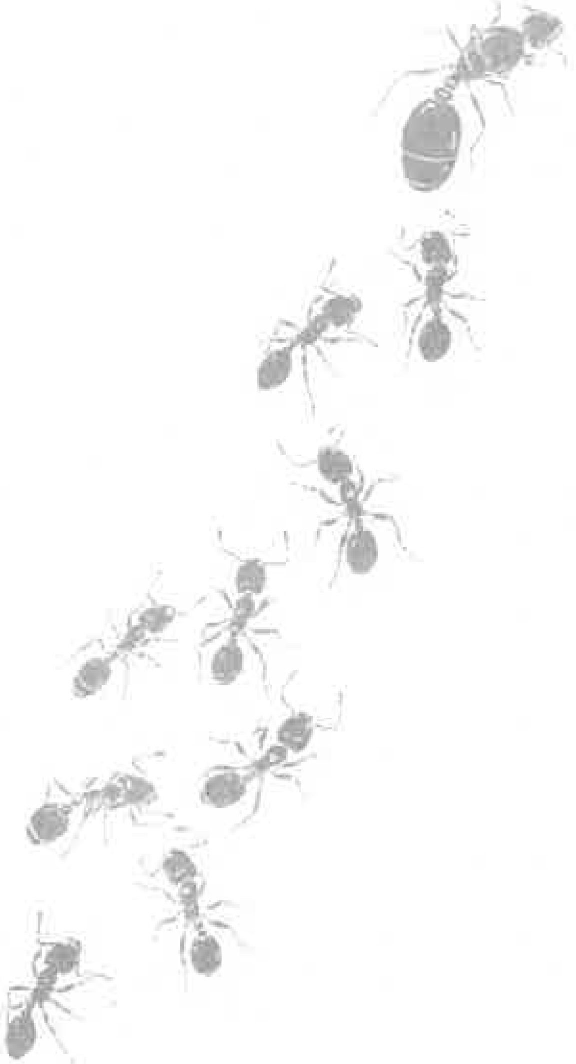
JOURNEY TO THE ANTS



A Story of Scientific Exploration

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and

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The Dominance of Ants

OUR PASSION IS ANTS, and our scientific discipline is myrmecology. Like all myrmecologists—there are no more than five hundred in the world—we are prone to view the Earth's surface idiosyncratically, as a network of ant colonies. We carry a global map of these relentless little insects in our heads. Everywhere we go their ubiquity and predictable natures make us feel at home, for we have learned to read part of their language and we understand certain designs of their social organization better than anyone understands the behavior of our fellow humans.

We admire these insects for their independent existence. Ants carry on in the midst of the shifting wreckage created by people, seeming not to care whether humans are present or not, so long as a little piece of minimally disturbed environment is left for them to build a nest, to search for food, and thereby to multiply their kind. City parks in Aden and San José, the steps of a Mayan temple at Uxmal, and a gutter in the streets of San Juan are among our research sites of past years, where on hands and knees we watched these minute creatures, unaware of our presence but the objects of our own lifelong curiosity and esthetic pleasure.

The abundance of ants is legendary. A worker is less than one-millionth the size of a human being, yet ants taken collectively rival people as dominant organisms on the land. Lean against a tree almost anywhere, and the first creature that crawls on you will probably be an ant. Stroll down a suburban sidewalk with your eyes fixed on the ground, counting the different kinds of animals you see. The ants will win hands down—more precisely, fore tarsi down. The British entomologist C. B. Williams once calculated that the number of insects alive on earth at a given moment is one million trillion (10^{18}). If, to take a conservative figure, 1 percent of this host is ants, their total population is ten thousand trillion. Individual workers weigh on average between 1 to 5 milligrams, according to the species. When combined, all ants in the world taken together weigh about as much as all human beings. But being so finely divided into tiny individuals, this biomass saturates the terrestrial environment.

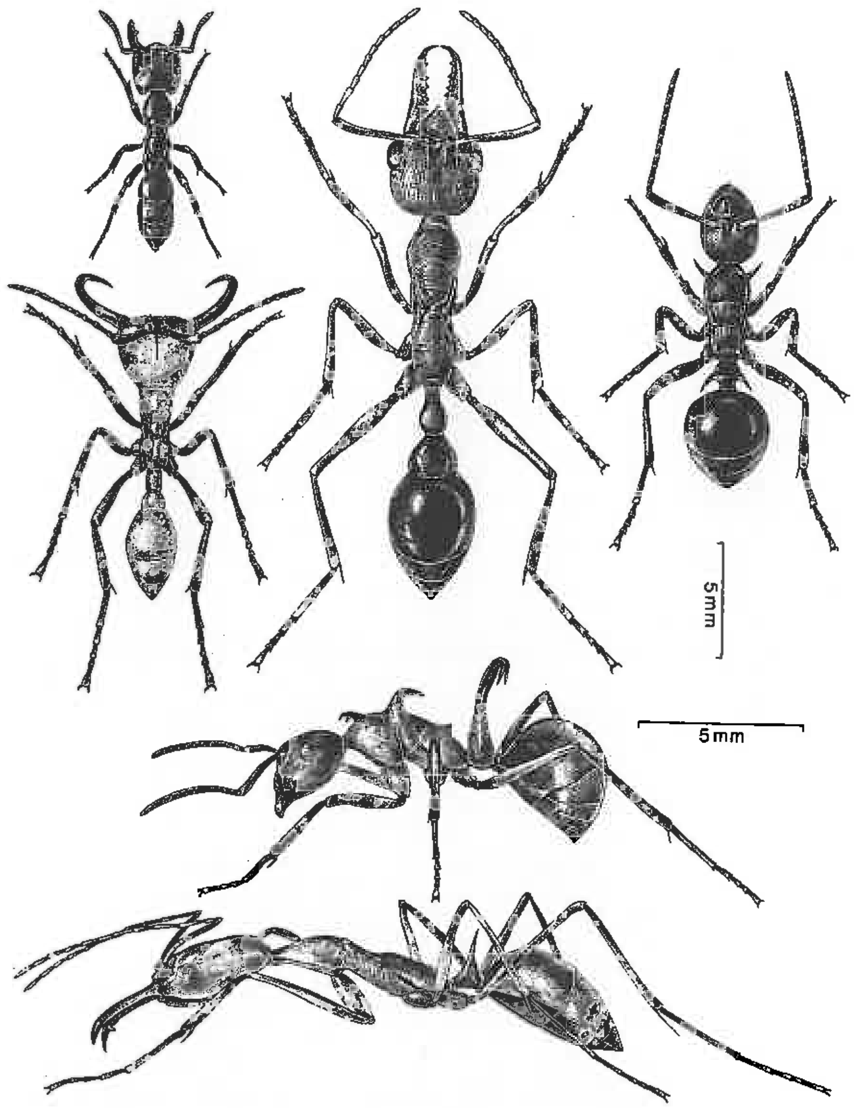
Thus in ways that become wholly apparent only when one's line

of sight is dropped to a millimeter of the ground surface, ants lie heavily upon the rest of the fauna and flora. They envelop the lives and direct the evolution of countless other kinds of plants and animals. Ant workers are the chief predators of insects and spiders. They form the cemetery squads of creatures their own size, collecting over 90 percent of the dead bodies as fodder to carry back to their nests. By transporting seeds for food and discarding some of them uneaten in and around the nests, they are responsible for the dispersal of large numbers of plant species. They move more soil than earthworms, and in the process circulate vast quantities of nutrients vital to the health of the land ecosystems.

By specialization in anatomy and behavior, ants fill diverse niches throughout the land environment. In the forests of Central and South America, spiny red leafcutters raise fungi on pieces of fresh leaves and flowers carried into underground chambers; tiny *Acanthognathus* snare springtails with their long traplike mandibles; blind, tube-shaped *Prionopelta* squirm deep into the crevices of decaying logs to hunt silverfish; army ants advance in teeming fan-shaped formations to sweep up almost all forms of animal life; and so on through nearly endless variations among the species in the pursuit of prey, corpses, nectar, and vegetable matter. Ants reach as far as insects can in the terrestrial environment. At one extreme, species adapted for life in the deep soil almost never come to the surface. High above them, large-eyed ants occupy the forest canopies, a few kinds living in delicate nests made of leaves bound with silk.

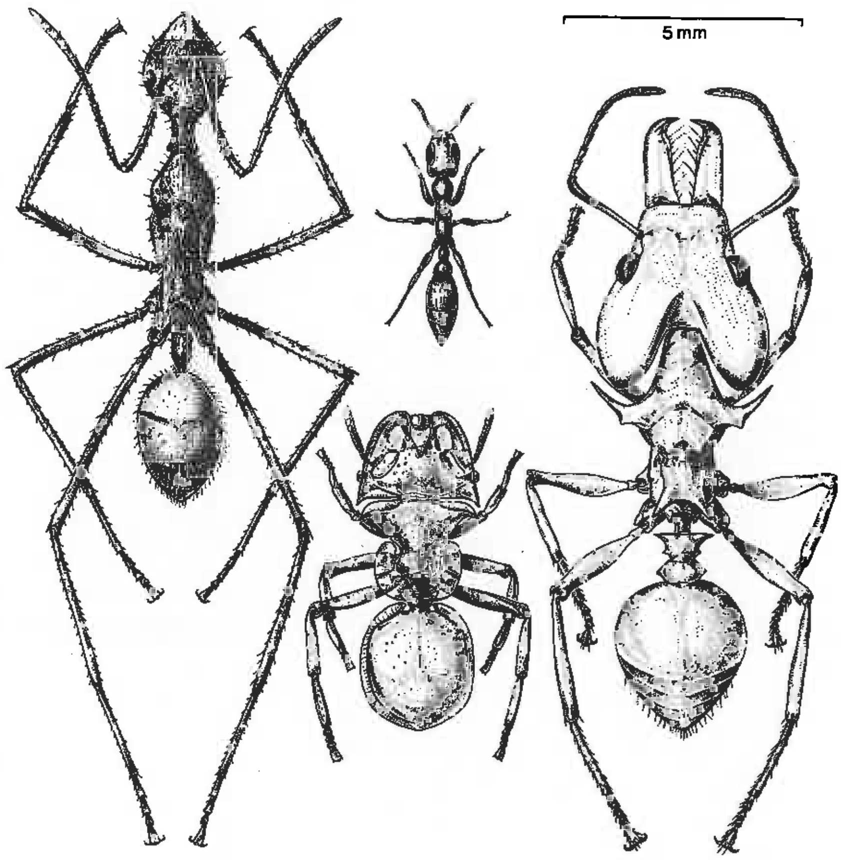
The dominance of ants has struck us in a particularly vivid manner during visits to Finland. In cool forests stretching north to beyond the Arctic Circle, we found that these insects still dominate the land surface. In mid-May on the southern coast, with the leaves of most of the deciduous trees still only partially emerged, the sky overcast, a light rain falling, and the temperature not rising above 12°C (54° Fahrenheit, uncomfortable for scantily clothed naturalists at least), ants were active everywhere. They teemed along forest trails, atop huge moss-covered boulders, and in the grassy tussocks of bogs. In a few square kilometers could be found 17 species, one-third the known fauna of Finland.

Mound-building Formicas, red and black ants the size of houseflies,

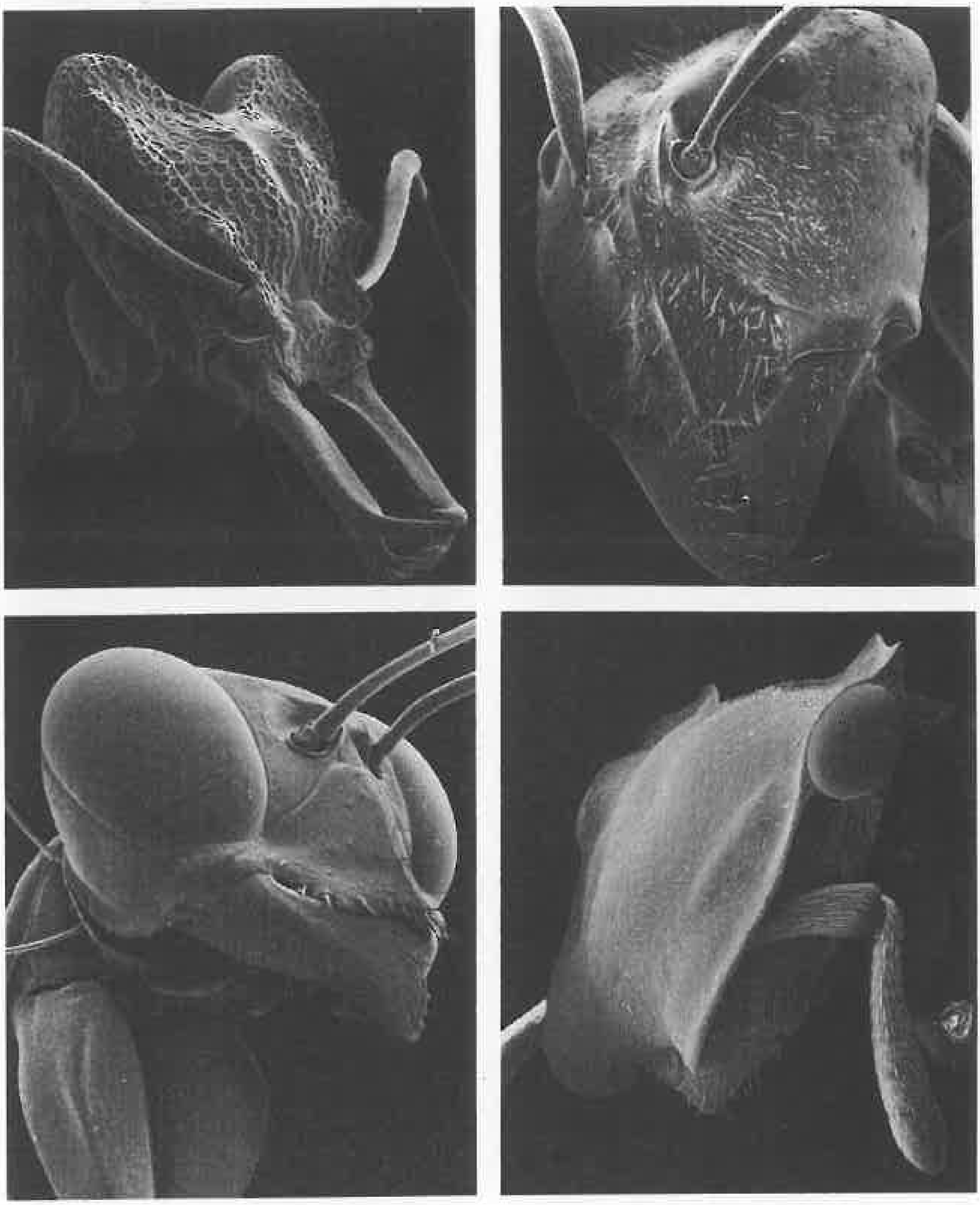


The extreme diversity of the 9,500 ant species of the world illustrated by worker ants. In the top center is a bulldog ant of the genus *Myrmecia;* to its left are a thick-bodied *Amblyopone* and a sickle-mandibled army ant of the genus *Eciton.* To the right of the bulldog ant is a multiple-spined *Polyrhachis,* and below it is another *Polyrhachis* and a long-mandibled *Odontomachus.* (Drawings by Turid Forsyth.)

