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How do dragonfly wings work? A brief guide to functional roles of wing structural components

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Insect wings have no flight muscles, except those situated in the thorax. However, they continuously respond to forces acting on them during flight. This ability is achieved by the specialised design of the wings and plays a key role in their aerodynamic performance. Dragonfly (Anisoptera) wings represent an extreme example of this automatic shape control among flying insects. The functionality of the wings results from complex interactions between several structural components of which they are composed. Here we put together the results of our recent works, to review the functional roles of some of the key wing components including vein, membrane, vein microjoint, nodus, basal complex and corrugation. Our results help to understand the relationship between the structure, material and function of each of these wing components in complex dragonfly wings. We further use our data to explain how the interactions between the wing components provide dragonflies with fully functional wings.

Keywords: stiffness; flexibility; deformability; crack resistance; morphology; Odonata

1. Introduction

With ∼97% hunting success rate, dragonflies are one of the most skilled predators in the animal kingdom (Olberg, Worthington, & Venator, 2000). Their impressive flight ability is a key feature that plays a large role in their success (Combes, Rundle, Iwasaki, & Crall, 2012). Dragonflies owe their skilled flight to the striking design of their wings (Wootton, 1991). Similar to wings of many other flying insects, dragonfly wings have two key elements: vein and membrane. However, what makes them unique among all other fliers is the high level of complexity of their wing design (Wootton, 2009).

Dragonfly wings consist of several structural components (Figure 1), which control the functionality of the wing system (Rajabi, Rezasefat, et al., 2016; Wootton, 1991; Wootton & Newman, 2008). In addition to transferring forces, redistributing stresses and minimizing stress concentrations, wing components create a balance between flexibility and stiffness. While the former is needed to generate high aerodynamic lift, the latter provides the necessary structural support (Mountcastle & Combes, 2013; Vanella, Fitzgerald, Preidikman, Balaras, & Balachandran, 2009; Zhao, Huang, Deng, & Sane, 2009).

Although wing components in different dragonfly species have evolved into various forms, they play similar roles in different wings (Wootton, 1991). Hence, in principle, it is possible to generalize the findings on wings of a certain species to many others. In recent years, in our research group, we have been trying to understand the link between the structure, material and

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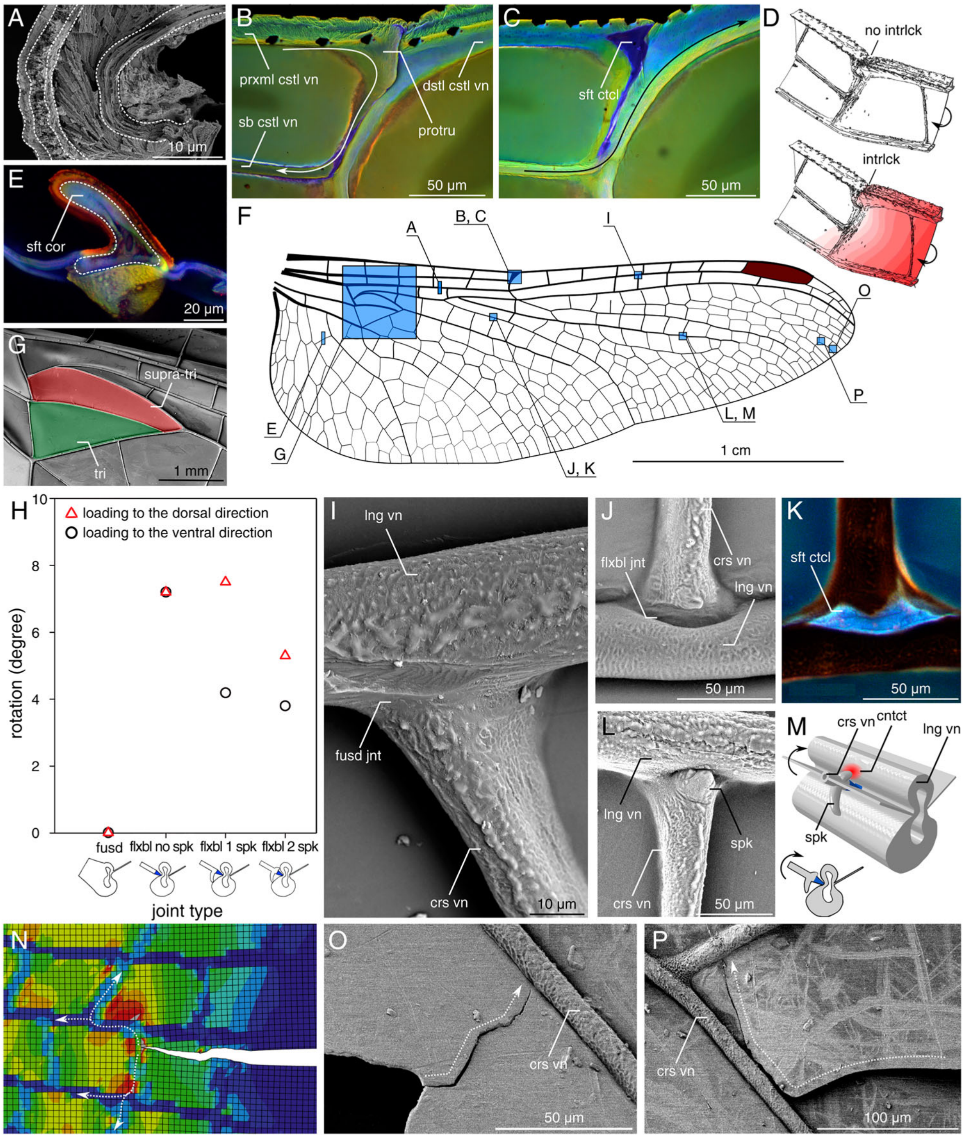

