Evolution

1. Fragata, I. *et al.* How much can history constrain adaptive evolution? A real-time evolutionary approach of inversion polymorphisms in *Drosophila subobscura*. *J.*

Evol. Biol. (2014). doi:10.1111/jeb.12533

Chromosomal inversions are present in a wide range of animals and plants, having an important role in adaptation and speciation. Although empirical evidence of their adaptive value is abundant, the role of different processes underlying evolution of chromosomal polymorphisms is not fully understood. History and selection are likely to shape inversion polymorphism variation to an extent yet largely unknown. Here, we perform a real-time evolution study addressing the role of historical constraints and selection in the evolution of these polymorphisms. We founded laboratory populations of *Drosophila subobscura* derived from three locations along the European cline and followed the evolutionary dynamics of inversion polymorphisms throughout the first 40 generations. At the beginning, populations were highly differentiated and remained so throughout generations. We report evidence of positive selection for some inversions, variable between foundations. Signs of negative selection were more frequent, in particular for most coldclimate standard inversions across the three foundations. We found that previously observed convergence at the phenotypic level in these populations was not associated with convergence in inversion frequencies. In conclusion, our study shows that selection has shaped the evolutionary dynamics of inversion frequencies, but doing so within the constraints imposed by previous history. Both history and selection are therefore fundamental to predict the evolutionary potential of different populations to respond to global environmental changes.

2. Civetta, A. & Reimer, A. Positive selection at a seminal fluid gene within a QTL for conspecific sperm precedence. *Genetica* (2014). doi:10.1007/s10709-014-9800-Male accessory gland proteins (ACPs) are associated with triggering postmating physiological responses in *D. melanogaster* females that can contribute to differential male reproductive success. Moreover, a large number of ACPs evolve rapidly and under positive selection among closely-related species of Drosophila. Here we have sequenced five candidate Acp genes (Acp53C14a, Acp53C14b, Acp53C14c, Acp53Ea and Acp54A1) within the previously mapped *D. simulans-D. sechellia* conspecific sperm precedences (CSP) locus from different *D. simulans* and *D. sechellia* strains. Polymorphism data analysis shows evidence of a selective sweep at Acp53Ea within *D. simulans*.

 Innocenti, P., Flis, I. & Morrow, E. H. Female responses to experimental removal of sexual selection components in *Drosophila melanogaster*. *BMC Evol. Biol.* 14, 239 (2014).

They investigated the effects of single and multiple matings on female fecundity and gene expression. The post-mating gene expression profiles of monogamous females differ significantly from promiscuous females, involving 9% of the genes tested (approximately 6% of total genes in D. melanogaster). These transcripts are active in several tissues, mainly ovaries, neural tissues and midgut, and are involved in metabolic processes, reproduction and signaling pathways. Our results demonstrate how the female post-mating response can evolve under different mating systems, and provide novel insights into the genes targeted by sexual selection in females, by identifying a list of candidate genes responsible for the decrease in female fecundity in the absence of promiscuity.

4. Jennings, J. H., Snook, R. R. & Hoikkala, A. Reproductive isolation among

allopatric Drosophila montana populations. Evolution 68, 3095-3108 (2014).

An outstanding goal in speciation research is to trace the mode and tempo of the evolution of barriers to gene flow. Such research benefits from studying incipient speciation, in which speciation between populations has not yet occurred, but where multiple potential mechanisms of reproductive isolation (RI: i.e., premating, postmating-prezygotic (PMPZ), and postzygotic barriers) may act. We used such a system to investigate these barriers among allopatric populations of *Drosophila montana*. In all heteropopulation crosses we found premating (sexual) isolation, which was either symmetric or asymmetric depending on the population pair compared. Postmating isolation was particularly strong in crosses involving males from one of the study populations, and while sperm were successfully transferred, stored, and motile, we experimentally demonstrated that the majority of eggs produced were unfertilized. Thus, we identified the nature of a PMPZ incompatibility. There was no evidence of intrinsic postzygotic effects. Measures of absolute and relative strengths of pre- and postmating barriers showed that populations can be driven by different contributions of both premating and PMPZ barriers occurring between different population pairs and without the evolution of postzygotic barriers.

