



Sciences biologiques,
Écologie et Environnement
**CONFÉRENCES
JACQUES-MONOD**



Roscoff (France), May 22-26 2013

Recent advances on the evolution of sex and genetic systems

Avancées récentes sur l'évolution du sexe et des systèmes génétiques

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Conference report

Rapport sur la conférence

PROGRAM OVERVIEW

The conference took place in Roscoff from May 22d to May 26th. 115 participants attended the conference (see below). The different sessions corresponded to different aspects of the evolution of reproductive systems:

Session 1: Advantages of sex and recombination

Session 2: Biology of sexual and asexual reproduction

Session 3: Inbreeding versus outcrossing

Session 4: The evolution of sex differentiation

Session 5: The evolution of sex chromosomes

PARTICIPANTS



Invited speakers

Each of the 28 invited speakers gave a 30 mn presentation.

AGRAWAL Aneil - Toronto, CANADA

BACHTROG Doris - Berkeley, USA

BARRETT Spencer - Toronto, CANADA

BARTON Nick - Klosterneuburg, AUSTRIA

CASTAGNONE-SERENO Philippe - Sophia-Antipolis, FRANCE

CHARLESWORTH Brian - Edinburgh, UK

CHARLESWORTH Deborah - Edinburgh, UK

DAVID Patrice - Montpellier, FRANCE

DE VISSER Arjan - Wageningen, THE NETHERLANDS

DELPH Lynda - Bloomington, USA

GIRAUD Tatiana - Orsay, FRANCE

GLEMIN Sylvain - Montpellier, FRANCE

HAAG Christoph - Montpellier, FRANCE

JOHNSON Marc - Toronto, CANADA
LENORMAND Thomas - Montpellier, FRANCE
LIVELY Curt - Bloomington, USA
MANK Judith - London, UK
MARAIS Gabriel - Villeurbanne, FRANCE
OTTO Sarah - Vancouver, CANADA
PANNELL John - Lausanne, SWITZERLAND
PERRIN Nicolas - Lausanne, SWITZERLAND
PORCHER Emmanuelle - Paris, FRANCE
ROZE Denis - Roscoff, FRANCE
SCHON Isa - Brussels, BELGIUM
SCHWANDER Tanja - Lausanne, SWITZERLAND
SHARBEL Timothy - Gatersleben, GERMANY
STADLER Tanja - Zürich, SWITZERLAND
VEKEMANS Xavier - Villeneuve d'Ascq, FRANCE

Among these invited speakers, 7 were from outside Europe, 11 from Europe (not including France) and 10 from France; 10 invited speakers were female.

Other participants

87 non-invited participants from 16 countries attended the conference. 16 contributed talks (of 15 mn each) were selected among the proposed abstracts:

CASTRIC Vincent - Villeuneuve d'Ascq, FRANCE
COELHO Susana - Roscoff, FRANCE
CORDAUX Richard - Poitiers, FRANCE
HANSSON Bengt - Lund, SWEDEN
JAQUIERY Julie - Le Rheu, FRANCE
MALONE John - Tallahassee, USA
MOUSSET Sylvain - Villeurbanne, FRANCE
NEIMAN Maurine - Iowa City, USA
REUTER Max - London, UK
RODE Nicolas - Ottawa, CANADA
SCHARER Lukas - Basel, SWITZERLAND
SCHOUSTRA Sijmen - Wageningen, THE NETHERLANDS
TSUCHIMATSU Takashi - Vienna, AUSTRIA
VAN DONINCK Karine - Namur, BELGIUM
VUILLEUMIER Séverine - Lausanne, SWITZERLAND
WRIGHT Stephen - Toronto, CANADA

All other participants presented posters during one of the two poster sessions. From these 87 participants, 9 were from outside Europe (Australia, Canada, Japan, USA), 39 from Europe excluding France (Austria, Belgium, Czech Republic, Denmark, Finland, Germany, the Netherlands, Spain, Sweden, Switzerland, UK) and 39 were from France. Finally, 25 participants were PhD students.

