

LEADING EDGE SECTION AND ASYMMETRIC TWISTING IN THE WINGS OF FLYING BUTTERFLIES (INSECTA, PAPILIONOIDEA)

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Summary

Insect wings are mounted on hinges, restricting the extent to which their bases can be supinated for the upstroke. The forewings of many insects therefore include devices that allow the distal part of the wing to twist relative to the base under aerodynamic loading in the upstroke, but restrict such twisting in the downstroke where the effect would be detrimental. In the broad forewings of butterflies, this asymmetric resistance to aerodynamic twisting seems to be a consequence of the curved section of the leading edge. The wing can be modelled as a cantilevered, thin cambered plate. Torsional tests on the forewings of four butterfly species and on a paper wing of curved section confirm the effect. Differences between the results for the four species appear to fit their morphological and kinematic differences. The nature of the mechanism is outlined.

Introduction

There is abundant evidence from high-speed photography and stroboscopic studies that the propulsive wings of insects generally twist in flight. Twisting is important in the instantaneous control of lift and thrust, and may be essential if enough net upward force is to be developed during the flapping cycle to support the weight of the insect.

It is convenient to distinguish between two kinds of twisting: rotation and internal torsion. Rotation of the whole wing ('active torsion' of Wootton, 1981) takes place mainly at the beginning and end of each half-stroke, as the wing changes from upstroke attitude to downstroke attitude and *vice versa*. It is usually actively initiated and is partly powered by thoracic muscles acting directly on the wing base or indirectly through the complex cuticular mechanisms of the laterothorax and axilla. In many cases, rotation is assisted by the momentum of the wing, since its centre of mass is commonly located behind the torsional axis. In Diptera at least, inertial torque appears to be enough to power the whole rotation process (Ennos, 1988*b*). Rapid rotation at stroke-reversal is incidentally involved in almost all the unsteady mechanisms of lift generation so far discovered or proposed and these are now believed to be significant in most kinds of insect flight (Dudley and Ellington, 1990).

Key words: butterflies, Papilionoidea, wings, flight, torsion.

At any stage in the flapping cycle, including the relatively steady phases while the attitudes of the wings are fairly constant, they may undergo internal torsion ('passive torsion' of Wootton, 1981). This is largely due to aerodynamic loading, since lift is commonly centred behind the torsional axis (Norberg, 1972; Wootton, 1981; Ennos, 1988*a,b*), but the wing's inertia, operating through its centre of mass, must also contribute substantially in the early stages of each half-stroke. These loads are opposed by muscular forces at the wing base and by the elasticity of the cuticle at the base and within the wing. The resulting torques create the familiar propellor-blade-like spanwise twist evident in many photographs and films of flying insects. The mechanical and aerodynamic significance of internal torsion has been discussed by Ennos (1988*a,b*) in Diptera and by Wootton (1981, 1992) for insects in general.

Insects differ markedly in the extent to which their whole wings twist between half-strokes. Locusts, for example, twist their wings rather little and generate significant lift only on the downstroke, both fore- and hindwings being effectively 'feathered' for the upstroke (Jensen, 1956; Zarnack, 1972, 1982; Cloupeau *et al.* 1979). At the opposite extreme, narrow-winged Diptera and zygoterous Odonata, which habitually fly slowly and may hover, twist their wings through very large angles and reverse the camber of the wings between the two halves of the stroke, generating a vertical weight-supporting force in both (Ennos, 1989*b*; Newman, 1982; Ruppell, 1989; Wootton, 1991).

Between these extremes lie many insects from a variety of orders, the twisting of whose wings between half-strokes is limited by structural features, the breadth of the base, the presence of a substantial rigid supporting zone at the trailing edge, and the coupling of forewings and hindwings on each side into a single aerofoil with insertions on both mesothorax and metathorax; but the distal regions of whose wings may nonetheless twist far enough for the generation of useful upstroke forces. This is only possible if the wings are capable of being twisted substantially along their length, and a range of devices are known that increase the wings' compliance to supinatory torsion. The effect of these devices is necessarily asymmetric, since increased compliance to pronatory twisting would be disadvantageous, reducing or eliminating the angle of incidence to the airflow.

Torsional asymmetry is achieved in different ways by different groups, but usually involves a degree of transverse or oblique ventral bending of at least the more posterior veins, often along local lines of flexibility. In many Plecoptera (Brodsky, 1981), Megaloptera (Wootton, 1981; Brodsky and Ivanov, 1983), Mecoptera (Ennos and Wootton, 1989), Trichoptera (Brodsky and Ivanov, 1983), Hemiptera (Betts, 1986; Wootton, 1993) and many Lepidoptera and Hymenoptera, this line is some way out along the span. In Diptera, when present, it is very near the base (Ennos, 1989*a*).

