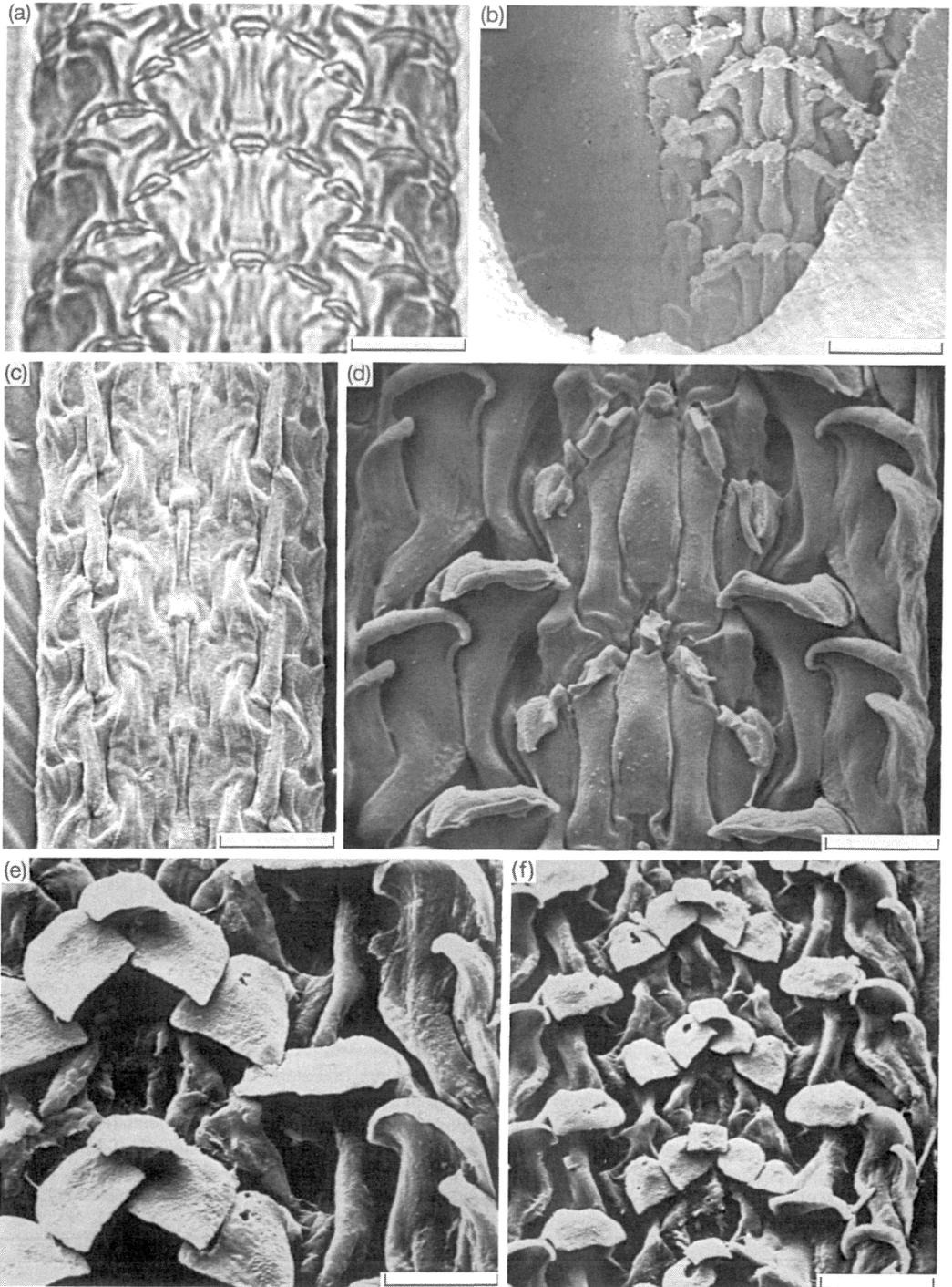


PLATE X. *Paralepetopsis floridensis*, shell, external anatomy and protoconch. All from Florida Escarpment. Anterior at top in vertical views. (a–c) Holotype shell, *Alvin* dive 1342. Length 9.4 mm. (a) Exterior, showing eroded apex. (b) Interior, showing horseshoe-shaped muscle scar closer to centre 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  $\mu\text{m}$ . (g) Dorsal view of protoconch showing lateral pouches. Scale bar = 200  $\mu\text{m}$ . (h) Complete shell, showing slightly offset protoconch, relative to anterior/posterior axis. Scale bar = 400  $\mu\text{m}$ .



