THE MECHANICAL PROPERTIES OF BIVALVE (MOLLUSCA) SHELL STRUCTURES

by JOHN D. TAYLOR *and* MARTIN LAYMAN

ABSTRACT. Bivalve shells are composed of a two phased composite material consisting of calcium carbonate and a largely protein matrix. The two phases are arranged into a number of distinct shell structures; these occur in discrete layers and their occurrence appears to be correlated with mode of life. Some mechanical properties of individual shell structures were tested; these included compression, bending, impact, and microhardness tests. Density and matrix content were also determined. Some structures were nearly twice as strong as bone. The relative strength is apparently related to the size of the microstructural units rather than to the matrix content, which is low. The possible functional significance of the various shell structures is discussed but it is difficult to see why any structure apart from nacre, which is both the strongest and the phylogenetically oldest, has been evolved.

RECENTLY much attention has been given to the mechanical properties of bone (Evans 1957; Currey 1964 and, with a good review, 1970; Bell 1969; and many others) but little attention has as yet been paid to other calcified tissues such as mollusc shells. In spite of the recent activity in the study of shell structures the only worker to have considered the microstructure of mollusc shells from a mechanical functional point of view is Wainwright (1969). Having studied the microstructure of molluscan shell materials for some years (Taylor *et al.* 1969; Kennedy *et al.* 1969) we were impressed by an apparent correlation between the type of shell structure and the mode of life of the animal concerned. We thus decided to investigate the mechanical properties of these materials in relation to their possible functional significance. The limitations imposed by the mechanical properties of the shell materials may have influenced the course of molluscan evolution; for instance this study might help to explain why certain possible shell coiling forms have never been utilized in nature.

The bivalve shell has obviously important functions in the protection of the animal, the maintenance of the mantle cavity and the support of the organs within it. In addition the shell plays an important part in the burrowing and boring processes (Trueman 1968). The shell is as functional as the more widely studied structures such as gills, siphons, stomachs, etc. Wainwright (1969) has stated that the mechanical function of the shell depends upon its ability to resist deformation and failure under environmental stresses; and that two main factors in shell architecture, shape, and construction materials, are involved in determining shell strength.

SHELL STRUCTURES

The bivalve shell, like bone (Currey 1964), may be considered as a material consisting of two phases retaining their separate identities (Wainwright 1969). The phases are crystalline calcium carbonate in the form of calcite or aragonite, and an organic matrix consisting largely of fibrous protein. The phases are arranged into various distinct fabrics which are recurrent throughout the Bivalvia and other molluscan classes. The mineralogy and micromorphology of these shell structures have been described in some

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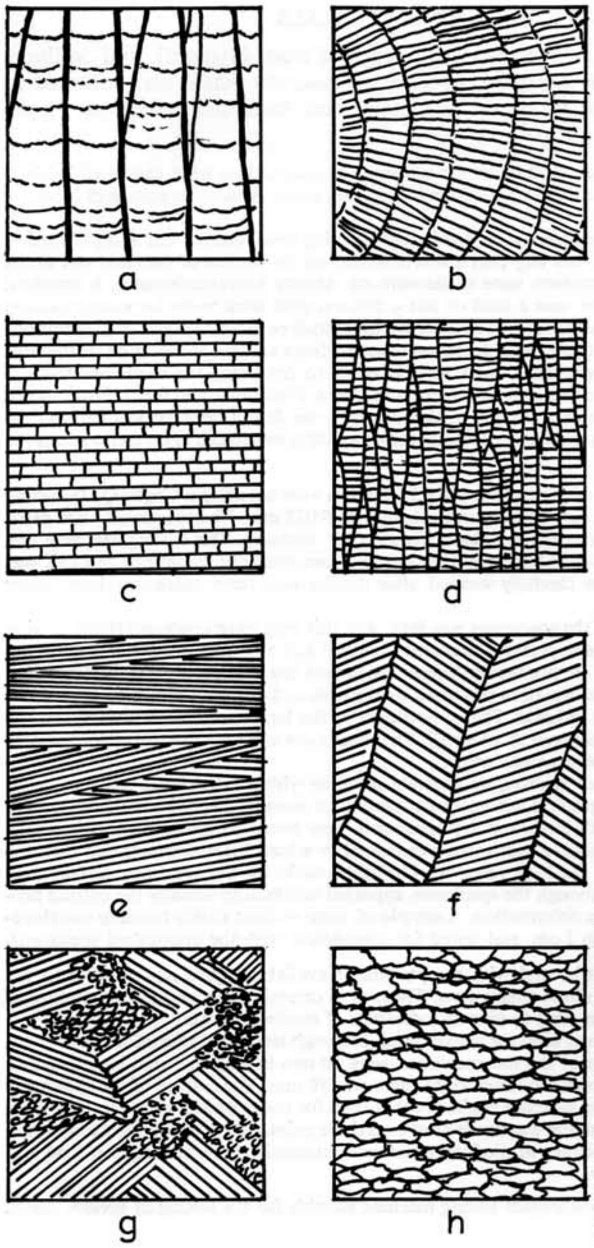
detail by Schmidt (1924), Bøggild (1930), Wada (1961), Wilbur (1964), Wilbur and Simkiss (1967), and Taylor *et al.* (1969 and in press).

