Neolepetopsidae, a new docoglossate limpet family from hydrothermal vents and its relevance to patellogastropod evolution

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(With 12 plates and 1 figure in the text)

Six new species of limpets from hydrothermal vents at spreading centres, hydrothermal vents on seamounts, or cold sulphide seeps are described in three new genera in the new family Neolepetopsidae. Anatomy is detailed separately by V. Fretter (1990). The family is considered to be a living descendant of the Palaeozoic-Mesozoic family Lepetopsidae (proposed herein), based on *Lepetopsis* Whitfield, 1882. Both families are placed in the new superfamily Lepetopsacea, new suborder Lepetopsina, order Patellogastropoda.

New genera and species are: *Neolepetopsis*, type species *N. gordensis*, from the Gorda Ridge, and three additional species: *N. densata*, from an active sulphide chimney near 12° N on the East Pacific Rise, *N. verruca* from a sulphide chimney near 21° N on the East Pacific Rise, and *N. occulta* from hydrothermal vents on the caldera floor of Green Seamount near 21° N; *Eulepetopsis*, type species *E. vitrea*, from hydrothermal vents at the Galapagos Rift and the East Pacific Rise near 21°, 13° and 11° N; *Paralepetopsis*, type species *P. floridensis*, from cool, hypersaline, sulphide seeps at the base of the continental slope off the west coast of Florida.

Inclusion in Patellogastropoda is indicated by plesiomorphic characters: symmetrical shell lacking coiled phase, no epipodium in adult, single dorsally arched jaw, docoglossate dentition with a licker below the tip of the radula, both left and right kidney, and gonad discharging through right kidney.

The radula differs from that of other patellogastropods in having the denticle caps delicate and non-mineralized, the shafts articulating with shafts and cusps of adjacent teeth in the row and with those in adjacent rows, and in having some capacity for longitudinal bending. The rachidian is well developed; the first two pairs of lateral teeth are regarded as homologues of the inner lateral teeth of *Patella*; the third lateral tooth is larger than the others and is considered a modified pluricuspid tooth; there are two pairs of plate-like marginals. Tooth morphology differs in each genus but all have a very long second lateral with a strong mid-shaft nub to articulate with the overhanging edge of the pluricuspid.

The neolepetopsid radula is interpreted as close to that of the patellogastropod archetype except for its lack of mineralization and reduction in the number of marginal teeth. The radula in living docoglossate outgroups (chitons and monoplacophorans) is mineralized and the teeth are articulating. Articulating teeth are therefore regarded as plesiomorphic in patellogastropods.

I speculate that articulating teeth may have been characteristic of Palaeozoic and early Mesozoic patellogastropods and that the non-articulating, straight-shafted and rapidly replaced teeth of extant Patellina may have arisen in the Mesozoic, a time at which patellogastropods of modern appearance underwent a radiation in shallow-water habitats.

Contents

Introduction

The recently discovered hydrothermal vent communities of the eastern Pacific have produced a number of new groups of high taxonomic rank and probable archaic origin (Newman, 1985; McLean, 1985). Among the new high-level taxa, the new families and superfamilies of archaeogastropod limpets have enabled the offering of new ideas about gastropod phylogeny, and engendered some controversial interpretations (McLean, 1981; Haszprunar, 1988a). Here I give the formal descriptions of a docoglossate group of limpets from hydrothermal vents and discuss the possible contribution of this group toward understanding the evolution of patellogastropod limpets.

The hydrothermal-vent habitat of the eastern Pacific has now been known for over a decade, following its initial discovery at the Galapagos Rift in 1977 (Lonsdale, 1977). Limpets from this habitat are tentatively assigned to eight families in seven superfamilies (McLean, 1988b). To date the following new superfamilies and families have been described: Neomphalacea, family Neomphalidae (McLean, 1981), anatomy described by Fretter, Graham & McLean (1981); Pyropeltidae in the existing cocculiniform superfamily Lepetellacea (McLean & Haszprunar, 1987); Lepetodrilacea, families Lepetodrilidae and Gorgoleptidae (McLean, 1988a), anatomy treated by Fretter (1988); Peltospiracea, family Peltospiridae (McLean, 1989a), anatomy studied by Fretter (1989). New slit-limpets of the superfamilies Scissurellacea and Fissurellacea have been treated by McLean (1989b) and Haszprunar (1989).

Six new species in three new genera of the new family Neolepetopsidae in the new superfamily Lepetopsacea are described herein. This family has earlier been referred to by Hickman (1983) as the "Group-C" limpets and by McLean (1985) as the "symmetrical" hydrothermal vent limpets. Unlike all other hydrothermal vent limpets (except Pyropeltidae), the shell is symmetrical, lacking an asymmetrically coiled juvenile phase.

Only brief information about the anatomical characters of the group is given here, as a detailed report on the anatomy in this group is soon to follow (Fretter, 1990). An earlier report that the heart is lacking (McLean, 1985) is no longer supported (Fretters, pers. comm.).

Hickman (1983) illustrated the radula of the species described here as *Eulepetopsis vitrea*, concluding that the radula did not fit into the standard classification of radular types. I have previously stated that the radula of these limpets provides no clues to relationships (McLean, 1985), but here I argue that this is a modified patellogastropod radula. A preliminary indication of the possible significance of this radula is mentioned (as a communication from me) by Haszprunar (1988a).

Protoconchs of neolepetopsid limpets are shed at a very early stage and were not available to Turner & Lutz (1984), Turner, Lutz & Jablonski (1985), and Lutz *et al.* (1986), who illustrated protoconchs typical of other hydrothermal-vent gastropods and limpets. Protoconchs of neolepetopsid limpets are figured here for the first time.

Newman (1985) estimated that some of the invertebrates of the hydrothermal-vent fauna are relics of the Palaeozoic and Mesozoic age, based on rank of endemism above the species level, geological record, and distribution. In earlier accounts of the newly discovered superfamilies Neomphalacea, Lepetodrilacea, and Peltospiracea (McLean, 1981, 1988a, 1989a), I could only surmise that the ancestors of those groups had an archaic origin. In the present case, however, there is better (though still speculative) evidence for a fossil record of a direct limpet ancestor.

Materials and methods

Neolepetopsid limpets are known from most of the major sites from which other hydrothermal vent limpets have been reported in the eastern Pacific. These are the Galapagos Rift and 2 major sites on the East Pacific Rise, near 21° N and 13° N, and a third, recently visited site near 11° N on the East Pacific Rise. One species is also known from the Gorda Ridge, first visited in 1988.

Unlike all other hydrothermal vent limpets previously described, which are restricted to hydrothermal spreading zones, one species of neolepetopsid limpet, *Paralepetopsis floridensis*, has been collected at a cold, hypersaline sulphide seep, at the base of the Florida Escarpment, where it is the only limpet species known, and one species, *Neolepetopsis occulta*, has been collected at a warm sulphide vent on a submarine volcano close to the East Pacific Rise near 21° N, where it too is the only limpet reported.

Neolepetopsid limpets have not been collected at 2 other East Pacific sites at which other limpet families are known, the Guaymas Basin and the Juan de Fuca Ridge. Earlier (McLean, 1985) I reported that one member of the Group-C limpets from the Guaymas Basin had a high profile, but the single specimen of that species was subsequently described as the pyropeltid lepetellacean *Pyropelta corymba* (McLean & Haszprunar, 1987).

The earliest discovered vent field, the Galapagos Rift, was first visited in February, 1977 (*Alvin* dives 723–733), and subsequently in January–February, 1979 (*Alvin* dives 877–896), and November–December, 1979 (*Alvin* dives 983–993). The initial account of the biota at the Galapagos Rift was given by Corliss *et al.* (1979). Hessler & Smithey (1983) discussed ecological relationships at the Galapagos Rift. A total of 7 limpet species was reported from the Galapagos Rift by McLean (1985), including the broadly distributed species described here as *Eulepetopsis vitrea*.

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, Smithey & Keller (1985) discussed ecological relationships. Fourteen limpet species were reported at 21° N (McLean, 1985); 2 of these are neolepetopsid species described herein: *Eulepetopsis vitrea* and *Neolepetopsis verruca*. The latter species has been collected only once at 21° N.

Green Seamount near 21° N was visited in February, 1982 (*Alvin* dive 1185), the only locality for *Neolepetopsis occulta*. Collection of the limpet was mentioned by Levin & Lonsdale (1983); further information about the habitat was given by Levin & Nittrouer (1987).

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 to 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 one is the broadly distributed *Eulepetopsis vitrea*.

The Florida Escarpment site was first visited in March, 1984 (*Alvin* dives 1342 to 1348), and again in October, 1986 (*Alvin* dives 1753 to 1759). The initial account is that of Paull *et al.* (1984), followed by further reports by Hecker (1985), Paull & Neumann (1987) and Commeau *et al.* (1987). The new limpet *Paralepetopsis floridensis* is known only from the Florida Escarpment site.

Jones *et al.* (1985) gave station data for all dives made by the *Alvin* and *Cyana* through 1985.

Two sites visited for the first time in 1988 also produced 2 more species of neolepetopsids: the type lot of *Neolepetopsis densata* was collected during an expedition to the East Pacific Rise near 12° N, *Alvin* dive 2003, in March, 1988. *Eulepetopsis vitrea* was also recorded from the same expedition. The Gorda Ridge was first sampled in June, 1988 (*Alvin* dives 2033–2044) and again in September, 1988 (U.S. Navy *Sea Cliff* dive 764). *Neolepetopsis gordensis* is as yet endemic to the Gorda Ridge. Van Dover, Grassle & Boudrias (1990) gave an account of the biological community.

Limpet specimens were collected with mechanical arms of the submersibles in the course of collecting substratum samples and general collecting of all organisms. Material was preserved upon reaching the surface and was originally fixed for 24 hours in 10% sea water 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 taken by expeditions of the *Alvin* were sorted and counted at Woods Hole Oceanographic Institution, following which the limpets were sent to me. Specimens collected by the *Cyana* expeditions were sorted at the Centre National de Tri d'Oceanographie Biologique, Brest, France, and sent to P. Bouchet at the Muséum National d'Historie Naturelle, Paris, and subsequently loaned to me.

Radulae were extracted from preserved specimens after dissolution of tissues with 10% NaOH for 48 hours, either air dried and coated with gold palladium for SEM examination, or mounted in non-resinous stain mountant (Turtox CMC-S) for light microscopy. Protoconchs and juvenile shells were examined with SEM. Protoconch lengths were taken directly from scale indications for the SEM micrographs. Specimens of *Paralepetopsis floridensis* and *Eulepetopsis vitrea* that had been preserved with the radula protruding were critical-point dried for SEM with shell attached.

Fossil specimens of *Lepetopsis* were examined at the National Museum of Natural History.

Repositories of the major series of type material are the Los Angeles County Museum of Natural History (LACM) and the United States National Museum (USNM). All figured specimens are deposited at the LACM.

Systematic descriptions
Superorder ARCHAEOGASTROPODA Thiele, 1929

Recent authors (Salvini-Plawen, 1980; Salvini-Plawen & Haszprunar, 1987; Haszprunar, 1988*a*, *b*; Hickman, 1988) have discussed the problems inherent in the 'archaeogastropod' concept, pointing out that Archaeogastropoda, as traditionally constituted (Thiele, 1929; Knight *et al.*, 1960), represents a grade. I follow Haszprunar (1988*a*, *b*) in a philosophy of classification that allows Archaeogastropoda to be expressly indicated in the classification as an orthophyletic grade and Patellogastropoda as a clade.

Order PATELLOGASTROPODA Lindberg, 1986

The docoglossan limpets have been regarded by most recent authors (e.g. Golikov & Starobogatov, 1975; Lindberg, 1986*b*; Haszprunar, 1988*c*, 1989) as differing from other archaeogastropods at the subclass or ordinal rather than subordinal level. Lindberg (1986*a*, *b*) has introduced a new ordinal name Patellogastropoda, to replace such subordinal names as Docoglossa Troschel, 1866, Patellina von Ihering, 1876, and other less well known names listed by Knight *et al.* (1960: 231). The name Patellogastropoda is more appropriate than Docoglossa, in that the adjective docoglossate applies to a type of radula found also in polyplacophorans and monoplacophorans, as well as limpets. In the present context the docoglossate limpet radula takes on another dimension, which also argues against continued usage of Docoglossa as an order or suborder. Because the term applies to a character state also present outside of Gastropoda, I have adopted Lindberg's term Patellogastropoda for the taxon.

Lindberg (1988*b*: 55) has recognized two suborders of Patellogastropoda based on characters of shell structure and radula: Patellina von Ihering, 1876, with the single superfamily Patellacea Rafinesque, 1815 (family Patellidae Rafinesque, 1815), and Nacellina Lindberg, 1988*b*, with two superfamilies, Nacellacea Thiele, 1891 (family Nacellidae Thiele, 1891) and Acmaeacea Forbes, 1850 (families Lottiidae Gray, 1840, Acmaeidae Forbes, 1850, and Lepetidae Dall, 1869). Subsequently, Lindberg (pers. comm.) has adopted an unranked higher classification that includes all the above taxa within the monophyletic suborder Patellina. As will be supported below by arguments based on radular characters, the neolepetopsids are regarded here as a sister taxon of all previously included members of Patellogastropoda. For present purposes, the suborder Nacellina is placed in synonymy of the suborder Patellina, which, as here defined, includes the superfamilies Patellacaea, Nacellacea and Acmaeacea. To express the sister group affinity of the new family Neolepetopsidae, the new suborder Lepetopsina is proposed.

LEPETOPSINA new suborder

Diagnosis. Patellogastropods with articulating radular teeth.

Remarks. Until now all extant patellogastropods (suborder Patellina) could be characterized as having non-articulating teeth. The Neolepetopsidae exhibit significant tooth articulation, a difference treated at the subordinal level in the discussion that follows. One new superfamily is included.

LEPETOPSACEA new superfamily

A single living family Neolepetopsidae and a single extinct family Lepetopsidae are here recognized, although additional, yet unrecognized, fossil families probably can be allocated here, as noted in the discussion section. The living family Neolepetopsidae is assumed to differ from all other possible fossil families in having non-mineralized denticle caps. The superfamilial and subordinal names are based on the Mississippian–Triassic genus *Lepetopsis* Whitfield, 1882, because I hypothesize that the suborder flourished in the Palaeozoic and that the Neolepetopsidae represent a single lineage surviving into the Recent in the deep-sea hydrothermal-vent community.

NEOLEPETOPSIDAE **new family**

Diagnosis. Shell with nearly central apex. Teeth non-mineralized: rachidian well-formed, two pairs of inner lateral teeth, a pluricuspid lateral tooth, and two pairs of plate-like marginals; inner edge of pluricuspid articulating with mid-shaft cusp of second inner lateral.

Description. Shell with apex central or anterior to centre, protoconch 400 μm in length, symmetrical but aligned about 10° to right of teleoconch axis, lost at early stage, attachment area sealed from within; teleoconch shell symmetrical. Shell with thin periostracum, exterior shell layer of prismatic calcite. Sculpture radial and concentric to nearly smooth. Muscle scar horseshoe-shaped, open anteriorly, narrow throughout, showing traces of muscle bundles; scar continued anteriorly by pallial line. Operculum lacking in mature stage.

External anatomy. Eyes lacking, cephalic tentacles long and tapered, non-papillate; mantle edge with fine, evenly-spaced papillae corresponding to radial ribs; epipodium lacking in adult. Nuchal cavity shallow, ctenidium lacking. Sexes separate, no external differences between sexes. Snout with small, laterally projecting oral lappets; single dorsally arched jaw prominent. Shell muscle horseshoe-shaped, not enlarged anteriorly or narrowed posteriorly; muscle in oval bundles.

Internal anatomy. Monotocardian, left and right kidneys present; gonad discharging via duct of right kidney (V. Fretter, pers. comm.).

Radula. Radula docoglossate with licker below anterior tip (V. Fretter, pers. comm.). Radular ribbon relatively small, denticle caps non-mineralized, delicate, not taking stain like the tooth shafts; teeth non-detachable, articulating with adjacent teeth in row. Rachidian tooth with narrow neck and tapered or quadrangular overhanging cusp. Three pairs of lateral teeth: two pairs of inner laterals, a pair of pluricuspid laterals, and two pairs of marginals. Overhanging cusp of first inner lateral long and tapered, second inner lateral with tapered overhanging cusp and very long shaft with accessory mid-shaft nub; pluricuspid tooth with long, narrow basal shaft and broad overhanging cusp; first marginal relatively large, with long narrow overhanging edge; second marginal reduced or vestigial.

Remarks. All members of this family are known from sulphide-rich habitats at abyssal depths.

Shells differ from those of most other patellogastropods in lacking colour patterns and in the striking transparency of the shell, at least when viewed from the interior. Interior views often reveal the surface detail of the exterior (Plates VIIb, VIIIb, Xb, XIb). Only by comparison with the exterior view is it evident that these are interior views. The eroded apical area is also characteristic.

External anatomy resembles that of the Lepetidae in having well-developed oral lappets. It differs from that of Patellidae and Nacellidae in lacking secondary gills and from that of Acmaeidae and Lottiidae in lacking a nuchal cavity gill. Its branchial condition is like that of Lepetidae, with neither a nuchal cavity gill nor secondary gills.

The radula is unlike that of all other patellogastropods in its non-mineralized teeth that are relatively small. Its most significant difference is that the teeth have complex structures for articulation with adjacent teeth, including a unique arrangement for articulation of the cusps of the pluricuspid with a basal projection on the shaft of the second inner lateral. Tooth cusps are delicate and easily degraded in the process of preparation for SEM, as discussed further in the discussion section. Designation of the lateral teeth as inner laterals and a pluricuspid tooth is based on tooth homologies established by Lindberg (1988a), shown here in Table I. Patellacea are similar in having a rachidian tooth and two pairs of inner laterals and a pair of pluricuspid teeth, but differ

TABLE I

Radular tooth fields and numbers in Patellogastropoda and outgroups (modified after Lindberg, 1988a, Table II)

Taxon	Rachidian	Inner lateral tooth pairs	Outer lateral tooth pairs	Marginal tooth pairs
Outgroups				
Polyplacophora	1	1	1 (2–3 teeth fused)	6
Monoplacophora (Neopilinidae)	1	1	2	2
Patellogastropoda				
Suborder Lepetopsina				
Superfamily Lepetopsacea				
Neolepetopsidae	1	2	1 (3–4 teeth fused)	2
Suborder Patellina				
Superfamily Patellacea				
Patellidae	1	2	1 (3–4 teeth fused)	3
Superfamily Nacellacea				
Nacellidae	0	1	1 (2–3 teeth fused)	3
Superfamily Acmaeacea				
Lottiidae	0	0	3	0–2
Acmaeidae	0	0	3	0
Lepetidae	0	0	2 (partial fusion)	2

in having three pairs of marginal teeth of different morphology. Nacellacea lack a rachidian, have only a single pair of inner laterals, a pair of pluricuspid teeth and three pairs of marginals. In Patellacea and Nacellacea the pluricuspid has strong cusps and is regarded as a fused tooth. Acmaeacea lack a rachidian and lack inner laterals; the three pairs of outer laterals are unfused in Acmaeidae and Lottiidae and the marginal teeth are two pairs or fewer.

