**ABSTRACT** 

Title of Document: STUDIES IN NEOTROPICAL ANT

DIVERSITY.

Jeffrey Sosa-Calvo, MS., 2007

Directed By: Dr. Theodore R. Schultz, Department of

Entomology

This study is divided into two parts: first, an inventory of the ant fauna of two plateaus in Eastern Suriname and, second, a series of taxonomical studies of ant genera belonging to the ant tribes Attini and Dacetini, and the ant subfamily Proceratiinae for the Neotropics. The first part describes the results of a rapid assessment program survey of the leaf-litter ant fauna that was conducted in Eastern Suriname with the goal of informing conservation decisions by mining companies, governments, and individuals. The second part deals with descriptions of three new species and 15 new distributional records for species in the genera *Pyramica*, *Strumigenys*, and *Acanthognathus* (Formicidae: Dacetini) for Panama and Guyana; a review of the ant subfamily Proceratiinae for Colombia; and the descriptions of three remarkable new species in the fungus-growing ant genus *Myrmicocrypta* (Formicidae: Attini) from Brazil.

### STUDIES IN NEOTROPICAL ANT DIVERSITY

By

Jeffrey Sosa-Calvo.

Thesis submitted to the Faculty of the Graduate School of the University of Maryland, College Park, in partial fulfillment of the requirements for the degree of Master of Science

2007

Advisory Committee: Professor Theodore R. Schultz, Chair Professor Charles Mitter Professor Maile Neel © Copyright by Jeffrey Sosa-Calvo 2007

## Acknowledgements

I am deeply grateful to my thesis advisor, Dr. Ted Schultz, for his unconditional help, for his patience at times when the progress on this research was slow, for being an excellent mentor and friend, for allowing me the freedom to work at my own pace, and for being a constant source of encouragement and inspiration for me. These years under his advisorship have been a major contribution in favor of my intellectual and personal development. Thank you for all you have done for me! I would also like to thank the other members of my advisory committee: Drs. Charles Mitter and Maile Neel. Their valuable comments, suggestions, expertise, and helpful advice improved this work considerably.

I would like to thank past and present members of the Smithsonian Ant Laboratory, Drs. Sean Brady, John LaPolla, and Ted Suman, as well as Nor Faridah Dahlan, Stephanie Johnson, Matthew Kweskin, Eugenia Okonski, Katrina Pagenkopp, and Lauren Spearman for their continuous support, advice, and encouragement. I am equally indebted to past and present members of the Mitter Laboratory for help and discussions.

For the loan of specimens, I am indebted to Tania Arias (UNAL-ICN), C. Roberto F. Brandão (MZSP), R.S. Camargo, Enrique Castillo (IAvH), Jacques Delabie (CEPEC), George Else (BMNH), Fernando Fernandez (UNAL-ICN), Michael E. Kaspari (Oklahoma University), John T. Longino (Evergreen State University), Chris Marshall (Oregon State University), Christian Rabeling (University of Texas at Austin), Roy Snelling (LACM), and M. Verhaag (SMNK). I would like to thank Ryan Badal (IOL) for his help conducting fieldwork in Suriname, and Eugenia

Okonski and Ted Suman (NMNH-SI) for their help sorting, mounting, and databasing specimens. Leeanne Alonso (CI), Greg Love (CI), and Kenneth Tjon (CELOS) provided invaluable support while doing fieldwork in Suriname. I am thankful to Scott Whittaker (NMNH-SI), who assisted me with the SEM photographs and to Natalie Barnett (ANIC), who prepared the photographs of *Pyramica panamensis*. I want to give special thanks to Barry Bolton for confirming the identity of the new species.

For comments and suggestions on early versions of these chapters, I thank Leeanne Alonso (CI), Carlos R. Brandão (MZSP), Diego F. Campos (UNAL), Hermogenes Fernandez (STRI), David Furth (NMNH-SI), Victor H. Gonzalez (Kansas University), Akito Kawahara (University of Maryland), John. S. LaPolla (Towson University), John Lattke (MIZA), John. T. Longino (Evergreen State University), Christopher Marshall (Oregon State University), Charyn Micheli (University of Maryland), Carlo Moreno (University of Maryland), and David R. Smith (NMNH-SI).

Special thanks go to the staff of the Department of Entomology at the National Museum of Natural History, Smithsonian Institution, and to the staff of the Department of Entomology at the University of Maryland for their support, encouragement, help, and friendship.

For financial support, I am particularly indebted to Dr. Ted Schultz, the Amazon Conservation Association, the Andrew W. Mellon Research Exploration Award, the Rapid Assessment Program of Conservation International, and the Smithsonian Institution's Biological Diversity of the Guiana Shield Program.

I want to thank all my friends, inside and outside of the Departments of Entomology at the Museum and at the University, for making my time outside the office enjoyable and for their support and encouragement during my time as a graduate student. I want to especially thank my past and present roommates, whom have been like a second family to me.

Finally, I would like to thank my parents Maria del Carmen and Humberto and my brother Diego Andres, who from a distance provided constant support and encouragement, necessary to get through the toughest moments. My brother Diego always managed to put a smile on my face and was always there when I needed him.

## Table of Contents

Acknowledgements	ii
Table of Contents	v
List of Tables	vii
List of Figures	viii
CHAPTER 1: Ants of the leaf litter of two plateus in Eastern Suriname	1
Abstract	1
Introduction	
Materials and Methods	4
Study sites	4
Data collection	
Data analysis	
Results	
Species richness estimates	
Diversity estimates	
Discussion	
Implications in conservation	
Acknowledgments	22
CHAPTER 2: Review of the ant tribe Dacetini (Hymenoptera: Formicidae) in	
Guyana	
Abstract	
Introduction	
Materials and Methods	
Systematic treatment.	
Pyramica dahlani, NEW SPECIES	
Pyramica mariae, NEW SPECIES.	
Key to Dacetini known from Guyana	
Dacetini species of Guyana	
Acknowledgements	
CHAPTER 3: Dacetine ants of Panama: New records and description of a new	
species (Hymenoptera: Formicidae: Myrmicinae: Dacetini)	
Abstract	
Introduction	
Materials and Methods	
Taxonomic treatment	
Genus Pyramica Roger 1862	
Genus <i>Strumigenys</i> F. Smith 1860	
Checkingt of Daccini of Lanama	ol

Acknowledgements	83
CHAPTER 4: Review of the subfamily Proceratiinae (Hymenop	otera: Formicidae) in
Colombia	
Abstract	
Introduction	
Diagnosis	
Biology	
Composition of the subfamily	
Tribe Proceratiini	
Genus Discothyrea Roger	
Genus Proceratium Roger	
Tribe Probolomyrmecini	
Genus Probolomyrmex Mayr	
Acknowledgements	
CHAPTER 5: Description of three remarkable new species of the growing ant genus <i>Myrmicocrypta</i> , with notes about the genus <i>Myrmicocrypta</i> , with notes about the genus <i>Myrmicocrypta</i> , within Attini	nus and its position
within Attini	
Abstract	
Introduction	
Materials and Methods	
Taxonomic treatment	
The genus <i>Myrmicocrypta</i> Fr. Smith	
Myrmicocrypta camargoi, NEW SPECIES	
Myrmicocrypta erectapilosa, NEW SPECIES	
Acknowledgements	
Acknowledgements	141
Appendices	142
Bibliography	143

# List of Tables

Table 1.1. Richness estimates and other summary values for the two localities studin eastern Suriname	
Table 1.2. Number of shared species and values of similarity indices for two sites (three transects) in Suriname	.12
Table 1.3. Species and number of individuals, for each species, collected at each locality in Suriname.	
Table 2.1. Dacetine ant species currently known from Guyana	.67

# List of Figures

Figures 1. $1-3$ . Taxonomic composition of the combined survey: 1) Total number of ant species by subfamily collected at both sites. 2) The eleven most speciose ant genera collected at both sites. 3) The fifteen most individual-rich genera collected at both sites. 9
Figures 1. 4 – 6. Assessment of the leaf litter ant inventory for each site. 4) Lely transect 1, 5) Lely transect 2, and 6) Nassau. The species accumulation curve plots the number of species ( <i>Y</i> -axis) and the number of samples ( <i>X</i> -axis). Abbreviations: Uni= uniques, Dup= duplicates, SOB= species observed, ICE= incidence-based coverage estimator.
Figure 1. 7. Assessment of the leaf litter ant inventory for each site. Combined Lely transects. The species accumulation curve plots the number of species ( <i>Y</i> -axis) and the number of samples ( <i>X</i> -axis). Abbreviations: Uni= uniques, Dup= duplicates, SOB= species observed, ICE= incidence-based coverage estimator
Figure 1. 8. Sample-based rarefaction curves. The forty samples of the combined Lely transect were rarefied down to twenty samples. The graph shows that the observed species richness at Nassau is included in Lely's 95% confidence interval (dashed lines). However, it is possible that with more sampling from Nassau, the species accumulation curve could start diverging from the one at Lely and its respective confidence interval.
Figures 2. 1 – 5. Holotype worker of <i>Pyramica dahlani</i> , new species. 1, full-face (dorsal) view. 2, closed mandibles. 3, dorsal view of petiole and postpetiole. 4, dorsal view of mesosoma. 5, lateral view
Figures 2. 6 – 11. Full-face (dorsal) and lateral views of: holotype worker of <i>Pyramica mariae</i> , new species (6, 8, 10) and <i>P. denticulata</i> (7, 9, 11)
Figures 2. 12 – 13. Relationships between head width and length (12), and petiole length and Weber's length (13) among <i>Pyramica denticulata</i> , <i>P. mariae</i> , and <i>P. enopla</i> . Measurements in millimeters.
Figures 3. 1 – 6. Frontal and lateral views. 1 – 2, <i>Pyramica cincinnata</i> . 3 – 4, <i>P. denticulata</i> . 5 – 6, <i>Strumigenys perparva</i>
Figures 3. 7 – 12. Frontal and lateral views. 7 – 8, <i>Pyramica fridericimuelleri</i> . 9 – 10, <i>P. nigrescens</i> . 11 – 12, <i>P. panamensis</i>
Figures 3. 13 – 15. Dorsal views. 13, <i>Pyramica fridericimuelleri</i> . 14, <i>P. nigrescens</i> . 15, <i>P. panamensis</i>

Figures 4.1 – 5. 1, antennal insertions ( <i>Discothyrea</i> ). 2 – 4, habitus of <i>Discothyrea</i> , <i>Proceratium</i> , and <i>Probolomyrmex</i> . Mesosoma lacking a promesonotal suture. 5, antenna of <i>Discothyrea</i>
Figures 4.6 – 10. <i>Discothyrea</i> species in frontal view. 6, <i>Discothyrea humilis</i> . 7, <i>D. nr neotropica</i> . 8, <i>D. sexarticulata</i> . 9, <i>D. denticulata</i> . 10, <i>D. horni</i> 95
Figures 4.11 – 15. <i>Discothyrea</i> species in lateral view. 11, <i>Discothyrea humilis</i> . 12, <i>D. nr neotropica</i> . 13, <i>D. sexarticulata</i> . 14, <i>D. denticulata</i> . 15, <i>D. horni</i> 96
Figures 4.16 – 18. <i>Proceratium</i> and <i>Probolomyrmex</i> species in frontal view. 16, <i>Proceratium mancum</i> . 17, <i>P. micrommatum</i> . 18, <i>Probolomyrmex boliviensis</i> 102
Figures 4.19 – 22. <i>Proceratium</i> and <i>Probolomyrmex</i> species in lateral view. 19, <i>Proceratium mancum</i> . 20, <i>P. micrommatum</i> . 21, <i>Probolomyrmex boliviensis</i> . 22, <i>P. petiolatus</i>
Figures 5. 1 – 6. <i>Myrmicocrypta camargoi</i> , new species. 1, 3, and 5 worker habitus (1, full-face (dorsal) view; 3, profile; and 5, dorsal view). 2, 4, and 6 gyne habitus (2, full-face view; 4, profile; and 6, dorsal view)
Figures 5. 7, 9, and 11 male habitus of <i>Myrmicocrypta camargoi</i> , new species. 8, <i>M. camargoi</i> gyne fore and hind wing. 10, <i>M. camargoi</i> male fore and hind wing. 12, <i>M. erectapilosa</i> gyne fore and hind wing
Figures 5. 13 – 18. <i>Myrmicocrypta erectapilosa</i> , new species. 13, 15, and 17 worker habitus (13, full-face (dorsal) view; 15, profile; and 17, dorsal view). 14, 16, and 18 gyne habitus (14, full-face view; 16, profile; and 18, dorsal view)
Figures 5. 19 – 21. Habitus of worker of <i>Myrmicocrypta samperi</i> , new species. 19, full-face view. 20, lateral view. 21, dorsal view

#### **CHAPTER 1:**

# Ants of the leaf litter of two plateaus in Eastern Suriname

JEFFREY SOSA-CALVO 1,2

1 Maryland Center for Systematic Entomology, Department of Entomology, University of Maryland, 4112 Plant Sciences Building, College Park, MD, 20742; email: sossajef@si.edu

2 Department of Entomology, National Museum of Natural History, Smithsonian Institution, POB 37012, NHB, CE518, MRC 188, Washington, D. C. 20013-7012.

#### Abstract

Ants possess numerous qualities that make them useful for conservation planning. Ants are: 1) dominant constituents of most terrestrial environments, 2) easily sampled in sufficiently statistical numbers in short periods of time, 3) sensitive to environmental change, and 4) indicators of ecosystem health and of the presence of other organisms, due to their many obligate symbioses with plants and animals. This study presents an inventory of the ant fauna of two plateaus (Lely and Nassau mountains) in Eastern Suriname. Suriname's ant fauna remains largely unknown. Suriname's position within the Guiana Shield, considered the largest undisturbed region of tropical forest in the world, makes it one of the most important places for tropical forest conservation and sustainable development. Suriname, like other developing countries, faces urgent ecological problems that threaten its rich biodiversity.

I present here the results of a rapid assessment program survey of the ant fauna that inhabits the leaf litter, hoping that this information may inform critical conservation decisions by mining companies, governments, and individuals.

#### Introduction

Due to rapidly declining diversity and disappearing habitats worldwide, systematists and ecologists have created a series of protocols to rapidly explore, understand, and catalogue our planet's extensive living resources. Invertebrates are an important component of the trophic structure of every ecosystem. Among all the invertebrates that live in the forest, ants possess numerous qualities that make them a cornerstone element for conservation planning. Ants are (1) dominant constituents of most terrestrial environments, (2) easily sampled in sufficient statistical numbers in short periods of time (Agosti et al. 2000), (3) sensitive to environmental change (Kaspari and Majer 2000), (4) indicators of ecosystem health due to their negative response to fragmentation (Alonso 2000), and (5) indicators of the presence of other organisms, due to the rich variety of interactions between ants and other organisms (Alonso 2000, Schultz and McGlynn 2000). For these reasons ant taxonomists, ecologists, and behaviorists created the Ants of the Leaf Litter protocol (A.L.L.) (Agosti and Alonso 2000). A.L.L. is a standardized methodology that can be easily repeated in different habitats at different times of the year (Agosti et al. 2000). Under this protocol datasets from different localities can be combined and analyzed at a variety of scales.

The ant fauna of Suriname remains unknown. Borgmeier (1934) reported 36 ant species from a study in coffee plantations in Paramaribo; Kempf (1961) reported 171 ant species belonging to 59 genera based on collections made by der Drift from April to October of 1959. In that survey, der Drift used pitfall trap samples, leaf-litter samples using Berlese funnels, and soil samples from primary forest, agricultural

fields, and pastures. Previous censuses of the Neotropical ant fauna by Kempf (1972), Brandão (1991), and Fernandez and Sendoya (2004) recognize 290 species for Suriname. The New World tropics are known to contain one of the richest ant faunas in the world, with more than 3000 described species (Fernandez and Sendoya 2004). As sampling becomes more exhaustive, this upper limit continues to increase. The La Selva Biological Station provides an instructive example. As a result of more than ten years of continuous sampling, La Selva accounts for almost 450 species (Longino et al. 2002).

Suriname's position within the Guiana Shield, considered the largest undisturbed region of tropical forest in the world, makes it one of the most important places for tropical forest conservation and sustainable development. The most important and urgent threats faced by Suriname are: 1) large-scale bauxite and gold mining, 2) small-scale gold mining, 3) large-scale logging, and 4) hunting. As pointed out by Haden (1999) the principal cause of deforestation and pollution is mining at both large and small scales. The extraction of gold is associated with water poisoning due to the large quantities of mercury or cyanide used. Common techniques to extract gold (i.e., suction-dredge placer and hydraulic) are responsible for erosion, siltation, and water turbidity (Haden 1999). This increasing pressure from mining and other resource-extraction industries threatens the pristine nature not only of Suriname but also of the entire Guiana Shield.

I present the results of a rapid assessment program survey of the ant fauna that inhabit the leaf litter, hoping that the information presented here will inform critical conservation decisions by mining companies, governments, and individuals.

#### **Materials and Methods**

Study sites

The Lely and Nassau plateaus are located in eastern Suriname on the Guiana Shield near the border with French Guiana and east of the man-made Lake Brokopondo, created in 1864 by swamping about 580 square miles of virgin rainforest. The Lely Mountains comprise a series of plateaus with a maximum elevation of 700 m. A preliminary plant survey of the Lely mountains (ter Steege et al. 2004) showed two types of forest. The first is a high mesophytic rain forest characterized by relatively well-drained soil and high (25 – 50 m) closed canopy. This type of forest is dominated by tree-species within the genera *Eschweilera, Couratari, Lecythis, Sloanea, Hymenaea, Virola,* and *Qualea*.

The second type of forest, a mountain savannah forest, is characterized by very low tree diversity. The mountain savannah forest was divided into three subcategories by ter Steege et al. (2004): 1) a dry forest dominated by *Croton* spp., *Micrandra brownsbergensis, Vriesea splendes*, and large numbers of species within the family Myrtaceae; 2) a humid type dominated by *Vriesea* spp., mosses, and epiphytes; and 3) a low moss forest with all tree trunks covered by dark brown mosses.

The Nassau Mountains comprise four plateaus ranging from 500 to 570 m. Nassau plateaus include primary and secondary rain forest, 'berg savannah' dominated by *Hevea guianensis, Micrandra* sp., and several Myrtaceae species (Banki et al. 2003), and limited patches of *Euterpe oleracea*, a palm found on the plateau in swamp-like areas. Nassau is also characterized by rocky soils and some

cleared areas (roads and an overgrown airstrip).

#### Data collection

I used a modified version of the A.L.L. protocol as described in Agosti et al. (2000). Two-hundred-meter linear transects were delimited at each locality (Lely= 2 transects, Nassau= 1 transect). A 1 x 1-m quadrat was sampled every 10 m. The leaf litter, rotten twigs, and first layer of soil present in the quadrat were shaken for about a minute using a wire sieve of 1-cm²-mesh size. The sifted leaf litter was then placed in a mini-Winkler sack and allowed to run for 48 hours. (For further information and discussion about this technique, see Agosti et al. 2000:133.) The alcohol-preserved samples were sorted to morphospecies in the laboratory using a Leica MZ16 stereomicroscope. Specimens of each morphospecies were mounted and identified to named species whenever allowed by current ant taxonomy.

#### Data analysis

The computer program EstimateS (version 7.5 for Mac) (Colwell 2005) was used to calculate species accumulation curves. Curve-smoothing was accomplished by randomizing sample order 100 times (Toti et al. 2000; Colwell & Coddington 1994). EstimateS was also used to compute the means of non-parametric species richness estimators that require presence/absence (incidence) data. These estimators differ in the way they calculate rare species. The estimators used for this study were:

(1) ICE, Incidence-based Coverage Estimator (Lee and Chao 1994), which relies on incidence data to quantify rarity (i.e., the number of uniques and duplicates) based on

species found in ≤ 10 sampling units (Chazdon et al. 1998; Longino 2000). (2) Chao 2, which (Chao 1987) relies on the number of uniques, i.e. species found in only one quadrat, and the number of duplicates, i.e. species found in exactly two quadrats (Chazdon et al. 1998; Longino 2000). (3) First-order Jackknife (or Jackknife 1), which is based on the number of uniques and on the number of the quadrats sampled (Chazdon et al. 1998; Magurran 2004). (4) Second-order Jackknife (or Jackknife 2), which is similar to Chao 2 and is based on the number of uniques and duplicates and the number of quadrats sampled. (5) Bootstrap estimator, which is based on the proportion of quadrats containing each species (Smith and Van Belle 1984; Chazdon et al. 1998). Chazdon et al. (1998) offer a list of the formulas and citations for these estimators.

To compare the taxonomic composition of the two sites, two similarity indexes were used. The first was the Sorensen index of similarity:

$$S = 2c/(a+b)$$

where a= number of species in site A, b= number of species in site B, and c= number of shared species in sites A and B. This index is considered to be one of the most effective presence/absence similarity measures (Magurran 2004). The second index employed was the Jaccard index:

$$Si = c/a + b - c$$

where, a= total number of species in sample A, b= total number of species in sample B, c= number of common (shared) species to sample A and B (King and Porter 2005). This is a modified version of the Jaccard classic index:

$$S_i = c/a + b + c$$

where, a= number of species that are unique for sample A, b= the number of species that are unique for sample B, and c= number of shared species in sites A and B.

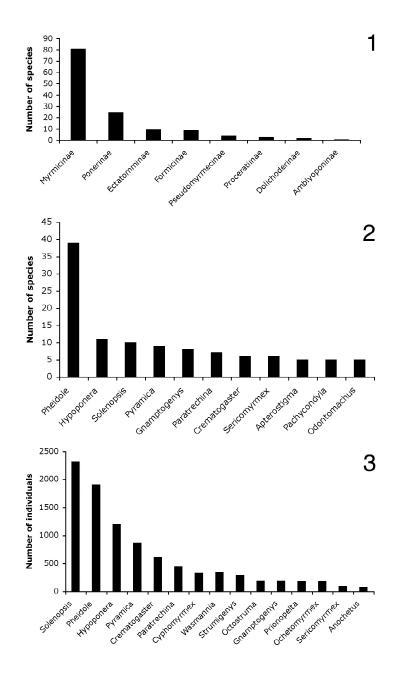
Due to the differences in sampling effort at the two sites (two transects at Lely and one at Nassau), sample-based rarefaction curves where computed using the program ECOSIM (version 7, for Windows) (Gotelli and Entsminger 2006) to compare total species richness between sites. Rarefaction estimates the species richness in a sub-sample of a size equal to that of the less-sampled site. The expected number of species is calculated using bootstrapped subsampling. Thus, the combined Lely transect (40 samples) was repeatedly subsampled in order to estimate the species richness present in a subset of 20 samples in order to compare it with Nassau (20 samples). Rarefaction curves were generated by random reordering (10000 pseudoreplicates).

#### Results

A total of 9484 individual ants were collected from 60 m<sup>2</sup> of leaf-litter samples (Table 1. 3). Of those 9484 individuals, 9298 worker specimens, representing 36 genera and 169 species, were collected. The combined transects at Lely accounted for 138 species whereas Nassau accounted for 96 species. The subfamily Myrmicinae (figure 1. 1) was represented by 81 species, followed by the Ponerinae with 25 species (48% and 15% of the total species, respectively). The most speciose genus (figure 1. 2) was *Pheidole* with 39 species (23% of the total) followed by the genera *Hypoponera* (11 species), *Solenopsis* (10 species), *Pyramica* (9 species), and *Gnamptogenys* (8 species). These four genera together accounted for 21.9% of the

total species richness. With respect to the number of individuals collected (figure 1. 3), *Solenopsis* ranks first (2316 individuals, 24.4% of total), followed by the genera *Pheidole, Hypoponera*, and *Pyramica* (1557 [16.4%], 1201 [12.7%], and 862 [9.1%] individuals, respectively). Among species, *Solenopsis* sp. 001 accounted for the largest number of individuals with 797 specimens collected, followed by *Pyramica denticulata* (767 individuals), and *Pheidole* sp. 006 (432 individuals).

This dataset contains a high number of unnamed morphospecies (102 out of 169 found), making it difficult to quantify the number of species that were not recorded by Kempf (1972) or Fernandez and Sendoya (2004), but it is estimated that at least 85 species (50.3% of the total species listed) represent new records for Suriname.



**Figures** 1. 1-3. Taxonomic composition of the combined survey: 1) Total number of ant species by subfamily collected at both sites. 2) The eleven most speciose ant genera collected at both sites. 3) The fifteen most individual-rich genera collected at both sites.

#### Species richness estimates

For none of the three individual transects (Lely= 2 and Nassau= 1), nor for the combined transects at Lely, does the randomized mean or the observed species accumulation curve reached an asymptote (Figures 1. 4-7). For Lely, on the one hand, the number of uniques (species detected in only one quadrat, regardless of their abundance within that quadrat) tends to reach a plateau or to continue increasing whereas the number of duplicates (species detected in only two quadrats) tends to decrease. For Nassau, on the other hand, the number of uniques tends to reach a plateau whereas the number of duplicates tends to increase. When both Lely transects are combined, both the number of uniques and the number of duplicates reach plateaus. The species estimator, ICE, for the combined Lely transects appears to approach an asymptote. However, for each of the transects considered separately the species estimator continues to increase, suggesting that more sampling is needed. Across the two sites, the greater number of species (138) was collected at Lely. In one Lely transect, 103 species were collected. For Nassau 96 species were recorded from a single transect. The data are inadequate for determining whether the difference in the numbers of species collected at the two sites reflects a genuine difference in species richness across the sites or whether it is an artifact of differing collection effort. Two separate 200-m transects of leaf litter samples were collected at Lely whereas a single 200-m transect was collected at Nassau. Rarefaction analysis (Figure 1. 8) found no difference between the species richness at both places. The figure suggests the possibility, however, that with more sampling at Nassau, the number of species observed might diverge from the lower 95% confidence limit for the

combined Lely transects. Previous studies of the diversity of the flora for both sites, including Brownsberg National Park, have shown that Lely contains a higher diversity while Nassau contains the lowest.

Richness estimates and other summary values for each transect, including the combined Lely leaf-litter sample, are listed in Table 1. 1. Each richness estimate is represented as the mean of 100 randomized iterations of sample order.

#### Diversity estimates

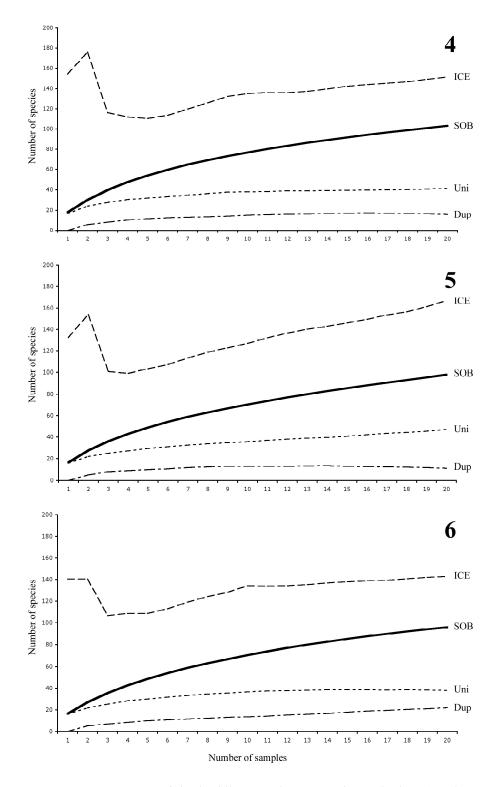
Values of the Sorensen similarity index and the Jaccard index (Table 1. 2) are equivocal about differences in species composition of the two communities (Lely vs. Nassau). The two transects at Lely share 64 species, whereas, based on separate comparisons between Lely transects 1 and 2 with Nassau, Lely and Nassau share a lower number of species (55 and 54, respectively). However, when both Lely transects are combined and compared with the one at Nassau, the number of shared species between Lely and Nassau increases to 67 species. This pattern is reflected by the value of each similarity index for both sites (Table 1. 2). Subjective comparison of the indexes computed for both sites suggests that the ant communities are similar. However, it is not possible to statistically analyze differences among the sites studied because the sample size is too small and because the observed species accumulation curves have not reached asymptotes for any of the three transects nor for the combined Lely transect. These results indicate that more sampling is needed at both sites to properly assess the number of species present.

 Table 1. 1. Richness estimates and other summary values for each locality.

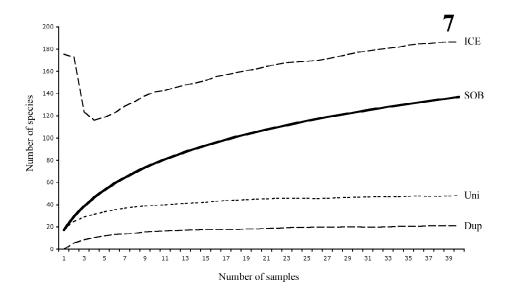
	Lely	Lely 2	Nassau	Lely (combined)
Observed richness	103	98	96	138
Number of samples	20	20	20	40
Number of adult workers	2730	2315	4253	5045
Number of uniques	41	47	38	48
Number of duplicates	16	11	22	21
ICE	151.4	166.77	142.87	186.61
Chao 2	155.53	178.41	128.82	191.86
Jackknife 1	141.95	142.65	132.1	183.8
Jackknife 2	165.21	175.57	147.54	209.96
Bootstrap Mean	120.31	116.68	112.74	157.91

**Table** 1. 2. Number of shared species and values of similarity indices for the two sites (three transects) in Suriname. See text for definition of indexes.

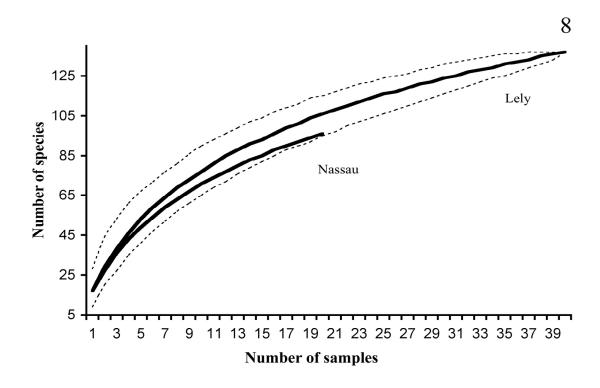
	Lely to Lely 2	Lely 1 to Nassau	Lely 2 to Nassau	Lely total to Nassau
Number of shared species	64	55	54	67
Sorensen's similarity	0.634	0.553	0.554	0.572
index				
Jaccard's similarity index	0.464	0.382	0.383	0.401



**Figures** 1. 4-6. Assessment of the leaf litter ant inventory for each site. 4) Lely transect 1, 5) Lely transect 2, and 6) Nassau. The species accumulation curve plots the number of species (*Y*-axis) and the number of samples (*X*-axis). Abbreviations: Uni= uniques, Dup= duplicates, SOB= species observed, ICE= incidence-based coverage estimator.



