

Sociogenomics Takes Flight

Gene E. Robinson

These are good times for research on social insects. The social Hymenoptera—ants, bees, and wasps—are emerging as valuable models for the study of molecular processes (1). The honey bee *Apis mellifera*, a social insect, has just been selected by the NIH's National Human Genome Research Institute to be among the next group of organisms to have its genome sequenced (2). Genes that are important for the organization of ant (3) and bee (4) societies have been identified during the past year, and the development of genomic resources such as expressed sequence tags and microarrays (5, 6) is quickening the pace of discovery. Some of the genes that are differentially regulated during the development of worker and queen honey bees have been identified (7), and provocative findings hint at even stronger genetic influences on caste determination in ants (8, 9). On page 249 of this issue, Abouheif and Wray (10) now formally welcome ants into the vigorous field of “evo-devo” with a fascinating description of changes in gene expression that are associated with the evolution of the wingless worker caste.

Winglessness in ants is part of a polyphenism, which can be defined as the “occurrence of several distinct phenotypes or forms in a given species, each of which develops facultatively in response to some cue from the internal or external environment” (11). Polyphenism is not limited to invertebrates, and accounts for some of the remarkable flexibility seen in life forms, including fish that switch sexes in response to changes in their social environment (12). Polyphenism has figured prominently in the evolution of one of the defining features of insect societies: a division of labor for reproduction.

Eggs of female social Hymenoptera can develop into either queens or workers (see the figure). Queens specialize in reproduction, whereas workers engage in little or no reproduction and perform all tasks related to colony maintenance and growth (13). A colony of social insects may have just one or a few queens but from tens to millions of workers. In many insect societies, there are profound morphological differences between queens and workers. For example, queens have huge ovaries and often lay thousands of eggs per day, whereas workers may completely lack ovaries. There are also morpho-

logical differences among worker castes in many species of ants, which reflects a further division of labor. Smaller workers care for the brood, whereas larger individuals become highly specialized as “soldiers” with powerful jaws and potent toxins.

Insects were the first group of animals to fly, more than 100 million years before reptiles and birds, and this trait is widely seen as a key evolutionary innovation underlying their spectacular success. Ant queens initially have wings but shed them after mating when they begin to establish a new colony. Workers, in contrast, are born completely wingless. This evolutionary reversal is thought to have given ants the mobility to search more efficiently for insects and other food sources in the ground, and thus figures prominently in their overwhelming ecological dominance (these tiny creatures constitute 10 to 15% of the entire animal biomass in most terrestrial environments) (14). With all known ant species sporting wingless workers, as well as some telling fossil finds (see the figure), ant specialists believe that worker ant winglessness evolved only once (10).

Abouheif and Wray (10) compared gene expression profiles during development of the queens and workers of several ant species. Their study draws on an elegant body of work (15) that has elucidated a hierarchical gene network underlying wing development in the fruit fly *Drosophila melanogaster* and other insects. These authors studied the expression of six wing development genes—*ultrabithorax* (*Ubx*), *extradenticle* (*exd*), *engrailed* (*en*), *wingless* (*wg*), *scalloped* (*sd*), and *spalt* (*sal*)—in the ant *Pheidole morrisi*. Meanwhile, they analyzed expression of *Ubx*, *exd*, and *en* in the ant species *Myrmica americana*, *Crematogaster lineolata*, and *Neomormica*

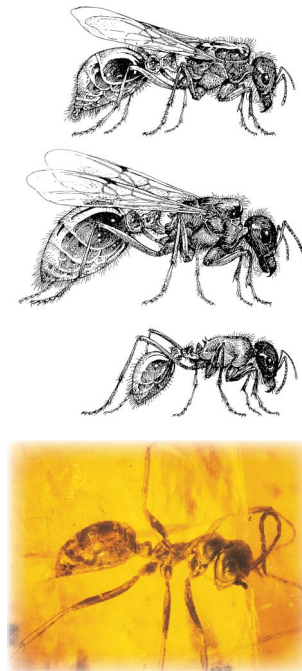
(*Formica*) *nitridiventris*. For queens, the results were straightforward: Wing development genes highly conserved in other insects showed the expected expression patterns in all

four species. (The same result was obtained for males, which also are winged.) For workers, the results were surprising. Expecting winglessness in the four ant species to be associated with a break at the same node of the genetic network, Abouheif and Wray instead observed different gene expression patterns in different species. For example, wing development in *C. lineolata* and *N. nitridiventris* workers was shut down toward the end of the process (no expression of *en*), but in *P. morrisi* workers the break occurred much more upstream, with no expression detected of any of the six genes. In *P. morrisi* soldiers, by contrast, five of the six genes showed normal expression and only *sal*, the most downstream gene examined, was silent, demonstrating differences in gene expression even for workers and soldiers of the same species.

