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Functional genetics and genomics in ants (Hymenoptera: Formicidae): The interplay of genes and social life

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Abstract

Ants are among the most remarkable and successful of animal taxa. The success of ants stems from their complex social systems, which originate, in part, from the genetic composition of individual society members. In this review, we evaluate progress in understanding how genetic information influences complex phenotypes in ants. We find that research on the structure of ant genomes has been strong in some areas, such as the exploration of chromosome number, genome size, and karyotype evolution. However, other areas of structural genomics concerned with gene number and genome content remain poorly studied. We also find that substantial progress has been made in successfully documenting genetic effects on phenotypic variation associated with ant social structure. For example, genetic variation influences sex determination in some ants and is associated with caste determination in several species. In addition, direct genetic control of queen and worker phenotypes has been discovered in some ant taxa. Advances have also been made in identifying genes whose patterns of expression are associated with ant social structure, development, and caste differentiation. Sufficient data are now available to address important questions regarding the relationship between the evolution of gene expression and phenotype. Finally, we review for the first time the growing sociogenomics literature in ants aimed at addressing the molecular bases for social life. Overall, substantial progress has been made in linking molecular genetic information to phenotypic variation in ants. However, many important research opportunities related to the molecular basis of complex phenotypes remain unexploited by the ant research community.

Key words: Caste, chromosome, evolution of development, genetics, gene expression, genomics, heritability, polyandry, polygyny, review, speciation.

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Introduction

Genes influence all biological processes. Every phenotypic characteristic displayed by an organism has some basis in its genetic composition. Moreover, phenotypic variation within and between species arises from genetic differences among individuals and populations. Consequently, a thorough appreciation of genetics is fundamental to understanding the diversity of life and the mechanisms underlying the success of biological entities.

Ants represent an important and fascinating group in which to investigate the relationship between genotype and phenotype. The importance of ants arises from several characteristics associated with their form, function, development, and evolution. First, distinct ant species display tremendous phenotypic differences (BOLTON & al. 2007). Thus, much can be learned about species differentiation by studying the genetic causes of phenotypic variation among ant taxa. Second, ants possess remarkable phenotypic diversity within species. In particular, the caste system that defines ants and other social insects represents a prime example of phenotypic plasticity, whereby the differential expression of genes leads to the production of divergent phenotypes (DEWITT & SCHEINER 2004, CARROLL 2005, SUMNER 2006). Consequently, studies of the molecular basis of ant castes will provide insight into how different phenotypes are generated from the same set of genes. Third, ants dominate terrestrial ecosystems by partaking in a variety of complex and unusual ecological interactions with conspecific and heterospecific taxa (e.g., group foraging behavior, social parasitism, mutualism; HÖLLDOBLER & WILSON 1990, BOURKE & FRANKS 1995, STADLER & DIXON 2005). Therefore, the study of the genetic mechanisms underlying ant interactions will lead to an understanding of how organisms come to be ecologically successful. Finally, and perhaps most importantly, ants are a critically important taxon in which to study the "molecular basis of social life" (i.e., sociogenomics; ROBINSON & al. 2005). The development of complex social behaviors displayed by ants originated from changes at the molecular level. Studies of such genetic changes can provide an understanding of how sophisticated group interactions arise from variation in genotype. Thus, while other social insect groups are worthy study subjects because they encompass taxa ranging from solitary to social, ants are of importance to the study of social behavior because they display a tremendous diversity of life histories and social patterns.

This review synthesizes recent research aimed at understanding the relationship between genotype and phenotype in ants. Our goal is to address the broad question of how gene function and genetic variation ultimately lead to divergent phenotypic characteristics in ants. Such research is critical to understanding the development of complex societies and behaviors that make ants successful.

Before proceeding with our discussion, however, it is important to describe what this review will not cover. First, this review does not incorporate studies that use genes as markers to address ecological or evolutionary questions (i.e., AVISE 2004). Genetic markers have been successfully used in hundreds of studies on ants to investigate questions related to breeding systems, population structure, kinship, and speciation (reviewed by BOURKE & FRANKS 1995, CROZIER & PAMILO 1996, PAMILO & al. 1997, ROSS 2001, STRASSMANN 2001, etc.). However, such investigations are generally not directly concerned with the functions of genes or the genetic causes of phenotypic variation. In addition, this review does not cover the extensive theoretical literature that attempts to explain the genetic underpinnings of complex social behavior (i.e., inclusive fitness theory; HAMILTON 1964, CROZIER & PAMILO 1996, LEHMANN & KELLER 2006). These theoretical issues do not directly address the function of specific, empirically-identified genes or genotypes. This review, in contrast, investigates how genes, genotypes, and patterns of gene expression affect phenotype. Hopefully, this review will help spur further research, ultimately elucidating the keys to the success of ants.

