JOURNAL OF MATERIALS SCIENCE 11 (1976) 1615–1623

Fracture in the crossed-lamellar structure of *Conus* shells

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Crossed-lamellar crystal architecture is the characteristic textural pattern of the calcium carbonate shell in many kinds of molluscs. By loading specimens from shells of the genus *Conus* in various orientations in bending tests it is shown that crossed-lamellar structure is highly anisotropic. This anisotropy is to be expected from the microscopic and submicroscopic structure, particularly the substructure of the primary lamellae and their orientation to one another, and from the paths taken by cracks travelling through layers of different orientation.

1. Introduction

Molluscs have a variety of characteristic structural arrangements of the material in their shells. The material is calcium carbonate in the form of either calcite or aragonite with a very tenuous matrix of protein [1–3]. The best known structural type is probably mother of pearl, or nacre; this consists of flat blocks of aragonite arranged in sheets about 0.3 to 1.0 μm thick with a thin layer of protein lying between each sheet and sending even thinner connecting membranes between the blocks. Nacre is found in the shells of members of three molluscan classes: the Bivalvia, Gastropoda, and Cephalopoda, but it is only one of several distinct types of crystal architecture found in bivalve shells [1]. Crossed-lamellar structure is according to Bøggild [3] the most specialized and the most common throughout the phylum, occurring in the Classes Bivalvia, Gastropoda, Polyplacophora and Scaphopoda. Its structure is very similar in the four classes, and it is not known outside the Mollusca. (For additional information on these classes see Appendix.)

In this study, we report on *Conus*, whose crossed-lamellar structure consists, as is most common in gastropods, of lamellae of aragonite. Each lamella is of the order of 40 μm thick and is composed of a stack of laths whose length is in the plane of the lamella and whose breadth is in the thickness of the lamella. These laths are themselves composed of many smaller lath-shaped aragonite crystals lying along the length of the laths (Figs. 1 and 2). In any lamella the laths are all orientated in the same direction, and this direction changes markedly from one lamella to the next, usually by about 70 to 90°. The lamellae do not always continue unchanged, they may become thinner and eventually disappear, as shown in Fig. 2. The protein part of the structure is extremely tenuous, about 0.5% by weight, and its detailed arrangement is uncertain.

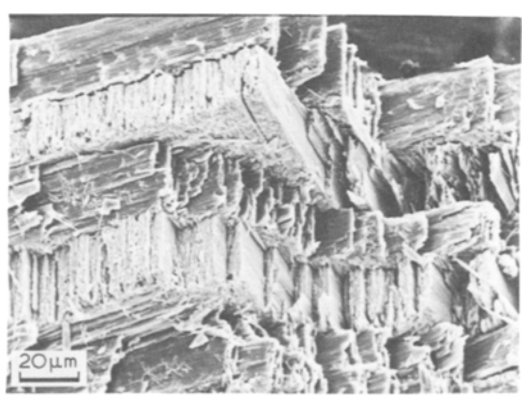

Figure 1 Fracture surface of crossed-lamellar structure. This is the middle layer of *Conus virgo*. Five lamellae are shown. The needle-like crystals making up the laths of each lamella are clearly visible.

