THE MECHANICAL PROPERTIES OF THE ABDOMINAL CUTICLE OF *RHODNIUS* LARVAE

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SUMMARY

1. The mechanical properties of loops of cuticle cut from the abdomens of 5th instar *Rhodnius* have been investigated. The cuticle shows pronounced viscoelastic behaviour.

2. Stress-relaxation tests show a continuously falling modulus over a wide range of times after the imposition of a strain.

3. Plasticized samples of cuticle show stress-relaxation curves which are shifted along the time axis towards earlier times by up to $\times 10^3$. The modulus at any particular time after the imposition of strain is about 10 times lower than that of the unplasticized cuticle.

4. It is concluded that the mechanical properties of this cuticle are determined, at least for maintained stresses, largely by the matrix material. Chitin microfibrils may act as a reinforcing filler for short-term, rapid stresses. The cuticular macromolecules are probably not extensively cross-linked by primary bonds, though secondary interactions between them are probably important in the viscoelastic properties of the cuticle.

5. Plasticization probably involves a change in either the number or the strength of secondary interactions between the cuticle macromolecules, or both.

INTRODUCTION

Rhodnius prolixus Stål. is a blood-sucking insect which takes infrequent and very large meals from its living hosts, resulting in considerable distension of its abdominal body wall. Bennet-Clark (1962) showed that this distension is facilitated by a temporary and reversible change in the mechanical properties of the abdominal cuticle which allows it to stretch more easily at the time of feeding. It has since been shown that this plasticization of the cuticle is under direct nervous control (Maddrell, 1966). Both Bennet-Clark and Maddrell used the same technique of inflating the abdomen of an experimental insect with compressed air at a constant pressure until it became shiny. The time taken to reach this end point was taken as a criterion of the extensibility of the cuticle. Although the forces acting in the abdominal body wall during inflation must be similar to those acting during feeding, the measures of 'plasticity' obtained using this method are not easily related to any conventional measures of a material's mechanical properties.

In the present work use has been made of loops of integument cut from the

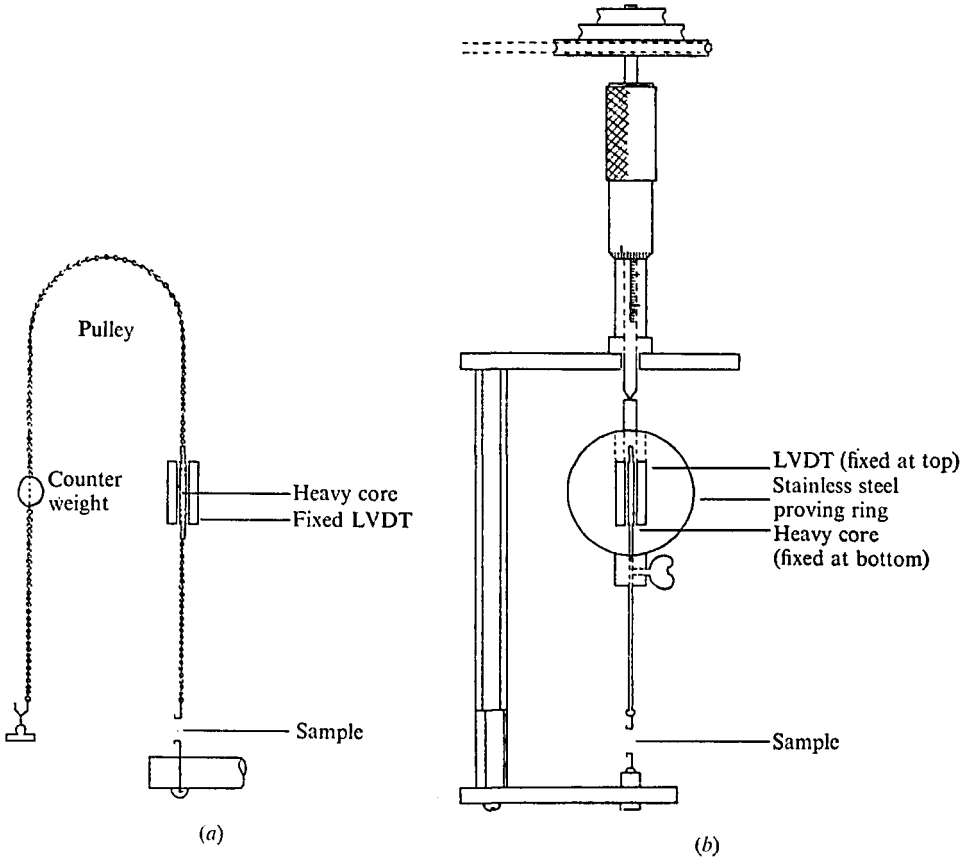* Present address: Department of Zoology, University of Bristol, Woodland Road, Bristol, BS8 1UG.

