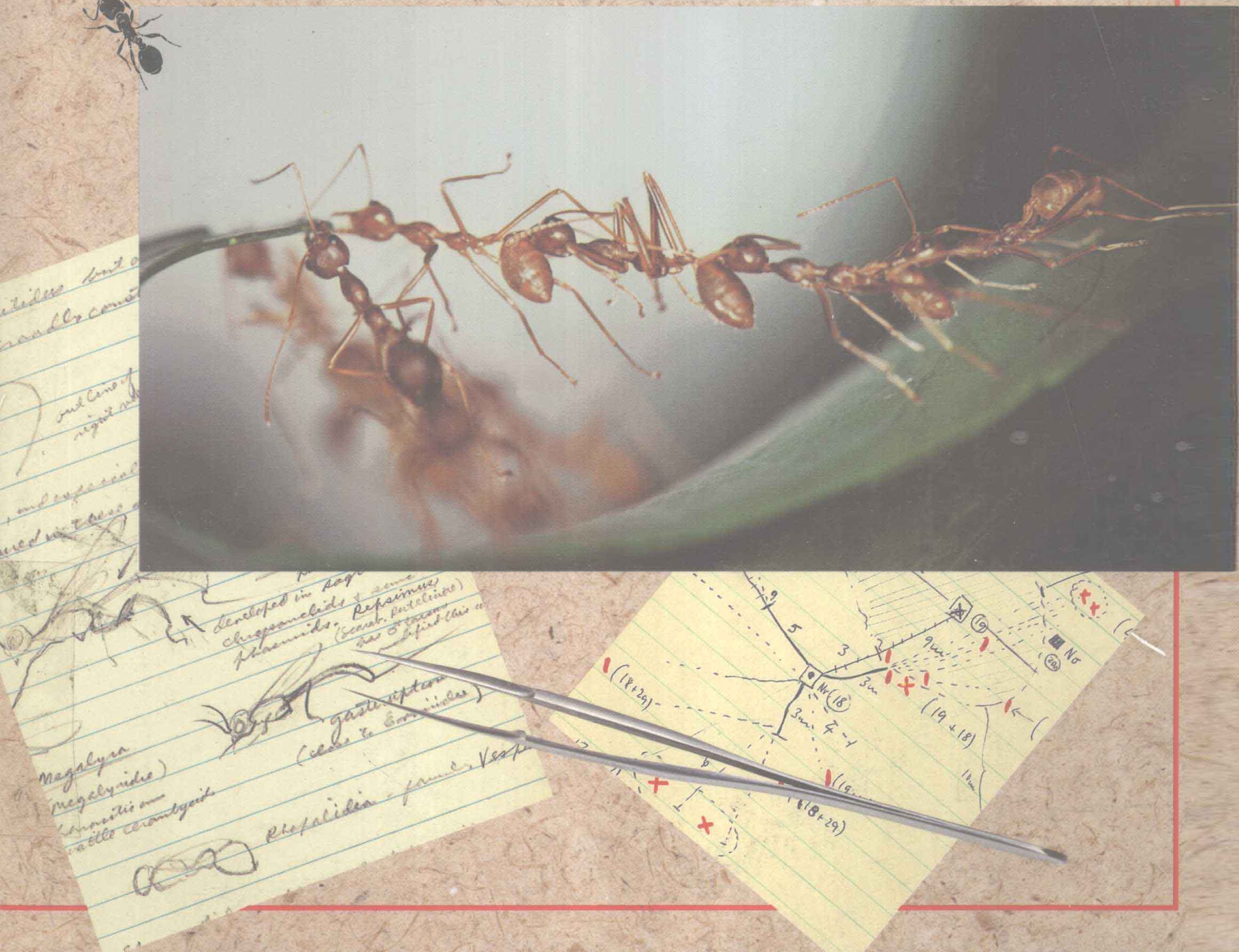
Journey to the Ants

A STORY OF SCIENTIFIC EXPLORATION

Bert Hölldobler & Edward O. Wilson



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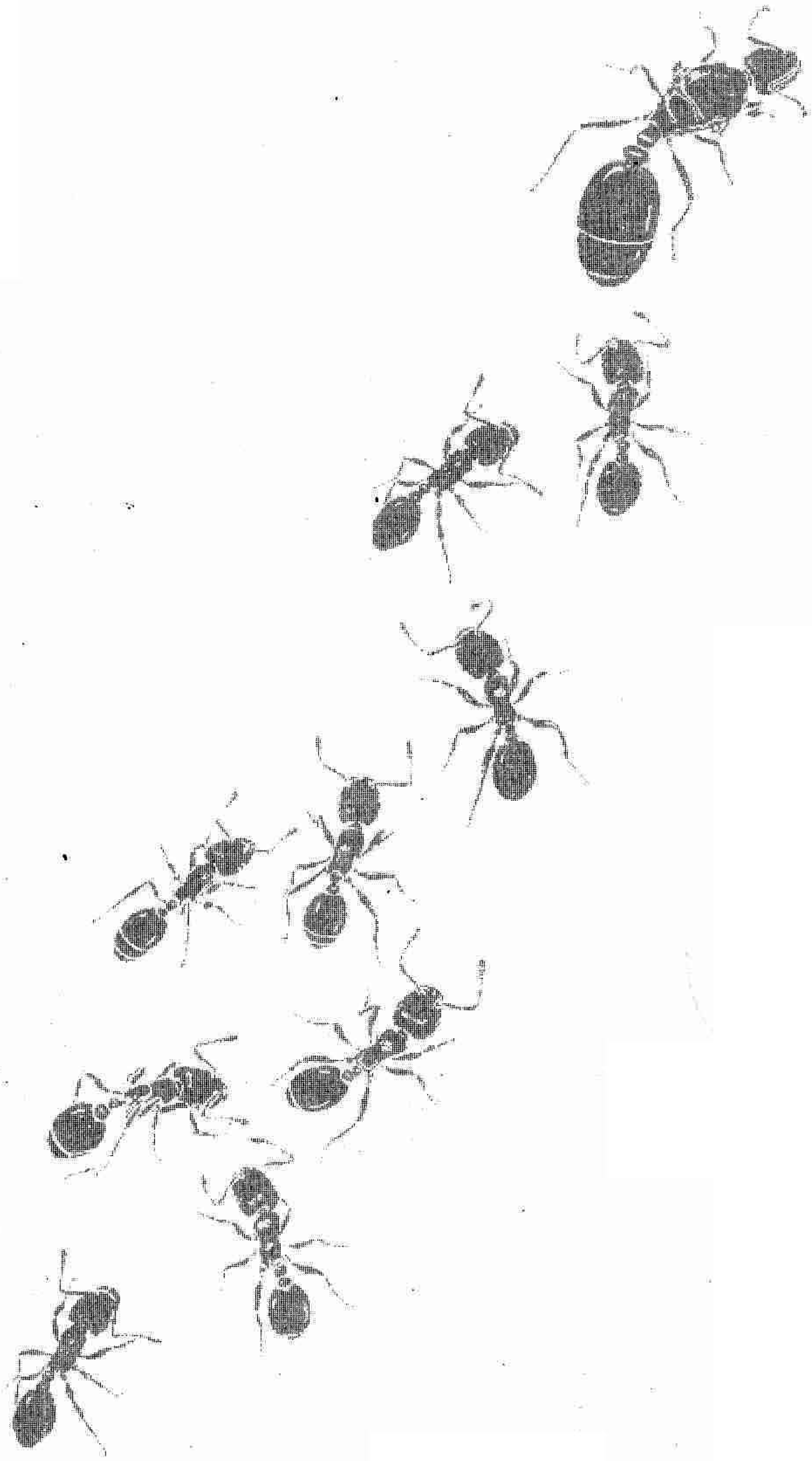

A Story of Scientific Exploration

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and

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The Belknap Press of
Harvard University Press
Cambridge, Massachusetts
London, England