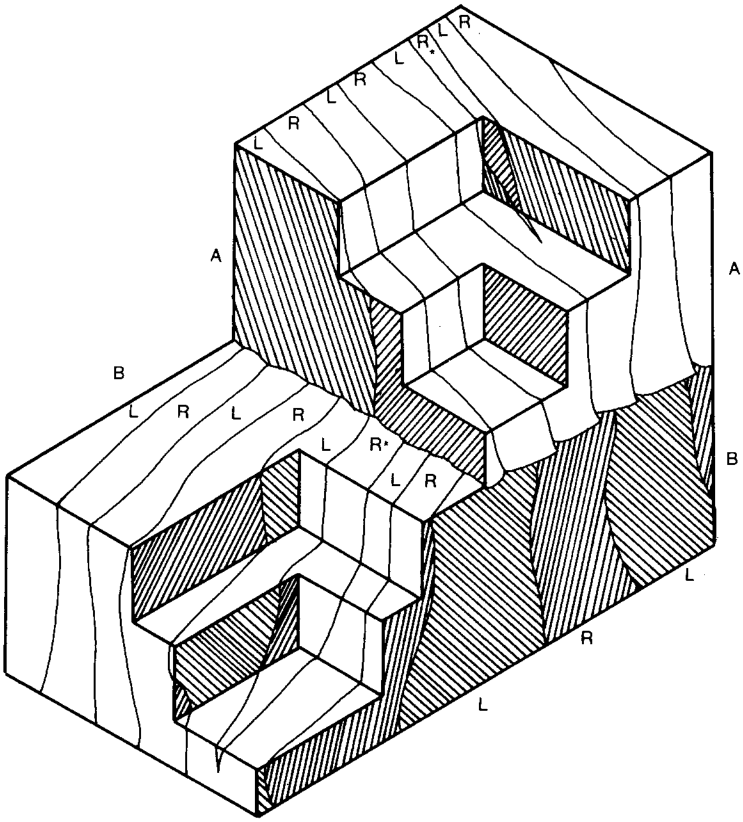

Figure 2 Schematic block diagram of crossed-lamellar structure. Shown here is the junction between two major blocks A, B of the structure, whose orientations differ by about 90°. In each block the lamellae are labelled "L", "R" and the laths are orientated approximately at right angles in the alternate layers. The orientation of the laths is shown where they outcrop on a face parallel to their long axis. Note two lamellae labelled "R*", which thin out and end.

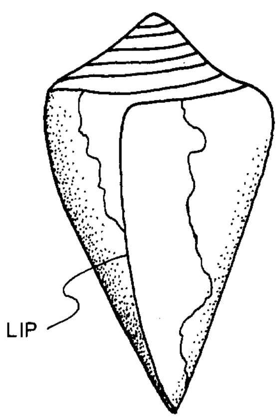

Figure 3 Shell of *Conus eberneus*. The conoid shape is characteristic of the genus. The lip is the most recently laid-down part of the shell. The two irregular lines mark repair lines: the shell has been broken back to these lines, probably by a crab, but the animal survived and repaired the damage.

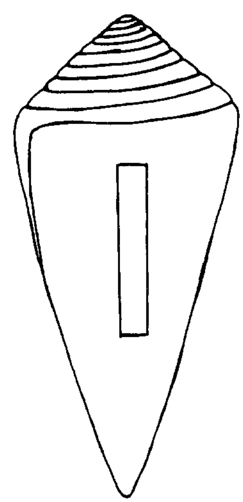

Figure 4 Diagram of the orientation of the longitudinal test specimens in relation to the whole shell.

Members of the genus *Conus* are predatory gastropods living in tropical regions. They have a most characteristically shaped shell (Fig. 3) [4]. The shell is made almost entirely of crossed-lamellar structure, and this is usually divided into three layers, of differing orientation. In the middle layer the lamellae are arranged with their short axis (their thickness) in the circumferential or transverse direction. The lamellae of the inner and outer layers have the short axis in the axial direction, that is, subparallel to the axis of coiling, or on a plane through it [5] (Figs. 4 and 5a). This arrangement was found to be so characteristic and

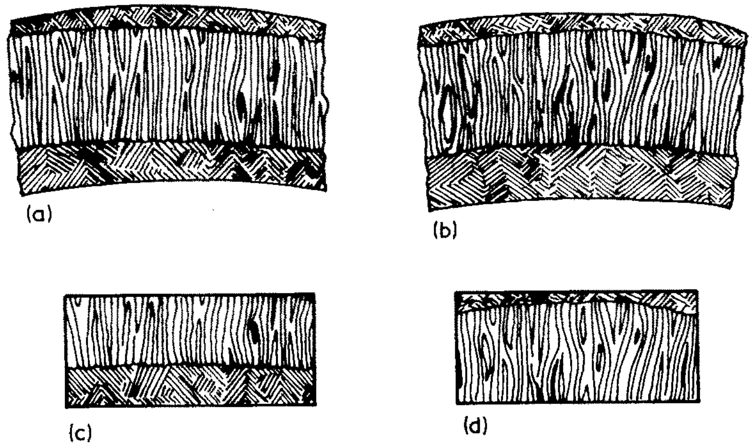

Figure 5 (a) and (b) show schematically the appearance of the three layers in transverse sections of axial blocks cut from the shell of *Conus miles*. The lamellae of the outer and inner layers are orientated so that their long axes are in the plane of the transverse section. The middle layer lies with its layers running approximately parallel to the long axis of the specimen. Both (c) and (d) were machined to rectangular prisms. (c) was prepared by cutting away as little of the inner layer as possible. (d) was prepared by leaving none of the inner layer.