Papilionid butterflies have no such transverse flexion lines, yet high-speed film and videotape of some 40 species flying freely in large enclosures shows that many of these are capable of some supinatory torsion (Fig. 1). Manipulation of the forewings of freshly dead butterflies strongly indicates that the necessary asymmetry in torsional rigidity is largely due to a previously undescribed effect of the cambered section of the wings' leading edge. This effect may prove to have wide importance in understanding insect wing design.

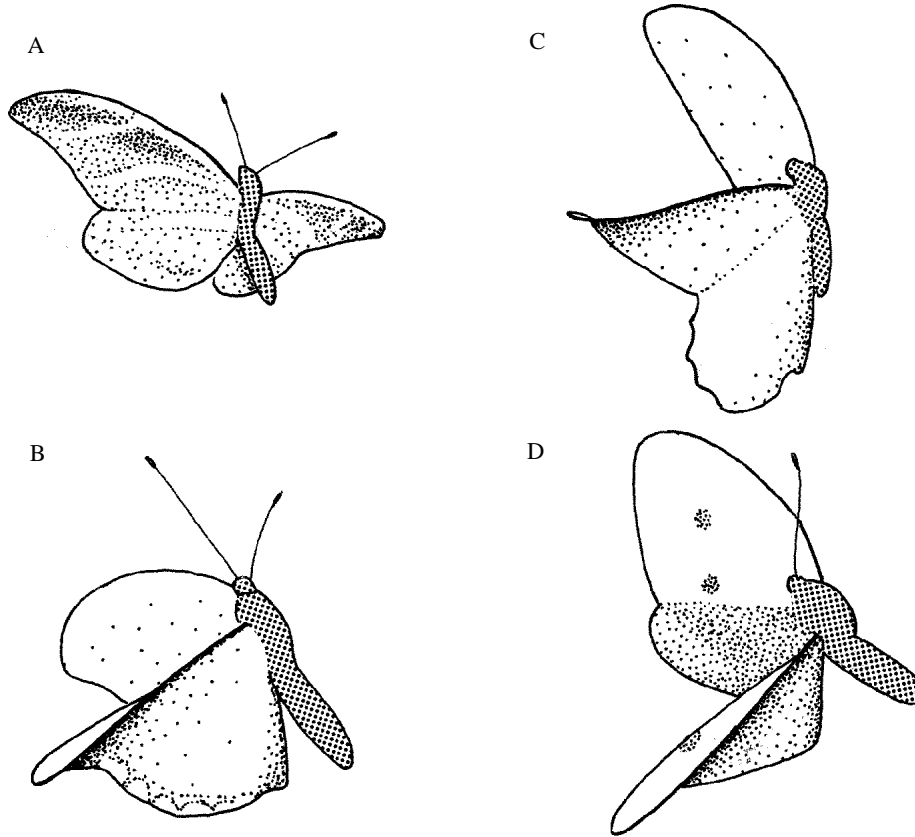


Fig. 1. Butterflies in mid upstroke at speeds near to hovering, showing varying degrees of supinatory torsion (from high-speed film). (A) *Heliconius charitonia*; (B) *Dryas julia*; (C) *Papilio rumanzowia*; (D) *Pieris brassicae*. Not to scale.

Morphology

The functional morphology of butterfly wings will be treated in detail elsewhere (R. J. Wootton, in preparation). Briefly, forewings and hindwings differ in size and shape and in some details of venation. They are not physically coupled in flight, but overlap appreciably, and normally beat in phase, acting as a single pair of aerofoils. However, they are capable of separating slightly, particularly during glides (Betts and Wootton, 1988), and far greater separations can occur momentarily (S. J. Bunker and R. J. Wootton, unpublished observations from high-speed film).

We are concerned here only with the forewing (Fig. 2). This is supported by a framework of thin-walled tubular veins, which taper to the margin. With the exception of the most anterior vein (subcosta, Sc) and the most posterior veins (the one or two anals), the framework consists of a large, often more or less elliptical, cell and of the distal extension of the radius (R), and the branches of the radial sector (Rs), the media (M) and the anterior cubitus (CuA), which radiate from the cell to the leading edge, the wing-tip and the outer trailing edge. The veins forming and emerging from this cell all lie in nearly

