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Design and mechanical properties of insect cuticle

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Abstract

Since nearly all adult insects fly, the cuticle has to provide a very efficient and lightweight skeleton. Information is available about the mechanical properties of cuticle—Young's modulus of resilin is about 1 MPa, of soft cuticles about 1 kPa to 50 MPa, of sclerotised cuticles 1–20 GPa; Vicker's Hardness of sclerotised cuticle ranges between 25 and 80 kgf mm^{-2}; density is 1–1.3 kg m^{-3}—and one of its components, chitin nanofibres, the Young's modulus of which is more than 150 GPa. Experiments based on fracture mechanics have not been performed although the layered structure probably provides some toughening. The structural performance of wings and legs has been measured, but our understanding of the importance of buckling is lacking: it can stiffen the structure (by elastic postbuckling in wings, for example) or be a failure mode. We know nothing of fatigue properties (yet, for instance, the insect wing must undergo millions of cycles, flexing or buckling on each cycle). The remarkable mechanical performance and efficiency of cuticle can be analysed and compared with those of other materials using material property charts and material indices. Presented in this paper are four: Young's modulus—density (stiffness per unit weight), specific Young's modulus—specific strength (elastic hinges, elastic energy storage per unit weight), toughness—Young's modulus (fracture resistance under various loading conditions), and hardness (wear resistance). In conjunction with a structural analysis of cuticle these charts help to understand the relevance of microstructure (fibre orientation effects in tendons, joints and sense organs, for example) and shape (including surface structure) of this fibrous composite for a given function. With modern techniques for analysis of structure and material, and emphasis on nanocomposites and self-assembly, insect cuticle should be the archetype for composites at all levels of scale.

Keywords: Cuticle; Chitin; Protein; Fibrous composite material; Stiffness; Strength; Toughness; Hardness; Material property charts; Materials selection

1. Introduction

From the functional point of view, the most important attribute of the majority of adult insects in their most advanced development is that they can fly. This imposes design requirements on both the material and the structure of the cuticle, which has to perform all the functions of a skin and a skeleton, and that at low weight. The cuticle is, praeternaturally, multifunctional: it not only supports the insect, it gives it its shape, means of locomotion, waterproofing and a range of localised mechanical specialisations such as high compliance, adhesion, wear resistance and diffusion control. It can also serve as a temporary food store and is a major barrier to parasitism and disease (e.g. fungal invasions). The fibrous composite cuticle derives its properties from its components, which can be varied in orientation (where applicable) and volume fraction to produce the wide range of mechanical properties: chitin nanofibres; type of protein; water content and degree of cross-linking of the protein; lipid; metal (Zn, Mn, Fe) ions; calcium carbonate. In this paper we first describe and review the formation and microstructure of cuticle, its fibrous composite microstructure and macroscopical shape as it is reported in the literature, then we analyse the remarkable mechanical performance of cuticle and compare it with that of other materials using material property charts and material indices generated for this purpose. The conclusion is that it is worthwhile to look to cuticle for inspiration for high material and structural efficiency.

2. Formation and microstructure of cuticle

The cuticle is secreted by a single layer of epidermal cells that covers the entire surface of the insect, extending

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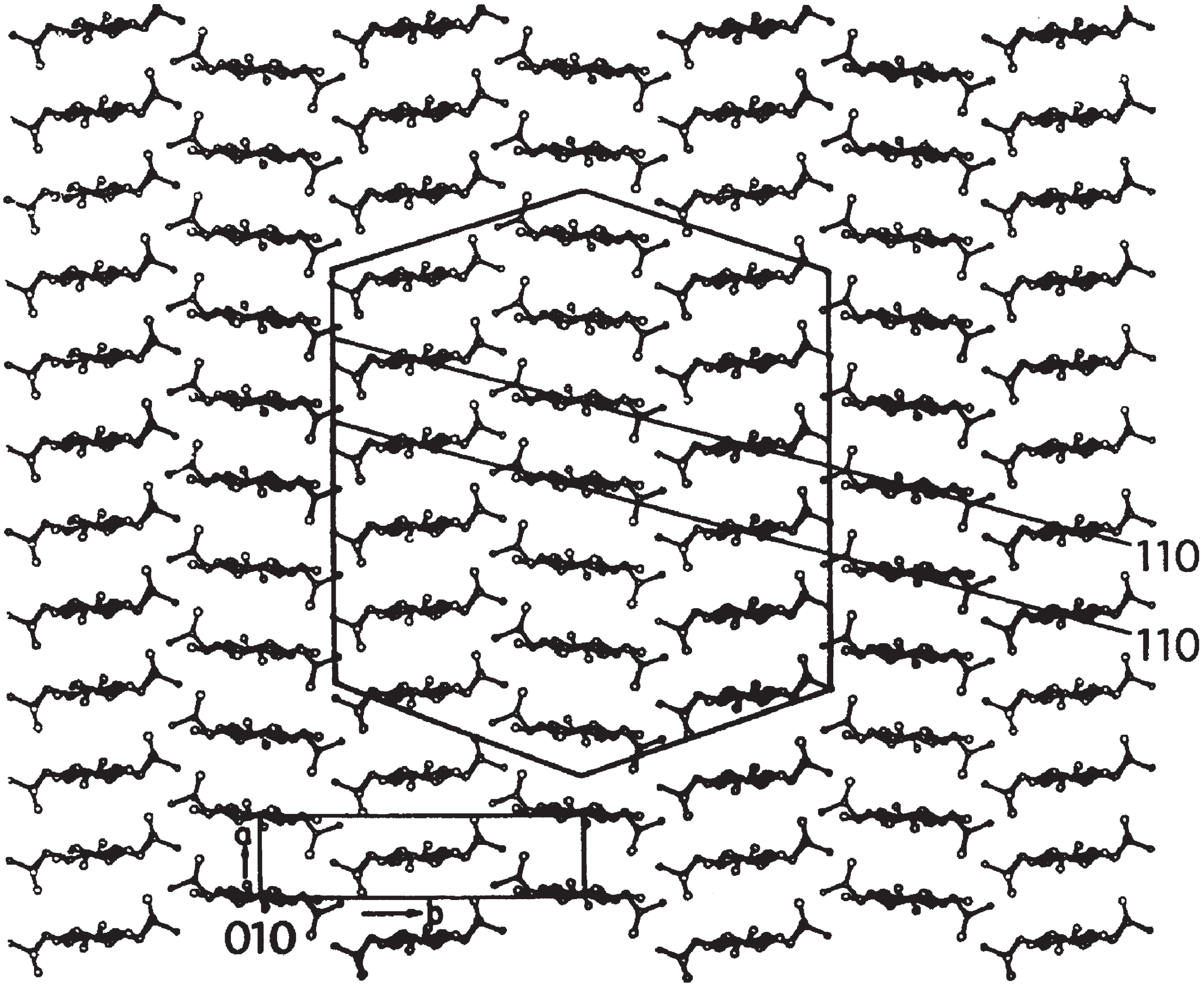

Fig. 1. End view of a chitin crystallite showing the typical section of a chitin nanofibre looking along the chitin chains which are extending out of, and into, the page in order to create the nanofibre.

into the tracheal system, fore- and hind-gut, and part of the genital system. Although it is composed of several layers (from the outside: cement and wax, then epicuticle, then exo- and endocuticle) most of the increase in understanding of mechanical properties has been in the exo- and endocuticular layers, which make up the bulk of the thickness. It can be as thin as 1 μm in the hindgut and over gills (e.g. Ephemeropteran larvae) and as thick as 200 + μm (elytra of large Coleoptera). For the rest of this review, 'cuticle' will mean just the exo- and endocuticular layers, unless otherwise stated. It is a composite material consisting of arrangements of highly crystalline chitin nanofibres embedded in a matrix of protein, polyphenols and water, with small amounts of lipid.

