

DROSOPHILA MELANOGASTER, DROSOPHILA SIMULANS: SO SIMILAR, SO DIFFERENT

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Drosophila melanogaster, Drosophila simulans: So Similar, So Different

Edited by

P. CAPY, P. GIBERT and J. BOUSSY

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Contents

Preface	1
<i>Drosophila melanogaster</i>, <i>Drosophila simulans</i>: so similar yet so different P. Capy, P. Gibert	5
<i>Biogeography and population structure: past and present</i>	
How two Afrotropical endemics made two cosmopolitan human commensals: the <i>Drosophila melanogaster</i>–<i>D. simulans</i> palaeogeographic riddle D. Lachaise, J.-F. Silvain	17
Mitochondrial DNA in the <i>Drosophila melanogaster</i> complex M. Solignac	41
<i>Wolbachia</i> infections in <i>Drosophila melanogaster</i> and <i>D. simulans</i>: polymorphism and levels of cytoplasmic incompatibility H. Merçot, S. Charlat	51
Historicity and the population genetics of <i>Drosophila melanogaster</i> and <i>D. simulans</i> M. Veuille, E. Baudry, M. Cobb, N. Derome, E. Gravot	61
Patterns of microsatellite variability in the <i>Drosophila melanogaster</i> complex B. Harr, C. Schlötterer	71
Molecular polymorphism in <i>Drosophila melanogaster</i> and <i>D. simulans</i>: what have we learned from recent studies? S. Mousset, N. Derome	79
The <i>sex-ratio</i> trait and its evolution in <i>Drosophila simulans</i>: a comparative approach D. Jutier, N. Derome, C. Montchamp-Moreau	87
A reanalysis of protein polymorphism in <i>Drosophila melanogaster</i>, <i>D. simulans</i>, <i>D. sechellia</i> and <i>D. mauritiana</i>: effects of population size and selection R. A. Morton, M. Choudhary, M.-L. Cariou, R. S. Singh	101
<i>Transposable elements and chromosomes</i>	
Transposable element dynamics in two sibling species: <i>Drosophila melanogaster</i> and <i>Drosophila simulans</i> C. Vieira, C. Biémont	115
Wanderings of <i>hobo</i>: a transposon in <i>Drosophila melanogaster</i> and its close relatives I. A. Boussy, M. Itoh	125
Mitotic and polytene chromosomes: comparisons between <i>Drosophila melanogaster</i> and <i>Drosophila simulans</i> S. Aulard, L. Monti, N. Chaminade, F. Lemeunier	137
<i>Geographical variability and adaptation</i>	
Comparative life histories and ecophysiology of <i>Drosophila melanogaster</i> and <i>D. simulans</i> J. R. David, R. Allemand, P. Capy, M. Chakir, P. Gibert, G. Pétavy, B. Moreteau	151

Comparative analysis of morphological traits among <i>Drosophila melanogaster</i> and <i>D. simulans</i>: genetic variability, clines and phenotypic plasticity	165
P. Gibert, P. Capy, A. Imasheva, B. Moreteau, J. P. Morin, G. Pétavy, J. R. David	
Ecological and genetic interactions in <i>Drosophila</i>–parasitoids communities: a case study with <i>D. melanogaster</i>, <i>D. simulans</i> and their common <i>Leptopilina</i> parasitoids in south-eastern France	181
F. Fleury, N. Ris, R. Allemand, P. Fouillet, Y. Carton, M. Boulétreau	
Relations between cuticular hydrocarbon (HC) polymorphism, resistance against desiccation and breeding temperature; a model for HC evolution in <i>D. melanogaster</i> and <i>D. simulans</i>	195
J.-D. Rouault, C. Marican, C. Wicker-Thomas, J.-M. Jallon	
Molecular analysis of circadian clocks in <i>Drosophila simulans</i>	213
A. S. Rogers, E. Rosato, R. Costa, C. P. Kyriacou	
A mutation in <i>Drosophila simulans</i> that lengthens the circadian period of locomotor activity	223
A. S. Rogers, S. A. Escher, C. Pasetto, E. Rosato, R. Costa, C. P. Kyriacou	
Sperm size evolution in <i>Drosophila</i>: inter- and intraspecific analysis	233
D. Joly, A. Korol, E. Nevo	
<i>Speciation: pre and post zygotic isolation</i>	
The nature of genetic variation in sex and reproduction-related genes among sibling species of the <i>Drosophila melanogaster</i> complex	245
R. J. Kulathinal, R. S. Singh	
Genetics of hybrid inviability and sterility in <i>Drosophila</i>: dissection of introgression of <i>D. simulans</i> genes in <i>D. melanogaster</i> genome	253
K. Sawamura, T. L. Karr, M.-T. Yamamoto	
A new hybrid rescue allele in <i>Drosophila melanogaster</i>	261
D. A. Barbash, J. Roote, G. Johnson, M. Ashburner	
Male-specific expression of the Fruitless protein is not common to all <i>Drosophila</i> species	267
D. Yamamoto, K. Usui-Aoki, S. Shima	
Genetic basis of sexual isolation in <i>Drosophila melanogaster</i>	273
A. Takahashi, C.-T. Ting	
Why there is a one-way crossability between <i>D. melanogaster</i> and <i>D. simulans</i>?	285
B. Moulin, T. Aubin, J.-M. Jallon	