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 XIId. 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

---

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  $\mu\text{m}$ . (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  $\mu\text{m}$ . (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  $\mu\text{m}$ . (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  $\mu\text{m}$ . (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  $\mu\text{m}$ . (f) Full width of radular ribbon. Scale bar = 40  $\mu\text{m}$ .

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 description 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 VIII f). 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 XII d), 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 VIII h. Lathic calcite is most commonly seen among bivalves—in certain pectinids, anomids 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 XII d), 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, XIId). 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

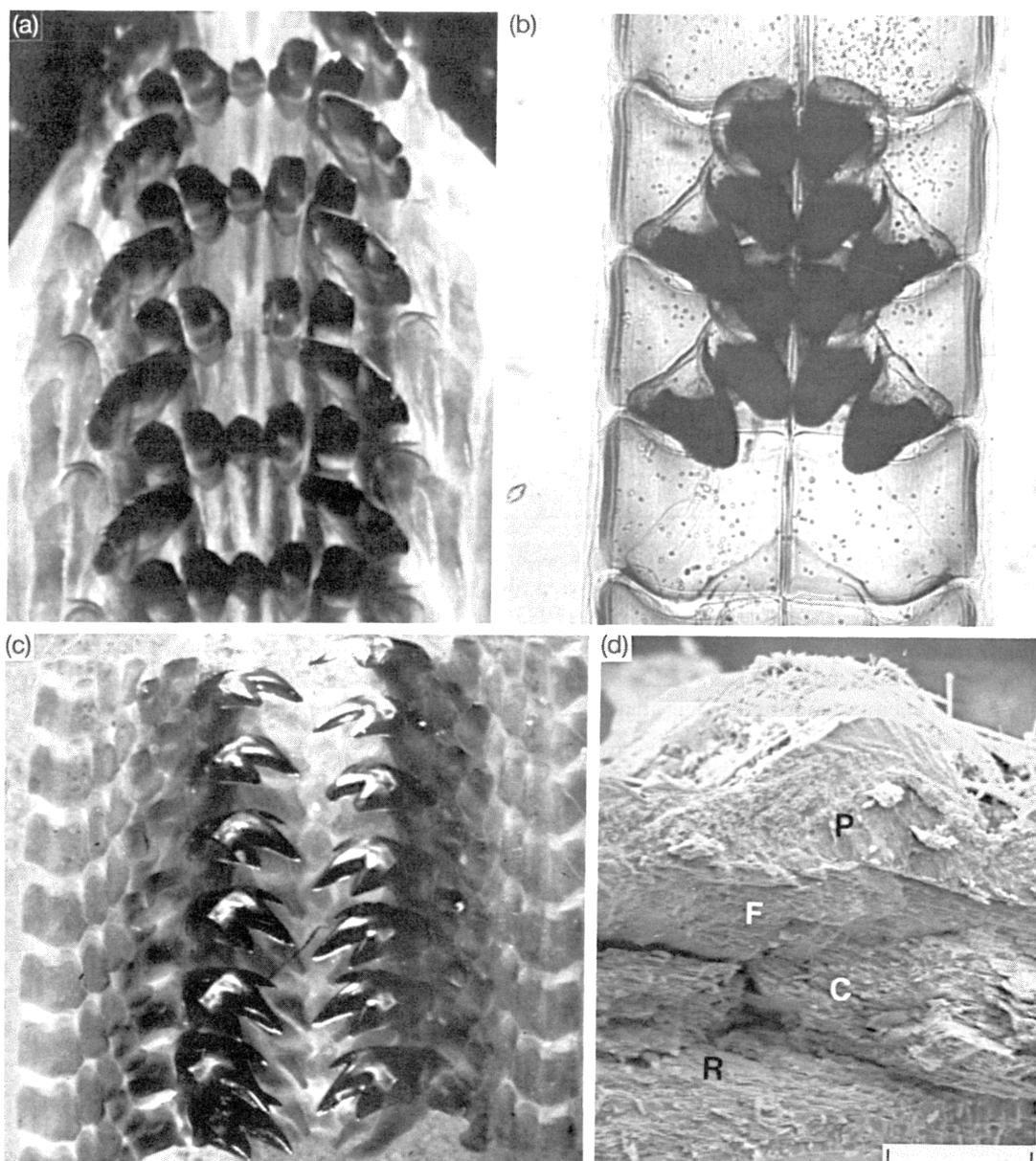


PLATE XII. Typical radulae of large species of Patellidae, Acmaeidae and Polyplacophora; shell structure of Neolepetopsidae. (a) *Patella (Ancistromesus) mexicana*. Full width of unmounted ribbon showing rachidian, two pairs of inner laterals, pluricuspid (fused outer laterals) with four separate cusps, 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  $\mu$ m.

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 XI d-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 IX b-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 IX e). 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 ( <i>Alvin</i> dive no.)					
<i>Neolepetopsis gordensis</i> (2040)	7.3	10.3	0.18	1.41	57.2
