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FUNCTIONAL WING MORPHOLOGY AND AERODYNAMICS OF *PANORPA GERMANICA* (INSECTA: MECOPTERA)

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Summary

The functional wing morphology of the wings of the scorpion fly *Panorpa germanica* L. was investigated using a combination of light microscopy, high-speed cinematography, wing manipulation and mechanical testing.

In rising forward flight the wings are flapped 40° out of phase along a shallow stroke plane, the forewings leading. Aerodynamic analysis suggests that unsteady effects are important in flight.

During the downstroke, both wings are straight and cambered, the chord being parallel to the body axis, which is angled 45° upwards from horizontal. Both wings are supinated at lower stroke reversal, the hindwing to a much greater extent, and flex ventrally halfway along their length for the first half of the upstroke. Flexion is parallel to the chord in the hindwing, but is oblique in the forewing, so distal forewing areas are supinated relative to proximal areas.

The behaviour of the wings is related to their structure. Spars at the leading and trailing edges of both wings support the wing during the downstroke, and flexion during the upstroke is facilitated by buckling of the weak ventral thyridium region. The oblique flexion seen in the forewing is due to its relatively longer leading edge spar.

The differences between the wings are, in turn, related to their pitch control mechanisms. The forewing has a well-developed clavus, like that of the forewing of a locust, and pitch is altered by relative movement of this and the leading edge, but only within a narrow range. Oblique flexion is necessary to invert the aerofoil. The weaker and less well-developed clavus of the hindwing, more similar to that of the Diptera, allows a greater degree of supination, effected largely by wing inertia. No oblique flexion is necessary.

Introduction

The morphology of insect wings has long been studied for the purposes of taxonomy, but it is only recently that attempts have been made to understand the

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functional significance of wing venation. Some of the basic principles underlying wing design were laid down by Wootton (1981), who drew attention to the widespread occurrence of supporting zones along the leading and trailing edges of insect wings, reminiscent of the mast and boom of sails, and of deformable zones in between them, reminiscent of the sailcloth. These zones are often separated by flexion lines, which allow relative movement, so altering the wing orientation and profile. In the forewing of the locust (Pfau, 1977, 1978; Wootton, 1979), for instance, the angle of attack of the distal wing region is controlled by alternately creating and eliminating the Z-shaped profile described by Jensen (1956). Weaknesses in the cross veins of many insect wings (including those of *Panorpa*) also allow camber to be set up in the deformable zones.

Ennos (1988*a*, 1989*a*) emphasized the importance of the low torsional rigidity of corrugated insect wings, such as are found in members of the Odonata and Diptera, in which the rear spars diverge serially from the V-shaped leading edge spar. In such wings, the aerodynamic forces encountered in flight will twist the wing, automatically causing a cambered profile to be set up. The wing therefore assumes an aerodynamically efficient propeller shape during each wing stroke.

Both principles may be used in the same wing, and flexion and torsion must, in fact, both occur if camber is to be set up in a wing. In flies, for instance, camber formation involves torsion of the leading edge spar and the cubitus vein, but also flexion of the base of the media (which hinges up and down at the arculus) and bending of the cross veins (Ennos, 1989*a*).

In this study the functional wing morphology of the scorpion fly *Panorpa germanica* (Mecoptera) is examined in the light of the structural principles outlined above, using the techniques of high-speed cinematography, manipulation and mechanical testing, which have been developed in previous studies.

The wings of these insects are superficially similar to those of members of other insect orders, the Megaloptera and the Plecoptera, which seem to have similar flight behaviour. Study of scorpion flies, therefore, might show the basic principles of wing design in such four-winged insects, which possess 'weak flight', driven by nonfibrillar flight muscles.

Scorpion flies are members of the Mecoptera, a relatively primitive order of the endopterygotes, which is widely regarded (see Hennig, 1981) as being the sister group of the Diptera. The study will therefore have phylogenetic implications, which are pursued more thoroughly by Wootton & Ennos (1989).

Wing morphology

The two wings of *Panorpa germanica* are illustrated in Figs 1 and 2 in stereo-pair photographs, a form which allows their three-dimensional nature to be more clearly seen.

The two wings are clearly similar in many ways. First, both are supported along the leading edge by a strong beam of V-shaped cross-section, supported at the points of the V by the costal (*C*), subcostal (*Sc*) and radial (*R*) veins.