A diversity of ants from South America. On the left is a long-necked *Dolichoderus;* on the right is a *Daceton,* with spines and long trap jaws. The center ants are *Pseudomyrmex* at the top and a flat turtle ant, *Zacryptocerus,* below. (Drawings by Turid Forsyth.)



Facing page
The diversity of ants illustrated by close portraits of their heads. Clockwise from the upper left: *Orectognathus versicolor* from Australia; *Camponotus gigas* from Borneo, one of the world's largest ants; a *Zacryptocerus* from South America; and *Gigantiops destructor* from South America. (Scanning electron micrographs by Ed Seling.)

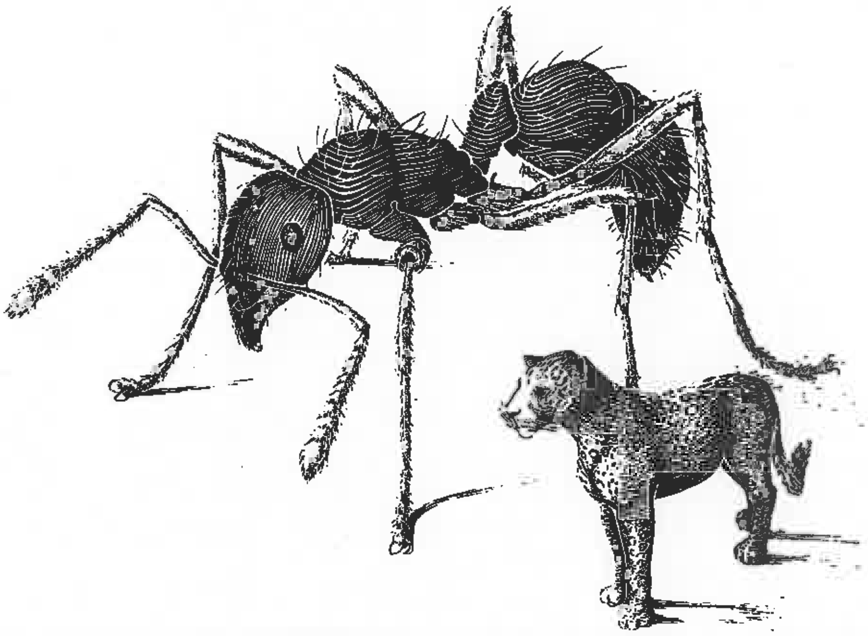


dominated the ground surface. The cone-shaped nests of several species, covered with freshly excavated soil and fragments of leaves and twigs, each housing hundreds of thousands of workers, towered a meter or more high, the equivalent for an ant of a forty-floor skyscraper. Ants seethed over the mound surfaces. They marched in columns several tens of meters long between adjacent mounds belonging to the same colony, their disciplined legions resembling heavy traffic on an intercity freeway as seen from a low-flying airplane. Other columns streamed up the trunks of nearby pine trees, where the ants attended groups of aphids and collected their sugary excrement. A small army of foragers deployed across the intervening terrain in search of prey. Some could be seen returning with caterpillars and other insects. Others were attacking colonies of smaller ants—in victory they carried the corpses of the defenders home for food.

In the forests of Finland ants are the premier predators, scavengers, and turners of soil. As we searched in company with Finnish entomologists under rocks, through the upper layers of humus, and in rotting pieces of wood strewn over the forest floor, we seldom found a patch of more than a few square meters anywhere free of these insects. Exact censuses remain to be made, but it seems likely that ants make up 10 percent or more of the animal biomass of that region.

An equal or even greater mass of living ants is found in tropical habitats. In the rain forest near Manaus, Brazil's principal city of the central Amazon, the German ecologists L. Beck, E. J. Fittkau, and H. Klinge found that ants and termites together compose nearly a third of the animal biomass: when all kinds of animals, large and small, from jaguars and monkeys down to roundworms and mites, are weighed, nearly a third of the weight consists of the flesh of ants and termites. These insects, along with the other two prevailing colonial forms, the stingless bees and polybiine wasps, make up an astonishing 80 percent of the insect biomass. And ants absolutely dominate in the canopies of the South American rain forests. In the high canopy of Peru they compose as much as 70 percent of the individual insects.

The diversity of ants in tropical localities is far higher than in Finland and other cold temperate countries. From one site of 8 hectares (20



In the Brazilian Amazon rain forest, the dry weight of all the ants is approximately four times that of all the land vertebrates (mammals, birds, reptiles, and amphibians) combined. The difference is represented here by the relative size of an ant *(Gnamptogenys)* and a jaguar. (Drawing by Katherine Brown-Wing.)

acres) in the Peruvian rain forest, we and other researchers have identified over 300 species. In a nearby locality we identified 43 species from a single *tree*, almost as many as occur in all of Finland, or all of the British Isles.

Although few such estimates of abundance and diversity have been attempted elsewhere, our strong impression is that ants and other social insects dominate terrestrial habitats in like degree throughout most of the rest of the world. All together, these creatures seem likely to constitute half or more of the insect biomass. Consider the following disproportion: only 13,500 species of highly social insects are known (9,500 of which are ants) out of a grand total of 750,000 insect species that have been recognized to date by biologists. Thus more than half the living tissue of insects is made up of just 2 percent of the species, the fraction that live in well-organized colonies.

We believe that the anomaly is due in large part to a struggle for existence based on harsh, direct competitive exclusion. The highly social insects, particularly the ants and termites, occupy center stage in the terrestrial environment, in the literal sense of having evicted silverfish, hunting wasps, cockroaches, aphids, hemipteran bugs, and most other kinds of solitary insects from the most desirable, stable nest sites. The solitary forms tend to occupy more remote and transient resting places, such as distant twigs, the extremely moist or dry or excessively crumbling pieces of wood, the surfaces of leaves, and the newly exposed soil of stream banks. As a rule, they are also either very small, or fast moving, or cleverly camouflaged, or heavily armored. At the risk of oversimplification, we envisage an overall pattern of ants and termites at the ecological center, solitary insects at the periphery.

How have ants and other social insects come to lord over the terrestrial environment? In our opinion their edge comes directly from their social nature. There is strength in numbers, if all the minions are programmed to act in concert. This quality is not, of course, unique to the insects. Social organization has been one of the most consistently successful strategies in all of evolutionary history. Consider that the coral reefs, which cover much of the floor of the shallow tropical seas, are composed of colonial organisms, sheetlike masses of anthozoan zooids, to be exact, which are distant relatives of the solitary and less abundant jellyfish. And that human beings, the most dominant mammals in geological history, are also by far the most social.

The most advanced social insects, those forming the biggest and most complicated societies, have attained this rank through a combination of three biological traits: the adults care for the young; two or more generations of adults live together in the same nest; and the members of each colony are divided into a reproductive "royal" caste and a nonreproductive "worker" caste. This elite group, which entomologists call eusocial (meaning "truly" social), is made up mainly of four familiar groups:

All of the *ants*, composing in formal taxonomic classification the family Formicidae of the order Hymenoptera, contain about 9,500 species known to science and at least twice that number of species remaining to be discovered, most of which are confined to the tropics.

Some of the *bees* are eusocial. At least ten independent evolutionary lines within the Halictidae (sweat bees) and Apidae (honeybees, bumblebees, and stingless bees) have reached the eusocial level. They contain about a thousand species known to science. A much larger number of bee species are solitary, including a large majority of the sweat bees.

Some of the *wasps* are also eusocial. About 800 species in the family Vespidae and a handful in the Sphecidae are known to have reached this evolutionary level. But they represent a minority, just as in the bees. Tens of thousands of other wasp species, scattered through many taxonomic families, are solitary.

All *termites*, composing an entire order on their own (the Isoptera), are eusocial. Descended from cockroach-like ancestors as far back as 150 million years ago, early in the Mesozoic Era, these curious insects have converged in evolution toward ants in superficial appearance and social behavior, but they have nothing else in common. About 2,000 species of termites are known to science.

In our view, the competitive edge that led to the rise of the ants as a world-dominant group is their highly developed, self-sacrificial colonial existence. It would appear that socialism really works under some circumstances. Karl Marx just had the wrong species.

The advantage of ants comes to the fore in the arena of labor efficiency. Consider the following scenario. A hundred solitary female wasps are pitted against an ant colony with the same number of workers, also all female. The two aggregations nest side by side. In a typical daily action, one of the wasps digs a nest and captures a caterpillar, a grasshopper, a fly or some other prey to serve as provender for her offspring. Next she lays an egg on the prey and closes the nest. The egg will hatch into a grublike larva, which will feed on the insect provided and in time emerge as a new adult wasp. If the mother wasp falters in any one of the serial tasks up to the sealing of the nest, or if she tries to perform them in the wrong sequence, the entire operation fails.

Nearby an ant colony, functioning as a *social unit*, overcomes all these difficulties automatically. A worker starts to dig a chamber to expand the colonial nest, where larvae will eventually be moved and fed to produce additional members of the colony. If the ant fails at any step of her sequence, all the necessary tasks will probably be finished anyway, so that the colony will continue to grow. A sister worker will simply move in and complete the excavation; other sisters can be counted on to transport larvae to the chamber, and still others to bring food. Many of the ants are "patrollers." On stand-by status, these individuals travel restlessly through the corridors and rooms, addressing each contingency they encounter, switching back and forth from one task to the other as needed. They complete the sequence of steps more reliably and finish in less time than could solitary laborers. They are like gangs of factory workers who move back and forth among the assembly lines according to momentary need and opportunity, improving the efficiency of the overall operation.

The grand strategy of social life becomes most obvious during territorial disputes and competition for food. Ant workers enter combat more recklessly than do solitary wasps. They can act like six-legged kamikazes. The solitary wasp has no such choice. If she is killed or injured, the Darwinian game is over, just as it would be if she had blundered during her labors and aborted the necessary rounds of nest construction and provisioning. Not so the ant. She is nonreproductive to start with and if lost will be quickly replaced by a new sister born back in the nest. So long as the mother ant queen is protected and continues to lay eggs, the death of one or a few workers will have little effect on the representation of the colony members in the future gene pool. What counts is not the total population of the colony but the number of virgin queens and males released into the nuptial flights that are successful at starting new colonies. Suppose that the war of attrition between ants and solitary wasps continues until almost all the ant workers are destroyed. So long as the queen lives through the encounter, the ant colony wins. The queen and surviving workers will rebuild the worker population rapidly, allowing the colony to reproduce itself by producing virgin queens and males. The solitary wasp, the equivalent of an entire colony, will long since have perished.

This built-in competitive superiority of colonies against wasps and other solitary insects means that colonies can retain prime nest sites and feeding areas for the natural life of the mother queen. In some species she lives more than twenty years. In others, where young queens return home after being mated, the colony has even greater potential: the nests and territories can be passed from one generation to the next. To heredity, then, is added the inheritance of property. The nests of mound-building ants, such as the Formica wood ants of Europe, often last for many decades, churning out queens and males year after year. Such colonies are in fact potentially immortal, even though the individual queens at their center are continually dying and being replaced.

There is still more to the power of the superorganism that is an ant colony. Building larger nests than individual solitary wasps and holding on to them for longer periods of time, ant colonies devise physical structures elaborate enough to regulate the climate. Workers of some species drive tunnels deep beneath the surface to reach soil containing more moisture. Those of others excavate galleries and chambers that radiate outward in a way that increases the flow of fresh air through their living quarters. During short-term emergencies architecture is augmented by rapid mass responses. In many species, when the nest dries out during droughts or excessive heat, workers form loosely organized bucket brigades, dashing back and forth in short lines, passing water from mouth to mouth, and finally regurgitating it onto the nest floor and walls. When enemies break through the nest wall some of the workers attack the invaders while others rescue the young or rush to repair the damage.

Colonial life may be an ancient phenomenon by human standards, but it is a relatively recent development in the overall evolution of the insects. It covers only about half of their geological time on earth. Insects were among the first creatures to colonize the land, arising as far back as the Devonian period, some 400 million years ago. They diversified richly in the swamps of the Coal Age that followed. By Permian times, about 250 million years ago, forests teemed with cockroaches, hemipteran bugs, beetles, and dragonflies not much different from those living today, mingled with beetle-like protelytropterans; protodonates, resembling huge dragonflies, with wings up to 3 feet across; and other insect orders now extinct. The first termites probably arose in the Jurassic or early Cretaceous Periods, roughly 200 million years before the present, and ants, social bees, and social wasps in the Cretaceous Period some 100 million years later. The eusocial insects as a whole, particularly the ants and termites, became dominant among the insects no later than the beginning of the Tertiary Period, 50 to 60 million years ago.

The sheer magnitude of this history, stretching back more than a hundred times beyond the entire life span of the genus *Homo*, presents a paradox. Why, if colonial life has such great advantages for insects, was it delayed for 200 million years? And why, 200 million years after the innovation finally occurred, aren't all insects colonial? These questions are better asked by turning them around: What advantages, not yet mentioned, might solitary life have over social life? The answer, we believe, is that solitary insects breed faster and do better with limited, ephemeral resources. By picking up the pieces left over by the ants and other eusocial insects, they fill transient niches.

It may seem odd to say that the highly social insects breed more slowly than their solitary counterparts. Colonies are after all little factories crowded with workers devoted to the mass production of new nestmates. But the fact of central importance is that the colony, not the workers, is the unit of reproduction. Where every solitary wasp is a potential mother or father, only one out of hundreds or thousands of the members of an ant colony can fill that role. In order to create virgin queens capable of founding new colonies, the mother colony—the superorganism, the unit of reproduction—must first produce a crop of workers. Only then can it reach the stage equivalent to sexual maturity in a solitary organism.

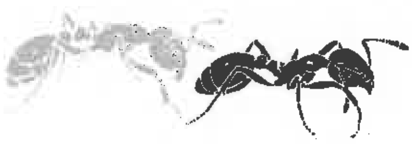
Being a massive organism, the colony must also have a large base from which to operate. It dominates the logs and fallen branches but concedes the scattered leaves and flakes of bark to the fast-moving, fast-breeding solitary insects. It controls the stable river banks but gives up the transient mud bars farther out. It spreads more slowly from one feeding place to the next because all the population must be mobilized before any one member can safely emigrate.

Solitary insects are therefore better pioneers. They can reach small windfalls in distant places—a seedling in a patch of new ground, a twig washed downstream, a new sprig of leaves—more quickly and flourish there for longer periods of time. Ant colonies in contrast are ecological juggernauts. They take time to grow up, they move about slowly, but once in motion they are very difficult to stop.

For the Love of Ants

DURING the 1960s and 1970s the scientific study of ants accelerated, swept forward by the general revolution in biology. In short order entomologists discovered that colony members communicate most of the time through the taste and smell of chemicals secreted from special glands throughout the body. They conceived the idea that altruism evolves by kin selection, the Darwinian advantage gained by the selfless care of brothers and sisters, who share the same altruistic genes and thus transmit them to future generations. And they established that the elaborate caste systems—queens, soldiers, workers, the signature trait of the ant societies—are determined by food and other environmental factors and not by genes.

