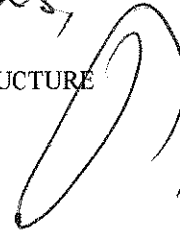


Regards,


Kat
1985

CONVERGENCE IN BIVALVE CONCHIOLIN LAYER MICROSTRUCTURE

Pieter W. Kat¹

ABSTRACT

Conchiolin layers occur within the shells of representatives of three brackish-water and marine bivalve superfamilies and are ubiquitous among freshwater Unionacea. Conchiolin layers examined exhibit a high degree of convergence in microstructure, despite their occurrence in distantly related taxa. These convergences are hypothesized to have arisen through similarity of response to similar selection pressures and constraints on the number of ways such conchiolin layers can be constructed. Conchiolin layers are hypothesized to broaden environmental tolerances of bivalves possessing them, since it allows such bivalves to inhabit waters of low calcium availability and affords some resistance to chemically boring predators.

INTRODUCTION

The way bivalves and gastropods construct their shells is of fundamental importance to their ability to resist desiccation and various types of predation, as well as the ease by which they move on and through the substratum (Stanley, 1969, 1981; Linsley, 1978; Vermeij, 1978; Palmer, 1979; Kat, 1981; Signor, 1983). Similarly, shell microstructural components can be important in increasing the durability and hardness of mollusk shells. For example, freshwater bivalves of the families Unionidae, Mutelidae and Margaritiferidae possess conchiolin layers within their shells which allow these bivalves to resist dissolution in acidic or poorly buffered fresh waters once the periostracum has worn away (Tolstikova, 1974; Tevesz & Carter, 1980; Kat, 1982, 1983a). Freshwater bivalves of the family Corbiculidae that lack such internal layers can suffer heavy mortality due to shell dissolution in habitats where co-occurring unionids suffer comparatively little damage (Kat, 1982).

Despite the occurrence of shell dissolution among marine taxa, the extent to which similar conchiolin layers occur in the shells of marine bivalves has not been adequately investigated. One notable exception is a study of the Corbulidae by Lewy & Samtleben (1979). Corbulids in general are slow and shallow burrowers, and inhabit marginal marine environments characterized by low salinity, oxygen content, and calcium carbonate availability. Lewy & Samtleben (1979) postulated that conchiolin layers among corbulids prevent shell dissolution in such habitats, and that these layers also can act as barriers to prevent chemically boring organisms from penetrating the shell. Many boreholes certainly terminate at the conchiolin layers of these bivalves (see Lewy & Samtleben, 1979, fig. 2E,F). Interestingly, the corbulid conchiolin layers apparently resemble those among the Unionidae in a number of structural features (Kat, 1982).

This study was undertaken to determine the extent to which conchiolin layers occur among brackish-water and marine bivalves, and the extent to which convergence in microstructural details occurs among distantly related taxa. Representatives of nine marine and brackish-water bivalve families (Arctiidae, Corbiculidae, Corbulidae, Hyatellidae, Mactridae, Psammobiidae, Solenidae, Solenocurtidae and Tellinidae) were examined and compared with bivalves of two freshwater families (Margaritiferidae and Unionidae). Species were chosen on the basis of occurrence in estuarine habitats and/or marine habitats with soft, organic-rich sediments. Such species often exhibit considerable shell wear in the umbonal region of the

¹Present address: National Museums of Kenya, P.O. Box 40658, Nairobi, Kenya.

valves and consequently can be expected to experience selection to reduce shell dissolution. The bivalve species examined are listed in Table 1.

MATERIALS AND METHODS

Specimens for this study were obtained from malacological collections at the Academy of Natural Sciences of Philadelphia and the National Museums of Kenya (Table 1). Use of such specimens involves a drawback, in that environmental information is often missing or presented in an extremely generalized fashion. Differences in environmental conditions experienced by various populations of a species could, for example, affect the relative sizes of various components of the conchiolin layers. However, experience with freshwater bivalves (see Kat, 1983a, b) indicates that, while environmental conditions can influence the number of layers deposited within the shell, microstructure of these layers is not affected by environmental differences among populations. All specimens examined were adults.

TABLE 1. Classification, habitat type, collection locality and catalogue numbers (KNML = National Museums of Kenya, Division of Mollusks; ANSP = Academy of Natural Sciences of Philadelphia) of the species examined. Species marked with an asterisk possess conchiolin layers.

