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

JAMES H. MCLEAN

Los Angeles County Museum of Natural History, Los Angeles, California 90007, USA

(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 Patellacea, 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 (1988*a*), 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
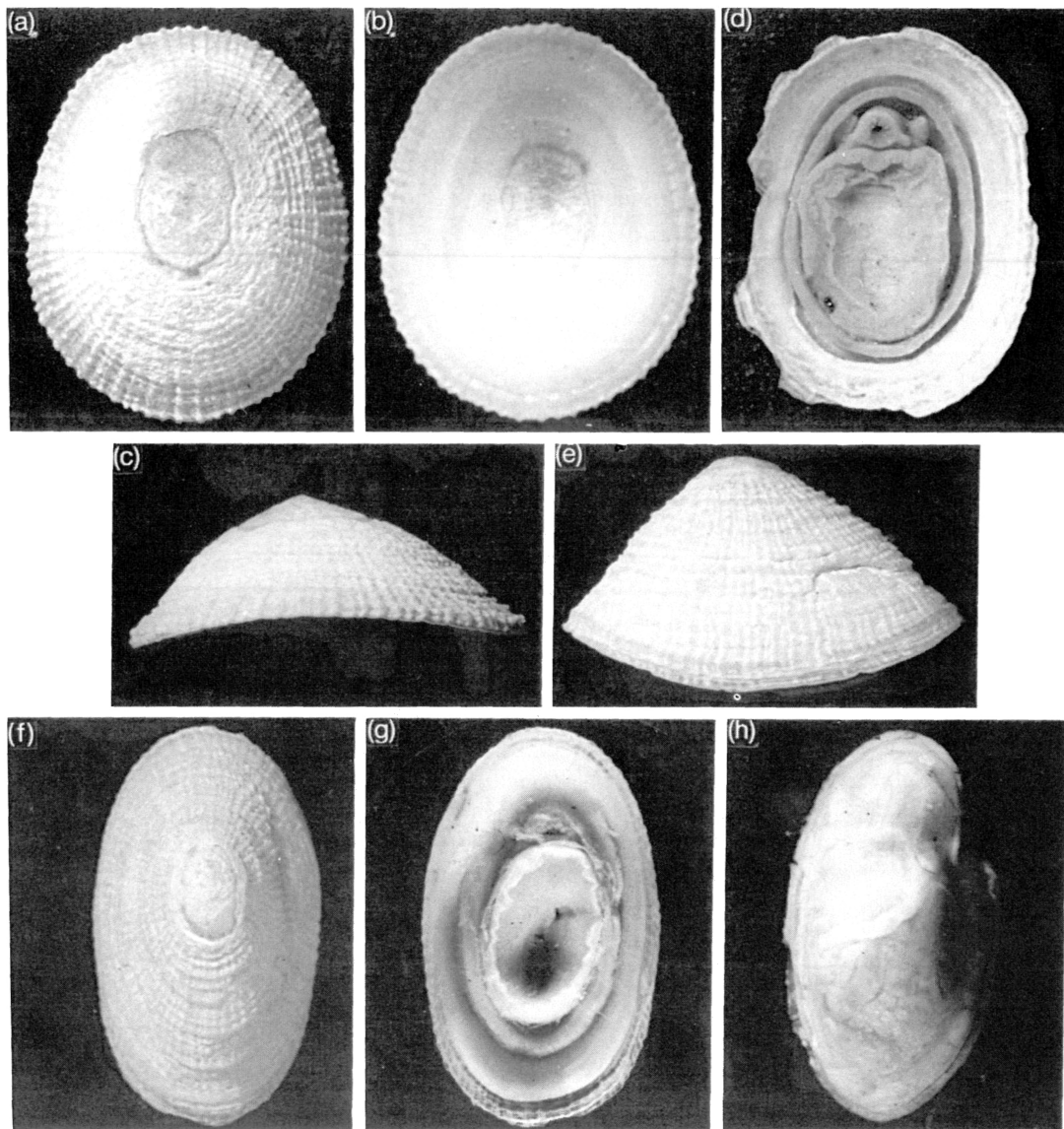
PLATE I. *Neolepetopsis gordensis*, shell and external anatomy. All from Gorda Ridge. Anterior at top in vertical views. (a–c) Holotype shell, *Alvin* dive 2040. Shell length 7·6 mm. (a) Exterior, apex eroded. (b) Interior, muscle scar poorly defined. (c) Left side. (d) Paratype, ventral view with body 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.
