

# A model for pattern formation in the development of the odonate wing

Seth Donoughe

Department of Biology, Department of Physics and Astronomy, Swarthmore College, Swarthmore, PA 19081, USA

18 May 2008

---

## Abstract

The wings of dragonflies and damselflies (Anisoptera and Zygoptera of the Odonata) are made of membranes supported by rigid veins. While the longitudinal veins are often highly conserved, the patterns of cross-veins are often quite variable, even between the left and right wings of an individual. Despite the high degree of variation, wings retain the key characteristics needed for agile flight including strength, flexibility, and corrugation. We propose a model to explain the development of unique, emergent patterns observed in odonate wings.

---

Odonates, which consist of dragonflies (sub-order: Anisoptera) and damselflies (sub-order: Zygoptera) are thought to have been the first aerial predators. They achieve stunning agility in the air with a wing design that remains largely unchanged since the Carboniferous. Odonate wings are composed of a thin cuticular membrane that is supported by a lattice of solid or hollow struts called veins. All together, the veins and membrane form a complex design within the wing that gives rise to whole-wing characteristics including flexibility and corrugation.

While the longitudinal veins in odonate wings are often highly conserved within species and even within families, some parts of the wing venation are highly variable (Fig. 1). These parts of the wings are distinct between individuals of the same species and even between the left and right wings of an individual. Here we analyze the wings of odonates from three families, seeking to apply and modulate existing pattern formation mechanisms to explain the unique structural vein designs in odonates as a group.

Little work has been done on odonate wing development, but a great deal of research continues to reveal more about the biomechanics of wings as functional biological structures. The findings of this research should inform our model and set standards for whether it is realistic. These can be reduced to two biomechanical wing attributes that should be explained by our model:

- 1) It is clear that wings need to be strong but light; as such, the model must *minimize the amount of vein material while maintaining structural integrity*.
- 2) Across the odonates *wings are stiffest at the leading edge and flexible in the region near the trailing edge*.