<i>Eulepetopsis vitrea</i> (1225)	14.6	5.3	0.18	0.36	29.4
<i>E. vitrea</i> (1225)	16.2	5.3	0.20	0.33	26.5
<i>E. vitrea</i> (991)	7.8	2.2	0.09	0.28	24.4
<i>Paralepetopsis floridensis</i> (1753)	7.0	6.6	0.13	0.94	50.7
Suborder Patellina (LACM locality no.)					
<i>Patella vulgata</i> (80-54)	33.4	52.0	0.8	1.56	65.0
<i>Nacella magellanica</i> (75-50)	33.6	70.0	0.65	2.08	107.7
<i>Cellana radiata</i> (77-123)	35.0	75.0	0.4	2.14	187.5
<i>Lottia pelta</i> (76-12)	32.9	28.0	0.6	0.85	46.7
<i>Acmaea mitra</i> (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, 1981b: 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 (1986a) 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,

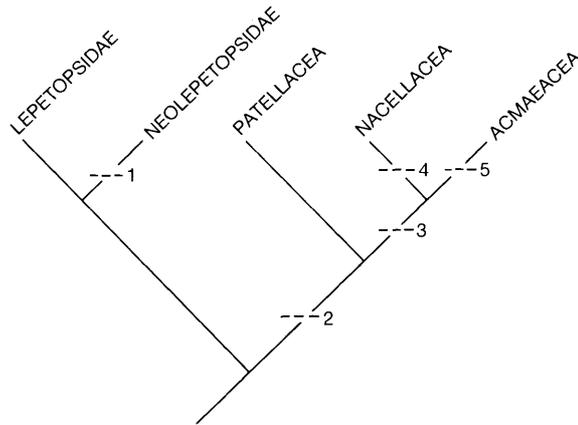


FIG. 1. Hypothesized events in patellogastropod radular evolution. The archetypal radula has mineralized, articulating teeth, a rachidian, two pairs of inner laterals, outer laterals fused to form pluricuspid tooth, and three pairs of marginals. 1, loss of mineralization, reduction of marginals to two 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 (1988*b*), 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 (1988*a, b*) regarded the Docoglossa (= Patellogastropoda) as the first major gastropod offshoot. He hypothesized (Haszprunar, 1988*a*) 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 (1981*a*) argued that there must be a coiled ancestor in patellogastropod evolution, based on asymmetrical protoconch alignment; Lindberg (1988*a*: 57) has mentioned further lines of evidence in support of a coiled ancestor. Haszprunar alone (1988*a*) 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 (1988*a*: 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, 1988*a, b*, 1989*a, 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.

