

AN APPROACH TO THE MECHANICS OF PLEATING IN DRAGONFLY WINGS

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Accepted 16 June 1986

SUMMARY

A structural engineering approach to the pleated wings of Odonata has been developed during a functional study of wing morphology in the group. The wing can be regarded as a folded plate structure within which each pleat-side acts as a deep plate-girder. Small cross-veins act as stiffeners within the girders, allowing the membrane to carry web shearing forces as pure tension, through a stressed-skin effect. Bending experiments confirm that the membrane significantly increases the rigidity of wing components. The properties of the membrane are unknown. It lacks birefringence, is very thin, and may be pure epicuticle. The advantages of stressed-skin construction are discussed, and possible modes of structural failure considered. The wing seems adapted to yield reversibly to unpredictable heavy loads.

INTRODUCTION

The wings of many insects are corrugated or pleated, at least in part. Those of Odonata are pleated almost throughout. The significance of pleating in stiffening the wing against spanwise bending is self-evident, but is only part of a complicated story. A simple, straight, corrugated membrane is rigid to deflection in one plane but may be very deformable in others; and the overall properties will be strongly influenced by the distribution and arrangement of any supporting members (Wootton, 1981).

An investigation by Newman (1982) of the comparative functional morphology of the wings of a range of Odonata has revealed great structural complexity, with wide variation – both between species and from place to place within a single wing – in vein section, in the situation and form of the cross-veins, and in the nature of their jointing with the longitudinal veins (D. J. S. Newman & R. J. Wootton, in preparation).

Any attempt at formal structural analysis is therefore certain to oversimplify, but may still reveal useful principles. The only such analysis of which we are aware is that of Rees (1975*a*), who calculated and compared the properties of flat and corrugated beams with and without supporting tubes. The beams had the same proportions as narrow longitudinal strips of insect wings. He concluded that corrugation increases

Key words: Odonata, dragonflies, wings, flight, engineering, pleating, membrane.

flexural rigidity, and hence reduces maximum stress experienced for a given loading, with little increase in mass. The inclusion of tubes along the pleat-lines, though increasing the mass, further increases rigidity and decreases maximum stress; and the tubes reduce the probability of catastrophic local buckling of the pleat-lines.

Rees' pleated sections were small, having only a single ridge and valley. They could not show all the properties of a pleated wing, in which adjacent pleats influence each other. We believe that a pleated wing is better analysed as a folded plate structure, behaving as described by Nilson (1961).

THE DRAGONFLY WING AS A FOLDED PLATE

The properties of folded plates

A folded plate structure may be thought of as carrying loads in two ways: slab action and line loading (Fig. 1A).

If a folded plate bears a uniformly distributed load from above, and is evenly supported below – as it would be if resting on a flat surface – then only slab action is seen. The load is carried transversely across the inclined plate-strips between the pleat-lines. Each plate-strip is loaded in compression, and must resist buckling.

If the plate is not evenly supported – for example if cantilevered – then the slab-loads are carried along the pleat-lines to the points of support. This is line-loading.

In either case, no pleat-line can be moved without causing deflection in the adjacent plate-strips. Pleat-line movement can be resolved into a component in the plane of each adjacent strip, and a component perpendicular to it (Fig. 1B). The resistance of each plate-strip to perpendicular deflection is minimal compared to its resistance to deflection in its own plane; and it follows that pleat-line deflections are primarily resisted by the 'in-plane' rigidity of the abutting strips. Each plate-strip acts in effect as a deep beam, which is further supported against bending and lateral buckling by all the other strips of the plate. Folded construction makes each plate-strip effectively edge on to the principal component of its load, and hence maximally rigid; and the total deflection of the folded structure is minimized.

In most man-made folded plates, each component strip is a deep beam of narrow rectangular cross section. By contrast, in the folded structure of a dragonfly wing each strip resembles a plate girder.

