

THE HIND WING OF THE DESERT LOCUST (*SCHISTOCERCA GREGARIA* FORSKÅL)

I. FUNCTIONAL MORPHOLOGY AND MODE OF OPERATION

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Summary

Detailed morphological investigation, mechanical testing and high-speed cinematography and stroboscopic examination of desert locusts, *Schistocerca gregaria*, in flight show that their hind wings are adapted to deform cyclically and automatically through the wing stroke and that the deformations are subtly dependent on the wings' structure: their shape, venation and vein design and the local properties of the membrane. The insects predominantly fly fast forwards, generating most force on the downstroke, and the hind wings generate extra lift by peeling apart at the beginning of the downstroke and

by developing a cambered section during the stroke's translation phase through the 'umbrella effect' – an automatic consequence of the active extension of the wings' expanded posterior fan. Bending experiments indicate that most of the hind wing is more rigid to forces from below than from above and demonstrate that the membrane acts as a stressed skin to stiffen the structure.

Key words: desert locust, *Schistocerca gregaria*, wing, flight, morphology, biomechanics.

Introduction

The economic importance, availability and docility of desert locusts (*Schistocerca gregaria*) and migratory locusts (*Locusta migratoria*) have made them ideal subjects for the study of animal flight; few insects have been so thoroughly investigated. In the 1950s, the classic, wide-ranging sequence of papers by Weis-Fogh and Jensen on the biology and physics of the flight of *Schistocerca gregaria* (Weis-Fogh and Jensen, 1956; Weis-Fogh, 1956a,b, 1964; Jensen, 1956; Jensen and Weis-Fogh, 1962) set new standards of excellence in insect flight studies and provided the foundation for a long series of subsequent investigations into the kinematics, aerodynamics, energetics, neurosensory physiology, behaviour and biochemistry of locust flight.

For a long time, little attention was paid to the functional morphology of the wings themselves. Jensen (1956) recognised that they change shape during flight, and described how the fore wings of tethered *Schistocerca gregaria* alter cyclically in profile through the stroke, flexing during the upstroke along two longitudinal lines, and flattening for the downstroke. He interpreted the resulting 'Z-shaped' upstroke profile as a device minimising drag and unfavourable lift, leaving useful force generation to the downstroke. The greater deformations that the hind wings undergo were acknowledged, but could not then be interpreted in aerodynamic terms. Later, Zarnack (1972, 1982) used stereophotography to investigate the changes in three-dimensional shape of the fore and hind

wings of tethered *Locusta migratoria*, but his aerodynamic conclusions were again limited; too little was known at that time of the significance of wing deformations in flight.

In the 1970s, developments in high-speed cine and still photography provided new, detailed information on the kinematics and deformations of wings in free flight in the laboratory and the field. Baker and Cooter (1979a,b) filmed swarms of *Locusta migratoria* and showed their wing movements to be far more varied than those described in the previous tethered studies. The authors recorded short periods of gliding, and found also that the hind wings often clapped together at the top of the upstroke, by then familiar in other insects as a component of mechanisms for unsteady lift generation (Weis-Fogh, 1973). High-speed photography of insects, including locusts, at closer quarters (Dalton, 1975) supplied information on wing deformations, which could be associated with morphological details. Wootton (1981) showed that insect wings in general include distinct areas variously adapted for support and for aeroelastic deformation, and he reinterpreted the cyclic change in the locust forewing section as a device by which the angle of attack of the distal, deformable, more aerodynamically effective part of the wing could be remotely controlled from the thorax via proximal rigid wing components.

Locust hind wings were recognised to be particularly interesting. It was clear that they played a far more important

role in force generation than the fore wings. The calculations of Jensen (1956) indicated that they were responsible for approximately 71% of the total lift and 75% of the thrust. Later, Cloupeau et al. (1979), working with tethered *Schistocerca gregaria*, measured lift values that were substantially higher than those of Jensen, but confirmed that the hind wings provide by far the greater part of the total aerodynamic force, most of it during the downstroke. They are therefore the principal locomotory organs of species legendary for long-range, high-endurance flight. Locusts migrate huge distances over unproductive country, and their flight system must be highly adapted for efficiency and durability. It is reasonable to assume that their hind wings represent an adaptive peak among wings of their type.

Locust hind wings exemplify a particular kind of wing, characteristic of Orthoptera, Dictyoptera and Phasmida. These wings have a corrugated structure, with rich venation, including many cross-veins dividing the membrane into many small cells. In particular, the anal and jugal areas are expanded into a broad 'vannus', supported by numerous veins radiating from the base and folding fanwise when at rest. Several other orders (Plecoptera, Trichoptera, Hemiptera and Coleoptera) include forms with an expanded hindwing fan, but this is supported by far fewer veins.

Wing corrugation, where the branches of the longitudinal veins alternately occupy ridges and furrows in the structure, provides considerable rigidity to bending across the span, but not to bending across the chord, i.e. along axes parallel to the longitudinal veins (Wootton, 1981, 1992). The degree of chordwise rigidity depends strongly on the form of the cross-veins and the presence or absence of lines of flexibility that cross them. Newman and Wootton (1986) compared the rigid components of dragonfly wings, in which the longitudinal veins are joined by numerous rigid cross-veins, with a series of plate-girders, joined edge to edge, with a zigzag cross section. They further showed, by a series of bending tests, that the membrane of the leading-edge spar of the large dragonfly *Aeshna cyanea* contributes to the rigidity of the structure by acting as a stressed skin, stiffening the cells against in-plane distortion. Other areas of the wing allow far more deformation by virtue of less robust cross-veins, often flexibly jointed to the longitudinal veins (Newman, 1982).

There are major differences between the wings of dragonflies and the hind wings of locusts. Dragonfly wings do not fold up at rest, whereas the most strongly corrugated area of the locust hind wing is a folding structure. Furthermore, dragonfly wings twist extensively in flight, generating weight support on both down- and upstrokes in association with slow flight and hovering. They therefore receive aerodynamic forces alternately from the dorsal and ventral sides. Locusts, in contrast, are more or less limited to fast flight and generate most of their force on the downstroke. Theirs are one-way wings, receiving aerodynamic forces mainly from below.

Locust hind wings therefore merit investigation on several counts: as high-performance representatives of a widespread and important kind of insect wing; as corrugated wings that

need both to function as aerofoils and to fold away; and as wings that are loaded mainly from one side, contrasting with those of the better-known Odonata. Finally, understanding the wings will fill a major gap in our extensive knowledge of the locust flight system.