Structure and organization of ant genomes

Genome size: An appreciation of the structure of genomes is necessary for understanding gene regulation and evolution. Recently, TSUTSUI & al. (2008) completed a major investigation of the evolution of ant genomes by determining the genome size of 40 ant species across several of the major subfamilies. In addition, LI & HEINZ (2000) and JOHNSTON & al. (2004) estimated genome size in *Solenopsis invicta*, and ARON & al. (2005) determined genome size in *Camponotus lateralis*. Overall, the available data indicate that most ants have haploid genome sizes near 300 megabases (Mb), which is small relative to other insects. However, genome size among different ant taxa varies substantially, with relatively large genomes (400 - 600 Mb) occurring in ponerine ants compared to other ant species. Thus considerable evolution of genome size has occurred within the ants since their origin.

Recent research has revealed that other, unusual genome size variation may exist within ant species. While males are typically haploid and produced by unfertilized eggs, ARON & al. (2005) discovered that male tissues actually differ in ploidy level. Ploidy variation in male ants results from endoreduplication, whereby the genome content of cells increases in particular tissues (EDGAR & ORR-WEAVER 2001). Endoreduplication occurs in the muscle tissue of most male Hymenoptera and is possibly associated with increased metabolic demands of flight.

Genome content: Within eukaryotic genomes, a large proportion of DNA does not get translated into proteins. Some untranslated DNA sequences code for functional RNA molecules that assist in transcription, translation, or gene regulation. Recent studies in ants have made headway into understanding some of these non-protein coding regions. HIRAI & al. (1994, 1996) and OHNISHI & YAMAMOTO (2004) investigated the location of ribosomal DNA (rDNA) within the genome of *Myrmecia*. They discovered that regions containing rDNA undergo dispersion with increasing chromosome number. As a result, the number of chromosomes carrying rDNA increases as chromosome number increases within ant taxa.

Transposable elements make up a large proportion of eukaryotic genomes. Repetitive DNA, including transposable elements, has been noted in ants for some time (ROBERTSON & MACLEOD 1993, BIGOT & al. 1994, ROBERTSON 1997, LORITE & al. 2002c, 2002d, 2004, KRIEGER & ROSS 2003, PALOMEQUE & al. 2006). Research suggests that these elements are active and important contributors to genome size expansion in ants.

Finally, considerable interest has focused on understanding the telomeres of ant chromosomes (OKAZAKI & al. 1993, MEYNE & al. 1995, LORITE & al. 2002a). Telomeres shorten with cell division and are believed to be an important determinant of cell aging (MONAGHAN & HAUSSMANN 2006). JEMIELITY & al. (2007) made the remarkable discovery that telomeres of male *Lasius niger* ants were shorter than those of queens and workers. Telomere length in male *L. niger* ants is thus consistent with their relatively short lifespans.

Genome structure: Chromosome number and structure are important aspects of the genetic organization of a species because variation in chromosome structure can affect species diversification (KING 1993, COYNE & ORR 2004). Ants represent excellent taxa in which to investigate the effects of chromosomal changes on species diversity because the Formicidae contain so many species and a great deal is known about chromosome structure of ants. To this end, IMAI & al. (1988) reported that over 500 ant species had been karyotyped! Since that time, several groups have continued studying chromosome structure and number in ants. For example, a series of investigations have extended our knowledge of chromosome number across several major ant genera (IMAI & al. 1990, FADINI & POMPOLO 1996, LORITE & al. 1996, 1998, 2000, 2002b, YAMAUCHI & al. 2001, MARIANO & al. 2003, 2004a, 2006).

These investigations have uncovered remarkable diversity in ant chromosome number. For instance, the ant *Myrmecia croslandi* has the fewest number of chromosomes of any diploid species (2n = 2) (CROSLAND & CROZIER 1986, MAJER & al. 2004). The greatest number of chromosomes found in any hymenopteran species also resides within the Formicidae; the ant *Dinoponera lucida* possesses 2n = 106 chromosomes (MARIANO & al. 2004b). Moreover, IMAI & al. (1988) reported that diploid chromosome number ranged from 2 to 84 in the genus *Myrmecia* alone, noting that *Myrmecia* is "the most karyologically diverse of all animal genera, and the Formicidae one of the most diverse of all animal families" (IMAI & al. 1990).