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- Bewick, E. R. & Dyer, K. A. Reinforcement shapes clines in female mate discrimination in *Drosophila subquinaria*. *Evolution* 68, 3082–3094 (2014).

- Cabral, L. G. & Holland, B. Courtship Song Does Not Increase the Rate of Adaptation to a Thermally Stressful Environment in a *Drosophila melanogaster* Laboratory Population. *PLoS ONE* 9, e111148 (2014).
- 8. Roseman, C. C. & Auerbach, B. M. Ecogeography, genetics, and the evolution of human body form. *J. Hum. Evol.* (2014). doi:10.1016/j.jhevol.2014.07.006
- Franssen, S. U., Nolte, V., Tobler, R. & Schlötterer, C. Patterns of linkage disequilibrium and long range hitchhiking in evolving experimental *Drosophila melanogaster* populations. *Mol. Biol. Evol.* (2014). doi:10.1093/molbev/msu320
- 10. Chang, C.-C., Ting, C.-T., Chang, C.-H., Fang, S. & Chang, H.-Y. The Persistence of Facultative Parthenogenesis in *Drosophila albomicans*. *PLoS ONE* **9**, e113275 (2014).
- 11. Amundson, R. Charles Darwin's reputation: how it changed during the twentieth-century and how it may change again. *Endeavour* **38**, 257–267 (2014).

Genitalia evolution

 Grieshop, K. & Polak, M. Evaluating the post-copulatory sexual selection hypothesis for genital evolution reveals evidence for pleiotropic harm exerted by the male genital spines of *Drosophila ananassae*. J. Evol. Biol. (2014).

doi:10.1111/jeb.12524

The male genital spines of *Drosophila ananassae* play an adaptive role in post-copulatory sexual selection. Whereas previous work on two Drosophila species shows that these spines function in precopulatory sexual selection to initiate genital coupling and promote male competitive copulation success, further research is needed to evaluate the potential for Drosophila genital spines to have a post-copulatory function. Using a precision micron-scale laser surgery technique, we test the effect of spine length reduction on copulation duration, male competitive fertilization success, female fecundity and female remating behaviour. We find no evidence that male genital spines in this species have a post-copulatory adaptive function. Instead, females mated to males with surgically reduced/blunted genital spines exhibited comparatively greater short-term fecundity relative to those mated by control males, indicating that the natural (i.e. unaltered) form of the trait may be harmful to females. In the absence of an effect of genital spine reduction on measured components of post-copulatory fitness, the harm seems to be a pleiotropic side effect rather than adaptive. Results are discussed in the context of sexual conflict mediating the

evolution of male genital spines in this species and likely other Drosophila.



2. Otti, O. Genitalia-associated microbes in insects. Insect Sci. (2014).

doi:10.1111/1744-7917.12183

Opportunistic microbes transmitted passively during mating might impose an energetic cost, as the immune system will need to be alert and will use resources to fight potential intruders. Through mating wounds and contaminated reproductive organs opportunistic microbes might be transferred to mating partners and even enter the body cavity. Females as the "receiving" sex are particularly likely to have evolved adaptations to avoid or reduce opportunistic infections. Males of several species show highly complex seminal fluids, which as well as containing components that influence a males' fertilization success, also possess antimicrobial substances. The role of antimicrobials in the reproductive process is not well understood. Some evidence hints at the protection of sperm against microbes, indicating a role for natural selection in shaping the evolution of reproductive traits. By highlighting the potential importance of microbes in sexual selection and their role in reproduction in general I will make a case for studies in sexual selection, especially the ones investigating post-copulatory processes, that should incorporate environmental, as well as genotypic variation, in reproductive traits.

