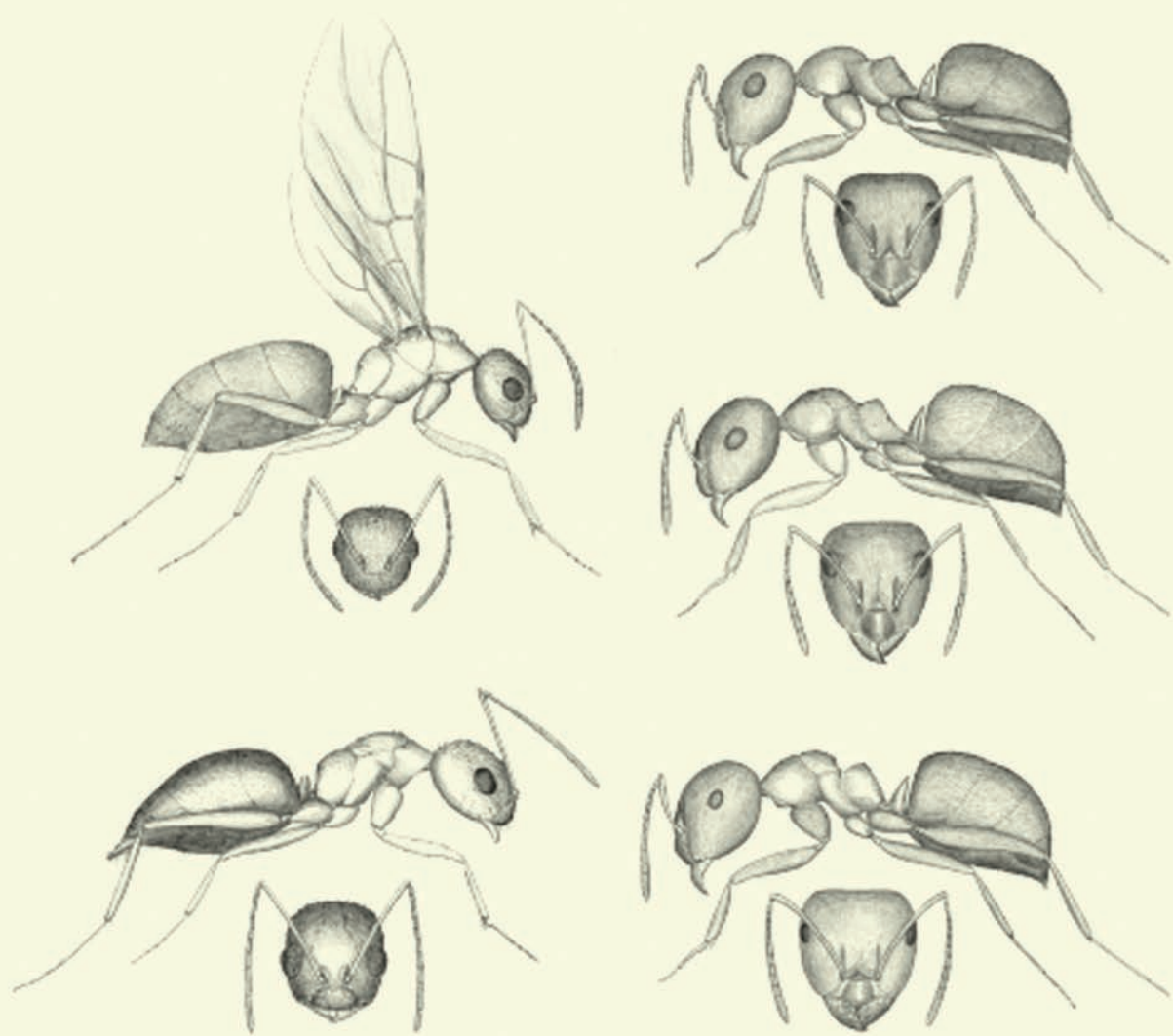


# ANTS OF FLORIDA IDENTIFICATION AND NATURAL HISTORY



MARK DEYRUP

# ANTS OF FLORIDA



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MARK DEYRUP

Archbold Biological Station, Venus, Florida, USA



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## ACKNOWLEDGMENTS

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Several myrmecologists became important ant-collecting companions, lending their knowledge and sharp eyes to many productive collecting expeditions. I am determined that the completion of this book will not mean the end of collaborations with my trusty friends Lloyd Davis, Stefan Cover, and Zachary Prusak. Edward O. Wilson sponsored and led several collecting trips, and has also consistently encouraged the Ants of Florida project. Thanks to all!

As mentioned above, I have been studying Florida ants for more than 30 years, with some distractions and detours along the way. Here, I acknowledge the work of myrmecologists, many of them friends or acquaintances, who have made timely contributions by revising groups of Florida ants, usually providing the Archbold Biological Station with authoritatively identified specimens after

completing the taxonomic work. These 30-year colleagues include (in no particular order) James Trager (revisions of *Nylanderia*, *Dorymyrmex*, *Formica*, *Solenopsis*, and *Polyergus*), Phillip Ward (*Pseudomyrmex*), William Mackay (*Temnothorax*), William Mackay and José Pacheco (*Solenopsis*), Barry Bolton (*Strumigenys* and *Tetramorium*), Clifford Johnson (*Crematogaster* and *Dolichoderus*), Roy Snelling (*Camponotus*), Marcio Naves (*Pheidole*), C. Baroni Urbani and Maria De Andrade (*Proceratium*), and John LaPolla and Robert Kalla (*Nylanderia*). I also gratefully acknowledge Barry Bolton, whose catalog of ants came in time to tremendously simplify all taxonomic work, and Norman Johnson, whose Hymenoptera Name Serve website gives access to the original descriptions of ants.

During my three-decade exploration of Florida ants, my understanding of the natural history of many species has depended on the contemporaneous work of additional colleagues. The encyclopedic treatise *The Ants* by Bert Hölldobler and Edward O. Wilson provided a natural history foundation for all my work. A series of studies by Walter Tschinkel and his team of myrmecologists has revealed often unexpected discoveries in the lives of many ecologically important Florida ants. Recently, James Wetterer has been presenting new perspectives on a long series of exotic Florida ants.

The distribution maps of Florida ants benefited from three different levels of assistance. Lloyd Davis collected thousands of voucher specimens from north Florida and compiled collection

information from specimens at the U.S. Museum of Natural History (Smithsonian). Clifford Johnson contributed a large collection of *Strumigenys*, including many specimens of rare species. The late Walter Suter allowed me to look through his Berlese funnel residues, which also yielded many new distributional records. The tabulation of the thousands of specimen records was done by Philipp Wiescher, who geo-referenced all the specimens preparatory to making distribution maps. The maps were designed and produced by Roberta Pickert, with recent updates by Vivienne Sclater.

Throughout my career in Florida entomology, the Archbold Biological Station has been my support, as a grouper might be supported

by a gloriously diverse and beautiful coral reef. The unique natural and intellectual properties of the Archbold Biological Station could never persist in our turbulent society without the faithful guardianship of the Archbold board of directors and executive directors. I thank both the board and the executive directors James Layne, James Wolf, John Fitzpatrick, and Hilary Swain for their support of the Ants of Florida project and other projects in entomology at the Archbold Biological Station. I particularly thank John Fitzpatrick, an ornithologist, for the suggestion of an illustration-based ant guide loosely based on the kinds of field guides that have been so successful in ornithology.

## INTRODUCTION

Purpose: This book is for those Floridians who live in proximity to a diversity of interesting ant species. Actually, that is all of us. This book is an invitation to detach from personal servomechanisms, flip open the airlock, extend the landing ramp, and take a pioneering step onto the exciting Planet of the Ants. It is a world that is amazing, intricate, beautiful, savage, and almost unexplored.

### ANTS ARE IN CHARGE OF THE STATE OF FLORIDA

Florida is crawling with ants. A cookie crumb dropped on the ground quickly attracts ants in almost any terrestrial habitat. If the cookie crumb is placed on the trunk or branch of a tree, patrolling ants carry it off. If the bait is buried in a perforated vial, it is found by ants that are moving freely through Florida's sandy soil. This suggests that virtually every meter of the whole state is being scoured for food by scavenging ants, and this ceaseless foraging covers an area many times that of the surface area of Florida, because it includes the leaves and stems of plants, and the volume of soil around their roots.

Not one of Florida's many ant species, however, is living on cookies. Florida's ants make their living by exploitation of all kinds of ecological systems, both natural and artificial. Some ants are ecologically specialized; there is an ant that subsists on spider eggs and another that lives in hollow mangrove twigs. Some ants are generalists; there are

ants that are equally at home in a forest or the edge of a parking lot, and ants that will attempt to grab any form of protein or sweets. Fortunately for us, we are very large as animals go, but if we were the size of beetles or caterpillars, we would realize the absolute necessity of discovering how to survive in a world ruled by ants.

Ants are a major force in Florida landscapes; this is one reason for learning about ants. A deeper reason might be curiosity about how the social behavior of a relatively small group of species has allowed them to dominate regions with a warm climate like that of Florida. Perhaps the study of ants may, in some people, provide a more basic reward: reassurance that the natural world around us can always astonish us with its intricate order.

### BECOMING AN ANT EXPERT

Theoretically, it should not be very difficult to become an expert on Florida ants. The number of known species, 239, is not daunting compared with that of groups such as birds or butterflies. This book attempts to make identification relatively easy and gathers together the highly fragmented literature in species-by-species accounts of biology. The main problem is that ants are small, requiring examination through a microscope. This means that collecting ants is part of becoming an ant expert. On the good side, collecting insects can be an enjoyable challenge, and few people care if a

small number of ants get collected. A single insecticide application on a lawn probably kills more ants than could be collected in a lifetime.

Ant experts are in more demand than one might expect. Most Floridians have ant stories or ant problems that they are happy to relate in hope of getting further information. There is often genuine curiosity behind the standard comment, "Interested in ants? Come to my house, you can have them all!"

## LEARNING TO IDENTIFY FLORIDA ANTS

### Illustrations

This book is intended to make it as easy as possible to identify and learn about Florida ants. It is designed for general naturalists as much as for entomologists or ant specialists. It obviously reflects modern field guides, which take advantage of the remarkable human ability to observe and remember small differences between species when standardized illustrations are provided in the form of "plates" of similar species. An important advantage of field guides is that the user's brain registers a large number of images while the user leafs through the plates, effortlessly increasing general expertise. The taxonomic keys that are traditional in entomological works are not included because it is unlikely that many users would prefer them to the "field guide" identification method. This book, of course, cannot aspire to be a field guide, as all ants are small and must be examined through a microscope to see any details. Eventually, one can become proficient at identifying many ants in the field, just as ornithologists can identify birds that are tiny dots against a cloud, but this is a skill not taught by books. Incidentally, the posture of the ants in the illustrations is not meant to be "natural." The appendages have been spread so they will not hide the body, and only appendages on the left side are included in the drawings.

**Plates 1 and 2** are diagrams showing the general morphology of ants.

### Diagnoses

Each species account begins with a small section on "Taxonomy and Similar Species." This section reminds the user of confusing similar species and confusing taxonomic uncertainties, if any.

## COLLECTING FLORIDA ANTS

Many of the diagnostic features shown in the identification plates can only be observed by moving a specimen this way and that under a microscope. This requires collecting, killing, and preparing specimens of ants. I usually kill ants by putting them in a vial of alcohol or in the freezer. The dead specimens are glued (I use Elmer's Glue) to a little, narrow triangle of stiff paper (I make points from leftover strips of heavy, smooth drawing paper). It is possible to order a point punch that makes these paper triangles. There are hundreds of specimens of ants displayed on the AntWeb site, providing dorsal and lateral views of properly prepared ant specimens. The insect labels associated with each specimen were temporarily removed from each specimen and photographed separately. Labels from recently collected specimens show the kind of information that should be included on the label.

Not many people collect Florida ants, so it is currently easy to make significant contributions to knowledge of Florida ants, such as new county records or range extensions within a county. These new records or other natural history discoveries should be associated with a small number of representative "voucher specimens" that provide a permanent confirmation that the ant is the purported species. These voucher specimens should end up in a permanent insect collection. All the dots on the range maps of ants in this book are associated with a voucher specimen, usually in the collection of the Archbold Biological Station, occasionally in the Florida State Collection of Arthropods or in the U.S. National Museum.

## DISTRIBUTION, NATURAL HISTORY, AND NAME DERIVATION

Each species has its own sections on distribution, natural history, and name derivation. Although there are maps showing known Florida distribution for most species, distribution outside of Florida is described, not shown in a map. The natural history section includes whatever is known to me about the biology of the species, widely varying from one species to another. The section on name derivation explains how the species got its name, or a suggested explanation if the reason for the name was not included by the author of the species.

This book is the result of years of study of Florida ants by the author and by many other entomologists. Knowing this, the reader may be surprised and disappointed by avowals of ignorance, for example, "knowledge of the distribution of this species remains incomplete," "the male of this species is unknown," "the function of these peculiar hairs is a complete mystery," and "this is apparently a species complex that includes one or more undescribed species." I apologize

for any sense of dissatisfaction such phrases may impart. There is still an enormous amount of research to be done on Florida ants, much of it relatively simple and requiring little fancy equipment. This book is a guide to what is known about the ants of Florida, but it is also a guide to what is not known about the ants of Florida. The reader will soon see that there are enough mysteries to absorb the energies of many generations of inquisitive naturalists.



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## ABOUT THE AUTHOR

**Mark Deyrup** grew up in New York City, home to a surprising number of insect species, including ants, which find a living even in sooty crevices and cracks between slabs of concrete. Inspired by this limited but interesting fauna, he went to Cornell University for an undergraduate degree in entomology. This was followed by a Peace Corps stint in Ecuador, a hot spot of biodiversity. After the Peace Corps, he got a doctorate in forest entomology at the University of Washington, followed by several years teaching

entomology at Purdue University. Since 1983, he has enjoyed an ideal entomologist's job, studying insect diversity and natural history at the Archbold Biological Station in Venus, Florida. He has published approximately 110 papers on subjects ranging from pygmy mole crickets that eat cyanobacteria beneath the surface of sandy areas, to a moth whose caterpillar hangs out in webs of social spiders. While working on the Ants of Florida project, he has described 12 new species of ants.



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## PART ONE

# An Overview of the Ants of Florida

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### INTRODUCTION

The following sections are an informal compendium of all the patterns that I see in the ant fauna of Florida. This includes not only patterns in distribution but also ecological patterns, the kinds of relationships between ants and humans, and even the trends in the nomenclature and research dealing with Florida ants. For an introduction to ant morphology see [Plates 1 and 2](#).

### FLORIDA ANT STATISTICS

There are 239 species of ants known in Florida. The ants of the state are relatively well known, and the users of this book should expect to find accounts of almost any ant they find. Two lines of evidence, however, suggest that there are some more species to be discovered: (1) Additional species have been accumulating, although at a slow rate, right up to the time of writing these words (2015); (2) several species have been collected in Florida only once or twice, a circumstance that always hints that there are more species to be found. Species that are very localized or difficult to collect (imagine a species that lives in hollow twigs at the tops of trees in Hell's Half Acre in Jefferson County) are likely to have been overlooked. The real number of species of ants in Florida is probably close to 245 or 250, excluding any new exotic species that may invade in the future. Any enthusiastic and ingenious ant hunter is likely to be rewarded eventually with species that have never been reported in Florida. Some of these ants will be species unknown to science. The best area to find unreported native species is the northern tier of counties in the Peninsula and

all of the Panhandle, a poorly studied area with localized and endemic species of animals in many groups, from frogs to beetles. Newly introduced species could turn up almost anywhere but are most likely to be found near major ports.

