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THE FUNCTIONAL MORPHOLOGY OF THE WINGS OF ODONATA

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The functional morphology of the wings of Odonata is reviewed in the light of recent detailed work on their structure, taken in conjunction with cinematographic analysis of dragonflies in unimpeded flight. Wing-corrugation, combined with a variety of types of cross-vein and of cross-vein/longitudinal vein links, provides resistance to transverse bending while allowing torsion and the development of camber. Controlled torsion, essential to flapping flight, is kept within limits by the pterostigma and by the structure of the leading edge spar, which permits more supination than pronation, so allowing the wing to generate lift on the upstroke and permitting slow, manoeuvrable flight and hovering. Camber and angle of attack are automatically maintained under aerodynamic loading by an array of internal mechanisms including the arculus, the quadrilateral of Zygoptera, the triangle and supratriangle of Anisoptera, and vein-curvature in a variety of broad-winged forms. The slender-based wings of Zygoptera, and their relatively short antenodal spars compared with those of the broader-based Anisoptera, seem to be associated with their generally slower flight.

INTRODUCTION

Dragonflies are unique in achieving spectacular levels of flight performance using wings of fundamentally archaic design. Richly-branched venation, abundant cross-veins, and extensive corrugation, with the longitudinal veins alternately occupying ridges and troughs in the membrane, are characteristic features of many Palaeozoic wings and of most hypothetical insect wing ground-plans. Indeed Odonatoidea are clearly recognisable in the mid-Carboniferous among the very earliest known winged insects (BRAUCKMANN & ZESSIN, 1989). In the Lower Permian, some 60 million years later, odonatoids already display a range of wing shapes (planforms) which parallel several distinct modern groups (WOOTTON, 1976), — and a far greater size-range than now : the span of the largest was some 16 times that of the smallest — compare a ratio of 10 to 1 today.

Not surprisingly the structure and functioning of the flight system of dragonflies have attracted much attention (see PFAU, 1986 for the most comprehensive account and for references to earlier work). Odonata were also among the first groups whose wing morphology was studied from a functional viewpoint. HERTEL (1966) put forward possible aerodynamic explanations for the sculpturing of the leading edge and the spines on the veins — since investigated in detail by D'ANDREA & CARFÌ (1988, 1989). NORBERG (1972) in an important study which seems to have been the first experimental investigation on the structural engineering of an insect wing, presented evidence that the pterostigma acts as an inertial regulator of wing pitching during flight. The significance of corrugation, with some reference to Odonata, was discussed by REES (1975a, b), and he (1975b) and NEWMAN, SAVAGE & SCHOUELLA (1977) demonstrated that at relevant size and airspeeds corrugated wings can perform at least as well as simple flat plates.

In a general discussion of wing functional morphology (WOOTTON, 1981) I drew attention to the fact that the function of corrugation in dragonfly wings varies with its position in the wing and with the local structure of the cross-veins and of their links with the longitudinal veins. This work was followed by a detailed comparative investigation by D. J. S. NEWMAN of the wings and flight of a selection of Odonata, combining high speed cinematography and computer analysis of insects in free flight, with detailed morphological study and some mechanical testing (NEWMAN, 1982 ; NEWMAN & WOOTTON, 1986). This work, sections of which are being prepared for publication elsewhere, was the first of a series of comparative studies in my laboratory on the wing biomechanics of selected insect groups. The present review draws extensively on NEWMAN's account, and incorporates relevant information from the later studies and some unpublished observations, in an attempt to summarize the current state and knowledge of the functional design of dragonfly wings.

RIEK & KUKALOVÁ-PECK (1984) have published a new interpretation of the venation of Odonata, based on fossil material. For ease of communication I here follow the traditional scheme, but without prejudice.

THE FLIGHT KINEMATICS OF ODONATA

In order to understand the structure of the wings it is necessary first to examine how they move and behave in flight. Plenty of information is now available. NORBERG (1975) filmed freely hovering *Aeshna juncea*, at about 500 frames per second, and his results were further analysed by SAVAGE, Newman & Wong (1975). G. Rüppell has taken many superb films, at a similar framing rate, of dragonflies flying freely in the field, and (Rüppell, 1989) has published an account of manoeuvres of 8 species of Zygoptera in 5 families and 12 species of Anisoptera in 2 families. D. J. S. Newman has filmed, at 2000 and 3000 frames per second, specimens of *Aeshna cyanea*, *Cordulegaster boltonii*, *Sympetrum striolatum*, *Calopteryx virgo*, *Calopteryx splendens*, *Ischnura elegans*, *Enallagma cyathigerum* and *Lestes sponsa* all flying freely in laboratory enclosures. Valuable information can also be obtained from the outstanding high speed still photographs of Stephen Dalton (1975, 1982).

