

Two Basic Mechanisms in Insect Wing Folding

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Two basic mechanisms in insect wing folding

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SUMMARY

Detailed comparison of patterns of folding in insect wings has shown that all those which fold transversely can be referred to two basic mechanisms, each consisting of four panels rotating hingewise about four folding lines, intersecting at a single point. The mechanisms, which have one degree of freedom, are in effect lever systems, whose velocity ratios change non-linearly as they operate. They are designated as 'Internal' (INT) and 'External' (EXT), and further specified by a plus or minus sign, derived from the convex or concave orientation of the folding lines. There are hence four possible combinations: INT−, INT+, EXT− and EXT+.

The two types are kinematically distinct. As INT unfolds, the effector panels move slowly at first and accelerate towards the end of the movement, whereas in EXT the effector panels move fast initially, then decelerate rapidly to their final position. Furthermore INT operates reversibly, whereas EXT usually needs to be closed elastically, or by an extraneous force. The principles of the two mechanisms are applicable to many other folding structures.

1. INTRODUCTION

The hind wings of many insects undergo folding when retracted to the resting position. Most usually the posterior, anojugal region becomes pleated along a series of radiating fold lines as the wing hinges backward to lie along the abdomen. In several groups, however – all winged Dermaptera, all winged Coleoptera, a few Blattodea – the hind wings additionally become folded transversely. This is usually associated with the need to tuck them under short, thickened, protective forewings, whose length is restricted to that of the metathorax and abdomen which they sheath. Larger, longer hindwings are then needed to provide the necessary aerodynamic forces for flight, but their potential vulnerability requires that they too should be protected, by folding to a length less than that of the forewings under which they lie. This has major mechanical, as well as geometrical implications: the muscles do not extend beyond the base of the wings, and transverse folding takes place far out along the span. The control of folding and unfolding is therefore remote, and must be achieved by leverage, by elastic energy storage and release, or by the action of other body structures.

The hindwing of the cockroach *Diploptera punctata* (Blattodea: Blaberidae) (see figure 1) nicely illustrates the two kinds of folding. The elliptical anterior area is capable of folding transversely, by means of a mechanism which is described below. The posterior area folds fanwise, along radial creases.

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Some implications of the geometry and mechanics of radially folding hindwing fans are explored elsewhere (Wootton 1995; F. Haas, unpublished data). We are here concerned with the mechanisms which underlie the usually far more complex transverse folding patterns. These have long attracted the attention of entomologists (Scudder 1876; Redtenbacher 1886; Moore 1900; Verhoeff 1917; Forbes 1924, 1926; Rehn 1951; Miller 1955; Kleinow 1966; Schneider 1975, 1978; Boulhard 1977; Hammond 1979; Danforth & Michener 1988; Kukulová-Peck & Lawrence 1993; Brackenbury 1994). With a few exceptions, however, previous accounts have tended to emphasise the variety of wing folding, rather than to seek common principles. We show here that virtually all folding patterns apart from fanwise folding consist of combinations of two basic mechanisms, which can be modelled both geometrically and mechanically. These models provide the basis for an analytic approach to all wing-folding in insects, and are relevant to the theory of folding structures in general and to their applications in technology (Kresling 1990).

2. THE BASIC MECHANISMS: DEFINITIONS AND COMMON FEATURES

The two mechanisms are illustrated as rectangular models in figure 2. Each consists of a 'knot' or origin in which four creases intersect at a single point. The four creases mark the borders of four panels, each named in figure 2*a* after its included angle at the point of intersection: thus the α -panel includes angle α . The creases are the hinges about which the panels move.

The mechanisms are folded and unfolded by the relative hingewise rotation of the δ - and γ -panels about