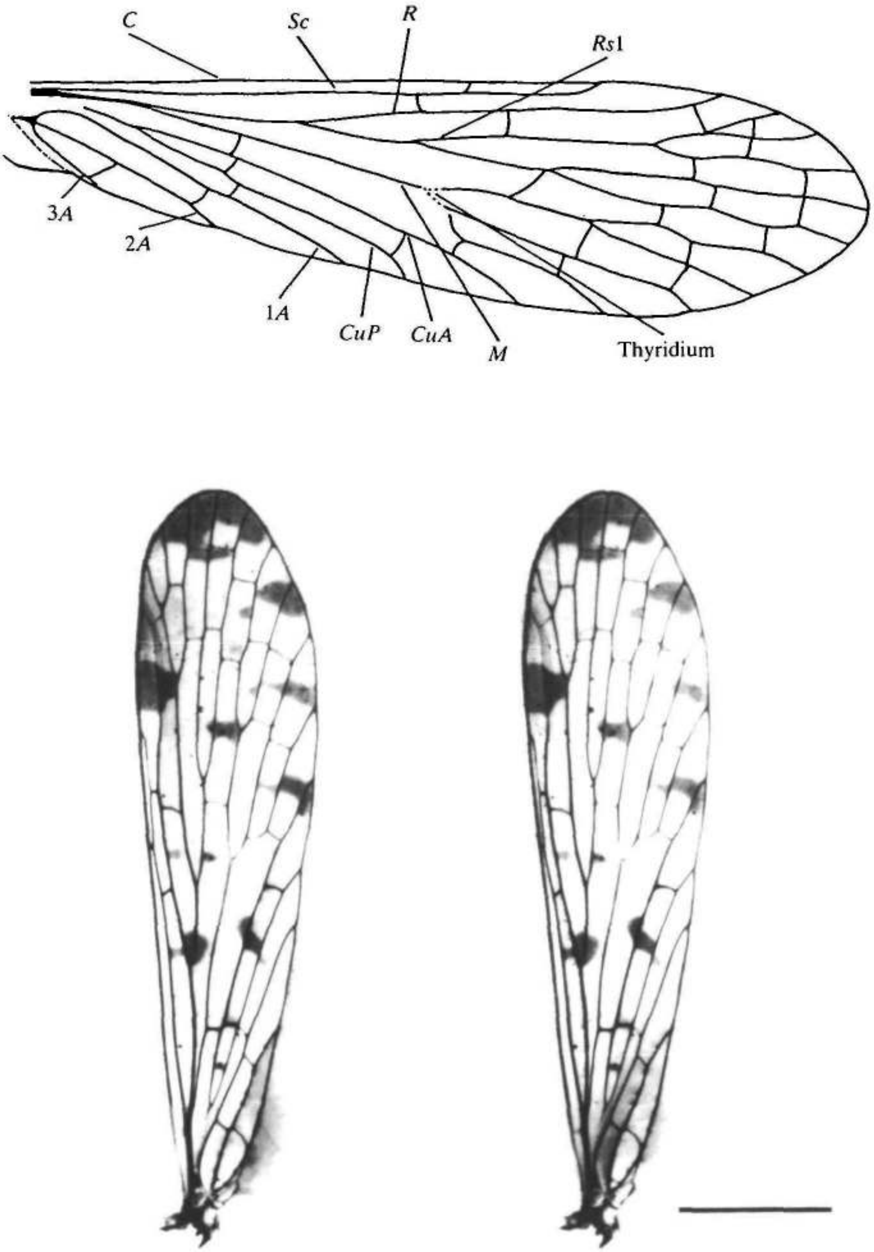

Fig. 1. The forewing of *Panorpa germanica*. The stereo pair shows the relief of the wing and weak, unsclerotized regions of veins can be clearly identified by their pale colour. Note the weakness at the thyridium, which allows ventral flexion, and the weakness of the cross veins which allows camber. *C*, costa; *Sc*, subcosta; *R*, radius; *Rs*1, first branch of the radial sector; *M*, media; *CuA*, anterior cubitus; *CuP*, posterior cubitus; 1, 2, 3*A*, first, second and third anal veins. Scale bar, 2 mm.

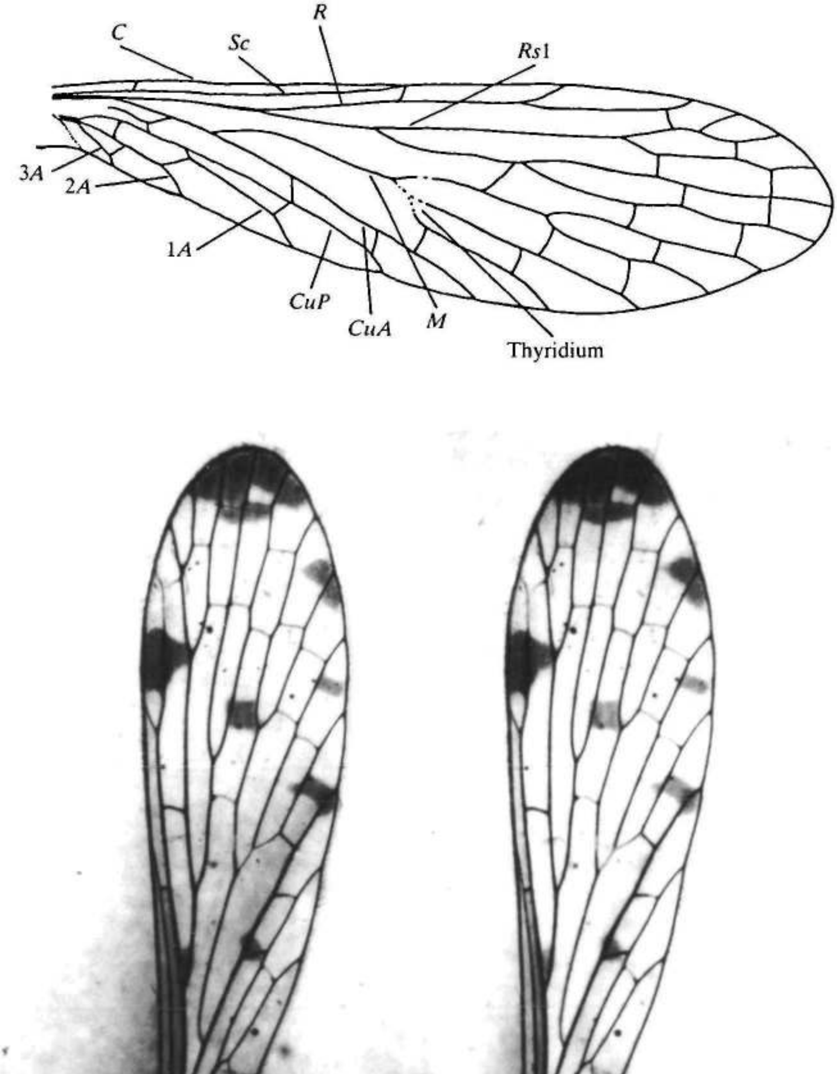

Fig. 2. The hindwing of *Panorpa germanica*. Note the differences from the forewing: the leading edge spar is shorter, as the subcosta ends more proximally; the anal veins are less well-developed; and the base of the stouter anterior cubitus (rather than that of the media) diverges from the radius. Abbreviations as in Fig. 1. Scale bar, 2 mm.

