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Genomic architecture of ant social evolution

Ants rank among the most ecologically dominant and evolutionarily remarkable insects on the planet, capturing the imagination of both curious children and thoughtful scholars alike. Aristotle, impressed by their division of labor and cooperative behavior, described them as "political animals". In Aesop's Fables, they are celebrated for their foresight and diligence in preparing for hardship. Traditional Chinese narratives similarly portray ants as modest creatures that, through collective effort, achieve extraordinary power and influence.

Charles Darwin was the first to articulate a scientific framework for understanding ant societies, acknowledging the evolution of neuter workers as a "special difficulty" for his theory of natural selection, since these individuals do not reproduce and therefore do not directly transmit their traits to offspring (Darwin, 1859). This apparent contradiction persisted until W.D. Hamilton, nearly a century later, introduced the theory of kin selection, which extended the logic of evolutionary advantage beyond direct reproduction. Through his formulation of "inclusive fitness"—the combined contribution of direct reproduction and indirect genetic gains from aiding relatives —Hamilton demonstrated that altruistic behaviors may evolve when the benefits to related individuals, weighted by genetic relatedness, exceed the costs to those expressing the behavior ($rB>C$) (Hamilton, 1964a, 1964b).

Despite sharing the same genetic blueprint, queens and workers diverge sharply in morphology, physiology, and behavior through caste-specific developmental trajectories. This division of labor parallels the structure of multicellular organisms, with queens functioning as the reproductive germline and workers as the non-reproductive somatic tissues—a configuration that optimizes collective fitness at the superorganism level (Wheeler, 1910). This organizational complexity exemplifies a major evolutionary transition in the history of life (Szathmáry & Smith, 1995). To date, over 15 000 ant species have been described, and their global biomass is estimated to equal approximately one-fifth that of humans, exceeding the combined mass of all wild birds and mammals (Schultheiss et al., 2022). Occupying a diverse array of terrestrial ecosystems, ants exert extensive and profound ecological influence through nutrient cycling, predation, and mutualistic interactions. As observed by the renowned biologist E.O. Wilson, their evolutionary trajectory represents the "ultimate expression of the social conquest of Earth" (Wilson, 2012).

What underlies the remarkable evolutionary success of ants? What genetic innovations gave rise to their complex social organization and explosive radiation? How are shared genomes developmentally programmed to generate the striking phenotypic divergence between queens and workers? These fundamental questions in evolutionary biology have been addressed through an unprecedented large-scale international collaboration involving 30 research institutions across China and worldwide, providing groundbreaking insights into one of the most elaborate social systems in the natural world (Figure 1) (Vizueta et al., 2025).

The international consortium generated and analyzed 163 high-quality ant genomes representing 12 of the 16 extant subfamilies and 97 of the 343 recognized genera. The findings revealed that the structure and evolution of ant genomes can be best understood through the lens of social evolution. Since their emergence in the Late Jurassic, approximately 157 million years ago, ant genomes have undergone extensive rearrangements, with structural dynamics correlating with lineage-specific diversification. Despite this genomic plasticity, conserved micro-syntenic blocks persist, often harboring genes with coordinated expression, including those showing caste-specific patterns, underscoring their significance in the evolution of ant society.

The ancestral reproductive strategy of ants, characterized by obligate lifetime monogamy (Boomsma, 2009) and haplodiploidy —where unfertilized haploid eggs develop into males and fertilized diploid eggs into females (Trivers & Hare, 1976) —established the groundwork for their social evolution by maximizing intra-colony relatedness. Over evolutionary time, ant reproductive strategies diversified to include pronounced queen-worker dimorphism, polygyny involving multiple reproductive queens per colony, the emergence of ergatoid queens with worker-like morphology, and systems lacking queens entirely, where reproduction is sustained by clonally reproducing workers. Conserved molecular pathways such as juvenile hormone, insulin, and mitogen-activated protein kinase (MAPK) signaling have undergone strong selection, with core components exhibiting caste-biased expression. Modulation of these pathways has shaped the gene regulatory networks driving the evolution of the diverse reproductive strategies observed in ants today.