Three genera are recognized: *Neolepetopsis* with four species, one from the Gorda Ridge, two from inactive sulphide chimneys along the East Pacific Rise, and one from a sulphide vent on a submarine volcano close to the East Pacific Rise; *Eulepetopsis* with one species from hydrothermal vents in the eastern Pacific; and *Paralepetopsis*, with one species from cold sulphide seeps off the west coast of Florida.

Genera differ in shell proportions and sculpture, but of more significance, there are substantial radular differences in cusp alignment and in the morphology of the tooth elements. The rachidian tooth is well developed in all three genera. It has a tapered tip in *Eulepetopsis* and *Neolepetopsis*, whereas is has a quadrangular overhanging cusp in *Paralepetopsis*. In *Eulepetopsis* it has strong lateral projections at shaft base. The first inner lateral tooth is fairly similar in each of the genera, but the second inner lateral tooth shows differences in the expression of the mid-shaft projection; it is most developed in *Neolepetopsis*. The pluricuspid tooth differs widely: in *Neolepetopsis* the inner edge of the shaft has a broad U-shaped indentation and the elongate cusp is subdivided; modifications of this tooth in *Paralepetopsis* and *Eulepetopsis* are less extreme. In *Eulepetopsis* there is a strong swelling or ridge on the outer edge of the shaft. The first marginal in the three genera has an inturned edge; that of *Eulepetopsis* is very large. The second marginal tooth is reduced in *Paralepetopsis* and *Neolepetopsis*; in *Eulepetopsis* it is vestigial.

Further discussion of character states and all consideration of relationships is deferred to the **Discussion** section.

Key to genera based on sculpture and shell proportions

1. Shell surface nearly smooth   2
   Shell surface with strong cancellate sculpture   ..   .. *Neolepetopsis*
2. Shell transparent, profile low ..   .. *Eulepetopsis*
   Shell opaque, profile high   ..   ..   *Paralepetopsis*

Neolepetopsis new genus

Type species: Neolepetopsis gordensis **new species**

Diagnosis. Surface sculpture of strong beads produced at intersections of radial and concentric ribs. Rachidian with tapered cusp and mid-shaft lateral projections; pluricuspid with broad U-shaped indentation on inner edge of shaft.

Remarks. Aside from the obvious difference in sculpture (noded in *Neolepetopsis*, compared to nearly smooth in both *Paralepetopsis* and *Eulepetopsis*), there are important radular differences. The cusp alignment of the first and second inner lateral teeth is higher than that of the other two genera; development of the mid-shaft projection of the second lateral tooth is strongest among the three genera; the U-shaped indentation in the base of the pluricuspid is most pronounced in *Neolepetopsis*. The two species for which the radula is known have differing renditions of the cusp edge of the pluricuspid, however.

Unlike *Eulepetopsis vitrea*, shells break cleanly. A broken edge of *N. occulta* was examined by SEM (Plate XIId), revealing four layers, as detailed in the **Discussion** section.

Four species are known: the type species *N. gordensis* from the Gorda Ridge, *N. densata* from an inactive sulphide chimney at 12° N on the East Pacific Rise, *N. verruca*, probably from an inactive sulphide chimney at 21° N on the East Pacific Rise, and *N. occulta* from hydrothermal vents on Green Seamount near 21° N. The latter three species are known from a single dive of the *Alvin*. None of the records includes information about other associated hydrothermal-vent fauna. The record for *N. densata*, which is specific as to the occurrence on an 'inactive sulfide chimney', is also specific to the absence of other kinds of vent fauna. It is therefore likely that each *Neolepetopsis* species requires sulphide substrata devoid of other megafaunal species.

The radula is known only for the type species and for *N. densata*. Although more material might suffice to show that *N. densata*, *N. verruca* and *N. occulta* represent variants of a single species, I have elected to name each in order to facilitate comparisons, as there are some morphological differences as well as distributional and habitat differences.

Neolepetopsis gordensis new species
(Plates Ia–h, IIa–g)

Type locality. Hydrothermal vents, Escanaba Trough on Gorda Ridge, off northern California (41° 00·4′ N, 127° 29·3′ W), 3271 m. Details of the association are unknown.

Type material. Holotype, LACM 2401, *Alvin* dive 2040 at type locality, 10 June 1988.
Paratypes. 22 specimens from 3 *Alvin* dives at type locality: dive 2035, 1 specimen LACM 2400; dive 2040, 8 specimens LACM 2402, 4 specimens USNM 860485; dive 2042, 8 immature specimens
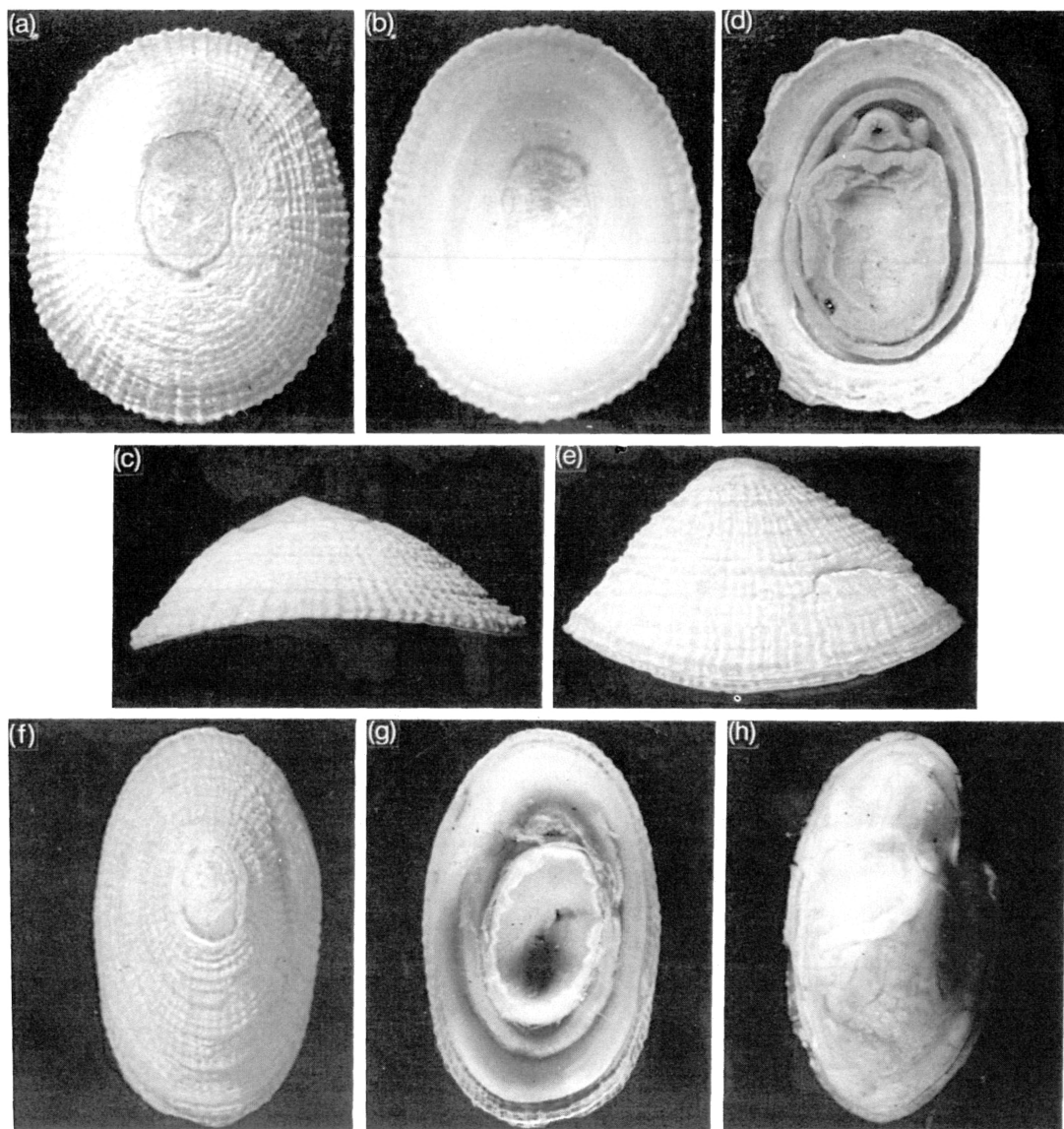
PLATE I. *Neolepetopsis gordensis*, shell and external anatomy. All from Gorda Ridge. Anterior at top in vertical views. (a–c) Holotype shell, *Alvin* dive 2040. Shell length 7·6 mm. (a) Exterior, apex eroded. (b) Interior, muscle scar poorly defined. (c) Left side. (d) Paratype, ventral view with body attached, showing contracted cephalic tentacles and oral lappets adjacent to mouth. *Alvin* dive 2040. Length 7·1 mm. (e–h) Laterally compressed form, *Sea Cliff* dive 764. Length 8·7 mm. (e) Left side, with raised ends. (f) Exterior, apex eroded. (g) Ventral view of contracted body attached to shell. (h) Dorsal view of detached body.
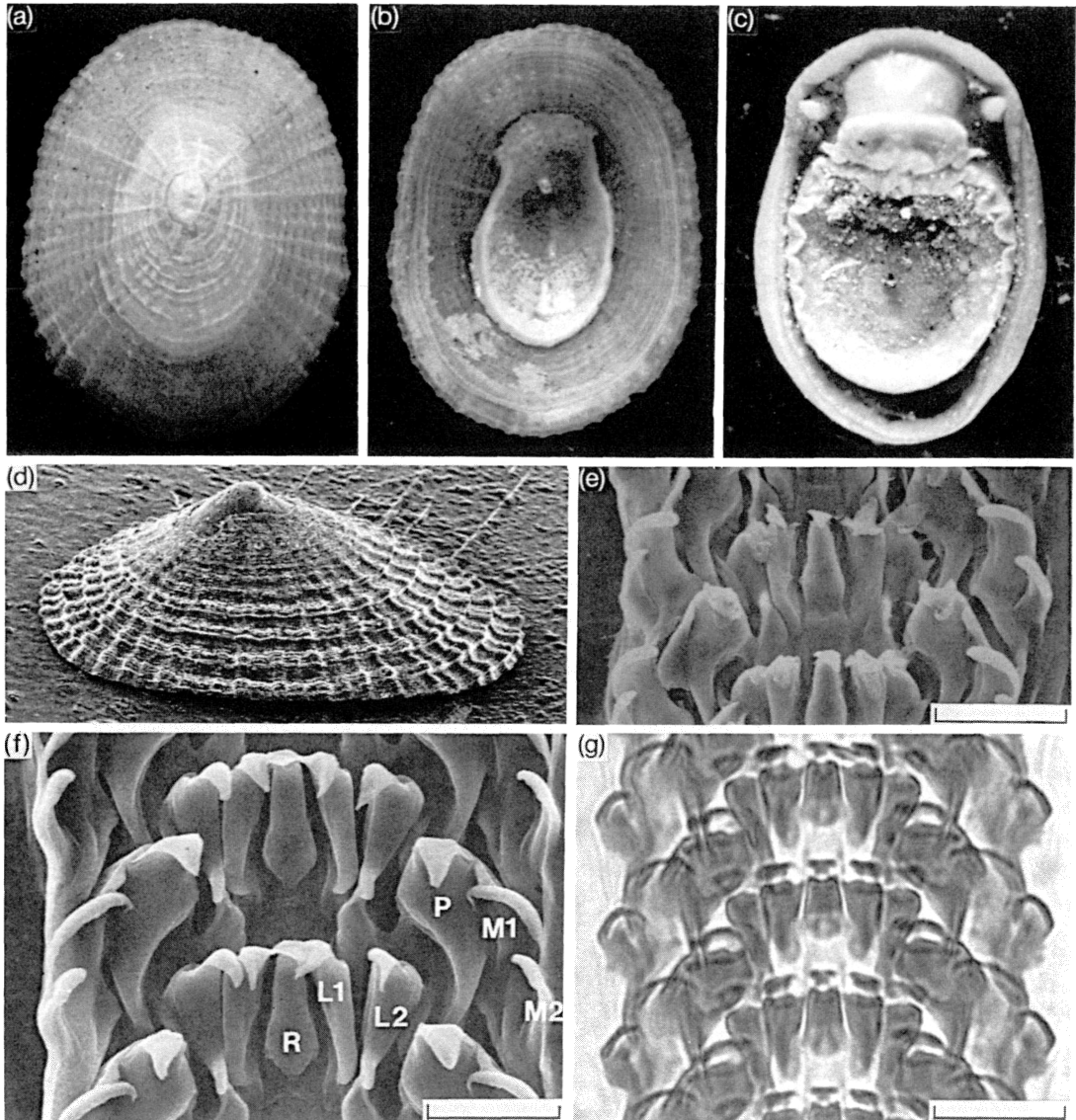
PLATE II. *Neolepetopsis gordensis*, shell, external anatomy and radula. All from Gorda Ridge. Anterior at top in vertical views. (a–c) Partially grown specimen, *Alvin* dive 2035. Length 5·0 mm. (a) Exterior. (b) Interior. (c) Ventral view of detached body, showing small oral lappets and sulphide particles attached to foot. (d) SEM view of immature shell from left side subsequent to loss of protoconch and early teleoconch sculpture. *Alvin* dive 2040. Length 2·9 mm. (e) SEM view of radular ribbon showing tooth degradation resulting from preparation for SEM. *Alvin* dive 2040. Scale bar = 40 µm. (f) SEM view of full width of radular ribbon, showing intact cusps on rachidian, inner laterals, pluricuspid, and marginals. *Sea Cliff* dive 764. Scale bar = 25 µm. Lettering: R, rachidian; L1, first lateral; L2, second lateral; P, pluricuspid; M1, first marginal; M2, second marginal. (g) Stained whole mount of radular ribbon. Shafts of rachidian, laterals and pluricuspid have taken stain; cusps of these teeth lack stain. *Alvin* dive 2040. Scale bar = 50 µm.

with missing or damaged shells, LACM 2403. 12 specimens (all compressed form) from US Navy *Sea Cliff* dive 764, Escanaba Trough, Gorda Ridge (41° 00′ N, 127° 29′ W), 3200–3250 m, 7 specimens LACM 2404, 5 specimens USNM 860486.

Description. Shell (Plate Ia–g, IIa, b, d) relatively thick, oval to oblong, slightly narrower anteriorly; profile moderate to high, highest point of shell at apex; shell margin not in same plane, sides raised relative to ends (Plate Ic) except in compressed form in which ends are raised relative to sides (Plate Ie). Apex on midline, two-fifths shell length from anterior. Protoconch lacking on present material on which all apices are eroded. Periostracum not apparent. Sculpture reticulate, concentric ribs weak, separated by broader interspaces; radial ribs strong, with narrower interspaces, producing scaly nodes on overriding concentric ribs. Shell interior transparent only on young specimens, revealing exterior pattern of sculpture. Innermost apical area opaque white, thickened on inner side. Inner outline of muscle scar well marked.

Dimensions of holotype: length 7·6, width 6·0, height 2·9 mm. Dimensions of figured compression form: length 8·6, width 5·0, height 5·2 mm.

Radula (Plate IIe–g). Cusps of inner lateral teeth descending slightly below that of rachidian tooth; cusps of pluricuspid and marginal teeth curving below cusps of inner laterals. Rachidian with laterally bulging base, narrow neck and tapered overhanging cusp. First inner lateral with tapered cusp like that of rachidian, shaft with indentation to accommodate basal extension of rachidian. Second inner lateral with similarly tapered tip, outward flange and prominent mid-shaft projection, its tip rounded; basal part of shaft extending below nub where it widens. Pluricuspid tooth with large, tapered overhanging cusp with a secondary cusp partially concealed by the first marginal; inner basal edge of pluricuspid with curved surface to accommodate cusp of second inner lateral below; basal extent of pluricuspid narrow, concealed by cusp of pluricuspid below. Shaft of first marginal long, overhanging edge broad. Second marginal reduced.

External anatomy (Plate Id, g, h, IIc). Cephalic tentacles tapered; oral disc with strongly defined lappets. Mantle edge contracted to position of shell muscle, edge with fine papillae. Muscle horseshoe-shaped, narrow throughout, in oval bundles.

Remarks. This is the largest and most robust of the *Neolepetopsis* species. Sculpture on the radial ribs is more scaly than that of other species of *Neolepetopsis*. Interior surfaces of large specimens are more opaque than those of other members of the family.

The pluricuspid tooth of this species is unique in the family in clearly showing a second, outermost cusp. Separation between the rows of teeth is most extreme in this species, producing a clear picture of the articulation possible between each tooth element and emphasizing the unique structure of the base of the second inner lateral, one of the hallmarks in the family Neolepetopsidae.

Comparisons between the light microscope radular preparations (Plate IIg) and the SEM preparation (Plate IIf) indicate that with SEM there is some lateral contraction: the ratio of segment width to segment spacing is 3·7 in the light microscope preparation, compared to 2·6 in the SEM preparation. However, there are no misleading differences between the two methods of preparation as there are with *Paralepetopsis floridensis*. The nub on the second lateral is not evident in the light microscope preparation. The cusps of *N. gordensis* are subject to degradation (Plate IIe) like those of all neolepetopsid species examined. Stain does not take on the cusps of the lateral teeth, as indicated by the unstained necks of these teeth in the light microscope preparation (Plate IIg).

