Biology and Physics of Locust Flight. V. Strength and Elasticity of Locust Cuticle

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Phil. Trans. R. Soc. Lond. B 1962 **245**, 137-169
doi: 10.1098/rstb.1962.0008

BIOLOGY AND PHYSICS OF LOCUST FLIGHT
V. STRENGTH AND ELASTICITY OF LOCUST CUTICLE

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(*Communicated by J. W. S. Pringle, F.R.S.—Received* 12 *February* 1959—*Revised* 22 *November* 1961)

[Plate 55]

CONTENTS

Elastic deformations of the cuticle play a major role in the energetics of flying locusts but the literature provides no relevant information about the elastic properties of any arthropod cuticle. The results are therefore discussed both in relation to locust flight and in relation to strength and elasticity of organic materials in general.

In *Schistocerca gregaria* Forskål there are two types of elastic cuticle, ordinary *solid cuticle* and *rubber-like cuticle*. The characteristic material in the latter type is a newly discovered protein rubber, *resilin*. Samples of both were studied under static and dynamic conditions.

The tensile properties of solid cuticle from various parts of the body (hind tibia, pleural wall, forewing) are similar to those of oak wood and of synthetic resins reinforced with cellulose; the static coefficient of elasticity ($d\sigma/d\epsilon$) is 800 to 1000 kg/mm^2 and the tensile strength 8 to 10 kg/mm^2, corresponding to an ultimate extension of 2 to 3 %. At moderate loads, the tensile and compressive moduli are of equal magnitude, but it is argued that the effect of tanning (hardening) is to increase the compressive strength and modulus rather than the tensile properties. Static loading results in lasting deformation. The dynamic modulus is of the same magnitude as the static modulus (forewing), at least up to 5 kg mm^{-2} s^{-1} and, provided the tension does not exceed 0·5 kg/mm^2, the loss factor is less than 0·1.

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The rubber-like sample (prealar arm) consists of parallel lamellae of chitin ($0{\cdot}2\,\mu$ thick) glued together by sheets of resilin (about $3\,\mu$ thick). It behaves like a solid when extended in the direction of the lamellae but otherwise like a rubber, the elastic modulus being $0{\cdot}2$ kg/mm^2. The swelling pressure of resilin does not play any direct role but swelling alters the geometry and, to a small extent, the elastic modulus. It is suggested that the animal controls the stiffness of its rubber-like structures by altering the swelling equilibrium chemically which, in a model experiment, is done by blocking the free amino groups.

Rubber-like cuticle does not encounter any permanent deformation which is attributed to the known lack of flow of pure resilin. Within the biological rate of deformation (up to 6 unit lengths per second), the dynamic stiffness remains within 4 % of the static value and the loss factor is only 0·03, i.e. less than for other natural or synthetic rubbers.

A three-component model of arthropod cuticle is suggested. It accounts for the enormous differences in mechanical properties between adjacent parts and also for the fact that strict structural and developmental continuity is observed between the parts. It has three components: (1) crystalline chitin, (2) a rubber-like protein which may act as a deformable matrix and which entraps, (3) water-soluble proteins which can undergo proper tanning.

1. Introduction

In locusts and in many other insects, the wing-bearing segments are elastic structures which tend to resist the wing movements during one part of the wing-stroke cycle and to feed back stored energy during the succeeding phase (Weis-Fogh 1961 *a*). The mechanics of this system is very intricate and will be dealt with in the succeeding part of this study (part VI, Weis-Fogh (in preparation)). The mere fact that such elastic forces exist and are important for flight immediately raises problems as to the mechanical properties of the materials from which the thorax is constructed. Three kinds of elastic materials are known to be of direct importance in locusts and other insects (Weis-Fogh 1958). These are: (1) the flight muscles which contain a passive elastic component of considerable strength and efficiency (Buchthal, Weis-Fogh & Rosenfalck 1957), (2) the ordinary *solid cuticle*, and (3) some little-known pads and ligaments of *rubber-like cuticle* (Weis-Fogh 1960). The present paper deals exclusively with the mechanical properties of the two types of cuticle as they are found in the mature desert locust under ordinary physiological conditions.

The term 'solid' refers to the fact that both the thin epicuticle, the tanned exocuticle and the less brittle endocuticle are dominated by materials in the solid state of matter. The external surface of rubber-like cuticle is also covered by thin epicuticle and the thick layers beneath it often contain lamellae of solid chitin, but the most important constituent is a specific protein, resilin (Bailey & Weis-Fogh 1961), which behaves like an almost ideal isotropic rubber provided it is swollen with water, as is always the case in the living animal (Weis-Fogh 1961 *b*, *c*).

Although most students of arthropod cuticle have emphasized the importance of its strength and elasticity (cf. Richards 1951, 1958), the present paper, with the possible exception of Herzog's (1926) study on 'chitin', seems to be the first attempt to obtain exact information about the coefficient of elasticity, tensile strength, permanent deformation, dynamic stiffness and mechanical damping. The results are therefore discussed not only in relation to flight but on a more general basis, particularly because the knowledge of arthropod cuticle is haunted by a growing amount of qualitative and controversial data (cf. Wigglesworth 1957). They are essential for the design and interpretation of the experiments to be reported in part VI.

A straightforward investigation of the material constants was rendered impossible for two reasons. First, the cuticle generally differs in composition from place to place and cannot be considered as homogeneous. Secondly, it was not possible to select representative samples which had a simple geometry. The first difficulty proved to be less important than anticipated, while the effect of the second was reduced by selecting a reasonably simple sample (the hind tibia) and comparing the results thus obtained with the less accurate measurements on thoracic cuticle and wings. For this reason the experiments on the hind tibia are given first and in greatest detail although they have no direct bearing upon the problem of flight.

2. Material and treatment

The methods are described in connexion with the results.

Insects

Adult desert locusts (*Schistocerca gregaria* Forskål, *phasis gregaria*, cage-bred at the Anti-Locust Research Centre, London) are very uniform in external geometry and, after maturity has been reached 2 to 3 weeks after the final moult, this also applies to cuticle thickness and dry weight; the latter increases about three times during the first weeks of adult life (Weis-Fogh 1952, figure 5). Samples were taken from mature insects if not otherwise stated.

Samples

The best-suited sample of *solid cuticle* is the tibia of the jumping leg (figure V, 1) which was used both in extension and compression. For comparison, ribbon-like pieces were cut from the pleural wall of the pterothorax and subjected to stretch. Finally, the entire forewing was suspended for cantilever experiments. As an example of *rubber-like cuticle* the prealar arm of the mesonotum was used partly because its structure is known (Weis-Fogh 1960) and partly because its elasticity is of importance for flight.

Changes in cuticle with age

When the solid cuticle has become tanned and has attained a slightly amber colour after the last moult, all external dimensions are fixed. In cross-section the cuticle of the tibia consists of an outer more dense exocuticle, 15 to $30\,\mu$ thick, and an inner colourless, laminate and solid endocuticle, 10 to $20\,\mu$ thick. The growth of the cuticle during the succeeding weeks concerns only the endocuticle, the final thickness of which ranges between 70 and $110\,\mu$ in the mature tibia (figure V, 2). In the young adult, the exocuticle therefore dominates, whereas the endocuticle is four times thicker in the mature locust. In spite of this, there was no significant difference in tensile strength per unit area or in the elastic coefficient between young and mature tibiae (see p. 145) so that, as a first approximation, the tibia can be treated as being homogeneous with regard to stretch.

The rubber-like structures also alter during the period of growth but only mature adults were used.

State of hydration

Solid cuticle becomes more brittle and perhaps also stronger when dried, but care was taken to avoid any significant alterations from the normal. The hind tibia was usually tested as soon as the cement which covered the cut ends had hardened, i.e. about 1 h after the leg had been removed from the locust. In the laboratory a fresh tibia with freely exposed ends lost water at a rate of 4 % by weight in 4 h so that the mounted tibia would probably lose less. Moreover, figure V, 6 shows that 48 h of storage without protection against evaporation had no appreciable effect upon the stress–strain relationship: the solid line refers to the left tibia tested 1 h after the removal (the usual condition for experiment), while the broken line is from the right tibia of the same locust after the above period of storage. In another control experiment, the one leg was tested in the usual way, while the other leg was mounted still connected to the living animal during the measurements. There was no difference between the results. In a few cases, samples were stored for 36 h in closed tubes before being mounted.

The rubber-like cuticle behaves like a solid when dried, but swells and becomes rubbery when water is admitted. Since the degree of swelling depends on the pH and on the mechanical constraint of the solid lamellae, the measurements were made in locust saline at pH 6·7 or in a buffer of similar acidity, unless otherwise stated.

Constants of elasticity

The *coefficient of elasticity* $E = \mathrm{d}\sigma/\mathrm{d}\epsilon$, where σ is the force per unit cross-sectional area (in $\mathrm{kg/mm^2}$) and ϵ is the relative elongation. In cuticle, Hooke's law does not apply, but in some experiments the *modulus of elasticity* (Young's modulus) was estimated, for the given situation defined as σ/ϵ. It is some mean value of the coefficient which varies with σ. The elastic modulus G of the rubbery protein is defined in another way (see p. 156).

3. Static properties of solid cuticle

(*a*) *Architecture of hind tibia*

The proximal and distal ends of the metatibia were cut, leaving a nearly straight and empty tube. The fresh sample was filled with and embedded in dentist's cement (Smith's Copper Cement) or soaked in monomer styrene and polymerized at 60 °C. The hardened block was ground on a carborundum stone in successive steps and the cross-sections photographed for determination of the area of the cross-section, its principal axes, and the moments of inertia of this area about the two principal axes, X and Y.

Figure V, 1 shows the hind tibia from the side together with the relative distance ξ of the cross-section from the proximal end and figure V, 2 shows the increase in wall thickness with age already referred to. The area of the cross-section varies with ξ (figure V, 3) and in this and other figures, the dimensions have been recalculated to those of a locust of standard size (Weis-Fogh 1952). The form of the cross-section also changes from the one end to the other, which means that the variation of the moment of inertia must be known in most experiments, as is illustrated in figure V, 4. Since there is some difference between male and female legs as well as some individual variation, the above quantities were therefore estimated for each sample used. The irregularities caused by the spines protruding from the posterior surface were excluded from the calculations because their effect upon strength and elasticity is negligible.

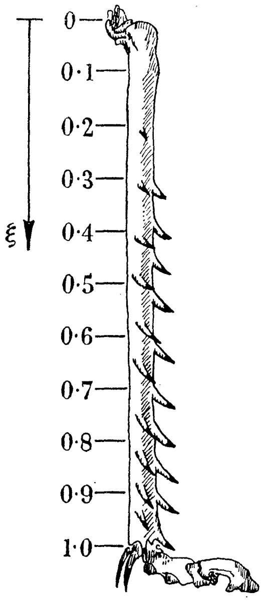


Figure V, 1. Side view of the hind tibia of an adult *Schistocerca gregaria*, from the proximal ($\xi = 0{\cdot}0$) to the distal end ($\xi = 1{\cdot}0$).

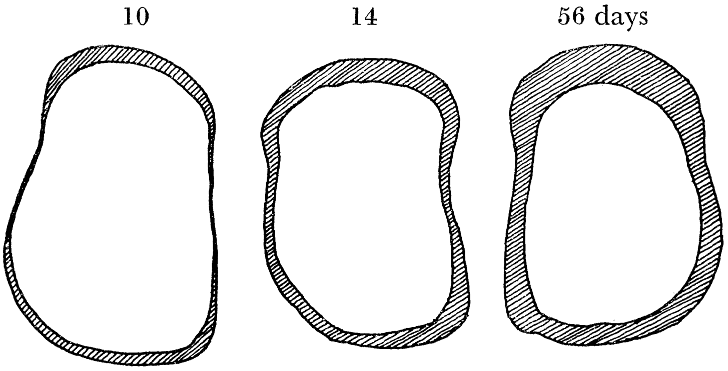


Figure V, 2. Cross-sections of three hind tibiae at the level of $\xi = 0{\cdot}3$ in adult locusts 10, 14 and 56 days after the final moult. The increase in wall thickness is due to endocuticle alone; two of the sections (14 and 56 days) are from the left and right leg of the same individual.

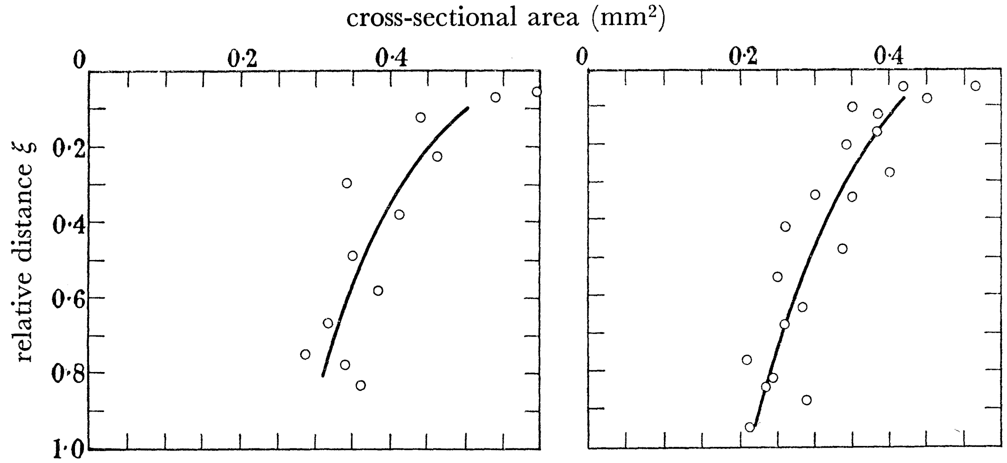


Figure V, 3. The variation of the cross-sectional area of the hind tibia with the relative distance ξ from the proximal end in eight males (left) and six females (right). All areas are recalculated to a locust of standard size.