Figure 1. (*Opposite.*) Structural components of dragonfly wings. (A) Ultrastructure of a longitudinal vein in the forewing of the dragonfly *Sympetrum vulgatum*. Veins consists of 3–6 cuticle layers and several sublayers. Dash lines show the borders between the layers. (B, C) Nodus of the hind wing of the dragonfly *Brachythemis contaminata* (dorsal view). The nodus consists of a knot-shaped structure, which protrudes from the proximal costal vein (B) and contains areas of soft cuticle, here in blue (C). White solid arrow in B shows the transition from the proximal costal vein to the subcostal vein on the dorsal side of the wing. Black solid arrow in C shows the transition from the subcostal vein to the distal costal vein on the ventral side. (D) While the soft cuticle provides the nodus with some level of deformability, the physical contact between the knot-shaped protrusion and the distal costal vein prevents large deformations by an interlocking effect. The upper and lower images here show a dorsal view of the nodus before and after loading until interlocking, respectively. Black arrows show the deformation direction. (E) Confocal laser scanning microscopy (CLSM) image of a cross vein in the forewing of the dragonfly *S. vulgatum*. Veins often have a soft, resilin-rich core (surrounded by the dashed line). (F) Hind wing of the dragonfly *S. vulgatum* showing the approximate location of each image. (G) Corrugated structure of the basal complex of the wing of the dragonfly *S. vulgatum*. Supra-triangle and triangle are painted in red and green, respectively. (H) Deformability of different microjoints under the same load. Fused and flexible microjoints provide wings with different levels of deformability. The deformability of the flexible microjoints varies depending on their structure and material properties. They also experience different deformations under the same

