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THE CONSTRUCTION OF A SUPERORGANISM

NOTE TO THE GENERAL READER

Imagine that 1 million years ago, long before the origin of humanity, a team of alien scientists landed on Earth to study its life-forms. Their first report would surely include something like the following: *This planet is teeming with more than 1,000 trillion highly social creatures, representing at least 20,000 species!* Their final report would surely contain the following key points:

- Most of the highly social forms are insects (six legs, two antennae on the head, three body parts). All live on the land, none in the sea.
- At maturity, each colony contains as few as 10 members to as many as 20 million members, according to species.
- The members of each colony are divided into two basic castes: one or at most a small number of reproductives and a larger number of workers who conduct the labor in an altruistic manner and do not, as a rule, attempt to breed.
- In the great majority of the colonial species—namely, those belonging to the order Hymenoptera (ants, bees, wasps)—the colony members are all female. They produce and care for males during short periods of time prior to the mating season. The males do no work. After the mating season, any of these drones that remain in the nest are expelled or killed by their worker sisters.
- On the other hand, in a minority of the highly social species, belonging to the order Isoptera (termites), a king typically lives with the queen, the reproductive female. Unlike hymenopteran workers, those of termites often belong to both sexes, and in some species, labor is divided to some degree between the sexes.
- More than 90 percent of the signals used in communication by these strange colonial creatures are chemical. The substances, the pheromones, are released

from exocrine glands located in various parts of the body. When smelled or tasted by other colony members, they evoke a particular response, such as alarm, attraction, assembly, or recruitment. Sound or substrate-borne vibrations and touch are also used by many species in communication, but ordinarily just to augment the effects of pheromones. Some signals are complex, combining smell, taste, vibration (sound), and touch. Notable examples are the waggle dance of honeybees, the recruitment trails of fire ants, and the multimodal communication of weaver ants.

- The social insects distinguish their own nestmates from members of other colonies by using receptors on their antennae to smell the hydrocarbons in the outer layer of their hard-shelled cuticles. They use different blends of these chemicals to identify different castes, life stages, and ages among their nestmates.
- Each colony is integrated tightly enough by its communication system and caste-based division of labor to be called a superorganism. The social organizations, however, vary greatly among the social insect species, and we can recognize different evolutionary grades of superorganismic organization. A "primitive" (less derived) grade is represented by several ponerine species, where members of the colony have full reproductive potential and there is considerable interindividual reproductive competition within each colony. Highly advanced grades are represented, for example, by the leafcutter ant genera *Atta* and *Acromyrmex* and the *Oecophylla* weaver ants, where the queen caste is the sole reproductive, and the hundreds of thousands of sterile workers occur as morphological subcastes that are tightly integrated in division of labor systems. These societies exhibit the ultimate superorganism states, where interindividual conflict within the colony is minimal or nonexistent.

- The superorganism exists at a level of biological organization between the organisms that form its units and the ecosystems, such as a forest patch, of which it is a unit. This is why the social insects are important to the general study of biology.

Such is the array of phenomena on which we two Earth-born biologists will now expand. The ants, bees, wasps, and termites are among the most socially advanced nonhuman organisms of which we have knowledge. In biomass and impact on ecosystems, their colonies have been dominant elements of most of the land habitats for at least 50 million years. Social insect species existed for more than an equivalent span of time previously, but were relatively much less common. Some of the ants, in particular, were similar to those living today. It gives pleasure to think that they stung or sprayed formic acid on many a dinosaur that carelessly trampled their nests.

The modern insect societies have a vast amount to teach us today. They show how it is possible to "speak" in complex messages with pheromones. And they illustrate, through thousands of examples, how the division of labor can be crafted with flexible behavior programs to achieve an optimal efficiency of a working group. Their networks of cooperating individuals have suggested new designs in computers and shed light on how neurons of the brain might interact in the creation of mind. They are in many ways an inspiration. The study of ants, President Lowell, of Harvard University, said when he bestowed an honorary degree on the great myrmecologist William Morton Wheeler in the 1920s, has demonstrated that these insects, "like human beings, can create civilizations without the use of reason."