Chitin is a fairly completely acetylated polysaccharide akin to cellulose. The monosaccharide units are joined by β-1,4 links that make the molecule very straight and ribbon-like. The chains are arranged anti-parallel (the α form) and combine into a highly crystalline structure within which the sugar residues are heavily H-bonded imparting stiffness and chemical stability. Within the body of the cuticle the chitin is assembled into nanofibres about 3 nm in diameter and about 0.3 μm long, each containing 19 molecular chains (Fig. 1) (Atkins, 1985). Although it has never been specifically measured, the stiffness of these nanofibres is at least 150 GPa, based on the observation that cellulose is about 130 GPa and the extra bonding in the chitin crystallite is going to stiffen it further (S. Eichhorn, personal communication). In suspension in water, chitin nanofibres are highly thixotropic (Vincent unpublished) and liquid crystalline (Murray and Neville, 1998). Stiffness and thixotropy are crucial properties for the self-assembly of the components of the cuticle. The number of chitin chains in the nanofibre is probably close to a minimum for internal stability of the crystallite; hence the nanofibres present the maximum surface area for interfacial interactions within the

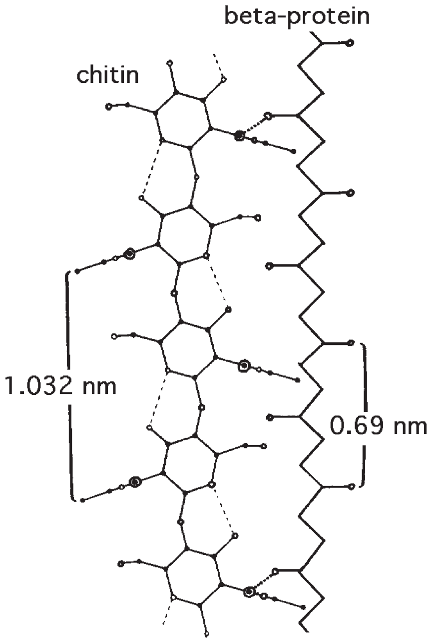

Fig. 2. Suggested bonding between a silk-like protein and chitin.

cuticle. However, larger nanofibres exist in some cuticles where resistance to compression may be important (Gardiner and Khan, 1979), but the optimisation of the size of the fibres in cuticle is unexplored.

The crystalline structure of α-chitin is important for the interaction of chitin with the protein matrix. Along the 010 face (the *c*-axis) the hydrogen chains are laterally spaced by 0.475 nm, the same as the lateral distance between the adjacent protein chains of an antiparallel β-sheet such as silk. Along the length of each chitin chain the space between adjacent residues is 1.032 nm. Twice this repeat (2.064 nm) is almost exactly the same as three times the repeat of a protein β-sheet (0.69 nm). Thus the lattice that appears on the 010 face of the chitin nanofibre can be related to the spacings in a chain folded sheet of protein β-sheet (Fig. 2) and the chitin is bonded to half the protein groups (Neville, 1993).

The protein is probably synthesised within, and is certainly secreted from, the epidermis (Locke et al., 1994). The protein has to produce a matrix of varying mechanical properties, which will also interact with and stabilise the chitin. It interacts with the chitin in a narrow zone (the Schmidt layer) where there is a relatively large amount of water (about 90%), presumably to drive the hydrophobic interactions between chitin and protein. Electrophoretic two-dimensional separation of extracted cuticular proteins on gels shows that they are many and varied. In soft cuticles such as the highly extensible soft intersegmental membrane cuticle of the female locust there may be only 20 or so (Vincent and Shawky, 1978) whereas in some of the stiffer cuticles in the same insect there may be 200 or more (Andersen et al., 1995). This complexity is probably more apparent than real, since the conditions of separation of the proteins on gels picks up slight differences in charge, which could be given by a single amino acid substitution in the sequence, which may not be so important in a structural protein. Also the proteins are probably not different in the different areas, as can be shown by immunological comparisons (Csikos et al., 1999).

The proteins can interact with each other giving well-defined complexes in the absence of H-bond breakers, suggesting that hydrophobicity is an important factor in their stabilisation; in general proteins from more highly evolved insects tend to be less hydrophobic (Hillerton and Vincent, 1983). Much of the protein, especially in softer, more hydrated, cuticles can be extracted with mild solvents such as simple buffers; the amount extracted is often increased at low temperatures, a behaviour characteristic of hydrophobic proteins. In some cuticles up to 70% of the total protein can be removed in this way.

The interaction of the remaining proteins with the chitin seems to be fairly consistent in that even in the softest of cuticles (in which the interactions are least developed) a strong solvent (e.g. 5% NaOH at 100C) is required to remove the protein from the chitin. X-ray diffraction of the ovipositor of the wood wasp *Megarhyssa* suggested that the proteins surround the chitin in a regular manner (Blackwell and Weih, 1980). Later work on this ovipositor, allied with more careful molecular modelling and the analysis of the crystalline structure of the chitin nanofibre, suggested that the protein is attached only to the 010 faces and that the other faces of the nanofibre are essentially bare of bound protein.

In recent years the increased amount of information on the amino acid sequence of these proteins allows much more detailed and interesting conclusions to be drawn about the nature of the matrix and its interactions both internally and with the fibrous phase. A conserved sequence was identified, and it was tentatively suggested that this sequence could be important in interactions with the chitin (Rebers and Willis, 2001). As noted above, this would necessitate its producing a β-sheet in the protein. This has recently been confirmed, and the protein has been shown, experimentally, to bind to chitin. Even so, the detailed nature of the chitin-protein bond in the cuticle is subject to speculation. The 3:2 relationship between the spacings of the chitin and protein residues along their respective chains accounts for only half of the bonds that the protein could make. Atkins (who has worked most recently with the chitin system) is of the opinion that one, at least, of these groups could react covalently with the few unacetylated side chains of the chitin (EDT Atkins, personal communication). This is still speculation, but while we cannot calculate the strength of the interfacial interaction between the chitin and the protein (fibre-matrix), we can at least put a lower bound on it, guessing that the shear strength of a single H-bond is of the order of 30 pN, and calculating that the area around each bond is about 10^{-18} m^2, then the shear strength will be about 30 MPa, or about half that measured for carbon fibres in a resin matrix.