Fig. 1. (a) Apparatus used for creep tests. The loops are subjected to a constant load rather than a constant stress. (b) Apparatus used for stress-relaxation tests and for determining stress–strain relationships at a constant rate of strain. Deformation of the stainless-steel proving ring, which acts as a force transducer, is measured by the movement of the transformer core (fixed at the bottom of the ring) through the LVDT (which is fixed at the top). The whole transducer assembly may be raised or lowered by the micrometer. (LVDT = linear variable differential transformer.)

abdominal body wall. This technique was used in some experiments by Bennet-Clark (1961), who ascribed its invention to T. Weis-Fogh. It allows the direct measurement of uniaxial stresses and strains in test samples of abdominal cuticle. Both normal and plasticized cuticle samples were tested in an attempt to define more fully the changes in mechanical properties which occur on plasticization.

METHODS

The insects used were 5th instar *Rhodnius*, 1–2 weeks after their last ecdysis. In any one experiment the insects were all taken from the same feeding batch.

Plasticization was in all cases induced by the injection of 10 μl of 10^{-4} M 5-HT solution in Ringer. The injection was made via a metathoracic leg from an 'Agla' micrometer syringe, an SWG 28 hypodermic needle making a snug fit with the cut leg. The composition of the Ringer solution is that given by Maddrell (1969). At this
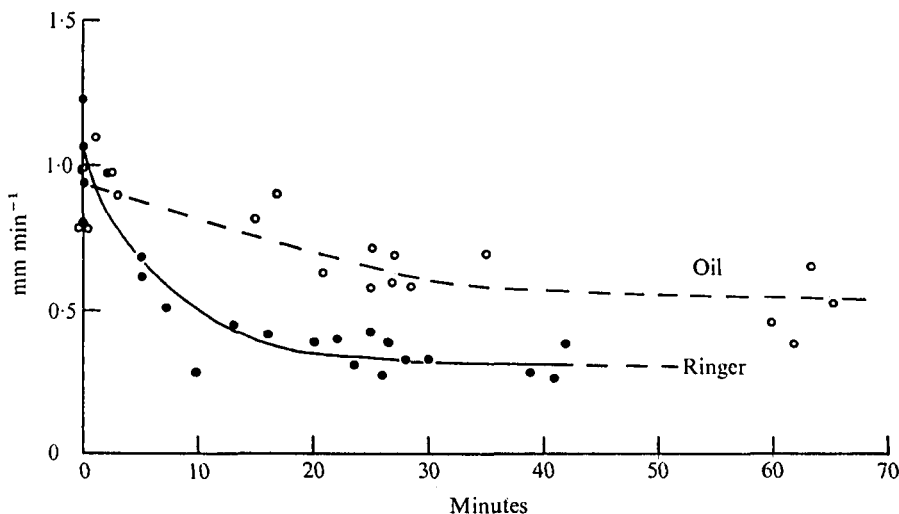
Fig. 2. The decay of the plasticized state in sample loops of *Rhodnius* abdominal cuticle in Ringer solution and in mineral oil. Plasticization was induced by the injection of 10^{-4} M 5-HT solution 30 min before the cuticle samples were taken from the insect. The rate of creep (mm min^{-1}) 30 sec after the imposition of a 5 g load was taken as a measure of the extensibility of the cuticle.

dosage 5-HT was found consistently to induce a maximal plasticization of the abdominal cuticle, greatly facilitating the performance of mechanical tests which would be difficult if partly fed insects were used. Evidence that the plasticization induced by 5-HT injection is produced in the same way as that induced naturally by feeding is to be found elsewhere (Reynolds, 1974 a).

Sample loops of cuticle were cut from the 4th segment of the abdominal body wall, transversely across the abdomen using the intersegmental membranes as guidelines for cutting. The length and width of the samples were checked using an ocular micrometer. Cuticle thickness was measured using frozen sections of unfixed material, where possible cut from the test sample itself. Where the test resulted in severe deformation of the test loop, another sample from the same insect was measured to give the initial thickness of the cuticle.