**Figure** 1. 7. Assessment of the leaf litter ant inventory for each site. Combined Lely transects. The species accumulation curve plots the number of species (*Y*-axis) and the number of samples (*X*-axis). Abbreviations: Uni= uniques, Dup= duplicates, SOB= species observed, ICE= incidence-based coverage estimator.



**Figure** 1. 8. Sample-based rarefaction curves. The forty samples of the combined Lely transect were rarefied down to twenty samples. The graph shows that the observed species richness at Nassau is included in Lely's 95% confidence interval (dashed lines). However, it is possible that with more sampling from Nassau, the species accumulation curve could start diverging from the one at Lely and its respective confidence interval.

#### Discussion

According to the censuses of Neotropical ants by Kempf (1972) and Fernandez and Sendoya (2004), Suriname possesses about 290 species. The few prior attempts to study the ant fauna of Suriname (Borgmeier 1934; Kempf 1961) report 54 genera and 171 species. Ant collecting in the interior in Suriname occurred sporadically from 1938 – 1958, conducted mainly by G. Geyskes in Paramaribo and Brownsberg Nature Park. The present survey was conducted in the eastern part of Suriname and recorded 169 ant species and morphospecies from three 200-m leaf litter transects (60 samples). Species richness estimators (figures 1. 4-7) suggest a much higher ant diversity for Suriname than indicated by any of the aforementioned studies. More leaf-litter samples from different localities within the country are needed to properly estimate Suriname's ant diversity and to develop future conservation strategies. Suriname's geographical position in the Guiana Shield, an ancient rock massif dating back to the Pre-Cambrian (~ 2.5 billion years ago) (Gibbs and Barron 1993), recommends it for biological resource conservation and sustainable development because of its large amount of remaining pristine forest. Approximately 90% of the total land area of Suriname remains intact or is only impacted to a limited extent by humans (Tropenbos International Suriname Program 2004).

Of all ecological communities, tropical rain forests are thought to have the greatest species diversity. In Costa Rica, for example, Longino et al. (2002) reported ca. 450 ant species in an area no greater than 1500 ha (La Selva Biological Station). LaPolla et al. (2007) recorded 230 species in eight localities in Guyana and estimated

a much higher ant diversity than the 330 species previously known for that country. Other surveys conducted in Borneo (Brühl et al. 1998) and Madagascar (Fisher 1999, 2005), with extensive field sampling over several years, have shown that the number of ant species is usually under-sampled. Based on these studies, extensive fieldwork will undoubtedly increase the number of ant species in Suriname.

The genus *Pheidole* is the most speciose genus at both sites, representing 23% of total ant species collected in this survey (with 39 species). The next most common genera Hypoponera, Solenopsis, Pyramica, and Gnamptogenys together accounted for almost 22% of total species collected (with 11, 10, 9, and 8 species, respectively) (figure 1. 2). The taxonomic dominance of *Pheidole* in most tropical forests is well known (Ward 2000, Wilson 2003) and the pattern found in Suriname is typical of leaf-litter samples taken at other localities in the Neotropics. In terms of the number of individuals collected per genus, *Pheidole* drops to second place with 1557 individuals. The genus *Solenopsis* ranked first with 2316 individuals collected. The genus, in which some species native from southern South America, has become of great economic importance worldwide due to their rapidly increasing range of expansion of its invasive species. In spite of its widespread distribution, the genus has not been taxonomically revised and the biology of many of its species remains unknown. Another ecologically dominant genus in Neotropical rain forests is Hypoponera, a prime candidate for conservation planning and long-term monitoring due to the distinct habitat preferences of its species, some preferring pristine forests and particular microhabitats and others preferring highly disturbed habitats (Longino 2007). However, the number of species identified here is likely underestimated due to

the lack of a taxonomical revision.

The rare ant genus *Thaumatomyrmex* was collected in Lely from four specimens (*T. ferox*). The biology of *Thaumatomyrmex* species been studied by Brandão et al. (1991), who showed that individuals use their enormous pitchfork-like jaws to remove the bristles that cover the body of polyxenid millipedes. This species was reported by LaPolla et al. (2007) from a very species-rich lowland forest and area of high endemism in Guyana.

The tribe Dacetini, which was recently revised by Bolton (2000), is represented in Suriname now by four genera, Acanthognathus, Daceton, Pyramica, and Strumigenys. According to Kempf (1972), Bolton (2000), and Fernandez and Sendoya (2004), this represents the first record of the genus *Acanthognathus* for Suriname. Within the genus *Pyramica*, there are five species that are here recorded for the first time for Suriname: P. auctidens (known previously from French Guiana), P. beebei (known from Colombia and Brazil), P. cincinnata (known from Brazil), P. crassicornis (known from Trinidad and Tobago to Paraguay), and P. halosis (known previously from Venezuela). Within the genus *Strumigenys*, two species are recorded for the first time: S. cosmostela (known from Mexico to Peru, including Brazil) and S. trinidadensis (known previously from Costa Rica to Brazil). A possible new species within the genus *Pyramica* was also collected. Members of the Dacetini tribe are promising tools for biodiversity planning. Their biology is relatively well-known, their taxonomy has been recently revised, and their diet is restricted to arthropods that inhabit the soil.

The recently established genus *Cryptomyrmex* Fernandez (Myrmicinae:

Adelomyrmicini), known from only two species from Brazil and Paraguay, was collected in Nassau. The species, *C. longinodus*, was originally described from soil samples from Brazil. Here, the distribution of the species and genus is extended. The biology of this intriguing ant remains unknown. The genus can easily be confused with *Adelomyrmex*, but close examination of the specimen reveals differences in the petiole and eyes, visible under light stereomicroscope, but not visible under Scanning Electron Micrography (SEM) (Fernando Fernandez, personal communication).

The data cannot reject the null hypothesis that differences in species richness between Lely and Nassau are due to the differing number of transects and samples collected (2 transects, 40 samples for Lely vs. 1 transect, 20 samples for Nassau). However, although rarefaction analysis indicates that the number of species observed for Nassau is contained within the 95% confidence interval for the estimated number of species at Lely, visual inspection of the species accumulation curve for Nassau suggests that it might, with more sampling, diverge from this interval (Figure 1. 8). Certainly the level of human-generated disturbance appears to be lower in Lely than in Nassau, where open roads, camps, mining, and hunting activities have resulted in a low animal population (ter Steege et al. 2005). If ant species richness in Nassau were lower than in Lely, this would accord with the results of ter Steege et al. (2004, 2005) and Bánki et al. (2003), which concluded that Nassau has the lowest plant diversity of the three areas, whereas Lely was the most diverse.

Similarity indices (Jaccard and Sorensen), although low, showed that the two samples within Lely are more similar to each other than either one is to Nassau (table 2). When the combined Lely samples are compared to Nassau, the number of shared

species between the two increases to 67. Although the indexes still suggest a low similarity between both sites, the fact that the species observed curve for both sites have not yet reached an asymptote, it is difficult to properly assess that the two sites are different. More sampling in this area is needed in order to statistically determine whether the ant communities at both sites differ or not.

#### Implications in conservation

With most of its landscape still intact, the time for Suriname to take action is now, before deforestation and mining become more widespread. Although the extraction of some natural resources is certain to happen, the rich fauna and flora of Suriname can be preserved with planning and with the creation of protected areas, such as the Central Suriname Nature Reserve. As demonstrated by Agosti et al. (2000), ants of the leaf litter can be important tools for conservation planning. Due to the large number of unnamed species found in this survey and to the low number of samples, it is difficult to properly assess the differences between the ant communities in both places. The presence of *Thaumatomyrmex atrox* in Lely, known to occur in relatively species-rich forests and in areas of high endemism (LaPolla et al. 2007), could indicate such an ecosystem. Based on the results reported here, I recommend conducting a more rigorous monitoring study with a larger number of samples from both localities, with the goal of properly evaluating the ant community present in each habitat, properly identifying species that reflect ecosystem health, and properly addressing conservation planning in both areas.

I observed the impact of several human-driven activities (logging, mining, and

hunting) on the physical environment at both places, clearly more significant at

Nassau. Ant communities are known to respond negatively to the loss of plant
diversity and to changes in soil microclimate resulting from deforestation

(Underwood and Fisher 2006). Although deforestation is not yet widespread at either

Lely or Nassau, I recommend the maintenance of large areas of intact primary forest
to serve as reservoirs of keystone species.

As pointed out by ter Steege (2005), constant pressure from mining activities in the surrounding areas of Nassau has resulted in a very low animal population, due to the hunting that accompanies small-scale mining. I observed that in Lely the pressure of such activity on mammals and birds is significant. Due to only a few people, small mammals, birds, and monkeys, among others, where found dead near the trails used by the local airstrip work crew. It is imperative that local people be educated to properly use their natural resources.

The conservation of these still-healthy forests should be a principal goal for the government, the mining companies, and the Surinamese people. One of the largest and richest pristine forests in the world remains intact within Suriname's borders, but it is threatened by uncontrolled logging, hunting, and mining. The enforcement of high environmental standards on resource extraction companies and of strong sanctions on illegal resource exploitation are needed in order to preserve the biodiversity of the Guiana Shield in Suriname.

## Acknowledgements

I would like to thank Ryan Badal (IOL) for his help during the fieldwork and Eugenia Okonski for her help sorting, mounting, and databasing the specimens. Greg Love (CI) and Kenneth Tjon (CELOS) provided invaluable logistical support. John LaPolla (NMNH) helped with statistics and discussions about ant diversity of the Guiana Shield. Ted Schultz (NMNH) made comments and suggestions on early versions of this report. I am indebted to Leeanne Alonso (CI) for the invitation to participate in this RAP.

**Table** 1. 3. Species and number of individuals, for each species, collected at each locality.

Species	Lely transect 1	Lely transect 2	Nassau
Acanthognathus lentus	2		
Acanthognathus ocellatus	4		
Acromyrmex sp. 001	1	1	
Acromyrmex sp. 002	8		
Acropyga guianensis			14
Anochetus horridus	4	1	7
Anochetus inermis	20	33	
Anochetus mayri	2		]
Anochetus targionii	11		
Apterostigma pilosum sp. 001		7	
Apterostigma pilosum sp. 002	4		
Apterostigma pilosum sp. 003			
Apterostigma pilosum sp. 004	24		1
Apterostigma pilosum sp. 005			3
Brachymyrmex sp. 001	7	5	24
Brachymyrmex sp. 002		1	
Brachymyrmex sp. 003	2		
Carebara sp. 001	1		
Carebara sp. 002	3		:
Carebara reticulata	20		
Carebara urichi	6		18
Crematogaster sp. 001	Ç	52	20
Crematogaster sp. 002	28	0-2	
Crematogaster sp. 003	99	4	
Crematogaster limata	18	5	
Crematogaster sotobosque	54	83	6
Crematogaster tenuicula	5.	3	Ü
Cryptomyrmex longinodus		3	
Cyphomyrmex cf. peltatus	25	21	6
Cyphomyrmex cirpenanas Cyphomyrmex rimosus	48	124	4
Discothyrea denticulata	5	121	•
Discothyrea sexarticulata	3	1	
Discothyrea sp. 001		1	
Dolichoderus imitator	3		•
Dolichoderus sp. 001	3		5
Ectatomma lugens			3
Ectatomma tugens Ectatomma tuberculatum	1		
Gnamptogenys horni	13	6	1:
Gnamptogenys interrupta	13	4	1.
Gnamptogenys moelleri	1	5	9
Gnamptogenys moettert Gnamptogenys pleurodon	59	1	1
Gnamptogenys relicta	39	1	4:
Gnamptogenys reticia Gnamptogenys sulcata	15		4.
Gnamptogenys tortulosa Gnamptogenys sp. 001	1		
Gnamptogenys sp. 001	1	13	
Hylomyrma sp. 001	1	13	3
Hylomyrma sp. 002			2
Hylomyrma sp. 003	02		1:
Hypoponera nitidula	92	4	50
Hypoponera sp. 001	121	1	3:
Hypoponera sp. 002	25		2;
<i>Hypoponera</i> sp. 003	3		

Species	Lely transect 1	Lely transect 2	Nassau
Hypoponera sp. 004	44	64	3
<i>Hypoponera</i> sp. 005	29	4	1
<i>Hypoponera</i> sp. 006	37	28	143
<i>Hypoponera</i> sp. 007	33		
<i>Hypoponera</i> sp. 008	21	4	52
<i>Hypoponera</i> sp. 009	97	108	174
<i>Hypoponera</i> sp. 010	1		
Leptogenys sp. 001	1		
Megalomyrmex sp. 001	3		5
Megalomyrmex sp. 002			1
Myrmelachista cf. mexicana			1
Ochetomyrmex sp. 001	93	39	52
Octostruma balzani	35	61	72
Octostruma iheringi	6		
Octostruma sp. 001		8	1
Octostruma sp. 002	1	7	
Odontomachus brunneus	2	3	17
Odontomachus hastatus			1
Odontomachus laticeps			1
Odontomachus scalptus			1
Odontomachus sp. 001	3	1	
Pachycondyla constricta	1	1	6
Pachycondyla harpax	6	9	
Pachycondyla pergandei	4		
Pachycondyla stigma		1	
Pachycondyla unidentata			9
Paratrechina sp. 001			10
Paratrechina sp. 002			70
Paratrechina sp. 003	27	98	138
Paratrechina sp. 004	7		
Paratrechina sp. 005	20		76
Paratrechina sp. 006			4
Paratrechina sp. 007	1	1	·
Pheidole sp. 001	11	8	19
Pheidole sp. 002		5	
Pheidole sp. 003		1	
Pheidole sp. 004		2	
Pheidole sp. 005	133	81	178
Pheidole sp. 006	29	173	261
Pheidole sp. 007	2)	5	201
Pheidole sp. 008		4	1
Pheidole sp. 009		2	1
Pheidole sp. 010		2	
Pheidole sp. 010		3	
Pheidole sp. 012	12	8	
Pheidole sp. 013	16	O	2
Pheidole sp. 013 Pheidole sp. 014	16	5	2
Pheidole sp. 015	3	10	
Pheidole sp. 015  Pheidole sp. 016	3	9	26
	7.4		20
Pheidole sp. 017	74	19	
Pheidole sp. 018	2	12	
Pheidole sp. 019	27	5	2
Pheidole sp. 020	27	6	215
Pheidole sp. 021	97	136	215
Pheidole sp. 022		24	

Species	Lely transect 1	Lely transect 2	Nassau
Pheidole sp. 023	22	6	94
Pheidole sp. 024		18	
Pheidole sp. 025	11	3	
Pheidole sp. 026			5
Pheidole sp. 027	1	1	
Pheidole sp. 028	1		
Pheidole sp. 029	16	2	
Pheidole sp. 030		1	14
Pheidole sp. 031	1	1	5
Pheidole sp. 032		2	15
Pheidole sp. 033	5	11	21
Pheidole sp. 034	1		
Pheidole sp. 035			1
Pheidole sp. 036		1	
Pheidole sp. 037			1
Pheidole sp. 038	1		
Pheidole sp. 039			1
Prionopelta amabilis	81	1	103
Pseudomyrmex sp. 001			3
Pseudomyrmex sp. 002			2
Pseudomyrmex sp. 003		1	
Pseudomyrmex sp. 004		1	
Pyramica auctidens	1	18	16
Pyramica beebei		10	
Pyramica cincinnata		11	
Pyramica crassicornis		1	
Pyramica denticulata	189	98	480
Pyramica halosis		3	5
Pyramica subedentata			22
Pyramica sp. 001	1	6	
Pyramica sp. 002		1	
Rogeria blanda			2
Rogeria curvipubens			11
Rogeria innotabilis	1		
Rogeria micromma		1	1
Sericomyrmex beniensis	4	7	
Sericomyrmex harekulli arawakensis	3		
Sericomyrmex impexus		10	1
Sericomyrmex myersi	7	1	
Sericomyrmex zacapanus	1	52	7
Sericomyrmex sp. 001			1
Solenopsis sp. 001	229	198	370
Solenopsis sp. 002	49	171	3
Solenopsis sp. 003	14	60	388
Solenopsis sp. 004	172	27	98
Solenopsis sp. 005	17	88	244
Solenopsis sp. 006	1,	47	23
Solenopsis sp. 007	17	24	15
Solenopsis sp. 007	31	27	13
Solenopsis sp. 000 Solenopsis sp. 009	3	21	
Solenopsis sp. 009 Solenopsis sp. 010	3	1	
Strumigenys cosmostela		4	
Strumigenys cosmosteta Strumigenys elongata	18	17	18
Strumigenys etongata Strumigenys perparva	114	61	49
Strumigenys perpurva Strumigenys trinidadensis	114	1	2
Strumtgenys trintadaensis	I	1	

Species	Lely transect 1	Lely transect 2	Nassau
Thaumatomyrmex ferox	4		
Trachymyrmex cf. bugnioni			17
Trachymyrmex sp. 001	3		
Tranopelta gilva			1
Wasmannia auropunctata	189	59	83
Wasmannia rochai			3
Wasmannia scrobifera	1	11	

### **CHAPTER 2:**

# Review of the ant tribe Dacetini (Hymenoptera: Formicidae) in Guyana

JEFFREY SOSA-CALVO 1,2, TED R. SCHULTZ 2, and JOHN S. LAPOLLA3

- 1 Maryland Center for Systematic Entomology, Department of Entomology, University of Maryland, 4112 Plant Sciences Building, College Park, MD, 20742; email: sossajef@si.edu
- 2 Department of Entomology, National Museum of Natural History, Smithsonian Institution, POB 37012, NHB, CE516, MRC 188, Washington, D. C. 20013-7012; email: <a href="mailto:schultzt@si.edu">schultzt@si.edu</a>
- 3 Department of Biological Sciences, Towson University 8000 York Road, Towson, Maryland 21252; email: jlapolla@towson.edu

## **Abstract**

The dacetine ants of Guyana are reviewed. One newly recorded genus, *Acanthognathus*, is added to the three dacetine genera previously known from Guyana. A total of 25 species of dacetine ants are reported from Guyana, 15 of which are new records. Among these 15 species, two new species of *Pyramica* are described, *P. dahlani* and *P. mariae*. *Pyramica dahlani* is remarkable because it lacks propodeal spines and possesses a very distinctive mandible morphology. *Pyramica mariae* belongs to the *gundlachi*-group and is probably closely related to *P. denticulata*. *Pyramica denticulata* is illustrated in order to show morphological differences from *P. mariae*. A key to the Guyana species and a modification version of Bolton's (2000) key are provided.

## Resumen

La hormigas dacetinas para Guyana son estudiadas. El género *Acanthognathus* es adicionado a los tres géneros de hormigas dacetinas conocidos anteriormente para Guyana. En total 25 especies son reportadas aquí para Guyana, de las cuales 15 constituyen nuevos registros para el país. Dentro de estos nuevos registros, se describen aquí dos nuevas especies en el género *Pyramica*, *P. dahlani* y *P. mariae*. *Pyramica dahlani* es fácilmente reconocida por la carencia de espinas en el propodeo y su distintiva morfología mandibular. *Pyramica mariae* pertenece al grupo *gundlachi* y está probablemente relacionada con *P. denticulata*. *Pyramica denticulata* es ilustrada tambien con el fin de mostrar las diferencias morfológicas que la separa de *P. mariae*. Una clave para identificar las especies de hormigas dacetinas que ocurren en Guyana es suministrada, al igual que modificaciones a la clave de Bolton (2000) para incluir las nuevas especies.

Keywords: Dacetini, *gundlachi*-group, leaf-litter survey, Myrmicinae, Neotropics, taxonomy.

## Introduction

Ants of the tribe Dacetini (subfamily Myrmicinae) vary greatly in size, morphology, and behavior (Hölldobler and Wilson 1990) and inhabit rotten wood, leaf-litter, soil, and trees (Hölldobler and Wilson 1990; Bolton 1998). With their striking morphological features and cryptic habits, the dacetine ants have long fascinated myrmecologists. The snapping mechanism of the mandibles in dacetine ants has been studied extensively (e.g., Acanthognathus Mayr [Dietz and Brandao 1993; Gronenberg et al. 1998]; Daceton armigerum (Latreille) [Gronenberg 1996]; Strumigenys F. Smith [Brown and Wilson 1959; Masuko 1984; Dejean 1987; Gronenberg 1996]). Bolton (1999) surveys mandibular morphology for all dacetine genera, categorizing mandibular action into two modes, kinetic and static pressure. Enigmatic spongiform tissue is encountered on the petiole, postpetiole, and first gastral segments of dacetine ants in the species Colobostruma cerornata Brown and in the genera *Pyramica* Roger and *Strumigenys*. It has been variously hypothesized that this tissue produces an allomone that is attractive to springtails (Collembola) on which most members of the tribe feed (Dejean 1985a), that it produces a pheromone necessary for nestmate recognition, or that it is involved in some kind of bacterial symbiosis (Kantarovich et al. 2006). In addition to springtails, some dacetine species consume a diverse variety of small arthropods (Wilson 1953; Dejean 1985b; Bolton 1998). Masuko (1984) suggested that the bizarre pilosity adorning the heads and bodies of most dacetine species serves to accumulate soil and other detritus, camouflaging the ants from their prey.

The ant tribe Dacetini (Formicidae: Myrmicinae) was constructed by Forel (1892; 1893a) and, since then, numerous authors have added new genera and species (Mann 1926; Wheeler 1927; Santschi 1931; Weber 1934; 1941; Donisthorpe 1948; 1949; and Brown 1948; 1949; among others). The tribe has been the subject of multiple generic-level monographic works by Brown (1948; 1949a, b, c; 1950a, b; 1952; 1953a, b; 1954; 1959a, b; 1964), Brown and Wilson (1959), and Brown and Kempf (1969), providing a detailed definition of the tribe, creating subtribes, creating new genera, and transferring some genera and species to the closely related tribe Basicerotini.

In the last decade, major changes in dacetine taxonomy have been proposed within a phylogenetic context. Baroni-Urbani and de Andrade (1994) expanded the tribal definition to include the tribes Basicerotini and Phalacromyrmicini (Myrmicinae) and synonymized the genus *Pyramica* under *Strumigenys*.

Subsequently, Bolton (1998; 1999) provided evidence supporting the monophyly of the tribe separate from the tribes Basicerotini and Phalacromyrmecini, revived from synonymy the genera *Mesostruma* Brown and *Pyramica*, and reduced the number of genera from 26 to 9, making the most dramatic changes in *Pyramica* and *Strumigenys*. Despite this extensive taxonomic reorganization, Bolton expressed concern that morphological data were insufficient to resolve the relationships of particular genera, and hoped that "perhaps when molecular data or even suitable characters from larvae and males are acquired, then the problem may become capable of resolution" (Bolton 1999; 2000). The most recent global revision of the tribe

(Bolton 2000) includes nearly 900 species, arranged in nine genera, of which 189 species, belonging to four genera, occur in the New World tropics.

Despite or perhaps because of extensive recent taxonomic work on the tribe, new species are still being discovered (Deyrup 2006; Sosa-Calvo et al. 2006). Bolton (2000) and Fernandez and Sendoya (2004) reported three dacetine genera and 10 species for Guyana. As a result of a recent leaf-litter survey in Guyana, here we increase the number of Guyana's dacetine ant species to 25, describe two new *Pyramica* species, and report for the first time *Acanthognathus* from the country.

### Materials and Methods

Specimens were examined and measured to the nearest 0.001 mm at various magnifications using a Leica MZ125 light stereomicroscope. All measurements are in millimeters, unless noted otherwise. Specimens were photographed using a JVC KY-F70B video camera mounted on a Leica M420 steromicroscope attached to an IBM Intellistation M Pro computer, on which composite images were assembled using Auto- Montage Pro Version 5.03.0018 BETA software® (Synoptics Ltd.). Images were cropped and enhanced using Photoshop CS2 Version 9® (Adobe Inc.). Scanning Electron Micrographs (SEM) of uncoated specimens were taken using a Philips XL-30 ESEM with LaB6 and a backscatter detector. Morphological terminology and abbreviations employed throughout follow Bolton (1994; 2000), with modifications where noted. Anatomical abbreviations are as follows:

- CI Cephalic Index: (HW/HL) X 100.
- GL Gaster Length: the length of the gaster in lateral view from the anteriormost point of first gastral segment (third abdominal segment) to the posteriormost point.
- HL Head Length: the length of the head in full-face (dorsal) view, including the occipital lobes and the anterior clypeal margin, excluding the mandibles.
- HW Head Width: the maximum measurable width of the head in full-face view, excluding the eyes.
- MI Mandibular Index: (ML/HL) X 100.
- ML Mandible Length: the exposed length of the closed mandibles, in full-face view, from the anterior clypeal margin to the apex of the mandibles.
- PI Petiolar Length Index: (PL/WL) X 100.
- PL Petiole Length: the straight line from the posterior-most margin of the petiole to the posterior-most margin of the metapleural lobe, in lateral view.
- PPL Postpetiole Length: the maximum length of the postpetiole in lateral view.
- PW Pronotal Width: the maximum measurable width of the pronotum in dorsal view.
- SL Scape Length: the maximum length of the antennal scape, excluding the condylar bulb.
- SI Scape Index: (SL/HW) X 100.
- TL Total Length: HL+ML+WL+PL+PPL+GL.

WL Weber's Length: the length of the diagonal connecting, in lateral view, the antero-dorsal angle of the pronotum to the posterior-most basal angle of the metapleuron. (= Alitrunk Length in Bolton [2000].)

Specimens examined were borrowed from and/or have been deposited in the following institutions:

BMNH: The Natural History Museum, London. U.K.

UGBC: Centre for the Study of Biological Diversity, University of Guyana, Georgetown, Guyana.

MCZC: Museum of Comparative Zoology, Harvard University, Cambridge, MA., U.S.A.

MZSP: Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil
USNM: National Museum of Natural History, Smithsonian Institution, Washington,
D.C., U. S. A.

## **Systematic treatment**

Pyramica dahlani Sosa-Calvo & Schultz, new species (Figures 2. 1–5)

Holotype worker, labeled: "GUYANA: Calm Water Creek along Essequibo River nr. Bartica; 58° 37.16' W 6° 28.06' N; 24.ix.2002; J.S. LaPolla; primary forest; litter sample." USNM ENT No. 00442119. (Deposited in UGBC.)

Paratype worker, labeled: "GUYANA: Mabura Hill camp at end of Rd. from Georgetown to Letham Rd.; 64 m; 58° 41.982' W 5° 9.313' N; 29 x 2002; J.S.

LaPolla et al.; primary forest; litter sample." USNM ENT No. 00441577. (Deposited in USNM.)

Diagnosis (worker): very small (TL= 1.38–1.42); eyes absent; mandibles linear, elongate, and in closed position leaving a gap between the basal mandibular teeth and the anterior portion of the clypeus; propodeum unarmed; ventral portion of the petiole lacking spongiform tissue.

Description (worker): *Head*: in full-face view, clypeus slightly concave anteriorly, with long apical spoon-shaped hairs extending over mandibular gap; mandibles sublinear and elongate; at full closure, mandibles contacting only in the apical halves of their lengths, leaving a gap between them basally; mandibles with total dental count of 10, the basal tooth acute, the rest rounded and flattened; teeth 1, 3, 5, 7, 9, and 10 larger than the rest; lateral dorsum of mandible with appressed simple hairs; eyes absent; sculpture on clypeal plate imbricate; sculpture on cephalic dorsum areolate and covered with flattened, spoon-shaped hairs; hairs on anterior margin (leading edge) of the scape spoon-shaped and directed basad; antennal scape narrowed basally, anterior margin of antennal scape abruptly expanded, being distinctly widest at the point of expansion; apicoscrobal hair absent. *Mesosoma*: dorsum of anterior portion of pronotum hairless; pronotal humeral hair absent; dorsum of promesonotum and dorsum and declivity of propodeum entirely areolate; propodeum lacking spines or denticles at its posterior margin; mesopleuron and metapleuron smooth and shiny; dorsal portion of mesosoma covered with appressed

spoon-shaped hairs (as on head) without erect hairs of any kind, lateral portions

hairless. *Metasoma*: petiole lacking ventral spongiform lobe, petiolar disc areolate

and covered with slightly appressed simple hairs; lateral surface of petiolar peduncle

smooth and shiny; ventral surface of petiole weakly sculptured; disc of postpetiole

weakly sculptured and shiny, covered with setae similar to those on petiole, but

narrower; ventral surface of postpetiole with a well-developed spongiform lobe

extending throughout entire length; lateral spongiform tissue overhanging the ventral

spongiform lobe; dorsal surface of first gastral segment smooth with some

longitudinal basigastral costulae. Individuals light yellow to dark yellow. Setae

throughout body lighter than integument.

Measurements: holotype and paratype: CI= 79 (82), HL= 0.34, HW= 0.28 (0.27),

MI= 26, ML= 0.09, PW= 0.18 (0.19), SI= 57 (59), SL= 0.16, TL= 1.38 (1.42), WL=

0.36(0.39). (n=2)

Etymology: Named after Ms. Nor Faridah Dahlan in recognition of her expertise and

hard work in support of Smithsonian ant research and in gratitude for her consistent

good will and friendship. JSC is deeply grateful to Faridah for all her help and care

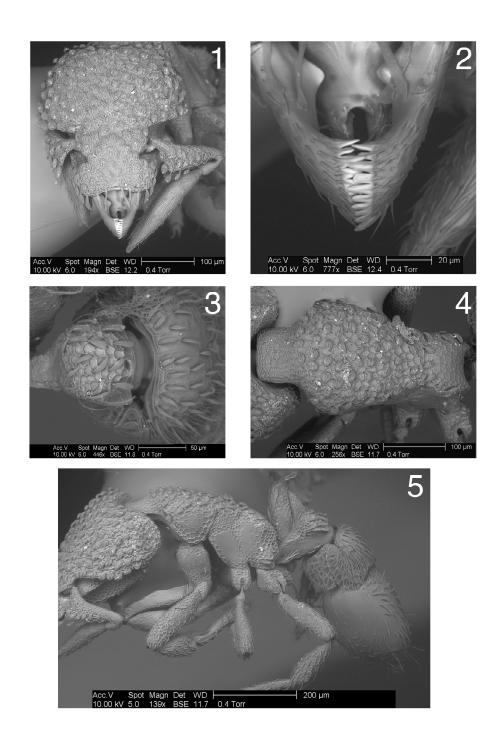
when he arrived in the United States for the first time.

Gyne and male: Unknown

35

Comments: *Pyramica dahlani* n. sp. seems to be related to members of the Nearctic *pergandei*-group, which includes: *P. angulata* (M.R. Smith), known from the southeast United States and Illinois, and *P. pergandei* (Emery), more widely distributed (Canada and United States). *Pyramica dahlani* shares with those species the following characters: i) mandibles short (MI=25–35) and, in frontal view, narrow and elongate, dentate only at the apical portion where they are in contact, leaving an edentate gap between them; ii) specialized mandibular dentition; iii) lateral clypeal margins, in dorsal view, extending beyond the line of the outer margin of the mandibles when closed; and iv) preocular carina broad and conspicuous. *Pyramica dahlani* differs from the species in the *pergandei*-group in four character states: i) total dental count 10 (15–16 in the *pergandei*-group), ii) lack of triangular teeth on the propodeum, iii) lack of a well-developed spongiform tissue on the ventral portion of the petiole, and iv) shorter antennal scape.