Printed in the United States of America

FOURTH PRINTING, 1995

Designed by Marianne Perlak

Library of Congress Cataloging-in-Publication Data
Hölldobler, Bert, 1936–
Journey to the ants: a story of scientific exploration /
Bert Hölldobler and Edward O. Wilson.
p. cm.
Includes index.
ISBN 0-674-48525-4 (cloth)
ISBN 0-674-48526-2 (pbk.)
1. Ants. 2. Insect societies. 3. Hölldobler, Bert, 1936– .
4. Wilson, Edward Osborne, 1929– . 5. Ants—Research.
I. Wilson, Edward Osborne, 1929– . II. Title.
QL568.F7H575 1994
595.79'6—dc20

94-13386
CIP

Preface

The Ants, the monograph we published in 1990, met with critical success and surprisingly wide public attention. But it is a technical book, aimed primarily at other biologists, as well as an encyclopedia and vade mecum of myrmecology, the scientific study of ants. And because exhaustive coverage is its primary aim, it is outsized, containing 732 pages of tables, figures, and double-columned text, measuring 26 by 31 centimeters in hard cover, and weighing 3.4 kilograms. *The Ants,* in short, is not a book one casually purchases and reads cover to cover. Nor does it try to convey in any direct manner the adventure of research on these astonishing insects.

Journey to the Ants condenses the best of myrmecology to a more manageable length, with less technical language and with an admitted and unavoidable bias toward those topics and species on which we have personally worked. Where special terms must be used because of the specialized nature of the subject, we define them on the spot.

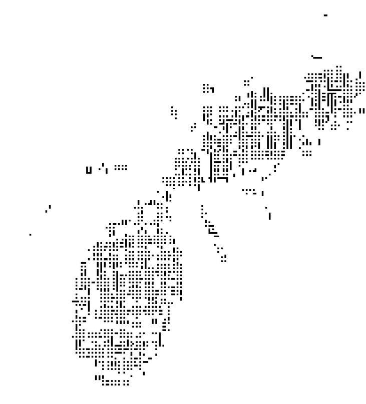
Our approach is thematic at the beginning, then opens out increasingly into natural history. We start with an explanation of why the ants have been so amazingly successful. The reason, we argue, is the swiftly applied and overwhelming power arising from the cooperation of colony members. Combined action at this level of efficiency is made possible by the advanced development of chemical communication: the release of a medley of substances from different parts of the body that are tested and smelled by nestmates and evoke in them, according to the substances released and the circumstance of the moment, respectively alarm, attraction, nursing, food offering, and a diversity of other activities. Ants, like humans, to put it in a nutshell, succeed because they talk so well.

The colony is the unit of meaning in the lives of ants. The workers' loyalty to it is nearly total. Perhaps as a result, organized conflict among colonies of the same species is far more frequent than human war. According to species, ants employ propaganda, deception, skilled surveillance, and mass assaults singly or in combination to overcome their enemies. In extreme cases, some fight by dropping stones on their adversaries, while others conduct slave raids to increase the size of their labor and fighting forces. But not all is harmony inside the warrior states, even those engaged in desperate territorial defense. Selfish behavior is common, especially during conflict over reproductive rights. Workers possessing ovaries sometimes compete with the queen by inserting eggs of their own into the communal nurseries. In the absence of the queen, and sometimes even in her presence, they fight for dominance. The ant colony, entomologists have discovered, is maintained by a Darwinian balance between survival by allegiance to the colony on the one side and the struggle for control within it on the other. The organization of the colony members is consequently complex and tight enough to create the equivalent of a giant, well-coordinated organism, the famous insect "superorganism."

The ants, we will show, arose amidst the dinosaurs about a hundred million years ago and spread quickly around the world. Like most such highly dominant life forms (humanity is a conspicuous exception) they have multiplied everywhere to create a plethora of species. The total number of kinds of ants at the present time probably numbers in the tens of thousands. In their expansion they have undergone a spectacular radiation of adaptive forms. This second aspect of their evolutionary achievement is the subject of the second half of the book. There we offer a tour of the whole range of formicid biodiversity, from social parasites to army ants, nomadic herders, camouflaged huntresses, and builders of temperature-controlled skyscrapers.

In our combined careers we have devoted more than eighty years of study to the ants, and we have many stories to tell, in the form of both personal anecdotes and accounts of natural history. We have also drawn heavily on the research of hundreds of other entomologists. We wish to share some of the excitement and pleasure that we and these other scientists have experienced. We hope our presentation will lead the reader to regard these insects as important in many ways to human existence.

