Achaete-scute, bristle:

Negre, B., and Simpson, P. (2015). The *achaete-scute* complex in Diptera: patterns of non-coding sequence evolution. J. Evol. Biol.

The *achaete-scute* complex has been a useful paradigm for the study of pattern formation and its evolution. *achaete-scute* genes have duplicated and evolved distinct expression patterns during the evolution of cyclorraphous Diptera. Are the expression patterns in different species driven by conserved regulatory elements? If so, when did such regulatory elements arise? Here we have sequenced most of the *achaete-scute* complex of the fly *Calliphora vicina* (including the genes *achaete*, *scute* and *lethal of scute*) to compare non-coding sequences with known *cis*-regulatory sequences in *Drosophila*. The organization of the complex is conserved with respect to *Drosophila* species. There are numerous small stretches of conserved non-coding sequence that, in spite of high sequence turnover, display binding sites for known transcription factors. Synteny of the blocks of conserved non-coding sequences is maintained suggesting not only conservation of the position of regulatory elements but an origin prior to the divergence between these two species. We propose that some of these enhancers originated by duplication with their target genes.



Sensory Organ Precursor Enhancer alignment

Otani, T., Oshima, K., Kimpara, A., Takeda, M., Abdu, U., and Hayashi, S. (2015). A transport and retention mechanism for the sustained distal localization of Spn-F-IKK during Drosophila bristle elongation. Development *142*, 2338–2351.

Stable localization of the signaling complex is essential for the robust morphogenesis of polarized cells. Cell elongation involves molecular signaling centers that coordinately regulate intracellular transport and cytoskeletal structures. In *Drosophila* bristle elongation, the protein kinase IKKɛ is activated at the distal tip of the growing bristle and regulates the shuttling movement of recycling endosomes and cytoskeletal organization. However, how the distal tip localization of IKKɛ is established and maintained during bristle elongation is unknown. Here, we demonstrate that IKKɛ distal tip localization is regulated by Spindle-F (Spn-F), which is stably retained at the distal tip and functions as an adaptor linking IKKɛ to cytoplasmic dynein. We found that Javelin-like (Jvl) is a key regulator of Spn-F retention. In *jvl* mutant bristles, IKKɛ and Spn-F initially localize to the distal tip but fail to be retained there. In S2 cells, particles that stain positively for Jvl or Spn-F move in a microtubule-dependent manner, whereas Jvl and Spn-F double-positive particles are immobile, indicating that Jvl and Spn-F are transported separately and, upon forming a complex, immobilize each other. These results suggest that polarized transport and selective retention regulate the distal tip localization of the Spn-F–IKKɛ complex during bristle cell elongation.



Model for bristle tip IKK ϵ –**Spn-F transport and retention.** (A) Transport and retention of the IKK ϵ –Spn-F complex. The IKK ϵ –Spn-F complex is transported to the distal tip by cytoplasmic dynein. Jvl is independently transported to the distal tip and interacts with Spn-F to retain the IKK ϵ –Spn-F complex there. (B) The shuttling movement of recycling endosomes. Rab11-positive recycling endosomes are transported by cytoplasmic dynein to the distal tip. IKK ϵ phosphorylates Nuf, a Rab11-dynein adaptor protein, and promotes motor switching. Specific pairings between cargo adaptors (Spn-F, Nuf) and regulatory molecules (Jvl, IKK ϵ) determine cargo fate.

Genitalia evolution:

Morgado-Santos, M., Pereira, H.M., Vicente, L., and Collares-Pereira, M.J. (2015b). Mate Choice Drives Evolutionary Stability in a Hybrid Complex. PLoS ONE *10*, e0132760.