A programme of research has therefore been carried out into the functional morphology and mechanics of the hind wings of *Schistocerca gregaria*. Some preliminary findings have already been published in summary (Wootton, 1992). In particular, the cyclic, semi-automatic development and loss of camber during the stroke, referred to as the 'umbrella effect', has been briefly described, and a general analytical, but highly simplified, model has been developed for its operation in orthopteroid and dictyopteroid wings (Wootton, 1995).

This study is perhaps the most complete investigation to date of the structural mechanics of any insect wing, and it appears in three parts. This paper deals with the morphology of the hind wing and its articulation, the deformations that it undergoes and their causes, control and significance. The second paper, Smith et al. (2000), will be concerned with the microstructure and mechanics of the membrane, and will measure, map and interpret the distribution of its material properties in different parts of the wing; the first time this has been done for any insect. The third paper, Herbert et al. (2000), will present a rigorous numerical model for the operation of the locust hind wing fan, the first model of any insect wing to incorporate vein geometry and precisely measured material properties, and will verify it both experimentally and with reference to existing kinematic information.

In the present paper, we describe the morphology of the wing in new detail, with particular attention to the form of longitudinal and cross-veins. We provide qualitative information on how the wings move and deform in free and tethered flight. We describe bending experiments aimed at investigating whether the asymmetric loading of the wing in the two half-strokes is reflected in differential resistance to dorsal and ventral loading and to what extent the membrane plays a supporting role as a stressed skin. Finally, we discuss how the two requirements of the vannus – to act as an aerofoil and to fold away – interact and are reflected in its structure.

Materials and methods

Adult desert locusts, *Schistocerca gregaria* Forskål, in the gregarious phase, were bought as required and kept in a constant-temperature room at 25°C.

Morphology

All morphological work was performed on freshly killed insects. Drawings were made from enlarged photographs, with frequent reference to the actual specimens.

Filming

Filming was carried out in the laboratory using a Hadland HiSpeed cine camera, operating variously at approximately 500 or approximately 700 Hz. Locusts were encouraged to fly

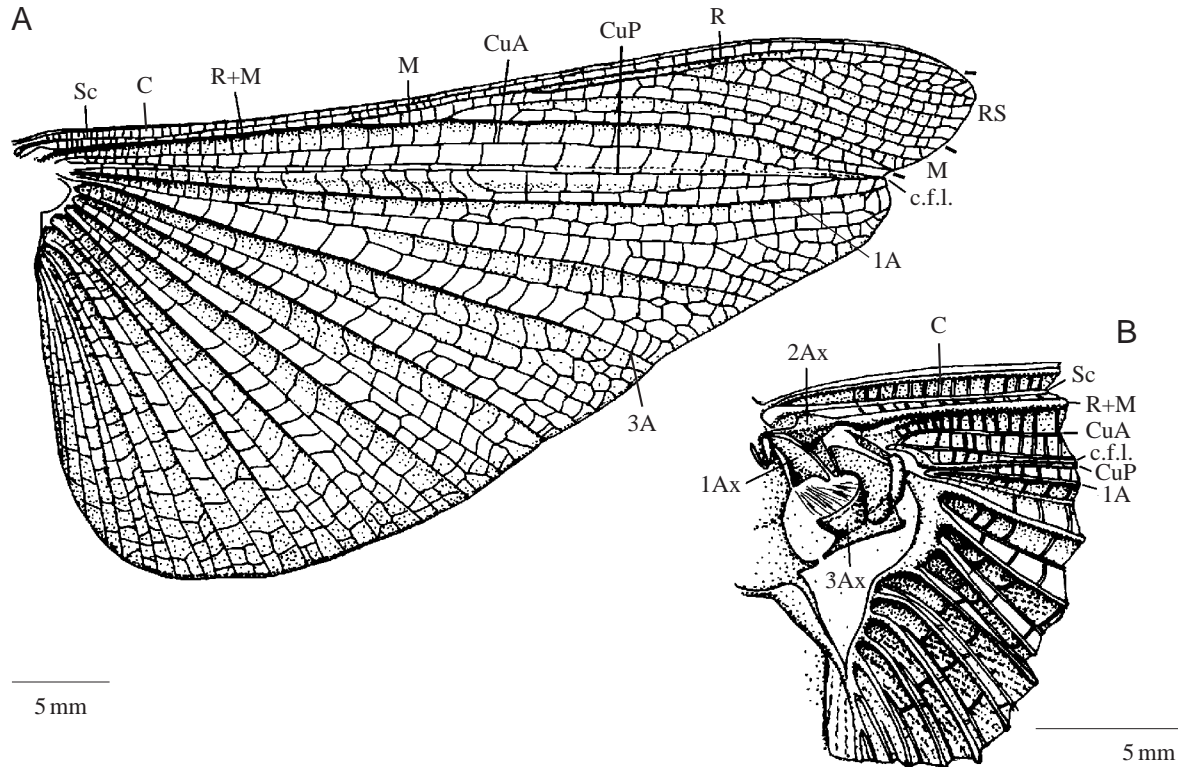


Fig. 1. The locust hind wing. (A) Dorsal view of the fully extended wing, showing venation, relief and the extent of the remigium and vannus. (B) The wing base, the axillary sclerites and their attachments to the thorax. c.f.l., claval furrow; C, costal vein; Sc, subcostal vein; R, radial vein; RS, radial sector vein; M, median vein; R+M, common base of R, RS and M; CuA, anterior cubital vein; CuP, posterior cubital vein; 1A, first anal vein; 3A, third anal vein. 1Ax, first axillary sclerite; 2Ax, second axillary sclerite; 3Ax, third axillary sclerite. The remigium is the area of the wing anterior to the claval flexion line, the vannus the area posterior to the line.

across an arena lined with reflective foil, illuminated by 4.2 kW of quartz-iodine lighting.

Tethered simulated-flight studies

To study the movements of the thoracic articulation and the deformations of the wings, locusts were tethered by attaching a loop of stiff wire to the pronotum, and held in the airflow from a simple open-ended wind-tunnel with a brush motor fan controlled by a variable resistor. Flow was smoothed by paper honeycombs within the tunnel. Flow rate was increased by degrees until the locust was 'flying' consistently and sustainedly with full hindwing extension in the downstroke. Stroboscopic illumination allowed the movements to be apparently slowed or 'stopped' at selected points in the stroke cycle. Details of the wing or axilla at these selected points could then be observed under a stereobinocular microscope on a long-arm stand.