The superorganisms are the clearest window through which scientists can witness the emergence of one level of biological organization from another. This is important, because almost all of modern biology consists of a process of reduction of complex systems followed by synthesis. During reductive research, the system is broken down into its constituent parts and processes. When they are well enough known, the parts and processes can be pieced back together and their newly understood properties used to explain the emergent properties of the complex system. Synthesis is in most cases far harder than reduction. For example, biologists have come far in defining and describing the molecules and organelles that compose the foundation of life. At the next higher major level of biological organization, biologists have further described in precise detail many of the emergent structures and properties of cells. But this achievement is still a long way from understanding fully how molecules and organelles are assembled, arranged, and activated to create a complete living cell. Similarly, biologists have learned the properties of many of the species that compose the living parts of a few ecosystems—for example, ponds and forest patches. They have worked out large-scale processes, including material and energy cycles. But they are far from mastering the many complex ways in which species interact to create the higher-level patterns.

Social insects, in contrast, offer a far more accessible connection between two levels of biological organization. The lower-level units in this case, the organisms, are relatively simple in the way they interact to create colonies, and thus, the colonies themselves are not nearly so complex in structure and operation as cells and ecosystems. Both of these levels, organism and colony, can be easily viewed and experimentally manipulated. As we will show in the chapters that follow, it is now possible to press far ahead in this fundamental enterprise of biology.

We will conclude this introduction with a guess. If alien scientists had landed to study Earth's prehuman biosphere, one of their first projects would have been to set up beehives and ant farms. This is our biased guess, because we have been fascinated by the social insects, and in particular the ants, during our entire scientific lives. The reader will find this slant throughout this book. We have chosen examples mainly from the ants and focused on those with which we are most familiar, but we repeatedly "glance over the fence," and especially to the honeybees, the best studied of the social insect species. This book is not intended to be as comprehensive a monograph as *The Ants* (1990). Rather, our intention here is to present the rich and diverse natural history facts that illustrate superorganismic traits in insect societies and to trace the evolutionary pathways to the most advanced stages of eusociality. Our intent in doing so is to revive the superorganism concept, with emphasis on colony-level adaptive traits, such as division of labor and communication. Finally, in presenting the subject this way, we visualize the colony as a self-organized entity and a target of natural selection.

In this book, we view the insect colony as the equivalent of an organism, the unit that must be examined in order to understand the biology of colonial species. Consider one of the most organism-like of all insect societies, the great colonies of the African driver ants. Viewed from afar, the huge raiding column of a driver ant colony seems like a single living entity. It spreads like the pseudopodium of a giant amoeba across 70 meters or so of ground. A closer look reveals it to comprise a mass of several million workers running in concert from the subterranean nest, an irregular network of tunnels and chambers dug into the soil. As the column emerges, it first resembles an expanding sheet and then metamorphoses into a treelike formation, with the trunk growing from the nest, the crown an advancing front the width of a small house, and numerous branches connecting the two. The swarm is leaderless. The workers rush back and forth near the front. Those in the vanguard press forward for a short distance and then turn back into the tumbling mass to give way to other advancing runners. These predatory feeder columns are rivers of ants coming and going. The frontal swarm, advancing at 20 meters an hour, engulfs all the ground and low vegetation in its path, gathering and killing all the insects and even snakes and other larger animals unable to escape. After a few hours, the direction of the flow is reversed, and the column drains backward into the nest holes.

To speak of the colonies of driver ants—or other social insects, such as the gigantic colonies of leafcutter ants (described in Chapter 9), the honeybee societies, or the termite colonies—as more than just tight aggregations of individuals is to conceive of superorganisms and invite a detailed comparison between the society and a conventional organism.