With its 239 species, Florida is one of the most ant-rich states, a fact strangely absent from the promotional literature of the Florida Tourist Bureau. One site in Florida, the Archbold Biological Station in Highlands County, has 128 species of ants, the most ants known for any site in the United States. Florida undoubtedly has more species of ants than any other eastern state, largely because its unique fauna of tropical and subtropical species is combined with the more widespread fauna of the southern Atlantic Coastal Plain, with elements of the southern Appalachians thrown in. The only other eastern state that has been carefully surveyed is North Carolina (Carter 1962; Guénard et al. 2012), which has 192 species, a remarkably high diversity that is attributable to North Carolina's great diversity in topography and habitats.

As one goes north from the Carolinas, the ant fauna inevitably diminishes because ants are basically creatures of warm climates, even though there are some groups of ants, such as the genera *Formica*, *Lasius*, and *Myrmica*, whose rich (and confusing) proliferation of species is almost entirely restricted to temperate regions.

Large southwestern states have even more ant species than Florida. California has 270 species (Ward 2005), New Mexico has 239 species (Mackay and Mackay 2002), and Arizona probably has even more species than New Mexico (Hunt and Snelling 1975). West Texas, with an area approximately twice that of Florida, has 184 species listed

(Cokendolpher 1990), and we already know of many additional species from the pine woods of East Texas and from the Brownsville area. It may still be difficult, however, to find a southwestern site with more than the 128 species known from a relatively small Florida site, so Florida may be able, in some sense, to retain its proud claim to being the “antiest” state for some time to come.

## NAMES OF FLORIDA ANTS

### On the Joys and Frustrations of Knowing the Names of Ants

Many naturalists will use this book primarily for identifying ants. Biologists know that the purpose of the scientific name of an organism is to provide a unique pair of code words under which is indexed the information about that organism. Every correct identification is a key to a file box of knowledge, whether in somebody’s head (“What do you know about *Temnothorax torrei*?”), or (formerly) in the indices of an abstracting journal, now replaced by electronic search engines, or the book you are holding in your hand. The knowledge-holding boxes, of course, are often empty. The enterprising Florida naturalist who encounters a small yellow ant, identifies it as *T. torrei*, and looks it up in the index of this book for the species account, still would not be able to find out how this species makes its living, because nobody knows. That too, however, is useful information. In the naturalist’s head, a new, empty file box has been set up, ready to receive any observations on *T. torrei*.

Field biologists are aware of another phenomenon: the possession of a name sharpens the senses. The mechanism in our brain that sifts sensory input is connected to our information files, and shunts into a spotlight of greater awareness the organisms that we recognize. To know more is to see more. This discussion is all by way of explaining what might seem an inordinate preoccupation with names in this book, and among many biologists, who are willing to argue for hours over the application of a name. This obsession has an adaptive basis, although, like other adaptive obsessions, it can easily get out of hand.

### Changing Names

The nomenclature of Florida ants is not quite settled. There are taxonomic problems about certain

species in approximately 10 of the 49 genera of Florida ants. This may be frustrating, but it is no great cause for concern, as biologists have not been given any deadline for finalizing the names of ants, or any other organisms. The great majority of names used here should remain stable. A residue of species may have their names changed for two reasons.

Generic names may be changed when the higher classification of a group of ants is revised. The Florida species of *Conomyrma*, for example, were returned to the genus *Dorymyrmex* in Shattuck’s 1992 revision of the Dolichoderinae. All such changes are made for the sake of the internal consistency in our classification of a group. There is no such thing as a biological genus concept, in the sense that there is a biological species concept. The use of the name *Conomyrma elegans* is not really wrong, because there could be no doubt which species was intended, and because a revision does not have the force of law, but most myrmecologists would agree that *Dorymyrmex elegans* is the current usage. Some names, *Colobopsis*, for example, are applied as a subgenus of *Camponotus* by some and as a full genus by others. This seems like a small difference in opinion that can eventually be resolved with a revision of the species groups of *Camponotus*, but the alleged misuse of a genus name can occasionally arouse as much pedantic petulance as the misidentification of a species.

Species names (or “specific epithets”) can change when our concept of a species changes. The Florida subspecies of *Leptogenys elongata*, *Leptogenys elongata manni*, was raised to species level some years ago, so we now recognize two species, *L. elongata* and *L. manni* (Trager and Johnson 1988). Names can change on lists because the name was mistakenly applied. Old records of *Monomorium minimum* from Florida probably all refer to two other species, *Monomorium viridum* and *Monomorium trageri* (DuBois 1986). Species names can change for the trivial reason that there was an earlier, disused name that takes priority, but most species name changes reflect advances in our understanding of the status of the particular species.

There will be some species-level name changes in Florida ants. We are, for example, waiting for names for several species of *Brachymyrmex*. *Crematogaster ashmeadi* might be a complex of at least two species. Working out correct species names has a biological significance, because species, when looked at in a particular area and era, have

an ecological and genetic integrity that is absent at the genus level and above.

This manual generally follows the subfamily classification outlined in Table 1 of Ward (2007) and the lists of genera from Barry Bolton's *A New General Catalogue of the Ants of the World* (1995, with on-line updates) and *Synopsis and Classification of Formicidae* (2003) with a few recent updates of particular genera.

### On English Names for Florida Ants

Most species of insects do not have English names or "common names" of any sort. There is a good reason for this. There are hundreds of thousands of species of insects, and most of these species can only be identified by a few experts. Many naturalists are interested in ants, but the number who can identify most of the species they see is very small. The specialists who can identify species of the genus *Crematogaster*, to take a typically difficult genus of ants, are quite satisfied to have only the single Latinized name for each species. They certainly do not want to deal with a batch of vernacular names, when they already know species by their formal scientific names, such as *Crematogaster atkinsoni* and *Crematogaster cerasi*. In practice, almost all our discussions of such species are with each other, as nobody else seems very interested. The term *common name* seems absurd in such a context: fewer people would know the species by its common name than by its scientific name. To make matters worse, if one gives a species a common name, for example, calling *Odontomachus ruginodis* the "West Indian Snapping Ant," this name might be unacceptable in Spanish-speaking countries such as the Dominican Republic and Cuba, where this ant also occurs, so they might want their own name.

I personally have had a reverence for the system of binomial nomenclature since the age of 9 or 10, when I began to teach myself scientific names, which I thought of as the "real names" of animals and plants. I remember my surprise when I discovered that scientific names are occasionally changed. I am still quite conservative about nomenclature, and find myself resentful of the attitude among some modern systematists that names of genera are bits of falsifiable trivia that can be changed whenever a vagrant intellectual breeze rustles the topmost twigs of some computer-generated phylogenetic tree. Fortunately,

ants have not suffered much in this regard, and most of the recent changes, such as transferring the Florida species *Iridomyrmex pruinosus* to the genus *Forelius* (Shattuck 1992), are broadly based in ecology, morphology, and phylogeny.

Although I was teaching myself scientific names of insects with flash cards while standing in line at the school cafeteria at the age of 15, I would not hold others to this standard of oddness. The world is largely populated with people who are less peculiar, even as teenagers. Scientific names are not at all the currency of ordinary conversation. They are likely to be seen as meaningless concatenations of syllables, difficult to remember, embarrassing to try to pronounce. I spend some of my time talking to gardeners and other informally trained naturalists, and have become painfully familiar with the looks, ranging from befuddled to hostile, that I get when I start to toss around scientific names. If I say "Caribbean Trailing Ant," I get an entirely different reaction than if I say "*Monomorium ebeninum*," even though the two names are equally unfamiliar. Sometimes, I think that there might be some brainstem response to a person who seems to interlard their conversation with foreign words from an alien tribe. Sometimes, I think it is simple resentment that I am providing an unintelligible name that will be impossible to remember. It does not matter; it is undesirable to have anything, including a mass of insect names intoned in Latin, standing between the naturalist and nature.

I have therefore concluded that all the ants of Florida should have English as well as scientific names. I am encouraged by the fact that better entomologists than I have made the same decision. In 1953, Jaques Helfer provided English names for the many orthopteroids in his manual of the group. In Charles Covell's field guide to eastern moths (1984), a book that finally made moths easily accessible to a generation of naturalists, each moth has a common name. He claims that most of these names were taken from a pre-existing list of common names (in Sutherland 1978), but the great majority of them cannot be found in that list, and are really from Holland's pioneering 1903 moth guide, or Covell invented them himself, with admirable aptness and brevity. Among guides to Florida insects, the books on dragonflies (Dunkle 1989), damselflies (Dunkle 1990), and grasshoppers (Capinera et al. 2001) include English names for all species. There are

only a few available English names for Florida ants, so I have coined almost all the common names in this book. The Entomological Society of America has allocated to itself the authority to establish “approved” common names (Sutherland 1978), but this list is restricted to the species “commonly of concern to entomologists,” which excludes almost all the ants of Florida. I doubt that I am the best person to make up names; many of the names in this book are more appropriate than concise—“the Woolly Pygmy Snapping Ant” is even clumsier than “*Strumigenys lanuginosa*.” Perhaps these names will become streamlined with usage.

### Subspecies Names for Florida Ants

Subspecific names have a dismal history in myrmecology. Specimens of ants that looked different might be given different subspecies names, even though the differences were related to caste, or to differences in the preservation of specimens. To make matters much worse, many ants were saddled with varietal names, so a specimen might have four or even five names attached to it. As Creighton (1950) pointed out, there was no simple way out of this “altogether horrendous maze of nomenclature.” Some of these names applied to ants that should really be considered distinct species, some applied to ants that were legitimate distinctive geographic subspecies, and a large number of them applied to variants that had no geographic basis and were different castes, or specimens that were discolored in preservation, or, as Creighton discovered in a surprising number of cases, distinguished by characters that seemed to be completely imaginary. Many Florida ants were caught up in this mess, but, largely thanks to Creighton, we have relatively few such problems remaining. Fossilized vestiges of these problems, like taxonomic coprolites, can still be seen occasionally. The Florida species *Odontomachus ruginodis*, for example, was described by W. M. Wheeler in 1905 as *Odontomachus haematodis insularis ruginodis*. The last name, referring to a “variety,” has no taxonomic standing, so *ruginodis* was not really the name of anything until 1935, when M. Smith used it as a subspecific name, *Odontomachus haematodis ruginodis*. This is why M. Smith, not Wheeler, is considered the author of *O. ruginodis* in the species account in this book. *Odontomachus ruginodis* was first recognized as a full species by E. O. Wilson in 1965. This little tangle and a few thousand similar cases are succinctly

dissected in Barry Bolton’s 1995 catalogue, a book that is a miracle of scholarship.

The flagrant abuse of the subspecies concept in ant taxonomy may have helped inspire Wilson and Brown’s general attack on the practice of designating subspecies (1953). To this day, American myrmecologists often avoid using the surviving subspecific names, and almost nobody names new subspecies of ants. But although the logic of the 1953 attack on subspecies is as cogent as ever, and continues to appeal to each new generation of young taxonomists, the usefulness of the geographic subspecies category persistently overwhelms all theoretical objections, and seems set to outlive all its detractors. The young want definitions that always work, but eventually we must always come back to working definitions. Although I am not about to name new subspecies of Florida ants, I recognize the legitimacy of geographic subspecies, and deal with them as they come up in the species accounts.

### One More Thing about Names: Author Names

Attached to the name of each ant is the name of the person who described it, or rarely, as in the case of *O. ruginodis*, the first person who used the name properly. When a species is transferred to a genus that is different from the genus in which it was first described, the author’s name goes in parentheses. The species *Conomyrma elegans* Trager, when transferred to *Dorymyrmex*, became *D. elegans* (Trager). I generally follow Bolton’s 1995 catalogue for author names. The use of an author name outside of a taxonomic treatise is, as the myrmecologist Bill Brown used to say, “An exercise in useless pedantry.” In this book, author names appear only in one place, at the beginning of each species account.

## ECOLOGICAL SIGNIFICANCE OF FLORIDA ANTS

### Ants as Predators

Most species of ants are predatory, as well as scavengers, and ready to attack any inadequately defended arthropod. Adult ants are not, strictly speaking, carnivorous, since they feed mostly on fluids, either sweet fluids such as nectar, or the juices of prey. The predaceous behavior of ants is inspired by the appetites of larvae back in the

nest, and the more food that can be found, the faster the nest grows. With this growth comes strength for nest defense and an ability to invest in the expensive business of producing queens and males that will disperse to new sites. Among more generalist predatory ants, there may be some targeting of the most available type of prey. This allows individual ants to become more efficient at finding and dealing with prey. This also makes these ants more important as regulators of ecosystems because they concentrate on species that are especially abundant.

### Anti-Ant Defenses

Few terrestrial or arboreal arthropods would be able to survive in Florida without anti-ant defenses, either behavioral, morphological, or chemical. Scientists studying the defenses of Florida arthropods often use generalist predatory ants as prototypic archpredators. Florida Carpenter Ants (*Camponotus floridanus*) were used to test the effectiveness of the morphological defense of the Palmetto Tortoise Beetle (*Hemisphaerota cyanea*), which uses adhesive pads on its feet to clamp itself down on a leaf when attacked (Eisner 1972). "Gin traps," rows of snapping teeth on the edges of pupae of lady beetles and many other insects, were tested with the Red Imported Fire Ant (Eisner and Eisner 1992). Peculiar detachable bristles on the millipede *Polyxenus fasciculatus* were shown to have the ability to hogtie Ashmead's Acrobat Ant (*C. ashmeadi*), which is often found under the bark of pine trees, along with the millipede (Eisner et al. 1996). The Florida Harvester Ant (*Pogonomyrmex badius*), which is a predator as well as a seed eater, was photographed being blasted by a species of Florida bombardier beetle (Eisner 1972). A pyralid caterpillar (*Laetilia* sp.) that feeds on scales on lignum vitae trees on Lignum Vitae Key defends itself with regurgitates against Florida Carpenter Ants, which guard the scales (Eisner et al. 1972). The Slender Crazy Ant (*Paratrechina longicornis*) was used as a bioassay to test the chemical defenses of the caterpillar of the Palmetto Borer Moth (*Litoprosopus futilis*) that feeds on palmettos in Florida (Smedley et al. 1993).

It is an absurd understatement to say that we have just begun to discover arthropod defenses against ants. In the sand soils of Florida, which are permeable to ants (as shown by tests with buried baits), every species of soil-dwelling arthropod

must have an anti-ant defense. The larvae of such arthropods, of which there are literally thousands of species, might be able to use active defenses, but the pupae must often depend on passive defenses, such as an impermeable cocoon or chemical deterrents. Consider the digger wasps in the families Sphecidae and Pompilidae: they stock their larval larders with paralyzed arthropods that would be ideal food for a great variety of scavenging and predatory ants. Although the underground groceries are safe from our eyes, they should not be at all safe from ants; it is like hiding hamburger in a hyena pit. We have to assume that these hundreds of species of digger wasps, and the sand-living bees as well, have potent defensive chemicals that can be smeared on the sides of the burrow to exclude ants from what would normally be a highly attractive resource. This is not quite hypothesis in vacuo: ant-repellent chemicals are known in social wasps (Jeanne 1970). Nonetheless, anybody who has ever dealt with an infestation of Pharaoh's Trailing Ants in their kitchen knows how persistent ants can be, even in the face of massive chemical assaults. An aggregation of sand wasp burrows can remain active for years, presumably protected by the minute amounts of whatever chemicals the wasps are able to produce from their various glands. Why haven't ants developed resistance to these defenses over the millions of years during which ants and digger wasps have been living side by side? The answer, as in the case of plant defenses against herbivores, is likely to be that there has been a long history of defense and counter-defense, culminating in a wide variety of defenses against ants. It would be gratifying to know just a few of them.