Unionoida			
Unionidae			
<i>Elliptio complanata</i> (Lightfoot)*	Freshwater	Maryland, U.S.A.	KNML 1134
<i>Caelatura leopoldvillensis</i> (Putzeys)*	Freshwater	Zaire	KNML 1135
<i>Lampsilis ochracea</i> (Say)*	Freshwater	Nova Scotia, Canada	KNML 1136
<i>Alasmidonta undulata</i> (Say)*	Freshwater	Nova Scotia, Canada	KNML 1137
Margaritiferidae			
<i>Margaritifera margaritifera</i> (Linnaeus)*	Freshwater	Nova Scotia, Canada	KNML 1138
Veneroida			
Solenidae			
<i>Glaucanome rugosa</i> (Reeve)*	Estuarine	Philippines	ANSP 52576
<i>Pharella acutidens</i> Broderip & Sowerby*	Estuarine	Philippines	ANSP 246162
<i>Siliqua costata</i> Say	Marine to brackish	Massachusetts, U.S.A.	KNML 1139
Corbiculidae			
<i>Polymesoda caroliniana</i> (Bosc)*	Estuarine	Georgia, U.S.A.	KNML 1140
<i>Geloina suborbiculata</i> (Pilsbry)*	Estuarine	Philippines	ANSP 224123
Mactridae			
<i>Rangia cuneata</i> Bosc	Estuarine	Virginia, U.S.A.	KNML 1141
Tellinidae			
<i>Macoma balthica</i> Linnaeus	Marine to brackish	Delaware, U.S.A.	KNML 1142
Solenocurtidae			
<i>Tagelus plebeius</i> Lightfoot	Marine to brackish	Delaware, U.S.A.	KNML 1143
Arcticidae			
<i>Arctica islandica</i> (Linnaeus)	Marine	Massachusetts, U.S.A.	KNML 1144
Psammobiidae			
<i>Gari californica</i> (Conrad)	Marine	California, U.S.A.	ANSP 34612
Myoida			
Corbulidae			
<i>Varicorbula gibba</i> (Olivi)*	Marine to brackish	England	KNML 1145
<i>Corbula luteola</i> Carpenter*	Marine to brackish	California, U.S.A.	ANSP 31262
<i>Corbula smithiana</i> Gould*	Marine to brackish	Australia	ANSP 33429
Hyatellidae			
<i>Cyrtodaria siliqua</i> (Spengler)	Marine	Florida, U.S.A.	ANSP 123641

Shells were embedded in clear plastic, radially sectioned with a circular rock saw, polished with a series of carborundum grit sizes, and etched for 5 sec in 5% HCl in preparation for scanning electron microscopy (SEM). During SEM, the specimens were tilted at an angle of about 25° to reveal clearly the microstructure of the reticulate portions of the conchiolin layers; the relative thickness of the outer homogeneous region of the layers is thus slightly distorted. Three specimens of each species, usually from different populations were examined to determine the amount of intraspecific variability in conchiolin layer microstructure.

RESULTS

Seven of the 14 marine and brackish-water bivalve species examined (see Table 1) possessed conchiolin layers. These seven taxa were distributed among two orders (Veneroida and Myoida) and three superfamilies (Solenacea, Corbiculacea and Myacea). In addition, conchiolin layers are ubiquitous among the Unionacea (Kat, 1983a). The study indicates a fundamental similarity in conchiolin layer microstructure among the taxa examined, but also that some differences exist. Dimensions of the conchiolin layers and their component parts are listed in Table 2. Details of the conchiolin layers of taxa examined can be summarized as follows.

Marine and brackish-water taxa

Varicorbula gibba (Olivi) (Fig. 1a)

The conchiolin layers of *Varicorbula gibba* were examined in detail by Lewy & Samtleben (1979), and this study confirms many of their observations. One and occasionally two (the Main Conchiolin Layer (MCL) and the Second Conchiolin Layer (SCL) of Lewy & Samtleben, 1979) conchiolin layers occur within the shell. The MCL extends from the umbonal region to the ventral margin of the left valve and to a groove between the pallial line and the ventral margin of the right valve. Corbulids in general are inequivalve, and the left valve fits into this groove in the right valve where the MCL emerges. The edge of the MCL was therefore compared to an elastic gasket by Lewy and Samtleben as it permits hermetic closure of the valves. The conchiolin layers are from 18-22 μm thick and are separable into two regions: an outermost homogeneous section and an innermost reticulate section composed of variously sized chambers of conchiolin that contain "cones" of calcium carbonate (see Lewy & Samtleben, 1979, fig. 5c-f; Fig. 1a of this study). The SCL lies under the MCL, is shorter than the MCL, and is similar in microstructure to the MCL, except that the homogeneous region of the SCL can be somewhat thinner.