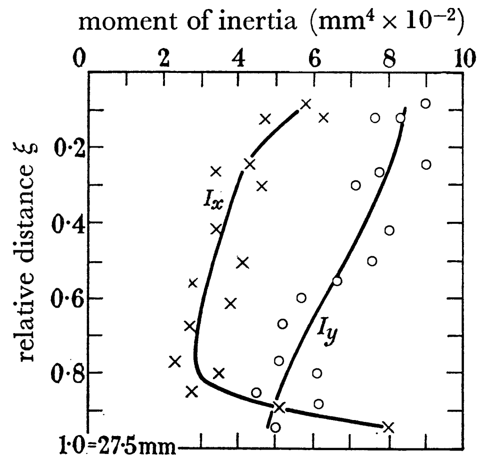


Figure V, 4. Example of the variation of the two principal moments of inertia of the cross-sectional areas (I_x and I_y) with the relative distance ξ from the proximal end in the two tibiae from the same full-grown female *Schistocerca.*

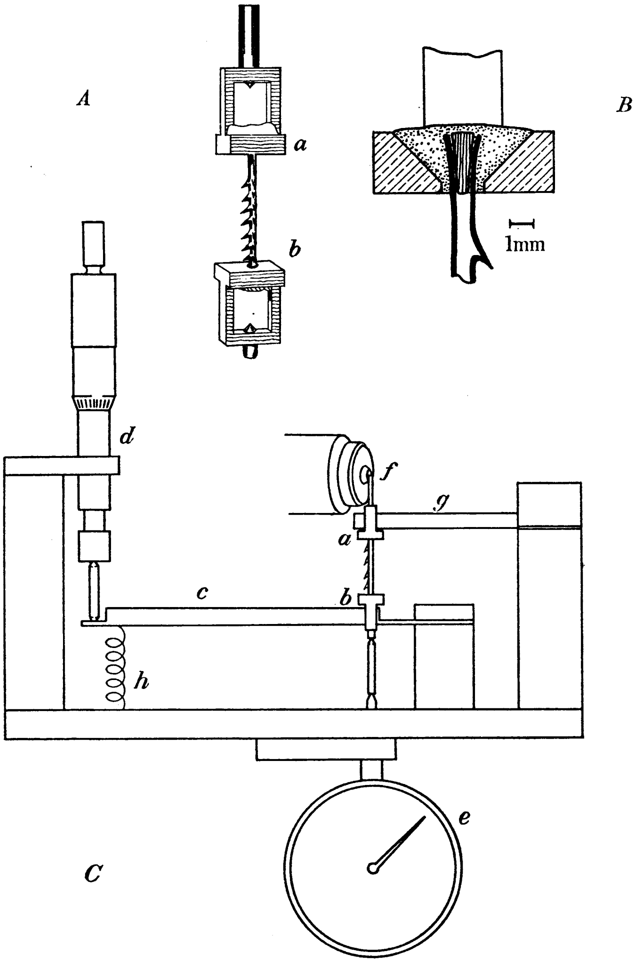


Figure V, 5. Mounting of hind tibia between steel stirrups (*A*), clamping of one end of the tube (*B*), and apparatus used for stretching (*C*). (*a*) Upper, (*b*) lower stirrup; (*c*) lower soft cantilever; (*d*) micrometer screw; (*e*) micrometer gauge; (*f*) front lens of microscope; (*g*) upper stiff cantilever; (*h*) spiral spring to prevent slacks.

(*b*) *Axial stretching of hind tibia*

Method

The irregular ends of a fresh hind tibia were removed and each end of the resulting tube was clamped in a steel 'stirrup' provided with a conical hole (figure V, 5*A*, *B*); the hole was filled with a paste of dentist's cement (dotted) and a short conical plug firmly pressed down into the bore of the tube, providing rigid clamping after about 30 min when the paste had become hard. The stirrups and the sample were kept centred and at a fixed distance (gauge 19·1 mm in females, 16·4 mm in males) during setting. The resulting piece was then attached vertically between the two horizontal cantilevers seen in figure V, 5*C*. The lower cantilever (*c*) is suspended by means of a blade of hardened steel and can be pressed downwards by the micrometer (*d*). The resulting depression of the lower stirrup (*b*) is read on the gauge (*e*, accuracy to within 10^{-3} mm). The tensional force thus produced is read as the deflexion (microscope with epicondenser, *f*) of the upper stiff cantilever (*g*). The accuracy was within 1·5 % at 2 kg force and 3 % at the lower limit of 0·2 kg.

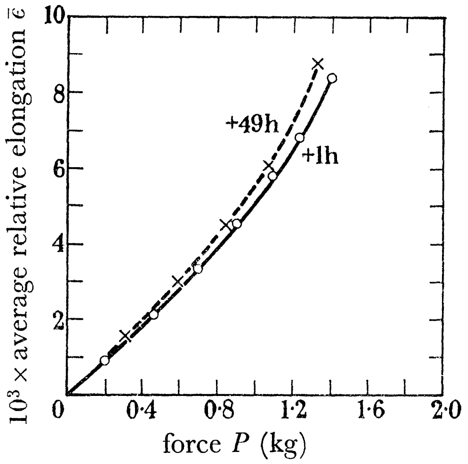


FIGURE V, 6. Measured relationship between the *average* relative elongation $\bar{\epsilon}$ and the applied force P in the two hind tibiae from the same individual. The one tibia was tested 1 h after mounting (solid line), the other after 2 days of storage without protection against evaporation (dashed line).

The readings were made not earlier than 1 to 2 s after the applied deformation and are referred to as static. The mounted sample did not alter its elastic properties in the course of an experiment and, as already mentioned, it could be left for 2 days in the laboratory without much alteration (figure V, 6).

Calculation

Figure V, 6 is a typical example of the non-linear relationship between the tensile force P and the average relative extension $\bar{\epsilon}$ of the *sample*. From such curves the problem was to deduce the relationship between the tension σ and the relative extension ϵ of the *material*. This is complicated by the fact that the cross-sectional area varies with ξ so that for every load different values of σ are present in the sample.

The variation of the cross-sectional area A with the distance x from the upper clamp is simple since $1/A(x)$ is almost linear. The procedure was to describe the load–extension curve of the sample as an algebraic function (using 1st, 2nd and 4th powers of P) and, by introducing $1/A(x)$, to calculate the corresponding algebraic function for the material. From the latter, the coefficient of elasticity $E = \mathrm{d}\sigma/\mathrm{d}\epsilon$ can be calculated for any value of σ.

The deviation of $1/A(x)$ from linearity introduced an error in the calculated tension–elongation curves of about 3 %. The remainder errors arose from the readings of force and elongation.

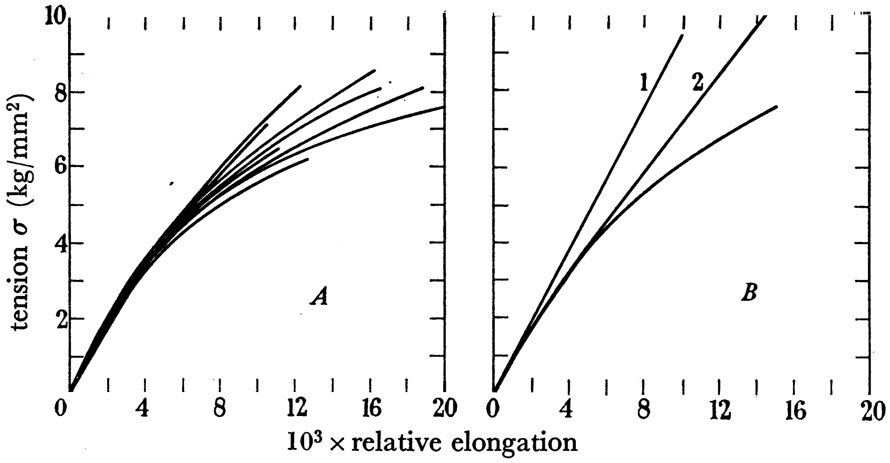


FIGURE V, 7. Calculated relationship between relative elongation ϵ and resulting tension σ (kg/mm^2) during axial extension of the hind tibia of mature *Schistocerca gregaria*. *A*, eight experimental curves. *B*, the average curve with the coefficient of elasticity indicated for $\sigma = 0$ (E_0) and for $\sigma = 3$ kg/mm^2 (E_3). Curve 1, $E_0 = 960$ kg/mm^2. Curve 2, $E_3 = 660$ kg/mm^2.

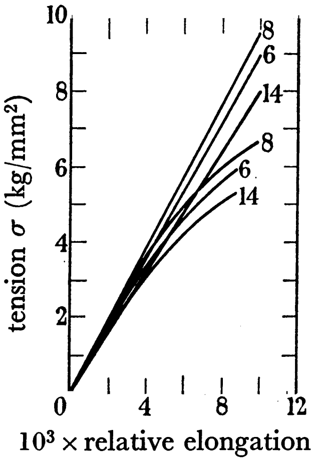


FIGURE V, 8. Relative elongation ϵ and tension σ in three hind tibiae of growing adults of *Schistocerca gregaria*, 6, 8 and 14 days after the final moult. The proportion between exocuticle and endocuticle has little influence upon the tensile properties.

Results

Figure V, 7*A* shows how the elongation ϵ varied with the tension σ in eight mature locusts and figure V, 7*B* is the average curve. As in most biological materials, the curves are non-linear and the coefficient of elasticity decreases with increasing tension. At zero load $E_0 = 960 \pm 80$ kg/mm^2 and at 3 kg/mm^2 it had decreased to $E_3 = 660$ kg/mm^2. In six of the experiments the ultimate tension (just before fracture) was $9{\cdot}6 \pm 0{\cdot}7$ kg/mm^2. The corresponding elastic extensibility is about $2\frac{1}{2}$ %.

It is of interest to know if the thickening of the cuticle seen in figure V, 2 is accompanied by any fundamental change in mechanical properties. Three tibiae from young, growing adults were therefore tested 6, 8, and 14 days, respectively, after the final moult (figure V, 8). The cross-sectional areas at $\xi = 0{\cdot}5$ were 0·120, 0·135 and 0·226 mm² (standard locust). Neither the course of the curves nor the actual values differ significantly from the results obtained with full-grown locusts. In the three cases E_0 was 810, 900 and 960 kg/mm² and, in two experiments, the ultimate tension was 11·4 and 9·9 kg/mm². From a mechanical point of view, the thickening of the cuticle with increasing age is equivalent to deposition of a material of nearly the same mechanical properties as those of the cuticle already laid down, i.e. there is only a slight difference between exocuticle and endocuticle with respect to stretch.

(*c*) *Axial compression of hind tibia*

Most parts of the skeleton are subjected to bending and therefore to compression as well as to tension. It was not possible to find a sample suitable for ordinary compression experiments; instead of this, an indirect estimate was made by applying Euler's formula to the relationship between the buckling of a slender column or strut and the axial stress applied. The tension at which buckling occurs depends upon the length of the strut, the moment of inertia of the cross-sectional area, and on the coefficient of elasticity. Euler's formula is only applicable provided the critical tension for buckling is small compared with the ultimate tension for compression; in the hind tibia the critical tension was about 0·7 kg/mm² or ten times less than the ultimate tension for stretch.

Method

A slender strut about 20 mm long was made by removing the two ends of the hind tibia. The deviation from a straight line did not exceed 0·3 mm. At each end, the tube was provided with a drop of dentist's cement which, under the influence of surface tension, hardened into a small centred ball (figure V, 9*A*). This rod (*a*) was placed vertically between the hemispherical sockets of the apparatus in figure V, 9*B*. Care was taken to centre the force by grinding the ends of the sample until no horizontal deflexion was observed at small loads. The column was quickly loaded and unloaded to prevent plastic deformations (lead shot in *f*) and then, by a stepwise increase in axial load, the buckling load was determined within 2%. Small unavoidable deviations from true axial loading rendered the estimates of E less accurate than those for stretch. The position of the fracture was noted and the cross-sectional areas determined as before.

Calculation

The variation of the cross-section of the *metatibia* makes it impossible to calculate the coefficient of elasticity directly according to Euler's formula. Since an analytical expression would be rather intricate, a numerical 'cut and try' method was adopted. It is illustrated by the following example.

The length l of the *metatibia* was 22·8 mm and buckling (about the axis for the smallest moment of inertia) took place at $0{\cdot}60\,l$ under a load of 0·507 kg. The variation of the smaller moment of inertia (I_x) with distance from the proximal end is illustrated in figure V, 10*A*; the ordinate to the right-hand side is in units of the smallest moment found (I_0). The figure also shows the supposed curve of bending (y_x) in relation to the maximum deflexion ($y_{\text{max.}}$) which was known to be near to 0·60 *l*. This curve divided by the relative moments of inertia gave the third curve on figure V, 10*A*, $(y_x/y_{\text{max.}})/(I_x/I_0)$. When the latter curve was multiplied by $y_{\text{max.}}/P$, the bending moments were obtained, *P* being the load at buckling.