### Ants as Specialized Predators

A portion of the diversity of life is derived from the fact that any general defense provides an exclusive resource to those species that are able to overcome that defense. This fuels evolutionary specializations and divergences, among the ants as in other groups. Hölldobler and Wilson (1990) have provided a list of specialized predators among the ants, including a number of species that occur in Florida. The largest group of species is among the dacetine ants: as far as is known, Florida species of *Strumigenys* are heavily dependent on Collembola (springtails) as prey. The relationship between the dacetine ants and the Collembola is discussed in

detail later, but the short version is that the only thing as fast as the spring-loaded leaping appendage of a springtail is the spring-loaded impaling mandibles of a dacetine ant. Other specialized predators among Florida ants listed by Hölldobler and Wilson are *Stigmatomma pallipes*, which feeds primarily on geophilomorph centipedes, *Leptogenys manni*, which feeds on oniscid sow bugs, and army ants (*Neivamyrmex*), which attack nests of other ants. In addition, the members of the genera *Proceratium* and *Discothyrea*, including several Florida species, are all likely to be specialized predators of arthropod eggs (Brown 1979). The Japanese myrmecologist Masuko, one of the finest observers of the natural history of ants, has discovered (1994) that two Japanese species of *Myrmecina* are specialized predators of armored oribatid soil mites, and there is every reason to believe that this remarkable behavior occurs in other *Myrmecina*, including species found in Florida.

All the known examples of specialized predators in Florida belong to the subfamilies Ponerinae, Ecitoninae, and Myrmicinae, groups that retain the ancestral stinging ability of ants. It has been suggested that the possession of a sting may be a preadaptation to prey specialization because it allows elusive or well-defended prey to be subdued quickly. This explanation may well be true, but one can't help thinking that if specialized predation had been concentrated in the stingless subfamilies Dolichoderinae and Formicinae, we would happily explain the phenomenon by claiming that immobilizing chemical sprays are the only good way to deal with especially fast or fierce prey that are difficult or dangerous to seize and handle. One would also expect the greatest degree of specialization in the fastest-moving ants, which would have the best ability to encounter and bring back scarce or dispersed prey; this is not at all the case. Returning to reality, additional specialized predators among Florida ants are most likely to be found among the species of Ponerinae and Myrmicinae. It would be worth taking note of prey and middens of species such as *Ponera notica*, *Hypoponera inexorata*, *Temnothorax smithi*, *Temnothorax bradleyi*, and also the species of *Proceratium*, *Discothyrea*, and *Strumigenys*, which may have interesting narrow specializations beyond the known predilections of their genera.

Most specialist predators among Florida ants are uncommon species compared to generalists that live in the same habitat, and their ecological effects are sure to be more subtle. In a simple

specialist predator and host system, predators lag behind the populations of hosts and may accentuate population fluctuations, but as soon as one is dealing with a complex of specialist and generalist predators, the system loses much of its predictability, even in models (Hassell and Godfray 1992).

### Cumulative Effects of Predatory Ants

The idea that ants control arthropod communities of Florida, and have helped shape the defensive adaptations of thousands of species, may seem extreme (or myrmecocentric), but it is supported by the devastation of Hawaiian arthropod communities when ants were introduced onto previously ant-free islands (Huddleston and Fluker 1968; Reimer 1994). This is not to say that ants alone rule Florida ecosystems; other groups such as nematodes and bacteria, beetles, and spiders are at least as important, and on a larger scale, humans have the ability to modify or destroy every habitat. It is, however, reasonable to believe that if Florida were divested of ants by means of some fantastic new insecticide, the whole state would suffer major biological perturbations. Since many species of arthropods, despite their defensive adaptations, have their populations repressed to some degree by ants, the most obvious effect would be the drastic increase of many other arthropods. On the scale of an individual plant, this has been shown by removing the extrafloral nectaries that certain plants use to attract predatory ants, and watching the resulting depredations by caterpillars (Beattie 1985).

### Ants as Seed Dispersers in Florida

The dispersal of seeds by ants is a phenomenon that was discovered approximately a hundred years ago, but received little attention until quite recently. If early myrmecologists observed ants carrying seeds, they probably assumed that the seeds themselves would be consumed by the ants. Twenty-five years ago, only 300 plants were known to have ant-dispersed seeds; today, the number is approximately 10 times that (Westoby et al. 1991). Ants are induced to disperse seeds by a fleshy, usually lipid-rich structure (called an elaiosome) attached to the seed, or more rarely, an attractive coating on the seed. After this edible treat is removed, the seed is discarded, usually in

a midden near the nest, where it may be buried by subsequent dumping. Seed dispersal by ants and other forms of seed dispersal have been compared by region and habitat (Willson et al. 1990), and it is clear that ants are major seed dispersers in only a few places: the fire- and drought-prone habitats of Australia, the droughty and nutrient-poor open shrub habitats of South Africa, and, to a much more limited extent, deciduous forests of eastern North America, where many spring-flowering herbs are dispersed by ants.

There are various theories to account for these patterns, and one might hope that these theories would tell us what to expect in Florida. Thompson (1981) suggested that spring-flowering woodland plants produce seeds at a time when the birds that are more normal seed dispersers are concentrating on collecting insects for their young, and less interested in fleshy fruits. We might, therefore, expect that there would be a good proportion of ant-dispersed seeds in the relatively small areas of hardwood forest in northern Florida where there are populations of spring-flowering herbs in genera that are often dispersed by ants, such as *Erythronium*, *Uvularia*, *Trillium*, and *Viola* (Thompson 1981). Ants in the genera *Lasius*, *Myrmica*, *Temnothorax*, *Tapinoma*, and especially *Aphaenogaster*, which are seed dispersers of violets in West Virginia (Culver and Beattie 1978), are also present in northern Florida. There are no published studies of seed dispersal by ants in northern Florida forests, but methods of Culver and Beattie (1978) could easily be adapted to northern Florida. The prevalence of ant-dispersed plants in open, scrubby, often fire-maintained habitats with nutrient-poor soils (Westoby et al. 1991) should make the heart of the Florida myrmecologist beat faster, because this habitat characterization fits most terrestrial habitats of Florida. With the abundance and diversity of ants available in these habitats, ant-dispersed plants should be common. Nobody has looked very carefully, but indications are not promising. The only widespread and diverse genus known to have elaiosomes is *Polygala*, although there are also a few species of open site *Viola*, mostly in northern Florida. There are probably many plants whose fresh seeds have never been examined for elaiosomes.

A particularly interesting case of seed dispersal by ants in tropical Florida was reported by Kaufmann et al. (1991), who studied seed dispersal in the exotic fig *Ficus microcarpa*. This species has a two-phase dispersal system: the fruits are eaten

by birds, and then the ants collect the seeds from bird droppings. This disperses the seeds from their original clump, and if the ant species is arboreal, the seeds may be taken up into the nest where they can grow epiphytically and eventually take over the tree. There is no reason why this bird-ant two-step system could not be the dispersal mechanism of some other Florida plants that have berries and small seeds, and the methodology of Kaufmann et al., while reasonably demanding, would not be impossible to replicate. The discovery of a complex ecological interaction such as the two-phase dispersal of fig seeds normally leaves ecologists smiling fondly over the intricacies of nature, but in this case, there was no joy in Dade County: the tree is an exotic species of fig (*F. microcarpa*) that seems poised to invade remaining natural tropical hammocks of the area. Accomplice ants that transport the seeds are *Paratrechina longicornis* and *Solenopsis invicta*, themselves exotics.

#### Ants as Seed Harvesters in Florida

Several species of Florida ants harvest and consume seeds. The most obvious of these is the Florida harvester ant, *P. badius*, which gathers large quantities of seeds, although it is also a predator and scavenger (Ferster and Traniello 1995). At some sites, one may see streams of foragers collecting seeds of scrub rosemary (*Ceratiola ericoides*), and after fires in sand pine scrub, these ants collect by the thousands seeds of sand pines (*Pinus clausa*) that are released from their serotinous cones by fire. The seed hosts of this ant in many natural communities in Florida are unknown, much less the impact of these ants on plant associations in which they live. Western species of seed-harvesting ants can have pronounced and unexpected effects on plant associations (Hölldobler and Wilson 1990), but it is unlikely that Florida species have such strong effects, because intensive flowering in many plant species is triggered by fires, rather than by seasonal rains that produce more or less dependable seed crops. On the other hand, in habitats dominated by long-lived perennials, such as the open habitats of Florida uplands, seed predators could have major and generally ineluctable effects, especially through maintenance of patchy distributions of plant species, if the ability of a plant species to establish itself in a spot that is temporarily available for long-term establishment is determined by proximity to a nest of seed-harvesting ants.

*Solenopsis geminata* is another Florida species that harvests seeds on a large scale. The largest workers are morphologically specialized as seed grinders (Wilson 1978). In experimentally seeded plots at a site in Mexico, Risch and Carroll (1986) showed that this ant changed the composition of plants in study plots. These researchers also discovered complex foraging behavior in *S. geminata*. They showed, for example, that when ants encounter small numbers of less preferred seeds mixed in with large numbers of their favorite seeds, the ants are more likely to bring back the less preferred seeds than if they encountered the less preferred seeds alone. The reverse is also true: preferred seeds are safer among a large number of less preferred seeds. When this kind of complexity crops up in an ecological experiment that has been drastically simplified, it does not make one feel that it will be easy to pin down ecological effects of ants in natural systems.

Several other species of Florida ants regularly harvest seeds. I have observed seed harvesting in *Pheidole littoralis*, *Pheidole adrianoi*, and *Pheidole metallescens*, and it almost certainly occurs in *Pheidole carrolli*. The only nest of *Solenopsis globularia* that I have seen had a chamber packed with small seeds. In open sandy habitats, seed harvesting is a conspicuous phenomenon, and it should be easy to discover many new relationships between specific plants and seed predators.

### Ants in the Diet

**Generalist Ant Predators:** We myrmecologists are so fond of expounding on the dominant role of ants in ecosystems that it is difficult for us to think of ants as victims. It is useful to remember that any group of superabundant organisms is likely to feature on the menu of numerous creatures. I have frequently seen ants in the stomach contents of Florida Scrub Lizards (*Sceloporus woodi*), Green Tree Frogs (*Hyla cinerea*), and Southern Toads (*Bufo terrestris*). Numerous insects and spiders eat ants opportunistically, including antlions (Myrmeleontidae), most species of which appear to be generalist predators. Flights of ants are a bonanza for general insectivores. Queen ants are especially choice, as they are usually plump with resources needed to found a colony, and generally unable to sting (except for some Ponerinae). After a night flight of ants, webs of night-weaving spiders (*Neoscona* spp.) may have bundles of alate *Pheidole* waiting to be stashed for

later consumption. Florida Scrub-Jays (*Aphelocoma coerulescens*) and Blue Jays (*Cyanocitta cristata*) come to road shoulders to harvest queen fire ants running along the pavement. Tree swallows (*Iridoprocne bicolor*) swoop through early flights of fire ants in the spring and are probably responsible for the winged but gaster-less mutilated queens that one finds crawling over the ground. Cuban Brown Anoles (*Anolis sagrei*) perched on shrubs bordering my driveway engage in frenzied footraces across the paving to seize recently landed fire ant queens and males.

**Specialized Predators:** Florida ants also face specialized predators. Ants comprise approximately 50% of the diet of Flickers (*Colaptes auratus*) (Moore 1995), and a single species of small ant, *Crematogaster pinicola*, makes up approximately 40% of the diet of the Red-Cockaded Woodpecker (Hess and James 1998). The Eastern Narrow-Mouthed toad (*Gastrophryne carolinensis*) is an ant specialist: at the Archbold Biological Station, the stomachs of 146 Narrow-Mouthed Toads were found to contain a total of 4859 individual ants, representing 43 species and comprising 95% of all food items (Deyrup et al. 2013). Specialized myrmecophilous insects may appear as commensals in Florida ant nests. These include Syrphidae of the genera *Microdon* and *Rhopalogaster*, an undescribed species of Histeridae in the genus *Terapus* associated with *Pheidole morrissi*, Staphylinidae in the genus *Adranes*, and others.

### FLORIDA ANTS AS PESTS OF HUMANS

The great majority of Florida's ant species do not bite or sting humans, and conduct their affairs in complete obscurity. The red imported fire ant (*S. invicta*) is the most extreme exception to this rule, and earns more attention than all other species combined. For many Floridians, the word ant is synonymous with fire ant, and any ant these Floridians see is considered a noxious pest. There is an increasing tendency for Floridians to label as pests any arthropods that occur in their yard or garden, certainly an untraditional and paranoid view of the outdoors. Some pest control operators and other professional entomologists seem to encourage this view, perhaps unintentionally. The idea that outdoor Florida is packed coast to coast with hostile and even dangerous ants and other arthropods is not only misleading, but unhealthy, as it needlessly raises our anxiety levels, drives us

indoors, and encourages us to permeate our living space with insecticides.

Out of almost 240 species of ants in Florida, only 7 can legitimately be considered outdoor pests. These species are *Solenopsis invicta* (the worst, by far), *S. geminata* (similar to *S. invicta*, but much less common), *Wasmannia auropunctata* (a minute stinging species, most common in south Florida), *Pseudomyrmex gracilis* (a casual stinging species that falls out of trees), *Hypoponera punctatissima* (there are scattered reports of many people being stung by alate queens when there are large flights of this species in south and central Florida), *Camponotus pennsylvanicus* (makes galleries in live trees in north Florida), and *C. floridanus* (establishes large, well-defended nests in outdoor installations such as pump housings and master switch boxes). These pest species are discussed in detail in their species accounts. Innocuous outdoor “yard ants,” such as species of the genera *Dorymyrmex*, *Crematogaster*, *Cardiocondyla*, *Cyphomyrmex*, and *Trachymyrmex*, should not be considered pests just because they presume to live near our homes (Plates 1 and 2).

Species that achieve pest status by regularly invading buildings are more numerous, including approximately 17 species. These species are *Monomorium pharaonis* (the most persistent and widespread species), *Monomorium floricola* (a south Florida species, not very common or persistent indoors), *Tapinoma melanocephalum*, *Brachymyrmex patagonicus*, *P. longicornis* and *Nylanderia fulva* (common species that persistently enter buildings, although the nests are usually outdoors), *Nylanderia bourbonica* and *Nylanderia steinheili* (species that regularly but infrequently enter houses), *S. invicta* (most likely to invade buildings when nests are flooded outdoors), *W. auropunctata* (relatively infrequent in buildings, but very irritating when it does move in), *Linepithema humile* and *Pheidole megacephala* (there are large populations of these invasive species in a few sites in Florida), *Technomyrmex difficilis* (a recent arrival that is proving to be even more of a household problem than *Paratrechina longicornis*), *Camponotus floridanus* and *C. inaequalis* (two of the species most often brought in for identification in south Florida; often nest in wall voids, behind cabinets, and in electric appliances), and *C. pennsylvanicus* (our only ant that does much excavating of sound timber; it is a relatively uncommon problem in northern Florida). The pest status of these species is discussed in their species accounts.

If doors and windows are left open, or if the structure of the house has large cracks, various

species of ants, and many other arthropods, are likely to wander in and out. Males and queens of many species are attracted to lights, and I have had some unusual ants, suspected of being termites, brought in for identification. When outdoor ants invade buildings, a small amount of detective work will usually reveal their mode of entry, and they can be excluded by a physical barrier or by a band of insecticide on the outside where they enter the building. Fumigating the building or attempting to eliminate all ants within foraging distance of the house is an expensive, sometimes unhealthy, last resort. These drastic treatments are profitable to exterminators, who are also the authorities who provide recommendations for methods of pest control. It is useful to remember that there can be a conflict of interest in these recommendations, even though most exterminators are undoubtedly responsible and well-trained individuals. When I get an inquiry about an invasion of ants in a building, I always recommend that the owner do a little research on their own to discover the identity of the ants and where they are coming from, before yelling for an exterminator. Since these ants are almost never a threat to human health or to the structure of the building, there is little to lose by doing a personal investigation of the problem. A good example would be ants invading a school building, a situation that could evoke a reflexive fear of lawsuits. Pesticide treatment is more likely to cause actual health problems than an ant infestation. A biology class assigned to analyze the case could get a more valuable lesson in biology and behavior than they would derive from any textbook, and possibly save the school a pile of money.