constant in all species of *Conus* studied that, in the course of an investigation into the strength of shells of animals from different habitats, it was possible to perform some additional experiments that gave considerable insight into the mechanism of fracture of this tissue.

2. Materials and methods

Sixty-six test pieces from fourteen shells of seven *Conus* species were tested in bending. The test pieces were cut in the axial direction (Fig. 4). The gauge length varied from 13 to 25 mm, the depth of the specimen from 1.15 to 4.05 mm. The length/depth ratio varied from 4.8 to 16, with the majority of test pieces having a ratio of about 9. The test pieces were of the full thickness of the shell and the rather low length/depth ratio of some test pieces was necessitated by the shape of the shell. The sides of the test pieces were polished square but, except where specifically stated below, the top and bottom surfaces were not machined so the specimens had a slightly irregular cross-section. The moment of inertia (I) of the specimen was calculated from the maximum depth; more accurate measurements showed that this approximation had only a trivial effect on the calculated value. The test pieces, which had mostly been previously dried out, were machined and tested wet. They were tested in three-point bending with the central loading point being on the morphological outer surface of the shell. Seven test pieces from one specimen of *Conus striatus* were cut with the long axis in the transverse direction. This was not possible in the case of the smaller species. The test pieces were loaded with a head speed of 1 mm min^{-1} and the maximum load was reached and fracture occurred in about 30 sec or less. When the test piece had broken, one broken end was polished flat and etched and an acetate peel made [1]. From this peel the thickness of the three layers of the shell was determined. The bending strength of the highest load borne was calculated according to: bending strength $= Mc/I$, where M is the bending moment, c is half the depth of the section, and I is the moment of inertia of the section. (We are aware that bending strength does not tell us anything much about the tensile strength.)

A further fourteen axial test pieces were prepared from two specimens of *Conus miles* and arranged in pairs randomly. One member of each pair was machined so that all the inner layer was removed, leaving the middle layer to bear the most extreme tensile stresses. The other member of each pair was ground so that most of the inner layer remained (Fig. 5). These specimens were machined accurately into rectangular prisms, and both members of the pair were of the same depth and breadth.

During the tests the test pieces were observed in an attempt to correlate events on the load deformation curve with events seen on the test pieces. In some additional tests the loading was stopped at various times and the specimen examined microscopically. The values for breaking strength of these specimens are not reported here.

TABLE I

Species	M.R.	% Inner	Modified M.R.	First crack
eberneus	94	35	222	44
	59	47	210	67
	149	33	332	56
	194	29	385	46
	176	29	349	56
	177	32	382	60
	252	20	394	69
	192	25	341	67
	200	35	473	63
striatus:	92	34	211	54
axial	129	32	279	47
	124	31	260	58
	162	28	312	62
	91	34	209	42
	97	42	288	57
	73	32	158	48
	91	33	205	65
	110	37	277	72
	138	28	266	72
	138	38	281	93
	97	36	237	75
	88	27	165	53
	73	37	184	63
	110	41	316	78
striatus:	227	34	–	–
transverse	242	32	–	–
	231	32	–	–
	269	29	–	–
	149	28	–	–
	143	26	–	–
	164	29	–	–
	231	29	–	–
pulicarius	105	35	249	?
	121	30	247	49
	104	31	218	33
	98	33	218	53
	138	32	298	45
	93	26	170	?
	168	28	324	63
	155	27	291	45
	107	34	246	54
	122	28	235	51

