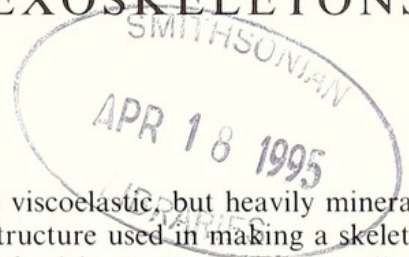


BIOMECHANICS OF TRILOBITE EXOSKELETONS

by NADINE V. WILMOT



ABSTRACT. Most skeletal materials, such as bone and insect cuticle, are viscoelastic, but heavily mineralized structures such as mollusc shell, are linearly elastic. The type of microstructure used in making a skeleton is related to required mechanical strength and to the metabolic cost involved in construction. The effects of composition, microstructure, and architecture on mechanical properties are discussed, and then related to trilobite exoskeletons. Due to their composition and internal organization, trilobite cuticles can be regarded as ceramics that behaved in a linearly elastic manner. The small size of the calcite crystals and the presence of an organic framework reduced the risk of crack formation and slowed the progress of fractures. As a result of its crystal arrangement, the thin outer prismatic layer would have had good compressive strength, but only poor crack-stopping abilities, whereas the underlying principal layer added bulk to the cuticle and deflected cracks. Structurally, trilobite exoskeletons are analogous to monocoque shells, that is, they are strong 'thin shells' with the same composition throughout and behave as a 'stressed skin'. The overall architecture of the cephalon and pygidium is of a series of modified domes, strengthened by the presence of the doublure, whereas thoracic segments are compromise structures which allow articulation as well as conferring mechanical strength.

THE ways in which materials respond to forces acting upon them are determined by their mechanical properties. Accommodation of the resulting stresses is a function of the composition, microstructural organization, and overall form (or architecture) of the specimen. The study of the mechanical characteristics of biological materials is part of the discipline known as biomechanics, a relatively new field with most research occurring from the 1970s onwards. Such research has concentrated on investigating the biomechanics of Recent skeletal materials such as bone (Currey 1969, 1975, 1979), insect cuticle (Hepburn *et al.* 1975; Vincent 1980), and mollusc shell (Taylor and Layman 1972; Currey and Taylor 1974; Currey 1976, 1980; Jackson *et al.* 1988) in order to compare their competencies. Various mechanical tests have been developed to measure the tensile, compressive, bending, and hardness characteristics of these materials by modification of standard engineering procedures. However, although the tests were basically the same, authors each followed their own individual techniques. Currey (1980) argued that sample preparation, size, and shape, would all have a bearing on the results obtained, and so demonstrated the desirability of a standard methodology.

These studies have demonstrated that not only do materials with the same composition have different mechanical properties, but also that biomechanics may not be the most important factor in their design; the metabolic cost involved in constructing a skeleton is also very important (Currey 1980). Some of the common terms used in biomechanical studies are explained at the end of this section.

The mechanical properties of biological materials have generally been related to composition and microstructure. The significance of the form of the organism has only been studied in depth for the Ostracoda (Benson 1974, 1975, 1981, 1982). Most testing of arthropod exoskeletons has been on insect cuticle, mainly because they are the most common arthropods today (see Vincent 1980 for review). However, such cuticles are uncalcified and behave as viscoelastic materials, in contrast to heavily mineralized exoskeletons which behave as ceramics and are linearly elastic. Consequently the biomechanics of trilobite exoskeletons, which were strongly calcified, are better compared with other mineralized skeletons such as mollusc shells, rather than insect cuticle. In the following sections the effects of composition, ultrastructure, and architecture on mechanical properties are discussed in turn, and the principles involved then related to trilobite cuticles.

Terminology

Stress (σ): force per unit area.

Strain (ϵ): a ratio to express the deformation created within a specimen when subjected to stress. It is the ratio of the change in size to the basic size.

Stiffness is a measure of the resistance of a material to deformation. It is measured by performing tensile tests (Currey and Taylor 1974; Joffe *et al.* 1975; Ker 1980), or compression tests (Taylor and Layman 1972; Currey 1976); both types of test have to be repeatable, that is, not incurring permanent damage to the specimen such as fracture.

Hardness measures the ease with which a material flows under a stress, and is related to the stiffness of the material and its plasticity. For details of tests see Taylor and Layman (1972) and Hillerton *et al.* (1982). It is useful for comparing viscoelastic materials, or ceramics with grain sizes of about 100 μm (Craig and Vaughan 1981).

Linearly elastic materials, such as ceramics, react immediately to the application of a stress, for as long as it is present, and on its removal immediately revert back to their pre-stressed state (Text-fig. 1A (i)). In a linearly elastic material, strain is directly proportional to stress and the stress/strain plot is linear:

$$\epsilon = \sigma/E,$$

where E is a constant (Young's modulus) and is a measure of the stiffness of the material.

Viscoelastic materials, such as insect cuticle, increasingly deform the longer a force is applied. Once the stress is removed, recovery is also gradual, so that any measurement of strain is time-dependent (Text-fig. 1A (ii)).

See Wainwright *et al.* (1976), Dorrington (1980), Gordon (1980), and Vincent (1980, 1982) for more details about linear elastic and viscoelastic materials.

COMPOSITION

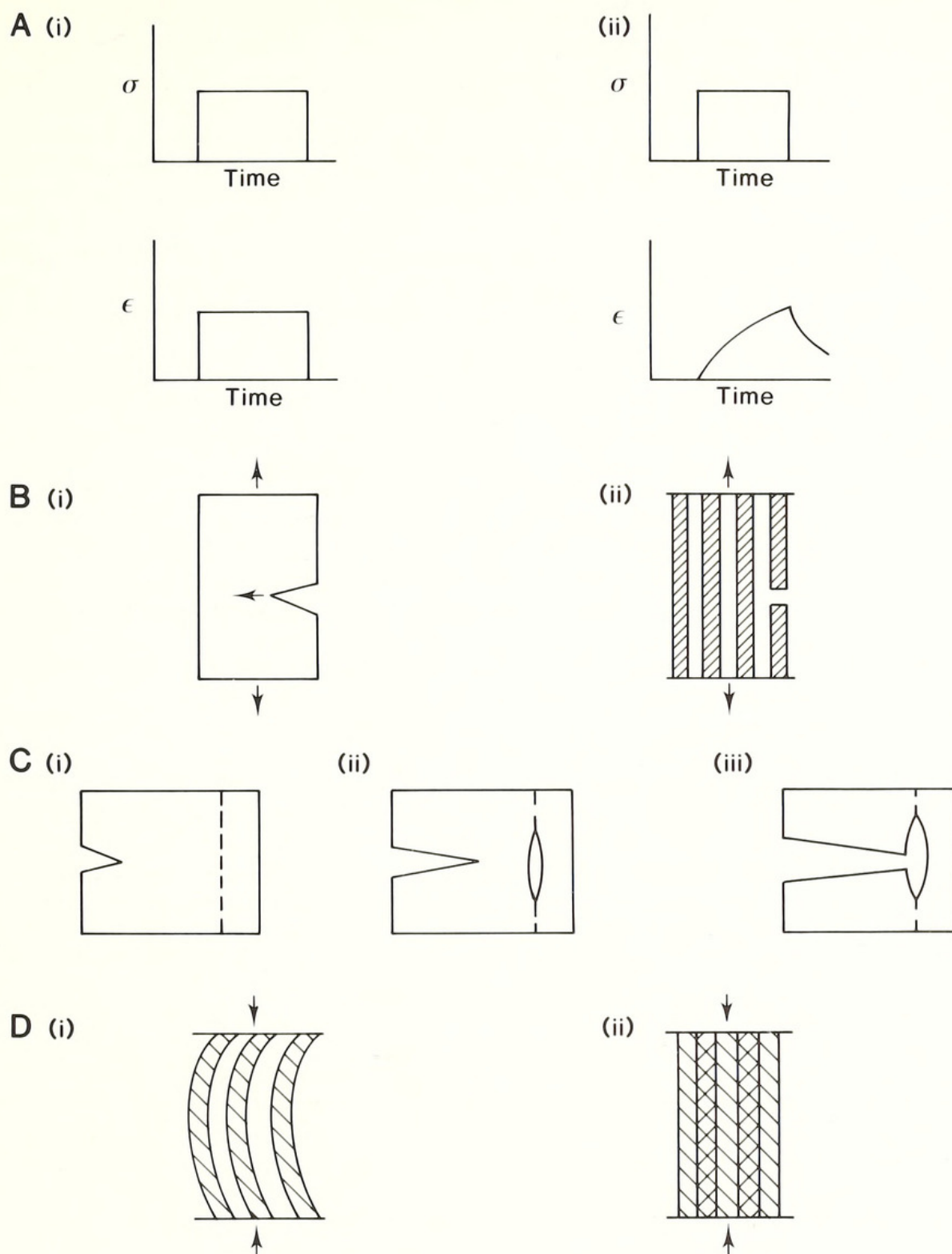
Every material has a unique response to both tension and compression, which is largely due to its composition and the strength of the bonds that maintain its atomic structure. For example, ceramics, characterized by ionic or covalent bonding, have great compressive strength.

Organisms are subject to both tensile and compressive forces, and their skeletons usually comprise a mixture of components, that is, they are composites. Tensile forces usually occur within the structure of the skeleton, or are created by support of the viscera, whereas compressive forces can be induced by walking, the surrounding water pressure, or predation.

Insect cuticle is one of the most efficiently constructed naturally occurring composites, being composed of chitin fibrils weakly bonded to a protein matrix. Chitin is very strong when subject to tensile forces, whereas the type of protein matrix determines stiffness (Hillerton 1984). The arrangement of these two components is also important (see below). Stiff and pliant insect cuticles owe their differences to their protein matrix compositions; the properties of the chitin fibrils are always the same (Hillerton 1984). Additional hardening can be generated by sclerotization, for example in locust incisors (Hillerton 1980). This involves the incorporation of phenols which become tightly bound within the cuticle, coupled with some loss of water (Vincent and Hillerton 1979).