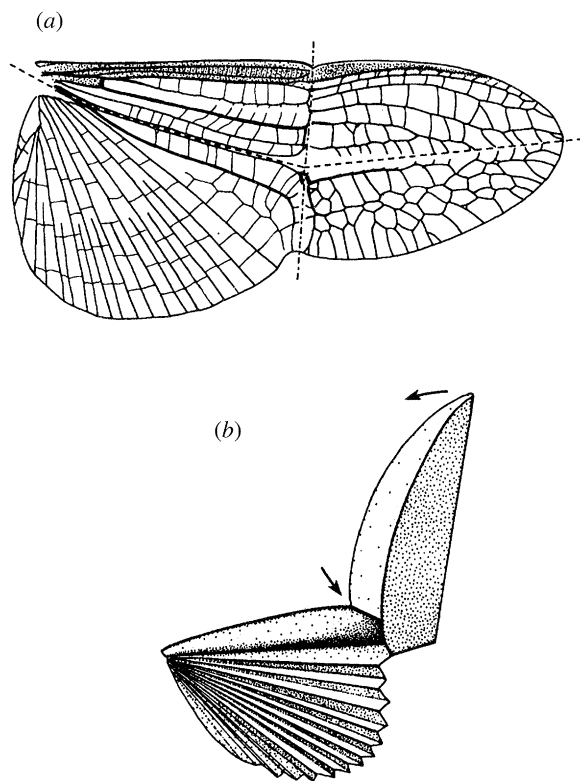


Figure 1. The hindwing of the cockroach *Diploptera punctata*. The anterior area is folded longitudinally and transversely at about half its length, forming an EXT+ mechanism. This is one of few cases known where a wing is folded by a single mechanism. In addition the posterobasal part is folded fanwise. (a) Dorsal view; (b) posterodorsal view of a stage in folding.

the crease OA between them. The changing angle between these panels is called the ‘opening angle’ of the mechanism, symbolized by ϵ .

This system of four panels has one degree of freedom (the degree of freedom is defined by Delarue (1992) as $M = 3 * P - 2 * C$; where one panel is fixed, P is the number of movable panels, and C the number of creases). The panels are movable and their relative position at any instant is unequivocally determined by the four angles around the knot and the opening angle, as defined below. For comparison, a system of three panels has zero degrees of freedom so that the relative positions of the panels are fixed. A system of five or more panels has more than one degree of freedom: the panels are movable but their relative positions are not unequivocally determined by the opening angle and angles around the knot; two or more panels may still move freely.

We distinguish the two basic mechanisms according to their folding pattern. In the first, here called the ‘Internal mechanism’ (INT, hereafter): as the mechanism folds, the crease OC moves between the δ - and the γ -panels, so that the α - and β -panels come to lie between them. In the second, the ‘External mechanism’ (EXT), OC moves outside the δ - and the γ -panels as the mechanism folds, so that the α - and β -panels come to lie on top of or under the δ - and the γ -panels. Figure 3 shows the two mechanisms at different stages in folding, in an xyz coordinate system.

We define the ‘configuration’ of a mechanism as the arrangement of convex and concave creases around the knot. For example (starting from the crease between the α - and the δ -panel, and going clockwise) a convex–convex–convex–concave arrangement is different from a convex–convex–concave–convex arrangement, and this has implications for the movement of the mechanism. Mechanisms are designated as of ‘+’ configuration if there are three convex creases around the knot, and as of ‘-’ configuration if there are three concave creases.

As each of the two types can have two configurations, there are four possibilities: types INT+, INT-, EXT+ and EXT-, which all behave differently with respect to the movement of OC (figure 2*a–d*). It must be stressed, however, that the distinction is only valid if the mechanisms operate in a coordinate system in which there are defined proximal–distal (x), anterior–posterior (y) and dorsal–ventral (z) axes, as in a real wing, with one panel fixed (in figure 3*a, b* the γ -panel is fixed in the x - y plane). If there is no such coordinate system, and the mechanism is freely turnable in all directions, then the distinctions vanish. Each of the mechanisms can be converted to another type or configuration by an appropriate turn. An INT mechanism turned in-plane through 90° becomes an EXT, and the ‘+’ configuration is clearly the ‘-’ configuration inverted. The distinction becomes important, however, in a structure like an actual wing which has a base, an apex, and defined dorsal and ventral faces.

Not all combinations of concave and convex creases are possible if the mechanism is to fold. In any mechanism, the absolute value of the difference between the number of convex and concave folds must equal 2 (Delarue 1992):

$$|n_{\text{convex}} - n_{\text{concave}}| = 2. \quad (1)$$

3. THE MECHANISMS: DIFFERENCES

To understand the following section the reader is recommended to compare the mechanisms practically by folding replicas of figure 2*a–d* with the creases made as indicated.

The two primary mechanisms, INT and EXT, differ in three further respects. All relate to the different movements, as ϵ changes, of the crease OC, where C represents the distal tip of the crease, and O its point of intersection with the others (origin).

(a) *The path of point C and the change in the velocity ratio*

The mechanisms are in effect lever systems, with the interesting property that the changes in position of the components are not linear with respect to ϵ ; velocity ratios and mechanical advantages change as the mechanisms fold and unfold.

