Flexural Stiffness in Insect Wings: Effects of Wing Venation and Stiffness Distribution on Passive Bending

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During flight, insect wings bend and twist dramatically, and the instantaneous, three-dimensional shape of wings may influence many aspects of flight performance. Insects have little control over this bending and twisting—wing deformations are largely passive and are controlled primarily by the architecture and material properties of the wing. However, our understanding of how insect wing design affects flexibility and passive wing deformation remains limited. Here, we discuss how insect wing venation affects overall bending stiffness, how stiffness varies throughout wings, and how these features of wing design affect passive bending.

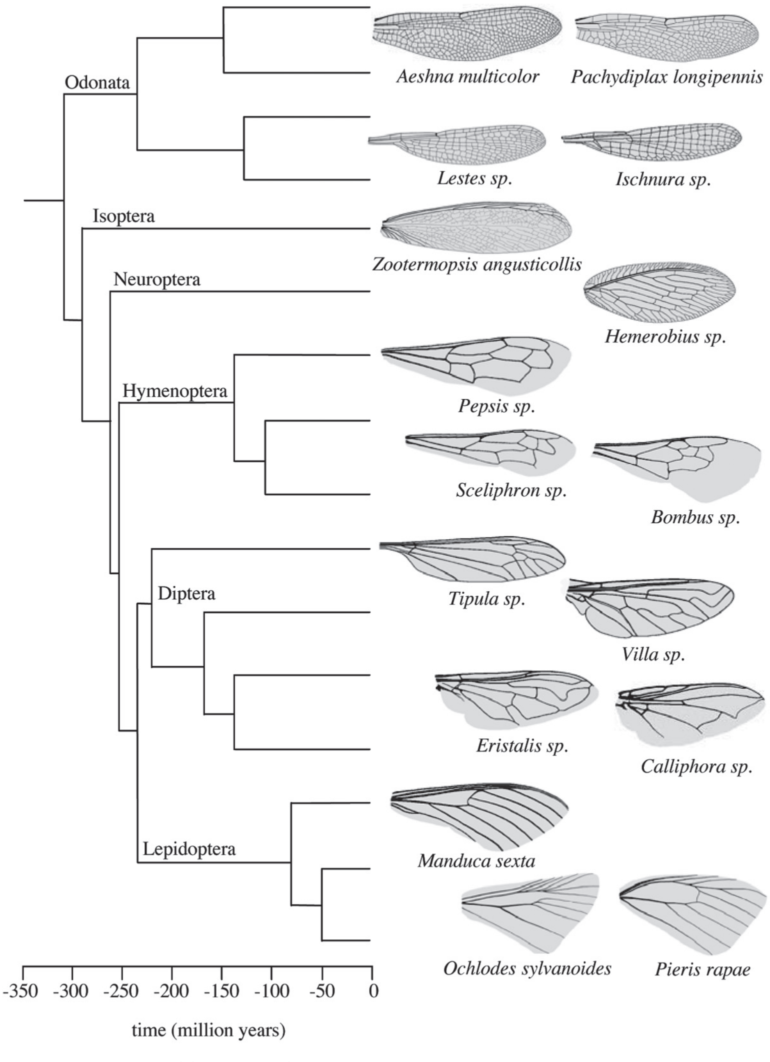

Fig. 1. Drawings of forewings from insects used in this study, arranged on the phylogenetic tree used to calculate independent contrasts. Veins are drawn at actual thickness; wings are not shown to scale. Genus and species names (when known) are shown under each wing, and orders are listed at their branching points (from Combes and Daniel 2003a).

The pattern of supporting veins in insect wings varies widely among insect orders and families. Given the large phylogenetic changes in wing venation pattern (Fig. 1), one might expect insect wings to display large mechanical differences that would affect their deformability during flight.

We examined the relationship between insect wing flexibility and venation by measuring flexural stiffness (*EI*) and quantifying venation pattern in 16 insect species from six orders. Flexural stiffness is a composite measure of the overall bending stiffness of a wing, combining the material properties of the wing (*E*, Young's modulus) and the geometric distribution of this material (*I*, second moment of area).