- 3. Tschopp, P. *et al.* A relative shift in cloacal location repositions external genitalia in amniote evolution. *Nature* (2014). doi:10.1038/nature13819
- 4. Herrera, A. M. & Cohn, M. J. Embryonic origin and compartmental organization of the external genitalia. *Sci Rep* **4**, 6896 (2014).
- Dines, J. P. *et al.* Sexual selection targets cetacean pelvic bones. *Evolution* 68, 3296– 3306 (2014).

 Murata, T. *et al.* β-catenin(C429S) mice exhibit sterility consequent to spatiotemporally sustained Wnt signalling in the internal genitalia. *Sci Rep* 4, 6959 (2014).

Evo-Devo

- 1. Haug, J. T., Haug, C. & Garwood, R. J. Evolution of insect wings and development new details from Palaeozoic nymphs. *Biol Rev* n/a–n/a (2014). doi:10.1111/brv.12159
- 3. Gerber, S. Not all roads can be taken: development induces anisotropic accessibility in morphospace. *Evol. Dev.* **16**, 373–381 (2014).
- Wilson, L. A. B. & Werneburg, I. Quantifying evolutionary development using non-model organisms: Integrating morphology, metrical frameworks, and gene expression. *J. Exp. Zool.* (*Mol. Dev. Evol.*) 322, 555–557 (2014).
- 5. Kraus, Y. *et al.* The embryonic development of the cnidarian *Hydractinia echinata*. *Evol. Dev.* **16,** 323–338 (2014).
- 7. Pantalacci, S. & Sémon, M. Transcriptomics of developing embryos and organs: A raising tool for evo-devo. *J. Exp. Zool. (Mol. Dev. Evol.)* n/a-n/a (2014). doi:10.1002/jez.b.22595

Genetics

 Yang, H. *et al.* Expression Profile and Gene Age Jointly Shaped the Genome-Wide Distribution of Premature Termination Codons in a *Drosophila melanogaster* Population. *Mol. Biol. Evol.* (2014). doi:10.1093/molbev/msu299
Widespread premature termination codon mutations (PTCs) were recently observed in human and fly populations. We took advantage of the population resequencing data in the Drosophila Genetic Reference Panel to investigate how the expression profile and the evolutionary age of genes shaped the allele frequency distribution of PTCs. After generating a high-quality data set of PTCs, we clustered genes harboring PTCs into three categories: genes encoding low-frequency PTCs (<1.5%), moderate-frequency PTCs (1.5-10%), and high-frequency PTCs (>10%). All three groups show narrow transcription compared with PTC-free genes, with the moderate- and high-PTC frequency groups showing a pronounced pattern. Moreover, nearly half (42%) of the PTC-encoding genes are not expressed in any tissue. Interestingly, the moderate-frequency PTC group is strongly enriched for genes expressed in midgut, whereas genes harboring high-frequency PTCs tend to have sex-specific expression. We further find that although young genes born in the last 60 My compose a mere 9% of the genome, they represent 16%, 30%, and 50% of the genes containing low-, moderate-, and high-frequency PTCs, respectively. Among DNA-based and RNA-based duplicated genes, the child copy is approximately twice as likely to contain PTCs as the parent copy, whereas young de novo genes are as likely to encode PTCs as DNA-based duplicated new genes. Based on these results, we conclude that expression profile and gene age jointly shaped the landscape of PTC-mediated gene loss. Therefore, we propose that new genes may need a long time to become stably maintained after the origination.

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- 3. Puerma, E., Orengo, D. J. & Aguadé, M. Evidence for a gene involved in multiple and diverse rearrangements in the Drosophila genus. *Mol. Biol. Evol.* **31**, 2998–3001 (2014).
- Mandal, A., Mandal, S. & Park, M. H. Genome-Wide Analyses and Functional Classification of Proline Repeat-Rich Proteins: Potential Role of eIF5A in Eukaryotic Evolution. *PLoS ONE* 9, e111800 (2014).
- Gilliland, W. D. *et al.* Normal Segregation of a Foreign-Species Chromosome During Drosophila Female Meiosis Despite Extensive Heterochromatin Divergence. *Genetics* (2014). doi:10.1534/genetics.114.172072
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- 9. Larracuente, A. M. The organization and evolution of the Responder satellite in species of the *Drosophila melanogaster* group: dynamic evolution of a target of meiotic drive. *BMC*

Evol. Biol. 14, 233 (2014).