In the fall of 1969, in the midst of this exciting period, Hölldobler knocked on Wilson's office door at Harvard University at the beginning of a term as Visiting Scholar. Although we didn't think of ourselves that way at the time, we met as representatives of two scientific disciplines, born of different national scientific cultures, whose synthesis was soon to lead to a better understanding of ant colonies and other complex animal societies. One discipline was ethology, the study of behavior under natural conditions. This branch of behavioral biology, conceived and developed mostly in Europe during the 1940s and 1950s, differed sharply from traditional American psychology by its emphasis on the importance of instinct. It also stressed how behavior adapts animals to those special parts of the environment on which the survival of the species depends. It singled out which enemies to avoid, which food items to hunt, the best places to build nests, where and with whom and how to mate, and so on through each step of the intricate life cycle. Ethologists were above all (and many so remain) naturalists of the old school, outfitted with muddy boots, waterproof notebooks, and sweat-soaked binocular straps chafing the neck. But they were also modern biologists who used experiments to dissect the elements of instinctive behavior. In combining these two approaches to become more scientific, they discovered "sign stimuli," the relatively simple cues that trigger and guide stereotyped behaviors in animals. For example, a red belly on



a male stickleback fish, really no more than a red spot to the animal eye, provokes a full territorial display in a rival stickleback male. The males are programmed to react to the splash of color and not to the look of a whole fish, at least not to what we as human beings see in a whole fish.

The annals of biology are now filled with such examples of sign stimuli. The smell of lactic acid guides the yellow-fever mosquito to its victim; a flash of ultraviolet reflecting wings identifies a male sulfur butterfly to the waiting female; a dash of glutathione in the water causes the hydra to stretch its tentacles in the direction of suspected prey; and so on bit by bit through the vast repertory of animal behavior, now well understood by ethologists. Animals, they realized, survive by responding swiftly and precisely to the fast-moving environment, hence the reliance on simple pieces of their sensory world. The responses in turn must often be complex, unlike the sign stimuli, and delivered in exactly the right manner. Animals are rarely given a second chance. And because all this repertory has to be accomplished with little or no opportunity to learn anything in advance, it must have a strong automatic, genetic basis. The nervous system of animals, in short, must to a substantial degree be hard-wired. If that much is true, the ethologists reasoned, if behavior is hereditary and shaped in a manner peculiar to each species, then it can be studied element by element, with the time-honored techniques of experimental biology, as though it were a piece of anatomy or a physiological process.

By 1969 the idea that behavior could be broken apart into atomic units had energized the entire generation of behavioral biologists to which we belonged. The effect was enhanced personally for us by the fact that one of the founders of ethology was a great Austrian zoologist who was a professor at the University of Munich in Germany with interests similar to our own. Karl von Frisch was and remains one of the most famous biologists in the world, praised for his discovery of the waggle dance, the elaborate movements in the hive by which honeybees inform their nestmates about the location and distance of food finds outside. The waggle dance remains to this day the closest approach to a symbolic language known in the animal kingdom. More generally, von Frisch was esteemed among biologists for the ingenuity and elegance of his many experiments on animal senses and behavior. In 1973 he shared the Nobel prize in Physiology or Medicine with his fellow Austrian Konrad Lorenz, former director of the Max Planck Institute for Behavioral Physiology in Germany, and with Nikko Tinbergen of the Netherlands, a professor at Oxford University in England, for the leading role the three men played in the development of ethology.

The second watershed tradition leading to a new understanding of animal societies was largely of American and British origin, with approaches radically different from those of ethology. It was population biology, the study of the properties of entire populations of organisms, how they grow as an aggregate, spread across the landscape, and, inevitably, retreat and vanish. The discipline relies as much on mathematical models as on field and laboratory studies of live organisms. Very like demography, it deduces the fate of populations by tracing the birth, death, and movements of the individual organisms, in order to plot overall trends. It also tracks gender, age, and the genetic makeup of the organisms.

As we began our collaboration at Harvard, we understood that ethology and population biology fit together wonderfully well in the study of ants and other social insects. Insect colonies are little populations. They can be understood best by following the life and death of the swarming legions that compose them. Their hereditary makeup, especially the kinship of their members, predetermines their cooperative nature. The things we learn from ethology about the details of communication, colony founding, and caste come together and make complete sense only when they are viewed as evolutionary products of whole colony populations. That in a nutshell is the basis for the new discipline of sociobiology, the systematic study of the biological basis of social behavior and of the organization of complex societies.

As we began conversations on this synthesis and our research agendas, Wilson was a professor at Harvard, 40 years old; Hölldobler, at 33, was on leave from a lectureship at the University of Frankfurt. Three years later, after a brief return to teach at Frankfurt, Hölldobler was invited to Harvard as a full professor. Thereafter the friends shared the fourth floor of the newly constructed laboratory wing of the university's Museum of

Comparative Zoology until, in 1989, Hölldobler returned to Germany to direct a department entirely devoted to the study of social insects in the newly founded Theodor Boveri Institute of Biosciences of the University of Würzburg.

Science is said to be the one culture that truly rises above national differences, melding idiosyncratic differences into a single body of knowledge that can be simply and elegantly expressed and generally accepted as true. We entered its domain by markedly different routes of academic tradition, but impelled by a common childhood pleasure in the study of insects and by the approval and encouragement of adults at a critical time of our mental development. To put the matter as simply as possible we, having entered our bug period as children, were blessed by never being required to abandon it.

For Bert, the beginning was on a lovely early summer day in Bavaria just before massive air raids brought World War II home to Germany. He was 7 years old and had just been reunited with his father, Karl, a doctor on duty with the German army in Finland. The elder Hölldobler had obtained a furlough to visit his family at Ochsenfurt. He took Bert on a walk through the woods, just to look around and talk. But this was not quite an ordinary stroll. Karl, an ardent zoologist, had a particular interest in ant societies. He was an internationally known expert on the many curious small wasps and beetles that live in ant nests. It was natural on this occasion for him to turn over rocks and small logs along the trail to see what was living underneath. Rooting through the soil to see its teeming life is, he understood well, one of the pleasures of entomology.

One rock sheltered a colony of large carpenter ants. Caught for an instant in the sunlight, the shiny blackish-brown workers rushed frantically to seize and carry grublike larvae and cocoon-encased pupae (their immature sisters) down the subterranean channels of the nest. This sudden apparition riveted young Bert. What an exotic and beautiful world, how complete and well formed! A whole society had revealed itself for an instant, then trickled magically out of sight, like water into dry soil, back to the subterranean world to resume a way of life strange beyond imagination.

After the war the Hölldobler home in the little medieval town of

Ochsenfurt, close to Würzburg, was filled with pets, at various times including dogs, mice, guinea pigs, a fox, fish, a large salamander called an axolotl, a heron, and a jackdaw. A guest of special interest to Bert was a human flea, which he kept in a vial and allowed to feed on his own blood, in an early attempt at scientific research.

Above all, encouraged by the example of his father and the loving patience of his mother, Bert kept ants. He gathered live colonies and studied them in artificial nests, learning the local species, drawing their distinctive anatomical traits, and observing their behavior. All the while his enthusiasms bubbled over. On top of everything else he collected butterflies and beetles as yet another hobby. He was imprinted on the diversity of life, the die was cast, and his hopes now centered on a career in biology.

In the fall of 1956, Bert entered the nearby University of Würzburg, intending to teach biology and other sciences in high school. By the time he took his final examination, however, he had lifted his horizons. He gained admittance to the graduate program of the university, now aiming for a doctoral degree. His teacher at this new level was Karl Gösswald, a specialist on wood ants. These large red and black insects, swarming by the millions per hectare, build mound nests that dot the forests of northern Europe. Gösswald wished to develop propagation methods by which the ants could control the caterpillars and other pests of the forest vegetation, without the intervention of insecticides. For generations European entomologists had noticed that whenever an outbreak of leaf-eating insects occurred, trees around the ant mounds remained healthy, with their foliage more or less intact. The protection was clearly the result of predation of the pests by the ants. Direct counts revealed that one wood-ant colony can harvest in excess of 100,000 caterpillars in a single day.

An early pioneer of forest entomology, Karl Escherich, spoke of the "green islands" that exist under the protective shield of the wood ants. Escherich was a student at the University of Würzburg in the 1890s, working under the tutelage of Theodor Boveri, at that time the most celebrated embryologist in the world. By fortunate coincidence, William Morton Wheeler, later to become America's leading myrmecologist, was at that time also an embryologist, and he visited Würzburg for two years as a young scholar. He was soon to switch his main research activity to ants. (Later, in 1907, he settled at Harvard as professor of entomology—thus he was Wilson's predecessor.) He conveyed his early enthusiasm for ants to young Escherich, who, partly as a result of Wheeler's influence, abandoned an interest in medicine and turned to forest entomology. His multivolume masterwork on the subject, completed in later life, influenced an entire generation of German researchers, among them Karl Gösswald. Initially, however, it was none other than Karl Hölldobler, then an advanced student of medicine and zoology at Würzburg, who introduced Gösswald to myrmecology. He encouraged the younger student to explore the rich ant fauna of the limestone area along the Main River in Franconia, a part of northern Bavaria. The work became the basis of Gösswald's doctoral thesis. So the two lineages run as follows: first, Wheeler–Escherich–Karl Hölldobler–Gösswald–Bert Hölldobler and, second, Wheeler–Frank M. Carpenter (Wilson's teacher at Harvard)–Wilson, starting in Würzburg with Wheeler, then separating, and finally, as we shall see, looping back to touch the German enterprise again at Harvard. Such is the reticulate structure of heritage in the scientific world.

Bert was far from exclusively guided by Gösswald while at Würzburg. Because of his father's friendship with other myrmecologists in the postwar years, he met many fellow enthusiasts before he entered the university. Among them were Heinrich Kutter of Switzerland and Robert Stumper of Luxembourg. Bert was attracted to forest entomology, but the mental gyroscope he had acquired as a child brought him back inevitably to the ants. At that time he was also inspired by Hans-Jochem Autrum, who gave lectures in zoology and, as one of the foremost neurophysiologists in the world, served as an inspiring role model.

One of Bert's first assignments, while he was still an undergraduate student, was a trip to Finland to conduct a north-to-south survey of wood ants. It was a full-time job, but Bert could not keep his eyes off the equally prominent carpenter ants, including the species that had conjured magic beneath the stone at Ochsenfurt. He felt nostalgia in visiting the forests of Karelia, where his father had spent the war under difficult and often dangerous conditions. Now it had become the scene for a leisurely exploration of a little-known fauna. Much of Finland was, and remains, a wilderness country, especially the northern reaches. Searching through its forests and glades, filled with mostly unstudied insect life, cemented Bert's commitment to field biology.

His mind was turning away from the kind of applied entomology emphasized by Karl Gösswald, and more toward the basic research favored by his instincts and early training. About three years after the Finland trip he learned of a graduate studies program at the University of Frankfurt headed by Martin Lindauer, one of von Frisch's most gifted students, and generally regarded as the great man's intellectual successor. In the 1960s Lindauer and his own protégés were in the midst of an exciting new wave of research on honeybees and stingless bees, and Frankfurt had become the center of what is aptly called the von Frisch–Lindauer school of animal behavior studies. Its tradition was not just a professional staff and a set of techniques but a philosophy of research based on a thorough, loving interest in—a *feel* for—the organism, especially as it fits into the natural environment. Learn the species of your choice every way you can, this whole-organismic approach stipulates. Try to understand, or at the very least try to imagine, how its behavior and physiology adapt it to the real world. Then select a piece of behavior that can be separated and analyzed as though it were a bit of anatomy. Having identified a phenomenon to call your own, press the investigation in the most promising direction. And don't hesitate to ask new questions along the way.

Every successful scientist has a small number of personal ways of coaxing discoveries out of nature. Von Frisch himself had two in which he attained great mastery. The first was the close examination of the flight of honeybees from hive to flowers and back again, a part of the life of bees that can be easily watched and manipulated. The second was the method of behavioral conditioning by which von Frisch combined stimuli, such as the color of a flower or the smell of a fragrance, with a subsequent meal of sugar water. In later tests, bees and other animals will then respond to the stimuli, provided they are strong enough to be detected. Using this simple technique, von Frisch was the first to demonstrate conclusively that insects can see color. He discovered that honeybees can also see polarized light, a capacity not possessed by human beings. The bees use polarized light to estimate the position of the sun, and take a compass reading, even when the sun is hidden behind clouds.

After Hölldobler completed the requirements for his doctoral degree at Würzburg in 1965, he moved to Frankfurt to work under Lindauer. The German doctoral students and young postdoctoral researchers he joined there were an outstanding group of young scientists, destined for leadership in the study of social insects and behavioral biology. They included Eduard Linsenmair, Hubert Markl, Ulrich Maschwitz, Randolf Menzel, Werner Rathmayer, and Rüdiger Wehner. Wehner was later to move to the University of Zurich, where he pioneered in the visual physiology and orientation of bees and ants.

This circle and these environs proved to be Bert's natural intellectual home. Given freedom to study the subject that had enchanted him since childhood, and encouraged by von Frisch himself, he set to work full time on new projects in the behavior and ecology of ants. In 1969 he received his habilitation, the equivalent of a second doctorate and the certification needed in Germany to become an instructor with classes of one's own. He began his new career by visiting Harvard University for two years, then returned briefly to teach at the University of Frankfurt, and in 1972 came back to Harvard. Thus began the main part of his twenty-year collaboration with Wilson.

In 1945, not long after Hölldobler's childhood encounter with the Ochsenfurt ant colony, Ed Wilson had recently moved from his hometown of Mobile to Decatur, a northern Alabama city named for Stephen Decatur, the War of 1812 hero renowned for his postprandial toast, "Our country! May she always be right; but our country, right or wrong." True to its honorand, Decatur was a municipality of right thinking and attention to civic duty. Having reached 16 years of age, Ed, also known as Bugs or Snake to his friends, believed he should be preparing for his future in a serious manner. The time had come to say farewell to the Boy Scouts of America, where he had earned the rank of Eagle Scout, to move past mere snake catching and bird watching, to defer involvement with girls—for a while anyway—and above all to give careful thought to his future career as an entomologist.

He believed that the best route was to acquire expertise on some group of insects that offered opportunities for scientific discovery. His first choice was the Diptera, the order of flies, and especially the family Dolichopodidae, sometimes called long-legged flies, glittering little metallic green and blue insects found dancing in mating rituals on the sunlit upper surfaces of leaves. The opportunities were extensive; over a thousand kinds occur in the United States alone, and Alabama itself was mostly unexplored. But Ed was thwarted from fulfilling this first ambition. The war had shut off the supply of insect pins, the standard equipment used to preserve and store specimens of flies. These special black, ball-headed needles were manufactured in Czechoslovakia, which at that time was still under German occupation.

He needed a kind of insect that could be preserved with equipment immediately at hand. So he turned to ants. The hunting grounds were the wooded lots and fields along the Tennessee River. The equipment, consisting of 5-dram prescription bottles, rubbing alcohol, and forceps, could be bought in small-town pharmacies. The text was William Morton Wheeler's 1910 classic *Ants*, which he bought with earnings from his morning delivery route for the city newspaper, the *Decatur Daily*.

Six years previously the seeds had been set for a career as a naturalist, but not in the outdoors of Alabama. At that time Ed's family lived in the heart of Washington, D.C., close enough for a short automobile drive to the Mall for Sunday outings and, more important for an embryo naturalist, within walking distance of the National Zoo and Rock Creek Park. Adults saw this part of the capital for what it was in human terms, a decaying urban neighborhood close to the high-energy center of government. For a 10-year-old, however, it was a region teeming with the fragments and emissaries of an enchanted natural world. On sunny days, carrying a butterfly net and cyanide killing jar, Ed wandered through the zoo to stand as close as possible to elephants, crocodiles, cobras, tigers, and rhinoceroses, and then, a few minutes later, he walked onto the back roads and woodland paths of the park to hunt for butterflies. Rock Creek Park was the Amazon jungle writ small, in which Ed, often accompanied by his best friend, Ellis MacLeod (now a professor of entomology at the University of Illinois), could live in his imagination as an apprentice explorer.