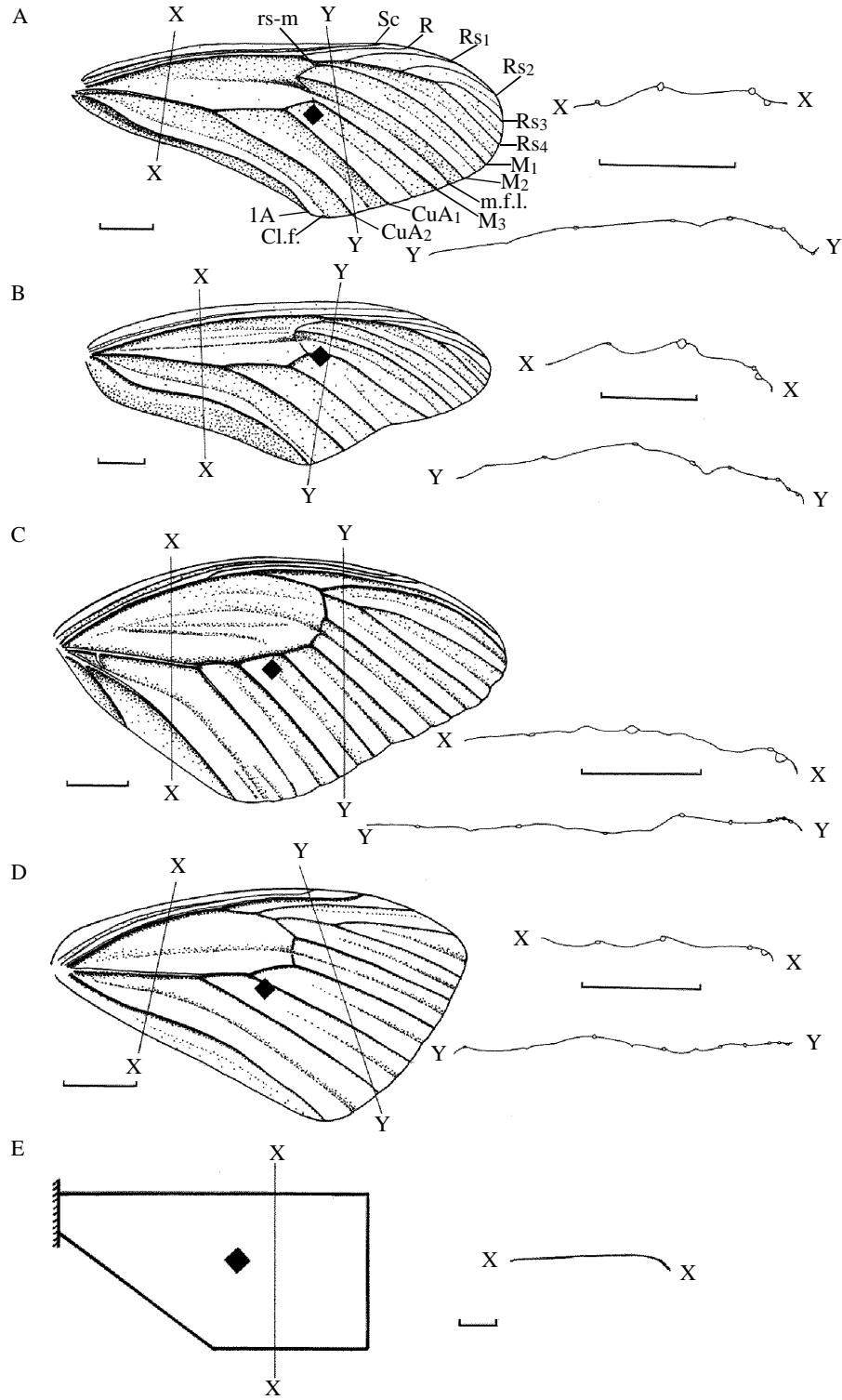


Fig. 2

Fig. 2 (A–D). Plans and two sections of the forewings of the species tested. The sections are drawn to larger scales. Diamonds show the positions of the centroids. (A) *Heliconius charitonia*; (B) *Dryas julia*; (C) *Papilio polytes*; (D) *Pieris brassicae*. (E). Plan and cross section of paper model wing. m.f.l., median flexion line; cl.f., claval furrow; Sc, subcosta; R, radius; $Rs_{1,2,3,4}$, branches of radial sector; $M_{1,2,3}$ branches of media; $CuA_{1,2}$ branches of anterior cubitus; 1A, first anal vein. rs-m, cross-vein linking Rs and M. X–X', Y–Y' show the positions of the transverse sections so labelled. Scale bars represent 5mm.

the same plane. Immediately adjacent to the radius lies the subcosta, a stout vein whose anterior edge lies significantly below the plane of the rest of the wing. In front of this is a band of membrane, with a slightly thickened margin which forms the leading edge. There is no costal vein.