The outer wing region of both is largely flat (as Wootton, 1981, commented), with strong longitudinal veins providing resistance to bending, but flexible, apparently unsclerotized cross veins, which would allow camber to be formed.

Both wings also possess a weakened, unsclerotized area of cuticle, the thyridium, at the point where the media (*M*) branches: a weakening which should allow flexion.

There are several differences between the wings, however, which could be structurally significant. The subcosta (*Sc*) is longer in the forewing, and the leading edge beam therefore extends further distally. The forewing possesses a strong basket-like framework of anal veins at the basal trailing edge, the clavus, which will provide support for this region; and a flexion line, the claval furrow (Wootton, 1979, 1981), separating this region from the rest of the wing. In contrast, the anal region of the hindwing is but poorly developed, with short, weak, anal veins with much lower relief, and a less obvious claval furrow.

Associated with this are differences in the media and cubitus (*Cu*) of the two wings. In the forewing, the two are approximately in the same plane, and the media diverges from the leading edge, whereas the base of the anterior cubitus begins free of other veins. In the hindwing, in contrast, the media is more clearly situated in a ventral corrugation, and the anterior cubitus in a dorsal corrugation of the wing membrane, so continuing the pattern of wing corrugation posteriorly. The media diverges at its rather weak base from the anterior cubitus, which has a strong base at the radius. This arrangement is very similar to that found in the Diptera (Ennos, 1989*a*).

The functional implications of these structural differences were examined by combining study of high-speed films of these insects with manipulations and mechanical tests on the wings.

High-speed cinematography

Methods

Insects were filmed in a Perspex flight box 45 cm high by 30 cm square. They were back-illuminated using an 800 W Redhead ciné light (Rank Strand Ltd), which was focused onto the image plane of a high-speed ciné camera (John Hadland Photographic Instruments Ltd). The focal distance was 75 cm and the aperture was set at f16, with a framing rate of around 2000 frames s^{-1}, calibrated by a timing light, which marked the film every millisecond. 16 mm Ilford Pan F film was used.

Insects were placed on a platform attached *via* a dowelling rod to a loudspeaker, and this was placed in the film frame. The platform was then vibrated at around 17 Hz to provoke flight, simultaneously triggering the camera. Four films of a male *Panorpa* were obtained using this method. Females tended to be more sluggish and, despite being flung from the platform, plummetted to the floor.

Immediately after filming, the insect was weighed, killed, and the series of wing measurements described by Ellington (1984*a*) and Ennos (1989*b*) were taken for each wing. The results are given in Table 1.

Table 1. *Morphological parameters of the wings of* Panorpa germanica

A	m (mg)	R (mm)	S (mm^2)	m_w (mg)	m_v (mg)
Forewing	17·0	11·4	49·1	0·175	0·054
Hindwing		10·2	42·9	0·125	0·047

B	Æ	$\hat{r}_1(s)$	$\hat{r}_2(s)$	$\hat{r}_3(s)$	$\hat{r}_1(m)$	$\hat{r}_2(m)$	$\hat{r}_1(v)$	$\hat{r}_2(v)$
Forewing	10·5	0·545	0·600	0·640	0·48	0·55	0·577	0·619
Hindwing	9·7	0·540	0·594	0·634	0·51	0·57	0·567	0·608

(A) Gross morphological parameters: mass, m; wing length, R; wing area, S; wing mass, m_w; wing virtual mass, m_v.

(B) Shape parameters: aspect ratio, Æ; non-dimensional radii of area, $\hat{r}_k(s)$, virtual mass, $\hat{r}_k(v)$ and mass, $\hat{r}_k(m)$.

Values are for the male *Panorpa germanica* which was filmed.

Results of filming

In all four films of the male scorpion fly, take-off was followed by acceleration into rising forward flight with noticeable banking.

Like most insects so far studied, *Panorpa* beats its wings with near simple harmonic motion back and forth approximately along a stroke plane. The stroke planes of the two wings are almost parallel, but to avoid contact, the forewings tend to be elevated above the plane containing the forewing base, whereas the hindwings are moved below the plane containing the hindwing base. The wing beat amplitude tends to be high, both wings often meeting dorsally in a classic 'clap-and-fling', but the hindwings tend to have the greater amplitude, and often meet ventrally as well. There seems to be some control of the relative phase of the two wings. At take-off, the wings move more or less in phase with a high stroke plane angle, but later in flight the forewings are advanced by around 40°, the opposite of the phase difference seen in locusts (Weis-Fogh, 1956), and very different from the 180° phase difference seen in the anisopterous dragonfly *Aeshna juncea* (Norberg, 1975) and in many of the Zygoptera (Newman, 1982). There must obviously be some aerodynamic interference between the wings, but we are at present unable to comment sensibly on this difficult aspect of flight.

Pitch changes occur in both wings. During the downstroke the chord of each wing is more or less parallel to the body (Fig. 3A), but at lower stroke reversal the hindwings are supinated by around 90°, until the chord lies at right angles to the body axis. The forewing, in contrast, supinates by a much lower angle at its base.

