Edward O. Wilson
and José M. Gómez Durán

Kingdom of Ants

José Celestino Mutis and the Dawn of Natural History in the New World

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THE JOHNS HOPKINS UNIVERSITY PRESS

Baltimore

Printed in the United States of America on acid-free paper
2 4 6 8 9 7 5 3 1

The Johns Hopkins University Press
2715 North Charles Street
Baltimore, Maryland 21218-4363
www.press.jhu.edu

LIBRARY OF CONGRESS CATALOGING-IN-PUBLICATION DATA

Wilson, Edward O.
Kingdom of ants : José Celestino Mutis and the dawn of natural history in the New World / Edward O. Wilson and José M. Gómez Durán.
p. cm.
ISBN-13: 978-0-80189785-6 (hardcover : alk. paper)
ISBN-10: 0-8018-9785-8 (hardcover : alk. paper)
1. Mutis, José Celestino, 1732–1808. 2. Botanists—Colombia—Biography. 3. Botanists—Spain—Biography. 4. Ants—Research—South America—History—18th century. I. Gómez Durán, José María. II. Title.
QK31.M8W55 2010
595.79’6092—dc22 2010011046

A catalog record for this book is available from the British Library.

Special discounts are available for bulk purchases of this book. For more information, please contact Special Sales at 410-516-6936 or specialsales@press.jhu.edu.

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Oh Sacred God!

How much time and perseverance

are needed to discover the secrets of nature!

JOSÉ CELESTINO MUTIS, SEPTEMBER 30, 1780

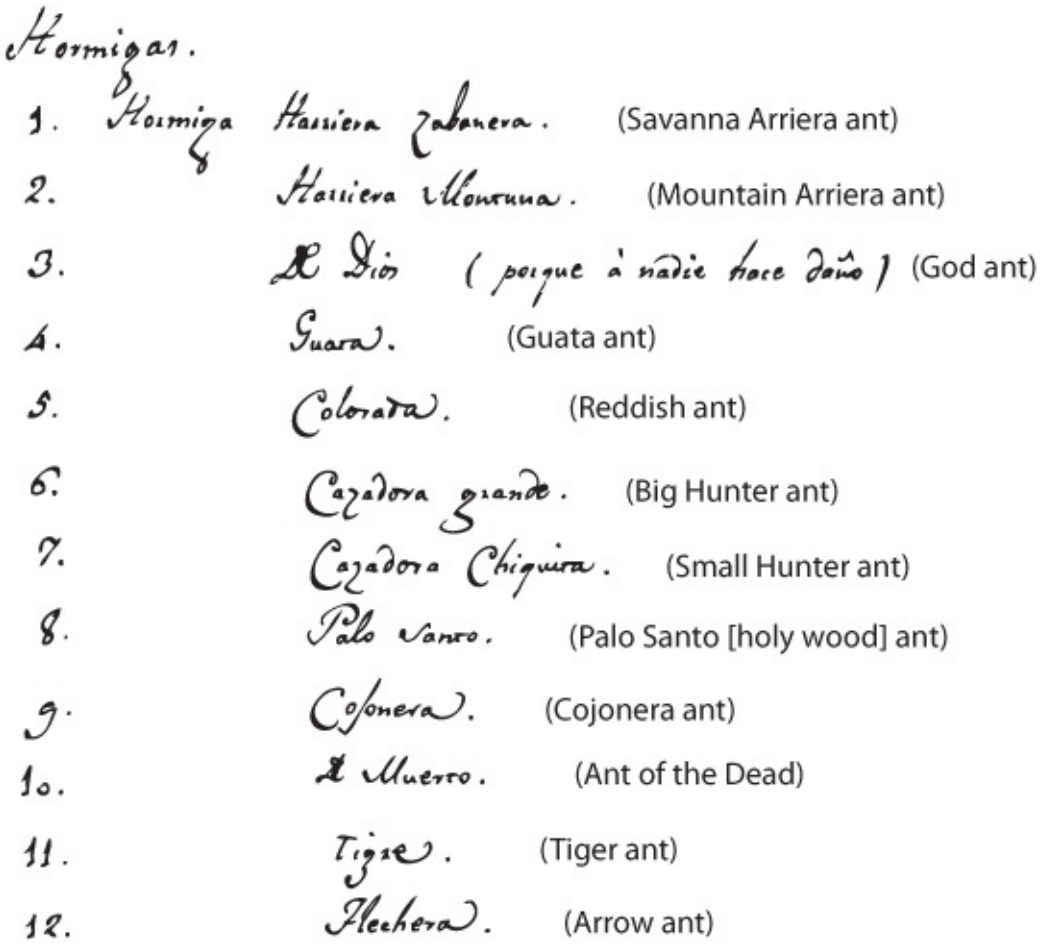
CONTENTS

Kingdom of Ants

PROLOGUE

Late in 1760 José Celestino Mutis, a young Spanish physician and botanist, arrived in the New World in what was then called the New Kingdom of Granada. In current political geography, this area constitutes the southern half of Central America and the northern part of South America. Mutis traveled from the Caribbean port of Cartagena de Indias up the Magdalena River on his way to the capital, which lay east on the high plateau of Santa Fe de Bogotá. Somewhere on the bank of the Magdalena, probably near the point of disembarkation at Mariquita, he walked into the tropical dry forest that lined the riverbanks. There he began a scientific study of a kind never before attempted. It was so esoteric it might not even have been previously imagined: he made a list of all the species of ants he could find.[1] It was in a sense a blind journey. Of the species he recorded, two kinds of the *arriera* (mule-train) ants had names the local people used. The rest he made up out of thin air. His list contained twelve species.

Thus began the earliest extended scientific program in entomology in the New World. In the four decades that followed, during a distinguished career as the first scientist and natural philosopher in what is now the nation of Colombia, Mutis accumulated a large amount of information on ants, and he wrote two books about his findings. Unlike his botanical research, both of these treatises were lost, and during the two centuries following Mutis' death in 1808, the substance of his extensive research was mostly forgotten. But not completely. That Mutis had done such work was known among scholars in Colombia and Spain in the nineteenth and twentieth centuries.



List of ant species in José Celestino Mutis' handwriting, with English translations (document catalogued as "Real Jardin Botánico de Madrid, Fondo Documental José Celestino Mutis, III, 11, 1, 20").

In the mid-1900s, the great Colombian historian Hernández de Alba discovered the complete diaries of Mutis.[2] He put the scattered pages in order, arranged them into a coherent series, and published them. Of the 1,200 published pages in the Alba collection, more than 100, inserted among Mutis' botanical observations, describe his findings. This material, rich in detail, amounts to Mutis' original field notes. In this work, for the first time, we have undertaken to reconstruct the substance and story of what this fascinating figure discovered. In doing so, we hope to reveal something about the dawn of natural history research in the New World.

CHAPTER 1

Who Was Mutis?

Today, José Celestino Bruno Mutis y Bosio is known to few outside of Colombia and Spain. Even there, his name rings familiar mostly to historians of the Spanish colonial era and to botanists specializing in the Neotropical flora. Yet this eighteenth-century scientist, Spanish by birth and Colombian by adoption, deserves a place in the explorer's pantheon of the New World. His was the broadest in education and scholarly research of all the pioneer naturalists of South America, save only the revered Alexander von Humboldt (1769–1859)—whom Mutis preceded by a full generation.

Mutis' forty-eight-year stay in Colombia, spanning most of his adult life, was far longer than Humboldt's four-year journey across northern South America. It vastly exceeded the two years artist and naturalist Maria Sibylla Merian (1647–1717) spent in the Dutch colony of Suriname, and it dwarfed the seven months' sojourn in Suriname by Carl Linnaeus' "apostle" David Rolander (1725–1793).

To the north, a number of explorers and collectors made important contributions on the fauna and flora of the West Indies. They included Gonzalo Fernández de Oviedo y Valdés (1478–1557) in the sixteenth century and in the seventeenth and eighteenth centuries, James Harlow (1660–1696), Joseph Donat Surian (?–1691), James Reed (collected during 1682–1693), Hans Sloane (1660–1753), Charles Plumier (1646–1704), Mark Catesby (1682–1749), Jean Baptiste René Pouppé Desportes (1704–1748), Patrick Browne (1720–1790), and Nikolaus Joseph Jacquin (1727–1817). Browne published his influential *The Civil and Natural History of Jamaica* in 1756, and Jacquin published the even more taxonomically important *Enumeratio Systematica Plantarum*…in 1760 and *Selectarum Stirpium Americanarum Historia* in 1763.

The collectivity of all these pioneers laid much of the foundation of tropical American botany, but none among them was comparable to Mutis in the breadth of his scientific and educational achievements.

In North America during the same period, only John Bartram (1699–1777), the leading scientific naturalist of the American colonies, can fairly be called the eighteenth-century peer of Mutis. The elder Bartram (his son William was a famous explorer and naturalist in his own right) created the twelve-acre Bartram Botanical Garden outside Philadelphia, the first such living collection in North America. With Benjamin Franklin, he founded the American Philosophical Society. Because of his prodigious efforts on behalf of systematic botany, including the large numbers of plant specimens he collected and distributed, Linnaeus called Bartram “the greatest natural botanist.” In 1765, George III appointed him Royal Botanist, a post he held for the remainder of his life.

True, Mutis published comparatively little, especially compared with the prodigious lifetime output of Bartram and Humboldt, and he made no appearance in salons and learned assemblages of America and Europe to lecture on wonders he discovered. (Humboldt became the most famous man in Europe after Napoleon, who is reported to have remarked upon meeting him, “I understand you are interested in botany, Mr. Humboldt; so is my wife.”)

Much of what Mutis wrote was lost or exists today only in fragments. But he brought the ideas of the Enlightenment and the institutions of science to the Spanish territories that constituted the New Kingdom of Granada, which mainly comprised present-day Colombia with adjacent parts of Venezuela and Ecuador and was a substantial part of the Spanish Empire. With the aid of a small team of assistants and supported by the Spanish crown, Mutis was the first to address the vast and largely unknown fauna and flora of northern South America. That region, encompassing the northern Andean highlands, the tropical dry and moist forests, and the broad savannas and wetlands, together with sections of both the Caribbean and western Pacific shallow marine waters, may be the biologically richest in the world. More than 1,700 species of birds are known to occur in modern Colombia alone.

To biology historians, Mutis is known chiefly as a botanist and unacknowledged apostle of Linnaeus. Yet, as we will now show, he was also the first in the New World to study the amazing habits of ants and termites, the dominant insects of tropical America. Among all of the explorer naturalists of the eighteenth century who focused on plants, vertebrate animals, and occasionally butterflies, Mutis alone looked down to the little creatures teeming at his feet.

CHAPTER 2

The Making of an Eighteenth-Century Naturalist

José Celestino Mutis began his career as a professor of anatomy and physician in the royal household of Ferdinand VI. In 1760, at age twenty-eight, he was appointed personal physician to Pedro Messía de la Cerda, the newly elected viceroy of the New Kingdom of Granada. The young doctor and scientist was eager to move to the Spanish colony. His intense interest in natural history was inspired by two Madrid naturalists, Miguel Barnades and Joseph Quer, the latter the director of the Botanical Garden of Soto de Migas Calientes. Like his great successor Alexander von Humboldt, Mutis saw in his visit to northern South America a unique opportunity to explore a rich and scientifically little-known part of the world.

Arriving in Santa Fe de Bogotá in 1761, Mutis thus found himself in an intellectual vacuum, and he became a polymath to fill it. His entrepreneurial spirit and energies in accumulating knowledge were extraordinary even for the times. Moving beyond his medical duties, he served as professor of mathematics, using that position to promote the ideas of the Enlightenment. He translated the writings of Isaac Newton and wrote original articles on the contributions of Copernicus and the Dutch physician and botanist Herman Boerhaave. He constructed the first astronomical observatory in the Western Hemisphere. His lectures at Santa Fe de Bogotá ranged across astronomy, geography, and meteorology. He built one of the largest scientific libraries in the world. He conducted mineralogical research at the mines of Montuosa Baja in Pamplona and Nuestra Señora del Rosario. Finally, amid all these enterprises, he did not neglect theology: in 1772, Mutis became a priest. Because of his passion for the Enlightenment, in 1774, Mutis was forced to defend himself before the Inquisition.

Throughout his long career, his focus never strayed from the studies of the natural world. In 1783, he accepted an appointment from the crown as the first director of the Royal Botanical Expedition to the New Kingdom of Granada, one

of a series authorized by Charles III to study natural history in remote parts of the world.[1] In this capacity, he hired artists and collectors and set out to write the *Flora of Bogotá*, in multiple volumes, and other works in botany and zoology.

However, perhaps as a result of the vertiginous array of activities to which Mutis committed himself, no volumes of the *Flora* appeared, and his personal published works remained otherwise sparse. He did nonetheless produce valuable series on the cinchona, the source of quinine and related compounds, some of which was posthumously put into book form in 1828 by Hernández de Gregorio entitled *El Arcano de la Quina*. A second book, *Historia de los Árboles de la Quina*, with systematic descriptions and illustrations of trees, was assembled posthumously from Mutis' notes and published in 1957.[2]

Then there were the ants to which Mutis turned soon after his arrival. The little insects (and some not so little) swarmed everywhere in the fields and forests of the New Kingdom. They demolished crops, hunted in formidable marching phalanxes, and were so abundant in houses that they often mingled with food and were accidentally eaten at meals. Mutis had seen nothing like these hexapod legions in Spain. He became obsessed with ants and elected to spend long hours puzzling over their diverse and strange habits.

The young scientist plunged into his myrmecological studies soon after arriving at Santa Fe de Bogotá in 1761. The Swede Carl Linnaeus, founder of the modern system of taxonomy in biology, had suggested this enterprise to Mutis.[3] Linnaeus' key work, the tenth edition of *Systema Naturae*, is the official foundation of the system from which priorities of scientific names are based to the present day. It had been published in 1758, only two years before Mutis' arrival in South America.

Linnaeus was acclaimed in his own lifetime as the world's greatest naturalist. His ambition was to classify all forms of plants and animals, not only in his native Sweden but also throughout the world. To further this project, which he believed entirely achievable, he recruited young men to travel to remote places and encouraged them to collect and annotate specimens during their visits. He called them his "apostles." Mutis was ideally suited to fill this role in northern South America.

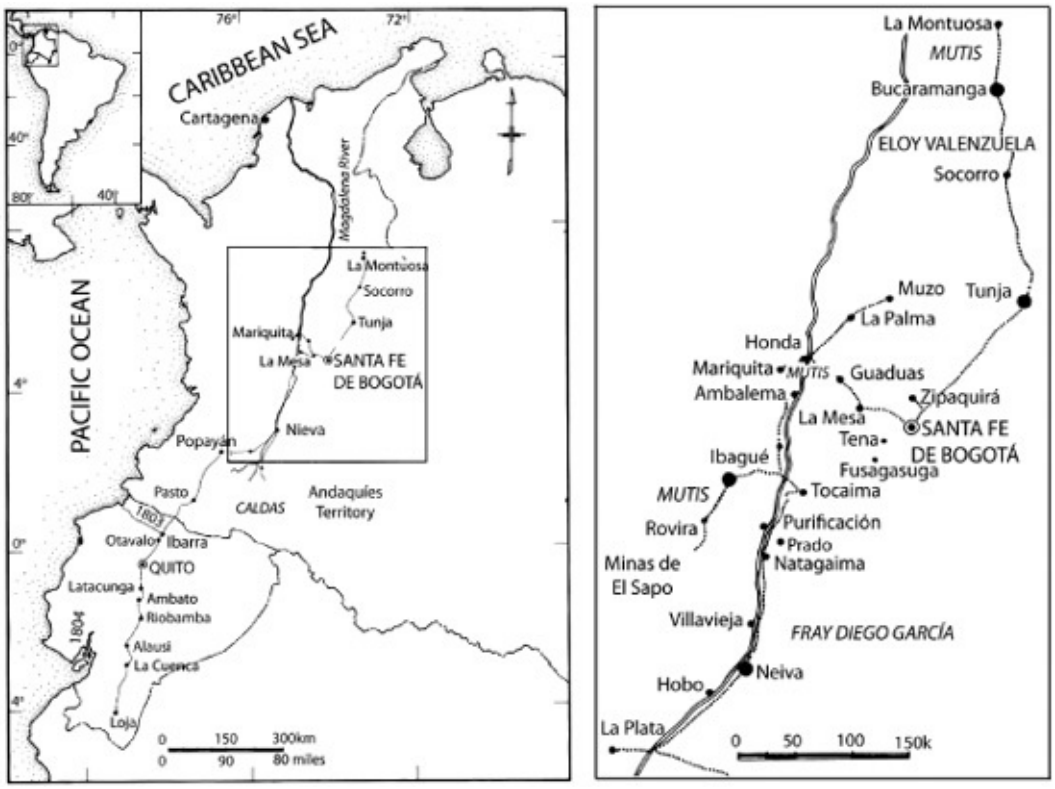
Mutis corresponded with Linnaeus, but perhaps because he never met Linnaeus personally and was not specifically a student of his, neither the Swedish sage nor later historians chose to add him to the official list of Linnaeus' seventeen apostles. We suggest that this omission be at least

informally corrected and that, as you read, you consider Mutis the honorary eighteenth apostle.