Why are there such broad variations in a trait that is thought to have evolved just once? Abouheif and Wray suggest that, after the wing development gene network was inactivated in a basal lineage, either a neutral evolutionary process or natural selection (perhaps related to pleiotropy) could

have acted in different species to change when wing development is halted. They also speculate that similar evolutionary lability underlies other polyphenisms, making it risky to generalize about molecular pathways on the basis of data from a single species. Their results provide a good example of how different genomes can achieve the same end in different ways, thus highlighting the importance of comparative genomics.

The heightened interest in social insects reflects the sense that the time has come to develop a comprehensive understanding in molecular terms of social life: how it evolved, how it is governed (16, 17), and how it influences all aspects of genome structure, gene expression and organismal development, physiology and behavior (18).



Winging their way to success.

Female ants can develop into either winged queens or wingless workers. Drawings depict a winged virgin queen (middle), a wingless worker (bottom) and a winged male (top) of the American harvester ant, *Pogonomyrmex barbatus*. Fossil evidence, such as this specimen in amber, indicates that winglessness evolved just once in the ants. Shown is a worker ant (subfamily *Sphecomyrminae*) in sequoia amber formed about 80 million years ago during the Upper Cretaceous. [Reproduced from (22) with permission]



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The nascent field of sociogenomics is predicated on two of the most significant ideas in biology to emerge from the latter half of the 20th century. First, many aspects of social life, including social behavior, have a biological basis and are thus influenced to some extent by genes and the forces of evolution (13). Second, the functions of many genes are highly conserved between invertebrates and vertebrates even for complex traits (15), so that much can be learned from strategically chosen models. Appropriately, social insects and developmental biology, the subjects of Abouheif and Wray's (10) paper, contributed profoundly to these hard-won insights.

Paradoxically, elucidation of the molecular biology of insect sociality is now possible because of a plethora of information about a nonsocial insect, *Drosophila*, as well as powerful new genomics techniques. This endeavor draws on rich traditions of research on social insects from the perspectives of evolutionary biology, ecology, ethology, neurobiology, and development, as the study by Abouheif and Wray (10) so nicely illustrates. The sequencing of the honey bee genome will provide a foundation for com-

parative analysis and facilitate gene identification in other social insect species. It will boost sociogenomics enormously and further enhance the value of social insects as models in diverse fields of biology.

By now, you're probably muttering that the only topic for which social insects have not been promoted in this article is world peace. In fact, I don't have to, because *The New York Times* (19) already did! In their news story entitled "A lesson in détente from the insect world" they discuss Giraud *et al.*'s (20) remarkable work on the Argentine ant *Linepithema humile*. This creature, normally a highly territorial species in its native habitat in South America, has in some parts of Europe become quite tolerant of individuals from other nests, forming a loose confederation that extends at least 6000 km and consists of millions of nests comprising billions of workers. Behavioral and genetic analyses suggest that here is a case where it might actually pay a society to fight less often with its neighbors. Politicians, but more importantly molecular biologists, would do well to "Go to the ant..."—and its cousins—and "consider her ways" (21). There is much to learn.