The most remarkable feature of the wing beat is the distortion of the two sets of wings. Both are straight and slightly cambered during the downstroke (Fig. 3A), but at the beginning of the upstroke both wings flex ventrally about halfway along the wing, probably at the thyridium. Flexion of the forewings is oblique to the wing chord (Fig. 3D), occurring more distally at the leading edge. As a result of thi

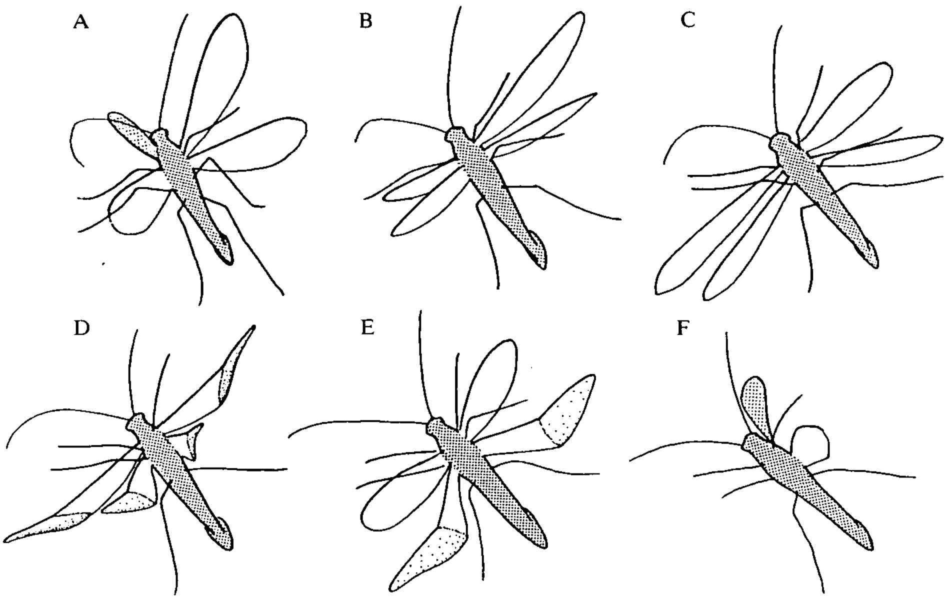

Fig. 3. The flight of *Panorpa germanica*. Consecutive film tracings from a single wing beat. The insect was in rising forward flight to the left and towards the camera. The hindwing lags behind the forewing throughout. (A,B,C) Downstroke, (D) early upstroke, (E) middle of hindwing upstroke, (F) start of the forewing downstroke. Note the ventral flexion in the wings during the upstroke: parallel to the chord in the hindwing, oblique to it in the forewing. Time between frames is 3·3 ms.

flexion, therefore, the distal area of the wing is supinated relative to the proximal part, so that it reaches a similar angle of pitch to the hindwing, but only for the first half of the upstroke, since flexion is lost relatively quickly (Fig. 3E). The flexion line along the rear wing, however, although curved, is approximately parallel to the wing chord (Fig. 3E). The distal wing area is therefore not supinated relative to proximal regions, but the wing seems to be supinated at its base. The flexion lasts for most of the upstroke and, because the flexion line is curved, causes a high degree of reversed camber, with the concave side on the morphological upper surface of the wing (Fig. 3D,E).

Film analysis

One flight sequence of the insect in forward rising flight was analysed using the program developed by Ellington (1984*b*) and the equipment described by Ennos (1988*b*). The analysis assumes that the wings are straight at all times. This was clearly not the case for the chosen sequence, which is that illustrated in Fig. 3, but flexion of the wing was only of the order of 20°, resulting in an apparent reduction in wing length of under 1·5 %; this is acceptable, given the difficulty of accurately identifying the points to be digitized. The program then calculated the following parameters.

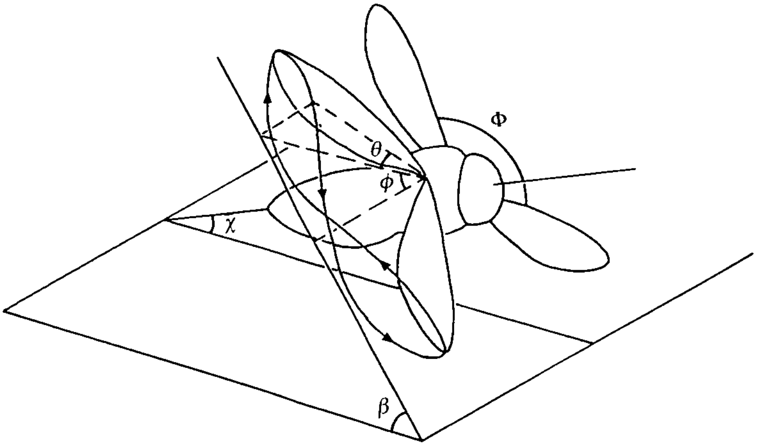

Fig. 4. Kinematic parameters measured for each wing pair during the flight sequence: body angle, χ; stroke plane angle, β; stroke amplitude, Φ; and instantaneous angular positions of the wings along the stroke plane, ϕ, and above the stroke plane, θ.

Body parameters

(i) The roll angle, η, of the insect. (ii) The angle of the body axis to the horizontal, χ (positive when the head is above the body).

Wing parameters

(i) The stroke plane angle, β, of each wing relative to the horizontal (positive when the wing moves downwards on the morphological downstroke). This is calculated by linear regression of the wing position in all the frames digitized. The stroke plane is defined as the plane parallel to this angle and passing through the wing base. (ii) The instantaneous position of the wings along the stroke plane, ϕ, positive when the wing is raised towards the top of the stroke. (iii) The instantaneous elevation of the wings above the plane, θ. From the minimum, ϕ_{min}, and maximum, ϕ_{max}, values of wing position, the stroke amplitude, Φ, can be found.

Some of these parameters are illustrated in Fig. 4.

Flight parameters

(i) Non-dimensional flight velocity, $\hat{V}$, measuring the speed of the insect in forewing lengths per wing beat. The advance ratio, J, defined by Ellington (1984*b*), is the ratio of flight velocity to the mean wing tip velocity, and is given by the equation $J = \hat{V}/2\Phi$. (Note that the hindwing is shorter than the forewing, so the value of J is greater than that calculated by simple use of this equation.) (ii) The flight trajectory angle of the insect, ξ, positive for upward flight.