Although a general description of the biotic community of the Gorda Ridge is available (Van Dover, Grassle & Boudrias, 1990), there is no explicit mention of the new species and I have not been able to obtain information about actual associations of these limpets with other vent animals. These authors report that the fauna of the active vent sites was dominated by slender vestimentiferan tube worms of the family Ridgeiidae. All specimens from *Sea Cliff* dive 764 were similarly mature specimens of the compressed form illustrated in Plate Ie–h. Such forms in other limpets are indicative of a life habit of attachment on cylindrical substrata of the same width as the limpet. In this case it may be that the limpets were attached to the vestimentiferan tubes.

Lepetodrilus fucensis McLean, 1988, the largest and most abundant limpet known from the Juan de Fuca Ridge, is here reported to be similarly abundant on the Gorda Ridge, which is part of the same ridge system. *Neolepetopsis gordensis* is as yet unknown from the Juan de Fuca Ridge.

Etymology: The specific name derives from the type locality of the Gorda Ridge.

Neolepetopsis densata new species
(Plates IIIa–g, IVa–d)

Type locality. On inactive sulphide chimney, East Pacific Rise near 12° N (11° 46′ N, 103° 47′ W), 2725 m. According to the original label this species was collected from an 'inactive sulfide chimney without megafaunal vent species.'

Type material. Six specimens from *Alvin* dive 2003, 25 March 1988. Holotype: LACM 2405, 3 paratypes LACM 2406, 2 paratypes USNM 860487.

Description. Shell (Plate IIIa–c, e–g) relatively thin, oblong, slightly narrower posteriorly; profile low, highest point of shell at apex; shell margin not in same plane, sides raised relative to ends. Apex on midline, one-third shell length from anterior. Protoconch (Plate IIIg) symmetrical, length 400 μm, retained on shells to length of 4·0 mm, detached and area sealed from within on larger shells. Apical area eroded on large specimens. Periostracum thin, greenish brown. Sculpture reticulate, concentric ribs strong, separated by broader interspaces; radial ribs broad, low, with narrower interspaces, producing concentrically drawn out nodes on overriding concentric ribs. Shell interior completely transparent, revealing exterior pattern of sculpture. Innermost apical area opaque white, thickened on inner side. Muscle scar not readily discernible.

Dimensions of holotype: length 7·3, width 5·5, height 1·4 mm. Dimensions of paratypes: length 6·9, width 5·3, height 1·3 mm; length 6·1, width 4·5, height 1·2 mm; length 5·3, width 3·6, height 0·7 mm; length 4·1, width 2·9, height 1·0 mm; length 3·9, width 2·6, height 0·8 mm.

Radula (Plate IVa–c). Cusps of inner lateral teeth in horizontal line with that of rachidian tooth; cusps of pluricuspid and marginal teeth descending in straight line below that of inner laterals. Rachidian with laterally expanded base, narrow neck and long, tapered overhanging cusp. First inner lateral with long tapered cusp like that of rachidian, shaft with indentation to accommodate basal extension of rachidian. Second inner lateral with long tapered tip, outward flange and prominent mid-shaft projection, its tip rounded. Pluricuspid tooth with broad overhanging cusp with inner and outer major points and two smaller points between; shaft with broad, U-shaped, basal-lateral indentation and flange connecting cusp edge to adjacent marginal. Shaft of first marginal broadly sinuous, overhanging edge broad. Second marginal reduced.

External anatomy (Plate IIId, e, IVd). Cephalic tentacles tapered; jaw dorsally arched; oral disc
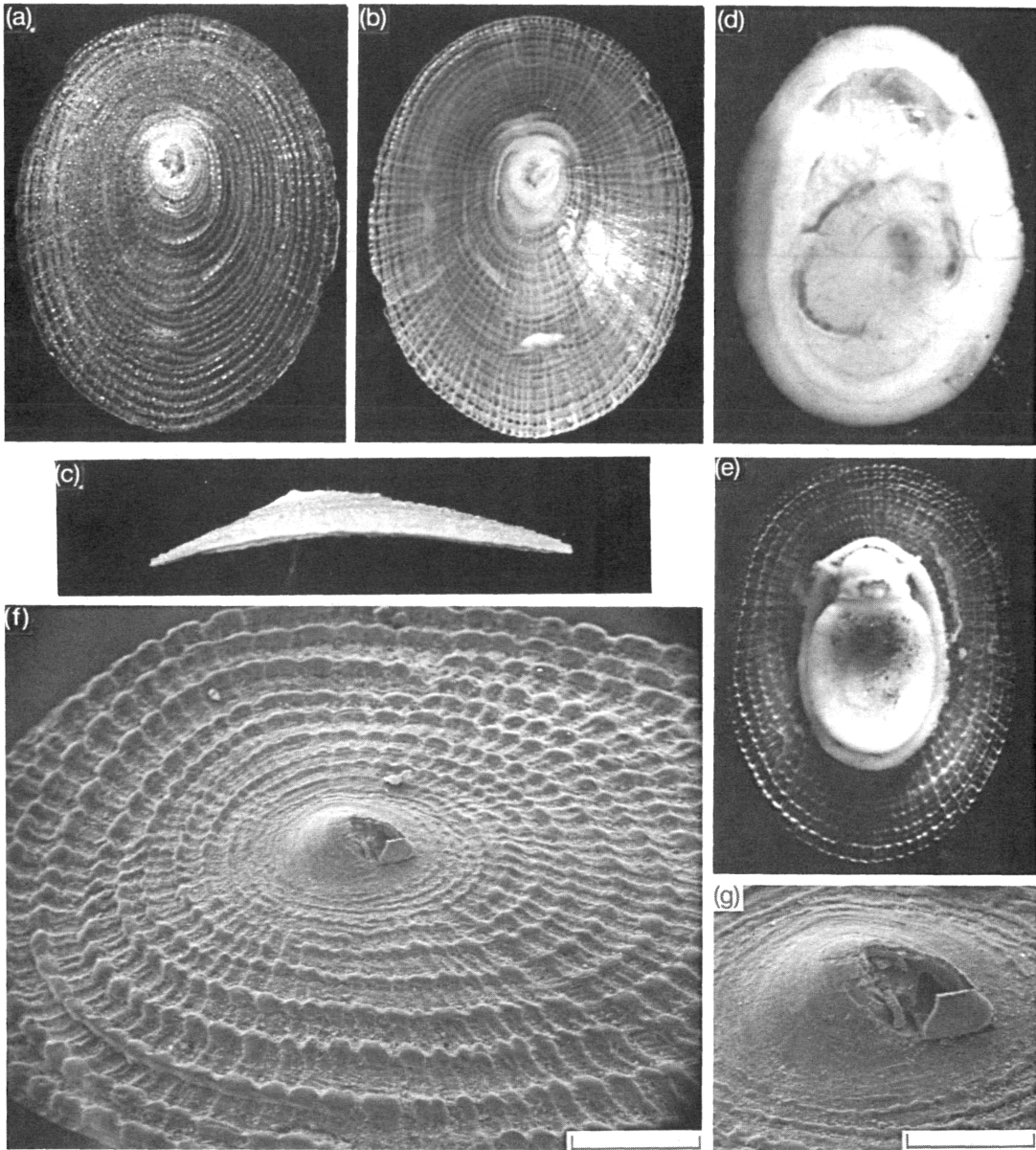
PLATE III. *Neolepetopsis densata*, shell and external anatomy. All from East Pacific Rise at 12° N, *Alvin* dive 2003. Anterior at top in vertical views. (a–d) Holotype, shell length 7·3 mm. (a) Exterior, apex eroded. (b) Interior, showing exterior sculpture by transparency and interior thickening near apex. (c) Left side. (d) Dorsal view of holotype body, showing horseshoe-shaped muscle scar and course of intestine. (e) Body of paratype attached to shell, showing oral lappets. Length 6·1 mm. (f, g) SEM views of exterior surface of small paratype specimen. (f) Oblique view of entire specimen, showing detail of sculpture. Scale bar = 400 μm. (g) Oblique view of broken protoconch from left side. Scale bar = 200 μm.
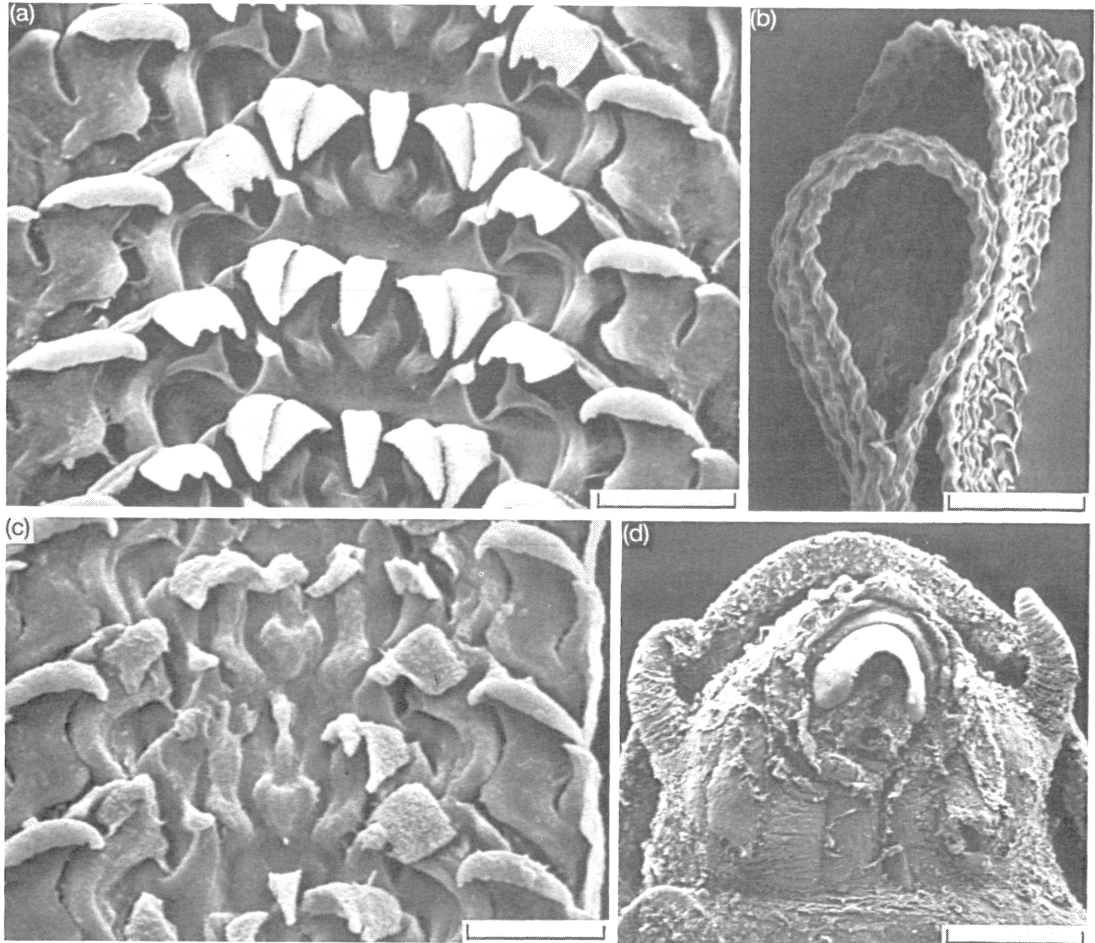
PLATE IV. *Neolepetopsis densata*, SEM views of radula and jaw. All from East Pacific Rise at 12° N, *Alvin* dive 2003. (a) Radular ribbon; rachidian, inner laterals, pluricuspid and marginals with intact cusps. Scale bar = 10 μm. (b) Folded piece of ribbon with degraded cusps. Scale bar = 40 μm. (c) Radular ribbon showing degradation resulting from preparation for SEM. Scale bar = 10 μm. (c) Critical-point dried specimen with exposed jaw. Scale bar = 200 μm.

with weakly developed posterior-lateral lappets. Mantle edge contracted to position of shell muscle, edge with fine papillae. Muscle horseshoe-shaped, narrow throughout, in oval bundles.

Remarks. Concentric sculpture in this species is denser than that of *N. verruca* (10 concentric ribs per mm between the 1 and 2 mm growth stage on the anterior slope compared to five in *N. verruca*). The nodes at the intersections of radial and concentric ribs are drawn out concentrically, rather than radially, as in *N. verruca*. Oral lappets are weakly developed in this species (Plate IVd), compared to other species in the genus.

None of the specimens showed any thickening of the shell close to the interior margin, as in

N. verruca or *N. occulta*, which suggests that shells of the latter two species are fully mature. The present specimens of *N. densata* are probably not yet mature and the species may reach larger sizes.

The absence at the type locality of other mega-faunal species is noteworthy and suggests that this species has exacting requirements for a sulphide substratum free of other vent fauna. As noted above, this is probably characteristic for at least the three southernmost occurring members of the genus.

Etymology: The specific name is derived from Latin, *densus*, thick, with reference to the closely-spaced concentric sculpture.

Neolepetopsis verruca **new species**
(Plate Va–g)

Reticulate Group-C, symmetrical limpet; McLean, 1985: 160.

Type locality. [Inactive sulphide chimney?], East Pacific Rise at 21° N (20° 51·0′ N, 109° 04·9′ W), 2593 m.

Type material. Two specimens from *Alvin* dive 915 at type locality, 22 April 1979.

Holotype, LACM 2407. The body of the holotype (Plate Ve, f) remains preserved, although the radula has been extracted. Paratype, LACM 2408 (Plate Vg), body lost during handling.

Description. Shell (Plate Va–d, g) relatively thick, oblong, slightly narrower anteriorly; profile low, highest point of shell at apex; shell margin not in same plane, sides raised relative to ends. Apex on midline, 2/5 shell length from anterior. Protoconch unknown (apical area eroded on present material); shell thickened on interior side. Periostracum thin, greenish brown. Sculpture reticulate, concentric ribs strong, separated by broader interspaces; radial ribs broad, low, with narrower interspaces, producing rounded nodes on overriding concentric ribs. Muscle scar not apparent on inner surface; thin edge of shell appears white; this represents the opaque outer surface of shell. The dark band along the margin (Plate Va, b, d) is a completely transparent zone; central to this zone there is a broad opaque zone showing coalescing lamellae under high magnification; fine, irregular radial ridges are also visible along the outer edge of the opaque zone; interior to this zone there is a completely transparent zone through which the opaque outer surface is visible. Apical area thickened on inner side, opaque white. Muscle scar within transparent zone, barely detectable, horseshoe-shaped, narrow, same width throughout, arranged in oval bundles.

Dimensions of holotype: length 6·0, width 4·6, height 1·5 mm. Dimensions of paratype: length 5·5 (anterior end damaged), width 4·6, height 1·3 mm.

Radula. Ribbon small, width 20 μm, tooth rows spaced at 12 μm apart (the ribbon of the holotype was mounted upside down for SEM; attempts to remount it failed).

External anatomy (Plate Vd, e, f). Cephalic tentacles tapered, jaw not projecting in single preserved specimen; oral disk with well-developed lappets. Mantle edge contracted to position of shell muscle; edge with microscopic papillae. Muscle horseshoe-shaped, narrow throughout, in oval bundles.

Remarks. As noted above under the discussion for *N. densata*, there are fewer concentric ribs in this species than in *N. densata* and the nodes are drawn out radially rather than concentrically. Shells of the two specimens have a thickened area inside the transparent margin (the opaque white
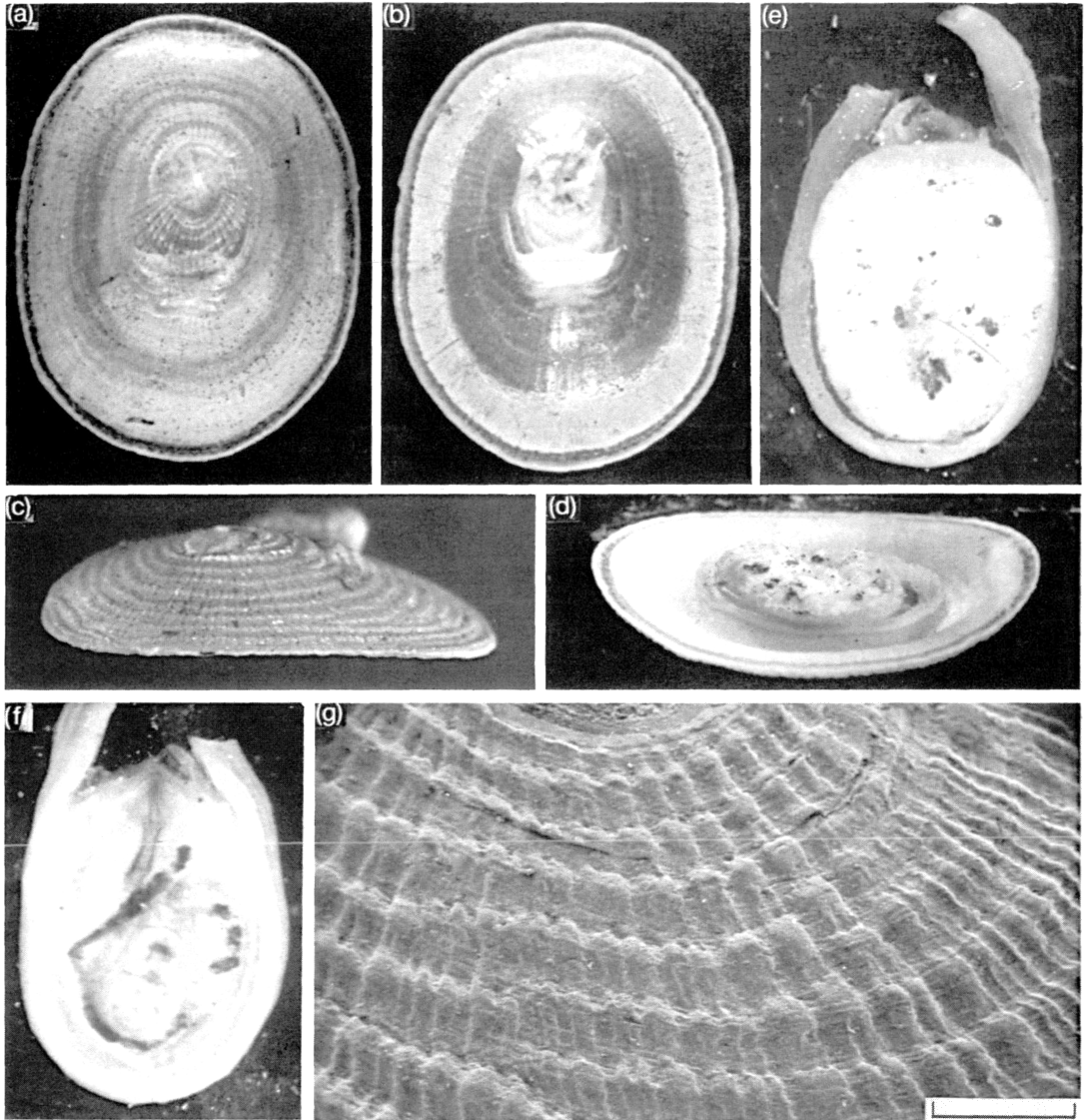
PLATE V. *Neolepetopsis verruca*, shell and external anatomy. All from East Pacific Rise at 21° N, *Alvin* dive 915. Anterior at top in vertical views. (a–d) Holotype shell. Length 6·0 mm. (a) Exterior, showing eroded apex. (b) Interior, showing thin layer of lamellar shell layer inside transparent margin and central area. (c) Left side. (d) Oblique ventral view from left side, contracted body still attached to shell. (e, f) Holotype body, mantle skirt cut on right side. Length 3·5 mm. (e) Ventral view, showing sulphide particles attached to foot. (f) Dorsal view, showing sulphide particles within intestine. (g) SEM view of paratype shell, showing detail of sculpture. Scale bar = 400 μm.

area in Plate Vb), which suggests that these specimens had ceased to increase in length and had restricted growth to thickening the shell on the interior.