The velocity ratio is defined (see, for example, Hughes & Hughes 1994) as:

$$\text{VR} = (\text{distance moved by effort}) / (\text{distance moved by load}). \quad (2)$$

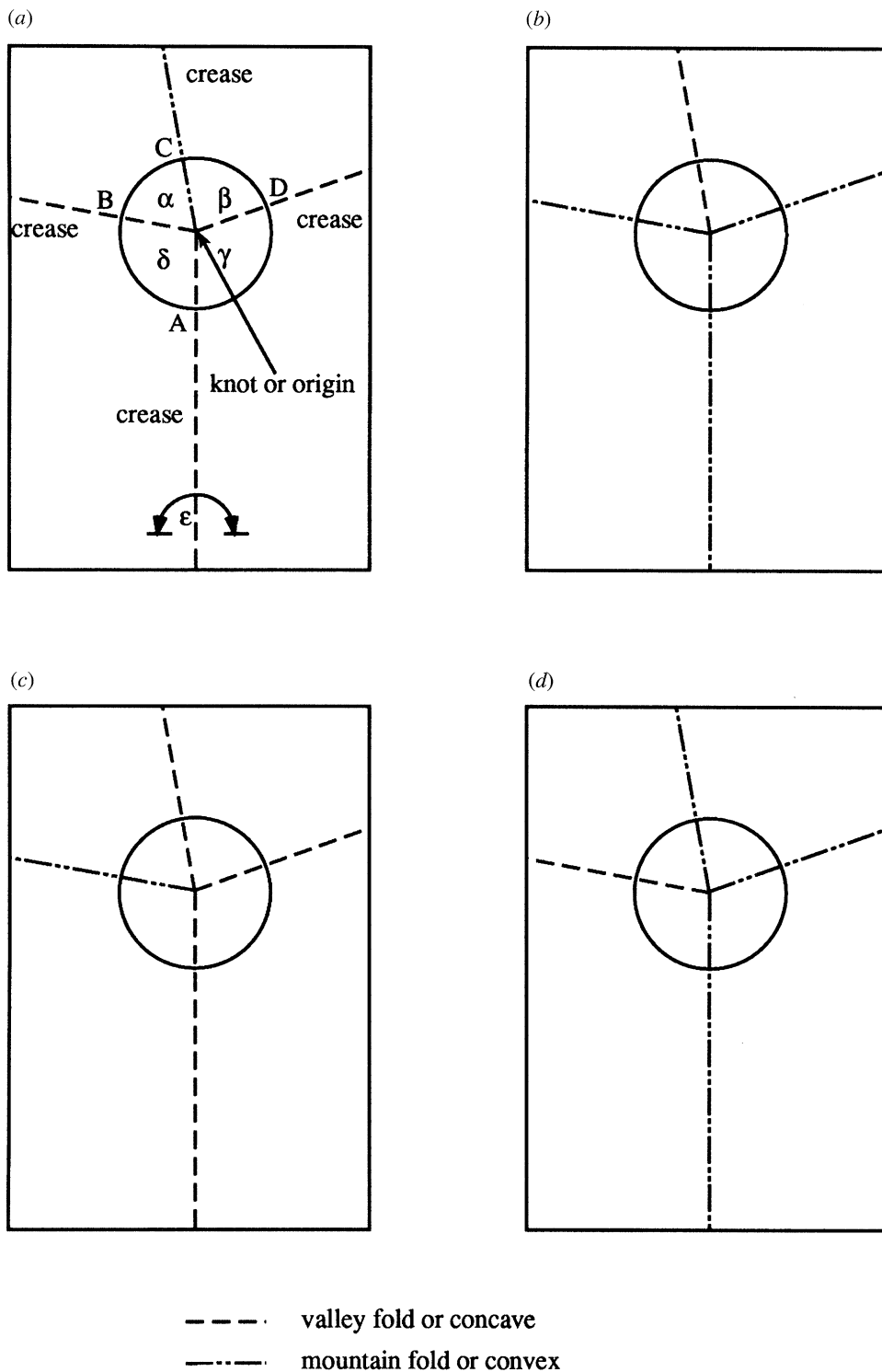


Figure 2. Top views showing the arrangements of creases in the two mechanisms in their four configurations. The definitions of angles and points as used in the analysis are shown in (a). Dashed lines represent a concave ('valley') fold, dashes and dots a convex ('mountain') fold. (a) INT-; (b) INT+; (d) EXT-; (e) EXT+.

Here, the numerator is equal to the distance moved by point B and the denominator is equal to the distance moved by point C, when the opening angle ϵ is changed.

To calculate the coordinates of point C (c_1, c_2, c_3) for any given angle ϵ , three simultaneous equations with three variables must be solved. The underlying assumption is that the panels are stiff and so the angles between the creases do not change. All four folding

lines are assumed to be of unit length. The dot product is used and so:

$$\cos \alpha = c_1 \cos \delta + c_2 \sin \delta \cos \epsilon + c_3 \sin \delta \sin \epsilon, \quad (3)$$

$$\cos \beta = \chi_1 \cos \gamma + c_2 \sin \gamma. \quad (4)$$

The third equation is given by the length of vector OC, assumed to be equal to one:

$$1 = c_1^2 + c_2^2 + c_3^2 \quad (5)$$

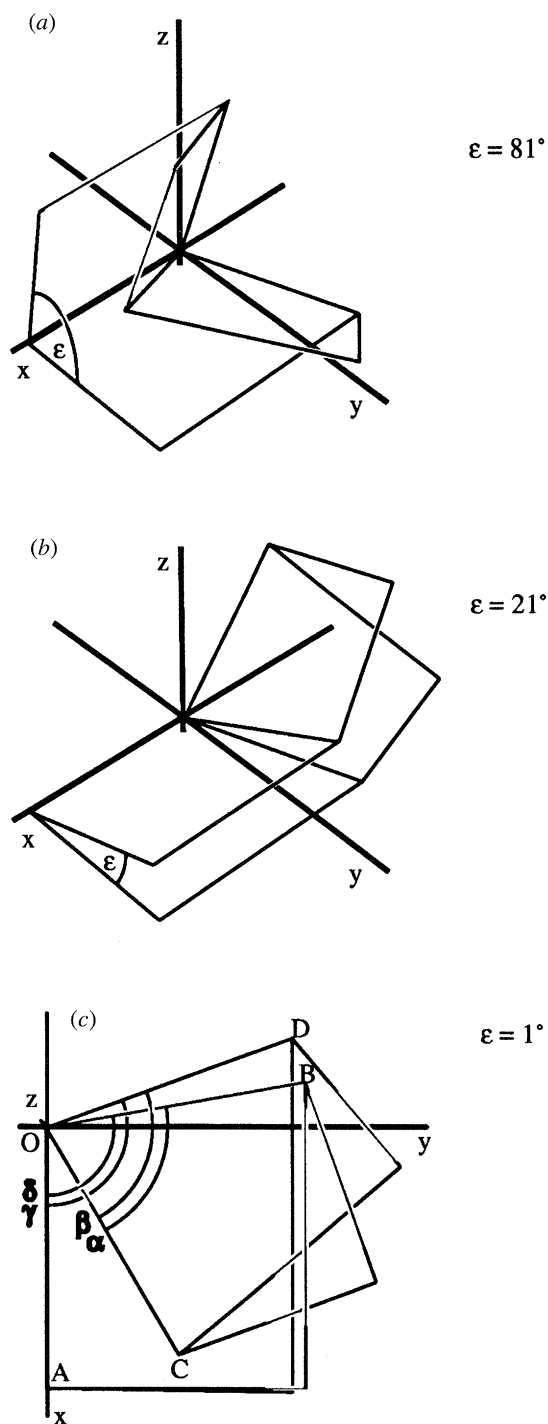


Figure 3. The two basic mechanisms at different positions during opening. (a) INT- mechanism and (b) EXT- with values of ϵ as shown. $\alpha = 70^\circ$, $\beta = 80^\circ$, $\gamma = 110^\circ$ and $\delta = 100^\circ$. (c) A fully folded ($\epsilon = 1^\circ$) INT- mechanism. For further explanation see text.

This quadratic equation has two computable solutions, given by adding or subtracting a root. Each represents one type of mechanism.

Figures 4 and 5 demonstrate the different behaviour of the mechanisms, with respect to the changes in velocity ratio and in the angles of OC to the X, Y and Z axes as a function of the opening angle ϵ . In an INT mechanism these angles change slowly until ϵ reaches ca. 90° , after which they rapidly increase. This

behaviour is also reflected in the velocity ratio. EXT has the converse behaviour: a rapid change of angles with small ϵ , and slowly changing angles with large ϵ .

The graphs in figures 4 and 5 were calculated using the same values for the angles α , β , γ and δ , and negative configurations: types INT- and EXT- respectively. Changing the configuration and the values of the angles around the origin O alters the shapes of the curves to some degree, but does not change their character: INT cannot become EXT. The kinematics are therefore specific to the type of mechanism and only modified in detail by the angles.

Summarising therefore: In INT, OC moves most rapidly, and the velocity ratio of the system is lowest, when the mechanism is almost open (ϵ close to 180°) (see figure 4). In EXT, OC moves most rapidly, and the velocity ratio of the system is lowest, at the beginning of the opening movement (ϵ close to 0°) (figure 5).

Figure 3 shows this clearly: in 3a ϵ is equal to 81° while the tip of OC is still close to the γ -panel. The mechanism shown is completely unfoldable, so the whole of the rest of the unfolding movement takes place in the remaining 99° of the value of ϵ . By contrast, the tip of OC in the EXT mechanism shown in 3b has almost reached its fully unfolded position while ϵ is only 21° .

The mechanical advantage of a lever system is defined as:

MA = force applied by the lever ('effort')/force applied to the lever ('load').

In a frictionless system this equals the velocity ratio, so the conclusions above apply equally to the mechanical advantages of the mechanisms. This clearly has implications in the transmission of forces within a wing.