The behaviour of cuticle loops subjected to a constant applied load was investigated using the apparatus illustrated in Fig. 1 (a). The d.c. output from the linear variable differential transformer (LVDT: obtained from Electromechanisms Ltd, Slough) was proportional to the linear displacement of the heavy core, which ran freely in the longitudinal axis of the transformer. Continuous monitoring of this output on a pen recorder (Servoscribe) thus provided a measure of the continuing deformation of the cuticle sample under a maintained uniaxial load. In all the creep experiments the load was 5 g weight.

The behaviour of the cuticle loops when subjected to an imposed strain was investigated using the apparatus which is shown diagrammatically in Fig. 1 (b). A known strain could be applied to the sample cuticle loop using a micrometer, either as a step increase in strain by advancing the micrometer rapidly by hand, or at a constant rate of strain using the belt drive from a small motor mounted on the apparatus. The output of the LVDT was again monitored continuously on a pen

recorder. Here, the output was proportional to the strain on the circular stainless-steel band, which acts as an essentially isometric force transducer registering the stress in the sample.*

The sample loops of cuticle were for the most part tested under light mineral oil, in order to prevent their drying out and to avoid the changes in the aqueous phase of the cuticle which might follow immersion in a bath of Ringer solution or other aqueous medium. The extensibility of plasticized cuticle loops, measured as the rate of creep 30 sec after the imposition of a 5 g load, was found to change rapidly when the loops were immersed in Ringer, decaying with a half-time of about 5 min to a level only a little higher than that shown by unplasticized samples. Plasticized cuticle loops immersed in mineral oil also showed a loss of extensibility with time, but changed their properties more slowly. The time course of these changes is shown in Fig. 2.

The temperature of the oil bath was noted for all experiments. Cuticle mechanical properties are dependent on temperature, so comparisons between the behaviour of samples were made from experiments performed at the same temperature. All the figures quoted in this paper are from tests performed at 25 °C.

It should be noted that *stress* is here defined as force per unit initial area, and is given in Newtons per square metre $(N\,m^{-2})$. *Strain* is defined as extension per unit initial length and is thus dimensionless. The *elastic modulus* (E) is defined as stress divided by strain, and has the units of stress $(N\,m^{-2})$. Rates of creep are given in mm min^{-1}.

RESULTS

The relation between stress and strain for both normal and plasticized samples of cuticle was investigated by subjecting cuticle loops to a constant rate of increasing strain. The rate of extension imposed on the samples was the same in all cases, being 0·18 mm min^{-1}. This corresponds to a strain rate of about 0·03 min^{-1}; the actual rate for any particular sample depended upon its exact dimensions which varied slightly from one sample to another. As shown in Fig. 3(a) and 3(b), the unplasticized cuticle loops showed a much higher stress for comparable extension than the plasticized cuticle samples. In effect, the plasticized cuticle showed a reduced elastic modulus. The modulus shown by the unplasticized sample in Fig. 3(a), taken from the straight section of the stress–strain curve, is $6·2 \times 10^7\ N\,m^{-2}$. In Fig. 3(b), the plasticized cuticle shows a modulus of $2·5 \times 10^6\ N\,m^{-2}$.

In fact the modulus value shown by the cuticle under these testing conditions was found to be strongly dependent on the rate of strain imposed, so that the actual values quoted above are not in themselves of great interest. This dependence of the modulus on strain rate is typical of materials showing viscoelastic behaviour.