The wing has two fully developed flexion lines, which pass from the axilla to the margin. The more anterior, a narrow band of flexible cuticle, bisects the elliptical cell, crosses its apex at a flexible section of the cross-vein-like base either of M_{2+3} or of M_3 , and runs to the outer posterior margin. This line, which originates between the bases of R+Rs and CuA, allows relative pronation and supination of the anterior section of the wing, creating and eliminating camber.

The second flexion line is the claval furrow, which lies in front of the more anterior anal vein, and allows the wing to be pronated and supinated relative to the narrow posterior clavus and to the hindwing.

Neither of these flexion lines appears to be in a position to influence distal torsion and, as we shall see, the asymmetric twisting behaviour of the wings persists when the lines are immobilised at the axilla. Its cause must lie elsewhere.

The most probable candidate appears to be the cambered cross section. The wing relief of butterflies has attracted little attention. It is most obvious in the membrane, which has deep grooves between and parallel to most of the longitudinal veins. The local effects of these grooves on wing section in flight have been discussed by Brackenbury (1991). In many – perhaps all – butterflies, however, the anterior strip of the forewing, immediately behind the leading edge, is deflected ventrally. The extent of the deflection, and the location of the posterior boundary of the strip, vary with species (Fig. 2). Of the four species studied here, the downward curve is least marked in *Pieris brassicae*, being confined to the basal area anterior to R, which forms its posterior boundary (Fig. 2D). In *Papilio polytes*, the boundary ridge follows the common stem of R and Rs, continues along Rs_1 , which lies close behind R and Sc, and runs to the wingtip along Rs_2 , which has curved anteriorly to lie adjacent to Rs_1 (Fig. 2C). The anterior strip is therefore narrow, but the camber is steep. In the Heliconiinae *Heliconius charitonia* and *Dryas julia* the posterior boundary ridge of the downwardly deflected strip follows R+Rs, Rs_{1+2+3} and Rs_{2+3} , and the strip is, therefore, relatively broader than in *Papilio polytes*. The anterior camber is clear in both species and particularly marked in the longer-winged *Dryas julia* (Fig. 2A,B).

Asymmetric behaviour of thin cambered plates

The dorsoventrally asymmetric flexural rigidity of thin cambered plates, including insect wings, has already been noted elsewhere (Wootton, 1981; Betts, 1986). A

cantilevered plate, point-loaded through the shear centre of its cross section from the concave side, is far more rigid than if loaded from the convex side. In the former case, the force tends to increase the camber, and hence the second moment of area of the cross section and the overall rigidity of the plate. In the latter, where loading is from the convex side, the force tends to flatten the curve, reduce the second moment of area and increase the flexibility, an effect which is utilised in coiled-steel tape measures.

If a thin cantilevered plate is loaded at a point some distance from the shear centre of its cross section, so that it is both bent and twisted, it again deforms asymmetrically according to the direction of application of the force. A point force applied to the concave side twists the plate, but this is rapidly arrested. A similar force to the convex side, however, causes a much greater deflection: the plate twists freely and tends to flex along an oblique line running anterodistally from the base of the posterior edge.

A butterfly forewing can be modelled in its entirety as a plate of this kind, or its ventrally curved anterior margin can be regarded as a narrow cambered plate with the rest of the wing attached along its posterior edge. If the centre of pressure lies behind the shear centre of the plate's cross section, its effect in each model will be essentially similar. Is the same true of the wing itself?

Materials and methods

To test the hypothesis that the curved section of the leading edge can contribute significantly to dorsoventrally asymmetric deformation, incremental torques were applied to isolated butterfly forewings by means of a specially constructed torsion balance and their angular deflections were recorded. A paper model of similar cross section was tested in the same way for comparison.

The species tested were as follows: *Heliconius charitonia* (Linnaeus) (F. Nymphalidae, Subf. Heliconiinae), three wings; *Dryas julia* Fabricius (F. Nymphalidae, Subf. Heliconiinae), two wings; *Papilio polytes* Linnaeus (F. Papilionidae), four wings; *Pieris brassicae* Linnaeus (F. Pieridae), three wings.

The heliconiines were selected because of the relatively high aspect ratio of their wings, their manoeuvrability and their capacity for hovering with a near-horizontal stroke plane. *Dryas julia* in particular has extended wing-tips, and high-speed film shows it to be very manoeuvrable, with considerable internal torsion (Fig. 1B).