(b) Reversability of folding

In both mechanisms, if the opening angle ϵ is increased from 0° to 180° , the mechanisms will unfold completely, so that the four panels come to lie in one plane. If however it is decreased to 0° again, then the INT mechanism will fold back to its original position. In the mathematical model of EXT, which assumes that the panels are infinitely rigid, OC will fold back as angle ϵ is decreased to 0° , provided that angles δ and γ are unequal. If they are equal the mechanism will remain unfolded, with the panels α and β coming to lie side by side in one plane, but with OC still extended. Moreover in a real example, any flexibility in the panel will effectively prevent an EXT mechanism from folding back whatever the values of angles δ and γ . In practical terms, an INT mechanism can therefore be actively unfolded and folded from the base (δ - γ panels), whereas EXT can only be unfolded; folding requires intrinsic elasticity, or some external agent.

(c) The limits of angle α

In INT, angle α must be less than angle δ to allow complete folding. The crease OC would otherwise be required to move beyond, i.e. through, the crease

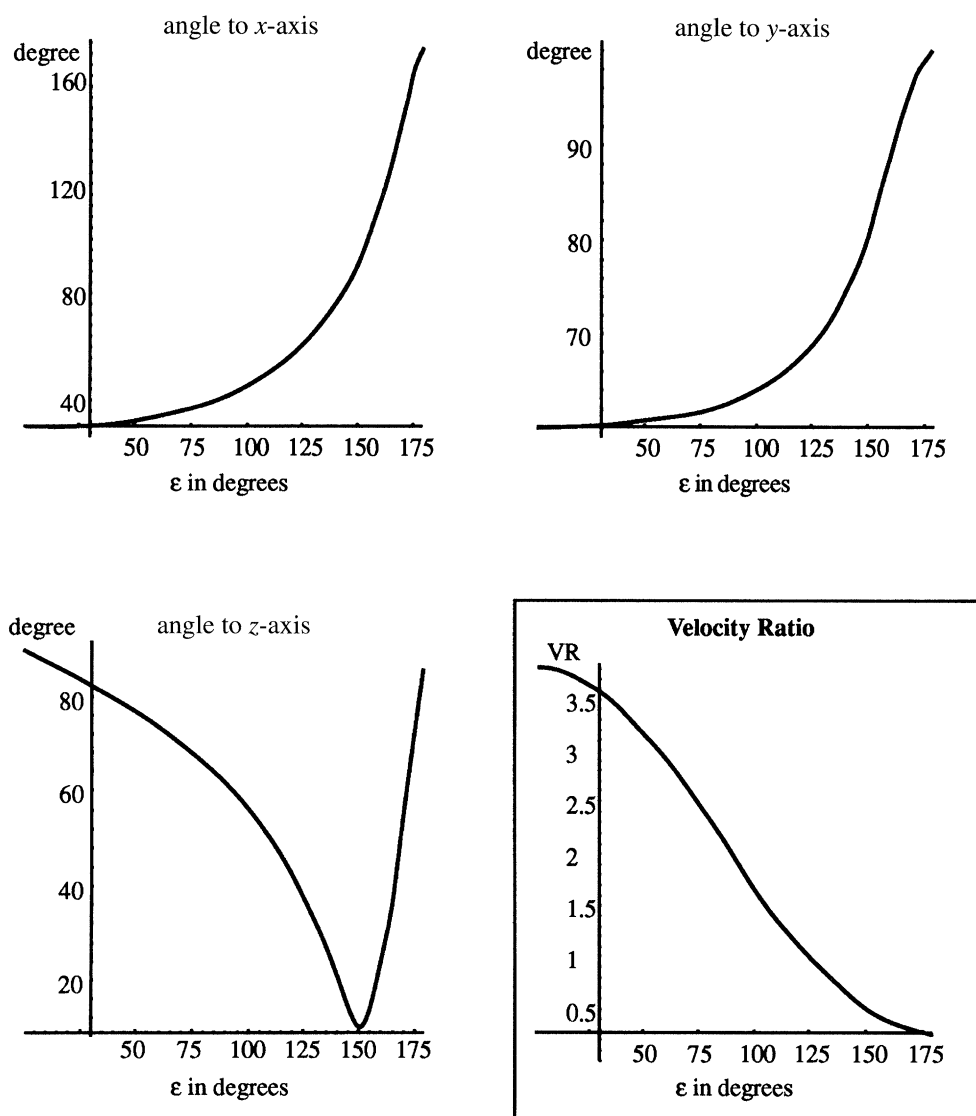


Figure 4. Variation with ϵ of the angles made by the folding line OC to the X, Y and Z axes during unfolding of an INT-mechanism. The angles demonstrate that OC moves slowly when ϵ is small and accelerates when it is increased. The inset shows the velocity ratio. The angles are $\alpha = 70^\circ$, $\beta = 80^\circ$, $\gamma = 110^\circ$ and $\delta = 100^\circ$.

between the δ - and γ -panels, which is clearly impossible. This restriction does not apply to an EXT mechanism.