Some marine arthropods harden their exoskeletons by reducing the amount of protein present (compared with terrestrial forms) and mineralizing their exoskeletons with calcium salts. It has been demonstrated for crustaceans that the greater the proportion of calcium salts, the harder the cuticle becomes (Welinder 1974; Abby-Kalio 1982). The type of mineralization is also important, for example the cuticle of the mantid shrimp *Gonodactylus* is mainly composed of calcium carbonate, but the harder outer surface of the smashing limb is predominantly calcium phosphate (Currey *et al.* 1982).

Sometimes organic matter is incorporated within the crystal lattice and alters the way in which



TEXT-FIG. 1. Responses of different materials to stress, based on Wainwright *et al.* (1976, fig. 2. 12), and Gordon (1980, figs 6 and 7). A (i), linearly elastic materials; A (ii), viscoelastic materials. B (i), continuous material is weak in tension, as cracks can advance unimpeded; B (ii), isolated elements are stronger in tension as cracks are unable to spread once the first element has broken. C, weak interfaces prevent the spread of cracks (Cook-Gordon mechanism): (i), crack formation begins; (ii), weak interface opens out in advance of the crack; (iii), progression of the crack is stopped. D, lateral bonds increase compressive strength: (i), isolated elements bend under compression; (ii), weak lateral bonds restrict movement.

the mineral fractures. This is exemplified by proteins within the calcite crystals of echinoderm plates (Berman *et al.* 1988). Although the concentration of protein is very small (only approximately ten molecules per 1×10^6 unit cells) these crystals are less brittle than inorganic calcite.

MICROSTRUCTURE

The size and arrangement of skeletal materials are of fundamental importance to the mechanical behaviour of the structure as a whole. In general, composites are stronger than pure materials. Cracks, generated in tensile conditions, are unable to propagate between isolated elements (Text-fig. 1B), hence chitin fibrils are extremely strong as they are composed of individual long chains of chitin molecules. If one chain is broken, the fracture does not spread to the others.

Weak interfaces within a material can also give strength due to the Cook–Gordon mechanism (Cook and Gordon 1964). As a crack propagates through a material, the weak interface opens up in advance. When the crack reaches the hole, its energy is dissipated and so is unable to continue (Text-fig. 1C). Wood behaves in this manner. Bonding between components can also increase compressive strength by creating greater resistance to bending (Text-fig. 1D).

Arthropod cuticle is a very efficient composite as it contains tension- and compression-resistant members. The chitin/protein fibrils are arranged in sheets parallel to the cuticle surface. Each sheet contains fibrils orientated in the same direction, but successive layers are rotated by a few degrees to produce a helicoidal structure. The typical laminated appearance of arthropod cuticle is due to this internal arrangement; each unit of 180° rotation of the helicoid corresponding to a single lamina (Bouligand 1965; Neville and Luke 1969; Neville 1970; Livolant *et al.* 1978). Consequently the cuticle is strong in tension along any plane parallel to the surface. Sometimes the sheets show preferred orientation along the direction of greatest stress (Wainwright *et al.* 1976), for example in the walking legs of spiders (Barth 1973), the hind limbs of coleopterans (Dennell 1978), the pedipalps of scorpions (Mutvei 1977; Dalingwater 1980), in *Limulus* cuticle (Mutvei 1977; Dalingwater 1980), and the legs of the Carboniferous eurypterid *Mycterops* (Dalingwater 1985). In such cases the cuticle is very strong along the plane of preferred fibre orientation but much weaker in other directions (Harris 1980).

The organic matrix of heavily mineralized skeletons is one of the most important factors in determining its mechanical properties. Most biomineralization is an 'organic matrix-mediated' process (Lowenstam 1981) where the organic matter forms a framework not only to control the nucleation, size, and orientation of the inorganic crystals, but also the physical behaviour of the shell (Krampitz *et al.* 1983). The organic matrix of crustaceans is a chitin-protein complex, and the proteins can be subdivided into water insoluble, and soluble fractions (Richards 1951) which are species-specific (Hackman 1974). This is also true in other marine invertebrates such as molluscs. Weiner *et al.* (1983) demonstrated that molluscan insoluble matrix (including chitin fibrils) forms a framework to limit the size and orientation of the crystals, which is very important mechanically, and also supports the soluble matrix that controls nucleation sites (see also the review by Mann 1988 concerning organic matrices).

The quantity and mechanical characteristics of the organic framework compared with the crystalline component can greatly influence the strength of a 'stony' (Wainwright *et al.* 1976) skeleton. As the matrix is much less brittle than the crystals it encloses, when sufficiently thick it can absorb some of the energy involved in crack propagation by plastic flow. If the organic matrix is thin, fractures are prevented from developing mainly by deflecting cracks as they reach crystal boundaries.

The size of the crystalline component of a stony skeleton (as controlled by the organic framework) is also very important. The larger the component, the more likely it is to contain flaws such as internal deformation or cracks. For linearly elastic solids at a given stress level, there is a 'critical crack length' or defect size at which fracture occurs. Hence it is advantageous for a ceramic to be constructed from small components to reduce the chances of containing defects. For calcium carbonate minerals in tension at 50 MN m^{-2} and 100 MN m^{-2} , the critical crack length is $2\text{--}8 \mu\text{m}$

(Wainwright *et al.* 1976). In general, heavily mineralized skeletal materials have grain sizes with one dimension smaller than $3\text{ }\mu\text{m}$ which minimizes fracture occurrence. Uniformity in size is also advantageous, to prevent weak links generated by larger components. The less organic matrix present, the more important it is for the crystal sizes to be small, so that if cracks do form, they frequently have to change direction at crystal boundaries: a process that requires additional energy. Hence fine-grained ceramic skeletons that contain only a small amount of organic matrix, are much stronger than a large inorganic crystal. This has been demonstrated for mollusc shells, which contain only 0.1–5% matrix (Currey 1980) and yet are stronger than inorganically precipitated calcite (Taylor and Layman 1972). Currey (1980, fig. 5) has illustrated the extremely good crack-stopping capabilities of molluscan nacre, which is composed of many thin sheets of aragonite separated by thin organic layers. A crack has to proceed along a very tortuous path in order to cross this type of microstructure. Therefore it is not surprising that most ceramic skeletons are fine grained and contain very few voids. When voids do occur, such as ducts, their function outweighs the structural weaknesses they induce (Wainwright *et al.* 1976).

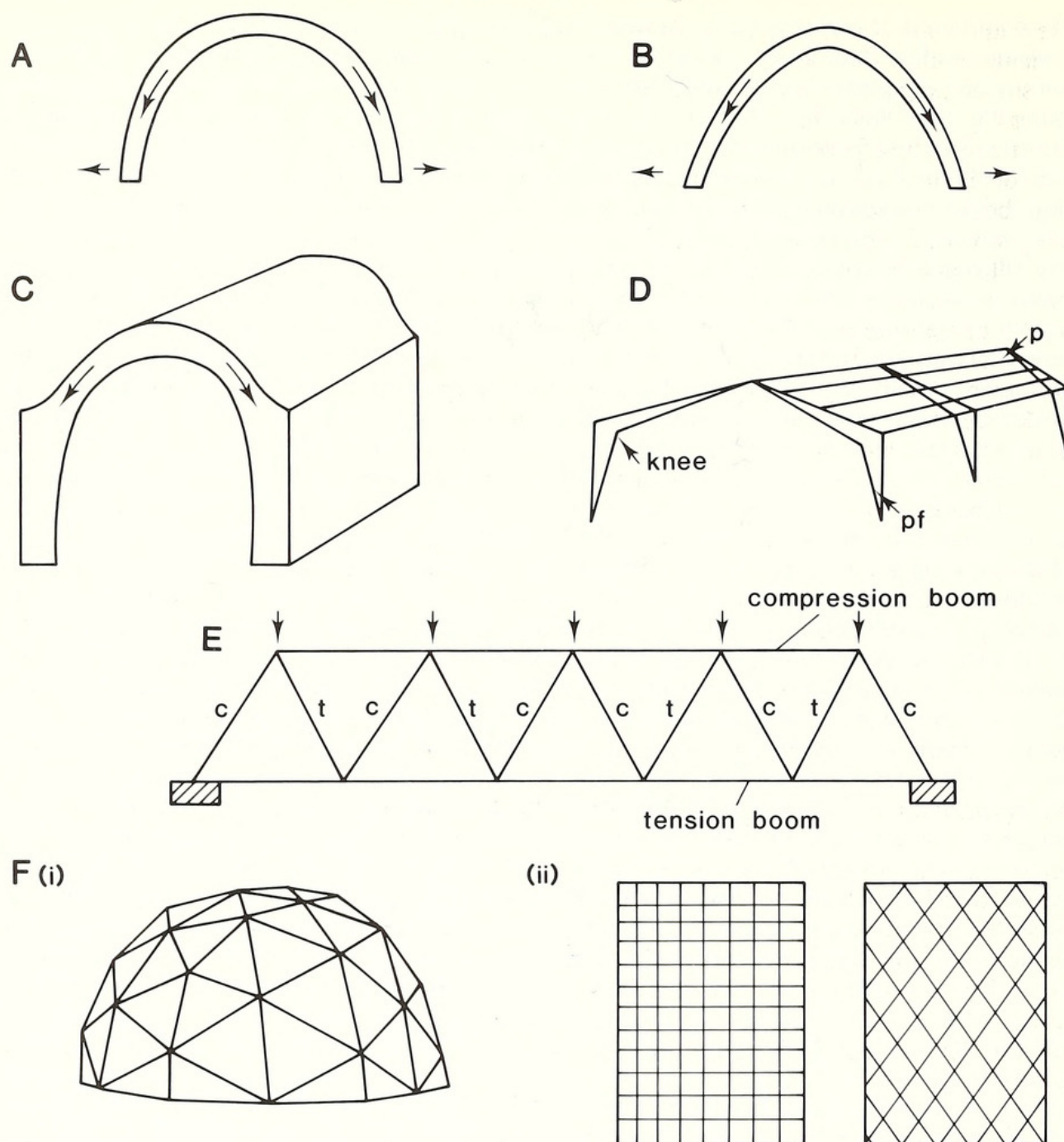
It can therefore be seen that the type of microstructure used to construct a skeleton will influence its mechanical characteristics. Mollusc microstructural types (described by Watabe 1984) have been found to exhibit different mechanical properties despite all being constructed from calcium carbonate. For example, nacre is the strongest, and crossed lamellar structure the hardest. However, mechanical strength may not be the most important factor involved in the design of a skeleton. Although nacre is the strongest of all types of molluscan microstructure and occurred first in the fossil record, weaker structural units are more commonly used today (Currey and Taylor 1974). There is a general correspondence between molluscan microstructure and mode of life (Taylor and Layman 1972; Currey and Taylor 1974; Currey 1976; Gabriel 1981). The development of other shell types may have been due to a necessity to protect against abrasion or chemical attack prevalent in some habitats, at which nacre is relatively poor (Gabriel 1981). The metabolic cost involved in secreting the material may also be more important than its overall strength (Currey 1980). It has been demonstrated that microstructures with a relatively high organic content are more 'expensive' to generate (Palmer 1983). A metabolically cheaper type of microstructure to construct, although of inferior quality to nacre, may be adequate for a particular lifestyle. Oyster shells, for example, are constructed from relatively weak microstructures (foliated structure and chalky deposits) and are prone to attacks from boring organisms; however, they can grow very quickly, which suits these animals' particular mode of life (Currey 1980).