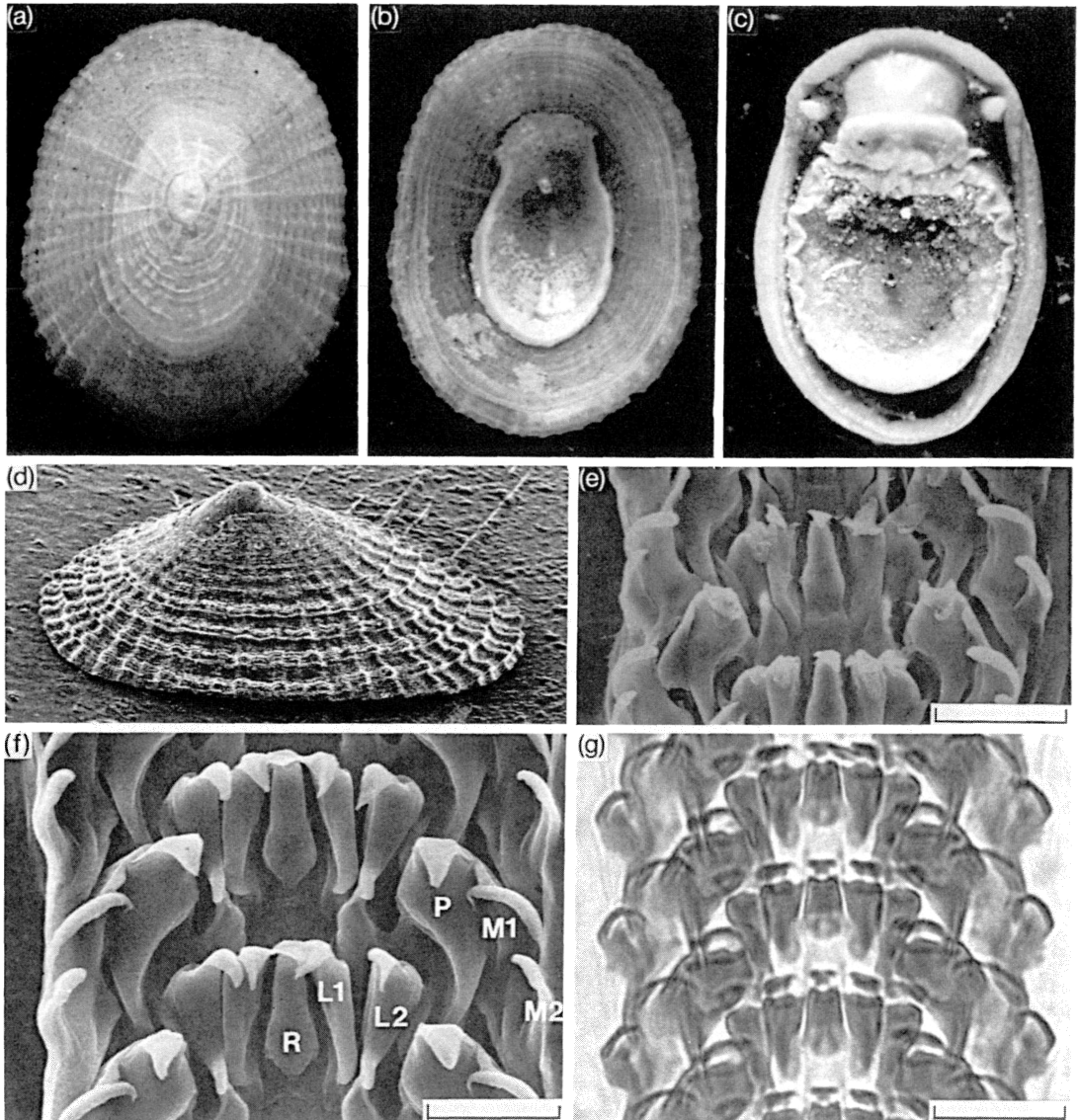
PLATE II. *Neolepetopsis gordensis*, shell, external anatomy and radula. All from Gorda Ridge. Anterior at top in vertical views. (a–c) Partially grown specimen, *Alvin* dive 2035. Length 5·0 mm. (a) Exterior. (b) Interior. (c) Ventral view of detached body, showing small oral lappets and sulphide particles 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