No pretence is made that this represented 'natural' flight. Tethered flight can differ from free flight even when every effort is made to simulate natural conditions (Gewecke, 1982). Indeed, stroboscopic illumination alone may influence the flight pattern. Here, the insect was not supporting its own weight, had no choice of airspeed and was unable to control its body angle relative to the flow, and any attempt to derive quantitative data on wing kinematics or wake structure would be valueless. Nonetheless, we believe the conditions to be

acceptable for qualitative study of the basic thoracic movements and alar deformations of the stroke cycle.

Bending tests

Bending tests were carried out (i) to determine the flexural rigidity of wing components to dorsal and ventral bending and (ii) to investigate whether the membrane operated as a stressed skin, contributing to the rigidity of the structure (Newman and Wootton, 1986).

The names and abbreviations of the relevant wing areas and veins are shown in Fig. 1A. All subsequent pictures of the complete wing are diagrammatic.

The hind wings were removed from newly killed locusts. Three kinds of specimen were isolated for testing, each representing a recognisable zone of the wing (Fig. 2). These were as follows. Zone A, the leading-edge spar, cut behind the common stem of the radial and median vein (R+M) and the first branch of the radial vein (R). Zone B, the rest of the remigium and anterior part of the vannus, including R+M and R as far as the point of separation of the radial sector vein (RS). R was cut through just beyond this point, so that RS was included in the specimen. R+M and the most proximal section of R are therefore part of both zone A and zone B and are necessary to provide basal support for both areas. Zone C, the vannus, separated just anteriorly to vein 3A.

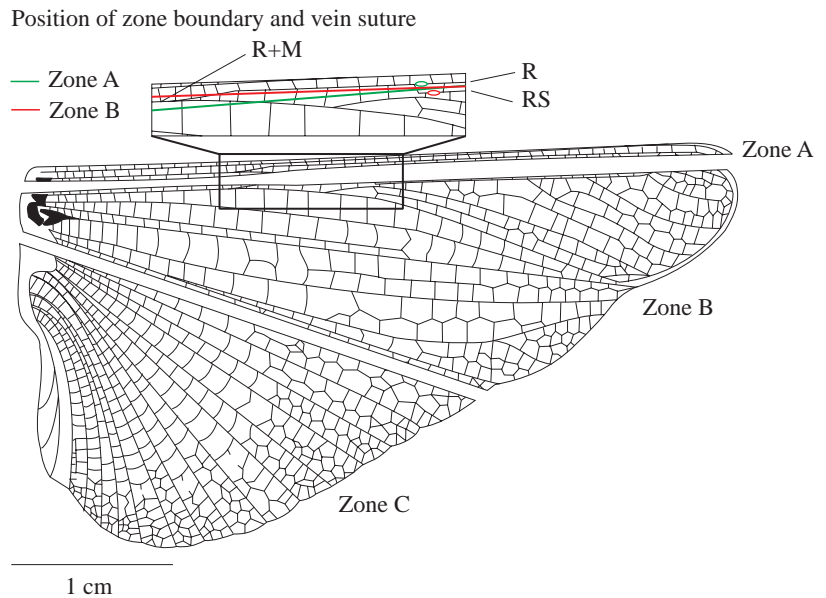


Fig. 2. Diagram showing the extents of the hindwing zones tested in the bending experiments. R+M, common stem of the radial, radial sector and median veins; R, radial vein; RS radial sector vein. The inset shows the location of the cuts delineating zones A and B.

Each specimen was mounted as a horizontal cantilever. Zone A specimens were clamped between two small blocks of balsa with a thin facing of compliant polyurethane foam. The bases of specimens of zones B and C were embedded in quick-setting epoxy resin to prevent crushing of the corrugated base by the clamps. The specimens were kept in a humid chamber until the resin had set, and high atmospheric humidity was maintained throughout the testing by adjacent pads of wet tissue.

Force/deflection curves were obtained with a rig similar to that used by Newman and Wootton (1986) for dragonfly wings. Mounted specimens were gripped in a clamp that could be moved vertically by a rack and pinion (Fig. 3). Vertical movement was measured by an isotonic lever transducer connected to a chart recorder. The specimens rested on a horizontal wire bar suspended from a tared torsion balance with a 10 g range. The specimens were moved down progressively, and at each increment the balance pointer was zeroed and the force read. In comparisons of dorsal and ventral rigidity, the specimen was marked along the line of contact with the bending wire and inverted in the clamp for the second test, ensuring that the wire contacted the wing along the same line. When investigating the effect of the membrane, the wing was first tested with the membrane intact; the membrane was then destroyed in each cell with a mounted needle, and the test was repeated.

The following comparisons were made for each zone. Two specimens were tested in each comparison, and five replicate sets of readings were taken in each test. (i) Intact, ventral loading (from ventral side) *versus* dorsal loading; (ii) ventral loading, membrane intact *versus* membrane cut; (iii) dorsal loading, membrane intact *versus* membrane cut.

Wing deployment tests

The torques required to deploy the hind wings of freshly killed locusts, whose direct and indirect flight muscles had

been removed, were measured using a test rig modified from that used by Wootton (1993) to investigate torsional rigidity in butterfly wings. The technique and apparatus are described in detail in Herbert et al. (2000). Wings were tested as quickly as possible to minimise desiccation. High ambient humidity was maintained by placing wads of wet tissue as close as possible to the specimen during the experiment.

Results

Morphology of the hind wing

The nomenclature of the wing follows that of Wootton (1979). Distinction is made between 'flexion lines', lines of flexible cuticle whose primary function is to facilitate profile change or transverse bending in flight, and 'fold lines', whose

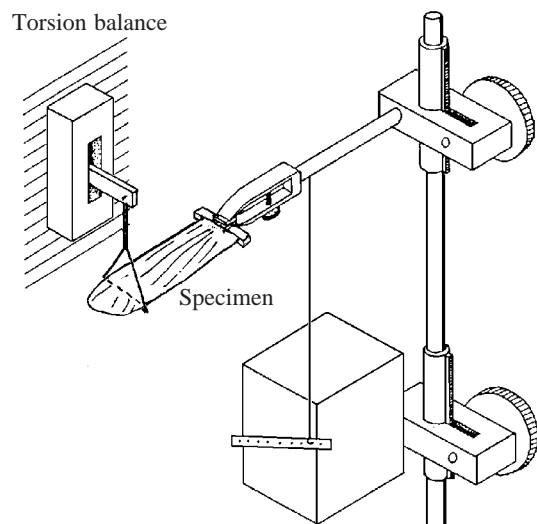


Fig. 3. The apparatus used for the bending experiments. See the text for an explanation.

