

SHELL STRUCTURES OF SELECTED GASTROPODS FROM HYDROTHERMAL VENTS AND SEEPS

Steffen Kiel

*Freie Universität Berlin, Institut für Geologische Wissenschaften, Fachrichtung Paläontologie,
Malteserstrasse 74–100, 12249 Berlin, Germany; steffen.kiel@gmx.de*

ABSTRACT

Shell structures of 24 gastropod species from hydrothermal vents and seeps are electron microscopically investigated, and the ecological and phylogenetic implications of their shell structures are discussed. The presence of prismatic complex crossed lamellar, and regularly foliated structure in the Neolepetopsidae provides further evidence for their position as sister group of the Acmaeidae. The Lepetodriloidae are considered to be derived from, or to have a common ancestor with the Fissurellidae based on their complex crossed lamellar structure and on the presence of shell pores. The earlier hypothesis that Peltospiridae derived from Neomphalidae by reduction of complex crossed lamellar structure cannot be supported; both groups show the same array of shell structures. It is shown that shell pores are a frequent feature in Neomphalidae and Peltospiridae. Dissolution of the inner shell walls is documented for *Bathynnerita naticoides*. The trend that small and thin-shelled gastropod groups tend to reduce their shell structure to intersected crossed platy, can also be observed in the vent/seep gastropods. Generally, their shell structures appear to reflect those of the phylogenetic group to which they belong, rather than being influenced by the peculiarities of the extreme environment they inhabit.

Keywords: Gastropoda, shell structure, deep-sea, hydrothermal vent, cold seep, phylogeny.

INTRODUCTION

Chemosynthetic ecosystems in the deep-sea harbor highly endemic faunas (Tunnicliffe et al., 1996). The gastropods that live there are no exception to this: 95–98% of the species and 70% of the genera are endemic to vents and seeps, and five families are found exclusively here (Warén & Bouchet, 2001). Origin and phylogenetic relationships of many of the endemic taxa are still debated.

Shell structures have only been described for three out of the about 125 gastropod species known from chemosynthetic ecosystems: *Neomphalus fretterae* (Batten, 1984), *Melanodrymia aurantiaca* (Hickman, 1984), and *Lepetodrilus elevatus* (Hunt, 1993). The scope of the present study is to provide an overview over the shell structures of the gastropod families present at chemosynthetic ecosystems, and to discuss their ecological and phylogenetic implications. Additionally, these data can help to clarify the identity of fossil vent and seep gastropods.

MATERIALS AND METHODS

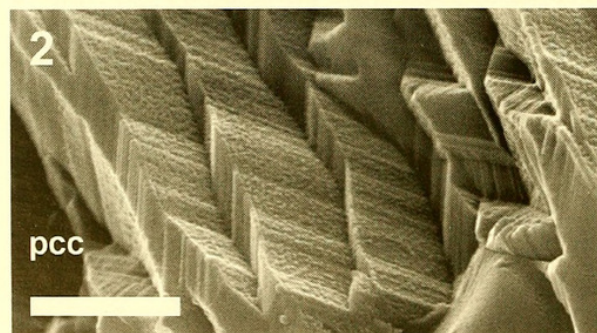
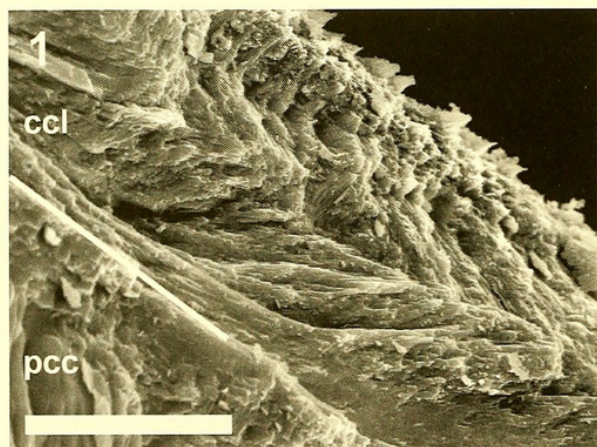
The majority of the material used here is from the study of Warén & Bouchet (2001), and was provided by the Muséum National d'Histoire Naturelle in Paris (MNHN). Three additional species were provided by the Natural History Museum of Los Angeles County (LACM).

All investigated specimens had the size of adult specimens as reported in the literature. The shell structure of protoconchs and ontogenetic changes in shell structures were not the subject of this study. Shell mineralogy was not studied, and is only inferred from the known mineralogy in related groups or is noted in cases when the structures have an unequivocal mineralogy. To observe the shell structures, pieces of shell were broken off the apertural region to obtain fresh fracture zones. The material was then mounted on stubs, coated with gold, and observed with several scanning electron microscopes in Paris and Hamburg.

The different types of shell structures were determined following the scheme of Carter & Clark (1985) and Hedegaard (1990, 1997). All figures in this study are oriented in a way that the outer side of the shell is up. The shell structures present in each species are listed from the outer side of the shell towards the inside. The taxonomic framework is that of Warén & Bouchet (2001).

Abbreviations in Figures

ccl	complex crossed lamellar
hom	homogenous
ica	intersected crossed acicular
icp	intersected crossed platy
nac	nacre
pcc	prismatic complex crossed lamellar
per	organic periostracum
rfo	regularly foliated
rsp	regular spherulitic prismatic
scl	simple crossed lamellar
spr	simple prismatic



FIGS. 1, 2. *Neolepetopsis* cf. *gordensis*. FIG. 1: Upper side of shell with the outer complex crossed lamellar layer and the prismatic complex crossed lamellar layer below (bar = 100 μ m). FIG. 2: Detail of the prismatic complex crossed lamellar layer (bar = 10 μ m).

RESULTS

Subclass Patellogastropoda Family Neolepetopsidae

The prismatic complex crossed lamellar and regularly foliated structures are always composed entirely of calcite (Hedegaard, 1990).

Neolepetopsis cf. *gordensis* McLean, 1990

- complex crossed lamellar (Fig. 1)
- prismatic complex crossed lamellar (Figs. 1, 2)

Mid-America Trench, Jalisco Block, 18°22'N–104°23'W; seep in 3,000–3,300 m (MNHN).

Eulepetopsis vitrea McLean, 1990

- prismatic complex crossed lamellar (Figs. 3, 4)
- regularly foliated (Fig. 5)
- simple prismatic

East Pacific Rise, NE of l'Île de Paques, site Rehu, 17°24'S–113°12'W; vent in 2,578 m (MNHN).

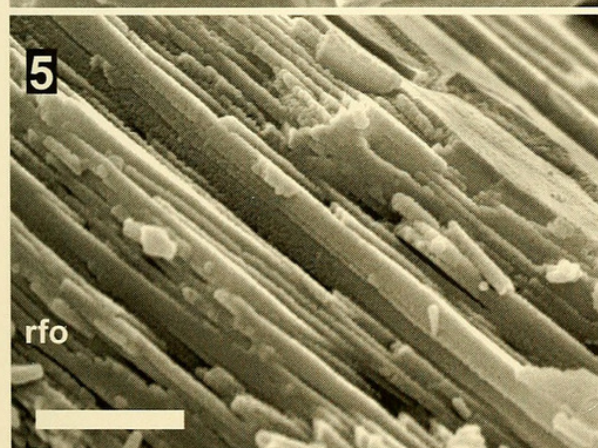
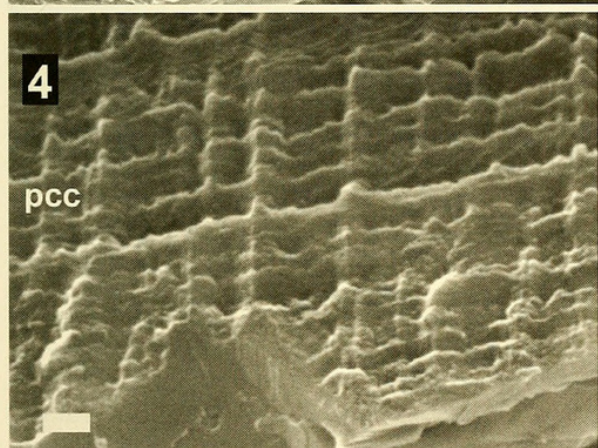
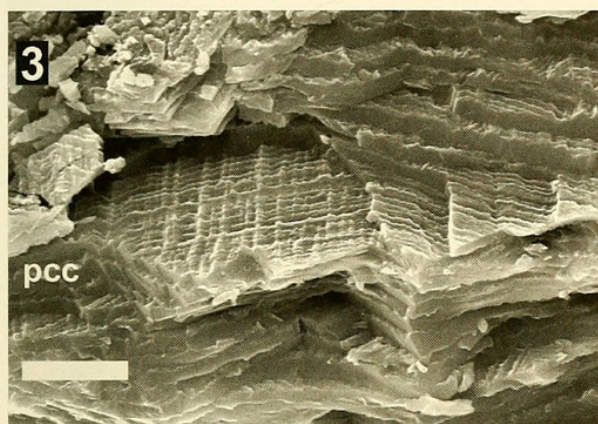
The prismatic complex crossed lamellar layer in this species has a very similar appearance as the "outer calcitic crossed lamellar" layer of *Patella crenata* described by Bandel & Geldmacher (1996). These authors compared their terminology only to those of Bøggild (1930) and MacClintock (1967), but not to those of the more recent works of Lindberg (1986, 1988) and Hedegaard (1990). However, due to their similarity the "outer calcitic crossed lamellar" layer of *Patella crenata* is here considered the same structure as prismatic complex crossed lamellar.

