## Evolutionary diversification at multiple levels of variation in *Drosophila*

Wing Shape

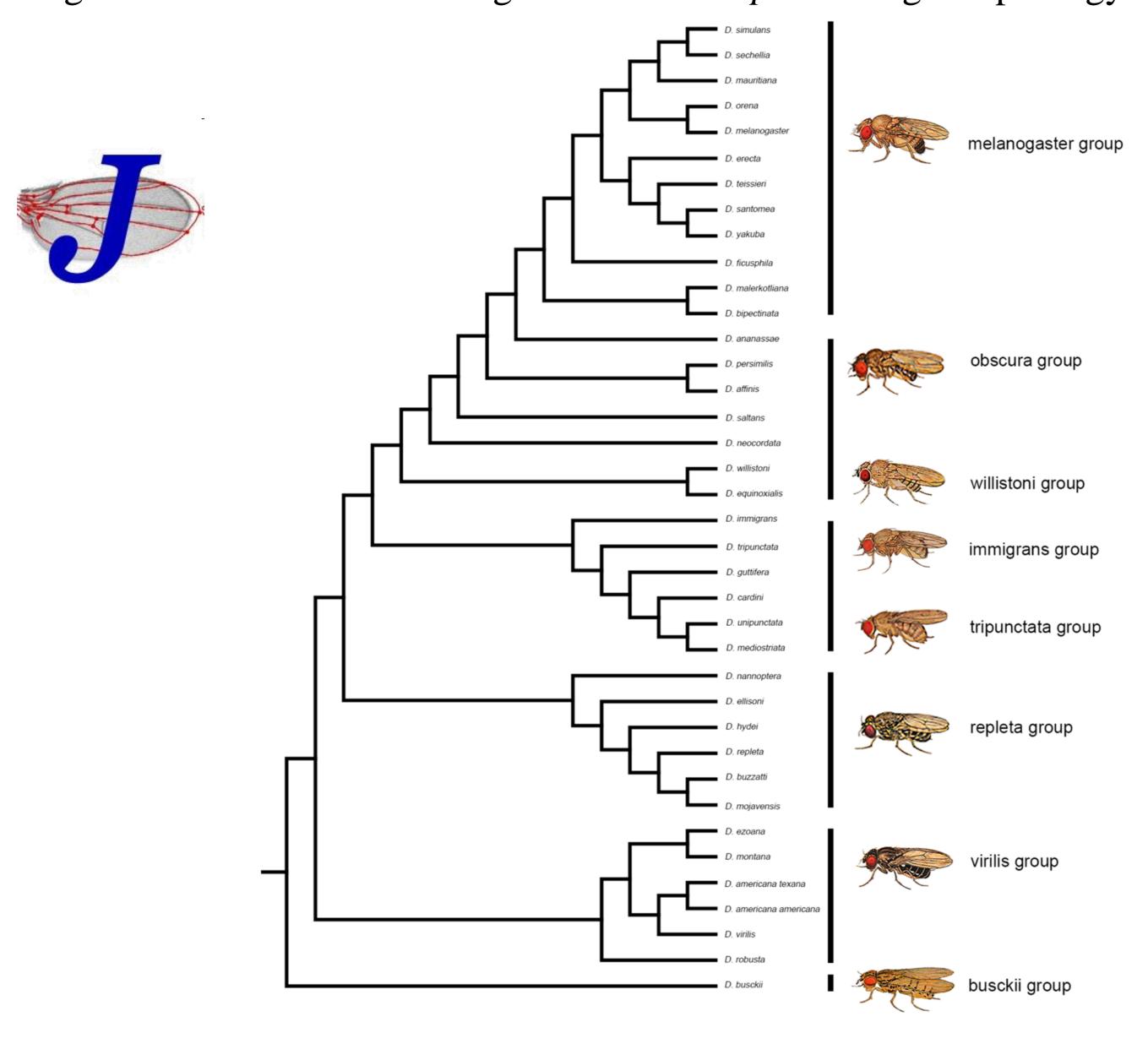
Hugo A. Benítez<sup>1</sup> & Chris Klingenberg<sup>1</sup>





Studying integration and modularity is essential to understand the evolution of shape because the coherence of recognizable parts of most organisms is dependent on their developmental origin and structure. *Drosophila* wing morphology has been used extensively as an important model trait in evolutionary biology, since its genetics and development are well known.

The objectives in this poster are to address questions that concern the pattern of divergence and evolution of integration in *Drosophila* wing morphology.