Financial support

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Scientific program

The goal of the conference was to gather researchers working on different aspects of the evolution of genetic systems (evolution of sex, mating systems, sexual differentiation, sex chromosomes) to assess the current state of the field and discuss open questions. In particular, important progress has been made possible over recent years thanks to new methodological tools (such as genomics/bioinformatics, statistical methods for comparative analyses, experimental evolution) and continued theoretical work; furthermore, field work has continued to bring important insights about the diversity of reproductive systems and their ecological and biological correlates. These different approaches were represented among the participants of the conference, with both theoreticians and empiricists working on a variety of topics and biological systems (including plants, animals and fungi). Theoretical approaches were represented in about 15 of the 44 oral presentations, genomics/transcriptomics approaches in about 16, field studies in about 9, while experimental evolution, comparative analyses and studies on the genetic control of reproductive systems were represented in about 3 presentations each (note that some presentations included results obtained using different types of approaches). This diversity of approaches was also represented during both poster sessions.

Session 1: Advantages of sex and recombination

Sessions 1 and 2 dealt with the evolution of reproductive modes (sexual vs. asexual) and the possible evolutionary benefits of sexual recombination. Session 1 included more theoretical presentations, while session 2 focused more on the genetical mechanisms leading to the loss of sex, the phylogenetical and ecological distributions of asexuals and the long-term evolutionary consequences of asexual reproduction.

Nick Barton (IST Austria) gave a review of the theoretical literature on the evolution of recombination, focusing on models including finite population size (indeed, stochastic fluctuations generated by finite population size have been shown to generally result in selection for recombination). New results on the rate of spread of beneficial alleles as a function of population size and genome map length were presented. Although these explanations based on finite population size are attractive, current estimates for the genetic variance generated by deleterious mutations, and for the rate of adaptive substitutions, seem too low to generate a strong benefit for recombination. However, it may be that most beneficial alleles only spread in part of the distribution range of a species, and/or that selection often fluctuates over time, which may generate stronger selection for sex and recombination. Tanja Stadler (ETH Zürich) presented new statistical approaches to infer rates of extinction and speciation from phylogenetic data, assuming that the rate of extinction may increase with species age. Indeed, a general observation is that asexual clades tend to be recent, which may be due to higher extinction rates of asexuals (caused by the accumulation of deleterious alleles and/or failure to adapt to changing environments, in which case extinction probability should increase over time). Datasets are needed in order to apply this new method to sexual and asexual clades. Thomas Lenormand (CNRS Montpellier) presented theoretical models on the evolution of gene expression in diploids, and possible consequences on the evolution of recombination. Indeed in diploids, an optimal rate of expression of a given gene can be achieved in a variety of ways (expression of only one of the two homologous genes, or equal expression of both genes) and selection may lead to a conflict over gene expression among promoters. In some cases, the consequences of this conflict may be reduced by modifier genes increasing recombination between promoters and coding sequences. Denis Roze (CNRS Roscoff) presented models on the evolution of sex and recombination in diploids, and showed that diploidy has important effects on selection for recombination as

soon as mating is not completely random. In general, dominance interactions among alleles tend to disfavor recombination (through an effect of recombination on correlations in homozygosity between genes) unless a particular form of epistasis (involving dominance) is also present. These effects are generally strong compared to effects that had been previously described using haploid models. Sijmen Schoustra (University of Wageningen) presented new experimental results using the fungus *Aspergillus nidulans*, showing that the magnitude of epistasis between beneficial alleles is proportional to the selection coefficient of these alleles (in agreement with phenotypic models of adaptation such as Fisher's geometrical model). Arjan de Visser (also from Wageningen) presented experimental results on another fungus (*Aspergillus niger*) obtained from generating different combinations of selected mutations at 5 different loci. The results showed evidence for widespread sign epistasis, where two individually deleterious alleles become favorable when combined. A theoretical model indicates that such sign epistasis should generally disfavor recombination. Possible explanations for the fact that recombination nonetheless generally favors adaptation were proposed (adaptive landscapes may be generally more complex and involve more evolutionary routes, and/or sign epistasis may be organized in genetic modules with little epistasis among modules). Finally, Maurine Neiman (University of Iowa) presented experimental results on the snail *Potamopyrgus antipodarum*, exploring whether differences in ploidy affect differences in reproductive success between sexual (diploid) and asexual (triploid or tetraploid) morphs. The results show an important variance in fitness components in both sexual and asexual morphs, while ploidy (triploid-tetraploid comparisons) seems to have little effect (at least under the benign laboratory conditions).