The letter from Linnaeus suggesting that Mutis study ants has been lost, but we know its content from Mutis' diary entry of July 3, 1761, written in Santa Fe de Bogotá:

> Still greater was the pleasure of corresponding with Mr. Linnaeus, an honor to which because of my young age I should not aspire. This gentleman is kind enough to write a generous and extensive letter requesting my own correspondence; he encourages me to make the pilgrimages; he clears the way for me to be honored as Academic in the Academy of Sciences of Uppsala; he promises to name a plant species after me; he gives me news of the current edition of *Fauna Suecica* and future ones of *Species Plantarum* and *Systema Naturae*; he tells me how much he would like to receive the collections I offered him; and he promises he will not fail to mention me whenever there is reason to cite my collections. He praised, in words worthy of our Viceroy's beautiful garments, the news that I communicated to Sir Alstroemer, who transmitted them by letter to Mr. Linnaeus in Sweden.
>
> He entrusts me very especially to work on the description of species of ants, their customs and economy, and to send him my works right away so that I might be admitted to the company of the sages of the Academy.[4]

Thus Mutis, at twenty-eight years old when he arrived in the New Kingdom of Granada, plunged into the task that Linnaeus had assigned him. He soon made his list of twelve kinds of ants found along the banks of the Magdalena River. At first, he had no idea of how to proceed. There was no literature on South American ants or on ants of the entire Western Hemisphere for that matter, and Mutis lacked training in entomology, a subject that scarcely existed in the mid-1700s.



The New Kingdom of Granada, and the travels of José Celestino Mutis and his assistants during the Royal Botanical Expedition, 1783–1816, including Francisco José de Caldas in Cauca and Ecuador to the south (*left*) and Fray Diego García to the southeast (*right*). From Benjamín Villegas and Pilar de San Pío Aladrén, eds., *Mutis and the Royal Botanical Expedition of the Nuevo Reyno de Granada*, vol. 1 (Bogotá: Villegas Editores; Barcelona: Lunwerg Editores; and Madrid: Real Jardín Botánico, 1992).

The bizarre catalog Mutis created on the banks of the Magdalena explains his unique circumstances. They help us understand why his efforts, some of which we are able to bring to light here for the first time, are reason to give him a special place in the history of biology. By 1761, the New Kingdom of Granada had a history of 200 years. It had been favored by competent governance, a solid economy, and a tolerable transportation system composed of riverboats, wagons, and mules. The ruling class was relatively well educated, with strong cultural ties to Spain and most European countries. As with most tropical regions in the eighteenth century, the natural history of the New Kingdom was still nearly void. Almost nothing was known about its insects.

When Mutis undertook entomology in New Granada, it was therefore as

though he had landed on an alien planet. In the French archives rested a remarkable manuscript, written in 1742–43 by René Antoine Ferchault de Réaumur, who described in detail the habits of some European ants. This could have served as a model for Mutis, but its existence remained unknown to scientists until it was translated and published in 1926 as *The Natural History of Ants* by the Harvard entomologist William M. Wheeler.[5] In 1747, the Reverend William Gould had published a brief set of observations entitled *An Account of English Ants*, but this admirable work was evidently not present in Mutis' large library.

In his *Systema Naturae* (tenth edition), Linnaeus had recognized seventeen species of ants. All were placed in the genus *Formica*, meaning, not surprisingly, "ant." Eight of the species were based on specimens from "*America meridionali*," that is, South America: (1) *Formica atrata* (in modern classification, *Cephalotes atratus*, the arboreal "turtle ant"); (2) *Formica cephalotes* (the leafcutter ant *Atta cephalotes*); (3) *Formica sexdens* (the leafcutter ant *Atta sexdens*); (4) *Formica foetida* (possibly a *Dolichoderus* species or some other dolichoderine with odorous secretions but more likely the New World tropical myrmicine *Pheidole jelskii*, a ubiquitous and extremely abundant myrmicine, whose soldier caste produces the strong fetid odor of skatole as a defense substance); and (5) *Formica haematoda* (*Odontomachus haematodus*, a large ponerine ant with long, traplike jaws). These five species are so abundant and conspicuous that they are among the first ants encountered even by beginning naturalists. Three of the South American forms described by Linnaeus are his "lost species": (6) *Formica bidens*, (7) *Formica omnivora*, and (8) *Formica saccharivora*. Authenticated specimens of these species have not been found in the Linnaean collections at London and Stockholm, and their identity remains unknown.

Linnaeus' first, brief attempt at binomial ant taxonomy was of little help to Mutis. The descriptions in *Systema Naturae* were sparse in the extreme, an unavoidable circumstance, because Linnaeus was trying to cover every kind of plant and animal in the world. Typical is the diagnostic of *F. omnivora*, allegedly the plague ants that vexed the West Indies in the sixteenth and eighteenth centuries. Firsthand descriptions of those who witnessed the plagues point to the fire ant, *Solenopsis geminata* (sixteenth century), and *Pheidole megacephala* (eighteenth century) as the pest species.[6] The specimens that Linnaeus had in hand may have been *P. megacephala*, but unfortunately, the specimens no longer exist. This is all Linnaeus had to say about *F. omnivora*:

F. thorace bidentato, petiolo binodoso, corpore testaceo, abdomine fusco.

Brown. jam. 440. Formica domestica omnivora.

Habitat in America *meridionali, consumens & dilacerans omnia cibaria*.

Thorax *lævis, adspersus punctis vix conspicuis elevatis*. Abdomen *fuscum, pilis albis vix manifestis*. Petiolus *nodis duobus teretiusculis*. Corpus *testaceum, minutissimum*.

At present, more than 14,000 living species of ants are known worldwide, of which at least a quarter occur in Central and South America. Hundreds among them might fit the diagnoses of Linnaeus' other lost species. Colombia is one of Earth's "megadiversity" countries, with a fauna and flora rivaled in richness only by Brazil. It is not unusual to find 200 or more ant species in a few square kilometers of natural terrestrial habitat, some of which remain undiagnosed and nameless in the twenty-first century.

Arriving on the edge of the great unknown forty years before Humboldt, seventy years before Charles Darwin, and nearly a century before Henry Walter Bates and Alfred Russel Wallace, young Mutis had no realistic concept of the immensity of the world he had chosen to explore. However, that may have been to his advantage in one respect. Keenly responsive to Linnaeus' request, he was determined to devise some sort of classification scheme on his own to begin investigating the ants of South America. He knew that if he could not tell one species from another, and if he failed to use consistent names to denote the ants in his notebooks, he had no chance of building a coherent account.

It is curious nonetheless that Mutis, an experienced taxonomist faced with this obvious challenge, did not follow Linnaeus by diagnosing his ants and termites and giving them two-part Latinized names. The only exception in his published correspondence is the "vixen ant," which he literally transcribed into *Formica vulpecula*. Even in this case, the species cannot be identified. The single specimen he found was a queen, possibly a *Monomorium* or *Tranopelta* in present-day classification. Mutis picked her up evidently after she had flown from her mother nest, mated, dropped her dehiscent wings, and was searching for a nest site to start a new colony. We do not hear of *F. vulpecula* again.

Nevertheless, the diaries of José Celestino Mutis, which were put away two centuries ago and now at last analyzed for their content on ants, [7] are invaluable in showing how a scientific discipline comes into existence, through zigzag steps. Mutis, working in isolation, not only was the first scientist to study ants in

the New World but also was one of only three in the entire modern world (the other two were the aforementioned René de Réaumur of France and the Reverend William Gould of England; none knew of the work of the others). In his diaries, he records his personal reflections. He experiences his emotions. He is thankful for the help he received (except to his servants, who just follow his orders). He is proud of the procedures he invents. He is frustrated by his many failures and thrilled by his discoveries.

Mutis was someone we would have liked to know in person if the barrier of time could be removed. His diaries reveal an honest man, privately as well as publicly—the first and absolute requirement of a successful scientist. He was truly modern in his uncompromising objectivity. Even though pre-Linnaean or primitively Linnaean in his taxonomy and virtually without guidelines, he operated strictly on the basis of the phenomena he could personally observe. He took clues from folklore, but he never entered them in the conclusions drawn in his diaries. He created hypotheses for testing, but he never trifled with fantasy. Keeping multiple hypotheses in mind, he returned repeatedly to the field to connect the dots and construct the best possible explanations he could.

The formal treatises that Mutis wrote may never be found. Sometime between 1765 and 1770, in a letter to a professor of medicine in Spain, he expressed his wish to write a book entitled *Natura, Mores, Oeconomia, Formicarum Americae*.Sometime between 1765 and 1770, Mutis sent observations that may have had that title, but they were lost in transit. In 1770, he wrote Linnaeus to repeat his earlier expressed desire to be a member of the Academy of Sciences of Uppsala:

> I can no longer conceal from you how much I wish to be associated with the illustrious members of the Society of Uppsala.

However, and oddly, no mention was made of the treatise on ants. In a subsequent letter, written on June 6, 1773, and the last-known letter Linnaeus received from Mutis, he announced an upcoming trip to Sweden by his own student Clemente Ruiz Pavón, who would bring, he said, a catalog of the plants of Santa Fe de Bogotá. Again, no mention was made of a treatise on ants.

In 1777, Mutis moved to the mines of Cerro del Sapo (Hill of the Toad), located near Ibagué in the Valle de San Juan. There he was to live for the next six years. Its ruins can still be seen amid the more or less natural environment in which he worked. At Cerro del Sapo, Mutis took up his studies of ants a second time and more intensely than in any other period in his life. This locality,

situated in lowland tropical dry forest, teemed with insects of great variety. It was, Mutis wrote,

> the court and center of all the American ants.

In the diary notes of that period, most of his known observations and thoughts about ants are found.

A disciple of Mutis, Pedro Fermín de Vargas, described the locale in 1805:

> The spot which he chose for his ordinary residence was truly romantic. His dwelling-house stood upon an acclivity commanding the most enchanting prospects over that extensive valley, through which the river Luisa winds its devious course: the groves of palm-trees, and all the rural scenery in the vale below, surrounded by a chain of hills that gradually rise one above the other, until they are lost among the clouds, afford a spectacle at once pleasing and romantic.[8]

His mentor Linnaeus died in 1778. But Mutis was undeterred. We know from his correspondence with the Swedish naturalists Pehr Jonas Bergius and Gustav Paykull, as well as Consul Gahn in Cádiz, that he had begun a new treatise on ants to replace the one lost. He still dreamed of membership in the Swedish academies, and finally, on November 17, 1784, he was elected to the academy at Stockholm. The next year, around the time he learned of this honor, he promised in a letter to send the new treatise to Paykull:

> Once I have completed this study I will send it to you.

This is, however, Mutis' last reference to the subject of which we have record. Neither Paykull's bibliography nor his letters conserved in the National Archives of Sweden contain any reference to Mutis or a manuscript on ants.

So, was there ever a second treatise? Despite Mutis' apparent silence on the matter, other sources confirm its existence. The first reference to it is from 1800, during Mutis' lifetime. A report by Antonio Josef Cavanilles,[9] director of the Botanical Garden of Madrid, includes a short description of its contents. From this one record, we can deduce the existence of the treatise and the date it was written. The information about the treatise was conveyed to Cavanilles by Mutis' student Francisco Antonio Zea, who was deported to Spain from the New Kingdom of Granada in 1795 for revolutionary activity. Therefore, the treatise

had to be written between 1785 (letter to Paykull) and 1795 (deportation of Zea).

In a letter to Humboldt,[10] Mariano Lagasca, who had been director of the Botanical Garden of Madrid, stated that the treatise never reached the Garden. Yet according to a handwritten note found among the personal papers of Marcos Jiménez de la Espada,[11] zoologist and historian of the naturalists of the West Indies, is this reference:

> Lagasca says that papers of Mutis about zoology, minerology, and geography may be kept among the geographical notes that were taken to the General Staff of the Army in 1817.

Further, in a note published in 1872, Espada states[12] that there was an unpublished treatise by Mutis about the ants and termites of America. According to Leoncio López-Ocón (personal communication, April 2006), a researcher of the History Institute of the Spanish National Research Council and an expert on Espada, it is almost certain that Espada saw the manuscript on ants, probably in Madrid. A similar opinion was expressed in 1868 by Pérez Arcas,[13] professor of zoology and cofounder with Espada of the Royal Spanish Society of Natural History, but noting that it was a published treatise. A third opinion was offered in 1886–1887 by Rodríguez Mourelo,[14] a professor of chemistry, who also knew Espada personally.

It can be established that a substantial portion of Mutis' personal library was lost during the first years following his death, which coincided with the beginning of the revolutionary events in New Granada. A document dated to the year 1816 in the General Archives of the Indies of Seville[15] gives the size of the inventory at near 4,000 items. After his visit to Mutis in Santa Fe de Bogotá in 1801, Humboldt described the collection as the largest he had ever seen, except for the one owned by Joseph Banks. A study by one of us (Gómez Durán) of more than 700 titles of the science and natural history section of the documents uncovered do not mention the ant treatise.

A final clue concerning the twisting trail of the lost treatise is a statement by the great Spanish historian and philologist Menéndez Pelayo[16] in his *La ciencia española* (1887–1888). Pelayo states that Jorge Tadeo Lozano had written a work called *Tratado de las hormigas de Nueva Granada* (*Treatise on the Ants of New Granada*). Pelayo did not specify whether the item was an unpublished manuscript or a published book. The provenance of this surprising note may be the following. When Mutis died in 1808, the Royal Expedition in the Kingdom

of New Granada was split into four divisions: (1) administration and drawings (headed by Salvador Rizo), (2) botany (Sinforoso Mutis, a nephew of José Celestino), (3) astronomy and geography (Francisco José de Caldas), and (4) zoology (Jorge Tadeo Lozano). Tadeo Lozano was in charge of preparing Mutis' zoological works, as well as his own *Fauna Cundinamarquesa*. Some papers of the latter, in particular on snakes, appeared in the *Semanario de Nueva Granada* (1808–1810). Otherwise, all of the zoological drawings and many of the manuscripts of the Royal Expedition appear to have been lost. Yet it may be possible that Lozano, who knew nothing about these insects, possessed a copy of Mutis' *Treatise on the Ants of New Granada*. In 1816, the Royal Expedition was terminated, and Lozano, Caldas, and Rizo were executed by the Spanish Army for revolutionary activities. The question remains, How did Menéndez Pelayo know of such a treatise, and why did he ascribe it to Lozano? More important, does a copy still exist?

CHAPTER 3

The Scientific Contributions of José Celestino Mutis

José Celestino Mutis' overall contributions to scientific natural history are considerable, extending well beyond his studies in systematic botany; and they are sufficient, in our view, to provide the great Spaniard a niche in the pantheon alongside Alexander von Humboldt and other early explorer naturalists of the New World. Yet Mutis has hitherto been largely unknown outside Colombia and Spain and celebrated only in the Spanish language. Before presenting our reconstruction of the lost treatises, it is important to summarize his contributions.

Mutis was one of the first scholars to conduct a sustained course of study in the scientific natural history of the Western Hemisphere. Before him came the aforementioned Maria Sibylla Merian (1647–1717), the famous German-born naturalist and illustrator. Her special artistic contribution was the accurate depiction of insects, and her main scientific contribution was the demonstration of the widespread occurrence of complete metamorphosis (egg-larva-pupa-adult) among insects. In 1699, the city of Amsterdam financed Merian's expedition to the Dutch colony of Suriname to collect and paint natural history specimens. For two years, she pursued these activities with distinction. Her most notable production from this period was the book *Metamorphosis Insectorum Surinamensium*.[1]

Another, lesser-known pioneer in South American natural history was Daniel Rolander (1725–1793). One of the seventeen men referred to as Linnaeus' "apostles," Rolander was able to finance his own travel to Suriname as the tutor of the children of a wealthy Dutch plantation owner. Sickly to start with, and understandably fearful of tropical diseases, Rolander remained in the colony for only seven months, from June 1755 to January 1756. During this period, it seems that he did relatively little tutoring but a large amount of specimen collecting and note taking on natural history. Unfortunately for his career, Rolander, on his return to Uppsala, had an argument with Linnaeus over his future employment and refused to turn over his collections. Whereupon Linnaeus broke into his

room and stole the specimens he most wanted to study. The rift was never healed, and Rolander's collections were eventually widely scattered. Sadly, his 700 pages of notes, written in difficult Latin, were ignored. Only recently has the manuscript been translated and made available for study. In a manner parallel to the Mutis epic, it has proved to be filled with original and generally accurate observations.[2]

Although Maria Sibylla Merian and Daniel Rolander were remarkable people who made significant scientific discoveries, neither came close to Mutis in the magnitude of their contributions to the scientific natural history of South America.

