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Arthropod Structure & Development 29 (2000) 137–146

ARTHROPOD STRUCTURE & DEVELOPMENT

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Elastic joints in dermapteran hind wings: materials and wing folding

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Received 23 May 2000; accepted 9 August 2000

Abstract

Representatives of Dermaptera probably have the most unusual hind wing venation and folding pattern among insects. Both correlate with unusual wing folding mechanics, in which folding is achieved from within the wing and unfolding is done by the cerci. In this account, the hind wings of the earwig *Forficula auricularia* were studied by means of bright field and fluorescence microscopy. Resilin, a rubber-like protein, was revealed in several, clearly defined patches. It occurs dorsally in the radiating veins, but ventrally in the intercalary vein. This distribution determines the folding direction, and resilin is the major driving mechanism for wing folding. Resilin stores elastic energy in broadened vein patches and along the folds. At the other locations, the mid-wing mechanism and central area, the primary function of resilin is suggested to be prevention of material failure. The arrangement of resilin patches is such that the wing cannot be unfolded from the thorax proper but must be unfolded by the cerci. In Dermaptera, the antagonistic movements of folding and unfolding are achieved in two different ways, resilin and cerci. To our knowledge this is unique.

Keywords: Dermaptera; Functional morphology; Joints; Kinematics; Materials resilin; Wing folding

1. Introduction

The wings of insects are typically thin, delicate and sensitive outgrowths of the body. However, in order to prevent damage, the fore wings are often thickened and stiff. They are rather narrow and are adapted to fit the shape of the abdomen. Clearly, fore wings which were both long and stiff would reduce the abdomen's motility and so rigid fore wings are usually shortened. The hind wings must have a certain size to be aerodynamically functional, which makes them larger than the thickened fore wings. In order to be completely covered by the fore wings, the hind wings must be folded.

The hind wings of earwigs (Dermaptera) are extensively folded and covered by the small, thickened and sclerotized fore wings (tegmina) (Fig. 1). The area of the unfolded wing is ten times greater than the area of the wing package. The folding pattern is so complicated that unfolding cannot be achieved by the thoracic musculature alone, as in cockroaches (Blattodea) and beetles (Coleoptera) (Haas, 1999). Earlier experiments by Kleinow (1966) have shown that the folding is achieved by intrinsic elastic forces and is still possible with the hind wing detached from the body. However, nothing was known about the mechanisms and materials involved.

High elasticity of the wing can be achieved by different mechanisms. One mechanism is a specific pleating pattern of the wing. Three-dimensionally pleated wings have asymmetric torsional rigidity depending on the direction of cantilever beam (Wootton, 1991). Another mechanism lies in the ultrastructure of thin membranous areas of wing cells.

In the vein joints of wings of Odonata, resilin, a rubber-like protein (Andersen and Weis-Fogh, 1964), is employed to enable controlled torsion, essential to flapping flight (Gorb, 1999a). In the hind wings of Coleoptera, the particular distribution of this material has at least two additional functions: wing folding, and preventing material fatigue during multiple folding–unfolding cycles (Haas et al., 2000). These findings suggest that dermapteran wings involve similar materials in the complex folding–unfolding cycles. This work was undertaken to examine resilin distribution in the dermapteran hind wing and to re-examine the processes of folding and unfolding, in order to investigate the close relationship between materials and folding properties.