Papilio polytes and *Pieris brassicae* were chosen for comparison. The former, like *Papilio rumanzovia* (Betts and Wootton, 1988), is capable of brief periods of hovering with an oblique stroke plane. *Pieris brassicae* has broad forewings and hovers predominantly with a vertical stroke plane (Ellington, 1980) and comparatively little torsion (S. J. Bunker and R. J. Wootton, unpublished observations).

The torsion balance is shown in Fig. 3. An aluminium disc, 38mm in diameter and 3 mm thick, is suspended on a 0.008mm guitar string, 300mm in length, glued to a sewing needle passing through the centre of the disc. The disc is mounted in the slotted end of an aluminium bar, with the needle passing above and below the disc through holes in the bar, reamed to minimise friction. The disc is, therefore, free to rotate about its centre, but not to swing laterally.

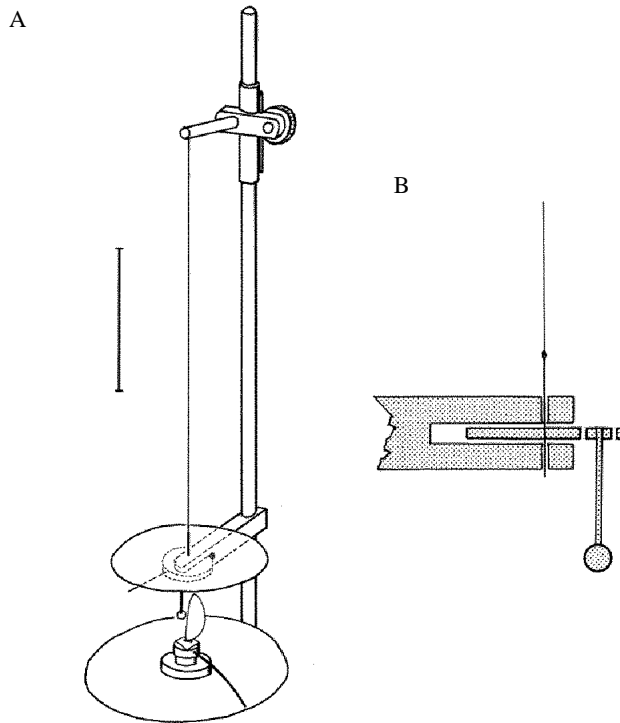


Fig. 3. The torsion balance. (A) The complete apparatus; scale bar represents 100mm. (B) Detailed section through the pendulum and its mounting.

The disc bears a slender wire pointer, running radially from the centre, whose angular position can be read against a 360° protractor mounted on the supporting bar. The whole apparatus is mounted on a clamp stand.

Beneath the pendulum, and coaxially with it, is placed another 360° protractor, on which is mounted a turned, centrally bored brass block. During testing, a wing is mounted vertically on a turned brass plate whose lower section fits into, and is rotatable within, the brass block on the lower protractor. The plate carries a pointer by which it can be rotated manually, so that the wing is turned about its torsional axis through an angle that can be read on the lower protractor.

Rotation of the wing brings it into contact with a plastic bead, 4.5mm in diameter, mounted on a stiff rod threaded into one of three holes in the lower side of the suspended aluminium disc. The latter is, in turn, rotated about its axis, against the torsional restoring force of the wire. The angular deflection of the wing can then be measured by subtracting the angular deflection of the disc from that of the lower pointer, and the applied force can be calculated from the deflection of the pendulum and the torsional rigidity of the wire.

The wire was calibrated in advance by suspending from it an aluminium bar of known moment of inertia (J), and timing its period of simple harmonic oscillation (T). Then:

$$\text{Torsional rigidity} = J(2\pi/T)^2.$$

The guitar string was found to have a rigidity of $4.93 \times 10^{-6} \text{ Nm rad}^{-1}$.

Fig. 2A–D shows the forewing plans, sections and centroids of the species tested. All wings were removed from freshly killed butterflies, together with the intact axilla and a small area of mesopleuron. The axis of torsion had been found before removal by probing the wing at a number of points along the span and noting the point of each chordwise section that did not move. The spanwise line joining these points was taken to be the torsional axis. The paper wing is shown in plan and section in Fig. 2E.

The nature of the load to be applied to the wing was carefully considered. A realistic distributed load was impracticable; a fine point load might be damaging. The spherical bead was a compromise. Selection of an appropriate point of application was also difficult. The centre of aerodynamic pressure of a flapping, twisting wing is impossible to find theoretically and certainly alters during the stroke cycle. The centre of mass is easily found, but the inertial contribution to the total torque will also vary through the cycle. The problem is compounded by the fact that the fore- and hindwings of butterflies act together as a single aerofoil, but are not physically coupled, so that the extent to which the hindwing contributes to the pattern of pressure on the forewing is unknown.