This species was collected from 21° N during the reconnaisance expedition of April 1979; no specimens were taken on the return expedition of April–May 1982. The position for dive 915 is one minute of latitude (one nautical mile) north of the rich hydrothermal-vent community that yielded specimens of *Eulepetopsis vitrea*, as well as other species from 21° N. No other species of limpets of any family were taken on *Alvin* dive 915, and the particular association of this species is unknown. Although no details of the microhabitat were provided with the original two specimens, iron sulphide particles were adhering to the foot. These particles were also present on the exposed surfaces of the peltospirid limpets *Nodopelta heminoda* and *Echinopleta fistulosa*, which were also first collected in 1979 (McLean, 1989a). The latter two species are definitely associated with the burrows and tubes of the pompei worm *Alvinella pompejana* Desbruyères & Laubier, 1980, which supports a community of living organisms at the base of the black smoker chimneys. It is therefore likely that *N. verruca* is also a member of this community, or that it came from an inactive sulphide chimney, as did *N. densata*.

The specific name is a Latin noun in apposition, meaning wart, with reference to the noded sculpture.

Neolepetopsis occulta new species
(Plate VIa–g)

Limpet; Levin & Lonsdale, 1983: 1017.

Type locality. On sulphide deposits on caldera floor, Green Seamount, near 21° N (20° 49·0′ N, 109° 17·0′ W), 1990 m. For further information about the expeditions to eastern Pacific seamounts see Levin & Lonsdale (1983) and Levin & Nittrouer (1987).

Type material. 38 specimens from type locality, *Alvin* dive 1185, 5 February 1982. Holotype, LACM 2409; 18 paratypes LACM 2410, 9 paratypes, USNM 860488.

Description. Shell (Plate VIa–d, f) relatively thick, oblong, broader anteriorly; profile low, highest point of shell at apex; shell margin not in same place, sides raised relative to ends. Apex on midline, 1/3 shell length from anterior. Protoconch unknown (apical area eroded on present material); shell thickened on interior side. Periostracum thin, greenish brown. Sculpture reticulate, concentric ribs strong, separated by broader interspaces; radial ribs less prominent than concentric ribs, narrow, low, with nearly equal interspaces, producing rounded nodes on intersecting concentric ribs. Shell interior transparent, showing the pattern of exterior sculpture. Innermost, apical area thickened on inner side and opaque white. Muscle scar not apparent on shell interior.

Dimensions of holotype: length 3·4, width 2·6, height 0·9 mm.

Radula. No trace of a radula was found after five attempts at clearing the soft parts in NaOH at room temperature. Sectioned specimens showed that a very small radula is present, however (V. Fretter, pers. comm.).

External anatomy (Plate VIc–e). Cephalic tentacles tapered, mouth with dorsally arched jaw; oral lappets well developed, triangular, with ventral nubs; mantle margin not showing any papillae.
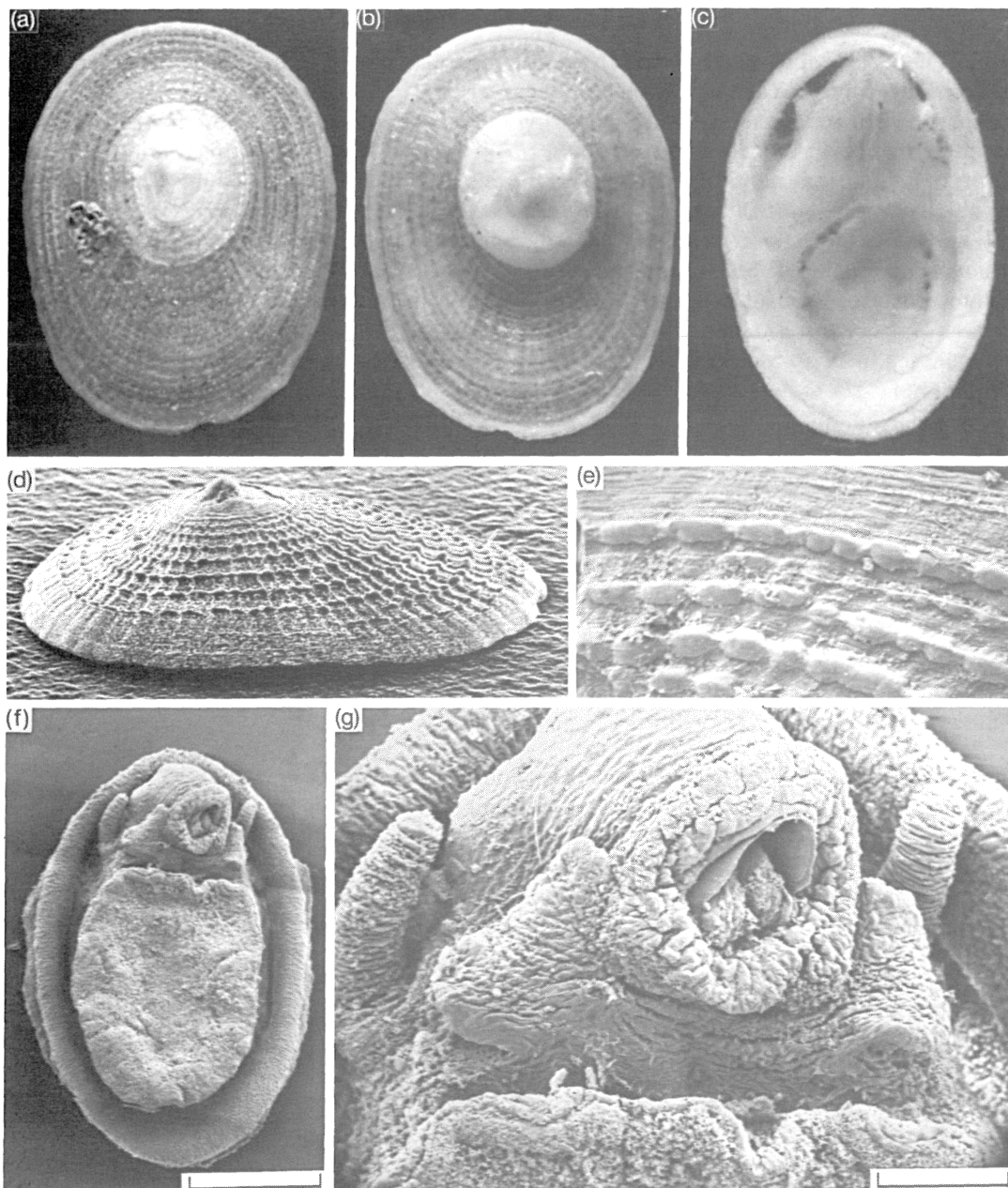
PLATE VI. *Neolepetopsis occulta*, shell and external anatomy. All from Seamount B, near 21° N, *Alvin* dive 1185. Anterior at top in vertical views. (a–c) Holotype. Shell length 3·4 mm. (a) Exterior, showing eroded apical area. (b) Interior, showing exterior sculpture by transparency, apical area thickened by secondary deposition. (c) Dorsal view of body, showing transparent mantle skirt over head and dark sulphide particles within intestine. Length 2·1 mm. (d) SEM view of immature shell from left side subsequent to loss of protoconch and early teleoconch sculpture. Length 2·6 mm. (e) SEM view of shell fragment, showing detail of sculpture. Scale bar = 200 μm. (f, g) SEM views of critical-point dried specimen. (f) Ventral view of entire animal. Scale bar = 400 μm. (g) Ventral view of head, showing jaw and oral lappets lateral to mouth, foot with opening of anterior pedal gland. Scale bar = 100 μm.

Remarks. Although there is a possibility that this could prove to be conspecific with *N. verruca*, there is a major habitat difference and a size difference. Specimens of *N. occulta* are smaller than those of *N. verruca* (maximum length 3·4 mm, compared to 6·0 mm). These specimens of *N. occulta* are considered mature, as the shell interior is thickened near the margin, comparable to that noted in *N. verruca* and large specimens of *E. vitrea*. Concentric sculpture is more crowded than that of *N. verruca*, being more comparable to that of *N. densata*, but not as crisply formed.

According to Levin (pers. comm.): 'only one active hydrothermal site (with water up to 13 C flowing downhill) was found during the survey. Most marked was the absence of large animal life characteristic of the 21 N and Galapagos vents . . . The limpets were preferentially distributed on a metallic grey material (possibly marquisite) on the sulfide rocks.' The habitat information is consistent with that provided for *N. densata* in the lack of other animal life.

Etymology: The specific name is a Latin adjective meaning concealed, suggested by the remote locality and exacting habitat requirements for this species.

Eulepetopsis new genus

Type species: **Eulepetopsis vitrea new species**

Diagnosis. Shell transparent, surface nearly smooth; profile relatively low; height about one-quarter the width. Rachidian with expanded base; pluricuspid with ridge to accommodate cusp of first marginal; second marginal vestigial.

Remarks. *Eulepetopsis* differs from *Neolepetopsis* in lacking beaded sculpture; the proportional height of *Eulepetopsis* is about half that of *Paralepetopsis*. The radula of *Eulepetopsis* differs from that of *Neolepetopsis* in having a much larger first marginal, and a vestigial second marginal. The second inner lateral is relatively large and the pluricuspid is unique in having a deep channel on its outer lateral surface.

Shell structure of *Eulepetopsis* is unique in the family, as indicated by the fact that shells do not break cleanly, instead breaking in steps, much like sheets of mica. The outer layer of the shell is composed of lathic calcite, which is the most transparent structure possible for a calcium carbonate shell (see **Discussion**).

A single species of *Eulepetopsis* is known, the broadly distributed *E. vitrea* from 21° N, 13° N, and 11° N on the East Pacific Rise and the Galapagos Rift.

Eulepetopsis vitrea new species
(Plates VIIa–i, VIIIa–j, IXa–f)

Group-C hydrothermal-vent limpet; Hickman, 1983; 87, figs 34, 35
[radula].
Translucent limpet; Hessler & Smithey, 1983: 742, figs 2, 6
[limpets visible in habitat photos].
Transparent Group-C symmetrical limpet; McLean, 1985: 160.

Type locality. Hydrothermal-vent community near 21° N on East Pacific Rise (20° 50·0′ N, 109° 06·0′ W), 2612–2633 m.
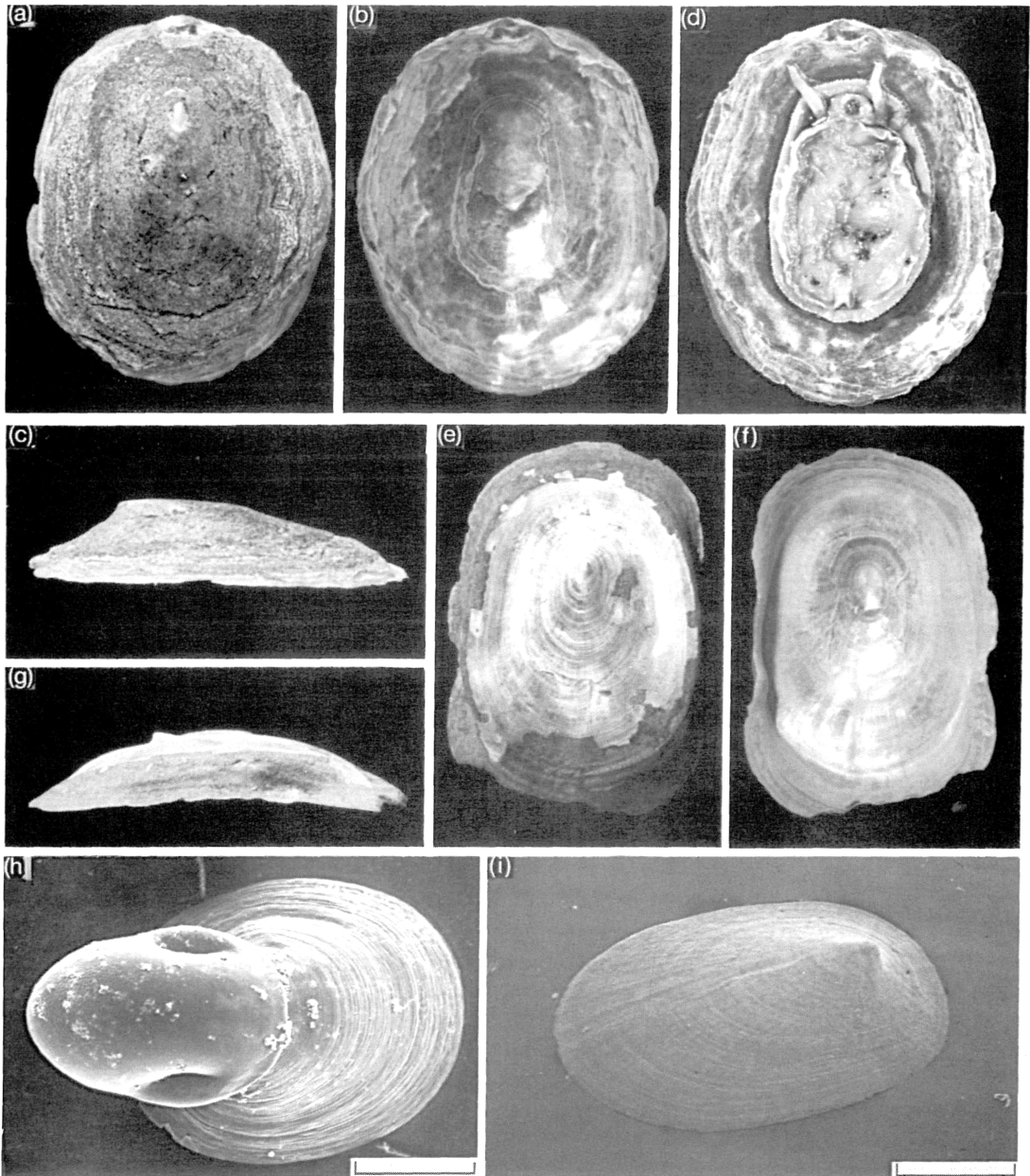
PLATE VII. *Eulepetopsis vitrea*, holotype, paratype, juvenile shell and protoconch. All from East Pacific Rise at 21° N. Anterior at top in vertical views. (a–d) Holotype, *Alvin* dive 1225. Length 16·9 mm. (a) Exterior, showing thick coating of mineral deposits. (b) Interior, showing muscle scar. (c) Left side. (d) Contracted body of holotype in shell, showing papillae at mantle margin. (e–g) Paratype with laterally compressed sides at later growth stage, showing flaking mineral deposits on shell. *Alvin* dive 1225. Length 14·5 mm. (e) Exterior. (f) Interior. (g) Left side. (h) Dorsal SEM view of protoconch and early teleoconch, showing lateral pouches first described by Morse (1910). From settling panel recovered at 21° N, courtesy C. Van Dover. Scale bar = 100 μm. (i) Oblique SEM view of juvenile shell from right posterior, protoconch lost. *Alvin* dive 1225. Scale bar = 1 μm.