The plasticized samples of cuticle were found to tolerate much higher strains before failing than unplasticized samples. The low tolerance of the unplasticized cuticle to high strains in these experiments is not shown by the unplasticized cuticle *in vivo*. Maddrell (1966) cut the abdominal nerve supply of 5th instar *Rhodnius* and allowed them to feed. Thus treated, they were unable to plasticize their abdominal cuticle, but nevertheless fed at the normal rate and took without mishap blood meals even larger than those of controls. The failure of the cuticle in the experiments reported
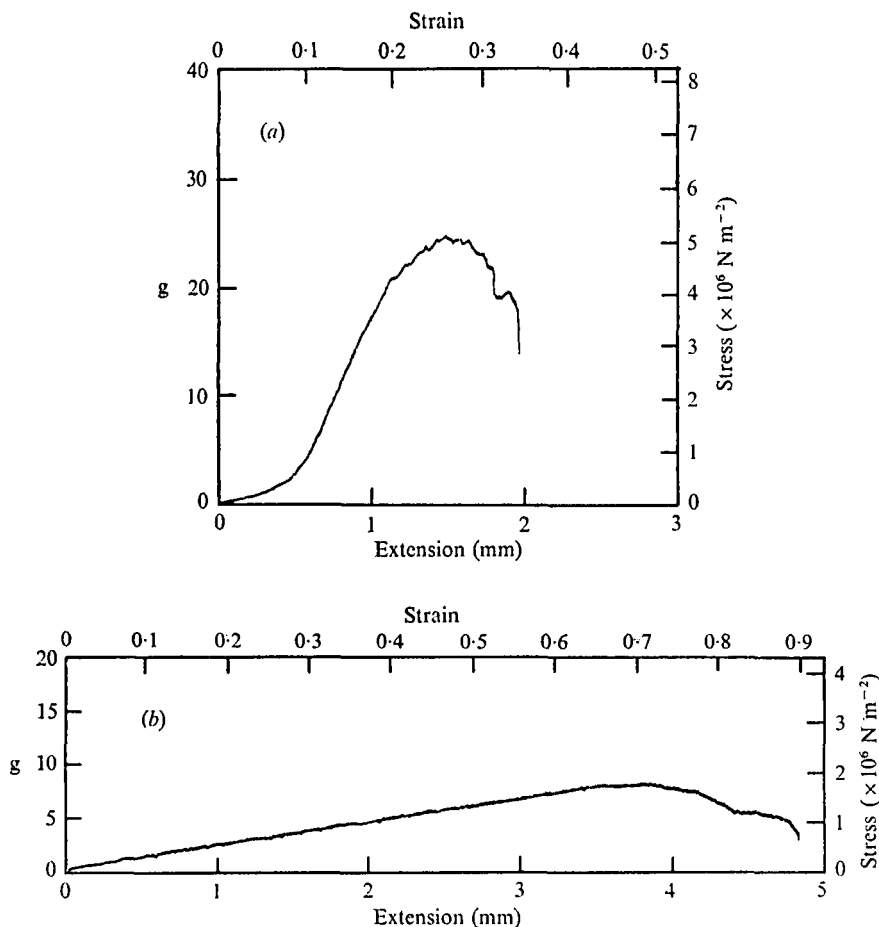
Fig. 3. The relation between stress and strain in samples of *Rhodnius* abdominal cuticle. (*a*) Normal cuticle. (*b*) Plasticized cuticle (from insects previously injected with 10^{-4} M 5-HT solution). In both cases the rate of extension was 0·18 mm min^{-1}, which corresponds to a strain rate of about 0·03 min^{-1}. Temperature = 25 °C.

here may well be due to the effect of straining the cuticle in one dimension only, perhaps resulting in reorientation of the chitin microfibrils within the matrix material. This would occur to a much lesser extent in normal feeding, when the cuticle is, of course, stretched in two dimensions. The stress would still not be uniformly distributed, however, being greater in the circumferential than in the axial dimension (Bennet-Clark, 1963). Some realignment of chitin 'micelles' was reported to occur in the *Rhodnius* abdominal cuticle on feeding by Nuñez (1963) on the basis of observations employing polarized light microscopy.

The low modulus associated with small strains (0–0·1) in the unplasticized cuticle samples is probably due to the unfolding of the ventral folds in the sternite cuticle, described by Wigglesworth (1933).