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PII: S1467-8039(00)00025-6

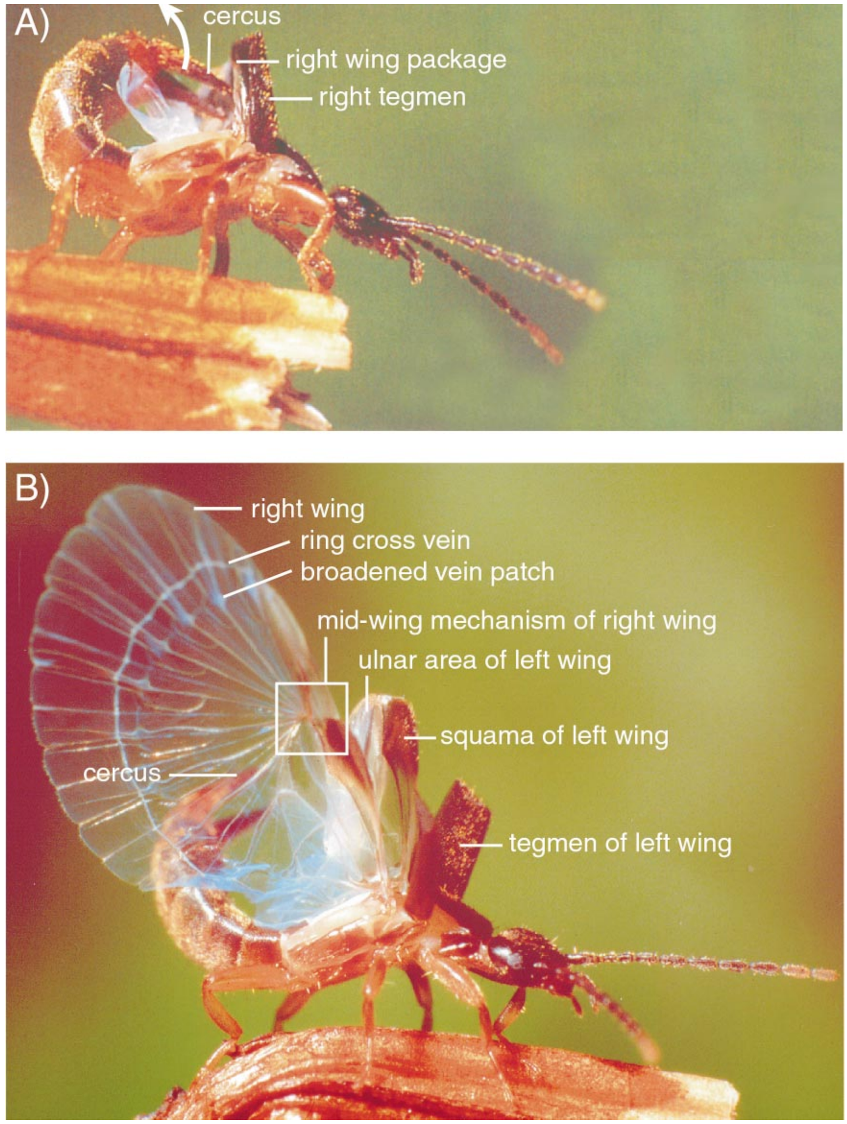

Fig. 1. *Labia minor* (Linnaeus, 1758) unfolding its wings. (A) Both wings are folded, and the cerci are beginning the process of opening the right wing. (B) The right wing is already completely unfolded by the cerci, while the left wing is still an erected wing package over the thorax. Squama and ulnar area assume an angle of about 90°, so that the cerci can interfere and unfold it. Photograph by courtesy of Christopher Timmins, with permission.

2. Materials and methods

2.1. Elasticity tests and modelling

In order to test the intrinsic elasticity of regions and patches in the wing, small areas or veins were mechanically isolated by cutting the wing membrane at different locations. In similar experiments, the broad attachment of the wing was cut, so that the wing attachment was not longer than the wing articulation proper. The movement of the isolated patches was observed, but no quantitative measurements were done. The kinematic model introduced by Haas and Wootton (1996) was developed to calculate the movements of the bistable basic mechanisms and to produce animated sequences. *Mathematica*™ 2.2 on Apple Macintosh™ was used for this purpose.

2.2. Resilin visualisation procedure

Wings of freshly killed specimens of *Forficula auricularia* (Linnaeus, 1758) were used. The wings were cut off, mounted on cover-slips in a water-soluble medium (Moviol, Höchst, Frankfurt, Germany), and observed with a fluorescence microscope (Axioscop, Zeiss Oberkochen, Germany) in bright-field in the UV band (excitation wavelengths 340–380 nm, emission 425 nm). It is known that the insect cuticle has a strong autofluorescence at wavelengths from blue–green area to deep-red. However, resilin has a blue autofluorescence at a very narrow band of wavelengths about 400 nm (Andersen and Weis-Fogh, 1964). This property makes it possible to reveal resilin in biologically native structures without immune labelling or other treatments.

The following procedure for picture acquisition was used.

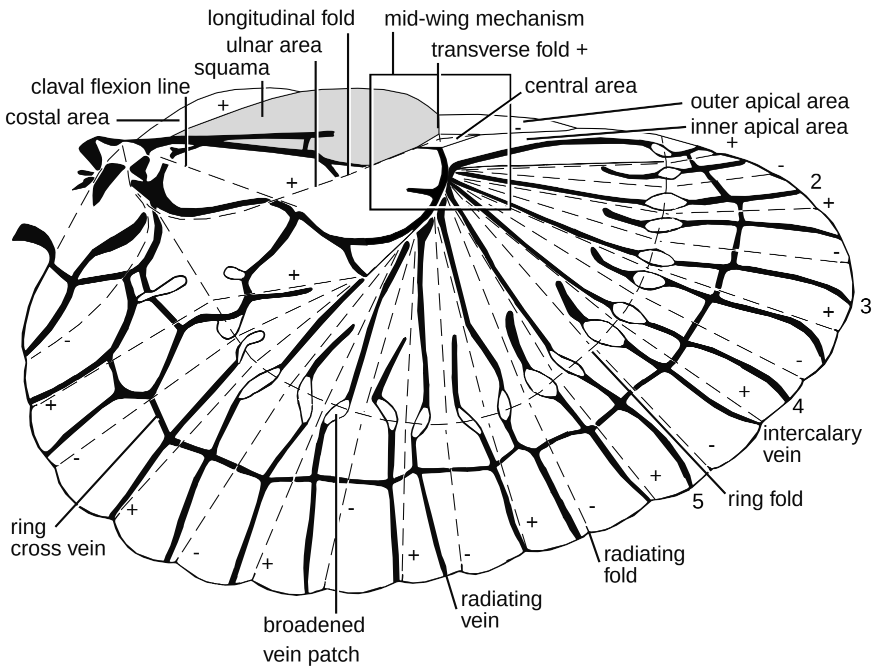

Fig. 2. Schematic view of dermapteran hind wing. The hatched squama is more sclerotised than the surrounding areas. Folding lines are dashed; +: convex or mountain fold; −: concave or valley fold. After Haas (1995), modified.

Pictures were taken using a Sony 3CCD Camera DXC-950P (Sony, Tokyo, Japan) and fluorescence microscopy (UV band) and bright-field microscopy of the same wing area and were afterwards mounted using computer imaging software. This enabled us to show the location of the fluorescence relative to the wing structures.