The mandibles of *P. dahlani* are similar to those within the *pergandei*-species group in that they contact in the apical third, producing a basal gap between the mandibles. This condition is different from the one found in species in the *ohioensis*-group, in which the masticatory margins contact through almost their entire lengths, and in which the mandibles are triangular rather than elongate. Elongated mandibles can be found in *gundlachi* and *argiola*-groups, the latter an Old World group introduced into the United States (*P. hexamera*). Mandibles in *P. hexamera* (Brown) are highly distinctive with an elongate and spiniform apicodorsal tooth and two long preapical teeth (see Bolton [2000] for further information). Species of the *gundlachi*-group share with *P. dahlani* the lack of a spongiform lobe on the ventral surface of



**Figures** 2. 1 - 5. Holotype worker of *Pyramica dahlani*, new species. 1, full-face (dorsal) view. 2, closed mandibles. 3, dorsal view of petiole and postpetiole. 4, dorsal view of mesosoma. 5, lateral view.

the petiole, but differ from *P. dahlani* in: i) mandibular length and morphology, ii) the presence of a pair of triangular teeth or short spines on the propodeum, and iii) the presence of pronotal humeral hairs and, in almost all species, a pair of laterally projecting apicoscrobal hairs.

Pyramica dahlani may also be related to P. paradoxa Bolton, known from a single worker individual collected in Costa Rica. Both species share the absence of propodeal spines; however, P. dahlani can be distinguished from P. paradoxa by the shape of the mandibles, and, in P. dahlani, the head and mesosoma strongly areolate with meso- and meta- pleuron smooth and shining. The head and mesosoma are mostly glabrous and shining in P. paradoxa. Although P. dahlani is not easily placed in any of the species groups defined by Bolton (2000), we hesitate to create a new species group and for now consider this new species incertae sedis.

# Modified version of key in Bolton (2000)

Pyramica dahlani will not key out to any known Pyramica species in either the Neartic or the Neotropical keys of Bolton (2000). The key to the Neotropical species can be modified as below to include P. dahlani. Numbering of key couplets follows Bolton (2000).

- 7. Dorsum of postpetiole (= disc) smooth and with weak costulae ... 7b
- Dorsum of postpetiole entirely reticulate-punctate... 12 (couplet 12 in Bolton)
- 7b. Cephalic dorsum with 1 or 2 pairs of standing hairs. Apicoscrobal and pronotal humeral hairs present ... 8 (couplet 8 in Bolton)
- Cephalic dorsum lacking standing hairs. Apicoscrobal and pronotal humeral hairs

Pyramica mariae Sosa-Calvo & Schultz, new species (Figures 2. 6, 8, and 10)

Holotype worker, labeled "GUYANA: Mt. Ayanganna montane forest; 1300 m; 59° 57.969' W 5° 22.483' N; 13.x.2002; T.R. Schultz, J. LaPolla, C. Marshall, R. Williams; litter sample." USNM ENT No. 00413858. (Deposited in UGBC.) Paratype 3 workers, same locality as in holotype. USNM ENT No. 00413859, 00442882, 00442883. (Deposited in MCZC and USNM.)

Diagnosis (worker): mandibles linear, elongate, and narrow; inner margin of mandibles with two clearly defined teeth, which are larger than the rest; labral lobes short with long trigger hairs at their apices; metapleuron smooth and shining; ventral portions of petiole and postpetiole lacking spongiform tissue.

Description (worker): possessing characters of the *gundlachi*-group and *gundlachi*-complex (Bolton 2000). *Head:* in full-face view nearly as broad as long; inner margin of the elongate mandibles slightly concave to more or less straight, with 4 teeth on the left mandible and 3 on the right, of which a pair of teeth are larger on each mandible (same in paratype); with 2 minute intercalary denticles between the apicodorsal and apicoventral fork teeth; labral lobes short, almost invisible in full-face view; trigger hairs long; eyes with 3 ommatidia in the longest row, with 6–7 ommatidia in total. Cephalic dorsum with a pair of erect hairs located near the posterior margin and with

another pair anterior to this; each upper scrobal margin with a short apicoscrobal hair

that projects laterally. *Mesosoma*: pronotum with a pair of short humeral hairs that

project laterally; mesonotum with a pair of short, erect, stiff hairs; mesopleuron and

metapleuron mostly smooth and shiny; dorsum of promesonotum, propodeum, and

propodeal declivity strongly reticulate. *Metasoma*: peduncle of petiole long, length of

petiole 3–3.5 times longer than its disc; petiolar disc reticulate-punctate, with a pair of

erect hairs on the posterior portion of the disc; ventral portion of petiole lacking

spongiform tissue; disc of postpetiole reticulate, ventral portion of postpetiole lacking

spongiform tissue; posterior portion of postpetiole disc with a row of 4 erect hairs;

first gastral tergite almost entirely reticulate except for a small portion at the posterior

portion of the tergite. Individuals light brown to brown.

Measurements: holotype and paratype: CI= 81 (78–92), HL= 0.52 (0.48–0.50), HW=

0.42 (0.38–0.46), MI= 73 (72–75), ML= 0.36 (0.36–0.38), PW= 0.27 (0.23–0.24),

SI= 71 (65–82), SL= 0.30 (0.30–0.31), TL= 2.47 (2.24–2.28), WL= 0.58 (0.55–0.56).

(n=4)

Etymology: Named in honor of the first author's mother, Maria del Carmen Calvo, in

gratitude for her encouragement and support.

Gyne and male: Unknown

40

Comments: *Pyramica mariae* n. sp. is clearly a member of the *gundlachi*-group (refer to Bolton [2000: 176–179 p.] for further information). Within the *gundlachi*-group, Bolton (2000) identified two complexes, *crassicornis* and *gundlachi*. *Pyramica mariae* belongs to the *gundlachi* complex and resembles *P. denticulata* (Mayr), *P. enopla* Bolton, and *P. vartana* Bolton. *Pyramica mariae* shares with *P. vartana* the smooth and shiny mesopleuron and metapleuron, but *P. mariae* can be distinguished from *P. vartana* by the form of apicoscrobal and pronotal humeral hairs, both short and stiff rather than long and filiform, and the disc of the postpetiole reticulate rather than smooth and shining.

Pyramica mariae is of similar size and color as P. enopla. However, P. mariae differs from P. enopla in that the apicoscrobal, humeral, and mesonotal hairs are short, erect, and stiff rather than long and filiform; the metapleuron is smooth and shining rather than reticulate; the dorsum of the petiole bears a single pair of hairs rather than two pairs of hairs; and the dorsum of the postpetiole lacks an anterior pair of hairs, which is present in P. enopla.

Pyramica mariae can easily be confused with P. denticulata (Figures 2. 7, 9, and 11), with which it shares the most character states. However, they can be separated by: i) Mandibular dentition: P. denticulata has 5–10 preapical denticles of similar size while P. mariae has 3–4 preapical denticles, two of which are larger than the rest. In Pyramica mariae, at least in the two specimens examined, there are 4 teeth on the left mandible and 3 teeth on the right mandible. ii) Mesosomal sculpture: The metapleuron in P. denticulata is reticulate whereas in P. mariae it is smooth and

shiny. iii) Petiole proportions: The petiolar peduncle in *P. denticulata* is relatively shorter (PI= 38–42) than in *P. mariae* (PI= 43–49) (Figures 2. 12 and 13).

The two specimens known of this species were collected in a leaf-litter sample extracted with a mini-Winkler. The leaf-litter sample was collected in a primary lower montane forest (1300 m). Other species in the *gundlachi*-group have been recorded from wet forest habitats from lowland rainforest to cloud forest and some in agro-ecosystems. *Pyramica denticulata*, the species perhaps most closely related to *P. mariae*, has been collected in lowland (< 1000 m) forests in Panama (Sosa-Calvo et al. in press) to subtropical forests in the wet Chaco region of Argentina (Theunis et al. 2005). Other than the collection data, nothing is known about the biology of *P. mariae*.

# Modified version of key in Bolton (2000)

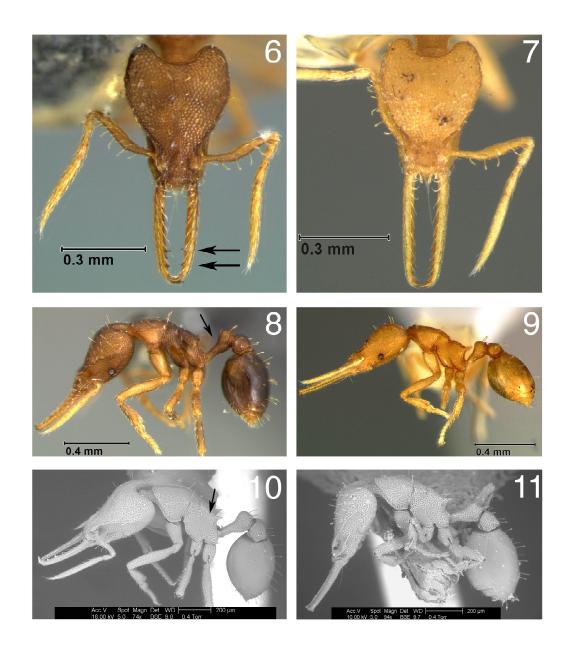
In Bolton's (2000) key, *Pyramica mariae* keys out to *P. denticulata*. The key can be modified as below to include *P. mariae*. Numbering of couplets follows Bolton (2000).

- 23. In lateral view, postpetiole lacking ventral spongiform lobe; sometimes a minute vestige is visible; mesonotum with a pair of erect hairs ... 23b
- In lateral view, postpetiole with a reduced ventral spongiform lobe but distinct; if lobe shallow then mesonotum with messy flagellate hairs ... 25 (couplet 25 in Bolton)
- 23b. Mandibles long, MI 72–85. Dorsum of pronotum lacking a pair of stiff erect hairs ... 23c

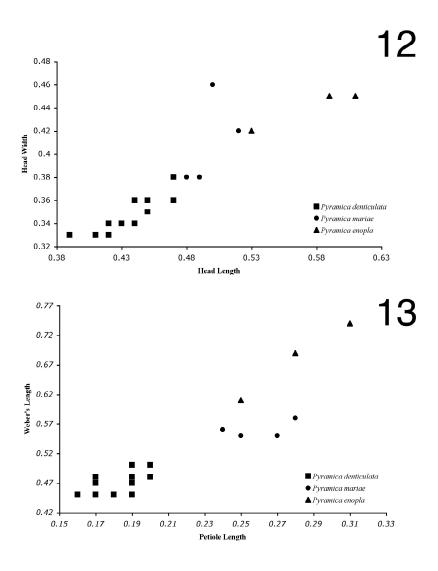
- Mandibles short, MI 58–65. Dorsum of pronotum with a pair of stiff erect hairs
   ... eggersi
- 23c. Inner margin of mandibles with 5–10 preapical denticles of similar size.

  Metapleuron densely reticulate. Peduncle of petiole short, PI 38–42 ...

  denticulata
- Inner margin of mandibles with 3–4 preapical denticles, two of which are distinctly larger than the rest. Metapleuron smooth and shiny. Peduncle of petiole elongate, PI 48–49 ... *mariae*, new species



**Figures** 2. 6 - 11. Full-face (dorsal) and lateral views of: holotype worker of *Pyramica mariae*, new species (6, 8, 10) and *P. denticulata* (7, 9, 11).



**Figures** 2. 12 - 13. Relationships between head width and length (12), and petiole length and Weber's length (13) among *Pyramica denticulata*, *P. mariae*, and *P. enopla*. Measurements in millimeters.

# Key to Dacetini known from Guyana

(Modified from Brown and Kempf [1969]; Bolton [1994; 2000])

- 1. Antenna 11-segmented ...2
- Antenna 4 to 6-segmented ...4
- 2(1). In lateral view the antennal scape passes below the eye when in resting position.

  Propodeal node bidentate. Palpal formula 5,3 ... Daceton armigerum
- In lateral view the antennal scape passes above the eye when in resting position.
   Propodeal node unarmed. Palpal formula 0,1 ...3
- 3(2). Sculpture on head and body strongly reduced, shining. Fossae on head and mesosoma small, shallow, and more widely spaced ... *Acanthognathus brevicornis*
- Sculpture on head and body strongly marked. Fossae on head and mesosoma larger
  and abundant with some rugulae present between them ... Acanthognathus
  lentus
- 4(1). Mandibles inserted on the sides of the anterior cephalic margin and converging towards the apex when closed. Inner margin of mandibles generally with numerous teeth or denticles ...5 (*Pyramica*)
- Mandibles inserted on the median portion of the anterior cephalic margin and diverging towards the apex when closed. Inner margin of mandibles with 0–2 preapical teeth ...18 (Strumigenys)
- 5(4). In full-face view, mandibles sublinear to linear, elongated and narrow; when

- closed contacting each other only in the apical halves or less of their lengths; either with an elongate space between the mandibles or their inner margin convex so that the margin touch, or nearly touch, near the midlength ...6
- In full-face view, mandibles either short and trap-like, or triangular to elongate-triangular; when closed contacting through most or all of their exposed length, lacking an elongate space between the mandibles or at most with a diastema basally between the basal lamella and the basal tooth ...12
- 6(5). In profile propodeum unarmed, declivity of propodeum with a carina on each side, but lacking any teeth or denticles. Ventral surface of postpetiole with well-developed spongiform lobe. Anterior portion of clypeus with long, spoon-shaped hairs that project over the mandibles. Eyes absent ... Pyramica dahlani
- In profile propodeum with denticles, teeth, or acute carinae. Ventral surface of
  postpetiole with a small spongiform lobe or spongiform lobe absent. Hairs on
  anterior portion of clypeus of different shape or absent. Eyes present ...7
- 7(6). Inner margin of mandible with a submedian tooth or denticle that is obviously enlarged at the midlength of the mandible. Apical fork with 3–5 intercalary denticles. Labral lobes very long and slender. ...8
- Inner margin of mandible with 2 or more denticles that may be minute and indistinct. Apical fork usually with 2 intercalary denticles. Labral lobes short
   ...10
- 8(7). Scape narrow basally; anterior margin of scape beyond base abruptly expanded

- and almost lobate at the subbasal angle, the scape distinctly widest at this point. Dorsolateral margin of head lacking an apicoscrobal hair ... *Pyramica crassicornis*
- Scape gradually broadening from base to apex; anterior margin convex but not abruptly expanded at the subbasal angle, the scape widest at or near its midlength. Dorsolateral margin of head with an apicoscrobal hair of some form ...9
- 9(8). Inner margin of mandible with only a single enlarged preapical tooth, located near the midlength. Larger species (HL 0.61–0.63, HW 0.41–0.43, AL 0.58–0.60) ... *Pyramica stenotes*
- Inner margin of mandible with two enlarged preapical teeth of approximately equal size. Smaller species (HL 0.50–0.52, HW 0.34–0.36, AL 0.46–0.50)
   ...Pyramica auctidens
- 10(7). In lateral view, dorsum of mesosoma with 4–6 pair of stout remiform standing hairs (not including those at humeri). Mandibles short (MI 49–54). In full-face view, inner margins of mandibles convex and, when entirely closed, touching at about the midlength ... *Pyramica subedentata*
- In lateral view, dorsum of mesosoma with only a single pair of standing hairs (not including those at humeri). Mandibles larger (MI 72–85). In full-face view inner margins of mandibles more or less straight to shallowly concave

...11

11(10). Inner margin of mandibles with 5-10 preapical denticles of similar size.

- Metapleuron entirely densely reticulate. Peduncle of petiole short, PI 38–42 .... *Pyramica denticulata*
- Inner margin of mandibles with 3–4 preapical denticles, two of which are distinctly much larger than the rest. Metapleuron in most of its surface smooth and shining. Peduncle of petiole elongate, PI 48–49 ... Pyramica mariae
- 12(5). With the head in full-face view, the anterior margin of the scape with projecting hairs, of which one or more, distal to the subbasal bend, distinctly curve toward the base of the scape. These hairs may be simple, spatulate, spoon-shaped, or wire-like ...13
- With the head in full-face view the anterior margin of the scape without projecting hairs that distinctly curve toward the base of the scape. Scape edge may have elongate simple straight or flagellate projecting hairs present; or may have entirely anteriorly or apically directed short hairs; or lacking hairs ...16
- 13(12). Disc of postpetiole smooth and shining ... Pyramica alberti
- Disc of postpetiole rugose or reticulate ...14
- 14(13). Promesonotum and side of mesosoma finely reticulate-punctate. Basal half or more of first gastral tergite sculptured. Basigastral costulae fine and numerous...15
- Promesonotum and side of mesosoma smooth and shining. First gastral tergite smooth and shining. Basigastral costulae vestigial or absent ... Pyramica thaxteri
- 15(14). Larger species (HL 0.77–0.80, HW 0.52–0.58, AL 0.75–0.85). Head

- dorsoventrally flattened. Hairs on antennal scape erect and stiff. Metapleuron densely reticulate ... Pyramica depressiceps
- Smaller species (HL 0.46–0.48, HW 0.30–0.32, AL 0.43–0.47). Head not dorsoventrally flattened. Hairs on antennal scape wire-like. Metapleuron smooth and shining. ... Pyramica cincinnata
- 16(12). In full-face view upper scrobe margin with an extremely long hair, much longer than the maximum length of the antennal scape ... *Pyramica villiersi*
- In full-face view upper scrobe margin lacking hairs, or, if present, hairs never as
   long as the maximum length of the antennal scape ...17
- 17(16). Head elongate (CI 68–70). Pronotal dorsum almost smooth. Ventral surface of petiole with a well-developed spongiform curtain ... *Pyramica beebei*
- Head short and broad (CI 91–96). Pronotal dorsum glossy with some feeble longitudinal costulae. Ventral surface of petiole with spongiform tissue vestigial or absent ... Pyramica glenognatha
- 18(4). Anterior margin of scape with all hairs curved or inclined toward the apex of the scape, without hairs that curve toward the base of the scape, and without a series of hairs at right-angles to the long axis of the scape shaft ...19
- Anterior margin of scape either with one to many hairs that distinctly curve toward
  the base of the scape, or rarely with hairs that are at right angles to the long
  axis of the scape shaft; never with all hairs obviously curved or inclined
  toward the apex of the scape ...20
- 19(18). In full-face view mandibles extremely large, exceeding maximum head length

- (MI 118–125). In dorsal view, bulla of femoral gland located close to the midlength on dorsum of each leg ... Strumigenys dolichognatha
- In full-face view mandibles short, not exceeding maximum length of the head (MI 41–48). In dorsal view, bulla of femoral gland located in apical quarter of dorsum of each leg ... Strumigenys godmani
- 20(18). Mandible without intercalary teeth or denticles that arise between the apicodorsal and apicoventral teeth, nor that arise from the dorsal base of the apicoventral tooth ... 21
- Mandible with 1 or 2 intercalary teeth or denticles that arise between the apicodorsal and apicoventral teeth, or that arise from the dorsal base of the apicoventral tooth ...24
- 21(20). Mandible without preapical teeth or denticles ... Strumigenys elongata
- Mandible with 1 or 2 preapical teeth or denticles ...22
- 22(21). Large species (HL 0.86–1.02, ML 0.50–0.56, AL 0.80–1.00). Ventrolateral margin of head in front of eye, and side of head above it, deeply concave; margin and side appear excavated or constricted in oblique dorsal view. ... Strumigenys precava
- Smaller species (HL 0.39–0.45, ML 0.20–0.30, AL 0.36–0.47). Ventrolateral margin of head in front of eye, and side of head above it, not deeply concave; margin and side do not appear excavated or constricted in oblique dorsal view ...23
- 23(22). Mandibles with one pair of preapical teeth or denticles. In full-face view

- upper scrobe margin with a row of 4–5 broadly spatulate to spoon-shaped hairs that are curved posteriorly ... *Strumigenys perparva*
- Mandibles with two pairs of preapical teeth, the basalmost one smaller that the one
  at midlength of mandible. In full-face view upper scrobe margin with a row of
  spatulate to spoon-shaped hairs that are all curved anteriorly ...Strumigenys
  dyseides
- 24(20). Apical fork of mandible with a single intercalary tooth or denticle that arises between the apicodorsal and apicoventral teeth, or arises from dorsal surface of apicoventral tooth ... Strumigenys trinidadensis
- Apical fork of mandible with two intercalary teeth or denticles that arise between
  the apicodorsal and apicoventral teeth; frequently represented by a distinct
  intercalary tooth accompanied by a less conspicuous or minute denticle
  ...Strumigenys cosmostela

# Dacetini species of Guyana

Acanthognathus brevicornis M.R. Smith, 1944

3 workers, 2 gynes, Base Camp, Mount Ayanganna, 5° 20.063' N, 59° 55.486' W, elev. 732 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.); 1 worker, Calm Water Creek, 6° 28.06' N, 58° 37.16' W, elev. 20 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.).

COMMENTS: Originally described from a worker and gyne collected on Barro Colorado Island, Panama. Almost nothing is known about the biology of this species.

Individuals have been collected nesting in hollow rotten twigs or in rotten wood on Neotropical rainforest. In Guyana, this species was collected from leaf-litter samples in lower montane sclerophyllous forest and evergreen forest known as "Wallaba" forest due to the presence of *Eperua falcata* Aublet (Leguminoseae). This constitutes the first record of the genus for Guyana. *Acanthognathus brevicornis* was previously known from Brazil and Panama (Brown and Kempf 1969; Bolton 2000; Fernandez and Sendoya 2004).

Acanthognathus lentus Mann, 1922

2 gynes, Iwokrama Forest Reserve, Whitewater Camp, 4° 43.890' N, 58° 50.992 W, elev. 60 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.).

COMMENTS: Originally described from a gyne and worker collected in Honduras. The biology of this species is poorly known. Brown and Kempf (1969) pointed out the similarity of this species with *A. ocellatus* and suggested that it might be a variant of *A. ocellatus*, but they did not synonomize them. Later, Kempf (1975) recorded this species for the first time from Brazil and confirmed it as a valid species. Individuals within the species have been collected in rotten logs. In Guyana, this species was collected from leaf-litter samples from lowland, evergreen, non-flooded forest in which *Chlorocardium* (Lauraceae) trees are often dominant. This constitutes the first record of the species for Guyana. *Acanthognathus lentus* has been recorded before from Brazil and Honduras (Brown and Kempf 1969; Bolton 2000; Fernandez and Sendoya 2004).

Daceton armigerum (Latreille, 1802)

7 workers, Iwokrama, Island in Essequibo River, 10 iv 1996, 4° 43.890' N, 58° 50.992 W, elev. ~60 m, hand collecting, 1° forest, tree, (TR Schultz and UG Mueller); 4 workers, Rupununi, Upper-Essequibo River, Kwatata, 3° 38.192'N, 59° 27.217'W, elev. 115 m, 25 x 2002, hand collecting, bush island, (TR Schultz)

COMMENTS: Originally described from several workers collected in Brazil.

Daceton armigerum is the only species in the genus and is largely restricted to the lowland rainforests of South America. This species forages and nests in trees, and displays a degree of polymorphism uncommon in dacetine ants. The biology, ecology, and behavior of this species were studied by Wilson (1962). In Guyana, this species has been hand-collected in lowland evergreen rainforest and, surprisingly, in "bush islands," small isolated clusters of trees on slightly elevated patches surrounded by seasonally flooding savannah.

Pyramica alberti (Forel, 1893b)

Cuyuni-Mazaruni Region: Kartabo (Wheeler).

COMMENTS: Originally described from workers and a queen collected on the Antilles Islands. In Guyana, this species has been collected in lowland rainforest in Kartabo, which is a village located ~6 miles from Bartica on the lower Mazaruni River. Colonies are usually small and can be found nesting in and foraging on dead wood, under tree bark, and in leaf litter.

Pyramica auctidens Bolton, 2000

1 worker, Kanuku Mountains, near Moco-Moco Falls, 3° 17.297' N, 59° 55.486' W, elev. 224 m, leaf-litter sample, 2° forest, (T.R. Schultz et al.)

COMMENTS: Originally described from three workers collected in French Guiana. In Guyana, the only specimen collected was in a leaf-litter sample from an evergreen, lower montane forest. Aside from these collection data, the biology of this species remains unknown. This represents the first record of the species in Guyana. *Pyramica auctidens* was previously known only from French Guiana (Bolton 2000). This species is also reported from Costa Rica in Fernandez and Sendoya (2004), but this seems to be a typographic error because, to date, there is no record of this species occurring in Costa Rica (Longino, personal communication).

Pyramica beebei (W.M. Wheeler, 1915)

1 worker, Iwokrama Forest Reserve, Whitewater Camp, 4° 43.890' N, 58° 50.992 W, elev. 60 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.); 9 workers: Base Camp, Mount. Ayanganna, 5° 20.063' N, 59° 55.486' W, elev. 732 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.).

COMMENTS: Originally described from a nest series containing workers, gynes, and males collected in Pará, Brazil. Wheeler received the specimens from a colleague that collected them under a "jungle mold at the feet of a single tree." The biology of this species remains unknown. In Guyana, this species was collected in the leaf litter of

lowland rainforest and in lowland forest dominated by *Chlorocardium* trees. This is the first record of the species for Guyana. *Pyramica beebei* has been collected in Colombia and Brazil (Bolton 2000; Fernandez and Sendoya 2004).

Pyramica cincinnata (Kempf, 1975)

2 workers: Base Camp, Mount. Ayanganna, 5° 20.063' N, 59° 55.486' W, elev. 732 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.).

COMMENTS: Originally described from Brazil. Sosa-Calvo et al. (in press) reported the presence of this species from a leaf-litter sample in a lowland rainforest of Panama. In Guyana, this species was collected from leaf-litter samples in a lower montane sclerophyllous forest. This represents the first record of the species for Guyana. Known previously from Brazil (Bolton 2000; Fernandez and Sendoya 2004) and Panama (Sosa-Calvo et al. 2006).

Pyramica crassicornis (Mayr, 1887)

No specific locality identified. This species was not collected in any of the leaf-litter samples of our survey.

COMMENTS: Originally described from Brazil. The species has been collected from Brazil, Paraguay, Trinidad, and Venezuela (Bolton 2000). Brown (1959c) reported it from Argentina and Kempf (1972) reported it from the Guianas.

Pyramica denticulata (Mayr, 1887)

(Figures 2. 7, 9, and 11)

47 workers, 4 gynes, Calm Water Creek, 6° 28.06' N, 58° 37.16' W, elev. 20 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.); 315 workers, 55 gynes, Iwokrama Forest Reserve, Whitewater Camp, 4° 43.890' N, 58° 50.992 W, elev. 60 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.); 195 workers, 11 gynes, Kanuku Mountains, near Moco-Moco Falls, 3° 17.297' N, 59° 55.486' W, elev. 224 m, leaf-litter sample, 2° forest, (T.R. Schultz et al.); 519 workers, 58 gynes, Base Camp, Mount.

Ayanganna, 5° 20.063' N, 59° 55.486' W, elev. 732 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.); 226 workers, 29 gynes, Mabura Hill, 5° 09.313' N, 58° 41.982' W, elev. 64 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.).

COMMENTS: Originally described from several workers from Brazil. The distributional range of *P. denticulata* has been recently extended to Central America by Sosa-Calvo et al. (2006). *Pyramica denticulata* appears to be the most common dacetine ant species in the forest in Guyana and was found in five of the eight areas sampled. According to Weber (1952), this species occurs in both primary and second-growth forest in leaf litter, rotten twigs, and low epiphytes. Lattke and Goitia (1997) reported the presence of this species in agro-ecosystems. In Guyana, this species was collected in lowland rainforest, forest dominated by *Chlorocardium*, "Wallaba" forest, and lower montane sclerophyllous forest (< 800 m).

Pyramica depressiceps (Weber, 1934)

Cuyuni-Mazaruni Region: Kartabo (Wheeler) (see information about the locality under *P. alberti*.)

COMMENTS: Originally described from a series of workers and males from Kartabo, Guyana. This species has been collected in wet forest habitats in Costa Rica, Panama, Colombia, and Peru (Longino 2006).

Pyramica glenognatha Bolton, 2000

8 workers, Iwokrama Forest Reserve, Whitewater Camp, 4° 43.890' N, 58° 50.992 W, elev. 60 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.); 2 workers, Kanuku Mountains, near Moco-Moco Falls, 3° 17.297' N, 59° 55.486' W, elev. 224 m, leaf-litter sample, 2° forest, (T.R. Schultz et al.); 1 worker, Falls Camp, Mount.

Ayanganna, 5° 22.332' N, 59° 57.563' W, elev. 1134 m, leaf-litter sample, 2° forest, (T.R. Schultz et al.); 1 gyne, Upper Forest, Mount Ayanganna, 5° 22.483' N, 59° 57.969' W, elev. 1300 m, leaf-litter sample, montane forest, (T.R. Schultz et al.).

COMMENTS: Originally described from two workers from Brazil. This species was collected from leaf-litter samples in lowland rainforest and high elevation forests or evergreen montane forest. Other than being collected in lowland and montane forests, the biology of this species remains unknown. This represents the first record of the species for Guyana. Previously known from Brazil (Bolton 2000; Fernandez and Sendoya 2004).

Pyramica stenotes Bolton, 2000

6 workers, Mabura Hill, 5° 09.313' N, 58° 41.982' W, elev. 64 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.).

COMMENTS: Originally described from four workers from Brazil. As pointed out by Bolton (2000), this species resembles *P. zeteki*, but can be distinguished by its larger size and more robust appearance. In Guyana, *P. stenotes* was collected in lowland evergreen, non-flooded forest dominated by *Chlorocardium* trees. This represents the first record of the species for Guyana. Previously known from Brazil (Bolton 2000, Fernandez and Sendoya 2004).

Pyramica subedentata (Mayr, 1887)

3 workers, Iwokrama Forest Reserve, Whitewater Camp, 4° 43.890' N, 58° 50.992 W, elev. 60 m, leaf-litter, 1° forest, (J.S. LaPolla et al.); 9 workers, Kanuku Mountains, near Moco-Moco Falls, 3° 17.297' N, 59° 55.486' W, elev. 224 m, leaf-litter sample, 2° forest, (T.R. Schultz et al.); 1 worker, Base Camp, Mount. Ayanganna, 5° 20.063' N, 59° 55.486' W, elev. 732 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.); 4 workers, Mabura Hill, 5° 09.313' N, 58° 41.982' W, elev. 64 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.).