Corbula luteola Carpenter (Fig. 1b)

The shell of *Corbula luteola* also contains two main conchiolin layers, but these layers differ in a number of aspects from those of *Varicorbula gibba*. First, seven to eight conchiolin layers are initiated in the umbonal region of the shell, but only two of these layers continue past the umbo to the ventral section of the valves. Second, the SCL in this species is apparently not deposited in a continuous sheet over the entire inner surface of the valve, as it pinches out near the middle of the valve and begins again near the ventral edge. And third, the microstructure of the conchiolin layers is different from that of *V. gibba*: the outer homogeneous section is thicker, and the inner reticulate region consists of dendritic structures oriented normal to the exterior of the valve. These dendritic structures are of different lengths and seem to end in organic sheets at the base of the layer. Calcium carbonate structures within the reticulate region could not be adequately observed since they largely dissolved during acid etching of the shells, perhaps indicating that these structures of *C. luteola* are more soluble than those of *V. gibba*.

Corbula smithiana Gould (Fig. 1c)

As was observed in the case of *Corbula luteola*, six to 10 conchiolin layers are initiated in the umbonal region of *C. smithiana*, of which at most two extend to the ventral edges of the

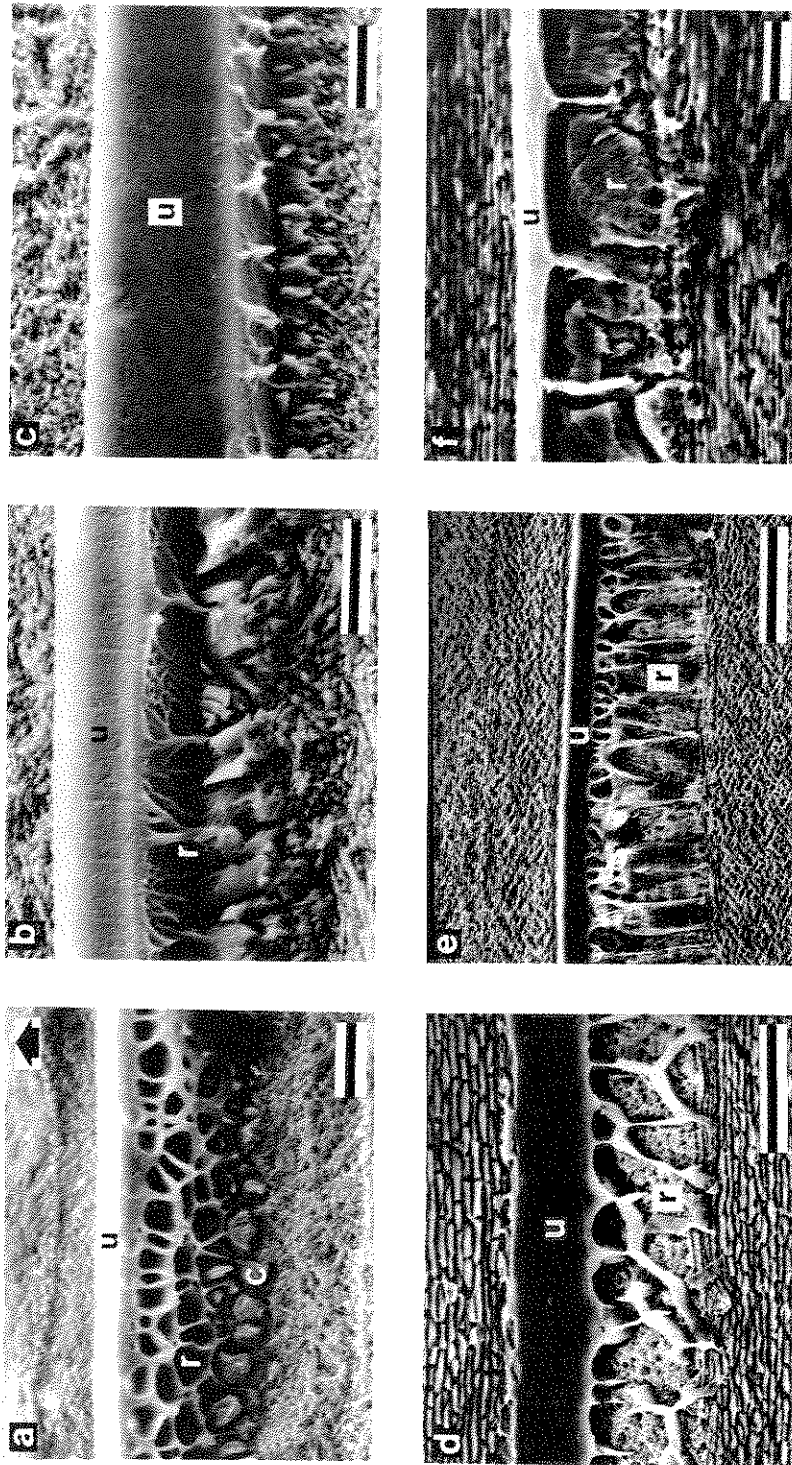


FIG. 1. Conchiolin layer of bivalve shells. a, *Varicorbula gibba*; scale bar = 10 μm . Arrow indicates direction to the outside of the shell. b, *Corbula luteola*; scale bar = 10 μm . c, *C. smithiana*; scale bar = 10 μm . d, *Elliptio complanata*; scale bar = 10 μm . e, *Margaritifera margaritifera*; scale bar = 20 μm . f, *Caelatura leopoldvillensis*; scale bar = 10 μm .
Abbreviations: c = calcareous structures within chambers of the inner reticulate region; r = inner reticulate region; u = outer homogeneous region.

TABLE 2. Dimensions of the conchiolin layers and their component sections.

Species	Conchiolin layer thickness (μm)		
	Total layer	Homogeneous section	Reticulate section
<i>Varicorbula gibba</i>	18-22	4-6	14-16
<i>Corbula luteola</i>	15-20	6-8	9-12
<i>Corbula smithiana</i>	16-22	14-18	2-4
<i>Glauconome rugosa</i>	4-8	4-8	—