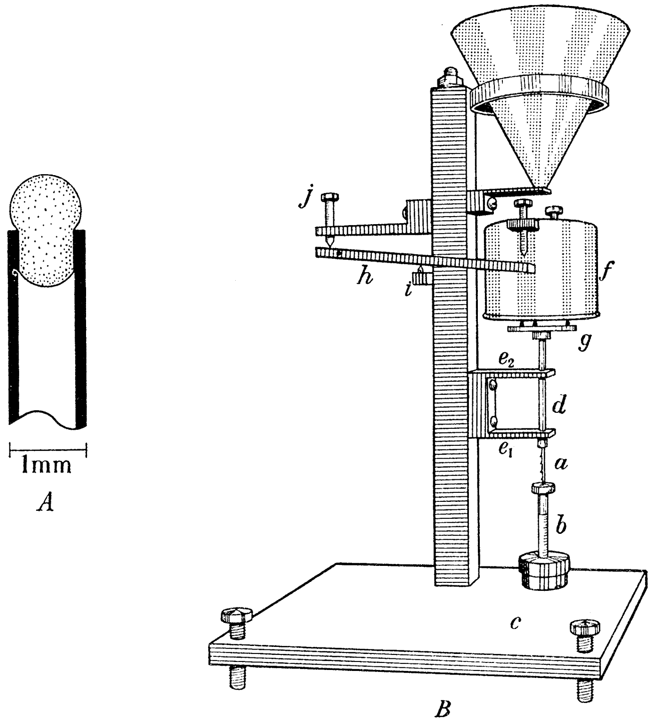


Figure V, 9. Mounting of tibia and apparatus used for buckling experiments. *A*, centred ball of dentist's cement at the cut end of a hind tibia. *B*, the apparatus: the tibia (*a*) is compressed between the adjustable platform (*c*+*b*) and the rod (*d*), guided by slide bearings (e_1, e_2); (*d*) is pushed downwards by the weight of the shot container (*f*) acting on the platform (*g*); the load is applied quickly but gently by means of the lever system (*h*, *i*) and the screw (*j*).

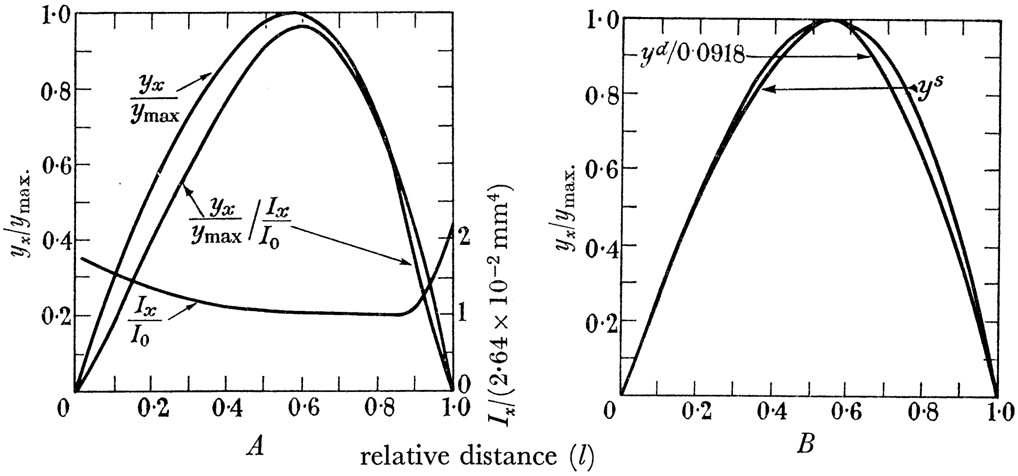


Figure V, 10. Method of deducing the coefficient of elasticity from buckling experiments. Full explanation in the text.

From the assumed elastic line of the column through the corresponding bending moments it is possible to calculate the elastic line of the column. This can be done by a double numerical integration of the above-mentioned curve representing the bending moments, followed by a division by EI_0.

If the assumed and the calculated lines are proportional, k being the ratio, and if the two expressions for the elastic line are reduced by the assumed value of $y_{\text{max.}}$ ($y_{\text{max.}} \neq 0$), k is determined by $kPl^2/(EI_0) = 1$. In the present example the 'best' value of k was 0·0918. Figure V, 10*B* shows that the assumed and the calculated line of elasticity are sufficiently near to each other to be used. The coefficient of elasticity then amounted to

$$E = \frac{0{\cdot}0918 \times 0{\cdot}507 \times 22{\cdot}8^2}{2{\cdot}64 \times 10^{-2}} = 915 \text{ kg/mm}^2.$$

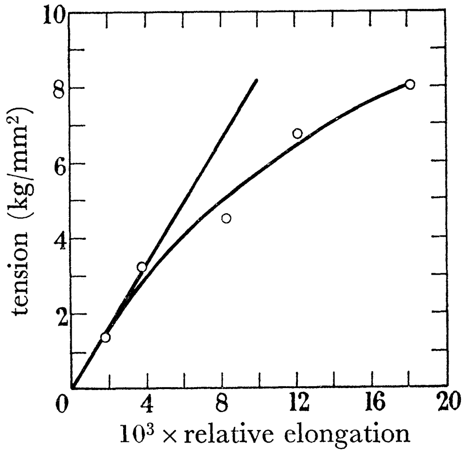


FIGURE V, 11. Relationship between relative elongation ϵ and the resulting tension σ in the solid cuticle of the pterothoracic pleuron (*Schistocerca gregaria*).

Result

In three hind tibiae from full-grown adults, the coefficient of elasticity was 825, 915 and 1010 kg/mm², or 920 kg/mm² in average. This applies to a tension of $-0{\cdot}7$ kg/mm². There is therefore no significant difference between the coefficient for stretch and compression at small loads.

(*d*) *Stretching of pleural cuticle*

A strip of the pterothoracic pleuron, 4·2 mm long and 0·052 mm² in cross-section, was extended in the stretching apparatus already described (figure V, 5); the resulting tension–elongation curve is seen in figure V, 11. The coefficient of elasticity E_0 was about 800 kg/mm² and the ultimate tension was about 8 kg/mm², i.e. of the same magnitude as in the hind tibia. Within the accuracy of estimate, the thoracic cuticle does not differ from that of leg cuticle.

(*e*) *Bending of forewing*

The forewings of the flying locust oscillate about eighteen times per second and are subjected to large, variable loads caused by acceleration of the wing mass and by wind forces. If the mechanical properties of solid cuticle are not the same throughout the skeleton, the differences are likely to be particularly marked in the wing.

Method

The proximal 2 or 3 mm of one forewing were clamped in plaster of paris. After setting, the cantilever thus obtained was loaded at the tip by placing a small piece of wire in a loop glued to the underside of the wing membrane. By lowering or raising a platform, loading and unloading were performed quickly and without shocks. The deflexions were measured by means of a vertical microscope (front lens 50 ×) fitted with an epicondenser. Small characteristic scratches in the membrane were focused and in this way deflexions were estimated with an accuracy to within 5×10^{-3} mm.

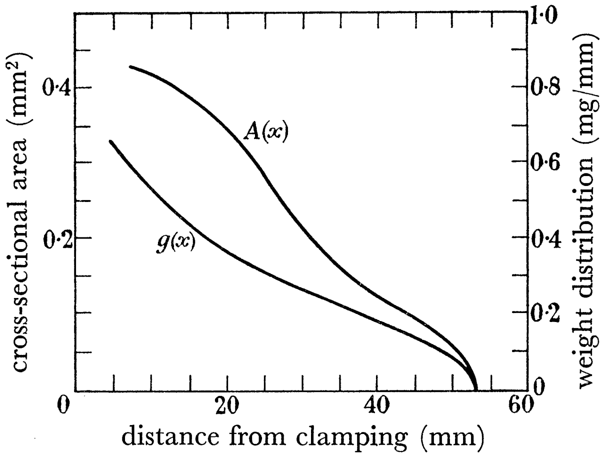


FIGURE V, 12. The variation of the cross-sectional area $A(x)$ and of the distribution of the wing weight $g(x)$ plotted against the distance x from the clamping of a locust forewing.

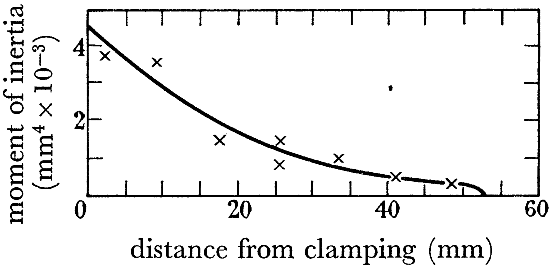


FIGURE V, 13. The variation of the moment of inertia of the cross-sectional area about a horizontal axis with the distance x from the clamping of a locust forewing.

Architecture

Seven cross-sections were made perpendicular to the long wing axis. Each section consists of rings (the veins) connected by thin lines of wing membrane. The length, width and wall thickness of veins and membranes were measured and the total cross-sectional area estimated. The area $A(x)$ varied with the distance from the fulcrum as seen in figure V, 12. The moment of inertia of the area about the horizontal axis is seen in figure V, 13 which is based upon photographs.

This method is not very accurate. An idea of the scatter is obtained by calculating the specific weight of the parts from their weights (cf. figure V, 12; $g(x)$) and the calculated volumes. The specific weight was 1·29, 1·38, 1·25, 1·09 and 1·17 respectively (average 1·20).

Permanent deformation and modulus of elasticity

When the wing tip was loaded by 30 mg, the immediate deflexion was 1·26 mm, increasing to 1·42 mm during the next 4 min. After 15 min the prolonged loading had caused a lasting deformation of 0·11 mm (figure V, 14). This plastic behaviour is typical for many organic solids and contrasts with the behaviour of the rubber-like cuticle (cf. figure V, 23). The measurements were therefore taken within the first few seconds of loading.

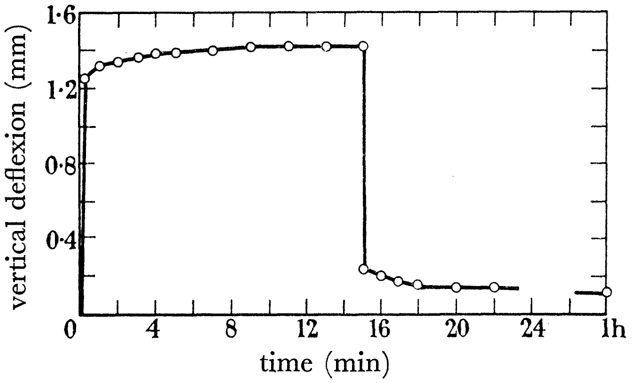


FIGURE V, 14. Flow and lasting deformations of a locust forewing suspended as a horizontal cantilever and loaded at the tip. The ordinate is the deflexion at the tip, and the abscissa is the duration of the isotonic load.

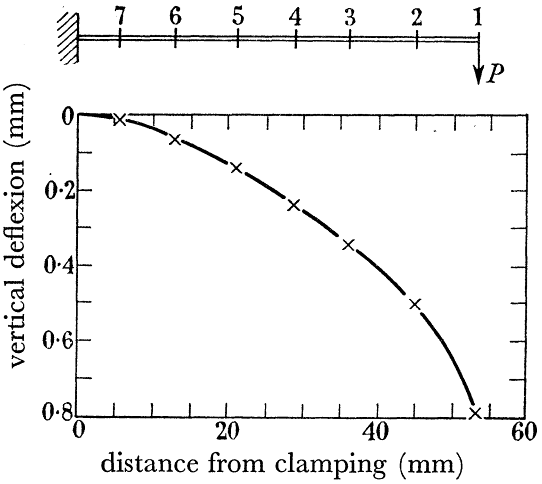


FIGURE V, 15. The vertical deflexion of a horizontally suspended forewing loaded at the tip (P) plotted against the distance x from the clamping.

The vertical deflexions were measured at the leading edge as well as at the trailing edge and at seven distances from the suspension. Each value is the mean of eight to ten single measurements. The result is seen in figure V, 15, where the ordinate is the downwards deflexion and the abscissa is the distance from the suspension. Since the moments of inertia are known, the curve of depression can be calculated provided the elastic modulus is assumed to be constant along the wing. By combining the calculated curve with the curve in figure V, 15, the modulus of elasticity is found as the unknown ratio (table V, 1). The average value is 870 ± 60 kg/mm^2, the accuracy of the single estimates in table V, 1 being ±20 %.

(*f*) *Conclusion*

The modulus of elasticity of solid cuticle in the pleuron and in the forewing is of the same order of magnitude as in the hind tibia, i.e. 800 to 1000 kg/mm^2, in spite of differences in structure and function of these parts. The tensile strength is also the same, 8 to 10 kg/mm^2 (pleuron only). The maximum elastic elongation is between 2 and 3 % with some plastic flow during prolonged loading.

TABLE V, 1. MODULUS OF ELASTICITY OF THE FOREWING OF A LOCUST

distance from clamping (mm)	10	20	30	40	50
modulus of elasticity (kg/mm^2)	600	740	1080	990	950

4. DYNAMIC PROPERTIES OF SOLID CUTICLE

In a flying insect most deformations are dynamic rather than static and two problems arise: does the modulus of elasticity change and is it possible to convert kinetic energy into elastic energy and back again without much loss, i.e. is the damping of the cuticle small?

(*a*) *Elasticity of oscillating forewing*

The forewing was suspended horizontally and induced to oscillate at its resonant frequency by means of sound waves from a loudspeaker fed from a sinusoidal electronic oscillator. The oscillation was observed in stroboscopic light (microscope). The curve of depression for a load on the wing tip was determined (cf. figure V, 15) and from this the stiffness against bending *EI* was calculated. Knowing the distribution of the weight along the wing, the bending line caused by the wing's own weight could be calculated. Assuming, as is normally done, that this line is proportional to the elastic line of the oscillation, the resonant frequency could be calculated, compared with the actual frequency, and the modulus of elasticity estimated.

In the experiment the resonant frequency was 68 c/s; assuming $E = 870$ kg/mm^2, the calculated frequency is 62 c/s. The difference is not significant within the accuracy of estimation. In the conduct of the static experiments, the rate of change in tension did not exceed 0·05 kg mm^{-2} s^{-1}. In the dynamic experiments it was about 5 kg mm^{-2} s^{-1}, i.e. 100 times larger. It is therefore concluded that the modulus of elasticity is of approximately the same magnitude in static and dynamic experiments when the rate of change in tension is kept within the above limits.