Moreover, in the length of his stay in South America, in his abiding devotion to the land he explored, in the breadth of his contributions to botany, astronomy, and now as revealed to entomology, Mutis was unique among eighteenth-century explorers of the continent. He was to be equaled or exceeded in the early nineteenth century only by Humboldt.

As we have learned from his diaries and correspondence and will report hereafter, Mutis was the first to conduct scientific studies of ants and termites in the Western Hemisphere. It was a good choice for a pioneering entomologist. Ants and termites are the dominant insects of South America, as they are throughout nearly all the rest of the world. Therefore, they profoundly affect the functioning of the ecosystems in which they live, and in tropical America at least, they are the leading economic pests.

Ants and termites, along with many species of bees and wasps, are the most social of all animals. In 1761, when Mutis first traveled up the Magdalena, the domestic honeybee (*Apis mellifera*) was the only social insect being studied with any exactitude. Ants and termites were largely ignored as worthy subjects of scientific research. That was a superb opportunity lost, for they represent among their numerous species every gradation, from the simplest, most primitive forms of colonial behavior to the most complex of any animals on Earth. As Mutis soon discovered, the immense diversity of the South American ants contains two "superstars," whose huge colonies and bizarre behavior attract the attention of even the most casual visitor to the countryside. They are, first, the leafcutters of the genus *Atta*, which collect large quantities of fresh vegetation to serve as substrate for fungus gardens within the nests; and, second, the army ants of the genus *Eciton*, whose legions of marauding foragers prey on other insects and whose colonies emigrate at frequent intervals from one bivouac site to the next.

Over the years, Mutis diligently addressed the natural history of these two kinds of ants in particular. He collected enough data to provide the broad outlines of their colony life cycles, food, nesting habits, and foraging patterns. He was also the first to distinguish the physical subcastes into which the worker castes are divided, and he came to understand how the subcastes divide labor. He observed communication among the workers, although he remained unaware that most of the signals used are exocrine secretions (pheromones) passed from one ant to another and read by smell or taste. It was not until the late twentieth century, and the development of microanalytic chemistry, that this phenomenon came to be well understood.

We will now present Mutis' observations in his own words, along with our interpretations of their meaning. For the most part, the material will be presented chronologically and then species by species. In some cases, the species, or at least the genera to which they belong, can be identified with reasonable certainty. In other cases, we will offer educated guesses, the best that can be done with existing knowledge.

CHAPTER 4

Mutis Seeks Advice

It is especially interesting to learn from José Celestino Mutis what ordinary people in such a remote place and era, uninitiated in any way to scientific natural history, saw in the ants and termites that swarmed about them. Mutis fortunately recorded some of what he heard when he sought advice from his new friends. What follows is Mutis' own account, with our commentary.

JULY 6, 1761 (SANTA FE DE BOGOTÁ)

> I had a long conversation with Mr. Gregorio Londoño, a fellow who is quite well informed about this country because of his curiosity and talents, and having been employed in such tropical lands as this for a long time. When I asked about ants, he promised to give me information about several species that he had discovered and their behavior. He told me that the destroyers of trees [the arrieras, or *Atta* leafcutter ants] always harm the distant trees, so that to know those responsible for the harm the farmers have to observe the land that is a bit distant from the crop and destroy the anthills that are there.
>
> He also told me that those kinds of ants fond of candy are so expert that even if the candy is suspended in the air, in the middle of a room, they contrive a way to take possession of it.

The expression "destroyers of trees" was no exaggeration. It refers to the mule-train ants (arriera ants), members of the genus *Atta*, which we nowadays call leafcutter ants. In 1761, these superabundant insects were major pests of many kinds of the cultivated crops of the New Kingdom of Granada. And nothing has changed. Today, the *Atta* leafcutters remain the most destructive agricultural pests throughout South America.

Mutis' new friend Gregorio Londoño sounds like a self-taught but competent rural naturalist of a kind still common in most countries around the world. His

observation that leafcutters often defoliate distant trees in preference to those closer to the nests has been confirmed by modern-day studies. The phenomenon would be a form of instinctive resource conservation. But it could equally well be explained as a result of the leafcutter foragers searching over long distances for the most succulent leaves and flowers.

The “candy-seeking ant,” cited by Mutis, could be any one of several species. One of the best candidates is the “crazy ant,” *Paratrechina longicornis*, an invasive species of possibly African origin. Noted for its extremely slender workers and its swift, zigzag running, *P. longicornis* is today one of the most widespread and abundant of all tropical tramp ant species in the world. Its colonies travel easily from port to port by hitchhiking in cargo. It is also among the ant species adapted to live in extreme habitats in which few other ant species are able to survive, including beaches, unvegetated rock outcrops, sidewalks, and houses. *Paratrechina longicornis* colonies survive in such places by specializing on temporary nest sites, such as a pile of dry leaves or a crack in a concrete sea wall. The workers swiftly evacuate the nests with even a slight disturbance. They are also more efficient than most other ant species in finding food and recruiting nestmates with the aid of short-lived odor trails. Could Mutis have seen them? One of us (E. O. Wilson), putting out sugar baits on the floor of an open-air restaurant in Mutis’ hometown of Mariquita, was not surprised to find they attracted swarms of this species within a half hour.

A second candidate for Mutis’ candy-seeking ant is *Pheidole megacephala*, an especially onerous pest ant introduced into the American Tropics from Africa. This species has recently been identified as the most likely eighteenth-century “plague” ant that often invaded houses. In addition, probably in symbiosis with mealybugs or some other sapsucking insects, it devastated sugarcane fields in Barbados, Grenada, and Martinique in the Lesser Antilles.[1] The plague peaked during 1760–1770, at the time Mutis began his studies on the ants of Colombia. Today, *P. megacephala*, given the common name “bigheaded ant” for the large head size of its soldier caste, is a major pest species in tropical regions around the world. These ants, like the crazy ants, are famous for their ability to invade houses and find food. They are also omnivorous. The small, slender minor workers scout independently for food items, and almost any edible particle attracts them: dead insects, table scraps, syrup, or almost anything that contains protein, fat, or sugar. They are notorious for destroying collections of dead insects left unprotected in laboratories and museums. If a particle is too large for a lone scout worker to carry, she leaves it and runs homeward, laying a trail from her poison gland. This substance, paid out through the tip of the scout’s

abdomen, attracts a force of nestmates. If the food source is large, others arriving at the scene add trail substances of their own, and the target area is soon teeming with hungry ants. Some of the colony’s large-headed soldiers come along as a protective force and perhaps to help cut large solids into pieces small enough for the minors to carry.

CHAPTER 5

Mutis Begins His Study of Ants

OCTOBER 29, 1761 (SANTA FE DE BOGOTÁ)

> After questioning Mrs. Mariana Dávila about the nearest place where I could go in search for ants, she told me that Trapiche de Serna was a very appropriate site for observing these tiny insects, as she had been amused to do while she was living there. She noticed, she said, that when the ants came out in very orderly squadrons to pick up their food, they were governed by bigger ants positioned at intervals, and then, ultimately by a yet bigger one. Also, while enjoying this delightful spectacle, she noticed several times that certain ants moved away from the regular path (as explorers) and returned to meet with the bigger ones. These then consulted with the largest one just mentioned—and suddenly the whole squadron changed direction, turning to the paths that the explorers had just left.
>
> She also reported that the spectacle of the hunter ants [army ants] was no less amusing. And said that she was afraid when she first saw this beautiful squadron suddenly coming into the house where she lived. Others warned her to leave the house at once in order to avoid the inevitable fright she would feel at the sight of all the little animals hidden in the cottage rooms emerging and leaving—because, when these creatures are harassed by the hunters, they escape hurriedly, hitting or attacking whatever is an obstacle to their flight. Despite having been warned in advance, she could not avoid the jump of a small lizard that fell on her shoulder while escaping from the hunters. These ants completely clear the rooms of any animal, heading for another house as soon as they have finished looting the first one.
>
> These phenomena are worthy of the most careful attention and study.

Mutis has thus been quickly attracted to the leafcutter and army ants, the two kinds that most dramatically distinguish the ant fauna of the New World Tropics. Their abundance, combined with the huge populations of the colonies and the conspicuous behavior of the worker castes, capture the attention of even the most casual observer. The arriera (mule-train) ants, the first of the two kinds

mentioned by Mariana Dávila, now known worldwide by the English vernacular names leafcutter, or gardener ants, compose the genera *Atta* and *Acromyrmex*. In Mutis' time, real mule-trains were a common means of overland transport in the mountainous terrain of the New Kingdom of Granada. The entomological allusion is to the long columns of worker ants bearing fresh fragments of leaves, flowers, and other plant parts from the field back to their nests. These long lines, formed by many hundreds of thousands of ants, move in an orderly fashion along conspicuous "highways," paths the width of a hand that the ants clear of seedlings and falling debris.

The second kind of ants mentioned by Mrs. Dávila, the "hunters," are known nowadays (in English) as army ants. The commonest species with larger workers belong to the genus *Eciton*. Most notable among these are the swarm raiders (*Eciton burchelli*). Each colony dispatches hundreds of thousands of workers all at the same time. The squadrons spread laterally as they move outward from the bivouac sites, forming a spread of running ants shaped like a reversed wedge, widest along the edge of the advancing front. The fierce workers flush every kind of animal in their path, capturing for food those they can seize and pin down, rejecting only a few kinds that are heavily armored or protected by toxic chemical defenses.

Often the armies pass through small human dwellings in their pathways, as described by Mrs. Dávila. For the people inside who are forced to leave for a short while, the onslaughts are a blessing. The ants clean out cockroaches and other house pests better than professional exterminators. Their services are free, and they leave behind no trace of their visits.

JANUARY 19, 1763 (CARTAGENA DE INDIAS)[1]

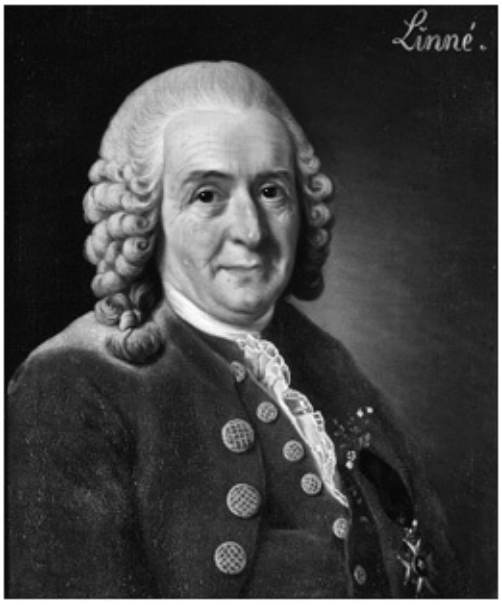
> On this day my Lady Mrs. Juana gave me a beautiful collection of ants, and we decided that I would stay in her village for 4 or 5 months while I started my field studies, with the goal of making a wide collection of natural history specimens. She also told me that while in the vicinity I would be able to collect a species of cinnamon tree, which is very distant [from my residence], and also samples of several other species of spice-bearing plants. At this point, I cannot express enough gratitude to this Lady, who is largely inclined to attend to people's needs, and was especially so to my own plans and particular interests. I am extremely grateful for all her sincere offers of future help, which I hope to accept in

the future.

However, of the helpful Mrs. Juana, we will hear no more.

JANUARY 31, 1763 (CARTAGENA DE INDIAS)

On this day, around the table, I heard Inquisitor Mr. Josef Humerez say that he thought that the *Theria*c flower is a very effective remedy against the *comejenes* [termites] that are already beginning to spread. This conjecture is supported by a recent story I was assured to be true. In a drawer filled with clothes there was, by chance, a jar of Theriac. The drawer, it was believed, had not been touched for a long time, and when it was finally opened, all the clothes inside were found to have been consumed by the comejenes—yet, much to the surprise of everyone present, a large number of comejenes were found dead lying around the jar of Theriac.



Carl Linnaeus, in 1775. His suggestion to José Celestino Mutis launched the first scientific study of ants in the Americas.

The *comejenes* are termites, of which a great variety occur in northern South America. The species described here can only be guessed. Termites, sometimes called white ants, are not even remotely related to ants in the insect evolutionary

tree. Their closest-living relatives are instead the cockroaches. Put another way, while ants are phylogenetically social wasps, termites are phylogenetically social protocockroaches. The “proto-” is added because termites are not directly descended from cockroaches of modern types but share a close common ancestry that dates back to the early Mesozoic era.

FEBRUARY 1, 1763 (CARTAGENA DE INDIAS)

> Very early in the morning Mr. Gregorio del Pozo paid his last visit in order to receive instructions for work in the savannas of Tolú, to where he was to travel the following day. When departing for this visit, he told me about the wonderful virtues of some herbs and—what I found most interesting—the small eggs [eggs, larvae, and pupae] of a certain caste of ants. I urged him to write everything down for me. I requested my nice old man to undertake some tasks for me, and he showed great pleasure in serving me. I asked him to gather various objects of natural history; but I was most eager to get a collection of ants, which are not lacking in the savannas.

With his “nice old man,” Mutis has adopted the practice of his mentor Carl Linnaeus of urging others to collect and write notes on species when they visited distant places. In this case, the destination is the savanna around the Colombian port town of Tolú. The “eggs” Mutis refers to are undoubtedly a combination of eggs, larvae, and pupae, usually white to light brown and easy to find in nests of any kind of ant. Usually, these immature forms are the offspring of the queen ant, but in some species, workers are able to add to the colony brood a few offspring of their own.

CHAPTER 6

Ants Are Transported by Ships

Small, sugar-loving ants have been carried on ships around the world for centuries, often disembarking to become onshore house pests. The invasives include the minuscule Pharaoh's ant, *Monomorium pharaonis*, and the equally tiny "sugar ant," *Tapinoma melanocephalum*. Both of these cosmopolitan "tramp" species are Old World tropical in origin. *Monomorium pharaonis* is an especially pernicious pest. Its colonies are spawned by multiple queens that mate and reproduce within the mother nest. They are also adapted to dry habitats and can spread into crevices in every warm part of a building. In large structures such as apartment houses and hospitals, the colony populations can grow into the millions.

FEBRUARY 3, 1763 (CARTAGENA DE INDIAS)

> I heard Mr. Joseph Vasco, Mayor of the Order of the Squadron, say that on board ships there lives a smaller species of ant that compensates for the damage they cause in the confectionary by way of other services they perform. He suggested commissioning several of the personnel on board to collect these insects for my treatise.

By "way of other utilities," Mayor Vasco evidently means the control of noxious insect pests, such as cockroaches. The following entry supports this supposition.

MAY 10, 1763 (CARTAGENA DE INDIAS)

> Some days ago I had asked Mr. Manuel Guin de Torres to pick up some ovaries [egg cluster or package] of cockroaches for me, and to record carefully in which day the mother deposited them. That would allow me

to discover how long it takes for the formation of a new generation. There was a problem however of knowing whether the development of the small offspring might suffer some damage when they are removed from the place where the mother deposits them and to which they are strongly stuck. Because the information I needed could only be settled by experimentation, I begged him again not to desist from the duty that he had taken upon himself. And sure enough, today I received, handed to me by an intermediary, two ovaries [egg packages] that Mr. Manuel had sent me from his ship, the El Dichoso. When I see him, I will make sure that all the procedures were followed necessary to make a proper study. I have put two ovaries outdoors, inside a glass container, so that fresh air is not lacking. In due course, I will report everything that happens. It will be necessary to watch the glass frequently so that the ants do not attack them. As with everything, ants do not neglect these [ovaries]; on the contrary, they show a big liking for them. In the ships, they constitute a special population that somehow moderates the propagation of the cockroaches, by means of the damage inflicted on them.

CHAPTER 7

Ant Plants and Plant Ants

Mutis discovers a remarkable symbiosis the hard way.