Preface

Comparison of closely related species is a powerful approach to understanding the changes that have occurred since their divergence from a common ancestor. The sibling species *Drosophila melanogaster* and *D. simulans* are probably the species pair for which the most genetic data are available. A workshop held at Gif/Yvette in January 2002¹ reviewed and discussed comparisons between these species, from their ecology and biogeography to their behavior and DNA polymorphism.

D. melanogaster and *D. simulans* are cosmopolitan human commensals, and they can often be found in the same geographical area and even emerging from the same larval food sources. However, this general similarity hides deep divergences for many traits, including courtship behavior, morphology, ecophysiology, chromosomes, enzymes, and DNA and protein polymorphisms.

D. melanogaster and *D. simulans* probably evolved in Africa, diverging about 3.4 million years ago. Based on their biogeography and patterns of mtDNA variability, it appears that *D. melanogaster* evolved in central Africa, whereas *D. simulans* likely evolved along the east coast or on Madagascar (D. Lachaise). *D. melanogaster* is largely a human commensal, and its world colonization was probably associated with early human activity and migration. The expansion of *D. simulans* worldwide is much more recent. The histories and phylogenies of the two species (as well as those of their siblings *D. mauritiana* and *D. sechellia*) have been analyzed using polymorphisms of *Wolbachia* strains (S. Charlat), microsatellite DNA (C. Schloetterer), genomic DNA (M. Veuille and S. Mousset) and mtDNA (M. Solignac).

D. melanogaster is less permissive than is *D. simulans* to the cytoplasmic incompatibility (CI) induced in crosses between flies bearing different *Wolbachia* strains, suggesting that host factors are involved. Five different *Wolbachia* variants, all inducing CI, can be detected in *D. simulans*, but only one is found in

D. melanogaster. In *D. melanogaster*, microsatellites reveal that West African populations are more closely related to non-African populations than to East African populations. East African populations are more variable than West African or non-African populations, suggesting that East African populations may more closely reflect African ancestral variability.

Ecophysiology, population dynamics and population structure are also important to understanding the evolution of the two species. Genetic diversity (θ) is higher in *D. simulans* (S. Mousset and R. Singh). Based on allozyme data, variability among populations (F_{st}) is higher in *D. melanogaster*. The effective population size (N_e) seems to be higher in *D. simulans*, but N_e and migration rate (m) are not independent. Migration rate could be an important factor, as shown by the dynamics of the two species in southern France (F. Fleury). Summer and fall populations of *D. melanogaster* seem to derive from winter populations maintained in the same site, while most of the sites where *D. simulans* is found in autumn are re-colonized every year from winter populations maintained in warmer regions (southern Europe). In other words, the migration rate of *D. simulans* in these regions seems to be higher than that of *D. melanogaster*.

Physiological analyses reveal that *D. simulans* is less sedentary, more sensitive to stress, more warm-adapted and more cold-tolerant. Shapes of reaction norms of different traits are generally similar and parallel for both species, but the mean values and phenotypic and genetic variabilities are generally different (P. Gibert and J. David). For instance, *D. simulans* is smaller and less genetically variable both within and between populations for morphological traits.

When the two species are in competition, *D. melanogaster* generally eliminates *D. simulans*. However, the dynamics of this elimination are not the same at different breeding temperatures, and at low temperature *D. simulans* is not eliminated. Moreover, in the presence of parasitoid wasps (*Leptopilina boulardi* and *L. heterotoma*), and depending on temperature, *D. simulans* may eliminate *D. melanogaster* (F. Fleury).

