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CHAPTER 1

Soil, Ants, and Life Underground

Under our feet lies a mysterious invisible realm. Heaps of soil in the shape of craters, mounds, or strewn pellets (fig. 1.1) hint at its existence. Although many creatures burrow in soil, most of this soil is brought up from below by ants during the excavation of their nests. Ant-made soil piles occur in a wide range of habitats and locations, from the rain forests of Uganda to the sidewalks of Los Angeles (to the degree that these sidewalks exist). Because ants vary enormously in body and colony size as well as in nesting habits, these deposits range from almost invisible to the obvious mounds of fire ants or Allegheny mound-building ants, or the colossal excavations of the leafcutter ants of tropical America, which can occupy as much belowground volume as a modest-sized house.

Fig. 1.1. A soil dump resulting from the excavation of a nest below. The generally crater-like form is typical of many ants, but far from all. Note the US dime for scale. This crater was formed by *Dorymyrmex bureni*. Author's photo.

The excavated soil tells little about the nest below. Conceivably, it suggests whether the nest is large or small, but rain, wind, and animals scatter soil piles, so even this deduction is unreliable. Nothing about the shape of the cavities, their arrangement in space, their depth, or their size is revealed by the excavated soil. Do the nests have a consistent architecture? Is there variation among ant species? How quickly do the ants create these nests? How do they use the space they create? These mysteries may not motivate many people into action, but to me they sound a strong call. What are the ants creating underground, and how does it serve them in their lives?

I am not the first biologist to ask such questions. Most of my predecessors have approached the challenge of revealing ant nest structure by first excavating nests in a range of soils and then publishing their findings as sketches or drawings of longitudinal or cross sections, or serial vignettes of nests (fig. 1.2). Some of these are crude sketches, some are more informative, and a few are excellent scale drawings (for example, fig. 1.2). Most of these were incidental to other studies—as far as I know, few were motivated primarily by a desire to describe the subterranean nest architecture. But all together, these studies give us a sort of "preview of coming attractions" that suggests that the study of ant nests and their role in ant biology might be very rewarding.

I began studying the mysteries of ant nest architecture almost unintentionally a couple of decades ago as a side project of my "regular" research. As I dabbled in this subject, I was increasingly drawn into revealing these mysteries as the main focus of my research. This book is mostly about my own exploration of the underground world of ants, based on the successes and failures of my ant research in the coastal plain forests of northern Florida over the last 25 years. Far beyond merely describing ant nests, I have approached the subject broadly, integrating nest architecture with relevant bits of physics, a touch of chemistry, some soil science, ant behavior, colony biology, ant ecology, ant natural history, some experimentation, and occasional personal adventures and ruminations. I hope to show the reader the attractions, problems, and rewards of pursuing a research subject with a passionate curiosity and a love of solving problems. Indeed, I have always found an aesthetic pleasure in working with