I thank those who have participated in the National Science Foundation sponsored cruises using the *Alvin*, in particular Carl J. Berg, Jr, J. Frederick Grassle, Barbara Hecker, Robert R. Hessler, Lisa Levin, Richard A. Lutz, Ruth D. Turner and Cindy Van Dover for directing limpet specimens to me. Many of these specimens (those from the Galapagos Rift and 21° N) were sorted, counted and forwarded from Woods Hole Oceanographic Institution by Isabelle P. Willimas. I thank Philippe Bouchet (MNHN) for allowing me to include the limpets from the Biocyarise and Biocyatherm expeditions to the 13° N site collected by the *Cyana* under the direction of D. Desbruyères. These specimens were sorted and counted under the supervision of M. Segonzac at CENTOB, Brest, France. Photographs of limpet bodies are the work of Bertram C. Draper. SEM micrographs were made at the University of Southern California with the help of C. Clifton Coney (LACM). SEM micrographs in Plates VIIIh–j and IXb–d were made with the help of David R. Lindberg, then at the University of California, Santa Cruz. Support for this work was provided by a grant from the Los Angeles County Museum of Natural History Foundation. I am grateful to David R. Lindberg for discussion throughout the course of this work. I thank Gerhard Haszprunar, Vera Fretter, Bruce A. Marshall, Winston F. Ponder, Anders Waren and Ellis Yochelson for helpful reviews of the manuscript and leads to references. I do not wish to imply that all have endorsed my conclusions, however.

#### REFERENCES

- Bandel, K. (1989). Larger gastropod units present in the Triassic of St. Cassian Formation. In *Unitas Malacologia, Tenth Int. Malacol. Congr., Tubigen, Abstracts*: 21. Meier-Brook, C. (Ed.).
- Banks, D. A. (1985). A fossil hydrothermal worm assemblage from the Tynagh lead-zinc deposit in Ireland. *Nature, Lond.* **313**: 128–131.
- Carter, J. G. & Clark, G. R., III (1985). Classification and phylogenetic significance of molluscan shell microstructure. In *Mollusks, notes for a short course*: 50–71. Broadhead, T. W. (Ed.). *Univ. Tenn. Dep. Geol. Sci. Stud. Geol.* **13**.
- Commeau, R. F., Paul, C. K., Commeau, J. A. & Poppe, L. J. (1987). Chemistry and mineralogy of pyrite-enriched sediments at a passive margin sulfide brine seep: abyssal Gulf of Mexico. *Earth Planet. Sci. Lett.* **82**: 62–74.
- Corliss, J. B., Dymond, J., Gordon, L. I., Edmond, J. M., Herzen, R. P. von, Ballard, R. D., Green, K., Williams, D., Bainbridge, A., Crane, K. & Andel, T. H. van (1979). Submarine thermal springs on the Galapagos Rift. *Science, Wash.* **203**: 1073–1083.
- Davis, J. R. A. & Fleure, H. J. (1903). *Patella*. *Proc. Lpool Biol. Soc.* **17** (LMBC Mem. No. 10): 193–268.
- Desbruyères, D., Crassous, P., Grassle, J., Khripunoff, A., Reyss, D., Rio, M. & van Praet, M. (1982). Données écologiques sur un nouveau site d'hydrothermalisme actif de la ride du Pacifique oriental. *C. r. hebd. Séanc. Acad. Sci., Paris* (III) **295**: 489–494.
- Desbruyères, D. & Laubier, L. (1980). *Avinella pompejana* gen. sp. nov., Ampharetidae aberrant des sources hydrothermales de la ride Est-Pacifique. *Ocean. Acta* **3**: 267–274.
- Desbruyères, D. & Laubier, L. (1983). Primary consumers from hydrothermal vent animal communities. In *Hydrothermal processes at seafloor spreading centers*: 711–734. Rona, P. A., Bostrom, K., Laubier, L. & Smith, K. L. Jr (Eds). New York: Plenum.
- Fretter, V. (1988). New archaeogastropod limpets from hydrothermal vents, superfamily Lepetodrilacea. Part 2. Anatomy. *Phil. Trans. R. Soc. (B)* **319**: 33–82.
- Fretter, V. (1989). The anatomy of some new archaeogastropod limpets (Superfamily Peltospiracea) from hydrothermal vents. *J. Zool., Lond.* **218**: 123–169.