Plate girders

A plate girder consists of two flanges separated by a thin, deep web, reinforced by transverse stiffeners (Fig. 2). When a girder is subjected to in-plane bending forces, the flange on the outside of the bend is in tension, the other in compression. The latter will tend to buckle, either laterally or in-plane. Lateral buckling in man-made girders is prevented by the wide section of the flange. In-plane buckling is resisted by the web, and particularly by the stiffeners, which are loaded in compression. If a plate girder is used as a cantilever, with the load passing down the long axis of the cross section, the web is sheared, and the rectangular panels between the stiffeners tend to be distorted into parallelograms. This distortion results in two mutually

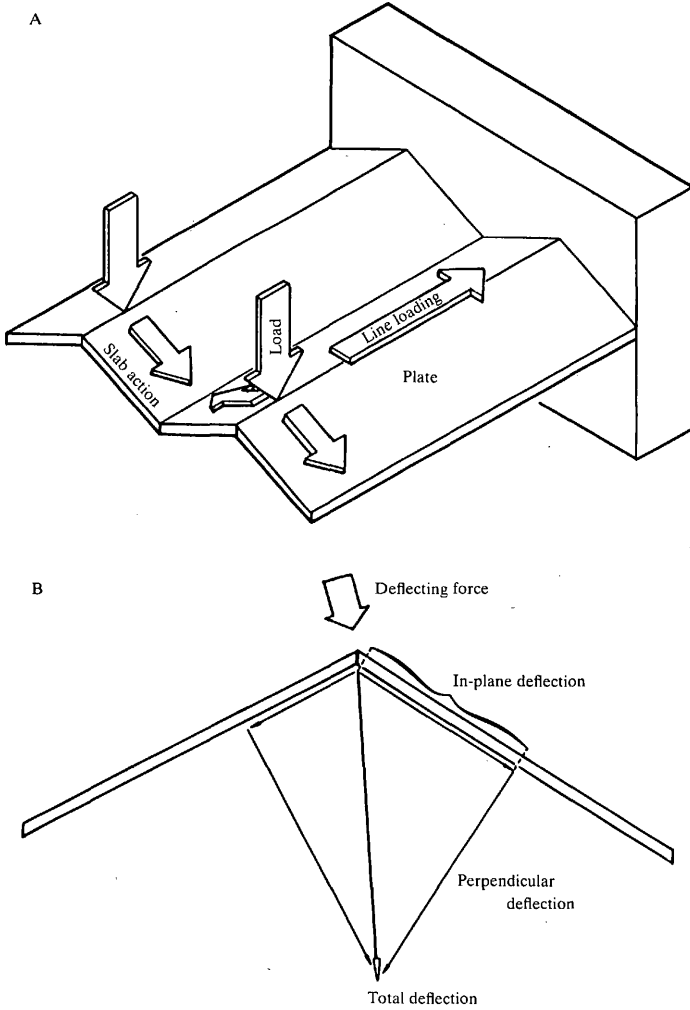


Fig. 1. (A) Slab action and line loading in a cantilevered folded plate. Applied loads are carried across the plates by slab action, and along the plates by line loading. (B) Pleat-line movement. The deflection of each pleat-side is resolved into a strongly resisted, in-plane component, and a weakly resisted, perpendicular component.

perpendicular forces of tension and compression at 45° to the direction of shear, across the whole of each panel. In initially square panels, the forces run parallel to the panel's diagonals; but in elongate panels their direction is perpendicular to the bisector of each of the expanding corner angles (Newman, 1982).

Since the panel material is thin it can only resist the tension, and buckles under the compressive force giving rise to small folds across the panel parallel to the tensile diagonal. This is a Wagner Tension Field. To a certain extent, the girder acts as a Pratt Truss, using all the panel material as a diagonal tensile member, and with the stiffeners in pure compression. If the stiffeners are effectively pin-jointed to the flanges, the tensile stresses in the web are evenly distributed across the panel (Hoadley, 1964). The panel material is acting as a 'stressed skin' or 'tension field system'. Thin sheets of material are commonly used in this way to stiffen frameworks: for example, in artists' canvases and aircraft fuselages.