COMMENTS: Originally described from several workers collected in Brazil. The biology of *P. subedentata* was described by Brown (1960), who states that members of this species are inhabitants of the leaf litter and more external soil layers in mesic

tropical forest. Nests are small, containing about 20 to 90 workers and one or more queens, and have been found in rotten twigs, leaf litter, or underground. In Guyana, *P. subedentata* was collected from leaf-litter samples in lowland rainforest and lower montane forest. Although this species has been collected in French Guiana, Suriname, and Venezuela, it has never been collected in Guyana, and this, to our knowledge, represents the first record of the species for the country. *Pyramica subedentata* has been collected from southern Mexico to southern Brazil (Brown 1960; Bolton 2000; Fernandez and Sendoya 2004).

Pyramica thaxteri (Wheeler, 1916)

2 workers, Base Camp, Mount. Ayanganna, 5° 20.063' N, 59° 55.486' W, elev. 732 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.).

COMMENTS: Originally described from several workers collected in Trinidad. The species was previously known only from Trinidad (Bolton 2000; Fernandez and Sendoya 2004), which makes this the first record of *P. thaxteri* for Guyana. Individuals of this species were collected from a leaf-litter sample in a lower montane forest. Its biology remains unknown.

Pyramica villiersi (Perrault, 1986)

15 workers, Iwokrama Forest Reserve, Whitewater Camp, 4° 43.890' N, 58° 50.992 W, elev. 60 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.); 1 worker, Kanuku Mountains, near Moco-Moco Falls, 3° 17.297' N, 59° 55.486' W, elev. 224 m, leaf-

litter sample, 2° forest, (T.R. Schultz et al.); 2 workers, Mabura Hill, 5° 09.313' N, 58° 41.982' W, elev. 64 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.).

COMMENTS: Originally described from a litter sample collected in French Guiana. In Guyana, this species was collected in both lowland rainforest and lower montane forests, and in non-flooded forest dominated by *Chlorocardium*. This represents the first record for the country. *Pyramica villiersi* has been previously recorded from Trinidad, French Guiana, Venezuela, Colombia, and Brazil (Bolton 2000; Fernandez and Sendoya 2004).

Strumigenys cosmostela Kempf, 1975

2 workers, 1 gyne, Base Camp, Mount. Ayanganna, 5° 20.063' N, 59° 55.486' W, elev. 732 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.).

COMMENTS: Originally described from two workers collected in Brazil on the forest floor. *Strumigenys cosmostela* has also been collected in Mexico, Costa Rica, and Peru. This represents the first record of this species for Guyana. The two workers and gyne reported here were collected from a leaf-litter sample in lower montane forest.

Strumigenys dolichognatha Weber, 1934

1 gyne, Iwokrama Forest Reserve, Whitewater Camp, 4° 43.890' N, 58° 50.992 W, elev. 60 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.); 1 worker, Base Camp,

Mount. Ayanganna, 5° 20.063' N, 59° 55.486' W, elev. 732 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.); 2 workers, Mabura Hill, 5° 09.313' N, 58° 41.982' W, elev. 64 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.).

COMMENTS: Originally described from a series of workers and males from a colony collected at Kartabo, Guyana. The ants were nesting in a rotten log lined with gray fungus (Weber 1934). *Strumigenys dolichognatha* has also been collected in lowland forest and lower montane forest (this study).

Strumigenys dyseides Bolton, 2000

4 workers, Calm Water Creek, 6° 28.06' N, 58° 37.16' W, elev. 20 m, leaf-litter sample, 1° forest, (J.S. LaPolla); 1 worker, Mabura Hill, 5° 09.313' N, 58° 41.982' W, elev. 64 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.).

COMMENTS: Originally described from a single worker collected in Colombia (Bolton 2000; Fernandez and Sendoya 2004). This represents the first record of the species in Guyana. In Guyana, the species was collected from leaf-litter samples in lowland non-flooded forest dominated by *Chlorocardium* trees and in "Wallaba" forest.

Strumigenys elongata Roger, 1863

2 workers, Calm Water Creek, 6° 28.06' N, 58° 37.16' W, elev. 20 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.); 1 worker, Iwokrama Forest Reserve,

Whitewater Camp, 4° 43.890' N, 58° 50.992 W, elev. 60 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.); 14 workers, Kanuku Mountains, near Moco-Moco Falls, 3° 17.297' N, 59° 55.486' W, elev. 224 m, leaf-litter sample, 2° forest, (T.R. Schultz et al.); 14 workers and 3 gynes, Base Camp, Mount. Ayanganna, 5° 20.063' N, 59° 55.486' W, elev. 732 m, leaf-litter sample, forest, (J.S. LaPolla); 8 workers, Mabura Hill, 5° 09.313' N, 58° 41.982' W, elev. 64 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.).

COMMENTS: Originally described from a single worker collected in Panama. *Strumigenys elongata* is a widely distributed ant (southern Mexico to Bolivia and southeastern part of Brazil). It is a common inhabitant of the leaf litter of wet and dry forests and agro-ecosystems (Lattke and Goitia 1997). *Strumigenys elongata* has been found nesting in and under rotten logs, under loose bark, and under epiphyte clumps (Brown 1954; 1962; Longino 2006). Observations by Brown (1954; 1962) suggest that this ant feeds exclusively on collembolans.

Strumigenys godmani Forel, 1899

Cuyuni-Mazaruni Region: Kartabo (Wheeler). (see information about the locality under *P. alberti*.)

COMMENTS: Originally described from a queen collected in Panama. This species and *Strumigenys mandibularis* Smith are perhaps the largest *Strumigenys* in the Neotropics (WL> 1.10). Colonies of *S. godmani* have been found in a rotten log in

cloud forest in Panama (Brown 1962) and Longino (2006) has observed workers foraging on the rainforest floor, in rotten wood, and under loose bark during both day and night collecting.

# Strumigenys perparva Brown, 1958

1 worker, 1 gyne, Calm Water Creek, 6° 28.06' N, 58° 37.16' W, elev. 20 m, leaf-litter sample, 1° forest, (J.S. LaPolla); 12 workers, 6 gynes, Iwokrama Forest Reserve, Whitewater Camp, 4° 43.890' N, 58° 50.992 W, elev. 60 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.); 5 workers, Kanuku Mountains, near Moco-Moco Falls, 3° 17.297' N, 59° 55.486' W, elev. 224 m, leaf-litter sample, 2° forest, (T.R. Schultz et al.); 11 workers, Base Camp, Mount. Ayanganna, 5° 20.063' N, 59° 55.486' W, elev. 732 m, leaf-litter sample, forest, (J.S. LaPolla); 9 workers, Mabura Hill, 5° 09.313' N, 58° 41.982' W, elev. 64 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.).

COMMENTS: Originally described from several workers and a gyne collected in Trinidad and Brazil. In Guyana, this species has been collected from leaf-litter samples from lowland rainforest, "Wallaba" forest, and lower montane forest.

# Strumigenys precava Brown, 1954

1 worker, Mabura Hill, 5° 09.313' N, 58° 41.982' W, elev. 64 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.); 2 workers, *Dycimbe* Camp, Mount Ayanganna, 5° 18.094' N, 59° 54.68' W, elev. 695 m, nest series, *Dicymbe* forest, in rotten log, (T.R. Schultz).

COMMENTS: Originally described from a series of workers collected in Guyana. This species is easily recognized by the strong preocular excavation, which it shares with *Strumigenys formicosa* Bolton (known from Ecuador). Nests of *S. precava* have been found in rotten logs in lowland rainforest and cloud forest in Panama and contain several hundred workers (Brown 1962). In Guyana, *S. precava* was collected in lowland rainforest and lower montane forest dominated by *Dycimbe* (Fabaceae) trees.

Strumigenys trinidadensis Wheeler, 1922

1 worker, Mabura Hill, 5° 09.313' N, 58° 41.982' W, elev. 64 m, leaf-litter sample, 1° forest, (J.S. LaPolla et al.)

COMMENTS: Originally described from a single specimen collected by sweeping foliage in Trinidad. Longino (2006) reports the presence of the species in a wet forest in Costa Rica and workers foraging on foliage and visiting extrafloral nectaries on an *Inga* sp. (Fabaceae) tree. Otherwise, the biology of *S. trinidadensis* remains unknown. Known previously from Trinidad, Costa Rica, Brazil, Panama, and Bolivia (Bolton 2000; Fernandez and Sendoya 2004), this represents the first record of the species in Guyana.

# Acknowledgements

We would like to thank Barry Bolton for confirming that these specimens represent new species. George Else (BMNH) loaned us type specimens of *Pyramica enopla* and *Strumigenys dyseides*. C. Roberto Brandão (MZSP) loaned us the type specimen of *P. cincinnata*. Ted Suman (USNM) sorted and prepared the specimens, Scott Whitaker (USNM) assisted with the scanning electronic micrographs, and Eugenia Okonski (USNM) databased and labeled the specimens. For corrections and comments on versions of the manuscript we thank David Furth, Victor H. Gonzalez, and Akito Kawahara. This project was supported in part by the NSF-IRCEB DEB 0110073 to TRS and by the Smithsonian Institution's Biological Diversity of the Guiana Shield Program to TRS and JSL.

**Table** 2.1. Dacetine ant species currently known from Guyana.

Table 2.1. Dacetine ant species currently known from Guyana.		
Taxon	Locality	Notes/ Reference
Acanthognathus brevicornis M.R.	CWC, MAB	New record
Smith	ICD	Nr. 1
A. lentus Mann	IFR	New record
Daceton armigerum (Latreille)	IFR, Essequibo River, Rupununi	Bolton 2000; Fernandez &
D : 11 (:(E 1)	Savannah	Sendoya 2004; this study
<i>Pyramica alberti</i> (Forel)	Kartabo	Bolton 2000; Fernandez &
D CL DI	TANA A	Sendoya 2004
P. auctidens Bolton	KMM	New record
P. beebei (Wheeler)	IFR, MAB	New record
P. dahlani Sosa-Calvo & Schultz	CWC, MHC	New species
n. sp.	MAD	NI
P. cincinnata (Kempf)	MAB	New record
P. crassicornis (Mayr)	Guyanas	Kempf 1972; Bolton 2000;
		Fernandez & Sendoya
D. I. C. I. (Marry)	Deal in Delevine Devel	2004
P. denticulata (Mayr)	Berbice Dubulay Ranch,	Bolton 2000; Fernandez &
	Morabukea, R. Mazaruni Forest,	Sendoya 2004; this study
D 1	CWC, IFR, KMM, MAB, MHC	D-14 2000- F 1 8-
P. depressiceps (Weber)	Kartabo	Bolton 2000; Fernandez &
D. alana aku atha Daltan	IED ZMM MAE MAII	Sendoya 2004
P. glenoghnatha Bolton P. mariae Sosa-Calvo & Schultz n.	IFR, KMM, MAF, MAU MAU	New record
	MAU	New species
sp. <i>P. stenotes</i> Bolton	MHC	New record
		New record
P. subedentata (Mayr)	IFR, KMM, MAB, MHC MAB	New record
P. thaxteri (Wheeler)		New record
P. villiersi (Perrault) Strumigenys cosmostela Kempf	IFR, KMM, MHC MAB	New record
S. dolichognatha Weber	Kartabo, IFR, MAB, MHC	Bolton 2000; Fernandez &
s. dollehognatha webel	Kaitauo, IFK, MAD, MITC	Sendoya 2004; this study
S. dyseides Bolton	CWC, MHC	New record
S. elongata Roger	Morabukea, CWC, IFR, KMM,	Bolton 2000; Fernandez &
S. elongala Rogel	MAB, MHC	Sendoya 2004; this study
S. godmani Forel	Kartabo	Bolton 2000; Fernandez &
S. goumant Poter	Kartaoo	Sendoya 2004
S. perparva Brown	Berbice Dubulay Ranch, CWC,	Bolton 2000; Fernandez &
s. perpurva biowii	IFR, KMM, MAB, MHC	Sendoya 2004; this study
S. precava Brown	Between R. Cuyuni & R.	Bolton 2000; Fernandez &
s. precuva biowii	Mazaruni, Kamakusa, MHC,	Sendoya 2004; this study
	MAD	Schuoya 2004, mis study
S. trinidadensis Wheeler	MHC	New record
5. II IIII UUUEIISIS WIICCICI	171110	INCW ICCUIU

Abbreviations for localities: CWC: Calm Water Creek, 6° 28.06' N 58° 37.16' W, elev. 20 m; IFR: Iwokrama Forest Reserve Whitewater Camp, 4° 43.890' N 58° 50.992' W, elev. 60 m; KMM: Kanuku Mountains near Moco-Moco Falls, 3° 17.297' N 59° 38.376' W, elev. 224 m; MAB: Base Camp Mount. Ayanganna, 5° 20.063' N 59° 55.486' W, elev. 732 m; MAD: Dicymbe Camp Mount Ayanganna, 5° 17.760' N 59° 54.632' W, elev. 717 m; MAF: Falls Camp Mount Ayanganna, 5° 22.332' N 59° 57.563' W, elev. 1134; MAU: Upper Forest Mount Ayanganna, 5° 22.483' N 59° 57.969' W, elev. 1300 m; MHC: Mabura Hill, 5° 09.313' N 58° 41.982' W, elev. 64 m. "New record" refers to a new record for Guyana.

### **CHAPTER 3:**

Dacetine ants of Panama: New records and description of a new species (Hymenoptera: Formicidae: Myrmicinae: Dacetini)<sup>1</sup>

JEFFREY SOSA-CALVO<sup>1, 3</sup> STEVEN O. SHATTUCK<sup>2</sup> AND TED R. SCHULTZ<sup>3</sup>

#### **Abstract**

Pyramica and Strumigenys are the most speciose dacetine (Formicidae: Myrmicinae: Dacetini) genera in the world. A new ant species in the Pyramica alberti group is described from leaf-litter surveys conducted in the Canal Zone, Panama. Pyramica panamensis new species, is similar to P. fridericimuelleri, P. nigrescens, and P. parsauga, but differs from those species in having strongly reduced eyes and a distinct promesonotal carina. A couplet is added to Bolton's (2000) key to Pyramica in order to accommodate the new species. New Central American records for two species in the dacetine genera Pyramica and one in Strumigenys are reported, and a checklist of the known Panamanian dacetine species is presented.

<sup>&</sup>lt;sup>1</sup> Maryland Center for Systematic Entomology, Department of Entomology, University of Maryland, 4112 Plant Sciences Building, College Park, MD, 20742. U. S. A. E-mail: sossajef@si.edu

<sup>&</sup>lt;sup>2</sup> CSIRO Entomology, GPO Box 1700, Canberra A. C. T. 2601, Australia. E-mail: <u>steve.shattuck@.csiro.au</u>

<sup>&</sup>lt;sup>3</sup> Department of Entomology, MRC 188, P.O Box 37012, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012. U. S. A. E-mail: schultz@lab.si.edu

<sup>&</sup>lt;sup>1</sup> Published manuscript (see appendix 1): Sosa-Calvo, J., S.O. Shattuck, and T.R. Schultz. 2006. Dacetine ants of Panama: New records and description of a new species (Hymenoptera: Formicidae: Myrmicinae: Dacetini). Proceedings of the Entomological Society of Washington, 18: 814-821.

Resumen

Los géneros *Pyramica* y *Strumigenys* contienen el mayor número de especies dentro

de los dacetinos (Formicidae: Myrmicinae: Dacetini) en el mundo. Se describe una

nueva especie dentro del grupo alberti, coleccionada en hojarasca en la zona del

Canal de Panamá, Panamá. Pyramica panamensis sp nov. es similar a las especies P.

fridericimuelleri, P. nigrescens, y P. parsauga, pero se diferencia de estas en la

presencia de ojos fuertemente reducidos y una carena promesonotal distintiva.

Adiciones a la clave taxonómica para la identificación de las especies del género

Pyramica para el Neotrópico (Bolton 2000) fueron necesarias para incluir P.

panamensis. Dos especies en el género Pyramica y una en el género Strumigenys son

reportados como nuevos registros para América Central, y se presenta una lista de las

especies conocidas dentro de la tribu para Panamá.

Key words: Central America, leaf litter, *Pyramica panamensis*, systematics,

taxonomy.

69

### Introduction

Ants (Hymenoptera: Formicidae) are one of the most ecologically important groups of insects due to their relative abundance in terrestrial ecosystems, especially in the tropics. Leaf-litter ants in particular are increasingly employed in biodiversity surveys (Agosti et al. 2000). Ants of the tribe Dacetini, worldwide in distribution and generally predaceous, are commonly encountered in such surveys. The tribe includes ants that are morphologically distinct (e.g., antennal segment numbers are reduced, mandibles are elongate and traplike; hairs, especially on the head, are scalelike; and spongiform lobes occur on the petiolar and postpetiolar segments). A recent revision of the tribe (Bolton 2000) permits the accurate identification of known species and, consequently, the recognition of species hitherto unknown to science. Intensive ecological work in Panama on ants, including dacetine ants (Kaspari and Weisner 2000, Kaspari et al. 2001), requires that Panamanian dacetine ant taxonomy remain current.

Of the nine dacetine genera, *Pyramica* Roger and *Strumigenys* Fr. Smith are the most speciose, *Pyramica* being more speciose than *Strumigenys* in the Neotropics (Bolton 2000), and the only ones with worldwide distributions. Both genera occur throughout the Americas, but are more abundant in the Neotropics (Brown 1962, Bolton 2000), where their mostly cryptic species are typically encountered inhabiting leaf litter, rotten wood, or soil (Brown 1953, Dejean 1991). Entomobryid and isotomid collembolans appear to be the main prey items of *Pyramica* and *Strumigenys*, but some species also feed on mites, termites, and ant larvae (Wilson 1954, Bolton 2000).

The New World tropics contain 85 described species of *Strumigenys* and 100 species of *Pyramica*. Here we present new species records for Central America and describe a new species, *P. panamensis*, within the *P. alberti* (Forel) species group. The *P. alberti* species group is broadly distributed in the Neotropical Region and frequently collected. *Pyramica panamensis* appears to be closely related to *P. fridericimuelleri* (Forel), *P. nigrescens* (Wheeler), and *P. parsauga* Bolton. A list of dacetine ants from Panama is presented, along with a modification of Bolton's (2000) key to accommodate *P. panamensis*.

### Materials and methods

Measurements and terminology follow Bolton (2000). Specimens examined were borrowed from or have been deposited in the following collections:

BMNH The Natural History Museum, London, U. K.
 JTLC J. T. Longino Collection, Evergreen State College, Olympia, Washington, U. S. A.
 MZSP Museu de Zoologia da Universidade de São Paulo, São Paulo,

Brazil

USNM National Museum of Natural History, Smithsonian Institution,
Washington, DC, U. S. A.

The holotype of *P. panamensis* was examined and measured using a Leica MZ125 stereomicroscope and photographed using a ProgRes 3012 digital camera (Jenoptik) attached to Leica MZ16 stereomicroscope. Specimens of *P. cincinnata* 

71

(Kempf), *P. denticulata* (Mayr), *P. fridericimuelleri*, *P. nigrescens*, and *Strumigenys perparva* Brown were photographed using a JVC KY-F70B video camera mounted on a Leica M420 microscope. All images were prepared using Auto-Montage Version 3.04 software (Synoptics Ltd.) and Photoshop (Adobe Inc.).

### **Taxonomic treatment**

Genus Pyramica Roger 1862

Pyramica cincinnata (Kempf 1975)

(Figs. 1-2)

This is the first record for this species for Central America. *P. cincinnata* has been recorded previously only from Brazil (Bolton 2000). The Panamanian specimens are slightly larger than the ones examined by Bolton (2000). Measurements (measurements in parentheses from Bolton [2000]): TL 1.85- 1.89 (1.6- 1.8), HL 0.47 (0.46- 0.48), HW 0.34 (0.30- 0.32), CI 72 (65- 68), ML 0.08- 0.09 (0.07- 0.08), MI 17- 20 (15- 18), SL 0.24 (0.20- 0.22), SI 68 (67- 69), PW 0.20 (0.19- 0.21), AL 0.52- 0.53 (0.43- 0.47).

Material examined.— 2 workers, labeled "PANAMA, Panama Prov.: Gamboa, Pipeline Road nr. Rio Frijolito; 09° 09' 00" N 79° 43' 56" W, 18 viii 2003; litter sample; J. Sosa-Calvo," "USNM No. 00445071, 00445072". PARATYPES: 2 workers, labeled "BRAZIL, Amazonas: Ponta Negra, N. of Manaus; Sept. 1962; W. L. Brown." Deposited in the MZSP.

72

# Pyramica denticulata (Mayr 1887)

(Figs. 3-4)

This is the first record for this species for Central America. *P. denticulata* has been recorded previously from Trinidad, Suriname, Guyana, French Guiana, Brazil, Bolivia, Paraguay, Venezuela, Colombia, Ecuador, and Argentina (Bolton 2000, Lattke and Goitia 1997).

Material examined.— 2 workers and 1 gyne, labeled "PANAMA, Panama Prov.: Gamboa, Pipeline Road between Rios Frijoles and La Seda; 72 m, 6 vi 2002 to 8 vi 2002; litter sample; C.J. Marshall," "USNM No. 00411461, 00411459, 00411798." 1 gyne, labeled "BRAZIL, Sao Paulo: Agudos, 4 iii 1953; berlese; W. Kempf." 3 workers, labeled "BRAZIL, Sao Paulo: Agudos, 6 iii 1955; C. Gilbert." 3 workers, labeled "SURINAME, (no locality), 15 vii 42; Geijskes (coll)."

### Pyramica panamensis new species

(Figs. 11-12, 15)

Diagnosis.—*Pyramica panamensis* is a member of the *P. alberti* species group and is most similar to *P. fridericimuelleri* (Figs 7-8, 13), *P. nigrescens* (Figs 9-10, 14), and *P. parsauga* Bolton. *Pyramica panamensis* can be distinguished from these species by the presence of small eyes and promesonotum with a complete median longitudinal carina.

Description.—*Holotype worker*: TL 1.8, HL 0.50, HW 0.35, CI 70, ML 0.11, MI 22, SL 0.28, SI 80, PW 0.23, AL 0.48. Possessing characters of *alberti* complex.

Masticatory margin of mandibles with a series of acutely triangular apical teeth (mandibles closed in holotype and basal region not visible). Anterior clypeal margin broadly and very shallowly convex between points where outer margins of closed mandibles intersect clypeal margin. Apicoscrobal hair flagellated, long, and fine. Eye very small, with only 2 ommatidia in longest row and only 4 in total. Promesonotum with a well-developed median longitudinal carina that extends through the entire length of pronotum and most of mesonotum. Pronotum dorsally entirely sculptured with fine punctation. Petiolar node in dorsal view slightly broader than long, with sides slightly converging anteriorly. Lateral spongiform lobes of node extending forward almost to anterolateral angles.

Gyne and male: Unknown

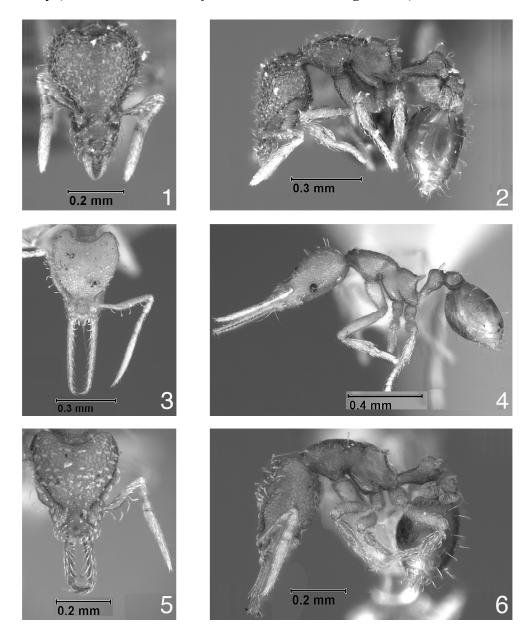
Type material.— Holotype worker, labeled "PANAMA: Panama Prov.: Gamboa, Pipeline Road between Rios Frijoles and La Seda; 72 m, 6 vi 2002 to 8 vi 2002; litter sample; C. J. Marshall," "USNM, No. 00410482."

Distribution and natural history.—*Pyramica panamensis* new species is known only from its type locality, Soberania National Park in Gamboa, Panama Province. This species was collected from leaf-litter samples taken in a successional rain forest containing P. cincinnata, P. denticulata, and S. perparva. None of the species closely related to P. panamensis (P. fridericimuelleri, P. nigrescens, and P. parsauga) are known from this particular lowland rain forest (Bolton 2000), although P.

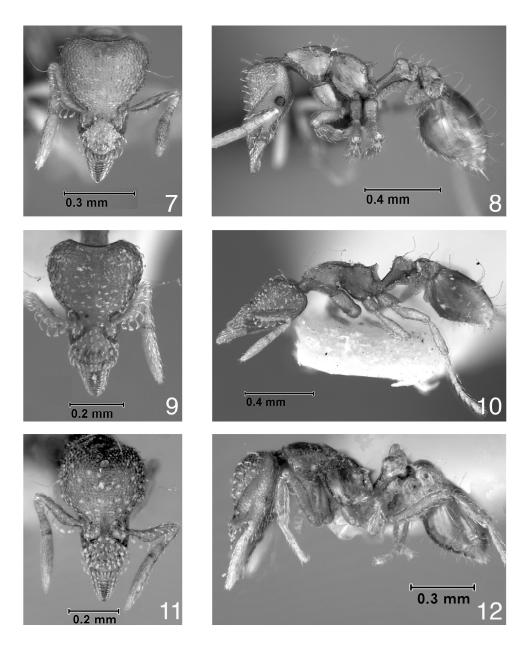
fridericimuelleri, the species apparently most closely related to *P. panamensis* and one of two species (the other *P. alberti*) within the *P. alberti* species group that occur in Panama, is found in the Chiriqui Mountains and Costa Rica. The other two species in the *P. alberti* group, however, are found in the northern part of Central America (*P. nigrescens*) or reported exclusively from Costa Rica (*P. parsauga*). The natural history of *P. panamensis* remains unknown.

Discussion.— The *P. alberti* group includes seven exclusively New World species. Of these seven species, P. conspersa, P. furtiva, and P. sublucida are known only from South America. P. alberti and P. fridericimuelleri are apparently more widely distributed, occurring in both Central and South America. Pyramica nigrescens and P. parsauga are known only from Central America. Pyramica panamensis shares with P. parsauga the reduced eyes (about 4 facets in total), but can be distinguished by promesonotal dorsum bearing a median longitudinal carina and dorsum of propodeum reticulate (smooth in *P. parsauga*). With *P. fridericimuelleri* and *P.* nigrescens, P. panamensis shares the fine median longitudinal carina on the promesonotal dorsum, the anterior clypeal margin, which in full face view is shallowly convex between the points where outer margins of the fully closed mandibules intersect the clypeal margin, and the sculpture on the dorsum of the mesosoma (most similar to P. nigrescens). Pyramica panamensis can be separated from P. fridericimuelleri and P. nigrescens by the compound eye compose of 4 facets (approximately 10 facets in *fridericimuelleri* and *nigrescens*), and the disc of the

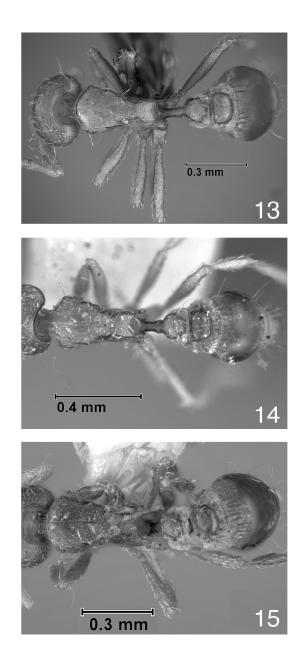
petiolar node slightly broader than long and with the sides only slightly converging anteriorly (intermediate between *fridericimuelleri* and *nigrescens*).



**Figures** 3. 1-6. Frontal and lateral views. 1-2, *Pyramica cincinnata*. 3-4, *P. denticulata*. 5-6, *Strumigenys perparva*.



**Figures** 3. 7 - 12. Frontal and lateral views. 7 - 8, *Pyramica fridericimuelleri*. 9 - 10, *P. nigrescens*. 11 - 12, *P. panamensis*.



**Figures** 3. 13 – 15. Dorsal views. 13, *Pyramica fridericimuelleri*. 14, *P. nigrescens*. 15, *P. panamensis*.

# Genus Strumigenys F. Smith 1860

## Strumigenys perparva Brown 1958

(Figures 3. 5-6)

This is the first record for this species for Central America. *S. perparva* has been recorded previously from Trinidad, Venezuela, Colombia, Bolivia, Guyana, Suriname, and Peru (Bolton 2000).

Material examined: 4 workers and 1 gyne, labeled "PANAMA, Bocas del Toro: Km 26 rd. to Chiriqui Grande; 09° 01' 34.92" N 82° 18' 20.04" W; 2 vi 2002 to 4 vi 2002; litter sample; C.J. Marshall," "USNM No. 00410903, 00410910." 1 gyne, labeled "Panama Prov.: Gamboa, Pipeline Road between Rios Frijoles and La Seda; 72 m, 6 vi 2002 to 8 vi 2002; litter sample; C.J. Marshall," "USNM No. 00445073." PARATYPE, 1 worker, labeled "BRAZIL, Sao Paulo: Agudos; 6 iii 1955; C. Gilbert." 2 workers, labeled "SURINAME, Tambahredjo; vi 1959; I. v. d. Drift."

# Modification of Bolton's (2000) Key to Neotropical *Pyramica* species

Here we add two couplets (number 48a and 48b) to Bolton's (2000, p. 137) key in order to accommodate *P. panamensis*.