- Fretter, V. (1990). The anatomy of some new archaeogastropod limpets (Order Patellogastropoda, Suborder Lepetopsina) from hydrothermal vents. *J. Zool., Lond.* **222**, 529–556.
- Fretter, V. & Graham, A. (1962). *British prosobranch molluscs: their functional anatomy and ecology*. London: Ray Society.
- Fretter, V., Graham, A. & McLean, J. H. (1981). The anatomy of the Galapagos Rift limpet, *Neomphalus fretterae*. *Malacologia* **21**: 337–361.
- Golikov, A. N. & Starobogatov, Y. I. (1975). Systematics of prosobranch gastropods. *Malacologia* **15**: 185–232.
- Haszprunar, G. (1988a). On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. *J. moll. Stud.* **54**: 367–441.
- Haszprunar, G. (1988b). A preliminary phylogenetic analysis of streptoneuro Gastropoda. In *Prosobranch phylogeny. Proc. Ninth Int. Malacol. Congr., Edinburgh, 1986*: 7–16. Ponder, W. F. (Ed.). *Malac. Rev.* (Suppl.) **4**.
- Haszprunar, G. (1988c). Anatomy and relationships of cocculiniform limpets, and its bearing on archaeogastropod systematics. In *Prosobranch phylogeny. Proc. Ninth Int. Malacol. Congr., Edinburgh, 1986*: 64–84. Ponder, W. F. (Ed.). *Malac. Rev.* (Suppl.) **4**.
- Haszprunar, G. (1989). New slit-limpets (Scissurellacea and Fissurellacea) from hydrothermal vents. 2. Anatomy and relationships. *Contr. Sci., Nat. Hist. Mus., Los Angeles County* No. 408: 1–17.
- Haymon, R. M. & Koski, R. A. (1985). Evidence of an ancient hydrothermal vent community, fossil worm tubes in Cretaceous sulfide deposits of the Samail Ophiolite, Oman. In *The hydrothermal vents of the eastern Pacific: an overview*: 57–65. Jones, M. L. (Ed.). *Bull. biol. Soc. Wash.* No. 6.
- Hecker, B. (1985). Fauna from a cold sulfur-seep in the Gulf of Mexico: Comparison with hydrothermal vent communities and evolutionary implications. In *The hydrothermal vents of the eastern Pacific: an overview*: 465–476. Jones, M. L. (Ed.). *Bull. biol. Soc. Wash.* No. 6.
- Hessler, R. R. & Smithey, W. M., Jr (1983). The distribution and community structure of megafauna at the Galapagos Rift hydrothermal vents. In *Hydrothermal processes at seafloor spreading centers*: 735–770. Rona, P. A., Bostrom, K., Laubier, L. & Smith, K. L., Jr (Eds). New York: Plenum.
- Hessler, R. R., Smithey, W. M., Jr & Keller, C. H. (1985). Spatial and temporal variation of giant clams, tube worms and mussels at deep-sea hydrothermal vents. In *The hydrothermal vents of the eastern Pacific: an overview*: 411–428. Jones, M. L. (Ed.). *Bull. biol. Soc. Wash.* No. 6.