TABLE II

Station data, number of specimens and disposition for dives yielding **Eulepetopsis vitrea**

Dive	Depth/m	Position	Date	Number specimens, habitat
		Alvin dives, East Pacific Rise near 21° N		
1211	2615	20 50·0′ N, 109 06·0′ W	17 APR. 1982	3, large shells, *Riftia* & clam wash
1213	2617	20 50·0′ N, 109 06·0′ W	19 APR. 1982	3, small, *Alvinella* wash
1214	2633	20 50·0′ N, 108 06·0′ W	20 APR. 1982	13, *Riftia* wash
1215	2616	20 50·0′ N, 109 06·0′ W	21 APR. 1982	2, juvenile, slurp sample
1218	2618	20 50·0′ N, 109 06·0′ W	24 APR. 1982	4, juvenile, clam & crab trap wash
1219	2612	20 50·0′ N, 109 06·0′ W	25 APR. 1982	31, all sizes, *Riftia* & clam wash
1220	2617	20 50·0′ N, 109 06·0′ W	26 APR. 1982	7, all sizes, washings
1221	2618	20 50·0′ N, 109 06·0′ W	04 MAY 1982	21, all sizes; 15 juveniles, *Riftia* & *Calyptogena* wash
1222	2614	20 50·0′ N, 109 06·0′ W	06 MAY 1982	4, juvenile, rubble from *Calyptogena* residue
1223	2616	20 50·0′ N, 109 06·0′ W	07 MAY 1982	12, all sizes; 10 juveniles, rubble samples
1225	2618	20 50·0′ N, 109 06·0′ W	09 MAY 1982	43, all sizes, rubble sample (holotype)
1226	2616	20 50·0′ N, 109 06·0′ W	10 MAY 1982	11, juvenile, *Riftia, Calyptogena* & *Alvinella* wash
		Cyana dives, East Pacific Rise near 12° N		
		(counts received from P. Bouchet)		
82–33	2633	12 48·6′ N, 103 56·7′ W	08 MAR. 1982	7
82–35	2633	12 38·6′ N, 103 56·7′ W	12 MAR. 1982	4
84–32	2635	12 48·1′ N, 103 56·9′ W	09 MAR. 1984	1
84–34	2630	12 49·1′ N, 103 56·9′ W	11 MAR. 1984	1
84–37	2630	12 46·6′ N, 103 56·7′ W	14 MAR. 1984	1
84–39	2635	12 48·6′ N, 103 56·7′ W	16 MAR. 1984	5
84–42	2635	12 48·6′ N, 103 56·7′ W	14 MAR. 1984	18
84–43	2635	12 48·6′ N, 103 56·7′ W	25 MAR. 1984	2
84–44	2635	12 48·8′ N, 103 56·8′ W	26 MAR. 1984	1
84–45	2635	12 48·8′ N, 103 56·8′ W	27 MAR. 1984	1
84–46	2635	12 48·6′ N, 103 56·7′ W	28 MAR. 1984	1
		Alvin dive, East Pacific Rise near 11° N		
1993	2600	11 26·3′ N, 103 47/3′ W	15 MAR. 1988	2, shells broken
		Alvin dives, Galapagos Rift		
733	2500	00 47·3′ N, 86 07·8′ W	16 MAR. 1977	1, large shell only
879	2495	00 48·2′ N, 86 04·1′ W	20 JAN. 1979	93, all sizes, mussel washings
880	2493	00 47·6′ N, 86 06·4′ W	21 JAN. 1979	371, all sizes, mussel washings
884	2482	00 48·1′ N, 86 07·0′ W	25 JAN. 1979	103, all sizes, rubble from mussels
887	2488	00 48·5′ N, 86 09·1′ W	12 FEB. 1979	11, juvenile and medium size, no habitat data
888	2483	00 47·1′ N, 86 08·5′ W	13 FEB. 1979	44, all sizes, mussel wash
890	2447	00 48·9′ N, 86 13·3′ W	15 FEB. 1979	34, all sizes, no habitat data
892	2454	00 48·3′ N, 86 13·8′ W	17 FEB. 1979	1, medium size, no habitat data
893	2578	00 46·8′ N, 86 01·9′ W	18 FEB. 1979	1, juvenile, rock shards residue
894	2457	00 48·2′ N, 86 14·9′ W	19 FEB. 1979	2, juvenile, amphipod trap
895	2482	00 47·9′ N, 86 09·3′ W	20 FEB. 1979	35, all sizes, clam box washings
896	2460	00 48·2′ N, 86 13·6′ W	21 FEB. 1979	7, juvenile, no habitat data
983	2457	00 48·0′ N, 86 13·0′ W	30 NOV. 1979	92, all sizes, washings
984	2451	00 48·0′ N, 86 13·0′ W	01 DEC. 1979	77, all sizes, mussel washings
989	2482	00 48·0′ N, 86 09·0′ W	06 DEC. 1979	66, all sizes; 80 juveniles, mussel & clam wash
990	2451	00 48·0′ N, 86 13·0′ W	07 DEC. 1979	14, all sizes, *Riftia* wash
991	2490	00 48·0′ N, 86 09·0′ W	08 DEC. 1979	236, all sizes, mussel & clam wash
993	2518	00 47·0′ N, 86 08·0′ W	10 DEC. 1979	1, juvenile, crab trap wash
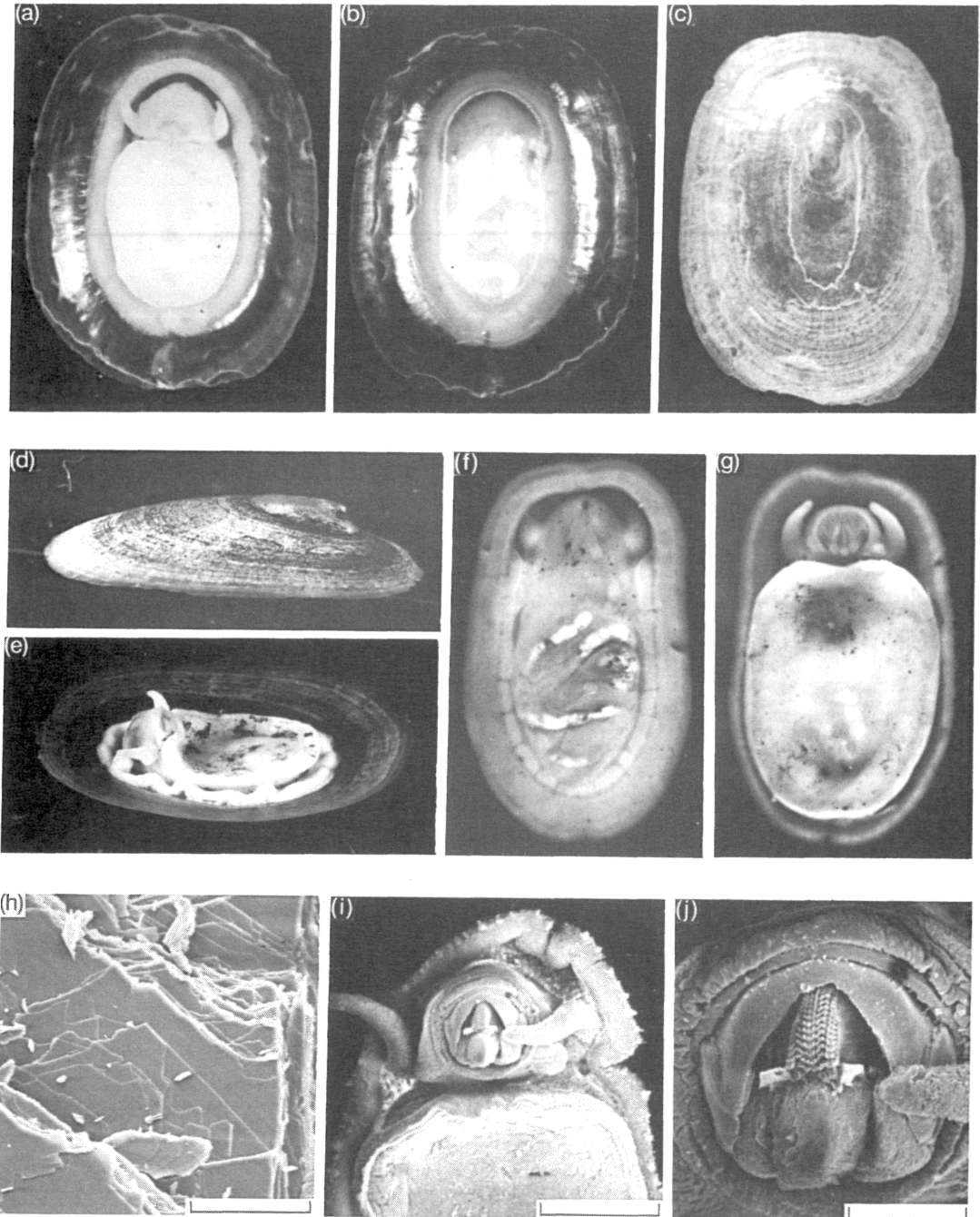
Type material. Holotype, LACM 2417, *Alvin* dive 1225 at type locality, 9 May 1982.

Paratypes. 179 specimens from 12 *Alvin* dives at type locality (Table II): dive 1211, 3 specimens LACM 2411; dive 1213, 3 specimens LACM 2412; dive 1214, 7 specimens LACM 2413, 6 specimens USNM 860489; dive 1215, 2 specimens USNM 860490; dive 1218, 4 specimens USNM 860491; dive 1219, 16 specimens LACM 2414, 15 specimens USNM 860492; dive 1220, 7 specimens USNM 860493; dive 1221, 11 specimens LACM 2415, 10 specimens USNM 860494; dive 1222, 4 specimens USNM 860495; dive 1223, 12 specimens LACM 2416, 10 specimens USNM 860496; dive 1225, 22 specimens LACM 2418, 20 specimens USNM 860497; dive 1226, 11 specimens LACM 2419.

Referred material. 42 specimens from 11 *Cyana* dives, East Pacific Rise at 12° N (Table II); 2 specimens from *Alvin* dive 1993, East Pacific Rise at 11° N (Table II); 1269 specimens from 18 *Alvin* dives at Galapagos Rift (Table II).

Description. Shell (Plate VIIa–i, VIIIa–e) oblong, anterior end slightly narrower than posterior; profile low, highest point of shell slightly posterior to apex; shell margin in same plane. Apex on midline one-quarter shell length from anterior end. Protoconch (Plate VIIh) symmetrical, length 400 μm, lost at early stage, broken off and sealed from within. Periostracum very thin; shell often coated with rusty appearing sulphide deposits; shells in fluid nearly transparent; dried shells with opaque white exterior surface. Sculpture of fine radial striae and concentric growth irregularities. Shell interior with metallic sheen when viewed at angle; completely transparent when viewed directly, revealing detail of exterior surface. Muscle scar barely apparent, not impressed in shell interior, positioned much closer to mid-dorsal line than to shell edge (Plate VIIb, VIIIc).

Dimensions of holotype: length 16·9, width 13·7, height 3·3 mm.

External anatomy (Plate VIId, VIIIe–g, i, j). Cephalic tentacles long and tapered. Snout with oral lappets, some preserved specimens with dorsally arched jaw and licker projecting (Plate VIIIj). Mantle edge thickened, after preservation contracted to position of shell muscle; edge appears smooth, but bears fine papillae under high magnification (Plate VIIIi). Muscle in elongate bundles (Plate VIIIf).

Radula (Plate IXa–f). Cusps of lateral teeth descending away from cusp of rachidian tooth. Shaft of rachidian tooth broad at base, with lateral projections, constricted at neck, overhanging

PLATE VIII. *Eulepetopsis vitrea*, shell, external anatomy and shell structure. Specimens from Galapagos Rift and East Pacific Rise at 21° N. Anterior at top in vertical views. (a–b) Intact specimen. Galapagos Rift, *Alvin* dive 879. Length 5·4 mm. (a) Ventral view. (b) Dorsal view, showing complete transparency of shell, course of intestine visible. (c) Dry shell. Dorsal view, showing fine radial and concentric sculpture. Details of interior show through: pattern of muscle scar (inner edge marked by white line), outline of muscle bundles readily apparent adjacent to this; pallial line continued anteriorly. Galapagos Rift, *Alvin* dive 879. Shell missing prior to measuring. (d, e) Intact specimen. 21° N, *Alvin* dive 1220. Length 11·5 mm. (d) Right side of shell, surface with light coating of black mineral deposits. (e) Oblique view of body in shell; foot with adhering sulphide particles. (f, g) Detached body. 21° N, *Alvin* dive 1220. Length 5·3 mm. (f) Dorsal view, head visible through transparent mantle skirt, narrow horseshoe-shaped shell muscle in discrete bundles, and sulphide particles in two loops of intestine. (g) Ventral view, mouth expanded to show jaw. (h) SEM view of fractured surface within shell, showing zigzag crystal edges indicative of lathic calcite. Galapagos Rift, *Alvin* dive 880. Scale bar = 40 μm. (i, j) SEM views of small, critical-point dried specimen (shell length 5·8 mm). Galapagos Rift, *Alvin* dive 879. (i) Ventral view of anterior showing mantle edge with fine papillae, cephalic tentacles, head with oral lappets, protracted jaw and radula. Scale bar = 1 mm. (j) Enlarged view of mouth; radula framed by jaw, attached to licker anteriorly (white horizontal strip between radula and licker is an artefact of drying process). Scale bar = 400 μm.
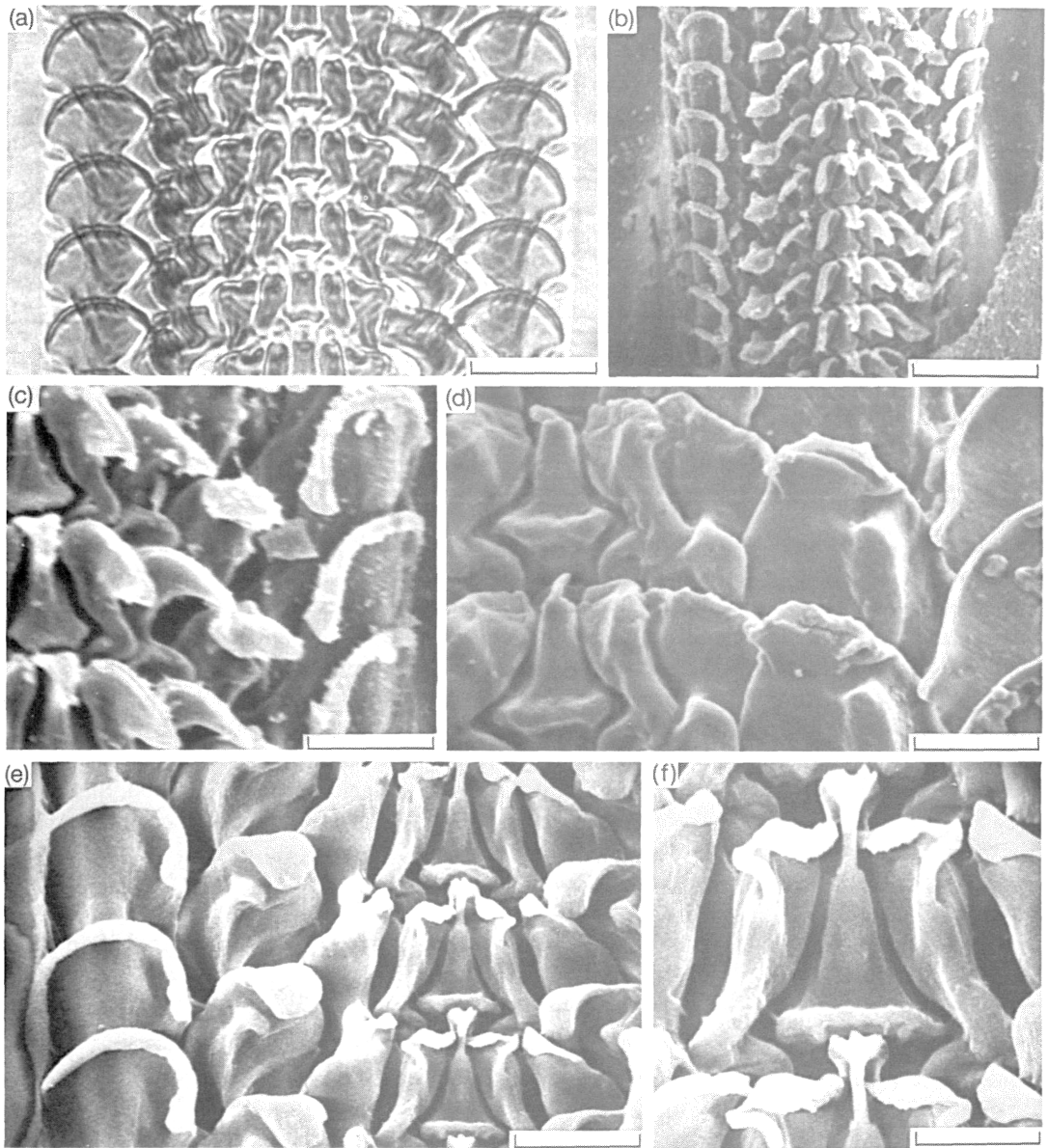
PLATE IX. *Eulepetopsis vitrea*, radula. Specimens from Galapagos Rift and East Pacific Rise at 21° N. (a) Stained whole mount of intact ribbon, showing the vestigial second marginal teeth at ribbon edge. Shafts of rachidian, laterals and pluricuspid have taken stain; delicate cusps of these teeth lack stain. East Pacific Rise at 21° N, *Alvin* dive 1225. Scale bar = 43 μm. (b, c) Enlarged SEM views of radula of same specimen as in Plate VIIIi, j, top to bottom reversed from those illustrations to show tooth rows in usual perspective. (b) Full width of radula; jaw edge visible in lower corner. Scale bar = 100 μm. (c) Enlarged view, showing rachidian, first and second lateral teeth, pluricuspid, and first marginal. Lateral teeth are seen from inner side due to longitudinal bending (see text). Scale bar = 20 μm. (d) SEM view of half row of radular ribbon from mature specimen, in which cusps of all teeth have been degraded in preparation; narrow base of pluricuspid concealed. Galapagos Rift, *Alvin* dive 880. Scale bar = 10 μm. (e, f) SEM views of radular ribbon of mature specimen (shell length 14·5 mm). Note constricted shaft near tip. East Pacific Rise at 21° N, *Alvin* dive 1225. (e) Half row of ribbon, showing rachidian, first and second inner laterals, pluricuspid with groove, and large first marginal tooth. Scale bar = 20 μm. (f) Enlarged view of rachidian and inner laterals. Scale bar = 10 μm.

cusp narrow, tapered. Shaft of first inner lateral tooth with indentation on inner side to accommodate basal projection of rachidian, overhanging cusp broad. Second inner lateral tooth much broader, its base accommodating projection of first inner lateral; mid-shaft nub prominent. Pluricuspid tooth with long, narrow base, outer edge with ridge and broad channel, overhanging cusp broad. First marginal tooth broad, overhanging edge narrow, its outer edge rising obliquely. Second marginal tooth vestigial.

Remarks. Here again an understanding of the radula of *Eulepetopsis vitrea* derives both from whole mount preparations and SEM preparations. Degradation of the cusps during preparation for SEM was so extensive that numerous attempts were necessary to achieve the results shown in Plate IXe, f. These views show a constricted neck on the rachidian and first laterals, corresponding to the unstained areas on the light microscope view (Plate IXa), in turn corresponding to the limits of the tooth degradation shown in Plate IXd. The SEM views have the advantage of showing the nub on the second lateral and the groove on the pluricuspid, while light microscope preparations reveal the remarkable fan-shaped structure of the first marginal and also show the vestigial second marginal, which had been completely undetectable in the SEM views.

The relatively large size of the fan-shaped first marginal teeth in this genus indicates a particularly important role in food gathering played by these teeth, compared to these teeth in the other two genera.

Teeth of a small specimen (shell length 5·8 mm) in which the radula was protracted on preservation are shown in Plate IXb, c. Here the ribbon is partially flexed longitudinally and the inner sides of the first and second inner lateral teeth are exposed. Cusps are longer on these teeth than those shown for a larger specimen (shell length 14·5 mm, Plate IXe, f).