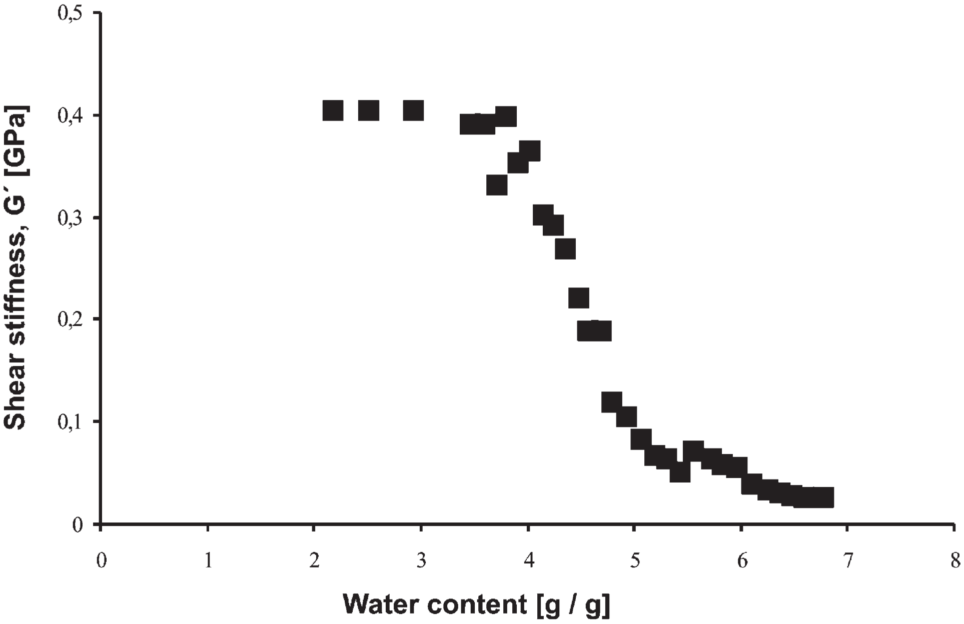

Fig. 3. Transition in shear modulus with change in water content of a sample of untanned maggot (*Calliphora* sp.) cuticle.

In the early stages of the development of the cuticle, before the insect has shed the cuticle of its previous stage, the amount of protein per unit chitin is much less than in the mature developed cuticle and the protein that is present shows much more β-sheet and so may be deduced to be interacting preferentially with the chitin. Therefore the addition of matrix material to chitin is at least a two-stage process; the chitin nanofibres are first coated with a specific protein, then the rest of the protein is added, interacting with the proteins already attached to the chitin.

Conformations other than β-sheets exist in cuticular proteins, although they have not been much explored. They have been mapped in some proteins. In particular the highly rubbery cuticle protein(s) called resilin now appear to contain β-turn structures similar to those found in elastin, a rubbery protein typical of vertebrate animals (Urry, 1983). The β-turn is present in many of the other cuticular proteins and so may form an important component of hydrated cuticles. When dehydrated, such structures revert to the glassy state, since water plasticizes proteins. Resilin is always highly hydrated.

3. Cuticle as a fibrous composite material

At the microstructural level the mechanical properties, such as the stiffness and strength, of insect cuticle are due to the extent of interaction of protein with the chitin by way of sheet structures, and the interactions of this protein with other matrix proteins and other components. Comparing the surface area available for bonding between matrix and chitin; if the minimum practical size for a carbon fibre is a diameter of 5 μm, but only half of the surface area of the chitin nanofibril is available for matrix bonding, then the surface area of chitin per unit volume of cuticle is 10^6 greater than the carbon fibre material. But with the huge surface area difference it is fairly obvious that the total fibre-matrix interaction per unit volume in insect cuticle is still 5×10^5 greater than carbon fibre composites.

'Soft' (compliant) cuticle commonly contains equal weight fractions of chitin and protein, and 40–75% water. 'Hard' (stiff) cuticles contain 15–30% weight fraction (dry) of chitin and only 12% water. Stiffness can vary from 1 kPa in the highly hydrated extensible intersegmental membrane of the locust, via about 1 MPa for the hydrated rubbery protein, resilin, to 60 MPa in the abdominal cuticle of *Rhodnius* (Reynolds, 1975) to 10 or more GPa in well-tanned isotropic cuticles and 20 GPa measured parallel to the chitin orientation in the tibial flexor apodeme of the locust (Ker, 1977). The mechanical properties of other parts of insects have been measured, such as the compressive and tensile stiffness of the hind tibia of the locust (Jensen and Weis-Fogh, 1962) which seems rather low at only 80 MPa, (but no discrimination was made between tanned exocuticle and the softer, relatively hydrated and less tanned, endocuticle). The stiffness of locust femoral cuticle is 2–6 GPa lower when there is more endocuticle, which is hydrated and therefore tends to be softer. Its tensile strength is 60–200 MPa, which is about 1–5% of the stiffness. Tensile strain is 1–2%, failure strain up to 5%. Although the stiffness of femoral cuticle in the locust goes down as the adult ages, due to deposition of softer endocuticle, the ratio of stiffness to weight remains constant over the fifth instar and first two weeks of adult life, suggesting similarity in usage of muscles or in jumping performance (Hepburn and Joffe, 1974). The development of calcification in a fly puparium (Roseland et al., 1985) and the 'strength' of beetle elytra (Grosscurt, 1978) have been measured with a

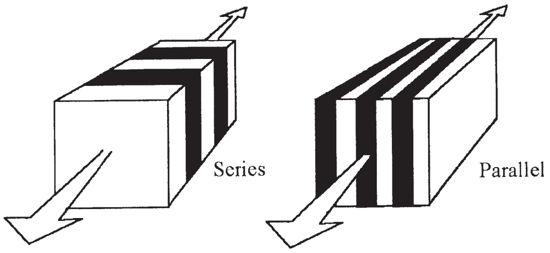

Fig. 4. Parallel (a) and series (b) limit models of platey or fibrous composite materials.

penetrometer, which involves measuring the force to push a pin through the material. Unfortunately this popular test, although very easy, is very difficult to interpret in terms of the mechanical parameters that are considered the most useful.

The most widely accepted version of stiffening (tanning, sclerotisation) of cuticle was suggested over 60 years ago (Pryor, 1940) but the fact that we are still uncertain of its mechanism makes one suspicious that the right trails are being followed.

Immediately after the old cuticle has been shed, the epidermal cells secrete into it a variety of substituted *ortho*-dihydroxyphenolic compounds. They are converted into the more reactive quinone form and, supposedly, cross-link the proteins making the matrix stiff, hydrophobic, insoluble and chemically inert. At the same time much water is lost from the cuticle (Fraenkel and Rudall, 1940), which can anyway, be stiffened just as much simply by the removal of water (Vincent, 1980). Indeed, the naturally sclerotised and stiffened material can be reversibly softened and made rubbery by soaking it in formic acid (Andersen et al., 1996), which breaks hydrogen bonds. This indicates that the secondary reactions made possible by the removal of water from the protein are much more important than the phenols in stiffening the cuticle, and that the control of stiffness is in general a matter of manipulating the water content. When the water has been removed the protein can form large amounts of β-sheet (Hackman and Goldberg, 1979) which is both chemically and mechanically stable.

