
"Tube-spine tapersnout limpet"; McLean 1985, p. 160.
"Limpet"; Baross & Deming 1985, p. 359, figs. 6a, b.

Type locality. East Pacific Rise at 21°N (20°50.0′N, 105°06.0′W), 2615–2622 m. Associated with *Alvinella* on black smokers.

Holotype. LACM 2321, *Alvin* dive 982 at type locality, 6 November 1979.

Paratypes. From 3 *Alvin* dives at type locality: dive 982, 9 specimens, LACM 2322, USNM 859950, MNHN; dive 1223, 12 specimens, LACM 2323, USNM 859951, MNHN; dive 1226, 4 juvenile specimens, LACM 2324, USNM 859952.

Description. Shell (Figs. 41–43) of limpet form, produced through one half whorl of growth, size medium for family (maximum length 8.8 mm). Outline of aperture elongate oval, sides nearly parallel, anterior slightly narrower than posterior; margin of aperture nearly in same plane, sides slightly raised relative to ends. Apex left of center, close to posterior margin. Protoconch scar (Fig. 46) dark brown, right side exposed, protoconch sculpture unknown. Early teleoconch growth lacking on posterior (columellar) slope until shell length of 2 mm; subsequent growth along posterior margin raises apex slightly above margin. Periostracum thin, only slightly extending over growing edge; large specimens coated with rust colored iron deposits. Background sculpture arising after shell length of 2 mm, of concentric growth ridges that produce crescent-shaped swellings aligned obliquely. Sculpture of spines arising at teleoconch length of 0.5 mm; spines twice as high as basal diameter, spaced 0.5 mm apart, obliquely aligned. Spines appear early on juvenile shell with nearly same strength as those produced at growing edges of large shells. Shell interior deeply pitted at position of major spines, indicating that spines are hollow. Shell interior with angular ridge posteriorly. Muscle scar narrow throughout, close to shell margin; narrowed but not interrupted posteriorly, anterior tips expanded inwardly, inserting on inner surface of angular ridge posteriorly; left arm of scar slightly longer than right. Dimensions of holotype: length 5.9, diameter 4.4, height 1.6 mm.

External anatomy (Fig. 44). Foot oval, with opening of anterior pedal gland, bluntly tapered posteriorly. Snout tapered, cephalic tentacles equal in size, thick at base (contracted in all specimens). Mantle edge unmodified. Epipodial ridge extending anteriorly to position of muscle extension, projecting, bearing numerous elongate tentacles. Mantle cavity extending to 1/3 depth of shell muscle, ctenidium with afferent and efferent membranes.

Radula (Figs. 47, 48) as described above for genus.

Remarks. Echinopelta fistulosa is not easily confused with any other hydrothermal vent limpet. It is unique in its sculpture of hollow spines, absence of the inturned periostracum and the left of center position of the apex in mature shells. In juvenile shells (Fig. 45), the apex is positioned to the right of center, as is true of mature shells in other species in the family.

Baross & Deming (1985, p. 359, figs. 6a, b) illustrated the shell of *Echinopelta fistulosa*, noting in the caption that this is the "most common limpet on outer face of active 'black smoker' at 21°N." This agrees with the finding that specimens are choked with iron sulfide particles (Fig. 44). They also noted that the exterior surfaces of these limpets were heavily colonized by microorganisms, which they illustrated in their figs. 7a–e.

This is the only peltospirid limpet known only from the East Pacific Rise at 21°N. The name means 'full of pipes', referring to the hollow spines.

***Hirtopelta* gen.n.**

Type species. Hirtopelta hirta sp.n.

Diagnosis. Shell of limpet form with laterally compressed sides; sides raised relative to ends; apex posterior. Periostracum shaggy, not enveloping shell edge. Background sculpture finely pustular, with larger, scattered collabral imbrications. Operculum multispiral, large.