## CONSERVATION OF FLORIDA ANTS

A solicitude for rare ants is unusual. Most people feel that there are far too many kinds of ants that are far too numerous. There are good reasons, however, why we should be concerned if species of ants are becoming rare or endangered. Even rare species may be ecologically important if they are rare because they are restricted to scarce habitats. A series of species, for example, seems to be restricted to the remaining scrub ecosystems in south and central Florida (*Odontomachus relictus*, *Dorymyrmex elegans*, and *D. flavopectus*) and are likely to be important members of these ecosystems (Deyrup 1989). There is the argument that we don't know whether rare

species might be “good for something” because no one has looked, and we will never know if the species disappear before they have been examined, and reexamined with the technology of the future (Eisner 1991). Associated with the rare ant *O. relictus* is the rare firefly *Pleotomodes needhami*, and we know that fireflies are hotbeds of unusual and potentially useful chemicals (Eisner 1991), and ants themselves, for that matter, have more glands than a wildlife photographer has pockets (Hölldobler and Wilson 1990). We should be modest in our judgment of which species are useful and attractive, and which species are useless and obnoxious, remembering that most hawks and owls were considered vermin in northern Europe and the United States until quite recently. Future generations may well have a more encompassing and sophisticated appreciation of biological diversity that is prevalent at the moment. Though few people (if any) expound on the clean, racehorse lines of *D. elegans*, or revel in the mysterious shifting patterns of ornate scales in the genus *Strumigenys*, it would be wrong to deny future generations those potential pleasures, or the intellectual and practical insights they might derive from them.

Although many of Florida’s ants are rare in collections, there is little evidence that most of these species are actually becoming rare and endangered. These species, as well as most native Florida species of plants and animals, are becoming less abundant as native habitats are being remodeled by the relentless influx of humans into the state, but this does not mean that populations of these species have been reduced to the point of concern. Our clearest examples of rare ants are those that seem to be dependent on a habitat that occupies a very small area in the state, and that area is steadily shrinking. These include the three species mentioned above that occur in Florida scrub habitat, and *Trachymyrmex jamaicensis*, which lives in hammocks in the Florida Keys, but is common only on Elliott Key. *Formica subsericea*, which had an isolated Florida population far south of its normal range, in an unusual habitat (Wilson and Francoeur 1974), has not been seen since it was first reported. The Florida slave-making ant *Polyergus oligergus* (King and Trager 2007; Trager 2013; Trager and Johnson 1985) appears to be both isolated and restricted in distribution. As we get more records and more ecological information, the number of rare and endangered species that we can recognize is sure to increase.

In addition to species that are endangered by habitat conversion, there are probably species endangered by the direct or indirect effects of introduced species. In the dark interstitial mazes of the soil, and in hollow twigs swaying in the tree tops, ant empires rise and fall in pitched mandible-to-mandible battles while we pass by oblivious. These replacements of one species by another should also become more evident as we accumulate enough records to track changes in the ant fauna.

Ants are, to say the least, unlikely flagships for conservation projects. In some cases, a list of all the rare and endangered species of a site is useful to establish the significance of the site; any rare ants should be on the list. For the most part, ants would be well advised to remain discretely in the background, allowing more showy or cuddly species to make public appearances and beg for money. There are situations, however, in which a nice illustration of an ant could be used to symbolize the specialness of the site, reminding the public that any really unusual place is likely to harbor a host of strange and interesting-looking tiny creatures, whose habits are usually a mystery.

## EXOTIC ANTS IN FLORIDA

As a young boy growing up on the lower East Side of New York City, on the way to school I used to walk up part of 14th Street, in those days a haunt of innocuous sleaze. Next to a movie theater that showed films that were considered racy (“Bridget Bardot in ‘Girl in a Bikini,’ Mon.–Sat.”) was a place with darkened plate glass windows that advertised “Exotic Dancers Nightly.” I had no real idea of what an exotic dancer might be, but I somehow knew not to ask my parents. I also knew intuitively that exotic dancers were less virtuous than nonexotic dancers, but at least as interesting. This is a good attitude for approaching exotic ants. They are not welcome members in natural communities, but they are extremely interesting. When I have found a new exotic ant in Florida, part of me exclaims “another new and exciting ant in Florida,” even while my more responsible persona is decrying “another new, evil exotic.” We should all fight the introduction of more invasive exotic species of ants and other organisms, but it is a bit hypocritical to consider exotics, such as the red imported fire ant, as evil organisms. These exotics are only manifestations or side

effects of our own unparalleled ability to invade and disrupt natural ecosystems.

Exotic ants have moved into Florida in such large numbers that one might suspect them of having read the enticing promotional literature provided by state agencies. With 57 species and counting, Florida has the dubious distinction of having the largest number of introduced ants of any state. The percentage of exotic ant species is also high, approximately 24%, as compared, for example, with North Carolina, with 16 species, or 8% (Guénard et al. 2012). The state with the largest proportion of exotic ants is Hawaii, which has no native ants and a 100% exotic ant fauna. The large number of exotic ant species in Florida is attributable to the warm climate of the state. The large percentage of exotic ant species in Florida is attributable to the isolation of the state with respect to the huge Neotropical ant fauna. Neotropical species suited to Florida, with the exception of some Caribbean species, have been forced to wait for transport by humans.

Exotic species are those that were brought to Florida by humans after the arrival of Europeans. There are no known examples of ants intentionally imported into Florida. The great majority probably arrived with plants in containers, or in plant material, or as stowaways in ships. The recent massive increase in air traffic increases the chance of species arriving as air passengers from almost any part of the world. Included as exotic ants are some species, such as *Pheidole obscurithorax*, that were brought to adjacent states and seem to have spread into Florida by their own powers.

Exotic ants in Florida are covered in their respective species accounts. A long discussion of exotic ants in Florida and their effects and origins is provided by Deyrup et al. (2000). This paper is available online. The checklist of Florida ants at the end of the Species Accounts section and before the Literature Cited designates which species were imported from the New World tropics and subtropics (33 species) and which species were from the Old World tropics and subtropics (24 species).

## MAPS OF FLORIDA ANTS

### The Quality of the Data—Not Very Good

Ant species are not uniformly distributed over Florida. For example, exotic species as a group are concentrated in the southern part of the peninsula,

and there are other distributional patterns, but these patterns are often lacking in detail. It might seem simple to stack up the distribution maps of a series of species to give us all kinds of brilliant ideas on the ecological factors that determine the distribution of various groups of ants in Florida. This book includes a distribution map for most species, and the sum of the collection sites (which appear as large dots) is more than 11,000. When one looks at a series of these maps, with the same state and county outlines, the same size dots, most of the collections and identifications by the same person, a fantasy can easily begin to build that these maps are equivalent and comparable. Unfortunately, as soon as organisms are transformed into dots, they become susceptible to being improperly juggled. A look at the distribution maps for one genus, *Hypoponera*, is depressingly instructive.

*Hypoponera opacior* (see map for this species in the map section) is a very common ant throughout the state, although it is never seen crawling about in the open. Gather a few liters of leaf litter from a moist or dry site from Pensacola to the Florida Keys, and *H. opacior* will be there in your Berlese funnel extract. This species is often absent from wet areas, but large gaps in the distribution map are not attributable to huge wetlands, but rather to a lack of sampling. Likewise, clusters of dots indicate favorite collecting areas. This species, because it is so common, indicates immediately how much remains to be done before it can be said that Florida has been adequately surveyed for ants. Large areas of the state have hardly been touched. The grouping of the dots is an artifact of collecting. There is no way to recognize these problems by looking at the map; one needs the information that this species turns up almost every time it is sought. Given this information, one might feel justified in shading the entire map of Florida to indicate the ubiquitous nature of *H. opacior*.

*Hypoponera inexorata* (see map for this species in the map section) is also widely distributed and also occurs (usually with *H. opacior*) in upland and mesic sites. This species, however, is much more rarely collected: during the entire study, approximately 90 specimens were collected, while the specimens of *H. opacior* must number in the tens of thousands. The enormous gaps on the map of *H. inexorata* might reflect the rarity of the species throughout its range, or they might reflect the patchy nature of some unknown habitat requirement, or they might reflect some problem with the sampling

method. The latter is probably the case; in most areas, this seems to be a subterranean species that seldom comes up into the leaf litter, so that one finds specimens by persistence in the more heavily sampled sites, and occasionally by luck on the less heavily sampled sites. We do not know nearly enough to consider shading the whole map because this species really might be absent from the western part of the peninsula and the northern edge of the Panhandle.

*Hypoponera opaciceps* (see map for this species in the map section) is almost always found in open, wet areas, such as marsh tussocks and the open edges of lakes. It is as widespread and dependably common as *H. opacior*, but much less commonly collected because the wet substrate it inhabits is harder to run through a litter extraction funnel, and there is less incentive to look for ants in soil of wet areas because there are far fewer species than in better-drained leaf litter where *H. opacior* occurs.

*Hypoponera punctatissima* (see map for this species in the map section) is a tropical exotic that prefers wet disturbed areas, such as heavily watered lawns, mulched shrubbery, seasonally wet pastures, and edges of ditches. It also lives in marsh tussocks, but cannot be found dependably in these natural habitats. The map of this species is particularly deceptive. *Hypoponera punctatissima* is probably present on every acre of the huge expanse of wet pasture, sugar cane fields, sod farms, and disturbed Everglades south of Lake Okeechobee, but since that area is generally inaccessible and faunistically boring, there is a big gap on the map. In contrast, the blank areas in the northern part of the map probably represent a genuine sporadic distribution of *H. punctatissima*, but there may be a sampling deficiency in north Florida as well. The northernmost part of Florida has such a diversity

of undersampled natural habitats that one is less inclined to spend time sampling lawns and foundation plantings in order to get records of weedy exotic ants.

So what does the publication of a locality map accomplish, beyond immortalizing a series of biases and fortuitous events? As in many other scientific studies, positive data are more useful than negative data. A site record is unequivocal, while the absence of a site record could be explained in several ways. Over a period, the failure to find a species in a well-collected area (such as Alachua County), using methods that work in other areas, begins to give some reality to the blank spots on the map. Even now, it appears that there are some recognizable broad patterns in the distribution of ants in Florida. One of the most valuable contributions of these maps is that they frequently enable naturalists to identify any range extensions.

*Spotting Future Biogeographic Changes:* The nonmethodical nature of most ant collecting should not prevent recognition of some future changes in the fauna. If some species becomes so locally dominant that it could not have been missed even in a cursory review of the fauna, it is safe to assume that such a species was previously rare or absent. I have applied this kind of evidence to suggest that species such as *Cyphomyrmex rimosus* and *Brachymyrmex patagonicus* are new to Florida, even though they were both present during the current survey. I am also hoping that my records of litter samples may be used to show future changes. Although the selection of sites for sampling has not been methodical, the amount of litter and the extraction technique have been consistent. I have taken thousands of samples and recorded the species of ants in each one. It should be possible to use these records to show gross changes, if any, in the litter fauna a few decades hence.

## PART TWO

### Species Accounts

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#### SUBFAMILY AMBLYOPONINAE

##### Genus *Stigmatomma*

##### *Saw-Toothed Ants*

When one first looks into the face of a worker *Stigmatomma* (pronounced **stig' ma tō' ma**), one can only be grateful that these ants are not the size of terriers. The long jaws, set with double rows of sharp, triangular teeth, are fearsome weapons. The prey of at least some species is relatively large and well-defended centipedes (Brown 1960a; Gotwald and Levieux 1972). Alex Wild provides a lively and profusely illustrated journal of a captive colony of *Stigmatomma oregonensis*, a species that appears closely related to the Floridian *Stigmatomma pallipes* (Notes from Underground, online, May 23, 2005). Workers in this colony killed centipedes by stinging and then carried the prey back to the nest, where they were repeatedly bitten, but not dismembered. Workers consumed hemolymph oozing from the centipedes, and eventually piled larvae on the prebitten centipedes. Queens and, less frequently, workers fed on larval hemolymph, puncturing the larvae in specific areas of the body. The larvae developed scars from this treatment, but otherwise seemed unharmed. This nonlethal cannibalism increased when the colony ran out of centipedes. Similar behavior occurs in the Japanese species *Strumigenys silvestrii* (Masuko 1986). The hemolymph-drinking behavior of *Stigmatomma* has inspired some myrmecologists to use the English name “vampire ants.” The appropriateness of this name, however, may be questioned in light of the recent spate of interest in the natural history of vampires. Vampirism specialists, whose

work may be scanned in the remarkable array of books currently appearing in the “Paranormal Romance” section of a large-chain bookstore, seem to disagree on whether vampire reproduction can even produce babies, and I know of no suggestion in the literature that vampires support themselves by feeding on the blood of their offspring.

The genus *Stigmatomma* was recently revived when the genus *Amblyopone* was divided into three genera; most of the species previously in *Amblyopone* have been transferred to *Stigmatomma*, which now includes 66 species (Yoshimura and Fisher 2012). *Stigmatomma* occurs worldwide except for arctic and subarctic areas (Brown 1960a). Most species live in moist habitats and forage underground; species in semiarid regions tend to remain deep in the ground (Brown 1960a).

**Name Derivation:** Apparently derived from *stigmata* (Greek), meaning “spot or dot,” and *omma* (Greek), meaning “eye,” probably referring to the tiny eyes of *Stigmatomma* workers.

*Stigmatomma pallipes* (Haldeman)—  
Common Saw-Toothed Ant ([Plate 3](#))

**Taxonomy and Similar Species:** *Stigmatomma pallipes* varies in size and color in such a way as to give the impression that there is more than one species involved. Usually, larger, blackish brown specimens are found in moist habitats, and smaller, reddish brown specimens are found in dry habitats, as if there were two species with different habitat preferences. The smaller and lighter forms were first considered a subspecies before they were regarded as a full species, *Amblyopone subterranea* (Brown 1949a). These forms, however,

are not distinguished by any known structural features, and one can put together a series of specimens that connects their extremes. These forms were eventually synonymized (Brown 1960a), but now and then I haul out a batch of specimens and check them again for structural differences. One of the problems with this and other species that vary in color is that sculptures of the integument and hairs show up better in darker individuals, increasing the apparent differences between light and dark individuals. The lingering question of whether there could be more than one species lumped under *pallipes* might someday be resolved by genetic analysis, if such analysis becomes as convenient and routine as its practitioners claim.

**Distribution:** Quebec, west to Wisconsin, south through Florida (Smith 1979), then west and south, possibly in a series of disjunct populations, into the Coastal Range of California (Ward 1988). In Florida, it is known throughout the state, but with many gaps that may reflect the cryptic and subterranean habits of the species in Florida.

**Natural History:** This species has been studied by several able myrmecologists, whose work has been summarized and augmented by Traniello (1982). The diet consists of fairly large, elongate arthropods, especially centipedes, but also beetle larvae (there are no records of millipedes as prey). The prey is seized, stung, and carried back to the nest. Workers may cooperate in subduing prey, but only one carries it back. Back at the nest, the prey is not dismembered, but the larvae are carried to it. Workers do not regurgitate food for larvae or for each other. The queen is said to squeeze larvae until a drop of clear liquid is regurgitated; this might be reexamined in the light of the non-lethal cannibalism seen in *S. oregonensis*. Workers and queens generally show few behavioral differences, except that mature queens do not forage. Workers do not change tasks as they mature. The genesis of colonies is not completely understood, but circumstantial evidence suggests that groups of 9–16 workers form small colonies with one or more queens, and these colonies, in turn, fission after the emergence of alates and workers in late summer. Within an area, workers from apparently isolated colonies are compatible. Alates leave the colony to mate, but usually return to the nest after mating. Alate females probably occasionally disperse and find new colonies removed from the parental population. In Florida, I often collect

males in Malaise traps, but I have only captured a few winged females.