(*b*) *Mechanical damping: hind tibia*

By means of dentist's cement the hind tibia was mounted between two clamps of mild steel (*a* and *b* in figure V, 16*A*). (*b*) was provided with a small vertical mirror which deflected a beam of light from the projecting lamp (*d*) in figure V, 16*B* on to the white screen (*e*). The tibia was deflected by current in the electromagnet (*f*). When the key was opened, the preparation started to oscillate in a horizontal plane, the bending taking place along the axis of the least moment of inertia of the cross-section. The oscillation of the light spot was recorded by means of a camera (*c*) which was turned downwards during the experiment. Figure V, 17 shows a damped oscillation of the tibia. Under the experimental conditions, air resistance was insignificant.

The formula for the oscillation is $x = a_0 \mathrm{e}^{-(\delta/\pi)t} \cos(2\pi t/T)$, where δ is the relative loss of kinetic energy during one half cycle from the moment the system passes the mid-line in one direction until it again passes it in the opposite direction; it is analogous to, but not identical with, the loss factor h in the experiments with rubber-like cuticle, the difference being that the latter systems did not pass the mid-line (cf. p. 159). In figure V, 17, δ is

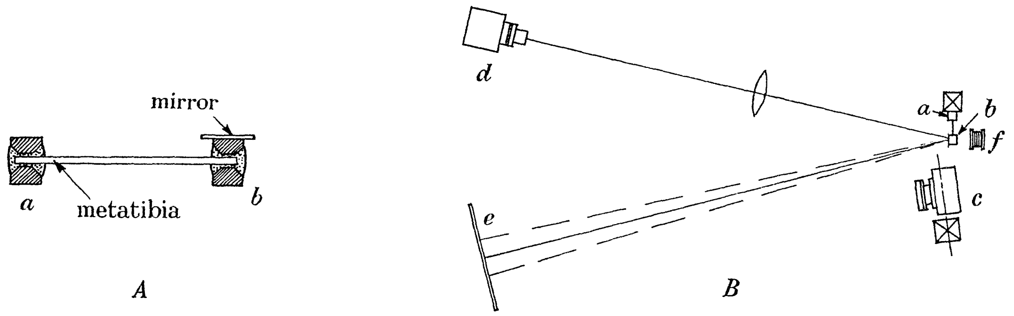


FIGURE V, 16. Method for recording a train of damped oscillations of the isolated hind tibia of *Schistocerca* (see the text).

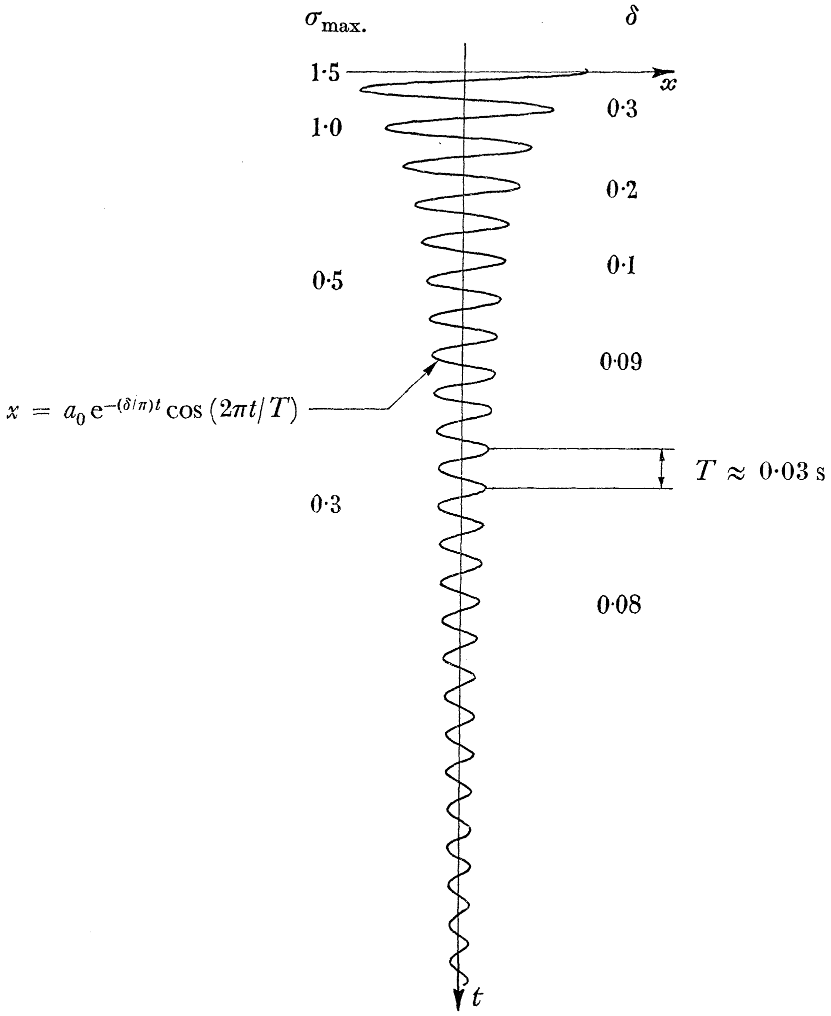


FIGURE V, 17. A train of damped oscillations of the hind tibia of a mature *Schistocerca*. The maximum tension encountered, σ (kg/mm^2), is indicated to the left of the curve and the loss factor δ to the right.

written to the right-hand side and the maximum tensions to the left-hand side. It is seen that δ decreases with decreasing amplitude or tensions. At high tensions, the loss is appreciable but when $\sigma_{\text{max.}}$ is less than 0·5 kg/mm^2, kinetic energy may be converted into elastic energy and regained as kinetic energy with a loss smaller than 10 %.

(*c*) *Conclusion*

The two types of experiment offer but limited information about the dynamic properties of solid cuticle. However, at the wing-stroke frequency of locusts (15 to 20 c/s) and when the tension does not exceed about 0·5 kg/mm^2, it is reasonably safe to conclude that (*a*) the dynamic modulus of elasticity is not appreciably different from the static modulus and that (*b*) the damping is sufficiently small for solid cuticle to be used as a material in elastic oscillating structures where it is essential to keep the loss factor small (0·1 or less).

5. Static properties of rubber-like cuticle

A large proportion of the elastic energy which passes in and out of the wing-bearing segments during a wing stroke is located in two rubber-like ligaments, the prealar arm (figure V, 18) which mediates the anterior suspension of the mesonotum and the main wing-hinge ligament (figure V, 21). Apart from epicuticle, the prealar arm consists exclusively of thin parallel lamellae of chitin separated by layers of isotropic resilin and this lamellar type predominates in the wing hinge which also contains a pad of pure resilin as well as some tough material (Weis-Fogh 1960; Bailey & Weis-Fogh 1961). The elasticity of pure resilin from dragonfly tendon is of the rubber-like type and depends both on the absolute temperature and on the degree of swelling, i.e. on the pH; it is particularly remarkable by its perfect elastic recovery and lack of flow (Weis-Fogh 1961 *b*, *c*).

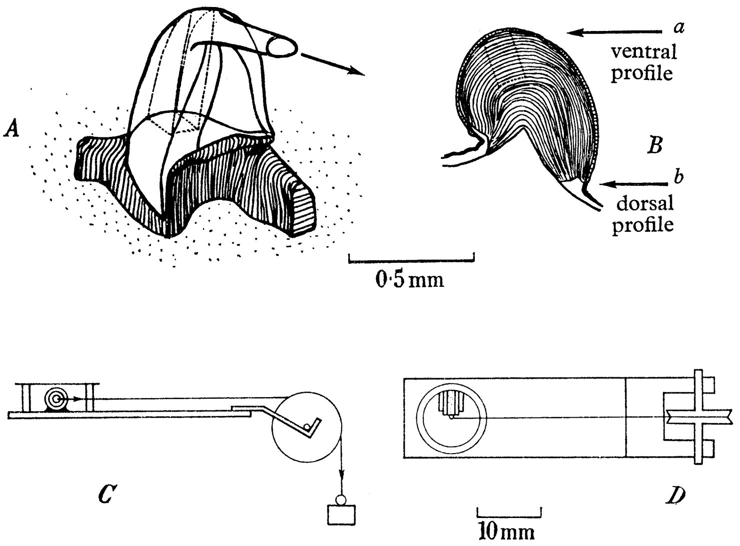


Figure V, 18. Morphology of the prealar arm of *Schistocerca gregaria* and apparatus used. *A*, the right prealar arm, as viewed from the dorsal side, with the base of solid, hardened cuticle (hatched) embedded in plaster of paris (dotted); the arrow indicates the direction of pull. *B*, cross-section of the prealar arm with the chitin lamellae indicated. The broken lines in *A* and *B* show the outlines of the preparation used to determine the elastic modulus (cf. figure V, 20). *C*, simple apparatus used for isotonic deflexions under the microscope, as viewed from the side, and *D* from above.

The aim has been to analyze typical laminated cuticle and to estimate the relative significance of the three components, chitin lamellae, resilin, and water, from a mechanical point of view.

(*a*) *Morphology and methods*

In the prealar arm there is an abrupt transition from the brown and solid cuticle to the hyaline arm itself which projects as a conical peg from its solid base (figure V, 18*A*). The tip of the cone extends into a very tough and thick ligament which connects the arm with the anterior tip of the basalar sclerite. The base was firmly embedded in plaster of paris at the end of a short length of glass tubing. The projecting, elastic part was deflected by an isotonic pull in the tough ligament perpendicular to the long axis of the cone; a short piece of platinum-iridium wire (0·06 mm in diameter) connected the ligament with a Nylon string which passed over a pulley with negligible friction. The tube was placed and clamped horizontally inside a larger horizontal tube fixed to a microscope slide inside a glass ring; the ring had a slit for the passage of the string (figure V, 18*C*, *D*). When placed on the turn-table of a polarizing microscope fitted with an eyepiece screw micrometer, linear and angular deflexions could be measured, to within 0·02 mm and 0·2°, respectively, and correlated with changes in birefringence. Thin pieces of pointed tungsten wire were inserted and used as points of reference.

In cross-section (figure V, 18*B*), the prealar arm is irregular with curved ventral and lateral sides and a V-shaped groove along its dorsal aspect. It is surrounded by a skin of the same apparent properties as the chitin lamellae of which there are about 100 with an average spacing of 3μ. According to the determinations of water, protein and solid matter, the lamellae are only about $0{\cdot}2\mu$ thick and the rubbery 'glue' therefore about fifteen times as thick. The lamellae are anchored in the solid base.

The elastic modulus was therefore calculated from the bending of a small cantilever shaped from the prealar arm by cuts parallel to its long axis (broken lines in figure V, 18). The resulting cross-sections were nearly rectangular but varied somewhat from base to tip. The ventral surface of the preparation was the natural one, the dorsal surface was the split surface between two laminae, and the lateral surfaces were cut normal to the laminae (cf. figure V, 20). A thin tungsten needle was inserted normal to the laminae and formed into a hook, protruding in the same direction as the tough ligament. The resulting, laminated cantilever was deflected isotonically (accuracy to within 20 mg and 0·004 mm) under the polarizing microscope. The cross-sections were measured from *camera-lucida* drawings at three different angles and at seven points along the axis.

All measurements were made at room temperature in 0·1 M buffer solutions of varying composition and pH.

(*b*) *Deformations, lamellae and skin*

The elastic modulus of the solid lamellae is probably several thousand times greater than the modulus of resilin. Since, moreover, the prealar arm is surrounded by a skin, the solid parts and the swelling pressure of water might be more significant than resilin for the large reversible deformations of which this type of cuticle is capable.

Deformations

When pulled parallel to the lamellae, the prealar arm stretches little and behaves more like a solid body. In compression and bending, however, the reversible deformation is very considerable, as is seen from the *camera-lucida* drawings in figure V, 19. The curve to the left-hand side shows how the linear deflexion in the direction of pull (abscissa) varies with the applied stress (ordinate). When the deflexion is as large as in this case, the strain is complex and this may account for part of the steep rise towards the end. But with forces up to 10 g, the curve is almost linear and this is the range and type of deformation normally encountered in flight (part VI); the dynamic experiments in §6 were confined mainly to this region.