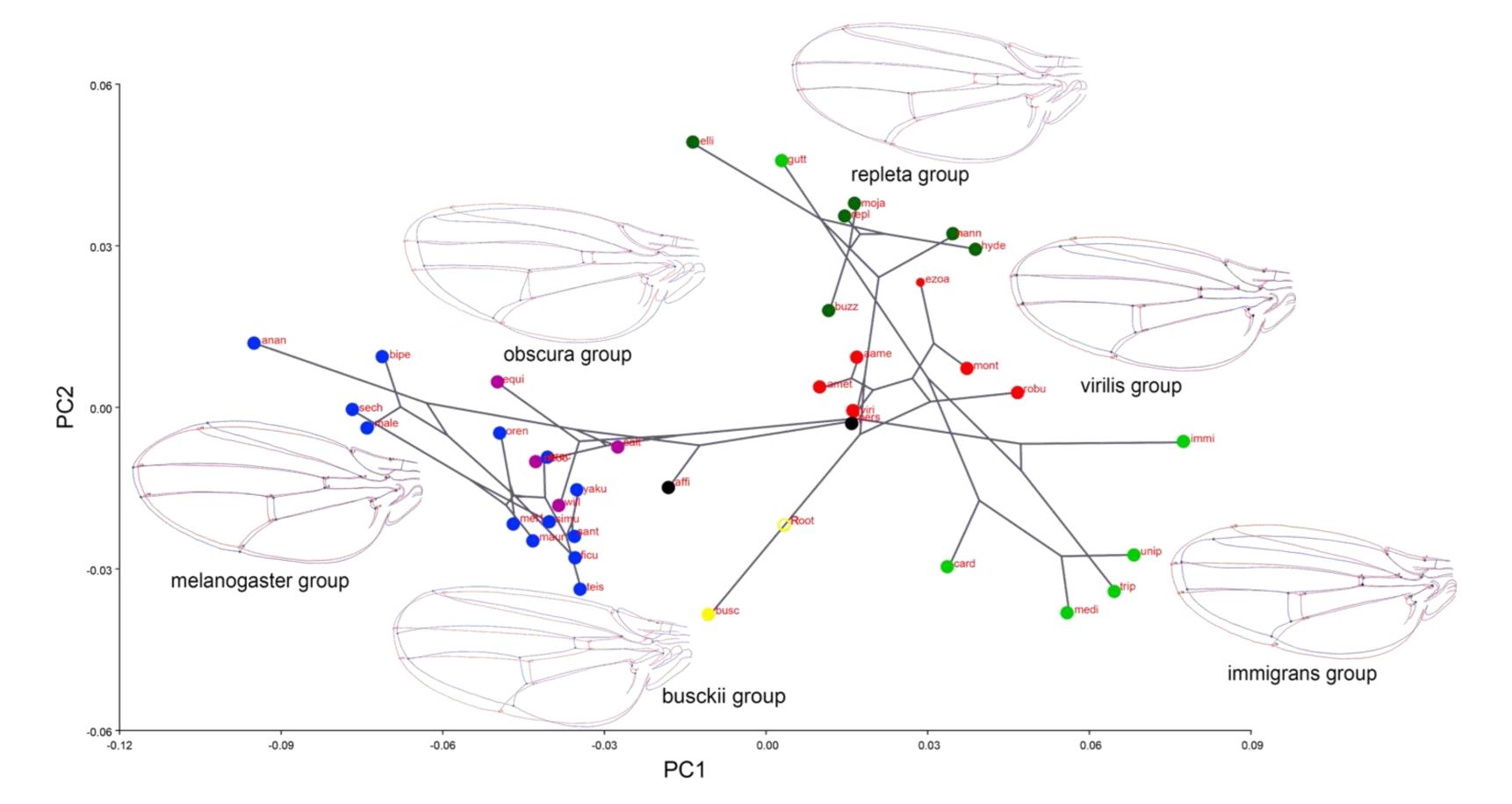
**Figure 1:** Reconstructed phylogeny using 38 species of *Drosophila* based on the phylogeny from Van der Linde et al 2010 [1], the fly pictures were taken of web of flybase (http://flybase.org).



## Question 1: Does the average shape evolve across the genus?

We used geometric morphometrics to analyze wing morphology in 38 species of *Drosophila*.

The comparative analyses were performed using a composite phylogeny of *Drosophila* (Fig. 1), which was used for mapping shape data by squared-change parsimony. To reconstruct the phylogenetic history of average shape change we projected the phylogeny into the shape tangent space, and we visualized the change using multivariate analysis of principal component (PCA) computed from the covariance matrix of the average shapes for the terminal taxa (Fig. 2). Wing shape evolved across the genus. Closely related species tend to be relatively close in shape space, which indicates the presence of a clear phylogenetic signal in the evolution of wing shape (permutation test with the null hypothesis of no phylogenetic signal: P< 0.0001).



**Figure 2:** Projection of evolutionary variation onto the phylogeny of *Drosophila* in the space of shape. The first two principal components (PCs) are used to display most of the variation of shape (PC1 vs PC2). Each branch has the abbreviation of the first 4 letters of the corresponding species.