Cuticle can be mechanically extremely sensitive to water content, suggesting that an important source of stabilisation is H-bonding (Nissan, 1976). In the soft cuticle of maggots, gradual reduction of water in the absence of tanning takes the cuticle through a transition of up to 10-fold increase in stiffness with a change in water content of only a few percent (Fig. 3, Vincent, unpublished). In some cuticles the insect can increase the water content so that the modulus decreases. This happens in the blood-sucking bug *Rhodnius*, for instance, which can change the pH of the cuticle from about 7 to below 6, thereby increasing the charge density of the cuticular protein and increasing the cuticular water content from about 26 to 31%, dropping its stiffness from 250 to 10 MPa and increasing its extensibility from 10% to more than 100% (Reynolds, 1975). A similar transformation happens in the locust extensible intersegmental membrane, but is here under hormonal control and the mechanism is obscure (Tychsen and Vincent, 1976).

The stiffnesses quoted so far are for in-plane deformation, such as extension, measured on the entire cuticle which, frequently, is multilayered with a plywood-like structure. Unidirectional composites are very anisotropic in-plane: the properties at one point in the body are not the same in every direction. The tensile and shear stiffnesses and strengths, for example, are much larger when fibres are aligned parallel to the applied load (Fig. 4b), the stiffness can be dominated by a relatively small proportion of high modulus fibres. When the fibres are aligned perpendicular to the applied load (Fig. 4a) the properties are dominated by the modulus of the matrix, as in the extensible intersegmental membrane of the locust (Vincent, 1981) where the matrix is eight orders of magnitude more compliant than the fibre.

If high stiffness in more than one direction is required, as is the case in most parts of the cuticle, 'laminating' unidirectional layers in a variety of directions produces the desired properties. In contrast to man-made lamellar composites in which the fibre direction can change abruptly, in cuticle the fibre direction from one lamella to the next changes gradually forming helicoidal connecting layers.

The overall elastic properties of the laminate cuticle depend on the properties of the laminae and their arrangement. The stiffness of the 'homogenised' cuticle with a plywood-like structure is about a third of that of a unidirectional lamella with the same chitin-fibre content. Further advantage can be taken through an asymmetrical lay-up. If, for example, the inner layer of the composite is more compliant than the outer, then appropriate beam bending puts the outer (sclerotised) layer in compression and the inner in tension. This already allows larger deformation before failure and increased elastic energy storage. If further unsclerotised cuticle is added to the tensile surface, the sclerotised layer can store even more elastic strain energy before failure, which also means that the material is tougher (Ker, 1977; Vincent, 1990). A compliant inner layer also increases the in-plane toughness both in crack opening (mode I fracture) and in tearing (mode III fracture) (Guild et al., 1978).

4. The shapes of cuticle

The mechanical performance of cuticle is further enhanced by its shape. This illustrates that what is true in engineering design also holds for biological structures: in design terms, material and shape are inseparable—only a shape optimised for a material (or vice versa) will lead to an efficient design, a phenomenon that is analysed in detail elsewhere in the work of Ashby and co-workers (Ashby, 1999; Weaver and Ashby, 1996, 1997; Wegst, 1996; Wegst and Ashby, 2004).

The cuticle is anything but a flat sheet. It is curved and

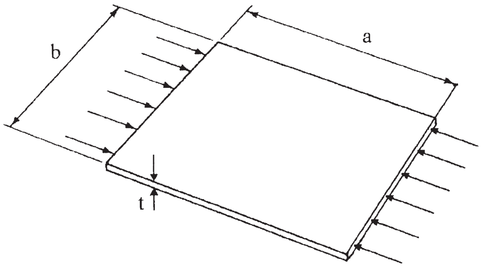

Fig. 5. Simple plate loaded in the plane and in danger of buckling, depending on the load and the morphology of the plate.

corrugated, and many regions of it have a closed form with a circular cross-section. Even the wings and elytra are stiffened as a result of their overall curved shaped. The exoskeleton is further stiffened by ribs, webs, stringers and flanges made from stiff, sclerotised cuticle, producing structures which resemble those of aerospace structures—in some parts, the cuticle even forms sandwich-like structures.

The reinforcements help to delay or prevent failure. A simple, un-reinforced plate loaded in compression on opposite sides with the other two sides free (Fig. 5) will fail the same way as a strut in a manner described by Euler: by compressive failure of the material if the ratio of length (a) to thickness (t) is low (<20), and by elastic instability (buckling) as the length increases for a constant thickness (Megson, 1990). The addition of flanges stabilises against buckling since it increases the effective thickness of the plate in selected areas effectively dividing the plate into shorter lengths.

In insects the position of the flange is identified by an external furrow or suture where the single layer of the cuticle folds inwards to form an internal ridge that commonly also functions as a muscle insertion or apodeme. A typical example is the pleural suture and ridge system of the pterothorax (Fig. 6). This stiffens the side of the thorax and, top and bottom, provides firm support for the wing and leg. In the simplest model with no constraints, the optimal design would have its compressive strength and critical buckling load the same so that the two modes of failure coincided. This has been observed in the somewhat similar structure of the hedgehog spine (Vincent and Owers, 1986) whose internal structure provides structural support until compressive failure occurs. Beyond this, the design considerations become more complex and imponderable, and no measurements have been made of this type of design in insect skeletons.

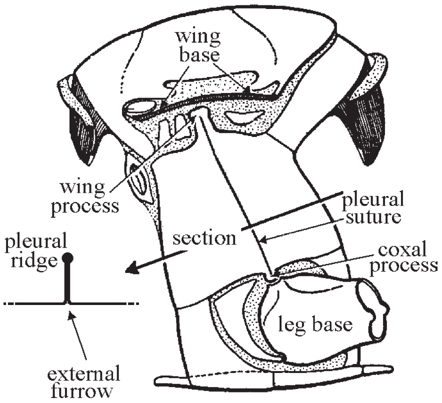

Fig. 6. Thoracic pleural suture and internal stiffening ridge. The wing process is made almost entirely of resilin.

Sclerites covering other parts of the insect are for containment rather than support and usually consist of very thin plates which, since they are not required to support loads in the plane, buckle elastically without loss of overall stability—here the cuticle is commonly less tanned, and thus is less stiff. The sclerites are connected by the untanned and hydrated arthrodial membrane, which is even softer and so can bend and stretch much more. In general these soft cuticles have a much higher content of chitin (50% dry weight) than do stiff cuticles (15–30% dry weight). This may be to do with strength (a softer cuticle may be easier to rupture) or may be to do with chemical stability—more chitin is necessary when the protein is hydrophilic and so more liable to remaining in solution without contributing to structural properties.

5. Cuticular design for various functions

So far we have considered cuticle as an efficient material for lightweight (aeronautical) applications—since one important, if not the most important, function of the cuticle is structural. However, the insect cuticle also has to form sensors, joints (elastic hinges and wear resistant articulations), wear resistant mandibles, devices for elastic energy storage, effective attachment systems, and a water and dirt repellent skin.

To illustrate the range in material properties of the cuticle and its adaptation to its various functions, we choose sensors, joints, mandibles and devices for elastic energy storage as examples and present material property charts to analyse them. Material property charts are graphs that show one material property (or a combination of properties) plotted against a second material property (or combination of properties)—for details see Ashby (1999), Wegst (1996), and Wegst and Ashby (2004). Logarithmic scales allow the accommodation of the vast range of biological materials within one chart.