PROBABLY BEFORE 1770 (VEGA DEL GUADUAL)[1]

One hot day in the Vega del Guadual, when I suffered from the [blazing] sun, I paused to stand with my shotgun beneath a somewhat thick-topped pyramidal tree. In a short time, I found myself covered with some red ants, stinging me so fiercely that, with difficulty, I first took off my shoes in order to get undressed, and then took off my shirt, beating my whole body with it [to shake off the ants]. However, since there were so many I had no other choice but to go into the river, shaking my clothes once I pulled them free. Returning to the house, and feeling inflamed all over, I told my story. The slave there told me that they were ants of *palo santo* [holy stick]. Accompanied by this mulatto I came back to the same place, where there were many trees of the same species and, in the open fields nearby, many medium-sized trees [of the same species] one half to three quarters of a *vara* [old Spanish unit of length: 1 vara = 0.84 meter] high, and one vara wide, without any leaf, resembling a wicker. When you touch the stems with your hand, a large number of ants pour out through some imperceptibly tiny holes, then swarm all over the stem with the same speed they show in stinging you. Thinking that the plant might be very beneficial, I was told by an Indian woman that the stems of the plant, as well as the liquid from its leaves and bark, cures the Gallic humor [syphilis]. I tried some of this material on an old Indian woman that I had in my house, who was very much distressed by such illness, in addition to leprosy of Carate [a kind of dermatitis], and wounds. In a little over a month after taking the palo santo medicine, she was free of all her sickness, and so agile that she survived many years.

The stinging ants, judging from this account of their behavior and of their arboreal nests, were surely members of the genus *Pseudomyrmex*. Further, their distinctive color points to the species *Pseudomyrmex triplarinus*, which lives as a symbiont on *Triplaris*, the small tree known in Colombia today as the palo santo. These ants are so aggressive and fast moving that just to brush against a tree occupied by them is comparable to being brushed by a nettle.[2]

An important principle that has emerged from observations of this kind is coevolution, the close adaptation of one species (the ant) to the other species (the plant). One of the symbionts can be parasitic or both can be mutually beneficial. In the latter case, each species tends to evolve traits of anatomy and behavior that accommodate its partner. Since this account almost 250 years ago, many such mutualistic symbioses have been discovered—although few by such a painful accident. The ants protect their plant hosts against herbivorous insects and other enemies, and the plants offer living quarters and in some cases specialized food, such as nutritious corpuscles, for their ant guests.

In general, the more dependent the ant species is to its host plant species, the more aggressive are its worker caste to invaders. Such tight reciprocity has been discovered in a large array of New World tropical trees and shrubs in addition to *Triplaris* and in partnership with ant species belonging to several genera. The latter include closely adapted species of *Allomerus*, *Azteca*, *Camponotus*, *Crematogaster*, and *Pheidole*. The conspicuous aggressiveness of such ants —*Camponotus femoratus* may be the most violently aggressive in the ant world —may occur because the colonies have no place to retreat. They must repel invaders from the plants in which they live, or perish.

CHAPTER 8

Mutis Learns about the Mule-Train (Leafcutter) Ants

José Celestino Mutis had a resolute objectivity and an unusual ability to describe phenomena of which neither he nor anyone else had prior knowledge from the literature. The following account, part of a tract entitled "Essay of the First Period Regarding the Insects, Birds, Ophidians, Plants and Fossils of the New Kingdom of Granada, Particularly in Warm Lands," was probably written between 1765 and 1775.[1] He addressed his subject with a minimum of speculation and in clear language immediately understandable to the modern reader.

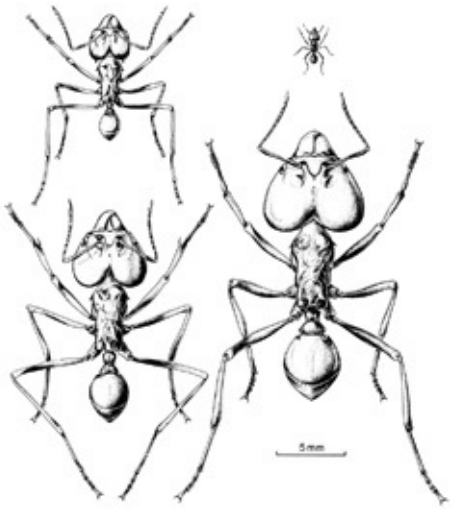
> Tijereta: it is an eagle that is thicker than a pigeon; when flying it shows a white stripe on its wings, and its unfolded tail looks like a Turkish moon or hocking knife. These birds gather in big flocks after the heavy showers of May and November, when the mother ants start their flight for the propagation of anthills. The eagles maneuver continuously, picking the ants out of the air, then instantly cutting off and flying away with their belly [the gaster, last major body segment], which is the soft and buttery part, while letting the legs, as well as the chest and the head, fall to the ground…. Ants: the number of species can reach twenty … arriera [leafcutter ants]: they are a plague that, before too long, will require help from the government so that the arrieras do not finish making unusable all the arable land of the tropical lowlands. They excavate the soil, while eating all the green vegetation in the sown lands, and [carrying away the vegetation] with intelligence and speed. The nests, which the ants dig below the ground, occupy a circuit of 4 to 6 *varas* in diameter. In this space all the floor is weak, especially after heavy showers, because [the subterranean part] is made of small vaults and chambers, one on top of the other, with passages and galleries to communicate. There, the ants store all the forage they can collect—at the expense of the farmland and in order to protect the litters of innumerable

worms [larvae] some of which develop, in due course, either into muletos [workers] destined solely for labor, or else into winged females [queens, and probably also males]; the latter leave the nests only in the rainy season, at which time they found anthills and propagate the species. The nests [often] settle in paths, making the ground sink and thus pose a serious risk for the horses and the load they carry. They also penetrate cracks in houses and in the foundations of walls, which they cause to fall down. The seeds sown on the lands are destroyed. In case the seeds do not get wiped out on the spot, then as soon as they begin to sprout, they suffer a new raid, which results this time in final devastation and utter ruin. The ants also climb up into the crop larders or else undermine its foundations, opening holes that burst onto the floor, allowing the ants to loot the grain and vegetables lying there. This insect, so tiny and despised by man that he does not regard it to be worthy of a thorough and meaningful persecution, is conquering much of this country and expelling the farmers from large sections of farmland, by turning it into infertile and unused wasteland. Streets, squares, and churches are not safe. An orchard cannot be maintained unless bananas or other coarse vegetables whose leaves the ants do not desire are grown. Each anthill contains millions of them, and their hills are not far between. When the arriera explorers and scouts announce, with reciprocal touches of their antennae, the existence of an orchard or a sown land, ants advance out of the west in a single column many individuals across and at full speed. They travel at five varas per minute, with more than a thousand passing by a particular spot. If they are discovered and suppressed, the arrieras return at the early hours of night, at the time of the crowing of the rooster, and at dawn. When caught in a heavy rainfall, they halt and take cover in scrub or underneath a tree trunk. Fortunately [for people], they do not know how to overcome the pits and spurts of water used [by farmers] to oppose them. But then they examine the narrowest side and there accumulate lots of their bounty, which, consisting of pieces of leaves piled close together, turn out to be a safe crossing for the whole column. Or else, if the surface is firm and consistent, they drill a hole that breaks open on the opposite side. By some means or other, they manage to overcome whatever obstacle is placed to stop them.

In order to destroy one of the entrenchments or nests [of the leafcutter ants], water or fire is needed, a treatment that costs no less than two pesos. It would be different if the authorities rule on this subject, which is becoming of the greatest importance day by day. These two pesos is the price of the time spent and blood spilled that the digger who dares to undertake such a task has to spend. No sooner has he made the first stroke with his shovel then the alarm sounds underground; the

signal spreads through all the chambers and storerooms, and all of a sudden the whole anthill is in a state of agitation and flurry, attacking the intruder with rage and swiftness. The first assaults take place on the legs of the digger. The ants then climb up his body and attack even his head. They pinch and they bite and they cut his skin deep enough to draw blood. The poor man kicks, shakes and maneuvers to the right and to the left. At times, he retreats to take a breath and remove the ones that bother him the most. His heated body and the abundant sweat show the terrible ordeal he has been through. If he regains the courage to repeat the attack, they receive him with more bravery of their own. Fresh clusters cling to him with such tenacity that he has to remove his shirt so as to rub them away, or to pull out one by one the nailing spikes [closed mandibles] that remain fixed after the rest of the body has been torn away.

The greatest cuts are made by the big-headed, or caporals, which, having sharper and proportionately stronger knifelike jaws, lance the flesh until blood spills. The scene usually lasts two or more hours and never ends until a fire is used to burn them, or a flood of water is applied to sweep them away and imprison them between clods of mud and earth. Meanwhile the *cubicularias* [servants of gentlemen and princes] and *camaristas* [maidservants of queens and princesses] have carried the progeny away from the point of intrusion and into hidden sites, from where one or more anthills will in short time renew the raids.



The worker castes of a leafcutter ant colony. The species depicted is *Atta laevigata*. From G. F. Oster and E. O. Wilson, *Caste and Ecology in the Social Insects* (Princeton, NJ: Princeton University Press, 1978).

In this essay, which might have been part of his first lost treatise, Mutis also recounts an attack by nightjars (bird family Caprimulgidae) on the immense aerial swarms formed by virgin queens and, we now know, males of the arriera (leafcutter) ants. The queens and males have left their mother nests to mate. The ponderous queens, the largest ants in the world, are joined by at least comparable numbers of males—not yet distinguished as such in this early account by Mutis—that have emerged from the same or other nests in the vicinity. The mating takes place in flight, and quickly, so that as many as five males are able to

inseminate each queen. The queen then stores the hundreds of millions of sperm thus acquired in her spermatheca, a small sac in her abdomen connected to the oviduct. From this organ, the sperm are paid out, one at a time through a valve the queen opens or closes. In the Hymenoptera as a whole, including the ants, fertilized eggs give rise to a female and unfertilized eggs to a male. The queen thus determines the sex of her offspring by either opening the valve to pass through a sperm as each egg moves down the oviduct, or closing it to stop sperm from reaching the egg.

As Mutis came to understand very well, the arriera nuptial flight is the beginning of the colony life cycle. The inseminated queen descends to the ground, painlessly breaks off her four membranous wings, and starts to explore the terrain. After finding a patch of soft, open soil, she excavates a vertical gallery, which she enlarges at the bottom to create a small chamber. This retreat becomes the first element of the nest, which is destined to grow to an enormous size and where she will spend the rest of her life. In the first chamber, the queen raises her initial brood of sterile workers (muletos) who assist her in rearing other workers. Thus begins a period of rapid population growth. The workers add galleries, and chambers multiply until the nests reach the mature size, as described by Mutis.

Mutis further observes the nightjars[2] as they snatch the flying queens in the air and tear off their “bellies” and then sever the posteriormost major parts of the ant’s body, which are “soft and buttery.”[3] The nightjar allows the anterior two parts of the body—the head and thorax (“chest”)—to fall to the ground, uneaten. It is easy to understand why the birds select the gaster. This rear part of the body is packed with ovaries and fat reserves. Queen leafcutter ants that successfully excavate nests rear their first brood entirely with nutrients drawn from the fat bodies, plus the nutrients metabolized from her once powerful but now useless wing muscles. As a result, the young queens never have to leave the safety of their underground retreats after they descend to the bottom chambers.

Human beings also harvest leafcutter queen gasters for food, which are to this day common items in the rural markets of northern South America. Small quantities also reach the North American markets as novelty items. Cooked in oil, they have a passable, nutty flavor, although fragments of the indigestible outer chitinous skeleton stick between the teeth. This myrmecophagy (ant-eating) also occurred in Mutis’ time, and probably for millennia before. In his diary entry of October 1, 1777, he notes,

> I have not yet been able to see the arriera-winged mothers to verify if these will be the ones that some Indians very much like to fry, as do the Americans [Spanish colonists] of a few towns like Barichara. These people are scornfully nicknamed *comehormigas* (ant-eaters).

Mutis assumed, as did other early observers, that the arrieras consume the fragments of leaves they harvest. He thought the material was also fed to the young larvae ("worms") destined to grow into workers in the early colony and, later, into new queens ("mother ants"). In assessing their part of arriera biology, Mutis missed making a major discovery. The large chambers of the leafcutter nests are filled with fluffy, spongelike masses, whose significance he did not choose to investigate. In fact, the mysterious material appears not to have stirred his interest at all. It remained for Thomas Belt, in his classic 1874 *The Naturalist in Nicaragua*, to recognize the far stranger truth.[4] The spongy masses are gardens, built from fresh vegetation chewed and fertilized with anal droplets. The modified material is then used as a substrate to raise the symbiotic fungus on which the ants feed. Because of their remarkable habit, leafcutters are today often called gardener ants.

The leafcutter foragers also, it turns out, receive partial sustenance from fresh sap they drink while scissoring off leaf and flower fragments. So Mutis and other early naturalists were not entirely wrong to assume a vegetarian diet for the ants. The queen and larvae, however, are fed entirely by fungi grown on the vegetative material after it has been carried into the nest. The queen receives, in addition, eggs laid by her worker attendants. The gray coloration of the garden is imparted by the tangled masses of fungal hyphae. The garden fungus is a basidomycete, but its sporophore, with the typical stalk and cap of a mushroom, is seldom allowed by the ants to grow out of the hyphal mass.

To transfer the fungus from the mother nests to the new nests, the young leafcutter queens tuck a wad of hyphae into a small cavity, the infrabuccal pocket, located on the floor of their mouths. When they have finished excavating their incipient nest, they spit the hyphal wad onto the floor of the chamber and use it to start the new garden. They then fertilize the growing fungal hyphae with their own secretions and surplus eggs.

As the garden grows, the newly emerging workers take over its care. In so doing, they employ a variety of techniques to keep the fungus culture pure. They weed out hyphae of invading fungus species, and they spread fungicides from exocrine glands on their bodies, which are toxic to alien fungi but not to the

cultivated species. Finally, they dispense antibiotic effluents from friendly bacteria carried as a thick layer on the bottoms of the middle parts of their bodies. The chemicals dispersed by these symbionts inhibit alien fungi in the same manner as the exocrine secretions of the ants. They inhibit alien fungi but do not harm the domesticated species.

Mutis misses these phenomena in his report—not surprisingly, since other scientists did not discover many of them for another 200 years—but he is able to record the discovery of others. In his facts-only style, he makes his mark as a pioneer and wholly independent observer of the habits of the leafcutter ants. He recognizes that some workers scout for fresh vegetation, and that on discovering a desirable patch, they use signals to attract nestmates to the site. He observes that when a nest is seriously disturbed, for example, torn open by a shovel, an alarm signal passes through the colony, and almost immediately, angry ants rush to the source of the disturbance. Mutis appears to believe that the messages are by touch, and such remained the opinion of entomologists well into the twentieth century. It is now known that most ant communication is by pheromones, chemical substances secreted by one individual to be smelled or tasted by others.[5] In the early 1960s, microanalytic techniques revolutionized natural products chemistry and made it possible to identify as little as a millionth of a gram—the amount, it turns out, typically carried by a single ant. Alarm pheromones released from the mandibular glands of *Pogonomyrmex* harvester ants, for example, have been found to comprise a mix of the ketone methylheptanone and alcohol methylheptanol. A medley of farnasenes is used as a recruitment signal by fire ants.

The leafcutter ant trail pheromones, identified by twentieth-century elements, have turned out to be extraordinarily efficient in meeting the needs of workers when recruiting nestmates over long distances. The trail pheromone of the North American leafcutter *Atta texana*, methyl-4-methylpyrolle-2-carboxylate, is extraordinarily potent. Entomologists have estimated that 1 milligram of this substance, which seems scarcely a trace to human beings but is roughly the quantity found in an entire colony, if laid out with perfect efficiency, is enough to lead a worker three times around the world. Even more impressive is the estimate that a milligram from the South American grass-cutting leafcutter *Atta vollenweideri* would suffice to lead a worker sixty times around the earth. Even at such an extreme degree of dispersion, the ants would still have plenty of this substance to guide them during their long hypothetical journey: 1 milligram spread out in such world-girdling trail would still comprise 2 billion molecules per millimeter of the trail.[6]

Mutis was also the first observer to note the existence of subcastes among worker ants. The soldiers (caporals), whose 5-millimeter-wide heads are grotesquely large compared with the rest of their bodies, are especially effective in combating mammals and other large predators. The soldiers' sharp mandibles, closed by massive adductor muscles that swell their heads, easily slice through human skin. This defense system was vividly described by Mutis. Smaller workers, comprising, in Mutis' expression, *camaristas* (distinguished maidservants of queens and princesses) and *cubicularias* (those under the orders of princes and gentlemen), attend the immature forms and repair damaged parts of the nests.