In the 18 years since we wrote *The Ants*, an astounding wealth of information has been revealed from the phylogenetic primitive (ancestral) ant species belonging to the poneromorph group, the subject to which Chapter 8 is devoted. Although some species of this group exhibit all the key superorganismic traits, such as castes, division of labor, and sophisticated communication (topics treated in Chapters 5 and 6), the societies of many other poneromorph species are characterized by intense competition among nestmates for reproductive privileges. Group members are organized in dominance hierarchies, which, from time to time, are challenged and overthrown by members of the society ready to take the top position. Although the division of labor and communication in these societies is quite primitive, the behavioral interactions among nestmates are complex, with dominance displays and submissive behaviors, chemical signaling of reproductive status, and even individual recognition. These societies exhibit superorganismic traits, but are far from possessing the ultimate superorganismic organization exhibited by the driver ants and the leafcutter ants. ■

Consider a honeybee gathering nectar from a flower bed. Although simple in appearance, the act is a performance of high virtuosity. The forager was guided to this spot by dances of her nestmates that contained symbolic information about the direction, distance, and quality of the nectar source. To reach her destination, she traveled the bee equivalent of hundreds of human miles at bee-equivalent supersonic speed. She has arrived at an hour when the flowers are most likely to be richly productive. Now she closely inspects the willing blossoms by touch and smell and extracts the nectar with intricate movements of her legs and proboscis. Then she flies home in a straight line. All this she accomplishes with a brain the size of a grain of sand and with little or no prior experience.

Our forager is part of a superorganism, a colony with many of the attributes of an organism but one step up from organisms in the hierarchy of biological organization. The basic elements of the superorganism are not cells and tissues but closely cooperating animals. To follow one bee home, to peer into the hive she enters, to observe the mass of nest inhabitants in their full organized frenzy is to understand why social insects—the colonial bees, wasps, ants, and termites—are species for species the most abundant of land-dwelling arthropods. Although they represent only 2 percent of the approximately 900,000 known insect species in the world, they likely compose more than half the biomass. In a patch of Amazonian rain forest near Manaus, where a measurement was actually made, social insects composed 80 percent. Ants and termites alone composed nearly 30 percent of the entire animal biomass in this same sample, and ants alone weighed four times as much as the combined mammals, birds, reptiles, and amphibians.[1] Social insects

1 | E. J. Fittkau and H. Klinge, "On biomass and trophic structure of the central Amazonian rain forest ecosystem," *Biotropica* 5(1): 2–14 (1973).

prevail at every level in all forests around the world except the coldest and wettest. In one sample from the canopy of Peruvian rain forest, ants made up 69 percent of all the individual insects.[2] In this specialized environment, they function not only as predators and scavengers but also as cryptic herbivores, collecting the rich sugary excrement of aphids, treehoppers, and other sap-feeding homopterous insects they tend like cattle.[3]

An odd parity exists between the social insects and humanity. About 6.6 billion individuals compose *Homo sapiens*, the most social and ecologically successful species in vertebrate history. And the number of ants alive at any given time has been estimated conservatively at 1 million billion to 10 million billion. If this latter estimate is correct, and given that each human weighs on average very roughly 1 or 2 million times as much as a typical ant, then ants and people have (again, very roughly) the same global biomass.[4]

WHY COLONIES ARE SUPERIOR

Environmental domination by ants and other social insects is the result of cooperative group behavior. When multiple workers address the same tasks, they use "series-parallel" operations: each worker can switch from one task to another as need demands, so that no task goes unattended for long and each step in the task is soon completed. Workers are also more inclined than solitary insects to be aggressive, even suicidal. There is little Darwinian loss in their bravery: individual casualties incurred during foraging and nest defense leave unharmed the rest of the colony, especially the all-important reproductive caste, and lost workers are soon replaced. In addition to this fighting edge, the enlarged insect power and coordinated actions

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2 | T. L. Erwin, "Canopy arthropod biodiversity: a chronology of sampling techniques and results," *Revista Peruana de Entomologia* 32: 71–77 (1989).

3 | J. H. Hunt, "Cryptic herbivores of the rainforest canopy," *Science* 300: 916–917 (2003).

4 | The number of insects alive on Earth at any given time has been calculated by ecologist Carrington Bonner Williams to be, to the nearest order of magnitude, 1 billion billion, or 10^{18}; see C. B. Williams, *Patterns in the Balance of Nature and Related Problems in Quantitative Ecology* (New York: Academic Press, 1964). We suppose that ants make up 10 percent, order of magnitude, of the individual living insects worldwide, with tropical forests and all other terrestrial and aquatic habitats considered collectively and the large numbers of tiny collembolans and comparably small insects included. We also suppose the average ant to have a dry weight of about 0.5 to 1.0 milligrams and humans to have an average dry weight of about 10 kilograms.

enable members of colonies to construct complex nests with superior defensive ramparts and interior microclimate control.