Paralepetopsis ferrugivora Warén & Bouchet, 2001

- prismatic complex crossed lamellar (Figs. 6, 7)

Mid-Atlantic Ridge, Lucky Strike; vent in about 1,650 m (MNHN). This specimen lacked any further details on its label, the depth is derived from the description of the Lucky Strike vent field (Van Dover et al., 1996). Hedegaard (1990) noted that the prisms of the prismatic complex crossed lamellar structure are always convex towards the outer side of the shell. This is also observed in the three neolepetopsids investigated here. Hedegaard (1990) also pointed out that these prisms show ribbed surfaces, which

he interpreted as the edges of the second order lamellae. This is also observed here, and these ribs have quite different appearances: in *Neolepetopsis* cf. *gordensis* they are fine tubercles (Fig. 2), in *Paralepetopsis ferrugivora* they are coarse and irregular (Fig. 7), and in *Eulepetopsis vitrea* they form a distinct grid-like pattern with tuberculate intersections (Fig. 4).



FIGS. 3–5. *Eulepetopsis vitrea*. FIG. 3: Outer prismatic complex crossed lamellar layer (bar = 10 μ m). FIG. 4: Close-up on the grid-like, ribbed surface of the prisms (bar = 1 μ m). FIG. 5: Regularly foliated layer (bar = 10 μ m).

Subclass Cocculiniformia
Family Pyropeltidae

Pyropelta musaica McLean & Haszprunar, 1987

- simple prismatic (Figs. 8, 9)
- simple crossed lamellar (Figs. 8, 9)
- simple prismatic (Fig. 8)

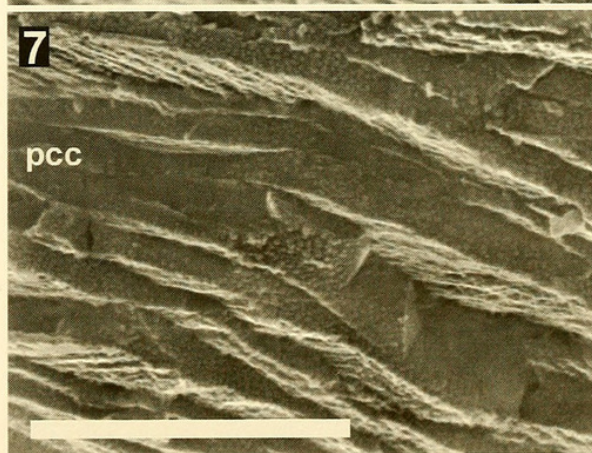
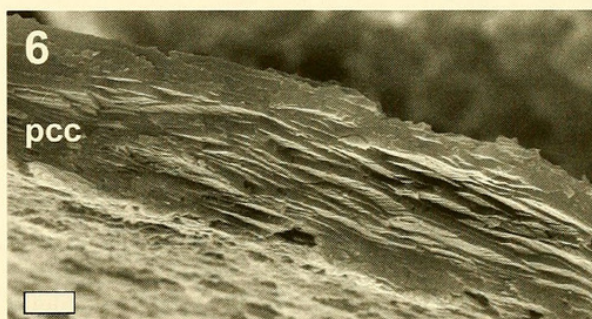
California, Santa Catalina Basin, between San Clemente and Santa Santa Catalina, 33°12'N, 118°30'W; whale bone from 1,240 m; (LACM 146909).

The shell consists of at least five alternating layers of simple crossed lamellar and simple prismatic structure, with the simple crossed lamellar layer becoming progressively thicker towards the outer side of the shell. The microcrystals of the simple crossed lamellar layers are not very densely packed.

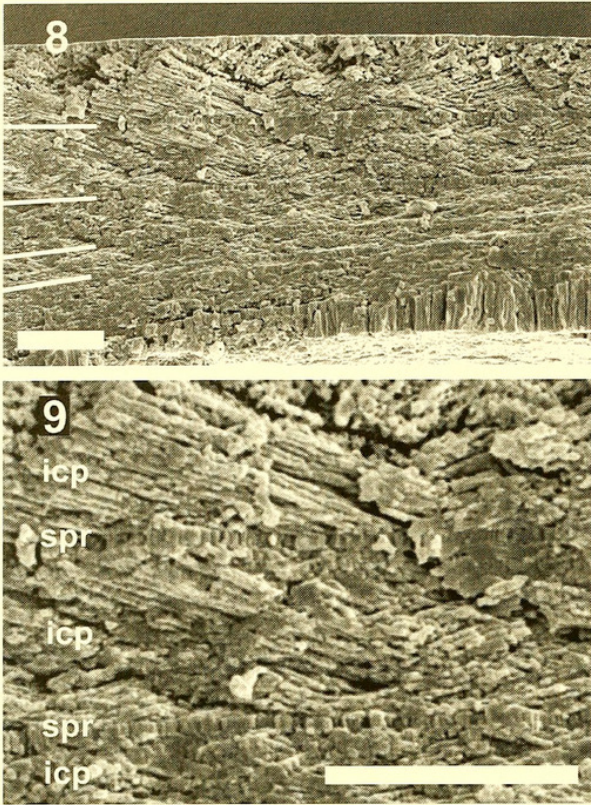
Subclass Vetigastropoda
Family uncertain

Sahlingia xandaros Warén & Bouchet, 2001

- simple prismatic (Fig. 10)
- intersected crossed acicular or platy (Fig. 10)
- homogenous (Fig. 10)



FIGS. 6, 7. *Paralepetopsis ferrugivora*. FIG. 6: Overview showing that the entire shell is composed of prismatic complex crossed lamellar structure (bar = 10 μ m). FIG. 7: Close-up on the prisms, showing their ribbed surface (bar = 10 μ m).



FIGS. 8, 9. *Pyropelta musaica*. FIG. 8: Cross-section showing five layers with simple crossed lamellar structure, with four thin layers with simple prismatic structure between them, marked by thin white bars (bar = 10 μm). FIG. 9: Close-up on three simple crossed lamellar layers (bar = 10 μm).

Alaska, Aleutian Trench, Kodiak Seep, 56°55.65'N, 149°32.90'W (LACM 1999-45); seep in 4,430 m. The crossed layer has a granular appearance making it difficult to distinguish between intersected crossed acicular or platy structure.