Each material is represented by a bubble. The width of the bubble reflects the range of the material's properties. In biological materials this range is due not only to the material's composition and microstructure but also to growth condition and age, and, probably most important, moisture content. Cuticle is an excellent example for this. The Young's modulus—density chart (Fig. 7) shows a remarkable range in Young's modulus for its small range in density (1–1.3 kg m^3): from 1 kPa for the intersegmental membrane, through the MPa range for wet and untanned cuticle of larva and puparium, to 20 GPa for tanned, dry

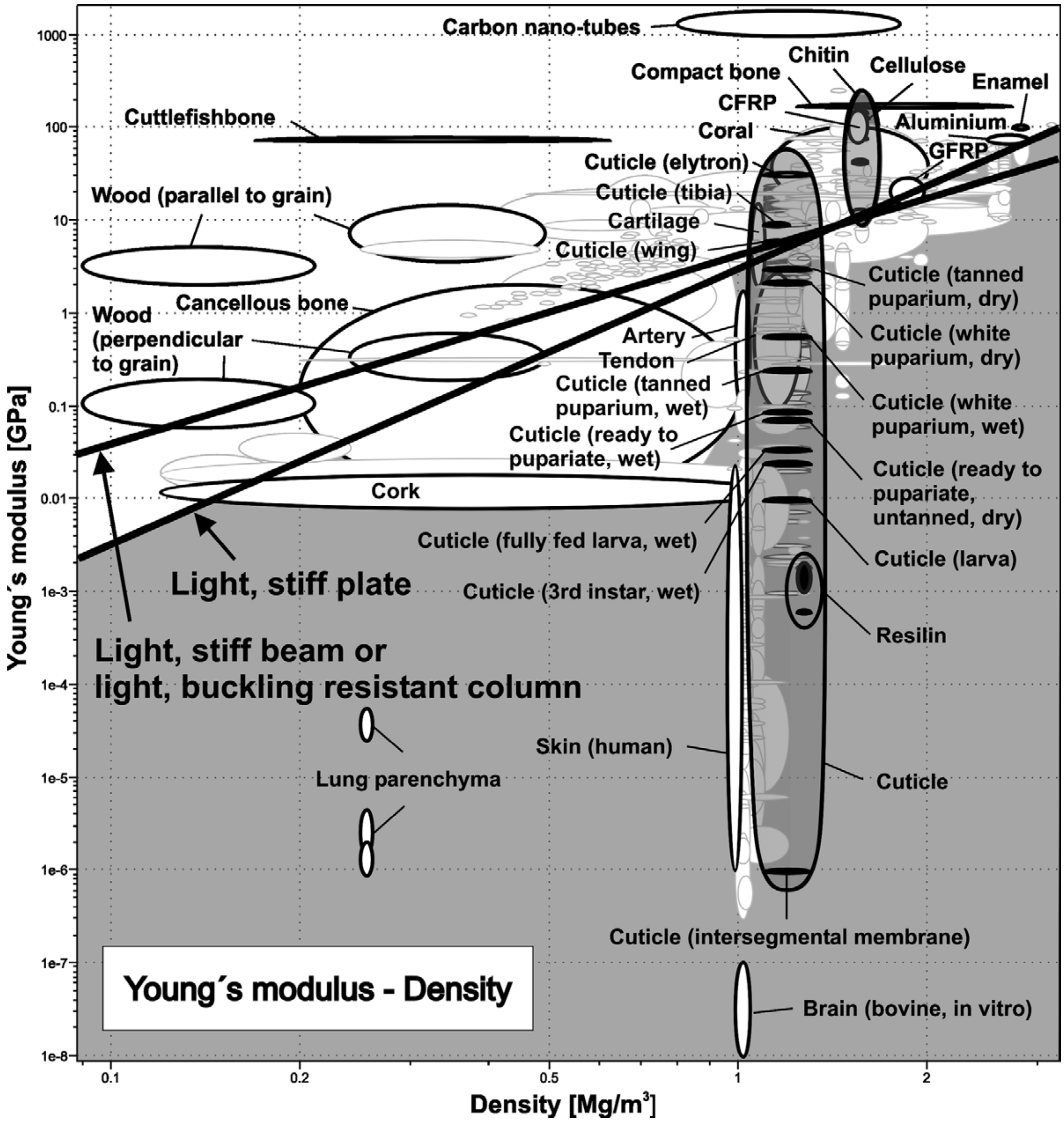

Fig. 7. A material property chart for natural materials, plotting Young's modulus against density. Guide-lines identify structurally efficient materials which are light and stiff. (Figure created using the Natural Materials Selector, Wegst, 2004.)

cuticle of the adult in wing, tibia and elytron, for example. Chitin nanofibres are (at a slightly higher density of 1.6 kg m^3) among the stiffest of the natural fibres. They have a Young's modulus of 150 GPa (S. Eichhorn, personal communication), which is comparable to that of cellulose and about 1/10 of the stiffness of the stiffest synthetic 'fibres': carbon nano-tubes.

Material property charts like Fig. 7 become more powerful in conjunction with materials indices, since they allow the objective comparison of the mechanical efficiency of materials in a given application (for derivations and details see Ashby (1999); Wegst (1996); Wegst and Ashby (2004)). The material index depends on the mode of loading: a light, stiff beam loaded in bending should have a high ratio of $E^{1/2}/\rho$ whereas a light, stiff plate loaded in bending should have a high ratio of $E^{1/3}/\rho$. The logarithmic scales of the property charts allow the indices to be plotted on them as straight lines of slopes 2 and 3, respectively. One guide-line for each is shown in Fig. 7: all materials on one line perform equally well, those above it are stiffer for the same weight and those below less stiff. Cuticle, again, spans a large range in performance: the efficiency in bending (beam and plate) of tanned, dry cuticle is as high as that of wood, aluminium, and even carbon-fibre reinforced polymers (CFRP)—typical aircraft materials), while that of the intersegmental membrane compares to that of human skin.

Where appropriate, we will use material property charts below, to compare the mechanical performance of cuticle with other natural and technical materials.

5.1. Sensors

The cuticle also represents a sensory barrier, in that the insect has to see and feel the outer world through it, with mechanical sensors like the campaniform sensilla which present an excellent example for an optimised combination of material and shape. The campaniform sensillum is a hole in the cuticle that, because it is generally not round but oval, can be deformed (dimensional measurement) more by strains (non-dimensional) in one direction than another. In the cockroach leg, two fields of sensilla with their long axes orthogonal to each other can detect intrinsic (proprioceptive) and extrinsic (extrareceptive) bending, compression, tension and twisting (Keil, 1997). The displacement of the hole is rotated through 90° by the mechanism of a dome that stretches across the hole, which takes the direction of displacement out of the plane of the cuticle so that it can be detected by a sense cell situated in the cuticular epidermis. But a hole introduces both compliance (which is what is needed here) and susceptibility to cracking (which is not needed). Generally holes are avoided by engineers and not regarded as an advantageous aspect of design. Insects design holes into their structure, but with remarkable care. The fibrous component (chitin) is orientated around the hole and so carries loads around it; in a man-made fibrous composite holes would frequently be drilled and the load-carrying fibres interrupted. A finite elements model of an oval hole drilled in a sheet of uniaxially orientated fibres, when stretched parallel to the fibres, developed high stress concentrations on either side orthogonal to the direction of strain, whence cracking would obviously start. With a formed hole the distribution of strain was much more even and the stress concentrations smaller and at the ends of the axis in line with the applied strain and so perfectly safe. Additionally, the fibres going around the hole tend to compress it, further increasing the deformation induced by stretching. At the limit the global strain is amplified locally nearly 10-fold (Skordos et al., 2002).