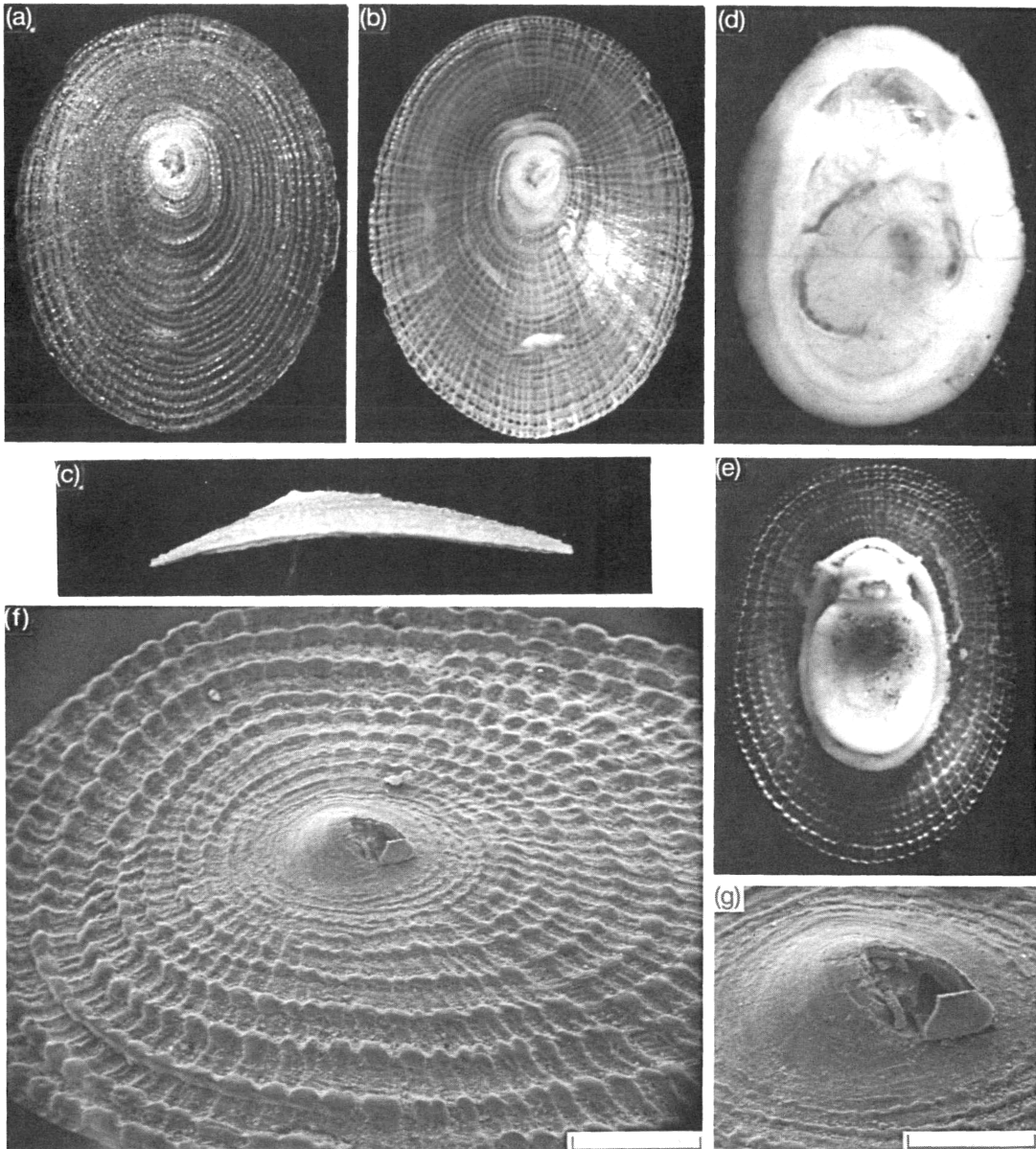
PLATE III. *Neolepetopsis densata*, shell and external anatomy. All from East Pacific Rise at 12° N, *Alvin* dive 2003. Anterior at top in vertical views. (a–d) Holotype, shell length 7·3 mm. (a) Exterior, apex eroded. (b) Interior, showing exterior sculpture by transparency and interior thickening near 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.