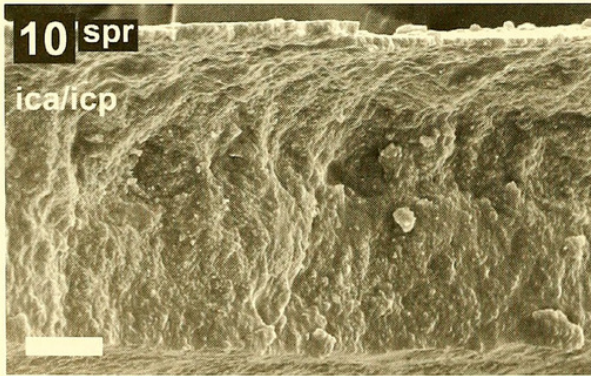
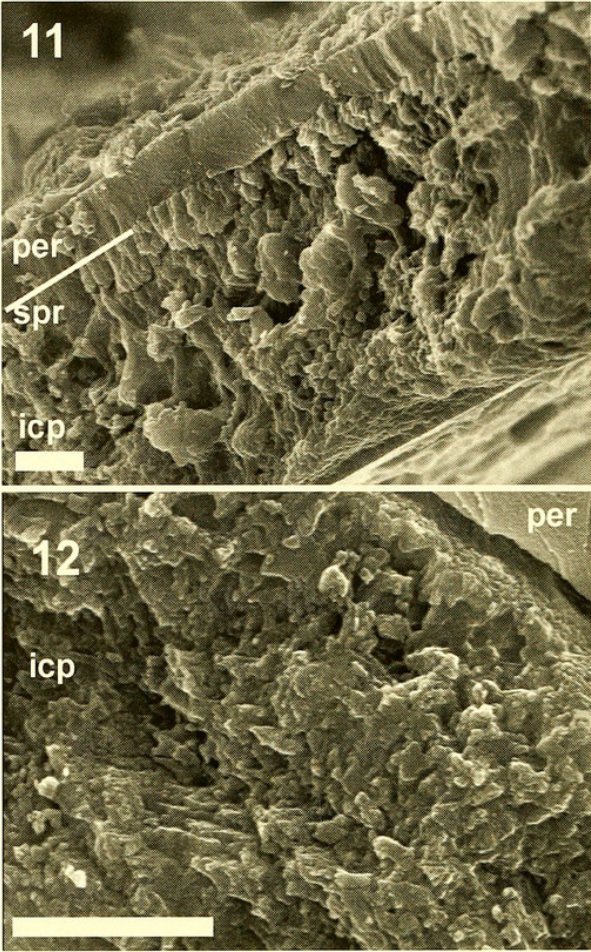


FIG. 10. *Sahlingia xandaros*, showing the thin outer layer of simple prismatic structure, the remaining shell is composed of intersected crossed acicular or platy structure (bar = 10 μm).



FIGS. 11, 12. *Protolira valvatoides*. FIG. 11: Organic periostracum, simple prismatic, and intersected crossed platy structure (bar = 10 μm). FIG. 12: Outer side of shell with organic periostracum and the intersected crossed platy layer (bar = 10 μm).

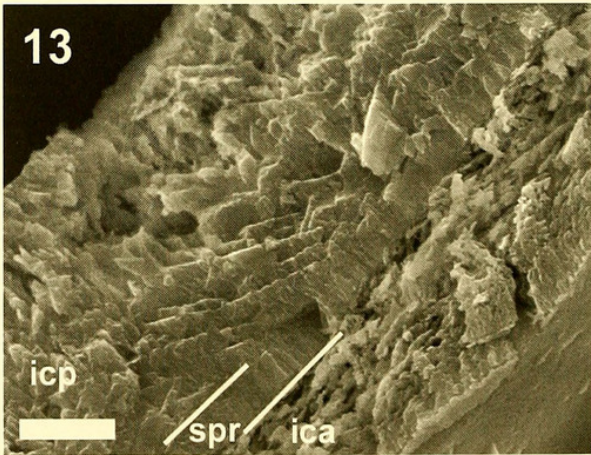


FIG. 13. *Bruceiella athlia*, showing the intersected crossed platy and simple prismatic layers, and the intersected crossed acicular layer below (bar = 10 μm).

Family Skeneidae

Protolira valvatooides Warén & Bouchet, 1993

- simple prismatic (Fig. 11)
- intersected crossed platy (Figs. 11, 12)
- simple prismatic (Fig. 11)

Mid-Atlantic Ridge, Lucky Strike, site Pagodas, 54°18.32'N–32°16.51'W; vent in 1,685 m (MNHN).

Many of the microcrystals have a granular appearance, and show cavities between each other.

Bruceiella athlia Warén & Bouchet, 1993

- intersected crossed platy (Fig. 13)
- simple prismatic (Fig. 13)
- intersected crossed acicular (Fig. 13)

Aleutian Trench, site Shumagin, 54°18.06'N–157°12.11'W; seep in 2,524 m (MNHN).

Many of the microcrystals have a granular appearance, and show cavities between each other.

Family Sutilizonidae

Sutilizona theca McLean, 1989

- simple prismatic (Fig. 14)
 - intersected crossed platy (Fig. 14)
- East Pacific Rise, 11°46'N, 103°47'W; vent in 2,715 m (Paratype LACM 2355).

Family Lepetodrilidae

Hunt (1992) used powder diffraction to show that the shell of *Lepetodrilus elevatus* is composed entirely of aragonite. It is therefore assumed that the shells of the lepetodrilids investigated here are also composed of aragonite.

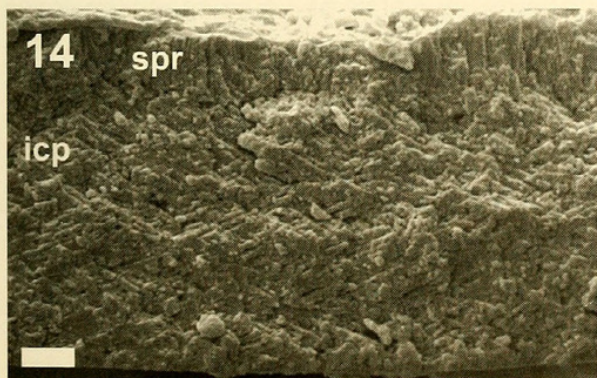


FIG. 14. *Sutilizona theca*, showing the thin outer layer of simple prismatic structure, the remaining shell is composed of intersected crossed platy structure (bar = 3 μ m).

Lepetodrilus pustulosus McLean, 1988

- simple prismatic (Fig. 15)
- complex crossed lamellar (Figs. 15, 16)

East Pacific Rise, sites Parigo, Genesis, Elsa, 12°48.52'N–103°56.48'W; vent in 4,808 m (MNHN).

There are occasionally fine pores perpendicular to the shell's surface, with an average diameter of 1 μ m (Fig. 16).

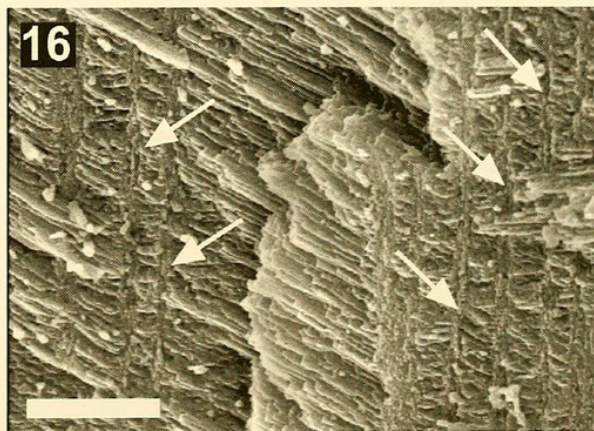
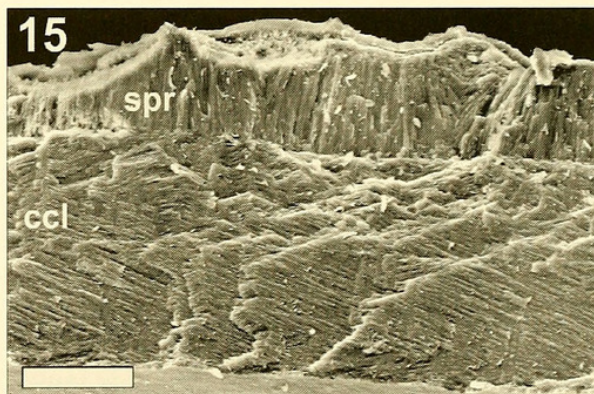
Pseudorimula midatlantica McLean, 1992