5.2. Joints

Very little is known of the joints of insects. Commonly they have to work under highly contaminating conditions such as dust and sand, and often in a moist environment. There are two types of joints. Those that are indeterminate and merely confer mobility in the form of elastic hinges, such as the sclerites in the abdomen, for example, and those that are determinate like head, leg and wing articulations.

Elastic hinges are readily analysed—they require a material which allows large deformation before failure. In material selection terms, this is reflected in a high ratio of tensile strength to Young's modulus of elasticity. Fig. 8 and the guide-line labelled 'Elastic hinge', illustrates this. On this graph, the materials below the line are better than those above. The ability of chitin and cuticle to form elastic hinges with large recoverable deflection is similar to that of tendon and grass, even when it is tanned and dry. With increasing moisture content and without tanning, it increases and is comparable to that of cartilage and spider silk.

Head, leg and wing articulations are complex, both in structure and function, and have been analysed little, but see Wootton (1999) for geometry and Gorb (2001) and Gorb and Scherge (2001) for structure and tribology. Investigations of the structure and measurements of the mechanical properties by nanoindentation of the head articulation of the dung beetle (*Geotrupes stercorarius*) and the rose chafer (*Pachnoda marginata*) indicate that the prothoracic part of the joint is rough (due to a regular pattern of hillocks) and much softer than the smooth corresponding surface on the head (Arzt et al., 2002; Enders et al., 2004). However, how structure and material combine in this system for wear resistance and friction control is yet unknown.

5.3. Resistance to wear

Wear resistance is required in ovipositors, claws and mouth-parts. Here we focus on mandibles of herbivorous insects. Wood, plant leaves and seeds are commonly hard, either because they are dense and dry or because they are reinforced by silica or calcium oxalate monohydrate crystals (Finley, 1999; Lucas et al., 2000). The cuticle of the cutting and grinding surfaces of the mandibles of these insects is reinforced (Hillerton et al., 1982; Chapman, 1995, 1998; Schofield et al., 2002). The hardness chart (Fig. 9) illustrates this: the Vicker's hardness of the cutting edge of dry mandibles compares to that of enamel and is about twice as high as that of the sheared face of the dry mandible and several times that of wet cuticle which has a hardness in the range of that of dentine.

Studies on a number of orders (Orthoptera, Phasmida, Lepidoptera, Hymenoptera, and Coleoptera) (Hillerton and Vincent, 1982; Robertson et al., 1984; Fawke et al., 1997; Quicke et al., 1998) revealed that the reinforcement against wear and tear is achieved by impregnating the sclerotised cuticle of the mandible with heavy metals (form unknown) such as Zn, Mn, or occasionally Fe. These metals are present in relatively large amounts ranging from a few to up to 16% of dry mass of the mandibular cutting edges and increase their hardness significantly, trebling it from about 25 to 80 kgf mm^{-2} (Chapman, 1995, 1998; Schofield et al., 2002, 2003). How the incorporation of metals into the cuticle hardens and stiffens the cuticle is not yet understood, similarly why metals are preferred to the more common mineralisation with Ca-salts.

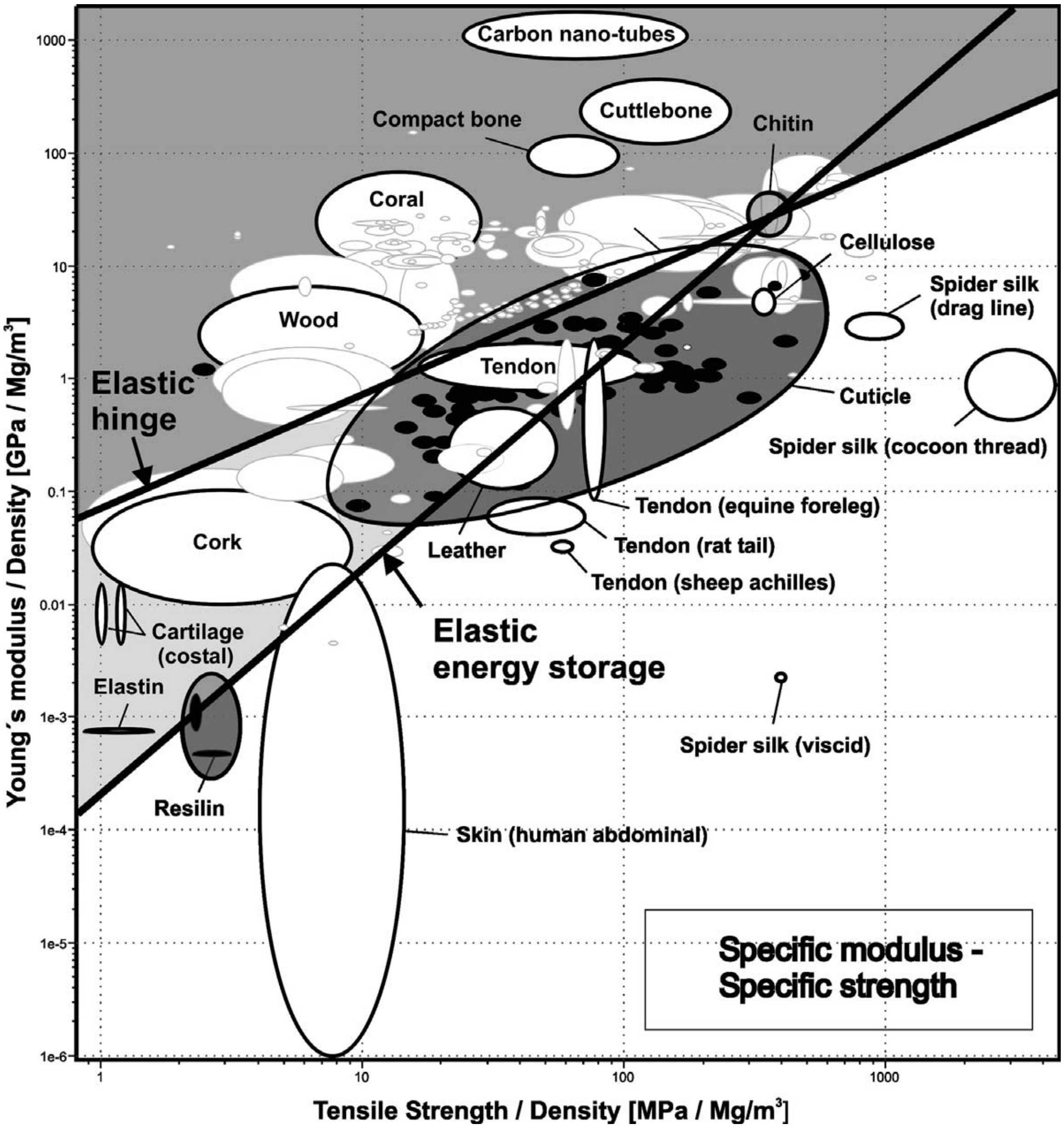

Fig. 8. A material property chart for natural materials, plotting specific Young's modulus against specific strength. Guide-lines identify materials which make good elastic hinges, and which store the most elastic energy per unit weight. (Figure created using the Natural Materials Selector, Wegst, 2004.)