3. Results

3.1. General design of the dermapteran wing

The hind wing of *Forficula auricularia* (Figs. 1 and 2) consists almost exclusively of a fan (= anal area) supported by radiating veins. In contrast to other insects' wings, these veins radiate from the centre of the wing and not from its articulation. The base of the radiating veins and the ulnar area are movably connected by the transverse fold. Radiating and intercalary veins are separated by radiating folds. Radiating and intercalary veins and radiating folds are crossed by the ring fold, which runs from the wing base to the anterior wing margin parallel to the posterior wing margin. Both radiating and intercalary veins are broadened where crossed by the ring fold.

The mid-wing mechanism (*Flügelmittelgelenk* of Kleinow, 1966) is the region where squama, ulnar area, outer and inner apical area abut (Figs. 1–3). This region is distinctly sclerotised with the exception of the central area (*Zwischenfeld* of Kleinow, 1966) and outer apical area (Fig. 3D). The four angles (α, β, γ, δ) in the mid-wing mechanism add up to 350° (Fig. 6A).

The claval flexion line (*konkave Längsfalte* of Kleinow, 1966), lies in the squama, runs from the wing articulation obliquely-posteriorly and crosses the longitudinal fold (Fig. 2).

The hind wing folds four times. It is folded fan-wise along the radiating folds, transversely along the ring fold and the transverse fold, and longitudinally along the fold between the squama and ulnar areas: the longitudinal fold. This four-fold folding is actually done in one combined movement after the wing stiffening mechanisms are released. The reader is encouraged to photocopy Fig. 2 and fold it according to the instruction (folding lines are dashed; + convex or mountain fold; − concave or valley fold). For a detailed description of the folding pattern see Kleinow (1966) and Haas (1994).

Each wing is attached to the body by a broad membranous area, extending the entire length of the notum. In the anterior half of this membrane lies the wing articulation, whose posterior margin is called the axillary cord. When the attachment of the wing was reduced to the wing articulation, the region of the axillary sclerites and pteralia only, the wing neither unfolded properly nor folded and returned to the resting position.

3.2. Basal vein coupling

The basal vein coupling is the hinge between the radiating veins and the ulnar area. Inferring from stereo microscopic observations, the basal vein coupling consists of a dorsal component, where the inner apical area and the fourth radiating vein meet, and a ventral component, where the