Previous studies have shown that assortative mating acts as a driver of speciation by countering hybridization between two populations of the same species (pre-zygotic isolation) or through mate choice among the hybrids (hybrid speciation). In both speciation types, assortative mating promotes speciation over a transient hybridization stage. We studied mate choice in a hybrid vertebrate complex, the allopolyploid fish *Squalius alburnoides*. This complex is composed by several genomotypes connected by an intricate reproductive dynamics. We developed a model that predicts the hybrid complex can persist when females exhibit particular mate choice patterns. Our model is able to reproduce the diversity of population dynamic outcomes found in nature, namely the dominance of the triploids and the dominance of the tetraploids, depending on female mate choice patterns and frequency of the parental species. Experimental mate choice trials showed that females exhibit the preferences predicted by the model. Thus, despite the known role of assortative mating in driving speciation, our findings suggest that certain mate choice patterns can instead hinder speciation and support the persistence of hybrids over time without speciation or extinction.

Brennan, P.L.R., and Prum, R.O. (2015). Mechanisms and Evidence of Genital Coevolution: The Roles of Natural Selection, Mate Choice, and Sexual Conflict. Cold Spring Harb Perspect Biol 7.
Denton, D., and Kumar, S. (2015). Studying Apoptosis in Drosophila. Cold Spring Harb Protoc 2015, pdb.top070433.

Genital coevolution between the sexes is expected to be common because of the direct interaction between male and female genitalia during copulation. Here **we review the diverse mechanisms of genital coevolution that include natural selection, female mate choice, male–male competition, and how their interactions generate sexual conflict that can lead to sexually antagonistic coevolution.** Natural selection on genital morphology will result in size coevolution to allow for copulation to be mechanically possible, even as other features of genitalia may reflect the action of other mechanisms of selection. Genital coevolution is explicitly predicted by at least three mechanisms of genital evolution: lock and key to prevent hybridization, female choice, and sexual conflict. Although some good examples exist in support of each of these mechanisms, more data on quantitative female genital variation and studies of functional morphology during copulation are needed to understand more general patterns. A combination of different approaches is required to continue to advance our understanding of genital coevolution. Knowledge of the ecology and behavior of the studied species combined with functional morphology, quantitative morphological tools, experimental manipulation, and experimental evolution have been provided in the best-studied species, all of which are invertebrates. Therefore, attention to vertebrates in any of these areas is badly needed.

Drosophila evolution:

Rogers, R.L., Cridland, J.M., Shao, L., Hu, T.T., Andolfatto, P., and Thornton, K.R. (2015). **Tandem Duplications and the Limits of Natural Selection in** *Drosophila yakuba* and *Drosophila simulans*. PLoS ONE *10*, e0132184.

Tandem duplications are an essential source of genetic novelty, and their variation in natural populations is expected to influence adaptive walks. Here, we describe evolutionary impacts of recently-derived, segregating tandem duplications in Drosophila yakuba and Drosophila simulans. We observe an excess of duplicated genes involved in defense against pathogens, insecticide resistance, chorion development, cuticular peptides, and lipases or endopeptidases associated with the accessory glands across both species. The observed agreement is greater than expectations on chance alone, suggesting large amounts of convergence across functional categories. We document evidence of widespread selection on the D. simulans X, suggesting adaptation through duplication is common on the X. Despite the evidence for positive selection, duplicates display an excess of low frequency variants consistent with largely detrimental impacts, limiting the variation that can effectively facilitate adaptation. Standing variation for tandem duplications spans less than 25% of the genome in D. yakuba and D. simulans, indicating that evolution will be strictly limited by mutation, even in organisms with large population sizes. Effective whole gene duplication rates are low at 1.17×10^{-9} per gene per generation in D. vakuba and 6.03×10^{-10} per gene per generation in D. simulans, suggesting long wait times for new mutations on the order of thousands of years for the establishment of sweeps. Hence, in cases where adaptation depends on individual tandem duplications, evolution will be severely limited by mutation. We observe low levels of parallel recruitment of the same duplicated gene in different species, suggesting that the span of standing variation will define evolutionary outcomes in spite of convergence across gene ontologies consistent with rapidly evolving phenotypes.

Magnacca, K.N., and Price, D.K. (2015). Rapid adaptive radiation and host plant conservation in the Hawaiian picture wing Drosophila (Diptera: Drosophilidae). Mol. Phylogenet. Evol. *92*, 226–242.