5.4. Devices for elastic energy storage

Elastic energy storage is important in the locomotion of insects for saving energy from one locomotory cycle to the next (e.g. resilin in the hinges of flapping wings (Jensen and Weis-Fogh, 1962) or as a power amplifier releasing energy more quickly than a muscle can (e.g. the flea (Bennet-Clark and Lucey, 1967; Rothschild et al., 1975) and the leafhopper (Gorb, this issue)). Some insects such as locusts and flea beetles use sclerotised cuticular tendons to store elastic energy (Bennet-Clark, 1975; Ker, 1977). How efficient the elastic energy storing devices resilin and cuticle are, can be evaluated using the specific modulus—specific strength chart (Fig. 8). The guide-line marked 'elastic energy storage' and the materials depicted below show that their efficiency to store elastic energy per unit weight is comparable to that of elastin, resilin's counterpart in vertebrate animals, tendon, skin and even spider silk.

Recovery by muscular relaxation is also possible through stiffening by recoverable elastic buckling (Kresling, 1991; Butler et al., 2004) and by shape recovery, as observed in tape-springs. Both are known in the technical world, the latter is found predominantly in deployable space-structures (Seffen and Pellegrino, 1999).

5.5. Failure of cuticle: fatigue and fracture

In addition to the elastic energy storage described above,

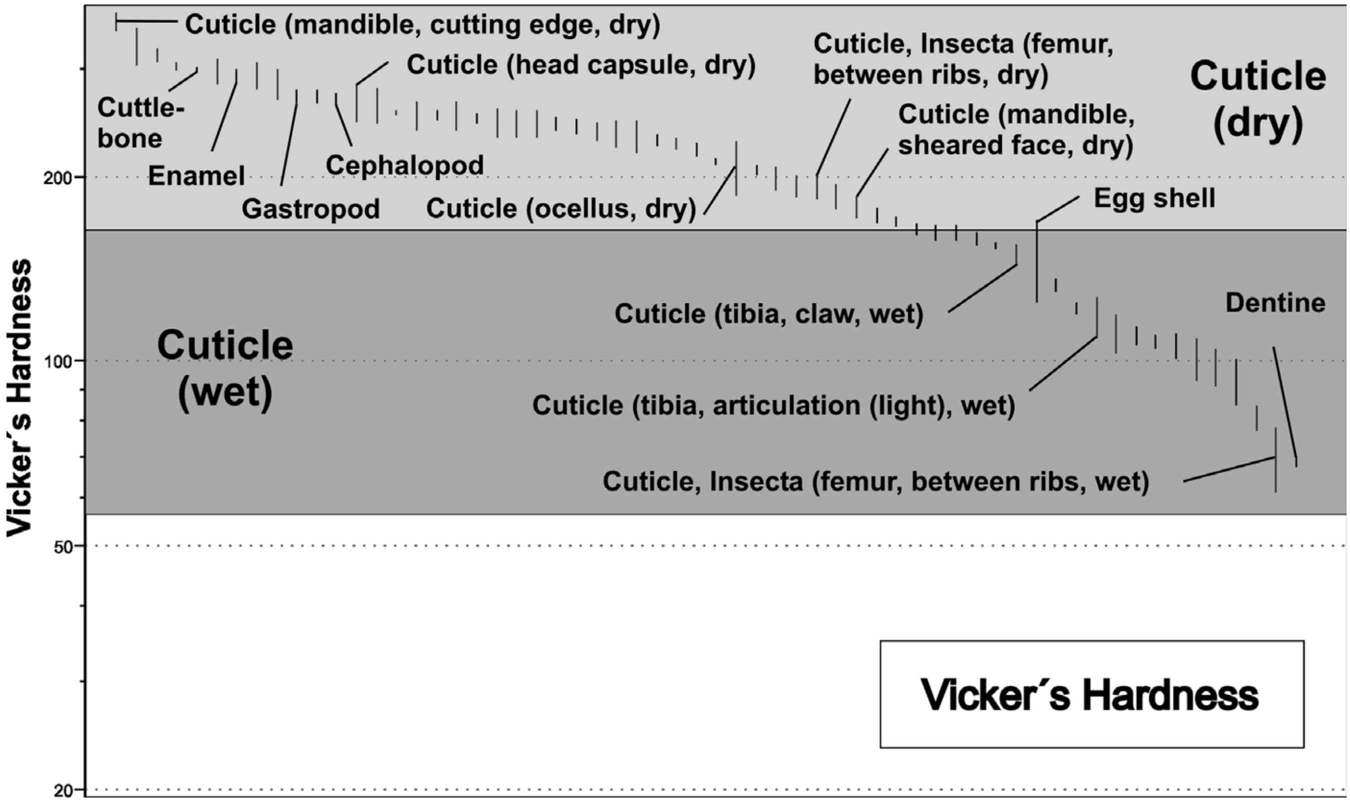

Fig. 9. A material property chart for natural materials, plotting toughness against Young's modulus. Guide-lines identify materials best able to resist fracture under various loading conditions. (Figure created using the Natural Materials Selector, Wegst, 2004.)

Haas et al. (2000a,b) suggest another function of resilin, namely that it prevents or delays material damage and failure by fatigue due to the repeated folding and unfolding in beetle wings, for example. To date, little has been done to investigate fracture and fatigue properties of cuticle, although many parts of the cuticle are, like the wing, subjected to high loads and a high number of loading cycles. Work by Hepburn and others is not valid, partly because they did not control the water content of the test samples so that drying out effects cannot be distinguished from actual fracture events, and partly because they did not use fracture mechanics, neither to design their experiments nor to analyse them. Casual observation shows that the veins in the wing are effective crack stoppers. Whether this is a purely geometrical or also a structural effect due to a site specific microstructure of the composite material is yet unknown.

The little data on the toughness (work of fracture) of cuticle is presented in Fig. 10. The guide-line marked 'absorb impact energy without failure' shows that cuticle performs as well as cork, nutshells and nacre by this criterion, but that horn, antler and skin, and the man-made glass- and carbon-fibre reinforced polymers (GFRP and CFRP), which lie above the line, are better. When, however, the criterion is that a given displacement must be supported without failure, then the materials above the guide-line 'large displacement without failure' are best. Cuticle, skin and aorta stand out here.