Above: Bert Hölldobler *(left)* as a 14-year-old entomologist hunting butterflies in a northern Bavarian field (1950), and Ed Wilson *(right)* at 13 years on an entomological expedition near his home in Mobile, Alabama (1942). *Below:* Hölldobler, on the left, and Wilson, on the right, examine a carpenter-ant nest in Bavaria, May 1993. (Bottom photograph by Friederike Hölldobler; top right photograph by Ellis MacLeod.)

On other days Ellis and Ed took streetcar rides to the National Museum of Natural History to explore the exhibitions of animals and habitats and pull out trays of pinned butterflies and other insects from around the world. The diversity of life displayed in this great institution was dazzling and awe-inspiring. The curators of the National Museum seemed knights of a noble order, educated to unimaginably high levels. The director of the National Zoo loomed even more heroic in this 1939 city of civic opportunity. He was William M. Mann, by odd coincidence a myrmecologist himself, a former student of William Morton Wheeler at Harvard who had studied ants at the National Museum and then transferred to the National Zoo as its director.

In 1934 Mann had published an article on his original scholarly interest, "Stalking Ants, Savage and Civilized," in the *National Geographic*. Ed eagerly studied the piece and then went out to search for some of the species in Rock Creek Park, excited by the knowledge that the author himself worked close by. One day he had an experience similar to Bert's epiphanous encounter with the carpenter-ant colony of Ochsenfurt. Climbing up a wooded hillside with Ellis MacLeod, he pulled away the bark of a rotting tree stump just to see what lived underneath. Out poured a roiling mass of brilliant yellow ants, emitting a strong lemony odor. The chemical substance, as later research was to reveal (by Ed himself, in 1969), was citronellal, and the worker ants were expelling it from glands in their heads to warn nestmates and drive off enemies. The ants were "citronella ants," members of the genus *Acanthomyops*, whose workers are nearly blind and completely subterranean. The force in the stump quickly thinned and vanished into the dark interior. But it left a vivid, lasting impression on the boy. What netherworld had been briefly glimpsed?

In the fall of 1946 Ed arrived at the University of Alabama, at Tuscaloosa. Within days he called on the chairman of the Biology Department, preserved ant collection in hand, thinking it normal or at least not outrageous for a beginning student to announce his professional plans in such a manner and to begin, as part of undergraduate studies, research in the field of his choice. The chairman and other biology professors did not laugh or wave him away. They were gracious to the 17-year-old. They gave him laboratory space, a microscope, and frequent warm encouragement. They took him along on field trips to natural habitats around Tuscaloosa and listened patiently to his explanations of ant behavior. This relaxed, supportive ambience was formative in a decisive manner. Had Ed gone to Harvard, where he now teaches, and been thrust into a packed assemblage of valedictorian overachievers, the results might have been different. (But perhaps not. There are many odd niches at Harvard where eccentrics flourish.)

In 1950, with bachelor's and master's degrees completed, Ed moved to the University of Tennessee to begin work on his Ph.D. There he might have remained, since the southern states and their rich ant faunas seemed world enough. But he had fallen under the spell of a distant mentor, William L. Brown, seven years his senior, who was just then completing a doctorate at Harvard. Uncle Bill, as he was to be affectionately called by fellow myrmecologists in later years, was a soulmate, fixated on the subject of ants. Brown took a global approach to these insects, thinking the faunas of all countries equally interesting. His spirit was deeply professional and responsible, seeking legitimacy for small creatures all too easily waved aside. Our generation, he explained to Ed, must revamp biological knowledge and reclassification of these wondrous insects, and assign them major scientific importance in their own right. And don't be intimidated, he added, by the achievements of Wheeler and other famous entomologists of the past. These people are overrated to a stultifying degree. We can and will do better; we must. Take pride, be careful in mounting your specimens, obtain reprints for ready reference, widen your studies to many kinds of ants, expand your interests beyond the southern United States. And while you are at it, find out what dacetine ants eat (Ed then confirmed that dacetines prey on springtails and other soft-bodied arthropods).

And above all, come to Harvard, which has the largest collection of ants in the world, for your Ph.D. The following year, after Brown had departed for Australia to conduct fieldwork on that little-studied continent, Ed did transfer to Harvard. He remained there for the rest of his career, in time attaining a full professorship and the curatorship of insects, positions previously held by William Morton Wheeler, and he even inherited Wheeler's old desk, complete with pipe and tobacco pouch in the lower right-hand drawer. In 1957 he visited William Mann at the National Zoo in Washington. The elderly gentleman, in his last year as director, gave Ed his library on ants. Then he took Ed and his wife, Renee, on a tour of the zoo—past the elephants, leopards, crocodiles, cobras, and other wonders, along the fringes of Rock Creek Park, and thus, for an enchanted hour, back into the dreams of Ed's childhood. He could not have known the thrill that the closure of the life cycle gave to the aspiring young professor.

The years at Harvard were crowded with work in the field and the laboratory. The result was more than two hundred scientific publications. Wilson's interests expanded occasionally into other domains of science and even human behavior and the philosophy of science, but the ants remained his talisman and enduring source of intellectual confidence. Twenty of his most productive years on these insects were spent in close contact with Hölldobler. Sometimes the two entomologists worked separately on their own projects, on other occasions as a two-person team, but always they enjoyed nearly daily consultations. In 1985, Hölldobler began to receive irresistibly attractive offers from universities in Germany and Switzerland. When it was evident that he might actually go, he and Wilson decided to write as thorough a treatise as possible on ants, to serve as a vade mecum and definitive reference work for others. The result was *The Ants*, published in 1990, dedicated to "the next generation of myrmecologists" and replacing at last Wheeler's magnum opus of 80 years' standing. It was the surprise winner of the 1991 Pulitzer Prize in General Nonfiction, the first unabashed scientific work to be so honored.

At this time our careers had come to a fork in the road. The examination of social insects, like most of the rest of biology, had reached a high level of sophistication that required ever more elaborate and expensive equipment. Where previously rapid advances in behavioral experimentation could be made by a single investigator with little more than forceps, microscope, and a steady hand, now there was and remains a growing need for groups of investigators working at the level of the cell and molecule. Such concentrated effort is especially needed to analyze the ant brain. All of ant behavior is mediated by a half million or so nerve cells packed into an organ no larger than a letter on this page. Only advanced methods of microscopy and electrical recording can penetrate this miniature universe. High technology and cooperative efforts among scientists with different specialties are also needed to analyze the almost invisible vibrational and touch signals used by ants in social communication. They are absolutely necessary to detect and identify the glandular secretions used as signals; some of the key compounds are present in amounts of less than a billionth of a gram in each worker ant.

The University of Würzburg offered the facilities to attain this level of expertise. Martin Lindauer, his mentor, had moved there in 1973 and was now retiring. The university decided to expand the study of social-insect behavior, and asked Hölldobler to accept a chair to lead a new group in behavioral physiology and sociobiology. He chose to go, and thus, a century after William Morton Wheeler's visiting scholarship, the link between Harvard and Würzburg was reestablished. The Leibniz Prize, a million-dollar research award from the Federal Republic given to build scientific fields in Germany, was awarded to Hölldobler shortly after his arrival. The Würzburg group is now proceeding strongly into experimental studies of the genetics, physiology, and ecology of the social insects.

A different urgency propelled Wilson onto a divergent path. The muse he celebrated had always been biological diversity—its origins, quantity, and impact on the environment. By the 1980s biologists had become fully aware that human activities are destroying biodiversity at an accelerating rate. They had made the first crude estimates of this erosion, projecting that, largely through destruction of natural habitats, fully one-quarter of the species on earth could disappear within the next 30 or 40 years. It was becoming clear that in order to meet the emergency, biologists must map the diversity around the world far more precisely than ever before, pinpointing the habitats that both contain the largest number of distinctive species and are the most threatened. The information is needed to assist the salvage and scientific study of endangered forms. The task is urgent and has only begun. As few as 10 percent of the species of plants, animals, and microorganisms have received so much as a scientific name, and the distributions and biology of even this group are poorly understood. Most diversity studies depend on the best-known—"focal"—groups, in particular mammals, birds and other vertebrates, butterflies, and flowering plants. Ants are an additional candidate for elite status, being especially suitable because of their great abundance and conspicuous activity throughout the warm season.

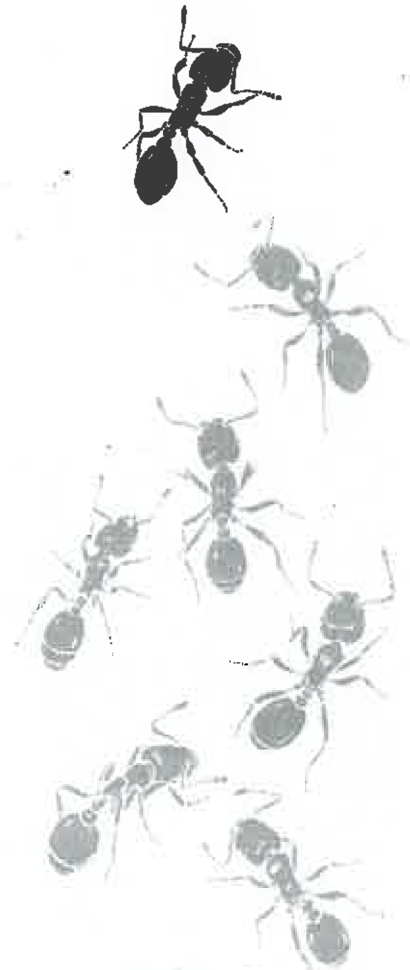
Now as in previous years, Harvard University has the largest and most nearly complete ant collection in the world. Wilson felt an obligation beyond a natural attraction to the subject to harness the collection in the effort to make ants a focal group of biodiversity studies. In collaborating with Bill Brown, now at Cornell University, he set out to scale the Mt. Everest of ant classification: a monograph on *Pheidole*, by far the largest genus of ants, with a thousand or more species to analyze and classify. Their effort when completed will include descriptions of 350 new species from the Western Hemisphere alone.

Hölldobler and Wilson still manage to meet and collaborate in field studies once a year, in Costa Rica or Florida. There they hunt for new and poorly known kinds of ants, Wilson to add to the full measure of diversity, Hölldobler to select the most interesting species for close study at Würzburg. Meanwhile, myrmecology is rising in popularity among scientists. The eccentric tinge is gone, although the netherworld has lost none of its alien mystery.

The Strangest Ants

DURING their hundred-million-year history, the ants have pressed to startling extremes of adaptation. Some of the most specialized forms are virtually beyond imagination—they could not have been easily fantasized in advance by the entomologists who were to stumble upon them in the field. What follows is a kind of formicid bestiary of our own making, a set of tales about species we have personally encountered that push the edges of the evolutionary envelope.

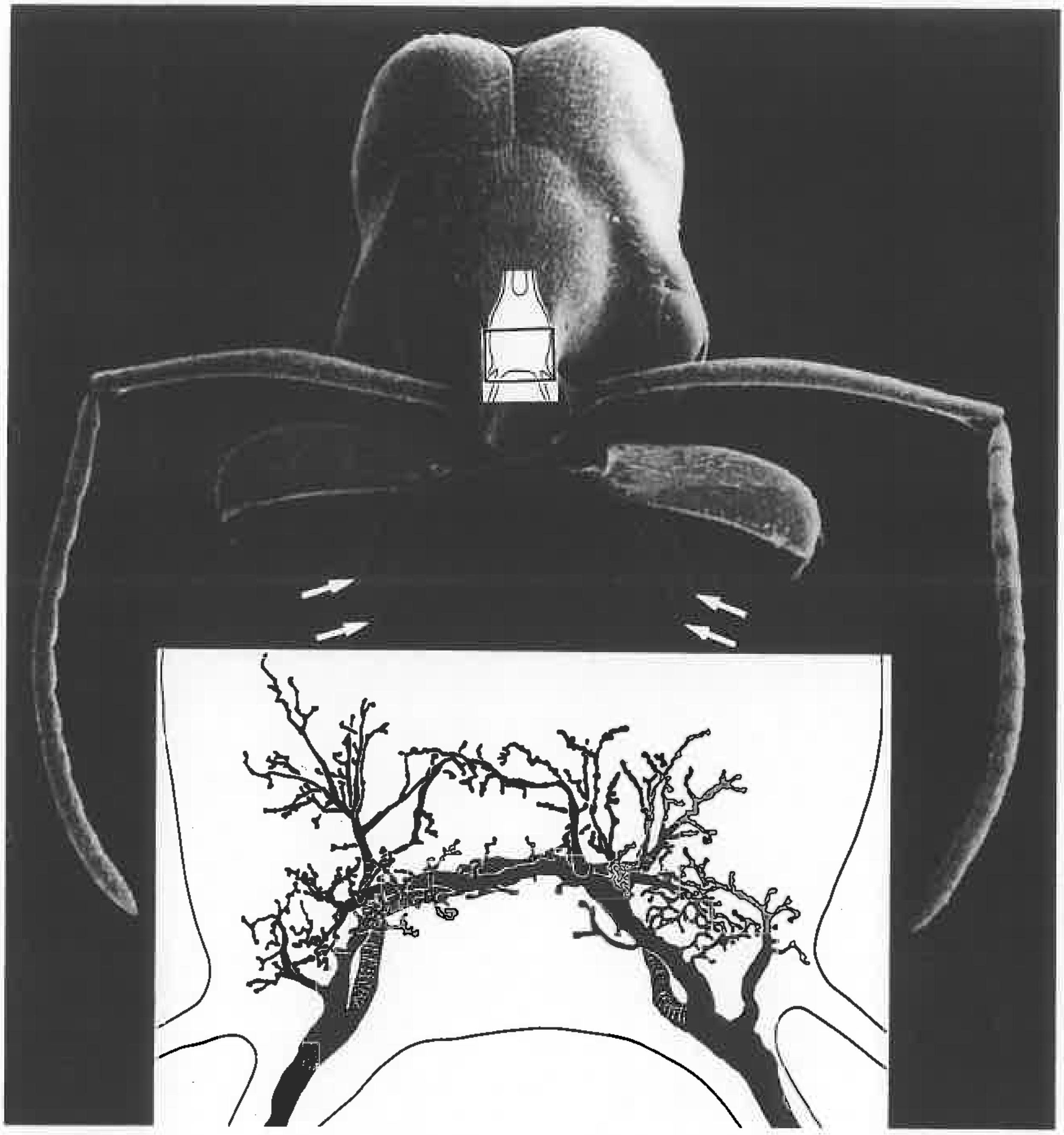
Our story begins in 1942, in a vacant lot next to the Wilson family home in Mobile, Alabama. At the edge of the weed-choked property was a fig tree that bore edible fruit late each summer, Mobile being located close to the American subtropics. Under the tree were scattered pieces of lumber, broken glass bottles, and roofing tiles. Around and beneath this rubbish Ed searched for ants. Just turned 13, he had set out to learn all the species he could find. He was startled to find one ant species radically different from anything he had seen before. Medium-sized, slender, dark brown, and very swift, the workers were armed with strange, thin mandibles that amazingly could be opened 180 degrees. When their nest was disturbed, the ants rushed about with their mandibles fully spread. Ed tried to pick them up with his fingers, but they snapped the mandibles shut like miniature bear traps, piercing his skin with sharp teeth, then followed through almost instantly by bending their abdomens forward and delivering a painful sting. So eager were the ants to attack that many of them snapped their mandibles together on empty air, making a clicking sound. The combined one-two punch was shocking. Ed gave up trying to excavate the nest and capture the colony. Later he learned that the species he had found was *Odontomachus insularis,* and that Mobile is at the northern limit of its range. *Odontomachus* is a genus of many species found in the tropics around the world.