We measured overall *EI* of wings in the spanwise direction (from base to tip) and the chordwise direction (from leading to trailing edge) by performing static bending tests. We attached each wing at the base (or leading edge), applied a known force at the tip (or trailing edge), and measured the displacement of the wing. We then calculated *EI* with a simple beam equation (see Combes and Daniel 2003a). We also digitized the wing venation of each species and derived five measures of venation pattern (Combes and Daniel 2003a). To remove the effects of phylogeny, we calculated standardized independent contrasts of venation and stiffness measurements and examined the correlations between these contrasts.

Our measurements show that *EI* is strongly correlated with wing size (Fig. 2), but the details of venation pattern do not appear to affect overall flexural stiffness (no significant correlations were found between contrasts of wing venation pattern and *EI*). The measurements also reveal a large anisotropy, or difference, between spanwise and chordwise flexural stiffness; spanwise *EI* is ≈1 to 2 orders of magnitude greater than chordwise *EI* in all species tested (Fig. 2).

To determine how wing structure may contribute to this pattern of stiffness anisotropy, we created a simplified finite-element model of a *Manduca* (hawkmoth) wing. To create this model, a digitized

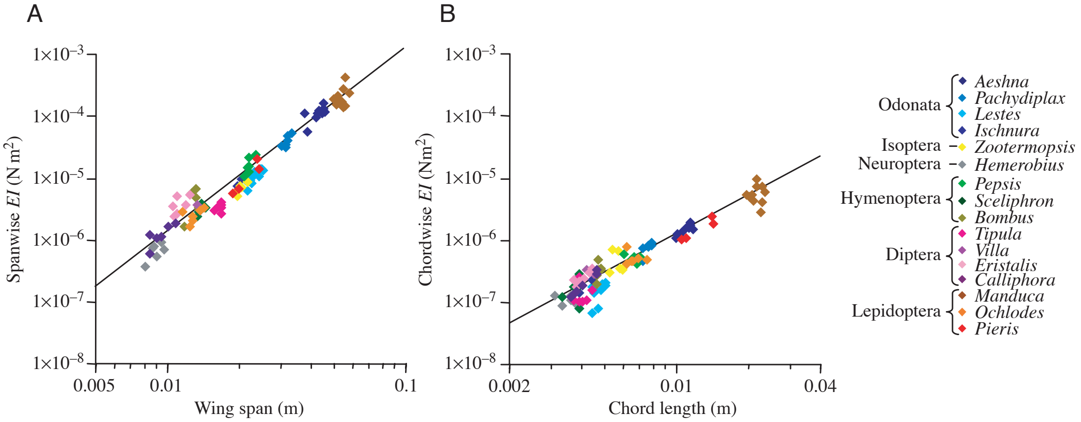

Fig. 2. Flexural stiffness *versus* span/chord length in 16 insect species. Individuals of each species are plotted in the same color. Axes are on a logarithmic scale. A. Spanwise flexural stiffness *versus* wing span; for log-log transformed data, $y = 2.97x + 0.08$, $r^2 = 0.95$. B. Chordwise flexural stiffness *versus* chord length; for log-log transformed data $y = 2.08x - 1.73$, $r^2 = 0.91$ (from Combes and Daniel 2003a).

image of the wing was discretized, or broken down into numerous elements (squares or triangles), each of which was given a certain thickness and Young's modulus (see Fig. 4A, left). This computational modeling technique allows us to solve a complex mathematical problem (how the entire wing responds to forces) by breaking it down into a number of simpler problems (how each element interacts with its neighbors). Our goal was not to reproduce the behavior of a real *Manduca* wing, but rather to create a general model to explore how adding or strengthening veins in certain regions of the wing affects overall flexural stiffness.

We increased the Young's modulus of certain veins in the model, applied a static force, recorded the resulting displacement, and then calculated overall *EI* of the virtual wing. We found that adding or strengthening veins in the leading edge of the wing dramatically increases spanwise flexural stiffness, generating the spanwise–chordwise anisotropy measured in real wings. The fact that clustered or thickened veins are found in the leading edge of nearly all insect wings suggests that this stiffness anisotropy may be a common functional feature among insects.