4. GEOMETRICAL RELATIONS AROUND A KNOT

For any mechanism to be capable of folding flat, certain geometrical rules have to be observed. Delarue (1992) and McShera (1992) stated that the sums of the angles of non-adjacent sectors around a knot must add up to 180° ; and this is true for any such mechanism, regardless of the type and configuration, which is in a single flat plane when open. Delarue did not, however, explain why it should be so. Furthermore it is not immediately apparent whether this is a special case of a general rule which also covers mechanisms in which the angles round the knot do not add up to 360° ; that is when the unfolded mechanism is not flat. If the sum of the angles around the knot is less than 360° , the surface forms an irregular pyramid; if greater than 360° the surface becomes frilled, with concavities and

convexities. Both types can be completely foldable if the geometry is correct.

Let the sum of the angles around the knot be S . Then:

$$\alpha + \beta + \gamma + \delta - S = 0. \quad (6)$$

It is clear from figure 5c that if the mechanism is to fold completely, the difference between the angles β and γ , and between α and δ must both equal angle AOC. Then:

$$-\alpha + \beta - \gamma + \delta = 0. \quad (7)$$

It follows that equation (6) = equation (7) and doing algebraic reformulation:

$$\alpha + \gamma = S/2. \quad (8)$$

Equation (8) shows that the sum of α and γ must equal half the sum of all the angles. In the model, α and γ are non-adjacent angles. Substituting (8) in (6) shows that the same rule applies to β and δ .

The same arguments apply to values of S other than 360° . The case stated by Delarue (1992) is therefore a special example of a general rule: the angles of non-