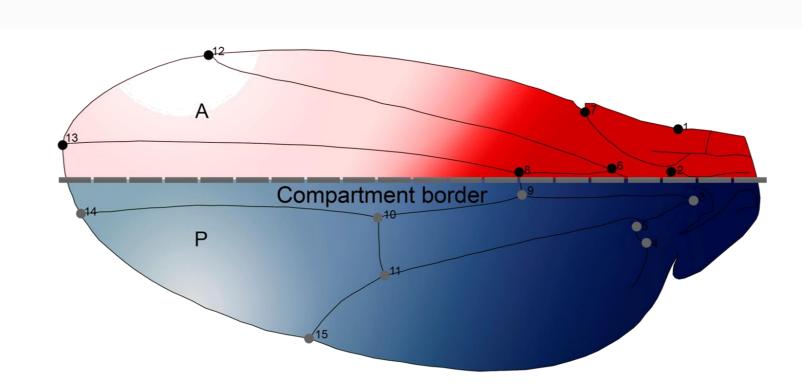
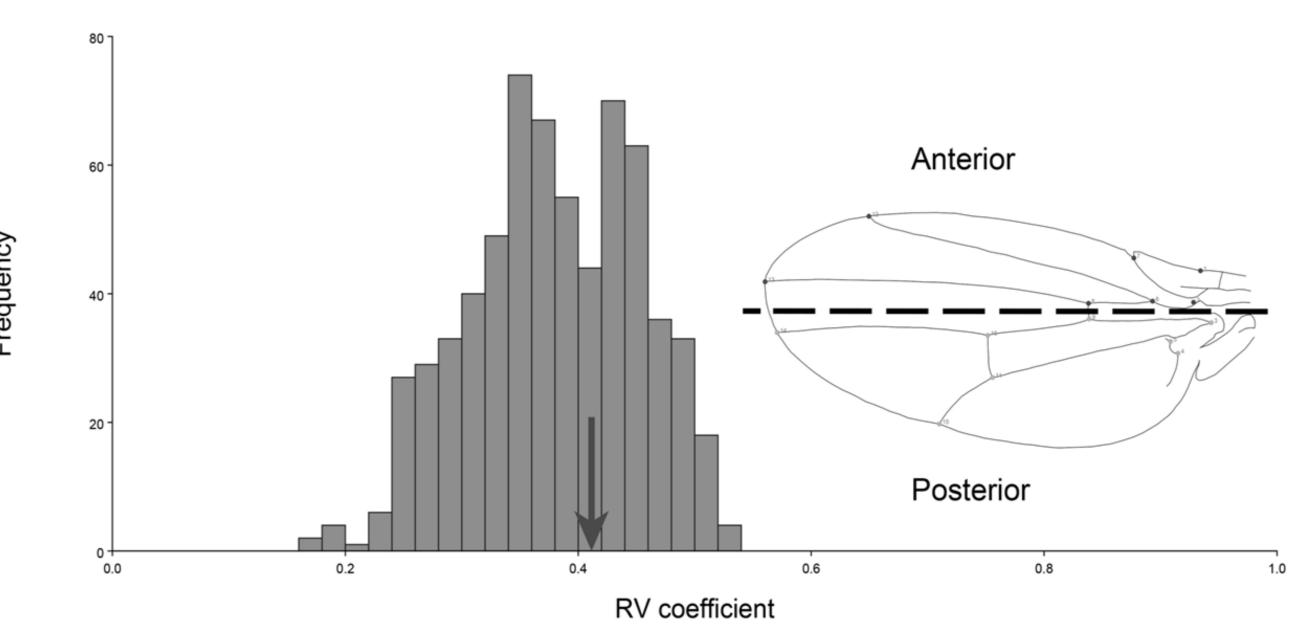


Figure 3: Developmental hypothesis of anterior and posterior wing compartments

## Question 2: Is the *Drosophila* wing a single integrated morphological unit, consistently across the whole genus?

We studied the pattern of covariation between anterior and posterior (A/P) parts of wing shape (Fig. 3) in the covariance matrix of independent contrasts for wing shape. To test the hypothesis that the anterior and posterior compartments are separate modules, we computed RV coefficient, which quantifies the strength of covariation between subsets of landmarks [2].