Species	M.R.	% Inner	Modified M.R.	First crack
rattus	259	7	299	?
	184	24	319	?
	93	31	195	79
	254	0	254	?
	146	27	274	53
	115	35	272	89
lividus	173	11	218	28
	91	33	203	18
	129	21	207	62
	143	31	300	18
	116	39	312	50
	83	37	209	42
	69	46	236	36
	73	37	184	15
	128	42	380	81
	141	36	344	43
	74	37	186	23
virgo	166	29	329	53
	169	35	400	41
	150	29	297	61
	175	32	378	35
literatus	109	34	250	32
	72	45	238	23
	91	43	280	41
	103	28	199	?
	86	46	295	18
	65	49	250	32
	69	41	198	52
	70	51	292	55
	72	47	256	55
	74	39	199	47
	67	41	192	30

Species	M.R. middle layer	M.R. inner layer	First Crack
miles	182	62	45
	175	69	44
	289	58	38
	194	55	39
	168	52	45
	141	53	51
	215	29	27

M.R.: modulus of rupture (bending strength) (MN m^{-2}).
% inner: percentage of the cross-sectional area of the specimen occupied by the inner layer.
Modified M.R.: modulus of rupture calculated as if the inner layer were absent (MN m^{-2}).
First crack: calculated stress (MN m^{-2}) at which the first sharp dip in the curve occurred. In some cases, shown by ?, there was no sharp dip.
In the case of *miles* the pairs of M.R. refer to pairs of specimens with the middle layer and inner layer bearing the greatest tensile stress.
"First crack" refers to the specimen with inner layer present.

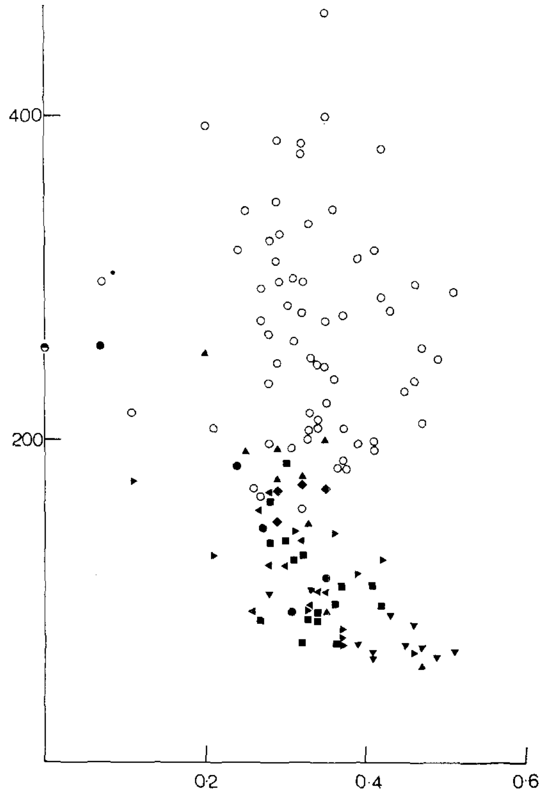

Figure 6 Bending strength of longitudinal specimens. Solid symbols: bending strength calculated directly according to the formula bending strength $= Mc/I$. Circle: *rattus;* square: *striatus;* triangle base to left: *lividus;* triangle, base to right: *pulicarius;* triangle, base up: *litteratus;* triangle, base down: *eberneus;* rhomb: *virgo.* Open circles: strength calculated as if the inner layer were absent. Abscissa: proportion of cross-sectional area occupied by inner layer. Ordinate: bending strength in $MN\ m^{-2}$. Although there are some significant between-species differences, the overall regression is highly significant and accounts for 58% of the variance.

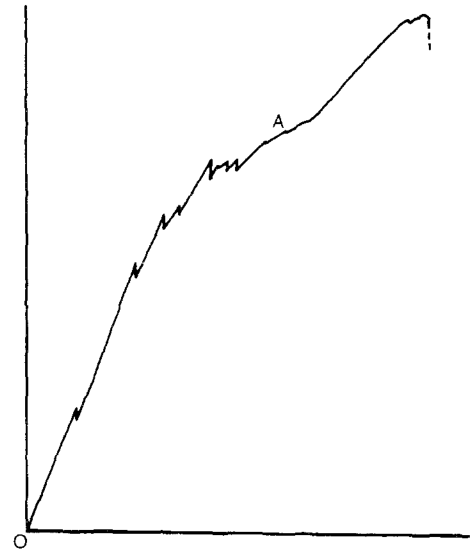

Figure 7 Load (ordinate) deformation (abscissa) curve of *Conus miles.* From 0 to A the curve shows the characteristic saw-tooth appearance given by cracking of the inner layer. Beyond this is the smoother curve characteristic of fracture of the middle layer.