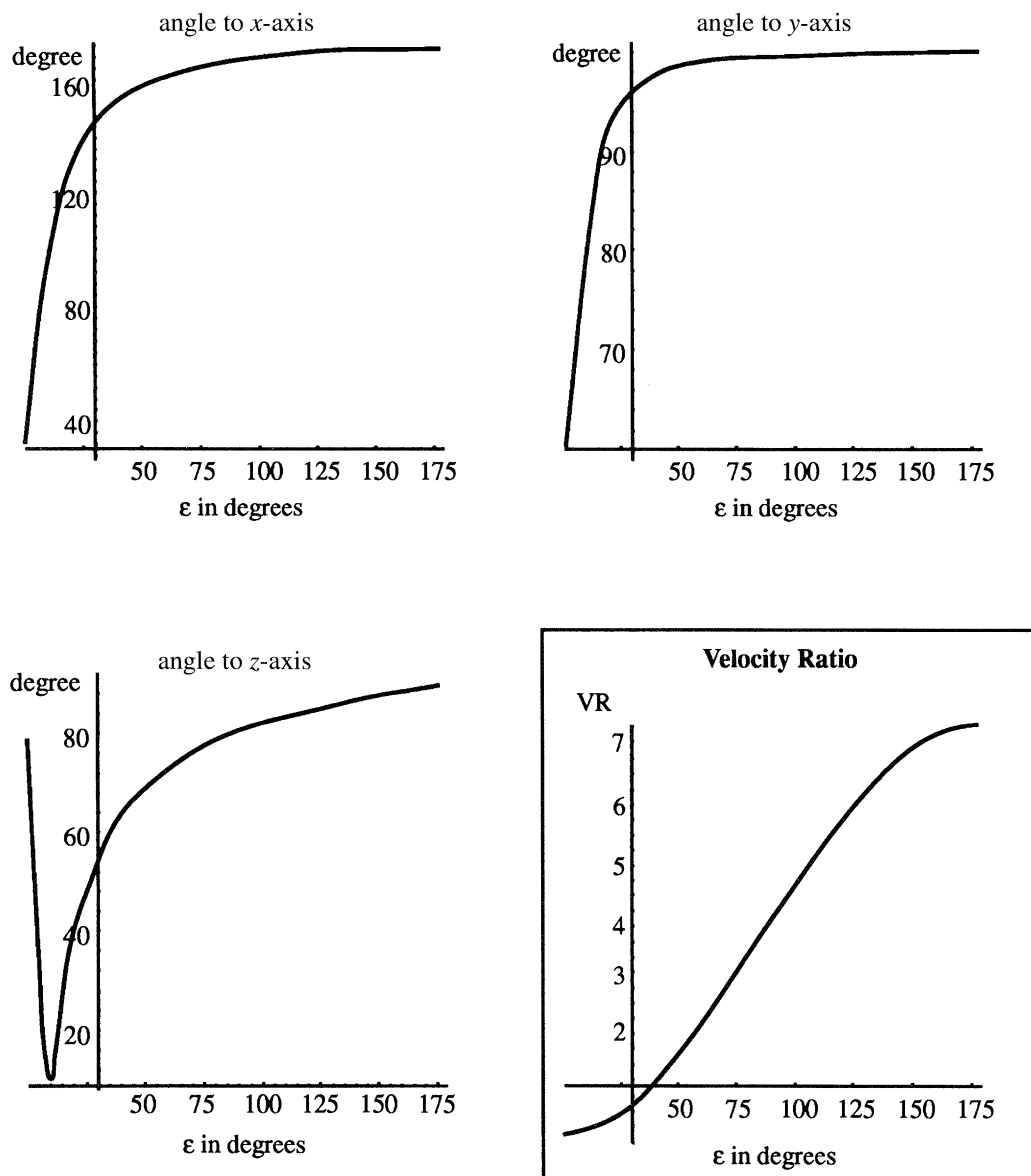


Figure 5. Variation with ϵ of the angles made by the folding line OC to the X, Y and Z axes during unfolding of a EXT– mechanism. The angles demonstrate that OC moves rapidly when ϵ is small and decelerates when it is increased. The inset shows the velocity ratio. The angles are $\alpha = 70^\circ$, $\beta = 80^\circ$, $\gamma = 110^\circ$ and $\delta = 100^\circ$.

adjacent sectors around a knot of four sectors must add up to half the sum of all the angles to allow the mechanism to undergo complete folding.

Clearly, the rules for complete unfolding ($S = 360^\circ$) and complete folding ($\alpha + \beta = S/2$) are independent. Mechanisms can therefore be designed which are completely foldable but cannot be unfolded to a flat plane.

5. HOW DO THE MODELS COMPARE WITH REAL WINGS?

A detailed comparative investigation of wing-folding mechanisms is currently in progress. Preliminary study indicates the following.

The anterior part of the hind wing of *Diploptera punctata* (see figure 1) shows a single mechanism of type EXT+. In almost no other insect wings do INT or EXT mechanisms occur in isolation. Instead mechan-

isms of several types and configurations occur linked together in various combinations. Figure 6a shows the hindwing, unfolded and folded, of *Zophobas rugipes* (Coleoptera: Tenebrionidae) and 6b illustrates schematically the arrangement, types and configurations of the folds in this wing. Note when mechanisms are linked the types and configurations of some components automatically determine those of the remainder.

With a few exceptions the membranes around the knots in wings are more or less flat; that is the angles around the knot add up to 360° . However measurements indicate that non-adjacent angles do not always add up to 180° . In the model this would prevent them from folding completely. In wings, the membrane is often rather crumpled and may show some extensibility; but it is also important to realize that real hind wings do not necessarily need to be completely folded into a flat plane. The actual requirement is to be folded