In the northern part of its range, the habitat of *pallipes* is usually moist woodland with a heavy canopy. It is sometimes difficult to believe that the same species could be in a cool, Appalachian rhododendron forest, and also in the dry scrub forests of Florida, but it is not so unusual for a species of ant to occur in different habitats in different parts of its range.

**Name Derivation:** From *pallio* (Latin), meaning “to be pale,” and *pes* (Latin), meaning “foot.” There is little contrast between the color of the feet and the body in Florida specimens, but some dark, northern individuals are more obviously pale-footed.

## Genus *Prionopelta*

### *Minute Three-Toothed Hunter Ants*

The genus *Prionopelta* (pronounced **pry’ on ō pel’ tuh**) includes 13 species widely distributed over the tropics, including Central and South America, Africa, Madagascar, New Guinea, and New Caledonia (Bolton 1995). These are small yellowish ants that probably never emerge in the open. Sifted from leaf litter, they could easily be mistaken in the field for one of the yellow, subterranean *Solenopsis*, but they move about with a slightly more undulating or squirming gait. Under the microscope, members of this genus display elongated, three-toothed jaws, gradually clubbed antennae, and a broad attachment between the petiole and the gaster. This last feature is shared with the genus *Stigmatomma*, and the two genera are now grouped together in the subfamily Amblyoponinae (Bolton 2003). There is one species in Florida.

**Name Derivation:** From *prion* (Greek), meaning “a saw,” and *pelta* (Greek), meaning “a small shield.” This refers to the expanded, serrate clypeus, seen in frontal view.

### *Prionopelta antillana* Forel—Caribbean Minute Three-Toothed Hunter Ant (Plate 3)

**Taxonomy and Similar Species:** *Prionopelta antillana* is an unmistakable species, thanks to its unusual mandibles, tiny eyes set far back on the head, and broadly attached petiole. It appears to be closely related to the mainland tropical species *Prionopelta amabilis*, and Brown (1960a) has suggested the two forms might be one variable species.

**Distribution:** *Prionopelta antillana* occurs in the Lesser Antilles and in northern South America (Brown 1960a). In Florida, it is known from a few sites in Marion County and one site in adjacent Sumter County. It has not been found in south Florida, where one might think that the climate might be more suitable. This species is small and cryptic, but it should have appeared in some of the thousands of litter samples that were collected in south Florida in the course of the Florida ant survey. My impression is that this species was imported directly into Marion County, and has spread slowly ever since. Eventually, it should occupy southern Florida. Although Marion County is not a logical point of entry for tropical ants, the city of Silver Springs has long promoted an image of tropical lushness. There is a botanical garden, which might be a possible source of exotic ants, and movies supposedly set in the tropics used the clear springs for photogenic and relatively safe and convenient locales. The most famous of these were the Johnny Weissmuller Tarzan movies shot in Silver Springs between 1932 and 1942, in which aquatic adventures in Silver Springs are jarringly intermixed with old footage from Africa and elsewhere. Perhaps tropical plants in containers were brought in for some scenes.

**Natural History:** Collected from soil and leaf litter in mesic hammocks and in sand pine scrub. A 2004 expedition to hunt for this species near the Big Scrub Campground in Ocala National Forest produced hundreds of workers from a dense population found under low, evergreen scrub oaks. No males or queens were seen. Colonies found on the island of Dominica in 2006 were in a very different situation: the chambers of the nest were in lumps of clay near a stream in a dense tropical forest. The biology of *antillana* has not been investigated, but the similar species *amabilis* has been studied by Hölldobler and Wilson (1986a). Colonies are in rotten wood, and a colony may be dispersed into more than one piece of wood. In feeding tests, the favored prey was *Diplura* of the family *Campodeidae*. Workers use fragments of old pupal cocoons to “wallpaper” the pupal galleries, probably to reduce moisture. Workers produce edible eggs and present them to the queen. Foraging workers show a “foot-dragging” behavior, and in a later paper, Hölldobler et al. (1992) show that a trail pheromone is exuded from a previously unknown gland in the hind basitarsi. The male is

known from collections, but apparently has not been described.

**Name Derivation:** From the Antilles; the type is from St. Vincent in the Lesser Antilles.

## SUBFAMILY PROCERATIINAE

### Genus *Discothyrea*

#### *Pygmy Egg-Eating Ants*

The species of *Discothyrea* (pronounced **dis’ kō thir’ ē uh**) are tiny roly-poly ants with an endearing infantile appearance. They may be recognized by their relatively huge antennal club and enlarged second gastral segment, with the terminal gastral segments tucked underneath. There are 27 known species (Bolton 1995), distributed from North America to Brazil, and from Africa and Taiwan to Australia and New Zealand (Brown 1958a). There is one species in the United States. Colonies are small (10–20 workers) and usually found in rotten wood, in leaf litter, or under stones (Brown 1958a). Like the related genus *Proceratium*, *Discothyrea* species seem to feed primarily on arthropod eggs (Brown 1958b, 1979). Queens of one African species even found their nests within spider egg sacs, which provide both food and lodging for the first generation of workers (Dejean and Dejean 1998).

**Name Derivation:** From *diskos* (Greek), meaning “a flat circular plate,” and *thyreos* (Greek), meaning “shield.” This refers to the peculiar plate (fused frontal lobes) that sticks out from between the antennae; this plate is somewhat rectangular in most specimens, but is described as semicircular in the type specimen.

#### *Discothyrea testacea* Roger— Southern Pygmy Egg-Eating Ant (Plate 4)

**Taxonomy and Similar Species:** There are no similar species in the United States. There is some variation in the shape and development of the plate between the antennae. The male is distinguished by its small size (under 2 mm), projecting clypeus, and characteristic wing venation. The latter has a small stigma and a large, complete, apically rounded marginal cell. This combination of features is not known for other Florida ants, so it should be possible to recognize the species from males taken in flight traps. The tiny size of the males, however, will still demand a sharp-eyed myrmecologist going through the trap sample.

Distribution: North Carolina through Florida, west into Oklahoma. Through most of its range, it is known from widely separated sites, probably because these ants are so small and difficult to find. The species was named in 1863 (Roger 1863) on the basis of a worker and queen found somewhere in “North America,” and apparently not seen again until 1948 (Smith and Wing 1954). This helps explain the absence of *D. testacea* from Creighton’s 1950 manual of ants. In Florida, persistent Berlese sampling at any upland or mesic site eventually seems to produce specimens.

Natural History: In Florida, this species occurs in both xeric and mesic habitats, including oak scrub, high pine, flatwoods, and temperate hardwood forest. One specimen was found in a tropical hammock in the Florida Keys. The diet is probably the eggs of other arthropods, especially spiders, but this awaits confirmation. A male, apparently the only one known, was found in a small colony in a hollow acorn buried in the leaf litter in Florida scrub habitat.

Name Derivation: From *testaceus* (Latin), meaning “having a shell,” probably referring to the first two gastral tergites, which conceal and protect the terminal abdominal segments.

## Genus *Proceratium*

### *Egg-Eating Ants*

Workers and queens of *Proceratium* (pronounced **prō ser ā” shum**) have the end of the gaster tucked under the first two segments, like that of *Discothyrea*, but lack the enormously enlarged antennal club. The genus, which is widespread in temperate and tropical areas, includes 78 species (some are fossil species), 45 of which were added in an exhaustive revision of the genus (Baroni Urbani and De Andrade 2003). Florida has six species, the largest number known for any state, although adjacent states probably have the same six species. This does not mean one can waltz down to Florida for one-stop shopping for *Proceratium*, as several species are extremely difficult to find, and none are a dime a dozen.

Almost all species of *Proceratium* spend their lives in concealment, usually in rotten wood or deep humus, but sometimes under stones in colder climates. Captive colonies may accept, usually reluctantly, various types of insect prey, but the main diet seems to be the eggs of arthropods, especially

spiders (Brown 1958b, 1979). The peculiarly modified gaster seems to have a defensive function. The hypertrophied second gastral tergite conceals the terminal gastral segments, it presents a hardened surface to enemies approaching from the rear, and it is equipped with a gland that probably produces defensive chemicals (Baroni Urbani and De Andrade 2003). Although unusual in ants, some insects in other groups have convergently evolved similar adaptations to provide rigid armor for the abdomen while maintaining flexibility for the terminal abdominal segments. Parasitic wasps of the genera *Chelonus* and *Ascogaster* (Braconidae) are good examples. The anteriorly directed terminal segments of the gaster have also been seen helping to manipulate and transport spider eggs (Brown 1979), but one would not claim that the abdominal modifications are a necessary adaptation for this purpose, as ants in general have no difficulty dealing with small round objects. *Proceratium* colonies are small, usually with 10–50 workers (Brown 1958a). In the North Temperate Zone, nuptial flights are usually in late summer (Brown 1958a).

There is often considerable variation in size, sculpture, and color within a species of *Proceratium*, and it is easy to look at a series of one of these species and imagine that there are additional undescribed species. With large series, these forms can usually be seen to intergrade. The revision by Baroni Urbani and De Andrade (2003) seems to have cleared up these problems in the Nearctic fauna.

Male *Proceratium* can be collected in Malaise traps or other flight traps, which may reveal the presence of a species whose colonies are difficult to find. At the Archbold Biological Station (Highlands County), *pergandei* is known only from males, although the ants of this site have been studied for more than 20 years.

Name Derivation: From the prefix *pro-* (Latin), meaning “in front,” and *keration* (Greek), meaning “a small, horn-like projection,” possibly referring to the projecting frontal carinae in the type species, *silaceum*.

### *Proceratium chickasaw* De Andrade— Chickasaw Egg-Eating Ant (Plate 5)

Taxonomy and Similar Species: This species is similar to the commoner and more widespread *pergandei*, but the rearward extension of the second gastral segment is longer and narrower, in lateral

view as long as the first tergite; the second gastral segment is covered with slender hairs that stand up on the surface and bend back at the ends, rather than being covered with uniformly decumbent hairs as in *pergandei*.

Distribution: Known from northwest Florida, west into Mississippi, and north into Tennessee (Baroni Urbani and De Andrade 2003). There are only few Florida collections, all from Liberty County.

Natural History: Florida specimens were collected from leaf litter in deep ravines along the Apalachicola River. These ravines are refuges for certain plants and animals of the southern Appalachian Mountains. It appears that no colonies have been found, which suggests that nests may be in the soil, rather than in rotten wood, where they would be more easily found. Males and queens are unknown.

Name Derivation: Named for the Chickasaw Indians of southeastern North America.

#### *Proceratium crassicorne* Emery— Emery's Egg-Eating Ant (Plate 6)

Taxonomy and Similar Species: *Proceratium crassicorne* is strikingly similar to *silaceum*, and the two species were synonymized by Creighton (1950) in a detailed and somewhat caustic account, not really softened by phrases such as, "I have no wish to seem unduly harsh..." In the recent revision of the genus (Baroni Urbani and De Andrade 2003), *crassicorne* is reinstated on the basis of a series of small, but consistent morphological differences, which do not occur together in nest series, and on the fact that the two forms often occur in the same area, or even at the same site. The two species are most easily distinguished, in my experience, by a difference in the density of the hairs on the gastral tergites, especially the second. In *crassicorne*, the small punctures from which the hairs emerge are close together, only one or two puncture-widths apart, when seen under a diffuse light, such as that of a fluorescent bulb. The second tergite of *silaceum* is sparsely punctate, with most punctures separated by several puncture-widths. When Creighton synonymized the two species, he included a commentary on the illusory nature of supposed differences in the shape of the petiole. Despite this, there really does seem to be a small but consistent difference in the shape of the petiole, with *crassicorne* less squared off above than *silaceum*, and the petiole of *crassicorne* less shining at

the base of the petiolar scale, the basal carina of the petiolar scale less developed, and the petiole more pubescent, especially the anterior face near the base. The frontal carinae of *crassicorne* project more above the surface of the head and are less expanded than those of *silaceum*. Several series of specimens of *silaceum* and *crassicorne* that I have seen from Arkansas suggest that in the western part of their ranges, the two species diverge in size, with *silaceum* larger than *crassicorne*.

Distribution: New York into north Florida, west into Missouri and Arkansas. In Florida, it is known from only two sites, one in Liberty County and one in Santa Rosa County.

Natural History: The habitat of *crassicorne* is hardwood forest, including ravines of the Florida Panhandle. It is not known whether there are any habitat differences between *crassicorne* and *silaceum*. The diet is probably arthropod eggs, especially those of spiders, but it is not clear which of the dietary records for *silaceum* (Brown 1958a,b) apply to that species and which apply to *crassicorne*. It would be necessary to look at voucher specimens. Males and queens are described and illustrated by Baroni Urbani and De Andrade (2003).

Name Derivation: From *crassus* (Latin), meaning "thick" or "stout," and *cornu* (Latin), meaning "horn." This refers to the thick antennal scapes in frontal view.

#### *Proceratium creek* De Andrade— Pocket Gopher Egg-Eating Ant (Plate 5)

Taxonomy and Similar Species: This species has a low, rounded petiole, similar to that of *pergandei*, but the antennal scapes are relatively longer, exceeding the posterior border of the head when the scapes are laid back against the head. The known workers are noticeably larger than those of *pergandei*, but since only about a dozen workers are known, there could be more variation than is known to date. Any specimen that appears to be an unusually large *pergandei* could be checked to see if it is this rare species, but so far no specimens have shown up in casual ant collecting.

Distribution: Known only from Thomas County, Georgia; Marion County, Arkansas; and Lafayette County, Florida; a male that is believed to represent this species was collected in a Malaise trap in Leon County, Florida.

Natural History: This remarkable ant causes one to wonder what other rare ants might still

be undiscovered in the soil beneath our feet. All but one of the specimens were collected in pitfall traps placed in the burrow systems of pocket gophers (*Geomys pinetis*) by Paul Skelley and Peter Kovarik in a study emphasizing the specialized scarabs that live with pocket gophers. Trapping in these burrow systems is not a simple affair: the gopher must be trapped and removed first, or it will fill the pitfall traps with sand. The trap is then set in the burrow system, and the excavation into the burrow is carefully covered with a board and soil (Skelley and Woodruff 1991). Although they can defend themselves with sharp teeth, pocket gophers are vegetarians and probably not a threat to insects that share their tunnels. It is not known whether *creek* is restricted to pocket gopher burrow systems, or whether they occasionally wander in there.

**Name Derivation:** Named for the Creek Indians of southeastern North America.

*Proceratium croceum* (Roger)—  
Angulate-Petiole Egg-Eating Ant (Plate 6)

**Taxonomy and Similar Species:** *Proceratium croceum* is similar to *crassicorne* and *silaceum*, but has a more squared-off petiole in lateral view and (in the worker) a slight concavity in the mesosomal profile when viewed from the side. It is also larger (worker is approximately 3 mm long) than Florida specimens of *crassicorne* and *silaceum* (workers are approximately 2.5 mm).

**Distribution:** Virginia into north Florida, west into Illinois, southwest into Oklahoma and Texas (Smith 1979). In Florida *croceum* is known from a small number of sites in the northern part of the state, from Levy County north and west.