ARCHITECTURE

The general shape of a structure will also influence the way in which it responds to stresses. Structural mechanics have only been applied in any depth to the design of ostracode carapaces, where exoskeletal features have been discussed in relation to common engineering or architectural structures (Benson 1974, 1975, 1981, 1982). Impact and compression testing of ostracode carapaces (Whatley *et al.* 1982) did not reveal any one factor that had overriding importance in conferring strength, though it has been demonstrated that the architecture of cirripede exoskeletons is more important than microstructure (Murdock and Currey 1978).

The importance of shape to the overall mechanical strength of a structure is best explained with reference to common architectural structures. The concept of 'strength through form' (Nervi 1951) has been successfully exploited in architecture from the 1950s. The various man-made constructional forms which have been developed follow well-understood engineering principles, and have many analogies with biological designs. (For an introduction to structural mechanics see Buckle (1977) and Cowan (1980).) Although buildings are many times larger in scale than biological constructions, the forces acting on skeletons generate stresses acting in similar directions.

The type of material to be used usually determines the type of structure that is produced. Due to their different mechanical properties, materials lend themselves to be used in certain ways: for example, stone is relatively weak in tension but possesses great compressive strength.



TEXT-FIG. 2. Space-spanning structures, A, hemisphere. B, dome. C, stone vault; thick walls counteract outward thrusts from the arch and ensure that the forces are deflected to the ground within the structural form (or else the building would collapse). D, portal frames (pf) and purlins (p); portal frames always have a shallow pitch, and the knee is strengthened by increased thickness or reinforcement; the weight and outward thrusts are absorbed by the foundations. E, truss: the girders of the truss act either in tension (T) or compression (C) to take up the load, and have flexible joints (based on Buckle 1977, fig. 8.1). F, space frames: (i), geodesic dome, based on triangular or diamond-shaped grids with flexible joints (from Buckle 1977, fig. 15.3); (ii), lamellar roofs of various shapes are based on horizontal or diagonal grids with rigid joints.

Some of the more common three-dimensional architectural structures are illustrated in Text-figure 2. A catenary is the shape a cable takes when suspended equally at both ends, and can be expressed mathematically as:

$$y = a/2(e^x + e^{-x})$$

where x and y are coordinates, e = exponential constant, a = variable. When inverted, this form is a catenary arch, on which vertical loads are directed evenly over the whole length. Its three-dimensional extension is the catenary dome (Text-fig. 2B). Although a hemisphere (Text-fig. 2A) encloses a given volume with less surface area than a catenary-shaped dome, the dome is structurally superior at resisting forces directed horizontally, and normally, to the crown. In both structures, the weight of the material is directed downwards, generating horizontal thrusts at the margins. These have to be counteracted either by ring beams, or some other sort of reinforcement such as increased thickness, which confines outward movement of the base.

A vault is another three-dimensional version of an arch, and also has outward thrusts at its base. For stone vaults (Text-fig. 2C), thick adjoining walls are necessary to counteract these horizontal moments and ensure that the thrusts are directed to the foundations within the building structure. This buttressing is essential to prevent collapse. Portal frames are space-spanning structures composed of straight members (Text-fig. 2D). The greatest shear and bending moments occur at the joint between the beam and the column, so the 'knee' is usually strengthened, either by thickening or adding reinforcing material. As with arches, shallower frames are subject to greater horizontal thrusts, and ties can be introduced between the supports to attain equilibrium. Purlins are beams that span between portal frames, and on which additional material can be placed such as roofing tiles. The load acts on the joints between the purlins and the portal frames.

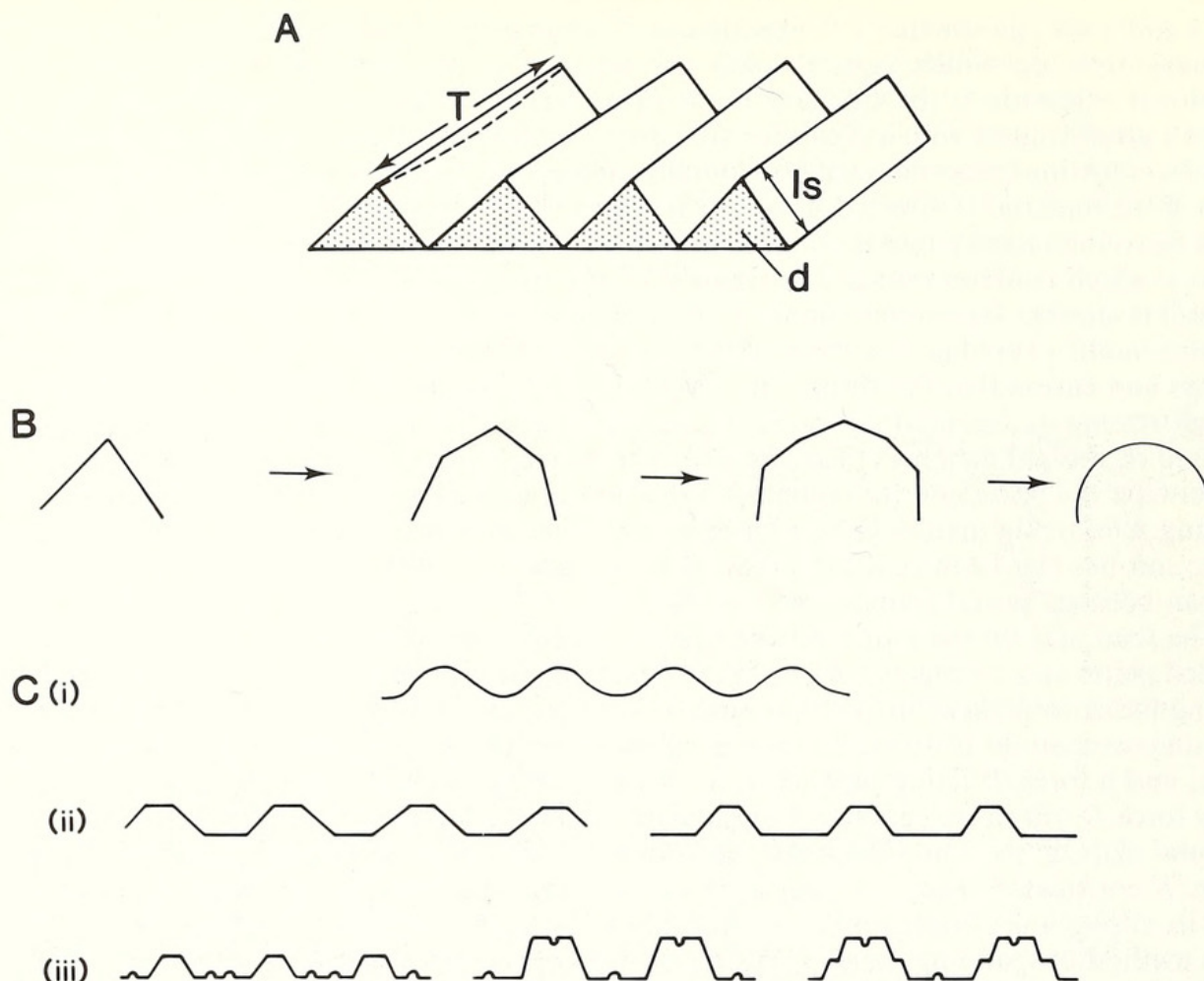
Folded plates and corrugated sheets (Text-fig. 3) are more economical in material than flat plates spanning the same area, as their shape imparts strength and so they can be thinner. A vertical load acting on corrugations is divided into two components: a force R acting at right-angles to the slab surface, and a force P acting parallel to it. P forces are resisted by 'skin stresses' within the slab, so only force R will cause bending. Consequently, much greater forces can be withstood than by a horizontal slab of the same thickness, on which all the force is directed perpendicularly to the surface. A corrugated sheet can withstand up to a hundred times its own weight in load (Cowan 1980): its strength is a function of its sinusoidal cross-section and its overall depth.

As a method of spanning space, a truss (Text-fig. 2E) is more economical in material than a solid beam, and there are many different types. Simply, the stresses from a vertically acting load are taken up by a series of members which act either in tension or compression. Space frames (Text-fig. 2F) can be likened to three-dimensional trusses. Various shaped, strong but lightweight lattices provide the necessary support for thin coverings. As in trusses, the members of the grid act either in tension or compression to transmit the stresses acting on the structure. The covering 'membrane' or 'skin' lies passively between the struts. An alternative type of space frame is the monocoque shell (Benson 1974, 1975), which does not have an internal grid. It is composed of the same material throughout to produce a strong thin shell, and all the load is transmitted through this thin 'stressed skin'.