- homogenous
- complex crossed lamellar

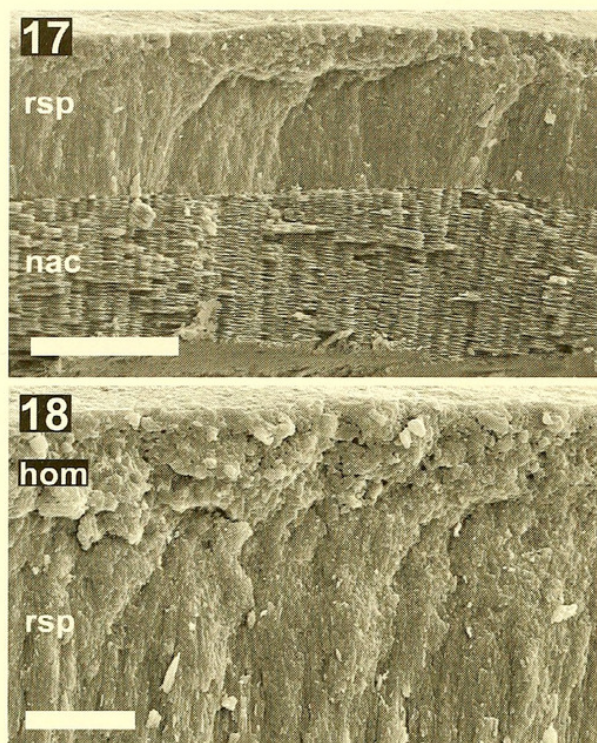
Mid-Atlantic Ridge, Snake Pit, site Elan, 23°23'N–44°56'W; vent in 3,520 m (MNHN).

There are occasionally fine pores perpendicular to the shell's surface, with an average diameter of 1–2 μ m.

Family Trochidae

Bathymargarites symplector Warén & Bouchet, 1989

FIGS. 15, 16. *Lepetodrilus pustulosus*. FIG. 15: Cross section showing the outer simple prismatic layer, and the inner complex crossed lamellar layer (bar = 100 μ m). FIG. 16: Close-up on the crossed lamellar layer, arrows indicate the fine, vertical pores (bar = 10 μ m).



FIGS. 17, 18. *Bathymargarites symplector*. FIG. 17: Overview showing the regular spherulitic prismatic upper layer, and the nacreous inner layer (bar = 50 μ m). FIG. 18: Close-up on the outer side of the shell showing the thin homogenous layer and the upper part of the regular simple prismatic layer (bar = 10 μ m).

- homogenous (Fig. 18)
- regular spherulitic prismatic (Figs. 17, 18)
- columnar nacre (Fig. 17)

East Pacific Rise 13°N; the label in the box indicates "same as Warén & Bouchet, 1993: 11–13, figs. 10A–E, 11A–B"; it is thus likely to be from a vent in 2,616–2,635 m (MNHN).

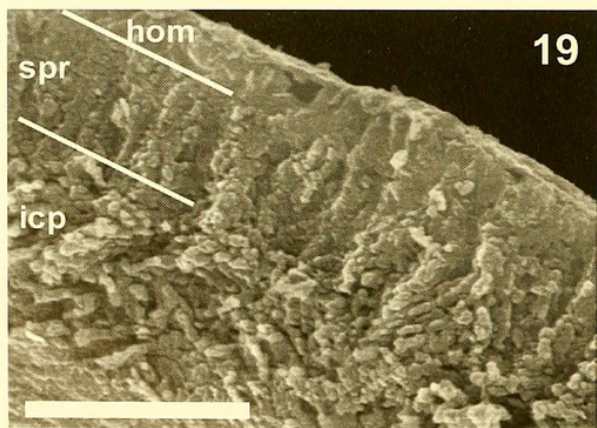


FIG. 19. *Retiskenea diploura*, the homogenous, simple prismatic, and intersected crossed platy structures merge into each other (bar = 10 μ m).

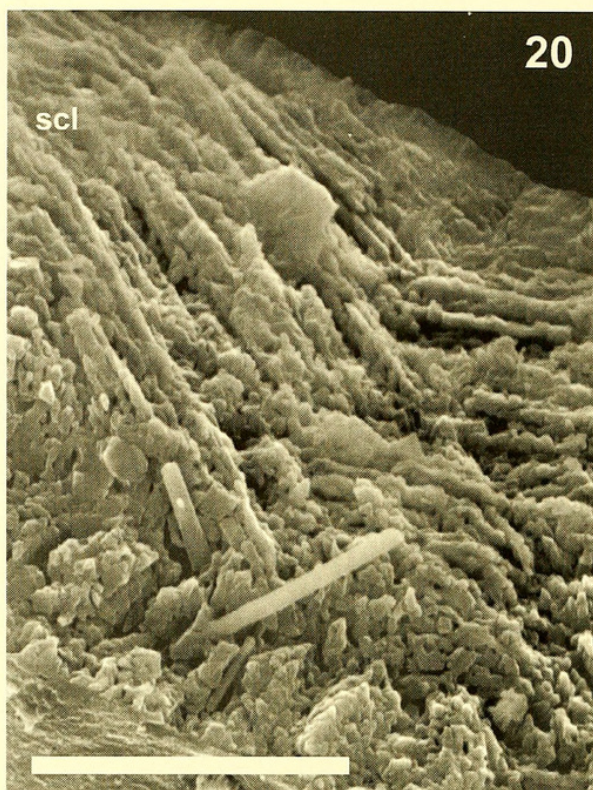


FIG. 20. *Melanodrymia aurantiaca*, view on the simple crossed lamellar structure (bar = 10 μ m).

Subclass uncertain
Family Neomphalidae

Retiskenea diploura Warén & Bouchet, 2001

- homogenous (Fig. 19)
- simple prismatic (Fig. 19)
- intersected crossed platy (Fig. 19)
- simple prismatic

Aleutian Trench, site Shumargin, 54°18.17'N–157°11.82'W; seep in 4,808 m (Paratype, MNHN).

The microcrystals of the crossed platy layer are not very densely packed and have a granular appearance.

Melanodrymia aurantiaca Hickman, 1984

- simple prismatic (Fig. 20)
- simple crossed lamellar (Fig. 20)
- simple prismatic (Fig. 20)

East Pacific Rise, sites Parigo, Pogosud, Genesis, 12°48.52'N–103°56.48'W; vent in 2,630 m (MNHN).

Hickman (1984) reported a thick layer with complex prismatic structure in this species. Hedegaard (1990) pointed out that Mac Clintock's (1967) "complex prismatic" structure is identical with the "simple crossed lamellar" structure of Carter & Clark (1985). Thus, the superficial differences between

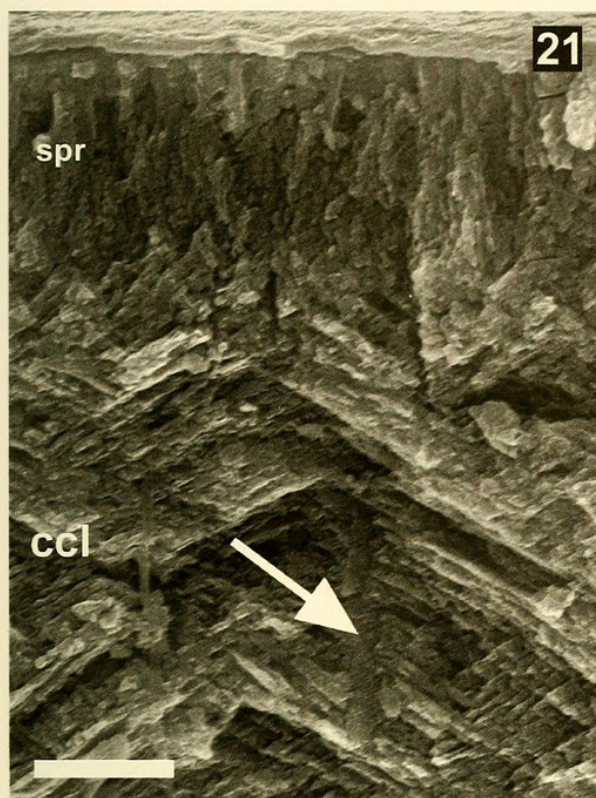


FIG. 21. *Cyathermia naticoides*, upper part of a cross-section with simple prismatic and complex crossed lamellar structure, arrow indicates a shell pore (bar = 10 μ m).