After consideration, the centroid of the forewing was selected as a reasonable application point. It is easily located by suspending a paper replica of the wing successively from two points near its perimeter and marking the intersection of the respective vertical lines from the two suspension points (Alexander, 1983). The centroid lies close to the centre of mass in each of the tested wings and may be as good an approximation to the centre of pressure as any other. It lies anteriorly and distally to the centroid of the whole wing couple. The centre of lift of a fixed wing is situated at about the quarter-chord, approximately level with the centroid of these forewings, but in a flapping wing it would probably lie more distally because of the spanwise velocity gradient. Furthermore, the presence of the hindwing would be expected to shift it behind the quarter-chord line of the forewing.

Each wing was mounted by glueing the section of mesopleuron to a square of thin polystyrene sheet with a quick-setting epoxy resin. The glue was applied to the axilla and to the extreme base of the wing itself, so as to immobilise the bases of the longitudinal flexion lines. While the glue was setting, which took about 5min, the wing was supported by entomological pins so that the torsional axis was exactly vertical. The wing was kept in a humid box until the glue had hardened fully, about 20min. The polystyrene square was then mounted on the brass plate with double-sided cellulose adhesive tape so that the torsional axis of the wing was in the exact centre of the plate, coaxial with the pendulum wire. The position of the bead was adjusted by screwing the probe to the appropriate height in the appropriate threaded hole in the disc.

The wing was loaded by turning the pointer attached to its base plate, so bringing the wing into contact with the bead, while rotating the disc and twisting the wire. A series of readings was taken at equal position intervals of the disc pointer, to give measurements of applied torque, and the angular deflection of the wing was found from the difference between the angular displacements of the two pointers. Each wing was tested five times in pronation and five in supination, the direction being alternated to eliminate creep. Pads of wet paper were placed as close as possible to the wings throughout the testing period,

which was generally shorter than 30min, in order to raise the air humidity and minimise cuticle dehydration.

Results

All the wings tested were significantly more compliant to supinating than to pronating torques. Repeated tests on individual wings gave consistent results with trivial variation.

Fig. 4A–D shows for each species the curves of pronatory and supinatory deflections against torque; the values are means for all tested wings. As the samples are small, the vertical bars show ranges, not standard errors.

The deflections vary nearly linearly with torque over the range used, and the regression coefficients for the mean data for each species, which are approximate measures of their torsional compliance, are given in Table 1.

Discussion

Ennos (1988a), examining wing torsion in three species of Diptera, used a torsion balance that applied a couple to the wing-tip, and so loaded the wing in pure torsion. He, too, found that the wings were more compliant to supinatory than to pronatory torques, but did not explain the mechanism.

The balance used in the present work measures the total deflection of the wing and so allows both torsion and bending, which clearly interact. Since the wing bases were immobilised in the experiments, it is clear that the observed difference in resistance to pronating and supinating torques is a property of the wings beyond their axillae. In the flying insect, this effect would be superimposed on the active pronation and supination of which the insect is capable and would allow the distal part of the wing to twist disproportionately in the upstroke, so rotating the net aerodynamic force vector in the direction of greater weight support and permitting slow flight and manoeuvring at low speeds.

The experimental results from the paper model, together with a great deal of unpublished, non-quantitative experience of manipulating various other models, support the contention that the curved leading edge section is, by itself, capable of producing this observed asymmetric rigidity. Modelling the wing in this way, we are treating it as a thin curved plate. It is important to examine the ways in which the real forewing differs from this simple model and how the differences might be expected to affect functioning.

Table 1. Mean compliance ($\times 10^6$ degrees Nm^{-1}) to angular point loading at the centroid

	Pronation	Supination
<i>Heliconius charitonia</i> (4)	23.3 \pm 1.9	36.8 \pm 3.1
<i>Dryas julia</i> (2)	32.1 \pm 3.2	60.1 \pm 2.9
<i>Papilio polytes</i> (4)	29.1 \pm 1.9	40.8 \pm 1.3
<i>Pieris brassicae</i> (3)	19.4 \pm 1.3	26.0 \pm 1.1

Values are means \pm S.D., figures in parentheses indicate the number of wings tested.