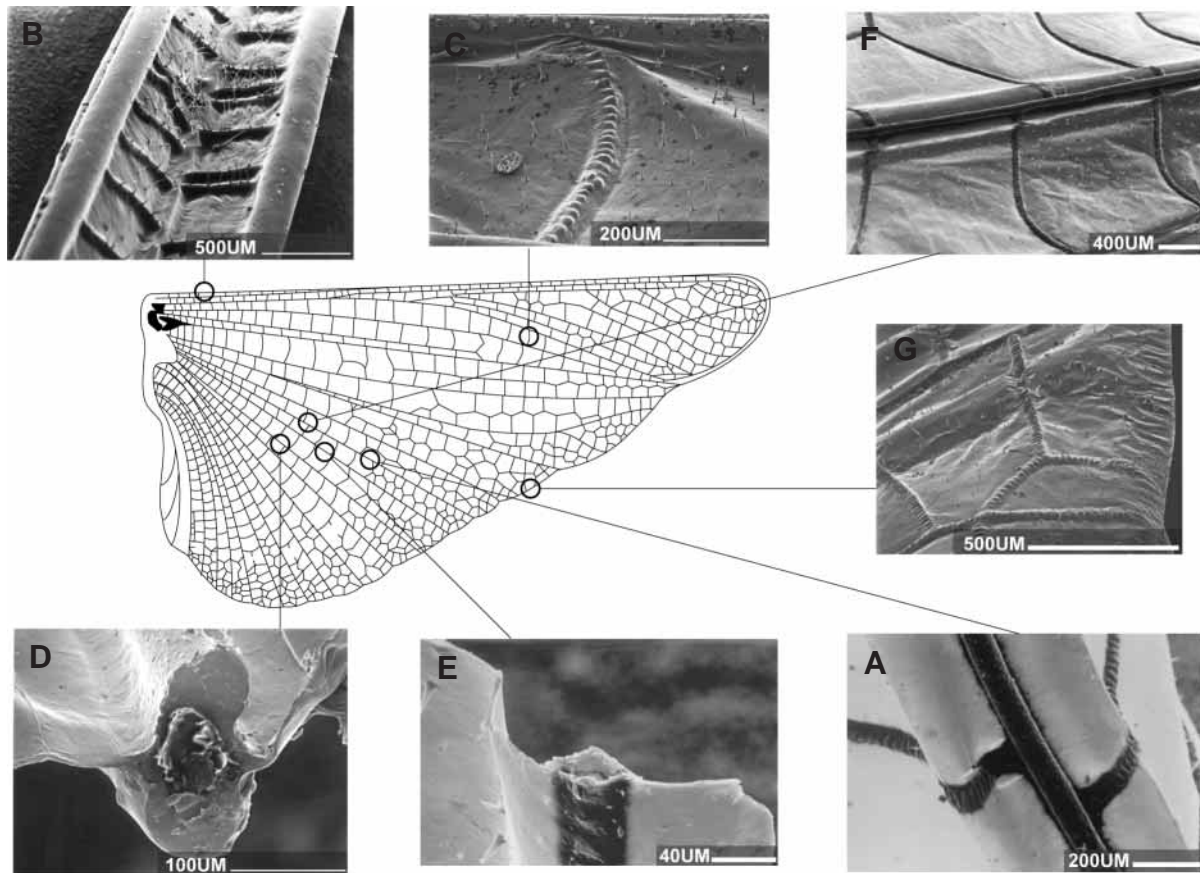


Fig. 4. Scanning electron micrographs showing the detailed form of the veins and membrane at various sites in the wing. (A) Detail of a longitudinal vein in the vannus, with adjacent fold lines crossing flexed and flattened cross-veins. (B) Detail of the leading-edge spar. (C) A flexible cross-vein in the remigium. (D) Cross section of a longitudinal vein on a ridge of the vannus. Note the thick walls and high section. (E) Cross section of a longitudinal vein in a trough of the vannus. Note the thin, flexible, annulated walls and the elliptical section. (F) Ridge vein, flexion lines, curved, flexible, annulated cross-veins and annulated trough vein in the vannus. (G) Vannus margin detail, showing the ends of reticulate veins and the crimped marginal band. UM, μm .

primary function is to allow the wing to fold up at rest, although they may incidentally also assist deformation in flight.

Fig. 1A is a dorsal view of a hind wing. Two areas can be distinguished. The remigium includes all the wing anterior to the claval furrow (c.f.l.), a flexion line that is present in most insect wings. Behind this is the vannus, an expanded, fan-like area with a series of radiating veins and fold lines. The anteriormost of the fold lines is very close to the claval furrow, so that the entire vannus effectively folds up fanwise at rest.

Whereas in the fore wing the remigium is the principal component, in the hind wing its area is far smaller than that of the vannus. Its venation is similar to that of the fore wing, but the cuticle is much thinner.

The veins of the vannus radiate from a curved, sclerotised bar, sigmoidal in shape (Figs 1A,B). The veins on the ridges arise directly from the bar, but are bent at the base. Those in the troughs arise in the membrane a millimetre or so from the bar. For most of their length, the ridge veins are stout, with a high cross-section, whereas those in the troughs are slender, with a cross section that may be circular or an ellipse whose

long diameter is in the plane of the membrane. The vannus is divided into panels by pairs of fold lines, the pairs alternately convex and concave. The panel behind the most anterior fold contains several longitudinal vein branches and is relatively broad. The next is less so, and from there to the inner (posteromesal) margin the panels are narrow and crossed by curved cross-veins, some of which join up to form a network towards the outer edge.

The fold-line pairs themselves consist of narrow strips of pliant cuticle on either side of each radiating vein (Fig. 4A,F). Where they cross the cross-veins, the latter are thinned and flexible. Both membrane and cross-veins are stable in the flexed position; removal of the cross-veins from an isolated piece of wing at a fold leaves the membrane flexed. In consequence, the whole fan is stable in the folded position: it needs to be actively pulled open and always folds up when released.