- 47. Basal lamella of mandible followed distally by a long edentate second lamella that extends forward about half exposed length of fully closed mandible, lamellae separated only by a minute cleft; mandibles relatively long, MI 27 33 ... *alberti*
- -. Basal lamella of mandible immediately followed distally by tooth row, without a

second lamella that extends forward for half exposed length of fully closed mandible; mandibles shorter, MI  $19-24\ldots48a$ 

48a. Eye small, with only 4 ommatidia in total ... 48b

- -. Eye larger, with 10 or more ommatidia in total ... 49
- 48b. Promesonotal dorsum without a median longitudinal carina. Pronotal dorsum entirely smooth and shining. Propodeal dorsum smooth and shining ... parsauga
- Promesonotal dorsum with a median longitudinal carina. Pronotal and propodeal dorsum entirely sculptured with fine punctation ... panamensis new species
- 49. Basal tooth row of mandible consisting only of narrowly triangular high acute teeth. Disc of petiole node in dorsal view as long as broad and with the sides of node converging anteriorly ... fridericimuelleri
- -. Basal tooth row of mandible consisting of alternating high narrow acutely triangular teeth and lower bluntly rounded broader teeth; tooth 4 from base particularly broad and rounded. Disc of petiole node in dorsal view much broader than long, roughly transversely rectangular, sides not converging anteriorly ... nigrescens

# Checklist of Dacetini of Panama (modified from Bolton 2000).

Genus Acanthognathus Mayr 1887

A. brevicornis M. R. Smith 1944

A. ocellatus Mayr 1887

Genus Pyramica Roger 1862 P. alberti (Forel 1893)

- P. brevicornis (Mann 1922)
- P. cincinnata (Kempf 1975)#
- P. crementa Bolton 2000
- P. denticulata (Mayr 1887)#
- P. depressiceps (Weber 1934)
- P. fridericimuelleri (Forel 1886)
- P. gundlachi Roger 1862
- P. lalassa Bolton 2000
- *P. margaritae* (Forel 1893)
- P. metopia (Brown 1959)
- P. myllorhapha (Brown 1959)
- P. panamensis new species#
- P. probatrix (Brown 1964)
- P. schulzi (Emery 1894)
- P. subedentata (Mayr 1887)
- P. trieces (Brown 1960)
- P. wheeleri (Smith 1944)
- P. zeteki (Brown 1959)

# Genus Strumigenys F. Smith 1860

- S. biolleyi Forel 1908
- S. cordovensis Mayr 1887
- S. deltisquama Brown 1957
- S. dolichognatha Weber 1934\*
- S. elongata Roger 1863

- S. emmae (Emery 1890)
- S. extirpa Bolton 2000
- S. fairchildi Brown 1961
- S. godmani Forel 1899
- S. humata Lattke & Goitía 1997
- S. lacacoca Brown 1959
- S. lanuginosa Wheeler 1905
- S. longispinosa Brown 1958
- S. louisianae Roger 1863
- S. ludia Mann 1922\*
- S. marginiventris Sanstchi 1931
- S. perparva Brown 1958#
- S. planeti Brown 1953\*
- S. precava Brown 1954
- S. rogeri Emery 1890
- S. smithii Forel 1886
- S. tococae W. M. Wheeler & Bequaert 1929\*
- S. trinidadensis Wheeler 1922
- \* From Kaspari's ants of the Barro Colorado Island Monument (BCIM), Panama, website (http://faculty-staff.ou.edu/K/Michael.E.Kaspari-1/K/Michael.E.Kaspari-1/bcnm\_ants\_home.htm). Specimens not seen by authors.
- # New record for Panama

Unmarked (with either \* or #) indicates recorded in Bolton (2000)

# Acknowledgements

We are indebted to C. Marshall for collecting the holotype specimen and to B. Bolton for confirming that this specimen represents a new species. Dr. C. R. F. Brandão loaned the paratype of *P. cincinnata*, Dr. J. T. Longino loaned specimens of *Pyramica fridericimuelleri*, and Dr. M. E. Kaspari loaned specimens of *Pyramica* and *Strumigenys* from Barro Colorado Island. Natalie Barnett (ANIC) prepared the images of *P. panamensis*. For corrections and comments on previous versions of this manuscript we thank A. Kawahara, J. S. Lapolla, J. T. Longino, D. R. Smith, and one anonymous reviewer. We are grateful to the Smithsonian Tropical Research Institute for providing logistical support and facilities in Gamboa and to the Autoridad Nacional del Ambiente for permission to collect ants in Panama. This work was supported by the NSF-IRCEB DEB 0110073 to TRS and the Andrew W. Mellon Research Exploration Award in Tropical Biology to JSC.

### **CHAPTER 4:**

# Review of the subfamily Proceratiinae (Hymenoptera: Formicidae) in Colombia

JEFFREY SOSA-CALVO<sup>1,2</sup> AND JOHN T. LONGINO<sup>3</sup>

### **Abstract**

The ant subfamily Proceratiinae includes the extant genera *Discothyrea* and *Proceratium* (Proceratiini), *Probolomyrmex* (Probolomyrmecini), and the extinct genus *Bradoponera* (Proceratiini). In the New World the subfamily includes 35 described species. Members of the subfamily are easily recognized by the following characters: antennal insertions completely to partially exposed; eyes vestigial or absent; and promesonotum fused, lacking mobility. Members of the tribe Proceratiini additionally share the distinctive character state of abdominal tergite IV strongly curved anterad with reduction of the respective sternite. Abdominal tergite IV is normal, i.e., plesiomorphic, in tribe Probolomyrmecini. Notes about the species that occur in Colombia are given.

<sup>&</sup>lt;sup>1</sup> Maryland Center for Systematic Entomology, Department of Entomology, 4112 Plant Sciences Building, University of Maryland, College Park, MD, 20742, U. S. A.

<sup>&</sup>lt;sup>2</sup> Department of Entomology, National Museum of Natural History, Smithsonian Institution, POB 30712, NHB-CE 518, MRC 188, Washington DC 20013-7012, U. S. A. Email: sossajef@si.edu

<sup>&</sup>lt;sup>3</sup> The Evergreen State College, Olympia WA 98505, U. S. A. Email: <u>longinoj@evergreen.edu</u>

### Introduction

The subfamily Proceratiinae, recently created by Bolton (2003), includes individuals that are rarely taken by conventional hand collecting. Leaf-litter sampling has proven so far to be the best collecting technique for obtaining members of this subfamily. The subfamily includes individuals that are relatively small to medium in size and usually found nesting in leaf-litter, rotten wood, or spider oothecas (egg sacs). To date, all genera, with the exception of *Discothyrea* Roger, have been subjects of taxonomic revision (Taylor 1965; Agosti 1994; O'Keefe and Agosti 1997; Baroni-Urbani and de Andrade 2003). Perhaps due to their cryptic habits, the natural history and behavior of most proceratiine species remain unknown.

The taxonomic keys presented here are, in part, based on previous work conducted by Taylor (1965), Agosti (1994), and O'Keefe and Agosti (1997) for *Probolomyrmex* Mayr and on the revision by Baroni-Urbani and de Andrade (2003) for *Proceratium* Roger. In contrast, the genus *Discothyrea* has never been the focus of revisionary work and the key presented here is restricted to the species of *Discothyrea* that occur in Colombia, based on keys previously proposed by Weber (1939), Borgmeier (1949), and Longino (2005).

# **Diagnosis**

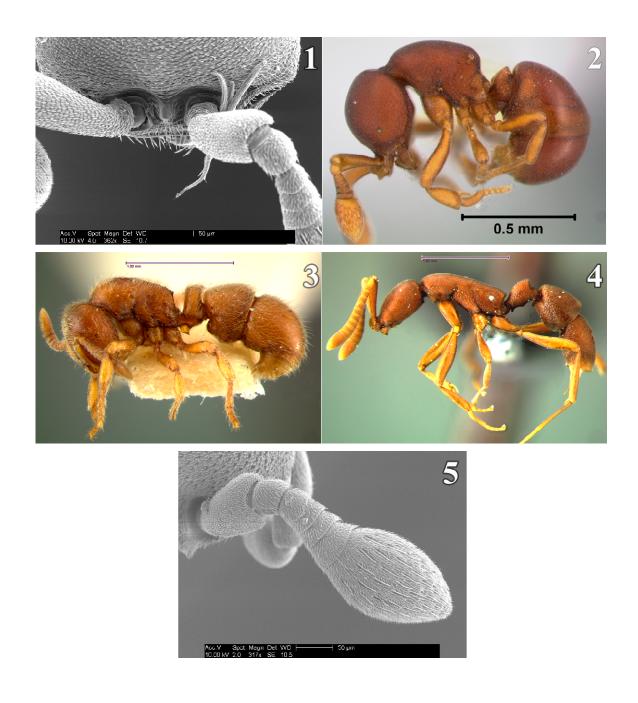
The newly created subfamily Proceratiinae shares several morphological characters with other subfamilies of the informal group poneromorphs (Bolton 2003). These characters include: i) mesosoma and gaster separated by a single segment, the petiole; ii) propodeal lobes present; iii) metapleural gland orifice always lacking a

dorsal cuticular collar; iv) helcium sternite retracted, overlapped by the tergite (differing only in *Discothyrea*) (Bolton 2003); v) spiracles of gastral segments III to V obscured by posterior margins of preceding tergites; and vi) sting apparatus always present and strongly developed. In addition to these characters, the subfamily possesses the following characters that serve to identify and separate its members from members of other subfamilies: i) antennal insertion mostly to completely exposed near the anterior margin of head; ii) clypeus reduced; iii) antennal sockets usually on a frontoclypeal platform that extends over the mandibles (figure 4.1), a character shared by all species in the genera *Discothyrea* and *Probolomyrmex* and by some *Proceratium*; iv) frontal lobes with torulus unfused; v) promesonotal suture fused, vestigial to entirely absent; vi) pronotum and mesonotum lacking the ability to move with respect to each other (figure 4. 2-4); vii) meso- and meta-tibia each with one spur, or mesotibia without one; viii) pretarsal claws simple; ix) orifice of metapleural gland simple and laterally positioned; x) individuals monomorphic and relatively small; xi) eyes absent or reduced.

### **Biology**

The natural history and biology of these ants are limited to a few behavioral studies that suggests a high degree of specialization. It has been reported that individuals of *Discothyrea* and *Proceratium* usually store and feed upon various arthropod eggs (Brown 1954, 1980). Brown, in observations with live laboratory colonies, found that individuals of *Proceratium* preferred spider eggs rather than body parts of insects. Most recently, Dejean and Dejean (1998) and Dejean *et al.* (1999),

working with *Discothyrea*, reported that species within the genus not only feed upon the spider eggs, but also construct their nests in spider oothecas, and suggested a new kind of leptobiosis called "arachnolesty" (Dejean et al. 1999). Taylor (1965) suggested that species of *Probolomyrmex* might have the same diet as those of the tribe Proceratiini, basing this conclusion on similarities in the morphology of the anterior portion of the head shared by all three genera. In contrast, Ito (1998) reported predation on millipedes in the family Polixenidae by *Probolomyrmex dammermani* Wheeler. Such behavior has been reported previously only for *Thaumatomyrmex* Mayr (Brandao et al. 1991; Eisner et al. 1996) and some Gnamptogenys Roger (Lattke 1990). The colonies of Proceratiinae species are small, generally containing no more than one hundred individuals (Menozzi 1925, Kennedy and Talbot 1939, Wesson and Wesson 1940, Brown 1958). The pupae of some species in the genera Discothyrea and Probolomyrmex have the unusual character of lacking cocoons; within the poneromorphs, this character is shared with some species in the genera Amblyopone Erichson, Ponera Latreille, and Simopelta Mann (Taylor 1967, Hölldober and Wilson 1990, Baroni-Urbani et al. 1992, Peeters 1997, Dejean et al. 1999).



Figures 4.1 - 4.5.1, antennal insertions (*Discothyrea*). 2, habitus of *Discothyrea*. 3, habitus of *Proceratium*. 4, habitus of *Probolomyrmex*. 2 - 4, Mesosoma lacking a promesonotal suture. 5, antenna of *Discothyrea*.

In the New World, proceratiines primarily inhabit leaf litter and soil. In tropical rainforests, they can be found nesting in small galleries or chambers in rotten wood or underneath rocks in dry forests. Some species have been found foraging and nesting in trees (Brown 1958, 1974). The absence or reduction of their eyes, the shape of their bodies (especially those of the genus *Probolomyrmex*), and their sparse representation in entomological collections strongly suggest that ants in this subfamily have hypogeous habits. If so, this subfamily could be much more abundant than is suggested by their current numbers in collections. It is known that several genera, when disturbed, remain motionless or play dead, making it extremely difficult for the collector to locate workers or colonies by direct examination of the leaf-litter.

# Composition of the subfamily

The subfamily Proceratiinae includes two tribes and three extant genera [Discothyrea, Proceratium (Proceratiini), and Probolomyrmex (Probolomyrmecini)] and an extinct genus [Bradoponera Mayr (Proceratiini)]. The subfamily is represented worldwide by almost 120 described species (Bolton 1995). In the new world, the subamily is represented by at least 35 species distributed from southern Canada through Argentina including some Caribbean islands (Cuba, Dominican Republic, and Trinidad and Tobago) (Weber 1939; Taylor 1965; Kempf 1972; Baroni-Urbani 1977; Agosti 1994; O'Keefe and Agosti 1997; de Andrade 1998; Baroni-Urbani and de Andrade 2003).

### **Tribe Proceratiini**

In addition to the morphological characters mentioned previously for the subfamily, the genera included in the tribe Proceratiini (*Discothyrea* and *Proceratium*) share the following characters: i) frontal lobes absent or vestigial, leaving the antennal insertions mostly to entirely exposed; ii) suture of promesonotum vestigial to entirely absent, i.e., both nota lacking mobility with respect to each other; iii) tergosternal fusion of petiole present and lacking laterotergites; iv) gastral tergite II enlarged and strongly arched, tergite much larger than gastral sternite II, which is greatly reduced (figures 4.2 – 4) (this character is also present in some other poneromorphs and in Agroecomyrmecinae) (Lattke 1994; Baroni-Urbani and de Andrade 2003; Bolton 2003); (v) antenna of worker and gyne with 6 to 12 segments, 13 in males.

# Genus Discothyrea Roger 1863

The genus *Discothyrea*, with 27 described species worldwide, is globally distributed throughout tropical and subtropical forests (Bolton 1994; de Andrade 1998). The genus includes very small individuals that primarily nest in leaf litter and rotten wood, with some in spider oothecas, consuming the spider eggs.

# **Diagnosis**

Although very similar to those within the genus *Proceratium*, individuals of *Discothyrea* can be distinguished, at least in the New World, by several morphological features: the lack of teeth or denticles on the inner (masticatory)

margin of the mandibles; a large last funicular segment, forming a terminal club that is of similar size or larger than the length of the remaining funiculus (figure 4. 5); antenna of worker and gyne with 6 to 9 segments (up to 12 antennal segments in Old World species), gradually increasing in size towards the apex (antennae in males filiform and 13-segmented); a variable palpal formula in the worker and gyne (5,4; 4,4; 4,3; 3,4; or 1,3), invariant in males (5,4); frontal lobes that are strongly reduced and fused forming a median vertical lamina that does not cover the antennal insertions; antennal scapes short, never surpassing the posterior margin of the head and broadened apically; eyes very small (one ommatidium) or absent (Brown 1958); gastral segment II strongly arched (this character state is shared with *Proceratium* and some *Gnamptogenys*), but usually abdominal tergites III and IV of almost the same size; helcium sternite convex, not overlapped by the tergite (as in dorylomorphs) (Bolton 2003).

The genus *Discothyrea* includes individuals that are difficult to identify due to their small size. Weber (1939) and Borgmeier (1949) developed taxonomic keys based on the worker and the gyne castes, using the number of antennal segments (7 or 9) to separate the species for the Neotropical region. Subsequently, Borgmeier (1954) described *Discothyrea sexarticulata*, in which the number of antennal segments is reduced to six. The use of antennal segment number for separating genera and species was questioned by Brown (1958), who synonymized under *Discothyrea* the genera *Prodiscothyrea* (with 10 antennal segments) and *Pseudosysphincta* (with 12 antennal segments). A complicating problem for the taxonomy of the genus is the difficulty in accurately counting the number of antennal segments. The funicular segments

between the apical segment and the pedicel are usually small, ringlike, and in some specimens, partially fused (Longino 2005). It is common to find individuals with nine antennal segments on one antenna and eight on the other. In spite of these problems, antennal segment number is useful in separating the species in Colombia, and it is employed in the key presented here. The position of the propodeal spiracles is another character state used in the key. The location of these spiracles varies, e.g., they may be: closer to the bulla of the metapleural gland (*D. humilis* Weber and *D. neotropica* Bruch), closer to the dorsal propodeal margin (some *D. denticulata* Weber), or intermediate in distance between the two (*D. sexarticulata* Borgmeier, *D. testacea* Roger, *D. horni* Menozzi, and in some *D. denticulata*). In addition, the spiracle may or may not project laterally as a tubercle in dorsal view.

To date, there are eight species of *Discothyrea* described for the Americas. The species *D. testacea* seems to be the only one present in the Neartic, while the other seven are distributed from Mexico through Argentina (Weber 1939; Borgmeier 1949; Smith and Wing 1954; Smith 1955; Alayo and Zayas-Montero 1977). However, the described species boundaries in the genus are relatively speculative and a exhaustive revision is needed. Due to the high diversity present in the tropics it is possible that the number of species in the Neotropical region have increased.

# Key to identify the species in the genus Discothyrea for Colombia

1. Propodeal spiracles located very close to the metapleural gland bulla (figures  $4.11-12)\dots 2$ 

92

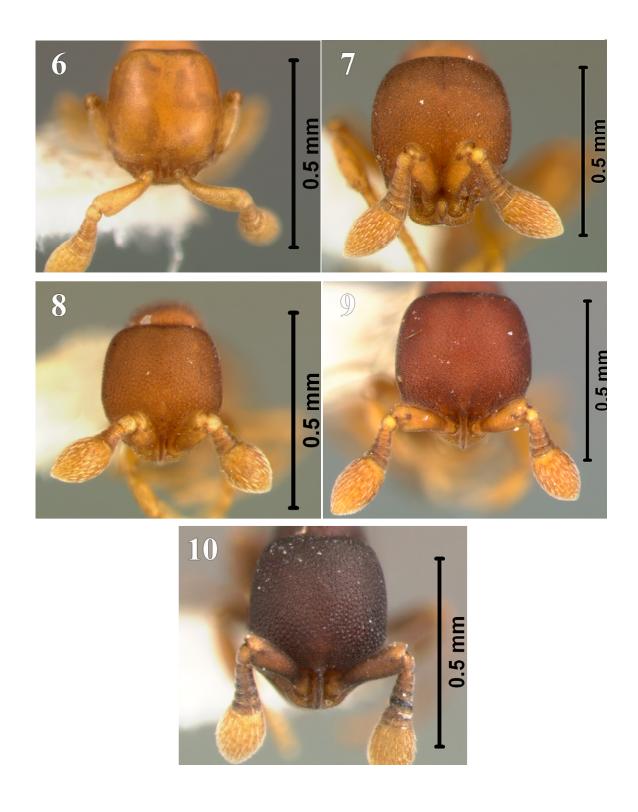
- Propodeal spiracles located distant to the metapleural gland bulla (figures 4.
   13 15) ... 3
- 2. Interantennal lamina reduced to a acute denticle (figures 4. 1, 4. 6) ... *D. humilis* Weber
- Interantennal lamina developed and convex in profile. With head in full-face view, interantennal lamina sligthly swollen (figure 4. 7) ... nr. *D. neotropica* Bruch
- 3. Antenna 6-segmented (figure 4. 8) ... D. sexarticulata Borgmeier
- -. Antenna 8-segmented (figures 4. 9 10) ... 4
- Propodeal spiracles located close to the dorsal border of propodeum or directed towards the median portion of propodeum (figure 4. 14).
   Interantennal lamina always with a median tooth (figure 4. 14)... D. denticulata Weber
- Propodeal spiracles always directed towards the mid lateral portion of propodeum (figure 4. 15). Interantennal lamina lacking a median tooth or denticle (figure 4. 15) ... D. horni Menozzi

# **Species in Colombia**

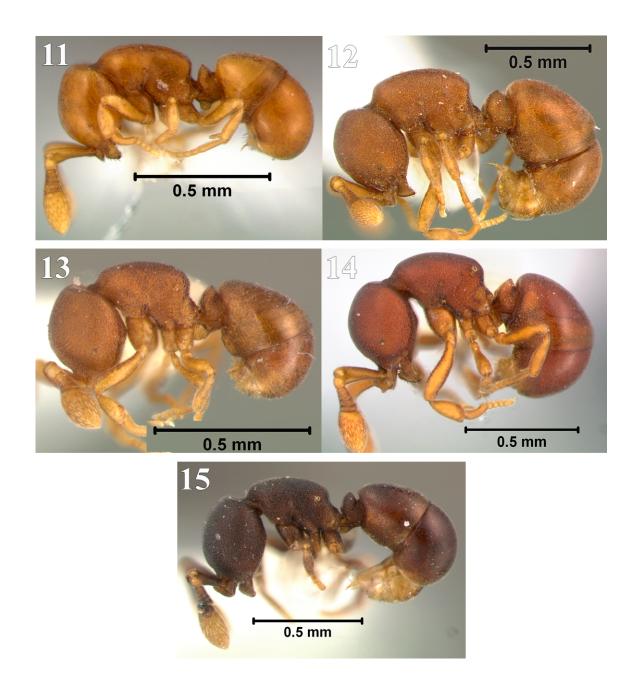
# Discothyrea denticulata Weber (figures 4. 9, 4. 14)

This species was established by Weber (1939) based on a worker collected from leaflitter samples in Guyana. In the same manuscript, Weber reports the presence of a "metatype" also collected in Guyana. Longino (2005), after close examination of the "metatype", indicated the presence of eight antennal segments rather than the seven segments as described by Weber. This species can be recognized for the number of antennal sengments (8), interantennal lamina developed and bearing a mid tooth or denticle, and body integument, including gaster, dull and finely punctate. The location of the propodeal spiracles can vary. We have examined specimens from Costa Rica, Colombia, and Guyana. In the specimens from Costa Rica the propodeal spiracles are located towards the mid portion of propodeum, when seen in profile. In the specimes from Guyana the propodeal spiracles are located closely to the dorsal portion of the propodeum, and in Colombia both forms can be found. Here we treat these specimens as the same species with the aim that a future revision of the genus can give more information about the variation presented here. This species shares the presence of 8 antennal segments with *D. horni*, but they can be separated from *D. horni* by the presence of a median denticle on the interantennal lamina and somewhat in the form of the anterior margin of clypeus: subtriangular in *D. denticulata* and convex to almost flat in *D. horni*.

This species has been collected in humid and dry tropical forests in Colombia from leaf-litter samples from Amazonas, Caquetá, Cauca, Nariño, Norte de Santander, Putumayo, and Valle del Cauca.



**Figures** 4.6 – 10. *Discothyrea* species in frontal view. 6, *Discothyrea humilis*. 7, *D. nr neotropica*. 8, *D. sexarticulata*. 9, *D. denticulata*. 10, *D. horni*.



**Figures** 4.11 – 15. *Discothyrea* species in lateral view. 11, *Discothyrea humilis*. 12, *D. nr neotropica*. 13, *D. sexarticulata*. 14, *D. denticulata*. 15, *D. horni*.

### Discothyrea horni Menozzi (figures 4. 10, 4. 15)

This species was created by Menozzi (1927) from an alate gyne collected in Costa Rica. Later, Menozzi (1931) described the worker from a single specimen also collected in Costa Rica. In the original description, Menozzi documented the presence of 9 antennal segments. However, we have seen specimens from Colombia and Costa Rica very similar to *D. horni*, in which the workers have 8 antennal segments. Such variation is more common among the tiny funicular segments (segments II and the apical one). Individuals within this species (at least for Colombia and Costa Rica) have the same number of antennal segments as D. *denticulata*. (See discussion in *D. denticulata*.)

This species has been collected in leaf-litter samples from rain and cloud forests in Caquetá, Bolivar, and Quindio, Colombia.

# Discothyrea humilis Weber (figures 4. 6, 4. 11)

This species was described by Weber (1939) based on a gyne collected from Barro Colorado Island, Panama. Individuals of this species can be easily separated from other *Discothyrea* species by the reduction of the interantennal lamina (in profile looking as a tooth between the antennal insertions), 7-segmented antenna, and smooth and shiny integument. The specimens from Colombia also have short hairs on the interantennal lamina that extend over the mandibles. This character state differs from the typical form described by Weber that is found from Panama to Costa Rica. However, we do not have enough evidence to consider this as a new species.

97

This species has been collected in wet tropical forest. In Colombia this species has been collected in forests of Amazonas and Caquetá.

# Discothyrea nr. neotropica Bruch (figures 4. 7, 4. 12)

This species was established by Bruch (1919) from a single specimen (gyne) collected from Alta Gracia, province of Cordoba, Argentina. At the time of discovery, D. neotropica was the first species known from South America. At the National Museum of Natural History (USNM), there is a deposited specimen (gyne) that was collected from San Fernando, province of Buenos Aires, Argentina (~600-1000 km of Alta Gracia). As with the specimen described by Bruch, the specimen from San Fernando has the median anterior margin of clypeus concave and, in profile, a swollen interantennal lamina. The specimen from San Fernando also possess 7segmented antenna as described by Bruch. Therefore we believe that the specimen deposited at the USNM could belong to the species D. neotropica. However, a more detailed study is needed to confirm our beliefs. We have examined specimens from Colombia and Venezuela (five and three workers, respectively) that are similar to the gyne from San Fernando. As the specimen from San Fernando, the specimens from Colombia and Venezuela have the median anterior margin of the clypeus concave and, in full-face view, swollen interantennal lamina. Such character state was not documented by Bruch (1919). Nonetheless, the specimens from Colombia and Venezuela differ from the specimen deposited at the USNM and from the description by Bruch, by the presence of nine antennal segments. However, the variation seen on

those specimens could be a result of the fusion of segments. Furthermore, the position of the specimen on the point makes it difficult to count the funicular segments.

Individuals from this species have been collected in dry, wet, and montane tropical forests and savannah. In Colombia this species has been collected from Caquetá, Bolivar, and Magdalena.

## Discothyrea sexarticulata Borgmeier (figures 4. 8, 4. 13)

This species was established by Borgmeier (1954) from six specimens (three gynes and three workers) collected in Brazil. It can be separated from the other species that occur in South America by the possession of six antennal segments, strongly reticulate-punctate body integument, and an interantennal lamina with a small median tooth (similar to the one in *D. denticulata* but smaller).

Kugler (1991), in his study on the sting apparatus of some poneromorphs, reported the presence of this species in Colombia from three workers collected from Magdalena. Here we extend the distribution of the species within Colombia to the Amazonas and Caquetá.

# Genus Proceratium Roger

Recently revised by Baroni-Urbani and de Andrade (2003), the genus *Proceratium* Roger 1863, is distributed throughout the tropical and temperate regions of the world. The Neotropic and Neartic regions contains 29 species, of which 24 are extant and 5 fossil species that have been found in Dominican amber. In Colombia, the genus is represented by five species (*P. catio, P. colombicum, P. mancum, P.* 

micrommatum, and P. transitionis). The species of Proceratium can be found nesting in rotting wood, the leaf-litter, under stones, or inclusive in tree branches (Brown 1958, 1974). It is believed that these ants, as species of Discothyrea, are predators of arthropods eggs, especially spider eggs (Brown 1958, 1980). Species within the genus are considered to have small colonies with a few individuals (Baroni-Urbani and de Andrade 2003 offer a extensive review on this matter). Due to their cryptic nature, these ants, as Discothyrea, are difficult to collect in the forest manually, which makes them to appear underrepresented in most entomological collections.

As a member of the tribe Proceratiini, *Proceratium*, similar to *Discothyrea*, has an inward curved gaster. This morphological character has been hypotezised to be used by these ants as a defense mechanism, most likely to block their nest entrance in the presence of intruders (Poldi 1964). Most recently, Baroni-Urbani and de Andrade (2003) reported the presence of a gland located on the fourth abdominal segment and proposed that such gland could be used to repell intruders (de Andrade and Baroni-Urbani 2002). This character has also been proposed as a way to manipulate the eggs preyed upon (Brown 1980).

# Diagnosis

Among other characters, members of the genus *Proceratium* can be distinguished by the presence of the following characters: i) masticatory margin of mandibles with 3-12 denticles (in worker and gyne) or 1-4 denticles (in males) (Bolton 2003); ii) a palp formula of 2,2; 3,2; 3,3; or 4,3 (in worker and gyne) and 5,3; 5,2; or 4,3 (in males); iii) a hammer-shaped joint of the maxillary palp II (Kennedy

and Talbot 1939; Brown 1958; Onoyama and Yoshimura 2002; Baroni-Urbani and de Andrade 2003); iv) a ventral process of the petiole; v) a sting apparatus developed and curved downwards; vi) simple pretarsal claws; vii) arolia of variable size; viii) since the antennal insertions are not located over a clipeal platform, the mandibles are exposed in frontal view.

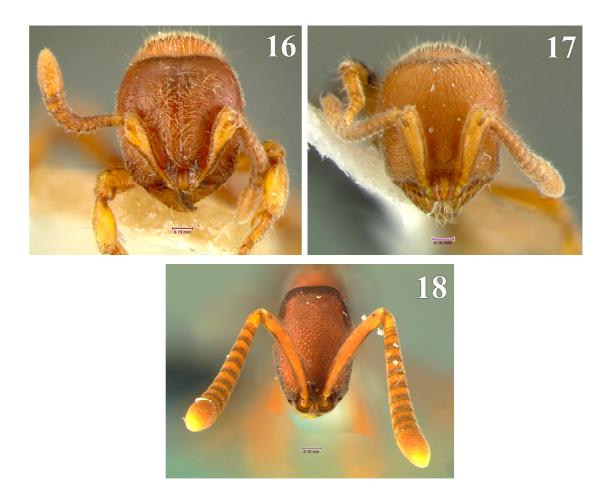
Baroni-Urbani and de Andrade (2003) presented three credible synapomorphies for the genus:

- Eyes of the worker either lacking or composed by minuscule, uniform
   ommatidia or by a "single convex facet." In *Discothyrea* and *Bradoponera* the ommatidia uneven or salient.
- ii. Apical antennal segment of worker or gyne short. Such apical antennal segment much longer in *Discothyrea* and *Bradoponera*.
- iii. Masticatory margin of mandibles of worker and gyne dentate, whereas mandibles in *Discothryea* and *Bradoponera* edentate.

**Key to identify the species of** *Proceratium* **in Colombia** (modified from Baroni-Urbani and de Andrade 2003)

- 1. Palp formula 3,2 ... 2
- -. Palp formula 2,2 ... P. mancum Mann
- 2. Mid tibiae lacking a pectinate spur ... 3
- -. Mid tibia with pectinate spur present ... P. transitornis de Andrade
- 3. Dorsum of propodeum with a protuberance covered by short hairs only ... 4

- Dorsum of propodeum lacking of a protuberance and covered by both long and short hairs ... P. micrommatum (Roger)
- 4. Gaster completely granulate ... P. colombicum de Andrade
- -. Anterior portion of gaster smooth ... P. catio de Andrade



**Figures** 4.16 – 18. *Proceratium* and *Probolomyrmex* species in frontal view. 16, *Proceratium mancum*. 17, *P. micrommatum*. 18, *Probolomyrmex boliviensis*.

## **Species in Colombia**

## Proceratium catio de Andrade

This species was established by de Andrade (2003) from an unique specimen collected in Valle del Cauca, Colombia at an elevation of approx. 1700 m. De Andrade also reported the presence of the possible gyne from two isolated collections in Risaralda and Gorgona Island, Colombia. The collection of the entire colony of *P. catio* or the use of DNA barcoding could further support the approach used by de Andrade. This species belongs to the *micrommatum* group, which includes the species *P. colombicum*, *P. micrommatum* and *P. transitionis*. *Proceratium catio* can be separated from *P. colombicum* by having a gaster that is incompletely sculptured rather than entirely sculptured. *Proceratium catio* can be distinguished from *P. micrommatum* by having a dorsum of propodeum with a bump covered by short hairs instead of dorsum of propodeum lacking such a bump and covered with both short and long hairs. *Procaratium catio* can be easily separated from *P. mancum* and *P. transitionis* by having mid tibiae without a pectinate spur.