The frequency, n, of the wing beat was then calculated using the light markers on the film. The time for a wing beat was measured between successive pronations of the forewing, estimated visually from the film. The downstroke-to-upstrok

Table 2. *Kinematics of flight of* Panorpa germanica

Sequence	χ	η	β	ϕ_{max}	ϕ_{min}	Φ	n (Hz)	d/u	$\hat{V}$	ξ	J
Forewing	46°	35°	8·0°	88°	−49°	137°	53	1·21	1·1	34°	0·23
Hindwing			6·5°	92°	−76°	168°	53	1·30			0·21

The table gives the body angle, χ; the roll angle, η; the non-dimensional flight velocity, $\hat{V}$ (in forewing lengths per beat) and the flight angle, ξ, for the insect; together with the stroke plane angle, β; the angle of the wing along the stroke plane at the top (ϕ_{max}) and bottom (ϕ_{min}) of the beat, and the stroke amplitude Φ; the wing beat frequency, n; the ratio of the downstroke to the upstroke duration, d/u, and the advance ratio, J, for each wing.

ratio, d/u, the relative duration of the two halfstrokes, was also estimated from the film.

The results for the *Panorpa* flight sequence are given in Table 2, and are also shown diagrammatically in Fig. 5, a figure similar to those in Ennos (1988*b*). The upper figure shows the inclination of the body, as a line with a cross-bar representing the head, and the wing bases, represented by large solid circles. The wing tip paths are shown as plots of θ, the instantaneous position above the stroke plane, against ϕ, the instantaneous position along the stroke plane. The scale is set by the arrows outside the paths, whose tips point at values of ϕ of 90° and −90°, and of θ of 0°, and thus mark the stroke planes. The non-dimensional flight velocity, $\hat{V}$, is shown as an arrow leaving the forewing base, and drawn to scale, so that a velocity of one forewing length per wing beat would be represented by a line the same length as the distance from the forewing base to its stroke plane arrows. In the lower diagram the positional angles, ϕ, of the wings are plotted as a function of non-dimensional time. The forewing is phase advanced by 40°.

Aerodynamic analysis of flight

Conventional aerodynamic analysis of insect flight assumes that the wing is operating under quasi-steady conditions (Ellington, 1984*d*). The average lift coefficient over a stroke is calculated and then compared with the maximum lift coefficient that can be achieved by aerofoils at the relevant Reynolds number. If the average lift coefficient is greater than the capabilities of the aerofoil, the insect must be using unsteady aerodynamics. The same is true if the force vector calculated from the analysis points in a different direction from that which is inferred from the trajectory of the insect.

The flight sequence of *Panorpa* was subjected to two forms of analysis. Since the advance ratio, $\hat{J}$, was around 0·2, the lift coefficient was calculated assuming that the insect was hovering. This might lead to a force asymmetry of around 40 % between the two strokes, but the force coefficient necessary should be little affected. The average lift coefficient was calculated using a modified version of equation 14 in Ennos (1988*b*) to take into account the use of two pairs of wings.

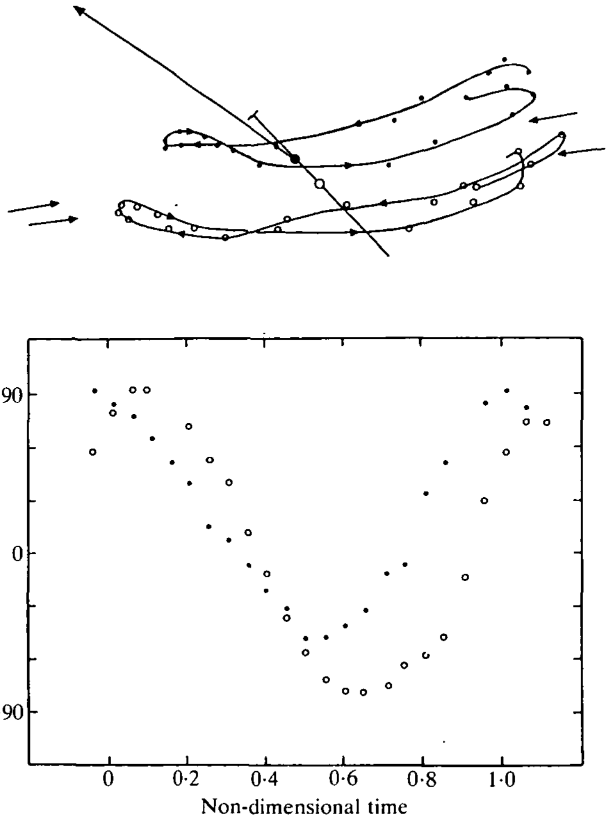

Fig. 5. Kinematics of the flight sequence of *Panorpa germanica*. The upper figure shows the wing tip paths relative to the wing bases (large circles), the orientation of the body, and the flight velocity (arrow from the base of the forewing). The lower figure shows the movement of the wings along the stroke plane through time. Solid circles show forewing position; open circles show hindwing position.

The terms relating to the stroke plane, $\cos\beta$, and the relative stroke plane, $\cos\beta_r$, were not included in the equation, since the induced velocity of flight in slow forward flight with two pairs of wings is unknown. A rough indication of the average lift coefficient is therefore given by a modified version of equation 14 of Ennos (1989*b*)

$$\bar{C}_L = \frac{4mg}{0{\cdot}96\rho\pi^2 n^2[SR^2\hat{r}_2{}^2(s)]_{f+h}}, \qquad (1)$$

where m is mass, g is the acceleration due to gravity, ρ is the density of air, n is the wing beat frequency, S is the area of each wing pair, and R is wing length, and the sum of fore (f) and hind (h) wings is taken. This yields a lift coefficient, $\bar{C}_L$, of 0·79, which is within the capabilities of aerofoils in steady flow.