The lower modulus of the plasticized cuticle shows that a given strain may be achieved at a lower stress in the plasticized condition. However, relatively little of the extension due to the imposition of a load on the cuticle loop is achieved immediately,
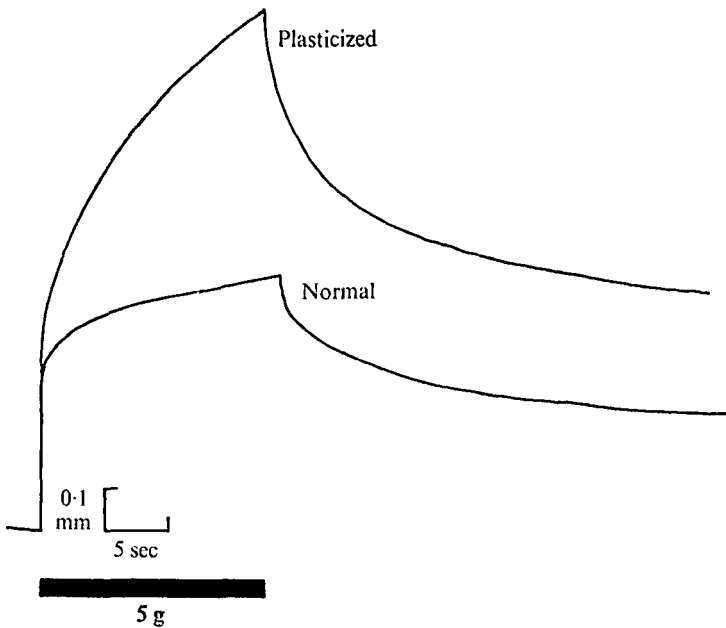
Fig. 4. Creep test on loops of cuticle from *Rhodnius* abdomens. Constant load of 5 g weight.
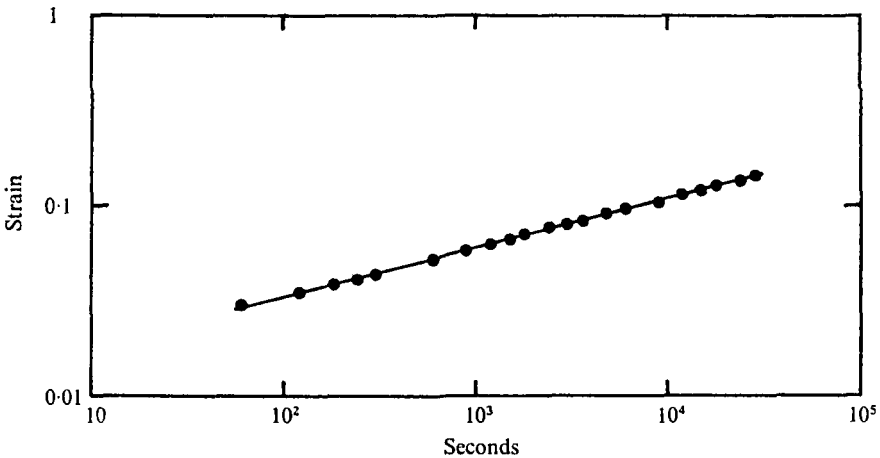Temperature = 25 °C.

Fig. 5. Creep test on a loop of unplasticized cuticle from *Rhodnius*. Log–log plot of extension.
Constant load of 5 g weight. Temperature = 25 °C. The test was discontinued after 8 h when
the sample showed no sign of failure.

as Fig. 4 shows. The results of such tests on loops of cuticle subjected to maintained
loads show that an initial rapid deformation is followed by a phase of slower extension,
or 'creep'. Most of the extension due to the load takes the form of creep. As can be
seen, the rate of creep for the plasticized cuticle samples is much greater than that for
the normal, unplasticized cuticle samples.

In these tests the cuticle loops continued to show creep so long as the load was
maintained. Using a load of 5 g, the plasticized samples generally ruptured after a
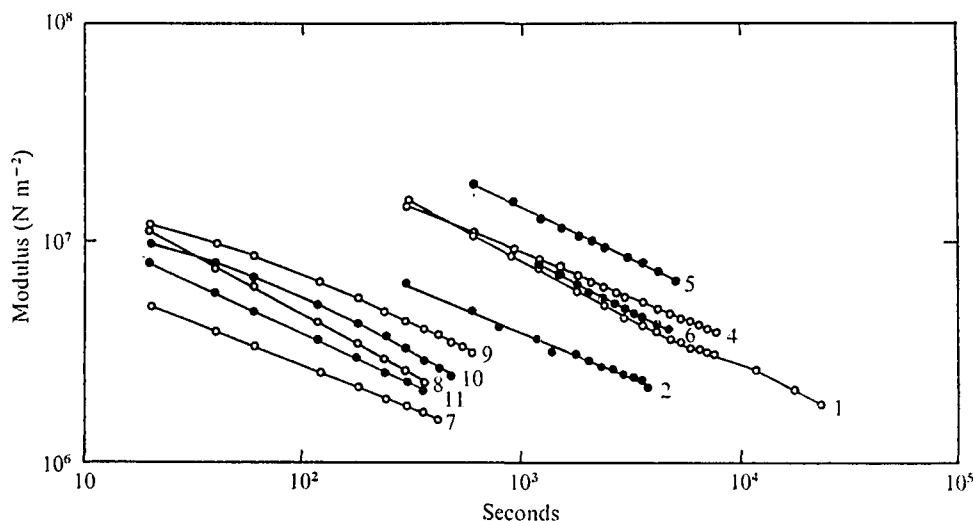
Fig. 6. Stress-relaxation behaviour of a number of samples of both plasticized and unplasticized cuticle from *Rhodnius*. All samples were subjected to an initial imposed strain of 0·15. Plasticization was induced by injection of 10^{-4} M 5-HT solution. Temperature = 25 °C. 1–6, Normal; 7–11, plasticized.

