

## Ongoing work

**Our team increasingly uses approaches of comparative genomics and population genomics, with the aim of studying the genomic mechanisms generating new species and allowing adaptation, using as models the events of rapid adaptation and diversification in plant pathogenic fungi, domesticated fungi, and domesticated plants.**

**We currently develop studies of comparative genomics and population genomics to study parallel adaptation of *Penicillium* species used for the fermentation of sausages (*P. salami* and *P. nalgiovense*). As for the cheese *Penicillium* fungi (see past achievements), they represent cases of parallel, recent and rapid adaptation events, in two phylogenetically distant lineages, on the same new human-made medium, rich in salt, lipids and proteins. We are carrying out experiments to test the existence of differentiated traits between the populations from sausage and those from other environments, which would indicate that an adaptation actually occurred. Using comparative genomics, we have detected very recent and specific horizontal gene transfers between the two *Penicillium* fungi used for the fermentation of sausages, and we are studying the functions of the genes they contain. We are also analyzing ca. ten genomes of each *Penicillium* species from cheese and sausage to study genetic diversity, to detect traces of selection, and to identify genomic regions involved in adaptation. We also develop approaches of genetic transformation to test the role of gene candidates identified in *Penicillium* fungi from cheese and sausage in the adaptation to the new human-made media.**

**We will also continue to develop our studies on the fungi used for cheese maturation to understand the genomic processes involved in the parallel adaptation of phylogenetically distant species to the same ecological niche.** We will in particular sequence the genomes of other species used for cheese maturation, phylogenetically distant to each other and to previously studied species. Thanks to the study of parallel adaptation events (of at least five independent lineages), our project will make it possible to test the existence of convergent adaptation events, to test if they occurred through shared genomic mechanisms and/or if the same traits/genes/genomic regions were targeted.

**We will also use approaches of comparative genomics to understand the mechanisms underlying adaptation and the formation of new species using as models the *Microbotryum* pathogenic fungi, causing the anther-smut disease sterilizing plants of the Caryophyllaceae family.** Indeed, there exists more than 100 species in this genus causing anther-smut disease, the various species being phylogenetically close but specialized on different host plants. There was thus an adaptive radiation, with specialization events on very different and well identified ecological niches, which makes it an excellent model to study the underlying genomic mechanisms of adaptation. We already obtained genome assemblies of exceptional quality for 20 pathogenic species of *Microbotryum* specialized on different plants. **This constitutes a unique material, making it possible to study poorly known processes, like the role of the gene gains and losses, chromosomal rearrangements, and localization in particular genomic regions.** Indeed, new sequencing technologies did not allow until one or two years ago to obtain information on the genomic structure, whereas it is essential to understand whether certain genomic areas, such as regions rich in transposable elements, telomeres, or chromosomal inversions, play a significant role in the processes of adaptation, by generating variability or by protecting beneficial association of alleles from recombination. **This constitutes a new frontier of research regarding the genomics of adaptation.**

**Another part of research in progress in the team relates to the study of the adaptive causes underlying the striking evolution of sex chromosomes, by again using fungi as useful eukaryotic models.** The sex chromosomes in plants and animals often show recombination

suppression (for example between X and Y in humans), which leads to differentiation and degeneration; for example, the Y chromosome is very small in humans, with very few genes and many repeated sequences. The current dominant theory to explain the suppression of recombination between the sex chromosomes in plants and animals, which often occurred in several successive steps (called evolutionary strata), is the existence of traits which are beneficial in males but deleterious in females, or conversely. There would then exist a selection to successively link the genes responsible for these traits to the sex-determinism genes. However, very little evidence of this process could be documented despite years of research. The fungi provide, here again, good models to test these hypotheses, because some have mating-type chromosomes with recombination suppression, whereas the mating types are not related to male and female functions. In fungi, the genes determining mating types control sexual compatibility, two haploid genotypes being compatible if, and only if, they have different alleles that mating-type genes, but without other different traits between the mating types.

The *Microbotryum* fungi were the first ones in which mating types were identified, at the beginning of the 20th century, and the first on which dimorphic mating-type chromosomes with suppressed recombination were described. For a long time, these chromosomes could not be assembled given their high quantity of repeated sequences. Thanks to the complete assembly of the *M. lychnidis-dioicae* genome that we have just obtained, we could show that the mating-type chromosomes are non-recombining across nearly 90% their length. Moreover, they present an exceptional degree of rearrangements and degeneration. Hundreds of genes were lost in one or the other mating type, and many deleterious changes were identified, in terms of replacement of amino-acids, sub-optimal gene expression or accumulation of transposable elements. Even more remarkably, we detected evolutionary strata on the mating-type chromosomes of *M. lychnidis-dioicae*, whereas there exist no male or female function in these fungi, all gametes displaying the same size. The mating-type chromosomes of *M. lychnidis-dioicae* thus present remarkable convergence with the sex chromosomes of plants and animals, despite lack of association with male and female functions. These results suggest that the dominant evolutionary theory explaining the evolution of sex chromosomes by differential optimal adaptation of males and females should be reconsidered. We are testing alternative hypotheses, such as a selection to shelter in a permanent heterozygous state the deleterious mutations which would accumulate in edges of the non-recombining regions. In addition, the unique material of extremely well assembled genomes of several *Microbotryum* species enabled us to show that the suppression of recombination has evolved many times independently and recently, by different chromosomal rearrangements, and with independent evolutionary strata. This is thus a case of remarkable evolutionary convergence, with likely a strong adaptive advantage, which we are trying to identify.

**Another axis of research which I develop with my team relates to the studies of introgressions between the cultivated apple tree and the European crab-apple tree, at the whole genome level, and on the adaptive or deleterious role of these introgressions.** Our recent work changed the view on the domestication of the apple tree and revealed a threat to the European crab-apple tree because of these introgressions (see “past achievements”). However, we had previously used only 35 genetic markers, in non-coding regions. We are now analyzing the sequences of the complete genomes apple trees. A first goal is to evaluate the importance of reciprocal gene flow between the domesticated apple tree *M. domestica* and the European crab-apple tree *M. sylvestris*, at the whole genomic level, both quantitatively and qualitatively. A second goal is to assess whether the European crab-apple tree contributed to traits selected by humans during domestication, such as disease resistance, climate or soil adaptation, or robustness. Reciprocally, we wish to determine if the introgressions of the European crab-apple tree by the domesticated apple tree threatens its persistence, or if in contrast they fostered adaptation, or if they are neutral. More generally, we wish to contribute to understand the evolutionary genomic processes of adaptation that occurred during

domestication. **These questions are to the forefront of evolutionary biology and have applied consequences, in terms of conservation of endangered species and varietal improvement.**

**In addition, we are collaborating with an INRA team (C. Lemaire, Angers) to study the consequences of the domestication of the apple tree on the fungus responsible for apple scab, *Venturia inaequalis*, by sequencing multiple genomes of various areas in Europe and Asia and various apple species. This is also a good model to understand the rapid adaptation to a new environment: the fungus responsible for the scab tree differentiated while adapting to the domestication of its host, and there exists several differentiated populations hybridizing in the zones of secondary contact between the various hosts. The fungal population on the cultivated apple tree appears more aggressive and more generalist than the populations on crab-apple trees. **Again, this is thus a good model to understand rapid adaptation to an anthropized environment and the generation of the biodiversity.****