Hickman's (1984) and my descriptions of the shell structures of *Melanodrymia aurantiaca* is likely to be only a difference in terminology.

Cyathermia naticoides Warén & Bouchet, 1989
 - simple prismatic (Fig. 21)
 - complex cross lamellar (Fig. 21)

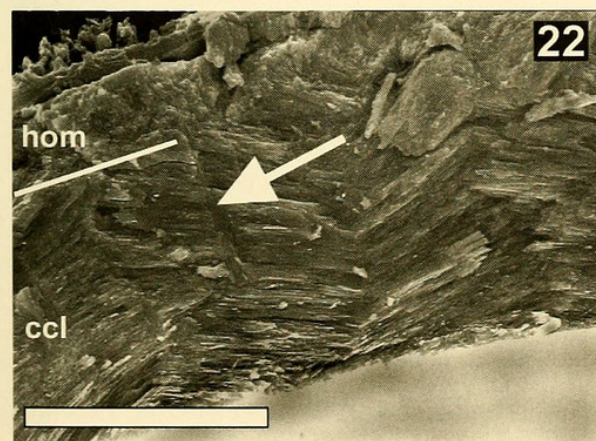


FIG. 22. *Pachydermia laevis*, homogenous and complex crossed lamellar structure, arrow indicates a shell pore (bar = 100 μ m).

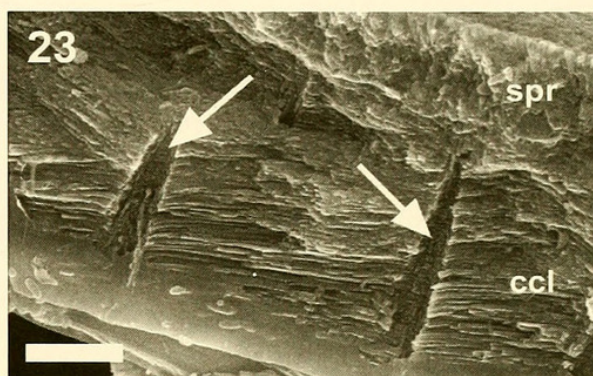


FIG. 23. *Peltospira smaragdina* has an outer layer with simple prismatic structure, and an inner layer with complex crossed lamellar structure, arrows indicate the broad shell pores (bar = 10 μ m).

East Pacific Rise, sites Julie, Genesis, Parigo, 12°48.96'N–103°46.62'W; vent in 2,630 m (MNHN).

Pachydermia laevis Warén & Bouchet, 1989

- homogenous (Fig. 22)
 - complex crossed lamellar (Fig. 22)
- East Pacific Rise, site Genesis, 12°48.56'N–103°46.58'W; vent in 2,630 m (MNHN).
 There are occasionally fine pores perpendicular to the shell's surface with an average diameter of 3 μ m (Fig. 22).

Planorbidella planispira (Warén & Bouchet, 1989)

- homogenous
 - complex crossed lamellar
 - simple prismatic
- East Pacific Rise, site Elsa, 12°48.09'N–103°46.34'W; vent in 2,630 m (MNHN).

Family Peltospiridae

Peltospira smaragdina Warén & Bouchet, 2001

- simple prismatic (Fig. 23)
 - complex cross lamellar (Fig. 23)
- Mid-Atlantic Ridge, Lucky Strike, site Sintra, 37°17.50'N–32°16.47'W; vent in 1,622 m (MNHN).
 There are occasionally fine pores perpendicular to the shell's surface, with an average diameter of 4 μ m (Fig. 23).

Ctenopelta porifera Warén & Bouchet, 1993

- homogenous, with traces of unidentified shell structures (Figs. 24, 25)
 - simple prismatic (Fig. 25)
- East Pacific Rise, sites Totem, Genesis, Elsa, 12°48.71'N–103°56.53'W; vent in 2,630 m (MNHN).

The shell is perforated by fine pores with an average diameter of 4 μm (Figs. 24, 25); these pores have not been observed in the internal septum.

Lirapex costellata Warén & Bouchet, 2001

- simple prismatic
- complex crossed lamellar
- homogenous
- simple prismatic

Mid-Atlantic Ridge, Lucky Strike, site Tour Eiffel, 37°17.32'N–32°16.51'W; vent in 1,685 m (MNHN).

Hedegaard (1990) presented shell structure data for three species he considered peltospirids. Among these, *Hyalogyrina glabra* has subsequently been assigned to the heterobranch family Hyalogyrinidae (Warén & Bouchet, 2001). The other two – *Xyloskenea costulifera* and *Bathyxyllophila excelsa* – were placed in the Skeneidae (Marshall, 1988), and

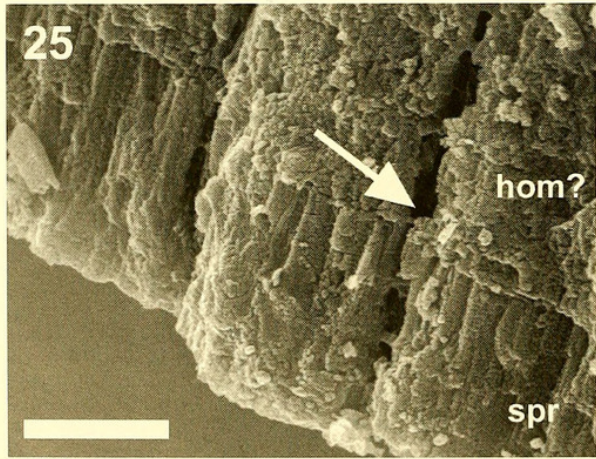
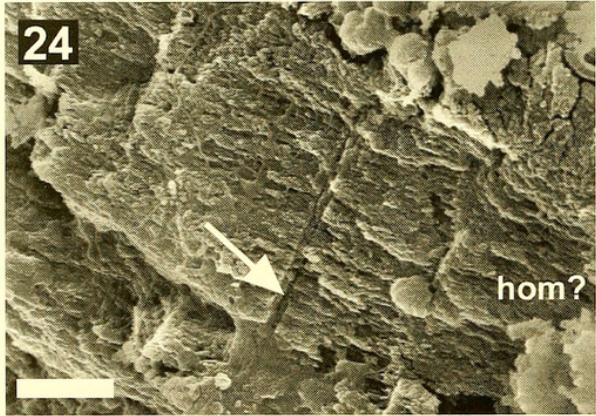
no subsequent work has been done on them. However, the Skeneidae are a heterogeneous group of small-shelled trochoids, and the assignment of *Xyloskenea costulifera* and *Bathyxyllophila excelsa* to either the Skeneidae or the Peltospiridae is still uncertain (Marshall, pers. comm., 2003).

Subclass Neritimorpha
Family Neritidae

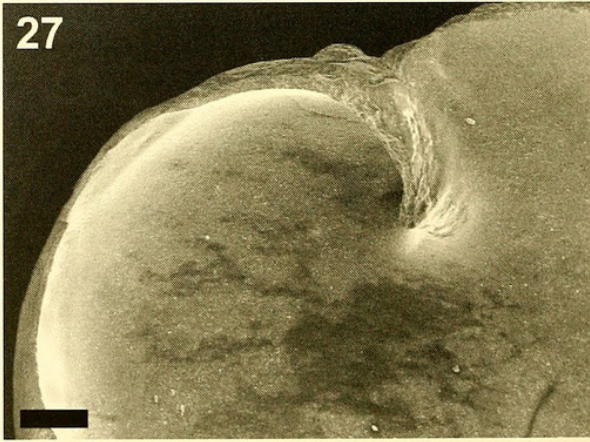
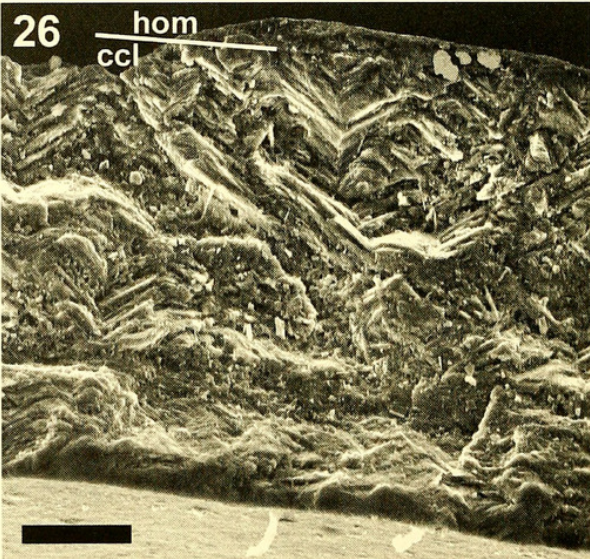
Bathynerita naticoidea Clarke, 1989

- homogenous (Fig. 26)
- simple cross lamellar (Fig. 26)
- simple prismatic

Louisiana Slope, Bush Hill Seep, 27°46.91'N–91°30.34'W; seep in 540–580 m (MNHN).