INFLUENCES OF TRILOBITE CUTICLE COMPOSITION AND MICROSTRUCTURE ON MECHANICAL BEHAVIOUR

Since the organic matrix has so much influence on the mechanical behaviour of heavily mineralized exoskeletons, no mechanical tests were performed in this study on fossil material, as any remaining organic matter will have been degraded. This has been proved for ostracodes by compression and impact tests on fossil and Recent specimens of the same species (Whatley *et al.* 1982), which were found to have different strengths. However, knowledge of trilobite microstructure (Wilmot 1988) can still provide much information on the likely mechanical properties of the exoskeleton.

Trilobite exoskeletons were heavily calcified, composed predominantly of low-magnesian calcite (Wilmot and Fallick 1989) with only a small proportion of organic matter. In this respect they can be categorized with other stony skeletons as behaving as ceramics. Remnants of the organic matrix have been obtained by decalcifying the cuticles in EDTA (Dalingwater 1969, 1973; Teigler and Towe 1975; Miller 1976; Dalingwater and Miller 1977). Although the composition remains uncertain, it may well have consisted of proteins and chitin fibrils as in all other arthropods.



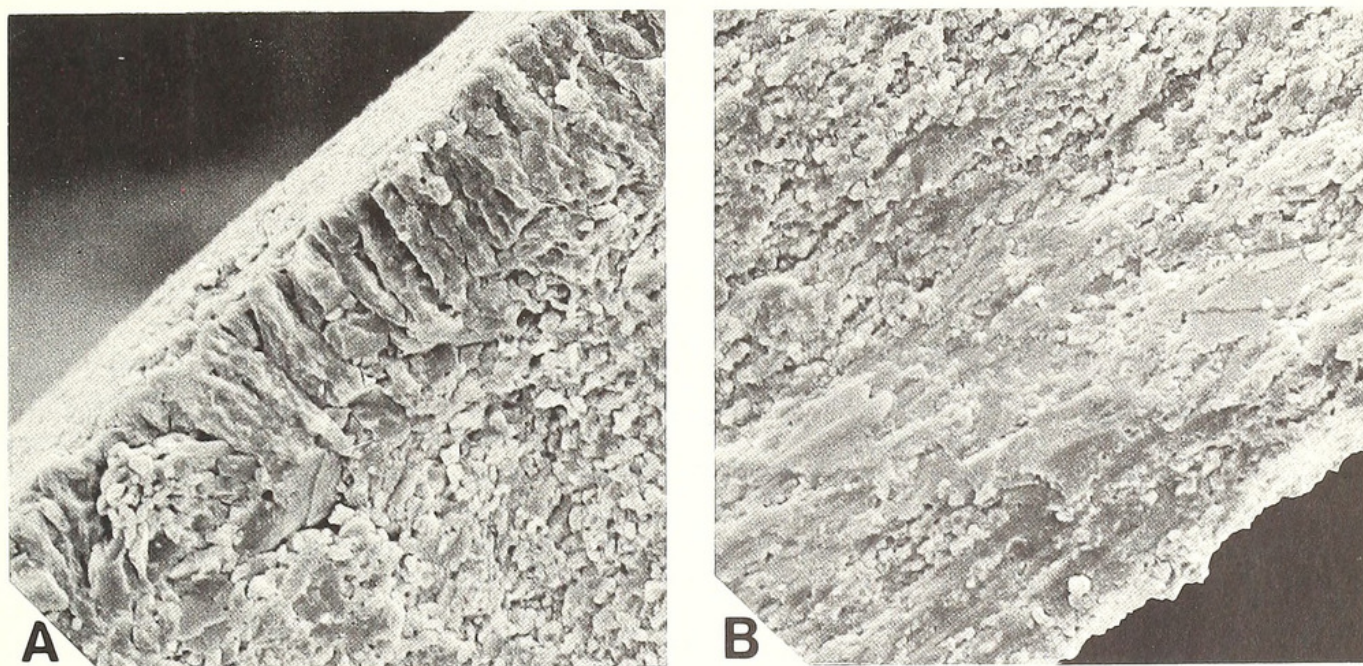
TEXT-FIG. 3. Corrugations. A, folded sheet: there is only a small local span (ls) so only thin slabs are necessary to resist the R and P forces; thin, end diaphragms (d) resist the thrusts (T) from the whole roof (based on Buckle 1977, fig. 14.7). B, the more folds in the folded sheet, the less local bending, enabling thinner slabs to be used, therefore sinusoidal corrugations are the strongest. C, examples of various profiles of corrugations used in buildings: (i), sinusoidal; (ii), trapezoidal (symmetrical and asymmetrical); (iii), stiffened trapezoidal.

Like all exoskeletons, trilobite cuticles were used both for protecting and supporting the viscera, and would have been subject to both tensile and compressive forces. Tensile forces parallel to the surface would have been present within the domed structure of the skeleton, and to a lesser extent generated by the suspension of the viscera. Compressive stresses would have been imposed by water currents and predators. To resist these, the exoskeleton contained tension elements, probably long chitin fibrils orientated parallel to the cuticle surface, and short calcite crystals strong under compression.

Unmineralized insect cuticle is stronger and stiffer than calcified crustacean cuticle; crustacean exoskeletons have to be thicker to compensate (Wainwright *et al.* 1976). However, calcification is very common in the marine environment as calcium ions are readily available. Hence it is much more economical for a marine invertebrate to construct an exoskeleton consisting of less protein and more calcium carbonate in comparison with its terrestrial counterpart (Wainwright *et al.* 1976). This probably explains why trilobite exoskeletons were heavily calcified.

Apart from agnostid exoskeletons which may have been constructed of only a thin, prismatic layer (Wilmot 1990a), most calcified trilobite cuticles comprise an outer prismatic layer with a thicker principal layer below. Sometimes the thin outer layer is finely laminated (Mutvei 1981; J. E. Dalingwater pers. comm.). Prismatic layer is a relatively thin layer of calcite crystals, approximately $1\ \mu\text{m}$ in diameter, orientated with their longer c -axes perpendicular to the outer

surface (Text-fig. 4A). It is not analogous to the molluscan prismatic layer which can have crystals up to several millimetres long, with each surrounded by a thick ($5\text{ }\mu\text{m}$) layer of organic matrix (Currey 1980). Trilobite principal layer forms 85–95% of the total cuticle thickness. It is finer grained, and has a much less regular crystal arrangement than the prismatic layer (Text-fig. 4B). Parallel laminations are sometimes preserved within this layer which may mark the former positions of organic material. The amount of organic matrix was low, with much less than $1\text{ }\mu\text{m}$ thickness between crystals. As in molluscan nacre (Currey 1980), fracture of trilobite exoskeletons mainly occurred through the thin layers of organic matter rather than through individual calcite crystals (unpublished observation, see Text-fig. 4). Except for eye lenses which were necessarily always of extremely high quality calcite, none of the cuticular crystals have two axes more than $3\text{ }\mu\text{m}$ long, so minimizing the risk of dangerously large internal defects.



TEXT-FIG. 4. Scanning electron micrographs of trilobite cuticular structure, exposed on a vertical fracture surface. *Phacops rana crassituberculata* Stumm, NMW.88.22G.41, Silica Shale, Silica, Ohio (Middle Devonian), $\times 1500$. A, prismatic layer with calcite crystals ($1 \times 10\text{ }\mu\text{m}$) orientated with their c-axes perpendicular to the surface; note that fracture has occurred between crystals, not through them. B, principal layer, with calcite crystals aligned parallel to the surface.

It has been argued above that the type of microstructure used is a compromise between the mechanical properties necessary for a particular mode of life, and the metabolic price that has to be paid in order to construct it. Trilobites, like other arthropods, regularly had to shed their exoskeletons in order to grow. Immediately after moulting, the organism would have been unable to move or feed properly, as well as being very vulnerable to predation, and so it would have been advantageous to mineralize the cuticle as soon as possible. It is therefore likely that rapidity of calcification was one of the main priorities involved in the selection of microstructure. Modern mollusc shells are stronger than crustacean cuticles (Wainwright *et al.* 1976), but such shells are gradually secreted throughout life. When trilobite cuticle was secreted, the prismatic layer formed first, with only a very thin principal layer present; as secretion continued, cuticle thickness increased by addition to the principal layer (Miller and Clarkson 1980). This suggests that the prismatic layer was relatively easy to generate, being calcified rapidly after ecdysis to give some degree of hardening to the cuticle. Bulk was added later to the exoskeleton to give greater strength. Prismatic layer may also have been effective against shell-boring organisms, as with molluscs (Gabriel 1981). Trilobite prismatic layer with its regular crystal arrangement was probably quite strong under compressive forces acting normal to the cuticle surface, but would have had poor crack-stopping capabilities. A

crack would have been able to travel unimpeded between crystals, and would only have been deflected on reaching the principal layer: hence the need for a thin principal layer even in newly secreted cuticle. The crack-stopping abilities of the principal layer can still be effective after millions of years: prismatic layer is often lost from trilobite cuticles when they are extracted from the rock matrix, whereas the principal layer remains intact (Miller 1976).

Unlike molluscs, trilobites only developed two kinds of exoskeletal microstructure. However, the overall thickness of the cuticles and the relative proportions of the different layers do vary considerably, which would have been of mechanical significance. Different types of cuticular ultrastructure may have been related to mode of life, or may just have been a phylogenetic trait, e.g. proetides have relatively thin prismatic layers.