Recent investigations have focused on understanding the effects that chromosome structure and number have on ant taxa. For example, BUSCHINGER & FISCHER (1991) investigated how chromosome polymorphism in the ant *Doronomyrmex kutteri* affects hybridization potential. They uncovered the surprising result that ants displaying different chromosome number could produce offspring that were fertile. IMAI & al. (1994, 2001) used the tremendous volume of information available on ant chromosome number to develop theory explaining changes in chromosome number. Their results indicate that chromosome number in ants increases due to fission of chromosomes. IMAI & al. further suggest that chromosome fission decreases potential problems associated with translocations and increases the potential for genetic divergence among species.

The rate of recombination between chromosomes is a critical determinant of the rate of evolution and adaptation within species (BUTLIN 2005). Recent studies have uncovered surprising results concerning the rate of recombination in ants. SIRVIO & al. (2006) discovered that recombination rates in both *Acromyrmex echinatior* and *Pogonomyrmex rugosus* were remarkably high relative to non-social taxa. High rates of recombination have also been uncovered in other social hymenopteran taxa, such as the bees *Bombus terrestris* and *Apis mellifera* (BEYE & al. 2006, WILFERT & al. 2006). Thus, recombination rates in social insects appear to rise above those in other animals, potentially facilitating the production of high levels of genotypic diversity among offspring. Increased genetic diversity may lead to increased colony success if genetic task specialization occurs among workers (FJERDINGSTAD & CROZIER 2006, OLDROYD & FEWELL 2007). Genetic diversity may also lead to greater resistance to disease (SCHMID-HEMPEL 1998, TARPY & SEELEY 2006). Thus the few available preliminary studies are consistent with the hypothesis that observed rates of recombination in social insect taxa have evolved in response to selective pressures associated with social lifestyles (WILFERT & al. 2007).

Genetic effects on ant phenotypic variation

Sex determination: The vast majority of Hymenoptera are haplodiploid (HEIMPEL & DE BOER 2008). Under haplodiploidy, haploid males are produced asexually by females, and females are produced sexually through the union of male and female gametes. In addition, sex is believed to be genetically determined in most social Hymenoptera. In particular, a single-locus complementary sex determination (sl-CSD) system has been proposed in many taxa (BEUKEBOOM & WERREN 2000), and has been identified as the primary mechanism for sex determination in *Apis* (BEYE & al. 2003). Under sl-CSD, individuals heterozygous at a sex determining locus develop into females, while haploid and hemizygous individuals develop into males (COOK & CROZIER 1995). Individuals that are homozygous at the sex determining locus also develop male phenotypes (COOK 1993), but these diploid males (if they survive at all) are generally sterile or produce sterile triploid offspring (COWAN & STAHLHUT 2004). Consequently, diploid males likely impart a serious load on the colonies that produce them (ROSS & FLETCHER 1986).

If sex is determined by sl-CSD, then either zero or fifty percent of brood should consist of diploid males after sib matings. Surprisingly, results of experiments conducted in ants such as *Plagiolepis pygmaea, Cardiocondyla obscurior,* and *C. batesii,* are not in line with these predictions (SCHREMPF & al. 2005, 2006, TRONTTI & al. 2005). All three species inbreed heavily under natural settings, with 83 % of all matings occurring between siblings in *C. batesii*. However, diploid males have not been detected in this taxon. Furthermore, extensive brother-sister matings in *C. obscurior* produced only a single diploid male. These data suggest that multiple loci may control the determination of sex in this species. Alternatively, diploid males may not develop sufficiently to be detectable or sex may not be determined through the CSD mechanism, as it is not universal among hymenopteran taxa (HEIMPEL & DE BOER 2008).

Worker-queen differentiation: The division of individuals into distinct castes is one of the hallmarks of advanced social insect societies. It has long been believed that the differences displayed by queen and worker castes result from environmental factors influencing developmental pathways (see below). Accordingly, environmental caste determination (ECD) has been theorized to be the only evolutionary stable mechanism for the maintenance of separate sterile and reproductive castes (QUELLER & STRASSMANN 1998). It is therefore surprising that several ants display genetic caste determination (GCD) in which the queen and worker castes belong to different genetic groups (reviewed by KELLER 2007, ANDERSON & al. 2008).