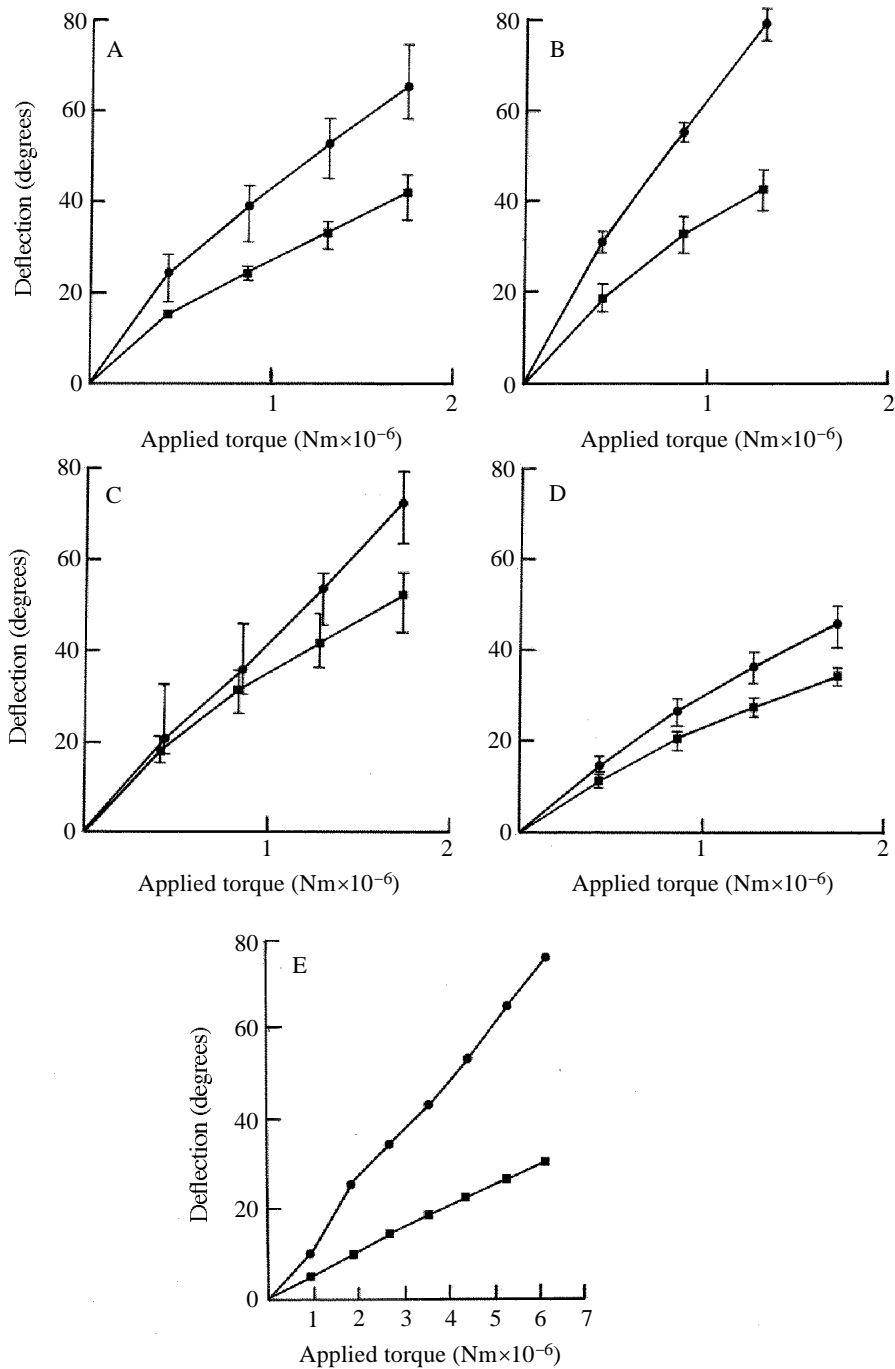


Fig. 4

Fig. 4. Torque *versus* mean deflection plotted for the forewings of the species studied. (A) *Heliconius charitonia*; (B) *Dryas julia*; (C) *Papilio polytes*; (D) *Pieris brassicae*. (E) Deflection curves for the paper model wing. Vertical bars show the range of values for the individual wings tested. See Table 1 for the numbers of wings tested. Squares, pronation; circles, supination.

The curved plate is made of a single material, of uniform thickness, whose properties are constant throughout. It has appreciable stiffness in compression, as well as in tension and shear.

In contrast, the wing is a framework of fairly rigid tubes, varying in section and perhaps in material properties both along their length and between individual tubes, linked by a membrane whose thickness and properties vary around the wing, but which is probably only significantly stiff in compression in the thickened band along the leading edge.