Plate girders and dragonfly wings

In the wings of dragonflies, the longitudinal veins appear to correspond to the upper and lower flanges of a plate girder (Fig. 3). The web consists of thin, transparent membrane, $2\text{--}3\ \mu\text{m}$ thick, divided into rectangular panels by the slender cross veins, which act as stiffeners. As the wing is pleated, each longitudinal vein acts as a flange common to two 'girders'. The veins are braced against lateral Euler buckling by the cross veins from each of the adjacent pleat-strips.

When the wing is subjected to aerodynamic and inertial forces, each 'plate girder' will deflect as if loaded down the long axis of its cross-section. As the joints between the cross-veins and the longitudinal veins are usually flexible (D. J. S. Newman & R. J. Wootton, in preparation) the panels will deform as described earlier, with the membrane in tension and the cross veins in compression. The membrane may then itself contribute to the rigidity of the wing.

Indirect evidence that this is so comes from the form of the slender cross-veins. When loaded in compression these would be liable to Euler buckling, which might

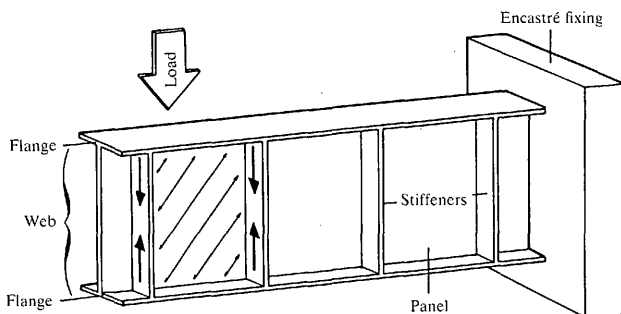


Fig. 2. A plate girder, cantilevered. Loading at the free end results in diagonal tension across the panels and compression in the stiffeners.

take place in any direction. In the absence of lateral support, their predicted cross-section would be circular. In fact many are elliptical or dumb-bell shaped in section, with the long axis of the section perpendicular to the membrane plane. This would decrease their stiffness in the plane of the membrane, were the latter not supporting them.

The idea that wing membrane may function both in support and as an aerodynamic surface is, we believe, new; but it cannot be assumed without experimental test. Much would depend on the properties, as well as the thickness, of the membrane, particularly its Young's modulus and the extent to which it is isotropic. Its Poisson ratio (strain normal to an applied force divided by strain parallel to the force) would seem to be unimportant: in the moderate distortion of a rectangular cell into a parallelogram, ample membrane contraction would be allowed by the shortening of one diagonal as the other lengthened (Newman, 1982).

The shear modulus of the membrane is unknown. If it were low, the sheared membrane would give little structural support. If the membrane were anisotropic, as might be true if it contained chitin fibrillae with a preferred orientation, the angle of the latter relative to the cell would be important. Alignment perpendicular to the bisector of the expanding angle would give maximal support; alignment parallel to the longitudinal veins would permit shearing, resulting in far less diagonal tensile stiffness.

RESULTS

We have investigated three aspects.

(1) Are the diagonal creases characteristic of Wagner tension fields visible in the cells of the loaded wing?