The best-described group displaying GCD is composed of *Pogonomyrmex* hybrid lineages found in the southwestern United States (HELMS CAHAN & al. 2002, JULIAN & al. 2002, VOLNY & GORDON 2002, HELMS CAHAN & KELLER 2003). Research has shown that queens and workers are sired by males belonging to genetically differentiated lineages. Further investigations have revealed that four pairs of complementary lineages exist throughout the southwestern United States (SCHWANDER & al. 2006). All four pairs of lineages are genetically isolated from each other and from the putative parent species. In fact, there is more genetic differentiation among the eight lineages than between the two *Pogonomyrmex* parent species.

Several studies have experimentally determined the costs associated with rigid GCD in *Pogonomyrmex* (JULIAN & al. 2002, HELMS CAHAN & al. 2004, 2006, ANDERSON & al. 2006b, SCHWANDER & al. 2006, VOLNY & al. 2006). For example, queens that mate with a high proportion of males from their own lineage are at a serious fitness disadvantage during colony founding. This disadvantage arises because queens are unable to regulate which castes they produce and intra-lineage offspring produced during colony founding do not develop into the workers necessary for successful colony establishment. Therefore, the total number of viable offspring decreases as the total number of intra-lineage offspring increases. Because queens must mate with at least one male from each genetic lineage in order to produce both workers and queens, the *Pogonomyrmex* system of caste determination leads to obligate polyandry.

Putative genetic mechanisms underlying *Pogonomyrmex* GCD have received some theoretical attention. VOLNY & GORDON (2002) proposed that zygosity plays a role in caste determination through the effects of a single genetic factor. HELMS CAHAN & KELLER (2003) proposed a more elaborate model and suggested that interspecific hybridization was responsible for the origin of the system. A third model proposed by LINKSVAYER & al. (2006) is based on interactions between nuclear and cytoplasmic genes. A fourth model returns to single-locus theory, but suggests a mutational origin of GCD rather than a hybrid one (ANDERSON & al. 2006a). Further work is necessary to determine which of these models, if any, are responsible for the presence of unusual, interdependent lineages found in *Pogonomyrmex*.

At least one other ant hybrid displays some type of GCD (HELMS CAHAN & VINSON 2003). *Solenopsis xyloni* hybridizes with *S. geminata* in certain regions of the United States. In hybrid zones, workers result from matings between *S. xyloni* queens and *S. germinata* males, while queens are produced by conspecific *S. xyloni* matings. This system appears similar to that of *Pogonomyrmex* and may represent the early stages of obligate hybridization.

Systems indicative of GCD have been discovered in several other ant taxa. PEARCY & al. (2004) found that *Cataglyphis cursor* queens are produced parthenogenetically by their queen mother, while workers result from sexual reproduction. Genetic studies investigating zygosity levels in queens and workers suggest that gynes are produced by automictic parthenogenesis. In the ants *Wasmannia auropunctata* and *Vollenhovia emeryi*, unusual reproductive mechanisms have also been discovered (FOURNIER & al. 2005, OHKAWARA & al. 2006). *Wasmannia auropunctata* and *V. emeryi* workers are sexually produced, while queens are produced parthenogenetically. Moreover, males are not produced parthenogenetically by their mother, as is typical in other ants. Remarkably, males are instead genetically identical to their father and may be produced by the elimination of the maternal genome from diploid zygotes.

Recently, HUGHES & BOOMSMA (2008) uncovered a case of "genetic cheating" in the leaf-cutter ant *Acromyrmex echinatior*. In this species, unlike the above-mentioned cases, GCD does not appear to be the product of hybridization or parthenogenesis, but rather the result of some patrilines producing more queen-destined offspring than workers. Thus, in this case, patrilines appear to vary in threshold response to environmental cues linked to caste development.

In all cases of GCD, the exact mechanisms underlying caste determination remain unclear. Nevertheless, these systems demonstrate that ECD is not the only evolutionary stable system by which insect societies can be maintained. Therefore, GCD poses the intriguing question: How many different ways can genotype influence caste in social insects?

