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## Focus

### Ant(gen)omics – what we have and what we need!

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The advent of next generation sequencing techniques has provided the ant community with the unique opportunity to open the black box of "the" ant socio-genome but at the same time swamped the community with an amount of data that is unprecedented in the history of social insect research (BONASIO & al. 2010, NYGAARD & al. 2011, SMITH & al. 2011a, b, SUEN & al. 2011, WURM & al. 2011). How will we analyze the onslaught of data and go beyond correlative research? How many more ant genomes do we need and which genomes should we prioritize? How will the field of myrmecology change and which research skills will future myrmecologists need? Finally, what can ant sociogenomics contribute to our understanding of the evolution and organization of ant societies in particular and genome evolution and gene regulation in general?

Within the next five years it will be feasible to include the costs of sequencing the genome, transcriptome and proteome of any individual ant species into a regular grant application. In fact there is concern that the accumulation of sequence data will soon outpace computer storage capacities (PENNISI 2011). At a recent meeting on social insect genomics organized by the Beijing Genomics Institute in Shenzhen, China a discussion among myrmecologists resulted in a prioritized list of about 40 ant species to be sequenced next (for the list see <http://ldl.genomics.org.cn/page/showinsects.jsp>).

However, here is the first roadblock for the keen investigator whose ant species has been sequenced: How can one access, process and analyze those data without the necessary training in bioinformatics? There are currently two approaches to solve this problem. First, the formation of a loose collaboration of individual researchers who have specialized in specific tasks and developed pipelines to assemble and annotate genomes or analyze specific gene families (= consortium). This has worked very well for many genomes in the past, but this might be problematic in the future because the experts are few and usually swamped with requests. A second approach is to hire one or two bioinformaticians and / or train graduate students. This might take some time but assembly, annotation and genome analysis programs will (hopefully) become more user friendly. The advantage of this second approach is that individual researchers will become less dependent on outside experts and more familiar with the genomics and transcriptomics data of their organism. The disadvantage is that it will

take much longer and the quality of the data and analyses may be more variable and sometimes questionable.

Assembly and annotation of an ant genome are the first steps in sociogenomics. Once a genome is annotated it can be compared to other genomes to determine what part is shared with other ants, social Hymenoptera, social insects, solitary insects or animals in general. Comparative genomics is a powerful approach and the seven published ant genomes are already providing important insights. For example, the gene families associated with chemical communication both generating (e.g., desaturases) and receiving (e.g., olfactory receptor proteins = Or) chemical signals or cues have been expanded extensively in comparison to solitary insects or the honey bee (e.g., SMITH & al. 2011a, b). These expansions probably reflect the elaborate use of chemical communication in ants. Communication is a hallmark of insect societies and a necessary part of the colony organization and regulation, e.g., by enabling colony recognition, caste determination (in the sense of when to produce reproductive brood and what sex ratio or minor-to-major-worker ratio should be produced), or nest building. Comparative genomics is however only one way to exploit the genome sequence. The other approach is to determine the genetic architecture (genes, gene effects, gene interaction) and regulation (expression, interaction between environment and gene expression) of social traits, although in many cases this will require additional data outside of the genomic sequence alone. Knowing the genetic basis underlying the signals involved in colony recognition, caste determination or nest building opens new possibilities to manipulate (e.g., by experimental gene knockdown using RNA interference) and finally better understand the mechanistic basis of communication in ant societies.

Reproductive and non-reproductive caste determinations are the two most prominent traits that characterize social insects. Although all ants or even all social Hymenoptera may share some common pathways or signaling cascades in determining caste (e.g., insulin signaling pathways, vitellogenin or juvenile hormone), the primary caste determination signal / trigger that determines which egg will develop into a queen, small or large worker differs dramatically between taxa (e.g., genetic versus environmental caste determination in *Pogonomyrmex barbatus*). This might turn out to be similar to the sex-determination system in insects, where many different primary sex determination signals exist (e.g., haplodiploidy, XY, WZ), but all feed eventually into the conserved sex-specific developmental pathways. Ants are ideal model organisms to study proximate and ultimate mechanisms of caste determination due to their high diversity in social organization and already known differences in proximate caste determination and developmental mechanisms (ABOUHEIF & WRAY 2002). For example, WURM & al. (2011) found that in *Solenopsis invicta* the number of vitellogenin genes has increased compared to the honeybee and other solitary insects. The different vitellogenin genes are also expressed in a caste-

specific manner which indicates a different way of regulation compared to the honeybee, where the single vitellogenin gene is up- or down-regulated in different castes. It is yet unclear whether this is causally involved in caste determination or related to differences in caste function. However, a logical next step would be to analyze the effect of individual vitellogenin-gene knockdowns on larval development.

In general, once we have identified the genes or proteins that determine a certain phenotype we can start to link the environmental, physiological or epigenetic factors that are employed in the regulation of these phenotypes. Once we understand how caste determination is organized in one ant species we can start to study and reveal the evolutionary changes that were necessary to develop different caste determination mechanisms. This will also shed light on the transition from a solitary to a social life style.

The phenotypic plasticity exhibited by all ant species and developed to an extreme in some leafcutter or army ants, or the intricate division of labor between workers of a leafcutter ant colony demonstrate that ant genomes have mastered the art of gene regulation to a degree rarely encountered in other animals. The first ant genomes have already provided an interesting glimpse into the diversity of these regulatory mechanisms but this is probably only the tip of the iceberg. For example DNA methylation, histone modification and caste- and stage-specific microRNA expression has been demonstrated in multiple ant genomes (BONASIO & al. 2010, SMITH & al. 2011a, b, SUEN & al. 2011, WURM & al. 2011).

The things we will learn following the approaches outlined above will have a broader impact on our understanding on how the genome and environment interact to produce an adaptive phenotype, the role of regulatory versus structural gene or genome changes in the evolution of novel phenotypes, and the genetic and regulatory basis of behavioral variability. These areas are already developed for the honeybee model organism but the social plasticity (i.e., colonies grow from a single founding queen to a colony with thousands of workers) and social variability (e.g., in colony size, composition and organization) of ants make them the ideal comparative model organism to study social complexity and organization. Ant genomics has already been implicated in biomedical research on aging, adiposity or behavioral disorders. It is clear that the next generation of myrmecologists that want to contribute to our understanding of the proximate and ultimate mechanisms

that rule insect societies need to become familiar and acquire skills in bioinformatics. However, they still need to know their ants, i.e., a deep understanding of the life history, behavior, physiology, anatomy, etc. of the study organism is essential to interpret the genomic data correctly and ask the right questions.

The advantage of having genomic data at disposal to resolve the ant tree of life comes in the form of the ability to choose the most suitable genes from an organism's entire gene set, i.e., those with clear orthology relations and the least level of saturation at the phylogenetic depth under investigation. Along similar lines, full gene repertoires may also be explored to identify genes evolving in clock-like fashion. This could improve divergence time estimates and help resolve the current controversy surrounding the timing of early cladogenetic events within ants.

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