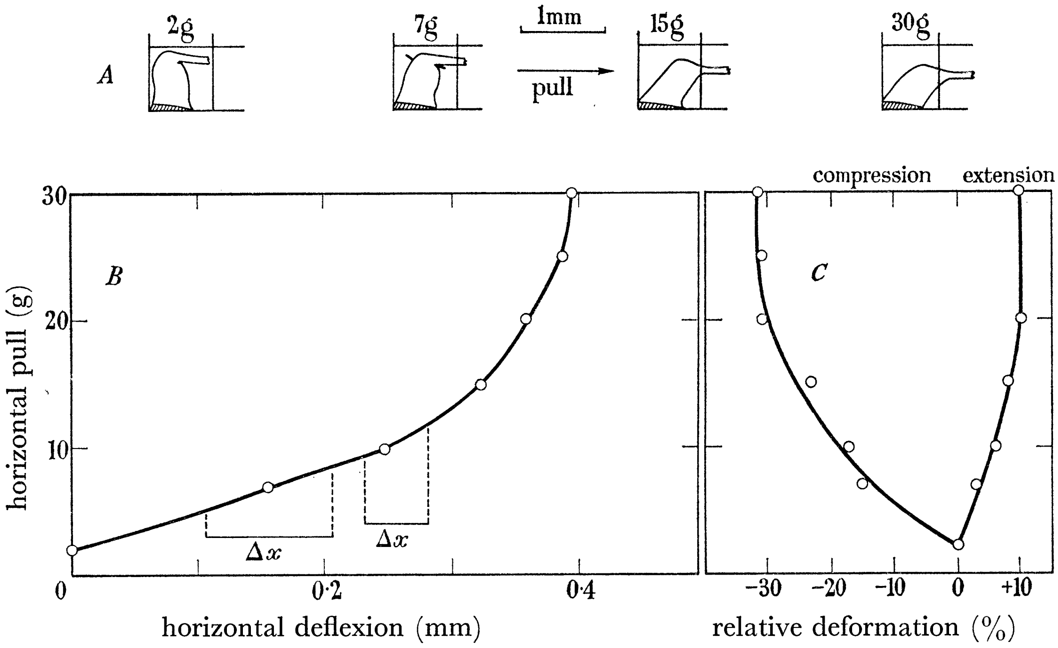
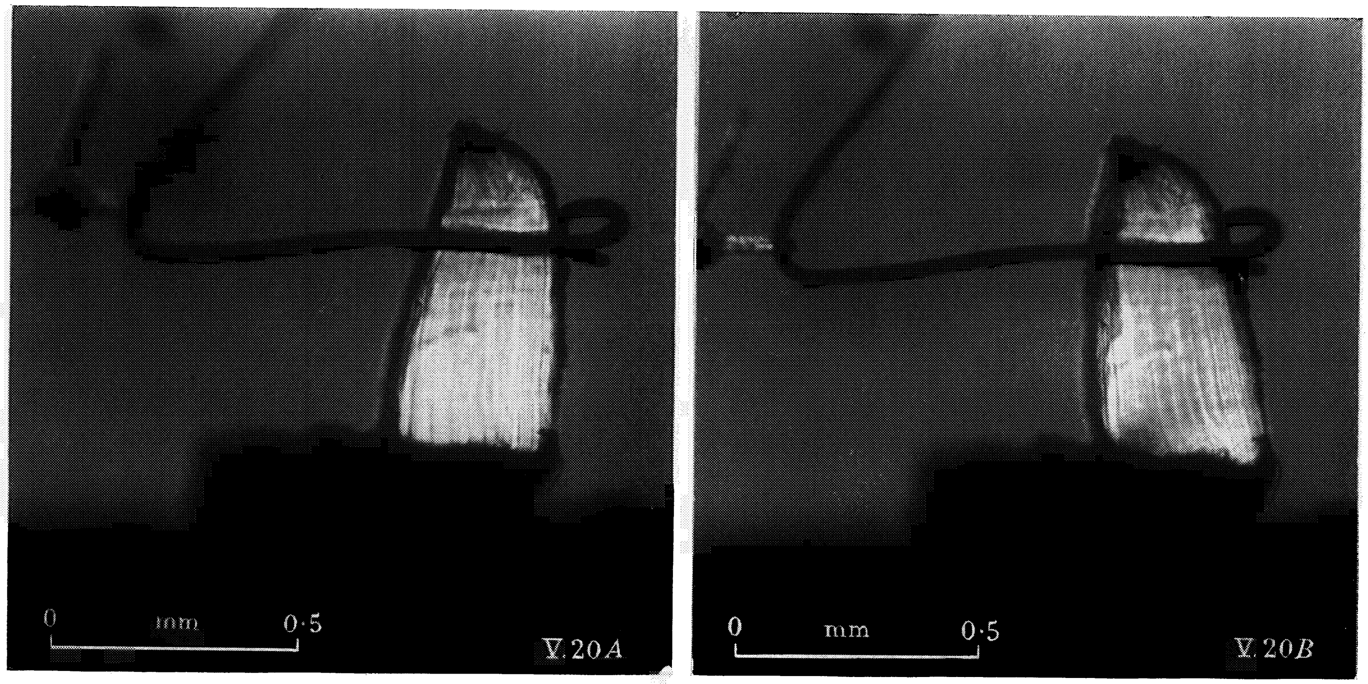


FIGURE V, 19. Reversible deformations of the prealar arm of *Schistocerca* as a result of an isotonic pull in the tough ligament at the tip (horizontal arrow in *A*). *A*, *camera-lucida* drawings from the side. *B*, the linear deflexion at the level of the tough ligament plotted against the applied force $\overline{F}$. *C*, the relative compression and extension of the outlines in figure V, 18*B* also plotted against the applied force. 25 °C, pH 6·7. Δx indicates the alternating strain in two dynamic experiments (§6).

Effect of lamellae

The curves at the right-hand side of figure V, 19 show the relative compression of the shortest of the two dorsal profiles (*b* in figure V, 18*B*) and the extension of the ventral profile (*a*). Compression is about three times more pronounced than extension over the entire range. This is consistent with the presence of thin lamellae of solid but flexible material which resist stretching but not bending or compression. The effect is to push the neutral layer towards the ventral side, i.e. towards the side subjected to extension. This interpretation was confirmed by the observed changes in birefringence when the structure was strained mechanically or by alteration of the swelling.

In the unstrained *cut sample* (figure V, 20, plate 55) the birefringence was positive in the direction of the lamellae at low and neutral pH. This birefringence is mainly form birefringence since unstrained resilin is isotropic; strained resilin becomes positively birefringent in the direction of extension and negatively birefringent in compression (Weis-Fogh 1960). By these criteria the neutral axis or layer was found to be situated, not in the



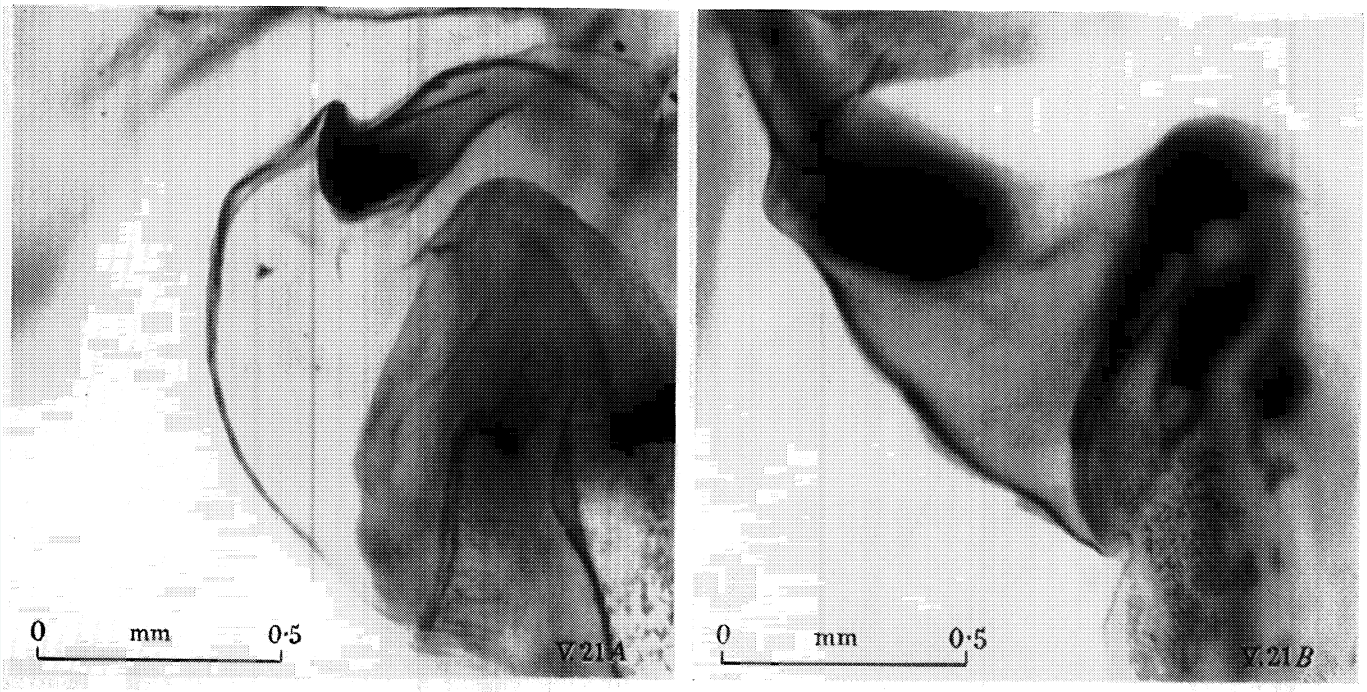


FIGURE V, 20. Small cantilever of rubber-like cuticle viewed from the edge of the chitin lamellae and placed between crossed Nicols (first-order-red gypsum plate). *A*, unstrained; *B*, strained within the linear range. In locust saline at pH 6·7.

FIGURE V, 21. Rubber-like hinge ligament of the right forewing of *Schistocerca gregaria*, viewed towards the head, ordinary light. *A*, with the forewings in the resting position 45° below the horizontal. *B*, after the forewings have been raised 45° above the horizontal by means of a downward push on the mesonotum. (From dehydrated preparations in balsam; similar deformations are observed in the fresh condition.)

middle, but further towards the extended side, about one-third or one-fourth of the thickness from the ventral surface. If the same sample was placed in alkaline buffer, the protein became more swollen and since the swelling was constrained parallel to but not normal to the lamellae, except at the base (cf. drawings in figure V, 22), the swelling was uneven so that the protein attained a predominant orientation normal to the lamellae. At pH 12·3 the intrinsic birefringence of the resilin thereby increased sufficiently to reverse the sign of the total birefringence from positive along the lamellae to negative. In such strongly swollen preparations, the neutral layer was pushed right over to the ventral surface, apparently because the lamellae had become expanded and taut by the swelling forces.

When the *intact prealar arm* was placed in buffered saline, the differences in thickness and orientation of the laminae prevented detailed optical observations, but when the sample had become swollen by immersion in Thoulet's solution (potassium mercury iodide, refractive index $n = 1{\cdot}52$) form birefringence was nearly abolished. As in the cut and swollen sample, the neutral layer could then be seen to be right over towards the ventral side. The thin lamellae therefore constrain swelling in directions parallel to their surfaces and, being solid but bendable, tend to diminish extension and to enhance compression of the interior.

In the more complicated *wing-hinge ligament*, compression is also the dominating type of strain in the animal, at least during some phases of the wing stroke, as is seen from figure V, 21, plate 55. In (A) the forewings are at rest in the downwards position but in (B) they have been raised above the horizontal by means of a downwards push on the mesonotum, imitating the action of the elevator muscles. The wavy outline of the cushion-shaped patch of rubber demonstrates the resulting compression. A similar situation is also observed after removal of the notum when the wings are turned upwards by a pull distal to the fulcra; this was the experimental condition for estimating the elastic efficiency of the hinge referred to on p. 161.

Effect of skin

The solid skin surrounding the prealar arm might act as the elastic wall of a 'turgor cell' inflated by the swelling pressure of the protein. It is difficult to disprove this possibility altogether. However, the following observations make it unlikely that the stress in the wall is of decisive importance. When the prealar arm or the wing ligament is cut by a razor, the cut surfaces remain flat and there is no bulging or change of external form so that the cut pieces fit precisely together. The intact form is actually determined by the content and only to an insignificant extent by the skin. When strongly swollen in alkaline solutions, the skin does restrict swelling but the mechanical effect is small and decreases with time. In bending, compression and probably also in extension normal to the lamellae, the solid parts should exert little influence compared with the resilin. When extended in the direction of the lamellae, rubber-like cuticle behaves more like a solid material than like a rubber. The swelling pressure has little mechanical significance.

(*c*) *Elastic modulus*

The deflexion d of the loaded tip of a cantilever of length l is $d = (\text{load} \times l^3)/(3EI)$. In the case of the cut samples, such as the one in figure V, 20, plate 55, the skin effect is absent and for small deflexions the formula is applicable as a first approximation. The major inaccuracy is due to the moment of inertia I partly because the exact position of the neutral layer was not known and partly because of some variation in the cross-section along the beam. Table V, 2 shows the rough estimates of E which could be obtained by this method at three degrees of swelling. The most probable values are in heavy types and equal 0·2 kg/mm^2. The estimates are based upon experiments in which the deflexion was proportional to the applied force within the range used. The elastic coefficient of natural and synthetic rubbers is about 0·05 to 0·5 kg/mm^2 at moderate degrees of deformation and swelling (cf. Meyer 1950; Roff 1956), or three to five orders of magnitude less than for skeletal materials and other solids. In bending and compression, there is therefore no doubt that the composite cuticle or the prealar arm is completely dominated by resilin, as far as its physics is concerned. This should also apply to the main wing hinge.

TABLE V, 2. MODULUS OF ELASTICITY OF RUBBER-LIKE CUTICLE

Approximate values of E in samples of the prealar arm from *Schistocerca gregaria*. The values in heavy type are those calculated by assuming that the neutral layer is flush with the ventral or tensile surface of the preparation and not situated midways between the dorsal and ventral aspects (ordinary type).

pH of saline	E (kg/mm^2) in sample		
	no. 1	no. 2	no. 3
1·8	0·3	—	**0·2** to 0·8
6·7	0·4	**0·5** to 1·8	**0·2** to 0·7
12·3	0·2	—	**0·2** to 0·8

The elastic modulus G derived from the kinetic theory of rubber elasticity is related to E by the equation $G = \frac{1}{3}E_0 v^{-\frac{1}{3}}$, where v is the volume fraction, i.e. the volume of the dry rubber over the volume of the swollen sample (see Treloar 1958). For locust resilin $v = 0{\cdot}42$ at pH 7 (Weis-Fogh 1960) so that table V, 2 indicates a value for G of not less than 0·09 kg/mm^2 which is somewhat higher than for dragonfly resilin (0·07 kg/mm^2; Weis-Fogh 1961 *c*).

(*d*) *Stiffness and swelling*

From the above equation it is seen that E for a swollen rubber decreases with the degree of swelling but not very steeply. Because of this, swelling may increase the moment of inertia of the cross-sectional area of a given sample more than it decreases its modulus so that the stiffness of the sample increases as a result. If, moreover, the rubber is placed inside a solid framework swelling may give rise to a hydrostatic pressure (turgor) and a corresponding increase in stiffness. The mechanical effect of swelling may therefore throw further light on the relative importance of the rubber and the solid parts, but it may also have an important bearing upon flight itself: shortly before the desert locust becomes a full migrant, as defined by laboratory criteria (Weis-Fogh 1952), the wing-hinge ligament increases its stiffness by 1½ to 2 times accompanied by a rather drastic decrease in damping (5 to 10 times, part VI). These important changes seemed to be caused by some chemical modification rather than by deposition of new hinge material.