Queen polymorphism: Several ant species are known to have a polymorphic queen caste. Variation in queen phenotype is often associated with alternative dispersal strategies during colony founding. For example, large queens disperse farther than their smaller, sometimes wingless, counterparts. Phenotypic variation observed among queens is believed to originate from environmental variation in many taxa (RÜPPELL & HEINZE 1999). However, in the ants *Harpagoxenus sublaevis*, *Leptothorax* sp. A, *Myrmecina graminicola*, and *Monomorium* sp. 10, queen polymorphism may have a genetic basis (WINTER & BUSCHINGER 1986, HEINZE & BUSCHINGER 1989, 2005, FERSCH & al. 2000, BUSCHINGER & SCHREIBER 2002). In these taxa, queens develop into either winged gynomorphs or wingless worker-like intermorphs (also known as ergatomorphs in *H. sublaevis*). Breeding experiments demonstrate that both morphs can be produced either by intermorphs or gynomorphs. However, gynomorphs result only from the mating of a gynomorph with a gynomorph-produced male. This result raises the possibility that gynomorphs are homozygous at a hypothetical genetic locus. Intermorphs, in contrast, can be produced through any other mating combination. Thus intermorph offspring are either heterozygous or homozygous for an intermorph allele at the hypothetical locus, suggesting the action of a dominant allele in preventing the development of gynomorphs.

Variation in queen size may also have a genetic basis in the fire ant *Solenopsis geminata*. Breeding experiments have demonstrated that queens produce daughters that are the same morphotype as themselves (MCINNES & TSCHINKEL 1995). In *Temnothorax spinosior* and *T. rugatulus*, similar results have been uncovered (HAMAGUCHI & KINOMURA 1996, RÜPPELL & HEINZE 1999). However, it is possible that size polymorphism in these ants results from genotype by environment interactions or maternal or colony effects. An understanding of the exact mechanisms governing variation in queen size in these species requires further research. Nevertheless, studies of phenotypic variation in ant queens demonstrate that genes may play a larger role in caste development than previously believed.

Worker subcastes: Worker ants frequently belong to subcastes that differ in size and undertake distinct tasks (OSTER & WILSON 1978). Recent studies have uncovered differences in the representation of subfamilies (individuals produced by either different patrilines or matrilines) among major and minor subcastes in *Camponotus consobrinus*, *Pogonomyrmex badius*, *Acromyrmex echinatior*, and *Eciton burchellii* (FRASER & al. 2000, HUGHES & al. 2003, HUGHES & BOOMSMA 2007, RHEINDT & al. 2005, JAFFE & al. 2007). These studies suggest that worker size variation can have a genetic basis and that task performance by workers may be influenced by genotype.

In *Acromyrmex echinatior* the effects of genes and environment on worker subcastes have been examined extensively (HUGHES & BOOMSMA 2007). Experimental work has discovered that workers with particular genotypes display a propensity to develop into workers of particular sizes when a colony's subcaste composition is altered. However, other lineages do not vary in the proportion of individuals in each subcaste regardless of environmental stimulus. These data suggest that *A. echinatior* retains some plasticity in subcaste determination, thereby allowing colonies to react to variable environmental conditions.

Genotype has also been found to play a role in worker task preference (but see BARGUM & al. 2004). In the polygynous ant *Acromyrmex versicolor*, workers vary in their task preference depending on their genotype (JULIAN & FEWELL 2004). In *Formica argentea*, *Camponotus planatus*, and *Leptothorax* sp. similar results have been uncovered (STUART & PAGE 1991, SNYDER 1992, CARLIN & al. 1993). Thus, as in species with dimorphic workers, it appears that genotype may contribute to variation in worker behavior in ants that display continuous size variation.

Finally, evidence has been uncovered pointing to the importance of genetic variation in colony survival and function. For example, queens in a few ant species are polyandrous (KELLER 1993, 1995, STRASSMANN 2001). Evidence now exists that the increased genetic variation arising from polyandry can benefit colony members. For example, in the polyandrous ant *Pogonomyrmex occidentalis* worker relatedness is negatively correlated with colony growth (COLE & WIERNASZ 1999, WIERNASZ & al. 2004). Thus multiple mating by a queen is beneficial to the colony she heads. Benefits may be derived from increased defense against pathogens and parasites that arise in genetically diverse colonies, or from increased efficiency of a genetically variable worker force.

Regulation of social structure: The fire ant gene *general protein-9 (Gp-9)* has garnered unparalleled attention in the study of genetic regulators of social organization (for in-depth review see GOTZEK & ROSS 2007). In *Solenop-*

sis invicta populations in the United States, the *b* allelic variant of *Gp-9* occurs in polygyne colonies. However, this allele is entirely absent in monogyne colonies, which exhibit only *B* allele homozygotes (ROSS 1997, ROSS & KELLER 1998, SHOEMAKER & al. 2006). Multiple heterozygous (*Bb*) queens are readily accepted into colonies where the polygynous *b* allele is present in workers at a threshold of roughly 5 - 15 % (ROSS & KELLER 2002), but these colonies reject *BB* queens. Colonies with only *BB* workers accept replacement *BB* queens, but reject *b*-allele replacement queens and secondary queens of any genotype (ROSS & KELLER 1998). In addition, *Gp-9 bb* queens suffer from low viability (HALLAR & al. 2007).