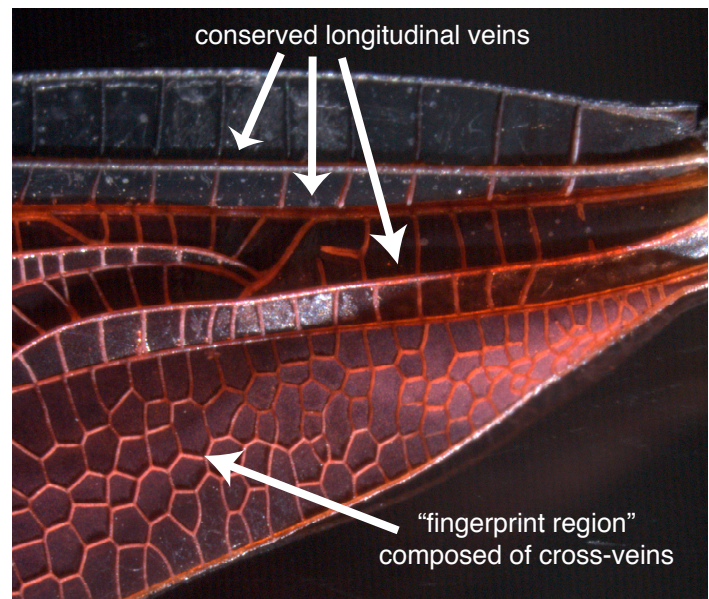
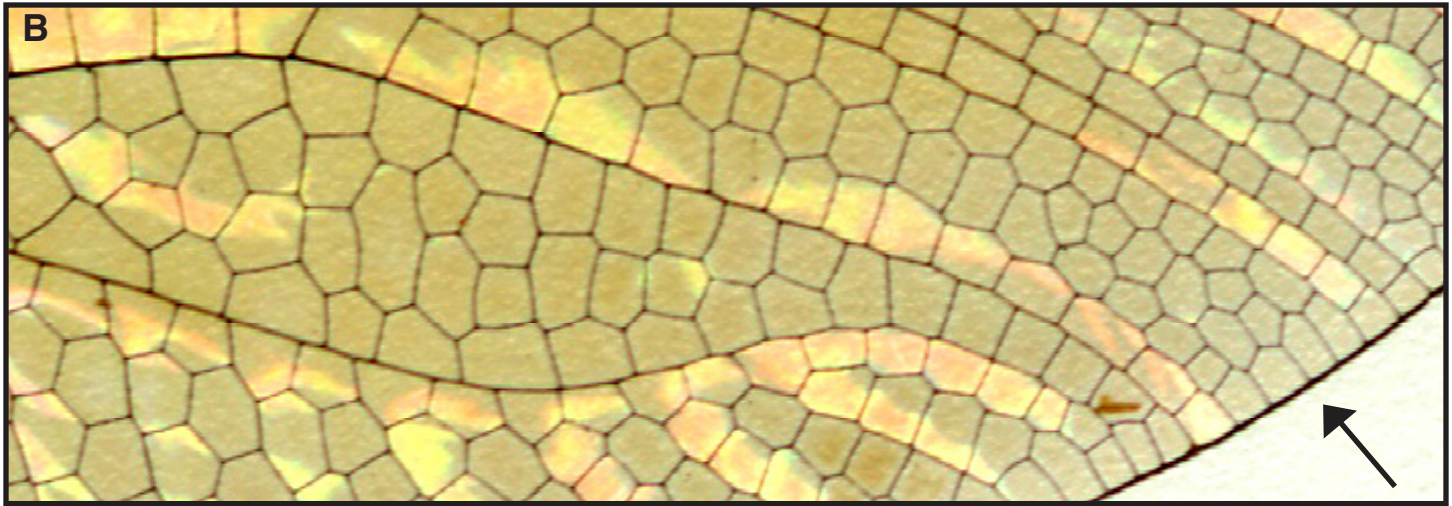
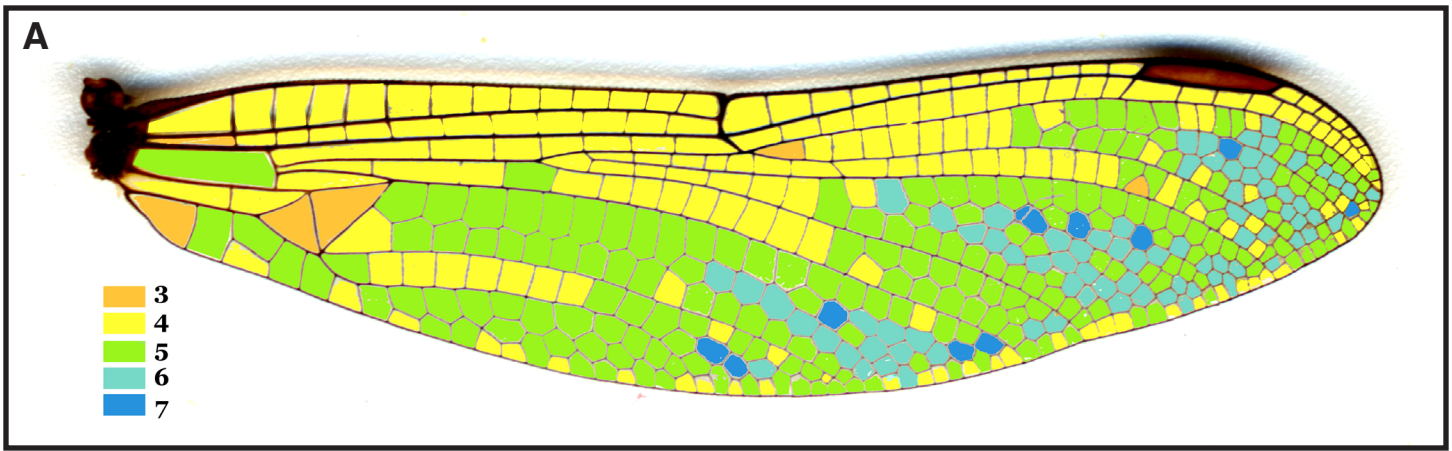


Figure 1. A wing from a *Heteraerina americana* damselfly.