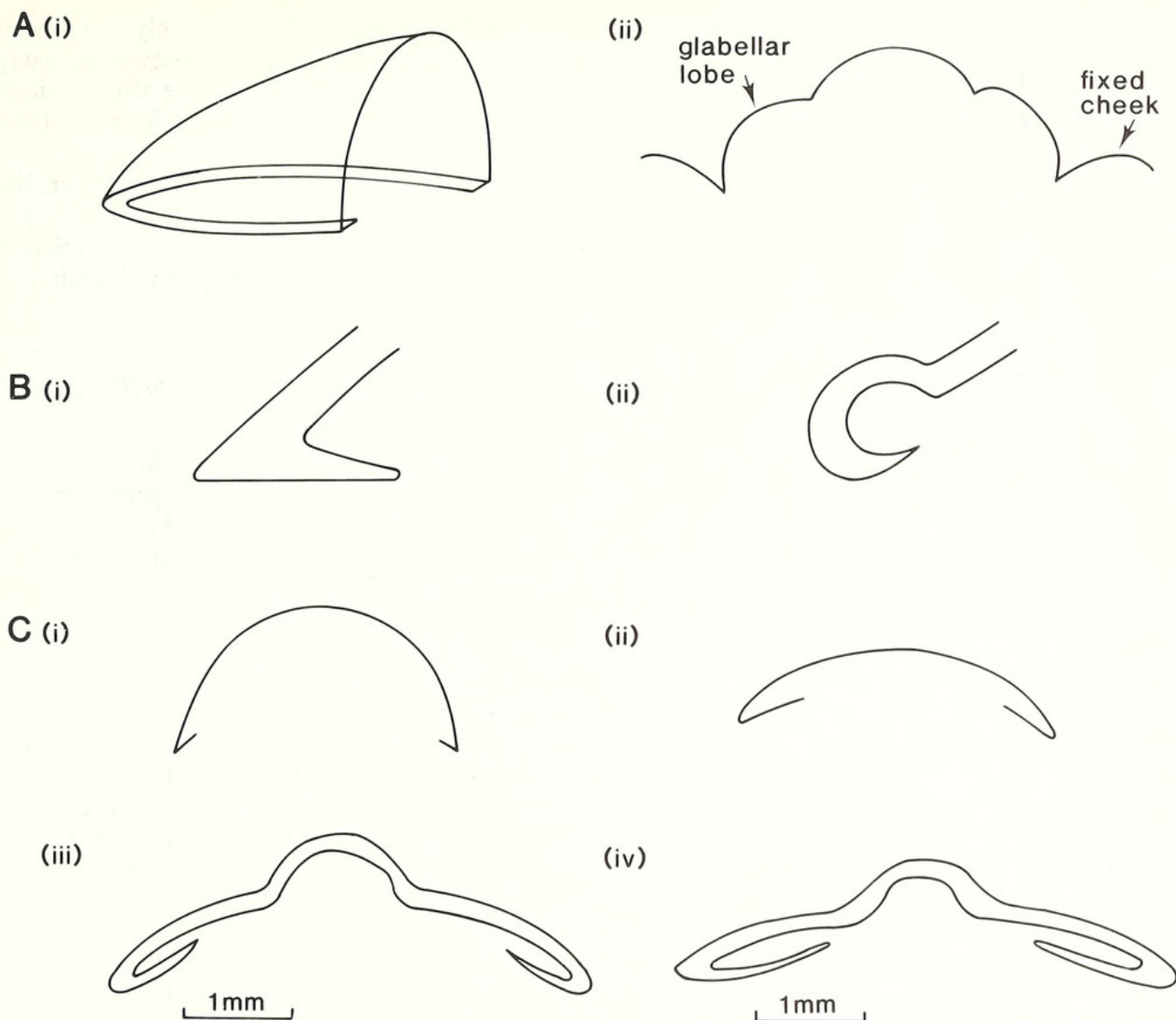
EFFECTS OF TRILOBITE ARCHITECTURAL DESIGN ON MECHANICAL STRENGTH

When assessing the design of an exoskeleton, it is important to consider the main function it provides for the animal. In trilobites, it seems likely that the exoskeleton developed primarily as a means of protection against predators, rather than just for muscle support. The high degree of calcification of the cuticle compared with other arthropods suggests an evolutionary bias for thicker exoskeletons and hence increased protection. Indeed, in low-oxygenated environments such as those existing in the 'Olenid Sea', predation was rare and the predominant trilobites only had very thin cuticles (Fortey 1985).

Other evidence suggesting a defensive function for the cuticle is the development of sophisticated enrolment mechanisms. This was a great advantage to trilobites, as they were able to curl up into 'balls' that enclosed vulnerable soft parts within the calcified exoskeleton. The cuticle then effectively formed a hard, protective outer casing with a much greater diameter than before, and the animal was therefore more difficult to attack. As cuticle thickness was fairly uniform throughout (increasing at muscle insertion areas), there were no major weak points in the 'ball' that could be exploited by predators. The margins of the exoskeleton, such as the borders of the cephalon and pygidium were often locked tightly together and, due to the doublure, were also thicker and stronger regions. Pleurae overlapping articulating facets greatly increased 'ball' thickness laterally. Detailed methods of trilobite articulation and enrolment are well known and will not be discussed further here: see Harrington (1959, pp. O70–O73, figs 49–51), Bergström (1973), and Fortey and Owens (1979) for further information.

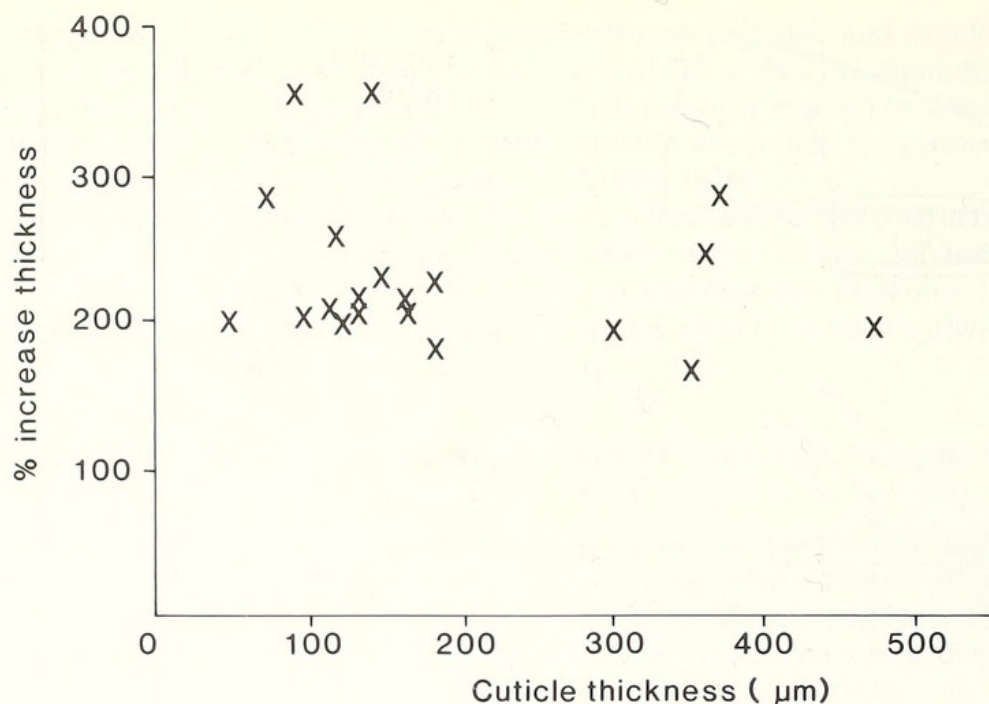
Although it can be seen that the trilobite exoskeleton was well developed for enrolment, the general shape was also mechanically strong for 'normal' life situations, and it is this aspect which will be discussed further below. For example, although the doublure may sometimes be involved in enrolment, incorporating coaptative devices (Clarkson and Henry 1973), this alone cannot explain its function for all trilobites. Schmalfuss (1981) suggested that doublures with terrace ridges supported a respiratory and feeding chamber below the animal, but this is unlikely to be true of pelagic species, or groups with long pygidial doublures (Fortey 1985). It is proposed here that the doublure acted primarily as a structural strengthening device, necessary for a dome-shaped exoskeleton.

Like most ostracode carapaces, the trilobite exoskeleton structurally most resembles a series of modified domes based on catenary arches (Text-fig. 5). The cephalon and pygidium can be regarded simply as half-domes. The horizontal thrusts at the margins of the domes are resisted by the doublure, which confers strength by increased thickness and a change of direction. The inner edge of the doublure marks the point of attachment of the ventral membrane, but although the latter was probably tough, its flexibility (Müller and Walossek 1987) would have given it negligible structural strengthening properties. Its main function would have been to constrain the positions of the body organs. As with the knee of a portal frame constructed of the same material throughout, the exoskeleton also had to be thicker at the doublure to resist shear forces acting at the change of direction. On average, cuticle thickness at least doubles at the doublure (Text-fig. 6). As slightly



TEXT-FIG. 5. General form of cephalon and pygidia. A (i), trilobite cephalon and pygidia can be regarded simply as half-domes; A (ii), generalized transverse section through a cranidium; the basic shape of a half-dome has been modified by addition of extra domes. B (i), the doublure gives strength to the domed structure by increasing thickness at the base, and a change of direction; B (ii), the shape of the doublure is also important; cylindrical doublures such as those of certain proetids are very strong. C, flatter domes exert greater thrusts at the margins and therefore need longer doublures: (i), (ii), diagrammatic representation of the relationship between convexity and doublure length; (iii), transverse section through the pygidium of *Proetus* (*Proetus*) *concinnus* (Dalman) (based on specimen NMW.88.22G.42); (iv), transverse section through the pygidium of *Warburgella* (*Warburgella*) *stokesii* (Murchison) (based on specimen NMW.88.22G.43); both these trilobites belong to the Proetacea yet have slightly different convexities, and hence dissimilar doublure lengths.

oblique sections through the doublure would give the impression of increased cuticle thickness, the minimum values recorded are the most significant. The width of the doublure is proportional to its strength (longer doublures affording more resistance to thrusts), therefore flatter domes which exert greater horizontal thrusts have to have longer doublures (Text-fig. 5c). However this general relationship is not necessarily valid for all trilobites, as factors such as doublure shape, ultrastructure, and overall cuticle thickness also exert an effect. Different types of trilobite doublure are illustrated in Text-figure 7. The addition of extra domes to parts of the exoskeleton such as the glabella (Text-fig. 5A (ii)) is also a recognized practice in architecture.