Effect of swelling

The solid curves in figure V, 22 show how the angular deflexion (abscissa) varied with the applied stress when the prealar arm was swollen to various extents. At low pH (1·8 to 5·6), the volume was minimum and increased gradually up to the most alkaline solution used, pH 12·3. Correlated with this swelling was a gradual increase in stiffness (force per unit deflexion).

The stiffness S of a simple cantilever is proportional to the elastic modulus E and to the moment of inertia of the cross-sectional area I, and inversely proportional to the third power of the distance l of the applied force from the clamping. Since $I \propto s^4$, where s is a linear dimension in the cross-section and provided that the neutral surface retains its relative position, $S \propto Es^4/l^3$. The swelling of the cross-section appeared to be equal in both directions and s increased from 1·00 to 1·22 (arbitrary units). The length l, on the other hand, only increased from 1·00 to 1·035, showing that the solid parts constrain the swelling of the isotropic rubber in the direction of the lamellae. As a result the volume increased by about 50%. According to the formula relating E with volume the elastic modulus should have decreased by about one-eighth. With all factors taken into account, the stiffness S should then have increased by a factor 1·8 as a result of the swelling. In actual fact, the factor was between 2·2 and 2·5, but the difference is not significant because the neutral layer tends to migrate towards the extension side when swelling increases. In a simple rectangular cantilever, a migration from the mid-line to the extension side would increase S by four times. The observed and the calculated change in stiffness are therefore in good agreement so that hydrostatic forces do not seem to play an essential role under any conditions.

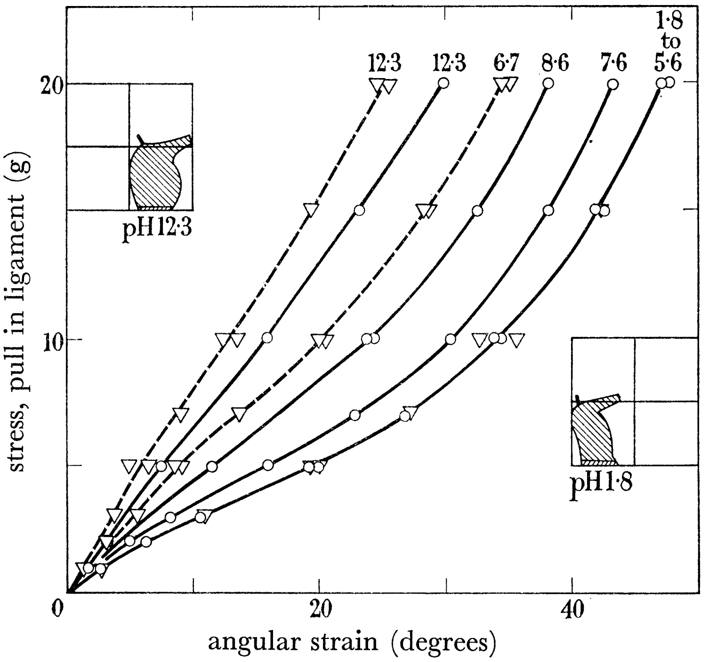


Figure V, 22. The effect of swelling upon the stress–strain curve of the prealar arm exposed to various hydrogen-ion concentrations (from pH 1·8 to 12·3 as indicated above curves), partly without any previous treatment (solid curves and circles) and partly after chemical modification caused by p-benzoquinone (dashed curves and triangles). The *camera-lucida* drawings show that swelling is constrained longitudinally and at the base (25 °C).

Probable control of swelling

In the locust, the pH is unlikely to vary nearly as much as in the experiment. Nevertheless, there is a possibility that the insect may control the amount of swelling and thereby the stiffness and the damping of its rubber-like structures. This is shown by the dashed curves and triangular symbols in figure V, 22 which derive from the same preparation after it had been treated in a saturated solution of industrial *p*-benzoquinone in a phosphate buffer at pH 7·6 for 40 h at room temperature. The prealar arm becomes deeply and permanently brown throughout but the protein remains in the rubbery state. The only mechanical change seems to be an alteration of the swelling properties which can be attributed to a blocking of the amino groups (see Gustavson 1956) and a corresponding shift of the isoelectric point towards the acid side. At neutral pH, for instance, the stiffness had doubled after the treatment compared with that of the fresh prealar arm. In the wing system most of the deformations are determined by the stroke angle which is almost constant and independent of the flight performance so that doubling the stiffness means doubling of the elastic recoil.

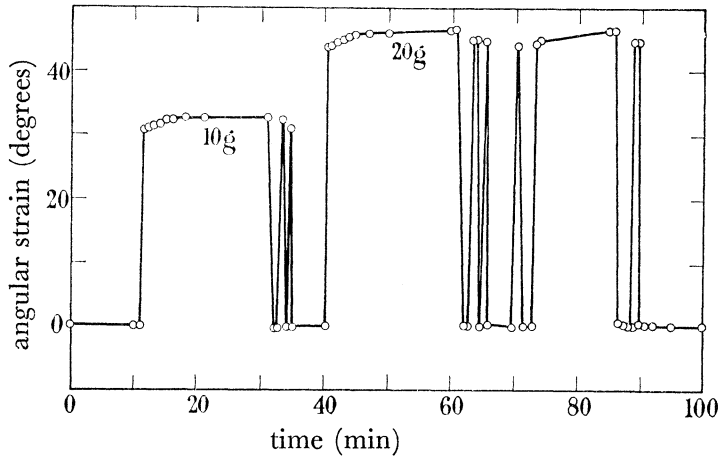


FIGURE V, 23. Angular deflexion of the rubber-like prealar arm plotted against the duration of the isotonic load (10 or 20 g). Note that the *apparent flow* is followed by *full elastic recovery* (cf. figure V, 14) (25 °C, pH 6·7).

It may then be possible for an insect to alter the degree of swelling by comparatively simple chemical modifications of the rubber-like protein and thereby to adjust the stiffness of a cuticular structure permanently or temporarily.

(*e*) *Lasting deformations*

From figure V, 14 we saw that solid cuticle, like most other skeletal materials, is subject to lasting deformation, the extent of which depends upon the magnitude and duration of the static stress. The experiment in figure V, 23 shows that the prealar arm behaves otherwise. The abscissa is the time in minutes while the ordinate is the angular deflexion of the long axis of the structure (arbitrarily defined by small needles). As in solid cuticle, the deflexion increases with increasing duration of the applied stress (10 and 20 g, respectively) but, in spite of this 'normal' behaviour, and in spite of the large deformations (cf. figure V, 19*A*), the prealar arm (1) returns to its external initial shape within 1 min or less after the release, and (2) has regained its original stiffness and recovered completely within 5 min. The last point is proved by the transient loadings following each of the static ones. This full elastic recovery is discussed on p. 167.

6. Dynamic properties of rubber-like cuticle

(*a*) *Method and definitions*

Mounting

The prealar arm was isolated in locust saline at pH 6·7, mounted in plaster of paris in a tube as already described and the plaster allowed to set for 12 h. The tough ligament was tied to the one end of a wire of platinum-iridium (20 mm long and 0·06 mm in diameter), slipping being prevented by means of a knot which pressed against the cut tip of the basalar sclerite. This wire and also the tough ligament could be considered rigid compared with the cuticle. The sample was not immersed in fluid but suspended in air and moistened with locust saline or with another buffer.

Apparatus

The other end of the wire was clamped to an electrically controlled vibrator which produces a sinusoidal strain of controlled amplitude ($\frac{1}{2}\Delta x$) and frequency both of which are independent of the stress set up in the preparation. The apparatus which is described in detail by Machin (1959) and Machin & Pringle (1959) incorporates a Solartron transfer-function analyzer. The following stresses were measured by electronic devices: the static force before the oscillation began and the average force $\overline{F}$ during the oscillation, the alternating component of force ΔF_0 in phase with the sinusoidal strain and the component ΔF_i 90° out of phase. The system measuring the dynamic stresses had a resonance frequency well above the range of operation. The measurements are correct to within 2% at frequencies from 10 c/s and upwards. Between 2 and 10 c/s the amplitude may be in error by a few per cent and the phase by a few degrees (either way).

Definitions and calculation

The static stress–strain curve in figure V, 19*B* is from a preparation used for dynamic experiments. The average stress $\overline{F}$ and the periodic strain Δx were adjusted so that the curve was practically linear within this range. Since $\overline{F}$ did not change with frequency in any of the experiments, the calculation is simple.

The *dynamic stiffness* $\Delta F_0/\Delta x$ increases with Δx and with the frequency. It equals the static stiffness at low frequencies but is given in per cent of its value at 10 c/s because the accuracy of the apparatus deteriorates below this frequency.

The *loss factor h* is defined as the ratio between the amount of energy irreversibly lost as heat during one half cycle and the total change in stored elastic energy during this period. In the case of simple viscosity the resistance is proportional to the rate of deformation $\mathrm{d}x/\mathrm{d}t$; the variation of this force with x is represented by an ellipse of area $A_1 = \frac{1}{4}\pi\Delta F_i\Delta x$. It is characteristic of the measuring instrument that it takes into account only the fundamental oscillation of the stress so that ΔF_i is the one axis of the ellipse and Δx the other. Since the change in stored energy equals the area A_2 of the trapezoid $A_2 = \Delta x\overline{F}$, we have for the loss factor $2h = A_1/A_2 = \pi\Delta F_i/4\bar{F}$; this expression is of course not valid when $\bar{F} = 0$, i.e. for oscillations about the unstrained position, but it suits the practical experiments as well as the technological tests on the resilience of rubbers.

The *elastic efficiency* is defined as $\eta_e = 1-h$. Expressed in per cent it equals the resilience for a sinusoidal strain. In the isolated thorax it shows how much of the energy stored at the top position of the wing has been converted into work or kinetic energy when the bottom position is reached.

(*b*) *Results*

Three complete experiments were performed with three prealar arms moistened with locust saline at pH 6·7. One experiment took place at 26 °C and the two others at 38 °C but since the results were essentially similar, they have been pooled. In addition, one of the preparations was tested in the least swollen condition (pH 1·8) and when strongly swollen (pH 12·3); this had no significant effect upon the dynamic properties of this sample and the results are therefore not given.

Table V, 3. Biological frequency range in experiments with prealar arm

average stress (g)	alternating stress ΔF_0 (g)	alternating strain Δx (mm)	biological frequency range (c/s)	symbol on curves
7·0	4 to 6	0·10 to 0·12	15 to 50	○
10·2	4 to 5	0·05 to 0·06		▽

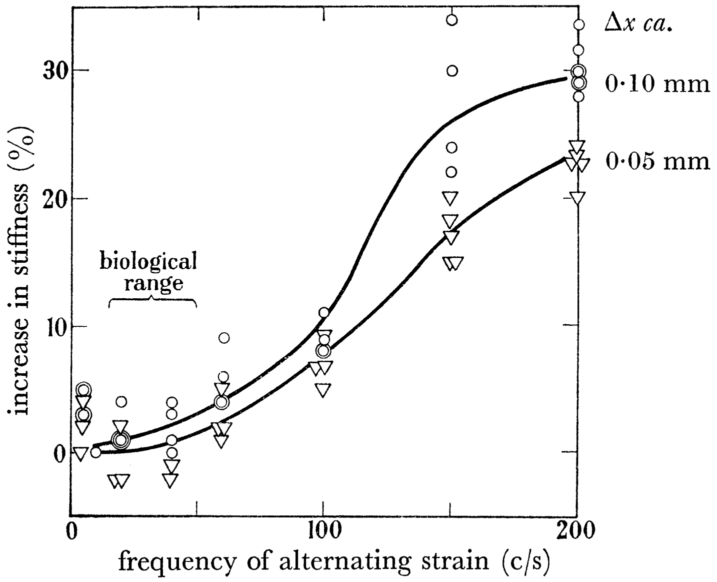


Figure V, 24. The percentage increase in stiffness of three prealar arms of *Schistocerca gregaria* plotted against the frequency of the sinusoidally oscillating strain at two amplitudes (26 to 38 °C, pH 6·7).

Relation to flight

The applied stresses and strains are shown in table V, 3 so as to relate the experimental rates of deformation with the flight rates. The wing-stroke frequency varies between 15 and 20 c/s. According to part VI, each prealar arm produces a periodic elastic force of this fundamental frequency and a peak-to-peak magnitude of 5 to 8 g. The upstroke lasts 0·4 of the total cycle and the downstroke 0·6 (part II). The natural rates of deformation should therefore correspond to the experimental rates within the frequency range of 15 to 50 c/s, called the biological range. This applies to the low as well as to the high value of $\bar{F}$ in figure V, 19. A rough calculation of the speed of deformation of the content of the prealar arm indicated that the average, linear rate of deformation at 50 c/s was about 6 l/s when averaged for the entire content and during one cycle, where l is the unit length of the content, i.e. mainly of the resilin.

Dynamic stiffness

Figure V, 24 demonstrates that the stiffness increases both with the frequency and with Δx, as was to be expected. The important feature is that the increase is very small up to about 100 c/s. The values obtained at 5 c/s are hardly significant because the apparatus is unsatisfactory for our purpose within this region. Within the biological range, the increase was negligible at the lower limit (15 c/s) and less than 5 % at the upper limit (50 c/s).