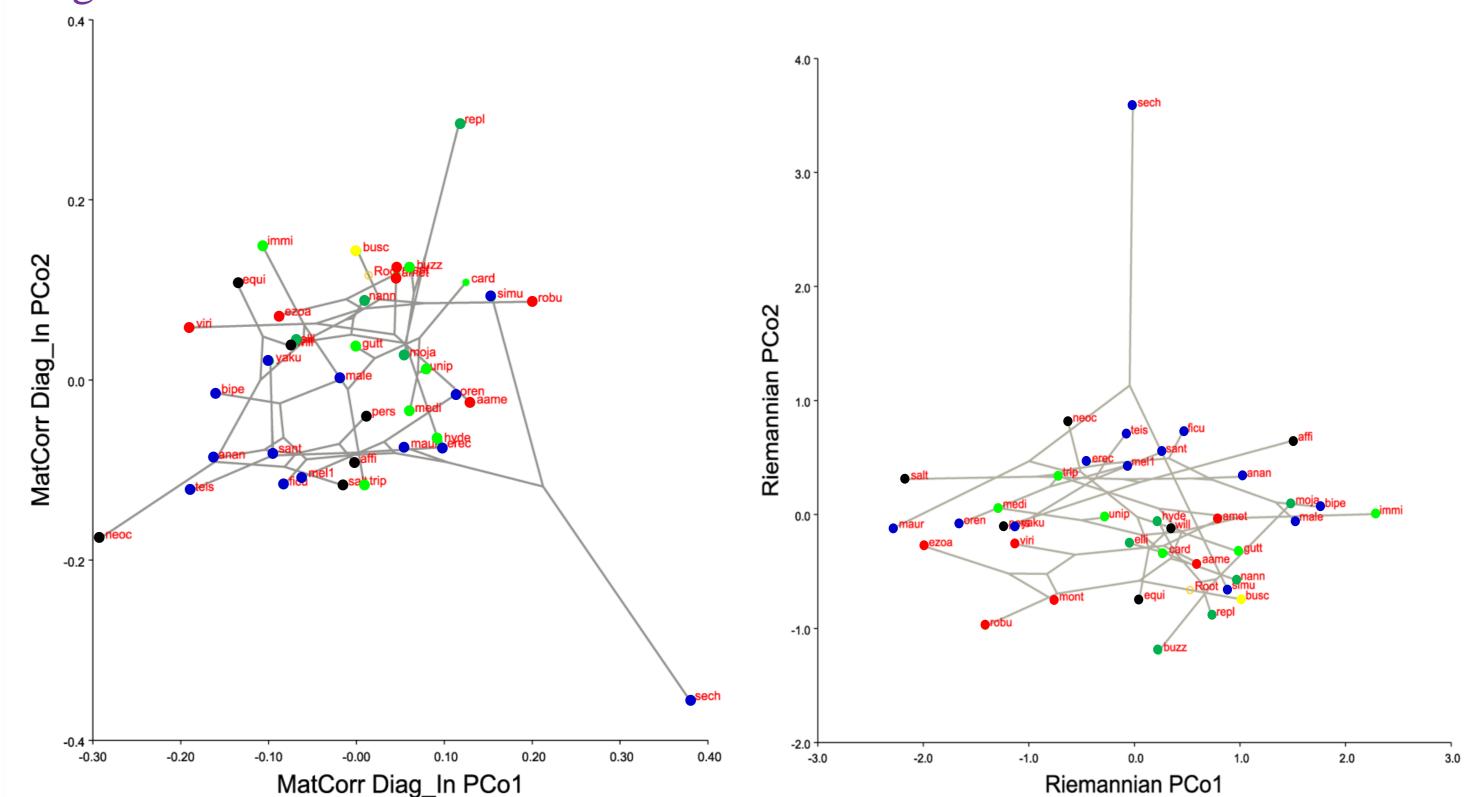
We found the two compartments of the wing are developmentally integrated. This is suggested by the independent contrasts analysis and a value of RV coefficient positioned in the middle of the RV coefficient distribution (RV=0.44; Fig. 4). This value indicates that the covariation between the two compartments is not weaker than expected between random partitions of landmarks. Therefore, our results suggest the *Drosophila* wing is a single integrated morphological unit across the species of the genus and that the anterior and posterior compartments are not separate modules.



**Figure 4:** Hypothesis of modularity by comparing the covariation between anterior and posterior developmental compartments of the wing with alternative partitions of the landmarks. Covariation of procustes coordinates of shape.

## Question 3: Does morphological integration evolve across the genus?

In order to compare the integration patterns between species, we use a principal coordinate analysis (PCoA) of the covariance matrix of average individuals, computed from matrix correlations and Riemannian distances [3; 4]. Both PCoA produce similar ordination patterns (Fig. 5): *D. sechellia* evolved a completely different covariance matrix compared to the other members of the *melanogaster* group in both graphs. Morphological integration evolved across the genus. Closely related species tend to be relatively close in their covariance matrices. Thus suggests a phylogenetic signal.



**Figure 5:** Comparison of PCoA onto the phylogeny of *Drosophila* with the two measures of distance between covariance matrices. A: PCoA with matrix correlation (diagonal blocks of the covariance matrices included). B: PCoA with the Riemannian distance measure.