This species is only known to be found from Colombia. The holotype was collected in Valle del Cauca and two gynes placed within the species were collected from Gorgona Island and Risaralda.

# Proceratium colombicum de Andrade

This species, described by de Andrade 2003 from a single individual collected in Nariño at almost 1000 m elevation, is the smaller member of the *micrommatum* 

species group. A detailed discussion of how this species differs from the other species of *Proceratium* found in Colombia is given under *P. catio*.

This species is only known from the type locality (Baroni-Urbani and de Andrade 2003).

# Proceratium mancum Mann (figures 4. 16, 4. 19)

This species was described by Mann (1922) from two workers collected from Honduras. This species constitutes the only of the *silaceum* species group found in Colombia. The *silaceum* species group, with 30 described species, is the largest group of *Proceratium* (Baroni-Urbani and de Andrade 2003). This species can be easily separated from other species in Colombia by having the palp formula 2,2 rather than 3,2 shown by the other four species.

This species is known from Antioquia, Caquetá, and Quindio, Colombia.

# Proceratium micrommatum (Roger) (figures 4. 17, 4. 20)

This species was erected by Roger (1863) from South America. Differences with other species of *Proceratium* from Colombia are given in *P. catio*.

This species is known from Guajira and Quindio, Colombia.

## Proceratium transitionis de Andrade

This species was established by de Andrade (2003) from a single worker collected from Santander, Colombia. Baroni-Urbani and de Andrade (2003) studied the phylogenetic relationships among the species of the genus and found out that *P*.

transitionis was the most basal species within the *micrommatum* species group. However, *P. transitornis* resembles the species of the *stictum*-group, it can be distinguished from all the species in the *stictum*-group by lacking the spine on the spur of the fore legs and by a reduction on the palp formula (3,2) rather than 4,3.

This species is known from Santander, Colombia (Baroni-Urbani and de Andrade 2003).



**Figures** 4.19 – 22. *Proceratium* and *Probolomyrmex* species in lateral view. 19, *Proceratium mancum*. 20, *P. micrommatum*. 21, *Probolomyrmex boliviensis*. 22, *P. petiolatus*.

# **Tribe Probolomyrmecini**

This tribe was recently elevated to taxonomical status by Bolton (2003) and includes the only genus *Probolomyrmex* Mayr (1901) and eleven described species worldwide. The diagnosis of the tribe is as in the genus.

## Genus Probolomyrmex

In 1901, Mayr created the genus *Probolomyrmex* from a specimen collected from Africa that present as remarkable characters the clypeus and frontal carinae fused, which appeared as a lobe over the base of the mandibles. Later, Santschi (1914) described the second specimen of *Probolomyrmex filiformis* from French Guinea. It would not be until almost a decade later when Mann (1923) described the first specimen within the genus from the New World, named *P. boliviensis*. The genus is now represented by four species distributed in the Americas (Taylor 1965; Agosti 1994; O'Keefe and Agosti 1997). Although, few studies about the behavior by Ito (1998) and Taylor (1965), the foraging habits of the ants within the genus remain unknown.

# Diagnosis

In addition to the characters mentioned previously for the subfamily, the tribe Probolomyrmecini has the following characters: i) workers lacking eyes; ii) mandibles small, triangular, and covered, laterally, by the clypeus; iii) promesonotum lacking of a visible suture; iv) tibiae with a pectinate spur; v) petiole lacking a fusion of the tergite and sternite; vi) in Probolomyrmecini abdominal tergite IV is not

strongly vaulted and its respective sternite is not strongly reduced, which is different to members within the tribe Proceratiini; vii) in males the frontoclipeal expansion is present, but is different from the one presented in workers and gynes; viii) stigma present on forewing; ix) antennae of workers and gynes 12-segmented, in males 13-segmented; x) palp formula 4,2; xi) mandibles of workers and gynes with 6-8 teeth, males with mandibles with a unique tooth; xii) and body and legs elongate.

**Key to identify the species of** *Probolomyrmex* **from the Neotropics** (modified from Agosti 1994; O'Keefe and Agosti 1997):

- Large ants and with antennal scapes elongate (Length of the body > 0.95 mm;
   scape index > 110). Body strongly sculpture ... P. boliviensis Mann
- Smaller ants and with short antennal scapes (Lenght of the body < 0.95 mm;</li>
   scape index < 110). Body fine and uniformely sculpture ... 2</li>
- 2. Process of petiole rectangular ... P. petiolatus Weber
- -. Process of petiole denticulate ... 3
- 3. Head small (Length of head < 0.62 mm; width of head < 0.37 mm). Antennal scapes short (Scape index= 99) ... *P. brujitae* Agosti
- Head large (Length of head > 0.62 mm; width of head > 0.37 mm). Antennal scapes larg (Scape index= 106) ... P. guanacastensis O'Keefe and Agosti

# Species in Colombia

# Probolomyrmex boliviensis Mann (figures 4. 18, 4. 21)

Established by Mann (1923) from specimens from Bolivia, it constituted the first species of the genus described for South America. This species can easily be identified for its size (Length of mesosoma usually more than 1 mm), elongate antennal scapes, and a finely sculptured body. Taylor (1965) revised the genus for the World and presents a detailed description of the biology of this species.

This species has been collected in Colombia from Antioquia and Magdalena.

# **Probolomyrmex petiolatus** Weber (figure 4. 22)

This species was established by Weber (1940) from specimens collected by Weber in Panama. Agosti (1994) later extended its distribution to the northern regions of South America (Colombia and Venezuela). This species is easily separated from *P. boliviensis* by the length (Length of the mesosoma usually less than 0.80 mm), short antennal scapes, wide head, and a rectangular process of petiole.

This species has been collected in Colombia from Meta (Agosti 1994).

# Acknowledgements

We are particularly grateful with Fernando Fernandez and Tania M. Arias for inviting us to participate in this book. For comments and suggestions on early versions of the maniscript, we thank Leeanne Alonso (CI), Carlos R. Brandão (MZSP), Diego F. Campos (UNAL), Hermogenes Fernandez (STRI), John Lattke (MIZA), Christopher Marshall (NMNH-SI), Charyn Micheli (NMNH-SI), and Carlo Moreno (University of Maryland). We are thankfull to Scott Whittaker (NMNH-SI) for helping with SEM photographs. This manuscript was supported, in part, by the NSF grants DEB-0205982 to Dr. M. Sharkey, NSF IRCEB 0110073 to Dr. T.R. Schultz, and the A.W. Mellon Research Exploration Award in Tropical Biology to J. Sosa-Calvo. JSC is thankful to Dr. Ted R. Schultz for access to the U.S. National Insect Collection at the National Museum of Natural History, Smithsonian Institution, and for use of the AutoMontage workstation there. JSC is also indebted to Enrique Castillo and the Alexander von Humboldt Institute for the loan of specimens and use of the Insect Collection in Villa de Leyva, Colombia.

## **CHAPTER 5:**

Description of three remarkable new species of the primitive fungusgrowing ant genus *Myrmicocrypta*, with notes about the genus and its position within Attini

JEFFREY SOSA-CALVO<sup>1, 2</sup> AND TED R. SCHULTZ<sup>2</sup>

1 Maryland Center for Systematic Entomology, Department of Entomology, University of Maryland, 4112 Plant Sciences Building, College Park, MD 20742, U.S.A. E-mail: sossajef@si.edu

2 Department of Entomology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, MRC 188 CE516, Washington, DC 20013-7012, U.S.A. E-mail: <a href="mailto:schultzt@si.edu">schultzt@si.edu</a>

#### **Abstract**

Three new Brazilian species of the fungus-growing ant genus *Myrmicocrypta* are described. All three species are unique within the genus due to the presence of erect pilosity. *Myrmicocrypta camargoi* sp. nov. is additionally unique because of its large size and pronounced sculpture, whereas, with their small size and effaced, tuberculate sculpture, *Myrmicocrypta erectopilosa* sp. nov. and *M. samperi* sp. nov. are more typical for the genus. The latter two species are closely related, but can be distinguished by differences in the frontoclypeal and hypostomal teeth, frontal lobes, mesonotal sculpture, and propodeal spines. All castes (workers, gynes, and males) are described for *Myrmicocrypta camargoi*, workers and gynes are described for *M. erectopilosa*, and only workers are described for *M. samperi*. Because the erect pilosity encountered in these species contradicts the state previously considered diagnostic for the genus, that of appressed, spatulate or squamiform pilosity found in

all other *Myrmicocrypta* species, we necessarily discuss the characters that define the genus *Myrmicocrypta* and assess its phylogenetic position within the tribe Attini.

**Key words:** Attini, fungus-growing ants, *Myrmicocrypta erectapilosa* sp nov., *Myrmicocrypta camargoi* sp nov., *Myrmicocrypta samperi* sp. nov., Myrmicinae, South America.

## Introduction

The ant genus *Myrmicocrypta* (Formicidae: Myrmicinae: Attini) was established by Fr. Smith (1860) based on an alate gyne collected in Sao Paulo, Brazil. The genus has never been revised; genus-level taxonomic actions consist of two synonymies (Emery 1894; Weber 1958) and the transfer of nine species to the attine genera *Mycetophylax* Emery and *Trachymyrmex* Forel (Emery 1913, 1922; Santschi 1922, 1929; Weber 1958). Currently the genus comprises 28 described species and subspecies (Kempf 1972; Hölldobler and Wilson 1990; Bolton 1995; Schultz and Meier 1995) distributed in the Neotropics from Southern Mexico through Northern Argentina (Kempf 1972). Except for Trinidad and Tobago, which are biotically indistinguishable from the mainland, the genus is unknown in the Caribbean (Wheeler 1922a; Weber 1958, 1968; see Kempf 1972 for distributional information).

The genus *Myrmicocrypta* is one of 13 genera within the monophyletic ant tribe Attini (Schultz and Meier 1995; Wetterer et al. 1998; Price et al. 2003; Schultz and Brady in prep.). Like all other attine ants, all *Myrmicocrypta* species, so far as their biology is known, cultivate fungus gardens upon which they depend for food (Wilson 1971; Garling 1979; Hölldobler and Wilson 1990; Mueller et al. 2005; Schultz et al. 2005). Chief among the putative synapomorphies uniting *Myrmicocrypta* species are the recurved, appressed, squamiform or spatulate setae present in workers and gynes (but not in males). Indeed, the first species described was named *M. squamosa*, of which the author, Fr. Smith (1860:74), wrote, "... covered on every part with separate and not very distant scales, which are of a glittering transparent white, – those on the scape of the antennae and legs most dense,

the flagellum alone being naked; . . . " (Fr. Smith 1860). This character state has been cited consistently in the subsequent taxonomic history of the genus and in identification keys (Fr. Smith 1860; Mayr 1865, 1887; Emery 1913, 1922; Mann 1916, 1922; Wheeler 1922b, 1925; Santschi 1936; Weber 1937, 1938, 1947, 1958, 1972; Borgmeier 1948; Hölldobler and Wilson 1990; Bolton 1994; Palacio and Fernandez 2003). Here, as part of a larger taxonomic revision and phylogenetic analysis of the genus currently in progress, we describe three new species of *Myrmicocrypta* in which this character state is contradicted, requiring a redefinition of the genus based on previously described as well as newly discovered synapomorphies.

## **Materials and Methods**

Specimens were examined at various magnifications using a Leica MZ125 light stereomicroscope. All measurements were taken to the nearest 0.001 mm and, unless otherwise noted, are in millimeters. Measurements of paratypes are listed within parentheses. Specimens were photographed using a JVC KY-F70B video camera mounted on a Leica M420 steromicroscope attached to an IBM Intellistation M Pro computer, on which composite images were assembled using Auto-Montage Pro® (Version 5.03.0018 BETA) software (Synoptics Ltd.). Images were cropped and edited using Photoshop CS2® (Version 9) (Adobe Inc.). The measurements, indices, and morphological terminology utilized throughout follow Gauld and Bolton (1988), Hölldobler and Wilson (1990), Huber and Sharkey (1993), Bolton (1994), and

Kugler (1994), with modifications where noted. Anatomical abbreviations are as follows:

- CI Cephalic Index: (HW/HL)\*100.
- EL Eye Length: in profile, the maximum diameter of the eye measured from the dorsal margin to the ventral margin.
- FLD Frontal Lobes Distance: in full-face view, the maximum horizontal distance between the outer borders of the frontal lobes.
- FLI Frontal Lobes Index: (FLD/HW)\*100.
- GL Gaster Length: in lateral profile, the length of the gaster from the anteriormost point of first gastral segment (fourth abdominal segment) to the posteriormost point of the last segment.
- HL Head Length: in full-face view, the maximum vertical distance from the posteriormost margin of the head to the midpoint of the anterior clypeal margin, excluding the mandibles.
- HW Head Width: in full-face view, the maximum horizontal width of the cephalic capsule excluding the eyes.
- MI Mandibular Index: (ML/HL)\*100.
- ML Mandible Length: in full-face view, the maximum diagonal-line distance from the base of the external mandibular insertion to the apical tooth.
- PL Petiole Length: in lateral profile, the straight-line distance from the posteriormost margin of the petiole to the posteriormost margin of the metapleural lobe.
- PPL Postpetiole Length: in lateral profile, the maximum length of the postpetiole.

- SI Scape Index: (SL/HW)\*100.
- SL Scape Length: in full-face view, the maximum length of the scape excluding the basal condyle.
- TL Total Length: HL+ML+WL+PL+PPL+GL.
- WL Weber's Length: in lateral profile, the diagonal length of the alitrunk as measured from the anteriormost dorsal extent of the pronotum to the posteriormost ventral angle of the propodeum.

The specimens examined were borrowed from and/or have been deposited in the following institutions:

CPDC Jacques Delabie Collection, CEPEC/CEPLAC, Itabuna, Bahia, Brazil.

IAvH Instituto "Alexander von Humboldt," Villa de Leyva, Boyacá,

Colombia.

INPA Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.

LACM Natural History Museum of Los Angeles County, Los Angeles,

California, U.S.A.

MCZC Museum of Comparative Zoology, Harvard University, Cambridge,

Massachussets, U.S.A.

MZSP Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

SMNK Staatliches Museum fuer Naturkunde Karlsruhe, Germany.

USNM National Museum of Natural History, Washington, DC., U.S.A.

## **Taxonomic treatment**

The genus Myrmicocrypta

*Myrmicocrypta* is currently regarded as relatively "primitive" for the tribe Attini, i.e., retaining many character states considered plesiomorphic for the tribe, including characters of wing venation (Kusnezov 1963); male antennal morphology (Kusnezov 1961); degree of queen/worker polymorphism (Wheeler 1910); monomorphism of the worker caste (Wheeler 1910; Emery 1912); larval morphology, including the form of the galea in some species (Schultz and Meier 1995); position on the integument of mutualistic *Pseudonocardia* Henssen (Actinomycetes) bacterial cultures (Currie et al. 1999); and the use, by the nest-founding gyne, of her shed forewing as a platform for the incipient garden (Fernandez-Marin et al. 2004).

Colonies of most *Myrmicocrypta* species are small, consisting of less than 200 individuals (Weber 1945; Murakami and Higashi 1997; Price et al. 2003). Nest form varies across species, usually consisting of either a single, spherical, shallow chamber in the soil or of a single, irregular chamber within rotting wood (Mann 1916; Weber 1941, 1945, 1947, 1968, 1969; Hölldobler and Wilson 1990; Murakami and Higashi 1997; JSC and TRS personal observation). Workers are cryptic foragers in the leaf litter and thus rarely hand-collected in the field. *Myrmicocrypta* species reportedly use a wide variety of organic matter as substrate for their fungus gardens, including arthropod frass, wood pellets, insect corpses, seeds, flower parts, dry leaves, and other plant debris (Weber 1941, 1945, 1947, 1966, 1968, 1969; Hölldobler and Wilson 1990; Murakami and Higashi 1997; Mueller et al. 2005). The only thorough study of *Myrmicocrypta* biology (Murakami and Higashi 1997) reports that *M. ednaella* Mann

garden substrate consists mainly of wood chips and occasional insect corpses and that adult workers feed primarily upon plant nectar and sap, which they share with other workers via trophallaxis.

Fr. Smith (1860) created the genus *Myrmicocrypta* based on an alate gyne collected in Sao Paulo, Brazil. Mayr (1865:24) briefly defined the genus, citing the characters: wings of gynes with short hairs, with submarginal cell enclosed, lacking stigma and lacking discal cell; and very reduced frontal lobes in workers and gynes. Forel (1885) created the genus *Glyptomyrmex*, based on a single male collected in Orizaba, Mexico, noting its resemblance to males in the genera *Apterostigma* Mayr and *Cyphomyrmex* Mayr. Mayr (1887) described the species *Apterostigma uncinatum*, based on a worker collected in St. Catharina, Brazil. After examining the type specimen and additional specimens (worker, gyne, and male) collected in Asuncion, Paraguay, Emery (1890:70) transferred this species to *Glyptomyrmex*. Referring to the description by Fr. Smith (1860) and reexamining the gyne, Emery (1894:224) synonomized the genus *Glyptomyrmex* with *Myrmicocrypta* and synonomized *G. uncinatus* with *M. squamosa*. Subsequently, Forel (1911:295) revived *uncinata* as a variety of *M. squamosa*.

Interestingly, in his description Fr. Smith (1860:74) points out a possible relationship between *Myrmicocrypta* and *Oecodoma* Latreille, a genus now regarded as a junior synonym of the attine leaf-cutting genus *Atta* Fabricius [Roger 1863:35]. Because, contrary to other authors of the day, Fr. Smith's (1858) concept of *Oecodoma* seemed to comprise our modern concept of the leaf-cutting attine genera *Atta* and *Acromyrmex* Mayr, this inference demonstrates a perceptive insight. Forel

(1885) was the first researcher to propose the monophyly of the Attini, grouping the seven genera known at the time (including *Myrmicocrypta*), three of which were regarded as "subgenera" of *Atta*. Six years later, however, he expanded the tribal definition to include additional genera ("the former Cryptocerides excluding *Cryptocerus* Latreille and *Procryptocerus* Emery"), none of which are fungusgrowers nor any longer considered to be attines. It was only after the fungus-growing behavior became known for multiple attine genera (Möller 1893; Forel 1893) that the tribal composition became relatively stable.

The Attini are morphologically heterogeneous, with few unreversed synapomorphies. The tribe is characterized by: (i) 11 antennal segments in workers and gynes, 13 in males (reduced to 12 in some Cyphomyrmex Mayr and Trachymyrmex Forel species, in Pseudoatta argentina Gallardo, and in all Sericomyrmex Mayr species); (ii) palpal formula of 4,2 (reduced to 3,2 in all Apterostigma species and in Pseudoatta argentina); (iii) anterior tarsus dilated, with the distal tarsomere long (reversed in some *Cyphomyrmex* species); (iv); larvae with short, narrow labrum; (v) larval mandibles fleshy, straight, and subconical; (vi) larvae with leg vestiges present as open integumental slits (Schultz and Meier 1995); (vii) obligate cultivation of fungi for food (Leucoprineaceae or, in some derived Apterostigma species, Pterulaceae) (Schultz et al. 2005); (viii) presence of a long unpaired median clypeal seta that arises from the border of the clypeus and clypeal apron, secondarily lost in all Apterostigma except A. megacephala Lattke and in Mycetophylax emeryi (Forel) (Lattke 1997, 1999; Brandão and Mayhé-Nunes 2001; Klingenberg and Brandão unpublished thesis).

Some, but not all, previous researchers have suggested that *Myrmicocrypta* is primitive within the Attini, i.e., that *Myrmicocrypta* species may be morphologically little diverged from the ancestral attine and that the genus may occupy a phylogenetic position near the root of the attine tree. Wheeler (1910) was the first to propose that Myrmicocrypta is the "most primitive" attine genus, based on low degree of worker/queen polymorphism and on the monomorphic worker caste. Emery (1912) produced the first phylogenetic diagram for the tribe, dividing it into two clades, one containing (Apterostigma + Myrmicocrypta), and the other containing (Cyphomyrmex + the rest of the attines). A year later he added *Mycocepurus* Forel to the clade containing Myrmicocrypta and Apterostigma, based on the relative size of the male antennal pedicel (Emery 1913), and subsequently reinforced this grouping (Emery 1922). Kusnezov (1955: 23) also hypothesized that the genera Myrmicocrypta + Apterostigma + Mycocepurus were primitive based on nest architecture, number of individuals per colony, fungal substrate, worker monomorphism, and defense behavior. He subsequently grouped the three genera together under the name Paleoatiini (Kusnezov 1963). The phylogeny of Schultz and Meier (1995), based solely on morphological characters of larvae, reconstructs Myrmicocrypta as paraphyletic with regard to both the remaining Paleoattini (*Mycocepurus* + *Apterostigma*) and the Neoattini.

The Paleoattini share a number of plausible synapomorphies including: i) the presence of a fenestra (clear spot) on the forewings of gynes, to our knowledge unique among ants (Emery 1913, 1922; Fernandez-Marin et al. 2005; Schultz unpublished); ii) inferior corner of the pronotum rounded, entirely lacking a spine,

tooth, or angle; iii) male antennal funicular segment I (pedicel) much shorter (almost as twice as short) than funicular segment II; iv) the presence of the *Pseudonocardia* actinomycete mutualist on the basisternum II under the forelegs (Currie et al. 1999); and v) hypostoma of workers and gynes bearing a pair of lateral teeth, secondarily lost in some *Apterostigma* and some *Mycocepurus*. The monophyly of the Paleoattini is also supported in molecular phylogenetic analyses (Schultz and Brady, unpublished). *Myrmicocrypta* can be separated from the other two Paleoattine genera by the characters listed in the following diagnosis.

# Genus Myrmicocrypta Fr. Smith, 1860

*Myrmicocrypta*, Smith, Journ. Ent. i. p. 73, t. 4. fig. 14-17 (1860). Type-species: *Myrmicocrypta squamosa* Junior synonymy of *Myrmicocrypta* 

*Glyptomyrmex*, Forel, Bull. Soc. Vaud. Sci. Nat. (2) xx. p. 50 (1885). Type-species: *Glyptomyrmex dilaceratum Glyptomyrmex* as junior synonym of *Myrmicocrypta* Emery, Bull. Soc. Ent. Ital. 26: 224 (1894)

Putative synapomorphies for the genus include:

## WORKER:

- 1) Antennal scapes bilobed at the base at the junction of the antennal condyle.
- 2) Posterior lateral margins of the clypeus, anterior to the frontal lobes, produced into a pair of blunt to acuminate frontoclypeal teeth.
- Area of propleuron adjacent to the inferior pronotal angle bearing a tooth, tubercle, or carina.
- 4) Postpetiole with lateral margins usually confluent with the anterior lateral margins of the gaster.

5) Body, of most species, typically covered with appressed to suberect squamate or spatulate hairs, reversed to erect or simple hairs in *M. erectapilosa* sp. nov. and *M. samperi* sp. nov.

#### MALE:

1) Propodeal spines extremely long and thin.

WORKER (Diagnosis): Monomorphic. Posterior border of head in full-face view convex, interrupted by a median concavity and sometimes by blunt tubercles but never by teeth or spines. Eyes of variable size, strongly convex, hemispherical, or globose. Lacking a ventral subocular prominence. Antennal scapes long, usually surpassing the occipital corners and bilobed at the base at the junction of the antennal condyle. Clypeal apron ("anteclypeus" of Brandão and Mayhé-Nunes 2001) always present as a smooth to weakly sculptured shiny strip. Posterior lateral margins of the clypeus, anterior to the frontal lobes, produced into a pair of blunt to acuminate frontoclypeal teeth. Frontal lobes narrow, in some species incompletely covering the antennal sockets, and always separated by a fingerlike posterior projection of the clypeus. Lateral corners of hypostoma with acute hypostomal teeth (hypostomal teeth rounded or absent in *Apterostigma* and *Mycocepurus*). Area of propleuron adjacent to the inferior pronotal angle bearing a tooth, tubercle, carina, or otherwise sculptured and bearing erect hairs (sculpture and setae absent in *Mycocepurus* and sculpture absent in *Apterostigma*). Promesonotum usually with spines or tubercles, rarely reduced to low ridges or carinae (as in Apterostigma), anteriorly with three pairs of spines or tubercles, but never with a crown of well-differentiated spines (as in

Mycocepurus). Petiole with a long peduncle and a well-defined petiolar node lacking spines but sometimes with a posterior carina (petiolar node ill-defined in Apterostigma and armed with a pair of spines in Mycocepurus). Postpetiole, in dorsal view, usually trapezoidal with or without posterior margin emarginate, the lateral margins usually confluent with the anterior lateral margins of the gaster. First gastral segment somewhat longer than wide; in dorsal view, its anterior and posterior margins straight, the lateral margins convex and anteriorly carinate. Sting present, protruding, and visible; frequently large. Body of most species covered with appressed to suberect squamate or spatulate hairs, in rare cases (described below) with erect or simple hairs (in Apterostigma hairs always long, simple, and flexuous [Lattke 1997, 1999], in Mycocepurus simple, short, and either erect, curved, or decumbent [Kempf 1963]).

Type- species: Myrmicocrypta squamosa Fr. Smith.

*Myrmicocrypta camargoi* Sosa-Calvo & Schultz, NEW SPECIES (Figures 5.1 – 5.11)

**Diagnosis (worker):** The largest known species of *Myrmicocrypta* (TL > 4 mm); body covered with erect setae; frontal lobes, in full-face view, convex laterally and, in profile, strongly protruding; antennal scapes covered with simple, sub-erect hairs; lateral mesonotal spines very long and knobbed at apex, with some spatulate hairs. **Holotype:** worker, labeled: "Brazil, Sao Paulo, Botacatu, 29-xi-2002, R.S. Camargo. Nest series, pasture." Holotype deposited in MZSP.

122

**Paratypes:** nine workers, same data as holotype. Deposited in IAvH (1), MCZC (1), MZSP (3), and USNM (4).

**Worker:** Measurements: TL= 4.58 (4.49 – 4.89); WL= 1.36 (1.33 – 1.46); HL= 0.97 (0.94 – 1.02); HW= 0.74 (0.72 – 0.80); SL= 1.13 (1.10 – 1.19); ML= 0.61 (0.58 – 0.69); EL= 0.12 (0.11 – 0.12); PL= 0.39 (0.39 – 0.42); PPL= 0.22 (0.21 – 0.23); GL= 1.03 (0.97 – 1.13); CI= 76 (76 – 81); SI= 153 (147 – 154); MI= 63 (60 – 71); FLD= 0.31 (0.28 – 0.34) (n= 10).

Description (worker). *Head*: almost 1.3x as long as wide (excluding the mandibles); posterior corners of the head in full-face view convex; head with scattered erect, spatulate hairs; in lateral view, frontal carinae posteriorly branching into projections of almost similar size and shape; the posteriormost the vertexal carinae; eyes with 7 – 8 ommatidia in longest row and 37 - 42 in total; eyes globose, and located posterior to the middle of the head at a level above the frontal lobes; antennal scapes very long and thin, slightly thickened at the apex; antennal flagellum incrassate, typical for Attini; antennal scapes surpassing the occipital corners by almost 1.5x the maximum distance between the frontal lobes; clypeus medially forming a slight angle, hyaline, brilliant, and imbricate; posterior margin of clypeal apron with a thick, long unpaired median seta (0.17 mm) and, on each side of median seta, with 6-7 simple appressed hairs; frontoclypeal teeth acute, covered with suberect, spoon-like hairs; mandibles with 8–10 teeth, increasing uniformly in size from base to apex; sculpture on dorsal surface of mandibles reticulate, frontal lobes expanded laterally (0.28 - 0.34 mm), covering the antennal insertions; in profile, frontal lobes strongly protruding;

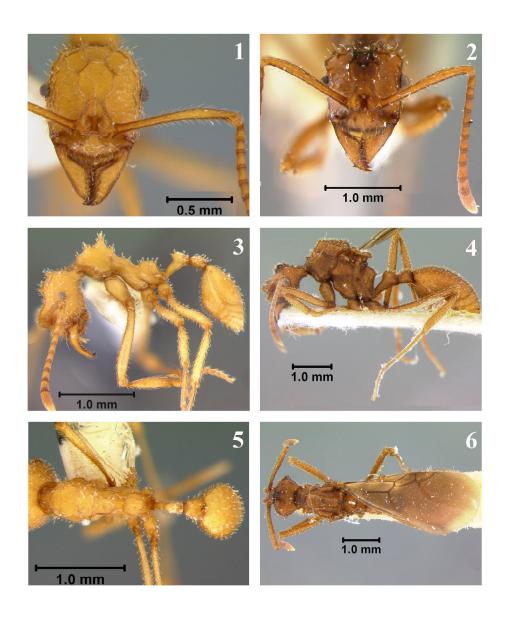
posterior margin of hypostoma with simple hairs that project over the hypostomal plate. Dorsum of hypostomal plate shiny and hairless; anterior-lateral margin of hypostoma with a pair of acute teeth; in profile, occiput drawn out posteriorly into an enlarged bilobed "neck" or "collar" that extends backwards covering the anteriorlateral portions of pronotum. Mesosoma: pronotum with the following sculpture: a pair of low anterior tubercles, a pair of humeral spines, a pair of lateral spines that are directed forward; propleuron, adjacent to the inferior pronotal edge, lacking distinct tubercles, the site bearing roughenings and erect, spatulate hairs. Mesonotum with the following set of cuticular projections: a pair of long, blunt lateral spines (the largest ones on the alitrunk), a pair of acute anterior spines, a shallow but conspicuous groove, a pair of small median spines, and a pair of small posterior spines (in some individuals the latter can be smaller than the former). In profile, base of propodeum flat and slightly longer than the declivity; both with thin lateral lamellae; propodeal spines short and blunt. Base of forecoxa with a conspicuous longitudinal carina. *Metasoma*: petiolar peduncle lacking ventral process; node of petiole, in dorsal view, longer than wide and, in lateral view, with anterior margin rounded and posterior margin flat; node of postpetiole, in dorsal view, slightly wider than long; posterior margin of postpetiole medially emarginate; in dorsal view, posterior margin of postpetiole as wide as the anterior margin of abdominal segment IV; dorsum of abdominal segment IV finely reticulate and covered with erect spatulate hairs; abdominal segment IV straight basally and margined at sides.

Individuals yellow to light ferruginous; pilosity spoon-shaped or spatulate, restricted mainly to spines and carinae; antennal scapes covered with simple, erect hairs; hairs on IV abdominal tergite short, erect, and spatulate.