TEXT-FIG. 6. Increase in cuticle thickness across the doublure.

Although, in sagittal section, a trilobite is much more elongated and therefore resembles a shallower dome than in transverse section, the thorax is well jointed, and dorso-ventral forces could have been taken up by flexure (Text-fig. 7A (iv)). However, the main purpose of the jointed thorax was for locomotion and enrolment.

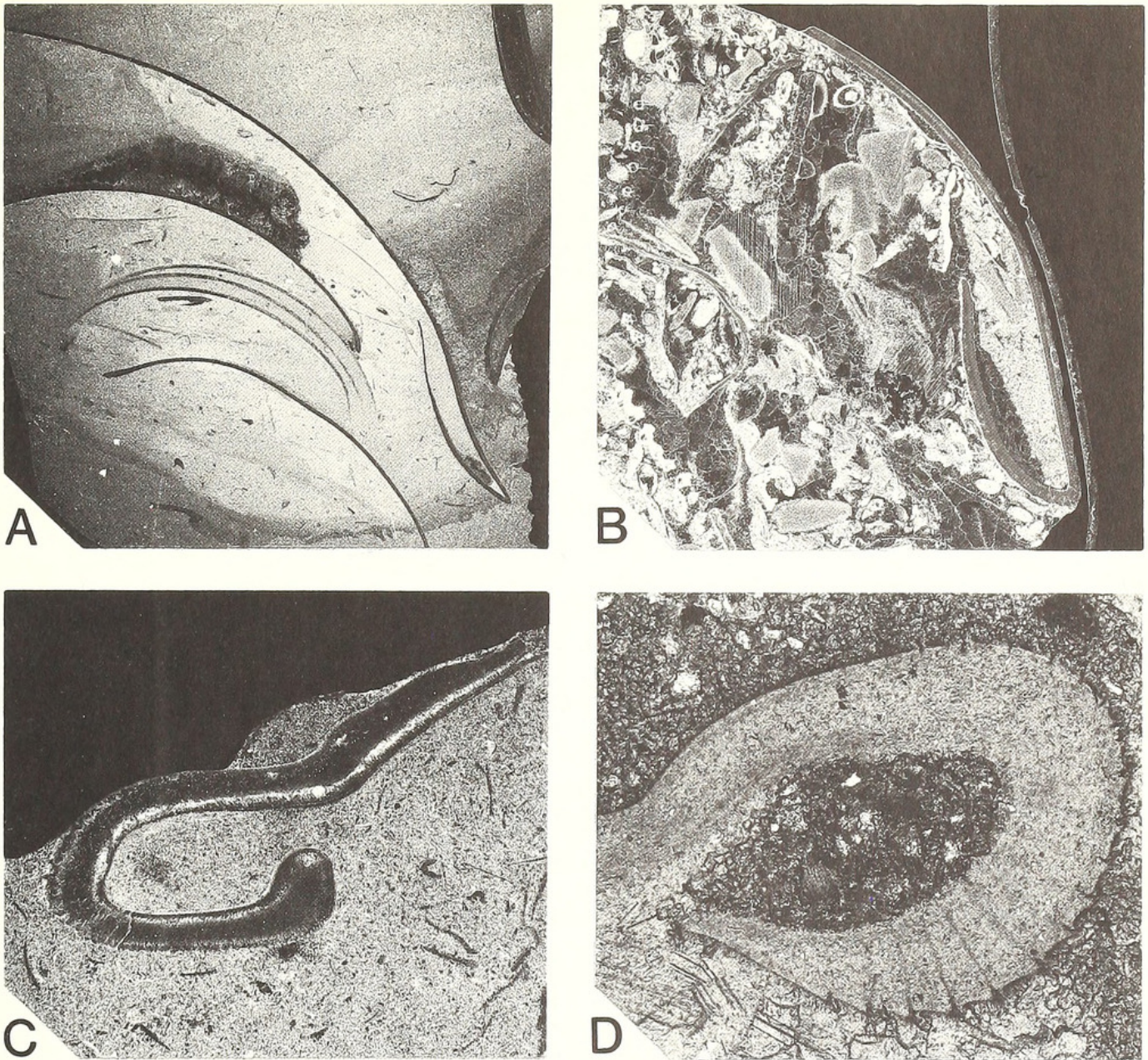
Trilobite thoracic segments are a compromise in structure between the necessary mechanical strength to protect and support the underlying organs, and permitting articulation. Some trilobites, such as certain illaenimorphs and homalonotids are characterized by their high convexity and effacement. Their thoracic segments resemble single arches (Text-fig. 8B) and are therefore structurally strong, and articulate only at the two fulcra (Lane and Thomas *in* Thomas 1978; Thomas and Lane 1984). The segments are arranged in an imbricate manner, and articulation is achieved by them sliding underneath one another (Thomas and Lane 1984, Text-fig. 2D). However, this is not common for trilobites as a whole.

Most trilobites have various structures on the anterior and posterior margins of the thoracic segments which enable them to articulate. These may include an articulating half-ring anterior to the axial ring, flanges from the proximal parts of the pleurae to the fulcra, fulcral processes with corresponding sockets, and articulating facets on the distal parts of the pleurae (Harrington 1959). Additionally, coaptative structures may exist on the cephalon and pygidium (Clarkson and Henry 1973; Henry and Clarkson 1975).

Many thoracic segments have the proximal parts of the pleurae extending horizontally from the axial furrows (Text-fig. 9). Although this is not very strong structurally, it is of great importance in articulation as the pleurae form a hinge plane. Strengthening of these thoracic segments is generated by the axial and pleural furrows (Bergström 1973; Müller and Walossek 1987) which are expressed ventrally as ridges (Text-fig. 9G), thus turning the cuticle into a folded sheet. Additional thickening of the exoskeleton in these areas also increases the strength of the structure, especially in areas of muscle attachment such as the axial furrows.

Other thoracic segments are intermediate in form between these two end members and resemble arches on arches, but with several articulating processes (Text-fig. 10). Therefore, although the cephalon and pygidium of a trilobite are well designed for mechanical strength, the shape of thoracic segments are also a function of their role in articulation.

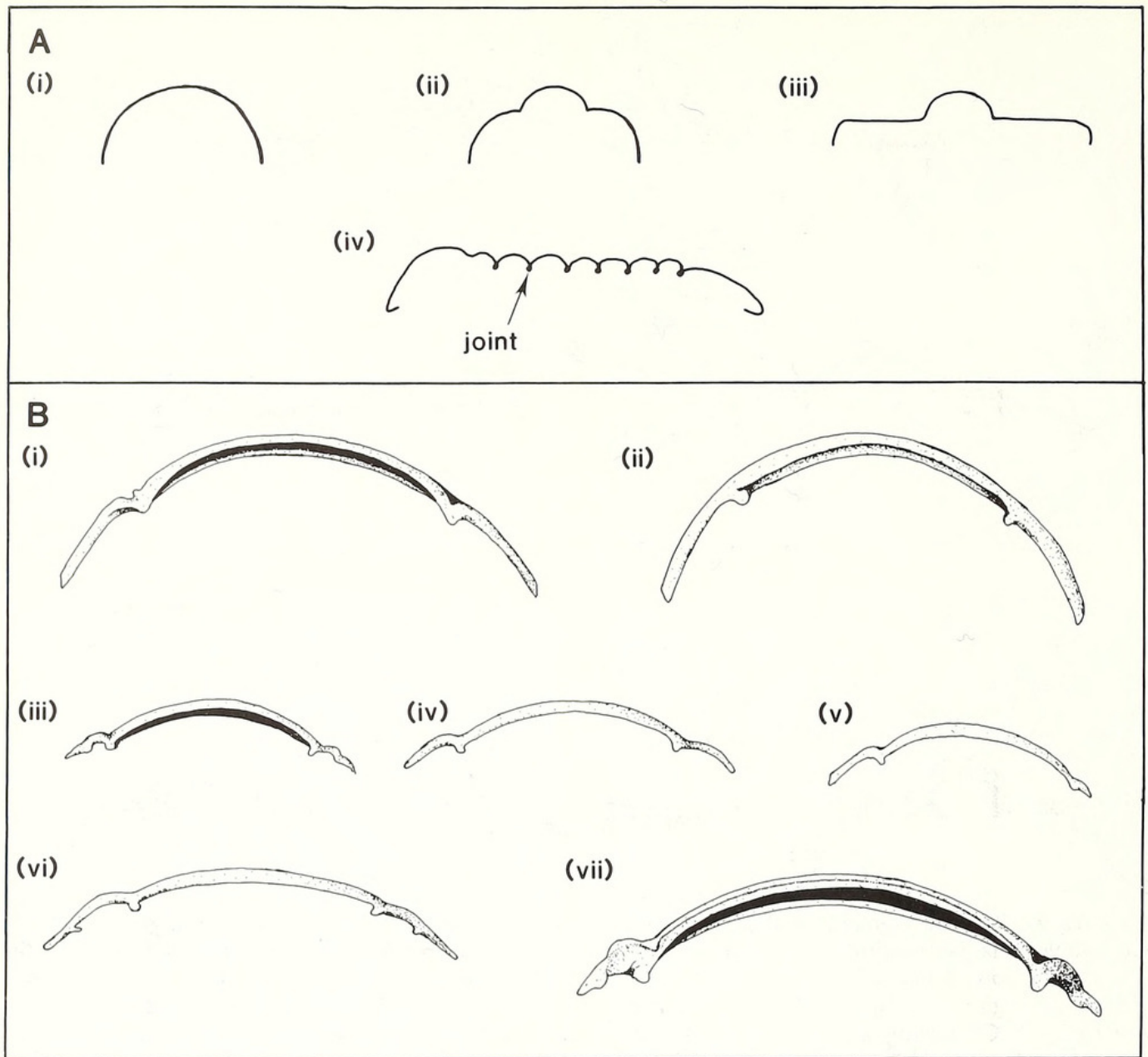
Occasionally a network of polygonal structures can be seen on the surface of trilobite cuticles, for



TEXT-FIG. 7. Different types of doublure. A, *Illaeus* sp. (JED) 2 Feb. 1966, pygidial doublure, Boda Limestone, Dalarna, Öland (Ordovician), $\times 15$. B, *Cybantyx anaglyptos* Lane and Thomas, NMW.88.22G.21, longitudinal section through pygidium, Much Wenlock Limestone Formation, Wren's Nest, Dudley (Wenlock), $\times 7$. C, *Dalmanites myops* (König), NMW.88.22G.20, longitudinal section through pygidium, Hill End Farm Borehole, Walsall (Wenlock), $\times 10$. D, *Warburgella* (*Warburgella*) *stokesii* (Murchison), NMW.88.22G.5, transverse section through the lateral border of a free cheek (note the canals opening out at the crests of the terrace ridges), Coalbrookdale formation, Daw End railway cutting, Walsall (Wenlock), $\times 70$.