Genetic factors involved in intra- or intergenomic conflicts can be used as markers of population dynamics and history. This includes data from *Wolbachia* and *sex-ratio* in *D. simulans*. Geographical distributions of *Wolbachia* strains (S. Charlat) are closely related

¹The workshop entitled “*Drosophila melanogaster*, *Drosophila simulans*: so similar, so different” that was held from 9 to 12 January, 2002 at the Centre National de la Recherche Scientifique (Lab. Populations, Génétique et Evolution) at Gif/Yvette (France) was financially supported by Kluwer Academic Publishers, the University of Paris XI and the Centre National de la Recherche Scientifique.

to those of mitochondrial types but are not similar to those of the components (distorters and suppressors) of the *sex-ratio* drive system (C. Montchamp-Moreau).

Polymorphisms of chromosomal inversions and of copy numbers of transposable elements suggest different genetic plasticities of the two species. *D. melanogaster* has a larger number of chromosomal inversions (more than 500 vs. 14 known in *D. simulans*, F. Lemeunier) and of mobile sequences (C. Vieira). Most of the inversions detected in *D. simulans* are described in populations originated from the recently colonized Japanese islands. The recent world colonization by *D. simulans* may be accompanied by a genome expansion involving increases in transposable element copy numbers. In *D. melanogaster*, the overall copy numbers of about 40 transposable elements in natural populations are higher in recent populations than in ancestral ones (about 1100 copies v.s. 940). These observations suggest that a correlation could exist between colonization and genome expansion.

A detailed analysis of the *hobo* element suggests three introductions into the *melanogaster* subgroup (I. Boussy). Two ancient introductions were into ancestors of the *melanogaster* and *montium* subgroups, and one quite recent one was into the ancestor of the *melanogaster* species complex, or into a member of the complex, followed by horizontal transfers or interspecific hybridization-mediated transfers. The sparse occurrence of *hobo* in the genus *Drosophila*, despite its ability to transpose even outside the genus, raises the question of the permissivity of *D. melanogaster* and *D. simulans* to transposable elements. *D. melanogaster* has been invaded or re-invaded by at least three different elements (*P*, *hobo*, and *I*) during the last century, while no such events have been reported for *D. simulans*. Is it due to the genetics and/or ecology of the species, or simply to differences in opportunity?

Several questions were discussed dealing with speciation and divergence between the two species. For instance, what could be the nature of genetic changes that occurred during the early stage of divergence? To answer this question R. Singh proposes focussing on sex and reproduction-related traits (SRR). These traits have often been shown to evolve more rapidly than other genes, as was illustrated for the *transformer* gene (*tra*). Such traits also could be more prone to being recruited for novel function, as was recently shown for *Sdic* in *D. melanogaster* and *Ocnus* (*ocn*) in the *melanogaster* subgroup.

What are the genes responsible for the postzygotic isolation between the two species, especially those involved in hybrid sterility and inviability? The effects of *Lhr* (lethal hybrid rescue), *Hmr* (hybrid male rescue), *zhr* (zygotic hybrid rescue) and *mhr* (maternal hybrid rescue) were discussed. Genes responsible for male inviability and female sterility in offspring of a cross with *D. melanogaster* as the female parent have been mapped using a *D. simulans* strain that produces fertile hybrid females. Introgression of a *D. simulans* chromosome region into a *D. melanogaster* genetic background shows that several genes probably contribute to male inviability, while female sterility could be due to a single gene (K. Sawamura). D. Barbash described a new hybrid rescue allele associated with a small deficiency of the chromosomal region 9D where the *Hmr* gene is mapped in *D. melanogaster*. The deficiency could be the result of a hybrid *P* transposable element insertion. This new allele suppresses high temperature hybrid female lethality.

Partial prezygotic isolation has been described between natural populations of *D. melanogaster*, a situation that is interpreted as representing the earliest stage of incipient speciation. C. Ting showed that the main effects responsible for the prezygotic barriers between Zimbabwe populations of *D. melanogaster* and cosmopolitan populations are localized on chromosome 3. The behavioral barriers are probably not due to a single gene but to several interacting genes. The other partial prezygotic isolation that has been described in *D. melanogaster*, between two Congolese populations, seems to be due to different mechanisms (Haerty & Capy, unpublished results).