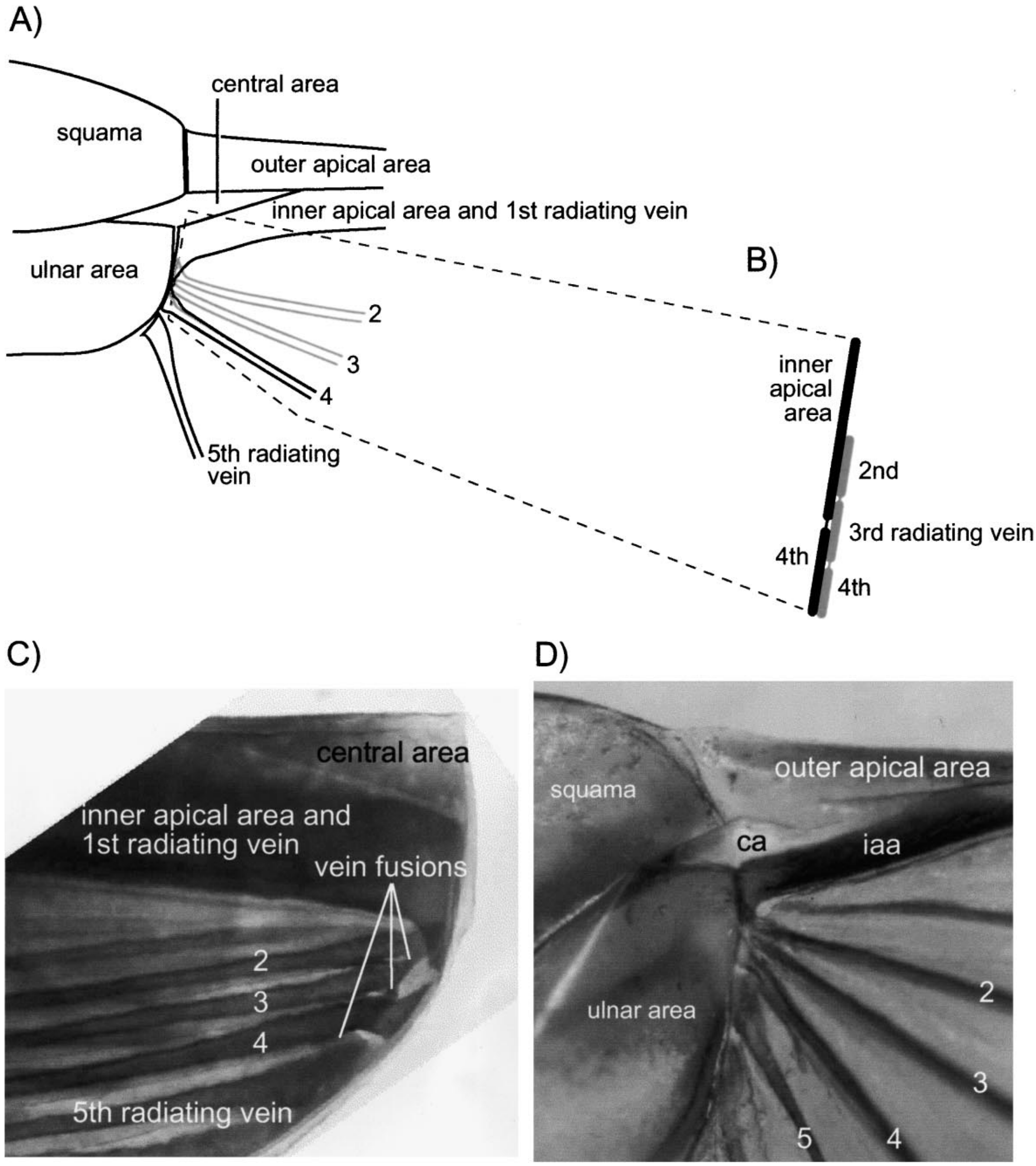

Fig. 3. The two components of the basal vein coupling. (A) Dorsal view. (B) Cross-section along line in (A). (C) Stereomicroscopic photograph of the basal vein coupling in the folded hind wing, showing vein fusions and overlapping of veins, ventral view. (D) Same as region as in (C) in the unfolded hind wing, dorsal view. ca — central area; iaa — inner apical area. cf. Fig. 5E and F.

inner apical area and the second radiating vein meet (Figs. 3, 5E and F). The third, fourth and fifth radiating veins are proximo-ventrally fused to the second radiating vein. The dorsal and ventral components are not staggered but overlap each other (Fig. 3).

Experimentally, the co-ordination of the movement of the veins is shown by a simple two-step experiment. In the first step, the connection to the inner apical area is destroyed, as well as the membrane between the veins, leaving the vein fusions untouched. Then one vein is chosen and moved and all other coupled veins move in the same way. However, if in the second step the vein fusions are destroyed, then the other veins do not move but stay as they are.

3.3. Broadened vein patches

Dissection of the radiating and intercalary veins showed that they bent along the broadened vein patches. If isolated, the radiating veins bent to the dorsal side and the intercalary veins bent to the ventral side. In each case the hind wing was unfolded and oriented in a natural horizontal position.

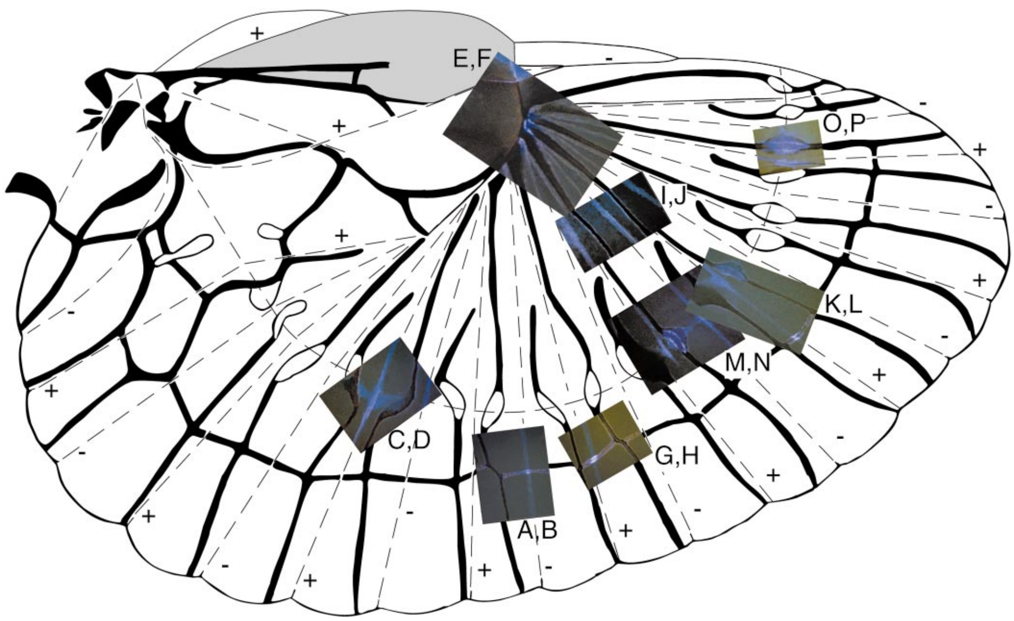

Fig. 4. Resilin distribution in a hind wing of *Forficula auricularia*, dorsal view. Blue autofluorescence shows the presence of resilin. (A)–(P) correspond to the individual pictures shown in Fig. 5.