FIGS. 24, 25. *Ctenopelta porifera*. FIG. 24: Outer layer with homogenous, and remnants of an unidentified structure, arrow indicates a shell pore (bar = 10 μm). FIG. 25: Lower side of shell with homogenous?, and simple prismatic structure, arrow indicates a shell pore (bar = 10 μm).



FIGS. 26, 27. *Bathynerita naticoidea*. FIG. 26: Mainly complex crossed lamellar structure, and thin, homogenous outer layer (bar = 100 μm). FIG. 27: View on the shell's interior showing that the inner walls are dissolved (bar = 100 μm).

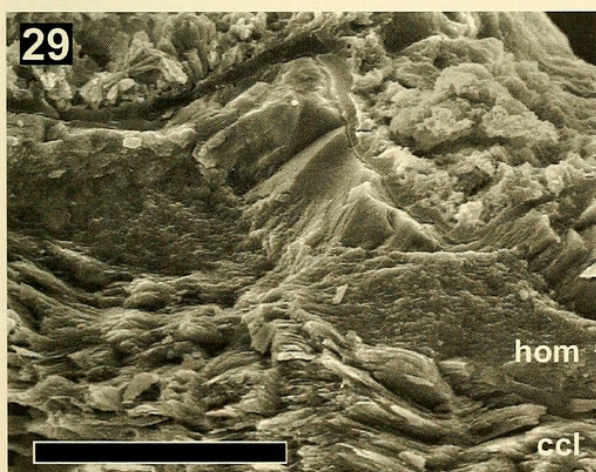
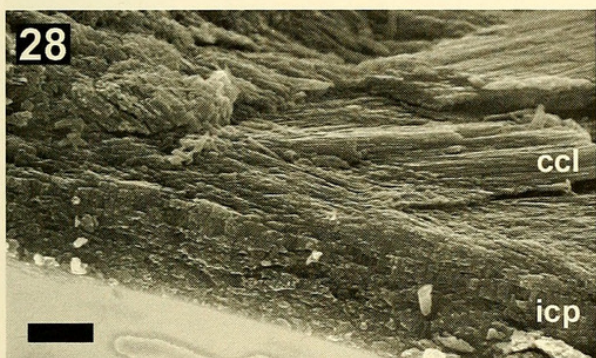
Hedegaard (1990) found the outer, homogenous layers of the five Neritidae investigated by him to be composed of calcite. It is thus likely that the thin homogenous outer layer of *Bathynnerita naticoidea* is also composed of calcite. The inner shell walls of *Bathynnerita naticoidea* are dissolved (Fig. 27). Dissolution of the inner shell walls is characteristic for the Neritidae, but has apparently never been documented for *Bathynnerita naticoidea*.

Family Phenacolepidae

Shinkailepas briandi Warén & Bouchet, 2001

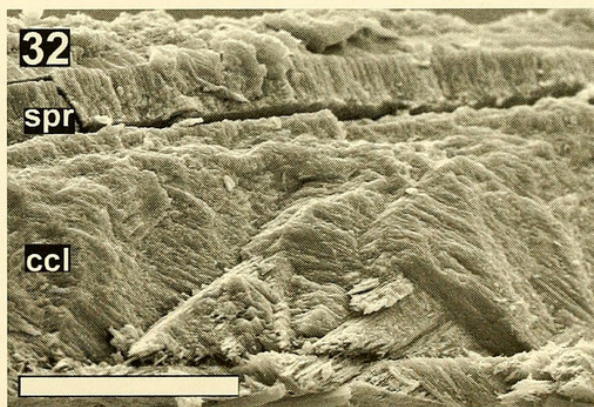
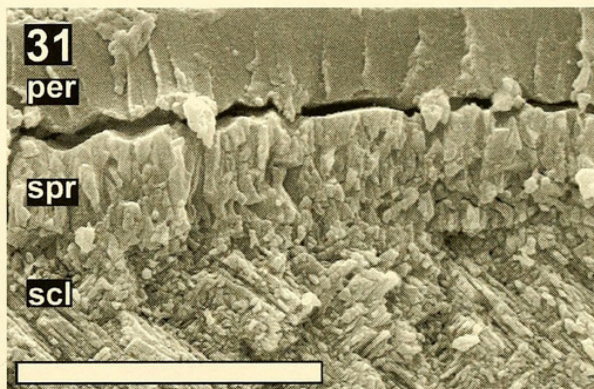
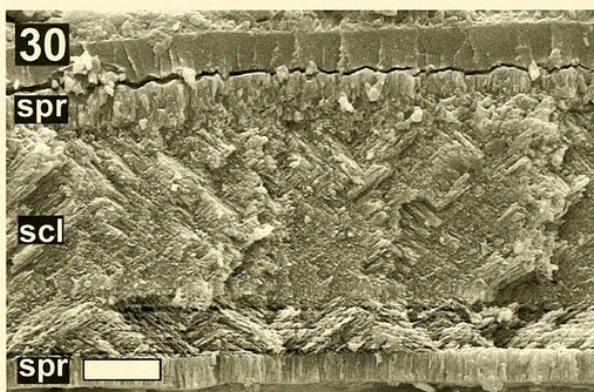
- homogenous (dense) (Fig. 29)
- homogenous (granular) (Fig. 29)
- complex crossed lamellar (Figs. 28, 29)
- intersected crossed platy (Fig. 28)
- simple prismatic

Mid-Atlantic Ridge, Lucky Strike, site Sintra, 37°17.50'N–32°16.47'W; vent in 1,622 m (MNHN).



FIGS. 28, 29. *Shinkailepas briandi*. FIG. 28: Inner side of the shell, showing the transition from complex crossed lamellar to intersected crossed platy structure (bar = 10 μ m). FIG. 29: Outer side of the shell showing the homogenous outer layer; the homogenous layer is very dense in the rib, and more granular away from the rib (bar = 100 μ m).

The homogenous outer layer that builds the ridges on the shell surface is similar to the outer layer described for *Phenacolepas pulchellus* by Hedegaard (1990). Hedegaard (1990) assumed that this layer has calcitic shell mineralogy, which is also likely in the species investigated here.



FIGS. 30–32. *Provanna variabilis*. FIG. 30: Overview showing the inner and outer, simple prismatic layers, and a central layer with complex crossed lamellar structure (bar = 10 μ m). FIG. 31: Close-up on the upper side of the shell, showing the slightly detached organic periostracum, and the transition from the outer simple prismatic to the complex crossed lamellar layer (bar = 10 μ m). FIG. 32: Inner simple prismatic layer is absent in this part of the shell (bar = 50 μ m).

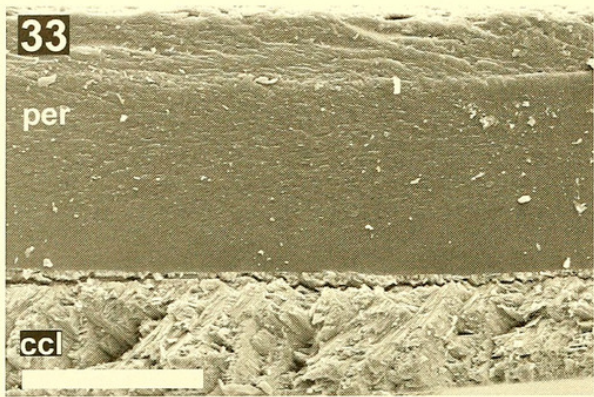


FIG. 33. *Alviniconcha hessleri*, the organic periostracum is about two and a half times thicker than the shell (bar = 100 μ m).