Four South American *Solenopsis* species also exhibit distinct monogyne and polygyne social forms associated with the presence of a *b*-like *Gp-9* allele (KRIEGER & ROSS 2002, 2005). Phylogenetic analysis of *Gp-9* sequences across fire ant taxa shows that "polygyne" *b*-like alleles form a nested clade within ancestral "monogyne" *Gp-9 B* alleles. Monogyne ancestry of the *Gp-9* allele supports a single evolutionary origin of polygyne *b*-like alleles by way of positive selection.

Solenopsis invicta Gp-9 is most similar to orthologs within the odorant-binding protein (OBP) family (KRIEGER & ROSS 2002, GOTZEK & ROSS 2007). Functionally, an OBP may directly regulate chemosensory queen recognition by workers. It must be cautioned, however, that the exact mode of expression and activity of *Gp-9* remains unknown. Unlike a putative chemosensory protein (ISHIDA & al. 2002) identified in the argentine ant, *Linepithema humile, Gp-9* expression is not limited to antennae. Further complicating inferences of proximate mechanisms, *Gp-9* genotype is associated with differences in queen fecundity (ROSS & KELLER 1998, DEHEER 2002) and worker and male adult body mass (GOODISMAN & al. 1999, 2007). These effects may result from the action of linked loci or components of a larger pathway to which *Gp-9* belongs. According to *Gp-9*'s complex functional implications, multiple hypotheses persist in explaining its role in the regulation of social structure (GOTZEK & ROSS 2007). Understanding the proximate mechanisms of *Gp-9* awaits further characterization of its biochemical properties and genetic interactions.

Gene expression and development in ants

Worker-queen differentiation: Changes in patterns of gene expression may drive phenotypic change and species divergence (CARROLL 2005). Within the Formicidae, a number of features have inspired study of how variation in gene expression drives the evolution of developmental programs. Chief among these is the key issue of how females develop into either queens or workers.

In ants, wing presence and absence is amongst the traits that typically demarcate the reproductive and nonreproductive female castes. A single evolutionary origin of developmental wing polyphenism is thought to have occurred some time around the origin of ants more than 125 million years ago (ABOUHEIF & WRAY 2002, MOREAU & al. 2006). Ants are thereby an ideal system for investigations of wing-patterning network conservation and robustness. ABOUHEIF & WRAY (2002) studied the expression of genes implicated in the regulation of wing development in the ant *Pheidole morrisii*. Patterns of expression in the wing development network were largely conserved in *P. morrisii* winged queens, winged males, and *Drosophila*. Of the *P. morrisii* wingless subcastes, workers exhibited no imaginal wing disc development but soldier larvae developed vestigial forewing discs. In soldier vestigial forewing discs, no activity was observed in one of six examined wing-development genes, although regulatory genes upstream of this interruption successfully specified forewing disc compartments. However, none of the examined wing-development genes exhibited activity in soldier hindwing sites or in workers. These results demonstrate that different points of network interruption have evolved between castes and within individuals.

Ants of the genus *Diacamma* present a case in which imaginal thoracic discs differentiate into male wings or evolutionarily derived structures in wingless females called gemmae (GOTOH & al. 2005, BARATTE & al. 2006). An integral wing development gene is downregulated in gemmae development, indicating either direct downregulation or an upstream interruption. To better understand the evolution of wing loss, ABOUHEIF & WRAY (2002) and BOWSHER & al. (2007) examined wing development in the wingless worker castes of four phylogenetically diverse ant species: *Neoformica nitidiventris*, *Crematogaster lineolata*, *Myrmica americana*, and *Solenopsis invicta*. *Neoformica nitidiventris*, *C. lineolata*, and *S. invicta* vestigial wing discs all shared a point of wing development interruption upstream to the interruption observed in *Pheidole morrisii*. Despite a presumed common origin of winglessness, observed network interruptions indicate molecular lability in the maintenance of homology. Furthermore, an evolutionary decoupling of patterning and growth is apparent, because taxa for which a shared wing-development network interruption is observed exhibit different rates of wing disc growth.