CHAPTER 9

Unending Struggles against the Mule-Train Ants

José Celestino Mutis' account establishes that in the late 1700s the arriera ants were the leading crop pests of the New Kingdom of Granada. Their depredations remain unabated in many tropical regions of South America. So intense were the attacks of these well-organized insects on most forms of cultivated plants, so difficult were the huge colonies to eradicate, and so resilient were the colonies, unless all are completely eradicated, that Mutis despaired for the future of agriculture in the New Kingdom, and so it was also in Brazil, which Portuguese settlers called the Kingdom of the Ants and had a saying, "Either Brazil will conquer the ants or the ants will conquer Brazil."

To control the leafcutters, the citizens of the New Kingdom of Granada were reduced, as noted in Mutis' account, to the expensive and bloody technique of digging into the nests and killing the inhabitants by fire or flooding. An alternative method, described by Mutis elsewhere in his accounts, was planting among crop trees colonies of the cacotaya ant, described as a large, black stinging species that builds its nest on the sides of trees. The cacotaya chases away other ants, including the dreaded leafcutters. This species cannot be identified with certainty today, but it was most likely the ponerine *Pachycondyla villosa*, a formidable ant that nests in the trees of northern South America. A second, less likely candidate is *Pachycondyla goeldii*, which lives in ant gardens —masses of materials built up by the ants that harbor miniature arrays of epiphytes.

What is truly remarkable about the use of the cacotaya, despite the almost casual attention Mutis gives to the technique, is that it is one of the earliest-known examples of planting ant colonies for the biological control of insect pests. The only other recorded case is the transfer of weaver ant colonies (*Oecophylla smaragdina*) into the citrus groves of southern China, a practice that began in early historical times.

There were other ways to fight the arriera ants in the eighteenth century, as

noted by Mutis in the following entry.

NOVEMBER 6, 1777 (MINES OF CERRO DEL SAPO)

From [Mr. Francisco] Ximénez I heard today that the way to prevent damage by arriera ants in corn fields is to plant yuccas [along the corn rows] because, given that they prefer this plant to the corn, they spend the time peeling the yuccas. I have been able to confirm this practice myself. It has also been observed that, although the ants peel the yuccas, the plant does not die. Rather, the root becomes *chumba* (in domestic terms), that is, hard and tasteless.

Mr. Ximénez also said that in order to banish the arriera ants from the anthill there is no more effective way than to toss some pot of broth into the anthill. He observed that by following this practice for a few days he did not see ants in that anthill again for fifteen days. And philosophizing in the way done by peasants (whose speeches must be [entirely] heard in order to get from them what is useful), he attributed the control to the salt, which he said must upset them. Other people advise putting salt in the entrances of the anthills during dry weather. On other occasions rascona ants (or rascaculas) attracted by the food enter in these anthills and kill the arrieras, especially the mothers [queens], which are very greasy.

Mr. Ximénez further noted that the mulattresses [brown arrieras] become very disturbed by the blazing sun, leaving them dead and almost dry, although they start to recover when the humidity rises again during the night. This breed of mulatto arrieras generally conducts its destructive harvesting at night, at least in some places. I also remember having seen during the past year a long row of arriera ants (I do not remember if they were mulattresses or red arrieras) that were all dead. I asked the peasant who accompanied me about the cause of the deaths, but he could not tell me the reason. Certainly, it could not have been a fight with others, because in that case the ants would have been found all together in a heap, rather than scattered along the path as I saw them. If I had known then [what I know now] about this species, it would have been less difficult for me to discover this point, because I could have found in my diaries the weather on those days. It is important that not a single thing observed in the field should be disregarded, and that any one thing however ridiculous it might seem [at the time] should be noted.

I have also heard Mr. Basilio Segura say a very effective way to driving the ants from an anthill is to put some grains of quicksilver down the entrance. He said that he has tried it out. However, [I believe that] these observations must be repeated to establish the truth.

CHAPTER 10

Ant Wars

In some species of ants, wars occur commonly, whereas in other species, the colonies avoid one another and wars do not ensue. In those where such aggression does occur, wars can be induced artificially simply by moving the nest of one colony close to the colony of another. The result is typically the destruction of the smaller and weaker colony. Such conspicuous aggression is less likely, however, in undisturbed natural habitats. The reason is that, when newly inseminated queens searching for a nest site happen to settle near an active colony of the same species, she is quickly killed by patrolling workers. If she succeeds in starting a small colony, it is eventually discovered and destroyed.

In short, the colonies of most ant species are highly territorial in their responses to other colonies of the same species, especially in the vicinity of their respective nests. In contrast, colonies belonging to different species usually just avoid one another. It is not unusual, especially in the cluttered ground litter of forests, to find many species nesting close to one another. In addition, the nest galleries and chambers are kept sealed off or else guarded by workers to protect them against invasion. Let us listen, now, as Mutis recounts a few things about the ant wars he observed.

NOVEMBER 7, 1777 (MINES OF CERRO DEL SAPO)

> Today, as I was going to the mine of La Concepción, I also saw the long-awaited spectacle of ants fighting. Undoubtedly, they had to be the two species of arrieras, mulatto and red ones. I still have not been able to find any traits to distinguish between these two species. [As noted] there is a difference in color, but I am not yet satisfied. It is true that the mulattresses are or seem to be more voracious and have different habits. These do not produce manure (as they call it here), whereas the red arrieras colonies have some squads of ants dedicated to this activity

continuously, casting the waste out day and night through separate nest entrances. I have constantly observed a colony at this task for ten months, whereas they normally leave at night to make their depredations. For the local people, who grew up in this country, a hostile response occurs between the two arriera species when the mulatto ones are put together with the red ones. Indeed, they hate and destroy each other. [At least] I strongly suspect that they were mulatto and red ones, because very near the narrow battlefield, there is a great anthill of red ones, whose raiders had to go to the side of the banana plantation to [reach the] mulattresses' anthills. When encounters occurred on a narrow path, fighting began. I believe they do not look for each other, because they'd certainly destroy one another. Rather, a battle is begun when it cannot be avoided.

NOVEMBER 10, 1777 (MINES OF CERRO DEL SAPO)

Walking along the plantation of bananas together with Mr. L. Lanneret, we came to the site of the ants' battlefield, and I was very pleased to see that this war had advanced so far ahead that the line of battle stretched six times the length of the one I saw on the first day; and the ground was covered by the dead bodies of these insects. Others with me began to question the war as the cause of the mortality, attributing [the deaths] instead to strong sunlight. But I reflected that if this had been the case, the same thing should have happened so that many other rows of ants would be arrayed through the whole area. Although I did find another mass of bodies about two hundred steps away, I can attribute this to another battle. There is no doubt: I saw them fight. Others tell me that this is the result of the efforts that the living make to bury the dead. I responded that the arrieras know how to carry bigger loads without these signs of rage and fury. Also, there are direct observations of fights occurring, with heads and bellies being cut off, which would certainly not happen if they were just carrying them out for burial. Besides, the sun does not shine as strongly in the present season as it does in other months of the year. The thing is that a very careful observation is needed to know for certain if this is the result of fighting or of sunstroke.

In connection with this event, the very curious and loquacious observer Mr. L. Lanneret said that he had observed, in May of this year, hostility between the tigers[1] and the arrieras, which were killed by the tigers with such a readiness that

just by stinging them the arrieras were destroyed on the spot.

NOVEMBER 12, 1777 (MINES OF CERRO DEL SAPO)

I had just begun writing down my observations when Mr. Bustos appeared, one of the main contributors to the materials in my diaries.

> I asked him about fights between the mulatto ants and the red ones. He answered that this was a constant fact that was beyond any doubt. I referred to what had been observed by us on the previous days, and my difficulties in distinguishing beyond doubt the mulattresses [mulatto workers] from the red ones when they were fighting. I always kept in mind the traits that Mr. Bustos had given me to tell them apart. But I was confused, because among the red ones there were brown ones, especially those of middle size that I call captains. These seem to govern the squad but do not regularly load the suppliers with food or the cleaners with excrement, which are the same color as that of the mulattresses. He offered to clear my doubts once again. Having gone to pick up the fruits of the big higuerón [fig-tree] at the entrance of the banana plantation, he saw the fight that was still going on with unspeakable destruction. He picked up some mulatto arrieras and some red arrieras, so that I could remove my doubts. The mulattresses, although brown, are recognizable by the head, which has a different color than the rest of the body. The color of the head is half-monkey (they call it monkey because those animals are a more or less tobacco color), and the local people say half-monkey because it is a bit like this color. The proper word for the color is testaceous—in other words light brown.

What precisely are the species of *Atta* leafcutters Mutis and the Colombian people of the day called the arriera (mule-train) ants? Of the genus occurring overall in the New World, from Texas to Argentina, three species are persistently common in Colombia: *Atta cephalotes*, *Atta colombica*, and *Atta sexdens*. In dry forest near Mariquita visited in 2007, E. O. Wilson and the Colombian ant expert Fernando Fernández found *A. colombica* abundant, and we observed a refuse pile near one nest. Since Mutis is clear on one difference between the two warring arriera (*Atta*) species, the red arrieras built refuse piles and the mulatto arrieras do not, we can reasonably assume that the red arrieras were *A. colombica*. *Atta cephalotes* does not build piles, whereas *A. sexdens*, the third species, does. But *A. sexdens* occurs more in grasslands and *A. cephalotes* in forests.[2] Putting all this together, it seems reasonable to suppose that Mutis' mulatto arrieras were *A. cephalotes*.

Wars between colonies of different species also occur but much less commonly and then usually between species that are either close in evolutionary ancestry, convergent in nesting, and food habits, or both. It is notable that Mutis had difficulty distinguishing *A. cephalotes* from *A. colombica*, the two antagonist species along the Magdalena. The two resemble one another closely, and both are forest dwellers with essentially the same nest preferences and food

requirements.

To make the record complete, not all colony-level conflict is territorial. Some species in the North Temperate Zone raid colonies of other species to enslave their young. Pupae, the last immature stage, are captured and allowed to emerge as six-legged adults in the slavemaker's nest. The captives learn by imprinting on the odor of the raiders, accept them as nestmates, and thereafter serve the raider colony as part of the workforce. The famous "war" between two species that Henry David Thoreau witnessed outside his cabin and described in *Walden* was most likely a raid by a red-and-black slavemaker in the *Formica sanguinea* group of species against a black species of the *Formica fusca* group, most likely *Formica subsericea*, an abundant inhabitant of the eastern North American woodlands. Curiously, for reasons not yet understood by ant biologists, no example of slavery (common in some ant species) has ever been found in tropical regions.

CHAPTER 11

Mutis Solves the Mystery of the Nomadic Pataloas

The Tropics are devoid of ant slavery, but they are headquarters of large numbers of ants whose colonies prey on the colonies of other ant species. Some ant species conduct raids to capture and eat the young of targeted colonies. Others raid wasp nests. These spectacular raids are witnessed by anyone who spends time in the forests of the tropical mainland. Hence, they could not fail to attract the scrutiny of José Celestino Mutis.

The army ants, or *pataloas* (Mutis also called them “hunter ants” and “vagabonds”), form huge colonies, with worker populations ranging into the hundreds of thousands. All the workers in an army-ant colony are daughters of the single queen mother. So powerful is the impact of the raider hordes on prey populations that the ants would run out of food if they remained in the same place for more than a few weeks. To survive, they must emigrate on a regular basis, and that is precisely what Mutis discovered. The army ants are the awesome roving Huns of the insect world.

What we now know, although Mutis could not have been expected to discover this during his long-term research, is that each army-ant colony follows a cycle in rearing its young that is tightly linked to its emigration from place to place. The cycle can be said to begin when the huge queen lays a mass of thousands of eggs. This event coincides with the transformation of all the larvae in the colony into the pupal stage. Each pupa has the external form of the final stage of development, in other words of six-legged adults. But it neither walks nor flies: all of its appendages are sealed within a soft, waxy exoskeleton. Inside the body of the pupa, the internal organs of the preceding, larval stage are breaking down and their tissues regrown and assembled as an internal body that fits into the exoskeleton. Each individual is enclosed in a silken cocoon (“tunic” to Mutis), spun by the larva before it metamorphoses into a pupa.

The eggs and the pupae are inactive, and their presence has little effect on the rest of the colony. The adult workers guarding them need only keep them safe

and clean. And because the workers do not have to feed growing larvae in this statary half of the cycle, they too are relatively inactive. They still conduct organized raids to collect prey but in lesser amounts than in the active half of the cycle, and they do not emigrate from one place to another.

When the eggs hatch into larvae, the new crop of adult ants simultaneously emerge from their pupal skins and cocoons. The appearance of these very active stages galvanizes the older workers. The colony then conducts more intense raids, and it emigrates to a new location each day. Both activities bring in an increased food supply, enough to feed the increasingly voracious growing larvae.

It is fascinating to read in Mutis' diaries how he puzzled over the intricacies of the army-ant lifestyle. He was the first to do so as a scientist. He had to make all the primary observations in the field by himself and in fragments of the cycle. There were no previously published accounts on which to build, only the casual and incoherent observations of local people to provide him with clues. He was further handicapped by an imperfect knowledge of the stages of the metamorphosis of the individual ant, which is the same as other holometabolous insects: egg to larva to pupa to adult.

Mutis found early on that the army ants (pataloas) are migratory and do not construct earthen nests. They occupy temporary bivouacs (as the retreats are called by modern entomologists) from which they construct their raids. Mutis writes that at least one species preys on other species of ants. This is most likely the common column raider *Eciton hamatum*.

NOVEMBER 12, 1777 (MINES OF CERRO DEL SAPO)

> In the early afternoon, a very happy Mr. L. Lanneret appeared, and told me to come see the place where the pataloa ants (hunters or army ants) were depositing their eggs [larvae], which they brought from another place. Indeed, we went down and saw an army of ants of this species that were carrying their offspring in their mouths, each one of them its own: some were depositing them in a hole against a stone and a bush of common straw, but others went on past in order to deposit them in another place similar to the first. I am becoming convinced that these ants, which I call vagabonds, do not have underground nests like other ant species, but place their brood between the straws and subsequently pile them together in dispersed heaps. This appears to be a kind of

incubation, a conjecture that needs to be confirmed in the future. Mr. L. Lanneret observed them again in the evening and assured me that the incubation appeared to have already begun, since a large number of them had gathered in that place. We could also see that they had brought many dead ants of another species. We wanted to know what the species were (they were certainly different from the pataloas), but it was not possible because the pataloas are to be feared for their very violent bites with the sting, I mean with the jaws, unlike the *flecheras* [arrow ants], that have a sting.

And although we were accompanied by Mr. A. Ribero, who is a man used to these phenomena, we could not proceed further with our investigations. These tiny insects had doubled their fury in the presence of their offspring, as if believing that we intended to remove them. Eventually, they overcame our efforts to study them altogether by forcing us to leave. By then they were already climbing over our bodies, and it was necessary to shake them off with much care in order to avoid their painful stings. I had already experienced the feel of these attacks. We guessed that the many dead ants [of other species] were destined to be the first meal of their offspring. This is backed by the following reflection. These ants do not eat herbs or grains, nor do they scavenge dead animals. Their [carnivorous] diet is proved by their habit of assaulting every living thing. We can reasonably suppose that not being able to move during the first days, they have to eat something that belongs to the animal kingdom and also does not rot. Such as ants.

And although I conjectured that [prey] might be [just] for feeding the mothers, in contradiction is the fact that they do not eat anything that is dead and that, as it happens with other animals, they must suffer from hunger during the days of incubation.

JULY 1, 1778 (MINES OF CERRO DEL SAPO)

Today, as I was walking across the banana plantation on my way to the orchard I am tilling, I discovered a column of black pataloas [army ants] that came and went. They were very close to a ditch and, seeing them loaded with their brood [most likely, larvae] a very common spectacle at this hill, I thought it would be a good occasion to discover their bivouac. I suspected that the origin of the column would not be very far, thinking they could not possibly have come from the other side of the ditch. I called the gardener right away and asked him to accompany me, for he was familiar with this terrain, where there could be some hidden snakes. We followed the way followed by the ants that were loaded. A few steps farther we came to the ditch and discovered that the huge army of ants had been using a great log that crossed over the ditch as a bridge. We moved round the log, and after a great struggle through the thick vegetation, we managed to reach the other side of the bridge, where the gardener discovered the place where the brood was concentrated. I then

proceeded to make the examination I strongly desired. Although I had seen this army of pataloas with their brood many times during several seasons, I had never been able to find the anthill. Although the immediate terrain proved very uncomfortable, I pushed close to the spot pointed out by the gardener. He was becoming weary and tired of the bites of the endless number of ants climbing onto him. We both suffered many bites of these furious insects, whose work we were disturbing.

