

Revealing Evolutionary Mechanisms by Mapping Pigmentation Character States and Developmental Mechanisms onto a Resolved Fruit Fly Phylogenetic Tree

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ABSTRACT

Since the origin of the 36 recognized animal phyla over 500 million years ago, subsequent evolution can be largely summarized as the diversification of physiological, behavioral, and morphological characteristics among these original 36 body plans. Diversification continues to this day and can be seen in humans as differences in coloration, lactose metabolism, and energy storage in fat tissue. As all animal characteristics are products of development, a key challenge for contemporary research is to reveal the ways in which development evolves through changes in the uses of genes. To meet this challenge, investigations must prioritize characteristics: that have recently evolved, the direction of character evolution is known, and for which the underlying genes can be studied by modern genetic manipulations. One ideal trait is the diverse coloration patterns observed on the abdominal tergites of fruit fly species from the *Sophophora* subgenus. Prior research has supported a scenario where melanistic pigmentation limited to the male abdomen evolved once within this clade through the evolution of a sexually dimorphic pattern of expression for the *bric-à-brac* transcription factor genes. My research challenges this scenario by looking at the patterns of pigmentation on the abdomens of species representing the diverse *Sophophora* species groups and interrogating the patterns of *bric-à-brac* expression during the development of the abdominal tergites. Success in this work will advance the fruit fly pigmentation model as exemplar of how diversity evolves through the re-working of developmental mechanisms.

What are the Genetic Differences Underlying Earth's Diversity of Life?

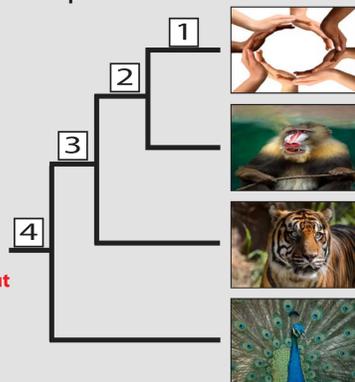
Diversity can be seen at different taxonomic levels of comparison:

1. Intraspecific level
2. Order Level
3. Class Level
4. Super-class level

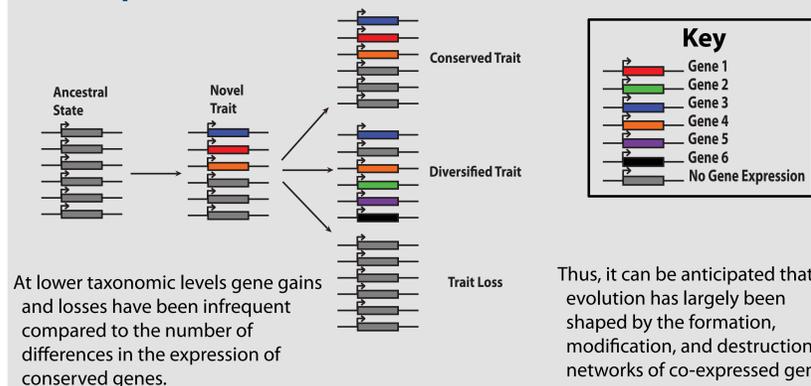
- How do novelties evolve?
- Which genes have been functionally changed?
- How have gene functions been modified?
- Are there trends in the types of genes changed and how are they modified?

To answer these questions requires knowing about the ancestral phenotypic and genetic makeup.

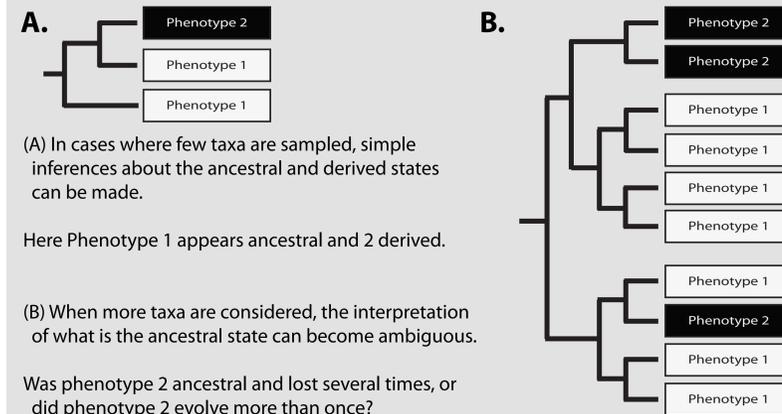
This is a challenge for traits and genetic material that the ancestral states cannot be obtained



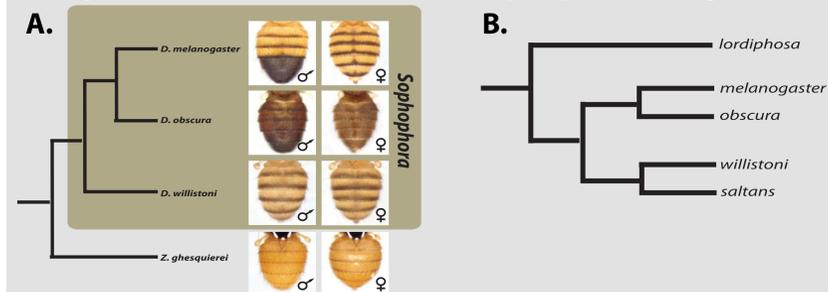
Conceptual Model for the Gene Network Basis of Evolution