The Hawaiian picture wing Drosophila are a striking example of adaptive radiation in specialist saprophages on an island system. We use DNA sequences from five nuclear genes with a total of 4260 nucleotides to provide a comprehensive phylogeny and biogeographic analysis of 90 species in the Hawaiian *Drosophila picture wing* clade. The current analysis indicates that the evolution of the *picture wing* clade took place more recently than previously suggested. The relationships of several morphologically anomalous taxa are resolved with strong support. Biogeography and host plant analyses show two periods of rapid divergence occurred when Kauai and Oahu were the main high islands, indicating that a combination of complex topographical features of islands and development of novel host plant associations was key to the rapid diversification of these lineages. For the past 2 million years,

host associations within lineages have been largely stable, and speciation has occurred primarily due to the establishment of populations on newer islands as they arose followed by divergence by isolation. The existence of several apparently relictual taxa suggests that extinction has also played a major role in assembly of the present Hawaiian *Drosophila* fauna.

Drosophila development:

Salvador-Martínez, I., and Salazar-Ciudad, I. (2015). **How complexity increases in development: An analysis of the spatial-temporal dynamics of 1218 genes in** *Drosophila melanogaster*. Dev. Biol. *405*, 328–339.

One of the most apparent phenomena in development is that it starts with something apparently simple and leads to something clearly complex with a specific and functional structure. At the level of gene expression it seems also clear that the embryo becomes progressively compartmentalized over time and space. However, there have not been any systematic attempts to quantify how this occurs. Here, we present a quantitative analysis of the compartmentalization and spatial complexity of gene expression in Drosophila melanogaster over developmental time by analyzing thousands of gene expression spatial patterns from FlyExpress database. We use three different mathematical measures of compartmentalization of gene expression in space. All these measures show a similar non-linear increase in compartmentalization over time, with the most dramatic change occurring from the maternal to the early gastrula stage. Transcription factors and growth factors showed an earlier compartmentalization. Finally, we partitioned the embryo space in 257 equally sized regions and clustered them depending on their expression similarity, within and between stages. This provides a global overview about the effective degree of differentiation and compartmentalization between body parts at each developmental stage and when and where in the embryo there are more changes, due to signaling or movement.

Left-right asymmetry:

Desvignes, T., Nguyen, T., Chesnel, F., Bouleau, A., Fauvel, C., and Bobe, J. (2015). X-Linked Retinitis Pigmentosa 2 Is a Novel Maternal-Effect Gene Required for Left-Right Asymmetry in Zebrafish. Biol. Reprod. *93*, 42.

Retinitis pigmentosa 2 (*RP2*) gene is responsible for up to 20% of X-linked retinitis pigmentosa, a severe heterogeneous genetic disorder resulting in progressive retinal degeneration in humans. In vertebrates, several bodies of evidence have clearly established the role of Rp2 protein in cilia genesis and/or function. Unexpectedly, some observations in zebrafish have suggested the oocyte-predominant expression of the rp2 gene, a typical feature of maternal-effect genes. In the present study, we investigate the maternal inheritance of rp2 gene products in zebrafish eggs in order to address whether rp2

could be a novel maternal-effect gene required for normal development. Although both rp2 mRNA and corresponding protein are expressed during oogenesis, rp2 mRNA is maternally inherited, in contrast to Rp2 protein. A knockdown of the protein transcribed from both rp2 maternal and zygotic mRNA results in delayed epiboly and severe developmental defects, including eye malformations, that were not observed when only the protein from zygotic origin was knocked down. Moreover, the knockdown of maternal and zygotic Rp2 revealed a high incidence of left-right asymmetry establishment defects compared to only zygotic knockdown. Here we show that rp2 is a novel maternal-effect gene exclusively expressed in oocytes within the zebrafish ovary and demonstrate that maternal rp2 mRNA is essential for successful embryonic development and thus contributes to egg developmental competence. Our observations also reveal that Rp2 protein translated from maternal mRNA is important to allow normal heart loop formation, thus providing evidence of a direct maternal contribution to left-right asymmetry establishment.

Protocols review:

Denton, D., and Kumar, S. (2015). **Studying Apoptosis in Drosophila.** Cold Spring Harb Protoc 2015, pdb.top070433.