The shell structures found in the Bivalvia belong to six main arrangements briefly described below and illustrated diagrammatically in fig. 1*a–h*. Further details can be found in the references cited; the nomenclature is largely retained from Bøggild (1930).

Simple prismatic structure consists of columnar crystals, polygonal in section, up to 200 μm in length and 9–80 μm in width, but the size is very variable. Each prism is surrounded by a sheath of matrix. The prisms are aligned normal to the shell exterior and are usually found as an outer shell layer. *Composite prismatic* structure consists of very small needle-like crystals 2 μm in width and up to 10 μm in length radiating from a central axis which is aligned parallel to the shell exterior. This structure is found only as an outer shell layer. *Nacreous structure* consists of tablet-like crystallites 2–10 μm in length and 0·4–3 μm in thickness, which are arranged in sheets and in section have the appearance of a brick wall. Another variety of nacre has the crystallites arranged into columns (*lenticular nacre*). Nacreous structures are usually found in the middle and inner layers of shells. In *foliated* structure the crystalline units are lath-like crystallites 2–4 μm in width, 0·2–0·5 μm in thickness and up to at least 20 μm in length, and are arranged in side to side contact into irregular sheets which have the same general orientation towards the shell margin and lie subparallel to the inner shell surface. *Crossed-lamellar* structure consists of lath-like crystals 5 μm in width and up to 20 μm in length arranged into lamellae. The lamellae are of variable size but some can be seen with the naked eye; in adjacent lamellae the crystallites are aligned in opposing directions. *Complex crossed-lamellar* structure is rather similar to crossed-lamellar, but consists of an intergrowth of blocks of crystallites arranged with four principal orientations. *Homogeneous* structure consists of small granular crystallites up to 5 μm in diameter with no obvious crystal form. The shell material deposited beneath the muscle attachment areas, the *myostracum*, has an irregularly prismatic structure.

The structures described above are found in discrete shell layers; certain combinations of structures are recurrent and show a distribution related to the probable phylogenetic history of the class.

The morphology of the organic matrix has been extensively studied by Grégoire (1967 with references), and in bivalves mostly consists of lace-like sheets which surround and in some cases are contained within the crystallites. The protein of the matrix resembles the keratin–myosin–epidermin–fibrin group of fibrous proteins (Degens *et al.* 1967; Wilbur and Simkiss 1968). The variation in amino-acid composition and amino sugars may be related to both phylogenetic and environmental effects. Proteins of the shell matrix group are characterized by a high degree of cross-linkage, a feature which will have an effect on mechanical properties and resistance to disaggregation. Variation in the amount and type of cross-linkage in the various shell structures has not yet been studied, and any possible effects upon shell strength are unknown. Surprisingly little is known of the total matrix content of the structural types. Hare and Abelson (1964) gave some general results which indicated a total protein content of 0·1%–5%, varying between various shell structures. The work of Hudson (1967), although based upon more exact layer separation and documentation, examined too few structural types to be of use in the present context.



TEXT-FIG. 1. Diagrammatic representation of the textures of bivalve microstructures as seen in sections normal to the shell surface.
(*a*) Simple prismatic structure
(*b*) Composite prismatic structure
(*c*) Sheet nacreous structure
(*d*) Lenticular nacreous structure
(*e*) Foliated structure
(*f*) Crossed-lamellar structure
(*g*) Complex crossed-lamellar structure
(*h*) Homogeneous structure

METHODS AND MATERIALS

The fresh specimens used in the tests were supplied from Plymouth and Millport marine laboratories, with the exception of *Tridacna maxima* which was collected at Malindi, Kenya. All dry and preserved specimens were from the collections of the British Museum (Natural History).

Microhardness. Tests were made on shell layers from seventy species from a wide variety of habitats and geographical localities and exhibiting all the shell structural types. A list of species and localities is available on request.

Specimens of separate shell layers were mounted in quick-setting resin, ground flat and polished to 3 μm. When the layer to be tested was very thin it was mounted on the surface of the resin and tested without further treatment. Indentations were made with an Akashi microhardometer, a standard Vickers diamond pyramid indenter, and a load of 500 g. Several tests were made for each specimen and the average taken. The material tested was at least five times thicker than the depth of indentation; tests were made at more than five times the indentation diagonal from another indentation or the edge of the specimen. Initially tests were made upon *Mytilus edulis* to determine the hardness variation within a layer and the effects of age and orientation upon hardness. Fresh, dry, and formalin-preserved specimens were tested in a preliminary survey. Little difference was found between wet and dry, so dry specimens were mostly used in the survey. Considerable variation was found in formalin-preserved specimens.

Compression tests. Test specimens of dimensions $8 \times 1{\cdot}5 \times 1{\cdot}5$ mm were cut using a Capco Q. 35 cutting machine, which produces parallel cuts and ensures accuracy to 0·025 mm. The specimens were glued to a Sindyano base which was attached to a base allowing 90° rotation. The cutting machine was lubricated and cooled by mineral oil which might conceivably penetrate the specimens, but this was unavoidable. The specimens were carefully washed after cutting and fresh specimens kept under water until tested.

The length to diameter ratio of the specimens was high, and this may have produced slight bowing which could reduce the values of compressive strengths obtained and also have some effect upon the modulus of elasticity. However, in producing longer specimens the stresses during cutting were reduced. There was little plastic deformation produced by the tests and as the specimen ends were cut parallel the tendency to bow was reduced. The convenience of the larger specimens outweighed the effect of buckling, which was considered to be small. The results are valid for comparative purposes even if the absolute values may have a small error.