In contrast to targeted approaches to the evolution of development (as discussed for wing development), genomic approaches can address molecular underpinnings of the full gamut of phenotypic differences between castes. For example, differential display screens in *Lasius niger* identified 16 genes differentially expressed between worker and queen adults (GRAFF & al. 2007). Three of these genes play a putative role in establishing a reproductive division of labor. Three genes are putatively associated with somatic maintenance, bearing potential relevance to longevity and immune function (Tab. 1). In addition, several differentially expressed genes had no orthologs with known function.

Small-scale functional gene expression studies have also provided insight into how castes develop. In the fire ant *Solenopsis invicta*, transcripts of a vitellogenin receptor were found only in the ovaries of reproductive alate virgin females and queens (CHEN & al. 2004). In addition, an important regulator of social structure, *Gp-9*, and two orthologs of the cytochrome P450 family of genes were upregulated in *S. invicta* workers versus queens (LIU & ZHANG 2004). Finally, TIAN & al. (2004) compared patterns of gene expression between alate, virgin queens and dealate, reproductive queens in *S. invicta*. They discovered differentially expressed genes implicated in flight muscle breakdown, immune function, and reproductive development.

A different approach to studying caste differences is driven by interest in specific phenotypic differences, such as life-span, which can vary by as much as ten-fold between queens and workers (Keller & Jemielity 2006). A correlation between Cu–Zn *superoxide dismutase 1* (*SOD1*) and longevity was found in *Drosophila* (Orr & Sohal 1994, Spencer & al. 2003). However, in the queen caste of *Lasius niger, SOD1* expression was not associated with increased lifespan (Parker & al. 2004). These contrasting results demonstrate that ants provide utility as a counterpoint to model organisms when investigating the molecular basis of important biological variation.

Morphological patterning and gene expression variation among life stages: Homeotic genes pattern the body axis of animals and are widely implicated in morphological evolution (Muller 2007). The evolutionary significance of the homeotic gene *Abdominal-A* has been investigated in ants (Niculita & al. 2001, Niculita 2006). A comparison of *Linepithema humile* and *Monomorium pharaonis* revealed that *Abdominal-A* shows spatial variation in expression during development. Similarity is high between *L. humile* and *M. pharaonis Abdominal-A* sequences, supporting the role of gene regulation, rather than protein level evolution, in the origin of phenotypic novelty by homeotic genes.

A greater understanding of the processes that underlie phenotypic divergence and plasticity may be obtained by increasing experimental genome coverage and by taking a comparative phylogenetic approach. Goodisman & al. (2005) utilized cDNA microarrays to assess gene expression patterns and development in the ant *Camponotus festinatus*. Interestingly, expression patterns of *C. festinatus* and *Drosophila melanogaster* differed greatly, with few of the identified *Drosophila* orthologs exhibiting similar patterns of expression between taxa. Organismal development inferences were also readily apparent, with a high proportion of genes highly expressed in *C. festinatus* larvae exhibiting protein metabolism and structural activity. Genes highly expressed in adults, meanwhile, had a greater diversity of function.

Conclusions and future directions

The coming decades of biological research will increasingly focus on determining how genetic information influences the formation of complex phenotypes. Ants are excellent subjects on which to focus such research efforts, because ant phenotypes extend beyond the individual and include the formation of complex social groups. The past years have seen significant progress in understanding how heritable information influences individual and group phenotypes in ants. However, this area of research in ants still lags behind other social insects. In particular, research on the honey bee, *Apis mellifera*, is progressing at a remarkable rate (e.g., The Honeybee Genome Sequencing Consortium 2006, Amdam & al. 2007, Grozinger & al. 2007), and advances are also being made in social wasps (Sumner 2006, Hoffman & Goodisman 2007, Toth & al. 2007, Toth & Robinson 2007) and termites (Scharf & al. 2003, Zhou & al. 2006). Ongoing research in other social insect species is exciting. However, greater advances must be made in ants because of their ecological and evolutionary importance.

We suggest that future research efforts in ants focus on making the link between genetic information and phenotype explicit. Genetic differences have already been identified as the basis of important phenotypic variation in ants. Research should now focus on determining the molecular mechanisms that produce this phenotypic variation. These efforts will not be easy and may rely on the improvement of classical genetic techniques, such as controlled crosses among closely related taxa. Progress in these areas will accelerate as the ability to sequence ant genomes becomes feasible. In such cases, comparisons of the genetic material among species, informed by known gene function inferred from model taxa, will provide insight into the genetic mechanisms responsible for the development of alternate phenotypes.

Tab. 1: Genes differentially expressed in adult ant queen and worker castes. The putative function of orthologous genes are provided when known. [1]Graff & al. (2007); [2]Chen & al. (2004); [3]Liu & Zhang (2004); [4]Valles & al. (2006); *also more highly expressed in *S. invicta* dealate versus alate queens (Tian & al. 2004).