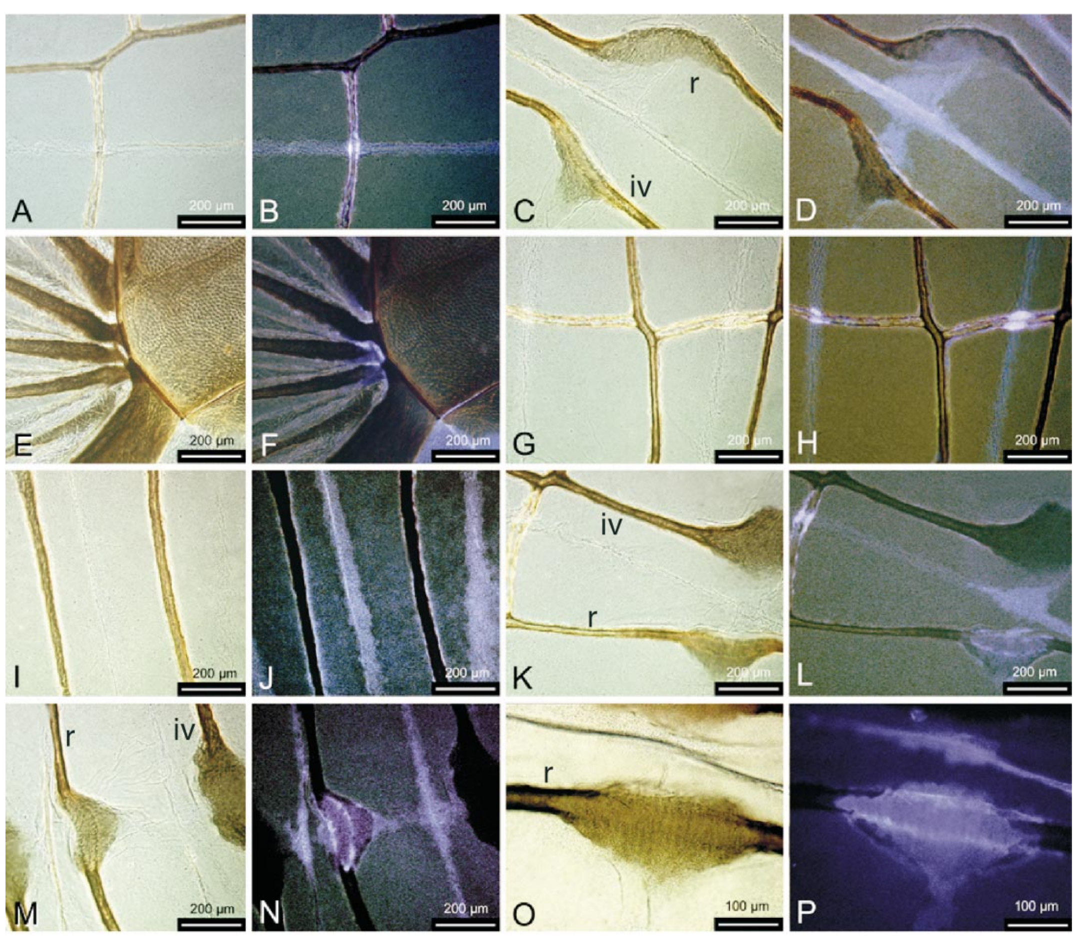

Fig. 5. Resilin distribution in a hind wing of *Forficula auricularia*, dorsal view. Blue autofluorescence shows the presence of resilin. (A, B) Radiating fold and ring cross-vein. (C, D) Broadened vein patches and radiating fold; note the different distribution of resilin in radiating and intercalary veins. (E, F) Basal vein coupling and posterior part of mid-wing mechanism. (G, H) Ring cross-vein at radiating fold. (I, J) Radiating fold. (K, L) Broadened vein patches and radiating fold; note the different distribution of resilin in radiating and intercalary veins. (M, N) Broadened vein patches; note the different distribution of resilin in radiating and intercalary veins. (O, P) Broadened vein patch of radiating vein. iv — intercalary vein; rv — radiating vein.

3.4. Resilin occurrence

Resilin has been found at the following locations in the wing (Figs. 4 and 5; in dorsal view). It occurs at the broadened vein patches of the radiating and intercalary veins (Fig. 5C, D and K–P). It has been possible to determine that a resilin (blue) layer lies dorsally in the broadened vein patches of radiating veins, while it is found ventrally in the broadened vein patches of the intercalary veins. In this case, the resilin is covered by the sclerotisation of the vein and not visible in the dorsal view. A slender resilin-bearing zone is found along the radiating folds (Fig. 5A, B, I and J). The basal vein coupling and the mid-wing mechanism also contain this protein (Fig. 5E and F).

4. Discussion

4.1. Resilin distribution and wing folding

Resilin is found at places in the hind wing where the folding forces are generated, i.e. the broadened vein patches of radiating and intercalary veins (Fig. 5C, D and K–P). The opposing bending directions of radiating and intercalary veins at first seem contradictory. However, during folding the veins are turned about their long axes and, as the fan becomes more and more folded, the veins turn from the horizontal position to a vertical position in the folded fan (Fig. 7A). In this new position the bending direction of radiating and intercalary veins is actually the same, now bending to the anterior (cf. the paper model). Accordingly the folding forces produced by the broadened vein patches in the radiating and intercalary veins are combined (Fig. 7A). In the paper model, it is sufficient to bend the veins about the broadened vein patches to the anterior to fold the whole wing. No other mechanism or interference is needed, so the model suggests that the wing is actually folded by the broadened vein patches, a mechanism remote from the articulation and distributed across the whole wing area.

The occurrence of resilin at the broadened vein patches described here, for the first time shows the material basis of this bending. It furthermore shows that the opposing bending directions are due to a different placement of a layer of resilin.

Resilin is also found along the radiating folds (Fig. 5A, B, I and J), probably supporting the wing folding by pre-stressing the folds either convexly or concavely, respectively, depending to the folding pattern. Thus, resilin along the radiating folding lines supports the broadened vein patches during folding and determines the folding direction to prevent false folding. The higher breaking strain of resilin (Weis-Fogh, 1961) (as compared to the surrounding cuticle) probably also prevents material fatigue along the folding line.