Testing was carried out using an Instron, an accurate machine with a high elastic stiffness, upon which a load *versus* compression graph is automatically plotted. A crosshead speed of 0·05 cm/minute was used throughout testing. Both fresh and dry specimens were tested to fracture and the results plotted on a stress/strain curve. Similar specimens were tested to a load below fracture and then the cross head velocity reversed and the load removed. Griffith's cracks on the specimen surface may influence the fracture strength; although the specimens appeared satisfactory visually the cutting process may have caused some surface deformation. A sample of nacre without visible banding was therefore polished on diamond paste to 1 μm, and tested for comparison with the unpolished specimens.

Bend tests. Bivalve shells are brittle, and with the equipment available it was not possible to cut specimens in a suitable shape for direct tensile tests. Thus, as in ceramics, the modulus of rupture as determined through bend tests was used to give an indication of tensile properties.

For bivalves a three point test was used for convenience, although the superiority of the four point test is recognized. The dimensions of the test specimens were 20 mm in length, 5 mm in width, and 1·5 mm in depth. The length between the lower knife edges was 16 mm. The cutting of the specimens was carried out on a Capco cutting machine similar to that used for compression tests. Dry and fresh wet specimens were tested. The bending was carried out on a three point test rig with an Instron testing machine. Displacement of the specimen at the load point was automatically plotted against load and the specimens tested until fracture.

Impact tests. There was no standard impact testing machine suitable for the testing of bivalve shells.

Either the machine was too large and lacking in sensitivity or the specimen size and shape were unsuitable. Consequently a simple test machine was constructed which, although unable to give absolute values of the energy absorbed, could give a comparison of the impact resistance of the various shell structures. The apparatus was modified from a crystal cleaver mounted in a wooden frame, with a hammer head replacing the cleaver blade and the specimens held against two blunt edges of metal. Portions of fresh shells containing one or more shell layers and periostracum were tested but as the shells were of different thickness, curvature, and ornamentation little direct information was obtained on shell structures. To obtain results for individual shell layers specimens of single structural types were cut to 5×1·5×1·5 mm on a Capco cutting machine and tested in both the fresh and dry states.

Density. The densities of individual shell structures were measured in two ways; by a standard weighing method and by a titration method using heavy liquids (Embrey 1969). The results obtained were closely comparable.

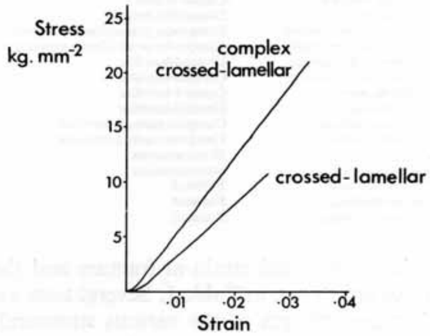
Total organic nitrogen content. A Kjeldahl digestion method was used, followed by steam distillation of the alkali treated digest. Initially this technique was applied on a semi-micro scale using up to 100 mg of shell. In view of the variability of the small quantities of nitrogen detected in some samples the amount of shell subsequently used was increased tenfold.

Pieces of individual shell structures were separated out, care being taken to remove all the periostracum. The shell was then digested over low heat with 6 ml of 50% sulphuric acid containing 1% selenium dioxide plus a small crystal of cupric sulphate. Prior to steam distillation into 0·01N sulphuric acid the digest was made alkaline by the addition of 14 ml of 10N sodium hydroxide. The quantities involved were within the scope of Quickfit semi-micro apparatus, and although the variation between samples of the same piece of shell structure was still high the limits appeared to narrow with the increased quantity of shell used.

Microstructures. Microstructures were studied by acetate peels of polished and etched sections of shells and by reflected light microscopy of polished surfaces. Surfaces and sections were also examined by scanning electron microscopy.

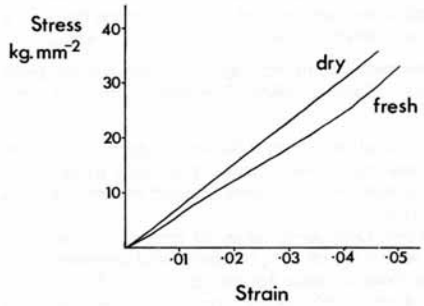
RESULTS

Compression tests. A graph of load versus compressive strain was automatically plotted during compression testing and then replotted as a stress/strain diagram (text-figs. 2–6). After minor adjustments (bedding down) most specimens exhibited a virtually linear relationship (text-fig. 2). This signifies elastic behaviour with the material obeying Hooke's law. The modulus of elasticity was obtained from the slope of the stress/strain curve. Deformation was elastic almost up to fracture, with possibly a small amount of 'plastic' deformation just before the point of fracture. Slight local deviations were observed in some curves; these were small and made no difference to the over-all form of the plot but indicated that the mechanisms of deformation, although apparently corresponding to Hookean elasticity, may be more complicated than for single phase materials.