few minutes of creep at a high rate, but the unplasticized cuticle continued to creep at an ever-decreasing rate over periods as long as 8 h, showing no sign of either coming to an equilibrium modulus or of failing (Fig. 5).

In stress-relaxation tests, where the cuticle loops were subjected to a maintained step strain, the stress resulting from the imposed strain declined with time, as shown in Fig. 6, in which the relevant data are plotted on a log–log scale. It is evident that the modulus for the plasticized cuticle is less than that of the unplasticized cuticle over a considerable range of times after the imposition of the strain. The length of time over which such experiments may be carried on is limited by the decay of the plasticized state *in vitro*. As explained in the Methods section, the extensibility of cuticle loops decays noticeably in a relatively short time. However, under mineral oil the properties of the plasticized cuticle loops would not have changed markedly in the 5 min allowed here for stress relaxation (see Fig. 2).

The stress-relaxation curves of a number of cuticle samples, both normal and plasticized, are plotted in Fig. 6. The curves are all fairly good straight lines on the log–log plot, with more or less similar slopes. The curves of the plasticized samples appear to be like those of the normal cuticle but are shifted to a greater or lesser extent towards earlier times on the abscissa. No sign was detected in any experiment of either a levelling off of the curve toward an equilibrium modulus or a rapid falling off toward zero.

DISCUSSION

Gosline (1971) has provided a brief summary of some current interpretations of the mechanical behaviour of synthetic polymers (which are, in general, homogeneous materials with a known, simple structure), and has attempted with some success to

apply these to the observed behaviour of a biological material, the mesogloea of the sea anemone (which is neither homogeneous nor very simple in structure).

Despite this encouraging start to a molecular biomechanics of complex tissues, it must be admitted that the insect cuticle is much more complex than is the mesogloea of the sea anemone, particularly in its highly organized ultrastructure (Neville, 1970). Caution must therefore be exercised in extending molecular interpretations of the behaviour of less highly organized materials to the insect cuticle, which shows a more complex organization than any man-made material.

The behaviour of the cuticle samples in the tests reported above is typically *visco-elastic* (Ferry, 1970). Such behaviour is shown by all polymeric materials to a greater or lesser extent, but is characteristic of materials which are cross-linked lightly or not at all. Visco-elastic properties are better investigated using creep and stress relaxation tests than by studying simple relations between stress and strain. The creep tests described here were performed under constant load conditions, rather than at a constant stress, which would have been very difficult to achieve using suitably small stresses. Consequently, these experiments, although a useful illustration of the consequences of the cuticle's visco-elastic properties, are unsuitable for detailed analysis. The stress-relaxation tests provide the material for the following discussion.

The behaviour shown in Fig. 6 is of a type generally referred to as transitional. Stress-relaxation curves of typical polymeric materials show a transition between the glass-like behaviour shown at very short times after the imposition of a strain and the behaviour typical of longer times, when an equilibrium modulus may be attained in the case of polymers which are cross-linked, or when the modulus may fall off to zero in the case of those which are not.

This interpretation of the transitional behaviour of the cuticle is almost certainly too simple. It is extremely likely that the chitin microfibrils present in the cuticle act as a reinforcing filler at short times after the imposition of the strain, so that the high modulus shown at short times cannot be regarded as simple glass-like behaviour. Behaviour at very short times was not investigated in the present experiments, but by the times of the first measurements, for both normal and plasticized cuticles, the modulus was already much less than that normally associated with glass-like behaviour. The role of chitin reinforcement in the cuticle is discussed further below.