Bert Hölldobler
Edward O. Wilson
January 3, 1994



JOURNEY
TO THE
ANTS

Contents

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.

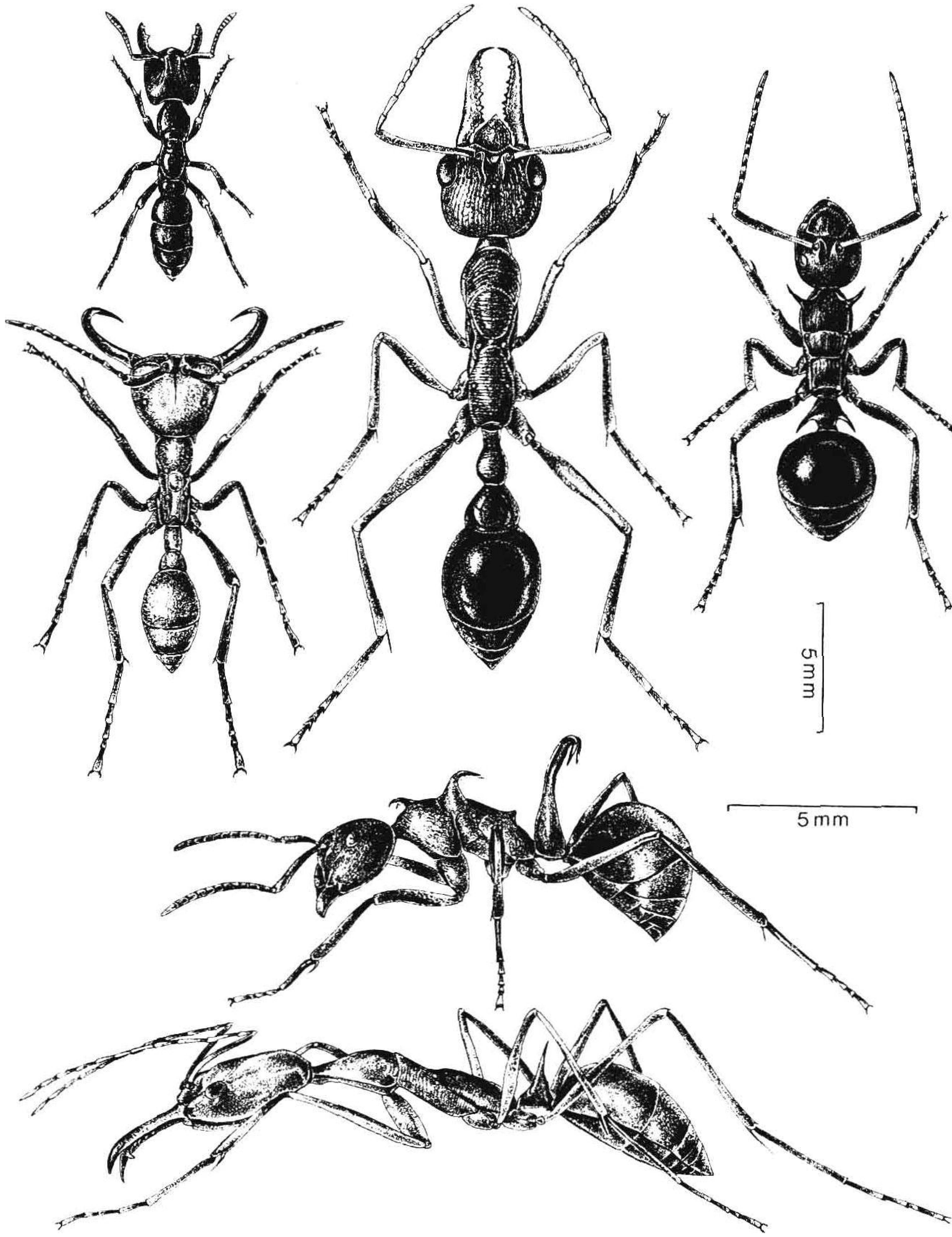
Thus in ways that become wholly apparent only when one's line

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.