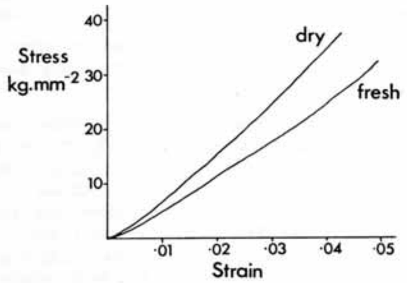


TEXT-FIG. 2. Stress/strain diagram for compression tests on the outer crossed-lamellar layer and the inner complex crossed-lamellar layer of *Tridacna maxima*.

A few specimens exhibited to a small degree behaviour which resembled that of an elastomeric material (text-figs. 3, 4). Materials showing this behaviour were of nacreous and homogeneous structures. The elastomeric-like characteristics were exhibited in the homogeneous structure of *Arctica islandica* in both the wet and dry states, but only in wet specimens of nacre. The single specimen of lenticular nacre examined also showed elastomer-like properties. In these samples a constant value of modulus could not be calculated and the value quoted is an average.



TEXT-FIG. 3. Stress/strain diagram for compression tests on sheet nacre of *Modiolus modiolus*.



TEXT-FIG. 4. Stress/strain diagram for compression tests on the middle homogeneous layer of *Arctica islandica*.

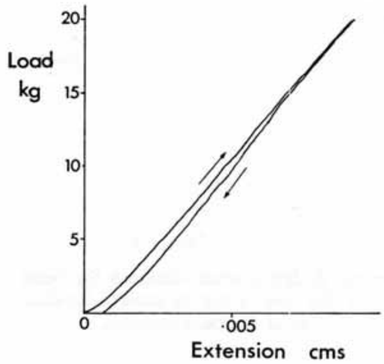
TABLE 1. Compression test results

Species	*Structure*	*Condition*	*No. of tests*	*Stress at fracture kg mm⁻²*		*Strain at fracture* $\times 10^{-2}$	*Modulus kg mm⁻²*
				Mean	*Std. dev.*		
Pinctada maxima	Sheet nacre	Dry	5	38·2	2·7	0·045	0·85
Pinctada maxima	Sheet nacre	Polished	2	42·3	..	0·044	1·0
Modiolus modiolus	Sheet nacre	Dry	4	39·3	4·8	0·050	0·80
Modiolus modiolus	Sheet nacre	Wet	4	33·4	6·8	0·050	0·62
Neotrigonia margaritacea	Lenticular nacre	Dry	1	30·6	..	0·036	0·89
Pinctada maxima	Calcite prisms	Dry	5	23·6	1·8	0·029	0·85
Codakia tigerina	Composite prisms	Dry	4	10·8	1·4	0·018	0·68
Mercenaria mercenaria	Composite prisms/homogeneous	Dry	3	23·8	4·6	0·024	0·99
Mercenaria mercenaria	Composite prisms/homogeneous	Wet	3	31·5	5·2	0·035	0·94
Glycymeris glycymeris	Crossed-lamellar	Dry	4	13·2	4·0	0·015	0·93
Glycymeris glycymeris	Crossed-lamellar	Wet	4	8·33	1·5	0·012	0·74
Tridacna maxima	Crossed-lamellar	Dry	5	14·5	1·6	0·019	0·78
Tridacna maxima	Crossed-lamellar	Wet	2	10·9	..	0·025	0·44
Tridacna maxima	Complex crossed-lamellar	Dry	6	24·4	5·4	0·032	0·78
Tridacna maxima	Complex crossed-lamellar	Wet	2	21·3	..	0·033	0·64
Arctica islandica	Homogeneous	Dry	6	37·4	5·8	0·043	0·93
Arctica islandica	Homogeneous	Wet	4	32·4	4·4	0·050	0·90
Pecten maximus	Foliated	Dry	3	20·3	4·4	0·029	0·74
Pecten maximus	Foliated	Wet	2	10·2	..	0·021	0·49
Crassostrea gigas	Foliated	Wet	3	0·64	0·1	0·005	1·34

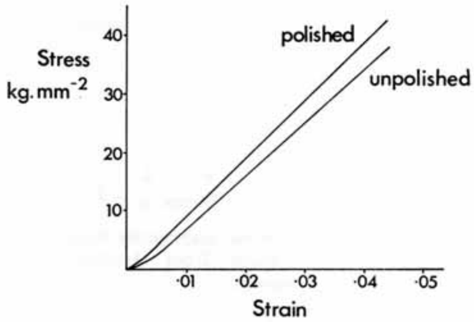
The stress and strain at fracture and the modulus of elasticity of the various structures are shown in Table 1. Several tests were carried out for most structural types. The fracture strength of the various structural types in descending order is nacre, homogeneous, composite prisms, homogeneous, complex crossed-lamellar, calcite prisms, foliated structure (*Pecten*), crossed-lamellar, composite prisms (*Codakia*), and the foliated structure of *Ostrea*. The two layers were tested together in *Mercenaria* because of cutting difficulties.

A typical result for the specimens which were loaded to about half the fracture stress and then unloaded is shown in text-fig. 5. Only a small amount of 'plastic' deformation occurred and in all cases the plot for unloading did not correspond to a straight line but tended to follow the load curve, showing a decrease in modulus at low levels of loading.

Wet fresh specimens (with one exception) displayed a slightly lower fracture strength than dry shells of the same species, and the modulus of elasticity was also lower. *Mercenaria mercenaria* showed a higher strength, but this may have been because different proportions of the two layers were tested in the two samples.



TEXT-FIG. 5. Load/unload diagram for compression tests on the sheet nacre layer of *Pinctada maxima*.