**Natural History:** This species lives in rotten logs and stumps in shady areas. Colonies are sometimes found beneath the bark of decaying pine logs. Cole (1940) found a colony of approximately 30 workers in a small nest in firm wood near the middle of a rotten log; he points out how easy it would be to miss the nests of this species unless one carefully dissects entire logs. Van Pelt (1958) found several nests in rotten pine logs. Haskins (1930) fed a captive colony on larvae and pupae of other ants, but the *croceum* larvae died before becoming full grown. It is probable, considering the diet of other species (Brown 1958a,b), that the normal diet is arthropod eggs. Males and queens are described and illustrated by Baroni Urbani and De Andrade (2003).

**Name Derivation:** From *krokos* (Greek), meaning “crocus,” a spring flower well known for its orange anthers used in cooking, referring to the orange color of this ant.

*Proceratium pergandei* (Emery)—  
Pergande’s Egg-Eating Ant (Plate 5)

**Taxonomy and Similar Species:** *Proceratium pergandei* belongs to a trio of Florida species (including *pergandei*, *chickasaw*, and *creek*) that have a low rounded petiole. Originally, species with this character state were placed in the genus *Sysphincta*, also spelled *Sysphincta*, which was synonymized with *Proceratium* (Brown 1958a). The antennal scapes of *pergandei* do not reach the posterior border of the head when laid back against the head (unlike *creek*), and the second tergite does not protrude rearward for a distance as great as the length of the first gastral tergite (unlike *chickasaw*).

**Distribution:** Massachusetts south into Florida, west into Colorado and eastern Texas (Baroni Urbani and De Andrade 2003). In Florida, it is known from Highlands County (males only) northward and west through the Panhandle.

**Natural History:** Nests have been found under stones (Wesson and Wesson 1940) and in dead wood (Brown 1979). In the sandy soils of Florida, it is probable that the nests are normally subterranean, as the species is known almost entirely from strays taken in leaf litter. A small colony (eight specimens) was found in a rotten pine stump below the surface of the ground. Paul Skelley collected several specimens from traps set up in burrow systems of pocket gophers (*G. pinetis*). Wesson and Wesson (1940) offered living and dead insects to a captive colony, but the only food accepted was the contents of the gasters of a few dead ants. Brown (1979) found a colony feeding on and storing spider eggs in a nest in rotten wood. The queen and male are described and illustrated by Baroni Urbani and De Andrade (2003).

**Name Derivation:** Named by Carlo Emery for Theodore Pergande (1840–1916), a German immigrant and Civil War veteran who provided biological observations and curatorial services for his ambitious, articulate, and exploitative boss, Charles Riley of the U.S. Department of Agriculture (Mallis 1971). Pergande is highly regarded among American myrmecologists for the quality of his specimens. He sent many species of ants to Emery and Forel for identification and description. William Wheeler

regularly corresponded with Pergande to obtain specimens and get details on the biology of ants.

*Proceratium silaceum* Roger—  
Common Egg-Eating Ant (Plate 6)

Taxonomy and Similar Species: *Proceratium silaceum* is very similar to *crassicorne*; the distinctions are discussed under that species. To make matters more confusing, *silaceum* is variable in size, color, and surface sculpture. Color is probably related to time since emergence of the adult, with recently emerged adults a golden yellow color. Some other poneromorph ants also seem to adopt their mature color slowly, and, unlike young adult myrmicines and dolichoderines, these callows may even be found foraging away from the nest.

Distribution: Southern Ontario, south into Florida, west into Illinois and Oklahoma, and south into the pine forests of eastern Texas. Records from Mexico and Central America have referred to the species *manicum* (Baroni Urbani and De Andrade 2003). In Florida, it is known from scattered sites from Highlands County northward and west through the Panhandle. With enough effort, it could probably be found in most mixed pine and hardwood forested areas through the northern half of the state.

Natural History: The habitat of *silaceum* is pine forests or mixed pine and hardwood forests. Nests are usually in rotten wood, but outside of Florida, nests have also been found under stones (Brown 1958a). Workers can also be found in litter samples, although they are never abundant. One Florida colony was found under bark flakes at the base of a living pine tree, and another was found between layers of asphalt roofing material that had been illegally dumped in a pine flatwoods site. Some colonies have been found with arthropod eggs stored in chambers, and egg-storing behavior with spider eggs also occurs in the laboratory (Brown 1958a). When supplied with spider eggs, captive colonies ignored other prey, including the eggs, larvae, and pupae of other ants (Brown 1958a). When provided with spider eggs, “the reflexed gastric tip is used to tuck the slippery eggs forward toward the mandibles when the eggs are being carried by the ants (Brown 1958b). The male and queen of *silaceum* are described and illustrated by Baroni Urbani and De Andrade (2003).

Name Derivation: From *sil* (Latin), a kind of yellowish earth or yellow ochre, hence *silaceus*, or “ochre colored.”

## SUBFAMILY PONERINAE

### Genus *Anochetus*

#### *Lesser Snapping Ants*

The genus *Anochetus* (usually pronounced **an ō kē”tus**) occurs throughout the tropics. It includes at least 97 species (Bolton 1995). This genus is closely related to *Odontomachus*, and members of the two genera are often similar in appearance. There can be no confusion between the genera in Florida, as we have only one species, *Anochetus mayri*, whose small size (approximately 4 mm) and double-pointed petiole immediately distinguish it from Florida *Odontomachus*, which are larger (9 mm or more) with a single petiolar spine.

Like *Odontomachus*, *Anochetus* has a snapping mechanism that can close the jaws with great force and speed, disabling small prey. Foraging is usually nocturnal, and prey is captured by ambush or slow stalking (Brown 1978). Nests are usually in hollow twigs in leaf litter, or in small cavities in soil, but there are some arboreal species (Brown 1978). *Anochetus kempfi*, a Caribbean species studied by Torres et al. (2000a), shows a number of interesting biological traits, including flightless queens, colonies that apparently reproduce by fission, and workers that attack males and some supernumerary queens. The eggs of this species are not left in chambers but are carried about by workers until they hatch.

Name Derivation: From the prefix *an-* (Greek), meaning “not” or “lacking,” and *ochetos* (Greek), meaning “aqueduct” or “ditch,” probably referring to the absence of a furrow or elongate depression found in some other ants, such as the furrows on the underside of the head of some species of *Odontomachus*.

*Anochetus mayri* Emery—  
Mayr’s Lesser Snapping Ant (Plate 7)

Taxonomy and Similar Species: In the Neotropics, there appears to be a confusing array of species similar to *A. mayri*, some of which may be geographic variants of that species (Brown 1978). There is some evidence that males may provide useful characters for separating the species in this complex (Brown 1978). The Florida population is introduced, most probably from the West Indies (Deyrup et al. 2000), but could have come from some other region. Florida specimens appear identical to specimens I have seen from Puerto Rico and St. John (the type locality is St. Thomas). In Florida and elsewhere in

the mainland United States, there is no danger of confusing *mayri* with any other species, unless additional *Anochetus* species are introduced.

**Distribution:** The geographic range of *mayri* will be uncertain until the taxonomy of the complex has been resolved. It clearly occurs in the Greater Antilles and nearby islands, and may range through southern Mexico into Bolivia as well (Brown 1978). In Florida, it was first discovered in 1987 in Miami-Dade County, and rediscovered in 2002 in Palm Beach County (Deyrup 2002). It seems likely that the species will expand its range in southern Florida, as Miami-Dade and Palm Beach counties have numerous nurseries for tropical and subtropical plants, as well as a population of mobile humans who take their landscape plants to new residences. It seems unlikely that this species could survive in colder parts of the state.

**Natural History:** The natural history of this species is largely unknown. Perhaps the presence of a population in Florida, a state well endowed with entomologists (although never too many), will lead to some research on the biology of the species. At the West Palm Beach site, numerous specimens, along with a variety of native and introduced ant species, were found by sifting deep litter beneath mature slash pines and oaks (Deyrup 2002). I have not seen males from the Florida population.

**Name Derivation:** Named in honor of Gustav Mayr (1830–1908), an enormously productive Austrian myrmecologist who described hundreds of species of ants, including many from North America. Gustav Mayr is also responsible for establishing approximately 48 generic ant names still in use today. *Anochetus* is one of these names.

## Genus *Cryptopone*

### *Pit-Jawed Ants*

The genus *Cryptopone* (in my experience usually pronounced **Krypt’ ō pōne**, but also pronounced **Krypt’ ō pō’ nē**) is a small, but widely distributed, genus of approximately 15 species. These ants are similar in structure to some species of *Ponera* and *Hypoponera*, but have a large shallow pit at the bases of the jaws. This pit (whose function is unknown) also occurs in some other genera of ponerine ants. The legs are short, and the middle tibiae have strong bristles on their outer faces. These bristles are probably used for digging and are apparently associated with unusual anterior mobility of the middle legs, which are often rotated forward in

preserved specimens. Similar bristles and spines occur on the middle tibiae of many fossorial Bethyilidae, Tiphiiidae, and even sand-swimming bees of the genus *Perdita*. One would expect such bristles to be more widespread in ants. It seems possible that while most digging ants employ their jaws to excavate passageways, *Cryptopone* species use their legs as well to force their way through rotten wood in search of prey. This is speculation, not based on observations of behavior.

**Name Derivation:** From *kryptos* (Greek), meaning “hidden,” and *pone*, in this case a contraction of “*Ponera*.” This genus was erected by Carlo Emery, who, as usual, provided no derivation for the name. His main concern seems to have been to distinguish *Cryptopone* from *Ponera*, and the “*crypto*” probably does not mean “hidden,” but rather refers to the “*crypt*,” sometimes used anatomically to mean a “*pit*” or “*recess*,” at the bases of the jaws.

### *Cryptopone gilva* (Roger)— Southern Pit-Jawed Ant (Plate 9)

**Taxonomy and Similar Species:** *Cryptopone gilva* is distinguished from somewhat similar species of *Ponera*, *Hypoponera*, and *Pachycondyla* by the stout bristles on the outer face of its middle tibiae and the pit at the base of the jaws; both these features are difficult to see without diffuse illumination, such as that from a fluorescent bulb. In the field, this species can, with practice, be identified by a combination of color (reddish brown) and size (bigger than *Ponera* and *Hypoponera*, smaller than *Pachycondyla*). This species appears under the name *Euponera gilva* in Creighton (1950).

**Distribution:** North Carolina (Carter 1962) south into Florida, west into Texas (Smith 1979), and south into Costa Rica. Presumably, there are populations somewhere between Texas and Costa Rica. In Florida, this species occurs from the northern border south into Highlands County.

**Natural History:** *Cryptopone gilva* lives in rotten logs in mesic to wet woodlands (Haskins 1931; Smith 1934). Haskins, in his study of the biology of *C. gilva* (1931), found that the brood is kept in large chambers, the eggs, larvae, and pupae usually separated, with some additional sorting of larvae by size. Larvae are active and “athletic,” responding to food before it has been presented by workers. Larvae feed on bits of arthropods; adults (in the laboratory) also consume sweets. Workers cover mature larvae with soil, which is removed

after the cocoon has been constructed. Larvae are not covered with soil from naked pupae, which are usually destroyed by the workers. Workers help young adults to emerge from their cocoons and appear to obtain some exudate from the newly emerged callows. The larval period (in the laboratory) is about three to four weeks, and the pupal period is about a month. Mature queens and males attempt to leave the nest within two weeks of emerging from their cocoons, so it is possible that there are no strongly synchronized mating flights. Colonies collected in the field may have several dealate queens, and Haskins believed that dispersal in this species might be by both fission of large colonies and solitary nest founding by young queens. Haskins also performed a series of interesting experiments testing the sensitivity of this species to various stimuli, but it is difficult for me to relate these to the field natural history of the species.

Name Derivation: From *gilva* (Latin), meaning “pale yellow.” This species is normally orange brown, and the type specimens may have been callow or discolored.

## Genus *Gnamptogenys*

### *Grooved Ants*

The combination of the conspicuous grooves on the head and body, and the one-segmented petiole separates this genus from all other Florida genera. *Gnamptogenys* (usually pronounced **Namp toj” en ēs**, but sometimes with the accent on the third syllable) is a genus of 99 species that ranges through most of the tropics, with the notable exception of Africa (Bolton 1995). As is often the case among the ponerine ants, some species seem to be specialized predators. A single introduced species occurs in Florida.

Name Derivation: From *gnamptos* (Greek), meaning “curved,” and *genys* (Greek), meaning “jaw” or “cheek,” referring to the strongly curved jaws, seen in lateral view.

### *Gnamptogenys triangularis* (Mayr)— Spine-Thighed Grooved Ant (Plate 4)

Taxonomy and Similar Species: Longitudinal grooves, covering the head and body, including the gaster, distinguish this species from other Florida ants. There is a sharp, curved spine on the hind coxa. The name *Gnamptogenys aculeaticoxae* has been applied to the Florida population, but this

name has been synonymized with *G. triangularis* (Lattke 1995).

Distribution: Native distribution is from Panama into Bolivia (Brown 1958a). In the United States, this species is known from several sites in Florida and Alabama. In Florida, it is known from only a few sites, and never seems abundant. At this point, it is one of Florida’s rarer exotics.

Natural History: This remarkable species has been studied in Venezuela by Lattke (1990). He found nests, containing approximately 80–120 workers, in fallen logs and branches. In four nests that he examined, the only prey remains were those of millipedes, whose disarticulated segmental rings surrounded the area near the nest entrance. Larvae were found with their heads thrust into the body of a dead millipede. Many millipedes secrete powerful defensive secretions, including cyanide (Eisner et al. 2005). Lattke found that both adults and larvae of *triangularis* are resistant to cyanide, surviving for more than three hours in a potassium cyanide killing jar that dispatched other ants in less than five minutes. The male has been described under the name *aculeaticoxae* (Santschi 1921).

Name Derivation: From *triangulus* (Latin), triangular; perhaps this refers to the outline of the mandibles in frontal view, or the frontal view of the head.

## Genus *Hypoponera*

### *Mini-Ponerine Ants*

The genus *Hypoponera* (usually pronounced **Hī pō pō” ne ruh**) occurs in tropical and warm temperate regions. There are 132 described species (Bolton 1995), but some of these are probably synonyms, and there must be a batch of undescribed species. Almost all species have cryptic habits, and there are probably subterranean species that have never been seen. In the mainland tropics, there are numerous well-marked species, but it is difficult to put names on specimens because the genus has never been reviewed. In a recent version of his website on the ants of Costa Rica, Longino lists nine undescribed species from that country alone. Apparently, there is a revision of New World species about to begin. There are only a few species in Florida, but there is a good chance that additional species will be imported. There are, for example, two species found in disturbed areas in the Bahamas that would undoubtedly thrive in the Florida Keys. One of these, tentatively identified as *Hypoponera parva*, is so small and cryptic that it could

be established for a long time in some restricted locale before anybody noticed. While there are many exotic *Hypoponera* that could probably live in Florida, there is no reason to believe that there are native species that remain undetected. Even subterranean species such as *inexorata* produce alates that are caught in flight traps, and I know of no unassigned alates.

Species of *Hypoponera* look similar to *Ponera*, but lack a translucent “porthole” found on the ventral part of the petiole of *Ponera*. This structure is inconveniently located, as it is normally hidden by the middle coxae. It is usually necessary to use a fine pin to raise the gaster slightly and reposition the hind legs; since the articulations are ball-and-socket joints, it is usually possible to make these adjustments to dry specimens without causing damage. Eventually, one becomes accustomed to more subtle and convenient differences between Florida species of *Hypoponera* and *Ponera*. The *Hypoponera* species have relatively longer legs, higher petioles, and less heavily clubbed antennae than the *Ponera*. Some large tropical species of *Hypoponera* are similar in general appearance to small *Pachycondyla*, but this is not a Florida problem.

In contrast to *Ponera*, queens of which seldom (if ever) appear in flight traps, queens of Florida *Hypoponera* fly readily. There are also flightless queens in the Florida species *opaciceps*, *opacior*, and *punctatissima*. The introduced species *punctatissima* has peculiar, large-headed ergatoid males that can occur in two sizes. Flightless males may not be unusual in the genus: two Japanese species each have two forms of males and two forms of queens, with various behavioral permutations (Yamauchi et al. 1996, 2001).