Figure 1. (*Caption Continued.*) load applied to the dorsal and ventral directions. Red triangles and black circles represent the rotation of the cross vein about the axis of the joint in the dorsal and ventral directions, respectively. The schemes below the image show two dimensional views of the microjoints. (I) fused microjoint. The intersecting veins in this type of joint have a large contact area. (J, K) flexible microjoint. They usually contain a patch of soft, resilin-rich cuticle. (L) Joint-associated spike. (M) Physical contacts between spikes and adjacent longitudinal veins restrain the deformation of vein microjoints. Inset in the left bottom corner shows a two-dimensional section of the model prior to the interlocking effect. Black arrows show the deformation direction. (N) Numerical simulation of crack propagation in insect venous wings. Cross veins transmit the stress to other veins and distribute it over a larger area. (O, P) Occurrence of cracks in naturally damaged wings. Cracks are deflected (P) or stopped behind veins (O, P). Dashed arrows show the crack path. The tip of the arrows shows where cracks were stopped. Abbreviations: cntct, contact; crs vn, cross vein; dstl cstl vn, distal costal vein; flxbl jnt, flexible joint; flxbl no spk, flexible joint with no spike; flxbl 1 spk, flexible joint with 1 spike; flxbl 2 spk, flexible joint with 2 spikes; fus, fused; fusd jnt, fused joint; intrlck, interlocking; lng vn, longitudinal vein; no intrlck, no interlocking; prxml cstl vn, proximal costal vein; protru, protrusion; sb cstl vn, subcostal vein; sft cor, soft core; sft ctcl, soft cuticle; spk, spike; supra-tri, supra-triangle; tri, triangle. (Reprinted with permission: A, E from Appel et al., 2015; B–D from Rajabi, Ghoroubi, et al., 2017; H from Rajabi, Ghoroubi, et al., 2015; K from Appel & Gorb, 2014; I, L from Rajabi, Ghoroubi, Darvizeh, et al., 2016; N from Rajabi, Darvizeh, et al., 2015; O, P from Rajabi, Schroeter, et al., 2017).

function of different components in dragonfly wings. In our studies, we have combined a variety of interdisciplinary approaches and modern research methods, including advanced microscopy and imaging techniques, mechanical testing, numerical modelling and 3D printing. In what follows, we will put our main findings together and use them to describe the function of some of the key wing components.

2. Supporting wing components: veins, membrane and corrugation

Several previous studies aimed to evaluate the effects of wing components on the wing response to external loads experienced during flight (partially reviewed by Sun & Bhushan, 2012). However, the extent to which each component can really influence the wing response remained unknown (Wootton & Newman, 2008). As it is almost impossible to fully address this issue only experimentally, we used a systematic numerical method to quantify the roles of three supporting components of dragonfly wings: veins, membrane and corrugation (Rajabi, Darvizeh, Shafiei, Taylor, & Dirks, 2016). To this end, we developed a reference wing model, with a high level of similarity to a real wing. Then, we selectively removed wing components from the reference model to determine their influence on both static and dynamic response of the wings.

According to our simulations, the axial and flexural stiffness of dragonfly wings are strongly influenced by longitudinal veins and corrugation. The torsional stiffness, in contrast, is mainly affected by longitudinal and cross veins. Membrane has, in general, the smallest effects on wing stiffness, among the wing components we have examined.

The effect of cross veins on the wing's response to external loads was quite surprising. Cross veins reduce the stiffness to weight ratio of the wings. This means that cross veins increase the weight of the wings rather than enhancing their structural stiffness. This finding, therefore, raises the question of what mechanical role cross veins play in the wing structure.

3. Specialised role of cross veins

In a recent study, we investigated the occurrence of cracks and fractures in dragonfly wings (Rajabi, Schroeter, Eshghi, & Gorb, 2017). Considering that most of the observed cracks were stopped or deflected behind veins (Figure 1O, P), our results suggested the effective role of veins, in particular cross veins, in increasing wing resistance against fracture. How can veins act as barriers for the crack advance?

To answer this question and to visualise the state of stress in a mechanically loaded wing, we used a numerical method (Rajabi, Bazargan, et al., 2017; Rajabi, Darvizeh, et al., 2015). Our results, presenting the first numerical simulation of crack propagation in insect venous wings, showed that when a propagating crack hits a cross vein it stops behind that vein (Figure 1N). The crack continues to grow only after the crack driving force exceeds the resistance of the vein.