4.2. The mid-wing mechanism as a bistable basic mechanism

The morphology of the mid-wing mechanism and basal vein coupling is more complex than previously suggested. Kleinow (1966) pointed out that the mid-wing mechanism acts as a bistable stiffening mechanism to keep the wing unfolded. Here, the mid-wing mechanism is re-interpreted as a basic mechanism after Haas and Wootton (1996) (Fig. 6). A basic mechanism consists of four plates (squama, outer and inner apical area) linked by four folding lines (transverse and longitudinal fold) meeting in one point (origin). Such a mechanism is deployed or unfolded by increasing the angle between the two basal plates. This angle is called the opening angle ε (Fig. 6B). It has been pointed out by Haas and Wootton (1996) that in order to be flat when unfolded ($\varepsilon = 180°$), the four angles around the origin must add up to 360°. If the sum of angles is less than 360°, the basic mechanism forms a pyramid and ε is less than 180°. Such a basic mechanism either ruptures or, if the plates are sufficiently strong and resilient, snaps to a second stable position beyond the flat unfolded situation. If the opening angle is increased beyond 180°, then the configuration suddenly snaps into a position symmetrically opposite to the first stable position (Fig. 6C). Consequently, basic mechanisms with a sum of angles less than 360° are bistable and usable as locking and stiffening mechanisms, provided there is some elasticity to avoid structural and material failure.

Our re-examination of the mid-wing mechanism shows that Kleinow's observation and the theoretical expectations for bistable mechanisms are perfectly congruent. The sum of angles α to δ is 350° in the mid-wing mechanism and the required elasticity is actually present as resilin in the central area (Fig. 5E and F). We assume that resilin in this situation serves two functions: — it stores the energy to keep the mid-wing mechanism in the locked position, which is necessary to prevent spontaneous folding during flight; — in addition, its higher breaking strain probably prevents material fatigue at this location. This assumption is supported by our observation that unfolded hind wings, when pressed flat on microscopic slides, rupture exactly at the mid-wing mechanism. Alcohol and the embedding medium dehydrate the resilin, thus rendering it brittle.

The question arises why the central area is significantly more compliant and membranous than its surrounding areas. Two paper models suggest an explanation. The first is a complete basic mechanism with a sum of angles of 350°. The second is the same basic mechanism with a rhombic piece around the origin, representing the central area, additionally cut out. If one compares the effort needed to snap each model from one stable position to the other, it proves to be much easier with the rhombic piece removed. This, in our view, strongly indicates the function of the membranous central area: it reduces the forces needed to change the stable

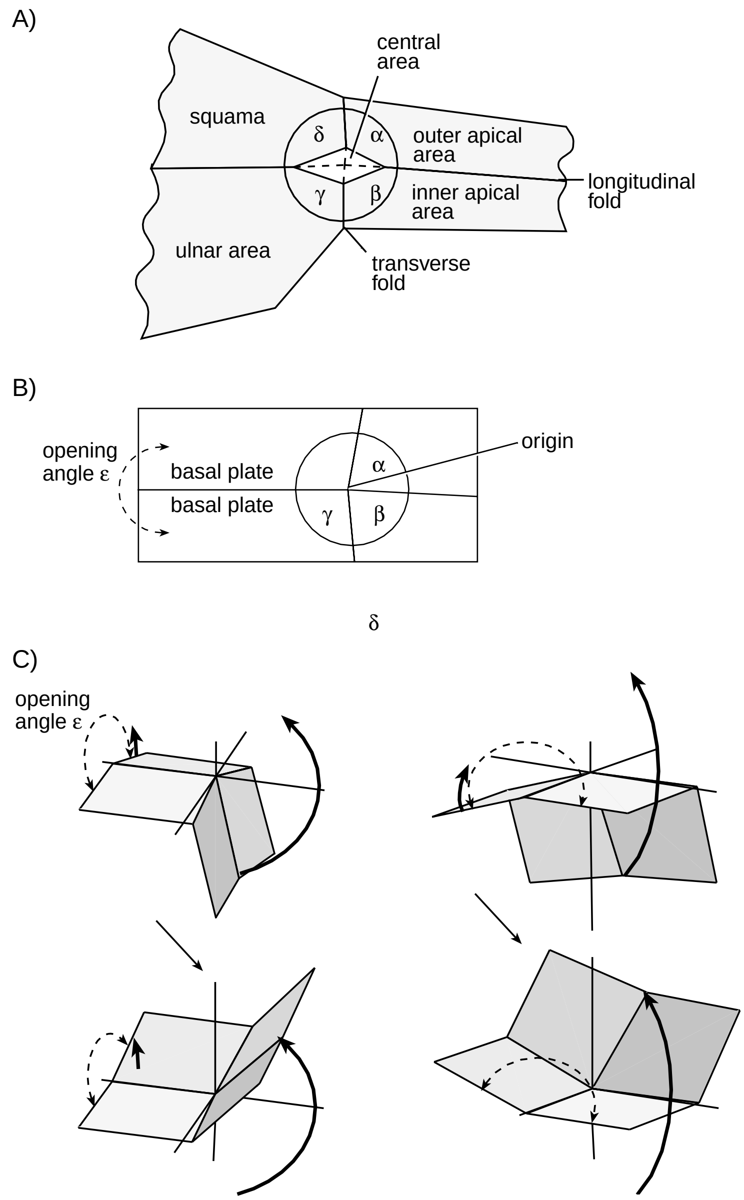

Fig. 6. Schematic view of mid-wing mechanism. (A) The angles α, β, γ, δ add to up only 350° hence the mid-wing mechanism is bistable and does not unfold flat. It is an indispensible stiffening mechanism to keep the wing unfolded during flight. (B) Mid-wing mechanism re-interpreted as a basic mechanism, after Haas and Wootton (1996). (C) Two frames of an animated sequence of a computer simulation, showing the snapping (thick arrows) from one stable position ($\varepsilon = 200°$, upper frame) to the other ($\varepsilon = 160°$, lower frame) in a basic mechanism with 350° sum of angles. The upper pair and the lower pair, respectively, show the same situation in different perspective.

positions and thus reduces the danger of damage from local high stresses.