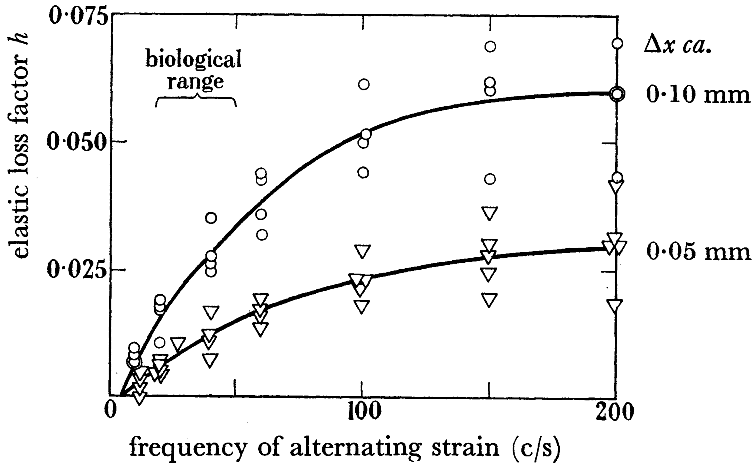


FIGURE V, 25. In the prealar arm the loss factor h (see the text) increases with the frequency of the oscillating sinusoidal strain and approaches a level. However, it is smaller than 7 % even at the highest frequencies used. 26 to 38 °C, pH 6·7. Same experiments, combinations and symbols as in figure V, 24.

Loss factor

Figure V, 25 demonstrates that the prealar arm absorbs very little of the energy it stores under normal conditions of work, maximally 3·5 % per half cycle and probably less than 2·5 %. In terms of elastic efficiency, η_e is 0·96 to 0·97, which is equal to the value found for the intact wing-hinge ligament *in situ* during a normal downstroke (part VI).

When, as here, the prealar arm is subjected to lateral deflexions of moderate amplitude, all the experiments show that its behaviour is governed by the rubber-like protein. Since another structure, the wing-hinge ligament, which has an equally large amount of this protein, also has an equally high efficiency in compression, it is justified to consider the elastic protein as being an exceptionally good rubber with rebound properties (resilience) hardly equalled by any known synthetic or natural product. Even at 200 c/s, the loss is reasonably small.

(*c*) *Conclusion*

Contrary to what might be expected, the rubber-like cuticle shows very little damping at frequencies below 100 c/s. It is therefore admirably suited for oscillating structures in which it is essential to reduce power expenditure. Since the elastic recovery after static strains is perfect and since the dynamic stiffness only varies by a few per cent from 0 to 50 c/s, the elastic characteristics of the highly elastic ligaments can be studied under static or semi-dynamic conditions.

7. DISCUSSION

(*a*) *Cuticle and flight*

Chabrier (1822) analyzed many of the ways in which elastic deformations of the cuticle assist the wing movements, but it is mainly the erroneous rather than the correct results that have survived in the literature. In more recent times it has been pointed out that the modified wings of Strepsiptera and Diptera, the halteres, to a considerable extent are moved by elastic forces during part of the stroke (Ulrich 1930, p. 608; Pringle 1948), but the problem did not become acute until the discovery of the so-called click mechanism in the thorax of many insects (Boettiger & Furshpan 1952; Pringle 1957) and until it was realized that flapping flight would be extremely expensive in energy (Sotavalta 1952) if the adverse effect of wing inertia is not counteracted by an elastic system (Danzer 1956; Weis-Fogh & Martin Jensen 1956 (part I)).

It is hardly possible to study the elements of an elastic structure as intricate as the insect thorax without the application of static and semi-dynamic methods. But such procedures presuppose that the elastic materials behave in nearly the same way in slow deformations as during actual flight. The investigation proves that this is the case in both types of locust cuticle. The way is therefore clear for the detailed analysis (in part VI) of the pterothorax as a spring system whose characteristics may be revealed by relatively simple techniques.

Limitations of solid cuticle

As an ideal elastic material, ordinary solid cuticle has some limitations of which one is its tendency to encounter permanent deformations when the load has a static component lasting for more than a few seconds. Where such conditions prevail for prolonged periods, as in certain parts of the flight system, counter-measures must be introduced. One obvious way is to incorporate into the fabric a resin-like material so as to decrease flow and to increase compressive strength and modulus (cf. table V, 5, asterisks). Actual adoption of this principle is indicated by the brown or dark colour of many parts of the wing system exposed to considerable forces but where hardness as such is of no major concern; a detailed analysis is still lacking. In most places the problem does not arise because the solid parts oscillate about their unstrained configurations.

Another limitation of solid cuticle may be of a more fundamental nature and finds its parallel in the skeletal system of vertebrates. It concerns loaded hinges which have the character of solid surfaces sliding past each other. Whether a lubricant is present or not, friction and abrasion are bound to occur. Both increase with load. In mammals, a cellular lining of spongy cartilage soaked in synovial fluid is essential in order to reduce friction

(MacConaill 1960; Lewis & McCutchen 1960) and make repairs possible. In the wings of locusts, the force normal to the hinge processes oscillates with a peak-to-peak amplitude of about 0·3 kg/mm^2 (part VI). This dynamic load is high even compared with loads on metal bearings. For ordinary lubricated journal bearings the permissible pressure for well-shaped hardened steel on bronze is 0·6 kg/mm^2; for mild steel on white metal it is 0·35 kg/mm^2 (Thomsen 1920). If dynamically loaded sliding hinges occur in the wing system, one should expect the composite cuticle to be greatly refined not only with respect to shape, lubrication, flow, cooling and hardness but also with respect to elastic loss (cf. Bowden 1957).

Advantages of rubber-like cuticle

The problems of lubrication, friction and abrasion of loaded hinges are avoided in the wing system of grasshoppers, dragonflies, cockroaches and presumably many other types. The hinge consists of two hard processes separated by a pad of rubber-like cuticle (figure V, 21) so that the friction between interphases has been replaced by a viscous resistance distributed throughout a bulky material. According to figure V, 25, the heat production due to this factor is small. Since there are no fillers involved, the internal abrasion should be negligible and the problem of fatigue of the material probably avoided because we are dealing not with crystalline materials but with a molecular three-dimensional network of highly flexible chains swollen with water (Weis-Fogh 1961 *c*). Moreover, the hinge material resilin can take up both compressive and tensile forces; it does not flow and it contributes positively to the elastic forces acting against the adverse forces from wing inertia. It therefore simplifies function, construction and maintenance in several ways.

Limitations or rubber-like hinges

There is another way of preventing the use of sliding hinges in the wing system, namely, by suspending the wing by means of tough ligaments which, at a given instant, are tense on one side and slack on the other, and vice versa. Tension hinges of this kind seem to be used in Hymenoptera, Diptera and Coleoptera (Weis-Fogh, unpublished). The reason for this difference may well be the rise in dynamic stiffness and damping at the frequencies with which these advanced forms move their wings (cf. figures V, 24 and 25). The successful application of rubbers is limited by such factors. In general, one should be hesitant in accepting the presence of loaded hinges of the sliding type in any wing system. Most authors take them for granted.

(*b*) *Cuticle as a material*

As has often been reviewed and discussed (cf. Wigglesworth 1948; Richards 1951), most solid cuticles and the soft intersegmental membranes appear to be laminated parallel to the surface. It is generally easy to split the endocuticle into laminae of various thicknesses, especially after treatment in glycerol and slight hydrolysis (Schulze 1926), but this also applies to the fresh tibia of the locust. After swelling or removal of tanned protein (Diaphanol), the same is true of most exocuticles. In the electron microscope, the lamellate appearance is less distinct (Richards & Anderson 1942) than in the light microscope, but polysaccharides as well as resilin are much less dense to electrons than most biological materials. Many solid cuticles, therefore, appear to be laminate or multi-ply structures in which partial or total removal of proteins discloses a microscopical system of thin sheets or true lamellae, mainly made up of chitin. This also applies to the other end of the scale: mild hydrolysis of the prealar arm completely removes the rubber-like 'glue' between the glossy chitin lamellae. In this particular case, the lamellae are continuous and clearly responsible for tensile rigidity and strength in directions parallel to their surface. The chitin lamellae anchor into and penetrate the hardened cuticle at the exceedingly sharp borderline between the two types, but it is not known whether they are continuous with the thin lamellae of the hard cuticle for any considerable length, as seems to be the case in some insect eyes (see p. 248 in Richards 1951).

A working hypothesis

The simplified picture which emerges is that of a laminate of *three components* (epicuticle and hypodermis being excluded): (1) a system of chitin lamellae parallel to the surface and of considerable tensile strength but not necessarily continuous, (2) a rubber-like 'glue' of protein between the lamellae which is cross-linked to different extents but which cannot be tanned by ordinary tanning agents and which is poor in tyrosine (Weis-Fogh 1960; Bailey & Weis-Fogh 1961), and (3) another protein which is rich in tyrosine and which may be water soluble (arthropodin, for instance) before being tanned to a resin-like material. Water may be considered as a fourth component. The laminae may be microscopical or submicroscopical but not of molecular dimensions. For the time being, this is but a working hypothesis which is brought forward not only as a basis for a discussion of the mechanical properties, but also in order to counteract the current tendency to consider insect cuticle as a mixed muco-polysaccharide-lipoid complex of which little analysis is possible.

It is essential to emphasize that the laminae are not of molecular dimensions because the molecular interlocking between chitin and protein proposed by Fraenkel & Rudall (1940, 1947) would result in essentially rigid and brittle materials. The other scheme makes possible all types of cuticle from very hard and brittle, through solid but flexible to truly rubber-like structures and in such a way that developmental and structural continuity may be observed between the various types right from the beginning of their formation. It is likely that the tough ligaments, the arthrodial membranes and the extensible plastic cuticles of some blood-sucking insects and ticks may force us to revise or extend the above picture. However, it may serve as a starting point for further enquiries.

Solid cuticle and fibrous materials

Most fibres owe their tensile strength to the longitudinal orientation of the molecular chains and to the secondary bonds formed between adjacent chains in crystalline parts of the fibre. Compared with such products (table V, 4; mainly from Roff 1956), the solid cuticle of locusts is of medium rigidity and of rather low tensile strength. The high value for dry 'chitin' (Herzog 1926) refers to the truly fibrous and crystalline 'Balkenlage' in the elytra of certain beetles and is, therefore, comparable to such materials as ramie and cotton fibres. It may have contained some non-fibrous protein in the meshes, but this is not likely to have much altered the results. Thor & Henderson (1940, cited from Richards 1951) worked with purified and apparently less oriented samples. In ordinary cuticle, the

TABLE V, 4. SOLID CUTICLE AND CHITIN COMPARED WITH ORGANIC FIBRES

Typical values for fibres from Roff (1956).

naterial and source	elastic modulus *E* in extension (kg/mm^2)	tensile strength (kg/mm^2)	extension at break (%)	specific gravity (g/ml.)	remarks
icle and chitin					
olid cuticle	960	9·6	2 to 3	1·2	present study
chitin',* dry	4500*	58*	1·3*	—	Herzog (1926)*
urified chitin dry	—	9·5	—	—	Thor & Henderson (1940)
urified chitin wet	—	1·8	—	—	
ural materials					
ellulose, ramie	2500 to 5000	90 to 110	4	1·6	highly oriented, polycrystalline, no primary interlockings
ellulose, cotton	600 to 1100	50 to 60	6 to 8	1·6	
rotein, silk fibroin	700 to 1000	35 to 60	20 to 25	1·3	
rotein, zein	250	12	20 to 25	1·3	mainly non-crystalline
rotein, wool keratin	100 to 300	15 to 20	30 to 40 (100)	1·3	complex (α to β transformation)
thetic materials					
olyesters, terylene	1000 to 1800	80	10	1·4	highly oriented, polycrystalline
olyamides, nylon 66	200 to 500	40 to 60	20 to 30	1·1	oriented, mainly crystalline
olystyrene fibres	250 to 400	5	2·5	1·1	non-crystalline

According to Herzog (1926) and Schulze (1926) this is an experiment performed with the truly fibrous 'Balkenlage' of dry elytra of the Goliath beetle (*Goliathus*); it remains unknown whether the resin-like protein component had been oved. *E* was calculated from Herzog's stress–strain diagram.

TABLE V, 5. COMPARISON BETWEEN 'SKELETAL' MATERIALS AND NON-CRYSTALLINE POLYMERS

ypical polymer values from Roff (1956). Figures in brackets refer to compression; * indicates that values in compression considerably higher than in tension.

material and source	elastic modulus *E* in extension (kg/mm^2)	tensile strength (kg/mm^2)	extension at break (%)	remarks
ticle				
pure resilin, dragonfly	0·2	0·3 (0·3)	300	Weis-Fogh (1961*c*)
rubber-like ligament, locust	0·2	—	—	*E* normal to lamellae
solid cuticle, locust	960	9·6	2 to 3	laminate
'Balkenlage', beetle	4500	58	1·3	fibrous, Herzog (1926)
her 'skeletal' materials				
human rib cartilage, wet	1	0·2 (1·6)*	—	Rauber (1876)
human tendon, wet	170	7	—	
oak wood	1000	9 (3·5)	—	
compact human bone	2000	11 (15)*	—	Rauber (1876), *E* in bending experiments
evea rubber				
unvulcanized	0·05	0·1 to 0·3	up to 1200	no interlockings
soft vulcanized	up to 0·5	3	700	few interlockings
hard vulcanized (ebonite)	350	7 (8)	4	space-networks, filled
sins and laminates				
protein, casein plastics	350	8 (25)*	2·5	formaldehyde tanned
phenol-formaldehyde:				
cast, unfilled	280 (600)*	7 (15)*	1 to 5	space-network
cellulose-filled	1000	6 (15)*	1 to 5	
paper laminate	1000 (5000)*	9 (20)*	1 to 5	shear strength normal to lamina 10 kg/mm^2, in plane 3 kg/mm^2
cotton laminate	850 (4500)*	8 (23)*	1 to 5	

chitin crystallites in the lamina are arranged parallel to the surface but otherwise more or less at random (Clark & Smith 1936). This also applies to the lamellae in the rubber-like cuticle, according to our own observations in polarized light. Although the protein is oriented to a certain extent (Picken & Lotmar 1950), the low birefringence of cuticle tells against any high degree of order. This is consistent with the mechanical properties of locust cuticle in table V, 4: they can be explained in terms of chitin lamellae mixed with some material of moderate tensile rigidity and strength (cf. keratin, zein and polystyrene).