Subclass Caenogastropoda
Family Provannidae

- Provanna variabilis* Warén & Bouchet, 1986
- simple prismatic (Figs. 30–32)
 - complex crossed lamellar (Figs. 30–32)
 - simple prismatic (Fig. 30)

Juan de Fuca Ridge, 47°57'N–129°04'W; vents in 2,212 m (MNHN).

In the innermost portion of the complex crossed lamellar layer the microcrystals are sometimes only loosely packed, although they are densely packed in the remaining part of the layer (Fig. 30). The inner simple prismatic layer may be present or absent at different parts of the shell (compare Figs. 30 and 32).

- Alviniconcha hessleri* Okutani & Ohta, 1988
- simple prismatic
 - complex crossed lamellar (Fig. 33)
 - simple prismatic
- Mariana Back Arc Basin, site Alice Springs, 18°12.59'N–144°42.43'E; vent in 3,630–3,655 m (MNHN).

Subclass Heterobranchia
Family Xylodisculidae

- Xylodiscula analoga* Warén & Bouchet, 2001
- intersected crossed platy (Fig. 34)
 - simple prismatic (Fig. 34)
- Mid-Atlantic Ridge, Lucky Strike, site Tour

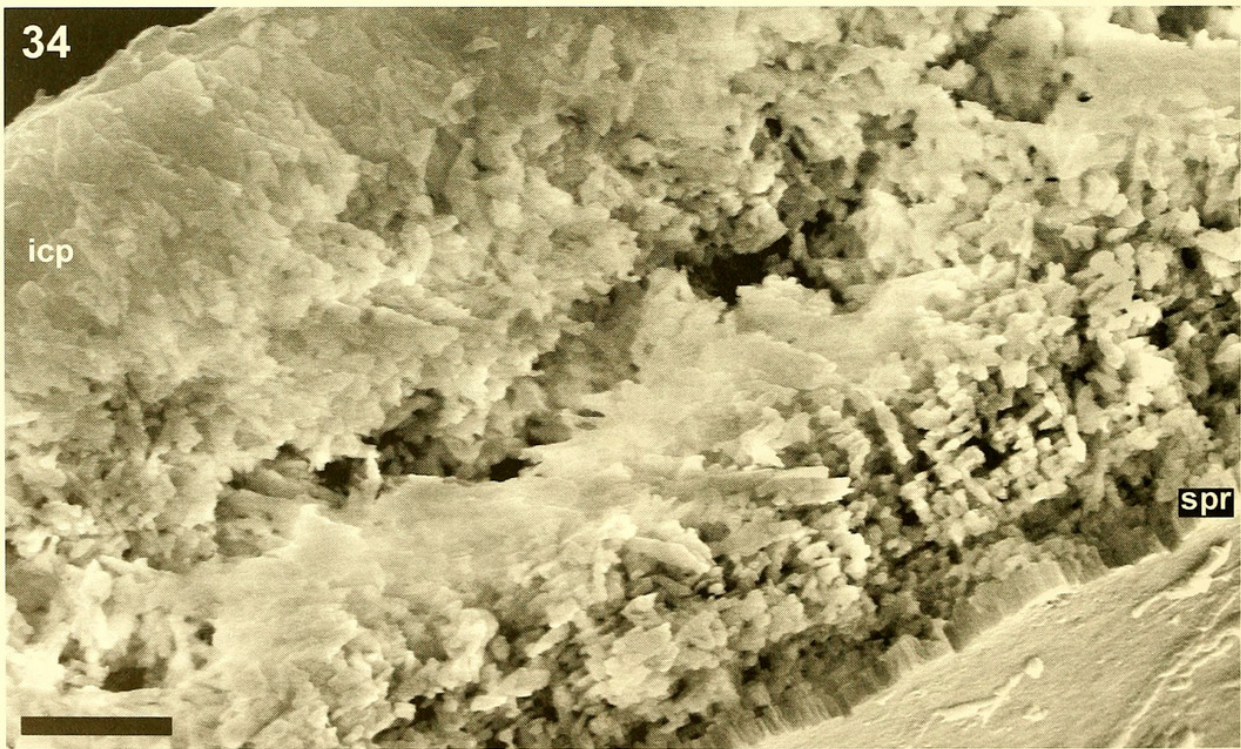


FIG. 34. *Xylodiscula analoga* has mainly intersected crossed platy structure, and a thin layer with simple prismatic structure at the inner side of the shell. The “smeared” area in the center of the picture and the loose packing of microcrystals probably indicate a high content of organic material (bar = 10 μ m).

Eiffel, 37°17.32'N–32°16.51'W; vent in 1,685m (MNHN).

The microcrystals are not very densely packed.

Family Hyalogyrinidae

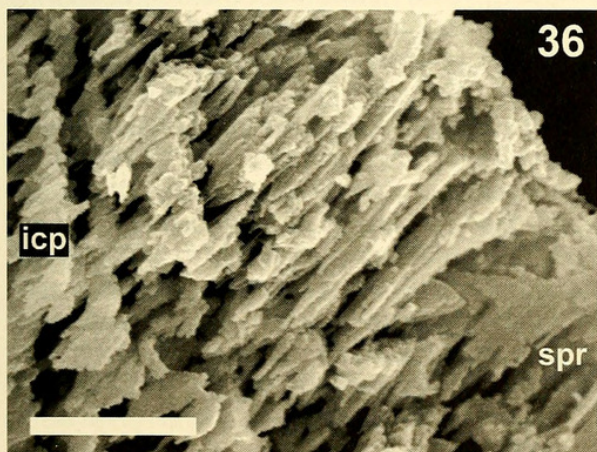
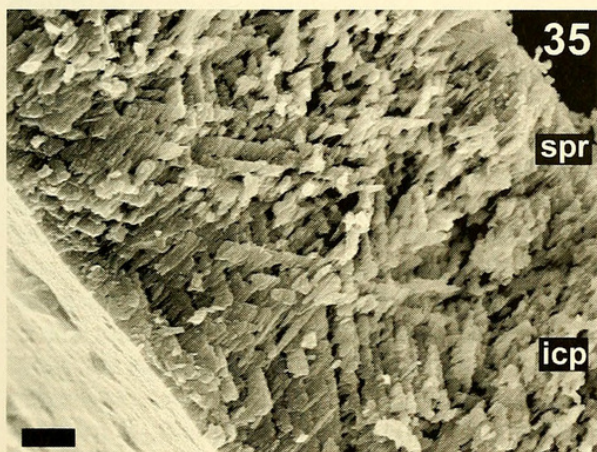
Hyalogyrina umbellifera Warén & Bouchet, 2001

- simple prismatic (Figs. 35, 36)

- intersected crossed platy (Figs. 35, 36)

Aleutian Trench, site Shumagin, 54°18.17'N–157°11.82'W; seep in 4,808 m (Paratype, MNHN).

This composition of shell structure is similar to that described for *Hyalogyrina glabra* (Hedegaard, 1990). The microcrystals are not very densely packed.



FIGS. 35, 36. *Hyalogyrina umbellifera*. FIG. 35: Thin outer layer with simple prismatic structure, and intersected crossed platy structure below (bar = 10 μ m). FIG. 36: Close-up on the transition from simple prismatic to intersected crossed platy structure, note the loose packing of the microcrystals (bar = 10 μ m).

DISCUSSION

Among the purposes of this study was to investigate whether the peculiarities of the vent/seep environment influence the shell structures of the gastropods groups living there. The microcrystals that build the shell structures are not very densely packed in several species (e.g., in *Retiskeneia diploura*, *Hyalogyrina umbellifera*, *Xylodiscula analoga*, and to a lesser extend also in *Pyropelta musaica*, *Protolira valvatoidea*, and *Bruceiella athlia*). Such loose packing is rarely observed in gastropods from shallow-marine environments, even in very thin-shelled species (Bandel, pers. comm. 2003; pers. observations). This loose packing is most probably the result of a high organic content in the shell. Loose packing occurs most frequently in small, thin shells with intersected crossed platy structure. This makes it at present impossible to distinguish whether it is related to the extreme vent/seep habitat, or to shell thickness and structure, or both.