Session 2: Biology of sexual and asexual reproduction

Curt Lively (University of Indiana) summarized a series of experiments and surveys in natural populations of the snail *Potamopyrgus antipodarum* that provide strong evidence for frequency-dependent infection by trematode parasites of different clonal lineages. The reported patterns suggest that parasites may prevent individual clones from going to fixation. An experimental evolution experiment with *Caenorhabditis elegans* further provided empirical evidence that fluctuating selection generated by parasites favours outcrossing. Tim Sharbel (IPK Gatersleben) described recent insights into the molecular basis of asexual reproduction through seeds (apomixis) in the plant species complex *Boechera holboellii*. Apomixis in this group varies quantitatively among individuals and is triggered by hybridization between sexual species, followed by polyploidization. Two likely candidate genetic regions associated with apomixis have been identified and functional characterization of these regions is the focus of ongoing research. Tanja Schwander (University of Lausanne) discussed different types of transitions from sexual reproduction to parthenogenesis and how they may generate variation among insect orders in the incidence of parthenogenesis. Of particular importance appears to be the sex determination system in the sexual ancestors, whereby the systems facilitating transitions to parthenogenesis (i.e., haplodiploidy) also allow for reversals from parthenogenesis to sex. Marc Johnson (University of Toronto at Mississauga) reported on the effect of sexual and asexual reproduction on the evolution of defense pathways in primroses. Consistent with expectations for reduced efficiency of selection in the absence of sex, independent losses of sex in this group are associated with a relaxed constraint on genes subject to purifying selection, but reduced positive selection for genes subject to positive selection. Karine van Doninck (University of Namur) described the genome structural organisation of the asexual bdelloid rotifer *Adineta vaga*. The long-term absence of meiosis in this species has apparently resulted in the loss of several genes involved in chromosome synapsis and has generated several unique features, including rearrangements and shuffling between allelic regions that no longer allow for the distinction of homologous chromosomes. Isa Schoen (University of Bruxelles)

reported on frequent origins of asexuality in Ostracods and hybridization events between sexual and asexual lineages, mediated by sexual males. Thus occasional fertilization of eggs laid by asexual females probably generated an increase in ploidy in some lineages, such that transitions to asexuality in the presence of sexual males lead to an increase of genome size. Philippe Castagnone-Sereno (Sophia Antipolis) summarized recent insights into genome characteristics of asexual knot nematodes (genus *Meloidogyne*). It was suggested that genome duplication and subsequent fixation of heterozygosity in this group could generate functional innovations facilitating the evolution of novel and complex adaptations under asexuality. Finally, Nicolas Rode (University of Ottawa) reported on rare events of sexual reproduction between bisexual and diploid asexual lineage, as well as within diploid asexual lineages, in the brine shrip *Artemia parthenogenetica*. Such rare sexual events would have generated triploid as well as tetraploid asexual lineages, whereby rare sex appears to also occur tetraploid lineages.