- Hessler, R. R., Smithey, W. M., Boudrias, M. A., Keller, C. H., Lutz, R. A. & Childress, J. J. (1988). Temporal change in megafauna at the Rose Garden hydrothermal vent (Galapagos Rift, eastern tropical Pacific). *Deep-Sea Res. (A)* **35** (10–11): 1681–1709.
- Hickman, C. S. (1977). Integration of electron scan and light imagery in study of molluscan radulae. *Veliger* **20**: 1–8.
- Hickman, C. S. (1983). Radular patterns, systematics, diversity, and ecology of deep-sea limpets. *Veliger* **26**: 73–92.
- Hickman, C. S. (1984). A new archaeogastropod (Rhipidoglossa, Trochacea) from hydrothermal vents on the East Pacific Rise. *Zool. Scr.* **13**: 19–25.
- Hickman, C. S. (1988). Archaeogastropod evolution, phylogeny and systematics: a re-evaluation. In *Prosobranch phylogeny. Proc. Ninth Int. Malacol. Congr., Edinburgh, 1986*: 17–34. Ponder, W. F. (Ed.). *Malac. Rev.* (Suppl.) **4**.
- Jones, H. D., Hawkins, S. J., Watson, D. C., Jack, E. M. & Kyriakides, M. A. (1984). The radular formula of *Patella* species. *J. moll. Stud.* **50**: 123–124.
- Jones, M. L., Bright, C. F., *et al.* (sic). (1985). Dive data of certain submersibles, hydrothermal and other sites. Appendix 2. In *The hydrothermal vents of the eastern Pacific: an overview*: 539–545. Jones, M. L. (Ed.). *Bull. biol. Soc. Wash.* No. 6.
- Kenk, V. C. & Wilson, B. R. (1985). A new mussel (*Bivalvia*, *Mytilidae*) from hydrothermal vents in the Galapagos Rift zone. *Malacologia* **26**: 253–271.
- Knight, J. B. (1941). Paleozoic gastropod genotypes. *Geol. Soc. Am. Spec. Pap.* No. 32: 1–510.
- Knight, J. B., Cox, L. R., Keen, A. M., Batten, R. L., Yochelson, E. L. & Robertson, R. (1960). Systematic descriptions (Archaeogastropoda). In *Treatise on invertebrate paleontology Part I (Mollusca 1)*: 169–310. Moore, R. C. (Ed.). Geol. Soc. Am., Univ. Kansas Press.
- Levin, L. A. & Lonsdale, P. (1983). Hydrothermal and other faunas of submarine volcanoes at 20 °N in the East Pacific Ocean. *Eos, Trans. Am. geophys. Un.* **64**: 1017.
- Levin, L. A. & Nittrouer, C. A. (1987). Textural characteristics of sediments on deep seamounts in the eastern Pacific Ocean between 10 N and 30 N. *Geophys. Monogr.* **43**: 187–203.
- Lindberg, D. R. (1981a). Is there a coiled ancestor in the docoglossan phylogeny? *Western Soc. Malacologists, Ann. Rep.* No. 13: 15.
- Lindberg, D. R. (1981b). *Acmaeidae*. Pacific Grove, California: Boxwood Press.
- Lindberg, D. R. (1986a). Radular evolution in the Patellogastropoda. *Am. Malac. Bull.* **4**: 115.