TEXT-FIG. 6. Stress/strain diagram of the unpolished and polished specimens of sheet nacre from *Pinctada maxima* showing the effect of the removal of some surface imperfections.

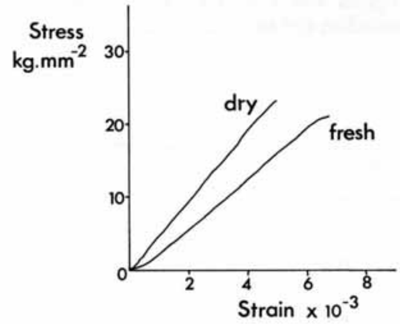
A statistical test for significant differences at the 5% level between the samples in the wet and dry states (*t*-test, see Bailey 1959) showed that most structures are significantly different, although two pairs, calcite prisms and the foliate structure of *Pecten*, and homogeneous and nacreous structures, were similar in strength.

The specimens of sheet nacre from *Pinctada maxima* which were polished to reduce surface cracks before testing showed slightly higher fracture stress and modulus of elasticity than the unpolished specimens (text-fig. 6).

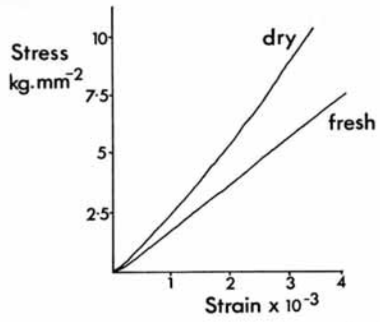
Bend tests. The data obtained from the automatically plotted load/displacement curve were used to calculate modulus and strain; these are shown in Table 2. Stress-strain curves are shown in text-figs. 7, 8. Because of the difficulties of cutting large enough test specimens of uniform structure, too few specimens were tested for statistical analysis.

The fracture stress was lower for compression tests and the modulus higher. Although the stress-strain plots approximate to a straight line, elastomer-like properties are seen in most cases (text-figs. 7, 8). The nacreous structure in both *Modiolus modiolus* and *Pinctada maxima* exhibited a small 'plastic' deformation range just before fracture. Again nacre is by far the strongest structure, but homogeneous was much weaker than under compression, being less strong than the crossed-lamellar layer of *Tridacna* and not much stronger than the prismatic layer of *Pinctada*. Again by far the weakest was the foliated structure of *Crassostrea gigas*. The fracture strengths of dry specimens were slightly higher than of wet ones.

Impact tests. Tests on individual shell layers showed that nacre was again the strongest structure (Table 3). It was followed in decreasing strength by homogeneous, calcite



TEXT-FIG. 7. Stress/strain diagram for bend tests on sheet nacre from *Modiolus modiolus*.



TEXT-FIG. 8. Stress/strain diagram for bend tests on the inner complex crossed-lamellar layer of *Tridacna maxima*.

TABLE 2. Bend test results

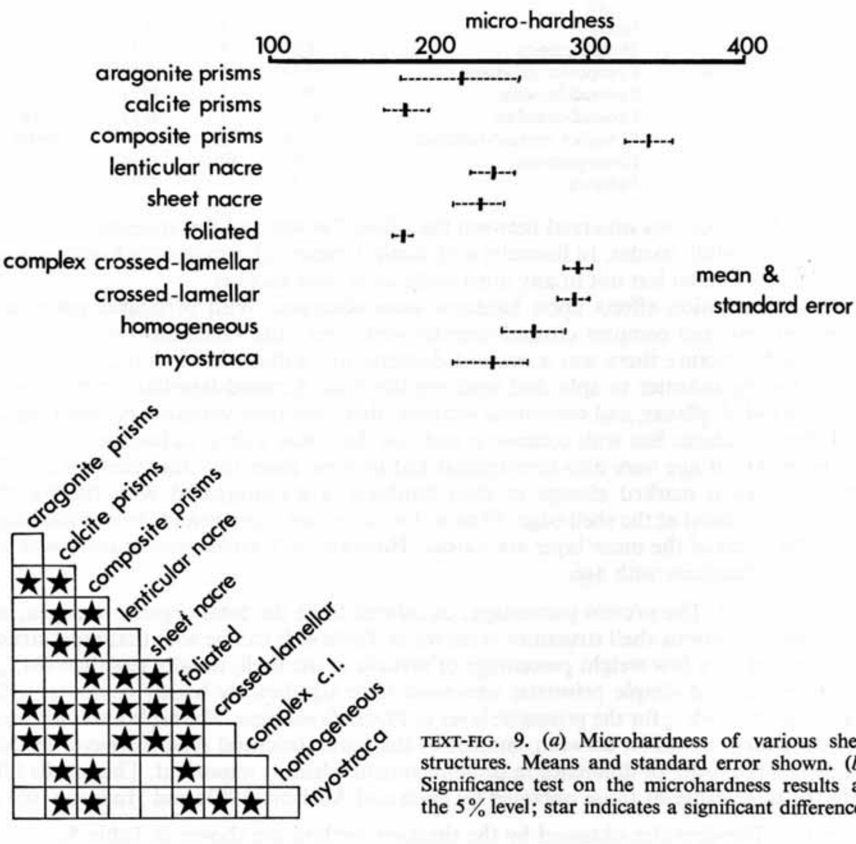
Species	*Structure*	*Condition*	*Load at fracture kg*	*Stress at fracture kg mm^{-2}*	*Modulus kg mm^{-2}*	*Strain* $\times 10^{-3}$
Pinctada maxima	Sheet nacre	Dry	17·6	36·08	4·7	7·7
Modiolus modiolus	Sheet nacre	Dry	11·6	23·8	4·69	5·0
Modiolus modiolus	Sheet nacre	Wet	10·4	21·3	3·15	6·7
Pinctada maxima	Calcite prisms	Dry	4·85	9·94	1·98	5·0
Tridacna maxima	Crossed-lamellar	Dry	5·75	11·79	3·20	3·68
Tridacna maxima	Crossed-lamellar	Wet	4·2	8·5	2·1	4·0
Tridacna maxima	Complex crossed-lamellar	Dry	4·25	8·71	2·57	3·4
Tridacna maxima	Complex crossed-lamellar	Wet	3·75	7·5	1·9	3·9
Arctica islandica	Homogeneous	Dry	5·25	10·76	3·11	3·46
Arctica islandica	Homogeneous	Wet	7·0	14·35	4·46	3·22
Crassostrea gigas	Foliated	Wet	0·2	0·41	8·29	1·4

