

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

JAMES H. MCLEAN

Accepted 25 February 1988

McLean, J. H. 1989. New archaeogastropod limpets from hydrothermal vents: new family Peltospiridae, new superfamily Peltospiracea.—*Zool. Scr.* 18: 49–66.

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*.

James H. McLean, Los Angeles County Museum of Natural History, 900 Exposition Blvd, Los Angeles, CA 90007, U.S.A.

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, 1988b). 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 1988b).

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 discussed 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 submersibles.

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'Océanographie Biologique, Brest, France, and sent to P. Bouchet at the Muséum National d'Histoire 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. Latero-marginal 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 auran-tiaca* (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 distin-

guished from lepetodrilid limpets (McLean 1988a) 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 | <i>Echinopelta</i> |
| Sculpture of scattered nodes | 3 |
| 3. Nodes crescent shaped | <i>Nodopelta</i> |
| Nodes irregular, elongate | <i>Hirtopelta</i> |
| 4. Sculpture of axial ridges on early teleoconch | <i>Peltospira</i> |
| Sculpture of fine concentric ridges | <i>Rhynchopelta</i> |

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 concur-

rently 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 pompeii worm *Alvinella*.

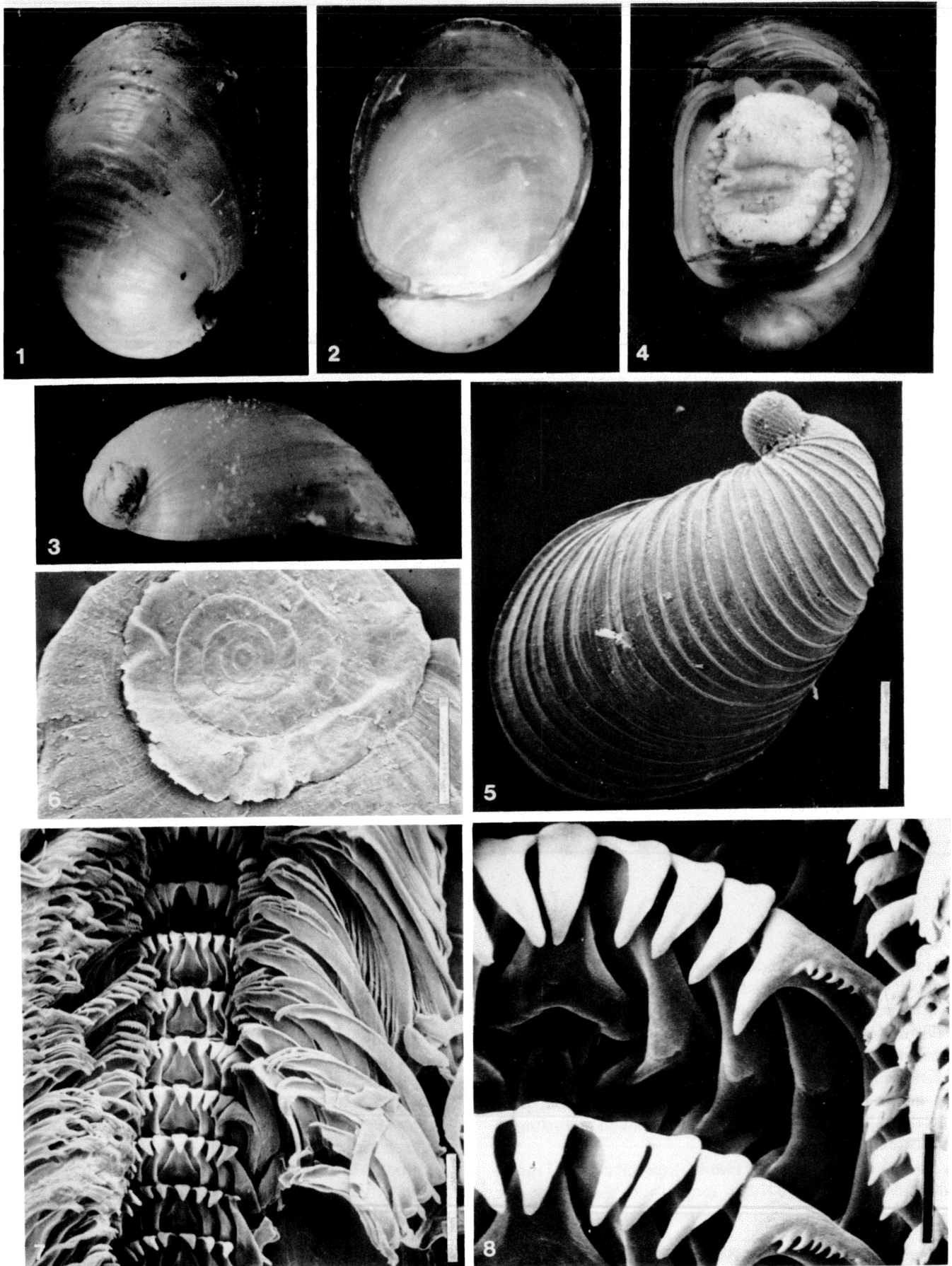
Holotype. LACM 2307, *Alvin* dive 1213 at type locality, 19 April 1982.