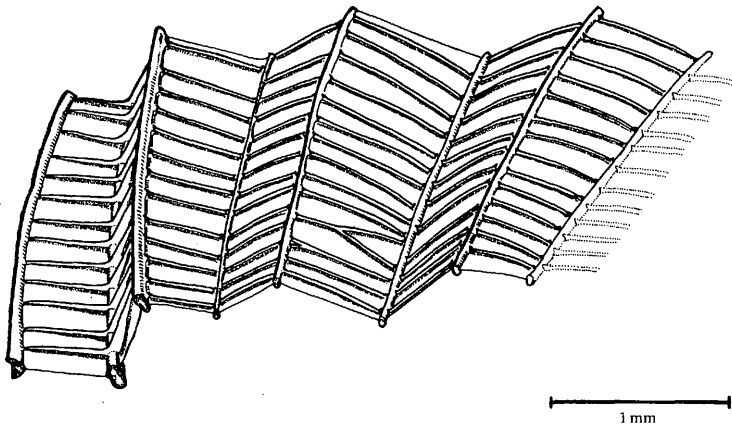


Fig. 3. *Calopteryx splendens*: part of the inner half of a right forewing; basal view.

- (2) Is there optical evidence for preferred chitin orientation?
- (3) Does removal of the membrane affect the flexural rigidity of isolated components of the wing?

Wagner tension fields

Wings of *Aeshna cyanea* (Müller), *Sympetrum striolatum* (Charpentier) and *Coenagrion puella* (L.) were detached from freshly-killed specimens, lightly clamped at the base, and pressed gently with a mounted needle, first from the dorsal side, then from the ventral.

In each case, parallel creases appeared in the membrane of many cells, orientated at approximately 45° to the longitudinal veins. The creases in the cells of adjacent panels, lying on either side of a ridge or a trough, were orientated mutually at right angles. When the direction of loading was reversed, the orientation of the creases in each cell altered through approximately 90°, as membrane which had previously been in compression was thrown into tension. Wagner tension fields were clearly present.

Chitin orientation

Wings of *Aeshna cyanea*, *Sympetrum striolatum* and *Coenagrion puella* were examined using an Olympus BH-2 stereomicroscope with polarizing attachment, both with and without a first-order red tint plate.

No birefringence was detected in the membranes of any of these species. This is in contrast to the desert locust, *Schistocerca gregaria*, and to the cockroach, *Blaberus*, on which parallel studies are in progress, and whose wing membranes show birefringence in many areas.

The absence of detectable birefringence in the membrane of Odonata is not surprising when one considers its thinness, 2–3 µm. The procuticle, if present, must be very thin indeed, and it may well be, as Dr A. C. Neville has suggested to us, that the membrane consists of epicuticle only, in which case there may be no chitin present.

The effect of membrane destruction on flexural rigidity

The four wings, including the humeral and axillary complexes, were severed in turn from a single, freshly killed male *Aeshna cyanea*. The proximal section of the leading edge spar, consisting of the costal, subcostal and radial veins, together with the fused base of the media, together with the linking cross-veins up to and including the nodus, was cut from the wing, and the base embedded in quick-setting epoxy resin glue (Devcon Corporation, Danvers, MA, USA) between two small panels of balsa.

Each spar in turn was mounted horizontally as a cantilever by clamping the balsa panels (Fig. 4). The clamp was mounted on a vertically moving rack-and-pinion

adjustment. The nodus of the spar was glued, using Evo-Stik impact adhesive, into a wire stirrup which was suspended from a torsion balance weighing up to 10 g. The clamp was connected by a vertical thread to an isotonic transducer (Washington, lever type T1), connected to a calibrated chart recorder (Washington 400 MD1).

The wing spar was loaded by racking the clamp down, and returning the pointer of the torsion balance to zero. The applied force was then registered on the torsion balance, and the deflection on the chart recorder. The spar was never loaded to the point of failure; the maximum deflection was 1 mm, so the force could throughout be assumed to be applied normal to the spar: no trigonometric correction was necessary.

A travelling microscope was used to ensure accuracy in zeroing the pointer of the torsion balance – potentially a serious source of error. Care was taken throughout to minimize water loss. Each wing was left on the dragonfly until needed for experiment. The dragonfly was kept in a plastic box in which the atmosphere was water-saturated; and the test spars were returned to the box while the epoxy resin was setting; a maximum of 7 min. During the bending experiments a soaked pad of paper tissue was held within 3 cm of the spar. The entire series of readings was completed within 4 h.