Although our measurements of overall *EI* provide information about the scaling and anisotropy of bending stiffness, the instantaneous shape of a flapping wing is influenced not only by overall stiffness, but also by the distribution of flexibility throughout the wing. To determine how wing flexibility varies spatially, we measured variation in flexural stiffness along two axes of the wing (spanwise and chordwise) in two species—the hawkmoth *Manduca sexta* and the dragonfly *Aeshna multicolor*.

We first measured continuous displacement by performing static bending tests as before, but also illuminated wings with lines of laser light along the bending axis and photographed wings before and after loading with a point force. The difference in the position of the laser line in these photographs provided us with the continuous displacement of the wing. To calculate *EI* along this axis, we used a continuous version of the beam equation (see Combes and Daniel 2003b) and rearranged the equation so that we were solving for displacement (along the wing) as a function of the *EI* distribution. We posed various alternatives for how flexural stiffness might vary along the wing (represented by simple mathematical functions), predicted the patterns of displacement that would result from loading, and then determined which *EI* distribution produced a pattern of displacement most similar to that measured in a real wing.

Our measurements show that flexural stiffness declines exponentially from wing base to tip and from the leading to the trailing edge in wings of *M. sexta* (Fig. 3A). In addition, we found that chordwise flexural stiffness declines far more sharply in male moths than in female moths; and the wings of male and female moths display a large dorsal/ventral difference in *EI*. Measurements on *A. multicolor* show that stiffness also declines exponentially in this species (Fig. 3B), despite large differences in wing shape and venation pattern between hawkmoths and dragonflies. This similarity

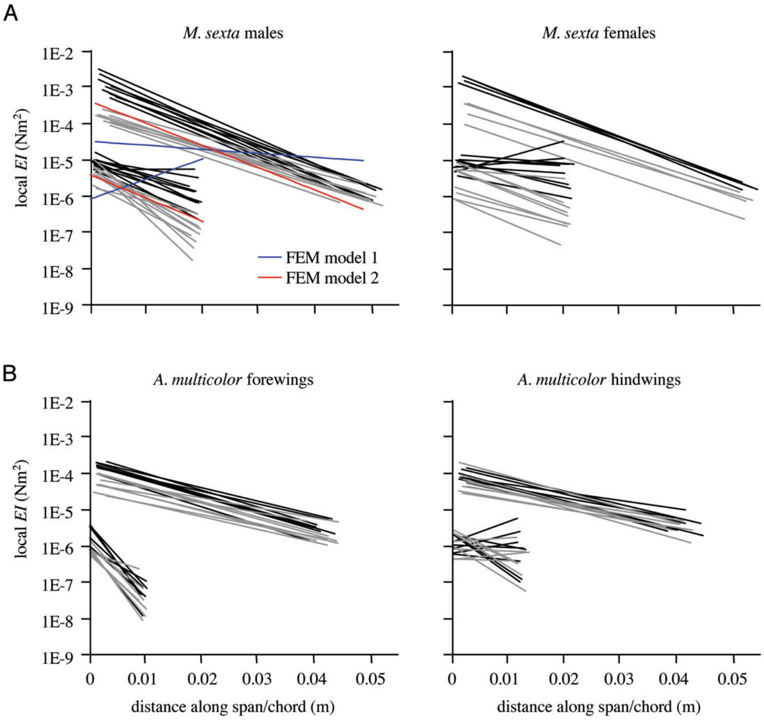

Fig. 3. Flexural stiffness distribution in wings of *Manduca sexta* and *Aeshna multicolor,* and in finite element models of *M. sexta* wings. In each graph, spanwise flexural stiffness is shown above (longer lines) and chordwise flexural stiffness below (both on a log scale); dorsal measurements are in black and ventral measurements in gray. Each line within these groups represents the flexural stiffness distribution of a different individual (from Combes and Daniel 2003b).