3. Results

The results are shown in Fig. 6 and Table I. It is apparent from Fig. 6 that the greater the amount of inner layer present the less the bending strength. This indicates that the inner layer may not be very strong in bending in the axial direction. The load-deformation curve for complete specimens had a most characteristic shape (Fig. 7); it was initially linear and then there was virtually always a sudden reduction in the load followed by several more reductions as the strain increased, with load increasing between each event. Observation of the test piece itself during loading showed that the sudden reduction in load occurred at the same time as the appearance of a crack on the surface of the inner layer. If the test piece was unloaded at this point, the crack could be examined, and it always extended right to the interface between the inner and middle layer (Fig. 8). This suggested that there is a strong possibility that the inner layer does not contribute greatly to the bending strength, so we recalculated the bending strength using a value for I and c that would be given if the inner layer did not exist. The results are shown in Fig. 6. Of course, since all the test pieces except one did have an inner layer, the values for bending strength are, as a result, higher. However, the overall negative relationship between bending strength and the thickness of the inner layer has now entirely disappeared.

The results from *Conus striatus*, the one species in which we were able to test pieces in both axial and transverse directions, are also informative. The mean value of bending strength of test pieces cut in the axial direction is 107.5 $MN\ m^{-2}$ ($S.D.$ = 25.8). Those cut in the transverse direction had a mean bending strength of 207.0 $MN\ m^{-2}$ ($S.D.$ = 47.7). The mean strength of the axially orientated test pieces, calculated as if they had no inner layer was 243.1 $MN\ m^{-2}$ ($S.D.$ = 51.7). There is no significant difference between these two latter means, $t_{21} = 1.64$, but the number of specimens is too small to draw any firm conclusions from this.

The results from the specimen of *Conus miles*, half of whose test pieces were prepared by grinding off the inner layer, are also striking. The

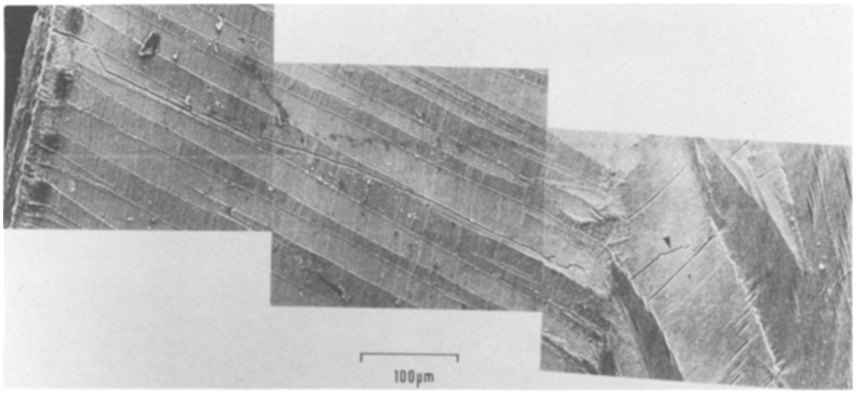

Figure 8 Montage of three scanning electron micrographs of a crack in *Conus miles.* The tension surface is at the left. The crack runs fairly directly until the boundary of the inner and middle layers, where it probably stops, although the crack marked with an arrowhead may be a short continuation of it. The other cracks in the middle layer are on the surface only, they occur in unloaded specimens and are caused by the grinding and etching.

mean strength for the test pieces with the inner layer present is 54.1 MN m^{-2}, for those with the inner layer removed it is 194.8 MN m^{-2}. The low value of 54.1 MN m^{-2} is probably caused by the fact that little of the middle layer remained in these specimens.