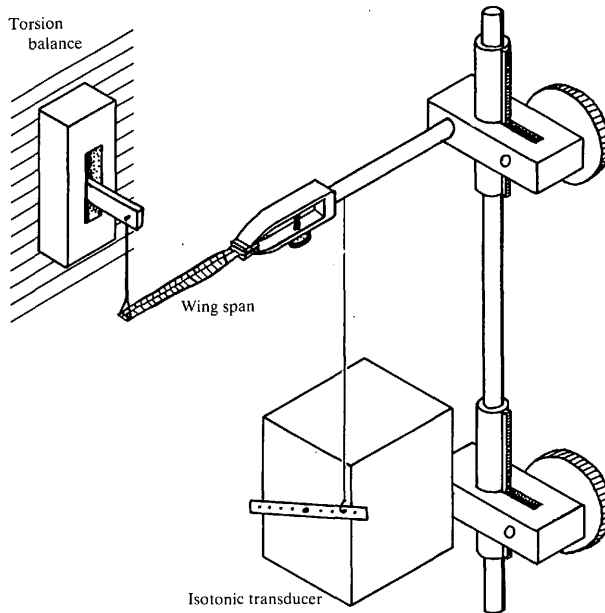


Fig. 4. Apparatus for testing flexural rigidity of wing components.

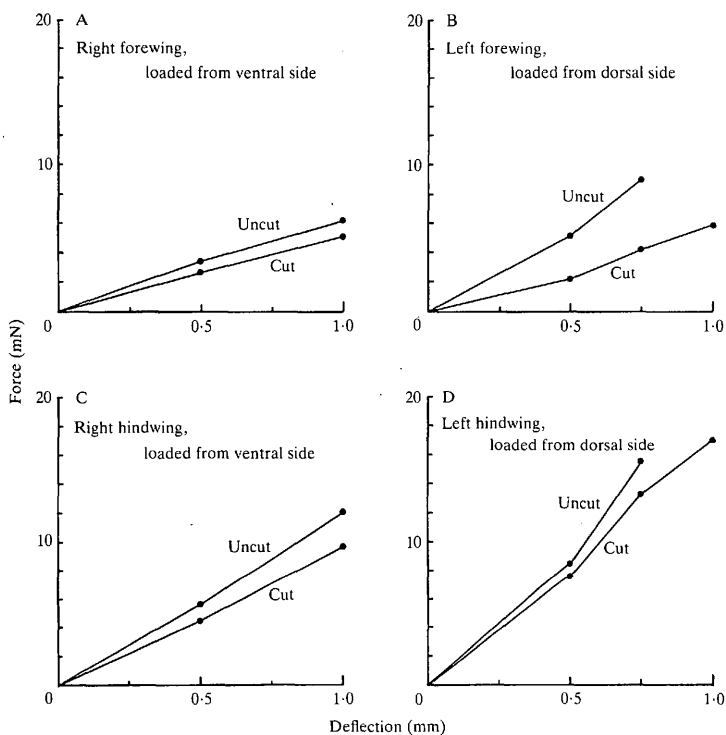


Fig. 5. The effect of cutting the membrane on the flexural rigidity of the leading edge spars of the fore- and hind-wings of *Aeshna cyanea*. (A) Right forewing, point-loaded at the nodus from the ventral side. (B) Left forewing, similarly loaded from the dorsal side. (C) Right hindwing, similarly loaded from the ventral side. (D) Left hindwing, similarly loaded from the dorsal side.

Four wings were enough to test the rigidity of the leading edge spars of a fore- and a hindwing to dorsal and ventral bending, with the membranes intact and destroyed.