It was not found possible to extend the times over which stress-relaxation behaviour was followed sufficiently to include that behaviour, typical of very long times, which would allow the differentiation of materials which are cross-linked and those which are not. This is unfortunate, as this is of considerable interest. It is clear, however, that the extent of any permanent cross-linking in the cuticle must be slight. The moduli of both normal and plasticized cuticle samples fall to about 10^6 N m^{-2} with time (see Fig. 6), so that any equilibrium modulus would need to be even less than this low value.

Such a high degree of extensibility is, as pointed out by Weis-Fogh (1970), quite incompatible with a model of the cuticle as a fibreglass-like material. In such a material mechanical properties would be determined largely by inextensible chitin microfibrils embedded in a protein matrix, the function of the matrix being largely to stop the spread of cracks (Cook & Gordon, 1964). The modulus of chitin in the pure crystalline form of the microfibrils is not known: it is certain to be very high. Herzog (1926)

sted individual *balkenlage* from the cuticle of the Goliath Beetle in which chitin microfibrils are now known to be unidirectionally oriented. E was $4 \cdot 5 \times 10^{10}\ N\ m^{-2}$. The true modulus of the individual microfibrils is probably even higher.

From this it is quite clear that the chitin microfibrils cannot be *directly* linked together to form a network within the cuticle. This does not preclude *indirect* linkage through the protein(s) of the matrix, however: indeed it seems likely that chitin is usually covalently linked to protein in arthropod cuticles to some extent (Hackman, 1960), so that it would be expected that chitin would form a part of any network which existed in the cuticle. As pointed out above, any such network in the *Rhodnius* abdominal cuticle would be very diffuse.

However, even if the chitin microfibrils do not form a network, it seems very likely that they can act as a reinforcing filler for the cuticle in which they are embedded early in the stress-relaxation process. In this way the chitin can provide strength for rapid stresses, while the properties shown by the cuticle in relation to longer, maintained stresses are determined largely by the more extensible matrix protein(s). The situation is rather similar to that described for sea anemone mesogloea by Gosline (1971), though the lower concentration of macromolecules in the matrix of mesogloea causes the moduli shown to be much lower than those of the *Rhodnius* abdominal cuticle. Because the collagen fibres in mesogloea are disposed circumferentially in the tissue, Gosline was able to show that these inextensible elements in the material provided short-term reinforcement, prolonging an early plateau in the stress-relaxation curve. This effect was more marked in the direction of preferred orientation of the collagen fibres. Collagen also contributed to the equilibrium modulus to a small extent, showing that its fibres must be indirectly linked into the network which determines the equilibrium properties.

In the abdominal cuticle of *Rhodnius* larvae, the chitin microfibrils are oriented in a uniform helicoidal array within the matrix (Reynolds, unpublished observations), and this provides for isotropic mechanical properties within the plane of the surface, so that it is not possible to assess the contribution of chitin to the cuticle's mechanical properties in this way.

The conclusion that permanent cross-links must be rare within the *Rhodnius* abdominal cuticle is in accord with Wigglesworth's (1933) observation that the abdominal procuticle does not become tanned after ecdysis (as it does in the rest of the body), and also with Bennet-Clark's (1961) finding that more than 85 % of the cuticle proteins from the abdomina of 5th instar *Rhodnius* could be extracted using 7 M urea solution, and therefore could not be covalently bound to other cuticle components. It seems likely that no extensive cross-linking of any sort goes on in this cuticle at the time of tanning, particularly since the abdominal cuticle is actually more extensible after the tanning process is complete than it was before it began (Reynolds, 1974 *b*). Wigglesworth (1970) suggested that primary bonds between structural lipids and cuticle proteins may help to stabilize the untanned cuticle of the larval *Rhodnius* abdomen to some extent. It seems unnecessary to propose such strengthening in the light of the mechanical properties shown by the cuticle loops in the experiments reported here.

The stress-relaxation behaviour shown by both normal and plasticized cuticle is of the transition type throughout the range of times which are likely to be of relevance

in the feeding insect's physiology. Such transitional behaviour is conventionally associated with the making and breaking of temporary interactions between the molecules of the stressed material. The interactions may take the form of entanglements between chains, or of local, and perhaps specific, attractive forces between molecules (Ferry, 1970). For a material composed of long, inhomogeneous polar molecules, as is the cuticle matrix, it may be supposed that the latter may be particularly important. These 'secondary interactions' (comprising hydrogen bonds, some weak covalent double bonds, van der Waals' forces, both attractive and repulsive electrostatic interactions between charges, and simple entanglements between chains) all involve much less energy than the stronger 'primary interactions' which are supposed to determine equilibrium mechanical properties.