Endowed with the advantages of colonial life, the social insects have managed to displace solitary insects, such as cockroaches, grasshoppers, and beetles, from the most favored nest sites and defensible foraging ranges. In the most general terms, social insects control the center of the land environment, while solitary insects predominate in the margins. Where social insects take territorial possession of the larger and more enduring spaces of the vegetation and ground, the solitary forms occupy the peripheral twigs, leaf surfaces, mudflats, and wet or very dry and crumbling portions of dead wood. In short, solitary forms tend to prevail over social insects only in the more remote and transient of living spaces.[5]

THE CONSTRUCTION OF SUPERORGANISMS

Reflection on the success of social life allows us to address a classic question of biology: *How does a superorganism arise from the combined operation of tiny and short-lived minds?* The answer is relevant to studies of lower levels of biological organization and the related question that also presents itself: *How does an organism arise from the combined operation of tiny and short-lived cells?*

The object of most research conducted on social insects during the past half century can be expressed in a single phrase: *the construction of superorganisms*. The first level of construction is sociogenesis, the growth of the colony by the creation of specialized castes that act together as a functional whole. Castes are created by algorithms of development, the sequential decision rules that guide the body growth of each colony member step by step until the insect reaches its final, adult stage. In the social hymenopterans (ants, social bees, and social wasps), the sequence is roughly as follows. At the first decision point, depending on its physiological condition, the developing female egg or larva is shunted onto one or the other of two paths of physical development. If the immature insect takes the path leading to more extended growth and development, it will turn into a queen upon reaching

5 | General accounts of the dominance of social insects and the reasons for it are given in E. O. Wilson, *Success and Dominance in Ecosystems: The Case of the Social Insects* (Oldendorf/Luhe, Germany: Ecology Institute, 1990); and B. Hölldobler and E. O. Wilson, *The Ants* (Cambridge, MA: The Belknap Press of Harvard University Press, 1990).

the adult stage. If it takes the other path, it will curtail growth and development and end up a worker. In some species of ants, the worker-bound larva encounters a second decision point on the road to adulthood, from which one path leads it to maturity as a major worker ("soldier") and the other to maturity as a minor worker.

These specialists, working together as a functional unit, are guided by sets of behavioral rules that operate in the following manner. If in a given context the worker encounters a certain stimulus, it predictably performs one act, and if the same stimulus is received in a different context, the worker performs a different act. For example, if a hungry larva is encountered in the brood chamber, the worker offers it food; if a larva is found elsewhere, the worker carries it, whether hungry or not, to the brood chamber and places it with other larvae. And so on through a repertory of a few dozen acts. The totality of these relatively sparse and simple responses defines the social behavior of the colony.

Nothing in the brain of a worker ant represents a blueprint of the social order. There is no overseer or "brain caste" who carries such a master plan in its head. Instead, colony life is the product of self-organization. The superorganism exists in the separate programmed responses of the organisms that compose it. The assembly instructions the organisms follow are the developmental algorithms, which create the castes, together with the behavioral algorithms, which are responsible for moment-to-moment behavior of the caste members.

The algorithms of caste development and behavior are the first level in the construction of a superorganism. The second level of construction is the genetic evolution of the algorithms themselves. Out of all possible algorithms, generating the astronomically numerous social patterns they might produce, at least in theory, only an infinitesimal fraction have in fact evolved. The sets of algorithms actually realized, each of which is unique in some respect to a living species, are the winners in the arena of natural selection. They exist in the world as a select group that emerged in response to pressures imposed by the environment during the evolutionary history of the respective species.

THE LEVELS OF ORGANIZATION

Life is a self-replicating hierarchy of levels. Biology is the study of the levels that compose the hierarchy. No phenomenon at any level can be wholly characterized without incorporating other phenomena that arise at all levels. Genes prescribe proteins, proteins self-assemble into cells, cells multiply and aggregate to form organs, organs arise as parts of organisms, and organisms gather sequentially into societies, populations, and ecosystems. Natural selection that targets a trait at any of these levels ripples in effect across all the others. All levels of organization are primary or secondary targets of natural selection. For example, the genes that distinguish the Africanized honeybee (or "killer bee"), which was accidentally introduced into Brazil in the 1950s, include induction of restless and aggressive behavior in workers. Under free-living conditions, Africanized colonies outcompete those of other strains. To some extent, they also penetrate and alter wild environments, including especially the canopies of tropical forests.