The dominant role of cross veins in toughening of insect wings was found to lie in their ability to distribute stress in their large network (Figure 1N). By this, cross veins reduce stress concentrations and shield the crack tip. The resistance of veins to crack propagation also arises from the properties of their complex multilayer architecture (Figure 1A). Veins in dragonfly wings consist of 3–6 cuticular layers, which most of them have several sublayers (Appel, Heepe, Lin, & Gorb, 2015; Rajabi & Darvizeh, 2013; Wang, Li, & Shi, 2008). We showed that the layers and sublayers trap a growing crack at their interfaces and slow down the crack propagation (Rajabi, Shafiei, Darvizeh, & Babaei, 2016; Rajabi, Shafiei, Darvizeh, Dirks, et al., 2016). In addition to this effect, veins contain a soft, resilin-rich core, which is highly extensible (area surrounded by dashed line, Figure 1E) (Appel et al., 2015; Rajabi, Shafiei, Darvizeh, Dirks, et al., 2016). This soft core improves the intrinsic toughness of the veins and contributes to their resistance against crack propagation (Rajabi, Shafiei, Darvizeh, & Babaei, 2016).

4. Vein microjoints: where flexibility and stiffness meet

Veins are connected to each other by joint-like structures, so called vein microjoints (Figure 1I–L). There are a variety of vein microjoints in dragonfly wings, of different sizes, shapes and material compositions (Appel & Gorb, 2011, 2014; Donoughe, Crall, Merz, & Combes, 2011; Gorb, 1999; Noorhidaya, Yazawa, Numata, & Norma-Rashid, 2018; Newman, 1982). Vein microjoints provide wings with different levels of local deformability. In accordance with their deformability level, they can be subdivided into two main categories: fused and flexible microjoints (Gorb, 1999; Newman, 1982). In the first category, the connected veins make a large contact area with each other (Figure 1I). However, in the second, there is no direct contact between the veins (Figure 1J) and they are often connected to each other via a patch of soft resilin-rich cuticle (Figure 1K) (Gorb, 1999).

The small size of microjoints makes it very challenging to perform any accurate mechanical measurement. Therefore, we used data from scanning electron microscopy (SEM) and micro-computed tomography (μCT) to develop detailed finite element (FE) models of the microjoints (Rajabi, Shafiei, Darvizeh, Dirks, et al., 2016). Using these models we comparatively studied the effect of geometric and material properties on the deformability of a variety of fused and flexible microjoints.

Our results show that vein microjoints significantly influence local deformation of dragonfly wings (Figure 1H). The resilin-rich cuticle, found in flexible microjoints, not only increases their deformability, but also reduces stress concentration under a given load. This was found to effectively reduce the risk of wing fracture in accidental collisions with rigid objects (Rajabi, Shafiei, Darvizeh, & Gorb, 2016).

We then combined single microjoint models and developed models of their combinations, based on previous observations on wings of different dragonfly species (Rajabi, Ghoroubi, Darvizeh, Appel, & Gorb, 2016). The results surprisingly revealed that a microjoint may behave very differently when surrounded by other types of microjoints. Hence, to estimate wing deformability, one should not only consider the presence of specific microjoint types, but also the way they are connected to each other.

Another interesting finding of our studies was related to the role of joint-associated spikes in wing deformability. Such spikes are located on either one or both sides of a cross vein adjacent to a longitudinal vein (Figure 1L). Our results showed that an external load causes the rotation of the cross vein about the axis of the joint. When a certain load is reached, the spike on the cross vein comes in contact with the adjacent longitudinal vein and acts as a "mechanical stopper", which avoids further rotation of the vein (Figure 1M). Therefore, according to our results, a microjoint can combine two different functions: flexibility and stiffness.

Spikes on the dorsal and ventral sides of cross veins often have different forms and sizes (Appel & Gorb, 2014). Spikes may even be present only on one side of the veins. These features can influence the deformability of vein microjoints in the dorsal and ventral directions (Figure 1H). This causes an asymmetry in microjoint deformation, which can further result in observable dorsal-ventral asymmetry in the deformability of the whole wing system (Rajabi, Ghoroubi, et al., 2015, 2016; Rajabi, Shafiei, Darvizeh, & Gorb, 2016).