The making and breaking of these secondary bonds is strongly affected by temperature. The energy associated with these bonds represents a potential energy barrier to the movement of long-chain molecules one past another, and is analogous to the activation energy for a chemical reaction. The effect of increased temperature on the stress-relaxation curve is to shift it along the time axis, so that prominent features of the curve, like the transition region with which we are concerned here, appear at earlier times. This is the 'time-temperature superposition principle'. For an increase in temperature, the modulus at any particular point in time will be less.

Plasticization in the *Rhodnius* abdominal cuticle acts like an increase in temperature.* It can be seen from Fig. 6 that the stress-relaxation curves for plasticized cuticles are parallel to those for normal cuticle samples, and are apparently shifted along the time axis to earlier times by up to $\times 10^3$.

It may be useful to point out that in correct usage the term 'plasticizer' is applied to an additive or solvent which 'lowers the temperature of a second order transition, or lowers the elastic modulus' of a material (Wordingham & Reboul, 1968). This is exactly what happens during plasticization of the abdominal cuticle in *Rhodnius*. Nevertheless, it appears that the use of the term in this way is unfamiliar to some biologists and may have caused confusion. This is probably due to rather loose usage in industrial practice. In the production of commercial plastics, the raw polymer, in powder form, is suspended in a solvent plasticizer. The term 'hardening' is employed to describe the process whereby the polymer is solvated by the plasticizer to form the finished product. In this process, the plasticizer is 'hardened' by the polymer, not vice versa.

The interpretation of the plasticization process in *Rhodnius* which the present experiments suggest is the following. The long-term mechanical properties of the abdominal cuticle in its normal state are determined largely by the matrix protein(s) of the procuticle, which shows little evidence of any extensive permanent cross-linking although cross-linking by means of secondary (weak) bonds must be important in determining the pronounced visco-elastic properties shown by this material. The reinforcing effect of the chitin microfibrils is evident only at shorter times. Plasticization of the cuticle is associated with a shift of the transition region of the stress-relaxation curve to earlier times. This is probably due to a reduction in the size of the

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* Bennet-Clark (1961) comments on the steep temperature dependence of the extensibility of the *Rhodnius* abdominal cuticle. A temperature increase of 4·5 °C halved the time to inflate a *Rhodnius* abdomen with compressed air at 10 cmHg pressure.

Potential energy barrier to flow, which is associated with the temporary interactions between cuticle macromolecules as they slip past one another. Such a reduction in the size of the potential energy barrier might be effected by reducing the number of secondary interactions affecting each macromolecule, or by reducing the amount of energy associated with each such interaction. Alternatively the extent of repulsive interaction between molecules might be increased. Some ways in which any or all of these possibilities might be achieved are discussed in another paper (Reynolds, 1975).

The extent to which strain is recoverable has not been investigated in these experiments. Much of the strain associated with visco-elastic behaviour in other systems which have been investigated (see Ferry, 1970) is recoverable, though for materials which are not permanently cross-linked by means of primary bonds, some permanent deformation is inevitable. Bennet-Clark (1971) shows some data on the extent to which recovery takes place in the abdominal cuticle of 5th instar *Rhodnius* after feeding up to the time of ecdysis to the adult. The recovery is very slow, continuing over the whole of the 21-day period to ecdysis, during which time the abdomen decreases in circumference from about twice that of the unfed 5th to about 1·2 times as large. A substantial part of the bulk of the blood meal is lost by excretion by about 3 h after feeding (Maddrell, 1964), so that the recovery of the abdominal cuticle must begin very soon after feeding is over. Bennet-Clark's figures show that very little of the strain in the cuticle associated with feeding is permanent. The stresses produced in the cuticle during feeding, although not uniform within the plane of the surface, do act in both dimensions. It has been pointed out earlier in this paper that the uniaxial stresses imposed on the cuticle loops under test conditions may well result in considerable realignment of the chitin microfibrils of the cuticle. Therefore, the recovery behaviour of cuticle loops strained in this way may differ from that shown by the cuticle *in vivo*.

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