<i>Geloina suborbiculata</i>	4-6	4-6	—
<i>Polymesoda caroliniana</i>	2-3	2-3	—
<i>Pharella acutidens</i>	2-3	2-3	—
<i>Elliptio complanata</i> *	15-23	5-8	10-15
<i>Lampsilis ochracea</i> *	4-6	4-6	—
<i>Alasmidonta undulata</i> *	5-8	5-8	—
<i>Caelatura leopoldvillensis</i> *	12-16	3-4	9-12
<i>Margaritifera margaritifera</i> *	50-70	10-12	40-60

*Freshwater taxa.

valves. Shorter layers all terminate close to the umbo of the shell, and these short layers lie above, between and occasionally below the longer conchiolin layers. *C. smithiana* has the thickest (14-18 μm) outer homogeneous section observed among the conchiolin layers of the corbulids and other taxa examined here. The reticulate region, on the other hand, consists of little more than small projections into the underlying calcareous layers. Details of the lower surface of the outer homogeneous region, however, are similar to those of *C. luteola*. Calcareous structures in contact with the lower surface of the conchiolin layer seem to consist of vertical prisms or lamellae.

Polymesoda caroliniana (Bosc) (Fig. 2b)

Conchiolin layers within the shell of *Polymesoda caroliniana* are limited to the umbonal region of the valves and are among the thinnest observed in this study. The entire layer is only 2-3 μm thick and consists entirely of a homogeneous region with highly pitted or rugose upper and lower surfaces where the conchiolin layer contacts calcareous shell layers. No more than two conchiolin layers were observed within the shell of specimens examined.

Pharella acutidens Broderip & Sowerby (Fig. 2d)

Conchiolin layers of *Pharella acutidens* are similar in thickness to those of *Polymesoda caroliniana*, but they are much less rugose. The upper and lower surfaces of the conchiolin layers of this species are almost flat. In some sections of the conchiolin layer, however, small, fingerlike conchiolin projections extend downward into the underlying shell layers. The relationship of these projections to the surrounding calcareous layers could not be determined: the etching process removed sufficient calcium carbonate to cause these delicate structures to collapse onto each other. It is clear, however, that some of these structures are detached from the conchiolin layer itself and must have been formed between crystals of the shell layer.