prisms, complex crossed-lamellar, and the very weak foliated of *Crassostrea*. The tests carried out on larger pieces of shell which had variable thickness and ornament are not listed here, but indicated the additional and maybe overriding effect of shape and ornament over shell structure as a factor controlling shell strength. The behaviour of the foliated structure in *Ostrea edulis* and *Placuna placenta* was interesting; in these specimens the cracks were not propagated through the whole structure but a localized hole was punched through the specimen by the test hammer.

Microhardness. The results of the microhardness survey of the shell layers are listed under the various shell structure types in text-figs. 9*a*, *b*, together with a *t*-test for

TABLE 3. Impact results (individual layers)

Species	*Structure*	*Impact number (N)*
Pinctada maxima	Sheet nacre	69
Modiolus modiolus	Sheet nacre	38
Tridacna maxima	Crossed-lamellar	14
Tridacna maxima (wet)	Crossed-lamellar	17
Tridacna maxima	Complex crossed-lamellar	17
Arctica islandica	Homogeneous	25
Arctica islandica (wet)	Homogeneous	28
Pinctada maxima	Calcite prisms	24
Crassostrea gigas	Foliated	5·5



TEXT-FIG. 9. (*a*) Microhardness of various shell structures. Means and standard error shown. (*b*) Significance test on the microhardness results at the 5% level; star indicates a significant difference.

differences significant at the 5% level. In some structures, such as aragonite prisms, there is considerable variation from species to species.

Composite prismatic structure is significantly harder than all other structures except possibly complex crossed-lamellar. The latter, crossed-lamellar, and homogeneous structures are of similar hardnesses and are harder than all remaining structures. The two varieties of nacre and aragonite prisms are all similar in hardness but harder than calcite prisms. Foliated structure is the softest structure. All structures, whether composed of calcite or aragonite, have higher hardnesses than the naturally occurring inorganic polymorph; that is 135 for calcite and 190 for aragonite.

TABLE 4. Protein percentage of shell structures, determined from organic nitrogen contents

Species	*Structure*	*Average % wt protein*	*No. of detns.*	*Minimum value*	*Maximum value*
Pinctada maxima	Nacre	2·3	3	1·57	3·06
Modiolus modiolus	Nacre	0·9	3	0·72	1·05
Pinctada maxima	Simple prisms	4·8	3	4·44	5·28
Mercenaria mercenaria	Composite prismatic	0·34	4	0·32	0·39
Glycymeris glycymeris	Crossed-lamellar	0·3	3	0·23	0·32
Tridacna maxima	Crossed-lamellar	0·17	3	0·13	0·19
Tridacna maxima	Complex crossed-lamellar	0·06	5	0	0·098
Arctica islandica	Homogeneous	0·4	10	0·14	0·55
Pecten maximus	Foliated	0·4	3	0·29	0·42

Little difference was observed between the values for wet and dry specimens, the dry ones being slightly harder. In formalin and alcohol-preserved samples the hardness was significantly altered but not in any apparently consistent manner.

Some orientation effects upon hardness were observed. With prismatic, nacreous, homogeneous, and complex crossed-lamellar structures little variation was found, but in foliated structure there was a marked decrease in hardness in sections, with a tendency for the indenter to split and separate the folia. Crossed-lamellar structure was tested in radial, planar, and concentric sections; there was little variation between radial and planar sections but with concentric sections there was a drop in hardness.

The effects of age were also investigated and in some cases the older parts of a shell layer showed a marked change in shell hardness when compared with the freshly deposited material at the shell edge. Thus in *Laevicardium crassum* and *Arctica islandica* the outer parts of the outer layer are harder. However in *Stavelia horrida* there was an increase in hardness with age.

Matrix content. The protein percentage, calculated from the total organic nitrogen, of fragments of various shell structures is shown in Table 4. It can be seen that most structures have a very low weight percentage of protein in the shell, usually less than 0·4%; but nacreous and simple prismatic structures have significantly higher contents, with a maximum of 4·8% for the prismatic layer of *Pinctada maxima*. The table also indicates the quite large variation between samples of the same structural type. However in this study it is the order of difference in protein content which is important. The results fall into the same range as those obtained by Hare and Abelson (1963) and Hudson (1967).