The remigium is deeply corrugated near the base, with veins on the ridges and in the troughs, but without fold lines. The leading-edge spar consists of three closely apposed longitudinal veins forming a girder with a V-shaped cross section (Fig. 4B). It and the base of the remigium appear to

form the main anterior supports for the wing. The cross-veins in these regions are short, straight and densely packed – a logical situation where the bending moments will be greatest – and become progressively more widely spaced distally. Many of the cross-veins in the posterior and posterodistal part of the remigium are long and curved. The scanning electron microscope shows the walls to be crimped (Fig. 4C), a common adaptation for flexibility (Wootton, 1981). Variations in the structure and geometry of the veins can be of the greatest functional importance, since they can strongly influence the local properties of the wing. They will be examined in more detail by Herbert et al. (2000).

The wing base and its articulation with the metanotum

The hindwing axilla, and the location, sense and roles of its flexion lines and fold lines were described by Wootton (1979). Fig. 1B shows the wing base, the axillary sclerites and their points of connection with the thoracic tergum. The principal hinge about which the wing is raised and lowered is slightly oblique, running posteroventrally between the first axillary sclerite (1Ax) and the anterior and median notal processes, between the third axillary sclerite (3Ax) and the posterior notal process, and across the apex of a sclerotised V-shaped structure formed by a posterolateral extension of the notum and the bar from which the jugal veins arise. The hinge line makes an angle of approximately 12° with the longitudinal axis of the thorax. 1Ax, however, is nearly triangular, with the result that the plane of the base of the remigium, which is hinged to 1Ax via the second axillary sclerite (2Ax), is approximately parallel to the thoracic axis.

The principal wing promoters are the basalar muscles, which pull on the basalar sclerite of the pleuron and, through this, on the anterobasal margin of the wing. The oblique wing hinge probably assists promotion, as a consequence of wing depression. At the top of the stroke, the wing is partly retracted, but it is pulled forward during the downstroke, so extending the fan. During the upstroke, the promoters relax, and the wing partly retracts. This promotion–relaxation cycle leads to deformations in the wing that profoundly influence its functioning.

Wing deformations during the stroke cycle

Fig. 5 shows tracings of single frames from several stroke cycles in a sequence of high-speed film of a locust flying obliquely away from the camera.

At the beginning of the downstroke (Fig. 5, frames 31, 33), the hind wings show the ‘near clap and partial peel’ described by Ellington (1984a,b) as a possible mechanism for obtaining transient high lift coefficients. The effect is known to be widespread in Orthoptera and Mantodea (Brackenbury, 1990, 1991) and has been modelled mathematically by Sunada et al. (1993). As the photographs of (Brackenbury, 1990, 1991, 1992) show, the peeling action is achieved by flexion of the vannus along lines parallel to the radiating veins, creating a shape that resembles part of the surface of a cone. This kind of deformation will here be referred to as ‘radial flexion’.

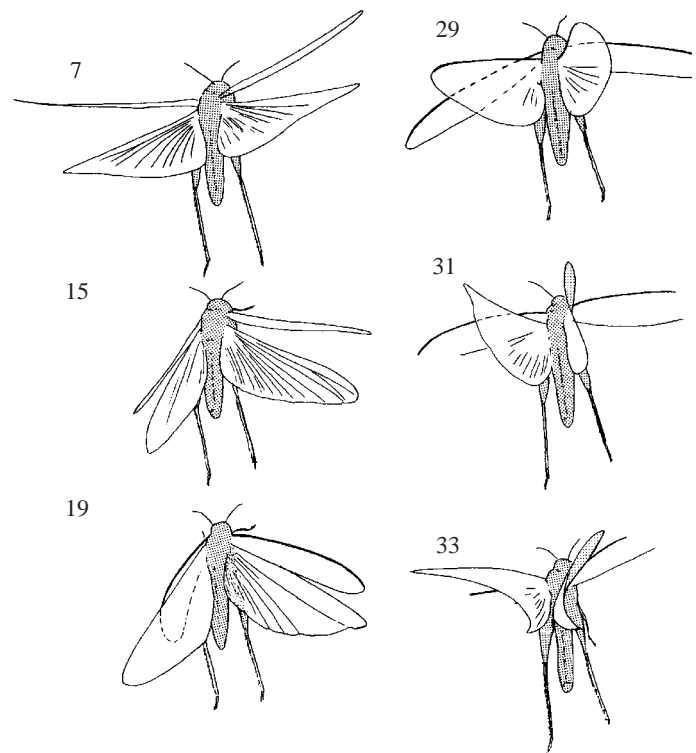


Fig. 5. Tracings from high-speed cine film recorded at 250 frames s^{-1} of a locust in free flight. Numbers represent the frames counted from the beginning of the sequence. An explanation is given in the text.

During the main translational part of the downstroke (Fig. 5, frame 7), the wing is fully extended, and the trailing edge can be seen to be lowered, so that the wing has evidently developed a cambered section. This results from the ‘umbrella effect’, described in greater detail below.

Fig. 5, frames 15 and 19 show the wing at the onset of the hindwing upstroke, with the wing partly retracted and effectively flat. Frame 29 shows the wing in mid-upstroke, showing slight radial curvature, concave dorsally. No chordwise camber is visible.

Fig. 6 shows two stereo pairs of a locust in tethered flight. Fig. 6B is in mid-downstroke and shows the wing fully extended and pulled forward. The trailing edge of the vannus is taut, with no corrugation, and chordwise camber is clearly visible. Fig. 6A shows the wing in mid-upstroke. It is partly retracted, and no camber is visible.

The camber is, therefore, apparently limited to the downstroke, in which the majority of the lift and thrust are generated, and serves two possible functions. These are the enhancement of lift and the maintenance of an effective angle of attack, by preventing the flexible trailing edge from swinging up into the wind.