Session 3: Inbreeding versus outcrossing

This session focused on the evolution of self-fertilization, in particular on the evolutionary forces that may favor selfing over outcrossing, the mechanisms leading to the loss of self-incompatibility and the long-term consequences of selfing. Anil Agrawal (University of Toronto) presented a new theoretical work exploring the hypothesis that low rates of outcrossing may be maintained in predominantly selfing species because of the advantages of recombination (since the "effective" recombination rate decreases as selfing increases). Multilocus simulations representing the spread of beneficial alleles at multiple loci and the evolution of a selfing modifier locus indeed indicate that low rates of outcrossing are generally maintained when selfing evolves to high rates, these low rates of outcrossing increasing with the fitness variance at selected loci. However, the spread of beneficial alleles may also cause transitions from outcrossing to high selfing, in particular when beneficial alleles tend to be recessive. Patrice David (CNRS Montpellier) presented theoretical and experimental results (both in the field and in the lab) on the evolution of selfing in hermaphroditic snails (*Physa acuta*). In this species all individuals may self-fertilize, but do so only after a given waiting time, if mates are unavailable. This waiting time (which determines the selfing rate) is heritable and can rapidly respond to selection (both in natural and laboratory environments); furthermore, it coevolves locally with the magnitude of inbreeding depression. Stephen Wright (University of Toronto) presented a genomic analysis of the consequences of the recent shift (< 200,000 years) from outcrossing to selfing in the angiosperm *Capsella rubella*. The data show evidence of an ongoing relaxation of selection in *C. rubella* (compared with its outcrossing sister-species *C. grandiflora*), which seems caused by a reduction in the effective population size in the selfing species. Séverine Vuilleumier (University of Lausanne) presented theoretical models exploring different scenarios for the transition between self-incompatibility systems involving 2 loci to systems involving a single locus (a transition that occurred multiple times in fungi). A first scenario involves linkage between the two loci, while a second involves the loss of function of one of the two genes. The transition occurs more easily under the second than under the first scenario. Sylvain Glémin (CNRS Montpellier) showed theoretical results on the effects of selfing on rates of adaptation, probabilities of extinction of populations following a change in environment, and interference between selected loci. Probabilities of fixation from standing variation generally decrease as selfing increases, while the genetic basis of adaptation is little affected by the dominance of mutations under selfing. Furthermore, selfing increases the probability that deleterious mutations hitchhike with beneficial alleles, generating a "cost of adaptation". Vincent Castric (CNRS Lille) presented a genomic study elucidating the basis of dominance interactions between self-incompatibility alleles in *Arabidopsis halleri*, showing that dominance is mediated by a repertoire of small regulatory RNAs coevolving with their target

sites (and providing one of the first examples of mechanism for the evolution of dominance interactions). Emmanuelle Porcher (MNHN Paris) presented different models for the evolution of selfing rates, incorporating both genetic effects (automatic transmission advantage of selfing, inbreeding depression) and ecological effects (pollen limitation, pollen discounting, geitonogamy). These models can explain the maintenance of mixed mating systems (involving both outcrossing and selfing), which cannot be explained from purely genetical models. Takashi Tsuchimatsu (Gregor Mendel Institute, Vienna) presented different studies involving genomics and laboratory crosses, demonstrating that the loss of self-incompatibility in *Brassicaceae* is due to the degradation of the male component of the self-incompatibility system. This result is consistent with theoretical predictions showing a stronger advantage of mutations in male components. Finally, Xavier Vekemans (University of Lille 1) presented genomic results on the consequences of whole genome duplication on the evolutionary dynamics of the self-incompatibility locus (S-locus) in *Brassicaceae*. In several cases, duplication was followed by a temporary loss of self-incompatibility, followed by the re-establishment of SI at a different genomic location and the quick increase in diversity at this new S-locus by negative frequency-dependent selection.