Each spar was tested by deflecting the node by two or three small increments, to a maximum of 1 mm, and the restoring force recorded for each value. The load was then removed, and the process repeated, to a total of ten times in all. The spar was then removed – still in its clamp, so no errors could be introduced by reclamping – and laid on a supporting strip of balsa. Without damaging the veins, the membrane in each cell was carefully destroyed by an X-shaped cut with an ophthalmic scalpel. The spar was remounted, and the testing continued a further ten times. Mean values and standard errors were calculated and plotted (Fig. 5). In every case the standard error was too small to appear in the graph.

The flexural rigidity of both fore- and hindwing leading edge spars, loaded both dorsally and ventrally, was significantly lowered by destruction of the membrane (Fig. 5). The extent by which it was reduced differed between specimens; but we have too few data to judge whether the differences are significant.

DISCUSSION

The advantages of stressed-skin construction

It is clear that the membrane contributes significantly to the flexural rigidity of the parts of the wing which we have tested. There is no reason to doubt that this is true elsewhere, although not necessarily throughout the whole wing. No highly deformable areas have been examined.

The primary function of the membrane is to provide an aerofoil surface, and any part which it may play in supporting the wing is a bonus. Yet the system would seem to be very efficient. In the range of Reynolds' number within which Odonata operate, wing corrugation seems to do no aerodynamic harm (Rees, 1975*b*; Newman, Savage & Schouella, 1977). The folded plate, stressed-skin structural arrangement would load the cross veins in compression only, and their design and location could be optimized for compression strength and stiffness.

Furthermore, the many high-speed films of freely flying dragonflies taken by D. J. S. Newman show that in most flight modes the wings turn right over, reverse their camber, and generate aerodynamic force in each half-stroke, so that the membrane is aerodynamically loaded alternately from the morphological upper and lower side. The inertial forces will also reverse as well as fluctuate. In each rectangular cell, therefore, the membrane across any diagonal will be loaded alternately in compression and in tension. A man-made truss subjected to alternate dorsal and ventral loading would require tension members across each diagonal, forming an 'X' within the rectangle. In the dragonfly wing the membrane serves the same function, with the stresses more evenly distributed.

Response to excessive loads

An insect in unimpeded flight has control over the inertial and aerodynamic forces to which its wings are subjected. From time to time, however, the wings may meet unexpected, excessive loads, due for example to sudden gusts of wind or to collision with obstacles. To dragonflies, which may fly for several weeks and which rely on flight for feeding and reproduction, it is vital that these forces cause minimal harm to the wings.

Two adaptive strategies are possible: to construct the wings so stiff and strong that they can resist all the forces which they encounter; or to build them to yield briefly, without damage, and to recover immediately.

Intuitively the second strategy seems preferable. Increased strength and rigidity needs thicker cuticle, some of it towards the wing tip, where most impacts occur; or deep corrugation; or both. The former would increase the moment of inertia,