It is easy to understand my joy when I saw this spectacle for the first time. We had to lie almost flat on the ground so that we could lift some leaves and view the arrangement taken by the colony. Despite all the care that we took in this task, it was impossible to hide our intent from these very watchful insects. We saw then that all the ants were clustered together—so closely that many of them fit in a small space. Inside each [small] cluster there is an egg [actually, larva] being incubated. In this position, the ants were bent with their heads and abdomens directed inwards. Also, they seemed clumsy until they felt attacked. When thus aroused they left the anthill to attack us, climbing up our feet and legs to take revenge for our unexpected visit. My curiosity satisfied, and not being able to stay longer at that site because of the large number of ants attacking us, I left the undergrowth, wishing to find the new storeroom for the offspring; because, having observed that there was an organized army of ants that came and went, I assumed that those coming again to carry another egg [larva] would deposit them in a common place.

I ordered my gardener, who was especially a target of the rage of these insects for going barefoot according to the custom of the country, to follow the path of the army. The new discovery was particularly troublesome because of the need to walk into weeds and undergrowth. But finally he found the place of the new deposit underneath an old log that was lying on the ground. I reached the site with difficulty and proceeded to examine the new lodging. The ants had already formed new aggregations for the incubation, each of which I estimated to be about four cubic inches in dimension, much smaller than the old aggregations. I also observed that the ants had not begun to excavate a nest in the ground but instead had settled on the sides of the log that touched the ground and along the upper part of the roof of the log, so that in the middle it seemed like a cluster hung in the air. Those already present had accommodated themselves by crowding closely one against the other.

Once my curiosity was satisfied I instructed the gardener to visit the anthill every day in the early morning, in order to continue my observations.

In this account, Mutis reports that the army-ant bivouacs are made up mostly of the bodies of the ants themselves. The ants form what appears to be “a cluster hung in the air.” In fact, close examination with a magnifying glass would have revealed to him (in case he could stay so close!) that the workers use their large hook-like claws, located at the ends of their tarsi (feet), to link themselves to others, claw to claw. They form chains and sheets of linked bodies that lie together in sheets to form a single mass. The surface of the mass, acting like a kind of living Velcro, adheres to the sides of tree trunks, tree cavities, and dead logs. The army ants thus dispense with the expensive and time-consuming excavation and assembly of materials required to build an ordinary nest. They are able to change their bivouacs simply by walking from one location to another and forming chains and sheets of their own bodies. Mutis continues:

1. What could be the reason these ants make the great effort to carry the offspring from one place to another through a distance of about one hundred [human] steps? And after the first scouts had undertaken the task of looking for a bridge that would help cross the ditch, in about seven steps? The gardener's answer to this question was that some other ants of another species would otherwise come to trouble them, forcing them to abandon the site. There was nothing illogical in this answer, but it had to be confirmed by observation. Although I could not make any solid objection to the gardener's conjecture, it did not satisfy me because, having observed these migrations of the pataloas very often, I doubted that aggression from other species are frequent. Anyway, it is repeated observation rather than conjectures that really counts in such cases. Thus, I leave to a future time the research of the migrations of the pataloas.

2. I wonder if other ants that are double the size and different in color, a bit big-headed, with great jaws like hooks and so similar to the other pataloas that even I get mistaken, are the same sex. They do not carry eggs and are few in comparison with the other ones. My guess is that these are the males of the species, but I cannot be sure.

3. Why do these migrations take place during the evening and through the rest of the night? I do not remember having seen these ants carrying brood in the mornings. Further, when the gardener went to check after mealtime he did not see this army marching across the same path, as I could gather from his answers to my questions. It seems to me that the reason for the nocturnal timing is the harshness of the sun, which greatly troubles insects. On harsh sunny days, it is very frequent to see long paths, especially those of the arriera ants, full of ants lying as if they had died from the heat of the sun. However, this idea will remain no more than a conjecture until, with more information on the timing of the migrations, we can find the real cause.

Mutis recognizes the emigrations made by the army ants, but he is puzzled by the high frequency with which they occur. His gardener suggests that the ants move so frequently because they are attacked by other kinds of ants. The gardener's hypothesis is reasonable, but Mutis remains skeptical and justifiably so. He has never seen such harassment. It will be 200 years before the migratory habits are satisfactorily explained. As Theodore C. Schneirla, Carl W. Rettenmeyer, one of the present authors (E. O. Wilson), and others demonstrated in the 1940s and 1950s, the colonies emigrate so much because, while the larvae are growing, the huge foraging expeditions soon begin to exhaust the local supply of prey. As giant predator superorganisms, they have to keep moving to new sites to keep eating. The emergence of the larvae and new adults serves to trigger the migratory phase of the cycle.

The big-headed ants in the army-ant columns with hook-like mandibles Mutis observed are soldiers, or major workers in modern terminology, the same caste that Mutis has recognized as the caporals, or *cabezones*, of the leafcutter ants. Like all the other working castes of ant colonies generally, these specialists are exclusively female. Males appear only for a short time before the mating season.

Army ants do not engage in the spectacular mating flights seen in the leafcutter ants. Instead, the males fly away from the mother colony and find another colony of the same species. On arrival, they are tolerated by the host

workers, who allow them to mate with one of the half-dozen virgin queens that have been reared by the colony. The huge queens are wingless, and unlike the leafcutter queens, they cannot start new colonies on their own. Instead, each army-ant colony multiplies by fission, during which it divides into two parts. One group of workers moves off with the old mother queen, the other with her daughter—the young, newly mated queen. No males or any of the surplus virgin queens survive the fission, and the social organization of both colonies quickly resumes the status quo ante.

CHAPTER 12

Mutis Measures the Size of an Army-Ant Colony

Next José Celestino Mutis shows his mettle as a scientist. He finds a way to estimate the enormous population size of an army-ant colony and then cross-checks his result by a second, independent method. Unfortunately, however, his summing of the two bivouacs, new and old, lead to a number well above that obtained by modern researchers. Mutis' estimates for the number of adult ants (3 million) is many times those made by T. C. Schneirla and C. W. Rettenmeyer in the 1960s and 1970s: for the column raider *Eciton hamatum*, they give 100,000 to 500,000, and for the swarm raiders of *Eciton burchelli*, 150,000 to 700,000.[1] Even so, Mutis was correct to speak of the colony populations as awesomely large. They are even more impressive when it is realized that all members are daughters of a single queen.

CONTINUATION OF JULY 1, 1778 (MINES OF CERRO DEL SAPO)

> 4. Because expressions like "a lot of" or "a very great deal of," *etc.* are too vague, I wondered which one to use in order to help lead to a more precise idea, somewhat near the truth, of the number of the many insects of this kind living in an anthill. Because it is absolutely impossible to count all of the ants, it is therefore necessary to make a cautious calculation.

From what I could observe, the columns of ants [pataloas] narrowed in some stretches and widened in others but never exceeded one inch in width all the way. This observation made, supposing an average of three quarters of an inch [translated from nine lines] in all distance, with six ants across and four ants in all the length of an inch, it makes 24 ants in every inch of the column. The column does not always go straight, but instead makes several turns. I estimated that the straight distance between bivouacs would be one hundred feet and the

true length of the column, with all its twists and turns, three hundred feet. Under the latter assumption, the whole length of the column would stretch to 3,600 inches and all the column would be formed by [at any given moment] 86,400 ants. Mighty army! Far below, however, the number in the whole anthill.

If again we suppose that half of this number returns in order to carry other offspring [larvae], then 43,200 offspring are transported in each trip. Prodigious progeny! Below, however, the true number. There were already many more in the new deposit and perhaps thirty times that many in the anthill. These ants march at great speed. Suppose that every three seconds they advance one inch, then in a period of 10,800 seconds or three hours, each ant carries a brood piece from the old anthill to the new one, and every three hours 43,200 offspring are deposited in the new anthill. And if we limited all the migration to a period of 18 hours, then 259,200 offspring would be deposited.

Under these assumptions, four eggs [larvae] are placed in the new anthill every second. Since the army is tireless in its activity of bringing and depositing, it means that every three seconds 12 offspring are deposited by the 12 coming ants, amounting to 4 offspring in every second. Hence, in a period of 64,800 seconds or the 18 hours time limit, a total of 259,200 offspring are transported.

In this same scenario, each ant will make three trips loaded, and therefore the number will rise to 777,600 offspring transported during the 18-hour time limit.

Let us make the calculation another way. Suppose that all the ant colony occupies 1 cubic foot, as based on my repeated efforts to determine the size of this space, then if each offspring occupies an average of one and a half lines (there are bigger and smaller ones, and even three sizes, according to my observations), there will be 729 offspring in each cubic inch if they were completely together. But since there must be a space double in size for the ants, we have to reduce the number to a third, making 243 eggs [larvae] in every cubic inch. Then, there will be 419,904 eggs [larvae] in 1 cubic foot, which, according to my estimate, is the space occupied by all the colony.

But if we take a figure that is in the middle of these two numbers then, as far as these calculations allow us, we arrive at 598,752 offspring.

This, as it can be seen, is just an estimation. And after reflecting on it, I have concluded that there are no more than 800,000 and no less than 500,000 offspring.

The number of ants employed for the incubation is certainly bigger. As I said before, those employed in the transport could be 86,400. Let us suppose that

there is double the number in the new bivouac—that is, 172,800. Assuming that there could be 4 cubic inches of the colony in this new bivouac, then in the old one, which is a cubic foot, 26 times the number of ants must have remained there, or 4,492,800. These added to the ants in the new lodging and the carriers make a total of 4,752,000.

Let us suppose, for a separate calculation, that for every offspring six ants are employed (usually there are more or less than that figure). Then, considering the number of offspring to be 600,000, the total number of ants employed in the task would be 3,600,000.

Let us make the calculation in yet another way. The numbers may seem incredible except for somebody who has seen the colonies. The ants link themselves together, adjusting their bodies so as not to leave any space between them you can notice. I believe that every six ants occupy the space of two cubic lines; therefore, there will be 1,200 ants in every cubic inch and 2,239,488 in a cubic foot.

Let us take now an intermediate number between these two, and it will make 3,495,744.

Finally, let us set this number to be 3,000,000 and the number of eggs to be 600,000, and it will be seen that the number of ants that are employed in the new generation is five times bigger.

Certainly, there is no other way to get an idea of the amazing number of these insects, being absolutely impossible for anyone to count them one by one.

CHAPTER 13

Mutis Tracks the Armies of Ants

None of Mutis' observations and commentary on the *Eciton* army ants better illustrates so well his passion for natural history and his commitment to the scientific method than his tracking of the colonies. At this stage of his work, he had begun to accumulate enough information about his pataloas to understand much of the complex forays and cycles of these extraordinary insects. But some of their secrets escaped him entirely, as indeed they did for many generations of scientists to follow. It is interesting to speculate what Mutis might have gone on to discover if someone transported from the future had given him, perhaps over a glass of fine port, with no more than 60 seconds and 100 words needed, a clue to those missing parts his successors took two centuries to add.

JULY 2, 1778 (MINES OF CERRO DEL SAPO)

Today, I went to my vegetable garden to ask the gardener about my ants. At his morning visit, he had found them perfectly settled and composed, having finished their entire emigration during the previous night. These visits amid weeds and thickets are usually hard. For this reason, I do not undertake such dangerous expeditions personally if it is not necessary to do so. Snakes and terrible insects abound in this place. On the other hand, there was no need to repeat the visit. For the purpose of counting the days that are spent in the incubation, it is sufficient for me to know that they still remain in their nest.

JULY 3, 1778 (MINES OF CERRO DEL SAPO)

Wishing to visit the anthill of the pataloas again in order to observe their behavior, I set out accompanied by the gardener. When I invited him to

make the inspection of the bivouac site, he told me that they had already left to another place. This news startled me, and when I asked him again how they had escaped his attention, preventing his following them again, he responded that they had stayed the night but had left before dawn. This statement is not quite true. He saw them in the morning and did not return in the evening. They must have started their new migration sometime in the previous afternoon and finished it during the rest of the night. For this reason, he did not find them this morning. I went with him to the site in order to make sure of this, and I only saw the vestiges of a portion of small tunics [pupal cases] of the offspring. I can conclude nothing about the tunics or membranes containing the insects. I don't know whether it is one or they are two or more. This negligence by my gardener has upset me very much.

JULY 5, 1778 (MINES OF CERRO DEL SAPO)

This afternoon, as I was going upwards from the vegetable garden to the offices, I discovered a column of pataloas. I quickly saw that they were transporting offspring. I invited those accompanying me to look for the place of the new bivouac in order to share those marvels. It was about five o'clock in the afternoon, and I suspected that the ants had started the migration a short time before. Because the land was free of obstacles, it was not very difficult for us to find the place of the new site. Indeed, around twenty steps away from the place where we saw them, we found a dead tree branch lying on the ground, and there we saw the cluster of those that were already depositing the offspring. I noticed again that they do not lay the offspring on the ground but instead cover them immediately with their own bodies. This circumstance suggests that from the beginning of the emigration a number of ants leave the old site to look for a new site, in order to shelter right away those offspring that are being brought. Because there is no doubt that the number of ants employed in the incubation exceeds that of the offspring, and since nearly all of them, with the exception of the big ones [major workers], travel loaded, it seems that they would not leave them abandoned at the new site, so that a number of them come back to finish the emigration. Whether the ones that leave first bring offspring I am not certain. I know for sure that they come and go and that the population at the new site increases steadily. Perhaps some of the outbound ones do not come back

and perhaps not every outbound one brings offspring.

Once I saw the new bivouac, I realized that the emigration had begun that same afternoon, deducing that much from the small number of ants that were there. That is, the volume of the cluster was similar to what I saw at the start of the first day of this month; and, comparing it with the great volume that I saw in the morning of the second day, and marking the conclusion of the process during that night, it can be easily deduced that it began in the afternoon and was concluded in the night. For this reason, I estimated that the duration of the emigration is eighteen hours.

We wanted to watch this beautiful spectacle, but the ants were becoming impatient of our visits, and obliged us to leave the site altogether. I expected to find them all fully composed the following morning.

JULY 6, 1778 (MINES OF CERRO DEL SAPO)

I wanted to visit the bivouac of my pataloas, and I went down in the morning to greet them. At this time, it was very easy to observe the ants, so long as we took care not to disturb them, because then they are relatively quiet. I called over everyone passing by who had joined me the previous afternoon, so that they could share this marvel. Again I observed that the ants squeeze in and press together so tightly that not only is it impossible to see an empty space, but even a single offspring. I observed that there were others employed in picking out of the heap the tunics, or shirts [abandoned cocoons], of the offspring. From the abundance of these spoils, I deduced that this task had begun during that night.

My naturalist, Mr. Andrés Ribero, came along this time and wanting to reward him for the pleasure he has given me with his news, I told him my news. I took him to the anthill, and he showed his talent as an observer by the pleasure he expressed on this occasion. He admitted frankly that he had never seen this remarkable phenomenon.

Since he was busy these days cutting trees for the collection of wood, I arranged to meet him on the following day. I predicted, from what I had already learned, that the migration to another nest would begin that afternoon.

JULY 7, 1778 (MINES OF CERRO DEL SAPO)

On the previous afternoon, when the emigration had begun, I had already invited my naturalist to observe the anthill on a daily basis. Yesterday, I forgot to write down this event, but since it is not very long ago, I note it here; my many occupations take my time and distract my attention, even for the notes of the day.

CONTINUATION OF JULY 6, 1778 (MINES OF CERRO DEL SAPO)

New expedition of the pataloas.