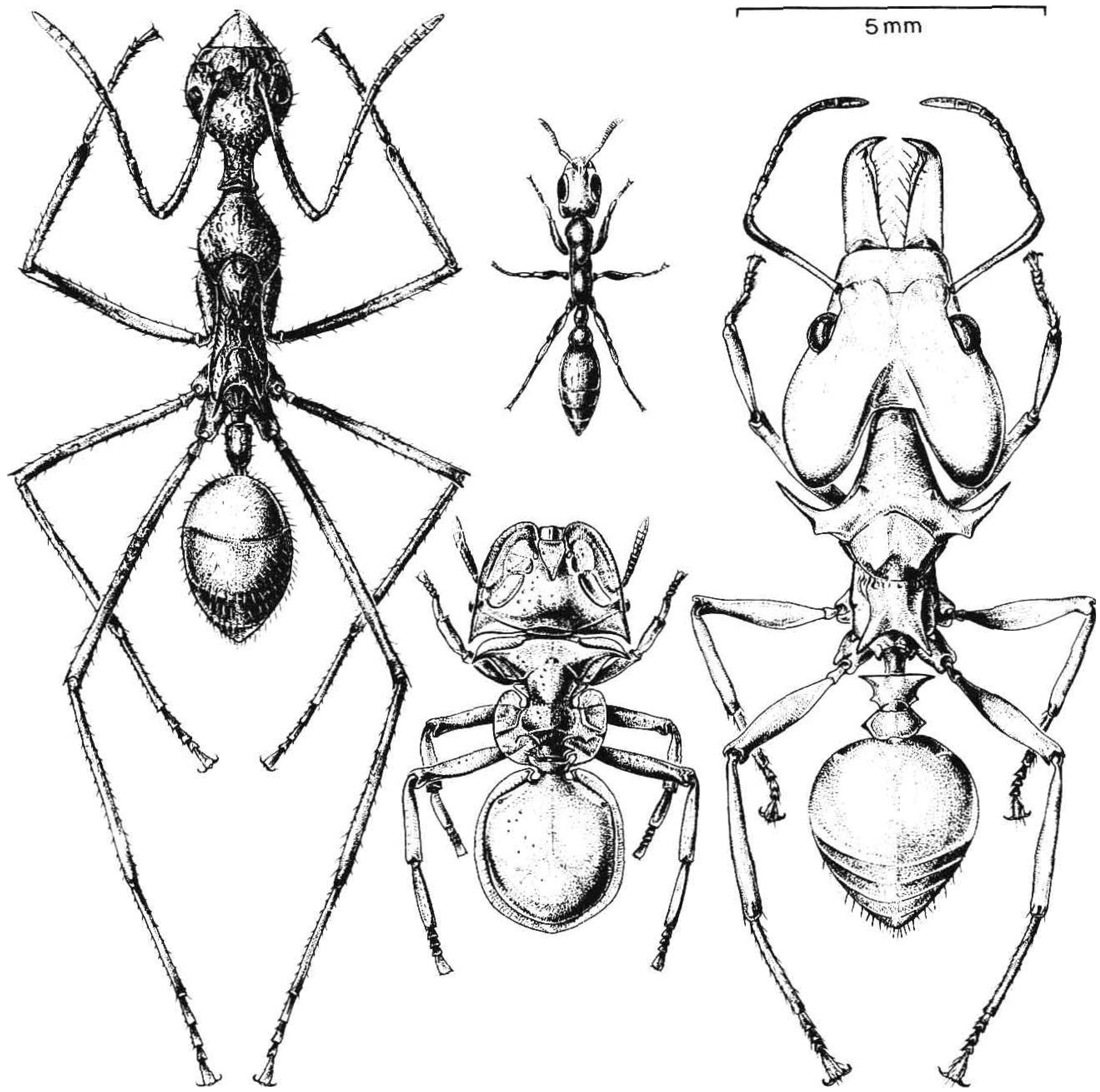
The dominance of ants has struck us in a particularly vivid manner during visits to Finland. In cool forests stretching north to beyond the Arctic Circle, we found that these insects still dominate the land surface. In mid-May on the southern coast, with the leaves of most of the deciduous trees still 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,