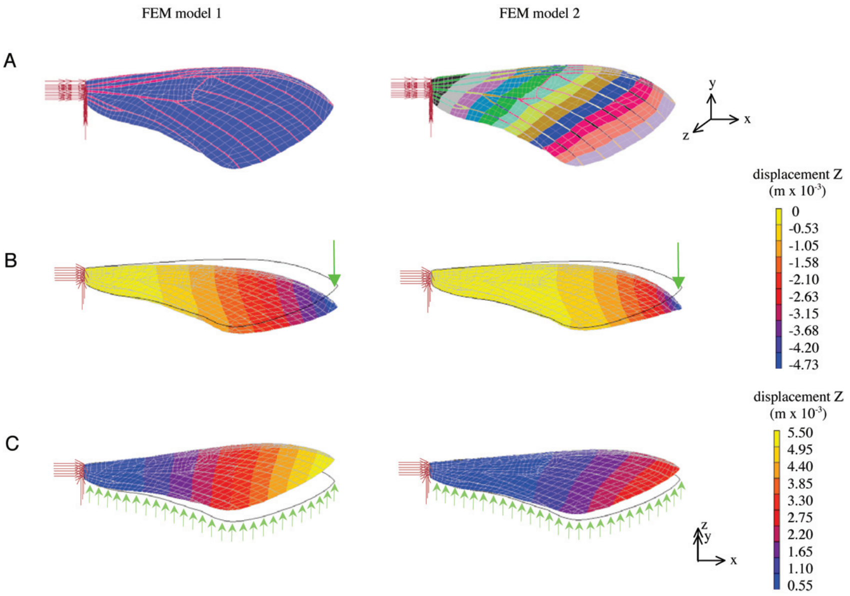

Fig. 4. Finite-element models (FEMs) based on *Manduca sexta* wings. A. FEMs 1 and 2 with colors representing different values of Young's modulus. Model 1 has fixed values of Young's modulus for vein and membrane elements; whereas Model 2 has values of Young's modulus that decline towards the tip and trailing edge. B. Results of static loading with a point force (green arrow). Displacement from original position (black outline) is indicated by the color bar. C. Results of static loading with a pressure force applied to the lower surface (green arrows), equivalent to the approximate pressure on a wing during steady flight (from Combes and Daniel 2003b).

in overall stiffness distribution between two very different species suggests that a sharp decline in *EI* toward the tip and trailing edge may be a common feature of many insect wings.

To determine how these stiffness patterns affect passive wing bending, we created two simplified finite element models with the same geometry, but with dramatically different spatial patterns of flexural stiffness. In one model, values of Young's modulus decline diagonally towards the tip, producing an exponentially declining *EI* distribution similar to the pattern measured in real wings (model 2, Figs. 3A, 4A). In a simpler model with fixed values of Young's modulus for veins and membranes, the spatial pattern of *EI* is very different from that measured in wings (model 1, Figs. 3A, 4A).

We compared patterns of bending in the two models in response to a static point load applied at the tip, static pressure force applied to the entire surface, or dynamic rotation around the wing base. In the model wing with exponentially declining flexural stiffness, both static and dynamic bending are concentrated near the tip and trailing edge of the wing, whereas bending in the simpler model occurs along the entire span (Fig 4; for movies of dynamic bending, see http://faculty.washington.edu/danielt/movies).

These results suggest that the sharply declining flexural stiffness measured in real wings helps maintain rigidity near the wing base, while localizing bending to the tip and trailing edge—regions of particular importance in controlling aerodynamic force production. The future integration of passive flexibility and spatial patterns of flexural stiffness into models of insect flight will be key in determining the functional significance of wing structure and dynamic bending to insect flight performance.

References Cited

Combes, S. A., and T. L. Daniel. 2003a. Flexural stiffness in insect wings. I. Scaling and the influence of wing venation. J. Exp. Biol. 206: 2979–2987.

Combes, S. A., and T. L. Daniel. 2003b. Flexural stiffness in insect wings. II. Spatial distribution and dynamic wing bending. J. Exp. Biol. 206: 2989–2997.

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