In all these one can recognise a fundamental wing-stroke pattern. Dragonflies usually — though by no means always — beat their fore and hind wings out of phase. The stroke is considerably inclined to the longitudinal axis of the body, due largely to the backwardly tilted terga of the pterothorax. The angle of the stroke plane to the horizontal varies between species and between manoeuvres within a species.

As the wing swings anteroventrally in the downstroke it develops a camber, most evident distally, and also a base-to-tip nose-down twist, like the blade of a propeller (Fig. 1a). Both are probably caused by the aerodynamic force,

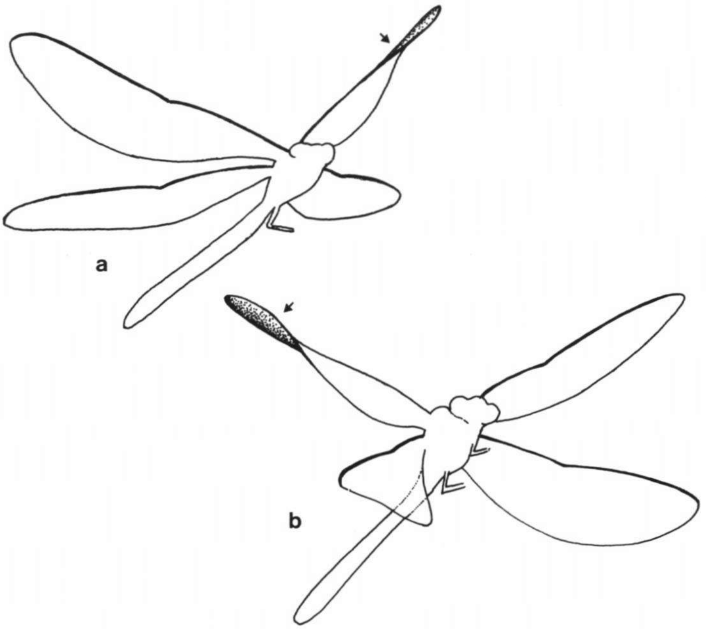

Fig. 1. Tracings from a high speed cine film of *Calopteryx splendens*, showing development of camber and torsion ; (a) downstroke, (b) upstroke.

which is centred behind the wing's axis of torsion (Norberg, 1972 ; Wootton, 1981 ; Newman, 1982), but the camber may be more than simple sail-like "bellying" — as will be discussed below.

At the end of the downstroke the wing undergoes sharp backward rotation (supination). Newman's films show that this involves the trailing edge swinging past the leading edge, apparently under its own momentum, as the latter decelerates and begins its acceleration into the upstroke. Newman (1982) concluded that supination is brought about substantially by inertial forces ; and this seems also to be true of Diptera, whose wings have features in common with those of Odonata (Ennos, 1988b).

Although the relative position of the plates of the axilla changes between half-strokes (Neville, 1960b) the wing base is capable only of limited torsion ; but the distal part of the wing seems almost invariably to be twisted enough to perform the upstroke with a positive angle of attack, so that weight-supporting force is generated on both half-strokes. The camber also becomes reversed, so that the actual upper surface (the morphological ventral surface) again becomes convex (Fig. 1b). At the top the wing again undergoes sharp, largely inertial torsion (pronation) to complete the stroke. At neither pronation nor supination does torsion occur simultaneously throughout the wing ; it travels inboard along the trailing edge as a wave, most clearly visible in the broad-winged *Aeshna*, *Cordulegaster*, *Sympetrum* and *Calopteryx* (Newman, 1982).

This basic pattern is subject to many variations in detail : in amplitude, timing, angular and torsional velocity, stroke angle and body angle ; controlling the mass and direction of the air accelerated downward by the wing-beat. Some of these variations are documented by Rüppell (1989) in his accounts of dragonfly flight manoeuvres.

To what extent Odonata make use of unsteady aerodynamic effects around the points of stroke-reversal is still disputed (Norberg, 1975 ; Savage, Newman & Wong, 1979 ; Somps & Luttges, 1985 ; Azuma *et al.*, 1985 ; Azuma & Watanabe, 1988) ; but it is in any case clear that a large proportion of the useful force is generated during the sweep of the up- and downstrokes. It is with these that we are most concerned in this paper.

STRUCTURAL PRINCIPLES

I have previously suggested (Wootton, 1981) that within nearly all orthodox insect wings can be recognised zones which are primarily adapted to be deformed by aerodynamic, inertial and remote muscular forces, and zones whose principal function is to support the wings and to limit their deformation. More recent work has shown this approach to be valid as a first approximation, but — as I predicted — to be over-simple. Primarily supporting zones undergo some deformation, and primarily deformable zones usually have internal supports and are adapted to deform in some ways, but not in others. All but the simplest wings are now better regarded as flexible aerofoils whose integrated design ensures that they deform predictably and usefully under loads. As such they are in a sense intermediate between "structures" and "mechanisms" in the orthodox meanings of engineers.