4.3. Claval flexion line as bistable mechanism

Kleinow (1966) reported that in an unfolded and stiffened wing the claval flexion line (Fig. 2) is active and “snapped in” (concave), while in a folded wing the claval flexion line is flat. He concluded that the claval flexion line is a stiffening mechanism to keep the wing unfolded. This assumption is supported by an simple paper model folded according to this instructions: take a sheet of paper and make a convex (+) or mountain fold, which corresponds to the longitudinal fold between squama and ulnar area. Then make a concave (−) or valley fold, which crosses the convex fold at an angle, which corresponds to the claval flexion line.

As long as the concave (claval) fold is flat or inactive the paper will bend along the convex (longitudinal) fold. However, when the concave fold is active, the sheet of paper becomes stiff, which is analogous to the situation in the unfolded wing.

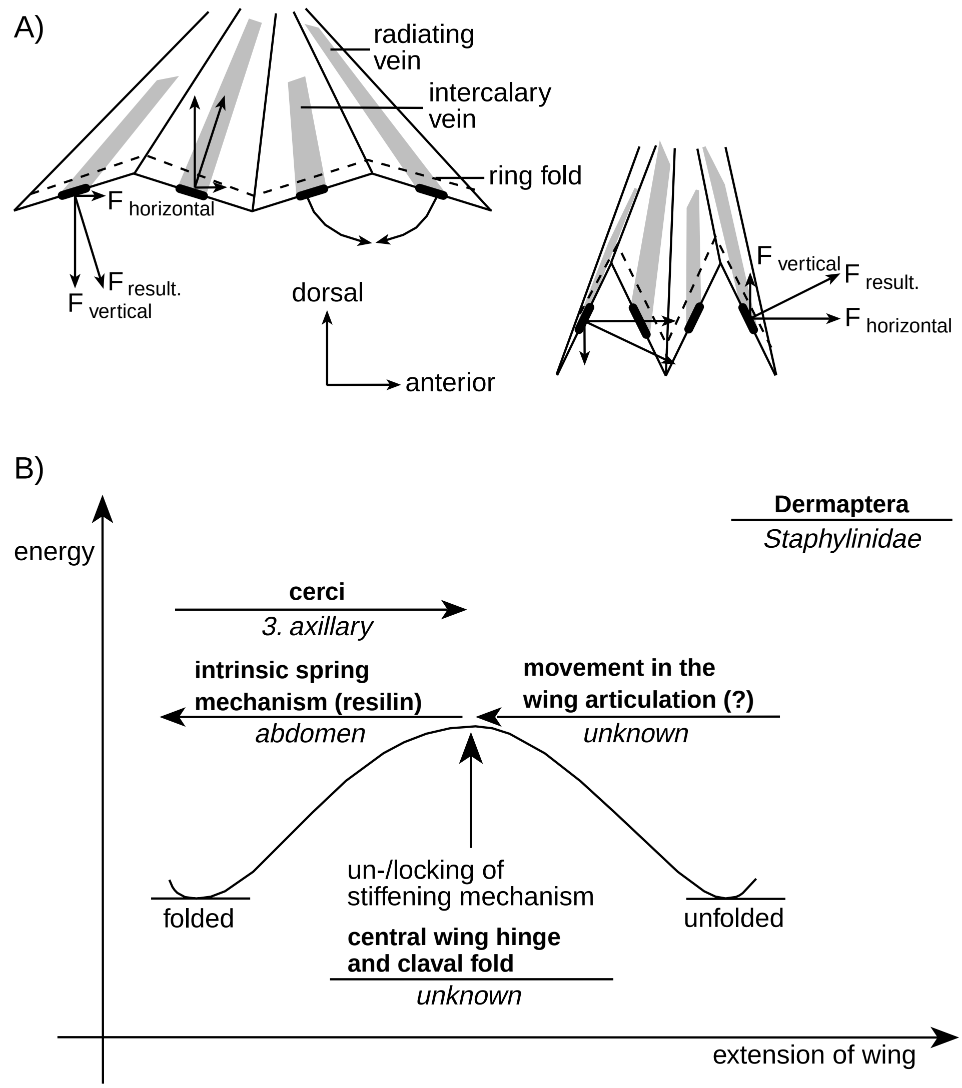

Fig. 7. (A) As a result of the different bending directions of the radiating (to dorsal side) and intercalary veins (to ventral side), the horizontal forces *F* horizontal of several broadened vein patches act synergistically and thereby increase the folding forces. Vertical forces *F* vertical of any paired radiating and intercalary vein counteract each other (left panel). In the partly folded fan (right panel), the broadened vein patches become arranged more vertically, and the situation is quite different. Through the torsion of the veins, *F* horizontal increases substantially, whereas *F* vertical decreases. The horizontal components of the forces generated by the broadened vein patches now fold the fan. (B) Diagrammatic summary of wing folding and unfolding in Dermaptera (bold, above arrow) and Stapyhlinidae (italics, below arrow). The movements of folding and unfolding are indicated by arrows.