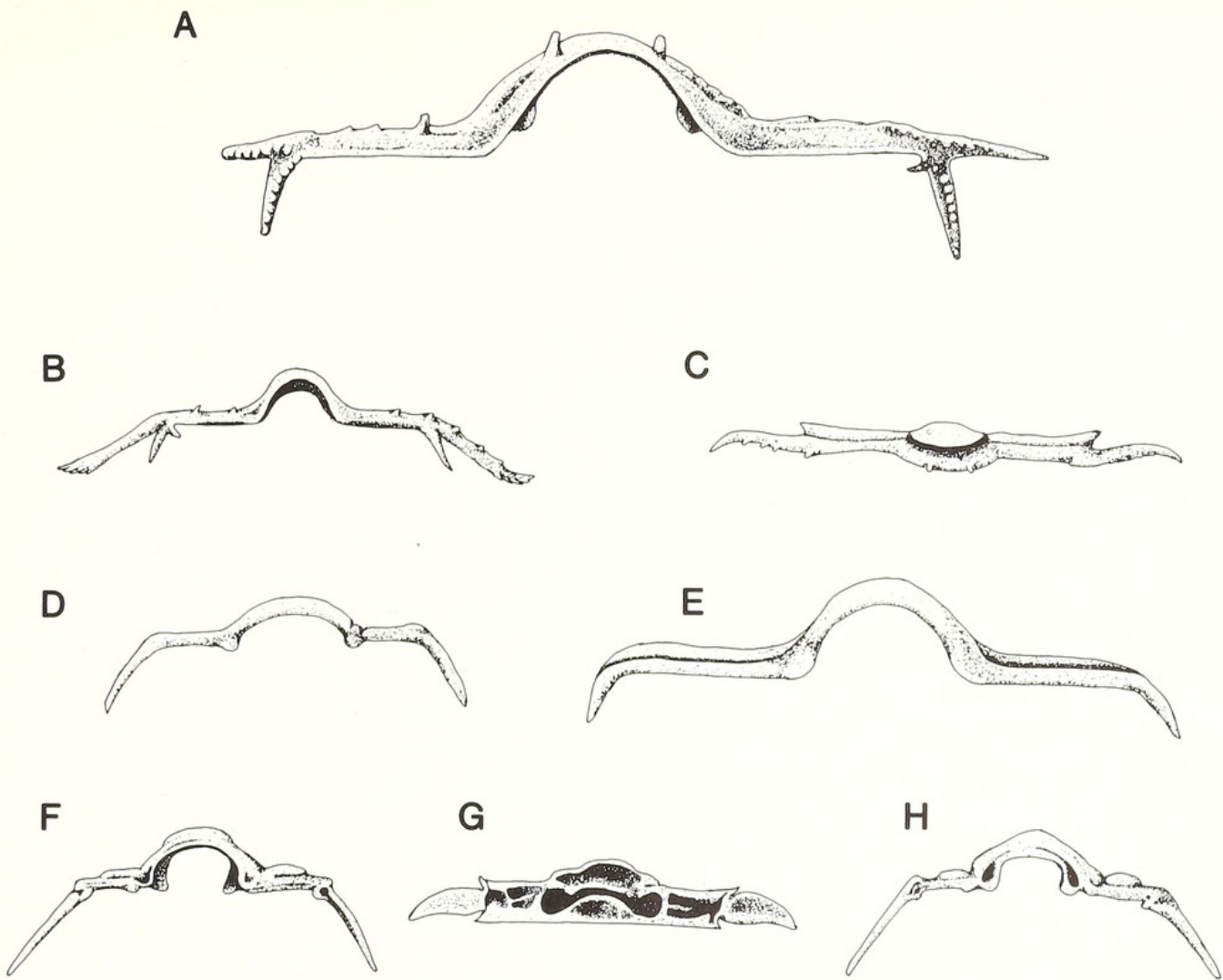
example *Homagnostus obesus* (Wilmot 1990a) which gives the appearance of space frames, such as geodesic domes. However, as trilobite exoskeletons were constructed predominantly from low-magnesian calcite, their space-enclosing structure is more analogous to the monocoque shell, which resists forces throughout its 'skin', not just in members of a grid system.

The polygonal structures may simply be the external expression of epidermal cells which generated the cuticle (Wilmot 1990b), but the network of ridges they create can give the 'thin shell' some additional strength. When examined in detail, the cell polygons are essentially curved plates with reinforced ridges on their edges (Text-fig. 11A, B). In section, the ridges are acting as T-beams



TEXT-FIG. 8. Trilobite thoracic segments. A, generalized forms of trilobite thoracic segments: (i), single arch; (ii), arch on arches; (iii), horizontal pleurae; (iv), simplified sagittal section through a trilobite, emphasizing the relatively low convexity compared with transverse sections, and the jointed nature of the thorax. B, single arch thoracic segments: (i), (ii), *Bumastus (Bumastoides) lenzi* Chatterton and Ludvigsen (Illaenidae), anterior and posterior views of thoracic segments, $\times 3.8$ (based on Chatterton and Ludvigsen 1976, pl. 5, figs 27 and 31). (iii)–(vii), *Failleana calva* Chatterton and Ludvigsen (Styginidae), thoracic segments (based on Chatterton and Ludvigsen 1976, pl. 6): (iii), anterior view, $\times 3$ (fig. 18); (iv), posterior view, $\times 4.3$ (fig. 21); (v), posterior view, $\times 2.9$ (fig. 24); (vi), posterior view, $\times 4.3$ (fig. 22); (vii), anterior view, $\times 3.5$ (fig. 27).

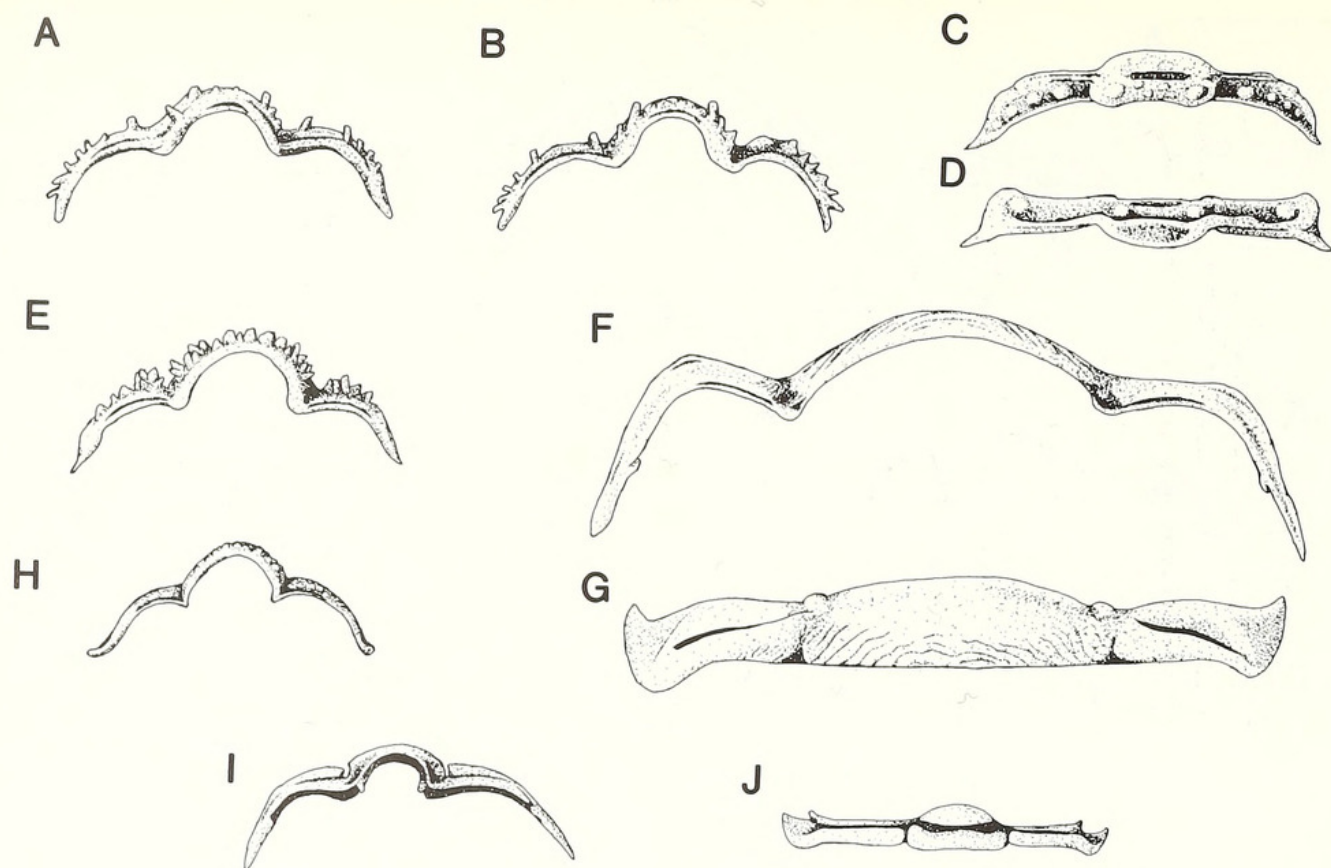
(Text-fig. 11c), which are much stronger than ordinary beams with columns since there are no joints. Although in architecture these are normally inverted, the principles involved remain valid for trilobites. Altogether, a strengthening meshwork has been produced over the external surface, the structural significance of which is most marked in thin cuticles such as those of agnostid trilobites, where the ridges can form as much as 15% of the total cuticle thickness. Such grids are rarely used in man-made structures as external meshes are subject to corrosion; as a compromise, they have to be placed within the structure. In this respect therefore, trilobite exoskeletons are better designed than most buildings, although an external mesh was applied to the Philips Pavilion, designed by Le