The wings of dragonflies illustrate these principles particularly well. We will consider first the implications of corrugation.

THE CORRUGATED WING

Dragonfly wings, like those of Ephemeroptera, show ***complete*** corrugation, with the stems of the main longitudinal veins alternately occupying ridges and troughs in the membrane, and this corrugation is continued beyond the primary forks of these veins by intercalary veins between the branches. The corrugation is deepest near the base, becoming more and more shallow towards the tip and the posterior margin. The veins too tend to be stoutest towards the base.

Corrugated wings, like corrugated iron roofs and pleated fans, are self-evidently resistant to transverse bending. REES (1975a) applied beam theory to corrugated sections, and showed that a pleated membrane stiffened by tubes at the apices of the pleats is a particularly rigid and strong structure. NEWMAN & WOOTTON (1986) suggested that a corrugated wing with cross-veins can be regarded as a 'folded-plate' structure, in which each panel — comprising two adjacent longitudinal veins and the cross-veins and membrane between them — behaves as a plate-girder, resisting bending by tension in one longitudinal vein, compression in the other longitudinal vein and the cross-veins, and diagonal tension in the membrane of each cell. Such a structure would respond similarly whether loaded from below or above. Reversing the direction of the applied force would convert all tensile stresses into compression stresses and vice-versa, except in the cross-veins, which would again be in compression.

NEWMAN & WOOTTON (1986) were able to show that the plate-girder analogy held good at least for the antenodal component of the leading edge spar (C + SC + R) of the wings of *Aeshna cyanea*, by bending isolated spars with the membrane in the cells first intact and then cut. Cutting the membrane appreciably reduced the rigidity of the spar to both dorsal and ventral bending, confirming that the membrane itself has a structural role — as a "stressed skin".

It is important, however, to appreciate that rigidity varies considerably from place to place within the wing. Four factors above all are important: the depth of the pleats, the rigidity of the longitudinal veins, the rigidity of the cross-veins, and the nature of their joints with the longitudinal veins. The latter two vary locally around the wing, but the two former tend to decrease from the base to the tip, and so accordingly does the flexural rigidity of the wing. This is appropriate — for three reasons. **First**, the aerodynamic and inertial bending moments on the wing in flight increase towards the base — see ENNOS (1989b) for a theoretical analysis based on the wings of Diptera. **Second**, the tapering of the veins tends to concentrate the mass of the wing towards the base, thereby minimising its moment of inertia and the energy expended in its acceleration and deceleration during the stroke. **Third**, the probability of accidental collision with obstacles or with other dragonflies in territorial or sexual encounters is probably greater towards the tips. Dragonfly wings, like those of most insects, cope with distal impact forces by yielding to them and recovering rapidly (NEWMAN & WOOTTON, 1986). They therefore need to be rigid enough to withstand the aerodynamic and inertial forces of normal flight, but compliant enough to allow local, non-destructive bending in response to sudden impacts. Where cross-veins are frequent, this can only be achieved by local flattening of the pleats (mode 3 yielding of NEWMAN & WOOTTON, 1986); and this is only possible if the cross-veins are flexible, or flexibly jointed to the longitudinal veins.

The forms of the cross-veins and of their junctions with the longitudinal veins are of fundamental importance. Most cross-veins are approximately circular or elliptical in cross-section, and lie in the plane of the membrane. In several places, however, there are found high-relief cross-veins which tie together groups of longitudinal veins into rigid, three-dimensional girders (Fig. 2). The most obvious are the humeral cross-vein and the deep "primary antenodal" cross-veins, usually two in number, but forming a complete series

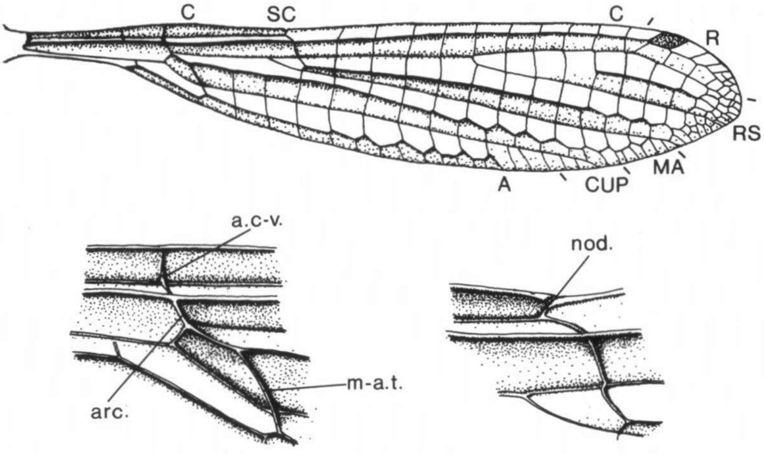

Fig. 2. Hind wing of *Enallagma cyathigerum* (Coenagrionidae), with enlargements of the nodal and arcular regions (nod. = nodus ; a.c-v. = antenodal cross-vein ; arc. = arculus ; m-a.t. = medio-anal tiebar).