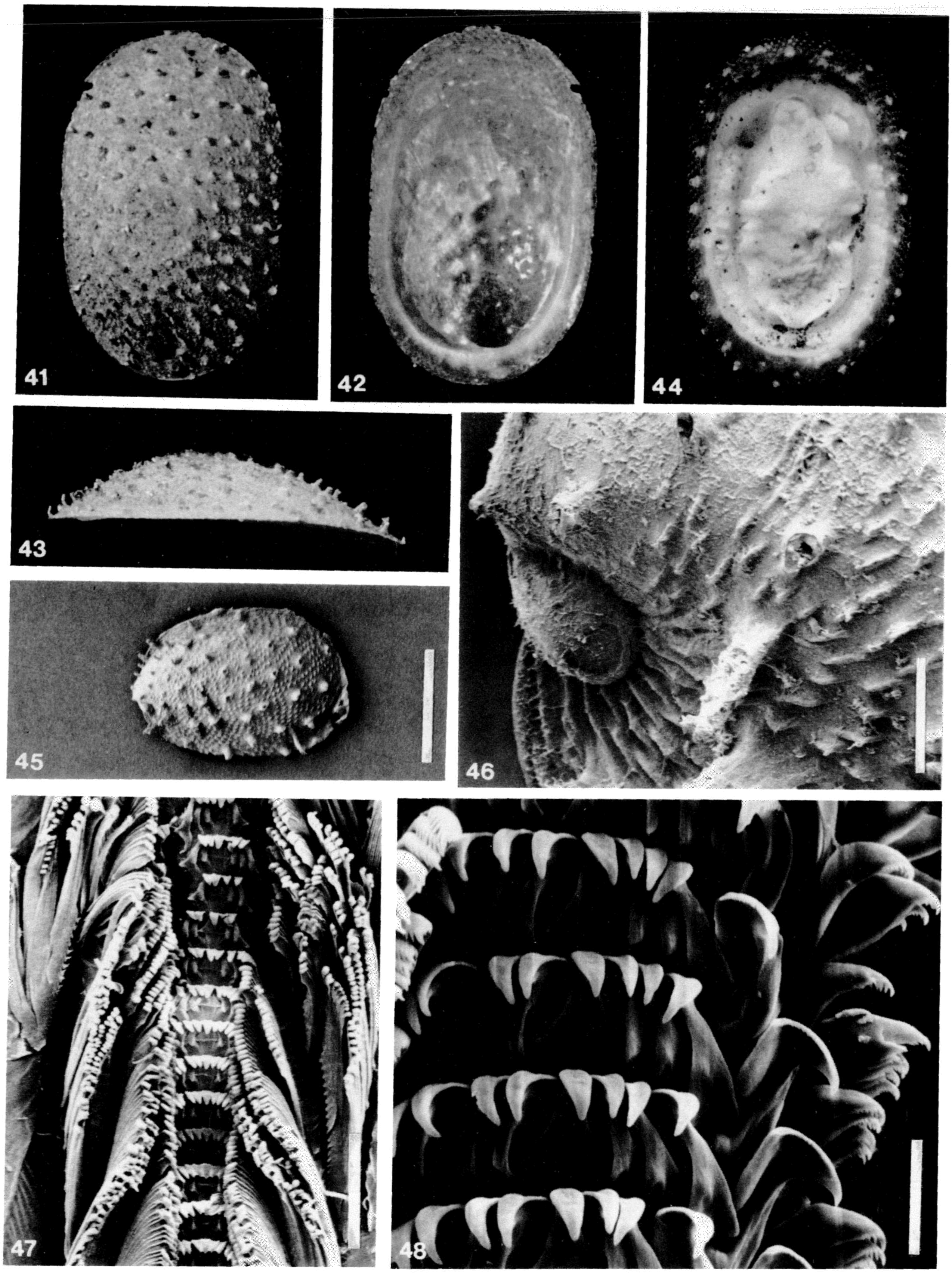
External anatomy. Mantle edge simple, epipodial ridge projecting, extending to head, bearing low tubercles. Snout not tapered, terminating in oral disc. Ctenidium exceptionally large.

Radula unusual for family, cusps of rachidian and laterals long, finely and sharply serrated on inner and outer edges; marginals with fine denticulation to match serration of laterals. Nub on shaft of laterals not evident.