I had predicted that on the afternoon of the sixth, toward four o'clock in the afternoon, the new emigration of the pataloas would begin. Towards one o'clock on Monday I retired to my room and the pataloas had proceeded from a place opposite the nest of my ants; and, not seeing them carrying offspring in their mouths, I thought they belonged to another colony. But later on, I very much regretted not having followed them, because they are relevant to the conjectures that I will refer to. Towards ten o'clock on the morning of this same Monday I saw this column, and I believe that only two or three or, rarely, four ants formed the width of it. They did not stop coming, always following the same course. This same column continued to at least one o'clock that day, when I left. Towards half past four in the afternoon I went downward and found the pataloa ants already coming from my nest with their eggs, along exactly the same path followed by the pataloas of the morning. For a long while, I observed the going of my pataloas; I went to the nest, which I saw was already in a general commotion at the outer layers of ants, although toward the bivouac center there reigned a deep stillness. Knowing for sure that it was the migration, I called one of those who had accompanied me on Sunday, in order to make all the explorations needed to discover the new nest. When we caught some ants, it seemed to us that only one tunic [pupal case] remained, while another one had been left in the old nest, as could be seen from the large amount of membranes existing there. We broke open several eggs [cocoons] and, indeed, there was only a little membrane covering the new pataloa ant, completely formed and with the same color and aspect as the living ones. Their situation is the same as that I have observed in the offspring of the arrieras [leafcutter ants], a matter that I will talk about in another part of my diaries—in case I find I have not written about it already. Those of the arrieras are pure white and extremely smooth and glistening. These are opaque and with the same color, although a bit pale, as they possess when fully mature. None of the pataloas whose membrane we removed gave a sign of life. I have observed this same condition with regard to the arrieras.

While observing this I noticed that on the same path followed this morning by the pataloas there were some heaps of dead ants, or at least they seemed dead to me. I certainly believed that the pataloas of my nest had killed them when they met. The majority were motionless, though some moved almost imperceptibly. They had been abandoned; those from the nest passed over them, ignoring them. This idea was so fixed on my mind that I told it to my companions, some of whom assumed, like me, that they were truly dead, and others that they had merely fainted from the harshness of the sun. But, in order to leave no loose ends, I will add here that I have very much regretted not having examined what place they went to and what place they came from, so that later this remaining scruple had not arisen. Because today, having deliberately examined the huge cemetery of dead ants, I did not find any vestige of carcasses, and so I was already certain that they returned to life from that apparent death. And from this I have grounds for thinking that the small squadron left the anthill (from a side opposite to that I was observing, something very feasible in these thickets where they hide and bustle) with the mission to serve as explorers in preparation for the impending emigration. This conjecture seems to be founded in wise Providence, because it does not seem fair that the ants set out carrying the offspring, traveling at random and without prior selection of the suitable place for such plentiful progeny. Therefore, it seems reasonable to believe that those ants, although suffering the brunt of the sun's heat (that certainly upset them a lot), left to make this exploration of the expense of [acquiring] an illness that lasts a few hours; then in the cool air of the night they were revived—as I have observed it. But the chance to observe more is gone—I lost the very beautiful moment to discover whether the pataloas send explorers to choose the new nest site before leaving the old one.

Let us continue with yesterday's story. My ants continued their incessant task, and I followed their movements that would lead me to the new place. In the first venture I lost them in a thicket, which left me frustrated. Next my naturalist, who is a good rustic, appeared, and we made a second attempt—but in vain. Finally, I insisted on searching for the site, even though night was

approaching, thus proving the power of perseverance. I decided to destroy another thicket, up to where we had followed them on the first time, and proceeding with this, my good rustic discovered the place where the ants were beginning to settle. The site was at the foot of a great bush of *Piñuela* [genus *Aechmea*]. Satisfied with this success, and after I had seen and noted the spot, we left with an agreement to return. Here ends yesterday's account.

CONTINUATION OF JULY 7, 1778 (MINES OF CERRO DEL SAPO)

We went to visit our ants, which were very precisely compressed into the bivouac, and still, with the exception of those casting off the shirts or membranes [cocoons] they were removing from the offspring. This operation of removing the cocoons is a task of the incubating ants and not of the offspring themselves, as in the case in chickens [pipping the eggs]. This interpretation is based on these two observations I made: first, the emerging ant does not give any sign of sensitive life; second, if it were acting on its own, it would first break the inner cover [pupal skin], and this is contrary to what I have observed, because once the outer cover is removed, the second, inner one, remains whole.

The entire external surface of this nest, from the only side where it could be seen, was so symmetrical and smooth, and also so perpendicular, that it seemed to have been leveled. I never tired of inspecting this beautiful spectacle. If you do not touch them, and if the ants do not perceive any invasion, they remain quiet, and those that throw the tunics [cocoons] away, continue their work. In the morning, there was a great many of the discarded tunics.

In the afternoon, I repeated my visit and found the colony calm, with no indication of imminent departure.

I estimated the size of the colony, that is, of the whole heap of ants, to be the same as the one I saw the first day. The distance from the old nest to the new one was also about the same.

JULY 8, 1778 (MINES OF CERRO DEL SAPO)

Who could believe that, today, on such a propitious occasion, I could forget about a matter that gives me so much pleasure as do the pataloas, as if I had never thought of my earlier observation? But such are my duties in the [mining] company these days, where I am conducting some important experiments on the melting of metals. As if there were no ants on this hill, I forgot about the pataloas completely, until lunch hour after one o'clock. Then I abandoned everything else and went to observe my ants. I found them still calm. But forgetfulness prevailed again, and later in the afternoon, when I should have visited them, it slipped my mind again.

JULY 9, 1778 (MINES OF CERRO DEL SAPO)

Now, free from my preoccupations of the day before, I went to visit the bivouac site. I was stunned when I found no ants at all, only a number of small discarded tunics [cocoons]. Not a single ant, dead or alive, remained in that place. I had to conclude that the colony had left the previous evening and [traveled] on through the whole night, in order to complete the rearing of the offspring.

From these observations, it can easily be inferred that it is a habit of this species of ants to brood their eggs [larvae, not eggs or pupae], taking them successively from one place to another. They perform these migrations not because of the attacks of other insects or animals that expel them from their nests. So what is the true reason for the emigrations? This is what I don't know. Could it be, perhaps, the annoyance that their own garbage may cause them? This is only a conjecture. I did not observe anything but the small tunics.

On today's morning, as I was walking towards the vegetable garden, I observed a column of pataloas. Perhaps they were the emissaries sent to explore the place for yet another emigration. The place has some thickets, so I chose not to follow them.

CHAPTER 14

Mutis Studies the Gender of Ants and Makes an Amazing Discovery

We now know that, with a very few exceptions, the males of all kinds of ants are radically different in anatomy from both reproductive females (queens) and nonreproductive females (workers). Males are permanently winged—unlike the queens, they are unable to shed their organs of flight. They have relatively small heads and usually reduced mandibles but exceptionally large eyes, with three prominent ocelli, or single-faceted small eyes, on the front center surface of the head. They possess prominent external genitalia at the tip of the rear segment of the three-part body. They are usually differently colored and darker than the queens and workers.

Although they are so strikingly different in appearance, males are seldom seen in the female-dominated societies they inhabit because males are present each year only during the short time leading up to the mating flight. At that hour, they emerge from the nest to fly forth in search of virgin queens. Their whole anatomy is designed for this single event. Successful or not, they never return to the nest and soon die.

While they are in the nest, and before their mating flight, males do no work. If the nest is disturbed, they retreat into the nest interior, leaving defense to the workers. Entomologists have never seen a male fight to protect its colony. Moreover, workers normally do not rear males at all until the colonies grow to nearly mature size. Some never produce males at all.

Aside from an opinion expressed by his mentor Carl Linnaeus, José Celestino Mutis had at first no way of knowing this important property of ant biology. He worked on the assumption that the colony workforce consists of both males and females. Further, in accordance with the vertebrate animal model, he also assumed that males would be big and aggressive. Stubbornly European in his worldview, he thought that the large-headed soldiers of some

species must be the males. How could these powerful and noble creatures be anything other than males? And how could we expect them to be neuter, like the female workers? So Mutis, on opening a nest of ants with both winged male and winged virgin queens, was prepared to conclude only the genuine and smaller adult males he saw were young queens still growing in size, destined to become full-sized queens that would mate with the wingless soldiers. This curious line of reasoning, which Mutis would in time correct through his later studies, is expressed in the following entry of his diary.

SEPTEMBER 18, 1778 (MINES OF CERRO DEL SAPO)

> But going back to my ants, the ones Mr. Bustos called *melcochas* [taffy ants], we were shown a beautiful spectacle. The moment that the small anthill was uncovered, all the species [castes] appeared (they are big ants, almost the size of the arrieras). There were many big and small females, all bearing wings and with three points on the head [ocelli, between the two large compound eyes] … The males are big-headed and bigger than the *espadones* [neuters; hence, workers]. Their color is dark brown. I greatly admired the large size of some eggs, or more exactly pupae, that enclose the ant for the transformation into a complete ant … I picked up a number of these to properly examine them in my satchel, but I did not want to leave the place without opening one of them. When I did so, I found an ant, one of the big mothers kind, which was already complete.

For the sake of truth and sincerity, which are necessary when observing, discovering, and writing down the creations of nature, I cannot silence the reflections I made just there, although they contradicted the system I had conceived about the sexes when I uncovered that pupa. They are as follows.

From observations of various ants of each species that I have made this year, and once I saw the feature of the mothers of the arriera ants, I assumed that nature would have made all the females of every species recognizable by the crown of the three points [ocelli]. I also assumed that the males dedicated to reproduction, propagation of the species, and protection of the offspring would be the big-headed ones that I find in all the anthills, and, finally, that the espadones [workers] would attend the incubation and provision of the needs of the anthill, and also the collecting of food—inferred from the fact that they are the only ones that move on the outside of the nest. I further decided that the other winged ants, also with a crown of three points, greater in number and much smaller than the big mothers, are the new little females that would later grow up to produce the new offspring. In other words, these smaller ones are just a variety based on age. I assumed that the big and very potbellied ones are the pregnant females.

I formed this system from proper, direct observations I had made. But today, with the opening of the big pupa [cocoon] and finding inside a big female ant, with wings and a much bigger head than those of the presumed young females, this system is already overturned.

Among the cucuncha ants well represented in my cabinet, I see both big and very small winged

ones. Among those inspected today, I saw the same phenomenon, and I do not doubt that the same caste forms exist in other species. The pupa I opened has already reached the full size of the large winged caste and is proportionately very much larger and different in proportion from the small winged ones belonging to the same anthill. I checked to see if they were born with the wings fully developed, and I found that they did not, but instead raise [expand] them later.

Given my observation that each one of the four varieties in each species is kept inside its pupa and shows a size proportionate to that they will have when adult; and assuming, according to my own observations, that when opening the pupa it will not be difficult to tell which of these varieties the insect or ant will belong to when grown, how then will the sexes be distinguished and classified?

The gentleman Linnaeus attributes wings to males and females. According to his opinion, based on the observations made on this subject, the females would be the big ones, and it seems that the Divine Providence would give them a bigger belly to contain the seeds of the new and numerous offspring. But then, which is the sex of the big-headed ones? It would be a difficult thing to say that they are espadones [neuters] dedicated to propagation as far as protection of the colony is concerned, but exempted from the task of reproduction.

And, assuming that there are infertile ants, would it be difficult to believe that there exist infertile males and that these would be the ones known so far as espadones, as well as infertile females and that these would be small and deprived of a belly able to contain the sperm? Does it not seem more likely that the instruments for the propagation of the species, being then the fertile males, are gifted by nature with the beauty, majesty, and greatness that show in the big-headed ones, and that this so noble feature does not belong to a group of ants as low as the small ones that look like the big ones?

Since I have not been able to find the right moments for the observation of ants in the act of mating, I cannot clear my confusion on these matters. I read Aristotle, excellent naturalist, and there I did not find anything about the features of males and females; also Pliny and his commentator Huerta; Jonston; Derham and his notes; and Lesser and his notes. In none of these authors did I find descriptions of the features of each sex.

No doubt this is a subject incompletely understood. Nevertheless, in attempting a resolution of this question it will be good to have in mind the following established principle: four different varieties of ants exist in every anthill.

Then, as he presses on, Mutis at last is able to find virgin queens and males in copula, forcing him to abandon his old assumption and accept the evidence of his own eyes.

JANUARY 8, 1779 (MINES OF CERRO DEL SAPO)

I thank God that today I got the greatest pleasure in making a discovery, in this case, one for which I have been yearning a long time. I wanted to see the union of male and female of some ants, to determine the features of each sex. It is necessary to live alone, away from other people, in order to learn the secrets of Nature; and my current state is very suitable for the purpose of studying the admirable and prodigious creations of Nature. I will now talk about my discovery.

Whenever it rains some winged ants emerge from the nests, in quantities depending on the

season. After today's heavy rains, with the air already calm, I could see some hens around the bilibili [*Guarea glabra*] tree opposite my room, behaving very vigilantly and apparently eating some insects. From this same tree, many winged ants have come out on such occasions. I immediately thought that I might be able to see some evidence of the coitus, to determine which caste was the male, because I have never had any doubt about the female. My desire grew stronger when a boy told me that he had seen them with their little rear ends joined. A short while after I had started watching I managed to see a cluster that had just formed, made up of eight ants that belonged, almost all of them, to the fifth [caste] variety, and of a single beautiful big female. This group had formed on the trunk of the tree, and after falling onto the ground due to the weight [of the cluster], the female came into view. I could then just barely see the union of a male, or one of this fifth [caste] variety of mine, with the female, which quickly detached from her mate and ran as if trying to hide in the grass. After a long while, I saw more clearly another such union, which lasted only moments—so briefly because other lustful males pressed in hurried disorder, piling themselves up onto the female that was in copula with the first male. In this mating, I noticed that the pair become perfectly joined at the tips of their abdomens, bending this part of their bodies a bit inward, the two of them forming a kind of arch, entwining their legs. I watched this same thing a second time, though not completely, because they approached so swiftly, stumbling into each other and tiring the female too much. The latter made every possible effort to escape and hide. Indeed, these males were extremely lustful, as I knew not only by the blundering running when they each sought the female but also by the fury with which they crowded together when they see another male in possession [of the female]. This was the aim of the jumps and flights of these males, gone crazy because of a female. A few months ago, on a similar occasion, when I observed the same [species of] ants and on this same tree, I had assumed that this was the case. But it remained no more than an assumption, because I did not see the union then as clearly and distinctly as I did today.

In several parts of my Diaries, I have expressed the belief that the big-headed ones might be the males. Logical that this was, I was always ready to change my opinion, and promptly. A good proof of this readiness is that when I discovered, after a long time, and not many months ago, this fifth variety [caste] and considering that this is an ant so different from the rest of its species, it occurred to me that this caste might be the male. But I was very distrustful, because it was the only one that I saw then.

Let us praise the Supreme Creator of so many marvels!

CHAPTER 15

Mutis' Other Ants

José Celestino Mutis made little progress as an ant taxonomist. That is entirely understandable: he was primarily a botanist, and insect taxonomy was mostly nonexistent in his time. Although he gained a great deal of experience identifying the plants of the New Kingdom, and was an advocate of the Linnaean system of taxonomy, he never applied that system to the ants whose habits he studied with such ardor. Further, even though he employed artists to illustrate the plants of the New Kingdom of Granada, many of which are today valued as artistic classics, he made no effort to illustrate the ant specimens in his cabinet. That effort would have made a huge difference to future entomologists. Even a crude sketch, combined with locality data, will often suffice to place a specimen to species, or at least to genus, in the present-day classification system.

Mutis' diaries nevertheless are filled with references to the ant species that he was able to distinguish in addition to the leafcutter (arriera) ants and army (pataloa) ants. A few were left unnamed. Most, however, were given a local native name or a nickname that Mutis deemed appropriate. Some of these species are recognizable or at least subject to an educated guess.

Unnamed. Occupies large ellipsoid carton nest attached to the trunk of a tree at Cerro del Sapo, a foot in diameter and two feet long, closely resembling that of nasute termites. Very large population. Workers fast-running in files, extremely aggressive, with irritating bite but no sting, and a distinctively sour odor. This species is unmistakably the dolichoderine ant *Azteca chartifex*, a common arboreal species in the forests of northern South America. Their nests are constructed, as noted by Mutis in this example, of "several overlapping sheets of solid matter," which today we know consists of processed vegetable matter. This *Azteca* species is also notable for the protection it inadvertently gives to oropendolas and social wasps, which often build their nests on the branches of trees close to but farther from the ground than those of the *Azteca*. They suffer no harm from the ants but benefit from the barrier provided against

enemies that might approach from the ground up the trunk or across from other parts of the tree.

Cucuncha. House ant at Cerro del Sapo. Closely similar to the arboreal *Azteca chartifex* just described but less aggressive. That would make the cucuncha ant a member of the subfamily Dolichoderinae. However, we are unable to place the species to genus or species.

Tiger ants. Common at Cerro del Sapo; with large-headed major workers (Mutis calls them males); black-headed; attack when nest is disturbed; bites painfully but does not sting; probably large. Almost certainly this species is *Camponotus atriceps* (formerly called *Camponotus abdominalis*), a very aggressive species whose abundant colonies occur widely through South America.