Glauconome rugosa (Reeve) (Fig. 2c)

Numerous (6-10) conchiolin layers occur within the shell of *Glauconome rugosa*. Most of these layers are located in the umbonal region of the shell, while one to two layers continue

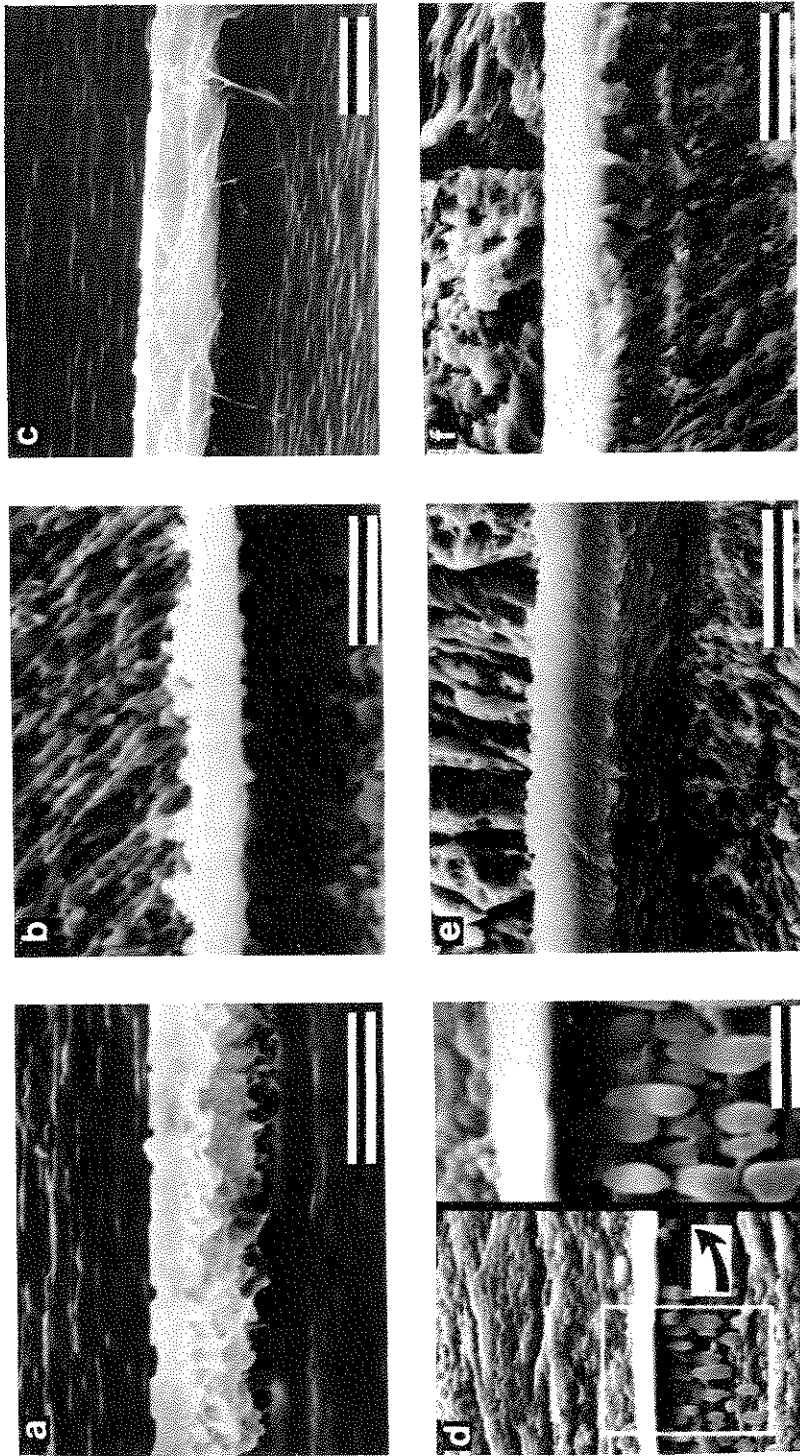


FIG. 2. Conchiolin layer of bivalve shells. a, *Alasmidonta undulata*; scale bar = 10 μm . b, *Polymesoda caroliniana*; scale bar = 5 μm . c, *Lamprolis ochracea*; scale bar = 10 μm . d, *Pharella acutidens*; region in box enlarged 2.5 at right. Scale bar = 10 μm on left, 4 μm on right. e, *Glauconome rugosa*; scale bar = 10 μm . f, *Geleina suborbiculata*; scale bar = 10 μm .

almost to the pallial line. The layers are simple in microstructure, consisting entirely of a homogeneous region of medium thickness (4-8 μm) with rugose surfaces.