Another interesting feature in certain Japanese species is trophallaxis (passing of liquid food from one adult to another), not otherwise known in the ponerines (Hashimoto et al. 1995). Larval *Hypoponera* resemble *Ponera* in having door knob-shaped tubercles that stick the larvae to the walls of nest chambers; the morphology and function of these have been studied by Peters and Hölldobler (1992).

My reading of the literature on *Hypoponera* gives me the impression that members of this genus are considered general predators feeding on small subterranean organisms. I have not come across any specifics on how any species actually makes its living. The microhabitats favored by three common Florida species (*opaciceps*, *opacior*,

and *punctatissima*) are consistent with a somewhat specialized diet on small fly larvae. This is just a guess.

Name Derivation: From the prefix *hypo-* (Greek), meaning in this case “less than,” and *ponera* (Greek), referring to the genus *Ponera* and roughly translating as “little *Ponera*.” The word *ponera* (Greek) means “toilsome,” but might be indirectly derived from *ponikos* (Greek), meaning “hardworking,” referring to the general reputation of ants.

*Hypoponera inexorata* (Wheeler)—  
Orange Mini-Ponerine (Plate 10)

Taxonomy and Similar Species: This species is distinguished by the combination of orange brown coloration and the shape of its petiole that tapers from top to bottom in lateral view. *Hypoponera punctatissima* may be orange brown, but has a lower and less tapering petiole; it is also conspicuously smaller when the two species are compared side by side. The mandibles of *inexorata* in frontal view are less convex along their outer edges than those of other Florida species, and are often described as “sinuate.” This feature is also best appreciated when there are specimens of other species for comparison, at least when one is dealing with Florida specimens. Wheeler’s drawing of one of the type series from Texas has curves that would probably meet the approval of Mae West. Male *inexorata* in Florida are large (more than 3 mm long), with well-pigmented wing veins and round eyes.

Distribution: South Carolina through peninsular Florida, west into Arizona, and south into Central America (Smith 1979). In Florida, *inexorata* is known from scattered localities around the state, reflecting its subterranean habits and consequent difficulty in collecting specimens. It is probably completely absent from extensive lowland areas.

Natural History: In Florida, the habitat of *inexorata* is dry coastal hammocks, Florida scrub, and sandhill. Specimens are found under objects on the sand, or occasionally extracted in ones and twos from leaf litter. In other parts of its range, it can be found under rocks, which provide a window into subterranean habitats not found in Florida. I have never seen an actual colony, and there is no evidence that this species has ergatoid males or flightless queens. I once observed a mating flight in scrub habitat on a June morning.

Name Derivation: From *in-* (Latin), meaning “in,” *ex-* (Latin), meaning “out,” and *ora* (Latin),

meaning “edge,” meaning “in and out edge,” referring to the sinuate outer edges of the mandibles in frontal view.

*Hypoponera opaciceps* (Mayr)—  
Granulate Mini-Ponerine (Plate 10)

**Taxonomy and Similar Species:** The nearly parallel front and rear faces of the worker petiole (in lateral view) and nonshining integument (thanks to minute, dense granulation) distinguish this species from other Florida *Hypoponera*. Wingless individuals with large eyes, probably ergatoid queens, occasionally occur in this species. There are six subspecies (Bolton 1995), most of which are probably synonyms or separate species. Males have pale, almost transparent wing veins and slightly elongate eyes.

**Distribution:** South Carolina through Florida, west to Colorado; Central and South America, West Indies, Southeast Asia, and Polynesia (Smith 1979). Reported from Nevada by Wheeler and Wheeler (1986) and from Arizona by Mackay and Mackay (2002). It was probably transported by commerce from the Neotropics to Pacific tropical areas (Wilson and Taylor 1967). It undoubtedly occurs in southern California and New Mexico in moist disturbed areas such as golf courses, edges of ditches, and low spots in lawns. This species is sometimes found in soil of potted plants in Florida and is presumably dispersed widely by the nursery trade. At this time, there is no good reason to believe that *opaciceps* is not native to Florida. It is common in wracks above high tide lines along Florida beaches, and it is easy to imagine that this species could have arrived by island-hopping through the Caribbean or by following the coast around the Gulf of Mexico. In Florida, *opaciceps* occurs throughout the state.

**Natural History:** In Florida, *opaciceps* forms small colonies in open or partially shaded areas. It is most common in wet or periodically flooded areas, where it tends to replace *opacior* in fallen logs, grass tussocks, and accumulations of organic matter (Van Pelt 1958). In wet pastures in Highlands County, it may coexist with high populations of *Solenopsis invicta*. It often occurs under piles of seaweed on coastal beaches and under heaps of detritus left by high water along lakes. It is not clear how *opaciceps* is able to burrow through mud without becoming dirty, but its dense covering of fine pubescence might have something to do with this trick, as in mole crickets (Gryllotalpidae) and the unrelated pygmy mole crickets (Tridactylidae).

It is a rapid colonizer of disturbed areas such as lawns and ditches, and is even able to move into areas that have recently been subjected to volcanic eruptions in Hawaii (Fellers and Fellers 1982). In southern Florida, alates may be found in flight in afternoon and evening any time of year. Alate queens can deliver a noticeable sting when they become trapped under clothing or stuck to the skin by sweat. Whatever water-repellent qualities this species may have, they are evidently not proof against human perspiration.

**Name Derivation:** From *opacus* (Latin), meaning “dark,” and *-ceps* (Latin), meaning “head,” possibly referring to the dark coloration of the head, although the entire body is a similar shade, but more likely meaning “nonshining,” referring to the conspicuously microgranulate surface of the head.

*Hypoponera opacior* (Forel)—  
Common Mini-Ponerine (Plate 10)

**Taxonomy and Similar Species:** Worker and queen *opacior* have the petiole in lateral view strongly narrowed above, like a narrow triangle, not more or less parallel sided as in *opaciceps*. This species is seldom orange like *inexorata*, and the outer borders of the jaws are smoothly convex, not slightly concave as in *inexorata*. This species is usually dark brown, but reddish brown, probably callow individuals can be found, and could be confused with *punctatissima*. The mesopleuron of *opacior* is slightly granulate, while that of *punctatissima* is smooth and shining. The petiole of *opacior* is more elevated than that of *punctatissima*, but this difference is best seen by comparing specimens of the two species. Queen *punctatissima* are dark brown, like those of *opacior*, but have a smooth and shining mesopleuron. Male *opacior* have light brown wing veins, unlike the transparent wing veins of *opaciceps*. Male *inexorata* have brown veins, but are at least 3 mm long, larger than male *opacior*. Wingless females with large eyes, probably ergatoid queens, occasionally occur in colonies of *opacior*.

There is some variation in size and color, as in many other ponerine ants, but I have not found any structural differences associated with this variation. I have looked at specimens from much of the range in the United States, and several Caribbean islands, and have a feeling that there may be two or more species included under the name *opacior*. There appear to be some small geographic differences in size and color, suggesting

that this species has not recently moved into an enlarged range, but occurs as various separate lineages. If this is the case, it would not be surprising if some populations had diverged into separate species.

**Distribution:** Virginia south through Florida and the West Indies, west into Oregon, south through Central and South America into Chile and Argentina (Smith 1979), assuming it is one species throughout this huge range. This species is not, apparently, known from the Old World tropics and subtropics, and there is no reason to consider it a tramp species. In some areas, especially in arid climates, the distribution of *opacior* may be localized and discontinuous: in a survey of the ants of Nevada, Wheeler and Wheeler (1986) found *opacior* only once. In Florida, *opacior* can be found wherever there is cursory sampling of ants in leaf litter.

**Natural History:** This is the most abundant species of *Hypoponera* in Florida, occurring in a variety of mesic and upland habitats, both open and shaded, including fields, Florida scrub, sandhills, flatwoods, and hardwood hammocks. In wet areas, it is usually replaced by *opaciceps* and *punctatissima*. This species forms small colonies in soil, in rotten logs, and in accumulations of leaf litter. Nests are often in hollow nuts or small hollow twigs. In south Florida, I have found alates in flight traps from May through December. Alate queens are able to sting when trapped against the skin; I have been stung when running, the queens caught in sweat on my arms and neck.

**Name Derivation:** From *opacior* (Latin), meaning “darker,” or “more opaque,” probably relative to some other lighter or more shining species of *Hypoponera* or *Ponera*, such as *punctatissima*.

*Hypoponera punctatissima* (Roger)—  
Pantropical Mini-Ponerine (Plate 11)

**Taxonomy and Similar Species:** The shiny mesopleural area of *punctatissima* distinguishes it from reddish (callow) specimens of *opacior*. It is much smaller than *inexorata* and lacks the large punctures on the front of the head of *inexorata*. This species is somewhat similar to *Ponera exotica* but the latter species has conspicuous punctures on the head, short antennae with a relatively large antennal club, and a porthole-like structure on the subpetiolar flange. According to Taylor (1968), *H. punctatissima* is a synonym of *Ponera ergatandria*, a name that appears in Creighton’s manual (1950) and Smith’s 1936 catalog.

Like many tramp species, *punctatissima* has accumulated a number of names, listed in Bolton (1995), probably because it has been collected in all sorts of out-of-the-way places, and because it is not a particularly distinctive species to begin with. It is possible, however, that myrmecologists have been flummoxed by another factor. *Hypoponera punctatissima* apparently only produces flightless males, which presumably have a strong tendency to mate with their sisters. This could, in theory, complicate taxonomy. If noticeable divergences arise in a lineage with sibling mating, it would be possible to have consistent sympatric forms that appear to be separate species. This is most likely to be seen in a tramp sib-mating species that has been imported two or more times from separate parts of its range. One might say that these forms have some of the characteristics of separate species, since they are sympatric and reproductively isolated. In such cases, entomologists tend to recognize distinct “species” of sib-mating or parthenogenetic lineages if they show distinctive morphological differences and if they also show ecological differences. Such “species by analogy” appear to be numerous in the Scolytinae, especially in the genera *Hypothenemus* and *Xyleborus*. In Hawaii, *punctatissima* has a light form found in dry areas and a dark form in wet areas. This suggests two functional species, but it is also possible that the color differences reflect direct environmental effects, which I think that I have seen in some other ants, such as *Ponera pennsylvanica* and *Stigmatomma pallipes*. Van Pelt (1958) also reports two forms of *punctatissima*, but one of these is probably *Ponera exotica*.

**Distribution:** Pantropical; in North America, colonies seem able to survive outdoors in Florida and southern Texas to California. It is of Old World origin (Delabie and Bland 2002). It is also able to survive in warm microhabitats around and under buildings and in warm, composting organic matter; this has allowed it to move into cold areas, including New England, the Upper Midwest, Scandinavia, Britain, and Iceland (Delabie and Bland 2002). This is a cryptic species whose wide range might not have been documented were it not for the large numbers of queens that emerge to disperse, stinging with relatively little provocation. In Florida, *punctatissima* is known from both the Peninsula and the Panhandle, but seems commonest in the south and central Peninsula.

**Natural History:** *Hypoponera punctatissima* occurs in small colonies in a variety of moist or well-drained

habitats. In south Florida, it is often found in rotten logs and large grass tussocks, and especially in accumulations of organic matter, often open or disturbed areas. The key to the housefly-like success of *punctatissima* lies in its predilection for dung and various kinds of middens, which humans and their livestock supply in inexhaustible quantities. Delabie and Bland (2002) have compiled a whole series of breeding sites, ranging from earthworm cultures to heaps of chicken manure, and suggest that *punctatissima* emerged out of Asia following the domestication and extensive use of horses. While reluctant to challenge this attractive “Valley of the Horses” hypothesis, it seems to me that *punctatissima* only requires stables and dung heaps in the northern part of its range, and could have spread on its own through the Old World tropics and subtropics, although it would have undoubtedly benefited from the organic middens our species has generously provided throughout our history.

The tendency for *punctatissima* to produce disproportionately large numbers of dispersing females is appropriate for a species that colonizes resource-rich resources that are often ephemeral. This dispersal, in turn, leads to problems with stinging alate queens, first mentioned by Smith (1936), who reported on a Florida outbreak in which the ants in sugar cane fields were so numerous as to annoy field workers “like mosquitoes,” also passing through screens to pester them by night. Many of the stings probably resulted from ants that got trapped in a film of sweat on the laborers’ bodies. In May of 1991, the Archbold Biological Station was sent packets of alate *punctatissima* from pest control and agricultural extension agents. The complaints included the presence of “big, biting swarms” in the afternoon, with many stings on the back, neck, and arms; ants entering through screens at night; ants attacking and stinging racehorses (the horse connection again); heavy attacks in schoolyards and at afternoon sports events. There were no reports of serious reactions. My experience is that the sting, while somewhat painful, does not linger like that of *Wasmannia auropunctata* or cause a pustule like that of *Solenopsis invicta*.

Colonies of *punctatissima* can include normal workers, alate or dealate queens, intercastes without wings but with larger eyes than those of workers (these are probably flightless queens), and two types of flightless males. The range of morphs in *punctatissima* is like that of the rare Japanese species

*Hypoponera bondroiti*, studied by Yamauchi et al. (1996), and it is possible that many of the complex reproductive behaviors found in *bondroiti* also occur in the common and easily available *punctatissima*. There is already an observation by Hamilton (1979) that male *punctatissima* fight until one has possession of the nest chamber where females emerge from their cocoons.

Name Derivation: From “*punctatissima*” (Latin), meaning “extremely punctured,” perhaps referring to the punctures on the head and body that are so numerous and tiny as to be almost invisible.

## Genus *Leptogenys*

### *Beaked Hunter Ants*

Members of the genus *Leptogenys* (pronounced **lep tō jen” ēz** or **lep toj” en ēz**) are long-legged, fast-moving ants. They usually lack teeth on the mandibles and the clypeus usually projects forward in a point, so that in frontal view it looks like the beak of a bird. Another unusual feature of the genus is the comb-like tarsal claws; the function of this apparent adaptation is unknown. Queens of most species are flightless and tend to look like workers. Approximately 236 species have been described (Bolton 1995; Lattke 2011), making *Leptogenys* one of the more speciose genera of ponerines. The genus occurs worldwide in the tropics, including species confined to isolated islands such as New Caledonia and Madagascar that have not been accessible for a very long time. There are also a few species whose distribution indicates that they have been transported by human commerce (Bolton 1975). One of these, *Leptogenys maxillosa*, apparently originating in Africa, has been found in Cuba (Bolton 1975) and might well survive in Florida, if it could get there. Southern Texas and northern Florida appear to be the northern limits of *Leptogenys* in the New World.

Neotropical species of *Leptogenys*, including 81 known species, tend to live in small colonies with only 20–30 workers (Lattke 2011). A few Old World species, such as *Leptogenys distinguenda*, have converged almost completely on an army ant way of life, with tens of thousands of workers (Gotwald 1995), but there are no known New World species with such habits (Lattke 2011). With the exception of the army ant–like species, *Leptogenys* seem to be specialized predators, usually feeding on terrestrial isopods (Lattke 2011).

Trager and Johnson (1988) suggest that the beak-like clypeus helps secure slippery, convex isopods as they are being carried back to the nest. One Old World species is a specialized predator of fungus-growing termites (Maschwitz and Schönegg 1983) and another specializes on earwigs (Steghaus-Kovak and Maschwitz 1993); it is always possible that species may be found with other strange prey preferences, as the habits of most *Leptogenys* species are not known.

*Leptogenys* species of the New World have recently been revised by Lattke (2011).

Name Derivation: From *leptos* (Greek), meaning “slender,” and *genys* (Greek), meaning “jaw,” referring to the long, slender mandibles.