An obvious correlation, although not related to the vent/seep habitat, is that between the presence of intersected crossed platy structure and shell thickness. This structure occurs more frequently in small, thin-shelled species than in larger, thicker-shelled ones. Hedegaard (1990) noted that among the Archaeogastropoda, intersected crossed platy structure dominates in species from small-shelled groups. In case of the vent/seep gastropods investigated here, this tendency can not only be observed among archaeogastropods, but also among the Heterobranchia, in the families Hyalogyrinidae and Xylodisculidae.

There are no apparent correlations between shell structures and depth or habitat.

Neolepetopsidae

Anatomical and molecular data indicate a sister group relationship of Neolepetopsidae and Acmaeidae (Lindberg, 1998; Harasewych & McArthur, 2000). The three neolepetopsids investigated here have prismatic complex crossed lamellar shell structure, which Hedegaard (1990) considered as apomorphy of the Acmaeidae. Hedegaard (1990) also pointed out that regularly foliated structure is present only in few acmaeids, and considered the reduction of this structure as an apomorphy of the Acmaeidae *sensu stricto*. Regularly foli-

ated structure is present in *Eulepetopsis vitrea*, but absent in *Neolepetopsis* cf. *gordensis* and *Paralepetopsis ferrugivora*. The position of the Neolepetopsidae as sister group of the Acmaeidae within the Acmaeoidea can thus be supported. However, it should be noted that the patellid *Patella crenata* also has prismatic complex crossed lamellar structure (Bandel & Geldmacher, 1996), raising some doubt whether this shell structure can actually be considered as an apomorphy of the Acmaeidae.

Pyropeltidae

Pyropelta musaica has simple crossed lamellar structure like the three cocculinids investigated by Hedegaard (1990), but a multi-layered occurrence of this structure separated by thin layers of a different structure as in *Pyropelta musaica* was not described. Neither does a fossil cocculinid from the Cretaceous show such a pattern (my data). A total of five investigated Cocculiniformia are far too few to propose this alternation of shell structures as an apomorphy of the Pyropeltidae. However, when future research confirms that this pattern does not occur in other cocculiniforms, it could be used for phylogenetic purposes, and also to identify members of the Pyropeltidae in the fossil record.

Sahlingia

Sahlingia xandaros has only simple prismatic and intersected crossed platy structures, which are not very conclusive for phylogenetic purposes.

Skeneidae

The two skeneids have the same shell structures as the three skeneids investigated by Hedegaard (1990).

Lepetodrilidae and Sutilizonidae

The Lepetodrilidae are considered here to be derived from, or to have a common ancestor with the Fissurellidae. The two decisive factors are their complex crossed lamellar structure, and their fine shell pores. Among the slit-bearing Vetigastropoda, the Pleurotomariidae, Haliotidae, and Seguenziidae have a nacreous shells (Bøggild, 1930; Erben & Krampiz, 1972; Bandel, 1979; Hedegaard, 1990; Harasewych, 2002) and are thus less

likely to be related. This also pertains to the Palaeozoic slit-bearing Porcellidae, for which nacre is inferred from the presence of nacre in its Mesozoic sister group, the Cirridae (Kiel & Frýda, 2004). The two remaining slit-bearing groups, Fissurellidae and Scissurellidae, have crossed lamellar structure (Batten, 1975; Bandel, 1998), have shell morphologies similar to those of the lepetodrilids, and are anatomically similar (Warén, pers. comm., 2003). Among these, only the fissurellids show shell pores as found in the lepetodrilids. Shell pores evolved independently in several groups of mollusks (Reindl & Haszprunar, 1996), can be present or absent in genera of the same family (e.g., Peltospiridae or Neomphalidae as shown herein), and may even be present or absent in species of the same genus – for example, *Shinkailepas briandi* without pores (herein) and *Shinkailepas myojinensis* with pores (Sasaki et al., 2003). However, shell pores have never been reported in scissurellids but frequently in fissurellids. Thus, the coincidence of similar shell shape, shell structure, and the presence of shell pores in both groups allows me to propose a close phylogenetic relationship between Fissurellidae and Lepetodrilidae.

The sutilizonid *Sutilizona theca* has intersected crossed platy structure, which is neither very conclusive for phylogenetic analysis, nor does it contradict previously suggested relationships (Haszprunar, 1988; Ponder & Lindberg, 1997; Warén & Bouchet, 2001).

Trochidae

Bathymargarites symplector has columnar nacre which is a common shell structure among the Trochidae (Wise, 1970; Erben, 1974; Hedegaard, 1990; Hickman & McLean, 1990). It is, however, the only gastropod with nacreous shell investigated here. Among other trochids from vents and seeps, nacre was reported from *Cataegis meroglypta* (McLean & Quinn, 1987; Warén & Bouchet, 1993), and from species of *Falsimargarita* (Warén & Bouchet, 2001).

Neomphalidae and Peltospiridae

Hedegaard (1990) proposed that the Peltospiridae is derived from the Neomphalidae by reduction of crossed lamellar structure. However, this was based on the incorrect higher taxonomic placement of his species – none of

them appears to belong to the Peltospiridae. Two of the three peltospirids investigated here show complex crossed lamellar structure, whereas two of the six Neomphalidae with known shell structure lack complex crossed lamellar structure. These new observations negate derivation of the Peltospiridae from the Neomphalidae, but do provide additional evidence that both families are related, as indicated by anatomical and molecular studies (Israelsson, 1998; McArthur & Tunnicliffe, 1998; Warén & Bouchet, 2001).

Shell pores in the Neomphalidae were first reported from *Neomphalus fretterae*, which has two types of pores, averaging 0.1 μm and 1.0 μm in diameter (Batten, 1984). Four out of the nine species of the Neomphalidae and Peltospiridae investigated here (including *Neomphalus fretterae*) have pores in their shells. In *Peltospira smaragdina*, *Pachydermia laevis*, and *Ctenopelta porifera*, the pores have an average diameter of 1.0–4.0 μm . The latter species has additional macropores 30.0–70.0 μm in diameter (Warén & Bouchet, 1993). The function of such shell pores is still controversial (Reindl & Haszprunar, 1996). Batten (1984) found the highest concentration of pores in *Neomphalus fretterae* around muscle insertion fields, and therefore interpreted them as muscle insertions. In the case of *Ctenopelta porifera*, Warén & Bouchet (1993, 2001) suggested the macropores to be related to chemosymbiosis.

Although the shell structure of the protoconch is not the scope of this study, Batten's (1984) interpretation of the multi-layered protoconch of *Neomphalus fretterae* deserves comment. Batten (1984) speculated that the three shell layers of the protoconch "may indicate that the veliger larval stage may have an extended planktonic mode." Calcification of the protoconch in archaeogastropods, however, takes place at the beginning of their benthic life, after the velum has been discarded (Bandel, 1982), and thus after the free-swimming larval stage. The additional inner layers have thus been built by the benthic juvenile or adult, possibly to strengthen the apical portion of the sub-limpet shell.

Neritidae and Phenacolepidae

Both investigated species, *Bathynnerita naticoidea* and *Shinkailepas briandi*, have crossed lamellar structures like their shallow-marine relatives. Likewise, both species have a homogenous outer layer with presumably

calcitic mineralogy. In this respect, both species differ from the neritilliid *Pisulina*, in which the thin outer layer has simple prismatic structure (Kano & Kase, 2000). In contrast to the classification of Warén & Bouchet (2001), *Bathynnerita* has recently been considered to be more closely related to the Phenacolepidae than to the Neritidae (Hodgson et al., 1998; Kano et al., 2002). Unfortunately, shell structures are too uniform among the two groups to provide further evidence to this hypothesis. The inner shell walls of *Bathynnerita naticoidea* are dissolved, a feature that is characteristic for all known neritoids, but had not yet been demonstrated for *Bathynnerita*.

Provannidae

The observed shells structures in the two provannids are similar to those of other caenogastropods (Bandel, 1990).

Hyalogyrinidae and Xylodisculidae

Both investigated species have homogenous and intersected crossed platy structure, whereas all other known heterobranchs have crossed lamellar structure (Bandel, 1990). This deviation might result from their small and thin shells, rather than being of phylogenetic importance.

In sum, the shell structures of the vent and seep gastropods appear to reflect those of the phylogenetic group to which they belong, rather than being influenced by the peculiarities of the extreme environment they inhabit.

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