Session 4: The evolution of sexual differentiation

This session dealt with the evolution of genders and sexual systems (hermaphroditism vs. dioecy, gynodioecy or androdioecy), the evolution of anisogamy and male-female differentiation. Spencer Barrett (University of Toronto) gave an overview of biological correlates of sex ratio biases in flowering plants. In particular, female bias is associated with sex chromosomes, which may be explained by different competitiveness of X and Y pollen during gametophytic selection (certation hypothesis). Studies on two *Rumex* species confirm this hypothesis, showing that pollination intensity and male proximity influence progeny sex ratios. Finally, a study on *Sagittaria latifolia* was presented, showing a variation of gender strategies across space, with hybridization between hermaphroditic and dioecious populations generating sub-dioecious populations. John Pannell (University of Lausanne) presented recent studies on the annual plant *Mercurialis annua* (in which the sexual system varies from dioecy through androdioecy to hermaphroditism) showing the importance of the evolution of sexual dimorphism in the evolution of gender strategies, and illustrating that mate limitation may render dioecious populations more vulnerable to the invasion of unisexuals. Lukas Schärer (University of Basel) proposed the idea that local sperm competition (competition between related male gametes) may be ubiquitous in nature and may limit the increase in male fitness with the number of gametes produced, thereby limiting the evolution of anisogamy and triggering the evolution of male secondary sexual characters. Richard Cordaux (CNRS Poitiers) showed that in the isopod *Armadillidium vulgare*, sex is often determined by cytoplasmic, feminizing endosymbionts (*Wolbachia*) while in some populations, a large piece of the *Wolbachia* genome has been transferred to the nucleus and determines sex (nuclear sex determination). Lynda Delph (Indiana University) presented a variety of experiments (using different approaches) highlighting the genetic architecture of sex differentiation in the dioecious plant *Silene latifolia*. Artificial selection experiments showed that sexually dimorphic traits, as well as between-sex correlations can respond to selection. QTL analyses showed that an important proportion of loci involved in such traits map on the sex chromosomes. Furthermore, quantitative genetics analyses of natural populations indicate that flower size is under stronger selection in males than in females. Tatiana Giraud (CNRS Orsay) presented general arguments and a theoretical model on the role of species selection on the maintenance of sex; she also presented a review of theory and data on the evolution of mating types in fungi, and recent results relative to the evolution of dimorphic mating-type fungal chromosomes. Sylvain Mousset (University of Lyon 1) demonstrated a pitfall in the

method of sister-clade comparisons, which had been previously used to conclude that dioecy may correspond to an evolutionary dead-end in Angiosperms. Indeed, the waiting time for the derived state (dioecy for example) is not taken into account in these previous analyses. Using a new method that takes into account this waiting time leads to the opposite conclusion: dioecious clades actually diversify faster than their sister clades. Finally, Christoph Haag (CNRS Montpellier) presented new results on sex determination in *Daphnia magna*. Although sex is usually determined by the environment in this species, some lines never produce males. This trait is coded by a single chromosomal region which exhibits strong suppression of recombination. Interestingly, recombination is also suppressed in the same region in the other lines (with environmental sex determination), indicating that the sex-determining mutation may have occurred in a genomic region in which recombination was already suppressed.

Session 5: The evolution of sex chromosomes

Judith Mank (UCL London) presented recent studies on sexual dimorphism in birds. Gene expression differs at many loci between males and females; furthermore, exaggerated male traits are correlated with higher expression of thousands of male-biased genes, although the magnitude of overexpression is small at each gene. Analysis of selected lines of poultry show that W chromosome expression responds to female-specific selection, and that relaxed female-specific selection affect W genes more than other genomic regions. Max Reuter (UCL London) presented data on sexual antagonism in *Drosophila*: analysis of a population separated for about 180 generations from a base population in which sexual antagonism had been shown (negative correlations between male and female fitnesses) demonstrated the loss of sexual antagonism. Genomic analyses will be performed to investigate the genetic basis of this evolutionary change. Deborah Charlesworth (University of Edinburgh) gave an overview of recent results on the evolution of sex chromosomes in plants, focusing on silene and papaya. Evidence for strata (of dS) was presented (in *S latifolia* and papaya), suggesting several events of loss of recombination; however, dioecious relatives of papaya may not have evolved recombination suppression. There is evidence for some Y degeneration in *S latifolia* (lower gene expression, higher K_A/K_S values); however, gene expression in the pollen may limit degeneration. In general, the cause of X-Y heteromorphism (deletions, accumulations of transposable elements) is still not well understood. Julie Jaquiéry (INRA Le Rheu) presented a model showing that the particular inheritance of X chromosomes in aphids should generate an accumulation of sexually antagonistic, male beneficial alleles on the X, while female beneficial alleles should accumulate preferentially on autosomes. Gene expression data fit the model predictions, with more male-biased genes on the X and more female-biased genes on autosomes. Sarah Otto (UBC Vancouver) presented theoretical results showing that certain forms of selection can maintain recombination on sex chromosomes, namely when an allele that is beneficial for daughters tends to be found at higher frequency on the X (which requires overdominance in males). Other forces may maintain recombination on sex chromosomes, such as selection for proper disjunction or Hill-Robertson interference. Doris Bachtrog (UC Berkeley) presented new results showing that the dot chromosome of *Drosophila* was ancestrally a differentiated X chromosome: genes located on the dot chromosome are X-linked in outgroup species while *Drosophila* X-linked genes are autosomal. This explains several puzzling aspects of the biology of the dot chromosome. Results relative to the evolution of sex chromosomes in ratite birds (showing limited suppression of recombination) were also presented. Susana Coelho (CNRS Roscoff) showed that sex in the model brown alga *Ectocarpus* is determined by large, non-recombining chromosomal regions that are highly divergent between male and female. Some signs of genetic degeneration are observed (high frequency of transposable elements, lower frequency of optimal codons). The limited expansion of the sex-determining region may be explained by the low level of sexual