In addition, a close visual inspection of wings themselves reveals two common design patterns that remain consistent through all odonates that should be explained by the model:

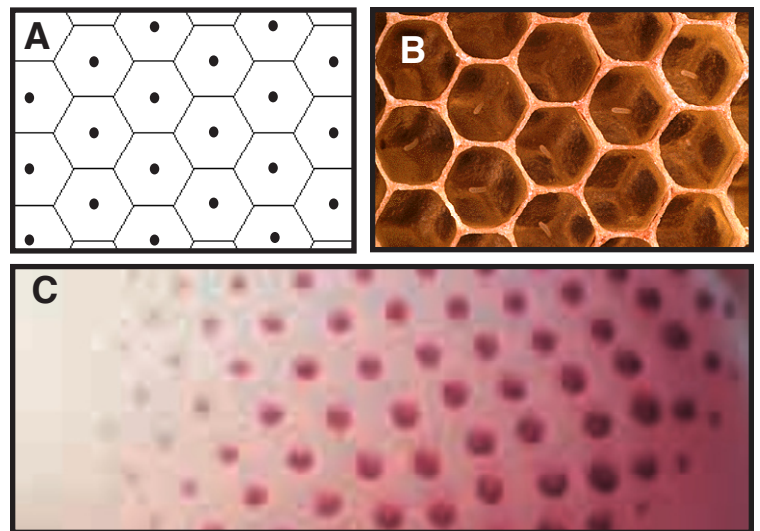
- 3) *Veins do not come together to form acute angles; cells tend to be pentagons, hexagons, and heptagons, generally resembling a hexagonal-like pattern (Fig. 2A).*
- 4) *Cells are larger near the leading edge and smaller near the trailing edge (Fig. 2B).*



**Figure 2.** **A.** Map of a dragonfly wing. Cells with 3, 4, 5, 6, and 7 sides are each assigned a different color. Note that the fingerprint region of the wing is predominantly composed of pentagons, hexagons, and heptagons. **B.** Magnified view of a dragonfly wing with the trailing edge indicated by an arrow. Cells decrease in size as one moves from the center of the wide to the distal edge.

To simplify this exercise, here we make the assumption that the fingerprint region of odonate wings can be accurately approximated by a uniform hexagonal space-filling pattern (Fig. 3A). Such a pattern is found rather commonly in nature, from honeycombs to feather arrangement on birds (Fig. 3B, C). It has been proven that a field of regular hexagons minimizes edge-length; given this we can collapse attribute 1 into attribute 3.

Furthermore, one observes that the thickness of structural veins decreases with cell size. If this holds true across all odonate wings, given that the stiffness of a region of the wing is proportional to the thickness of the veins in that region, we can collapse attribute 2 into attribute 4. Here we show data from three odonates supporting the notion that cell size is proportional to the thickness of adjacent veins. Finally we propose a simple model for wing vein development that explains our two remaining wing attributes.



**Figure 3.** **A.** Space-filling pattern of regular hexagons. In nature, this pattern can be observed as the edges of the hexagons (**B**) or the centers of the hexagons (**C**). **B.** Honeycomb built by bees. **C.** Skin tissue from a developing chick; dark spots are stained feather buds.