It is more difficult to calculate the direction of the force which would be produced by a quasi-steady aerofoil, since this involves a lengthy integration of th forces produced by each wing section at each stage of the wing beat. A much simpler analysis was therefore developed, based on the assumption that an equal but opposite circulation is built up around the wing at stroke reversal for each halfstroke (Ennos, 1989*b*, in which equations 2–4 are derived). In this case the instantaneous lift produced by each wing is directly proportional to its velocity to the first power ($L = \rho\Gamma u$, where Γ is the circulation). It was also assumed that drag was a constant fraction of the lift so $D = L/K$, where K is the lift-to-drag ratio of the aerofoil. Both lift and drag are therefore assumed to vary linearly with the local wing velocity and so can be averaged over a wing beat.

The motion of the wing consists of the superimposed flapping and body motion (see fig. 9 in Ennos, 1989*b*) whose aerodynamic effects can now be viewed separately. The flapping motion produces lift at right angles to the stroke plane and the drag forces produced by each halfstroke cancel out. Body motion, meanwhile, results in drag on the wings opposing the motion, but produces no net lift, since the opposite circulations during the two strokes will produce equal and opposite lift forces.

The two net forces which result can be added to give the expected force vector whose direction, ψ_C, relative to vertical can be calculated. The ratio of the two forces depends on the relative flapping to flight velocity [at the centre of the circulation a distance $\hat{r}_1(v)R$ from the wingbase] and on the lift-to-drag ratio, so:

$$D/L = \hat{V}/2K\hat{r}_1(v)\ . \tag{2}$$

K, the lift-to-drag ratio of the aerofoil, falls with Reynolds number and is given approximately by the equation:

$$K = 0{\cdot}30Re^{0{\cdot}344}\ , \tag{3}$$

where *Re* is the Reynolds number of the aerofoil, given by:

$$Re = 4\Phi nR^2/\nu\mathcal{R}\ , \tag{4}$$

where $\mathcal{R}$ is the aspect ratio of the wings and ν is the kinematic viscosity of air. The relative magnitudes of the lift and drag forces produced by the two wings in the flight sequence were calculated and the two force vectors were added to give the estimate of the direction of the resultant force, ψ_C.

Table 3 gives values of *Re*, K, D/L and ψ_C for the two wings. The direction of the force that would be produced by each wing, if equal but opposite circulation were being created for each stroke, was almost vertical. During the sequence, however, the insect was flying forwards, and was also accelerating. It was clear that it was actually producing a net force which was angled well forwards. The model was clearly inapplicable. The insect was either producing greater circulations on the upstroke than on the downstroke, which would result in the wing encountering enhanced drag as it moved backwards during the upstroke (assuming a constant lift-to-drag ratio), a situation which would therefore shift the net force forwards, or the wings may have been used at a high angle of attack on the upstroke to propel the insect using drag, without producing much lift.

Table 3. *Equal circulation estimate of force vectors in the forward flight of* Panorpa germanica

Wing	β (degrees)	*Re*	K	D/L	ψ_C (degrees)
Forewing	8·0	415	2·39	0·17	0·1
Hindwing	6·5	445	2·44	0·15	−0·4

The stroke plane angle, β, and the Reynolds number, *Re*, for each wing; and the ratio of lift to drag coefficient, K, which results; and the ratio, D/L, of drag opposing body motion to the lift produced by flapping.

ψ_C is the inclination of the force vector, calculated assuming equal but opposite circulations.

Wing manipulations and mechanical tests

The structural behaviour of the wings was examined by subjecting them to mechanical tests. Wings were removed from the body of freshly killed insects and basally glued to a microscope slide using 5 min epoxy resin glue, so that the wing formed a cantilever. The glue in no case reached the base of the cubitus, so the mechanical behaviour of the main wing region would not be affected. Point forces were then applied to the wing at the approximate aerodynamic centre of pressure, point *P* on Fig. 6, using the force transducer described by Ennos (1988*a*). The point of the transducer was advanced by 0·5 mm, and the displacement of the wing along the three chords, *A*, *B* and *C* (Fig. 6) was measured with a calibrated eyepiece in a stereo microscope. In all cases the forces required were too low (less than 2×10^{-5} N) to measure. At the same time the wing was examined to find the mode of deformation.

The wings were also manipulated, while they were still attached to the body, to investigate the mechanisms by which the wing pitch could be altered.

Results

The behaviour of the wings of the five different insects tested was consistent and qualitatively similar. The displacements of the forewing (Fig. 7) and the hindwing (Fig. 8) of one of the test animals are given as an example of the results obtained.

The wings were both resistant to dorsal flexion, and displacement upon loading from below was limited to positive camber and torsion, as in the flies tested by Ennos (1988*a*). In both wings the media hinged upwards from its base, and the leading edge spar and cubitus rotated, just as in the Diptera.

Ventral flexion of the wings, however, occurred relatively easily, along the flexion lines shown in Fig. 6. Since these were both curved, flexion caused the outer wing regions to assume the marked reversed camber that was seen in films, while inner wing regions remained relatively flat. The orientation of the flexion lines in the two wings was noticeably different, being more oblique in the forewing, so that it reached the leading edge more distally. As a result, th