dimorphism in this species. Nicolas Perrin (University of Lausanne) reviewed recent data on sex chromosomes in amphibians, showing that sex chromosomes are rarely heteromorphic, due to 2 mechanisms: rare recombination events between the X and the Y (demonstrated in *Hyla arborea*), and frequent turnover of sex chromosomes (demonstrated in ranid frogs). In this last case, it seems that some chromosomes are co-opted more frequently to become sex chromosomes (possibly because they carry important genes for sex differentiation). Brian Charlesworth (University of Edinburgh) presented results on the evolution of regions with reduced recombination in the *Drosophila* genome. These regions consistently show lower levels of neutral variation, and higher rates of protein sequence evolution. Analyses of non-synonymous site variation suggests that this last effect corresponds to the fixation of weakly deleterious mutations, and that adaptive evolution is reduced in these genomic regions. Quantitative patterns are consistent with a scenario involving Hill-Robertson interference between large numbers of weakly selected sites. Bengt Hansson (Lund University) presented an analysis of a neo-sex chromosome in passerine birds, showing a lower genetic diversity on neo-Y genes, moderate synonymous and weak non-synonymous divergence between neo-Z and neo-W and lower GC content on the neo-W than on the neo-Z, confirming hypotheses on neo-sex chromosome evolution. Gabriel Marais (CNRS Lyon) presented results on Y chromosome degeneration in the dioecious plant *Silene latifolia*. Comparisons between X and Y BACs show that the Y chromosome has lost 20-40% of its genes; the rate of gene loss is comparable to what is known in *Drosophila*. Furthermore, RNA-seq data indicate lower rates of gene expression on the Y, while X-linked expression increases as Y-linked expression decreases, indicating X dosage compensation. Finally, John Malone (Florida State University) presented analyses of gene expression in engineered *Drosophila* in which gene dose was reduced from two to one. Expression was reduced compared to the wild-type, but the response was gene-specific and highly heterogeneous. Dosage compensation is thus a gene-specific response, largely mediated by interactions with the rest of the transcriptome.

Conclusion and perspectives

We think that the conference has met its initial objectives in providing a general overview of the latest developments of research on the evolution of genetic systems, establishing links between different research questions (e.g., T Lenormand's presentation on gene expression and the evolution of recombination, or A Agrawal's presentation on recombination and the evolution of selfing rates), illustrating the importance of the different types of approaches used (quantitative genetics, genomics, field studies, comparative phylogenetics, mathematical modelling...) and the power of recent methods (genomics in particular). Many of the participants declared that a conference covering these different topics was extremely useful and timely, and that the overall quality of the presentations was outstanding. Invited speakers were present during all sessions and easily accessible; the poster sessions were both very interactive. All participants agreed that organizing another conference on the same topic in a few years would be extremely useful. Tanja Schwander agreed to become the president for this next conference, and Thomas Lenormand (CNRS Montpellier) to be the vice-president. A general suggestion for the next conference is that the overall number of oral presentations could be reduced, in order to leave more time for questions and general discussions.

Finally, we would like to stress that the CNRS staff for the Jacques Monod conferences (Nathalie Babic, Alain Paoli) have been extremely helpful during the preparation and the course of the conference.