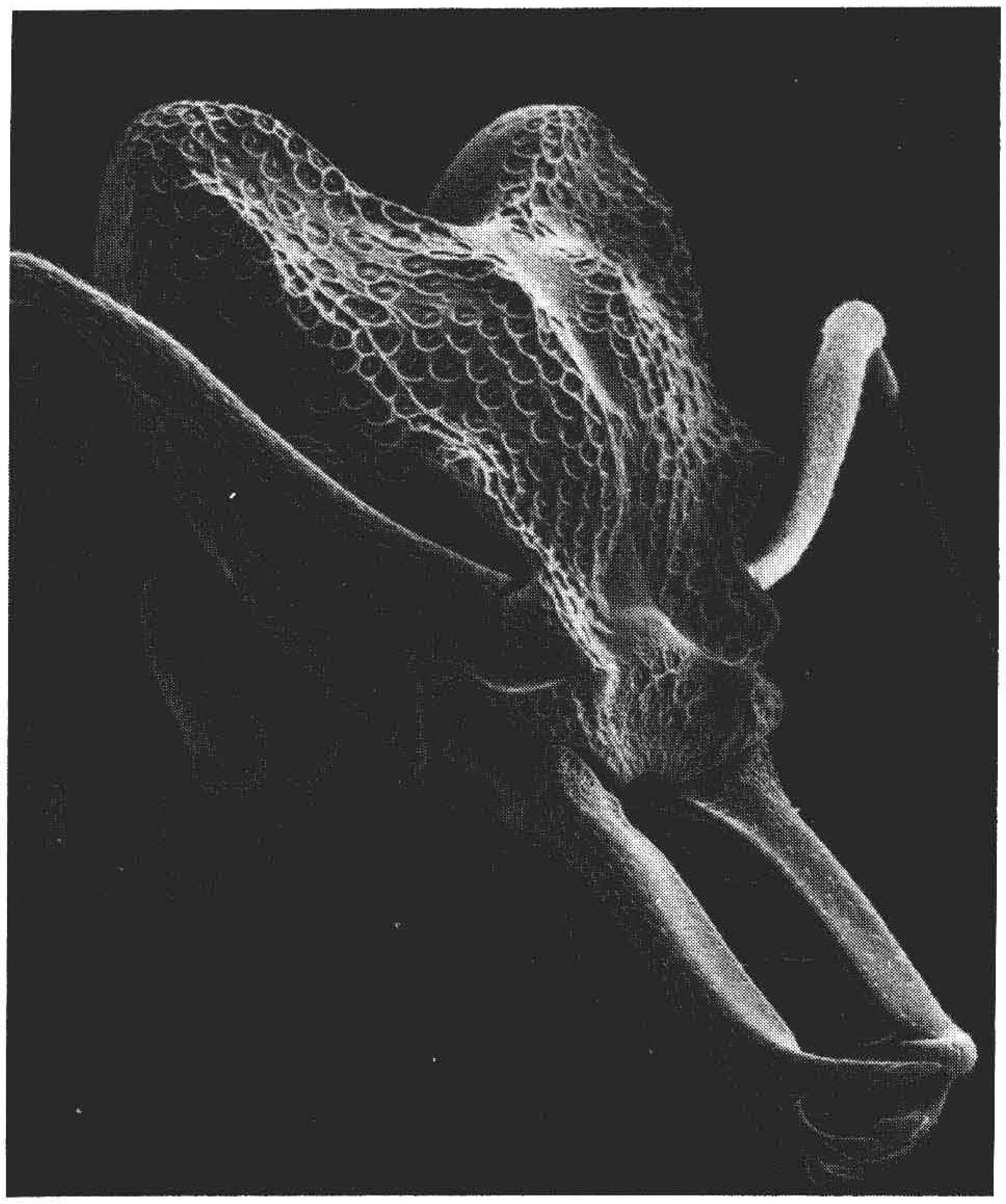


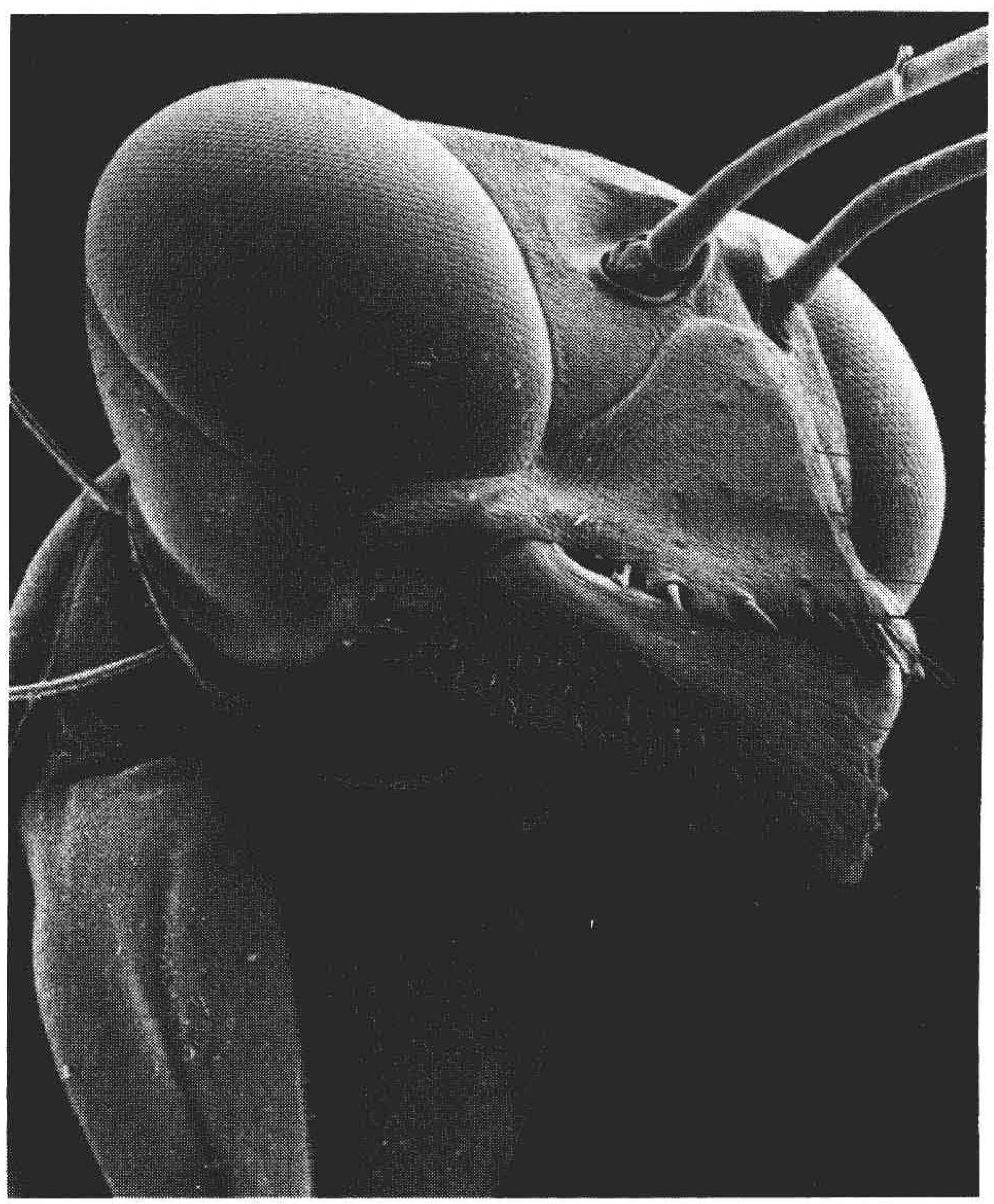
The extreme diversity of the 9,500 ant species of the world illustrated by worker ants. In the top center is a bulldog ant of the genus *Myrmecia;* to its left are a thick-bodied *Amblyopone* and a sickle-mandibled army ant of the genus *Eciton.* To the right of the bulldog ant is a multiple-spined *Polyrhachis,*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