Cuticle and other materials

In table V, 5 rubber-like and solid cuticles are compared with other skeletal materials as well as with typical non-crystalline polymers and their laminates. The differences between various cuticles are even greater than between soft cartilage and compact bone. As to the properties listed here, solid cuticle resembles oak wood.

The modulus and strength of pure resilin equal those of other soft, unfilled vulcanizates although natural rubber is stronger in the dry state. Addition of fillers and stronger vulcanization (cross-linking) may increase the modulus to about one-third of that of solid cuticle and the strength to about the same level (ebonites). Vulcanization alone cannot do so because a sharp optimum is soon reached beyond which the strength decreases abruptly (cf. Bueche 1957*a*). It is therefore clear that, in all circumstances, pure cross-linked resilin can account only for rather small values of modulus and strength.

With regard to non-crystalline materials (e.g. polystyrene, table V, 4) and space polymers (e.g. formaldehyde-treated casein, various synthetic resins), a common feature is the comparatively low coefficient of elasticity in extension, about one-third of that for cuticle. The tensile strength of these materials and of their laminates is of the same order as in cuticle. Another general feature is that both the coefficient and the strength are increased several times in compression (marked by an asterisk in table V, 5). These generalities may have an important bearing upon our understanding of arthropod cuticle, the role of tanning and the incorporation of minerals (cf. bone). A soft laminate cuticle may have considerable strength parallel to its surface but little rigidity in compression and flexion. If such a cuticle is soaked with a protein which eventually becomes tanned to an all-embracing resin, this process need not result in any large increase in tensile strength or modulus but it is bound to cause a considerable increase in compressive strength and modulus and therefore in flexion rigidity. This is probably the essential point in hardening whether it happens as a result of tanning or by incorporation of minerals.

The failure to demonstrate any significant difference in *tensile* strength and elastic coefficient between young (mainly tanned exocuticle) and old tibiae (mainly softer endocuticle) is in accordance with the above view. It is obviously necessary to investigate the properties in *compression* for both cuticular layers separately, since the cantilever experiments and the buckling of the tibia may be misleading on this particular point (but not for the cuticle as a whole). It may be that the supposedly smaller values for the thick endocuticle in compression happen to be compensated by the larger values for the thin exocuticle.

On the whole, the known properties of solid locust cuticle agree well with similar properties of cellulose-filled resins and of true laminates made from resin and paper or cotton, i.e. with combinations of particles or sheets of crystalline polysaccharides with some kind of a space-network, whether an actual resin or a hard vulcanizate. In the latter case, however, the rigidity to compression is not likely to be nearly as high as after true protein tanning. These results therefore support Pryor's views as given by Wigglesworth (1948). In future investigations, more attention should be paid to variations in modulus and strength with the nature and direction of the strain.

(*c*) *The significance of resilin*

Resilin is a space-network of thermally agitated polypeptide chains held together at intervals by covalent cross-links. The cross-linking is almost perfect since the material is completely insoluble although the chains are strongly solvated by water. Since secondary links seem to be absent (cf. Weis-Fogh 1961 *c*), a deformation which does not break primary bonds has no permanent effect; after the strain the material will regain the initial, most probable external and internal configuration. This explains the full elastic recovery of the rubber-like cantilever in figure V, 23. What happens is that the felt-like lamellae of chitin tend to flow and therefore to decrease the rigidity of the structure as a whole but the resilin does not flow. Since it dominates the behaviour, the structure takes up its external shape almost immediately after removal of the load but, since it acts as a glue between the lamellae, the minute dislocations of the solid parts (flow) set up small strains in the rubber adjacent to them. The immediate return is therefore only apparent, as is seen from the quick loadings after the prolonged ones, but it becomes complete within a few minutes because of the restoring forces in the rubber.

Figure V, 25 also needs some comment. One may expect that since the loss factor depends on viscosity it should increase linearly with frequency; in actual fact it approaches a constant value. This is known in many polymers and can be understood as a sequence of elastic elements with different, independent viscosity elements distributed along the equivalent chain (Pelzer 1957), an idea which agrees well with the molecular structure of swollen resilin.

A comparison between figures V, 17 and V, 25 indicates that, even at large strains, the small loss factor of rubber-like cuticle (resilience 96 to 97 %) is due to the presence of resilin, the loss factor of which must be even smaller. The resilience of glass is 95 %, of steel and natural rubber about 90 %; some synthetic rubbers may give slightly higher values (see Buist 1961). We have been unable to find figures as high as those for resilin. The loss factor of rubbers depends *inter alia* on how perfectly the molecules have become cross-linked into a network with stable entanglements (Bueche 1957 *b*). The high resilience of resilin therefore indicates that it is a particularly complete and regular molecular network.

The work on solid cuticle was done in 'Vindlaboratoriet', The Technical University of Denmark. The investigation of the rubber-like cuticle took place in Cambridge University, Department of Zoology. It is a pleasure to thank Professor Sir James Gray, F.R.S., and Professor V. B. Wigglesworth, F.R.S., for excellent working conditions and Professor J. W. S. Pringle, F.R.S., and Dr K. E. Machin for their active interest and help. The work was supported by a grant from The Department of Scientific and Industrial Research. The Anti-Locust Research Centre, London, provided the locusts.

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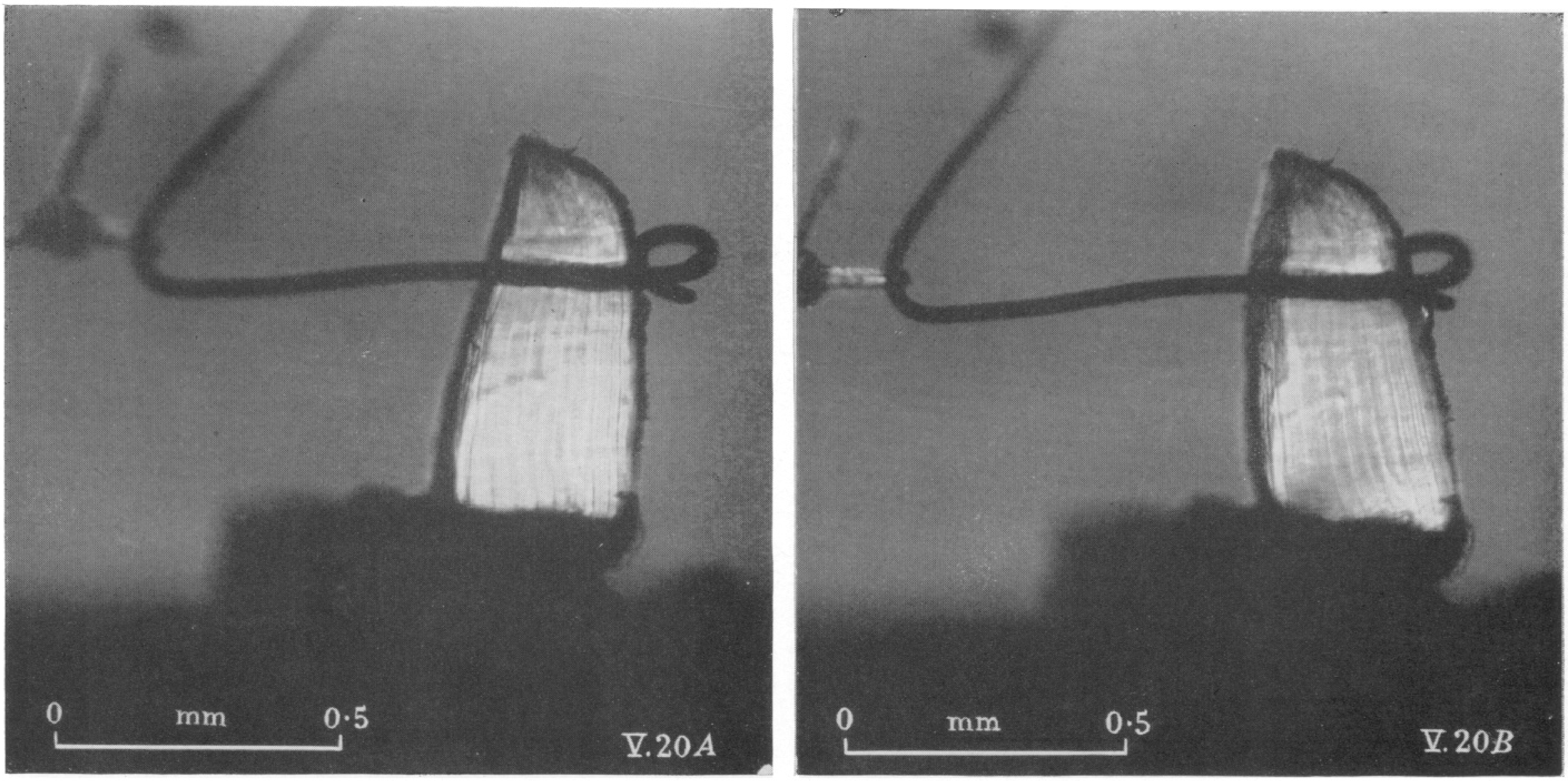

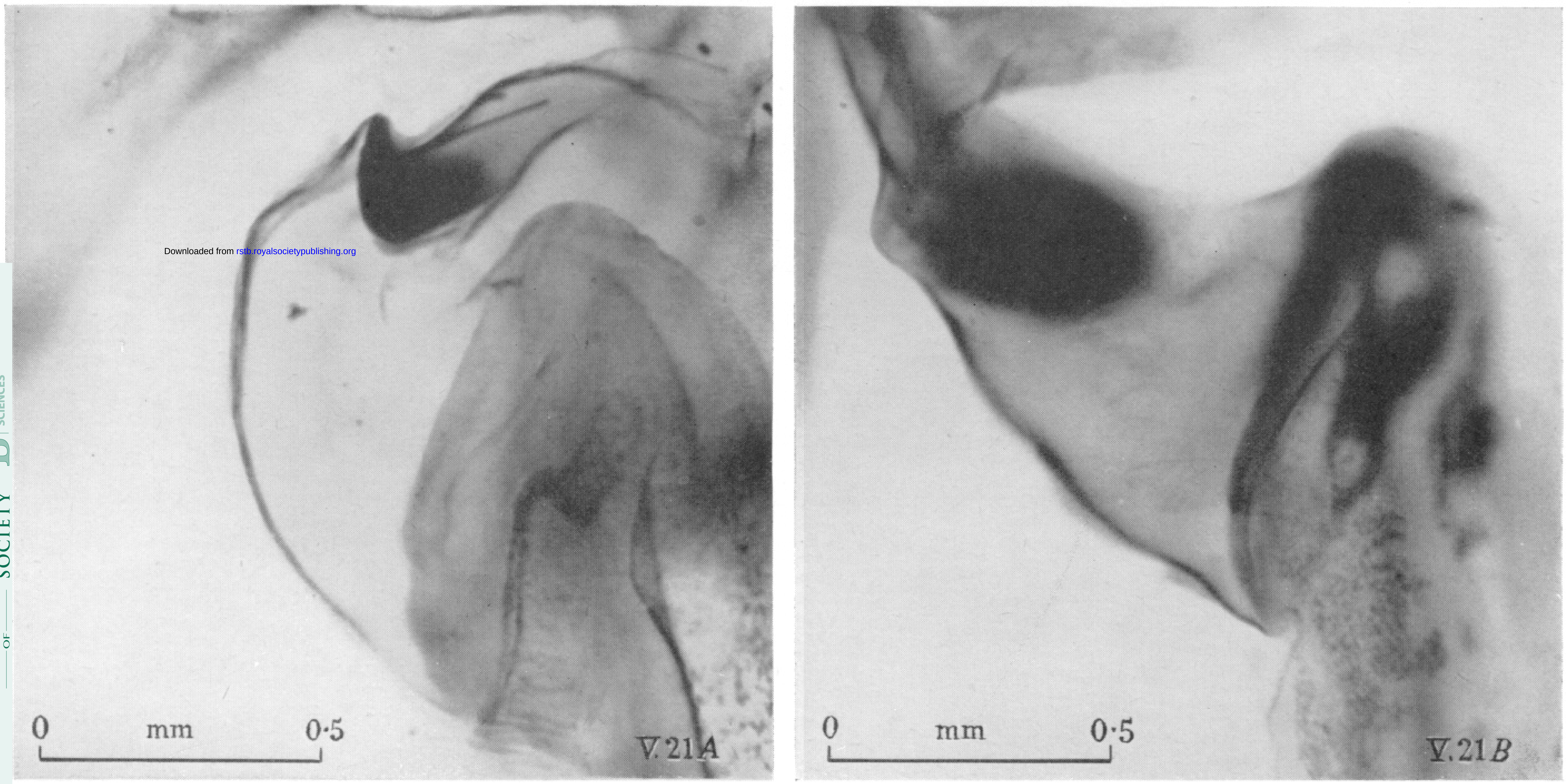

FIGURE V, 20. Small cantilever of rubber-like cuticle viewed from the edge of the chitin lamellae and placed between crossed Nicols (first-order-red gypsum plate). *A*, unstrained; *B*, strained within the linear range. In locust saline at pH 6·7.

FIGURE V, 21. Rubber-like hinge ligament of the right forewing of *Schistocerca gregaria*, viewed towards the head, ordinary light. *A*, with the forewings in the resting position 45° below the horizontal. *B*, after the forewings have been raised 45° above the horizontal by means of a downward push on the mesonotum. (From dehydrated preparations in balsam; similar deformations are observed in the fresh condition.)