Fifty years later, Bert Hölldobler, in the course of research on the predatory ants of the subfamily Ponerinae, began a detailed study of *Odontomachus bauri,* a species closely similar to the one encountered by Wilson. He and his associates Wulfila Gronenberg and Jürgen Tautz at the University of Würzburg became fascinated by

the blinding speed and force of the jaw closure. So hard is the blow that when the tips of the mandibles strike a hard surface the ant flips itself backward through the air. The researchers set out to record the mandibular closure with the aid of ultra-high-speed cinematography, recording at 3,000 frames a second. To their astonishment they found that the movement of the jaws is not merely fast: it is the fastest of any anatomical structure ever recorded in the animal kingdom! The full strike, from the instant at which the fully opened mandibles start to close to the instant they clash together, takes from between a third of a millisecond to a full millisecond—that is, one-three-thousandths to a thousandth of a second. Previously, the fastest recorded movements had been the jump of a springtail at 4 milliseconds, the escape response of a cockroach (40 milliseconds), the foreleg strike of a preying mantis (42 milliseconds), the tongue "shoot" of a rove beetle to catch prey (1–3 milliseconds), and the leap of a flea (0.7–1.2 milliseconds). The *Odontomachus* mandible is only 1.8 millimeters long, but its spiked tip moves at a velocity of 8.5 meters a second. If the ant were human, its response would be the equivalent of swinging the fist at about 3 kilometers a second—faster than a rifle bullet.

The *Odontomachus* trap-jaw workers can catch any known living creature, provided they can get it within range of their mandibles. They hunt with their jaws open and locked into position, ready for the pull of the massive adductor muscles. A long sensitive hair projects forward from the base of each mandible. During the hunt the *Odontomachus* worker sweeps her antennae back and forth in front of the head. When the smell organs on her antennal surface identify either a prey or an enemy, the ant jerks her head forward, causing the tips of the hairs to touch the target. Inside the mandibles are huge nerve cells that respond to pressure on the hairs. Their axons, the elongated cell stems, are the largest ever recorded in either insects or vertebrates. Their size, Hölldobler's coworkers found, allows them to conduct impulses at extremely high velocity. The reflex arc, running from the receptor cells in the jaw to the brain and back out to the motor cells of the mandibular muscles, takes only 8 milliseconds, the shortest duration recorded in any animal to date. When the electric discharge completes the arc, so that the impulse



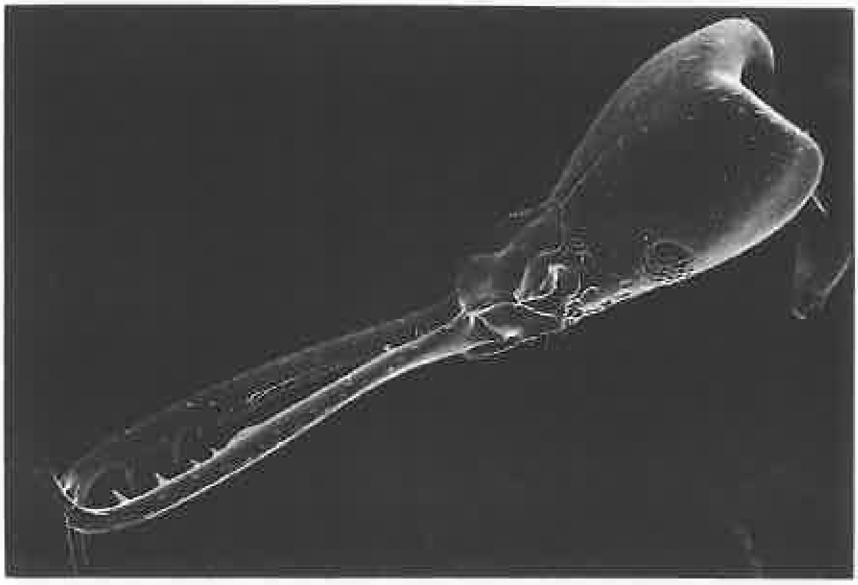
The powerful and swift trap jaws of *Odontomachus.* Here the mandibles of a worker have been opened fully; the arrows point to the sensitive trigger hairs that project forward. The inset reveals the portion of the brain entered by the gigantic nerve cells from these trigger hairs. In the lower drawing this portion of the brain is enlarged, and the nerves are shown in black. (Drawing by Wulfila Gronenberg.)

reaches the muscles, the mandibles close within a millisecond, completing the full behavioral response.

The *Odontomachus* mandibles are filled mostly by giant sensory cells surrounded by air space; the resulting lightness enhances their startling velocity. When they snap together the jaws stun smaller creatures or at least pierce them with the terminal teeth, holding them still while the ant bends its abdomen forward to insert its sting. The mandibular strike is powerful enough to cut some soft-bodied insects in half.

The superfast mandible strike of *Odontomachus* also serves a second, wholly different function. The workers use it as a transport device when attacking intruders. By pointing their heads downward toward a hard surface and closing the mandibles, the ants are able to catapult themselves up into the air—and onto nearby enemies. When Bert Hölldobler touched a nest of a large *Odontomachus* species in a tree at La Selva, Costa Rica, as many as 20 workers snapped their mandibles and sailed about 40 centimeters through the air onto his body. As soon as they landed they began stinging him. Bert stepped back involuntarily. He understood at once how the colonies of this species protect their otherwise vulnerable homes, the walls of which are little more than a thatching of dry vegetable materials.

Other ants with heads like snares are abundant in tropical and warm temperate regions around the world. The *Odontomachus*-like armamentarium has originated many times independently in the course of evolution. As a college student in the late 1940s, Wilson turned his attention to one of these groups, the dacetines, small ants known to hunt springtails. Many species live in Alabama, including members of the genera *Strumigenys, Smithistruma,* and *Trichoscapa,* which until that time had remained almost entirely unstudied. Wilson set out to find all the dacetines he could, searching through woodlands and fields in the central and southern parts of the state. He housed the colonies, which were typically composed of a single queen and a few dozen workers, in artificial nests made from blocks of plaster of Paris. The construction was modified from a design introduced a half century earlier by the French entomologist Charles Janet. To observe his dacetines as closely as possible Wilson carved holes in half of the upper surface to create little chambers and connecting galleries similar to those excavated by the ants



A trap-jawed worker of a Central American species of *Acanthognathus;* the extremely long and slender mandibles are used to capture springtails and other small, swift insects.

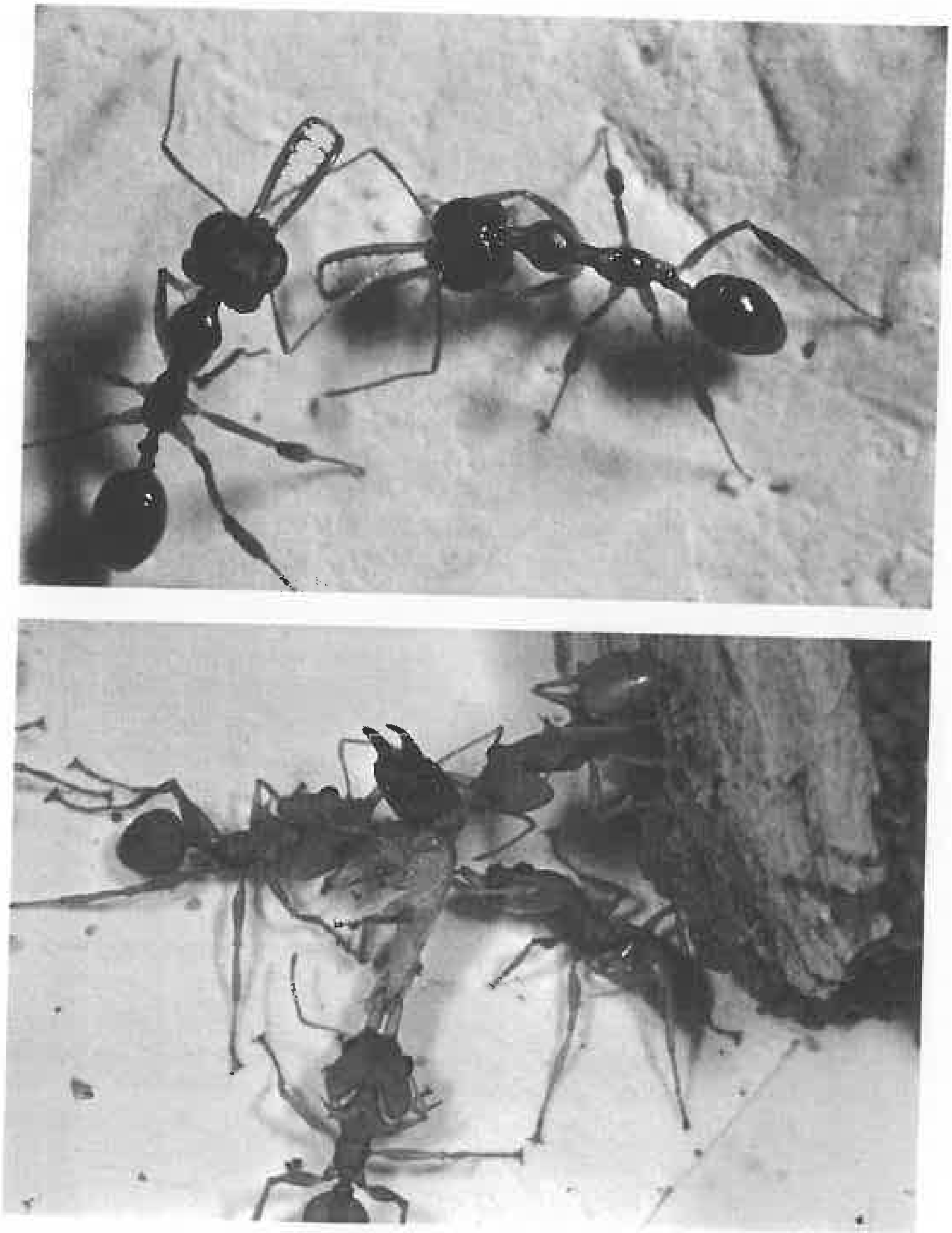
themselves. Into the other half he dug a much larger chamber to serve as the foraging arena of the ants. Then he covered the entire surface with a plate of glass to create a transparent roof. On the floor of the arena he scattered bits of soil and decayed wood to simulate the natural floor of the forest. Into this space, finally, Wilson placed live springtails, mites, spiders, beetles, centipedes, and other small arthropods collected from habitats where the dacetines lived, in order to see which would be hunted by the dacetines—and in what manner. The entire block of plaster was small enough, about the size of two doubled fists, to be fitted onto the stage of a dissecting microscope. So with minimal effort Wilson was able to watch both the dacetine colony in the brood chambers and the workers hunting in the foraging arena, virtually all at the same time.

There are two basic kinds of trap-jawed ants among the dacetine species. One has extremely long, slender mandibles, which the ants open 180° or more, as in *Odontomachus,* and then close with a convulsive snap, impaling the prey on the sharp terminal teeth. The ants move about a great deal while hunting, and stalk insects only for relatively brief periods of time once they have located them. The second group has shorter jaws, which can be opened only about 60 degrees. These short-mandibled dacetines, Wilson discovered, are masters of stealth. As soon as a huntress becomes aware of an insect nearby, she freezes in a crouching position and holds this stance briefly. Then if at an angle to the prey, she slowly turns to face it. She next begins to creep forward, in a movement so slow that it can be detected only by persistent and careful watching and by noting the position of her head relative to bits of soil. Several minutes may pass before the ant comes into striking position. If the prey moves in any way during the stalk, the dacetine freezes again and waits a while before resuming forward movement. Finally she comes within range, whereupon she touches the prey very gently with the tips of the long sensitive hairs that project forward from her head, and closes her mandibles with an explosive snap.

The dacetines studied by Wilson in his miniature terraria displayed a general liking for small soft-bodied arthropods, including symphylans, which resemble centipedes, and diplurans, which look like miniature silverfish. But most of all they relish springtails, tiny wingless insects that possess a forked, taillike appendage beneath the body (the furcula) allowing them to bound instantly and far away at the slightest hint of danger. The release and downward swing of the furcula is one of the fastest movements known in the animal kingdom, exceeded only by the mandibular snap of the *Odontomachus*. The small dacetine ants, using stealth and a convulsive snap of the trap jaws, are among the few animals able to capture springtails consistently.

In later studies Keiichi Masuko, known for solving the riddle of the leptanilline army ants, used his extraordinary powers of observation to add a new twist to the dacetine story. The little workers, he found, smear soil and other detritus on their own bodies, evidently as an odor camouflage to allow a closer approach to the prey. In still another extension, Alain Dejean of France found that the workers exude an odor attractive to springtails, holding them in place longer as the ants make their approach.

Over the years Wilson and William Brown, in the course of hunting dacetine ants during expeditions to various parts of the tropics, pieced together the likely evolution of the miniature stealth hunters. About 250



Two trap-jawed ants: a species of *Myrmoteras* from southeastern Asia *(above)* and *Daceton armigerum* of South America *(below)*.

dacetine species are known worldwide, composing 24 genera, and they vary enormously among themselves in size, anatomy, and behavior. Their history evidently proceeded as follows. The more primitive forms, like the living species of *Daceton* in South America and *Orectognathus* in Australia, were large ants that foraged over the ground and onto low vegetation. They used trap jaws to catch a wide variety of small to moderate-sized prey, such as flies, wasps, and grasshoppers. In some lines originating from these ancestral forms, the workers drastically reduced their size and began to hunt minute, soft-bodied insects and other arthropods living in the soil. Some of the extreme species came to restrict themselves entirely to the capture of springtails. At the same time the social structure was altered to accommodate this change to a reduced, secretive lifestyle. The colonies grew smaller, the workers became uniform in size (in contrast to the maintenance of major and minor workers in the larger dacetines), and the ants abandoned the use of odor trails to recruit nestmates to prey.

This sketch of dacetine history, mostly completed by 1959, was one of the first attempts to reconstruct the evolution of social organization in a group of animals as shaped by changes in food habits and other dimensions of ecology.