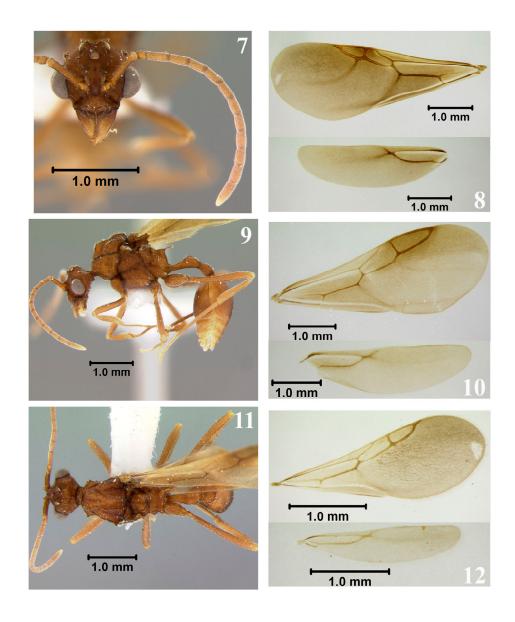
**Queen:** 1 gyne labeled: "Brasil: Jatai, Goiás, Faz. Aceiro; 30 x 1962; Exp. Dep. Zool. Cerrado" (MZSP); 1 gyne labeled: "Sao Paulo, Botucatu; 5 x 1991; (BH Dietz)" (MZSP).

Measurements: TL= 7.42 – 7.51; WL= 2.13 – 2.18; HL= 1.20 – 1.24; HW= 1.05 – 1.13; SL= 1.44; ML= 0.42; EL=0.22 – 0.25; PL= 0.67 – 0.72; PPL= 0.38 – 0.39; GL= 2.15 – 2.22; CI= 85 – 94; SI= 127 – 137; MI= 67 – 69; FLD= 0.42 – 0.43 (n= 2).

Description: quite similar to the worker except for the differences of the caste. *Head*: excluding mandibles, slightly longer than wide with lateral and posterior margins straight; occipital margin with raised carina; posterior ocelli very small and concealed by the frontal carina, median ocellus small (0.06 mm in diameter) and covered posteriorly by a horizontal carina; frontal carinae as in the worker; mandibles with 11 teeth; clypeus as in worker and with a long unpaired median setae (length= 0.24 mm). *Mesosoma:* anterior pronotal and humeral spines well developed; lateral spines bearing small tubercles; inferior margin of pronotum rounded; in profile, propleuron slightly obtuse angulate adjacent to the inferior pronotal edge; anterior pronotal spines connected by a weak carina, easily visible in fronto-dorsal view; mesoscutum with notauli carinate and extending through the entire length of mesoscutum; median line short and fading out at almost half the length of mesoscutum; parapsidal sutures present at each side of notauli, long, and well developed; transscutal articulation



**Figures** 5. 1-6. *Myrmicocrypta camargoi*, new species. 1, 3, and 5 worker habitus (1, full-face (dorsal) view; 3, profile; and 5, dorsal view). 2, 4, and 6 gyne habitus (2, full-face view; 4, profile; and 6, dorsal view).



**Figures** 5. 7, 9, and 11 male habitus of *Myrmicocrypta camargoi*, new species. 8, *M. camargoi* gyne fore and hind wing. 10, *M. camargoi* male fore and hind wing. 12, *M. erectapilosa* gyne fore and hind wing.

present; margin of axilla carinate and with posterior tubercles; lateral margins of mesoscutum carinate; scuto-scutellar sulcus deep and with posterior margin of mesoscutum projecting as spines, medially emarginate; scutellum without lateral projections and ending posteriorly as two prominent spines; base of propodeum, on each side, with a lamella that extends through all its length and continues partially on the declivity of propodeum forming an angle, but lacking spines; mesopleuron divided medially by a deep sulcus. *Metasoma*: peduncle of petiole, on each side, with a dorsal longitudinal lamella that runs almost its entire length; node of petiole, in dorsal view, with carinate porsterior margins; postpetiole as in worker; abdominal segment IV finely reticulate-punctate. *Wings*, fore wing (length 4.80 mm) with very reduced fenestra, which appears as a rounded spot near the apical margin (figure 5.9); hind wing (length 3.57 mm) with one closed cell.

Head and body dark ferruginous; gaster yellowish to light ferruginous; wings smoky. Pilosity as in worker.

**Male:** 2 males labeled: "Brasil: GB, Rio de Janeiro (Floresta da Tijuca); iv 1966, (M. Alvarenga, col.); 2 males labeled: "Brasil: Espirito Santo, Santa Teresa, xi 1928. (O. Conde col.)." Measurements: TL= 5.96 – 6.34; WL= 1.90 – 1.98; HL= 0.90 – 0.94; HW= 0.77 – 0.83 (including eyes= 1.08); SL= 0.48 – 0.54; ML= 0.48 – 0.58; EL= 0.37 – 0.40; PL= 0.64 – 0.73; PPL= 0.23 – 0.33; GL= 1.64 – 1.86; CI= 82 – 92; SI= 58 – 70; MI= 53 – 62; FLD= 0.25 – 0.29 (n= 4).

Description. Head: triangular; occipital corners strongly angulate; ocelli larger than those in gynes (mid ocellus= 0.12 mm in diameter), concave on its anterior margin; a very small tooth-like tubercle behind each posterior ocelli; frontal carina extending posterad and forming a sort of low tubercle; a median carina extends between the frontal lobes to the anterior margin of median ocellus; dorsum of mandibles finely punctate; masticatory margin with 8-9 teeth gradually diminishing in size toward base; outer margin of mandibles slightly convex; body of clypeus with a raised median carina that emerges at the setal socket and that extends posterad and splitting into two carinae that curve at the level of the frontoclypeal teeth. Such carinae continuing anteriorly reaching the posterior margin of the clypeal apron; antennae with 13 segments; antennal scapes barely surpassing posterior cephalic margin, shorter than funicular segments I-III combined; funicular segment II 2.3x longer than funicular segment I (antennal pedicel); posterior margin of head, in profile, concave and bearing a median longitudinal carina that originates at the occipital carina; occipital collar not at all produced into a neck. Mesosoma: pronotum with humeral and lateral spines short and acute, anterior spines absent; in fronto-dorsal view, anterior spines replaced by a longitudinal carina that connects the lateral spines; inferior margin of pronotum rounded; propleuron, adjacent to the inferior pronotal edge, bearing a group of very low tubercles and with simple hairs; mesoscutum and scutellum as in the gyne; in lateral view, propodeal spines long and spatulate; sides of basal portion and declivity of propodeum with a low carina. *Metasoma*: petiole pedunculate; node of petiole, in profile, low and convex; petiole with longitudinal carina that extends dorsally along its entire length; node of petiole longer than wide;

node of postpetiole wider than long; abdominal segment IV finely reticulate. *Wings*: as in the female but lacking fenestra. Forewing length= 4.56 - 4.68 mm; hindwing length= 3.25 - 3.47 mm.

Individuals ferruginous in color; antennae and legs testaceous; pilosity on antennal scape simple and appressed; head and mesosoma with hook-like hairs mostly on carinae and tubercles; consisting of simple appressed or decumbent hairs; abdominal segment IV with very short, simple appressed hairs.

ETYMOLOGY: It gives us great pleasure to name this striking and unusual fungusgrowing ant after its discoverer, R.S. Camargo.

# *Myrmicocrypta erectapilosa* Sosa-Calvo & Schultz, NEW SPECIES (Figures 5.12 – 5.18)

**Diagnosis:** Individuals with body covered by erect, simple hairs; sculpture on mesosoma reduced, frontal lobes triangular and partially covering the antennal insertions.

Holotype: worker, labeled: "Brazil: Amazonas 4832; Manaus- RS 2108; 21 x 93 C5; AB Casimiro P. Coleção do Laboratório de Myrmecologia # 62 (CEPEC)"
Paratype: 3 workers, labeled: "Brazil; Amazonas; Manaus BR. 174 Km 45 EEST 51;

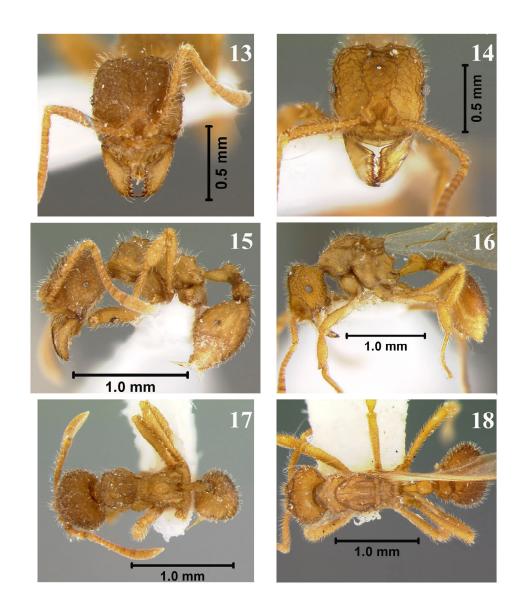
13 ix 1991; AY Harada and AG Bandeira." (INPA)

**Worker:** Measurements: TL= 3.33 (3.22 – 3.25); WL= 0.91 (0.84 – 0.87); HL= 0.71 (0.66 – 0.69); HW= 0.63 (0.57 – 0.60); SL= 0.65 (0.60 – 0.63); ML= 0.45 (0.44 – 0.47); EL= 0.06 (0.05); PL= 0.33 (0.29 – 0.36); PPL= 0.15 (0.16); GL= 0.78 (0.70 –

0.76); CI= 89 (86 – 87); SI= 103 (103 – 107); MI= 63 (67 – 69); FLD= 0.24 (0.21 – 0.22) (n= 4).

Description: Head: 1.13 – 1.15x as long as wide (excluding the mandibles); posterior margin convex with a shallow concave notch medially (vertexal area), but without projections; head covered mainly with erect and suberect hairs; integument evenly rugose; frontal carinae vestigial; eyes very small (8 ommatidia total) and located closer to occipital corner than to insertion of mandibles; antenna incrassate and with 11 segments, both typical for the Attini; antennal scape slightly wider at midpoint; hairs on antennal scape long and erect or semi-erect; antennal scapes surpassing the cephalic corners by near 1.8x their apical width; clypeal apron convex, transparent, and shiny with some shallow longitudinal striae and with five pairs of simple, long slender, appressed hairs that originate at the posterior margin of clypeal apron and overhang the mandibles; medially with an unpaired long (0.14 - 0.16 mm), thick seta; frontoclypeal teeth acuminate and covered with simple erect hairs; mandibles with 6 – 7 teeth increasing in size from base to apex; dorsal surface of mandibles reticulate and with appressed hairs, the latter more concentrated on outer margin of mandible; frontal lobes, in full face view, triangular and partially covering the antennal insertions; hypostomal teeth short and acute; hypostomal plate small, lacking hairs, smooth, and shiny; occiput not extended into a "neck" or "collar." *Mesosoma*: pronotal humeral and lateral spines knoblike, anterior pronotal spines absent; dorsum of pronotum with a median longitudinal carina that emerges at the anterior margin of pronotum and extends posteriorly to almost at the level of the lateral mesonotal

spines; dorsum of pronotum matte and sometimes with low wrinkles; inferior pronotal margin rounded; propleuron, adjacent to the inferior pronotal edge, with one or two very low tubercles, and bearing simple hairs; all mesonotal spines reduced to carinae; anterior propodeal spines absent; posterior propodeal spines short and blunt; base of propodeum, in profile, flat and as long as the declivity of the propodeum; declivity of propodeum with a very reduced, but conspicuous lamella on each side. Metasoma: petiole pedunculate; ventral process of petiole, in profile, very small and with a narrow carina that extends through all of the ventral petiolar length; node of petiole, in profile, rounded; node of petiole, in dorsal view, ellipsoidal and with a longitudinal carina; node of postpetiole 1.6x wider than long; posterior edge of postpetiole, in dorsal view, slightly emarginate; postpetiole, in profile, longer than high and dorsally convex; in dorsal view, disc of postpetiole wider than long (1:1.6 – 1:1.9); base of abdominal segment IV, where it attaches the postpetiole and anteriorlateral edges, carinate; dorsum of abdominal segment IV finely reticulate. Individuals uniformly brown ferruginous; antennal scapes, head, and mesosoma covered with simple, erect hairs on the body restricted mainly to carinae or tubercles; hairs on dorsum of abdominal segment IV hook-like.



**Figures** 5. 13 – 18. *Myrmicocrypta erectapilosa*, new species. 13, 15, and 17 worker habitus (13, full-face (dorsal) view; 15, profile; and 17, dorsal view). 14, 16, and 18 gyne habitus (14, full-face view; 16, profile; and 18, dorsal view).

**Gyne:** 3 alate gynes labeled: "Brazil, Mato Grosso, Sinop, 55° 37'W 12° 31'S, x 1974 (Alv. & Roppa Col.) (12725); 1 alate gyne labeled: "Brazil, Mato Grosso, Sinop, 55° 37'W 12° 31'S, x 1974 (Alv. & Roppa Col.) (12580); 1 dealate gyne labeled: "Brasil; Amazonas; Manaus BR. 174 Km 45 EEST 51; 13 ix 1991; AY Harada and AG Bandeira." (INPA).

Measurements: TL= 4.11 – 4.24; WL= 1.13 – 1.19; HL= 0.76 – 0.81; HW= 0.69 – 0.71; SL= 0.68 – 0.75; ML= 0.50 – 0.53; EL= 0.11 – 0.12; PL= 0.40 – 0.46; PPL= 0.19 – 0.22; GL= 1.05 – 1.13; CI= 88 – 92; SI= 96 – 106; MI= 63 – 68; FLD= 0.27 – 0.29 (n= 5).

Description: characters similar to those in worker with modifications expected for caste and with the following differences: *Head*: frontoclypeal teeth, in lateral view, large and acute; frontal carina extending posterad to almost the level of the midocellus and splitting into two low carinae, the vertexal ones being more conspicuous; ocelli small (maximum length of middle ocellus= 0.06); occipital collar (neck) well-developed, with both upper and lower tubercles knob-like, the lower one, in some cases, slightly bigger. *Mesosoma*: dorsum of pronotum conspicuously rugose; humeral and lateral pronotal tubercles present; propleuron, adjacent to the inferior pronotal edge, somewhat angulate and bearing several curved hairs; mesoscutum overall rugose; mesoscutal sulcus, in dorsal view, conspicuous and short, not extending more than 1/3 the length length of mesoscutum; notauli shallow and almost inconspicuous; parapsidal lines conspicuous and extending near to the anterior margin

of mesoscutum; scuto-scutellar sulcus present and conspicuous; scutellum posteriorly bidentate, dorsally rugose; propodeum with a pair of short denticles; declivity of propodeum with a reduced, but conspicuous lamella on each side. *Metasoma*: petiole as in the worker, with longitudinal ventral carina inconspicuous; postpetiole 2.5x wider than long, with a pair of latero-posterior projections; dorsum of first gastral tergite densely reticulate; base of abdominal segment IV with widely spaced costulae; base of abdominal tergite IV with conspicuous antero-lateral carina, as in the worker. *Wings*: fore wings (length= 2.73 - 2.83 mm) with a small crescent-shaped fenestra located on the apex of the wing; apical margin, beginning at the end of the R1 vein through the end of the claval furrow, with erect simple hairs; hind wing (length= 2.06 - 2.08 mm) with six hamuli and with one closed cell; apical margin, beginning at the last hamuli to the end of the anal vein, with erect simple hairs (figure 5.12). Individuals dark yellow or light brown; wings smoky. Pilosity as in the worker.

ETYMOLOGY: The name *erectapilosa* derives from the latin erectus= standing and pilosum= hair and refers to the erect hairs present in this species, the first such species to come to our attention.

# *Myrmicocrypta samperi* Sosa-Calvo & Schultz, NEW SPECIES (Figures 5.19 – 5.21)

**Diagnosis:** very similar to individuals of *M. erectapilosa*. Frontal lobes vestigial, failing to cover the antennal insertions; hypostomal teeth long and slightly curving at the apex; vertexal carina present; humeral and lateral pronotal spines acute; dorsum of pronotum smooth and shiny.

**Holotype:** 1 worker labeled: "Brazil: Amapa, Serra do Navio (Silverstone, leg)." (LACM 42302)

**Paratypes:** 3 workers, same locality as in holotype (LACM 42302); 1 worker labeled: "Brazil, Amazonas, Manaus, 9 v 2003, (C. Rabeling and M. Verhaagh, leg.)." (USNM)

**Worker:** Measurements: TL= 3.54 (3.28 – 3.29); WL= 0.96 (0.91 – 1.01); HL= 0.76 (0.72 – 0.76); HW= 0.66 (0.62 – 0.67); SL= 0.71 (0.66 – 0.72); ML= 0.51 (0.45 – 0.51); EL= 0.06 (0.05); PL= 0.34 (0.31 – 0.32); PPL= 0.19 (0.16 – 0.19); GL= 0.78 (0.72 – 0.80); CI= 87 (86 – 88); SI= 108 (105 – 109); MI= 67 (63 – 67); FLD= 0.12 (0.11 – 0.12) (n= 5).

Description: *Head*: head almost 1.2x longer than broad; posterior margin convex, convexity interrupted by two knob-like tubercles in the vertexal area; integument rugulose and matte; frontal carinae obsolete or vestigial; eye very small with 7-9 ommatidia in total; eyes above middle of head; antennal scape reticulate and long, surpassing the occipital corners by twice its apical width; clypeal apron convex and

medially slightly angulate, hyaline, and dorsum with longitudinal striae; median unpaired seta thick and long (length 0.13 - 0.15 mm) originating near the posterior margin of the apron; anterior margin of clypeal apron with 8 simple hairs (4 at each side of the median hair) that extend over the mandibles; clypeus with 2 blunt frontoclypeal teeth covered with simple, erect hairs; mandibles with 6-7 teeth decreasing in size from apex to base; dorsal surface of mandibles striolate; frontal lobes strongly reduced, exposing antennal insertions; hypostomal teeth large and slightly curved; occipital "collar" (neck) reduced, with short and blunt teeth; antennal scape wider near its apex than at the rest of its length; anterior edge of the antennal scape minutely denticulate and, in full-face view, bearing suberect to erect hairs, posterior margin of scape bearing appressed to subdecumbent hairs. *Mesosoma*: dorsum of pronotum smooth and shining with low humeral tubercles; stout and blunt lateral spines; lacking anterior and inferior pronotal spines; propleuron, adjacent to the inferior pronotal edge, with a broadly obtuse angle and with some subdecumbent or suberect, simple or lanceolate hairs; mesonotum with lateral tubercles reduced to carinae, anterior tubercles low; mesonotal groove matte without hairs, in some individuals with a short, rudimentary longitudinal median carina; median mesonotal tubercle low; posterior mesonotal tubercles blunt apically and slightly larger than the median tubercles; metanotal groove with a median longitudinal carina that extends from the posterior portion of mesonotum through the anterior portion of the propodeum; propodeum lacking anterior spines or tubercles, although in some individuals angulate; posterior propodeal spines long and acute; basal and declivous areas of the propodeum with a narrow lateral lamella that extends to the propodeal



**Figures** 5. 19 - 21. Habitus of worker of *Myrmicocrypta samperi*, new species. 19, full-face view. 20, lateral view. 21, dorsal view.

lobe; base of propodeum flat, in profile subequal to declivity of propodeum.

*Metasoma*: petiole pedunculate; node of petiole, in profile, with a carina that arises on the anterior and posterior margins of the node giving it a subquadrate appearance (the posterior margin usually most prominent); node of petiole longer than broad, in dorsal view; postpetiole broader than long, in dorsal view; posterior margin of postpetiole emarginate medially; latero-posterior margins of postpetiole, in dorsal view, with inferior wing-like projections giving it a trapezoidal shape; shape of postpetiole, in profile, longer than higher (1:1.2-1:1.3); dorsum of abdominal segment IV finely reticulate-punctate; base of abdominal segment IV lacking a carina on its anterolateral margin.

Individuals brown ferruginous; pilosity restricted to wrinkles, tubercles, spines, carinae, appendages, and antennal scapes, absent elsewhere. Legs and antennal scapes strongly reticulate.

**Gynes and males:** unknown.

ETYMOLOGY: It gives us great pleasure to name this species after Dr. Cristian Samper, who as founder and Director of the Alexander von Humboldt Biological Resources Research Institute, as Director of the National Museum of Natural History, and as Acting Secretary of the Smithsonian Institution has promoted, supported, and encouraged scientific research.

Discussion: *M. samperi* is similar to *M. erectapilosa* but differs from it by having simple, curved hairs, whereas in *M. erectapilosa* hairs are entirely erect; frontoclypeal teeth blunt (large and acute in *M. erectapilosa*); hypostomal teeth longer, larger, and slightly curved at tip (short, small, and straight in *M. erectapilosa*); frontal lobes narrow (triangular as in *M. erectapilosa*) exposing part of the antennal condyles; vertexal spines present; humeral and lateral spines acute (spines reduced in *M. erectapilosa*); dorsum of pronotum smooth and shiny (matte in *M. erectapilosa*); in profile, node of petiole subquadrate (rounded in *M. erectapilosa*). *M. samperi* can be separated from other *Myrmicocrypta* species by the presence of simple, semi-erect hairs.

## Acknowledgements

We are indebted to R.S. Camargo for collecting the type specimens of *M. camargoi*, to C. Rabeling and M. Verhaag for collecting specimens of *M. samperi*, and to A.B. Casimiro, A.Y. Harada, and A.G. Bandeira for collecting the specimens of *M. erectapilosa*. Jacques Delabie (CEPEC), Enrique Castillo (IAvH), Roy Snelling (LACM), C. Roberto F. Brandão (MZSP), Christian Rabeling (U. of Texas at Austin), M. Verhaag (SMNK), and Ana Harada loaned us specimens. This research was supported in part by the NSF-IRCEB DEB 0110073 to TRS.

# **Appendices**

### ENTOMOLOGICAL SOCIETY OF WASHINGTON

c/o Department of Entomology National Museum of Natural History Smithsonian Institution P.O. Box 37012, MRC 168 Washington, D.C. 20013-7012 Phone: 202 382-1783

Fax: 202 384-7822 e-mail: dave.smith@ars.usda.gov

April 15, 2007

Mr. Jeffrey Sosa-Calvo Department of Entomology University of Maryland College Park, MD 20742

Dear Mr. Sosa-Calvo:

This is in response to your request to use illustrations or other material from your article published in the *Proceedings of the Entomological Society of Washington*.

The *Proceedings* is not copyrighted. However, for the record, you are welcome and have permission to use any material you wish from your articles in the *Proceedings*.

Sincerely,

David R. Smith,

Daw A Amit,

Editor

# Bibliography

#### CHAPTER ONE

- Agosti, D. and Alonso, L. E. 2000. The ALL protocol: a standard protocol for the collection of ground-dwelling ants In: *Ants, Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti, J. Majer, L. E. Alonso and T. R. Schultz (Eds.). Washington, DC: Smithsonian Institution Press.
- Agosti, D., J. D. Majer, L. E. Alonso, and T. R. Schultz. 2000. Ants: Standard methods for measuring and monitoring biodiversity (Eds.). Washington, DC: Smithsonian Institution Press.
- Alonso, L. E. 2000. Ants as indicators of diversity In: : *Ants, Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti, J. Majer, L. E. Alonso and T. R. Schultz (Eds.). Washington, DC: Smithsonian Institution Press.
- Bánki, O. S., H. ter Steege, M. J. Jansen-Jacobs, U. P. D. Raghoenandan. 2003. Plant diversity of the Nassau Mountains, Suriname. Report of the 2003 Expedition.
- Bolton, B. 2000. The ant tribe Dacetini, with a revision of the *Strumigenys* species of the Malagasy Region by Brian L. Fisher, and a revision of the Austral epopostrumiform genera by Steven O. Shattuck. Memoirs of the American Entomological Institute, 65: 1 1028.
- Borgmeier, T. 1934. Contribuição para o conhecimento da fauna mirmecólogica dos cafezais de Paramaribo, Guiana Holandesa (Hym. Formicidae). Arquivos do Instituto de Biología Vegetal, 1: 93 113.
- Brandão, C. R. F. 1991. Adendos ao catálogo abreviado das formigas da região

- Neotropical (Hymenoptera: Formicidae). Revista Brasileira de Entomologia, **35**: 319 412.
- Brandão, C. R. F., J. L. M. Diniz and E. M. Tomotake. 1991. *Thaumatomyrmex* strips millipedes for prey: a novel predatory behaviour in ants, and the first case of sympatry in the genus (Hymenoptera: Formicidae). Insectes Sociaux, 38: 335 344.
- Brühl, C. A., M. Mohamed, and K. E. Linsenmair. 1998. Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. Journal of Tropical Ecology, 15: 265 177.
- Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. Biometrics, 43: 783 791.
- Chazdon, R. L., R. K. Colwell, J. S. Denslow, and M. R. Guariguata. 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forest of northeastern Costa Rica. In: *Forest biodiversity research, monitoring, and modeling: conceptual background and Old World case studies*. F. Dallmeier and J. A. Comiskey (eds.). The Parthenon Publishing Group.
- Colwell, R. K., J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society (Series B), 345: 101 118.
- Colwell, R. K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application published at: http://purl.oclc.org/estimates.

- Fernandez, F. and S. Sendoya. 2004. List of Neotropical ants (Hymenoptera: Formicidae). Biota Colombiana, 5: 3 93.
- Fisher, B. L. 1999. Improving inventory efficiency: A case study of leaf litter ant diversity in Madagascar. Ecological Applications, 9: 714 731.
- Fisher, B. L. 2005. A model for a global inventory of Ants: A case study in Madagascar. Proceedings of the California Academy of Sciences, 56: 86 97.
- Gibbs, A. K. and C. N. Barron. 1993. The geology of the Guyana Shield. Oxford University Press, Oxford. 246 pp.
- Gotelli, N. J. and G. L. Entsminger. 2006. EcoSim: Null models software for ecology.

  Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465.

  http://garyentsminger.com/ecosim.htm.
- Haden, P. 1999. Forestry issues in the Guyana Shield region: A perspective on Guyana and Suriname. European Union Tropical Forestry. Overseas Development Institute, London.
- Kaspari, M. and J. D. Majer. 2000. Using ants to monitor environmental change. In:
  Ants, Standard Methods for Measuring and Monitoring Biodiversity, D.
  Agosti, J. Majer, L. E. Alonso and T. R. Schultz (Eds.). Washington, DC:
  Smithsonian Institution Press.
- Kempf, W.W. 1961. A Survey of the ants of the soil fauna in Surinam (Hymenoptera: Formicidae). Studia Entomologica, 4: 481 524.
- Kempf, W.W. 1972. Catalogo abreviado das formigas da região Neotropical (Hymenoptera: Formicidae). Studia Entomologica, 15: 3 344.
- King, J. R. and S. D. Porter. 2005. Evaluation of sampling methods and species

- richness estimators for ants in upland ecosystems in Florida. Environmental Entomology, 34: 1566 –1578.
- LaPolla, J. S., T. Suman, J. Sosa-Calvo, and T. R. Schultz. 2007. Leaf litter ant diversity in Guyana. Biodiversity and Conservation, 16: 491 510.
- Lee, S. M. and A. Chao. 1994. Estimating population size via sample coverage for closed capture- recapture models. Biometrics, 50: 88 97.
- Longino, J.T. 2000. What to do with the data? In: *Ants, Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti, J. Majer, L. E. Alonso and T. R. Schultz (Eds.). Washington, DC: Smithsonian Institution Press.
- Longino, J. T., J. Coddington, and R. K. Colwell. 2002. The ant fauna of a tropical rain forest: Estimating species richness three different ways. Ecology, 83: 689 702.
- Longino, J.T. 2007. Ants of Costa Rica. Genus *Hypoponera*(http://academic.evergreen.edu/projects/ants/genera/hypoponera/key.html)
- Magurran, A. E. 2004. Measuring biological diversity. Blackwell.
- Schultz, T. R. and T. P. McGlynn. 2000. The interactions of ants with other organisms. In: *Ants, Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti, J. Majer, L. E. Alonso and T. R. Schultz (Eds.).
  Washington, DC: Smithsonian Institution Press.
- Smith, E. P. and G. van Belle. 1984. Nonparametric estimation of species richness. Biometrics, 40: 119 129.
- ter Steege, H., O. S. Bánki, T. R. van Andel, J. Behari-Ramdas, and G. Ramharakh.

- 2004. Plant diversity of the Brownsberg Nature Park, Suriname. Report of the Nov Dec 2003 Expedition.
- ter Steege, H., O. S. Bánki, M. Jansen-Jacobs, G. Ramharakh, and K. Tjon. 2005.

  Plant diversity of the Lely Mountains, Suriname. Draft Report of the Nov –

  Dec 2004 Expedition.
- Toti, D. S., F. A. Coyle, and J. A. Miller. 2000. A structured inventory of

  Appalachian grass bald and heath bald spider assemblages and a test of
  species richness estimator performance. The Journal of Arachnology, 28: 329

   345.
- Tropenbos International Suriname Programme. 2004. Issues paper: Information issues in the Suriname forest sector. 117 pp.
- Underwood, E.C. and B. Fisher. 2006. The role of ants in conservation monitoring: If, when, and how. Biological Conservation, 132: 166 182.
- Ward, P. S. 2000. Broad-scale patterns of diversity in leaf litter ant communities. In:
  Ants, Standard Methods for Measuring and Monitoring Biodiversity, D.
  Agosti, J. Majer, L. E. Alonso and T. R. Schultz (Eds.). Washington, DC:
  Smithsonian Institution Press.
- Wilson, E. O. 2003. Pheidole in the New World. Harvard University Press, Cambridge, Massachusetts, 793 pp.

## **CHAPTER TWO**

Baroni-Urbani, C. & de Andrade, M. L. 1994. First description of fossil Dacetini

- ants with a critical analysis of the current classification of the tribe. (Amber Collection Stuttgart: Hymenoptera, Formicidae. VI: Dacetini.) Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie), 198: 1 65.
- Bolton, B. 1994. Identification guide to the ant genera of the world. Harvard University Press, Cambridge, Massachusetts, 222 pp.
- Bolton, B. 1998. Monophyly of the dacetonine tribe-group and its component tribes.

  Bulletin of the Natural History Museum (Entomology Series), 67: 65 78.
- Bolton, B. 1999. Ant genera of the tribe Dacetonini. Journal of Natural History, 33: 1639 1689.
- Bolton, B. 2000. The ant tribe Dacetini, with a revision of the *Strumigenys* species of the Malagasy Region by Brian L. Fisher, and a revision of the Austral epopostrumiform genera by Steven O. Shattuck. Memoirs of the American Entomological Institute, 65: 1 1028.
- Brown, W. L., Jr. 1948. A preliminary generic revision of the higher Dacetini.