As ecosystems change by biological invasions, such as those of the Africanized honeybees, or by shifts in climate or by any other means, the relative abundances of the species composing the ecosystems also change. Some species are likely to drop out and new ones invade. As a consequence, the selection pressures on the individuals and societies are altered, with eventual consequences for the inherited traits of at least some of the species.

The dynamism of ecosystems is consequently eternal. Biological hierarchies are reverberating systems within which, depending on the histories of the species and the environmental niches they occupy, social order may or may not evolve.

The principal target of natural selection in the social evolution of insects is the colony, while the unit of selection is the gene. Because the traits of the colony are summed products of the traits of the colony members and those traits differ genetically among the members, as well as from one colony to the next, the evolution of the social insects is grounded in the flux of changing gene frequencies across generations. That flux in turn reflects the complex interplay of behavior both by colonies and the individual members that compose them.

EUSOCIALITY AND THE SUPERORGANISM

The sociobiology of insects is most effectively constructed with the concept of the superorganism, with reference to both its origin and evolution. Which of the insect societies deserve to be designated a superorganism? In the broadest sense, the term *superorganism* is appropriate for any insect colony that is eusocial, or "truly social," and that means combining three traits: first, its adult members are divided into reproductive castes and partially or wholly nonreproductive workers; second, the adults of two or more generations coexist in the same nests; and third, nonreproductive or less reproductive workers care for the young. For those who prefer a stricter definition, the term *superorganism* may be applied only to colonies of an advanced state of eusociality, in which interindividual conflict for reproductive privilege is diminished and the worker caste is selected to maximize colony efficiency in intercolony competition.[6]

In the chapters that follow, we will draw examples from insects and arthropods at all levels of social evolution, with emphasis on the eusocial species. The ants, for example, are all eusocial,[7] and they also vary enormously, according to species, in the complexity of their social organization. Specifically, they differ widely in mature colony size and the degree to which the workers are specialized for particular tasks. They further vary substantially in the rate of information exchange among colony members, the number of kinds of behavioral acts performed by the colony as a whole, and the amount of collaboration by workers in the performance of these acts, as well as in the architecture of their nests, including the homopterous "cattle" sheds and other physical structures they build.

At one end of the spectrum in the social evolution of ants are the anatomically primitive *Prionomyrmex* (formerly *Nothomyrmecia*) *macrops* "dawn ants" of Australia and species of the cosmopolitan genus *Amblyopone*. Their colonies, with fewer than 100 workers, employ only elementary communication signals. They engage in little or no division of labor other than that distinguishing queens and workers, and they build simple nests. At the opposite extreme of the spectrum are the mighty *Atta* leafcutters, doryline driver ants, ecitonine army ants, and *Oecophylla* weaver ants, whose colonies of hundreds of thousands to millions of workers contain advanced caste systems. These "civilized" species employ complex division of labor and communication systems, and they build elaborate nests, such as the silken pavilions of

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6 | H. K. Reeve and B. Hölldobler, "The emergence of a superorganism through intergroup competition," *Proceedings of the National Academy of Sciences USA* 104(23): 9736–9740 (2007).

7 | Among the ant species that have fewer than the full complement of eusocial traits are the workerless parasites. In addition, several ponerine species, such as *Pachycondyla* (formerly *Ophthalmopone*) *berthoudi*, whose mated sister workers reproduce (that is, they are "gamergates"), there is an absence of strict overlap between generations and no castes; see C. Peeters and R. Crewe, "Worker reproduction in the ponerine ant *Ophthalmopone berthoudi*: an alternative form of eusocial organization," *Behavioral Ecology and Sociobiology* 18(1): 29–37 (1985). Also, a few ant species reproduce by parthenogenesis; hence, there are no castes, and all members of each colony are clones; see K. Tsuji, "Obligate parthenogenesis and reproductive division of labor in the Japanese queenless ant *Pristomyrmex pungens*: comparison of intranidal and extranidal workers," *Behavioral Ecology and Sociobiology* 23(4): 247–255 (1988).

the *Oecophylla* weaver ants or, in the case of the ecitonine army ants, shelters created by an acrobatic interlocking of their own bodies.