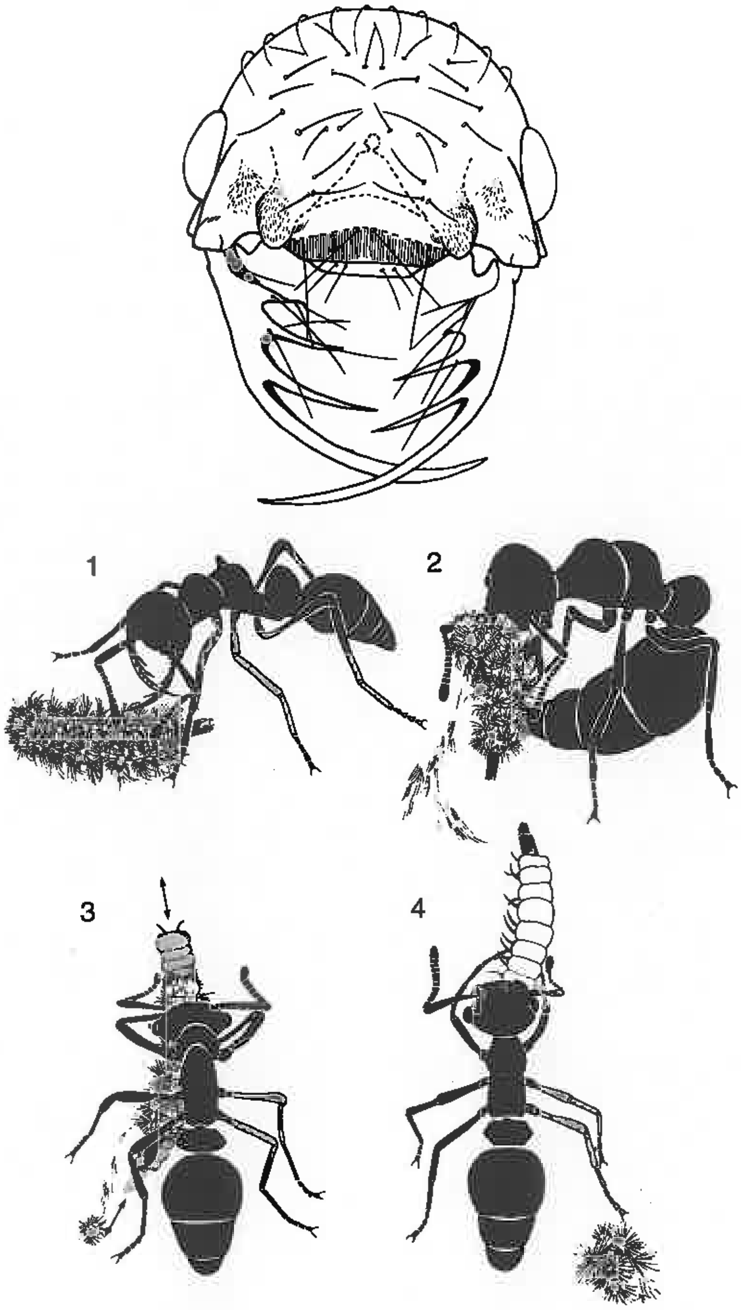
The jaws of an ant are the functional equivalent of the hands of a human being. They are used to pick up and manipulate soil particles, food items, and nestmates. They serve as weapons for the defeat of enemies and the capture of prey. The size and shape of the jaws therefore provide clues to the kinds of lives ants live and the nature of the food the workers gather. And of all the ants in the world, those with the strangest mandibles are not *Odontomachus* and the dacetines but the species of the ponerine genus *Thaumatomyrmex*. The head capsule of the worker is short, almost globular, and set on each side by large, convex eyes. The huge mandibles project forward like a basket, the struts formed of long thin teeth resembling the tines of a pitchfork. When the mandibles are closed tightly against the mouth in repose, the tips of the extremely long terminal teeth extend past the rear border of the head like a pair of horns. The name *Thaumatomyrmex* means, appropriately enough, "marvelous ant."

Marvelous indeed—and just how are those spectacular jaws used? Are they trap jaws, or do they fill some other, wholly unsuspected role? For years myrmecologists speculated on the natural history of *Thaumatomyrmex*—where it nests and the creatures it hunts. Unfortunately, members of the genus are among the rarest ants in the world. Although the several known species are distributed variously from southern Mexico to Brazil (with one found only on Cuba), no more than a hundred specimens exist in all the museums of the world. Just to find a single living worker is considered a major accomplishment. Until recently no live colony had ever been studied in the laboratory.

Wilson had managed to collect just two workers in his entire life, one in Cuba and the other in Mexico. It was his burning ambition for many years to locate a colony and solve the mystery of the stupendous jaws. In 1987 he devoted a week to this task at the La Selva Field Station and Biological Station of the Organization for Tropical Studies, in northeastern Costa Rica, a locality where several specimens had been recently collected. During that time he did nothing but walk along trails and across the undisturbed forest floor, head bent, desultorily kicking at leaves and fallen tree branches, in search of the distinctive black, shiny form of the basket-headed workers. He found not a single one. In frustration, he next published an article in *Notes from Underground,* the myrmecological newsletter. The message in essence: "Will someone please find out what *Thaumatomyrmex* eats, and put my mind at rest?"

Within a year three young Brazilian scientists, C. Roberto F. ("Beto") Brandão, J. L. M. Diniz, and E. M. Tomotake, had the answer. They came across two workers, in separate locations in Brazil, carrying dead polyxenid millipedes. They also located a fragment of a colony and kept it under observation in the laboratory, during which time the workers accepted polyxenid millipedes while ignoring other kinds of prey offered them. Millipedes have two legs on every segment of their body, and are sometimes called thousand-legs. Most are elongate, cylindrical creatures with hard, calcareous exoskeletons. Polyxenid millipedes are very different in general appearance, however. Relatively short, soft-bodied, and covered by long, densely packed bristles, they are the porcupines of the millipede world.

The *Thaumatomyrmex* are porcupine hunters. Their extraordinary



The tropical American species of *Thaumatomyrmex* are among the rarest ants in the world. They also have the most bizarre mandibles, with which they capture porcupine-like polyxenid millipedes. In the sequence below, a worker strips the bristles from a polyxenid before dismembering and eating it. (From an article by C. R. F. Brandão, J. L. M. Diniz, and E. M. Tomotake.)

mandibles are nicely adapted to overcome the defense of the polyxenids. Brandão and his collaborators learned that on encountering one of the millipedes, the ant drives the spikelike teeth of her mandibles past its bristles and into the body, and then carries her prey home. Inside the nest she uses coarse hairs on the pads of her forefeet to strip off the bristles of the millipede, like a cook plucking a chicken for the pot. Then the ant consumes the millipede, starting at the head and proceeding back to the tail. Occasionally it shares some of the remains with adult nestmates and the larvae. On learning of this startling discovery, Wilson was happy to know the secret of *Thaumatomyrmex* at last, disappointed not to have come close to discovering or even guessing the answer himself, and at another level a bit sad to know that the ant netherworld had one less challenge to offer.

Another mystery recently solved was the natural history of big, dark ants in the genus *Basiceros*. The workers' heads are elongate, their integument thick and coarsely sculptured, and their bodies cloaked with a mixture of bizarre club-shaped and feathery hairs. Like the pitchfork-jawed *Thaumatomyrmex*, the species of *Basiceros* are widely distributed in the forests of Central and South America, yet until recently few had been seen alive. Virtually nothing was known about their natural history.

The rarity of *Basiceros* turns out to be an illusion, because the ant itself is a master of illusion. In 1985, while collecting in the biological reserve at La Selva, we learned how to locate colonies of the local species with relative ease. We discovered that the ant, *Basiceros manni*, is actually quite common. The trick in hunting it is to look for the white larvae and pupae, which stand out from the dark rotting wood in which the ants build their nests. The workers and queens themselves are extremely difficult to locate unless one knows exactly where to look and then stares at that spot closely. The ants are superbly camouflaged to the human eye, and presumably also to the eye of visually searching predators such as birds and lizards. The ants are easily lost sight of as they walk over the ground, and they become virtually invisible when they come to a halt. The effect is achieved in part by the extreme slowness of the *Basiceros manni* workers. They are among the most sluggish ants we have encountered during years of field experience around the world. They are slow-motion huntresses, creeping about in search of insects, which they stalk carefully and seize with a sudden snap of their jaws. Inside the nest, the entire worker force often stands perfectly still for minutes at a time, even holding their antennae rigidly in place. For the observer used to the eternal bustle of most ant colonies, the effect is eerie. When moving workers are disturbed by being uncovered or touched by a pair of forceps, they freeze into immobility for up to several minutes, in contrast to most other kinds of ants, which dash frantically away.

Not only are the *Basiceros* phlegmatic in the extreme, they are also the dirtiest ants in the world. Most ants are scrupulously clean. They stop frequently to lick their legs and antennae and wipe their bodies with combs on their legs and brushes of hairs on their feet. In some species more than half the behavioral acts of the ants are devoted to cleaning their own bodies, and a large portion of the remainder involves washing nestmates. The *Basiceros* devote only 1 to 3 percent of their repertoire to personal grooming. The bodies of older workers are encrusted with dirt. The phenomenon is not the result of neglect and poor hygiene, but is a quality sought by the ants. It is part of the camouflage technique of the species. By the time the workers are old enough to forage outside the nest, they blend in almost perfectly with the soil and rotting litter they walk on.

The camouflage of the *Basiceros* is enhanced by anatomical design. The collection of fine particles is accomplished by two layers of hairs on the upper surface of the body and legs. Long hairs with splintered ends, shaped like bottle brushes, scrape off and capture minute soil particles. Beneath them, like bushes in a forest undergrowth, feather-shaped hairs anchor the particles close to the body surface.

We successfully cultured *Basiceros* colonies in artificial nests back at Harvard by feeding them vestigial-winged fruit flies, which the ants hunted in their usual slow motion. The workers had no natural dark soil to add to their exoskeletons, but they did have the fine dust of the plaster of Paris walls and floor from which we had built the laboratory nests. And so over time the older workers began to turn white—they became ghost ants, camouflaged in an environment in which no *Basiceros* had previously lived.

The exact opposites of the stealthy dacetines and *Basiceros* are ants that flaunt bright colors in sunlight. They subscribe to a basic rule of natural history that holds both on the land and in the sea: if an animal is beautifully colored and acts with relative indifference to your presence, it is probably poisonous or well armored with jaws or spines. On the floors of Central and South American rain forests, the bodies of poison-arrow frogs are dazzling spots of color in various combinations of red, black, and blue. The frogs make only a half-hearted attempt to hop away when approached, and they sometimes sit still if you try to pick them up. Don't. The mucus of a single individual is toxic enough when ingested to kill a human being. Amerindian hunters, in order to immobilize monkeys and other larger animals, add a trace of the material to the tips of their arrows and blow darts.

In Australia, red and black bulldog ants, a centimeter or more in length and packing a sting as powerful as that of a wasp, can be spotted from a distance of 10 meters. Around their nests they are fearless and belligerent, and they have excellent vision. The workers of some species literally bound toward human intruders, taking sizable forward leaps into the air.

Some of the most colorful and insouciant ants in the world occur in Cuba. They are members of the genus *Leptothorax*, until recently placed in a genus of their own, *Macromischa*, because of their special anatomical properties. There are dozens of species on the great island, almost all of which are found nowhere else. Jewels of Antillean natural history, they come in many sizes, shapes, and colors, including yellow, red, and black. But the most arresting of all are slender species that shine metallic blue and green in the sunlight. The workers forage in open spaces, often in columns, on limestone walls and low woody vegetation.

When Wilson was 10 years old, he was enchanted by the following passage in a *National Geographic* article by William Mann: "I remember one Christmas Day at the Mina Carlota, in the Sierra de Trinidad of Cuba. When I attempted to turn over a large rock to see what was living underneath, the rock split in the middle, and there, in the very center, was a half teaspoonful of brilliant green metallic ants glistening in the sunshine. They proved to be an unknown species."

Imagine! Prospecting in a faraway place for new species of ants that resemble living emeralds. Mann named the species *Macromischa wheeleri,* in honor of his Ph.D. adviser at Harvard, William Morton Wheeler. The image was still vivid in Wilson's mind in 1953 when, as a Ph.D. student at Harvard, he arrived at the same locality, Mina Carlota, to collect ants. As he climbed a steep, forested hillside, he turned over one soft limestone rock after another in search of ants, as had Mann. Some cracked, some crumbled, and most stayed intact. For a while, no green ants appeared. Then one rock broke in half, exposing a teaspoonful of the metallescent workers of *Leptothorax wheeleri.* There was a special satisfaction in repeating Mann's scientific discovery in exact detail four decades later. It was a reassurance of the continuity of the natural world, and of the human mind.

Continuing deeper into the Sierra de Trinidad, Wilson encountered another *Leptothorax* species whose workers glistened with golden reflections in the sunlight. The color resembled the scintillations of tortoise beetles found in many parts of the world. The hue (as well as the metallic blues and greens of other species) is almost certainly produced by microscopic ridges on the body that refract strong light. But why should such an unusual effect be evolved in the first place? It is a fair guess that the ants are also poisonous and thus use the color to warn off predators, perhaps the anole lizards that also abound in the same habitats. A few other ants in the world have turned golden. Some species of *Polyrhachis* in Australia and Africa have evolved sheets of golden hairs on their abdomens, which may serve to advertise the sharp spines they carry on their thoraxes and waists.

Let us close our bestiary with absolutely the rarest, or at least the most elusive, of all the ants we have ever known. In 1985 Hölldobler was searching along the edge of second-growth woodland at La Selva, our favorite tropical study site. He poked at a curious small cluster of dried, thatchlike vegetation about chest high in the foliage of a small tree. Out poured more than a hundred workers of a new species belonging to the ant genus *Pheidole.* The ants ran in erratic looping patterns to form a spreading pattern away from the nest. There was nothing unusual about this response—ants usually rush out to defend their homes—except that in this case the workers looked astonishingly like termites of the genus *Nasutitermes.* These termites are abundant in the trees of La Selva and elsewhere throughout the New World tropics. Their huge spherical nests, built from hardened feces, contain tens of thousands of workers. The soldier caste, called nasutes, possess long, noselike projections on the head from which they squirt streams of sticky, noxious fluid. The nasutes swarm out in large numbers whenever the nest walls are ruptured. Few enemies the size of frogs or smaller can withstand their attacks.

The *Pheidole* discovered by Hölldobler resembled the nasutes only superficially, but the deception was convincing. At first he thought they were actually termites. The movements of the charging workers were nearly identical to those of *Nasutitermes.* Even more persuasively, the coloration of the *Pheidole* soldiers is unique for ants of this genus but close to that of the termite soldiers. If our interpretation is correct, the ant, which we later named *Pheidole nasutoides,* is the first known case of an ant mimicking a termite. In this role, it presumably bluffs predators that have learned to avoid the heavily armed nasutes.

For the remainder of our visit to La Selva that year we searched hard for more colonies of *Pheidole nasutoides,* in order to make a close study of its natural history and to test the mimicry hypothesis. But we never found another. In later trips, sometimes separately and sometimes together, we continued the search, but still had no luck. We are puzzled by this failure, and eager to learn more about *Pheidole nasutoides.* It is possible that the ant is simply very rare, limited to extremely sparse populations like those of the spear-toothed *Thaumatomyrmex.* Or it may be normally a dweller of the high canopy, a zone we and others have yet to explore. Perhaps the nest had fallen from a branch higher up. Eventually someone will learn the answer, and the puzzle will be solved. There is no need to fear that the world of ants will then grow one bit less interesting. By that time other strange phenomena will certainly have come to light, leading new generations to adventures in the field.

How Ants Control Their Environment

ANT COLONIES control and change the environment to their liking by means of mass action and division of labor among the workers. Temperature regulation is a prime example of this social power, one vital to the success of the ants. For some reason still unknown, these insects require an unusual amount of heat. With the exception of the primitive Australian *Nothomyrmecia macrops* and a very few other cold-temperate species, ants function poorly below 20°C (68°F) and not at all below 10°C (50°F). Their diversity declines steeply from the tropics to the north temperate zones. Colonies of any kind are scarce in the shaded portions of old-growth northern coniferous forests, and only a very few cold-adapted species live on the tundra. No native species of any kind exists in Iceland, Greenland, or the Falkland Islands. Ants are also largely absent from the slopes of heavily forested mountains in the tropics above 2,500 meters (8,200 feet). In contrast, a legion of species swarm in the hottest and driest places, from the Mojave and Sahara Deserts to the dead heart of Australia.