5. Nodus: a specialised microjoint

The nodus is a microjoint located almost in the middle of the costal vein of dragonfly wings (Figure 1B, C). In contrast to all other vein microjoints, the nodus is not the intersecting point of two or more veins, but rather where a vein breaks. At this point, on the dorsal side, the proximal costal vein bends and merges with the subcostal vein (solid arrow, Figure 1B). On the ventral side, the subcostal vein makes a transition to the distal costal vein (black arrow, Figure 1C). The proximal and distal parts of the costal vein in this region connect to each other with a soft, resilin-rich cuticle (bluish regions, Figure 1C).

In two separate studies, we investigated the influence of the structure and material composition of the nodus on its function in dragonfly wings (Rajabi, Ghoroubi, Stamm, Appel, & Gorb, 2017; Rajabi, Stamm, Appel, & Gorb, 2018). We found that the presence of the soft cuticle makes the nodus a flexible microjoint. The flexible nodus facilitates the twisting of the leading edge spar, which is known to be a lift enhancing mechanism (Ennos, 1988a; Wootton, 1993). The nodus, however, contains a knot-shaped structure, which protrudes from the proximal costal vein (Figure 1B), and plays a similar role as that of the spikes in typical vein microjoints. When a critical load is reached, the distal part of the costal veins comes in contact with the nodal protrusion, which is located on the proximal costal vein (Figure 1D). This physical contact between the two parts results in an interlocking effect and restrains the displacement of the nodus, converting it to a stiff joint (Rajabi, Ghoroubi, et al., 2017). This is an important effect which prevents the loss of the aerodynamic function of the wings under large loads.

6. Basal complex

The basal complex is a high-relief structure at the wing base (Figure 1G). It consists of a thick cross vein, known as the arculus, and two triangular wing domains, so called supra-triangle and triangle. With its relatively thick and highly corrugated structure, the basal complex plays an important role in stiffening the wing (Rajabi, Ghoroubi, Malaki, Darvizeh, & Gorb, 2016; Wootton, Kukalová-Peck, Newman, & Muzón, 1998).

Interestingly, this wing component has also a strong influence on how wings deform during flight. Our studies showed that, under an external load, the basal complex rotates and pushes down the trailing edge (Rajabi, Ghoroubi, Malaki, et al., 2016). The downward rotation of the trailing edge is expected to enhance wing camber formation and, therefore, increase lift. Both the quality and quantity of this rotation depend on the geometric characteristics of the basal complex and, to a great extent, determine the deformation pattern of dragonfly wings.

7. Secret of wing functioning: a balance between flexibility and stiffness

Studies on flight aerodynamics have shown that flexible wings are capable of producing significantly greater lift in comparison with stiff wings (Ifju et al., 2006). The reduced torsional stiffness of flexible wings facilitates the development of a cambered section in flight. The latter consequently improves the aerodynamic performance of the wings (Ennos, 1988b). A similar strategy is used in dragonfly wings (Mountcastle & Combes, 2013), and likely in those of many other flying insects (Du & Sun, 2010; Nakata & Liu, 2011; Young, Walker, Bomphrey, Taylor, & Thomas, 2009). Many of the wing components mentioned earlier, such as flexible microjoints, nodus and patches of soft cuticle, provide wings with an increased structural flexibility. However, the flexibility is needed to only a limited extent. A very flexible wing would not be able to withstand flight forces. Hence, a balance is needed between flexibility and stiffness. The latter is achieved not only by supporting wing components, such as veins, corrugation, and membrane, but also by reducing the level of flexibility of deformable wing components, such as vein microjoints and nodus, as the applied load increases.

There are still many components of dragonfly wings, such as the pterostigma, flexion lines, spikes, etc., which have not yet been adequately studied. Future research may focus on the role of these structural components in the wing system. The interactions among different wing components is another unexplored area. Given the importance of such interactions in the functionality of dragonfly wings, they promise a fruitful area for future research.

Data accessibility

All supporting data are made available in the article.

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