Between the two extremes, occupying almost every conceivable point in the gradient of social complexity, are thousands of other ant species. Together they provide a clear view of the likely evolutionary origins of the intermediate and advanced grades of superorganisms.

A BRIEF HISTORY OF INSECT SOCIOBIOLOGY

The concept of the superorganism is venerable in its own evolution. It arose during a period of intense interest in evolutionary philosophy in the late nineteenth and early twentieth centuries. A succession of prominent thinkers, including Ernst Haeckel, Herbert Spencer, and Giti Fechner, wrote of the hierarchical structure underlying order in the entire universe, and they expatiated on the unique properties that emerge within each level of the grand order of creation. William Morton Wheeler, in his famous 1911 essay "The Ant-Colony as an Organism," brought the concept explicitly into sociobiology. "The ant-colony is an organism," he wrote, "and not merely the analogue of the person."[8] The colony, Wheeler pointed out, has several diagnostic qualities of this status:

1 | It behaves as a unit.
2 | It shows some idiosyncrasies in behavior, size, and structure, some of which are peculiar to the species and others of which distinguish individual colonies belonging to the same species.
3 | It undergoes a cycle of growth and reproduction that is clearly adaptive.
4 | It is differentiated into "germ plasm" (queens and males) and "soma" (workers).

Wheeler, in his later summary work *The Social Insects, Their Origin and Evolution* (New York: Harcourt Brace, 1928), was also the first to call the social insect colony a superorganism. He reinforced the concept of social homeostasis, consisting of the physiological and behavioral processes by which the colony keeps itself

8 | W. M. Wheeler, "The ant-colony as an organism," *The Journal of Morphology* 22(2): 307–325 (1911).

in optimal condition for growth and reproduction. "We have seen," he explained, "that the insect colony or society may be regarded as a super-organism and hence as a living whole bent on preserving its moving equilibrium and integrity."

The history of insect sociobiology can be fruitfully viewed as the evolution of the superorganism concept as it has waxed and waned and waxed again.[9] Of all the species whose colonies rank as advanced superorganisms, the best known, and indeed one of the best-known animal species of any kind, is the honeybee *Apis mellifera.*[10] Advanced superorganisms also exist among the termites, reaching an apogee among the mound-building macrotermitines of the African tropics. But the social insects that boast the greatest number of such extreme species, that embrace the largest number of evolutionary lines, and that have been studied across the most species, especially during the last several decades, are the ants. These insects also happen to have been the focus of our own personal research and will be the principal subject of the accounts to follow.

In general, bees and wasps offer the important advantage to scientists of many living species still at the earliest and intermediate stages of colonial evolution; thus, they display most clearly the likely evolutionary origins of social life itself. Ants and termites, on the other hand, reveal little of the first stages of colonial evolution, because all their species are eusocial; but in compensation, they have the most to tell us concerning the evolution of superorganisms. Of these two hegemonic groups, ants are by far the more diverse—more than 14,000 species of ants are known versus about 2,000 species of termites—and their biology has been better studied.

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9 | Because in addition to cooperation, conflict also occurs or at least has the potential to occur due to some forms of opposing interests among genetically differing members of the same colony, F. L. W. Ratnieks and H. K. Reeve have suggested that *superorganism* as a unit term is problematic and might better be replaced by reference to "community of interests," with some behaviors having superorganismic qualities and others not; see F. L. W. Ratnieks and H. K. Reeve, "Conflict in single-queen hymenopteran societies: the structure of conflict and processes that reduce conflict in advanced eusocial species," *Journal of Theoretical Biology* 158(1): 33–65 (1992). We disagree, holding that while ambiguities do exist, the term *superorganism* is sufficiently clear-cut and more than sufficiently heuristic to justify using it to denote a fundamental unit of biological organization. See also T. D. Seeley, "The honey bee colony as a superorganism," *American Scientist* 77(6): 546–553 (1989).