Extant ant species are broadly classified into two major clades: poneroids and formicoids. Poneroids represent the basal ant lineages that retain relatively simple social structures, including small colony sizes, minimal queen-worker dimorphism, and reproductive flexibility whereby workers often preserve mating capacity. In contrast, formicoids, comprising over 90% of extant ant species, have evolved highly

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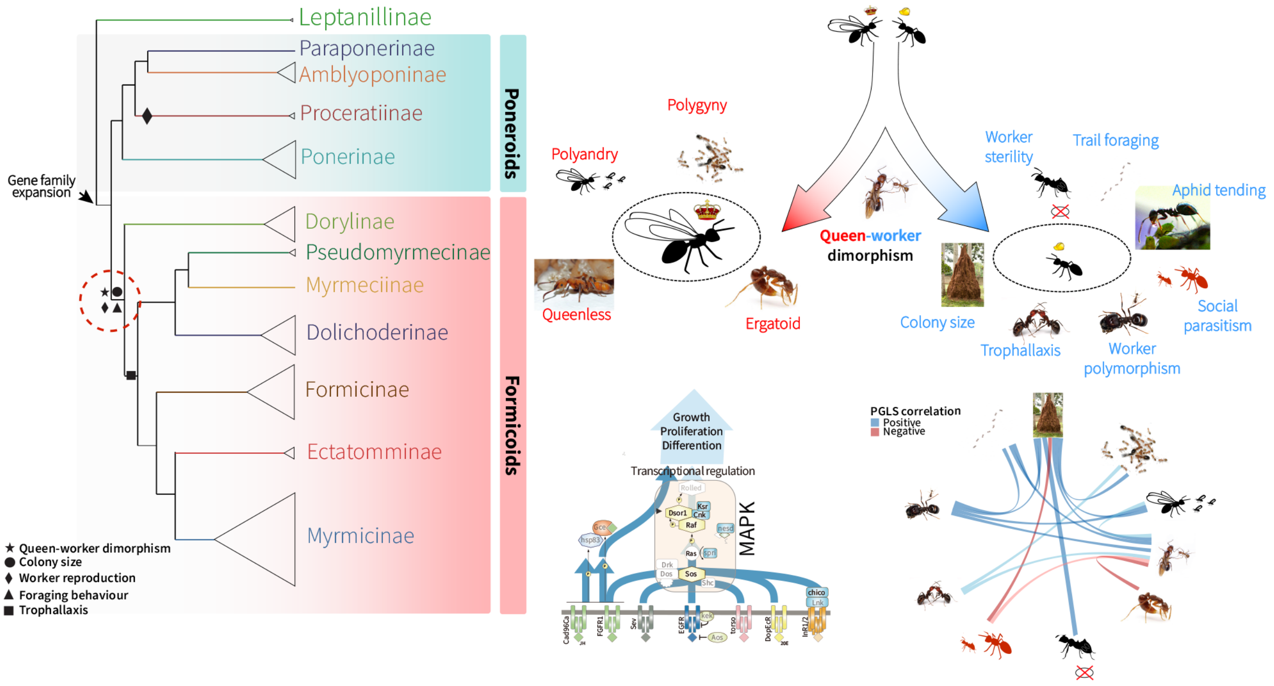

Figure 1 Genetic architecture and trait interactions in the evolution of sociality in ants

Illustrative phylogeny depicts key genomic and phenotypic transitions during ant evolution. Multiple gene family expansions occurred in the ancestor of extant poneroid and formicoid ants, while the formicoid ancestor represents a concentration of genes under positive selection. Triangle size reflects species abundance within each branch. Following the emergence of reproductive division of labor, social systems diversified to include increased queen-worker dimorphism, polygyny, polyandry, ergatoid castes, and queenless colonies. Concurrently, workers evolved a suite of specialized traits, including large colony size, trophallaxis, worker polymorphism, sterility, trail foraging, aphid tending, and social parasitism. These traits form modular and co-evolving networks that drive varying levels of social complexity. Underlying this diversification are pleiotropic gene networks and conserved pathways, including juvenile hormone, insulin, and MAPK signaling, which coordinate the developmental and behavioral architecture of ant societies.

sophisticated social systems characterized by extreme caste differentiation, massive colony sizes, and sterile worker castes that often include specialized subcastes such as soldiers.