A toughening mechanism frequently observed in biological materials is to join brittle layers by a thin, more ductile one. Whether the gradual helicoidal change in fibre direction from one layer to the next has this effect and acts as a crack stopper, has also not been investigated yet. What has been observed, however, is that cracks can be repaired by an injection of protein followed by tanning, or simply by localised tanning on its own (Lai-Fook, 1966).

5.6. Structure and function of cuticle surfaces

Most parts of the exoskeleton are covered with protuberances ranging from relatively flat scales in the micrometer range to long hairs and brush-like structures of several 10 s of μm in size which themselves have a complex geometry (Gorb and Scherge, 2001; Gorb, 2001): long, stiff spines for defence, scales and bristles for generation of sound, structural colour (camouflage, mimicry, species and sex recognition), prevention of water loss and thermoregulation (reflection of sunlight, insulation), aero- and hydrodynamic efficiency through the creation of turbulence which act as air and water bearings, respectively, long bristles as tools for grooming, food sampling and food filtering, and spines for food grinding, both in the mouth-parts and also in the digestive system. The essential water and dirt repellence of the exoskeleton is achieved (as on the lotus leaf) through the combination of a hydrophobic surface chemistry with

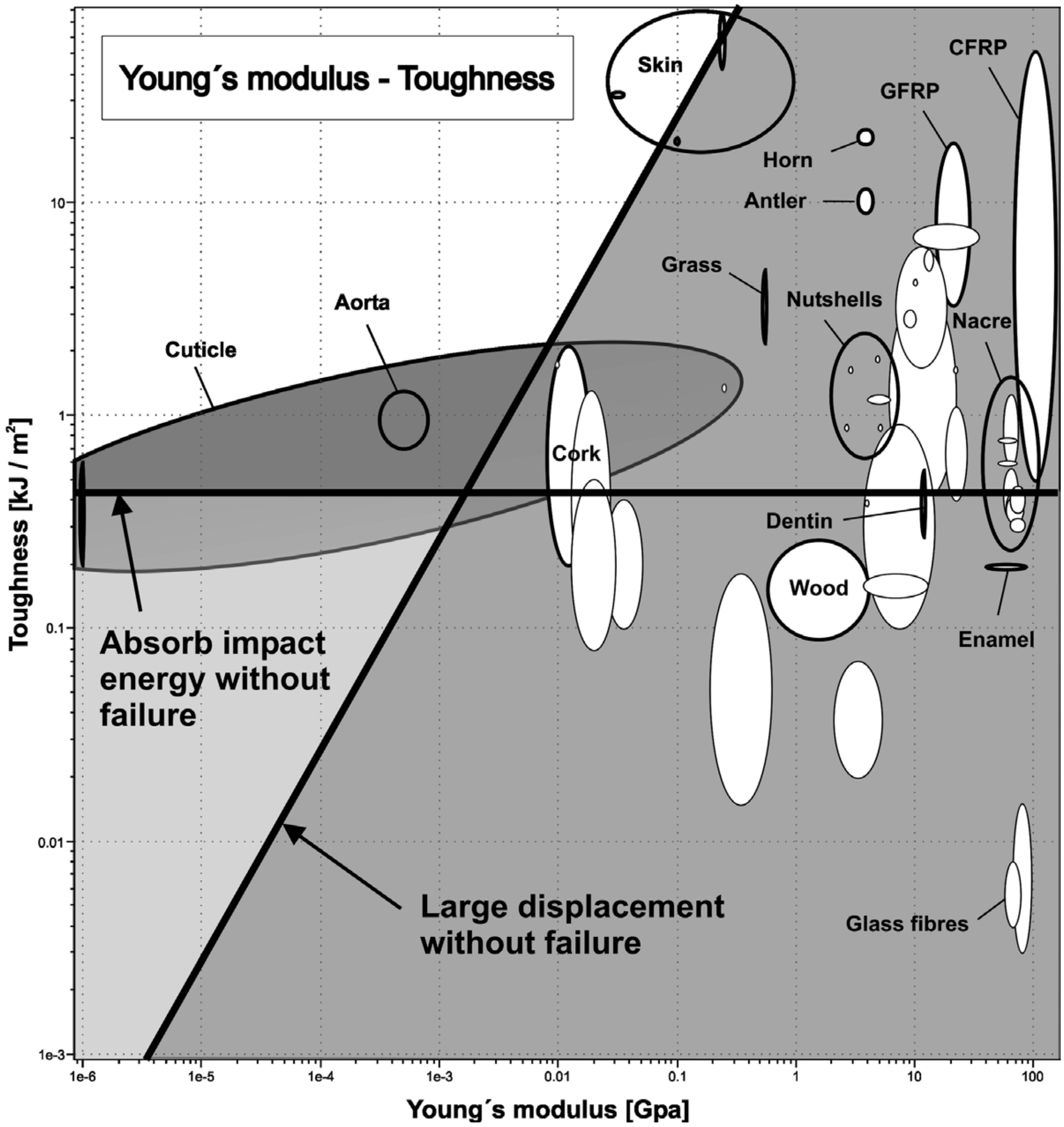

Fig. 10. A material property chart, plotting Vicker's hardness for a range of natural materials. The materials in the light grey zone have a hardness like dry cuticle, those in the dark grey that of wet cuticle. (Figure created using the Natural Materials Selector, Wegst, 2004.)

cuticular protuberances in the range from 0.1 to 1.0 μm (Wagner et al., 1996). There is also a large range of attachment devices, both hairy and smooth (Nachtigall, 1974, Gorb and Scherge, 2001; Gorb, 2001). In the form of hooks, brushes, snap and lock-and-key mechanisms they allow the organism to attach to the substratum, to interlock body parts, to attach during copulation and to associate one organism with another for phoresy, predation and parasitism.

6. Learning from cuticle

Our current understanding of cuticle derives from two streams—the application of biochemistry to the origin of the structure, and the application of principles of structural and materials science to the structures which we see. We can gain technical benefit from both these streams: from the disruption of the biochemistry we can acquire control of pest insects and, with more difficulty, we can derive principles of construction and multifunctionality from structural insights. Success in the development of biomimetic materials suitable for industrial production may be found in the application of the principles of design optimisation identified in biological materials—and in the awareness that material and shape always go hand in hand, that the one needs to be analysed in parallel with the other.

Bearing this in mind, cuticle with its great variety of structures and functions presents an immense source of inspiration. Adhesive-free and reversible attachment systems, wear resistant articulations with variable frictional properties, functional surfaces, mechanosensors, hardening and stiffening of polymers through metal incorporation, a specific fibre alignment for wear resistant surfaces, fatigue and fracture resistance, and the structure and properties of the fibre composite which allow the cuticle to fulfil all the complex requirements imposed on it by the environment in which the organism lives, are examples. The use of nanofibres, resembling chitin, in composite design for improved mechanical properties is another.

However, in order to derive the maximum benefit it is probably necessary to unwind our analysis so that we can generate the structures of interest by defining the chemistry and chemical environment of the components. Usefully large structures can be generated in this way (think of the size of some marine crustaceans and of the insects which flew in the forests of the Carboniferous era), so perhaps this is a fruitful direction for the interdisciplinary associations (such as this review!) which insect cuticle can inspire.

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