Geloina suborbiculata (Pilsbry) (Fig. 2f)

Conchiolin layers of *Geloina suborbiculata* consist of homogeneous layers of medium thickness (4-6 μm), with a slightly developed reticulate region. No more than two such layers were observed to occur in the shell, and they are restricted to the region of the umbo.

Freshwater taxa: Margaritiferidae and Unionidae
(Fig. 1d, e, f; Fig. 2a, c)

Five species were selected from a more exhaustive survey of conchiolin layers among the Unionacea (see Kat, 1983a) to demonstrate the variety of conchiolin layer microstructures present among this freshwater group of bivalves. Conchiolin layers range from thick and complex (*Elliptio complanata* (Lightfoot), Fig. 1d; *Margaritifera margaritifera* (Linnaeus), Fig. 1e) through layers of intermediate complexity (*Caelatura leopoldvillensis* (Putzeys), Fig. 1f; *Alasmidonta undulata* (Say), Fig. 2a) to thin and comparatively featureless layers (*Lampsilis ochracea* (Say), Fig. 2c). Unionid species can possess conchiolin layers divisible into two types within the shell: thin and undifferentiated, and thick and more complex. Unionid complex layers can generally be divided into three regions: an outer homogeneous portion, a central, reticulate portion consisting of chambers of various shapes and sizes formed by sheet-like lamellae, and an inner, thin homogeneous layer (Kat, 1983a). Margaritiferids, on the other hand, possess only one type of layer, a thick complex band also composed of three regions: an outer, homogeneous portion, a central, vacuolated portion, and an inner, reticulate portion composed of widely spaced lamellae that form chambers filled with blocks of subprismatic shell material (Tolstikova, 1974; Kat, 1983a).

DISCUSSION

Given that the bivalve species possessing conchiolin layers belong to three separate orders, and that therefore these layers are likely of polyphyletic origin, the degree of convergence exhibited among the microstructure of these conchiolin layers is surprising. The similarities include the following.

1. Overall dimensions of the layers. For example, the conchiolin layers of *Geloina suborbiculata* (4-6 μm) and *Glaucanome rugosa* (4-8 μm) are similar in dimension to those of freshwater taxa such as *Alasmidonta undulata* (5-8 μm) and *Lampsilis ochracea* (4-6 μm) examined here, and *Anodonta cataracta* Say (4-8 μm), *Strophitus undulatus* (Say) (3-5 μm) and *Lampsilis splendida* (Lea) (3-6 μm) examined earlier (Kat, 1983a). Also, the size of the reticulate region of the conchiolin layers of *Varicorbula gibba* (14-16 μm) and *Corbula luteola* (9-12 μm) compares closely with those of *Elliptio complanata* (10-15 μm) and *Caelatura leopoldvillensis* (9-12 μm). Nevertheless, marine taxa such as *Polymesoda caroliniana* and *Pharella acutidens* possess thinner conchiolin layers (2-3 μm) than have been observed among freshwater taxa (Kat, 1983a). Overall dimensions of the conchiolin layers and their component regions do not seem affected by environmental conditions among freshwater taxa, and have therefore been useful in taxonomic analyses (Kat, 1983a, b). More work needs to be done with marine taxa, however, to determine if constancy of dimensions of conchiolin layers among different environments is a general trend.

2. Location of the conchiolin layers. With the exception of the corbulids, conchiolin layers examined here are generally not deposited over the entire inner surface of the shell, but are localized in the umbonal region. Among unionids and margaritiferids, for example, conchiolin layers are deposited as patches of various sizes concentrated below the umbo.