4. Discussion

The general results are clear – the third or inner layer cracks rather easily if it is loaded in the axial direction but much less easily if it is loaded transversely; in fact, the results of calculating the bending strength as if the inner layer were absent produces values not significantly greater than those from specimens that either were loaded transversely or that had had the inner layer removed. The strength of the inner layer, calculated from the value of the bending moment at the first sharp reduction in load is reasonably constant in most species; the great majority of values lie between 40 and 75 MN m^{-2}. The correlation between the load at the first crack and the difference between this load and the final load is insignificant (r_{52} = −0.114). This indicates, as one might expect, that the behaviour of the inner layer has no effect on the final strength of the specimen.

The microscopic and submicroscopic structure of the cracked surfaces shows that these results are reasonable. When an axial specimen is bent, the inner layer fails at several cross-sections, usually first underneath the central bar. These failures result in a fast crack, with fairly smooth surfaces, travelling to the boundary of the inner and middle layers. The crack is like a crack travelling between the layers of plywood. However, when the crack reaches this boundary it cannot travel further because of the nature of the middle layer. In general, at each point where it reaches the middle layer there will be a direction, at about 45° to the direction it had been travelling previously, that the crack can move in rather easily. This is because the laths in the middle layer can be pulled apart in this direction. However, although the crack may start to travel for many microns in this direction it is brought to a halt because the crack front on each side of the point we are considering is travelling at about 90° to it (Fig. 9). In order for the crack as a whole to advance it must do more than pull the laths apart, it must also break them across their

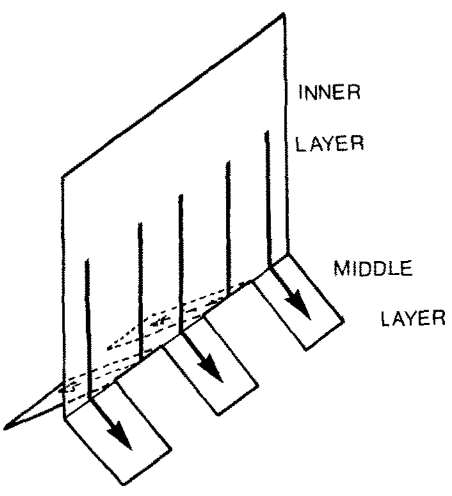

Figure 9 Highly schematic drawing of the geometry of the crack surface as it reaches the interface between the inner and middle layers.