No other limpet has such a transparent shell, allowing anatomical details to show through the shell (Plate VIIIb).

There are no apparent differences among populations occurring at the Galapagos Rift, 11° N, 13° N and 21° N.

As is evident in illustrations of Hessler & Smithey (1983), this species occurs widely on the basalt substratum and on mussels (*Bathymodiolus thermophilus* Kenk & Wilson, 1985). Shells that are iron-coated appear black in the photographs. Although a few specimens were recovered from washings of the vestimentiferan *Riftia pachyptila* Jones, 1981, it is evident from the collection data in Table II that the largest samples came from mussel washings. Specimen counts of the limpets from *Alvin* dive 1214 at 21° N, which were obtained by washing a *Riftia* sample, produced 14,574 specimens of *Lepetodrilus elevatus*, 1853 specimens of *L. pustulosus* (McLean, 1988a), but only 13 specimens of *E. vitrea*.

The only known specimen of *E. vitrea* having an intact protoconch was recovered from a settling panel placed at 21° N (Plate VIIh, courtesy C. Van Dover). The apical area of other small specimens is sealed from within (Plate VIIi).

Most samples have shell lengths ranging from 8–12 mm; specimens from dive 1225, from which the holotype was selected, include some exceptionally large specimens (maximum length 16·9 mm, holotype), including some that have developed compressed sides at later stages of growth (Plate VIIe–g).

Etymology: The specific name is a Latin adjective meaning glassy or transparent.

Paralepetopsis **new genus**

Type species: ***Paralepetopsis floridensis* new species**

Diagnosis. Shell opaque, surface with faint radial sculpture, shell height about one-half the dimension of width; rachidian tooth with quadrate cusp; pluricuspid with tapered shaft and long overhanging edge.

Remarks. Paralepetopsis differs from *Eulepetopsis* in higher shell proportions. Its radula is unique in the family in having the rachidian and inner laterals with straight rather than tapered cusps. The rachidian, inner laterals and pluricuspid have relatively straighter shafts, not having the basal projections of *Eulepetopsis*. Of the three genera, the mid-shaft projection of the second inner lateral is least developed in *Paralepetopsis*. As in *Neolepetopsis*, but unlike *Eulepetopsis*, the second marginal is well developed in *Paralepetopsis*.

   This genus is as yet known only from a single species from cool, hypersaline, sulphide seeps in the western Atlantic, at the base of the continental slope off the west coast of Florida.

Paralepetopsis floridensis **new species**
(Plates Xa–h, XIa–f)

Limpet; Paull *et al.*, 1984: 956; Hecker, 1985: 466.
Florida Group-C symmetrical limpet; McLean, 1985: 160.

Type locality. On shells of mytilid bivalves, hypersaline sulphide seeps at base of continental slope, Florida Escarpment off south-western Florida (26° 03·0′ N; 84° 54·0′ W), 3270 m.

Type material. Holotype, LACM 2420, *Alvin* dive 1343 at type locality, 9 March 1984.

   Paratypes. 47 specimens from 3 *Alvin* dives at type locality: dive 1343, 3 specimens LACM 2421; dive 1753, 11 specimens LACM 2422, 8 specimens USNM 860498; dive 1755, 8 specimens LACM 2423, 6 specimens USNM 860499.

Description. Shell (Plate Xa–c), elliptical in outline, anterior end slightly narrower; profile moderately high, highest point of shell at apex: shell margin in one plane. Apex on midline, two-fifths shell length from anterior end. Protoconch (Plate Xf–h) symmetrical, length 400 μm, retained only on shells to length of 1·5 mm, detached and sealed from within on larger shells. Periostracum thin, light tan. All slopes straight to slightly convex. Sculpture of fine radial striae and concentric growth irregularities. Shell interior with transparent margin, 0·5 mm in width; area between margin and muscle scar with fine lamellae running parallel to edge, visible under high magnification and making surface opaque. Muscle scar well marked, horseshoe-shaped, narrow thoughout, weakly impressed in shell interior and indicating muscle bundles. Muscle position slightly closer to mid-dorsal line than to shell edge.

   Dimensions of holotype: length 9·4, width 6·8, height 3·3 mm.

   External anatomy (Plate Xd, e). Cephalic tentacles long and tapered, snout with oral lappets, mouth with dorsally-arched jaw. Mantle edge with fine papillae. Muscle narrow, arranged in oval bundles (Plate Xd).

   Radula (Plate XIa–f). Cusp position of lateral and marginal teeth descending away from that of rachidian tooth in nearly straight line in inverted-V. Shaft of rachidian three times longer than wide, overhanging cusp broad, quadrangular, with pointed tips at corners. Shaft of first inner
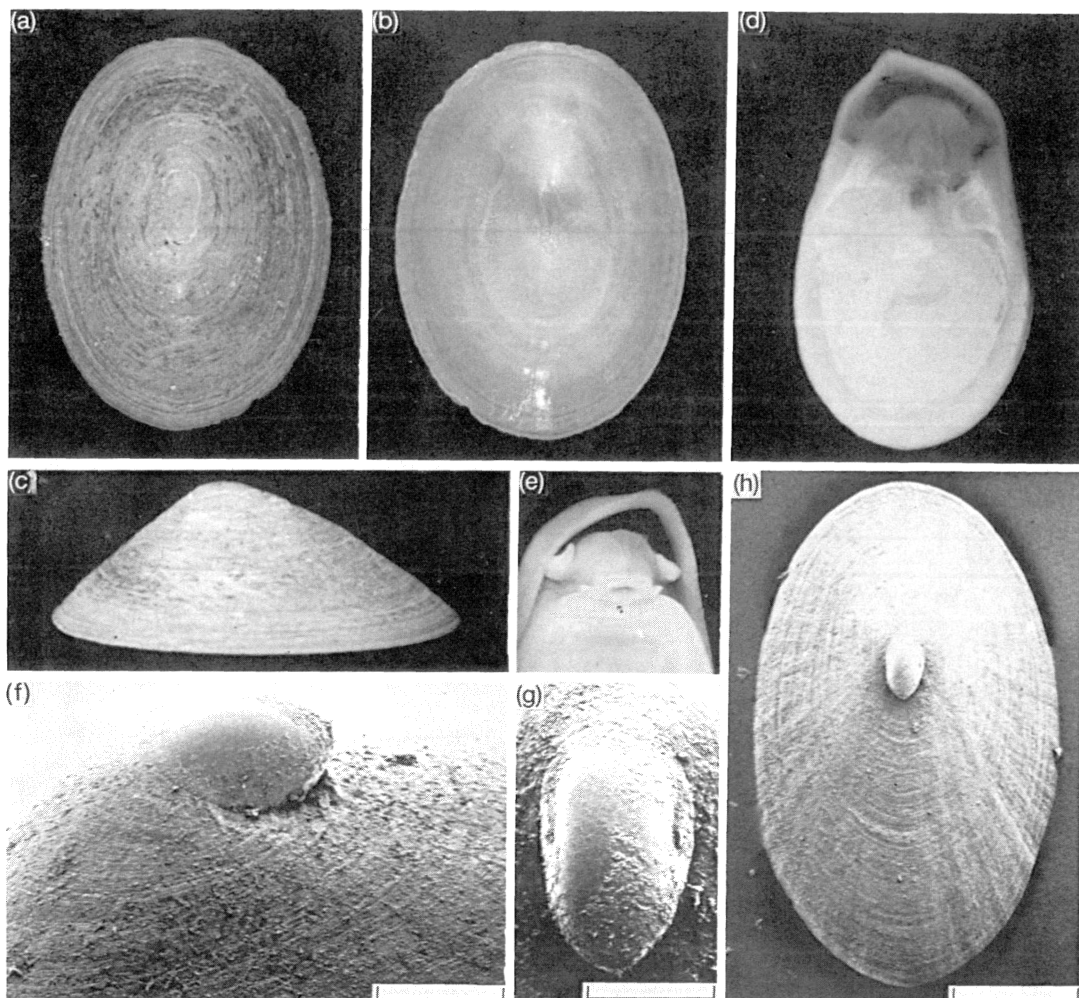
PLATE X. *Paralepetopsis floridensis*, shell, external anatomy and protoconch. All from Florida Escarpment. Anterior at top in vertical views. (a–c) Holotype shell, *Alvin* dive 1342. Length 9·4 mm. (a) Exterior, showing eroded apex. (b) Interior, showing horseshoe-shaped muscle scar closer to centre than to margin. (c) Left side. (d, e) Body of holotype. Length 7·0 mm. (d) Dorsal view, showing mantle skirt transparent above head, narrow shell muscle in bundles. (e) Ventral view of head and foot, showing contracted cephalic tentacles and small, pointed oral lappets lateral to mouth. (f–h) SEM views of juvenile shell with intact protoconch. *Alvin* dive 1755. (f) Oblique view of protoconch from anterior left side. Scale bar = 200 μm. (g) Dorsal view of protoconch showing lateral pouches. Scale bar = 200 μm. (h) Complete shell, showing slightly offset protoconch, relative to anterior/posterior axis. Scale bar = 400 μm.
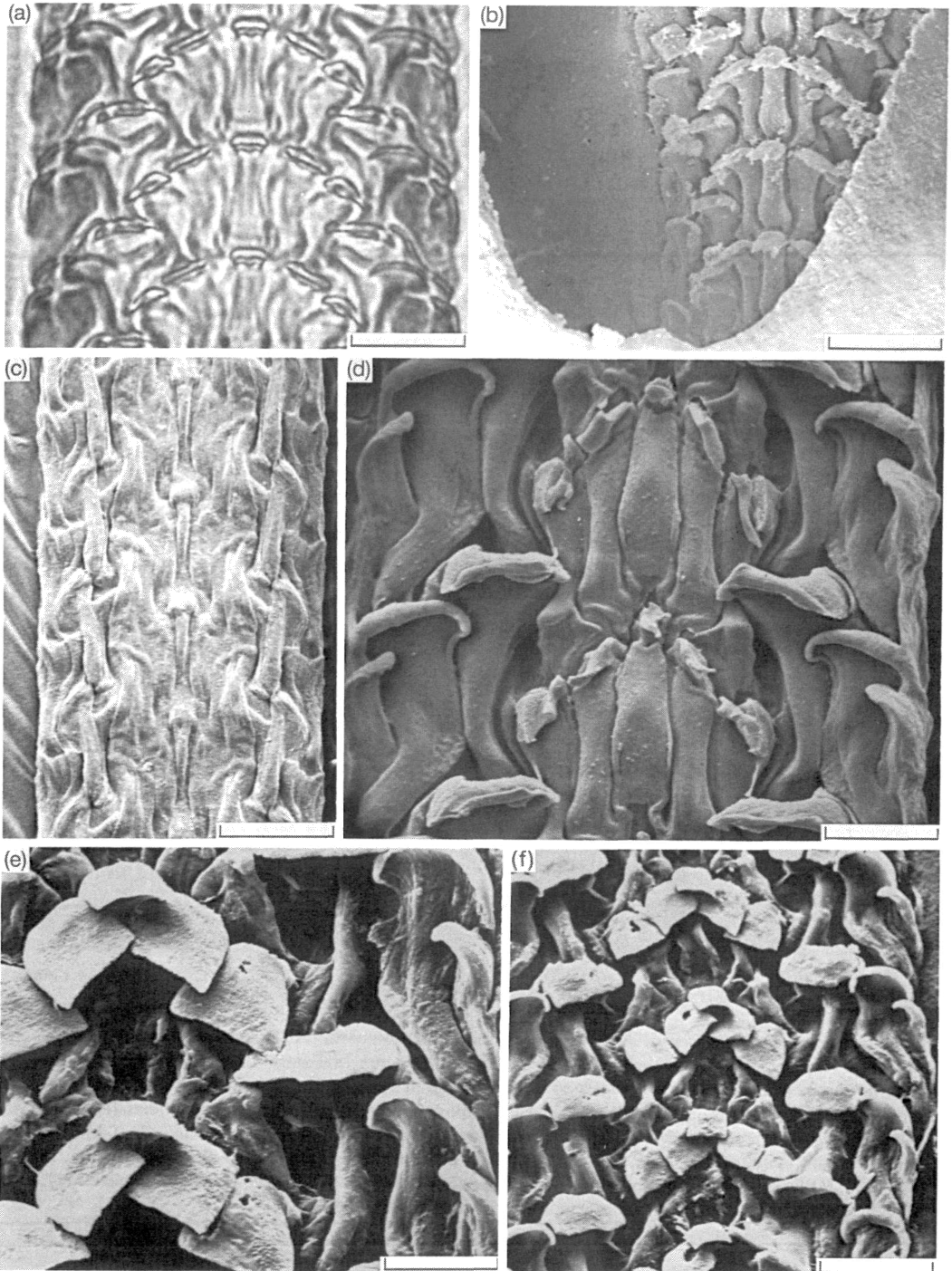
lateral more slender than that of rachidian, overhanging cusp elongate, base of shaft extending below that of rachidian. Shaft of second inner lateral bowed and with mid-shaft projection to articulate with overhanging edge of pluricuspid. Pluricuspid with large, nearly quadrate cusp, shaft very long, narrow at base. Shaft of first marginal broad, overhanging edge curled, descending toward edge of ribbon. Second marginal reduced.

Remarks. Paralepetopsis floridensis is the only limpet of any family known from a cold sulphide-seep habitat.

The light microscope preparation of the radula (Plate XIa) shows the outlines of the teeth in normal relative positions and reveals the great length of the lower shaft of the pluricuspid, which extends behind the pluricuspid of the row below. It also shows the weak link between the shaft and cusps, corresponding to the pattern of tooth degradation in Plate XId. However, it does not show the mid-lateral projection on the second laterals that are only apparent in the SEM views. The SEM preparation in which the cusps survived (Plate XIe, f) is misleading because of the shrinkage of all teeth, causing the rachidian and laterals to overlap and mistakenly giving the impression that the cusps of the laterals are sharply tapered, rather than straight across, as is apparent from the light microscope preparation.

According to Hecker (1985), the limpets live epifaunally on clumps of a large (yet unnamed) mytilid that occurs in a band along the base of the escarpment and in scattered patches extending to 30 m out on the abyssal plain. Water emanating from the seeps at the juncture of the escarpment base and abyssal plain sediments has the ambient bottom temperature of about 4·5 °C, is hypersaline and sulphide-rich. This community is thought to be widely distributed at the base of Florida Escarpment 'and possibly other carbonate escarpments' yet to be sampled (Paull *et al.*, 1984; Paull & Neumann, 1987). Similar escarpments occur off Yucatan and on the eastern edge of the Bahamas.

Etymology: The specific name derives from the type locality, the Florida Escarpment.

Presumed fossil record of **Lepetopsacea**

Shells of *Neolepetopsis* and *Paralepetopsis* species have a striking morphological resemblance to the late Palaeozoic genus *Lepetopsis* Whitfield, 1882, which was well represented in the Permian and probably represented in the Triassic (Yochelson, 1960: 245). I consider that there is a direct connection between the fossil genus and the genera now restricted to the deep-sea sulphide habitat, and make the assumption that the extinct, shallow water members would have had mineralized teeth, as do all extant patellogastropods away from the sulphide habitat (see **Discussion**).

The fossil members have yet to be assigned to a family that differentiates them from other

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PLATE XI. *Paralepetopsis floridensis*, radula. All from Florida Escarpment. (a) Stained whole mount of full width of radular ribbon. *Alvin* dive 1753. Scale bar = 32 μm. (b) SEM view of specimen with protracted radula and jaw, critical-point dried, showing radula framed by jaw. The inner edge of the jaw is shown at the lower edge of the frame, the radula reversed top to bottom in order to show teeth rows in usual perspective (compare with similar view in Plate IXb). *Alvin* dive 1753. Scale bar = 40 μm. (c) SEM, basal view of intact ribbon, showing strong interlock between tooth rows; longest teeth on both sides are the shafts of the pluricuspids. *Alvin* dive 1755. Scale bar = 40 μm. (d) SEM, radular ribbon, cusps of rachidian, inner laterals and pluricuspid degraded in preparation, cusps of two marginals intact, showing interaction of shafts and articulation with adjacent teeth. *Alvin* dive 1755. Scale bar = 20 μm. (e, f) SEM views of intact radular ribbon, showing rachidian with straight edge and pointed corners, inner laterals, pluricuspid and marginals. Teeth are close together (due to drying process), compared to (a). *Alvin* dive 1755. (e) One half row of teeth. Scale bar = 20 μm. (f) Full width of radular ribbon. Scale bar = 40 μm.

Palaeozoic limpets. Yochelson's (1960: 245) description of *Lepetopsis* serves below as the description for a new family based on this genus.

LEPETOPSIDAE **new family**

Diagnosis. 'Patelliform gastropods with subelliptical to lozenge-shaped margin; position of apex nearly central to somewhat anterior, strongly anterior only in species doubtfully referred to the genus; shell commonly low in relation to height and width so that lateral surfaces slope at an angle of less than 45 degrees from the horizontal; muscle scar horseshoe-shaped, opening anteriorly and high in shell; outer surface smooth or marked by concentric ornamentation; ribs radial from apex, present in some species' (Yochelson, 1960: 245).

Type genus: Lepetopsis Whitfield, 1882. Mississippian—Triassic.

Remarks. This decription agrees with the shell morphology of the neolepetopsids. They have the subelliptical shape (without marked narrowing of either end), relatively low profile, muscle scar closer to the apex than the margin, and the apex just anterior to centre. *Neolepetopsis* species have concentric sculpture predominating over radial; the muscle scar is relatively thin throughout, closer to the apex than to the margin, the apex just anterior to centre. *Neolepetopsis* has an eroded apical area at all sizes; similarly eroded apices are evident in illustrations of various species of *Lepetopsis* (Yochelson, 1960, pl. 57; Newell, 1935, pl. 35).

Other useful references to *Lepetopsis* are: Knight (1941) for an illustration of the type species, *L. levettei* (White, 1882); Newell (1935) for illustrations of two Mid-Pennsylvanian species; Lipman & Langenheim (1983) for depositional information: 'It is thought to have been deposited in a quiet-water lagoon behind a crinoidal, or locally oolitic, bar. . . .' They noted that 'these interpretations of a quiet depositional environment contrast with the high-energy rocky shoreline habitat of modern patellids.'