How is it generated? It can easily be simulated manually by pulling on the leading edge of the hind wing of a dead locust. The wing is stable in the folded position and work needs to be done to deploy it against the elastic resistance of the cuticle. Fig. 7A shows sections at three levels along the span of hind wings fixed when deployed through angles of 60° , 65° and

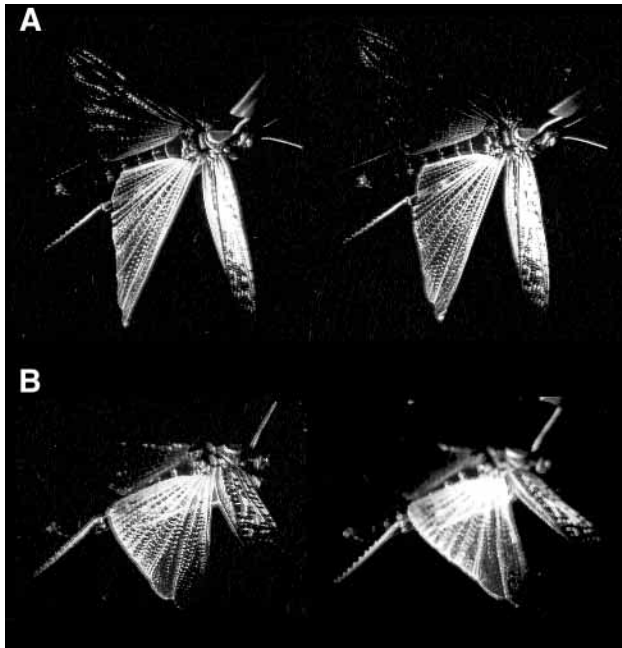


Fig. 6. Two stereo pairs of a tethered locust flying in an airstream. The pairs should be viewed by the 'crossed eyes' method of fusion. The use of a stereo-viewer will create a concave, rather than a convex, image. (A) Mid-upstroke, with the wings partly retracted. (B) Mid-downstroke, with the wings fully extended and the vannus cambered.

85°. In actual flight, the wing may be deployed through as much as 90°, as can be seen in photographs of *Locusta migratoria* (Brackenbury, 1992, plate 45).

Fig. 7B shows a typical torque-deployment curve for a locust wing derived as described in detail by Herbert et al. (2000). All wings tested show a very similar pattern. Comparatively little torque is required to open the folds of the vannus, but this is complete at approximately 0.9 rad (approximately 60°) deployment. Thereafter, the torque required to extend the wing further rises sharply as the load is taken by the now taut, though curved, wing margin, by the sprung cuticular V formed by the posterolateral extension of the notum and the bar from which the jugal veins arise and, in compression, by the anal and jugal veins.

It appears that the generation of camber in the downstroke results directly from the active promotion of the wing, by the combined action of the direct basalar muscles, acting on the leading edge and the indirect depressor muscles lowering the wing anteroventrally about the inclined wing hinge. As the wing is extended and depressed, the fan unfolds progressively until the trailing edge is taut. Further force tends to pull the perimeter in towards the base and compresses the radiating vannal veins, causing them to bend slightly. The veins in the troughs of the corrugations, with their smaller cross sections and thinner, often annulated, walls (Fig. 4C,F), are far more flexible than the ridge veins and tend to buckle upwards into their plane, reducing the stiffening effect of the corrugations and facilitating the curvature. The effect is enhanced by the fact that all the vannal veins are curved, the longer, more anterodistal ones slightly, the

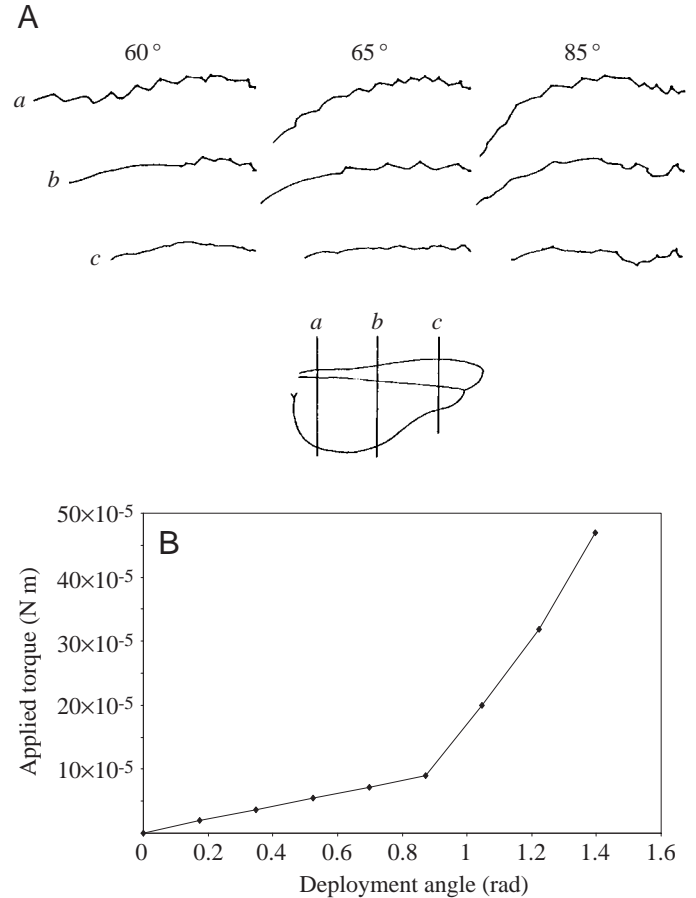


Fig. 7. (A). Sections of locust hind wings, manually extended through angles of 60°, 65° and 85°, showing the camber developed at three places (*a*, *b* and *c*) along the wing. (B) Torque/deployment curve of a locust hind wing. An explanation is given in the text; see Herbert et al. (2000) for details of the methods.

shorter inner ones markedly so. The latter lie in the plane of the membrane when the vannus is folded, but extension twists them out of plane, maximising the curvature proximally. The whole process is made possible by the shape of the vannus, which resembles a truncated logarithmic spiral and causes the tension in the perimeter and the compression forces in the vannal veins to increase around the spiral towards the base and, hence, to resist the extending force; without this, the wing would simply be pulled away from the body (Wootton, 1995).

Bending tests

Fig. 8 shows the results for one of the two specimens tested in each comparison.