in Calopterygidae, and a series whose height diminishes distally in many Libellulidae. These act like angle-brackets, rigidly maintaining the V-shaped cross-section of the leading edge spar proximally to the nodus : the stiffest and strongest supporting beam in the wing. Similar high-relief veins are the medioanal tiebar which holds together MA, CUP and 1A at the distal end of the discoidal cell in Zygoptera ; and the composite vein linking SC, R and RS at the nodus. The latter rigidly couples the end of the concave antenodal component of the leading edge spar, formed by C, SC and R, to the dorsally convex postnodal component, comprising C, R and RS1. The complex behaviour of this spar in flight will be discussed below.

In contrast, flexible or flexibly-jointed cross-veins are essential if the wing is to bend significantly along axes parallel to the longitudinal veins — which is essential if the wings are to develop camber in flight. NEWMAN (1982) found 6 or 7 different kinds of cross-vein junction in the species which he studied. Some were rigid, some flexible both dorsally and ventrally, some one-way only.

THE TORSION-WING

The wings of Odonata have a rigid, relatively straight leading edge, and a curved, flexible trailing edge, without obvious firm support. This kind of wing, which is also typical of Diptera, Isoptera, and some Neuroptera, and is paralleled in the wing-couples of those Hemiptera, Hymenoptera and Lepidoptera in which the hindwing is small and closely linked to the claval region of the forewing, allows extensive twisting at the top and bottom of each stroke. It is therefore characteristic of groups which generate force which supports the insects' weight on both downstroke and upstroke, and are hence capable of slow flight, approaching or including hovering. Rapid flight is not precluded, and the groups which have wings of this kind include the majority of the most versatile and manoeuvrable fliers.

TORSION, VEIN ALIGNMENT AND CAMBER GENERATION : THE ENNOS EFFECT

During a comparative study of the mechanics of wings and flight in Diptera, A. R. ENNOS discovered that wing torsion and camber generation are often intimately linked. In Diptera the leading edge is supported, basally at least, by three parallel veins forming a girder of V-shaped cross-section. Such a spar, with an open section, is resistant to bending, but is not too hard to twist. ENNOS (1988a) showed that the wings of Diptera conform well with a model in which a series of parallel veins diverge posterodistally at an acute angle from a twistable leading edge (Fig. 3a). In flight the aerodynamic

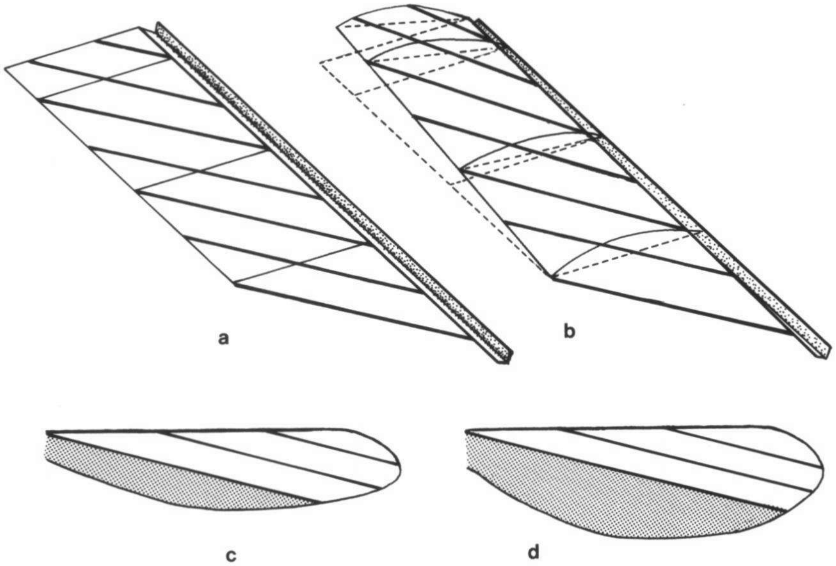

Fig. 3. The Ennos effect (a, b). Pressure applied to the wing from below twists the leading edge spar, raises the veins which diverge from it, and automatically creates camber (redrawn after Ennos, 1988a). — Two diagrammatic wings (c, d), of different aspect ratio, in which the supporting veins diverge at the same angle from the leading edge spar. In the broader wing a far greater area (shaded) is left without support.

force raises these veins, twists the leading edge nose-down, and in so doing automatically generates camber (Fig. 3b), the height of which is inversely proportional to the tangent of the angle at which the veins diverge from the leading edge spar. The mechanism operates whether the wing is loaded from above or below, and so is effective on both downstroke and upstroke.