- Charlesworth, B. & Campos, J. L. The relations between recombination rate and patterns of molecular variation and evolution in Drosophila. *Annu. Rev. Genet.* 48, 383–403 (2014).
- 11. Artieri, C. G. & Fraser, H. B. Transcript length mediates developmental timing of gene expression across Drosophila. *Mol. Biol. Evol.* **31**, 2879–2889 (2014).
- 12. Gilles, A. F. & Averof, M. Functional genetics for all: engineered nucleases, CRISPR and the gene editing revolution. *EvoDevo* **5**, 43 (2014).

Sensory Organ

 Jiang, Y., Boll, W. & Noll, M. Pox neuro control of cell lineages that give rise to larval poly-innervated external sensory organs in Drosophila. *Dev. Biol.* (2014). doi:10.1016/j.ydbio.2014.10.013

The Pox neuro (Poxn) gene of Drosophila plays a crucial role in the development of poly-innervated external sensory (p-es) organs. However, how Poxn exerts this role has remained elusive. In this study, we have analyzed the cell lineages of all larval p-es organs, namely of the kölbchen, papilla 6, and hair 3. Surprisingly, these lineages are distinct from any previously reported cell lineages of sensory organs. Unlike the well-established lineage of mono-innervated external sensory (m-es) organs and a previously proposed model of the p-es lineage, we demonstrate that all wild-type p-es lineages exhibit the following features: the secondary precursor, plla, gives rise to all the three support cells - socket, shaft, and sheath, whereas the other secondary precursor, pllb, is neuronal and gives rise to all neurons. We further show that in one of the p-es lineages, that of papilla 6, one cell undergoes apoptosis. By contrast in Poxn null mutants, all p-es lineages have a reduced number of cells and their pattern of cell divisions is changed to that of an m-es organ, with the exception of a lineage in a minority of mutant kölbchen that retains a second bipolar neuron. Indeed, the role of Poxn in p-es lineages is consistent with the specification of the developmental potential of secondary precursors and the regulation of cell division but not apoptosis.

 Couturier, L., Trylinski, M., Mazouni, K., Darnet, L. & Schweisguth, F. A fluorescent tagging approach in Drosophila reveals late endosomal trafficking of Notch and Sanpodo. *J Cell Biol* 207, 351–363 (2014).

Signaling and endocytosis are highly integrated processes that regulate cell fate. In the Drosophila

melanogaster sensory bristle lineages, Numb inhibits the recycling of Notch and its trafficking partner Sanpodo (Spdo) to regulate cell fate after asymmetric cell division. In this paper, we have used a dual GFP/Cherry tagging approach to study the distribution and endosomal sorting of Notch and Spdo in living pupae.

- Fritzsch, B., Jahan, I., Pan, N. & Elliott, K. L. Evolving gene regulatory networks into cellular networks guiding adaptive behavior: an outline how single cells could have evolved into a centralized neurosensory system. *Cell Tissue Res* 1–19 (2014). doi:10.1007/s00441-014-2043-1
- Miller, S. W., Rebeiz, M., Atanasov, J. E. & Posakony, J. W. Neural precursor-specific expression of multiple Drosophila genes is driven by dual enhancer modules with overlapping function. *PNAS* 111, 17194–17199 (2014).
- 5. Short, B. Red and green traffic signals. *J Cell Biol* **207**, 319–319 (2014).
- Espositoa, R. *et al.* The ascidian pigmented sensory organs: structures and developmental programs. *Genesis* (2014). doi:10.1002/dvg.22836

Asymmetry

1. Chouvenc, T., Basille, M., Li, H.-F. & Su, N.-Y. **Developmental instability in incipient** colonies of social insects. *PLoS ONE* **9**, e113949 (2014).