Zone A

Both specimens tested to compare the results of loading from the ventral side with those of loading from the dorsal side showed the leading-edge spar to be significantly more rigid to loading from the dorsal side than the ventral side (Fig. 8A). Eventual failure in dorsal loading was by local upward, probably harmful, buckling of the subcostal vein (*Sc*) in the trough of the

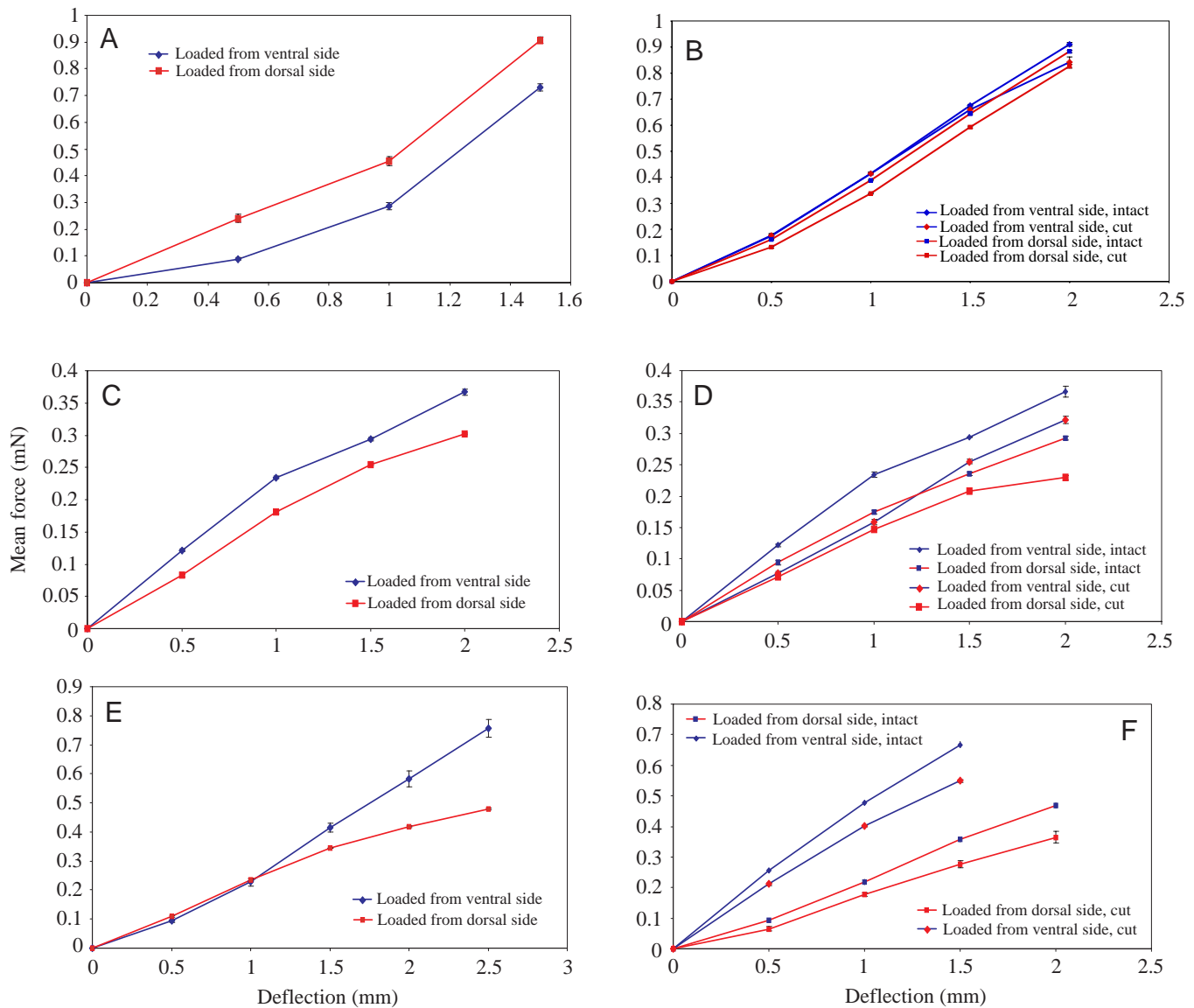


Fig. 8. Typical force/deflection curves of hind wing components for zones A, B and C (see Fig. 2 for definition of zones). Red lines represent samples loaded from the morphologically dorsal side, blue lines from the ventral side. Blue symbols indicate that the membrane was intact, red symbols that the membrane had been destroyed. Each pair of curves represents a different sample. (A) Zone A, loaded from the dorsal and ventral sides. (B) Zone A, two specimens loaded from the dorsal and ventral sides with membranes intact and cut. (C) Zone B, loaded from the dorsal and ventral sides. (D) Zone B, two specimens loaded from the dorsal and ventral sides with membranes intact and cut. (E) Zone C, loaded from the dorsal and ventral sides. (F) Zone C, two specimens loaded from the dorsal and ventral sides with membranes intact and cut. Values are means \pm S.E.M., $N=5$.

spar. Failure in ventral loading occurred by flattening the spar by gentle, non-destructive buckling of the costal vein (C) into the plane of Sc and the radial vein (R), involving flexion of the cross-veins between C and Sc. Tests to discover the effect of cutting the membrane (Fig. 8B) demonstrated that rigidity to dorsal loading was slightly, but noticeably, reduced by destroying the membrane. However, rigidity to ventral loading was unaffected by destroying the membrane.

Zone B

Tests on two specimens showed zone B to be significantly

more rigid to loading from the ventral side than from the dorsal (Fig. 8C). Tests on three specimens demonstrated that cutting the membrane lowered the rigidity; a fourth test was inconclusive. Fig. 8D shows two examples loaded from the dorsal and ventral sides.

Zone C

Both tests showed the vannus to be significantly more rigid to loading from the ventral side than the dorsal side (Fig. 8E). Failure to loading from above occurred by buckling of the slender trough veins into the plane of the stouter veins on the

ridges (Mode 3 failure of Newman and Wootton, 1986). In all specimens tested, destroying the membrane lowered rigidity to both dorsal and ventral loading. Fig. 8F shows two examples loaded from the dorsal and ventral sides.

Discussion

From information in Baker and Cooter (1979a) and from the new high-speed film and tethered flight information, the basic locust hind wing stroke appears to be as follows (Figs 5, 6). During the upstroke, the wing is somewhat retracted and the vannus is relatively flat, or may show some radial curvature, achieved by flexion along the fold lines that lie alongside the veins (Fig. 5, frame 29). At the top of the stroke, the remigium pronates, and the vannus initially again curves along the radii, but is now dorsally convex (Fig. 5, frame 33). Then, as the remigium swings forward and down, the fan is actively extended and develops chordwise camber by the umbrella effect (Fig. 5, frame 7, Fig. 6B), depressing the trailing edge and probably enhancing lift. At the end of the downstroke, the wing retracts enough to lose the camber, the remigium supinates slightly and the next upstroke begins.