- Lindberg, D. R. (1986b). The Patellogastropoda: a new 'old' order. In *Unitas Malacologica, Ninth Int. Malacol. Congr., Abstracts*: 44. Heppel, D. (Ed.). Edinburgh: National Museums of Scotland.
- Lindberg, D. R. (1986c). Name changes in the 'Acmaeidae.' *Veliger* **29**: 142-148.
- Lindberg, D. R. (1988a). Heterochrony in gastropods, a neontological view. In *Heterochrony in evolution*: 197-217. McKinney, M. L. (Ed.). Plenum Publishing Corporation.
- Lindberg, D. R. (1988b). The Patellogastropoda. In *Prosobranch phylogeny. Proc. Ninth Int. Malacol. Congr., Edinburgh, 1986*: 35-63. Ponder, W. F. (Ed.). *Malac. Rev. (Suppl.)* **4**.
- Lindberg, D. R. (1990). Systematics of *Potamacmaea fluviatilis* (Blanford) a brackish water patellogastropod (Patelloidinae: Lottiidae). *J. moll. Stud.* **56**: 309-316.
- Lipman, E. W. & Langenheim, R. L. Jr (1983). *Lepetopsis franae*, n. sp., a new patellid gastropod from the Bird Spring Group, Virgilian, at Arrow Canyon, Clark County, Nevada. *J. Paleont.* **57**: 602-605.
- Lonsdale, P. (1977). Clustering of suspension feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers. *Deep-Sea Res.* **24**: 857-863.
- Lutz, R. A., Bouchet, P., Jablonski, D., Turner, R. D. & Waren, A. (1986). Larval ecology of mollusks at deep-sea hydrothermal-vents. *Am. Malac. Bull.* **4**: 49-54.
- MacClintock, C. (1967). Shell structure of patelloid and bellerophonoid gastropods (Mollusca). *Bull. Peabody Mus. nat. Hist.* **22**: 1-40.
- Marshall, B. A. (1986). Recent and Tertiary Cocculinidae and Pseudococculinidae (Mollusca: Gastropoda) from New Zealand and New South Wales. *N. Z. J. Zool.* **12**: 505-546.
- McLean, J. H. (1981). The Galapagos Rift limpet *Neomphalus*: Relevance to understanding the evolution of a major Paleozoic-Mesozoic radiation. *Malacologia* **21**: 291-336.
- McLean, J. H. (1985). Preliminary report on the limpets at hydrothermal vents. In *The hydrothermal vents of the eastern Pacific: an overview*: 159-166. Jones, M. L. (Ed.). *Bull. Biol. Soc. Wash.* No. 6.
- McLean, J. H. (1988a). New archaeogastropod limpets from hydrothermal vents, superfamily Lepetodrilacea. 1. Systematic descriptions. *Phil. Trans. R. Soc. (B)* **319**: 1-32.
- McLean, J. H. (1988b). New archaeogastropod limpet families in the hydrothermal vent community. In *Prosobranch phylogeny, Proc. Ninth Int. Malacol. Congr., Edinburgh, 1986*: 85-87. Ponder, W. F. (Ed.). *Malac. Rev. (Suppl.)* **4**.
- McLean, J. H. (1989a). New archaeogastropod limpets from hydrothermal vents: new family Peltospiridae, new superfamily Peltospiracea. *Zool. Scr.* **18**: 49-66.
- McLean, J. H. (1989b). New slit-limpets (Scissurellacea and Fissurellacea) from hydrothermal vents. Part 1. Systematic descriptions and comparisons based on shell and radular characters. *Contr. Sci., Nat. Hist. Mus., Los Angeles County* No. 407: 1-29.
- McLean, J. H. & Haszprunar, G. (1987). Pyropeltidae, a new family of cocculiniform limpets from hydrothermal vents. *Veliger* **30**: 196-205.
- Morris, T. E. & Hickman, C. S. (1981). A method for artificially protruding gastropod radulae and a new model of radula function. *Veliger* **24**: 85-90.
- Morse, E. S. (1910). An early stage of *Acmaea*. *Proc. Boston Soc. Nat. Hist.* **34**: 313-323.
- Newell, N. D. (1935). Some mid-Pennsylvanian invertebrates from Kansas and Oklahoma: II. Stromatoporoidea, Anthozoa, and Gastropoda. *J. Paleont.* **9**: 341-355.
- Newman, W. A. (1979). A new scalpellid (Cirripedia): A Mesozoic relic living near an abyssal hydrothermal spring. *Trans. S. Diego Soc. nat. Hist.* **19**: 153-167.
- Newman, W. A. (1985). The abyssal hydrothermal vent invertebrate fauna: A glimpse of antiquity? In *The hydrothermal vents of the Eastern Pacific: an overview*: 231-242. Jones, M. L. (Ed.). *Bull. Biol. Soc. Wash.* No. 6.
- Newman, W. A. & Hessler, R. R. (1989). A new hydrothermal verrucosomorph (Cirripedia; Sessilia): the most primitive living sessile barnacle. *Trans. S. Diego Soc. nat. Hist.* **21**: 259-273.
- Paull, C. K., Hecker, B., Commeau, R., Freeman-Lynde, R. P., Neumann, C., Corso, W. P., Golubic, S., Hook, J. E., Sikes, E. & Curray, J. (1984). Biological communities at the Florida Escarpment resemble hydrothermal vent taxa. *Science, Wash.* **226**: 965-967.
- Paull, C. K. & Neumann, A. C. (1987). Continental margin brine seeps: their geological consequences. *Geology, Boulder, Colo.* **15**: 545-548.
- Powell, A. W. B. (1973). The patellid limpets of the world (Patellidae). *Indo-Pacif. Mollusca* **3**(15): 75-206.
- Runnegar, B. (1984). Crystallography of the foliated calcite shell layers of bivalve molluscs. *Alcheringa* **8**: 273-290.
- Salvini-Plawen, L. V. (1980). A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia* **19**: 249-278.
- Salvini-Plawen, L. V. & Haszprunar, G. (1987). The Vetigastropoda and the systematics of streptoneurous Gastropoda (Mollusca). *J. Zool., Lond.* **211**: 747-770.