Investigated the stress imposed on individuals of incipient colonies by comparing the developmental instability of individuals between incipient and mature colonies of two Coptotermes species, *C. formosanus Shiraki* and *C. gestroi* (Wasmann). We assessed the developmental instability by measuring the asymmetry of morphological traits from the head capsule of the soldier caste. Soldiers from incipient colonies of both species displayed strong asymmetrical traits in comparison to soldiers from mature colonies. We suggest that homeostatic conditions for optimal development are reached as the colony matures, and confirmed that the incipient colony remains a critical bottleneck where individuals are exposed to high developmental stress.

2. Watanabe, H. *et al.* Nodal signalling determines biradial asymmetry in Hydra. *Nature* **515**, 112–115 (2014).

In bilaterians, three orthogonal body axes define the animal form, with distinct anterior-posterior, dorsal-ventral and left-right asymmetries. The key signalling factors are Wnt family proteins for the anterior-posterior axis, Bmp family proteins for the dorsal-ventral axis and Nodal for the left-right axis. Cnidarians, the sister group to bilaterians, are characterized by one oral-aboral body axis, which exhibits a distinct biradiality of unknown

molecular nature. Here we analysed the biradial growth pattern in the radially symmetrical cnidarian polyp Hydra, and we report evidence of Nodal in a pre-bilaterian clade. We identified a Nodal-related gene (Ndr) in *Hydra magnipapillata*, and this gene is essential for setting up an axial asymmetry along the main body axis. This asymmetry defines a lateral signalling centre, inducing a new body axis of a budding polyp orthogonal to the mother polyp's axis. Ndr is expressed exclusively in the lateral bud anlage and induces Pitx, which encodes an evolutionarily conserved transcription factor that functions downstream of Nodal. Reminiscent of its function in vertebrates, Nodal acts downstream of β -Catenin signalling. Our data support an evolutionary scenario in which a 'core-signalling cassette' consisting of β -Catenin, Nodal and Pitx pre-dated the cnidarian-bilaterian split. We presume that this cassette was co-opted for various modes of axial patterning: for example, for lateral branching in cnidarians and left-right patterning in bilaterians.

 Shiratori, H. *et al.* Self-regulated left-right asymmetric expression of Pitx2c in the developing mouse limb. *Dev. Biol.* 395, 331–341 (2014).

Methods

 Wong, W. H. *et al.* 'Direct PCR' optimization yields a rapid, cost-effective, nondestructive and efficient method for obtaining DNA barcodes without DNA extraction. *Mol Ecol Resour* 14, 1271–1280 (2014).

The direct PCR can be successfully optimized for a wide range of other invertebrate taxa that need routine barcoding (flies: Culicidae, Drosophilidae, Dolichopodidae, Sepsidae; sea stars: Oreasteridae). Key for obtaining high PCR success rates is optimizing (i) tissue quantity, (ii) body part, (iii) primer pair and (iv) type of Taq polymerase. Unfortunately, not all invertebrates appear suitable because direct PCR has low success rates for other taxa that were tested (e.g. Coleoptera: Dytiscidae, Copepoda, Hymenoptera: Formicidae and Odonata). It appears that the technique is less successful for heavily sclerotized insects and/or those with many exocrine glands.

 Cicin-Sain, D. *et al.* SuperFly: a comparative database for quantified spatiotemporal gene expression patterns in early dipteran embryos. *Nucleic Acids Res.*

(2014). doi:10.1093/nar/gku1142

SuperFly (<u>http://superfly.crg.eu</u>) is a relational database for quantified spatio-temporal expression data of segmentation genes during early development in different species of dipteran insects (flies, midges and mosquitoes). SuperFly has a special focus on emerging non-drosophilid model systems. The database currently includes data of high spatio-temporal resolution for three species: the vinegar fly *Drosophila melanogaster*, the scuttle fly *Megaselia abdita* and the moth midge *Clogmia albipunctata*. At this point, SuperFly covers up to 9 genes and 16 time points per species, with a total of 1823 individual embryos.