TEXT-FIG. 9. Thoracic segments with horizontal pleurae. A, *Ceratocephala lacinata* Whittington and Evitt (Odontopleuridae), posterior view of thoracic segment, $\times 10$ (based on Whittington and Evitt 1954, pl. 8, fig. 8). B, C, *Acidaspis* (*Acidaspis*) *lesperancei* Chatterton and Perry (Odontopleuridae), posterior and anterior views of thoracic segment, $\times 10$ (based on Chatterton and Perry 1983, pl. 21, figs 15 and 16). D, *Nanillaenus mackenziensis* Chatterton and Ludvigsen (Illaenidae), anterior view of thoracic segment, $\times 2.9$ (based on Chatterton and Ludvigsen 1976, pl. 4, fig. 15). E, *Dolichoharpes* aff. *D. reticulata* Whittington (Harpedidae), posterior view of thoracic segment, $\times 7$ (based on Chatterton and Ludvigsen 1976, pl. 7, fig. 24). F–H, *Ceraurinella typa* Cooper (Cheiruridae), anterior, ventral and posterior views of thoracic segment, $\times 2$ (based on Whittington and Evitt 1954, pl. 11, figs 1, 4, 5).

Corbusier at the Brussels Exhibition in 1958. As the building was a temporary exhibit, corrosional effects were unimportant.

Additional structures on trilobite exoskeletons acting as T-beams occur on the ventral surfaces of some effaced cuticles (Text-fig. 11E). For example, the pygidium of *Leiolichas* is strengthened by a series of radiating ribs (Thomas and Holloway 1988, pl. 9, fig. 208). As mentioned previously, ridges on the ventral surface are generally more prominent than the corresponding dorsal furrows, although this is probably primarily for muscle attachment rather than for strengthening purposes. Other larger-scale features such as terrace ridges will have strengthened the exoskeleton by increasing the thickness of the cuticle. As most terrace ridges only have relief on the external surface of the exoskeleton, they acted mechanically as reinforcing ridges to the 'sheet', and often occur on the margins or doublure where strains were greatest. Those that have relief on both dorsal and ventral surfaces of the cuticle (Wilmot 1988) will have acted as folded plates.



TEXT-FIG. 10. Arch-on-arch thoracic segments. A–D, *Dimeropyge virginensis* Whittington and Evitt (Dimeropygidae), thoracic segments, $\times 15$ (based on Whittington and Evitt 1954, pl. 3, figs 8, 11, 1, 5). E, *Dimeropyge clintonensis* Shaw (Dimeropygidae), posterior view of thoracic segment, $\times 15$ (based on Chatterton and Ludvigsen 1976, pl. 18, fig. 11). F, G, *Isotelus parvirugosus* Chatterton and Ludvigsen (Asaphidae), posterior and dorsal views of thoracic segment, $\times 2.9$ (based on Chatterton and Ludvigsen 1976, pl. 2, figs 19 and 20). H, *Acanthoparypha chiropyga* Whittington and Evitt (Cheiruridae), posterior view of thoracic segment, $\times 3.2$ (based on Whittington and Evitt 1954, pl. 29, fig. 25). I, J, *Encrinuroides rarus* (Walcott) (Encrinuridae), posterior and dorsal views of thoracic segments, $\times 5.5$ (based on Chatterton and Ludvigsen 1976, pl. 15, figs 40 and 41).

CONCLUSIONS

1. For the first time, the mechanical characteristics of a trilobite exoskeleton have been related to its composition, microstructure, and architecture.

2. Trilobite cuticles are best regarded as ceramics which are linearly elastic, as they were predominantly composed of low-magnesian calcite with only a small proportion of organic matter.

3. Calcification was probably the most economical method of strengthening the cuticle in the marine environment, due to the abundance of the relevant ions.

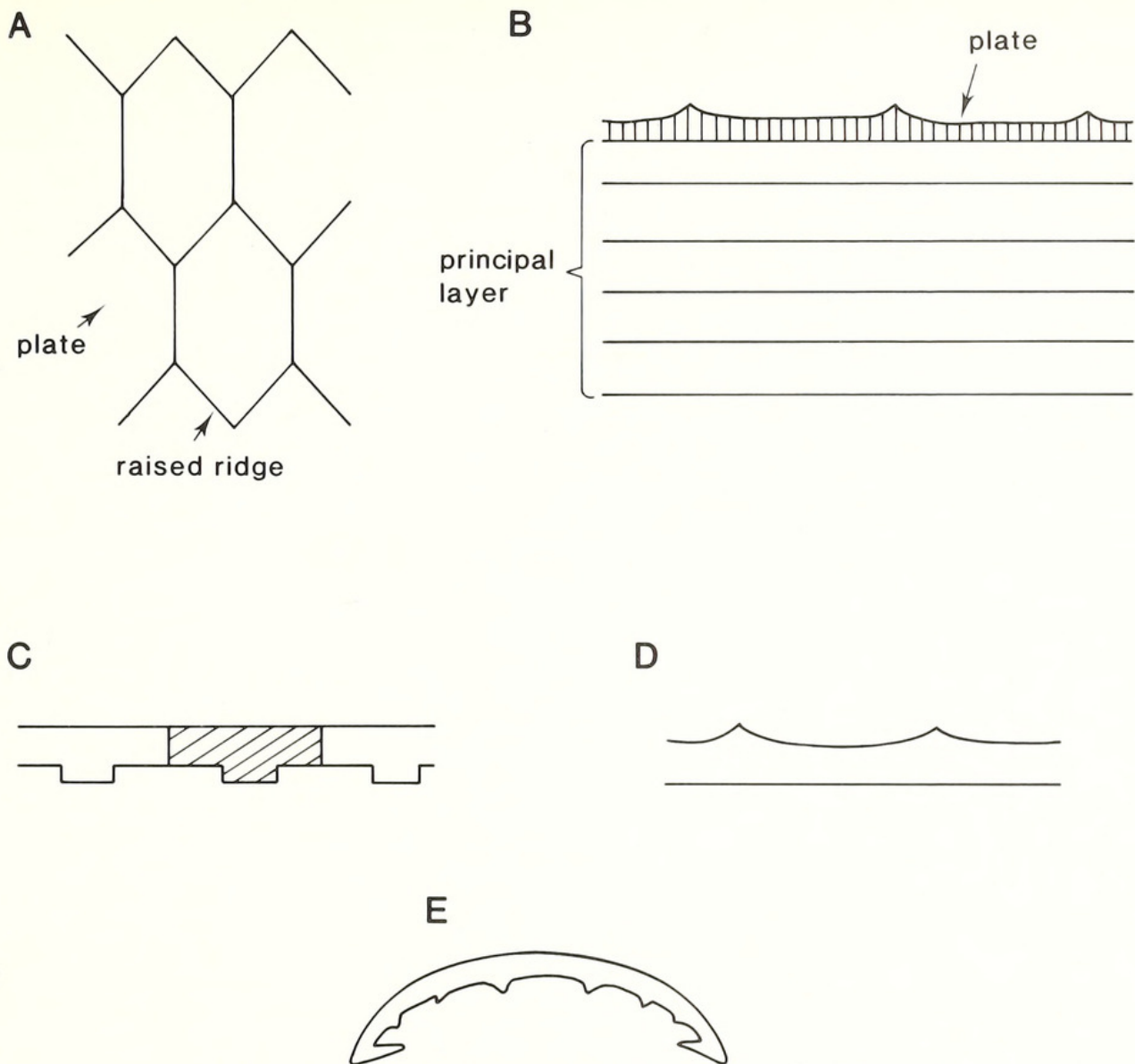
4. Trilobite exoskeletons were composites that could resist both tensile and compressive forces.

5. The small size of the calcite crystals reduced the risk of crack formation, and the progression of fractures was slowed by the changes of direction at each crystal boundary.

6. Prismatic layer was probably the easiest microstructure to generate, being rapidly calcified after ecdysis, and would have been strong under compressive forces acting normal to the cuticle surface. The underlying principal layer functioned as a crack-stopper and added bulk to the exoskeleton.

7. The relative proportions of prismatic layer to principal layer would have been of mechanical significance.

8. Structurally, the trilobite exoskeleton is a monocoque shell in the form of a series of modified



TEXT-FIG. 11. T-beams. A, plan view of cell polygons on trilobite cuticle. B, schematic transverse section through trilobite cuticle, not to scale. C, T-beam, as used in architecture. D, transverse section through an agnostid cuticle. E, schematic transverse section through an effaced pygidium showing ribs on ventral surface.

domes. The doublure, cell polygons, and terrace ridges all strengthened the cuticle. Strongly convex trilobites had shorter doublures than shallower forms.

9. The shape of thoracic segments is a compromise between mechanical strength and their function as articulating structures.

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