In free flight, this basic stroke will be modifiable as needed, in amplitude and probably also in the stroke-plane angle, the shape of the wing tip path and the timing of pronation and supination. If the amplitude is high, the wings will approach each other dorsally, sometimes meeting at the top of the stroke (Baker and Cooter, 1979a) and peeling apart by radial flexion, sometimes performing the 'near clap and partial peel' described by Ellington (1984a,b) and shown in Fig. 5 (frame 33). Both these kinematic patterns are believed to generate extra lift.

The two types of curved section, radial curvature and chordwise camber, are both most evident in the vannus, although the whole wing is to some extent involved. Less conspicuously, in the downstroke, some camber is also visible in the distal part of the remigium, which is shallowly corrugated and supported by parallel veins running distally and slightly posteriorly. This is more noticeable in the fore wing, where the corresponding area, in tethered 'flight' at least, also shows some pronatory torsion in the downstroke and in free flight can flex ventrally during the upstroke. In the hind wing, such torsion and ventral flexion appear to be limited by the broad posterior area.

An important feature of the locust hind wing is the close functional coupling of its principal deformations in flight and its ability to fold at rest. Radial curvature makes use of the vannal fold lines, whose primary function is in folding; and the development and loss of chordwise camber are a direct consequence of the active deployment and partly passive retraction of the vannus, which folds up automatically by elastic recovery of the membrane and cross-veins when the promotory musculature is relaxed.

Wing promotion during flight requires work to be done against this resistance. The folds in the membrane and cross-veins need to be actively flattened, and camber development

requires that the trough veins buckle dorsally towards the plane of those on the ridge. Furthermore, close examination of the wing stroboscopically arrested in tethered 'flight' indicates that appreciable strains are developed in the plane of the membrane. During the downstroke, oblique tension creases appear in the individual cells in most of the wing, but most spectacularly in the vannus. All the tension creases are directed posterodistally. During the upstroke, they vanish from most parts of the wing, although they may remain in the innermost region of the vannus. Each cell appears to act as a Wagner tension field, and in the vannus at least the stresses seem to be transmitted along the panels as a direct consequence of the wing's extension, with in-plane deformation of the cross-veins. All these tension creases represent stored elastic energy, which is a direct cost of flight. The energy involved in deploying the wing in each downstroke can be approximately measured from the area under the curve in Fig. 7B. Some 7.8×10^{-5} J is required to extend the fan and another 14.7×10^{-5} J to further extend the 'umbrella' to 80° . This can be compared with estimates of the aerodynamic cost of flight. Assuming quasi-steady aerodynamics and perfect energy storage, Weis-Fogh (1976) quotes a cost of 0.86 WN^{-1} for a 2 g locust flying at 3.5 m s^{-1} . Assuming a wing-stroke frequency of 15 Hz, this is 1.1×10^{-3} J per wing stroke, approximately 2.5 times the estimated cost of full deployment of both hind wings. From our measurements, the umbrella effect would be a significant proportion of the cost of the stroke.

Economy is a prerequisite for long-range travel, and it is reasonable to expect that the structure of the vannus at least will reflect the need to minimise the cost of necessary deformation. In contrast, the leading-edge spar and the base of the remigium are primarily supporting structures. The functional differentiation between these wing components is clearly reflected in the details of the wing's morphology and in the results of the mechanical tests.

Most aerodynamic force comes from below, and the tests confirm that most of the wing is more rigid to bending from below than from above. However, the leading-edge spar shows the contrary. This is a generally stiff structure formed by three longitudinal veins, more-or-less circular in cross section (Fig. 4B), linked together by numerous short, straight, strut-like cross-veins into a three-dimensional cantilevered truss. The cross-veins increase in frequency towards the base, where the bending moments are greatest, and the spar is V-shaped in cross section. Girders with this section are usually more compliant to loading from below than from above, because the section tends in the former case to flatten and in the latter to become higher: the second moment of area becoming lower and higher, respectively. Interestingly, cutting the membrane reduces the rigidity of the spar to bending forces from above, but not from below. This hints at a degree of pre-stress in the membrane, and further evidence for this will be presented by Smith et al. (2000). In a wing, it is important that any bending that does take place, e.g. through impacts and collisions, should be safe and reversible. In the locust, it seems that ventral bending of the anterior spar of the wing is strongly resisted, or

limited to the flatter distal end, while damage from any dorsal bending would be minimised by the flexibility of the cross-veins between C and Sc, which allows the section to flatten non-destructively and to recover.

Overall rigidity in the posterior, fan-like part of the wing during the downstroke is essential and is evident from the bending tests, even though the vannus was mounted flat in the experiments. The tendency of the vannus to develop camber by the 'umbrella effect' will greatly enhance this rigidity.

However, the process of camber formation involves significant deformation within the vannus. Some components are necessarily compliant, and this is clear in their morphology. The radiating veins of the ridges and troughs of the vannus are quite different in form. The ridge veins have a high cross section (Fig. 4D). These are certainly the primary veins of the vannus; many other Orthoptera have no veins in the troughs, while some have incomplete 'intercalary' veins formed by the secondary alignment of components of a network of cross-veins. The trough veins of the vannus of locusts are clearly unusually complete intercalary veins and presumably reflect adaptations for relatively high-performance flight. They are comparatively slender, their cross sections are circular, tending towards ellipses in the plane of the membrane, and their walls are thin and often annulated (Fig. 4E). This facilitates their bending up towards the plane of the far less flexible ridge veins, contributing to camber generation in the umbrella effect.

The cross-veins of the vannus and to some extent in the broader, more deformable part of the remigium are also adapted for compliance: they are slender, usually curved and, hence, long and they are often annulated (Fig. 4F). Towards the perimeter of the vannus, the cross-veins become reticulate, perhaps providing reinforcement and minimising tearing in an area that will be subject to circumferential tension during the downstroke. An annulated band just inside the vannus margin probably minimises the likelihood of a tear beginning (Fig. 4G).

When examined in detail, the locust hind wing emerges as a highly complex structure adapted region by region to the local requirements of folding and force generation in flight. Two aspects need further consideration. First, it is clear that the membrane plays an important part in the various aspects of wing functioning, and it seems probable that its roles vary around the wing. Its material properties can be expected to vary locally in association with these roles; these are investigated by Smith et al. (2000). Second, the 'umbrella effect', a remarkable example of remote, semi-automatic shape control, deserves more detailed investigation. Wootton (1995) derived a general model for the effect, with many simplifications. Herbert et al. (2000) will derive and experimentally verify a sophisticated numerical model, specifically for the locust hind wing vannus, with most of the simplifications eliminated.

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