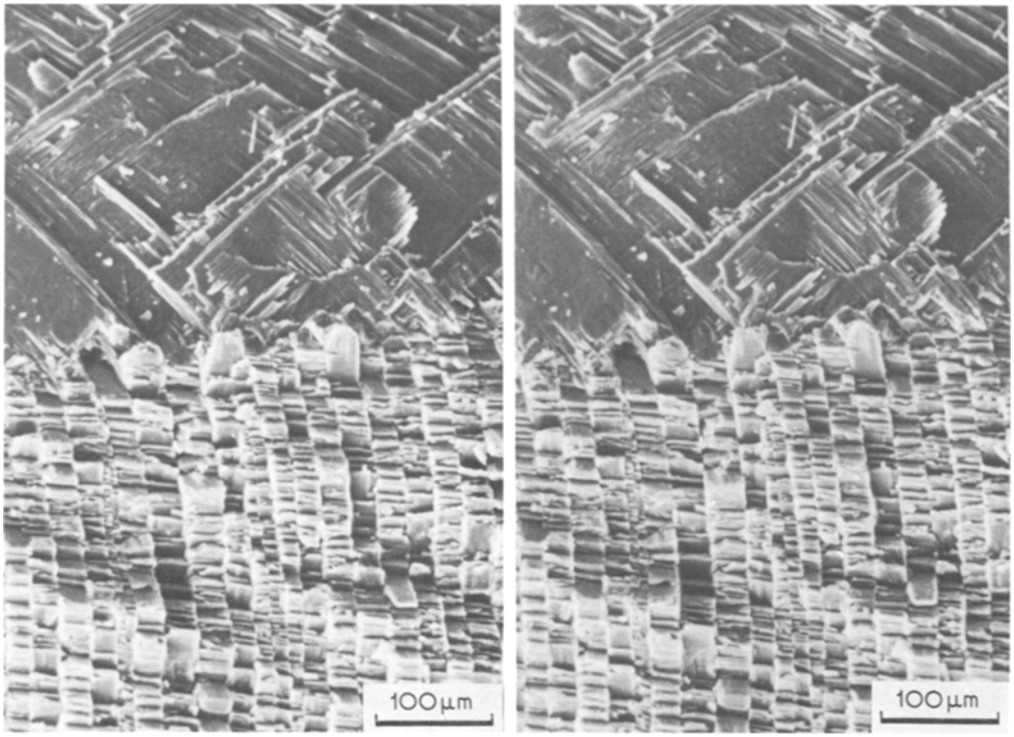

Figure 10 Stereopair of fracture surface at a boundary between inner and middle layers.

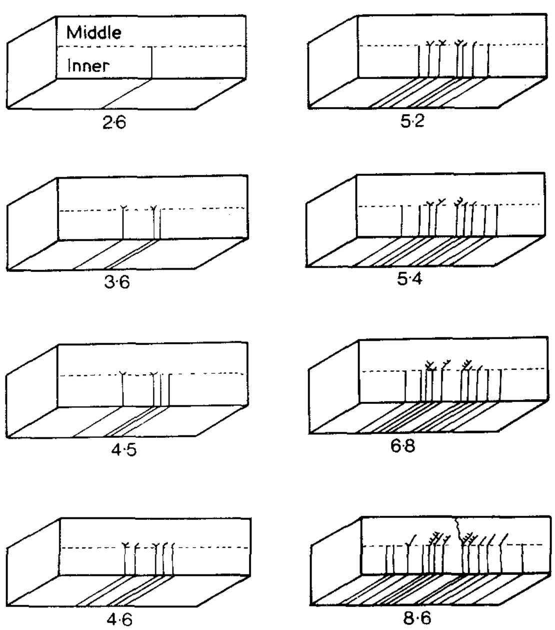

Figure 11 Diagram, approximately to scale, of the visual appearance of a test specimen under progressively greater loads. These are indicated by the figure (of kg load). The tension surface is on the lower side. The cracks all travel immediately to the junction of the inner and middle layers shown by the dotted line, but invade the middle layer only with difficulty.

length (Figs. 1 and 10). This has two effects; the local stress required to do this is considerably higher than that required to fracture the inner layer, and the amount of energy absorbed is very much greater. The difference in behaviour of layers with different orientations under the influence of loads is striking: the inner layer breaks with a series of sharp cracks, while the middle layer splits slowly apart, rather like wood in bending though without, of course, absorbing as much energy as wood. When the first crack appears under the central bar, the inner layer on each side of this is released from stress, and so the next cracks to form are some distance away from it (Fig. 11). As the load increases, cracks can be seen starting to pursue a tortuous course into the middle layer.

Crossed-lamellar structure is shown, therefore, to be highly anisotropic. Its bending strength in one direction is about 70 MN m^{-2}, in a direction at right angles to this it is about 200 MN m^{-2}. These findings are entirely consistent with the structure. In the weak direction the aragonite crystals can be pulled apart from each other; in the strong direction the laths cannot be pulled apart from each other, each one must be broken across its long axis.

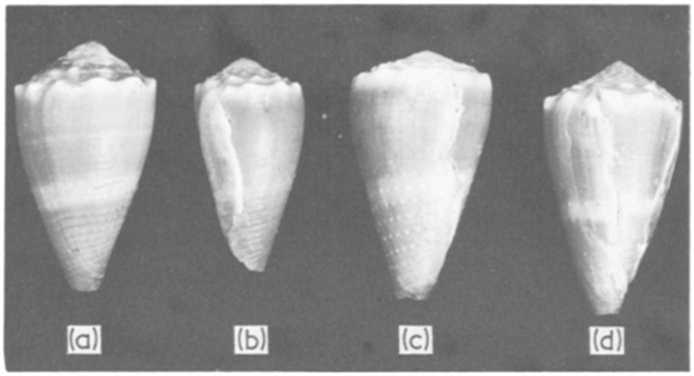

Figure 12 Four shells of *Conus lividus*, showing scars left following repair of shell after attacks by crabs: (a) (which is 45 mm long), no repair scars; one thickening near the lip, indicating a temporary cessation of growth, is visible; (b) one scar is visible close to the outer lip; (c) one scar is visible further from the outer lip; (d) three scars close to each other are visible.