Ennos suggested that Odonata would also prove to conform to the model ; and Coenagrionoidea, Lestinoidea and *Hemiphlebia* in particular appear from their design to be near-perfect examples. Experiment confirms this : application of a point force close to the theoretical centre of pressure of isolated wings gives precisely the predicted result ; and high speed photographs of Odonata in free flight (e.g. Dalton, 1975, pl. 8 ; Dalton, 1982, pl. 23) beautifully demonstrate the effect.

TRAILING EDGE DEPRESSION : VEIN-CURVATURE ; THE PTEROSTIGMA ; THE ARCULUS ; AND THE DISCOIDAL CELL

Norberg (1972) recognised an important potential shortcoming of wings with a flexible trailing edge. Lacking rigid posterior support, they will tend under aerodynamic loading to behave like flags, rotating to lie parallel to the relative airflow, generating no lift and perhaps developing destructive flutter. It is therefore crucial that mechanisms exist to limit this tendency, and to maintain the wing at an effective angle of attack. NORBERG provided good theoretical reasons, supported by experimental evidence from *Aeshna juncea*, that in many insects the pterostigma provides such a mechanism, by acting as a counterweight in front of the torsional axis, regulating the extent to which the wing pitches up into the wind.

It has since become clear that several of the most notable characters in the dragonfly wing are adaptations to depress the trailing edge and so maintain a functional angle of attack.

The ENNOS model, in its simplest form (Fig. 3) does not in itself assist, since all the veins which diverge from the leading edge spar tend to be raised by the aerodynamic force. Furthermore, since they leave the spar at an acute angle, they inevitably reach the trailing edge well towards the tip, leaving the posterobasal area unsupported ; and the broader the wing, the larger the unsupported area (Fig. 3c, d).

However, as ENNOS (1988a) demonstrated, this is substantially overcome if the diverging veins curve posteriorly. As in the simple model, the aerodynamic force raises the veins to an extent which increases from the base to the tip. In being lifted each vein tends to twist that immediately behind it, in a tail-down sense. If the veins are curved, this twist significantly lowers the trailing edge — below the level which it would occupy if unloaded.

Curved longitudinal veins are characteristic of many Odonata, particular among Calopterygoidea and Anisoptera ; and comparison of a range of species shows a marked correlation between curved veins and wing breadth. *Calopteryx virgo* and *C. splendens*, for example, have broad wings and curved veins, whereas the more slender-winged *C. angustipennis* has far straighter veins. Members of the genus *Sapho* have immensely broad wings, with strongly-curved veins. In two specimens of *Euphaea masoni* which I have examined in the British Museum the female has slender wings with straight veins, the male broad wings with curved veins.

It may be noted here that vein curvature combined, as here, with corrugation has an additional effect, which results from its tendency to be flattened by the airflow. NEWMAN (1982) showed that a pleated structure in which the pleats are curved cannot be flattened out to a planar surface, but instead takes up a curved shape, which is actually part of the surface of a cone. In a dragonfly this would tend to complement the Ennos effect in generating a cambered section.

A third mechanism serving to keep down the trailing edge is provided, in some Odonata at least, by the arculus. This is a transverse ridge vein near the base of the wing, from which arises in Odonata the stem of the radial sector (RS1), and the anterior median vein (MA). In freshly-killed Coenagrionidae and *Lestes sponsa*, at least, point pressure from below in the radial sector field, in the region where the aerodynamic pressure would be expected to be centred, tends to raise RS, and in so doing to impart a nose-down twist to the leading edge and a tail-down rotation to the cubitoanal region, which is transmitted to the anal vein and thence to the trailing edge by the oblique discoidal cell and the high-relief medioanal tie-bar, linking MA, CUP and 1A into a single rigid spar (Fig. 4). This effect parallels the situation in Diptera (Ennos, 1989a), where the arculus appears similarly to have developed in association with a flexible trailing edge, a high degree of wing torsion, and slow manoeuvrable flight (Wootton & Ennos, 1989).

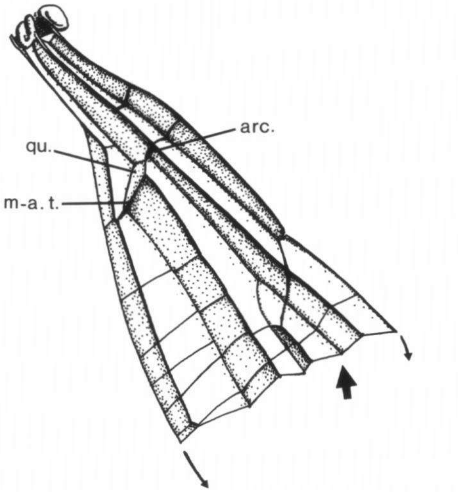

Fig. 4. Hind wing base of *Enallagma*, to show the mode of action of the arculus, quadrilateral and medioanal tiebar. Upward pressure in the field of the radial sector raises RS about a hinge at the arculus, and tends to rotate the leading edge spar and the posterior part of the wing in opposite directions. Torsion of the rather stiff leading edge is limited ; but the posterior area, supported basally by the quadrilateral and medioanal tiebar, is automatically lowered (arc. = arculus ; m-a.t. = medioanal tiebar ; qu. = quadrilateral).