Densities. The densities obtained by the titration method are shown in Table 5.

TABLE 5. Density measurements

Species	*Structure*	*Density*
Pinctada maxima	Nacre	2·74
Modiolus modiolus	Nacre	2·74
Pinctada maxima	Prismatic calcite	2·56
Codakia tigerina	Composite prisms	2·94
Mercenaria mercenaria	Composite prisms	2·66
Glycymeris glycymeris	Crossed-lamellar	2·80
Tridacna maxima	Crossed-lamellar	2·76
Tridacna maxima	Complex crossed-lamellar	2·80
Arctica islandica	Homogeneous	2·72
Crassostrea gigas	Foliated	2·52
Pecten maximus	Foliated	2·67

DISCUSSION AND CONCLUSIONS

Two aspects of shell strength may be discussed. Firstly, how does the shell behave as a material, and secondly, what is the functional significance, if any, of the properties of the material? The first of these questions is the easier to approach.

Our work supports the hypothesis that the bivalve shell behaves as a composite material in a manner similar to that of bone. The behaviour of the material does not resemble that of a single phased solid; for although the lack of 'plastic' deformation suggests a behaviour like a ceramic, the slight elastomer-like behaviour may indicate the role of the organic matrix. Both the compressive and tensile strengths of shell are remarkably high and most are similar to bone. Currey (1970) has recently reviewed the results of many tests by various workers on bone and quotes values of 9·0–23·7 kg mm^{-2} for compression and 8·2–14·1 kg mm^{-2} for tension. The variation depends upon the histology, orientation, and condition of the specimen, and the nature of the test. Although most shell structures fall within this range, nacre is much stronger both in compression and bending; the maximum for compression is nearly twice the highest recorded for bone. Homogeneous structure is also much stronger than bone in compression but does not perform as well under bending. Currey (1964) thought that skeletal materials such as mollusc shells would not behave as normal two phase substances, considering that the small amount of matrix present would not act as a very efficient arrestor of cracks. Molluscan shells thus show what appear to be very high strengths considering the nature of the constituent materials. By comparison, bone has approximately 40% weight of collagen. As can be seen from Table 4 the material with the highest strength, nacre, has one of the highest matrix contents. However, prismatic structure, which has quite a low strength, has a much higher protein content. Homogeneous structure, which is extremely strong in compression, has a low protein content. There is thus no obvious correlation between matrix content and strength; there may be some relation to the type of matrix but this has not been studied.

A possible significant factor in the strength of the various structures is the size of the largest microstructural units. Thus crossed-lamellar structure consists of small crystals arranged into much larger blocks, whereas in nacre and homogeneous structures the individual crystallites are the largest units present. Small cracks developing in the crystallites would have their energy dissipated at the many crystallite boundaries in nacreous and homogeneous structures, whereas there will be a tendency for cracks to travel along the boundaries of the larger units in crossed-lamellar and prismatic structures.

All the shell structures are harder than inorganic calcite and aragonite. This property may indicate the rubber-like nature of the matrix; the indenter stress is probably distributed to other parts of the shell and stored as elastic energy which is released when the indenter is raised.

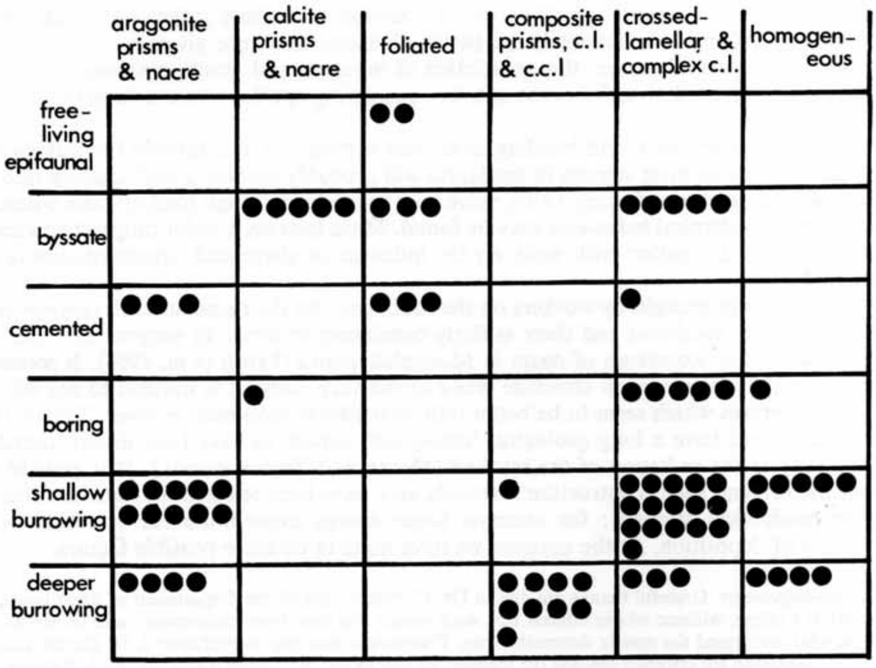
Recent research on bone has shown a relation between compressive strength and apparent density (Galante, Rostoker, and Ray 1970). In the shells examined we could find no such relationship. Although *Crassostrea gigas* has a low compressive strength and a low density, composite prismatic structure has a high density and a low compressive strength. Bone however incorporates many holes into its structure which possibly act as crack stoppers (Currey 1964). Comparable structures are generally absent in bivalves, although the cavities and chalky layers of oysters may possibly serve a similar function. The layered arrangement in the shell of materials having different properties may also act as a crack-stopping mechanism.