This localization of conchiolin layers corresponds to the areas of the shell that are most often damaged by dissolution. The conchiolin layers of corbulids generally extend from the umbonal to the ventral region of the valves, and Lewy & Samtleben (1979) proposed that these layers not only retard shell dissolution but also seal the shell commissure and prevent shell penetration by boring organisms, which do not necessarily concentrate their activities in the umbonal region of the shell. Nevertheless, *Corbula luteola* and *C. smithiana* were both observed to possess numerous (6-10) conchiolin layers in the umbonal region, only two of which extended to the ventral parts of the shell. Why some conchiolin layers terminate in the umbonal region while others are secreted over more extensive parts of the inner surface of the shell is not known.

3. Construction of conchiolin layers. All conchiolin layers examined here consist of at least an outer, homogeneous region, and some taxa possess an additional inner, reticulate region. Both layers are in intimate contact with the surrounding shell layers, and conchiolin layers do not separate regions of different microstructure within the shell. Unionids that possess complex layers also can possess simple layers composed entirely of a homogeneous region: I have proposed elsewhere that unionid complex layers could result from elaborations on simple layers (Kat, 1983a). This is not true of marine and brackish-water taxa examined here nor of the margaritiferids, which possess only one type of layer in the shell. The complex conchiolin layers of corbulids examined in this study exhibit a remarkable number of similarities to those of the Unionacea. The most striking similarity is the division of complex layers into upper, homogeneous and lower, reticulate regions, and that the reticulate regions are generally composed of chambers or cells of conchiolin that enclose calcareous material of different microstructure from the rest of the shell (these differences are perhaps due to different crystallization environments). For example, the rounded chambers apparent in the conchiolin layer of *Varicorbula gibba* (Fig. 1a) are quite similar in appearance to those of *Elliptio complanata* (Fig. 1d) and *Margaritifera margaritifera* (Fig. 1e). Also, the chambers of the conchiolin layer of *Corbula luteola* (Fig. 1b) are similar in appearance to those of *Caelatura leopoldvillensis* (Fig. 1f) examined here and *Lampsilis radiata* (Gmelin), *Anodonta gibbosa* Say and *E. dariensis* (Lea) examined earlier (Kat, 1983a). However, the calcareous structures within the conchiolin reticulate region of *V. gibba* are of different microstructure than those of *E. complanata*, and the peculiar, fingerlike conchiolin structures associated with the conchiolin layer of *Pharella acutidens* have no parallel among freshwater taxa.

Why conchiolin layers exhibit convergences among these distantly related taxa could be due to similarities of response to similar selective pressures, constraints on the number of pathways by which the mantle can secrete a conchiolin layer, or both. For example, there seems to have been strong and ubiquitous selection for conchiolin layers firmly attached to the surrounding shell layers by pitted and rugose upper and lower surfaces. Such conchiolin layers could probably better withstand scour and the efforts of boring predators once the surmounting shell layers have been removed. It is not clear, however, why conchiolin layers composed of two or three different portions evolved in the lineages examined, and why they exhibit strong convergence in microstructure. The addition of a reticulate region to the homogeneous portion of a conchiolin layer certainly thickens the entire structure (although negligibly so in the case of *Corbula smithiana*), and inclusion of calcareous material within conchiolin layers could render the thickened layer more structurally sound. Incorporation of a chambered reticulate region might afford more flexibility than a completely homogeneous layer of equal thickness. Such flexibility could be important when underlying shell material has to be protected by conchiolin layers once the overlying shell has worn away. Conchiolin layers would then be performing a role analogous to that of the periostracum, and it is interesting to note that the periostracum and conchiolin layers are similar in microstructure among margaritiferids. Also, complex conchiolin layers among corbulids have been observed to deter chemically boring predators (Lewy & Samtleben, 1979), despite the ability of such predators to penetrate organic as well as mineral components of the shell (Carriker et al., 1978; Carriker,

1981). Since many corbulids exhibit boreholes that terminate at the conchiolin layers, it would be interesting to determine why boring predators terminate their activities at these layers, and whether it was a function of the complexity of the layer itself.

Despite the discussed advantages to incorporation of conchiolin layers in the shell, Lewy & Samtleben (1979) proposed that the presence of such layers within corbulid shells structurally weakens the valves which often split apart when the conchiolin layers are destroyed during fossilization. It is uncertain, however, whether shells possessing conchiolin layers are more susceptible to crushing by predators such as fishes and crabs (Vermeij, 1978; Palmer, 1979) than shells that do not have such layers, and therefore whether the incorporation of conchiolin layers compromises shell strength in living bivalves. The interdigitation of conchiolin layers with surrounding shell layers would seem to argue against a loss of shell structural integrity, but it is possible that very thick, almost entirely homogeneous conchiolin layers like those observed in *Corbula smithiana* could render the shell more easily breakable by crushing and shearing forces. This could explain the apparent paucity of such thick homogeneous layers among the taxa examined here and in Kat (1983a), and might be an additional advantage to thickening conchiolin layers by addition of a reticulate region rather than by addition of more homogeneous material.