In Calopterygoidea the medioanal tie-bar is short and transverse, and lies some way distally to the arculus. The mechanism nonetheless operates rather similarly. Raising RS twists the whole spar formed by MA, CUP and 1A, and the trailing edge is depressed by a complex, 3-dimensional conformation of the veins in the anal field, bearing some resemblance to that in the libelluloid hind wing — see below.

In Anisoptera the function of the arculus appears to be augmented and to some extent superseded by a mechanism associated with the triangle and supratriangle. These form a high-relief zone of the wing bounded distally by convex veins (part of MA, and the relic of the medioanal tie-bar), proximally by a concave vein (the zigzag-shaped CUP), and crossed by a new concave vein.

Point pressure from below on virtually any point between R and CUP has the effect of sharply depressing the proximal part of the trailing edge. The means by which this is achieved is rather complex and not fully understood. It may vary in detail between families, and in Libelluloidea seems to operate differently in the fore and hind wings. In essence, raising the distal part of the wing raises the distal apex of the triangle and supratriangle, levering the posteroproximal part of the wing downwards about an oblique fulcrum. In *Aeshna*, *Cordulegaster* and the fore wing of *Sympetrum* (Fig. 5a), this fulcrum seems to lie along a line which crosses the supratriangle from the point where MA leaves the arculus to the proximal end of the groove which separates supra-triangle from triangle. The effector arm of the lever thus includes most of the triangle, which in Libellulidae is particularly long, and the distal parts of CUP and 1A. In the hind wing of *Sympetrum* (Fig. 5b) both morphology and functioning are rather different. The fulcrum runs from the base of CUP to the posterior apex of the triangle, which hence lies wholly anteriorly to the fulcrum, and cannot contribute to the effector arm. This role is taken over by the 'anal loop', a large sock-shaped groove in the broad postanal area, characteristic of Libelluloidea, though developed to a variable extent in different members of the group.

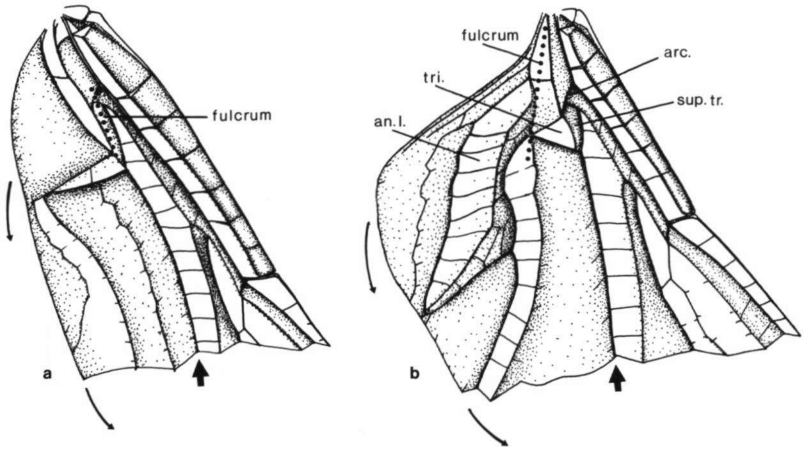

Fig. 5. Fore wing (a) and hind wing (b) bases of *Sympetrum striolatum*, showing the action of the supratriangle and triangle. Pressure from below raises their common distal apex, and lowers the posterior part of the wing about a line fulcrum which is differently situated in the two wings (an.l. = anal loop ; arc. = arculus ; sup.tri. = supratriangle ; tri. = triangle).

Several mechanisms, therefore, contribute to the crucial task of holding down the trailing edge and maintaining an appropriate distribution of angle of attack and camber along the wing. It is of course misleading to consider any of them in isolation: they certainly interact in a complex manner with each other and with the forces which are actively applied to the wing base by the thoracic musculature.

ASYMMETRIC TORSION : THE LEADING EDGE SPAR

Dragonfly wings are mounted not on axles but on flexible hinges: the wing bases can only be twisted to a limited extent. On the downstroke, when the main part of the wing is more or less in the same plane as the hinge, it is close to the limit of pronation; but at the bottom of the stroke it undergoes extensive twisting into the upstroke position. Some of this occurs at the hinge itself; but most takes place distally to the arculus. The torsional compliancy of the wing itself is therefore asymmetrical: starting from the flat position, it can be supinated far more than it can be pronated.

Two factors contribute to this. First, a one-way flexion line in the convex pleat immediately behind the basal part of R allows the pleat to close up when the wing is loaded from above, but not to open further under pressure from below. The second factor is a curious property of the leading edge spar which may prove to be significant in many other insect groups. It is described here for the first time.