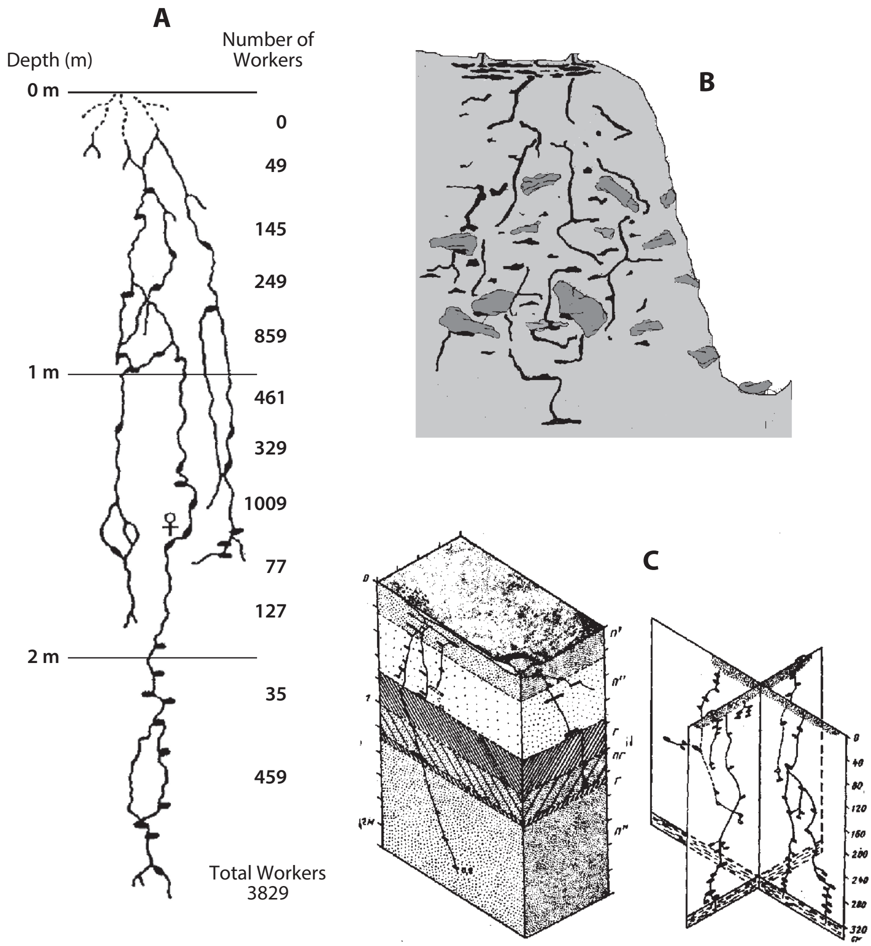

Fig. 1.2. Examples of published drawings of subterranean ant nests, two with scales. Rendering the three-dimensional nature of such nests with drawings is difficult. *A*, from Kondoh (1968); *B*, from Talbot (1964); *C*, from Dlussky (1981).

the "objects of nature" rather than the abstract concepts that are so fashionable (and admittedly important) in modern biology. I believe the reader will find aesthetic pleasure in these objects, too, and will be charmed by the lives of the ants that create them.

I think of myself as a sort of pioneer, mapping and describing an unknown land. This is because biology always begins with a description, and it is no surprise that the infant field of ant nest architecture should begin with a description before taking up a range of brainy hypotheses to explain the observations. It is also probably no surprise that progress in research depends on having available or inventing the methods needed for answering the relevant questions. Throughout the history of science, various fields have blossomed as a result of the invention of a new instrument or process, be it the microscope, the microtome, or any number of other inventions. The field of ant nest architecture is no exception, even though the methods are simpler and more mundane than a synchrotron, a nuclear magnetic resonance instrument, or a confocal microscope. A remarkable amount of interesting stuff can be learned with shovels, plastic bags, a modest ability to count, and a homemade kiln. In an era of high-tech science, I offer a story about the pleasures of low-tech shoestring science.

THE ANTS

The creators of this mysterious underground realm are the ants. In my experience, most people are aware of ants, those pesky creatures that mob the spilled sweet drink on their kitchen counter or make dirt piles on their pristine lawns, but few are aware that the world of ants is like another universe, an alien world. It thus seems prudent to start with a brief sketch of ant biology and diversity.

Ants are social insects whose ancestors diverged from the ancestors of wasps some 100 to 140 million years ago. Their societies (usually colonies) are distinguished by a strong division of function among individuals, such that only one or a few individuals are capable of laying fertilized eggs (the queen or queens), while most of the others are more or less sterile and carry out most of the work (the workers). All of the individuals with a social function are females. Males are produced only for mating with queens and are usually present for only weeks out of the year. Typically, a colony is a family whose mother is the queen and whose daughters are the workers. Daughters are full sisters if their mother mated with a single male, and half sisters if she mated with multiple males. At the individual level, ants are typical of insects with a complete metamorphosis, developing from egg to larva to pupa to adult. Sociality has built on this basic insect plan by affecting how ants develop into adulthood, producing either sterile workers or adults with fully developed sexual organs that are capable of mating and reproducing.

Sociality has made the ants an enormously successful group of animals, dominating many ecosystems in most of the warmer parts of the world. Their biomass—that is, their total weight—often exceeds that of any other animal group in their habitat. About 14,000 species have been described, but at the rate of discovery of new species, it is likely that the final count will be 20,000 to 40,000. For example, in his exhaustive sampling of the ecosystems of Madagascar, my colleague Brian Fisher has personally discovered and named over 1,000 new ant species. When queried about the number of ant species, ant experts usually estimate between 20,000 and 30,000, reasoning that much of the world remains poorly explored for ants and other insects. Many of these new species probably already reside in museums, waiting to be described by ant taxonomists, who, unlike the ants, are in short supply.

With their diversity and abundance, it is not surprising that ants occupy a wide range of habitats. Many species are scavengers and predators; some are herders of livestock such as aphids, mealybugs, and scales; still others are specialized predators of such tidbits as spider eggs, or of difficult prey ranging from hairy millipedes to springtails; some are communal nomadic hunters settling temporarily in camps; some gather wild seed crops; and some farm fungus on beds of caterpillar droppings or leaf fragments. Here in the coastal plain pine forest of Florida (where I do much of my research), it is common for all of these lifestyles to be represented in a plot as small as a medium-sized suburban lot.