In cool habitats ants seek heat for the rearing of their larvae. This, in simplest terms, is why colonies are concentrated so heavily beneath rocks in the cold temperate zone, and why the best way to find entire colonies with the queen near the surface is to turn over rocks, preferably in the spring when the ground is first warming up. Rocks have excellent thermoregulatory properties, especially those that are flat and set shallowly in the soil, with a large fraction of their surface exposed to the sun. When dry they have a low specific heat, meaning that only a small amount of solar energy is needed to raise their temperature. Hence during the spring, when ant colonies most need to move into action quickly, the sun warms the rocks and underlying soil more rapidly than it does the surrounding soil. The difference allows the workers to forage, the queen to lay eggs, and the larvae to develop sooner than rivals confined to bare soil. The same thermoregulatory principle holds for the spaces beneath the bark of decaying stumps and logs. In spring the queen, workers, and brood crowd together in such cavities, while retreating through passage-

ways to the cool interior of the wood only when the outer chambers become overheated.

Ant species in tropical forests, enjoying a sufficient warmth almost all the time, display a very different nesting preference. Most inhabit small pieces of rotting wood on the ground. A small number nest in bushes and trees or in rotting logs, and still fewer live entirely in the soil. Where rocks occur on the ground, they are seldom chosen by ants for cover.

The complete adaptation to ground life of ants gives them a special opportunity to regulate their surrounding temperature on an hourly basis. Their nests are typically excavated from beneath rocks or the bare ground surface vertically into the soil, or else from spaces beneath the bark of rotting wood into the heartwood and around the heartwood surface to encompass portions of the wood facing the soil. This geometry allows workers to move the eggs, larvae, and pupae quickly within the nest to reach the chambers best suited for growth. Colonies of most species manage to keep all stages of brood in the warmest chambers within 25°-35°C whenever these temperatures are available.

The earthen nests also permit the ants to avoid overheating in the hottest environments. Even desert specialists die if forced to stay above ground in the summer sun for more than two or three hours. Surface temperatures above 50°C, which are reached in some deserts, cause death within minutes or even seconds. The ants nevertheless manage to flourish by constructing nests deep within the soil, where temperatures stay close to a comfortable (for ants) 30°C even on the hottest days.

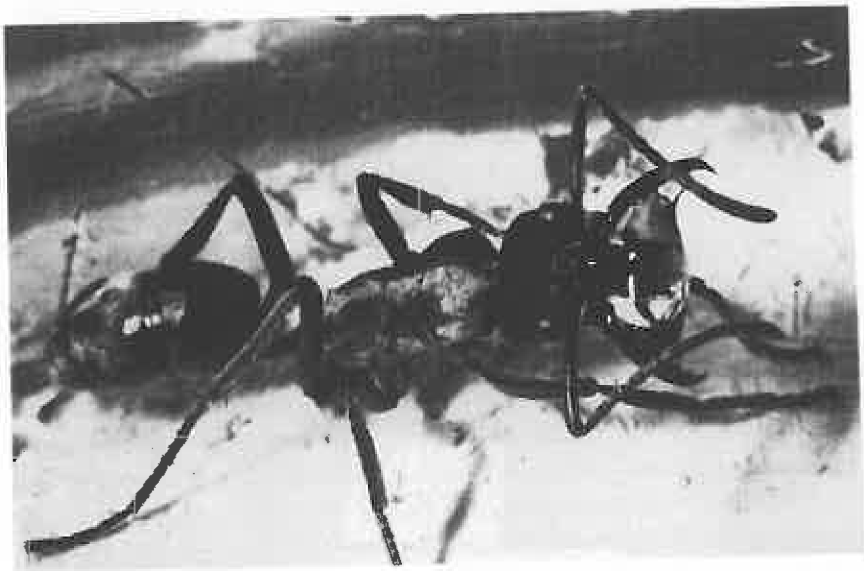
The most sophisticated climatic regulation is achieved by ants that build mounds. These structures are far more than piles of earth excavated to create large underground dwellings. They are intricate in design, symmetric in shape, rich in organic materials, perforated with dense systems of interconnected galleries and chambers, and often thatched with fragments of leaves and stems or sprinkled with pebbles and bits of charcoal. True mounds are cities above the ground, filled with ants and their brood. They are found most commonly in habitats subject to extremes of temperature and humidity, such as bogs, stream banks, coniferous woodlands, and deserts.

The mounds best understood through research to date are the large structures created by ants of the genus *Formica* in cold temperate zone climates. The massive constructions of the red and black wood ants, including *Formica polyctena* and closely related species, are familiar sights in the forests of northern Europe. Rising as much as 1.5 meters (5 feet) above ground level, the mounds are designed to raise the temperature of the ants inside, which are then able to forage earlier in the spring and rear new broods more quickly. The outer crustlike layer reduces loss of heat and moisture, while the enlarged area of the surface exposes the nest to more sunlight. The mounds of some *Formica* species also have longer southern slopes, which further increase the amount of solar energy collected. These slopes are so consistently oriented that for centuries the nests have been used as crude compasses by natives of the Alps. Additional heat comes from the decay of plant materials gathered within the mound and from metabolism of the tens of thousands of ants working together in crowded quarters.

Some ants, such as the *Pogonomyrmex* harvester ants of the American deserts and grasslands, decorate the surface of their mounds variously with small pebbles, fragments of dead leaves and other vegetation, and pieces of charcoal. These dry materials heat rapidly in the sun and serve as solar energy traps. On the high plains of Afghanistan, colonies of *Cataglyphis* sprinkle their mounds with small stones. The habit may be the basis of the legend of ant gold mining reported by Herodotus and Pliny. Herodotus placed the Afghan mining ants near the town of Caspatyros in the country of Pactyike, which has been identified as either modern-day Kabul or nearby Peshawar. It is well known that gold is found in rock and alluvial soil in this part of Afghanistan, and nuggets might occasionally have been brought to the surface by ants along with the pebbles used in temperature regulation. In a somewhat similar fashion, *Pogonomyrmex* harvester ants in the western United States regularly add fossil bones of small mammals to the outer decoration zones of their nest surfaces. Paleontologists routinely inspect the mounds early in their expeditions to see if there are any skeletons still buried in the vicinity.

The greatest peril of the physical environment faced by ants is not excessive heat or cold or drowning (most can live under water for hours or even days), but drought. Colonies of most species need an ambient

A foraging *Pachycondyla villosa* worker brings a water droplet into the nest, where it will be shared with nestmates and daubed onto the walls and floor of the nest to humidify the interior.



humidity higher than that of ordinary outside air, and they face death within hours if exposed to very dry air. Ants therefore employ a diversity of techniques, some approaching the bizarre, to raise and regulate humidity in the nest chambers. Mounds, for example, appear to be constructed to keep not just the temperature but also the moisture of the air and soil within tolerable limits. The thick crust and thatching reduce evaporation, and in addition nurse workers move the immature forms up and down through the vertical passageways to reach optimum humidity. They place the delicate eggs and larvae in moister rooms and the pupae in the drier ones, the latter usually closer to the surface.

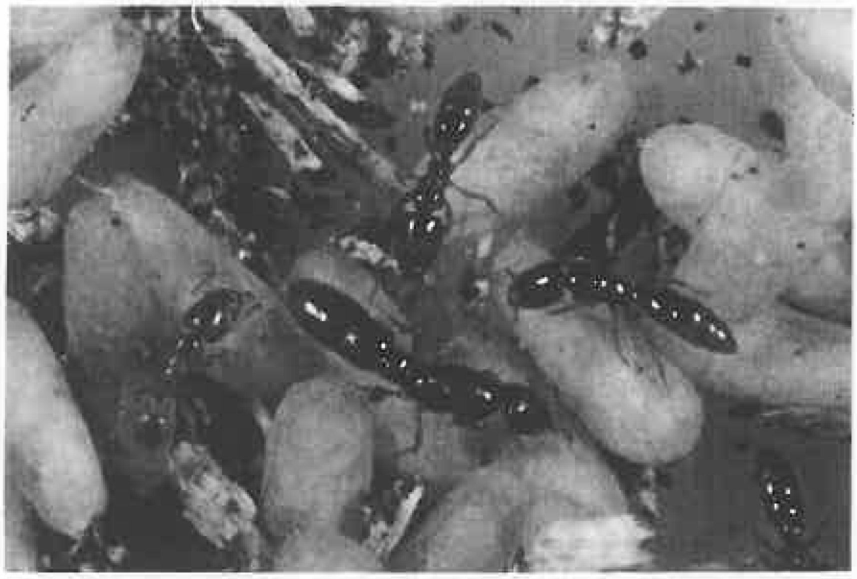
A radically different form of humidity control is practiced by *Pachycondyla villosa*, a giant ponerine hunting ant found from Mexico to Argentina. During the dry season colonies living in arid habitats are in constant danger of desiccation. Gangs of workers make repeated trips to collect dew from nearby vegetation or water from any other source they can find. They gather the droplets between their widely opened mandibles and carry them back to the nest, where they pause and allow thirsty nestmates to drink some of the excess. The remainder of the water is then fed to larvae, daubed onto cocoons, and placed directly onto the ground. Using this bucket brigade the *Pachycondyla* foragers keep the interior of the nest much moister than the surrounding soil.

A strange variation on water collecting is used by the Asiatic hunting ant *Diacamma rugosum.* In the dry scrub woodland of India workers decorate the entrances of their nests with highly absorbent objects such as bird feathers and dead ants. In the early morning hours the dew forming on this material is gathered by the *Diacamma* workers. During the dry season the droplets appear to be the only source of water for the ants.

Still another and equally strange form of humidity control is "wallpapering" by *Prionopelta amabilis,* a tiny, primitive ponerine found in Central American rain forests. The colony typically constructs nests in logs and other fragments of rotting wood on the forest floor, materials that are saturated with water a large part of the year. The problem experienced by these little ants is thus the opposite faced by that of the ponerines in dry woodland. Too much surface moisture can impede the development of young ants. Eggs and larvae can be kept on bare wet surfaces of the wood, but the pupae need a drier environment. The workers solve the problem by papering over some of the rooms and galleries with fragments of pupal cocoons from which adults have previously emerged. Sometimes the pieces are piled on top of one another to form several layers. The rooms have drier surfaces than others left bare, and the workers take care to move the pupae into them.

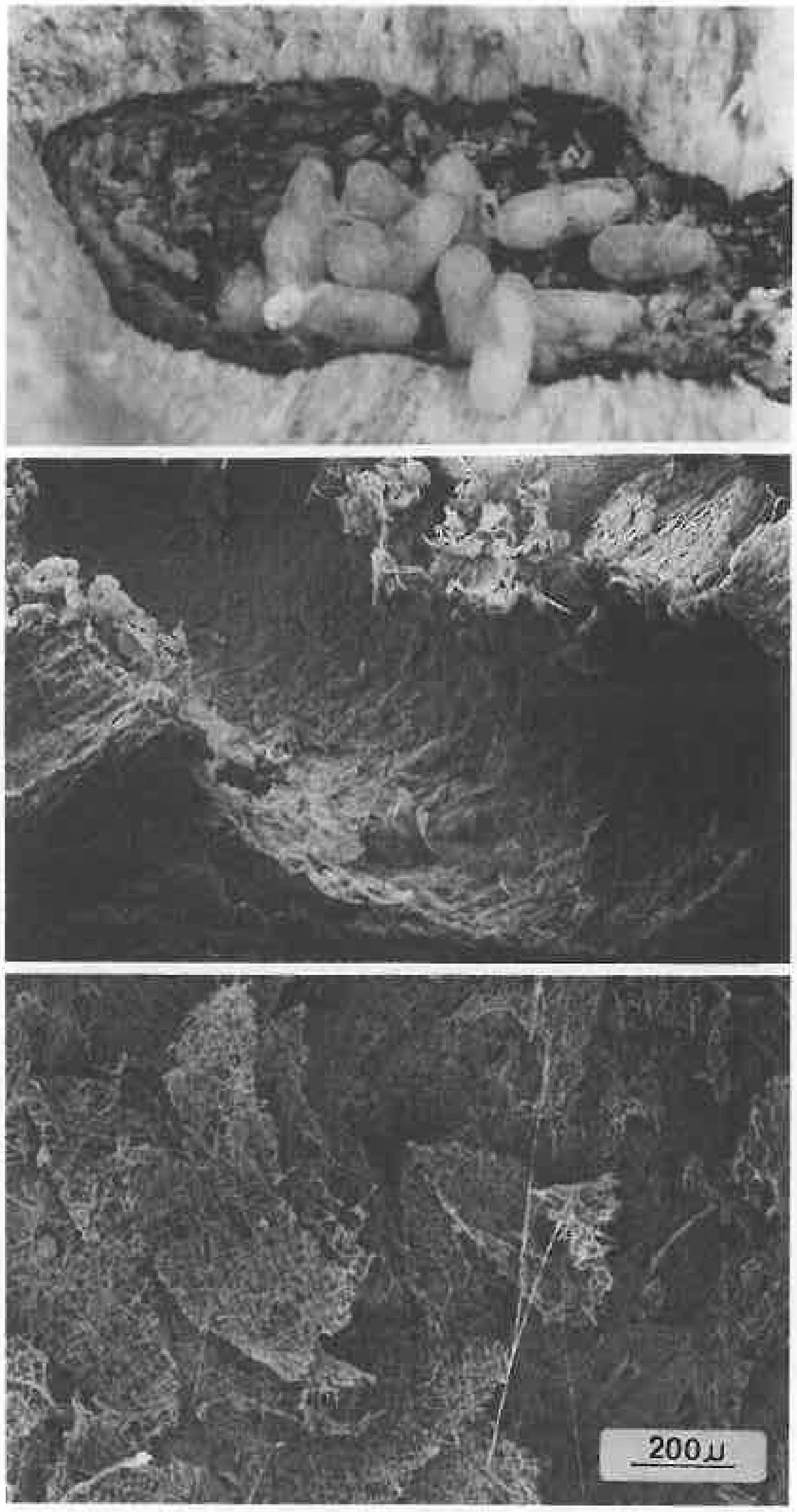
Nests located in the moist soil or in rotting wood are ideal growth chambers for countless bacteria and fungi that are potential health hazards for the ants. Nevertheless, ant colonies are rarely struck by bacterial or fungal infections. The reason for this remarkable immunity was discovered by Ulrich Maschwitz. He found that the metapleural glands in the thorax of adult ants continuously secrete substances that kill bacteria and fungi. Most remarkably, the fungus cultivated by the leafcutter ants *Atta* is not affected by the secretions, but all other foreign fungi or bacteria attempting to invade the *Atta* fungus garden are totally eliminated.

A queen of the miniature tropical American ant *Prionopelta amabilis,* surrounded by her daughter workers and cocoons containing both worker and queen pupae.



Ants as a whole have achieved a dominance across many land habitats enjoyed by few other groups of insects. Their numerical success has allowed them to alter not just their nest environments but the entire habitats in which they live. Harvesting ants, species that regularly include seeds in their diet, have an especially high impact. They consume a large percentage of the seeds produced by plants of many kinds in nearly all terrestrial habitats, from dense tropical forest to deserts. Their influence is not wholly negative. The mistakes they make by losing seeds along the way also disperse plants and compensate at least in part for the damage caused by their predation.