Comparative genomic analyses revealed that in the last common ancestor of both clades, several key gene families associated with chemosensation, cuticular hydrocarbon synthesis, digestion, and endocrine regulation underwent significant expansion. These molecular innovations suggest that the genomic foundations required for social living were already well-established in early ants. The ancestral formicoid lineage exhibited an exceptional concentration of genes under positive selection, indicating a period of intense adaptive evolution. Adaptive changes in genes, particularly in caste-related genes regulating reproductive capacity, lipid metabolism, and brain development, appear to have driven the evolution of extreme queen-worker dimorphism and enhanced social complexity, facilitating niche diversification and supporting the remarkable evolutionary radiation of formicoid ants.

Alongside the evolution of reproductive division of labor, worker castes diversified further, exhibiting either continuous or discrete polymorphism. In several lineages, this diversification gave rise to specialized subcastes such as soldiers. Genes associated with worker polymorphism are frequently enriched in functions related to juvenile hormone signaling and neural development. Among them, the transcription factor *gcm*, which regulates glial cell differentiation, consistently shows elevated expression in minor workers relative to major workers across multiple species. This expression pattern likely facilitates glial specialization, potentially driving behavioral differentiation between worker subcastes.

Over the course of their evolutionary history, ants have acquired a diverse array of adaptations supporting the emergence and maintenance of complex social systems. However, accurately quantifying social complexity remains a major challenge in evolutionary biology, as it arises from the integration of numerous interacting traits. Traditional characterizations based on qualitative terms such as “simple” or “complex” obscure the underlying trait architecture. By reconstructing the evolutionary history of individual social traits, a more nuanced understanding can be gained, revealing distinct patterns of trait co-emergence and mutual exclusion. For instance, large colony size consistently co-occurs with queen-worker dimorphism, worker polymorphism, trail-based foraging, worker sterility, and aphid tending, while showing mutual exclusivity with social parasitism. These associations define a modular and dynamic system in which colony size and queen-worker dimorphism serve as central organizing features, driving the elaboration of other social traits and generating a spectrum of organizational complexity across ant societies.

The coevolution of biological traits in ants is underpinned by a set of overlapping genes with pleiotropic effects that operate within shared regulatory networks. These genes tend to cluster into functionally integrated modules, mirroring the modular structure of the traits they influence. Notably, selection pressures on these genes dynamically shift with social complexity, with genes under intensified selection in highly complex societies often experiencing relaxed selection in simpler systems, and genes under intensified selection in simpler societies showing reduced pressure in more complex ones. This modular regulatory pattern suggests the recurrent co-option of ancestral genetic elements for novel social functions throughout ant evolution.

The emergence of sociality in ants marks a major evolutionary transition, enabling unprecedented levels of organismal complexity and conferring substantial advantages in survival and productivity. Through an extensive international collaboration, researchers have assembled a comprehensive dataset linking ant genomic architecture to a broad spectrum of biological traits. Despite these advances, many intriguing questions remain unresolved—for example, the mechanisms by which queens evade the typical trade-off between fecundity and lifespan, the developmental processes that translate identical genomes into phenotypically distinct adult castes, and the genetic and regulatory basis by which collective behaviors are orchestrated and diversify across species. Future research is expected to draw on this extensive dataset through interdisciplinary approaches to uncover the mechanistic foundations of these mysteries. Such efforts hold strong potential to advance understanding of animal social evolution and the core principles driving major evolutionary transitions in organismal complexity.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

W.L., G.D., Z.X., and G.Z. wrote the draft manuscript. All authors revised, read, and approved the final version of the manuscript.

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