Shared characters of shell morphology are here regarded as sufficiently close to relate the neolepetopsids to a late Palaeozoic and early Mesozoic ancestor, the genus *Lepetopsis*. The hydrothermal-vent habitat is also a quiet environment, into which a limpet from a quiet depositional environment could enter.

Lepetopsis has been assigned to the Palaeozoic family Metoptomatidae, a family provisionally placed in the Patellacea by Knight *et al.* (1960: 231), who noted, with reference to their placement: 'The Metoptomatidae are seemingly represented by undescribed species and genera occurring as far back as early Middle Ordovician time. Their derivation is uncertain, but it seems probable that they arose from the early pleurotomarian stem or even from the still more primitive bellerophonts. No direct evidence can be cited to indicate that this family was docoglossate, but on the other hand, there is not yet enough evidence to establish it as a superfamily unrelated to but convergent with the Patellacea.'

The genus *Metoptoma* Philipps, 1836, which ranged from the Mississippian to Permian, has a type species with a posterior apex (Knight, 1941: 194, pl. 2, figs 3a–c; Knight *et al.*, 1960: 232, fig. 143.2), which is a discrepancy that serves to dissociate it from *Lepetopsis*, for the latter has a central apex. Yochelson (1960: 244) noted: 'The difference between the relatively high muscle scar in *Lepetopsis* and the much lower scar in *Metoptoma*, coupled with the pronounced difference in shape and position of the apex, may be fundamental. However, the erections of new families, or monotypical subfamilies within the Metoptomatidae, is not an attractive position in the present

state of our knowledge.' Despite Yochelson's reluctance, exactly that must now be done to limit the present discussion to *Lepetopsis*. I here propose the family name Lepetopsidae for *Lepetopsis*, using Yochelson's above quoted diagnosis for *Lepetopsis* for that of the family. Yochelson (1960: 245) further stated: 'Superficially, *Lepetopsis* appears to be similar to the Recent genus *Patella* Linnaeus. It differs in having the muscle scar rather high in the shell.' Preservation of muscle scars of *Lepetopsis* have not been good enough to result in any comment as to whether the muscle is configured in oval bundles.

Although I can cite no apparent differences based on shell characters, it would not be prudent to place *Lepetopsis* in the Neolepetopsidae, in view of the great differences in age and habitat. Loss of mineralization in the radula, which is hypothesized to be the key distinction between the extinct and living families, should have been accompanied by other changes at the family level.

Discussion

Study of internal anatomy of the neolepetopsid limpets confirms that these are patellogastropods (Fretter, 1990). It has previously been noted (McLean, 1985), based on preliminary work of Fretter, that two kidneys are present and that the gonad discharges through the right kidney. Further characters (Fretter, pers. comm.) include the licker below the tip of the radula (shown in Plate VIIIj), a structure found in all patellogastropod species, but nowhere else, and the single large, dorsally-arched jaw, which is unique to patellogastropods.

Here I discuss the affinity of the group to the Patellogastropoda on shell and radular characters, concluding that the neolepetopsid radula is significant for patellogastropod evolution and higher classification. I have argued in the preceding section that a Palaeozoic fossil record for the superfamily can be tentatively recognized.

Shell characters

Position of apex. The slightly anterior of centre position of the apex of neolepetopsids is similar to that of patellids, unlike that of nacellids and lottiids, in which it is generally closer to the anterior margin.

Protoconch. The protoconch characters of neolepetopsids are common to the order Patellogastropoda. The neolepetopsid protoconch resembles that of lottiid patellogastropods in its expression of the lateral folds or lateral pouches (Plates VIIh, Xg), first described by Morse (1910) and Thompson (1912). They are also observed in most families of cocculiniform limpets (as illustrated by Marshall, 1986). The significance of this character in patellogastropods needs to be further examined, as the pouches are not apparent in the protoconch of *Patella coerulea* (L.) illustrated by Waren (1988).

The neolepetopsid protoconch has its anterior-posterior axis offset about 10° to the right of the anterior-posterior axis of the teleoconch (Plate Xh). This angle of offset is somewhat less than is typical for other patellogastropods. Lindberg (1981a) indicated that the patellacean protoconch is offset as much as 20° to the right of the anterior-posterior axis of the teleoconch (see also Wingstrand, 1985, figs 2B, C). As in other patellogastropods, the neolepetopsid protoconch is lost at a very early stage and the area sealed from within. Although Davis & Fleure (1903) stated for *Patella* that 'the larval shell shows the beginnings of a spiral,' modern authors admit no indication of a coiled phase in the teleoconch in any patellogastropod.

Muscle scar. The muscle scar (and shell muscle) of the neolepetopsids is like that of other

patellogastropods in being horseshoe-shaped, open anteriorly, of consistent width throughout, and constricted into bundles (Plate VIIIf). It tends to be narrower and closer to the mid-dorsal line than that of most other patellogastropods. As in other patellogastropods, a narrow pallial line joins the anterior arms of the muscle scar.

Shell structure. Shell structure of all neolepetopsid species needs to be studied in detail and the observations reported here are preliminary. Neolepetopsids have a periostracum, which is otherwise unknown in the suborder, except for the brackish to freshwater lottiid genus *Potamacmaea* (Lindberg, 1990). In general appearance, shells of the neolepetopsid genera look like the shells of lepetids, especially in lacking colour patterns. Unusual features are the high transparency of the shell of *Eulepetopsis* and the fact that shells in that genus are also unique in not breaking cleanly, as well as the general interior transparency of most species.

Advances in knowledge of patellogastropod shell structure started with MacClintock (1967), followed by papers of Lindberg (see especially 1981*b*, 1986*c*, 1988*b*) and Stutzel (1984), who studied *Patella*. Terminology has recently been standardized by Carter & Clark (1985). There are a number of possibilities for different sequences of structural layers, character states that have been used successfully by Lindberg (1986*b*, 1988*b*) to distinguish monophyletic clades. In Lindberg's classification, the most primitive shell structure is represented in *Patella* (Patellacea), in which foliated, calcitic shell structures form the exterior layers, including the exteriormost layer forming the shell margin and the intermediate area outside the muscle scar. In the more derived Nacellacea and Acmaeacea, the exteriormost surface is formed of prismatic calcite, with other possibilities for the intermediate layers. In all groups the central area within the muscle scar always is at least partially composed of crossed-lamellar, aragonitic layers.

Based on my SEM preparation of a fractured edge of *Neolepetopsis occulta* (Plate XIId), D. R. Lindberg (pers. comm.) has identified four layers from outermost to inner: prismatic, foliated, concentric crossed-lamellar, and radial crossed-lamellar. In the case of *Eulepetopsis vitrea* in which shell transparency is extreme, the exterior prismatic layer has the crystallography of lathic calcite (Carter & Clark's lath-type fibrous prismatic), as shown in Plate VIIIh. Lathic calcite is most commonly seen among bivalves—in certain pectinids, anomiids and ostreids (Waller, 1972, 1978; Runnegar, 1984). These groups are noted for shell transparency; in fact, no other shell structure is known to produce a completely transparent shell.

According to Lindberg (pers. comm.) the shell structure of *Neolepetopsis occulta* (Plate XIId), which is more typical of the family than that of *Eulepetopsis vitrea*, represents 'a structure similar, if not identical, to that of acmaeids (*Acmaea* and *Pectinodonta*) and lepetids.' Thus the shell structure characters imply a closer affinity of the Lepetopsina to the Acmaeacea than to the Patellacea.

External anatomy

The lack of epipodium in the adult, presence of the single, dorsally-arched jaw, presence of fine papillae at the mantle edge, the overall shape of the head, including the oral lappets, are characters of the Neolepetopsidae that are in general agreement with these characters in all patellogastropods. Oral lappets comparable to those of neolepetopsids are found in lepetid and some acmaeid patellogastropods. As in other patellogastropods, there is no operculum in postlarval stages.

Radular characters

Unlike evidence from the shell and external anatomy, which clearly indicates patellogastropod

affinity for the Neolepetopsidae, the evidence provided by the radula is enigmatic. Nevertheless, I have reached conclusions about this radula and its possible phylogenetic significance.

Previous assessments. The first published account of the Group-C radula was that of Hickman (1983, figs 35, 36), based on SEM examination of the species here described as *Eulepetopsis vitrea.* She noted that there is a projection on the shaft of the second lateral tooth that articulates with the cusp of the third lateral tooth. Now that the radula of four species in three genera are known, it is apparent that all have a similar mid-shaft projection on the second lateral tooth, and that the shaft of this tooth is longer than that of other teeth in the row. This particular feature is unknown elsewhere, whether among docoglossate or rhipidoglossate plans. Hickman concluded that the Group-C radular plan represented a new pattern not falling under previous classifications of radular types. She also noted that in some cases the cusps had apparently failed to form.

In my preliminary assessment of each group of hydrothermal-vent limpets (McLean, 1985), I reported that radular characters of the Group-C limpets provided no clues to relationships, except that the general appearance was comparable to that of the cocculiniform family Lepetellidae, in which each lateral tooth in the row is also dissimilar in morphology to that of other lateral teeth in the row.

Method of preparation. The radula of neolepetopsids has presented difficulties in preparation for SEM in that the cusps of the teeth frequently appear to be worn or malformed throughout the length of the ribbon, as noted by Hickman (1983). It is now clear that this is due to an inherent weakness in the cusps. Radular ribbons prepared for optical light microscopy show that the cusps survive the treatment in 10% NaOH for 48 hours, but that those treated further for SEM by air-drying and vacuum-coating are degraded in the process, so that the teeth in most preparations then appear to be defective (Plates IIe, IVe, IXd, XId). Repeated efforts to obtain good preparations for SEM have ultimately succeeded, but I cannot even suggest methods by which to duplicate the results achieved here. To my knowledge, this is the only gastropod family in which the preparation process for SEM may severely degrade the tooth cusps. All radulae prepared for scanning contract to some extent during the drying process, whereas those prepared for optical microscopy have the advantage of remaining unaltered. In the Neolepetopsidae the best understanding of radular characters has resulted from combining information derived from both methods of preparation. Stained whole mounts show the teeth in their normal perspective and also reveal that the cusps do not take stain. I have no explanation for this apparent chemical or structural characteristic of the cusps, but it correlates with their ready capacity for degradation. The SEM preparations are effective in revealing surface topography of the teeth, including the raised nature of the mid-shaft nubs, the presence and significance of which would not even have been noted in the optical preparations. It is clear that there is much to be learned from both techniques, as advocated by Hickman (1977), despite the more recent tendency to use only SEM for the study of radulae.

Tooth-row homologies. Table II gives an analysis of tooth counts for patellogastropod superfamilies and polyplacophoran and monoplacophoran outgroups, based on Lindberg (1988a, table 2), to which I have added corrections and my interpretation of the tooth counts for neolepetopsids.

The robust rachidian tooth of all three genera of Neolepetopsidae has its counterpart in some species of the Patellidae (Plate XIIa; see also Powell, 1973, pl. 104, fig. 3). In Patellidae a rachidian may be present or absent, but if present it is often reduced to a very slender element. The neolepetopsid rachidian, however, is a major element with a long, tapered cusp (except that it is straight across in *Paralepetopsis*). In all three genera it is as well developed as the first lateral tooth. In the Nacellacea and Acmaeacea, which Lindberg (1988b) considers the most advanced
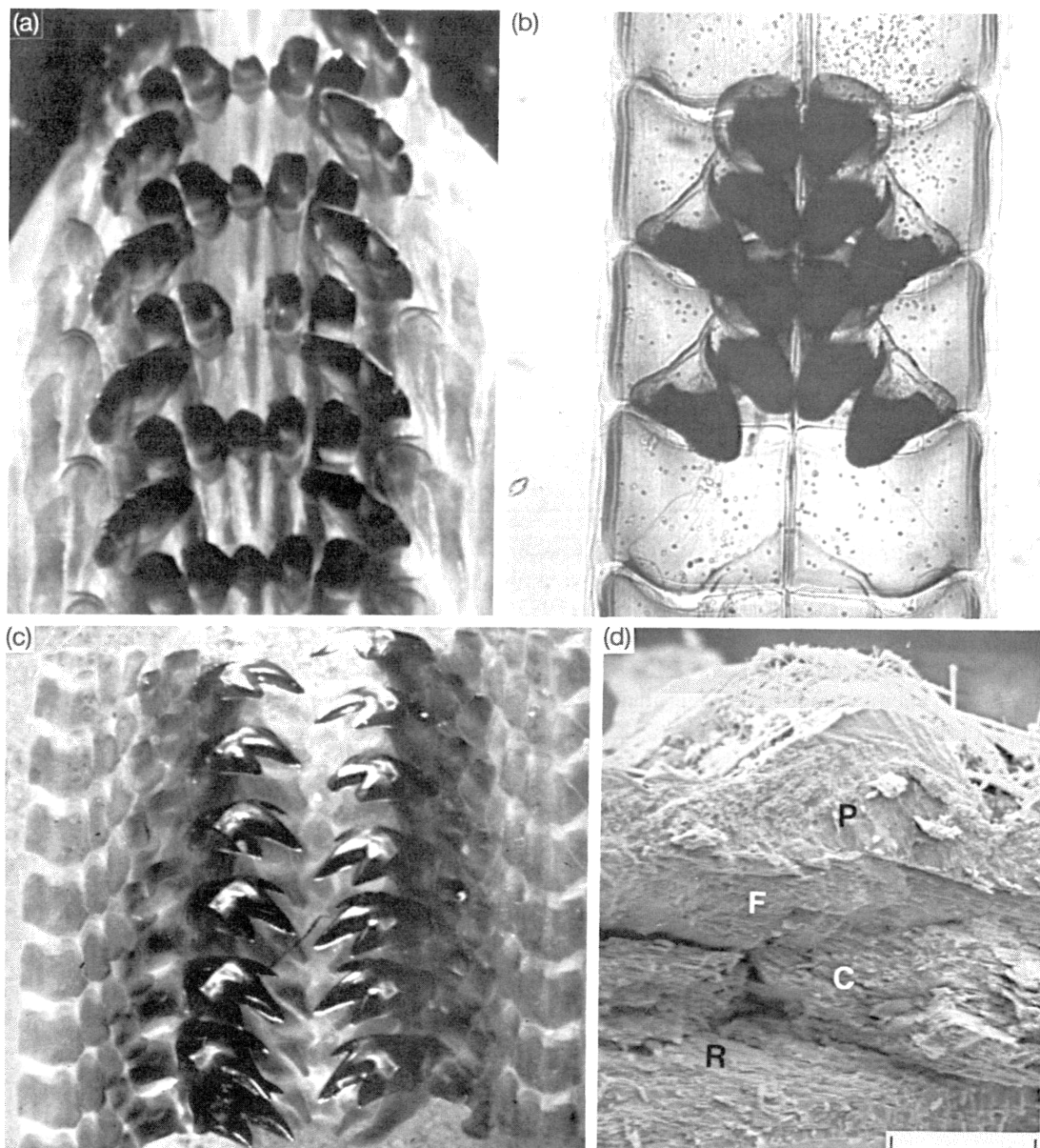
PLATE XII. Typical radulae of large species of Patellidae, Acmaeidae and Polyplacophora; shell structure of Neolepetopsidae. (a) *Patella* (*Ancistromesus*) *mexicana*. Full width of unmounted ribbon showing rachidian, two pairs of inner laterals, pluricuspid (fused outer laterals) with four separate cusps, all with mineralized denticle caps, and three pairs of unmineralized marginals, naturally opaque. Tenacatita Bay, Jalisco, Mexico, LACM 66-55. Width of ribbon 2 mm. (b) *Acmaea mitra*. Full width of ribbon (unstained light microscope preparation) showing three pairs of unfused outer laterals with dark denticle caps; teeth rows stripped from lowermost segment to show basal plates. Arroyo Frijoles, San Mateo County, California, LACM. Width of ribbon 0·7 mm. (c) *Cryptochiton stelleri*. Full width of unmounted ribbon showing dark denticle caps only on pluricuspid teeth; other teeth naturally opaque. Depoe Bay, Oregon, LACM 71–85. Width of ribbon 5 mm. (d) *Neolepetopsis occulta*. SEM view of fractured edge, with exterior node at top. Four layers are visible: P, prismatic; F, foliated; C, concentric crossed-lamellar; R, radial crossed-lamellar. *Alvin* dive 1185. Scale bar = 20 μm.

superfamilies, it is lacking. The presence of a well-developed rachidian in the neolepetopsids is a distinctly primitive character, clearly relating the group to the Patellacea.

Individual tooth pairs are not readily comparable to those of other patellogastropods. The third tooth in the row is difficult to interpret and the relatively broad, outermost teeth are very unlike the marginal teeth of previously known groups. However, the third tooth is too large to be considered comparable to the third lateral tooth of Acmaeacea. It can only be compared to the pluricuspid tooth of the Patellacea (Plate XIIa). In the case of *Patella*, authors are in agreement (e.g. Fretter & Graham, 1962; Jones *et al.*, 1984; Lindberg, 1988a) that the pluricuspid tooth represents a fusion of three to four originally separate outer lateral teeth. A pluricuspid tooth is lacking in Acmaeacea (Plate XIIb). In the Acmaeacea, the tooth homologies with Patellacea are explained by considering the inner laterals of *Patella* to be lacking and the remaining teeth to be unfused outer laterals. I favour the designation of the third neolepetopsid tooth as a reduced pluricuspid because in each genus it is the broadest tooth and in the type species of *Neolepetopsis* there are two well-differentiated cusps (Plate IIe).

Further affinity to the Patellacea is suggested by the tooth row alignment, in which the rachidian and first two lateral teeth form a row that is more anteriorly placed than the other teeth in the row. This stepped arrangement is most readily apparent in *Neolepetopsis* (Plate IIe). Overall views of the radula of *Paralepetopsis* (Plate XId–f) indicate a break between second and third teeth in the row, but here the cusps of the rachidian and inner laterals are not aligned straight across. In all genera the lower placement of the cusp of the third tooth enables it to interact with a nub on the shaft of the second tooth. Although not observed in *Patella* (Plate XIIa), such an interaction would make sense in *Patella*, in which a cusp on the second tooth would serve to shield that tooth from contact with the massive edge of the pluricuspid. Thus, the only functional explanation for these nubs (a hallmark of the family) is consistent with the assumed affinity to the Patellidae.

The remaining two teeth are designated as marginals. In their broader, plate-like form they are more reminiscent of the outer marginals of neopilinid monoplacophorans than of other extant patellogastropods. My conclusions about tooth row homologies are summarized in Table I.