### *Leptogenys manni* Wheeler— Eastern Isopod Ant (Plate 12)

Taxonomy and Similar Species: *Leptogenys manni* looks slightly like similar-sized species of *Aphaenogaster*, but is even more slender, with an elongate gaster. The beak-like clypeus and elongate jaws are diagnostic. There is a closely related similar species west of the Mississippi, *Leptogenys elongata*. The distinctive males, which are orange with thick dark antennae and brown wings, can easily be picked out of light trap and Malaise trap samples; these help establish the range of the species.

Distribution: Known only from Florida, but undoubtedly occurs in southern Georgia, as it occurs at Tall Timbers Research Station (Leon County) just a mile or so from the Georgia border. There are scattered records through peninsular Florida, but as yet no Panhandle records west of the Ochlockonee and Apalachicola Rivers. This distribution suggests that the species was eliminated from much of its eastern range during cool periods of the Pleistocene, spreading back from southern Florida relatively recently but limited in its western expansion by north–south rivers.

Natural History: *Leptogenys manni* occurs on the Archbold Biological Station, as males have been collected at flight traps and at lights, and workers have occasionally been found in bowl traps filled with water and a little detergent. There are no observations, however, of this species out foraging, and it is probable that colonies are nocturnally active. This is a reasonable assumption, as isopods, the normal prey of *L. manni*, are also nocturnal (Hornung 2011). Elsewhere in Florida, *L. manni* is usually found in undisturbed

mesic woodlands where limestone is at or near the surface (Trager and Johnson 1988). Terrestrial isopods have a relatively high requirement for calcium as the exoskeleton is calcified with calcite crystals and calcium carbonate (Hornung 2011). Nests of *L. manni* are often marked by a midden of isopod shells; examination of these middens suggests that *manni* prefers the native isopod *Porcellionides virgatus* rather than introduced species of *Armadillidium* (Trager and Johnson 1988). Colony reproduction is almost certainly some form of fission of mature colonies, but the process, not surprisingly, has not been observed. In the case of a species such as *manni*, there is no obvious reason why a new colony must begin with a large number of workers, so it is possible that a new colony is founded by a queen with a retinue of just a few workers. Males fly May through October (Trager and Johnson 1988). Continuously operating flight traps at the Archbold Biological Station captured males July–December 1983–1986, with the great majority (69 out of 77) in September–November, 40 in October alone.

Name Derivation: William Wheeler named this species for his former graduate student William Mann, who sent Wheeler the type specimens from Florida (Wheeler 1923). Wheeler and his graduate student did not operate on quite the same wavelength. Wheeler was a brilliant and versatile academician who enjoyed a well-organized field expedition. Mann, by his own admission, was forever yearning for adventurous collecting trips to exotic places. After several such trips, Wheeler insisted that Mann settle down and write his dissertation. Around that time, Mann’s world was “completely demolished” by overhearing Wheeler turn down an offer to have Mann accompany an expedition to Borneo. He recovered from this shock in time to finish his doctorate and head off on an extended trip to the South Seas to collect ants and other animals, as related in his book, *Ant Hill Odyssey* (1948). After a series of productive ant-hunting safaris, eventually Mann displayed his own brand of versatility, becoming director of the National Zoo in Washington, DC.

### Genus *Odontomachus*

#### *Snapping Ants*

The genus *Odontomachus* (usually pronounced **Ō’ don tō mak’** us, but sometimes **Ō’ don tōm’**)

**a kus**) occurs around the world in the tropics, including some remote islands in Melanesia. These are large stinging ants that are easily agitated, and would not seem preadapted as stowaways, but there is good evidence that two species are exotic in Florida, so the powers of independent dispersal may not be as great in some species as myrmecologists have assumed. There are approximately 60 described species (Bolton 1995), reduced from approximately 160 names. *Odontomachus* species are conspicuous ants, often with some intraspecific variation. In the early days of myrmecology, this resulted in a chaotic horde of specific taxa that were sorted and disciplined by Brown in his review of the genus (1976). Four species are known from Florida. North American species were reviewed by MacGown et al. (2014).

Members of this genus are distinguished from most other Florida ants by their elongate, apically bent jaws, and the absence of a conspicuous constriction between the first and second segments of the gaster. These features also occur in *Anochetus*, but the Florida species of *Anochetus* is only 4 mm long, much smaller than any species of *Odontomachus*, and has two points on the petiolar apex when viewed in front or at the back.

*Odontomachus* species are famous for the speed of their mandibular snap, which requires only 0.33–1.00 milliseconds, the fastest animal movement known (Gronenberg et al. 1993). This is achieved by using stored tension, as in, for example, a crossbow. The jaws are cocked open and locked into place, and then tension is put on the massive jaw-closing muscles that run back into the rear lobes of the head. A trigger device releases the jaws, which snap closed with sufficient force to stun or crush prey, or drive off predators (Carlin and Gladstein 1989). A drawing of the jaw-snapping mechanism is provided by Barth (1960). The ends of the jaws are thickened, but the apical teeth often show wear or breakage from snapping shut. Despite these formidable jaws and an effective sting, Florida representatives of *Odontomachus* are not especially bold, and often retreat for a few minutes after stunning a prey, perhaps to allow dissipation of defensive chemicals (Brown 1976; Ehmer and Hölldobler 1995). This even allows at least one species, *Odontomachus bauri* (not a Florida species), to kill and carry off nasute termites, which squirt a glue of noxious chemicals (Ehmer and Hölldobler 1995). Although all species of *Odontomachus* are probably predaceous, at least one

species, *Odontomachus chelifer*, consumes arils on the seeds of a tropical tree and may have a role in seed dispersal (Piso and Oliveira 1998). The Florida species *Odontomachus brunneus*, which often occurs in open wet areas, could conceivably be a disperser of wetland milkworts (*Polygala* spp.). Several species are attracted to sweets (Oliveira and Hölldobler 1989), and this attraction can be seen, in a mild form, in Florida species.

There are behavioral studies of several tropical species, and these might serve as models for studies of Florida species, two of which are easy to find, and would make good research subjects. Oliveira and Hölldobler (1989) found that the forest species *O. bauri* uses forest canopy patterns in orientation, and foragers are able to recruit nest mates to bait by raising the level of foraging activity, but not by laying a trail to the bait. Medeiros et al. (1992) studied dominance hierarchies in queens of the polygynous species *O. chelifer*. Brandão (1983) studied division of labor in the Brazilian species *Odontomachus affinis*.

Name Derivation: From *odontos* (Greek), meaning “tooth,” and *machetes* (Greek), meaning “fighter” or “warrior,” referring to the toothed jaws and defensive behavior of *Odontomachus* species.

*Odontomachus brunneus* (Patton)—  
Southeastern Snapping Ant (Plate 8)

Taxonomy and Similar Species: The long, dense, appressed pubescence on the gaster distinguishes *brunneus* from other Florida species. Groups of these flexible hairs often cling together, a feature not seen in other Florida species. The pubescence of *haematodus* is also relatively dense, but the hairs are not flexible, and stand up from the surface of the gaster. The male is brownish yellow, with huge, protruding ocelli, each as wide as the space between the eye and the lateral ocelli. The males of Florida *haematodus* that I have seen are also brownish yellow but do not have extraordinarily large, protruding ocelli. Within the Southeast, there is some variation in workers, but apparently based on habitat rather than geographic variation. Specimens from dry habitats are often smaller and paler than specimens from wet habitats. Southeastern records of *insularis* (Smith 1979) actually refer to *brunneus*; *insularis* is a valid West Indian species that is not known from Florida. In the Neotropics, the entire *haematodus* complex designated by Brown (1976), which includes all of the five or six species found in the United States,

needs some review, preferably with the inclusion of worker-associated males. In *Odontomachus*, male morphology has, at least in some cases, diverged more conspicuously than worker morphology (MacGown et al. 2014). The recognition of *ruginodis* as a species separate from *brunneus* (Deyrup et al. 1985) and *relictus* from the southwestern *clarus* (Deyrup and Cover 2004b) depended heavily on obvious differences among the males of these species.

**Distribution:** Southern Georgia, throughout Florida, although rare in the western Panhandle. There are records from Alabama (MacGown and Forster 2005), but the published records from Baldwin County (Deyrup and Cover 2004b) are from specimens of *haematodus*, which I identified through the sides of vials without taking them out to examine them more carefully. I have not seen specimens from the West Indies. Records from Central and South America, south into Paraguay and Bolivia (Brown 1976), are uncertain, as they date from a time when *brunneus* was combined with *ruginodis*, an apparently widespread and adaptable species. Biogeographically, therefore, *brunneus* allows highly disparate hypotheses. In North America, it could be a disjunct, possibly introduced, population of a widespread Neotropical species, or it could be an ancient, possibly Arctotertiary, endemic species. My gut feeling is that *brunneus* is restricted to southeastern North America. The name *brunneus* was first applied to a population from southeastern North America (Patton 1894), so this name should remain stable for the species in North America.

**Natural History:** This species occurs in both well-drained and poorly drained habitats, and nests may be in soil or in rotten wood. Van Pelt (1958) studied *brunneus* at the Welaka State Forest in Putnam County. He found many colonies in various habitats, including swamp forest, flatwoods, mesic forest, upland scrub, and sandhill. Nests were in various microhabitats: deep leaf litter, fallen logs, at the bases of trees, and open or sparsely vegetated sandy areas. At the Archbold Biological Station, Highlands County, *brunneus* is in moist areas and mesic hammocks, but is replaced by *relictus*, or occasionally *ruginodis*, in dry upland habitats.

Workers sometimes emerge to forage on cloudy days, but are generally nocturnal. The powerful jaws are not used as assertively as one might expect, and there are preliminary indications that

*brunneus* is sensitive to chemical defenses. Foragers approach prey tentatively, and recoil immediately after striking (Brown 1976). There may be a delay before the prey is carried away; Brown (1976) suggests that this delay is a reaction to possible chemical defenses, which are allowed to dissipate before the prey is retrieved. Alex Wild (unpublished student notes in the files of the Archbold Biological Station) twice observed *brunneus* retreating hastily when confronted by aroused workers of *Dorymyrmex bureni*, a small species that can release strong-smelling defensive compounds. Van Pelt (1958) reported accumulations of head capsules in several nests of *Formica archboldi* and suggested the possibility that *brunneus* is a regular prey of *F. archboldi*. If predation is involved, it is more likely that *brunneus* is subdued by chemical means than by jaw-to-jaw combat.

Some aspects of the natural history of *brunneus* are known in great detail, thanks to Walter Tschinkel and his students and colleagues, who have studied ants in the Tallahassee area for several decades. Other research achievements of Tschinkel and his diverse team are discussed under *Solenopsis*, *Trachymyrmex*, *Pogonomyrmex*, *Pheidole*, *Dolichoderus*, and *Prenolepis*.

Colony organization was described by Powell and Tschinkel (1999). Colony structure is complex, but derived from a relatively simple mechanism of ritualized dominance contests between pairs of ants. Persistent losers end up at the periphery of the nest, whereas persistent winners are near the brood and near the queen, who is the most dominant individual in the colony. Persistent winners have larger ovaries and may be able to produce unfertilized (male) eggs. Persistent losers are probably important in foraging and in nest maintenance and defense. During a food shortage, contests intensify, resulting in more peripheral workers and more foraging. This class system is apparently based on dominance contests and stabilized by different work zones within the nest.

Nest architecture of *brunneus* varies with habitat. In wet areas, nests are often in rotten logs or branches on the ground; such nests have not been studied. In well-drained sandy areas, *brunneus* constructs elaborate nests consisting of a slender shaft with varying numbers of chambers along its length (Cerquera and Tschinkel 2010). Nests sometimes take advantage of cavities left by other animals or expand into hollow roots. Nests extend to a depth of 18 to 184 cm.

Hart and Tschinkel (2012) studied the seasonal cycle of *brunneus* in a well-drained sandy habitat in the Tallahassee area. Like most North American ants, *brunneus* produces larvae that will become males and queens once per year, in this case in spring. The effort of rearing sexual broods, added to the effort of raising worker larvae, depletes the energy reserves of the workers, as measured by the contents of the fat body (a storage organ found in most insects). In fall, after all larvae have matured, the fat content of workers quickly recovers. In winter, colonies are in a quiescent state.

The mating arrangements of *brunneus* might be unusual. Young queens still bearing their wings have been observed foraging away from the nest, rather than waiting in the nest for conditions appropriate for a mass emergence of males and queens (Hart and Tschinkel 2012). Males seem to fly around extensively. I find large numbers of males, but no females, in flight traps and at lights. When males and queens of other species of ants emerge en masse, as occurs in many species, there is no guarantee that couples will find each other, and these mass emergences usually attract predators. Young *brunneus* queens might incur a risk during foraging expeditions outside the nest (Hart and Tschinkel 2012), but might compensate by enjoying the comfort and security of the nest until the time they are out foraging and meet one or more roving males. An example of such a mating system is provided by the unrelated ant *Myrmecina graminicola* (Buschinger 2003). There is always the possibility that there are mass emergences of male and female *brunneus*, and normal mating aggregations; nobody knows what all those nocturnally active males are actually doing.

Name Derivation: From *brun* (Anglo-Saxon), Latinized to *brunneus*, meaning “brown.”

*Odontomachus haematodus* (Linnaeus)—

Two-Spined Snapping Ant (Plate 8)

Taxonomy and Similar Species: This widespread and variable tropical species is most clearly differentiated from a series of similar species by a pair of well-developed spines, usually of unequal lengths, located immediately in front of the hind coxae (Brown 1976). The discovery of these spines was a taxonomic triumph for aficionados of *Odontomachus*, but the spines can be difficult to see. The specimen must be viewed underneath from in front, and the hind coxae should be at right

angles to the body (or removed). It helps raise the gaster so that the spines are not seen against the background of the gaster. If the specimen is astride a point between the second and third coxae, the spines are embedded in glue and covered by the point. One would not want to search for the spines on every specimen of *Odontomachus* found in Florida, so it is fortunate that there are alternative character states available for preliminary identification. The hairs on the gaster are densely arranged but do not lie flat on the gaster like those of *brunneus*, but stand up slightly off the surface, as can be seen by scanning the gaster from the side. There are no conspicuous ridges across the back of the petiole, as in *ruginodis*. The first gastral tergite of *relictus* is glassy smooth, with sparse hairs that are almost as far apart as they are long. The first gastral tergite of *haematodus* is covered with fine, wavy, transverse sculpture, and the hairs are close-set; the distance between them is less than a third of their length. Close-up photos of workers and males of *haematodus* have been published by MacGown et al. (2014).

Distribution: Guyana, west to the Andes; southeastern Brazil, the Amazon Basin, south into northwestern Argentina (Brown 1976). In southeastern North America, *haematodus* occurs as an exotic from southern Louisiana east into the western Florida Panhandle (MacGown et al. 2014). The debarkation point for this species is unknown, but likely to be Mobile or the Port of New Orleans. The earliest collection is from Alabama in 2001; the most recent is from Florida in 2006. I would not have predicted the establishment of this species in the Southeast, but it does fit a pattern of species that may have come from subtropical South America to ports on the Gulf of Mexico. Other species that may fit this pattern are *Solenopsis invicta*, *Brachymyrmex patagonicus*, *Cyphomyrmex rimosus*, and *Pheidole obscurithorax*. Two widespread species of *Odontomachus* that might be adapted to Florida, or at least the southern Peninsula, are *bauri* and *insularis*.

Natural History: This species is common in lowland tropical and subtropical forests (Brown 1976). In the Southeast, it has been collected in mesic disturbed areas (a zoological park, a residential area) and in salt marshes. It is probable that this species will prove poorly adapted to sandy uplands in Florida, but might spread widely through wet and mesic habitats, unless it is limited in its spread by competition with *brunneus*.