- Skinner, B. J. (1983). Submarine volcanic exhalations that form mineral deposits: an old idea now proven correct. In *Hydrothermal processes at seafloor spreading centers*: 557–568. Rona, P. A., Bostrom, K., Laubier, L. & Smith, K. L., Jr (Eds). New York: Plenum.
- Spiess, F. N., Macdonald, K. C., Atwater, T., Ballard, R., Carranza, A., Cordoba, D., Cox, C., Diaz Garcia, V. M., Francheteau, J., Guerrero, J., Hawkins, J., Haymon, R., Hessler, R., Juteau, T., Kastner, M., Larson, R., Luyendyk, B., Macdougall, J. D., Miller, S., Normark, W., Orcutt, J. & Rangun, C. (1980). East Pacific Rise: Hot springs and geophysical experiments. *Science, Wash.* **207**: 1421–1433.
- Stutzel, R. (1984). Anatomische und ultrastrukturelle Untersuchungen an der Napfschnecke *Patella* L. unter besonderer Berücksichtigung der Anpassung an den Lebensraum. *Zool., Stuttg.* **46** (135): 1–50.
- Thiele, J. (1929). *Handbuch der systematischen Weichtierkunde. I. Loricata/Gastropoda (Prosobranchia)*. Jena: Gustav Fischer Verlag.
- Thompson, W. F. (1912). The protoconch of *Acmaea*. *Proc. Acad. nat. Sci., Philad.* **1912**: 540–544.
- Tunncliffe, V. (1988). Biogeography and evolution of hydrothermal-vent fauna in the East Pacific Ocean. *Proc. R. Soc. (B)* **233**: 347–366.
- Turner, R. D. & Lutz, R. A. (1984). Growth and distribution of mollusks at deep-sea vents and seeps. *Oceanus* **27**: 54–62.
- Turner, R. D., Lutz, R. A. & Jablonski, D. (1985). Modes of molluscan larval development at deep sea hydrothermal vents. In *The hydrothermal vents of the eastern Pacific: an overview*: 167–184. Jones, M. L. (Ed.). *Bull. biol. Soc. Wash.* No. 6.
- Van Dover, C. L., Grassle, J. F. & Boudrias, M. (1990). Hydrothermal vent fauna of Escanaba Trough (Gorda Ridge). In *Gorda Ridge: a seafloor spreading center in the United States' Exclusive Economic Zone*: 285–287. McMurray, G. R. (Ed.). Springer Verlag.
- Waller, T. R. (1972). The functional significance of some shell microstructures in the Pectinacea (Mollusca: Bivalvia). *Int. geol. Congr., Montreal, Can.* **24** (Section 7, Paleont.): 48–56.
- Waller, T. R. (1978). Morphology, morphoclines and a new classification of the Pteriomorpha (Mollusca: Bivalvia). *Phil. Trans. R. Soc. (B)* **284**: 345–365.
- Waren, A. (1988). *Neopilina goesi*, a new Caribbean monoplacophoran mollusk dredged in 1869. *Proc. biol. Soc. Wash.* **101**: 676–681.
- Waren, A. & Bouchet, P. (1989). New gastropods from East Pacific hydrothermal vents. *Zool. Scr.* **18**: 67–102.
- White, C. A. (1882). Fossils of the Indiana rocks. *Indiana Dept. Geol. nat. Hist. Ann. Rep.* No. 11: 347–402.
- Whitfield, R. P. (1882). On the fauna of the Lower Carboniferous limestones of Spergen Hill., Ind., with a revision of the descriptions of its fossils hitherto published, and illustrations of the species from the original type series. *Bull. Am. Mus. nat. Hist.* **1**(5): 39–97.
- Wingstrand, K. G. (1985). On the anatomy and relationships of Recent Monoplacophora. *Galathea Rep.* **16**: 7–94.
- Yochelson, E. L. (1960). Permian Gastropoda of the southwestern United States. *Bull. Am. Mus. nat. Hist.* **119**: 205–294.
- Yochelson, E. L. (1988). A new genus of Patellacea (Gastropoda) from the Middle Ordovician of Utah: The oldest known example of the superfamily. *Mem. Inst. Min. Technol. New Mex.* No. 44: 195–200.