Water ants. House ant at Cerro del Sapo. Very small; often attracted to food on the table but not detected until eaten; twojointed waist; timid and inoffensive. Mutis also called it the *maravilla* (marvelous) ants or *bizcochuelera* (biscuit) ants. Probably Pharaoh's ant (*Monomorium pharaonis*), a tiny myrmicine house pest of Asiatic origin inadvertently spread around the world by human commerce.

Savanna sabuco ants. These ants are unmistakably myrmicines of the very abundant genus *Crematogaster*. Many of the species nest or at least forage on trees, and Mutis' specimens were found foraging "all along" a little tree in the field. But what is definitive is his mention of the heart-shaped abdomen of the workers, one of the diagnostic traits of the genus in modern taxonomy.

Ant of the dead. Mutis selected this odd name simply because the first specimen he saw, in 1761, was dead. These "exquisite ants," which Mutis observed on the bilibili tree (*Guarea glabra*) next to his house at Cerro del Sapo is clearly a member of the exclusively arboreal myrmicine tribe Cephalotini, possibly the very conspicuous *Cephalotes atratus*. The species was one of seventeen kinds of ants described (as *Formica atratus*) by Linnaeus in the *Systema Naturae* in 1758. Mutis was fascinated by the heavily armored body structure of the workers, including articulated body plates, lateral spines, and grooves along each side of the head into which the antennae can be completely folded. (Had this species been found in Japan, Mutis might have called it the samurai ant.)

Guata ants.

> The Guata ant bites terribly; it is bright red, moves about underground until it finds meat, fat, or some other animal matter, which it devours quickly, burying itself once again. (Mutis)

This species is unmistakably *Labidus caecus*, an army ant that is almost strictly subterranean. It is widely distributed in the tropical and subtropical parts of the Western Hemisphere.

CHAPTER 16

How Good a Scientist Was Mutis?

José Celestino Mutis' sustained passion for natural history, so evident in the diaries and correspondence, his objectivity and honesty, his willingness to learn from others, and his readiness to change his mind (most of the time) in the face of new evidence, are traits that mark him as a true scientist of the Enlightenment.

In hindsight, however, it is a failing that Mutis, despite his devotion to Carl Linnaeus, did not adopt the system of classification introduced in the *Systema Naturae* of 1758. The main reason for this lapse may have been that Mutis was more interested in scientific natural history than taxonomy. Although he made excellent annotated collections of plants, the illustrations of which were superb, he evidently never thought of doing the same for his ants.

Even a Linnaean classification of the ants of the New Kingdom of Granada would have been unnecessary if only Mutis had made drawings of the species he studied. Then, it would have been relatively easy today to place his subjects to genus and even to species. We are certain of the identity of the ants on which Mutis worked intensively, the leafcutter and army ants, and the few other species we have noted, but we are forced to rely much more on guesswork for the remainder. Mutis can be easily forgiven this lapse. He was just following fashion. In the late 1700s, scientists and their artists worked diligently on illustrations of plants, vertebrate animals, and a few colorful butterflies and beetles of striking appearance, but they chose to illustrate only a very few of the aesthetically less pleasing denizens of the soil and vegetation.

Yet Mutis must be judged, in our opinion, not by these shortcomings. His great achievement was to overcome the daunting challenges he faced as a scientific naturalist in an entirely new world. In this respect, Mutis was unique. He had no previous information on which to build. There is in history no pre-Mutisian. Working as the first entomologist ashore on an unknown continent, he did his best with what he had. We must understand that the difficulty he overcame was deeper than the simple lack of prior knowledge; it was that he did

not even know what questions to ask.

Science is a cumulative endeavor. New knowledge is not just factual addenda entered into journals and textbooks. Good science also raises new issues and new questions. A young scientist entering a field of research usually encounters an array of problems already laid out by previous scientists. He asks himself, “What additional discoveries can I make about this or that phenomenon? Does it exist elsewhere? What are its causes and meaning?” Neither the great Linnaeus nor anyone else could open that door for Mutis. He had to do everything and think through everything mostly on his own.

Scientific knowledge grows exponentially and thus often slowly at the start of a discipline. In this case, it was more than a century after Mutis’ research that Auguste Forel, during a visit in 1896, made the first intensive collecting trip to Colombia, [1] and more than a century after that before a Colombian entomologist, Fernando Fernández, [2] conducted extensive research on ants in his own country. The oldest ant specimen published from Colombia of which we are aware is a soldier of *Pheidole praeusta* Roger, collected in 1820 by an unknown person and housed in the Paris Museum of Natural History.

Might Mutis’ lost treatises have made a difference to the study of ant biology had they been published in his lifetime or at most shortly afterward? They probably would have stimulated earlier attention to the most spectacular species, the leafcutter and army ants, and especially so if presented with some of the flair displayed by Alexander von Humboldt and John James Audubon. Meanwhile, Mutis lives on in memory as a pioneer scientist struggling virtually alone, thrilled by the wonders around him, and never deterred by the handicaps he faced in unraveling them.

Epilogue

In 1808, Mutis died. Coincidentally, in the same year, the revolution began that was to break apart the New Kingdom of Granada and give birth to the modern states of Spanish South America. Heroes and martyrs abounded before and during this tumultuous period—Miranda, O'Leary, Páez, Santander, Sucre, and, of course, Simón Bolívar, the liberator himself, with a cast of thousands. When freedom was won, the new nations created from New Granada inherited the quiet but imperishable and immensely important cultural legacy left by José Celestino Mutis.

Beneath the feet of all this humanity teemed the arrieras and pataloas and all the other marvelous ants that so absorbed Mutis' attention. Their study was a gift of inspiration he received in a letter from Carl Linnaeus. It is interesting to reflect that both the three decades of the revolution and half-century of Mutis' dedication to New Granadan culture, when placed in the deep history of the continent's living environment, shrink to less than an eye blink of time.

In deeper history, the arriera and pataloa ants had been there for more than 20 million years, working with metronomic precision their impact on the environment. Unless humanity manages to wreck the planet altogether, they will still be there millions of years into the future. Mutis, the first to probe into their mysteries, will be remembered by their presence for a long time to come.

Acknowledgments

We are very grateful to Fernando Fernández and Cristián Samper for the invaluable help given to E. O. Wilson on a trip to Colombia in 2007, during which Wilson was able to visit many of the sites important to Mutis' research on ants. We also thank Stefan Cover for his good advice on the identity of Mutis' ants, and Santiago Madriñán-Restrepo for information on the early naturalists of the West Indies. Finally, the book has been substantially improved by the research and editing, as well as the enhancement of many of the illustrations, by Kathleen M. Horton.

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ISBN 13: 978-0-8018-9785-6
ISBN 10: 0-8018-9785-8

The Johns Hopkins University Press
Baltimore
www.press.jhu.edu

1. Real Jardín Botánico de Madrid, Fondo Documental José Celestino Mutis, III, 11, 1, 20.

2. Guillermo Hernández de Alba, comp. and ed. *Diario de observaciones de José Celestino Mutis (1760–1790)*, 2 vols., Instituto Colombiano de Cultura Hispánica (Bogotá: Editorial Minerva, 1957–1958; new ed., 1983).

1. The expeditions to study natural history organized and supported by the Spanish crown during the second half of the seventeenth century included Peter Löfling to the Orinoco region (1754–1756); J. Dombey, H. Ruiz, and J. Pavón to the viceroyalty of Peru (1777–1788); Juan de Cuéllar to the Philippines (1785–1795); V. Cervantes, M. Sessé, and M. Mociño to the viceroyalty of New Spain (1787–1803); Alejandro Malaspina to the American coasts, Philippines, New Zealand, and Australia (1788–1794); and Baltasar Manuel Boldo to Cuba (1796–1799). Among them, and the longest in duration, was the Royal Botanical Expedition to the New Kingdom of Granada (1783–1816), led by José Celestino Mutis until his death in 1808.

2. A detailed account of the botanical contributions of Mutis during the fruitful period before his appointment as director of the Royal Botanical Expedition in 1783 has been provided by José Antonio Amaya in *Mutis Apóstol de Linneo: Historia de la Botánica en el Virreinato de la Nueva Granada* (*1760–1783*), vol. 1 (382 pp.), vol. 2 (683 pp.) (Bogotá: Instituto Colombiano de Antropología e Historia, 2005). This compilation contains a large number of previously unpublished letters and unpublished manuscript pages and is an invaluable contribution to Mutisiana.

3. The Linnaean system is binomial (two names for each species), Latinized in the choice of names, and hierarchical. The *wolf,* for example, received the name *Canis lupus* Linnaeus (the custom developed after Linnaeus of adding the name of the scientist who first gives a formal description and name to the species). The name *lupus* denotes the species, and *Canis* is the genus to which it belongs (the genus contains not only the wolf but also the domestic dog *Canis familiaris* L., and other wolflike animals). Multiple genera (plural of genus) with similar traits are clustered into taxonomic families; in this example, the dog-like animals are in the family Canidae. Similar families are grouped into orders; in this case, the dog-like, cat-like, and many other forms are grouped into the order Carnivora. The Roman military influence in the hierarchy and terminology is obvious.

4. Translation of Mutis’ diary entries by Enrique Gómez Durán and José María Gómez Durán.

5. In 2006, the Réaumur book was translated into Spanish by José María Gómez Durán and Xavier Roig as *Historia natural de las hormigas* (Madrid: Ed. Vision Net).

6. The likely identities of the two plague ant species were analyzed and reported by one of us (E. O. Wilson) in “Ant Plagues: First Environmental Crises of the New World,” *Nature* 43 (2005): 32 and, in greater detail with biological evidence, in E. O. Wilson, *Nature Revealed: Selected Writings* (Baltimore: Johns Hopkins University Press, 2006).

7. In the course of our work on the Mutis papers, José María Gómez Durán also discovered a long-forgotten article that mentioned ants and termites, extracted from the original Mutis diary for the first eleven days of October 1778 and not present in other records or bibliographies. It was published in 1874–1875 in *Revista mensual de filosofía, literatura y ciencias* (*Monthly Journal of Philosophy, Literature and Science*). The journal was edited in Seville in six volumes spread from 1869 to 1875. The Mutis piece appears in the final volume under the title “Observaciones sobre hormigas y comejenes hechas en Sta. Fé de Bogotá, por Mutis, en Octubre de 1778. Fragmentos entresacados de los diarios correspondientes a los once primeros dias de dicho mes, y existentes en el Jardín Botánico de Madrid.” The connection may be this: one of the founders of the journal was Antonio Machado Núñez, a zoologist and friend of Miguel Colmeiro. Colmeiro was at that time director of the Madrid Botanical Garden and cofounder, with Jiménez de la Espada and a few other naturalists, of the Spanish Society of Natural History in 1871. In a meeting held by that institution in 1872, Espada mentioned the existence of unpublished observations on ants and termites by Mutis.

8. This account is inserted by Charles König and John Sims in “Some Account of Don Joseph Celestine Mutis, Chief of the Spanish Botanical Expedition to Santafé de Bogotá in South America,” *Annals of Botany* 5 (1805): 490–500.

9. A. Joseph Cavanilles Palop, “Materiales para la historia de la Botánica,” *Anales de Historia Natural* 2, no. 4 (1800): 3–57.

10. Miguel Ángel Puig-Samper, J. Luis Maldonado, and Xosé Fraga, “Dos cartas inéditas de Lagasca a Humboldt en torno al legado de Mutis,” *Asclepio* 56, no. 2 (2004): 65–86.

11. Archivo de la Biblioteca General de Humanidades, Madrid. Fondo Marcos Jiménez de la Espada 0010/01/031.

12. Marcos Jiménez de la Espada, “Noticia de un trabajo inédito de Mutis sobre hormigas y comejenes americanos,” *Anales de la Sociedad Española de Historia Natural*, vol. 1 (1872).

13. Laureano Pérez Arcas, “Trabajos zoológicos realizados en España, sobre todo en los siglos más florecientes de su historia,” in *Discursos leídos en las sesiones públicas de recepción de los señores Académicos Numerarios de la Real Academia de Ciencias Exactas, Físicas y Naturales* (Madrid), no. 25 (1868), 37 pp.

14. José Rodríguez Mourelo, “Clemente (D. Simón Rojas): Historia, progresos y estado actual de las ciencias naturales en España,” in *La España del siglo XIX. Colección de conferencias históricas celebradas durante el curso de 1885–86*, vol. 2 (Madrid: Ateneo Científico, Literario y Artístico de Madrid; Librería de Don Antonio San Martín).

15. “Imbentario de la librería de la Casa que fue la Botánica al cargo del Dr. Mutis,” Santafé, 16 de Octubre de 1816. General Archives of the Indies, Seville, Audiencia de Santafé, legajo 667.

16. Marcelino Menéndez Pelayo, *La ciencia española*, 2 vols. (Madrid: Librería General de Victoriano Suárez, 1887–1888).

1. Natalie Zemon Davis, *Women on the Margins: Three Seventeenth-Century Lives* (Cambridge, MA: Harvard University Press, 1995).

2. Stephanie Pain, “The Forgotten Apostle,” *New Scientist* 195 (2007): 41–45.

1. E. O. Wilson, *Nature Revealed: Selected Writings* (Baltimore: Johns Hopkins University Press, 2006).

1. Real Jardín Botánico de Madrid, Fondo Documental José Celestino Mutis, III, 3,1, 1, p. 75 (this number appears at the upper right corner of the document).

1. Real Jardín Botánico de Madrid, Fondo Documental José Celestino Mutis, III, 5, 1, 44. (This document found among Mutis' manuscripts, with a different handwriting from that used by Mutis, could be attributed to one of his collaborators.)

2. The *Triplaris* symbioses are not simple. During a brief visit in 2007 to dry tropical forest near Mariquita, in the Magdalena Valley, E. O. Wilson investigated two palo santo trees. One contained an aggressive colony of the dolichoderine ant genus *Azteca*, which bit the skin fiercely but did not sting. The second contained stinging workers of an unidentified species of *Pseudomyrmex* other than *triplarinus*.

1. The essay is catalogued as “Real Jardín Botánico de Madrid, Fondo Documental José Celestino Mutis, III, 11, 1, 26.” It was transcribed in *Escritos científicos de don José Celestino Mutis*, comp. by Guillermo Hernández de Alba (Bogotá, Colombia: Instituto de Cultura Hispánica, 1983).

2. The traits given by Mutis of the birds hawking leafcutter queens—white wing stripes, concave tail in flight—narrow the species to three possibilities: the Lesser Nighthawk (*Chordeiles acutipennis*) and Nacunda Nighthawk (*Podager nacunda*), which are resident, and the transient, migratory Common Nighthawk (*Chordeiles minor*).

3. In myrmicine ants, including the leafcutters of the genus *Atta*, the gaster is anatomically the fourth segment of the basic hymenopteran abdomen, plus the successive segments; the second and third abdominal segments have been thinned and narrowed at each end to create the two segments of the “waist,” that is, the combined anterior petiole and posterior postpetiole; and the first abdominal segment, nowadays called the propodeum, is fused to the thorax. The full arrangement gives the ant much greater flexibility in moving the posteriormost major segment of the body, the gaster.

4. The discovery of the bizarre symbiosis was inevitable but took a long time. In 1869, the great Brazilian naturalist Fritz Müller wrote to his brother Hermann about his own belief in its existence, and in 1874, Charles Darwin sent a copy of Belt's book and asked him to confirm the phenomenon. This Müller was able to do. See David A. West, *Fritz Müller: A Naturalist in Brazil* (Blacksburg, VA: Pocahontas Press, 2003).

5. See E. O. Wilson, *The Insect Societies* (Cambridge, MA: Belknap Press of Harvard University Press, 1971), and B. Hölldobler and E. O. Wilson, *The Ants* (Cambridge, MA: Belknap Press of Harvard University Press, 1990).

6. The research identifying the *Atta* trail pheromone and its potency is reviewed by Bert Hölldobler and Edward O. Wilson in *The Superorganism* (New York: W. W. Norton, 2009) and *The Leafcutter Ants* (New York: W. W. Norton, 2010).

1. Probably ants of the genus *Camponotus* and most likely *Camponotus atriceps* in modern classifications.

2. Neal A. Weber, *Gardening Ants: The Attines*, Memoir 92 (Philadelphia: American Philosophical Society, 1972).

1. References and discussion in B. Hölldobler and E. O. Wilson, *The Ants* (Cambridge, MA: Belknap Press of Harvard University Press, 1990).

1. Auguste Forel, *Out of My Life and Work*, trans. Bernard Miall (London: George Allen & Unwin, 1937).

2. Fernando Fernández, ed., *Introducción a las hormigas de la región Neotropical* (Bogotá, Colombia: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, 2003).