Finally, there is the question of the adaptive significance of this arrangement. The shells of most species of *Conus* are quite thick, and the thickness is generally uniform throughout the last whorl [6, 7]. In epifaunal species such as *C. lividus* (Fig. 12), this serves as a defence against predatory crabs, particularly of the genus *Carpilius*, family Xanthidae (AJK, personal obs.; G. Vermeij, in prep.). Although crabs can break off the relatively thin outer lip of a fully grown *C. lividus*, the shell is usually too strong for them to break where it has reached its full thickness. The snail responds to attack by withdrawing into the shell beyond this point, thus losing its outer lip but avoiding falling prey to the crab. The *Conus* later repairs its shell, but a record of the attack is left as a scar (Fig. 12). The distribution of scars from crab attacks on a sample of 39 *C. lividus* from Hawaii (Fig. 13) indicates that up to four scars may be found on the last whorl of a single specimen. The average number of scars was 1.2 per last whorl. The type of loading exerted by crabs is equivalent to bending in the transverse direction, which *Conus* shells are much better at withstanding than loading in the longitudinal direction. To this extent, then, the arrangement of the inner layer seems adaptive. The question we might then ask is why is not the whole shell arranged in this way? There are various possible answers to this, but at least until we have a knowledge of the other kinds of loading to which the shells are exposed and of, for instance, the modulus of elasticity of the layers loaded in different directions it is probably not worthwhile speculating.

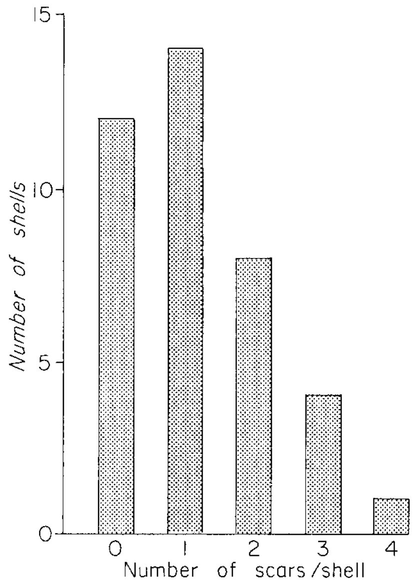

Figure 13 Frequency distribution of scars on the last whorl following repair of shell after attacks by crabs. The sample includes 39 specimens of *Conus lividus*. The mean number of visible scars is 1.2 per last whorl.

Appendix. The larger classes of living Mollusca

Class Polyplacophora – The chitons: coat-of-mail shells.
Class Gastropoda – The univalves: snails and slugs.
Class Bivalvia – The bivalves: clams, oysters, etc.
Class Scaphopoda – The tusk shells.
Class Cephalopoda – The squid, octopus, cuttlefish and nautilus.

Acknowledgements

J.D.C. wishes to acknowledge the support of the Science Research Council with a grant to study the mechanical properties and fracture of invertebrate hard tissue. A.J.K. acknowledges support by a John Simon Guggenheim Memorial Fellowship and NSF Grant BMS 75-03303.

References

1. J. D. TAYLOR, W. J. KENNEDY and A. HALL, *Bull. Brit. Mus. Nat. Hist. (Zool.) Suppl.* **3** (1969) 1.
2. *Idem, ibid* **22** (1973) 253.

3. O. B. BØGGILD, *K. danske Vidensk. Selsk. Skr.* **2** (1930) 232.
4. A. J. KOHN and A. C. RIGGS, *Syst. Zool.* **24** (1975) 346.
5. L. R. COX, in: "Treatise on Invertebrate Paleontology", edited by R.C. Moore (University of Kansas Press, 1960) **I** p. 84.
6. A. J. KOHN and V. R. MEENAKSHI, *Amer Zool.* **13** (1973) 1335.
7. *Idem,* in preparation.

Received 4 February and accepted 22 February 1976.