The obvious success of freshwater members of the families Sphaeriidae, Dreissenidae and Corbiculidae, and the wide environmental tolerances of the other taxa examined here which lack conchiolin layers underline the fact that such layers are not a necessity for life in fresh, brackish and marine waters in which shell dissolution occurs. Even though bivalves without conchiolin layers often experience destruction of shell layers, high rates of compensatory shell secretion seem sufficient to prevent lethal shell dissolution in many of these species. Nevertheless, possession of conchiolin layers could allow a bivalve species to occupy a broader range of habitats both in terms of calcium availability and presence of chemically boring predators than bivalves that do not possess such layers.

ACKNOWLEDGEMENTS

My thanks are extended to Pat Shipman and Jenny Rose for their help during SEM sessions, and to the anonymous reviewers for their suggested improvements to the manuscript. This study was supported in part by a National Capital Shell Club Scholarship and Biomedical Research Support Grant 5-S07-RR07041-14.

LITERATURE CITED

- CARRIKER, M.R. 1981. Shell penetration and feeding by naticacean and muricacean gastropods: a synthesis. *Malacologia*, 20: 403-422.
- CARRIKER, M.R., WILLIAMS, L.G. & VAN ZANDT, D. 1978. Preliminary characterization of the secretion of the accessory boring organ of the shell-penetrating muricid gastropod *Urosalpinx cinerea*. *Malacologia*, 17: 125-142.
- KAT, P.W. 1981. Shell shape changes in the Gastropoda: shell decollation in *Rumina decollata* (Pulmonata: Subulinidae). *Veliger*, 24: 115-119.
- KAT, P.W. 1982. Shell dissolution as a significant source of mortality for *Corbicula fluminea* (Bivalvia: Corbiculidae) inhabiting acidic waters. *Malacol. Rev.*, 15: 129-134.
- KAT, P.W. 1983a. Conchiolin layers among the Unionidae and Margaritiferidae (Bivalvia): microstructural characteristics and taxonomic implications. *Malacologia*, 24: 298-311.
- KAT, P.W. 1983b. Patterns of electrophoretic and morphologic variability in a widely distributed unionid: an initial survey. *Neth. J. Zool.*, 33: 21-40.
- LEWY, Z. & SAMTLEBEN, C. 1979. Functional morphology and palaeontological significance of the conchiolin layers in corbulid pelecypods. *Lethaia*, 12: 341-351.
- LINSLEY, R.M. 1978. Locomotion rates and shell form in the Gastropoda. *Malacologia*, 17: 193-206.
- PALMER, A.R. 1979. Fish predation and the evolution of gastropod shell structure: experimental and geographic evidence. *Evolution*, 33: 697-713.
- SIGNOR, P.W. 1983. Burrowing and the functional significance of ratchet sculpture in turritelliform gastropods. *Malacologia*, 23: 313-320.

- STANLEY, S.M. 1969. Bivalve mollusk burrowing aided by discordant shell ornamentation. *Science*, 166: 634-635.
- STANLEY, S.M. 1981. Infaunal survival: alternative functions of shell ornamentation in the Bivalvia (Mollusca). *Paleobiology*, 7: 384-393.
- TEVESZ, M.J. & CARTER, J.C. 1980. Environmental relationships of shell form and structure of unionocean bivalves. In: Rhoads, D.C. & Lutz, R.A. (Eds.), *Skeletal growth of aquatic organisms*. Plenum Press, New York. 750 pp. [pp. 295-322].
- TOLSTIKOVA, N.V. 1974. Microstructural characteristics of freshwater bivalves. *Paleontol. J.*, 8: 55-60.
- VERMEIJ, G.J. 1978. *Biogeography and adaptation*. Harvard University Press, Cambridge, Massachusetts. 416 pp.

PIETER W. KAT

*Department of Earth and Planetary Sciences
The Johns Hopkins University
Baltimore, Maryland 21218, U.S.A.*