Two implications of this difference require comment. First, a force applied to the uniform plate would be transmitted through the structure by the material as a whole, whereas a force applied to the wing would be transmitted variously as tension or compression by the veins, but only as tension by the membrane. The precise distribution of forces induced in a real wing by a distributed aerodynamic load or by a point load close to the presumed centre of aerodynamic pressure is at present impossible to determine, but it seems clear that torque would be transmitted to the leading edge spar – Sc, R and the branches of Rs, and the membrane anterior to and between them – primarily by the cross-vein rs-m (Fig. 2A) This would be levered up in pronation and down in supination by the applied force centred behind it. The spar, with its curved section, would deflect in much the same way as the anterior band of the uniform plate, and the wing-tip would similarly twist more easily in supination. Second, the curved plate deflects by bending as well as twisting. The leading edge spar of the real wing is stiffened by the veins, which might therefore interfere with the effect.

This proves not to be the case; indeed, the veins may actually assist the mechanism. Manipulation of a series of models consisting of cantilevered strips of thin, cambered plastic sheet, stiffened with long rods at various distances from one edge (Fig. 5A) shows that the rods further inhibit pronatory twisting, which tends to bend rods close to the leading edge, but that they hardly affect supinatory twisting, which indeed does not require significant bending in the spar. This is confirmed, rather against intuition, by applying a couple to the end of a simple slender cambered plate. One edge bends down, the other stays nearly straight; their roles are exchanged when the direction of the couple is reversed (Fig. 5B). These experiments may perhaps explain the torsional asymmetry of Ennos' Diptera (Ennos, 1988*b*). If his mounted wings were even slightly cambered, a supinating couple would easily depress the trailing edge, which has no supporting vein, but the corresponding deflection of the leading edge by a pronating couple would be resisted by the flexural rigidity of the anterior veins.

The results of the present experiments show some differences between the four butterfly species. Since the samples were small, these are suggestive rather than conclusive, but they conform well with what we know of the wing morphology and kinematics. The difference between pronatory and supinatory rigidity is least in *Pieris*

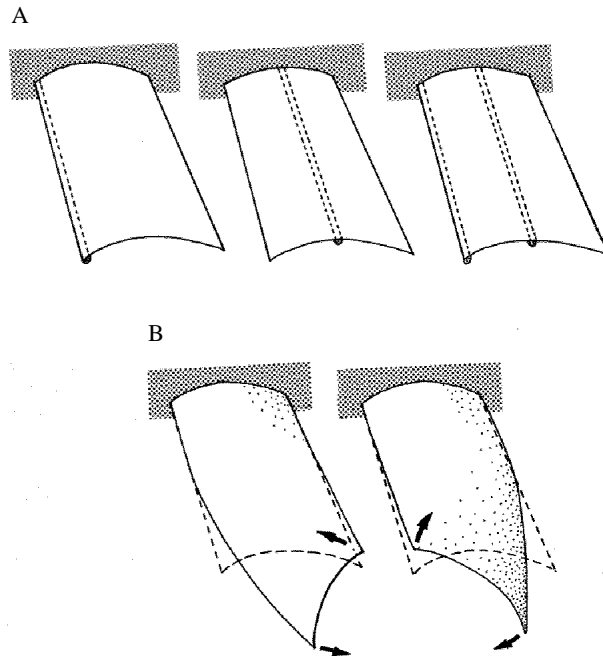


Fig. 5. (A) Plastic sheet models used in qualitative investigations of the effect of stiffening rods on twisting behaviour. (B) Effect of a couple applied to the end of a cantilevered thin cambered plate. The arrows show the direction of the torque. Further explanation in the text.

brassicae, whose leading edge camber is confined to the basal part of the wing and which hovers with a vertical stroke plane (Ellington, 1980), with little internal wing torsion. It is most marked in *Dryas julia*, whose wings are strongly cambered and twist extensively as the insects hover and manoeuvre. *Papilio polytes* and *Heliconius charitonia* show intermediate patterns in torsional asymmetry, camber and torsion in flight (S. J. Bunker and R. J. Wootton, original observations; Fig. 1).

Curved or corrugated leading edge spars are common in insects, and the form of their sections may prove to be an important regulator of their torsional properties. I have suggested elsewhere that the complex leading edge morphology of the wings of Odonata, in which the spar changes abruptly from dorsally concave to dorsally convex at a point called the 'nodus', partway along the wing, may be associated with the partitioning of torsion along the spar and again with torsional asymmetry. The position of the nodus in different families may be correlated with greater or lesser degrees of within-wing torsion, in association with different flight habits (Wootton, 1991).

The present investigation further confirms the significant role of camber in supporting insect wings and in controlling, without necessarily inhibiting, their aeroelastic deformations. It also hints at a possible approach to more rigorous analysis of the engineering of these complex, delicate structures, by modelling them in the first instance as thin, deformable plates, and then as space-frames.

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