Challenges with Inferring Ancestral and Derived Phenotypes



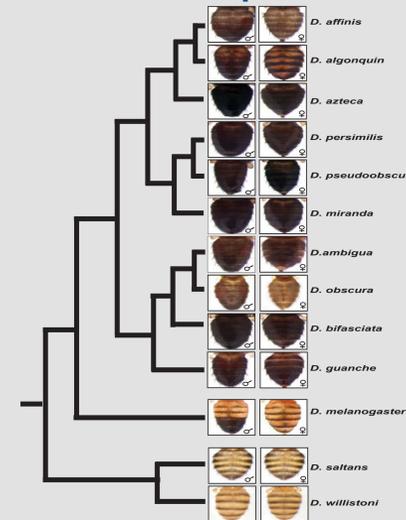
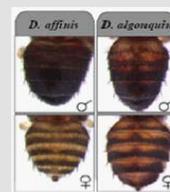
Pigmentation Evolution in the *Sophophora* Subgenus



- (A) Working model, based on limited taxa sampling, is that monomorphic pigmentation is the ancestral state in *Sophophora* and dimorphic pigmentation is derived.
- (B) However, the *Sophophora* subgenus includes many different species groups and hundreds of extant species. We were curious whether a more thorough taxa sampling would support or contradict the working model.

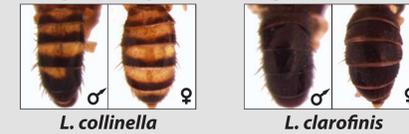
Hidden Dimorphism in *Obscura* Group

We identified that species exist in the *obscura* group with sexually dimorphic pigmentation raising the possibility that dimorphism existed in the most recent common ancestor of the *melanogaster* and *obscura* species groups.



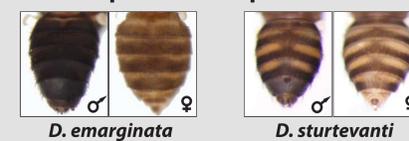
Saltans and *Lordiphosa* Groups Include Dimorphic Species

A. *Lordiphosa* Species Group



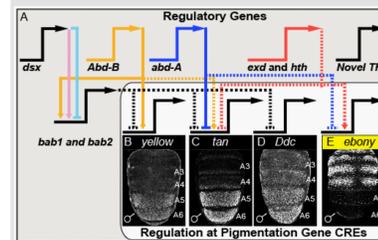
We found that dimorphic species reside in the *Saltans* and *Lordiphosa* species groups too. Thus dimorphic pigmentation is observed in several species groups among the major lineages of *Sophophora*.

B. *Saltans* Species Group



This raises uncertainty as to whether dimorphism was ancestral and frequently lost, or alternatively whether dimorphic pigmentation evolved on multiple occasions.

Using Gene Network Structure to Reveal Homology or Convergence

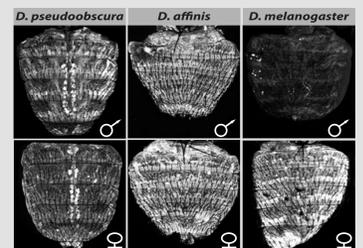


The *Drosophila melanogaster* pigmentation gene regulatory network has been well studied.

A cornerstone feature of the network shaping male-limited expression of pigmentation enzymes is the drastically reduced expression of the Bab transcription factors in the male abdomen.

Bab1 Expression Hints to an Independent Origin of Dimorphism

In a monomorphic and a dimorphic pigmented species of the *obscura* group, we found nearly equivalent expression of Bab1 in the male and female abdomens.



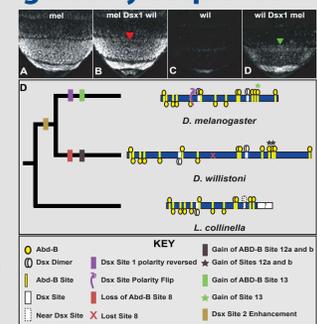
This suggests that Bab expression differs in this species group, and that tergite pigmentation is not repressed by the Bab transcription factors.

The Molecular Evolution of a Bab Regulatory Sequence

Female specific Bab expression is controlled by a regulatory element known as the dimorphic element which has binding sites for the Abd-B and Dsx transcription factors.

This element and binding sites are conserved in the monomorphic species *D. willistoni*, but a Dsx binding site's polarity is inverted that leads to spatially-limited regulatory activity.

We found that a *Lordiphosa* species has the inverted site polarity too, supporting the conclusion that Bab regulation is a novel feature of dimorphic pigmentation for *D. melanogaster* and closely related species.



CONCLUSIONS AND FUTURE DIRECTIONS

Our data supports a scenario where sexually dimorphic pigmentation evolved on multiple occasions in the *Sophophora* subgenus and through unique inputs of transcriptional regulatory proteins.

Our future work will prioritize revealing how dimorphism evolved to be made at the levels of pigmentation enzyme genes and their upstream transcriptional regulators.

REFERENCES

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2. Williams TM, Selegue JE, Werner T, Gompel N, Kopp A, Carroll SB: **The regulation and evolution of a genetic switch controlling sexually dimorphic traits in *Drosophila*.** [Internet]. *Cell* 2008, **134**:610–23.

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