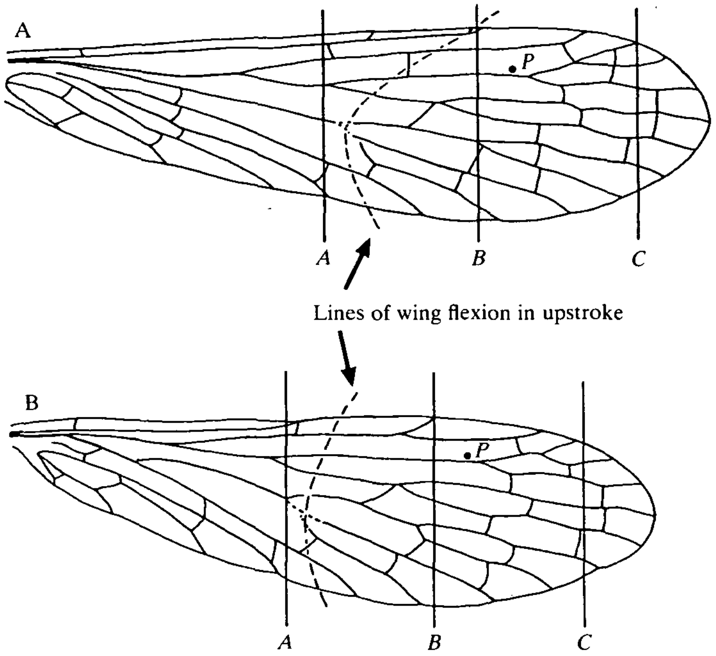

Fig. 6. Forewing (A) and hindwing (B) of *Panorpa germanica*, showing the point, *P*, at which the point force was applied during tests. Displacement of the wing was investigated along the cross-sections *A*, *B* and *C*. Ventral flexion in each wing occurred along the broken line.

displacement of the leading edge of the forewing at cross-section *B* was noticeably less than in the hindwing, and the forewing was consequently supinated more than the hindwing.

The pitch of both wings could be altered extremely easily, most of the rotation occurring at the wing base as in the Diptera (Ennos, 1987). The base of the hindwing of *Panorpa* has the clavus poorly developed, and it should exert little control on the pitch of the main wing region, as in Diptera. The base of the forewing, however, has a well-developed clavus, which is set at a constant pitch angle. Pitch changes of the wing therefore require flexion at the claval furrow, and dorsal or ventral movement of the clavus, a situation reminiscent of that in locusts.

Discussion

The mechanical behaviour of the wings and the distortions they consequently underwent in flight are clearly related to their structure.

In reacting to forces from below, both wings camber and twist slightly, just like the wings of flies, because the wing is supported front and rear by strong spars which prevent flexion. Both are easily twisted, however, and the major vein supporting the mid-wing region, the media, can be flexed up and down at its rather weak base, especially in the hindwing. An upward force, therefore, causes the

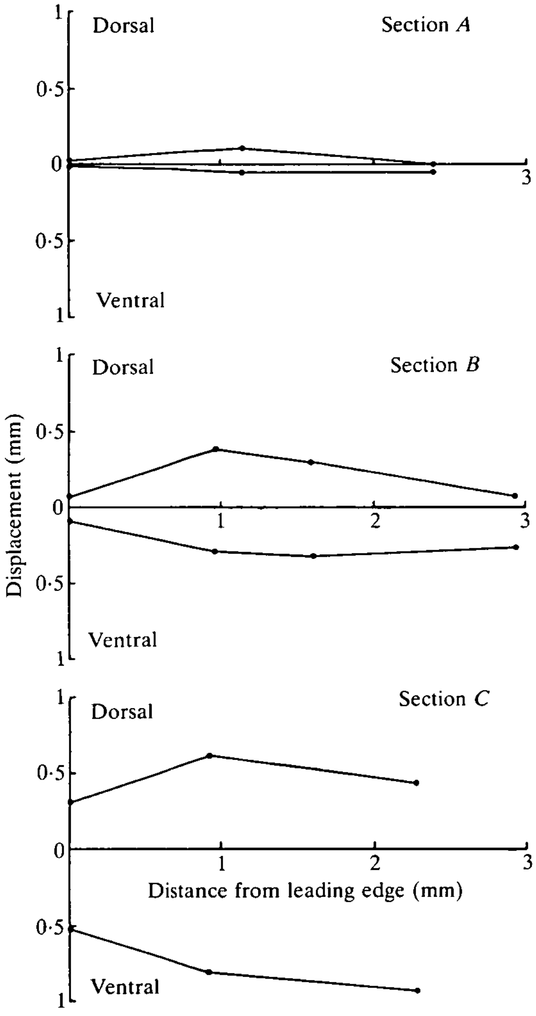

Fig. 7. Results of the point force test on the three chordwise sections *A*, *B* and *C* of the forewing of *Panorpa germanica* (see Fig. 6). Dorsal movement results from a force applied from below: ventral movement from a force applied from above. Note the formation of opposite camber when force is applied from below and above, respectively, and the greater displacement of outer wing regions (section *C*) to forces from above, because of ventral flexion. The outer wing region is supinated by a force from above (lower curve in *C*) because of the oblique flexion line.

media to flex upwards, while the spars twist to allow camber to be formed, just as in the Diptera (Ennos, 1989*a*). The arrangement of relatively strong longitudinal veins and weak cross veins in the distal wing region (Wootton, 1981) allows camber, while preventing transverse flexion.