Gene	Upregulated in caste	Species	Putative function
Vitellogenin	queen*	*L. niger*[1], *S. invicta*[2]	yolk protein precursor, somatic maintenance
Yellow g	queen*	*L. niger*[1]	reproductive development
Serine proteinase inhibitor	queen	*L. niger*[1]	somatic maintenance, immune defense
Histone 2a	queen	*L. niger*[1]	somatic maintenance, immune defense
Thrombin inhibitor protein	queen	*L. niger*[1]	enzyme inhibitor
Pheromone-binding protein ASP1	worker	*L. niger*[1]	odorant binding
Gp-9	worker	*S. invicta*[3]	regulation of colony social structure (see text)
Hypothetical membrane alanyl aminopeptidase	worker	*L. niger*[1]	unknown
Cytochrome P450	worker	*S. invicta*[3]	biosynthesis and degradation pathways
Glutathione S-transferase	worker	*S. invicta*[4]	unknown

Another important area of future research in ants will center on how the expression of genetic information results in phenotype. Ants are ideal subjects for such assays because of the diversity of alternate phenotypes that they produce. Recent studies have begun to demonstrate how variation in gene expression causes changes in phenotype in ants. Indeed, a number of investigations have been driven by a genomic ideology – implementing large-scale, multigene approaches to address developmental questions (TIAN & al. 2004, GOODISMAN & al. 2005, GRAFF & al. 2007). These efforts should be considered precursors to an era of comparative ant genomics in which unprecedented evolutionary inference will address the remarkable feat of evolution embodied by the ants. Additional data arising from more detailed studies (e.g., WANG & al. 2007) will eventually allow for cross-species comparisons that will be particularly useful in understanding how the evolution of gene expression affects society formation. Future studies should incorporate phylogenetically diverse ants into developmental gene expression studies. Such studies will provide more information about the rate at which gene expression patterns evolve and address a greater breadth of phenotypic traits and developmental processes. Overall we are optimistic that the coming years will see major progress in understanding how ants develop important and diverse forms.

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Zusammenfassung

Ameisen zählen zu den bemerkenswertesten und erfolgreichsten Tieren. Der Erfolg der Ameisen fußt auf ihrem komplexen Sozialsystem, welches zum Teil aus der genetischen Architektur der Einzelindividuen der Sozietät herrührt. In diesem Übersichtsartikel evaluieren wir den Fortschritt im Verständnis dessen, wie genetische Information komplexe Phänotypen bei Ameisen beeinflusst. Wir befinden, dass die Erforschung der Struktur von Ameisengenomen in manchen Bereichen weit gediehen ist, beispielsweise hinsichtlich Chromosomenzahl, Genomgröße und Karyotypenevolution. Andere Bereiche der strukturellen Genomik allerdings, wie etwa jene von Genzahl und Genomzusammensetzung, sind nach wie vor wenig untersucht. Beträchtlichen Fortschritt zeigen wir in der Dokumentation genetischer Effekte auf die phänotypische Variation auf, die mit der Sozialstruktur der Ameisen zusammenhängt. Als Beispiel sei genannt, dass genetische Variation die Geschlechtsbestimmung bei manchen Ameisenarten beeinflusst und bei einigen Arten mit der Kastenbestimmung in Zusammenhang steht. Ausserdem konnte bei einigen Arten eine direkte genetische Kontrolle von Königinnen- und Arbeiterinnenphänotypen nachgewiesen werden. Ebenfalls vorangekommen ist die Identifizierung von Genen, deren Expressionsmuster mit Sozialstruktur, Entwicklung und Kastendifferenzierung zusammenhängen. Wir haben inzwischen ausreichend Daten, um wichtige Fragen den Zusammenhang zwischen Phänotyp und Evolution der Genexpression betreffend zu behandeln. Abschließend fassen wir – erstmals überhaupt – die wachsende Literatur zur Soziogenomik von Ameisen zusammen, also der Erforschung der molekularen Grundlagen ihres sozialen Lebens. Insgesamt können wir von substanziellen Fortschritten in der Verknüpfung von molekulargenetischer Information und phänotypischer Variation bei Ameisen berichten, zeigen aber gleichzeitig auf, dass viele wichtige Gelegenheiten zur Erforschung der molekularen Basis komplexer Phänotypen noch darauf warten, von Ameisenforschern ergriffen zu werden.

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