Obviously the strength of the shell does not merely depend upon the strength of the construction materials. It depends upon an interaction with other architectural features such as shell shape, thickness, and ornamentation which may be equally or more important than shell structure. The independent study of the contribution of each of these factors to shell strength is at present extremely difficult.

What sorts of stresses is the bivalve exposed to during its life? These may be of two main types; static, for instance sediment pressure and water movements; or dynamic, for instance boring activities, impact loading by pebbles and rocks, or biting by predatory fish, crabs, and birds. At first consideration it might be thought that the greatest stresses on the shell would occur during the burrowing process. Wainwright (1969) found, however, that even under severe adduction no strain could be detected in the shell, but if an object was placed between the valves then near breaking strains were recorded. It has been shown for *Tridacna gigas* that large forces of the order of 500 kg are exerted during adduction (Maynard and Burke 1971). However, measurements of tension in adductor muscles of most bivalves suggest that stresses on the shell are fairly low (Trueman, *personal communication*).

If the shell structure combination used by each bivalve family (Moore 1969) is plotted against the generalized mode of life, we find certain correlations (text-fig. 10). For instance, a combination of calcite prisms and nacre or foliated structure is associated with an epifaunal byssate, or cemented life. The layer combination of composite prisms, crossed-lamellar, and complex crossed-lamellar structures appears strongly associated with deeper burrowing. The combination of crossed-lamellar and complex crossed-lamellar, although found in a variety of modes of life, is more closely associated with shallow burrowing. Families having aragonite prisms and nacre are also associated with shallow burrowing, but here the families largely inhabit fresh or deeper marine waters.

As seen in text-fig. 10, foliated structure is confined to epifaunal species. In the oyster *Crassostrea gigas* it was the weakest of all structures in all the tests, but for the free-living swimming *Pecten maximus* it was much stronger and had a compression strength higher than crossed-lamellar structure. Oyster foliated structure was weak under impact, although whole shells of *Ostrea edulis* and *Placuna placenta* did not crack but the test hammer punched a hole through them. The oyster may rely upon the thickness of the shell and cavities full of water or chalky material for protection. Furthermore the pallial attachment around the adductor muscle enables extensive withdrawal of the mantle into the shell cavity.



TEXT-FIG. 10. Diagram showing mode of life and shell structure combination for each bivalve family. In some cases families have two distinct modes of life; these have been entered twice. Families from Moore (1969).

The very high strength of nacre has in some cases enabled a very thin shell to be used which might not have been possible with other structures. In forms such as the Pholadomyidae and the Laternulidae the shells are so thin as to be transparent; the outer prismatic layer is very thin and most of the shell is made up of nacreous structure. Nacre is also used frequently in epifaunal shells of low convexity. This was carried to an extreme in a Cretaceous *Inoceramus* whose shells reached lengths of up to 2 metres; much of the thin shell consisted of nacre (E. Kauffman, *personal communication*).

The shell structures most commonly employed by burrowing forms, crossed-lamellar, complex crossed-lamellar, and composite prismatic have the highest hardness values but do not have the highest compressive and tensile strengths. The high hardness values indicate good abrasion resistance which may be a desirable property in actively burrowing species which regularly move through sediment. It is noteworthy that burrowing forms which employ the softer nacreous and prismatic structures are usually fairly sedentary and inhabit fine sediment substrates in quiet conditions. Chave (1964) has indicated that skeletal durability is controlled by the micro-architecture of the shell. In some families (Nuculanidae, Thraciidae) there has been an apparent evolutionary trend towards homogeneous structure from nacro-prismatic structure (Taylor *et al.* 1969, Taylor and Morris *unpubl.*). It is conceivable that these rather more actively burrowing groups have favoured the better abrasion resistance given by the homogeneous structure. However, this association of hardness and abrasion resistance with burrowing is speculative, for some actively burrowing species retain a largely intact periostracum.

Both the compressive and bending tests were carried out at relatively low rates of loading. However most stresses in predation will probably involve a high loading rate. Therefore as for bone (Currey 1970), more tests are needed at high loading rates where a different mechanical behaviour may be found. More tests on a wider range of species are also needed together with work on the influence of shape and ornamentation on strength.

It is generally thought by workers on the Mollusca that the nacreous shell represents the 'primitive' condition and there is fairly convincing evidence to support this idea; for instance the occurrence of nacre in Monoplacophora (Erben *et al.* 1968). It seems therefore that the strongest structure was evolved very early; it is difficult to see why other structures which seem to be better only in hardness have been evolved. The shell structure types have a long geological history and appear to have been differentiated very early in the radiation of the bivalves (Morris and Taylor *unpubl.*). It is possible that the original shell construction materials may have been selected for reasons other than mechanical strength; for example lower energy expenditure for secretion or rapidity of deposition. At the moment we have no data on these possible factors.

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JOHN D. TAYLOR
Department of Zoology
British Museum (Natural History)
Cromwell Road
London S.W. 7

MARTIN LAYMAN
23 Park Road
Smallfield
Horley
Surrey

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