Ventral flexion occurs more easily than dorsal flexion, because the weak thyridium region lies on a ventral corrugation of the wing membrane. When

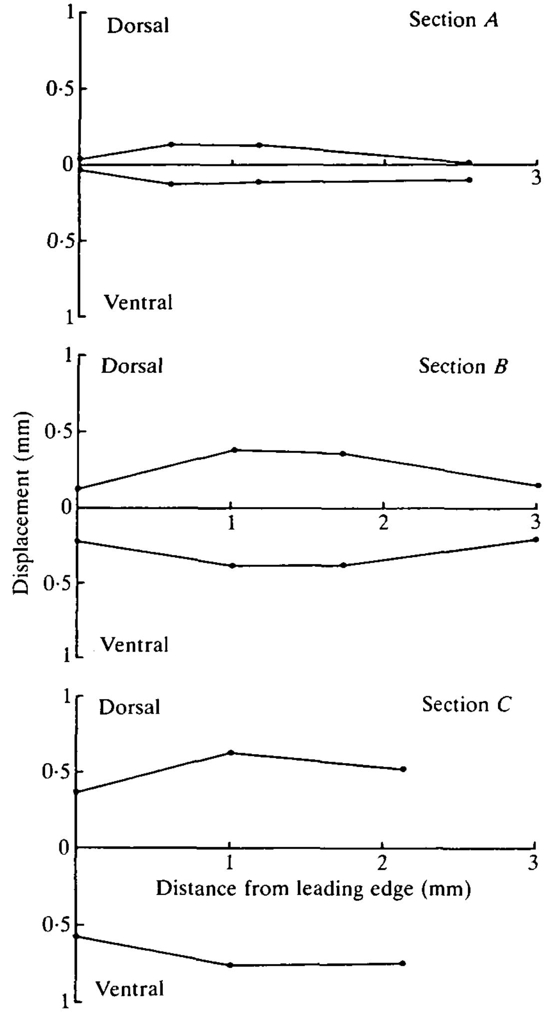

Fig. 8. Results of the point force test on the hindwing of *Panorpa germanica*. Results are similar to those for the forewing, but forces from above result in less supination of the distal wing (section *C*).

force is applied from above, therefore, it will be put under compression and will buckle fairly easily, destroying the corrugated wing pattern, and allowing the wing to bend (Wootton, 1981). No such weakening occurs dorsally.

The contrasting orientation of the flexion lines across the two wings is due to the differences in the length of the leading edge spar. In the hindwing the spar ends around halfway to the tip, and flexion can therefore occur relatively proximally, whereas in the forewing it extends much closer to the tip, since the subcosta is relatively longer, so the flexion line must be oblique. Towards the trailing edge, flexion is prevented proximally by the rather stout anterior cubitus.

The difference in the orientation of the flexion line causes differences in the relative pitch of the distal wing region, which is supinated relative to the proximal region in the forewing at the start of the upstroke, but not in the hindwing. This compensates for the lower degree of supination that occurs at the base of the forewing, so the distal areas of fore- and hindwings will have similar values of angle of attack at the start of the upstroke. The low degree of supination at the base of the forewing is clearly related to the presence of the well-developed anal region, which in life will be under the control of direct muscles, and will prevent large degrees of rotation.

At present we cannot state with any certainty what aerodynamic mechanisms the insect was using. Clearly, however, the aerofoil was reversed between the two strokes (so that the morphological dorsal surface became the functional lower surface for the upstroke), as in many hovering insects, such as members of the Odonata, Diptera and Hymenoptera, and unlike the flight of locusts and most birds. Indeed, analysis showed that the upstroke was probably producing larger forces than the downstroke. This may have been related to a high angle of attack or the high reversed camber produced during ventral flexion of the wings. The wings do not straighten quickly after ventral flexion, however, so it is unlikely that the upstroke lift was increased by the mechanism seen in *Calliphora* and many other flies (Ennos, 1989*a*,*b*), in which the unsteady circulation created by the 'flex' mechanism (Ellington, 1984*c*) may be increased by delaying and speeding up wing rotation (Ennos, 1989*b*).

Reversal of the aerofoil involves marked changes in wing pitch between halfstrokes. The base of the forewing, actively controlled by direct muscles, does not seem to be able to supinate adequately. The wing has to flex along an oblique flexion line in order to supinate the distal wing region. The hindwing, with its weaker clavus, in contrast, supinates easily, and seems to be under less direct control.

The two wings, in summary, show many interesting contrasts, which reflect differences in the extent to which they are actively controlled, and may shed light on the changes that occurred during the acquisition of asynchronous flight musculature. The forewings of *Panorpa* are, in many ways, similar to the forewings of locusts. Control of the wing pitch is effected by relative movement of the anterior and posterior supporting zones, which in both insects are separated from the intervening deformable zone by flexion lines. The changes in pitch made possible by this arrangement are adequate in locusts, in which the aerofoil is only feathered on the upstroke (Jensen, 1956), but are not adequate to allow reversal of the aerofoil. In smaller insects such as *Panorpa*, therefore, which can fly only at low advance ratios, and therefore may need to reverse the aerofoil, an oblique ventral flexion line is necessary to allow the aerofoil to achieve the correct angle of attack. Such oblique flexion lines are seen in many insects which likewise possess strong clavuses and synchronous wing musculature, for instance the alder fly, *Sialis* (Wootton, 1981).

The hindwings of *Panorpa* are far more similar to the wings of the Diptera. The narrow wing base and less well-developed anal region of the wing both suggest th pitch changes are effected to a greater extent automatically at the end of each halfstroke by wing inertia, as in flies (Ennos, 1988*b*). The hindwings can twist by over 90° at the base, so no oblique flexion is necessary to reverse the aerofoil. The supporting function of the anal veins along the trailing edge is taken over in the hindwing by the anterior cubitus, which is stouter and has a stronger base at the radius. The base of the media is weaker and it hinges up and down at its divergence from the cubitus, so allowing camber to be set up automatically in the main wing region. This arrangement is strikingly similar to that in the arculus of Diptera (Ennos, 1989*a*).

The fore- and hindwings of *Panorpa* may show similarities to functional stages along the development of flight in small insects. The direct muscular control seen in larger insects still occurs in the forewings of *Panorpa*, and oblique wing flexion is required to allow reversal of the aerofoil. Reduction of the rear wing clavus allows the wing to rotate to a much greater extent, which should improve its aerodynamic efficiency. As a result, however, the control of wing pitch has to be effected, to a greater extent, automatically by the inertial and aerodynamic forces set up during flight. In turn, this might simplify acquisition of asynchronous flight.

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