The apoptotic machinery is highly conserved throughout evolution, and central to the regulation of apoptosis is the caspase family of cysteine proteases. Insights into the regulation and function of apoptosis in mammals have come from studies using model organisms. Drosophila provides an exceptional model system for identifying the function of conserved mechanisms regulating apoptosis, especially during development. The characteristic patterns of apoptosis during Drosophila development have been well described, as has the apoptotic response following DNA damage. The focus of this discussion is to introduce methodologies for monitoring apoptosis during Drosophila development and also in Drosophila cell lines.

Interesting papers:

Altenhein, B., Cattenoz, P.B., and Giangrande, A. (2015). The early life of a fly glial cell. Wiley Interdiscip Rev Dev Biol.

Throughout evolution, glia have key regulatory roles in neural development and function. Typically, they control the response to developmental and/or pathological signals, thereby affecting neural proliferation, remodeling, survival, and regeneration. Such complex biology depends on the plastic features of glial cells, but also on the presence of different classes of glial cells, hence the importance of understanding the cellular and the molecular mechanisms underlying their development. The fly community has made major breakthroughs by characterizing the bases of gliogenesis and here we describe the glial lineages as well as the glial promoting factor active in the embryo of *Drosophila melanogaster*.

Vensko, S.P., and Stone, E.A. (2015). Recent progress and open questions in Drosophila dosage compensation. Fly (Austin) 0.

Sexual dimorphism is observed in many traits across diverse taxa, and often it is quite extreme. Within a species, individuals of opposing sex can appear strikingly different, reflecting differences at the molecular level that may be similarly striking. Among the most extreme cases of such molecular sexual dimorphism is the quantity of sex chromosomes that each sex possesses. Hemizygous sex chromosomes are common to many species, and various mechanisms have evolved to regulate transcriptional activity to ensure appropriate sex chromosome-to-autosome gene expression stoichiometry. Among the most thoroughly investigated of these mechanisms is *Drosophila melanogaster's* male-specific lethal (MSL) complex-mediated dosage compensation. In *Drosophila*, the male X chromosome transcription is upregulated approximately two-fold in somatic tissues to counterbalance the effects of sex chromosome hemizygosity on transcript abundance. Despite dramatic advances in our understanding of the *Drosophila* dosage compensation, many questions remain unanswered, and our understanding of its molecular underpinnings remains incomplete. In this review, we synthesize recent progress in the field as a means to highlight open questions, including how the MSL complex targets the X chromosome, how dosage compensation has shaped evolution of X-linked genes, and the degree to which MSL complex-mediated dosage compensation varies in activity across somatic tissues.

Kinghorn, K.J., Castillo-Quan, J.I., Bartolome, F., Angelova, P.R., Li, L., Pope, S., Cochemé, H.M., Kofler, R., Nolte, V., and Schlötterer, C. (2015). **Tempo and Mode of Transposable Element Activity in Drosophila**. PLoS Genet. 11, e1005406.

The evolutionary dynamics of transposable element (TE) insertions have been of continued interest since TE activity has important implications for genome evolution and adaptation. Here, we infer the transposition dynamics of TEs by comparing their abundance in natural *D. melanogaster* and *D. simulans* populations. Sequencing pools of more than 550 South African flies to at least 320-fold coverage, we determined the genome wide TE insertion frequencies in both species. We suggest that the predominance of low frequency insertions in the two species (>80% of the insertions have a frequency <0.2) is probably due to a high activity of more than 58 families in both species. We provide evidence for 50% of the TE families having temporally heterogenous transposition rates with different TE families being affected in the two species. While in *D. melanogaster* retrotransposons were more active, DNA transposons showed higher activity levels in *D. simulans*. Moreover, we suggest that LTR insertions are mostly of recent origin in both species, while DNA and non-LTR insertions are older and more frequently vertically transmitted since the split of *D. melanogaster* and *D. simulans*. We propose that the high TE activity is of recent origin in both species and a consequence of the demographic history, with habitat expansion triggering a period of rapid evolution.