This wealth of ant species is not evenly distributed on the earth. Rather, the number of ant species by region declines with increasing distance from the equator. Tropical regions, especially in the humid tropics, host between 4,000 and 6,000 ant species, but away from the equator this drops rapidly until at latitudes greater than 50° north or south, there are fewer than 50 species. I once collected a sample of *Leptothorax muscorum* at almost 70° N latitude on the Arctic slope of Alaska north of the Brooks Range. Only two ant species in the Arctic region extend from North America across Siberia, and the colony I found was nesting in a rare sandy bank facing south, soaking up every calorie of sunshine it could get, perched as it was only a few centimeters above the permafrost. In winter, the nest and everything in it froze solid—a life on hold, not to be resumed until the spring thaw. Its life could define the word "tenuous."

Of course, larger areas have more ant species, so equivalent-sized countries must be compared. Ecuador and Finland are not very different in size, but Ecuador has over 700 ant species, while Finland is home to only 64 species. An area of 16 hectares in the Peruvian Amazon yielded almost 500 species of ants. Brazil and the United States are pretty similar in size, yet the United States has only about 800 species while Brazil has over 1,400, and once Brazil is fully explored, it will probably yield many more.

Myrmecologists have speculated and argued for decades about which group of insects gave rise to the ants. For a long time, the consensus was that the closest relative of the ants was a wasplike creature similar to modern tiphiid wasps. These wasps seek out the larvae of beetles, paralyze them with a sting, and then lay an egg on them. The larva hatching from this egg then grows and develops by consuming the beetle larva. More recently, molecular methods have been used to determine the degree of relatedness of various insect groups and to arrange them into family trees (phylogenetic trees). Basically, the sequence of base pairs in the DNA of groups of organisms changes with time, so the number of pairs in a long DNA sequence that differ is a measure of both the time (more or less) the two lines have evolved separately, and the degree to which they are (or are not) related. Recent studies of many families of ants, bees, and wasps have shown that ants are most closely related to bees and stinging wasps. In the language of taxonomists, they are "sister groups." Bees, of course, collect and feed on pollen, whereas ants (at least the more primitive ants) and most wasps are carnivorous or parasitic. However, what ants, most bees, and most stinging wasps have in common is that they build or find nests and bring "stuff" (pollen, prey, nest material) back to the nest. Wasps outside this group tend to find their prey and parasitize it in place rather than haul it back to a central place. The collection of "stuff" is probably the part of the life history and behavior that predisposes these sister groups to evolve sociality, because it makes parents and offspring more likely to associate in the nest. Given other favorable factors, this group can evolve sociality. It is notable that sociality has evolved six to eight separate times in the bees and once in the ancestral ant, all of whose descendants are social.

Nest construction thus facilitated the evolution of sociality, because living in a nest and returning "stuff" to it predisposes insects to form related groups and thus evolve cooperative behavior. In other words, nesting behavior predates the evolution of both ants and sociality. Modern social insects share a particular set of life history features—that is, characteristics of the stages and phases of their life cycle—and ways in which these meet the life challenges of the species: (1) daughters remain in the nest with their mother and sisters (generations overlap); (2) sisters care for younger sisters rather than their own offspring (communal brood care) and coincidentally care for their mother, too; (3) some individuals specialize in laying eggs, and others in rearing them and doing other necessary work (division of labor or function). It is easy to imagine that a mother ant, bee, or wasp that repeatedly hauls "stuff" back to the nest to feed to her developing offspring would eventually share that nest with her adult daughters, and they with their younger and contemporary sisters. The presence of a brood would trigger the brood-tending behavior of the sisters, and various nutritional and perhaps hormonal conditions would suppress the reproductive capability of the daughters. Should such a combination of a mother (queen) and her suppressed daughters (workers) be more successful in producing the next generation than the daughters trying it on their own, then this nascent sociality would be favored by natural selection, and social evolution would be on its way. Such social evolution eventually passes a point of no return when the workers are no longer capable of being queens, as happened in the ants. After that point, ants were no longer able to ask, "Should I be social or should I go it alone?" They were irreversibly committed.

In addition to nest construction and stuff collection, a particular mode of sex determination in these hymenopterans predisposes them to become social. Whereas females develop from fertilized eggs like most animals, males develop from unfertilized eggs. This means that females are diploid (have two sets of chromosomes), and males are haploid (have one set). All of the male's sperm carries the same set of genes. If the queen mates with a single male, math tells us that sisters are 75% related to one another (i.e., 75% of their genes are the same), whereas they are only 25% related to their brothers. So if sisters are going to help each other reproduce, they are surely not going to include their less-related brothers. The very high relatedness among sisters makes forfeiting their own reproduction to help their sisters reproduce pay off, genetically speaking, because their sisters bear so many of the same genes. Multiple fathers decrease the strength of this selection, but once sociality evolves, even this confers some advantages. In any case, the high relatedness among females produces a strong selective pressure to evolve sociality, and this is one reason all-female sociality evolved seven to nine times in this evolutionary lineage.