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 than 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 μ m.—6. SEM view of operculum, scale bar 400 μ m.—7. SEM view of radular ribbon, scale bar 40 μ m.—8. SEM view showing rachidian, 4 laterals and tips of marginals, 4th lateral with denticulation matching that of marginals, scale bar 10 μ m.

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 “*Calypptogena* 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 μ m (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 than 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.).

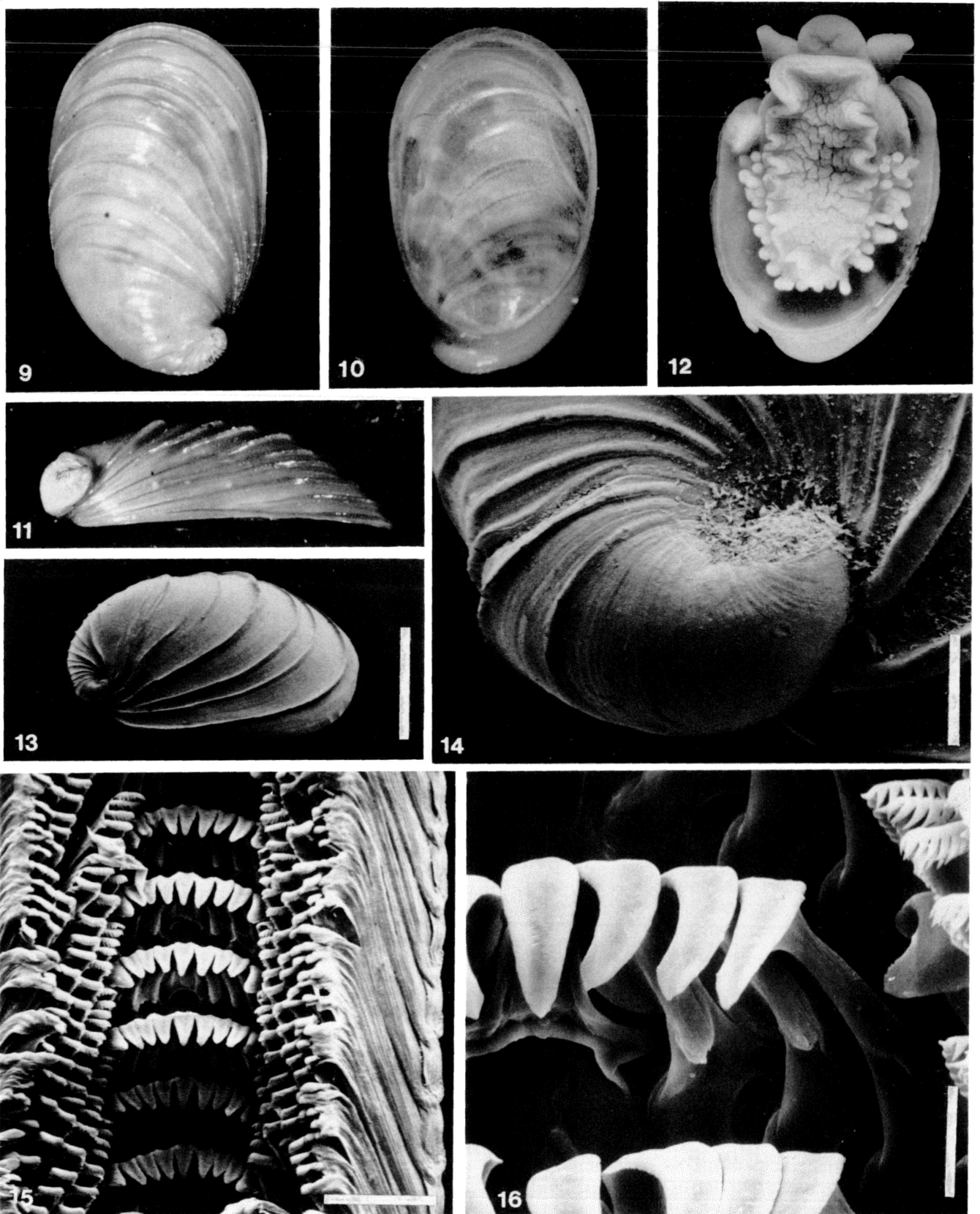
Although there is a major size difference between the two species *Nodopelta heminoda* and *N. subnoda*, they have a clear affinity in sharing sculptural and mantle margin characters. The two species differ in radular characters, as detailed in the comparisons under each species. The protoconch is known 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 μ m.—15. SEM view of radular ribbon, scale bar 40 μ m.—16. SEM view showing rachidian, 4 laterals and tips of marginals, scale bar 4 μ m.

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