As far as the nodus, the leading edge is occupied by the concave spar described above, formed by C, SC and R, rigidly tied together by the three-dimensional humeral cross-vein and primary antenodals. Beyond the nodus, SC is absent, and the leading edge spar, now formed by C, R and RS1, is dorsally convex. The post-nodal section of the spar is far more resistant to pronation than to supination. This unexpected property is due to the fact that the twisting force, whether inertially or aerodynamically derived, is applied at the posterior edge. A beam of inverted V-shaped section, to which an upward force is applied at one edge only, undergoes torsion without significant bending. If instead a downward force is applied to an edge the beam both twists and bends, which allows far more rotation than does torsion alone (Fig. 6).

Taking the spar as a whole: the antenodal component now appears to be a stiffening and strengthening member, whose three-dimensional cross-veins provide flexural and torsional rigidity; basally reinforcing the dorsally convex postnodal component, which is the principal torsion member and provides much of the necessary torsional asymmetry.

This difference in properties between the antenodal and postnodal regions helps to explain the nodus. The latter consists of an alignment of cross-veins

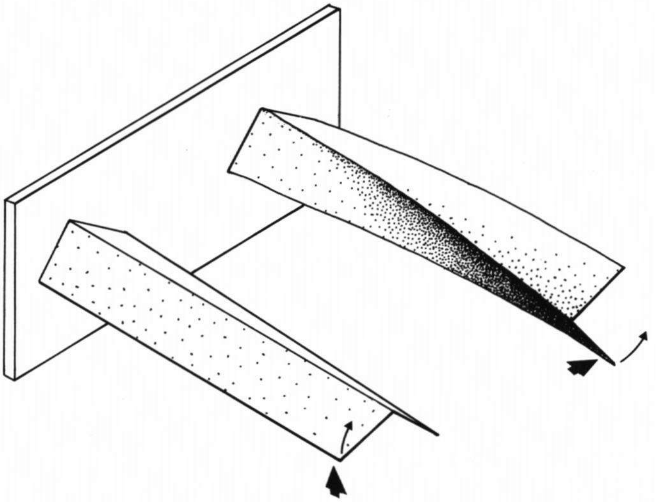

Fig. 6. Asymmetric torsional rigidity of a cantilevered beam of inverted V-section subjected to clockwise and anticlockwise forces applied at one edge.

between C and RS at the point where SC ends, and a band of soft cuticle on the ventral side of C. High speed photographs and cine film show no significant transverse bending at the nodus, so it is not — like similar structures in other insects — the site of a transverse flexion line. The most probable function is shock-absorption (NORBERG, 1972; NEWMAN, 1982), and its significance becomes clear when one considers the stress-concentrations which will inevitably develop at a sharp junction between two spars with very different torsional properties. The cross-veins of the nodus provide reinforcement, and the band of soft cuticle will serve to absorb the potentially destructive energy of the twisting wing.

WING SHAPE AND FLIGHT BEHAVIOUR

We have much to learn about the functional significance of wing shape in insects. It is nonetheless possible to form some tentative conclusions as to the relationship between planforms and flight behaviour in Odonata.

The mean speeds of a series of points along the wing of a flapping insect increase more or less linearly from the base to the tip. If the insect is flying slowly in still air the speed of the extreme wing base will be low — the same as that of the body — and the ratio of the airspeed of the tip to that of the base at any instant during the active stroke will be high. If the insect is flying fast, however, the wing base will also be moving fast, and the ratio of wing tip speed to wing base speed will be lower.

The distribution of aerodynamic force generation along the wing length is more complex, as many factors are involved ; but it is clear that very little lift or thrust will be developed by the basal section of the wing of a hovering or slow-flying animal, and that an insect which always flies slowly will derive little advantage from a broad wing base. By contrast an insect which makes frequent use of fast forward flight will benefit from a broad base, which will generate useful aerodynamic forces without unduly increasing the moment of inertia of the wing.

This generalisation fits well with our knowledge of flight behaviour in several insect groups : Neuroptera, where the narrow-based wings of the slow-flying Myrmeleontidae contrast with the broad-based wings of the fast, predatory Ascalaphidae ; Diptera, where narrow-based, often petiolate wings are characteristic of slow-flying Nematocera, broad-based wings of more rapidly flying forms. Within Diptera the Asilidae, which to some extent parallel Odonata in their predatory habits, include the slow-flying genus *Leptogaster* which has petiolate wings, while stouter, faster-flying genera like *Asilus* have broader wing bases.

In Odonata narrow-based wings seem generally to be associated with slower flight. NEVILLE (1960a) timed the flight speed in still air of a range of species in the field. Values varied between 0.9 and 3.1 m s^{-1} for coenagrionid and lestid Zygoptera, between 2.7 and 11 m s^{-1} for Anisoptera. RÜPPELL's figures (RÜPPELL, 1989) are similar : maximum speeds for Zygoptera (Calopterygidae, Lestidae, Platycnemidae, Pseudostigmatidae) between 1.4 and 2.5 m s^{-1}, for Anisoptera (Aeshnidae and Libellulidae) between 4 and 10 m s^{-1}.