References

1. R. E. Page *et al.*, *Genetics* **160**, 375 (2002).
2. www.nhgri.nih.gov/NEWS/sequencing.html (2002).
3. M. J. Krieger, K. G. Ross, *Science* **295**, 328 (2002).
4. Y. Ben-Shahar *et al.*, *Science* **296**, 741 (2002).
5. C. W. Whitfield *et al.*, *Genome Res.* **12**, 555 (2002).
6. R. Kucharski, R. Maleszka, *Genome Biol.* **3**, RESEARCH0007 (2002).
7. J. D. Evans, D. E. Wheeler, *Genome Biol.* **2**, RESEARCH0001 (2002).
8. G. E. Julian *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **99**, 8157 (2002).
9. V. P. Volny, D. M. Gordon, *Proc. Natl. Acad. Sci. U.S.A.* **99**, 6108 (2002).
10. E. Abouheif, G. A. Wray, *Science* **297**, 249 (2002).
11. H. F. Nijhout, *Insect Hormones* (Princeton Univ. Press, Princeton, NJ, 1994).
12. R. D. Fernald, *Novartis Found. Symp.* **244**, 169 (2002).
13. E. O. Wilson *Sociobiology: The New Synthesis* (Belknap, Cambridge, MA, 1975).
14. B. Hölldobler, E. O. Wilson, *The Ants* (Belknap, Cambridge, MA, 1990).
15. S. B. Carroll, J. K. Grenier, S. D. Weatherbee, *From DNA to Diversity: Molecular Genetics and the Evolution of Animal Design* (Blackwell Science, Malden, MA, 2001).
16. G. E. Robinson *et al.*, *BioEssays* **19**, 1099 (1997).
17. G. E. Robinson, *Trends Ecol. Evol.* **14**, 202 (1999).
18. G. E. Robinson *et al.*, www.nhgri.nih.gov/DER/Sequencing/proposal.html (2002).
19. H. Fountain, "Ideas & trends: united we expand; a lesson in détente from the insect world," *New York Times*, *Week in Review*, 21 April 2002, p. 5.
20. T. Giraud *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **99**, 6075 (2002).
21. Proverbs 6: 6.
22. B. Hölldobler, E. O. Wilson, *Journey to the Ants* (Harvard Univ. Press, Cambridge, MA, 1994).

PERSPECTIVES: APPLIED PHYSICS

Squeezing X-ray Photons

Till H. Metzger

Almost 150 years ago, Maxwell formulated the equations that govern electromagnetic wave propagation. The equations predict that in materials in which the index of refraction changes in a stepwise fashion, a discrete set of modes should be observed. The polarization, shape, and amplitude of these modes or "guided waves" can be controlled through the design of the waveguide.

Guided waves have found many uses, from efficient radiation sources to communication technology, but x-rays have proven difficult to control. On page 230 of this issue, Pfeiffer *et al.* (1) report an important advance toward using guided waves to create coherent hard x-ray beams with small spot sizes. These beams will help to decipher the structure and dynamics of nanometer-scale objects.

The art of guiding waves has been developed at different times for different parts of the electromagnetic spectrum. Cavity resonators of microwaves and radar were known long before the invention of lasers and optical fibers. Hard x-rays are the last frontier, requir-

ing interfaces perfect enough to support mode propagation and guiding of 0.1-nm radiation.

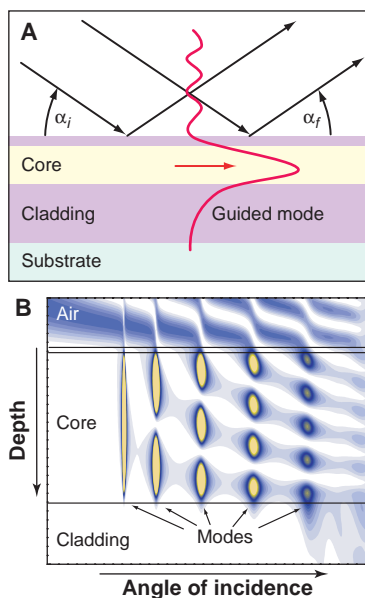
Such precision seemed impossible to achieve until Spiller and Segmüller demonstrated that x-rays can propagate in suitable planar thin-film structures (2). More recently, Feng *et al.* introduced the concept of resonant beam couplers (see the first figure) (3). These structures enable efficient coupling of x-rays into planar waveguides. A thinned surface cladding is used, thereby avoiding coupling of the beam through the front end. The latter would inevitably lead to large losses, because the diameters of available x-ray beams are orders of magnitude larger than the guiding layer.

The resonant beam coupler principle has boosted research into

x-ray waveguides, leading to new devices that could produce x-ray beams with submicrometer diameters (4, 5). New applications included diffraction with nanometer-sized beams (6) and phase contrast projection microscopy (7) (see the second figure). But all these efforts were limited to planar thin-film structures in which the beam is confined to one dimension. The most interesting applications require a two-dimensionally confined beam.

Pfeiffer *et al.* (1) now report the first proof of principle that resonant beam coupling can be realized in two dimensions. They show that x-ray reso-

nant beam coupling can be realized in two dimensions. They show that x-ray reso-



Resonant beam coupling. (A) In thin-film sandwich x-ray waveguide, resonant modes can be excited at certain grazing angles α_i in the waveguide channel (yellow) by coupling a parallel beam through the cap layer. The resonantly enhanced beam propagates parallel to the surface and exits at the edge of the structure. (B) Electrical field intensity as a function of incidence angle. A discrete set of modes (resonances) is observed in the waveguide, with the number of nodes and antinodes characteristic for the resonant wave propagation.

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