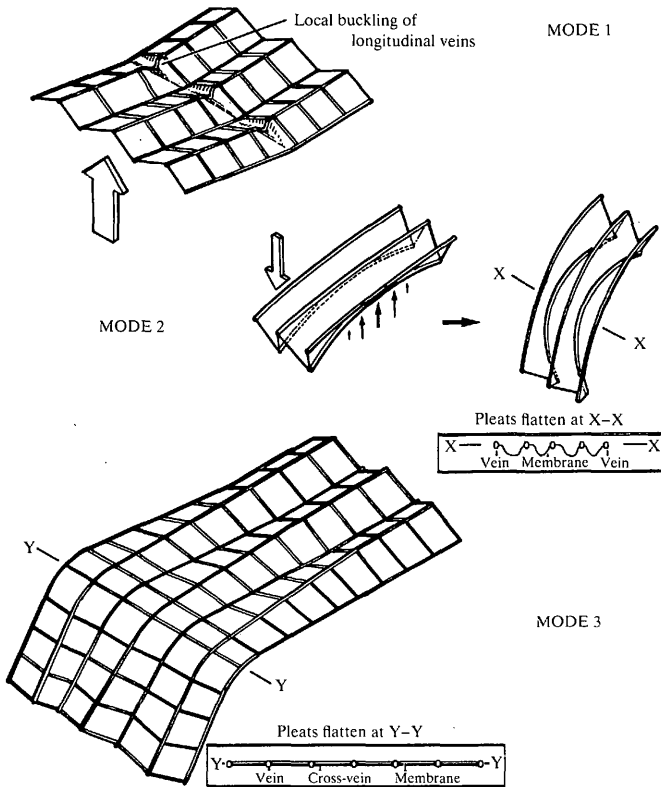


Fig. 6. Three modes of yielding in pleated wings. See text for explanation.

to the detriment of flight performance. The latter might well bring adverse aerodynamic effects.

By contrast, a lightly built wing which deflected under high loads, with rapid recovery, could be virtually unbreakable, since its behaviour need never permit individual structural elements to be over-stressed.

Manipulation, and some high-speed ciné films, confirm that dragonfly wings do indeed yield reversibly when overloaded.

Failure by buckling of the pleated wing structures, which we have described, can occur in three modes, each resulting in extreme bending and loss of spanwise rigidity (Fig. 6). All can be induced in isolated wings by manipulation.

In Mode 1 the wing fails by local buckling of the longitudinal veins in compression, leading to a kinked, chordwise fold across the pleats.

In Mode 2 failure is by Euler buckling in compression of alternate longitudinal veins up between the adjacent veins, followed by a smooth, chordwise fold in the now flattened surface.

In Mode 3 the pleats flatten out, and a smooth, chordwise fold develops.

Mode 1 must be avoided. Manipulation shows that local buckling of longitudinal veins, with the formation of plastic hinges, tends to cause permanent damage and weakness. Moreover, although the buckling might in life be reversed hydrostatically, the process would be slow, and the insect temporarily incapacitated.

Modes 2 and 3 both involve smooth, non-destructive bending, in which the vein section is only moderately flattened. Recovery, in each case brought about by cuticle elasticity, is rapid, and would cause minimal interruption of normal flight.

Both probably occur in flight, although only Mode 3 bending has been seen in high-speed films, of *Aeshna cyanea* and *Sympetrum striolatum* in collision with the walls of the enclosure in which they were flying (Newman, 1982).

Mode 2 failure, which is easily induced artificially in the pleating near the wing base of the Coenagriidae *Pyrrhosoma nymphula* and *Enallagma cyathigerum*, is favoured where cross-veins are widely spaced, so that the longitudinal veins have little lateral support. Where cross-veins are more frequent, Mode 3 failure is usual, and it is probably general when the shallowly pleated wing tips brush against obstacles.

It should be appreciated that the ready, quickly reversible yielding of the wings under excessive loads is a consequence of the relative thinness and flexibility of the longitudinal veins which the pleated structure allows. Insects with flatter wings, relying on stout longitudinal veins alone for flexural rigidity, tend only to have recourse to sharp, non-catastrophic bending in the distal parts of their wings, where the veins are comparatively slender. More proximally, bending is only permitted at special points or lines of flexibility, like the costal breaks of many Diptera, and the nodal line of cicadas.

In combining rigidity to spanwise bending under normal conditions with the capability of yielding reversibly under excessive loads, the pleated, densely veined wings of Odonata demonstrate one elegant solution to insects' stringent requirement for stiff, durable, ultra-light aerofoils for high-performance flapping flight. Other groups, for example Ephemeroptera, Orthoptera, Dictyoptera, some Neuroptera, and some extinct Orders, have adopted similar solutions. We have found that considering these pleated wings as space-frames, with or without stressed-skin support, is particularly useful in unravelling their functional morphology. The mathematics for analysing comparable man-made structures is available; but the subtlety of insect wing construction, and in particular the local variation in the form of the component members and their interconnections, and of the property of the cuticle, ensure that rigorous structural analysis is still far from practicable.

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