NEWMAN's films (NEWMAN, 1982) suggest that the slow flight of coenagrionoid and lestinoid Zygoptera is associated with generally shallow stroke-plane angles, and with a high degree of torsion. The latter in turn is probably made possible by the relatively proximal position of the nodus, reflecting the relative shortness of the rigid antenodal spar. The extreme is reached in Pseudostigmatidae, whose nodus is usually situated no more than 0.14 of the wing length from the base — compare 0.37 for *Enallagma cyathigerum*, *Ischnura elegans* and *Pyrrhosoma nymphula*, 0.42 for *Calopteryx virgo* and *C. splendens*, and 0.5 for the fore wings of *Aeshna cyanea* and *Sympetrum striolatum* (original observations, Fig. 7). Degree of torsion is hard to measure from film, but RÜPPELL's data (RÜPPELL, 1989, table II) suggest that *Megaloprepus caerulatus* is capable of twisting its wing through c. 130 degrees ; compare 120 degrees in *Lestes viridis* in rising flight , 115 degrees in *Calopteryx splendens* and 75 degrees in *Aeshna cyanea*, both in fast forward flight. These figures are very approximate, and represent different manoeuvres, but they do illustrate the remarkable degree of wing torsion of which Zygoptera in general and Pseudostigmatidae in particular are capable.

The significance of wing breadth is less clear. Both Calopterygoidea and Anisoptera show a wide range of wing aspect ratios, but the flight of closely-

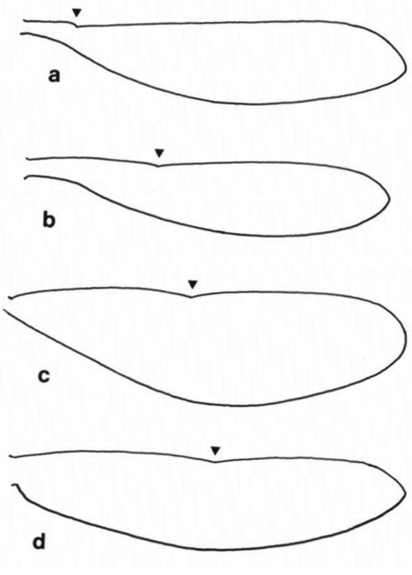

Fig. 7. The relative position of the nodus in selected wings. a : *Megaloprepus caerulatus* (Pseudostigmatidae) ; b : *Pyrrhosoma nymphula* (Coenagrionidae) ; c : *Calopteryx virgo* (Calopterygidae) ; d : *Sympetrum striolatum* (Libellulidae). Not to scale.

related broad- and narrow-winged forms has not been studied comparatively. There is good evidence that unusually expanded hind wings in Anisoptera are sometimes associated with the habit of frequent gliding (HANKIN, 1921), and CORBET (1962) has stressed the value of gliding to migratory species. ENNOS (1989c) has shown theoretically that rather broad wings may aid gliding performance in the size range which insects occupy.

Gliding is less common in Zygoptera, but RÜPPELL (1989) records *Megaloprepus caerulatus*, whose wings are not conspicuously broad, performing long shallow glides.

CONCLUSIONS

It is clear that the exceptionally skilful, versatile flight capabilities of Odonata reflect an extensive range of kinematic patterns, brought about by the interaction of complex thoracic controls with an array of largely automatic mechanisms which are built into the structure of the wings themselves. Corrugation allows strong, light aerofoils, resistant under normal conditions to transverse bending — though capable of yielding locally to absorb sudden impacts — but permitting the development of camber, and of the torsion which is the key to so much of the functioning of the wing. The leading edge spar provides anterior support, and restricts pronation while permitting considerable supination, so that the insects are able to gain weight support on the upstroke and so fly slowly and hover. Posterior support, and effective angle of attack and profile are maintained variously in different groups by the linked effects of vein-alignment, vein-curvature, arculus, quadrilateral and medioanal tiebar, triangle, supratriangle and anal loop.

Much is still poorly understood : the functional significance of differences in wing proportions, in vein branching patterns, in triangle and supratriangle shapes, in surface microstructures. To clarify these quantitative information, gathered where possible in the field, is needed on the flight performance and behaviour of more species in all families — particularly those, like Libellulidae, which show great diversity. Taken in conjunction with a thorough morphometric analysis, information of this kind should be particularly illuminating, with implications which go far beyond Odonata. Given that the functional morphology of the thorax of dragonflies is perhaps better known than that of any other order, and that their aerodynamics, neurophysiology and behaviour are all being intensively studied, we are within reach of a remarkably full and well-integrated understanding of the flight of these most fascinating of insects.

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