Jordi Cohen

Learning to fly

Overcoming the obstacles

The problem of the origin of flight as a means of locomotion is of special importance to the field of evolutionary biology. The reason for this is that the acquisition of the ability to fly must necessarily represent a radical and abrupt departure from the roles previously assumed by the host organism. Such a dramatic change can be put on the same footing as other discrete adaptations such speciation, or the formation of eyes, etc., all of which are still largely unexplained by our current interpretation of evolutionary theories. On one hand, developing the ability to fly (or see) requires so many interoperating components that the probability of a sudden coordinated mutation bestowing flight would be as low -- literally -- as that of seeing a horse give birth to a Pegasus. On the other hand, it has been difficult to explain these major events in terms of gradual mutations, because, firstly, the new ability cannot be the result of a gradual adaptation brought on by natural selection unless the host *already* possesses that ability (e.g.: wings cannot be selected for their flight-enhancing properties if the organism doesn't fly!). Secondly, the ability cannot be acquired until *all* of the required components needed for that ability are present. There lies the problem. At first glance, flight cannot be selected for if it is not present, but to be present, it needs to have been selected for.

The hurdles to be surmounted in order to achieve an airborne lifestyle are tremendous. The organism needs the right size of wings, as well as the appropriate muscular and nervous components to make them work. Furthermore, the organism's own morphology must enable it to acquire sufficient lift and, in addition to that, it must be able to dynamically control its body orientation and posture in order to stay airborne.

I will examine recent scientific investigations [1,2] that propose a plausible answer to the origin of flight in insects. The authors claim that insect flight has evolved in a *gradual* manner from a different form of locomotion. What is interesting about these results is that they hinge on phylogenetic methods, combined with a morphological and functional comparison of different species.

From water to air

An interesting form of locomotion -- skimming -- intermediate between flight and water skating has been observed in a certain species of stonefly. This stonefly (which possesses the ability to fly), upon contact with a water surface, will lower its hind legs and skim the water while maintaining an upright position and flapping its wings. Other stonefly species also display other similar behaviors, such as 6- and 4-leg skimming, sailing, and skimming combined with brief jumps in which the insect flies clumsily. The more flight-

like is the locomotion, the more the species is advantaged. For example, hind-leg skimming (in which the insect practically flies, but uses the water surface to be steadied) is about 1.4 times faster than 6-leg skimming, helping in overcoming predators and river currents. The basic idea is that skimming might have provided the incentive for the development of a rugged flight machinery in insects: skimming can be achieved with small wings and weak flight muscles and it is also much safer than other hypothesized flight-selecting behaviors such as gliding and flapping.

Although it is well accepted that insect flight might be derived from skimming, it has been unclear whether the skimming behaviors seen in stoneflies are precursors to flight. It had been previously suggested and assumed that water skimming resulted from a loss of the ability to fly. One measure of the ability to fly is the number of cross-veins in the insect's wings (veins are the visible "fibers" in an insects otherwise transparent wings, and cross-veins are those veins that are organized laterally). A previous study had reported that the number of cross-veins in the Nemouroidea super-family of stoneflies (in which skimming was first observed) was much reduced compared to the rest of the Plecoptera order (stoneflies). This would mean that the ability to fly of the Nemouroidea taxon has been lost, or greatly reduced.

Phylogenetic insight

A new, much more complete, phylogenetic analysis has been performed on the Plecoptera order [2] that suggests an opposite conclusion. By using outgroups (unrelated species that are used to indicated which node in the tree is the oldest) and extensive phylogenetic methods, it has been shown that the Nemouroidea are in fact a *basal* taxon of the Plecoptera, meaning that they are the most ancient group (the phylogenetic tree is shown in figure 1). This has important consequences because it would mean that the low number of cross-veins might be an ancestral trait.

A cursory glance at the entire phylogeny of the Plecoptera reveals that various skimming behaviors and/or weak flying ability are widely distributed throughout the tree. This observation lends additional credibility to the fact that the common ancestor to the Plecoptera might have had these characteristics (weak flight, low number of cross-veins, skimming behavior). Additionally, fossil evidence shows that 260 million year-old Nemouridae fossils (which is the basal clade) has a relatively unchanged number of cross-veins, while fossils for the more modern derived clades (after the asterisk in figure 1) have much fewer veins than their descendants, demonstrating an adaptation towards better flight.

Conclusion

This study shows how phylogenetic information can be used to complement an analysis of morphological traits (such as number of cross-veins) in order to infer new results. A previous analysis that relied too much on morphological traits to infer descendance was shown to have produced erroneous results. Combining morphological data with genealogical data has been shown to be a very powerful tool, but this technique cannot be

used when the genealogy is derived from morphological comparisons, and this is where phylogenetics comes in handy.

The study described above seems to suggest that insect flight (at least in the Plecoptera family) is an adaptation that has occurred gradually. The flight machinery has been developed incidentally to improve skimming abilities.

References

[1] Kramer M. and Marden J., *Nature* **385** (30), 403-404 (1997)

[2] Thomas M., Walsh K. *et al., Proceedings of the Nat'l Acad. of Sciences of the U.S.A* **91** (24), 13178-13183 (2000)

[MISSING FIGURES]