ANT NESTS

Ant nest architecture originated about 100 to 140 million years ago when the ancestor of all modern ants dug the ancestor of all modern ant nests. Today, the many thousands of ant species and their nests are the descendants of this ancestral ant and her nest. However, in the humid tropics, about half of the ant species nest in trees, often reaching a huge abundance. I once fogged two rain forest trees in Guyana with a "knock-down" insecticide to collect the arthropods living in them. About 90% of the resulting rain of insects onto our collecting sheets were ants, and most were a single, superdominant species of *Azteca*. With increasing latitude both north and south, ant species nest less frequently in trees and more frequently in the ground. This shift probably occurs because of the seasonally harsh desiccating and/or freezing conditions of life in trees in temperate climates. At my latitude in Florida, only a few of the hundred or so species nest only in trees. Most nest in the ground or in rotting wood or make temporary nests in existing shelters.

Each of the ground-nesting ant species builds a more or less distinctive nest, differing not only in size but also in architectural details from those of other species. In modern biology, these differences are best explained by evolution.

A 1973 essay by the evolutionary biologist Theodosius Dobzhansky of fruit fly genetics fame was titled "Nothing in Biology Makes Sense Except in the Light of Evolution." By this he meant that there is overwhelming evidence that all life on Earth is related and can be arranged into family trees that make sense as the outcomes of evolutionary descent. Evolutionary explanations are a core of modern biology, from molecules to behaviors to societies. The diversity of ant nest architecture, like the diversity of organisms, must also be the outcome of evolution and can therefore be arranged (at least in theory) into family trees that show lines of descent of closely related organisms or architectures as branches. To work toward this goal with respect to nest architecture, the reader will have to allow me a good deal of latitude because my sample size is small. Nevertheless, the exercise can be educational and is undertaken in chapter 9. From the outset, I must make clear that what evolved is not the ant nest—which is just hollow space in dirt—but the behavior of the ants that dig the nest. The nest is essentially the product, or "fossil," of the ants' behavior. Much complexity is hidden in this simple claim, for "behavior" includes not only the lone actions of individual workers, but also how these workers are affected by the behavior of other workers and by the cues and feedbacks emanating from the nest as it is constructed by dozens to millions of workers in the dark, without a leader or a blueprint. It is, in the currently popular phrase, self-organizing. How this self-organization works during nest excavation is largely still a mystery but is one of the central questions of the field.

THE MEDIUM

To those of us who move freely in sunlight and air, soil is the dense, granular medium on which we walk, in which plants are rooted, on which our houses are built, and on which we place asphalt in parking lots. We have no experience that would allow us to imagine moving through soil. Most creatures that live in soil move through it by creating cavities, and much of this activity involves excavating soil and dumping it on the surface, out of the way. This is what ants do when they create their subterranean nests. But most soils also have abundant empty pore space, and some soil-dwelling creatures are so small that they can move in the spaces between soil clumps or grains, or they can exploit the ample pore space by pressing grains aside to gain passage. Some ants such as the minuscule thief ants are so small that they are probably capable of doing this. Their wide-ranging, dispersed, threadlike passages are rarely accompanied by soil dumps on the surface. When these passages intersect with the nests of larger ants, the thief ants steal and eat the brood of the larger ants.

In the coastal plains of Florida, soils barely qualify as "soils" among soil scientists, who describe them as mere sedimentary deposits because they show little or no formation of zones or horizons. Indeed, most of the coastal plains are stranded coastal dunes running more or less parallel to the current shore. The lower interdune valleys form a network of sluggish streams that gradually drain the shallow water table to the Gulf of Mexico. An elevation difference of 1 to 2 m separates the wetlands from the dry uplands. The wetland soils are dark, organic, and mucky, while the upland soils are almost pure sand, with charcoal dust darkening the top 10 cm to gray. This soil is so sterile that no farmer, native or immigrant, was ever foolish enough to try to farm it, reprieving the pine forest from destruction. Competition for nutrients is intense because 85% of the nutrients are in the top 15 cm of soil. Getting a share of these nutrients on their way down to the water table requires plants to capture them before their neighbors do. Roots are sparse below about 20 cm.

This is the environment in which I began my field studies of ants, lured by the diverse and abundant ant fauna that proclaimed its presence, like name tags, through distinct patterns of soil dumps. It seemed likely that this surface distinction also reflected distinction underground, and it was this underground distinction that I wanted to reveal.

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