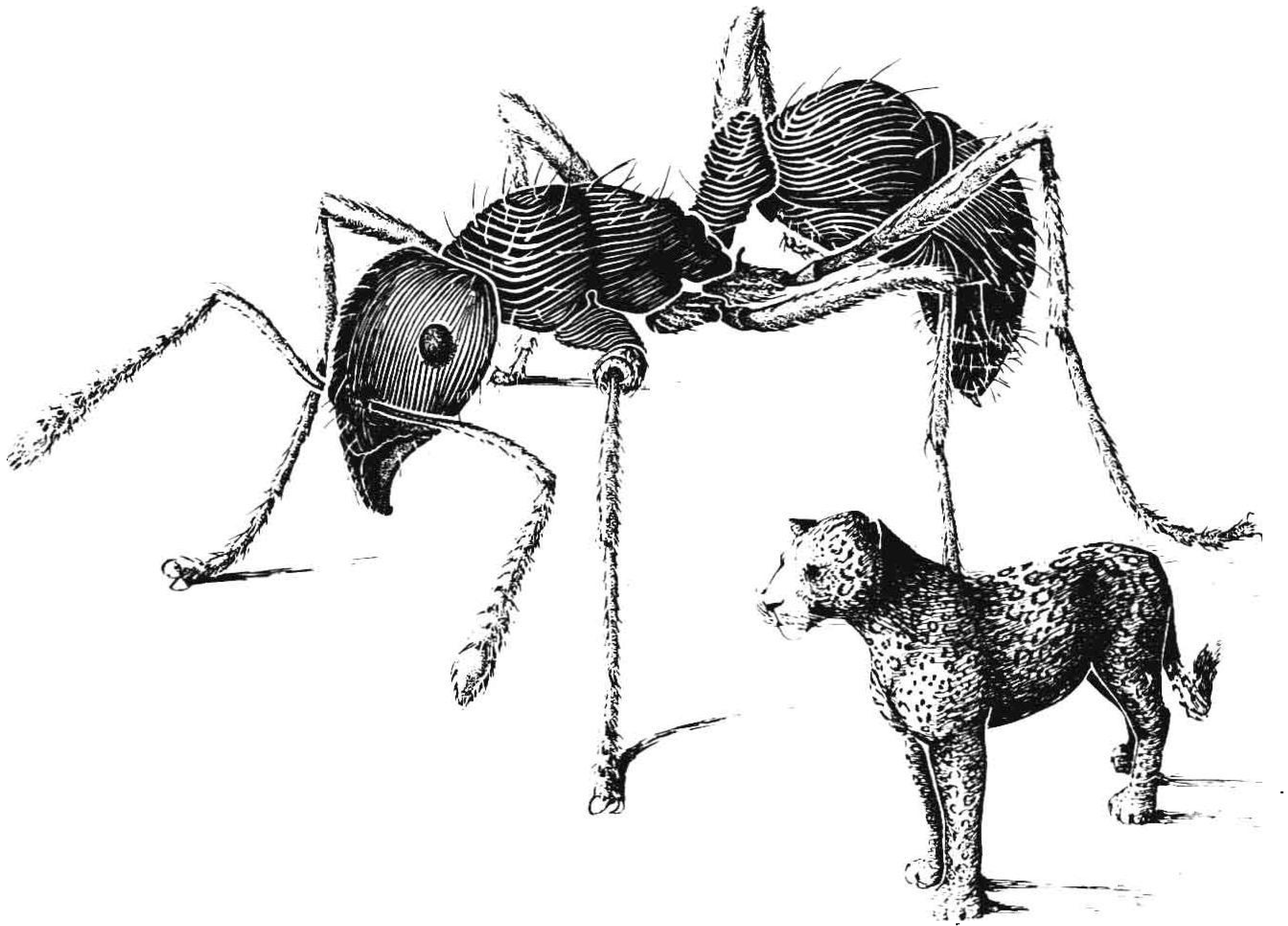


dominated the ground surface. The cone-shaped nests of several species, covered with freshly excavated soil and fragments of leaves and twigs, each housing hundreds of thousands of workers, towered a meter or more high, the equivalent for an ant of a forty-floor skyscraper. Ants seethed over the mound 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-