Longitudinal bending. According to recent definitions (e.g. Fretter & Graham, 1962; Haszprunar, 1988a), the docoglossate radula undergoes no longitudinal bending. Yet it is evident from the illustration of a protracted radula in a young specimen of *E. vitrea* (Plate IXb–c) that the radula of neolepetopsids does undergo a limited degree of longitudinal folding, enough to splay the first and second inner lateral teeth more than 45° (over 90° from left to right) to reveal the inner sides of these teeth. This radula is therefore not entirely docoglossate in a functional sense. However, it does not achieve the complex longitudinal folding at the bending plane, as illustrated by Morris & Hickman (1981, figs 2–9) for an artificially protracted rhipidoglossate radulae. It is therefore functionally intermediate between the docoglossate radula of other patellogastropods (stereoglossate condition of Haszprunar, 1988a) and a rhipidoglossate radula (flexoglossate condition of Haszprunar, 1988a), in which there are large numbers of marginal teeth.

Tooth articulation. A major distinctive feature of the neolepetopsid radula is the articulation of bases and shafts of all teeth with adjacent teeth in the row and with teeth in the adjacent rows. There are complex arrangements of lateral projections and sockets at the bases of the shafts, including the unique articulation between the base of the second inner lateral and the inner edge of the pluricuspid. In *Neolepetopsis*, there is a curved depression on the pluricuspid that accommodates the entire inner edge of the second inner lateral. In *Eulepetopsis*, there is a good fit between the first marginal and the groove on the pluricuspid (Plate IXe). In their formative stage, the edges of the ribbon are folded together, keeping these teeth in contact. The morphology of the

TABLE III

Lengths and widths of patellogastropod radular ribbons, compared to shell lengths (all in mm)

Species	Shell length (sl)	Radula length (rl)	Radula width (rw)	rl/sl	rl/rw
Suborder Lepetopsina (*Alvin* dive no.)					
Neolepetopsis gordensis (2040)	7·3	10·3	0·18	1·41	57·2
Eulepetopsis vitrea (1225)	14·6	5·3	0·18	0·36	29·4
E. vitrea (1225)	16·2	5·3	0·20	0·33	26·5
E. vitrea (991)	7·8	2·2	0·09	0·28	24·4
Paralepetopsis floridensis (1753)	7·0	6·6	0·13	0·94	50·7
Suborder Patellina (LACM locality no.)					
Patella vulgata (80–54)	33·4	52·0	0·8	1·56	65·0
Nacella magellanica (75–50)	33·6	70·0	0·65	2·08	107·7
Cellana radiata (77–123)	35·0	75·0	0·4	2·14	187·5
Lottia pelta (76–12)	32·9	28·0	0·6	0·85	46·7
Acmaea mitra (1464–42)	32·0	44·0	0·9	1·38	48·9

inner laterals of *Eulepetopsis* also indicates a close fit when the edges of the ribbon are curled inward.

Such interactions are unknown in other patellogastropod radulae, in which the teeth act independently, with no articulation between the long shafts of adjacent teeth in the row (Plate XIIa, b). The capacity for articulation in neolepetopsids is certainly a correlate of the capacity of the radula to bend longitudinally. Major articulation between teeth is a character shared with the polyplacophoran outgroup and to a lesser extent with the neopilinids, and it is therefore plesiomorphic to docoglossate radulae in general.

Size. *Neolepetopsis gordensis* and *Paralepetopsis floridensis* have relatively long radulae, compared to those of *Eulepetopsis vitrea*, in which the radular length is only about one-third the length of the shell (Table III). The former two genera are within the shell to radular length ratios of typical shallow-water members of Patellina, in which radula lengths approach or greatly exceed shell lengths (Table III).

Lack of mineralization. The neolepetopsid radular ribbon differs from that of other patellogastropods in that the denticle caps are unmineralized, appearing uniformly transparent under magnification. Whether these teeth are completely lacking mineralization should be determined, however. In other patellogastropods the shafts of the teeth are translucent yellow and the caps of the lateral teeth are sharply demarcated in dark brown or black (Plate XIIa, b). The entire length of the neolepetopsid radula is comparable to the first 10% of the length of the ribbon of other patellogastropods at the nascent end, where the fully formed teeth are lacking pigmentation, in a condition prior to mineralization.

Neolepetopsids can be considered paedomorphic with respect to arrested radular development, maturity being attained prior to the radular mineralization that characterizes all other patellogastropods.

Lack of mineralization is probably not related to depth nor to the chemistry of the hydrothermal environment, as there are vent-associated species of Lepetidae and Acmaeidae (to be described separately) in which mineralization is not lost.

The tooth cusps of neolepetopsids correspond to the denticle caps in species of shallow-water *Patellina*. The fact that these cusps do not take stain and are easily degraded in the process of preparation for SEM can be understood as a phylogenetic result of demineralization of the denticle caps in the Neolepetopsidae.

Functionally, the loss can be understood in terms of less need for hardened, mineralized teeth when a shallow-water food source of calcified algae is replaced by a food source of uncalcified sulphur bacteria in the hydrothermal-vent habitat.

Tooth attachment. The neolepetopsid radula is comparable to the radula of the patellacean *Patella* in that no damage is done to it by cleaning in room-temperature 10% NaOH for 48 hours. Polyplacophoran radulae are also unaffected by such treatment. In contrast, such treatment of radulae of nacellacean or acmaeacean species makes the teeth easily detachable with a fine brush. Radular ribbons and teeth are chitinous, but in the latter two superfamilies the bond between the teeth and the basal plates is alkaline soluble (as was noted for Acmaeacea by Lindberg, 1981*b*: 14). To observe this, I placed one dissected buccal mass for each of the species in Table III in 10% NaOH for 24 hours. The teeth of *Patella vulgata* remained attached, and those of *Nacella magellanica*, *Cellana radiata*, *Lottia pelta* and *Acmaea mitra* were readily detached, but I also noted that the teeth in the unpigmented, unmineralized portion of the ribbons for all species were not weakened by the process and could not be separated from the basal membrane with a fine brush. It is therefore not clear whether the firmly attached condition of the neolepetopsid teeth correlates with lack of mineralization or indicates an affinity with Patellacea, in which there evidently are phylogenetic constraints against easily detached teeth.

Lack of basal plates. Another correlation between the patellogastropods with non-detachable teeth (Patellacea and Lepetopsacea) and those with detachable teeth (Nacellacea and Acmaeacea) is that the ribbons of the former do not show the clear-cut division into segments by tooth rows as do the Nacellacea and Acmaeacea. In the Nacellacea and Acmaeacea, the basal plates that correspond to each tooth row form quadrangular segments that remain after the teeth are stripped away (Plate XIIb). Basal views of neolepetopsid ribbons show no subdivisions into segments (Plate XIc). Lindberg (1986*a*) regarded the increasing complexity of the basal plates in the sequence leading from Patellacea to Nacellacea to Acmaeacea as a major trend in radular evolution. Thus, it is evident that the lepetopsacean radula is primitive both in absence of basal plates and retention of teeth on the ribbon.

Summary of radular characters. The neolepetopsid radula is unique among patellogastropods in the following characters: (1) articulating bases and shafts of all teeth; (2) lack of mineralization of denticle caps; (3) having a limited capacity to bend longitudinally; (4) mid-shaft projection of second inner lateral tooth articulating with edge of pluricuspid; (5) delicate condition of tooth cusps (not taking stain and easily degraded).

Primitive characters shared with Patellacea are: (1) presence of a well-formed rachidian tooth; (2) presence of two pairs of inner lateral teeth; (3) outer lateral teeth represented by pluricuspid tooth; (4) firmly attached condition of the teeth; (5) lack of segmentation of the basal ribbon.

Position of Lepetopsina within Patellogastropoda

A complete analysis of character states, including those of anatomy and shell structure cannot be accomplished until those details are published. On the basis of evidence from anatomy, Fretter (pers. comm.) believes the affinity of Neolepetopsidae to be somewhat closer to the Acmaeacea than the Patellacea. Shell structure, as noted above, also suggests affinity to Acmaeacea. However,
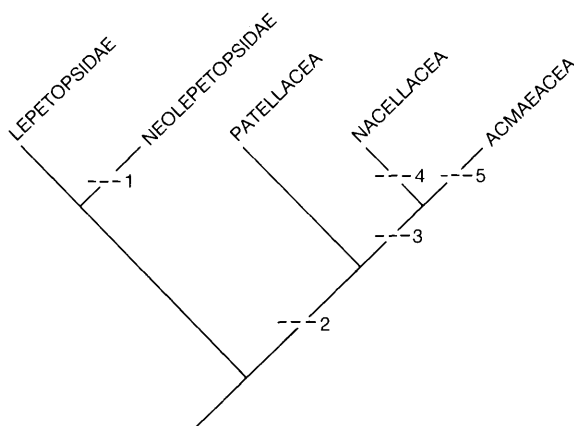
FIG. 1. Hypothesized events in patellogastropod radular evolution. The archetypical radula has mineralized, articulating teeth, a rachidian, two pairs of inner laterals, outer laterals fused to form pluricuspid tooth, and three pairs of marginals. 1, loss of mineralization, reduction of marginals to two pairs. 2, loss of articulation within and between tooth rows. 3, loss of rachidian tooth. 4, loss of first pair of inner laterals. 5, loss of remaining pair of inner laterals, outer laterals no longer fused, marginals reduced to two pairs or less.

the entire suite of radular characters points to an affinity nearer to the Patellacea, except that the loss of mineralization is secondary and altogether outside the main line of radular evolution in the Patellogastropoda.

Despite contradictory evidence from anatomy and shell structure (which can possibly be explained as convergence), I proceed on the assumption that tooth articulation in neolepetopsids is the most significant character (in essence a set of characters), one that is plesiomorphic for the entire suborder and basic to patellogastropod evolution. It therefore supports a basal position for the Lepetopsacea and justifies the recognition of a sister group Lepetopsina equivalent to the Patellina. This assumption has the advantage of support from outgroup comparison. Because tooth articulation is characteristic of polyplacophorans, the neopilinid monoplacophorans, and the neolepetopsids, it is a plesiomorphic character and, if the weighting of this character is correct, it therefore follows that extant Patellina (Patellacea, Nacellacea and Acmaeacea) may be the aberrant limpets in having lost the capacity of the teeth to interact with others in the row or with adjacent rows (Fig. 1). However, because the character(s) of articulating teeth is plesiomorphic, its loss, by itself, does not indicate whether the loss has occurred once or many times in the Patellina as here defined. Further evidence as to the polyphyly or monophyly of Patellina can be obtained from a cladistic analysis based on many more characters than are available to me. The assumption here that the loss of tooth articulation occurred once is speculative.

The Palaeozoic and early Mesozoic fossil record of the Patellogastropoda is poorly known (see Knight et al., 1960) and subject to controversial interpretation (see Yochelson, 1988, and references therein). The fossil record of extant patellogastropod taxa is taken only to the Cretaceous by Lindberg (1988b), although Bandel (1989) notes the presence of 'species of modern appearance' in the St. Cassian Triassic. I offer a speculative scenario of patellogastropod evolution as follows: The divergence between articulating teeth (suborder Lepetopsina) and non-articulating teeth (suborder Patellina) may have taken place near the Permian-Triassic transition, coinciding with a rapid radiation of species of modern appearance. Earlier patellogastropods from shallow

water environments would certainly have had mineralized teeth (to cope with calcareous algal food sources), but there is now good reason to expect that they had articulating teeth. All Palaeozoic patellogastropods may therefore be tentatively assigned to the suborder Lepetopsina. Straight-shafted, non-articulating teeth of extant patellogastropods are evidently effective and are rapidly replaced with wear, which may be a correlate of the present success of Patellina in high-energy, shallow water habitats.

Haszprunar (1988a, b) regarded the Docoglossa (= Patellogastropoda) as the first major gastropod offshoot. He hypothesized (Haszprunar, 1988a) that 'the gastropod archetype' would have had a 'stereoglossate radula of the neopilinid/lepetid type,' for which he depicts a rachidian plus two lateral teeth and two marginal teeth. Such a low number of lateral teeth represents an advanced condition in patellogastropods. According to Lindberg's analysis of tooth counts in patellogastropods and outgroups (shown here in Table I), it is more likely that there would have been a minimum of three interactive laterals (two inner, plus a four-cusped pluricuspid) and three marginals, which is the primitive number in extant Patellogastropoda and closer to the number in Polyplacophora (Fig. 1). Although Polyplacophora have only one pair of inner laterals, they have a strongly developed pluricuspid, as do the basal patellogastropods Lepetopsacea and Patellacea. The low number of teeth now known in the deep-water to abyssal neopilinids is not relevant to the number of teeth that would have been present in basal monoplacophorans of shallow-water habitats of the Palaeozoic.

Lindberg (1981a) argued that there must be a coiled ancestor in patellogastropod evolution, based on asymmetrical protoconch alignment; Lindberg (1988a: 57) has mentioned further lines of evidence in support of a coiled ancestor. Haszprunar alone (1988a) has argued that the docoglossate gastropod archetype was a primary limpet and that coiling is a derived character of non-docoglossate groups.

On the origin of the rhipidoglossate radula

Haszprunar (1988a: 390) stated: 'Recent investigations by McLean (pers. comm.) revealed that the radula of the group-C hot-vent limpets might reflect an intermediate condition between the docoglossate and the rhipidoglossate radula. Although being still stereoglossate this type has a well-developed rachis tooth, non-mineralized lateral teeth, and lacks basal plates. All these characters are present in the rhipidoglossate radula, whereas the radula of Polyplacophora, Tryblidiida and Docoglossa [= Patellogastropoda] have a weakly developed rachis tooth, mineralized lateral teeth and basal plates. The latter conditions are thus primitive for Gastropoda. Indeed, the group-C hot-vent limpets have the only type of stereoglossate radula, from which an evolution of the rhipidoglossate type appears possible.' Although the development of discrete basal plates is an apomorphy only of the patellogastropod superfamilies Nacellacea and Acmaeacea, Haszprunar's statement still holds. I add to it the observation that there is some longitudinal bending (partial flexoglossate condition) in the neolepetopsid radula (indicated in at least a young specimen of *Eulepetopsis vitrea*, Plate Vb, c), and that the significant tooth-articulation is also in accordance with the rhipidoglossate plan.

A radula transitional between the docoglossate and rhipidoglossate plans would have been unmineralized and would have had the tooth configuration of the gastropod archetype described above: three interactive laterals (two inner, plus a four-cusped pluricuspid) and three marginals. Unmineralized homologues of the pluricuspid should have had the capacity for either reduction or enlargement, as in the enlarged outer lateral of many rhipidoglossate groups.

I do not mean to suggest that the neolepetopsid radula itself is an intermediate example, only that some of its features provide clues as to how the wide differences between the two basic plans could be bridged by a common gastropod ancestor.

Time of entry to the hydrothermal-vent community

I have earlier offered my views concerning age and origin of the new families of hydrothermal vent limpets (McLean, 1981, 1985, 1988a, b, 1989a, b, and references therein) and will therefore summarize rather than repeat the details of the same arguments here. I note again that all the hydrothermal-vent limpets are derived from archaeogastropod (docoglossate or rhipidoglossate) stocks to the clear exclusion of taenioglossate stocks.

The Lepetopsacea, as well as the other newly described superfamilies from the hydrothermal-vent community (Neomphalacea, Lepetodrilacea, and Peltospiracea) differ at the superfamily level (or higher) from archaeogastropod superfamilies living in other marine habitats. Because they are not derivatives of established families their origin must be placed in the same time frame as the origin of other living archaeogastropod superfamilies, which are traceable to the late Palaeozoic and early Mesozoic. This was a time at which archaeogastropods were the dominant component of the gastropod fauna, and a time at which the fossil record indicates a greater diversity at the family level than today (Knight et al., 1960). The ancestors of the Lepetopsacea, as well as the Neomphalacea, Lepetodrilacea and Peltospiracea, would have escaped the extinction that befell other (in most cases unknown) shallow-water members of their groups by invading the deep-sea hydrothermal-vent habitat. 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 (Newman, 1979; McLean, 1981, 1985).

The hydrothermal-vent habitat has existed throughout geologic time (Skinner, 1983); fossil vent communities with worm-like tubes have been reported in sulphide deposits of Carboniferous (Banks, 1985) and Cretaceous age (Haymon & Koski, 1985). Although individual vent sites have a relatively short duration and are subject to faunal succession (Hessler et al., 1988), the composition of the hydrothermal-vent community should remain stable over geologic time because the toxicity of the sulphide environment should deter invasions of new predators, providing a refuge for archaic forms and enabling their continued radiation in the habitat.

Admittedly, the evidence presented here for the direct lineage between the Permian-Triassic Lepetopsidae and the Recent Neolepetopsidae is based on morphological characters that are subject to convergence. Hickman (1984) and Waren & Bouchet (1989) noted that many mollusc families have rapid evolutionary histories and these authors do not rule out relatively recent invasion and evolution of hydrothermal-vent faunas. The only completely convincing fossil evidence for the antiquity of vent faunas is seen in barnacles: Newman (1979) and Newman & Hessler (1989) have described two endemic genera that are surviving relics of suborders that first appeared in the Mesozoic.

Some indication of the minimal time of origin of the Neolepetopsidae derives from consideration of the biogeographic implications of the distribution of *Neolepetopsis gordensis* and *Paralepetopsis floridensis*, the two neolepetopsid species occurring at sites that are non-contiguous with the East Pacific Rise. Tunnicliffe's discussion (1988) of biogeographic relationships between the fauna of the Juan de Fuca/Gorda Ridge and East Pacific Rise was based on the premise that the two ridge systems have been disjunct for approximately 35 million years. *Neolepetopsis* must

therefore have at least an Oligocene origin to have species on both ridge systems. Hecker (1985 and references therein) noted that deep-sea sulphide habitats would be provided by a volcanic arc in the Central American Seaway during the Eocene, allowing for faunal interchange between species now known from the Florida Escarpment and the East Pacific Rise. The separation of *Paralepetopsis* from *Eulepetopsis* and *Neolepetopsis* can therefore be understood as no younger than Eocene. Knowledge of faunas of more distant vent sites, combined with similar considerations of plate tectonics and vicariant events will provide a framework for further elucidations of evolutionary histories of vent faunas.

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