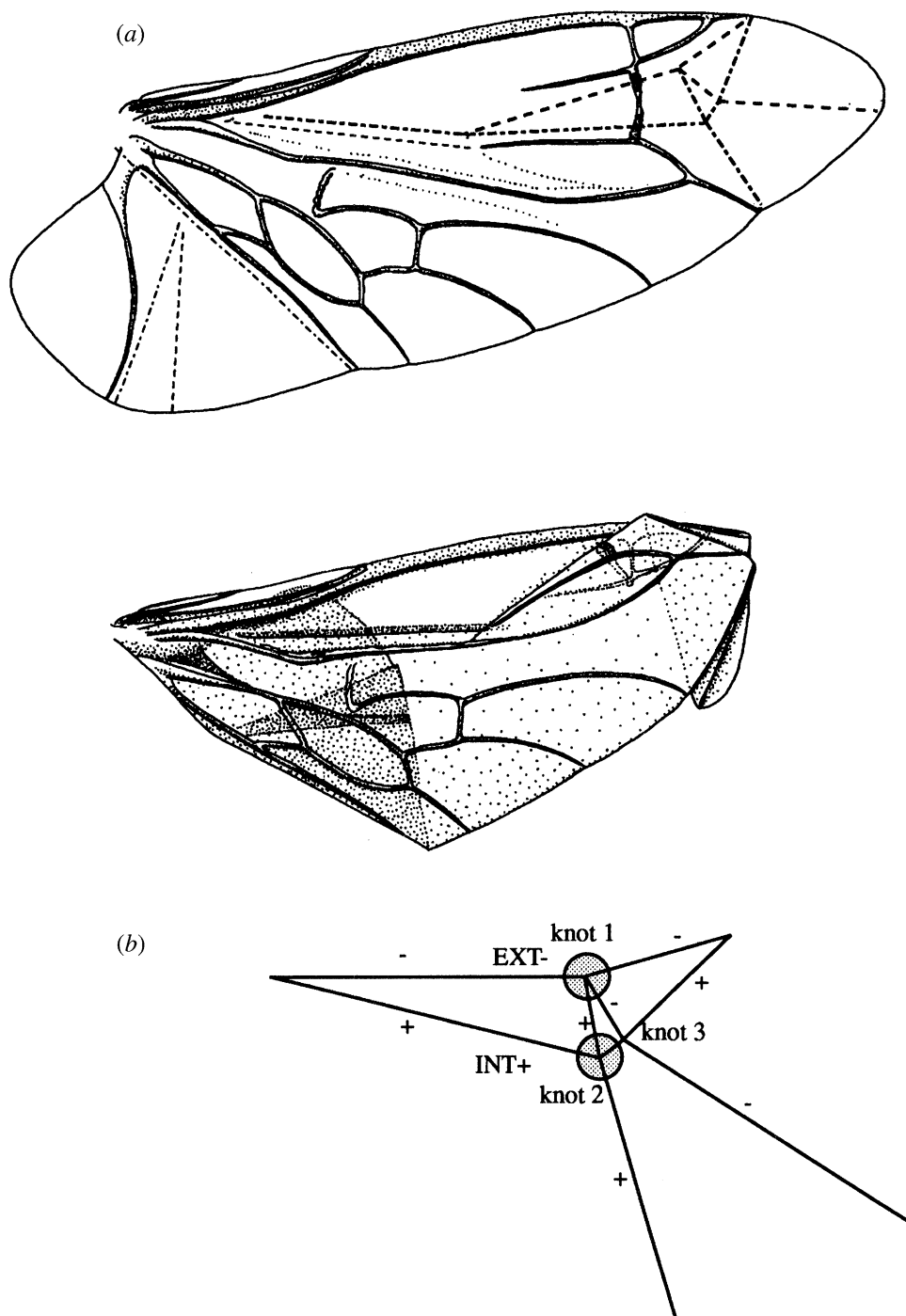


Figure 6. (a) The unfolded and folded hindwing of *Zophobas rugipes*, (Coleoptera, Tenebrionidae) dorsal view, showing the folding pattern. (b) Schematic view of the folding pattern of the tip. The two circles demark two knots of folding mechanisms type EXT- and type INT-. The configuration of these knots determine the configuration of the third knot and so of the remaining folding lines. The angles are, for knot 1: 80°, 22°, 100°, 158°; for knot 2 114°, 120°, 66°, 60°; for knot 3 74°, 106°, 98°, 82°.

into a space of appreciable depth, between the folded fore wings and the dorsal surface of the abdomen, both of which may be curved.

6. HOW ARE TRANSVERSE UNFOLDING AND FOLDING ACHIEVED?

The mechanisms which have been described operate as levers. Can the entire unfolding–folding process be explained as a series of linked levers, powered by the

basal muscles, and opening–closing fold after fold in a chain reaction from the wing base to the tip?

Clearly this can only be part of the story. We have seen that EXT mechanisms, once open, can hardly be levered closed. Furthermore, in many beetles (Forbes 1926) there are mechanisms near the wing tip which at first sight seem independent of the more proximal mechanisms. Paper models with similar folding patterns show that these distal mechanisms can often in fact be unfolded from the base, so a base-to-tip

kinematic chain from the base to the tip may be a reality. However wing membrane is more inclined to buckle in compression than most paper, so only tensile forces are transmissible. To achieve both folding and unfolding other factors must often be involved.

Insect wing cuticle can store energy elastically. Folding and unfolding can involve elastic recovery from an actively maintained unstable shape to a stable shape, or a 'click' from one stable condition to another. Local rigidity in compression can be provided by veins and other thickened sclerotized areas. Active wing extension by the forceps has been demonstrated in Dermaptera (Kleinow 1966), and folding by the abdomen in some Coleoptera (Kaufmann 1960; Hammond 1979). Hydraulic mechanisms for unfolding have been postulated (Schneider 1975), but have not so far been confirmed. Brackenbury (1994) has shown that the wings of beetles flex appreciably along the folding creases in flight, and it may be that aerodynamic and inertial forces play a part in their extension.

7. CONCLUSION

Examination of a very wide range of insect wings has shown that the two basic mechanisms described here provide a suitable foundation for the analysis of nearly all cases in which transverse folding takes place. Together with the fanwise folding whose geometric and mechanical relations are discussed elsewhere (Wootton 1995; F. Haas, unpublished data) they account for the great majority of wing folding patterns. A computer programme is currently under development which will be capable of producing animated sequences of the basic mechanisms and of more complex folding patterns, and will provide a useful tool in describing the kinematics of wing folding processes.

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