## Methods

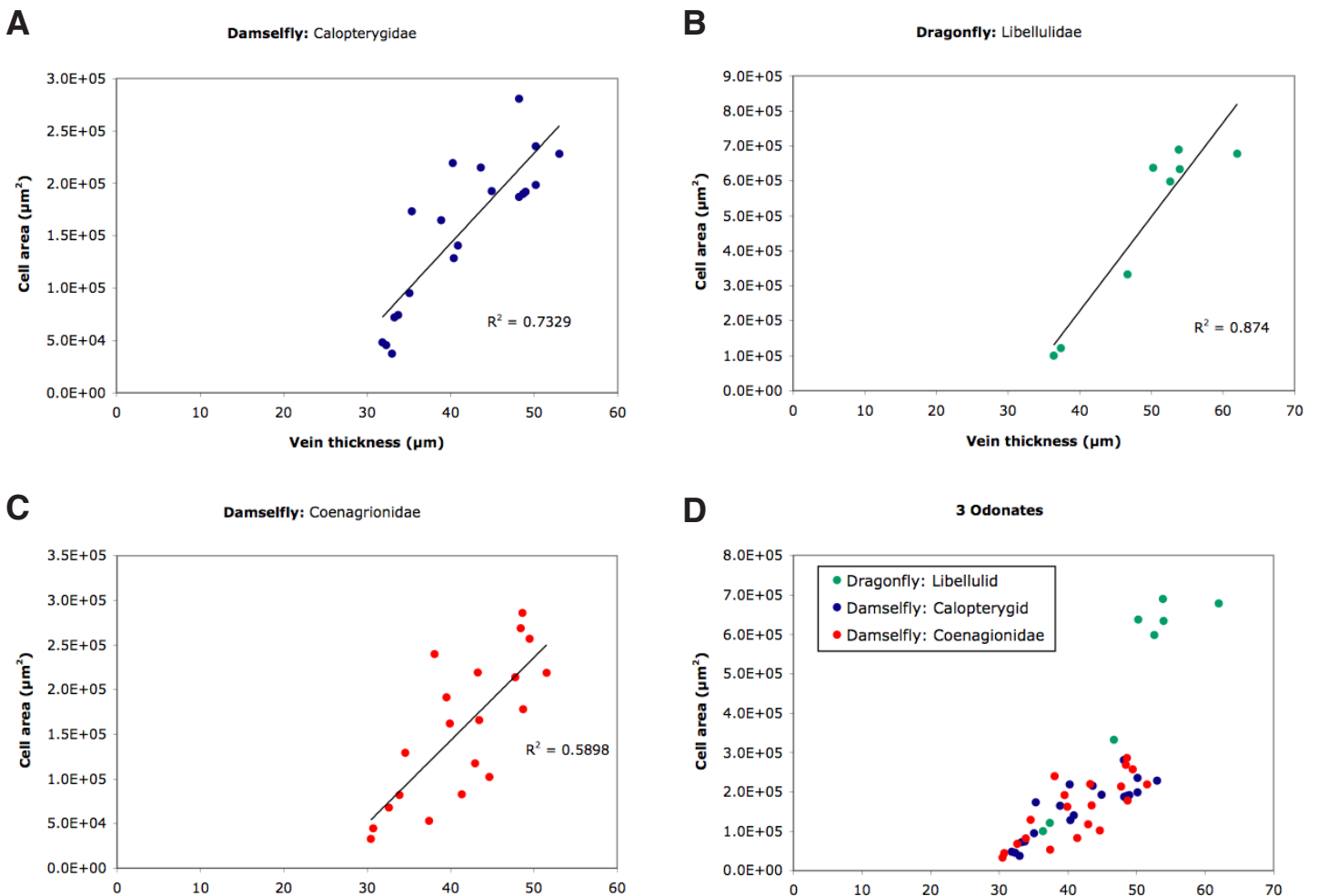
Three odonates were caught in the Crum woods at Swarthmore College, PA. Specimens were anesthetized with ether and the wings dissected from the bodies, which together were used for identification (Fig. 4). Wings were mounted on glass slides and scanned at 600 dpi resolution. ImageJ was used to measure cell areas and vein thicknesses on a series of randomly selected cells from within the fingerprint region of the wings.

## Results

Despite this relatively small sample size, it seems reasonable that there is a relationship between vein thickness and cell size (Fig. 5A-C). The plot for the combined dataset (Fig. 5D) suggests that there is a minimum vein thickness, seemingly constant for each of the three species studied.



**Figure 4.** The three odonates were from different families: **A.** Calopterygidae. **B.** Libellulidae. **C.** Coenagrionidae.



**Figure 5.** Preliminary measurements seem to indicate that there is a relationship between cell size and the thickness of adjacent veins. **A.** Family Calopterygidae (n = 20). **B.** Family Coenagrionidae (n = 20). **C.** Family Libellulidae (n = 8). **D.** Combined data.



**Figure 6.** A scanning electron micrograph of the cross-section of a dragonfly longitudinal vein .

### A model for odonate wing pattern formation

1) The hollow, highly conserved longitudinal veins develop first<sup>1</sup> (Fig. 6).