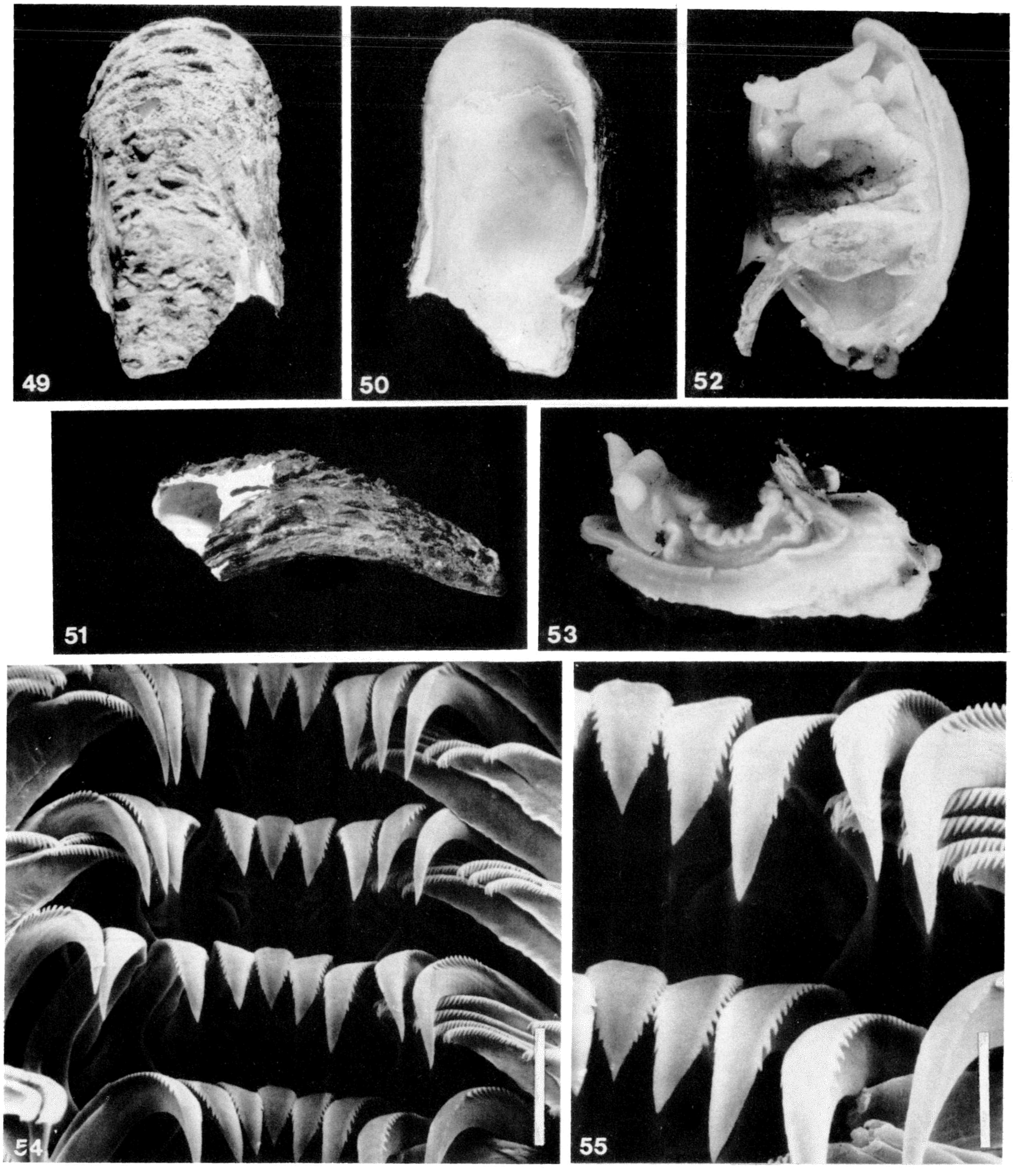
Remarks. This monotypic genus is based on an imperfectly known species, as shells of the two known specimens were badly damaged. Although one other species, *Peltospira operculata*, has a relatively large operculum, *Hirtopelta* has a much simpler development of the epipodium and a completely different mode of shell sculpture. *Hirtopelta* is also unique in having laterally compressed sides, although there is a possibility that the incomplete holotype is deformed.

The radula has the basic features of the peltospirid plan, but is the most unusual among the peltospirid limpets in having the cusps of the rachidian and laterals sharply serrate on both edges, with the marginals displaying a similar pattern. This radula is comparable to that illustrated by Warén & Bouchet (1989, figs. 28, 29) for *Pachydermia laevis* and undoubtedly indicates a close relationship between the two species, although shells seem to have no features in common.

This species also differs from the other peltospirid limpets in having a broad tip to the snout, rather than the tapered tip that led to the vernacular name 'tapersnout' for the family. The snout of *Pachydermia laevis* is shown



Figs. 41–48. Echinopelta fistulosa sp.n., from 21°N.—*41–43*. Holotype shell, exterior and interior (anterior at top) and lateral (right side) views. Length 5.9 mm.—*44*. Ventral view of paratype body in shell.—*45*. SEM view of juvenile shell showing early sculpture, scale bar 1 mm.—*46*. Apical area of same specimen showing protoconch scar, scale bar 100 μm.—*47*. SEM view of radular ribbon, scale bar 100 μm.—*48*. SEM view showing rachidian, 4th lateral and inner marginals folded back, scale bar 20 μm.



Figs. 49–55. Hirtopelta hirta sp.n., from 13°N.—*49–51.* Holotype shell, exterior and interior (anterior at top) and lateral (right side) views. Length 11.5 mm (incomplete).—*51, 52.* Ventral and right side views of holotype prior to sectioning, note torn operculum.—*54.* SEM view of central portion of radular ribbon, scale bar 20 μm.—*55.* SEM view of rachidian, 4 laterals and inner marginals, scale bar 10 μm.

relatively broad by Warén & Bouchet (1989, fig. 34). However, *P. laevis* is said to have a relatively small gill, unlike the large gill of *H. hirta*. Differences in snout morphology and radular morphology are indicative of feeding differences between this genus and other peltospirid genera. Anatomical studies may show that this is a family level difference.

The name means shaggy-shield, referring to the coarseness and irregularity of the sculptural elements.

Hirtopelta hirta **sp.n.** (Figs. 49–55)

"Haliotiform tapersnout limpet"; McLean 1985, p. 160.

Type locality. East Pacific Rise at 13°N (12°48.6′N, 103°56.7′W), 2630–2635 m.

Holotype and paratype. MNHN, *Cyana* dive 82-35 at type locality, 12 March 1982. 2 broken specimens only; the larger holotype specimen preserved with nearly intact body (Figs. 52, 53), subsequently sectioned for study by V. Fretter; body of the smaller specimen the head end only (used for radular preparation).

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 narrrow 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.

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