"Go to the ant thou sluggard; consider her ways": Solomon thus praised harvester ants for the industry they display in gathering seeds and their storage of the excess bounty in underground granaries. Writers of the ancient world were well aware of harvesting ants, because they lived in dry Mediterranean environments where the prudent habit is exceptionally well developed. The dominant species they encountered were most likely *Messor barbarus,* which occurs in the Mediterranean



The workers of *Prionopelta* "wall-paper" the interior of their nests with fragments of discarded silk cocoons *(top)*, evidently as a form of humidity control. Scanning electron micrographs *(center* and *bottom)* disclose the relatively dry surfaces of the fragments on which cocoons containing living pupae are placed.

region and south through Africa; *Messor structor,* which is absent in Africa, but ranges all the way from southern Europe to Java; and *Messor arenarius,* which is abundant in the deserts of North Africa and the Middle East. These middle-sized, conspicuous ants are often serious grain pests, and it is to them that Solomon, Hesiod, Aesop, Plutarch, Horace, Virgil, Ovid, and Pliny almost certainly allude.

The first scientific observers of ants in the modern era, from the early 1600s to the early 1800s, were skeptical of the classical accounts despite the long list of authors who repeated the claim. And justifiably so, since without exception their experience was limited to northern Europe, one of the few parts of the world where the phenomenon is rare to nonexistent. When European naturalists paid closer attention to ants in warmer, drier climates, the activity was reconfirmed. During a sojourn in southern France in the early 1870s, Reverend J. Traherne Moggridge, an American entomologist, explored seed harvesting by *Messor barbarus* and *Messor structor* in detail, establishing that the ants collect seeds from at least 18 families of plants. He confirmed the reports by Plutarch and other classical authors that the workers bite off the radicle to prevent germination, then store the deactivated seeds in granary chambers in the nests. In a remarkably modern addendum, Moggridge went on to prove that harvesters play an important role in dispersing plants by accidentally abandoning viable seeds in the nest vicinity or failing to deactivate them before they sprout inside the nest chambers.

In the last century exacting studies by biologists after Moggridge have touched on every aspect of the natural history of harvesters almost everywhere they occur, from Eurasia, Africa, and Australia to North and South America. One important finding is that the ants strongly alter the abundance and local distribution of flowering plants. They are especially potent in deserts, grasslands, and other arid habitats where harvesting is most intensive. They tip the balance in competition among some species of plants while promoting a balance in numbers among others. In so doing, they rearrange the distribution of species in local floras.

Harvesting by ants reduces the vegetative mass of plants as well as their reproductive power. Experiments performed in Arizona by James Brown and other ecologists revealed that when ants are removed from desert plots, annual plants grow in at double the ordinary density within just two seasons. In similar experiments performed in Australia by Alan Andersen, seedling numbers increased fifteen-fold.

Harvesting ants also often aid the exploited species by dispersing them more widely than would otherwise be the case. In the Arizona deserts, many seeds survive long enough to take root in the refuse piles around harvester nests, and thus certain plant species are scattered across the barren land from one nest site to another. These plants and the harvesters can be said to exist in a loose form of symbiosis. The plants "pay" the ants a certain fraction of their seeds in return for transport of another fraction of their seeds to the nest perimeters, which are rich in nutrients and nearly free of competitors.

By means of this unintentional manipulation, harvester ants exert powerful effects on the life and death of certain plants. They are keystone species, deciding by their presence alone which of the plants flourish and which fail. In croplands of the Mexican tropical lowlands fire ants *(Solenopsis geminata)* reduce the abundance of weeds among the domestic plants; they also cut the number of species of insects on the plants to one-third. The ants prefer some kinds of seeds over others. As a result, a few plant species are lifted to dominance while their competitors are driven to extinction. In other cases an equilibrium is reached. Plants that would otherwise eliminate competitors are cropped to low enough levels by the ants so that all coexist indefinitely.

Harvesting, with its unintended consequences, is only one of many symbioses that have existed between ants and plants for as long as tens of millions of years. By the middle of the Cretaceous Period, when dinosaurs still reigned, primitive sphecomyrmine and ponerine ants were on the rise; at the same time the flowering plants were diversifying and spreading around the world as the newly dominant form of vegetation. An intricate coevolution of the plants and insects as a whole was under way. Many of the plant species had come to depend on moths, beetles, wasps, and other insects for pollination, while an even greater number of insect species subsisted on nectar and pollen obtained during the pollination process. Another legion of insects fed on the foliage and wood of the flowering plants. The plants responded by evolving various combinations of thick cuticles, dense spines and hairs, and chemical defense substances such as alkaloids and terpenes, including chemicals that we humans now use in small doses as medicines, insect repellents, drugs, and condiments.

Into this lively theater of coevolution the ants entered. As the Cretaceous drew to a close, the ants increased in diversity and abundance, seized new roles as pollinators and seed dispersers, and appropriated parts of the plants as nest sites. An entomologist returning to early post-Cretaceous times, about 60 million years ago, would find familiar-looking ants swarming over familiar-looking vegetation.

Complex symbioses were fashioned among the thousands of species of ants and plants living together. The relationships found today are often parasitic, with ants exploiting plants and giving nothing in return. In other combinations they are commensalistic, with one partner making use of the other but, as in the case of ants occupying the dead hollow stems of trees and bushes, neither harming nor helping it. Of far greater general interest, however, are the mutualistic symbioses, from which both partners benefit. Ants use cavities supplied by the plants for nest sites, as well as nectar and nutritive corpuscles for food. In return, they protect their plant hosts from herbivores, transport their seeds, and literally pot their roots with soil and nutrients. Some pairwise combinations of ants and plants have coevolved so that each is specialized to use the other's services. The pacts of mutualism have produced some of the strangest and most elaborate evolutionary trends found in nature.

The classic case of complete interdependence is the symbiosis between members of the woody genus *Acacia* in Africa and tropical America and the ants living in them. Among the combinations, the American bull's-horn acacias and their ants have been the most thoroughly documented. The acacias, which are among the dominant shrubs and trees in dry forests, seem thoroughly designed to shelter and feed ants. Their thick pairs of thorns (the "bull's horns") are distributed at regular intervals up and down the branches. They are hard-shelled and inflated, and their pulp-filled centers serve as ideal shelters for ants. Nectaries exuding sugary liquid are located at the base of the feathery compound leaves. The workers need only step out of the entrance holes they have cut into the thorns and run a few centimeters in order to drink from droplets of the nectar. To these amenities the acacias add nutritious little buttons that sprout from the tips of the leaflets. The corpuscles, called Beltian bodies, are easily plucked off by the ants. All the evidence suggests that the dominant inhabitants of the acacias—slender stinging ants of the genus *Pseudomyrmex*—are able to thrive on nectar and Beltian bodies alone.

In return the ants protect the acacias from their enemies. They are crucial to the high success, indeed the very survival, of the plants. This side of the symbiosis was proven in a field experiment performed in the early 1960s by the American ecologist Daniel Janzen. During the course of studies in Mexico, Janzen, then a young graduate student, noticed that acacia shrubs and trees lacking *Pseudomyrmex* ants suffered greater damage from insects. They were also partly overgrown by competing plant species. When Janzen removed ants from occupied trees, by spraying with insecticides or clipping off the branches and thorns in which the *Pseudomyrmex* lived, he found that the acacias came under heavy attack by their insect enemies. Coreid bugs and treehoppers sucked on the shoot tips and new leaves; scarabs, leaf beetles, and caterpillars of assorted moths browsed on the leaves; and buprestid beetle larvae girdled the shoots. Other plants grew in more closely and shaded the stunted shoots.

In nearby occupied trees, those left untouched by Janzen, the ants attacked the invading insects, driving off or killing the great majority. Alien plants that sprouted within a radius of 40 centimeters of the acacia trunks were chewed and mauled by the ants until they died. Up to a fourth of the entire worker force of the occupied trees was active on the plant surfaces at any given time, day and night, constantly patrolling and cleaning the surfaces.

As Janzen's experiment proceeded, the ant-occupied trees thrived, while the empty trees progressively declined. In 1874 Thomas Belt, the naturalist who first recorded the symbiosis, had concluded that the *Pseudomyrmex* ants "are really kept by the acacia as a standing army." This view has now been firmly proved.

Similar ant-plant symbioses abound in tropical forests and savannas

The bull's-horn acacias of tropical America harbor ants of the genus *Pseudomyrmex* in a close symbiotic relationship. In the upper photograph the nest entrance used by the ants is shown; in the foreground can be seen a row of nipplelike extrafloral nectaries from which the ants feed. In the lower photograph a worker collects nutritious Beltian bodies from the tips of the acacia leaflets. (Photographs by Dan Perlman.)

around the world. They have been the subject of an explosion of research in recent years. Ulrich Maschwitz and his collaborators, for example, have discovered a string of new symbioses in the rain forests of Malaysia, linking surprising new combinations of ant and plant species. Similar reports are coming in from Africa and both Central and South America. At the present time we know hundreds of plant species in more than 40 families that possess special structures to house ants. Many also supply nectar and food bodies, in the acacia manner. Among them are the legumes (including acacias), euphorbs, madders, melastomes, and orchids. The ants that depend on the symbiosis to some degree are equally diverse, including hundreds of species in 5 subfamilies.

Ants that are completely dependent on symbiotic plants are also among the most aggressive in the world. Those large enough to attack mammals, including human beings, are well-armed, quick and vicious. It is as though they have no other place to go, and with their backs to the wall they are prepared to make an extreme response to every provocation. The acacia ants swarm out almost instantly to mount and sting an offending arm and hand. When a person stands upwind and close by an acacia bush, some of the workers run to the edge of the leaves and strain to reach him, apparently aroused by his body odor alone. Larger and even more aggressive *Pseudomyrmex* ants inhabit *Tachygalia*, a small understory tree of South American forests. To brush one's bare skin against a sprig of *Tachygalia* is like touching a nettle. The punishment in this case, however, is delivered by dozens of ants that sprint onto the body, instantly begin to sting, and hold on until picked off. As we have walked through the rain forest undergrowth distracted, often rather carelessly in the typical naturalist's manner, we have felt the familiar burning sensation on some exposed part of our body and thought immediately: *Tachygalia!*

But the most effectively aggressive ant species in the world, exceeding even the tachygaliaphilic *Pseudomyrmex*, may be *Camponotus femoratus*, a large, hairy and decidedly unpleasant ant of South American rain forests. When disturbed in the slightest, the workers boil out in an angry mass over the nest surface. Just the close presence of a human being is enough to trigger the reaction. Diane Davidson, an American entomologist who has studied ant-plant symbiosis extensively, described the behavior in a letter to us as follows: "When I approached to within 1–2 m of their nests, workers of this species typically began to run back and forth and frequently jumped or fell onto me. Workers of all size classes of this polymorphic species attempted to bite, but usually only the major castes were capable of breaking the skin with their mandibles and causing a stinging sensation by simultaneously biting and spraying formic acid into the wound."

These ants happen to live not in the cavities of plants, but in ant gardens, which constitute the most complex and sophisticated of all symbioses between ants and flowering plants. The gardens are round masses of soil, detritus, and chewed vegetable fibers assembled in the branches of bushes and trees, ranging in size from golf balls to soccer balls, within which are grown a variety of herbaceous plants. The ants collect the materials for the nests. The ants gather the seeds of the symbionts and place them in the nests. As the plants grow, nourished by the soil and other materials, their roots become part of the framework of the gardens. The ants in turn feed on the food bodies, fruit pulp, and nectar provided by the plants.

The ant gardens of Central and South America contain many plant species, representing at least 16 genera, that are found nowhere else. These specialized forms include arums such as *Philodendron*, bromeliads, figs, gesneriads, pipers, and even cacti.

The plants limited to the gardens appear to be full symbiotic organisms. The ants transport their seeds to favorable sites within the nests, including the brood chambers, at least in part because the ants find them attractive and may even confuse their odors with those emitted by their own larvae. Some of the attractants have been identified, including 6-methyl-methylsalicylate, benzothiazole, and a few phenyl derivatives and terpenes. The growth of the plants is promoted by the activities of the ants. The ants in turn are less fully committed to the gardens. The diet supplied them by the plants is not restrictive; all the known garden-ant species forage away from the gardens to collect other kinds of food. Yet the ants that engage the symbiosis, including the ferocious *Camponotus femoratus*, seem to know they have a good thing going. At least they act as though their lives depended on it.

Epilogue: Who Will Survive?

LOCKED INTO THEIR chemosensory world, ants are oblivious to human existence. They experience reality for the most part through sensory devices projecting from their hard exoskeletons in the form of hairs, pegs, and plates. Their strange tripartite brains process information received primarily from a space of only a few centimeters around their bodies. They are, furthermore, aware of no more than a few minutes and hours of time into the past, and they have no mental construct of the future. It has been thus for tens of millions of years in the past, and so it will continue into the indefinite future. That difference in scale can never be abolished for a tiny creature imprisoned within an exoskeleton.

Because ants exist in a fractal world of centimeters, they are part of what human beings can profitably view as microwildernesses. Each colony grows and reproduces in a habitat contained by as little as two buttresses of a tree, the bark of a fallen log, or the soil beneath a scattering of stones. "Real" wilderness as human beings consider it, viewed over distances of hundreds of kilometers (again, a matter of perceptual scale), is everywhere threatened. Most of the forests and grasslands may vanish or be corroded almost beyond recognition, but some ant colonies will persist somewhere, and they will continue to cycle through their hereditary routines as though they were in a pristine world before the arrival of humankind. The superorganisms make no concessions, understand no mercy or variance given on their behalf, and will always be as elegant and pitiless as we now witness them, until the last one dies. But we are unlikely to see that happen. Their microwildernesses will outlast our own human-scale ecosystems.

Ants have lived on Earth for more than ten million of their generations; we have existed for no more than a hundred thousand human generations. They have evolved hardly at all during the past two million years. In the structure of our brain, we have undergone in the same period of time the most complex and rapid anatomical transformation in the history of life. Like a secondary rocket catching fire, our cultural evolution has accelerated change still more in a span of several centuries, exceeding the rate of organic evolution by

orders of magnitude. We are the first species to become a geophysical force, altering and demolishing ecosystems and perturbing the global climate itself. Life would never die through the actions of ants or of any other wild creatures, no matter how dominant they became. Humanity, in contrast, is destroying a large part of the biomass and diversity of life, a success that perversely measures our own biological dominance.

If all of humanity were to disappear, the remainder of life would spring back and flourish. The mass extinctions now under way would cease, the damaged ecosystems heal and expand outward. If all the ants somehow disappeared, the effect would be exactly the opposite, and catastrophic. Species extinction would increase even more over the present rate, and the land ecosystems would shrivel more rapidly as the considerable services provided by these insects were pulled away.

Humanity will in fact live on, and so will the ants. But humankind's actions are impoverishing the earth; we are obliterating vast numbers of species and rendering the biosphere a far less beautiful and interesting place for human occupancy. The damage can be fully repaired by evolution only after millions of years, and only then if we let the ecosystems grow back. Meanwhile let us not despise the lowly ants, but honor them. For a while longer at least, they will help to hold the world in balance to our liking, and they will serve as a reminder of what a wonderful place it was when first we arrived.