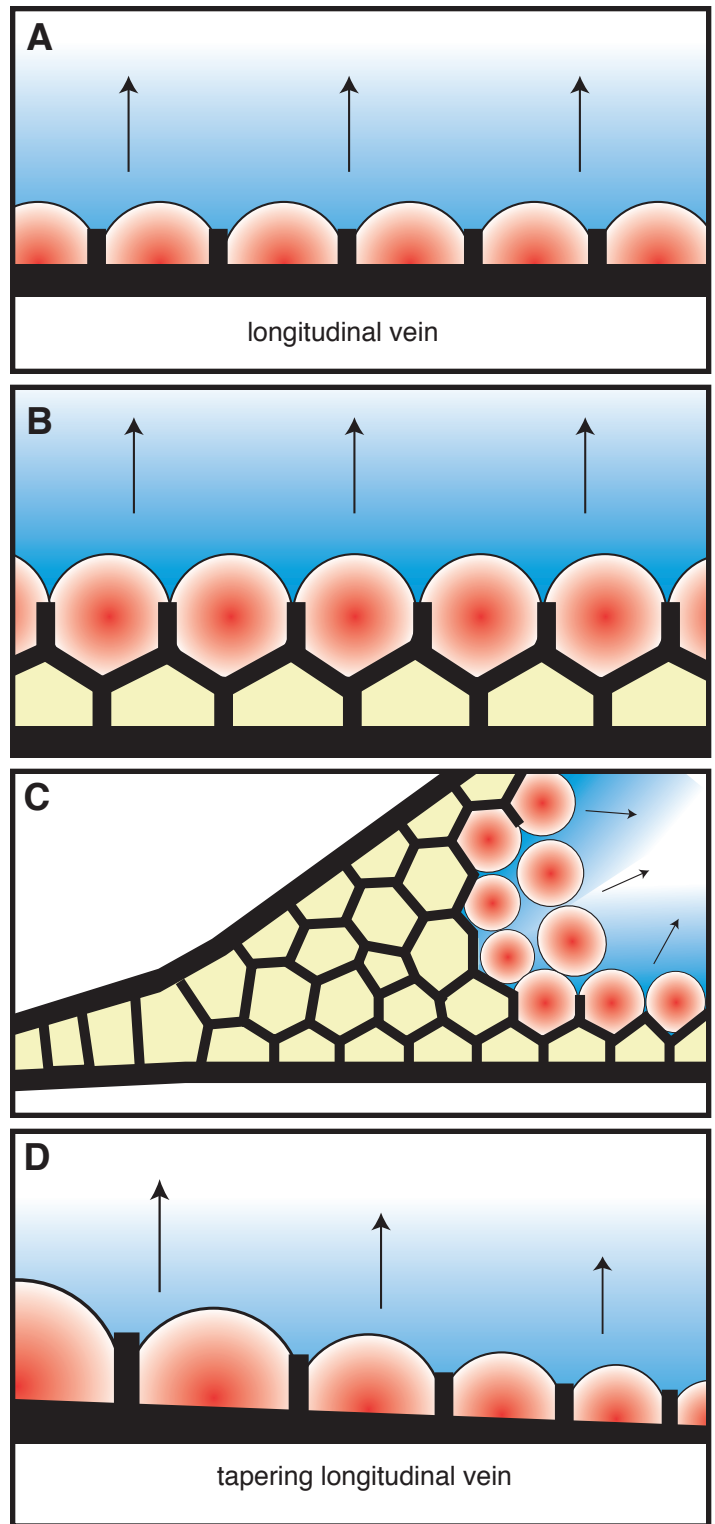
2) The longitudinal veins release a factor, here called A, which diffuses into the proto-wing. As with many Turing bifurcation reaction-diffusion systems, A activates a second factor, B, which simultaneously activates itself and inhibits A. Initially, this results in a series of peaks of factor B along the longitudinal vein.

3) Every peak of factor B is the center of an inhibitory contact circle, each of which will become a cell in the developing wing. Veins are built simultaneously, with new material being deposited at concentration minima of factor B (Fig. 7A). Cells continue developing further and further away from the longitudinal veins, until the area is filled (Fig. 7B).

4) With an initial, uniform factor A concentration and no boundaries, this would become a perfectly hexagonal array. Bounded by non-parallel longitudinal veins, however, pentagons and heptagons, are also needed to fill the space (Fig. 7C).

5) The size of the contact circles is dependent on the diffusion coefficients and the rate at which factor A is released from the longitudinal veins. We propose that factor A is released from a longitudinal vein at a rate that is proportional to the cross-sectional area of the vein. Thus a tapering longitudinal vein would be surrounded by cells of decreasing size (Fig. 7D).

While this model seems promising, this is certainly a preliminary study. Future work should include measurements on a much wider sampling of odonates to confirm these findings. The next, more ambitious step, would be to experimentally examine the mechanisms of wing development themselves.



**Figure 7.** Vein patterns emerge as a result of a reaction-diffusion system. Factor A is shown blue and factor B is shown as red. Newly formed cells are colored yellow. See body of text for explanations.

<sup>1</sup> It has been proposed that these veins evolved from the trachea on the gills of the predecessor to odonates; additional venation, therefore, likely evolved later, perhaps under the control of other developmental factors. This would explain why only the conserved longitudinal veins are hollow, while the cross veins in the fingerprint regions are not.