4.4. Unfolding of wings

If all the described patches of resilin fold the wing rather than unfold it, energy has to be put into these patches by some external means. This is done by the cerci during unfolding. In order to unfold the wing, the wing package is erected, and thus opened a little, over the thorax by the thoracic musculature. Then the abdomen bends over, the cerci interfere with the wing package behind the ring fold and the wing is unfolded by means of a repeated wiping movement. This is done separately for each wing (Kleinow, 1966), (Fig. 1, own observation).

The basal vein coupling (Fig. 3) ensures the synchronisation of the vein movements during unfolding (Kleinow, 1966; own observation). The wing is unfolded by the cerci, which insert in the partly unfolded wing package. Owing to their shape, the cerci will contact only a small area in the wing package, close to a single vein. In order to transmit the force to the other veins, which resist unfolding by the forces generated in the broadened vein patches, the veins are linked by cross-veins. Besides synchronising the movement, this also prevents high local forces and rupture of the membrane.

Thus, the cerci, driven by the abdominal musculature, put the elastic energy into the resilin patches. These in turn will fold the wing after flight — and after the stiffening mechanisms are released (Fig. 7B; Dermaptera in bold, above arrows; direction of movements indicated by arrows). The stiffening mechanisms — the mid-wing mechanism and claval flexion line — are probably released by movements in the wing articulation, driven by the thoracic musculature (Kleinow, 1966). These movements seem to be so subtle that they were not observed yet. Most arthropod and vertebrate limbs possess two sets of muscles for antagonistic movement. However, there are several exceptions to this general mechanism. Spider legs are bent by muscles but partly extended by hydraulic pressure acting within the leg (Parry and Brown, 1959). The same is true for the mouthparts of larval Odonata (Tanaka and Hisada 1980; Parry, 1983; Olesen, 1972) and staphylinid beetles (Betz, 1996; Kölsch and Betz 1998). Elastic hinges used in returning movements are known from the jumping mechanism of fleas (Bennet-Clark and Lucey 1967; Rothschild et al. 1975) and beetles (Furth et al. 1983), the postcervical neck sclerite of Odonata (Gorb, 1999b), bug mouthparts (Edwards, 1983) and insect claws (Gorb, 1996). None of these require the help of an additional appendage or body part, such as the cerci or legs, for retraction of the extended structure. To our knowledge, the hind wings of Dermaptera and Coleoptera (Haas, 2000) are the only natural structures in which the antagonistic movements of the kinematic chain are achieved with different body parts.

4.5. Comparison of Dermaptera and Staphylinidae

The Dermaptera and Staphylinidae (Coleoptera) are very similar in their superficial appearance: the wings are covered by short fore wings and the abdomen is free and highly moveable. However, this situation undoubtedly evolved independently because Dermaptera and Staphylinidae are certainly not sister groups; the latter belong to the holometabolous Coleoptera, while the former to the Paurometabola (Kristensen, 1991).

The wing folding of the Staphylinidae has been examined by Blum (1979) and Haas (1999), who found that wing folding is completely different compared to Dermaptera. In the staphylinid wing, the anal area is small and the remigium comprises almost the whole wing area. The wing area of the unfolded wing is about four times greater than that of the wing package (Haas, 1998). The venation is reduced to two major veins, the Radius anterior (RA) and the Media posterior (MP1 + 2) (Kukalová-Peck and Lawrence, 1993), which are separated in a scissors-like movement to unfold the wing. This separation is probably driven by the muscles of the 3rd Axillary which also remote the wing (Haas, 1999; Haas and Beutel, 2000). The wings are folded simultaneously by anteriorly directed, pendulum-like movements of the abdominal tip, folding and pushing the wings under the elytra (Blum, 1979). The wings of the Staphylinidae have not been examined for resilin. A stiffening fold has not been found, although one is present in Coccinellidae (Haas et al., 2000).

As in Dermaptera, the Staphylindae use different body parts for the antagonistic movements; however, their roles are exchanged (Fig. 7B; Staphylinidae in italics, below arrows; direction of movements indicated by arrows). In Staphylinidae the abdomen is used to fold, not to unfold, the wings. Unfolding is achieved by thoracic muscles, and there is no indication so far that it is done by some mechanism located within the wing span. Furthermore, the wings are unfolded simultaneously and not sequentially, as in Dermaptera.

In all respects — folding and venation pattern, usage of thorax and abdomen — the Staphylinidae are ‘typical’ Coleoptera with somewhat more densely folded wings. The similarity of Staphylinidae to the Dermaptera is superficial only.

Acknowledgements

Discussions with Prof. Dr U. Schwarz (MPI für Entwicklungsbiologie, Tübingen, Germany) on the structure and properties of biomaterials are greatly acknowledged. Many thanks to Christopher Timmins, Exeter, UK, for permission to use his splendid photographs of wing unfolding in a lesser earwig, *Labia minor* (Fig. 1). This work is supported by the Federal Ministry of Education, Science and Technology, Germany to SG (project BioFuture 0311851). Part of the work originates from a Master of Philosophy Dissertation done at the Department of Biological Sciences, the University of Exeter, UK, which was supported by the German Academic Exchange Service.

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