  Transactions of the American Entomological Society, 74: 101 129.
- Brown, W. L., Jr. 1949a. Revision of the ant tribe Dacetini: III. *Epitritus* Emery and *Quadristruma* new genus (Hymenoptera: Formicidae). Transactions of the American Entomological Society, 75: 43 51.
- Brown, W. L., Jr. 1949b. Revision of the ant tribe Dacetini: IV. Some genera properly excluded from the Dacetini, with the establishment of the Basicerotini *new tribe*. Transactions of the American Entomological Society, 75: 83 96.
- Brown, W. L., Jr. 1949c. Revision of the ant tribe Dacetini. I. Fauna of Japan, China

- and Taiwan. Mushi, 20: 1-25.
- Brown, W. L., Jr. 1950a. Revision of the ant tribe Dacetini: II. *Glamyromyrmex*Wheeler and closely related small genera. Transactions of the American Entomological Society, 76: 27 36.
- Brown, W. L., Jr. 1950b. Revision of the ant tribe Dacetini: V. The delimitation of *Arnoldidris*, new genus (Hymenoptera: Formicidae). Transactions of the American Entomological Society, 76: 143 145.
- Brown, W. L., Jr. 1950c. Preliminary description of seven new species of the dacetine ant genus *Smithistruma* Brown. Transactions of the American Entomological Society, 76: 37 45.
- Brown, W. L., Jr. 1952. The dacetine ant genus *Mesostruma*. Transactions of the Royal Society of South Australia, 75: 9 13.
- Brown, W. L., Jr. 1953a. The Neotropical species of the ant genus *Strumigenys* Fr. Smith: group of *mandibularis* Fr. Smith. Journal of the New York Entomological Society, 61: 53 59.
- Brown, W. L., Jr. 1953b. Revisionary studies in the ant tribe Dacetini. American Midland Naturalist, 50: 1-137.
- Brown, W. L., Jr. 1954(1953). A preliminary report on dacetine ant studies in Australia. Annals of the Entomological Society of America, 46: 465 471.
- Brown, W. L., Jr. 1958. The Neotropical species of the ant genus *Strumigenys* Fr. Smith: Group of *ogloblini* Santschi. Journal of the New York Entomological Society, 65: 133 137.
- Brown, W. L., Jr. 1959a. Some new species of dacetine ants. Breviora, 108: 1 11.
- Brown, W. L., Jr. 1959b. The Neotropical species of the ant genus *Strumigenys* Fr.

- Smith: Group of *gundlachi* (Roger). Psyche, 66: 37 52.
- Brown, W. L., Jr. 1959c. A revision of the dacetine ant genus *Neostruma*. Breviora, 107: 1-13.
- Brown, W. L., Jr. 1960. The Neotropical species of the ant genus *Strumigenys* Fr. Smith: Group of *gundlachi* (Roger). Psyche, 66: 37 52.
- Brown, W. L., Jr. 1962. The Neotropical species of the ant genus *Strumigenys* Fr. Smith: Synopsis and key to the species. Psyche, 69: 238 267.
- Brown, W. L., Jr. 1964. The ant genus *Smithistruma*: a first supplement to the world revision (Hymenoptera: Formicidae). Transactions of the American Entomological Society, 89: 183 200.
- Brown, W. L., Jr. & Wilson, E. O. 1959. The evolution of the dacetine ants.

  Quarterly Review of Biology, 34: 278 294.
- Brown, W. L., Jr., & Kempf, W. W. 1969. A revision of the Neotropical dacetine ant genus *Acanthognathus* (Hymenoptera: Formicidae). Psyche, 76: 87 109.
- Dejean, A. 1985a. Etude éco-éthologique de la prédation chez les fourmis du genre *Smithistruma* (Formicidae: Myrmicinae: Dacetini) II. Attraction des proies principales (collemboles). Insectes Sociaux, 32: 158 172.
- Dejean, A. 1985b. Etude éco-éthologique de la prédation chez les fourmis du genre Smithistruma (Formicidae: Myrmicinae: Dacetini) III. La capture des proies chez S. Emarginata. Insectes Sociaux, 32: 241 – 256.
- Dejean, A. 1987(1986). Etude du comportement de prédation dans le genre *Strumigenys*. Insectes Sociaux, 33: 388 405.
- Deyrup, M. 2006. Pyramica boltoni, a new species of leaf-litter inhabiting ant from

- Florida (Hymenoptera: Formicidae: Dacetini). Florida Entomologist, 89: 1 5.
- Dietz, B.H. & Brandão, C.R.F. 1993. Comportamento de caça e dieta de *Acanthognathus rudis* Brown & Kempf, com comentários sobre a evolução da predação em Dacetini (Hymenoptera, Formicidae, Myrmicinae). Revista Brasileira de Entomologia, 37: 683 – 692.
- Donisthorpe, H. 1948(1947). A third instalment of the Ross collection of ants from New Guinea. Annals and Magazine of Natural History (11), 14: 589 604.
- Donisthorpe, H. 1949(1948). A new genus and species of dacetine ant from New Guinea. Entomologist's Monthly Magazine, 84: 281.
- Fernandez, F. & Sendoya, S. 2004. List of Neotropical ants (Hymenoptera: Formicidae). Biota Colombiana, 5: 3 93.
- Forel, A. 1892. Attini und Cryptocerini. Zwei neue *Apterostigma*-Arten.

  Mitteilungen der Schweizerischen Entomologischen Gesellschaft, 8: 344 349.
- Forel, A. 1893a. Sur la classification de la famille des formicides, avec remarques synonymiques. Annales de la Société Entomologique de Belgiques, 37: 161 167.
- Forel, A. 1893b. Formicides de l'Antille St. Vincent. Récoltées par Mons. H. H. Smith. Transactions of the Entomological Society of London, 1893: 333 418.
- Forel, A. 1899. Biologia Centrali-Americana; or, contributions to the knowledge of

- the fauna and flora of Mexico and Central America. Insecta. Hymenoptera. 3 (Formicidae). London. 169 pp.
- Gronenberg, W. 1996. The trap-jaw mechanism in the dacetine ants *Daceton* armigerum and *Strumigenys sp*. The Journal of Experimental Biology, 199: 2021 2033.
- Gronenberg, W., Brandão, C.R.F., Dietz, B.H., & Just, F. 1998. Trap-jaws revisited: the mandible mechanism of the ant *Acanthognathus*. Physiological Entomology, 23: 227 240.
- Hölldobler, B. & Wilson, E.O. 1990. The Ants. Belknap Press, Cambridge, Massachusetts, 732 pp.
- Kantarovich, S., Nardi, J., and Suarez, A. 2006. Exploring the form and function of the "sponge body" gland in the Dacetini. Poster. Memoirs of the XV meeting of the International Union for the Study of Social Insects (IUSSI).
- Kempf, W.W. 1972. Catálogo abreviado das formigas da regiãão Neotropical (Hymenoptera: Formicidae). Studia Entomologica, 15: 3 344.
- Kempf, W.W. 1975. Report on Neotropical dacetine ant studies (Hymenoptera: Formicidae). Revista Brasileira de Biologia, 34: 411 424.
- Latrielle, P.A. 1802. Histoire naturelle des fourmis, et recueil de memoires et d'observations sur les abeilles, les araignees, les faucheurs, et autres insectes. Paris, 445 pp.
- Lattke, J. & Goitia, W. 1997. El género *Strumigenys* (Hymenoptera: Formicidae) en Venezuela. Caldasia, 19: 367 396.
- Longino, J.T. 2006. Ants of Costa Rica.

- http://www.evergreen.edu/ants/AntsofCostaRica.html (August 23, 2006)
- Mann, W.M. 1922. Ants from Honduras and Guatemala. Proceedings of the United States National Museum, 61: 1 54.
- Mann, W.M. 1926. Some new Neotropical ants. Psyche, 33: 97 107.
- Masuko, K. 1984. Studies on the predatory biology of oriental dacetine ants

  (Hymenoptera: Formicidae) I. Some Japanese species of *Strumigenys*, *Pentastruma*, and *Epitritus*, and a Malaysian *Labidogenys*, with special

  reference to hunting tactics in short-mandibulate forms. Insectes Sociaux, 31:

  429 451.
- Mayr, G. 1887. Südamerikanische Formiciden. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien, 37: 511 – 632.
- Perrault, G.H. 1986. *Gymnomyrmex villiersi*, nouvelle espèce de Guyane [Hymenoptera, Formicidae]. Revue Française d'Entomologie, 8, 1 4.
- Roger, J. 1863. Die neu aufgeführten Gattungen und Arten meines Formiciden-Verzeichnisses, nebst Ergänzung einiger früher gegeben Beschreibungen. Berliner Entomologische Zeitschrift, 7: 131 – 214.
- Santschi, F. 1931. Fourmis de Cuba et de Panama. Revista de Entomologia, 1: 265 282.
- Smith, M.R. 1944. A key to the genus *Acanthognathus* Mayr, with the description of a new species (Hymenoptera: Formicidae). Proceedings of the Entomological Society of Washington, 46: 150 152.
- Sosa-Calvo, J., Shattuck, S.O. & Schultz, T.R. 2006. Dacetine ants of Panama: New

- records and description of a new species (Hymenoptera: Formicidae: Myrmicinae: Dacetini). Proceedings of the Entomological Society of Washington, 108: 814 821.
- Theunis, L., Gilbert, M., Roisin, Y., & Leponce, M. 2005. Spatial structure of litter-dwelling ant distribution in a subtropical dry forest. Insectes Sociaux, 52: 366 377.
- Weber, N.A. 1934. Notes on Neotropical ants, including the descriptions of new forms. Revista de Entomologia, 4: 22 59.
- Weber, N.A. 1941. Four new genera of Ethiopian and Neotropical Formicidae.

  Annals of the Entomological Society of America, 34: 183 194.
- Weber, N.A. 1952. Biological notes on Dacetini (Hymenoptera, Formicidae).

  American Museum Novitates, 1554: 1 7.
- Wheeler, W.M. 1915. Two new genera of myrmicine ants from Brazil. Bulletin of the Museum of Comparative Zoology of Harvard College, 59: 483 491.
- Wheeler, W.M. 1916. Ants collected in Trinidad by Professor Roland Thaxter, Mr. F. W. Urich, and others. Bulletin of the Museum of Comparative Zoology of Harvard College, 60: 323 330.
- Wheeler, W.M. 1922. The ants of Trinidad. American Museum Novitates, 45: 1 16.
- Wheeler, W.M. 1927. The physiognomy of insects. Quarterly Review of Biology, 2: 1-36.
- Wilson, E.O. 1953. The ecology of some North American Dacetine ants. Annals of the Entomological Society of America, 46: 479 495.

Wilson, E.O. 1962. Behavior of *Daceton armigerum* (Latreille), with a classification of the self-grooming movements in ants. Bulletin of the Museum of Comparative Zoology, Harvard University, 127: 401 – 422.

#### CHAPTER THREE

- Agosti, D. J. D. Majer, L. E. Alonso, and T. R. Schultz. 2000. Ants. Standard

  Methods for Measuring and Monitoring Biodiversity. Smithsonian Institution

  Press, Washington and London.
- Bolton, B. 2000. The ant tribe Dacetini, with a revision of the *Strumigenys* species of the Malagasy Region by Brian L. Fisher, and a revision of the Austral epopostrumiform genera by Steven O. Shattuck. Memoirs of the American Entomological Institute, 65: 1 1028.
- Brown, W. L., Jr. 1953. Revisionary studies in the ant tribe Dacetini. American Midland Naturalist, 50: 1 137.
- Brown, W. L., Jr. 1962. The Neotropical species of the ant genus *Strumigenys* Fr. Smith: synopsis and key to species. Psyche, 69: 238 267.
- Dejean, A. 1991. Gathering of nectar and exploitation of Aphididae by *Smithistruma emarginata* (Formicidae: Myrmicinae). Biotropica, 23: 207 208.
- Kaspari, M. and M. D. Weiser. 2000. Ant activity along moisture gradients in a Neotropical forest. Biotropica, 32: 703 711.
- Kaspari, M., J. Pickering, J. T. Longino, and D. Windsor. 2001. The phenology of a Neotropical ant assemblage: evidence for continuous and overlapping reproduction. Behavioral Ecology and Sociobiology, 50: 382 390.

- Lattke, J. and W. Goitia. 1997. El género *Strumigenys* (Hymenoptera: Formicidae) en Venezuela. Caldasia, 19: 367 396.
- Wilson, E. O. 1954[1953]. The ecology of some North American dacetine ants.

  Annals of the Entomological Society of America, 46: 479 495.

#### CHAPTER FOUR

- Agosti, D. 1994. A revision of the South American species of the ant genus *Probolomyrmex* (Hymenoptera: Formicidae). Journal of the New York Entomological Society, 102: 429 – 434.
- Alayo, P., and L. Zayas-Montero. 1977. Estudios sobre los Himenópteros de Cuba.

  VII. Dos nuevas especies para la fauna mirmecológica cubana. Poeyana, 174:

  1 5.
- Baroni-Urbani, C. 1977. *Discothyrea stumperi* n. sp. du Bhoutan, premier representant du genre dans le subcontinent Indien (Hymenoptera: Formicidae). Archives Institut Gry- Ducal de Luxembourg, 37: 197 200.
- Baroni-Urbani C., B. Bolton, P. S. Ward. 1992. The internal phylogeny of ants (Hymenoptera: Formicidae). Systematic Entomology, 17: 301 329.
- Baroni- Urbani, C. and M. L. de Andrade. 2003. The ant genus *Proceratium* in the extant and fossil record (Hym: Form). Monografie XXXVI. Museo Regionale di Scienze Naturali- Torino. 492 pp.
- Bolton, B. 1995. A new general catalogue of the ants of the world. Harvard University Press, Cambridge, MA. 504 pp.
- Bolton, B. 2003. Synopsis y classification of Formicidae. Memoirs of the American

- Entomological Institute, 71: 370 pp.
- Borgmeier, T. 1949. Formigas novas ou pouco conhecidas de Costa Rica e da

  Argentina (Hymenoptera: Formicidae). Revista Brasileira de Biología, 9: 201

   210.
- Borgmeier, T. 1954. Uma nova *Discothyrea* com seis articulos antenais

  (Hymenoptera: Formicidae). Revista Brasileira de Entomologia, 1: 191 194.
- Brandão, C. R. F., J. L. M. Diniz, and E. M. Tomotake. 1991. *Thaumatomyrmex* strips millipedes for prey: a novel predatory behaviour in ants, and the first case of sympatry in the genus (Hymenoptera: Formicidae). Insectes Sociaux, 38: 335 344.
- Brown, W. L. 1954. Predation of arthropod eggs by the ant genera *Proceratium* and *Discothyrea*. Psyche, 64: 115.
- Brown, W. L. 1958. Contributions toward a reclassification of the Formicidae. II.

  Tribe Ectatommini (Hymenoptera). Bulletin of the Museum of Comparative

  Zoology Harvard Collection, 118: 175 362.
- Brown, W. L. 1974. A remarkable new island isolate in the ant genus Proceratium (Hymenoptera: Formicidae). Psyche, 81: 70 83.
- Brown, W. L. 1980. A remarkable new species of *Proceratium* with dietary and other notes on the genus (Hymenoptera: Formicidae). Psyche, 86: 337 346.
- Bruch, C. 1919. Descripcion de una curiosa ponerina de Cordoba "*Discothyrea neotropica*" n- sp. Physis, IV: 400 403.
- de Andrade, M. L. 1998. First fossil records of the ant genus *Discothyrea* in

- Dominican and Mexican Amber (Hymenoptera: Formicidae). Fragmenta Entomologica, 30: 201 214.
- de Andrade, M. L., and C. Baroni-Urbani. 2002. What are they doing with their curved gaster? Notes from Underground, 10: 5.
- Dejean, A., and A. Dejean. 1998. How a ponerinae ant acquired the most evolved mode of colony foundation. Insectes Sociaux, 45: 343 346.
- Dejean, A., A. Grimal, M–C. Marherbe, and J-P. Suzzoni. 1999. From specialization in spider egg predation to an original nesting mode in a "primitive" ant: a new kind of leptobiosis. Naturwissenschaften, 86: 133 137.
- Eisner T., M. Eisner, and M. Deyrup. 1996. Millipede defense: Use of detachable bristles to entangle ants. Proceedings of the National Academy of Sciences, 93: 10848 10851.
- Hölldobler B, and E. O. Wilson. 1990. The Ants. Belknap- Harvard University Press, Cambridge. 732 pp.
- Ito, F. 1998. Colony composition and specialized predation on millipedes in the enigmatic ponerine ant genus *Probolomyrmex* (Hymenoptera, Formicidae).

  Insectes Sociaux, 45: 79 83.
- Kennedy, C. H., M. Talbot. 1939. Notes on the hypogaeic ant, *Proceratium silaceum* Roger. Proceedings of the Indiana Academy of Sciences, 48: 202 210.
- Kempf, W. W. 1972. Catálogo abreviado das formigas da região Neotropical. Studia Entomologica (N. S.), 15: 3 344.
- Kugler, C. 1991. Stings of ants of the tribe Ectatommini (Formicidae: Ponerinae).

  Insecta Mundi, 5: 153 166.

- Lattke, J. E. 1990. Revisión del género *Gnamptogenys* Mayr en Venezuela (Hymenoptera: Formicidae). Acta Terramaris, 2: 1 47.
- Lattke, J. E. 1994. Phylogenetic relationships and classification of ectatommine ants (Hymenoptera: Formicidae). Entomologica Scandinavica, 25: 105 119.
- Longino, J.T. 2005. Ants of Costa Rica Web Page.

  <a href="http://www.evergreen.edu/ants/genera/Discothyrea/specieslist.html">http://www.evergreen.edu/ants/genera/Discothyrea/specieslist.html</a>
- Mann, W. M. 1922. Ants from Honduras and Guatemala. Proceedings of the United States National Museum, 61: 1 54.
- Mann, W. M. 1923. Two new ants from Bolivia. (Results of the Mulford Biological Exploration. Entomology). Psyche, 30: 13 18.
- Mayr, G. 1901. Sudafrikanische Formiciden, gesammelt von Dr. Hans Brauns.

  Annalen des k. k. Naturhistorischen Hofmuseums Wien, 16: 1 30.
- Menozzi, C. 1925. Res Mutinenses. Atti della Società dei Naturalisti e Matematici di Modena, 3: 22 47.
- Menozzi, C. 1927. Formiche raccolte dal Sig. H. Schmidt nei dintorni di San Jose di Costa Rica (Hymenoptera: Formicidae). Entomologische Mitteilungen, XVI: 266 277.
- Menozzi, C. 1931. Contribuzione alla conoscenza del "microgenton" di Costa Rica.

  Bolletino del Laboratorio di Zoologia Generale e Agraria della Facolta Agraria in

  Portici, 25: 259 274.
- O'Keefe, S. T., and D. Agosti. 1997. A new species of *Probolomyrmex*(Hymenoptera: Formicidae) from Guanacaste, Costa Rica. Journal of the New York Entomological Society, 105: 190 192.
- Onoyama, K., and Yoshimura, M. 2002. The ants of the genus *Proceratium*

- (Hymenoptera: Formicidae) in Japan. Entomological Science, 5: 29 49.
- Peeters, C. 1997. Morphologically "primitive" ants: Comparative review of social characters, and the importance of queen- worker dimorphism. In: Choe J, B. Crespi (eds). The evolution of social behavior in insects and arachnids.

  Cambridge University Press, Cambridge.
- Poldi, B. 1964. Alcune osservazioni sul *Proceratium melinum* Rog. e sulla funzione della particolare struttura del gastro. Atti dell'Accademia Nazionale Italiana di Entomologia. Rendiconti, 11: 221 229.
- Roger, J. 1863. Die neu aufgefuhrten Gattungen und Arten meines Formiciden-Verzeichnisses, nebst Erganzung einiger fruher gegeben Beschreibungen. Berliner Entomologische Zeitschrift, 7: 131 – 214.
- Santschi, F. 1914. Formicides de l' Afrique occidentale et australe du voyage de Mr. le Professeur F. Silvestri. Bolletino del Laboratorio di Zoologia Generale e Agraria della R. Scuola superiore d' Agricoltura in Portici, 8: 309 385.
- Smith, M. R. 1955. Remarks concerning the types of five species of ants described by Roger or Forel (Hymenoptera, Formicidae) Bulletin of the Brooklyn Entomological Society, 50: 98 99.
- Smith, M. R., and M. W. Wing. 1954. Redescription of *Discothyrea testacea* Roger, a little-known North American ant, with notes on the genus (Hymenoptera: Formicidae). Journal of the New York Entomological Society, 62: 105 112.
- Taylor, R. W. 1965. A monographic revision of the rare tropicolitan ant genus *Probolomyrmex* Mayr (Hymenoptera: Formicidae). Transactions of the Royal Entomological Society of London, 117: 345 – 365.

- Taylor, R. W. 1967. A monographic revision of the ant genus *Ponera* Latreille.

  Pacific Insects Monographs, 13: 1 112.
- Weber, N. A. 1939. New ants of rare genera and a new genus of Ponerinae ants.

  Annals of the Entomological Society of America, 32: 91 104.
- Weber, N. A. 1940. Rare ponerine genera in Panama and British Guiana (Hym: Formicidae). Psyche, 47: 75 84.
- Wesson L. G. Jr., R. G. Wesson. 1940. A collection of ants from Southcentral Ohio.

  American Midland Naturalist, 24: 89 103.

#### CHAPTER FIVE

- Bolton, B. 1994. Identification guide to the ant genera of the world. Harvard University Press, Cambridge, Massachusetts, 222 pp.
- Bolton, B. 1995. A new general catalogue of the ants of the world. Harvard University Press, Cambridge, MA. 504 pp.
- Borgmeier, T. 1948. Die Geschlechtstiere zweier *Eciton*-Arten und einige andere Ameisen aus Mittel- und suedamerika (Hym. Formicidae). Revista de Entomologia, 19: 191 206.
- Brandão, C.R.F. and A.J. Mayhé-Nunes. 2001. A new fungus-growing ant genus, *Mycetagroicus* gen. nov., with the description of three new species and comments on the monophyly of the Attini (Hymenoptera: Formicidae). Sociobiology 38(3B): 639 665.
- Currie, C.R., J.A. Scott, R.C. Summerbell, and D. Malloch. 1999. Fungus-growing ants use antibiotic-producing bacteria to control garden parasites. Nature, 398: 701 704.

- Emery, C. 1890. Studi sulle formiche della fauna neotropica. Bollettino della Societa Entomologica Italiana, 22: 38 – 80.
- Emery, C. 1894. Studi sulle formiche della fauna Neotropica. Bollettino della Societa Entomologica Italiana 26: 137 – 241.
- Emery, C. 1912. Études sur les Myrmicinae. Annales de la Societe Entomologique de Belgique 56: 94 105.
- Emery, C. 1913. Études sur les Myrmicinae. Annales de la Societe Entomologique de Belgique 57: 250 262.
- Emery, C. 1922. Hymenoptera, Fam. Formicidae, subfam. Myrmicinae. Genera Insectorum 174C: 207 397.
- Fernandez-Marin, H., J.K. Zimmerman, W.T. Weislo. 2004. Ecological traits and evolutionary sequence of nest establishment in fungus-growing ants (Hymenoptera, Formicidae, Attini). Biological Journal of the Linnean Society, 81: 39 48.
- Fernandez-Marin, H., J.K. Zimmerman, W.T. Weislo, and S.A. Rehner. 2005. Colony foundation, nest architecture, and demography of a basal fungus-growing ant, *Mycocepurus smithii* (Hymenoptera, Formicidae). Journal of Natural History, 39: 1735 1743.
- Forel, A. 1885. Études myrmécologiques en 1884; avec une description des organes sensoriels des antennes. Bulletin de la Societe Vaudoise des Sciences Naturelles 20: 316 380.
- Forel, A. 1893. Sur la classification de la famille des formicides, avec remarques

- synonymiques. Annales de la Societe Entomologique de Belgique, 37: 161 167.
- Forel, A. 1911. Ameisen des Herrn Prof. v. Ihering aus Brasilien (Sao Paulo usw.) nebst einigen anderen aus Südamerika und Afrika (Hym.). Deutsche Entomologische Zeitschrift 1911: 285 312.
- Garling, L. 1979. Origin of ant-fungus mutualism: a new hypothesis. Biotropica, 11: 284 291.
- Gauld, I., and B. Bolton. 1988. The Hymenoptera. Oxford University Press. 344 pp.
- Hölldobler, B. and E.O. Wilson. 1990. The Ants. Belknap Press, Cambridge, Massachusetts, 732 pp.
- Huber, J. and M.J. Sharkey. 1993. Structure, pp. 14 59. In: Hymenoptera of the world, an identification guide to families. Agriculture Canada Research Branch Monograph No. 1894E. 668 pp.
- Kempf, W.W. 1963. A review of the ant genus *Mycocepurus* Forel, 1893 (Hymenoptera: Formicidae). Studia Entomologica (N.S.) 6: 417-432.
- Kempf, W.W. 1972. Catálogo abreviado das formigas da região Neotropical. Studia Entomologica (N.S.) 15: 3-344.
- Kugler, C. 1994. Revision of the ant genus *Rogeria* (Hymenoptera: Formicidae) with descriptions of the sting apparatus Journal of Hymenoptera Research 3: 17 89.
- Kusnezov, N. 1955. Evolución de las hormigas. Dusenia, 6: 1 34.
- Kusnezov, N. 1961. Evolution der Ameisen. Symposia Genetica et Biologica Italica 12: 103 – 121.

- Kusnezov, N. 1963. Zoogeografía de las hormigas en Sudamerica. Acta Zoologica Lilloana 19: 25 186.
- Lattke, J. 1997. Revisión del género *Apterostigma* Mayr (Hymenoptera: Formicidae).

  Arquivos de Zoologia 34(5): 121 221.
- Lattke, J.E. A new species of fungus-growing ant and its implications for attine phylogeny (Hymenoptera: Formicidae). Systematic Entomology, 24:1-6.
- Mann, W.M. 1916. The ants of Brazil. Bulletin of the Museum of Comparative Zoology of Harvard College 60: 399 490.
- Mann, W.M. 1922. Ants from Honduras and Guatemala. Proceedings of the U.S. National Museum 61: 1 54.
- Mayr, G.L. 1865. Reise der Oesterreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859, unter den befehlen des Commodore B. von Wuellerstorf-Urbair. Zoologischer Theil. Formicidae. Vienna. 119 pp.
- Mayr, G.L. 1887. Südamerikanische Formiciden. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 37: 511 – 632.
- Möller, A. 1893. Die Pilzgärten einiger südamerikanischer Ameisen. Botanische Mitteilungen aus den Tropen, 1893: 1 127.
- Mueller, U.G., N. Gerardo, T.R. Schultz, D. Aanen, D. Six. 2005. The evolution of agriculture in insects. Annual Review of Ecology and Systematics 36: 563 569.
- Murakami, T., and S. Higashi. 1997. Social organization in two primitive attine ants, *Cyphomyrmex rimosus* and *Myrmicocrypta ednaella*, with reference to their fungus substrates and food sources. Journal of Ethology, 2: 135 – 139.

- Palacio, E.E., and F. Fernandez. 2003. Claves para las subfamilias y géneros. Pages 233 260. In: Fernandez, F. Introducción a las hormigas de la región Neotropical. Instituto Humboldt, Bogotá. 424 pp.
- Price, S. L., T. Murakami, U.G. Mueller, T.R. Schultz, and C.R. Currie. 2003. Recent finding in fungus-growing ants: Evolution, ecology, and behavior of a complex microbial symbiosis. In: Genes, behaviors, and Evolution of social insects (T. Kikuchi, N. Azuma, and S. Itagashi, Eds.), Hokkaido University Press, Sapporo, Japan.
- Roger, J. 1863. Verzeichniss der Formiciden-Gattungen und Arten. Berliner Entomologische Zeitschrift 7(suppl.): 1 65.
- Santschi, F. 1922. Myrmicines, dolichodérines et autres formicides néotropiques.

  Bulletin de la Societe Vaudoise des Sciences Naturelles 54: 345 378.
- Santschi, F. 1929. Nouvelles fourmis de la République Argentine et du Brésil. Anales de la Sociedad Científica Argentina 107: 273 316.
- Santschi, F. 1936. Fourmis nouvelles ou intéressantes de la République Argentine.

  Revista de Entomologia 6: 402 421.
- Schultz, T.R., and R. Meier. 1995. A phylogenetic analysis of the fungus-growing ants (Hymenoptera: Formicidae: Attini) based on morphological characters of the larvae. Systematic Entomology, 20: 337 370.
- Schultz, T.R., U.G. Mueller, C.R. Currie, and S.A. Rehner. 2005. Reciprocal illumination: A comparison of agriculture in humans and ants. Pp. 149 190 in: *Ecological and Evolutionary Advances in Insect-Fungal Associations*

- (Fernando Vega and Meredith Blackwell, editors). Oxford University Press, New York.
- Smith, F. 1858. Catalogue of the hymenopterous insects in the collection of the British Museum. Part VI. Formicidae. London. 216 pp.
- Smith, F. 1860. Descriptions of new genera and species of exotic Hymenoptera.

  Journal of Entomology 1: 65 84.
- Weber, N. A. 1937. The biology of the fungus-growing ants. Part I. New forms. Revista de Entomologia, 7: 378 409.
- Weber, N. A. 1938. The biology of the fungus-growing ants. Part 4. Additional new forms. Part 5. The Attini of Bolivia. Revista de Entomologia 9: 154 206.
- Weber, N. A. 1941. The biology of the fungus-growing ants. Part 7. The Barro Colorado Island, Canal Zone, species. Revista de Entomologia 12: 93 130.
- Weber, N. A. 1945. The biology of the fungus-growing ants. Part 8. The Trinidad, B.W.I. species. Revista de Entomologia 16: 1 88.
- Weber, N. A. 1947. Lower Orinoco River fungus-growing ants (Hymenoptera: Formicidae, Attini). Boletin de Entomologia Venezolana 6: 143 161.
- Weber, N. A. 1958. Evolution in fungus-growing ants. Proceedings Tenth International Congress of Entomology 2: 459 473.
- Weber, N. A. 1966. Fungus-growing ants. Science 153: 587 604.
- Weber, N. A. 1968. Tobago Island fungus-growing ants (Hymenoptera: Formicidae).

  Entomological News 74: 141 145.
- Weber, N. A. 1969. A comparative study of the nests, gardens and fungi of the fungus-growing ants, Attini. Proceedings of the VI. Congress IUSSI: 299 307.

- Weber, N. A. 1972. Gardening ants, the attines. American Philosophical Society, Philadelphia. 146 pp.
- Wetterer, J. K., T. R. Schultz, and R. Meier. 1998. Phylogeny of fungus-growing ants (Tribe Attini) based on mtDNA sequence and morphology. Molecular Phylogenetics and Evolution 9: 42 47.
- Wheeler, W.M. 1910. Ants, their structure, development and behaviour. Columbia University Biological Series, No. 9. 663 pp.
- Wheeler, W.M. 1922a. The ants of Trinidad. American Museum Novitates 45: 1-16.
- Wheeler, W.M. 1922b. Keys to the genera and subgenera of ants. Bulletin of the American Museum of Natural History 45: 631 710.
- Wheeler, W.M. 1925. Neotropical ants in the collections of the Royal Museum of Stockholm. Part I. Arkiv for Zoologi 17(A8): 1 55.
- Wilson, E.O. 1971. The insect societies. Belknap Press, Harvard University, Cambridge, MA. 548 pp.