10 | R. F. A. Moritz and E. E. Southwick, *Bees As Superorganisms: An Evolutionary Reality* (New York: Springer-Verlag, 1992); T. D. Seeley, *The Wisdom of the Hive: The Social Physiology of Honey Bee Colonies* (Cambridge, MA: Harvard University Press, 1995); The Honeybee Genome Sequencing Consortium (C. W. Whitfield, G. E. Robinson, et al.), "Insights into social insects from the genome of the honeybee *Apis mellifera*," *Nature* 443: 931–949 (2006); and R. E. Page Jr. and G. V. Amdam, "The making of a social insect: developomental architectures in social design," *BioEssays* 29(4): 334–343 (2007).

To gain perspective at this point from our narrative, the following thumbnail sketch of the history of myrmecology (the scientific study of ants) might be helpful.

Leaving aside pioneering but minimally influential works of René Antoine Ferchault de Réaumur (*Mémoires pour Servir à l'Histoire des Insectes* [Amsterdam: Pierre Motier, 1737]) and the Reverend William Gould (*An Account of English Ants* [London: A. Millar, 1747]), the modern scientific study of ants can fairly be said to have been launched in 1810 by Pierre Huber's *Recherches sur les Moeurs des Fourmis Indigènes* (Paris: Chez J. J. Paschoud). For the next 150 years, myrmecology consisted largely of taxonomy and natural history. This foundational descriptive work was rich and productive, and it continues unabated today: possibly half the species remain undiscovered, and of those given a scientific name, only a tiny fraction—1 percent or fewer—have been examined intensively in the field or laboratory. Much of the pleasure in the study of ants still consists of discovering new forms of social behavior and ecological adaptations in little-known groups, nowadays mostly in the tropics, and applying that knowledge to improve reconstructions of ant evolution.

Since around 1950, the number of researchers and publications in myrmecology has grown exponentially, while the range of topics addressed has expanded at nearly equal pace. At the risk of oversimplification, the history of this past six decades can be encapsulated as follows.

From the 1950s through the 1970s, researchers worked out much of the basic plans of chemical communication, the evolution of caste systems, and many of the physiological factors that determine caste in a diversity of ant species. This work played a key role in the foundation of sociobiology.

In the 1970s and 1980s, sociobiology was established as a new discipline built on physiology, ecology, and evolutionary theory. In this synthesis, the social insects were given a central role. Toward the end of this period, attention was focused especially on the forces of selection that shape colony structure and life cycles. But ants in particular came to play an important role in general population and community ecology, particularly in studies of communal foraging and competition.

The 1990s and early 2000s saw important advances in analyzing the self-organization of colonies based on simple rules of individual worker behavior. A productive branch of population genetics also emerged: sociogenetics, the analysis of genetic relatedness among colonies and members as well as the hereditary basis of some forms of social behavior. It was quickly followed by a first effort at sociogenomics, the decoding of entire genomes in the search for the genes critical for social evolution. In 2006, the complete sequencing of the honeybee genome was announced.

Although each decade saw the appearance of newly popular topics, with small research industries growing around them, studies on those enjoying earlier favor continued without interruption. The two oldest subjects, systematics and scientific natural history, actually experienced a renaissance during the 1980s and 1990s and accelerated during the 2000s.

All this research has created a linkage, albeit still tenuous in places, across all levels of biological organization, from molecule to ecosystem. We think it timely to attempt the revised synthesis based on that perception. In upgrading the concept of the superorganism as an organizing theme, we will address not just the analogies frequently cited for a century between organisms and superorganisms but also, and at increasing depth, the principles by which the two entities are built and maintained.

The chapters that follow expand on the tentative conclusions just cited. We trust that our exposition will make clear the substantial importance of social insects for general biology. The content is also arranged to present sociobiology as it truly is, in its full range, aligning cause-and-effect explanations from genetics to behavioral science and ecology. By shifting emphasis back toward empirical studies of colony-level selection, the prime mover of social evolution, we aim also to promote a more fruitful union between sociobiology and behavioral ecology. Finally, by stressing the algorithms that direct the self-construction of colonies, we hope to assist in establishing more clearly the relevance of sociobiology to the general principles of developmental biology and systems theory.