Behavior is an important component in such prezygotic isolation. M. Ritchie asked whether 'speciation genes' are the same as those that contribute to variation within species. From a QTL analysis of the interpulse interval of courtship song within *D. melanogaster* and between *D. simulans* and its sibling, *D. sechellia*, different chromosome regions are detected, and in both cases no sex-linked QTL is observed. This suggests that the answer to the question is 'no'.

Among the factors that might be involved in the reproductive isolation between the species is sperm length. The distribution of this trait allows us to discriminate among the two species. The mean value and the variability are lower in *D. simulans*. A detailed analysis of populations of the two species in 'Evolution Canyon' in Israel shows the existence of clinal variations in sperm length in association with drought for *D. melanogaster*, but not for *D. simulans* (Joly).

D. melanogaster and *D. simulans* have different cuticular hydrocarbon profiles. Cuticular hydrocarbons partly function as pheromones. In *D. melanogaster* sex-specific compounds are detected, while in *D. simulans* the compounds of the two sexes are similar. In *D. simulans*, some differences exist between Yaoundé (Cameroon) populations and the other populations from eastern Africa. For *D. melanogaster* males, differences are also detected between eastern and western populations of Africa. These cuticular hydrocarbons are also involved in the resistance to desiccation. Tropical populations are more protected against desiccation in both species. It is suggested from an analysis of the melting points of the different compounds that the lipidic phase, which covers the cuticle, is liquid and that longer chains of carbons provide better protection against desiccation. One of the main compounds involved in this protection could be 7-pentacosene. A simple mathematical model based on the kinetics of lipid elongation and decarboxylation was proposed to explain the differences observed between temperate and tropical populations of the two species. Variation in the kinetics of the decarboxylation is enough to account for the observations. The absence of variation among populations of *D. simulans* from temperate regions could be the result of a recent dispersion (J. Rouault and J.M. Jallon).

In behavior, the general activity of the adults plays an important role. This activity can be affected by several genes, including those involved in circadian rhythm, such as the *period* gene (*per*). In this gene the number of threonine–glycine repeats has an impact on rhythmic behavior. The mean threonine–glycine repeat number of *per* is different in the two species and varies within each species between populations. For *D. melanogaster* there is a cline in the repeat number in Europe, but not for *D. simulans*. However, in both species there is some evidence for balancing selection's maintaining different numbers of repeats (C. Kyriacou).

The courtship song is known to be an important signal involved in sex and species recognition. Analysis of the ontogeny of the courtship song of males shows that young imagoes of both species have

similar IPIs (inter-pulse intervals) but differences can be detected during the maturation of the adults (B. Moulin). In *D. simulans* there is almost no variation with age, while maturation is required for *D. melanogaster* males to develop a mature, successful courtship song.

Courtship is also affected by genes like *fruitless* (*fru*). Mutants of *fru* are characterized by enhanced male-to-male courtship and by the lack of the male-specific muscle of Lawrence. Due to *transformer* (*tra*), the primary *fru* transcript is differently spliced in males and females, and the male-specific presence of Fru protein appears to be due to translation repression in females by *tra*-binding (D. Yamamoto).

As well studied as *D. melanogaster* and *D. simulans* are genetically, there continues to be a lack of ecological, biogeographic, and population dynamics data for the two species. Questions about the equilibrium of natural populations of both species are not solved. It is quite possible that the genes under selective constraints in *D. melanogaster* are not the same as those in *D. simulans*. *D. melanogaster* and *D. simulans* are cosmopolitan, while all the other members of the *melanogaster* subgroup are endemic to particular regions of Africa. A major question, then, is how these species became colonizers. To answer this question, comparisons of recent and ancestral populations of *D. melanogaster* are appropriate, if ancestral populations can be identified, as are detailed analyses of the recently colonizing species, *D. simulans*.

During this workshop, it became apparent that an integrated view is needed to understand the evolutionary history of these species. The beauty of working with *D. melanogaster* and *D. simulans* is that so many genetic tools are already available that questions can be addressed at quite sophisticated levels. The papers presented here are enthusiastically offered by the authors as evidence of this promise, and as bases for future work. Moreover, the complete genomic sequence of *D. simulans* would be of the greatest interest for these endeavors.

P. CAPY, Gif-sur-Yvette, France
 P. GIBERT, Gif-sur-Yvette, France
 I. BOUSSY, Chicago, IL, USA